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Abstract

Background: Theories of density-dependent habitat selection provide two solutions for co-existence of competing species. The niche compression hypothesis predicts that species reduce their respective niche breadths in response to inter-specific competition. Alternatively, if the species have similar resource preferences, the subordinate species may be forced to expand its niche to incorporate secondary resources. Aim: Determine whether grazing ungulate species partition the resource by compression or expansion of dietary niches. Organisms: Black wildebeest (Connochaetes gnou) and blue wildebeest (C. taurinus). Methods: Stable carbon and nitrogen isotope analysis of faeces. Isotopic niche breadths are compared across allopatric and sympatric wildebeest populations in South African grasslands. Results: Stable carbon and nitrogen isotope niche breadths of the two wildebeest species were virtually identical. In sympathy, however, black wildebeest had a narrower δ13C niche breadth (indicating almost exclusive use of C4 grass), whereas blue wildebeest had a wider δ13C niche breadth (indicating significant contributions from C3 sources). Blue wildebeest also had a wider δ15N niche breadth than sympatric black wildebeest. Moreover, the δ13C niche breadths of sympatric black wildebeest and blue wildebeest were narrower and wider, respectively, than those of allopatric populations of either species. Conclusions: Isotope niche dynamics across allopatric and sympatric populations arise due to the combined effects of competition and habitat heterogeneity on resource use. Although results for black wildebeest resemble niche compression, this hypothesis cannot explain patterns observed in blue wildebeest. Expansion of the blue wildebeest niche, and restricted niche breadth of black wildebeest, is consistent with predictions of a shared preference model in which black wildebeest are the dominant competitor. When competition is operating, differences in the way species use secondary resources can have an important role in structuring grazer assemblages.
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Influence of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis

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Abstract

Background: Theories of density-dependent habitat selection provide two solutions for co-existence of competing species. The niche compression hypothesis predicts that species reduce their respective niche breadths in response to interspecific competition. Alternatively, if the species have similar resource preferences, the subordinate species may be forced to expand its niche to incorporate secondary resources.

Aim: Determine whether grazing ungulate species partition the resource by compression or expansion of dietary niches.

Organisms: Black wildebeest (Connochaetes gnou) and blue wildebeest (C. taurinus).

Methods: Stable carbon and nitrogen isotope analysis of faeces. Isotopic niche breadths are compared across allopatric and sympatric wildebeest populations in South African grasslands.

Results: Stable carbon and nitrogen isotope niche breadths of the two wildebeest species were virtually identical. In sympatry, however, black wildebeest had a narrower $\delta^{13}C$ niche breadth (indicating almost exclusive use of $C_4$ grass), whereas blue wildebeest had a wider $\delta^{15}C$ niche breadth (indicating significant contributions from $C_3$ sources). Blue wildebeest also had a wider $\delta^{15}N$ niche breadth than sympatric black wildebeest. Moreover, the $\delta^{13}C$ niche breadths of sympatric black wildebeest and blue wildebeest were narrower and wider, respectively, than those of allopatric populations of either species.

Conclusions: Isotope niche dynamics across allopatric and sympatric populations arise due to the combined effects of competition and habitat heterogeneity on resource use. Although results for black wildebeest resemble niche compression, this theory cannot explain patterns observed in blue wildebeest. Expansion of the blue wildebeest niche, and restricted niche breadth of black wildebeest, is consistent with predictions of a shared preference model in which black wildebeest are the dominant competitor. When competition is operating, differences in the way species use secondary resources can have an important role in structuring grazer assemblages.

Keywords: centrifugal community; grassland; grazer; niche compression; wildebeest
Introduction

Interspecific competition for resources is an important factor driving niche dynamics of wildlife species and the structure of communities (Chesson, 2000; Sinclair et al., 2006). Models of density-dependent habitat selection attempt to explain the niche dynamics that lead to resource partitioning and, ultimately, enable species to stably co-exist. The outcome most commonly predicted is niche compression, whereby species packing leads to each species using a relatively smaller portion of the available resource; niche breadths can only expand when the species are released from competition (MacArthur and Pianka, 1966). However, the niche compression hypothesis requires that species have distinct preferences (Rosenzweig, 1981). When competing species have shared preferences, at least one (the subordinate) should expand its range of resource use to include a less-preferred ‘secondary’ niche space that it utilizes efficiently (Rosenzweig, 1981; Rosenzweig and Abramsky, 1986). In this way, co-existence is achieved because species differ in their exploitation of secondary niches. The ‘outwards’ expansion of niches can lead to a centrifugal community structure (Rosenzweig and Abramsky, 1986).

Niche dynamics of species in a shared preference system are explained using ‘isolegs’ – lines in state space representing equal choice amongst individuals (Rosenzweig, 1981). Isolegs are an extension of the ideal free distribution (IFD) model of Fretwell and Lucas (1970), which states that species become less selective as their densities increase. But, isoleg theory incorporates the combined density of competitors in a two-species system. Consider two syntopic species with distinct preferences: at low densities each selects only its preferred niche (e.g. habitat, or food resource). As the density of the first species increases, the value of the preferred niche declines with increasing utilization. Assuming optimal behaviour, the species will then expand its niche range to include secondary resources, concordant with the IFD (Fig. 1a). When
the density of the second species increases above the isoleg, the first species will be competitively excluded from the secondary niche and select only its preferred habitat (an outcome similar to that predicted by niche compression). In a shared preference system, however, both species’ isolegs cross the density axis of the dominant species because the subordinate is more sensitive to changes induced by its competitor (Rosenzweig and Abramsky, 1986; Tregenza, 1995). The subordinate thus tolerates a wider niche – increases in density of the dominant species result in the subordinate including its secondary resource, possibly using only this resource, whereas the dominant is forced into its secondary niche by large increases in its own numbers (Fig. 1b).

In discussions about the role of competition in community structure, grazing ungulate assemblages have proved an interesting paradox. These assemblages comprise many species sharing a single food source (grass) (Bell, 1971; Murray and Brown, 1993; Prins and Olff, 1998; Sinclair, 1985). Although resource partitioning has been shown along dietary (feeding height, forage quality) and spatial niche axes (Bell, 1971; Codron et al., 2008b; Cromsigt and Olff, 2006; Jarman, 1974; Kleynhans et al., 2011; Murray and Brown, 1993; Murray and Illius, 2000), extensive niche overlap is a persistent feature of these systems (Arsenault and Owen-Smith, 2008). Simulation models of exploitation competition generally converge on exclusion, or at best unstable co-existence, as the most likely outcomes in the absence of a spatially heterogeneous resource (Murray and Baird, 2008; Murray and Illius, 1996; but see Farnsworth et al., 2002). Notably, most predictions for grazer community structure reflect the niche compression hypothesis. Patterns resembling centrifugal-type niche expansion have been found in some temperate ungulate communities (Gordon and Illius, 1989; Stewart et al., 2003), but those studies included species from different feeding guilds (grazers, browsers, and mixed-feeders). To
our knowledge, no studies of resource partitioning amongst grazers have explicitly contrasted niche dynamics under the compression vs. expansion models.

Niche compression and expansion can both lead to niche shifts (change in mean along a continuous resource use axis), but the two processes can be difficult to differentiate in the field (Ward, 2009; Ward and Seely, 1996), e.g. if at high densities both species utilize only their secondary niches. A robust investigation of how competition influences niche dynamics requires knowledge of patterns that emerge when competition happens and when it does not (Gordon and Illius, 1989; Holt, 1987). In grazers, resource partitioning is most often studied by field observations of diet, from where dietary overlap indices are calculated for axes like plant species and plant parts utilized (e.g. Mysterud, 2000). Acquiring comparative data across contexts (i.e. with and without competition), however, invokes time and labour constraints, and experimental exclusions are difficult with such large animals (Gordon and Illius, 1989).

One approach to niche dynamics across environmental and ecological contexts is stable isotope analysis. This tool has been exploited to study resource partitioning in a variety of wildlife assemblages (Codron et al., 2009; Crawford et al., 2008; Michaud et al., 2008; Newsome et al., 2007; York and Billings, 2009). The premise is that isotope compositions of animal tissues are consistent with those of their resources, archiving information about diet and habitat preference. For herbivores living in subtropical African savannas, body tissue and faecal $^{13}\text{C}/^{12}\text{C}$ ratios track differential consumption of $^{13}$C-depleted C$_3$ (trees, shrubs, forbs) vs. $^{13}$C-enriched C$_4$ (mainly grass) foods, as well as other aspects of habitat use such as relative openness and proximity to water (Cerling and Harris, 1999; Codron et al., 2007; Tieszen et al., 1979; Vogel, 1978). Herbivore $^{15}\text{N}/^{14}\text{N}$ ratios also reflect trophic behavior if food groups differ in N isotope composition (Codron et al., 2009), although qualitative inferences are often difficult
because herbivore $^{15}$N-abundances are influenced by diet quality, climate, stress, and ecophysiology (Ambrose, 1991; Robbins et al., 2010; Sponheimer et al., 2003b).

We used stable isotope analysis of faeces to investigate niche dynamics of two closely-related grazer species, the black wildebeest *Connochaetes gnou* (Zimmermann, 1780) and blue wildebeest *C. taurinus* (Burchell, 1823), co-occurring in the grassland biome of the central interior of South Africa. Black wildebeest are endemic to this region, while blue wildebeest are more frequently associated with tree/grass savanna habitats and have a wider distribution extending northwards as far as East Africa (Skinner and Smithers, 1990). The species have similar diets, feeding mainly on short grass when available (Helm, 2006; Murray and Illius, 2000; Skinner and Smithers, 1990; Van Zyl, 1965). Morphology of their feeding apparatus does not differ, although black wildebeest show less variation in dental morphology and thus may be more specialized (Brink, 2005; Codron and Brink, 2007). Resource partitioning between species with such similar trophic adaptations could yield important insights into ecological separation and co-existence of grazers in general. Moreover, while their distributions overlapped historically (Skead, 1980), co-occurrence is more common today because many game ranches stock both species despite legislation imposed to prevent hybridization (S. Vrahimis, pers. comm.). Their interaction in confined areas likely has consequences for persistence of populations and their combined effects on ecosystems (Helm, 2006).

A previous study found that sympatric black and blue wildebeest partition the stable isotope axes (Codron and Brink, 2007): here we investigate whether this partitioning is due to resource competition, by testing the hypothesis that isotope niche breadths differ between allopatric and sympatric populations of each species. We look at patterns during the dry season only, when grass becomes limiting and competition more likely (Arsenault and Owen-Smith,
We contrast predictions of the niche compression hypothesis with those of niche expansion in a shared preference system. The expectation was that compression would lead to narrower isotope distributions along a continuous axis of one or both species in sympatry (Figs 2b, 2c), whereas niche expansions would manifest as wider isotopic ranges in sympatry (Fig. 2d), or even a shift in the absolute range of one species (Fig. 2e).

**Materials and Methods**

**Study Area**

The study focused initially on wildebeest populations in three small (< 11 000 ha) nature reserves in the grassland biome of the South African interior: the Gariep Dam Nature Reserve (GNR), Maria Moroka Park (MM), and Soetdoring Nature Reserve (SNR) (Fig. 3). Black wildebeest and blue wildebeest occur sympatrically at GNR, while the other two reserves are inhabited by black wildebeest only. The grassland biome is typically a homogeneous, open landscape, with mostly high grass productivity and little or no tree cover (Mucina and Rutherford, 2006). GNR extends furthest west, partly incorporating the Nama Karoo biome, but even in these parts (eastern non-succulent Karoo) grasslands are dominant (Mucina and Rutherford, 2006). Topography is mainly flat, but the grasslands extend eastwards over the escarpment, where altitude rises as high as ~2 500 m above sea-level, before descending to near sea-level. Climate varies from arid to semi-arid; mean annual precipitation decreases from ~600 to ~400 mm from east to west, and falls mainly in the austral summer between October and March. A characteristic feature of the more arid western areas (where the bulk of this study was carried out), is a high density of naturally-occurring seasonal pans (Janecke et al., 2003).
Materials and Data

Faeces and plants were collected from GNR, MM, and SNR during the dry season (June) of 2008. Faeces were sampled by locating animals and following them on foot until defecation. Specimens were collected moist, avoiding contamination by soil or insects. Representative local vegetation was collected for baseline isotopic data. Three circular sampling transects (5 m diameter) were established at random localities within each reserve, from where foliage of the most abundant grass, tree and forb species was sampled. Faeces and plants were oven-dried at 60°C for 24 h, and then mill-ground to a homogeneous powder through a 1 mm sieve using a hammer mill. Stable isotope ratios were determined by combustion of samples in an automated elemental analyzer (Carlo Erba, Milan, Italy), and introducing resultant CO₂ and N₂ gases via continuous flow to a Delta XP Mass Spectrometer (Finnigan, Bremen, Germany). Isotope ratios are presented in conventional delta (δ) notation, in units per mil (‰), relative to the Vienna PeeDee Belemnite (VPDB) and atmospheric N₂ standards for δ¹³C and δ¹⁵N, respectively. Standard deviations of repeated measures of laboratory standards (Merck Gel, lentil, and chocolate powder) were less than 0.1 ‰ and 0.3 ‰ for δ¹³C and δ¹⁵N, respectively. These analyses also yielded percent nitrogen (%N, by weight) of each specimen, providing a proxy for plant crude protein content, and diet quality from faeces (Holecheck et al., 1982).

The sample for GNR was expanded by including faecal isotope data for both wildebeest species from a dry season month (May) in 2006 (Codron and Brink, 2007). For comparison, we also included data for allopatric blue wildebeest populations from reserves elsewhere in South Africa: the Northern Basalt Plains (NBP) of the Kruger National Park, and Hans Merensky Nature Reserve (HM) (Codron et al., 2007). These reserves lie in the savanna biome (see Fig. 3), but the NBP is an arid (~400 mm rainfall per annum), open grassland permeated with a network
of seasonal pans (Grant et al., 2002), and is thus comparable to habitats in the grassland biome. HM is a more densely wooded savanna. The NBP and HM data are represented by faeces collected monthly over a complete seasonal cycle (i.e. one year); to derive a sample comparable with present data we extracted data for only two dry season months (June 2004 and May 2005; see Table 1).

Data Analysis

Comparisons between groups were made with δ¹³C values, δ¹⁵N values, and %N as continuous dependent variables, and “Reserve” or “Species” as categorical factors. Data were compared using one-way ANOVA, or the non-parametric Kruskal-Wallis alternative when residuals were not normally distributed (plant δ¹⁵N and %N). For plant data, multiple comparisons tests were performed with Tukey’s HSD. For faeces we used Dunnett’s T post hoc tests for multiple comparisons, because we hypothesized a priori that group variances would be unequal between sympatric and allopatric populations (Fig. 2); this test avoids the assumption of equal variance in the ANOVA. For comparisons of niche breadth, we used F-tests to compare variances between groups. Analyses were performed in STATISTICA v8.0 (Statsoft_Inc, 2007).

Variation in stable isotope composition of dietary baselines influences consumer isotope compositions, which blurs the relationship between ecological and isotopic niches (Codron et al., 2007; Post, 2002). To account for these effects, we converted raw δ values to estimates of isotopic niche space using the linear two-source mixing equation:

\[
\delta_{\text{niche}} = \frac{\delta_{X_{\text{consumer}}} - \delta_{X_{\text{C3 plants}}}}{\delta_{X_{\text{C4 plants}}} - \delta_{X_{\text{C3 plants}}}}
\]

where X refers to the C or N isotope in the system. Mean (or medians in the case of non-normal δ¹⁵N data) values for local C₄ (grass) and C₃ (tree/forb foliage) were used as end-members in the
above equation (data in Table 1). It is important to note that this approach is only partly analogous with the more common conversion of δ values to ecological “p space” (Newsome et al., 2007), because we make no assumptions about variation in consumer-diet fractionation factors. Thus, output of the above model is not constrained to a proportion between 0 and 1, but simply depicts niches along a relative scale where the highest values correspond most closely to values for C<sub>4</sub> vegetation. We used these estimates of “δ niche space” as dependent variables in our analyses, because they account for regional variations in plant δ<sup>13</sup>C and δ<sup>15</sup>N, and we highlight cases where this approach yielded disparate results compared with raw data.

**Results**

**Variations in Baseline (Plant) Isotope Composition**

All grasses sampled had δ<sup>13</sup>C values consistent with C<sub>4</sub> vegetation (-15.0 ‰ to -11.7 ‰, n = 106) and values for tree and forb foliage were all consistent with C<sub>3</sub> vegetation (-29.7 ‰ to -24.3 ‰, n = 70). Plant δ<sup>13</sup>C values did not differ by much between habitats, although significant differences were found between SNR and NBP for C<sub>4</sub> grass (mean difference = 0.8 ‰; Tukey’s p = 0.002), and between GNR and SNR for C<sub>3</sub> foliage (mean difference = 1.6 ‰; Tukey’s p = 0.011; Table 1). Variance in δ<sup>13</sup>C values for both plant groups did not differ between regions (Levene’s p = 0.898 for C<sub>4</sub> and 0.967 for C<sub>3</sub>).

Plant δ<sup>15</sup>N differed across regions, in that values for C<sub>4</sub> grass were ~2.0 to 3.5 ‰ higher at NBP compared with the other reserves (H<sub>4,106</sub> = 50.146; p < 0.05), and values for C<sub>3</sub> foliage were ~2.5 ‰ higher at NBP compared with SNR and HM (H<sub>4,70</sub> = 24.299; p = 0.013 and p < 0.001, respectively).
Grass %N was highest in the two savanna reserves (NBP and HM), and significantly lower in at least two of the grassland reserves (GNR and MM; $H_{4,106} = 43.551; p = 0.034$ and $< 0.0001$, respectively). Nitrogen content of C$_3$ foliage was also highest at NBP and HM, and lowest at GNR ($H_{4,70} = 22.797; p = 0.025$ and $p < 0.001$, respectively).

Comparative Isotope Niches of the Two Wildebeest Species

$\delta^{13}C$ values of all wildebeest faeces were consistent with C$_4$-dominated (grass-based) diets (-17.0 ‰ to -12.8 ‰, $n = 131$). The overall means and SD’s were similar for the two species (Dunnett’s $p = 0.587$; $F_{70,59} = 1.113, p = 0.338$; Table 2), and their respective distributions in $\delta^{13}C$ niche space were almost identical (Dunnett’s $p = 0.842$; $F_{70,59} = 1.325, p = 0.134$; Fig. 4a). A $\delta^{13}C$ niche shift did, however, emerge amongst the sympatric populations at GNR: here, black wildebeest had, on average, higher values (more strongly C$_4$; Dunnet’s $p = 0.028$), but a smaller niche variance than blue wildebeest ($F_{35,34} = 8.323, p < 0.0001$).

Mean faecal $\delta^{15}N$ for black wildebeest was higher than for blue wildebeest, both overall (mean difference = 0.5 ‰; Dunnet’s $p < 0.001$) and in sympathy at GNR (mean difference = 0.9 ‰; Dunnet’s $p < 0.001$). However, after accounting for regional differences in plant $\delta^{15}N$, the overall difference did not persist (Dunnet’s $p = 0.186$; Fig. 4b), and the situation amongst sympatric populations became reversed, i.e. the estimated $\delta^{15}N$ niche of black wildebeest was lower than that of blue wildebeest (Dunnet’s $p < 0.0001$), whereas blue wildebeest values were more similar to those of local C$_4$ grass. Variance in faecal $\delta^{15}N$ for the two species was similar ($F_{59,70} = 1.074, p = 0.385$), but after controlling for plant variations it emerged that black wildebeest had a narrower $\delta^{15}N$ niche breadth than blue wildebeest (SD = 0.61 and 1.09,
respectively; $F_{70,59} = 3.169, p < 0.0001$). At GNR, however, variance in δ¹⁵N was smaller in black wildebeest than blue wildebeest ($F_{35,34} = 3.135, p < 0.0001$).

Faecal N content of black wildebeest was lower and less variable compared with that of blue wildebeest (Dunnet’s $p < 0.0001$; $F_{70,59} = 1.651, p = 0.025$), but at GNR the distribution of faecal %N values was similar for both species (Dunnet’s $p = 0.632; F_{35,34} = 1.326, p = 0.206$; Fig. 4c).

Niche Dynamics across Populations

Mean faecal δ¹³C values of black wildebeest differed between all three populations studied (Dunnett’s $p < 0.0001$ for all comparisons; Table 2). The sample with the most positive values in δ¹³C niche space (most similar to C₄ plants) was at MM, while the SNR population utilized the least positive δ¹³C niche space, and the GNR sample had an intermediate range of values (Fig. 5a). Further, the sample from GNR had lower variance compared with both MM ($F_{13,34} = 2.799, p = 0.008$) and SNR ($F_{10,34} = 6.842, p < 0.0001$), whereas δ¹³C niche variance of MM and SNR were not different ($F_{10,13} = 1.962, p = 0.127$).

Faecal δ¹⁵N values for black wildebeest were lowest at MM (Dunnett’s $p < 0.0001$), whereas values for GNR and SNR did not differ (Dunnett’s $p = 0.288$). However, mean δ¹⁵N niche was lower at SNR compared with both other reserves (Dunnett’s $p < 0.0001$; Fig. 5b), suggesting the former result was likely due to the low grass δ¹⁵N values at MM (see Table 1). There were no significant differences in δ¹⁵N variance between the three reserves ($F$-test $p = 0.066$ to 0.4683), although some comparisons were associated with low statistical power (minimum 0.36 for variance ratio of 80%).
Mean faecal %N, and associated SD’s, of black wildebeest did not differ between reserves (Dunnett’s $p = 0.141$ to $0.992$; $F$-test $p = 0.098$ to $0.270$; Fig. 5c).

For blue wildebeest, faecal $\delta^{13}$C values were significantly lower at GNR compared with NBP (Dunnett’s $p < 0.001$) and HM (Dunnett’s $p = 0.017$; Table 2), but the differences between GNR and NBP did not persist after adjustment for variations in plant $\delta^{13}$C (Dunnett’s $p = 0.691$; Fig. 5a). Variance in $\delta^{13}$C of blue wildebeest was higher at GNR and HM compared with NBP ($F_{35,14} = 2.708$, $p = 0.025$ and $F_{19,14} = 4.376$, $p = 0.004$, respectively), but was not different between GNR and HM ($F_{19,35} = 1.616$, $p = 0.107$).

Mean faecal $\delta^{15}$N values for blue wildebeest did not differ between reserves (Dunnett’s $p = 0.273$ to $0.999$; Table 2), but a lower $\delta^{15}$N niche emerged for HM after accounting for variations in plant data (Dunnett’s $p < 0.0001$; Fig. 5b). The HM sample also showed relatively large variance in $\delta^{15}$N niche space ($F$-test $p < 0.0001$).

Mean faecal %N for blue wildebeest was highest at NBP, followed by HM, and was lowest at GNR (Dunnett’s $p = 0.046$ to $< 0.0001$; Fig. 5c). Variance of faecal %N at GNR was greater than at NBP and HM ($F$-test $p < 0.001$).

**Discussion**

Stable Isotope Evidence for Influences of Competition

Faecal stable isotope distributions reflect similar dietary niches for black wildebeest and blue wildebeest across the range of habitats studied here. But differences did emerge where the two species live sympatrically, at GNR. Here, the faecal $\delta^{13}$C niche of black wildebeest was higher ($^{13}$C-enriched) and had a narrower range than that of blue wildebeest, suggesting the former foraged more selectively. The species’ $\delta^{15}$N niches also differed at GNR, with black
wildebeest being more $^{15}$N-enriched relative to local C$_4$ grasses than blue wildebeest. Further, results showed that the isotopic niches of both species at GNR differed from those of their allopatric conspecifics, indicating that interspecific competition was an important driver of niche dynamics. Black wildebeest at GNR had a narrower faecal $\delta^{13}$C niche breadth compared with both allopatric populations of this species, whereas the $\delta^{13}$C niche breadth of blue wildebeest at GNR was wider than the allopatric population from the NBP, but not HM.

Relatively small sample sizes ($n < 20$ in some reserves) used here represent a possible limitation, but the pattern of isotopic niche overlap with partitioning emerging in sympatry appears quite robust, especially for $\delta^{13}$C data. For one, data for the sympatric populations reflect similar trends over two study years (2006 and 2008). Further, the strong overlap in $\delta^{13}$C distributions of the two species is consistent with carbon isotopic evidence for dietary similarity over longer time periods, recorded from analysis of tooth dentine collagen (Codron and Brink, 2007). Our aim here was to advance this knowledge by gaining insights into niche dynamics of sympatric vs. allopatric populations in the grassland biome, where the two species’ ranges overlap (but co-existence was likely less frequent prior to contemporary management practices). This was achieved for black wildebeest, but comparative data for allopatric blue wildebeest populations were necessarily taken from two habitats in the savanna biome: an open grassland and a woodland savanna. Nonetheless, we found stronger similarities in blue wildebeest $^{13}$C and $^{15}$N isotopic niches between ‘grassland-sympatric’ with ‘grassland-savanna’ habitats than either compared with the woodland savanna (HM), implying that the grassland savanna (NBP) provided a suitable baseline (allopatric) habitat for our purposes.

Overall, our study demonstrates an effective method for tracking niche dynamics of herbivores across ecological and environmental contexts. Using a sampling approach analogous
to conventional removal experiments (e.g. Schoener, 1983), but which are logistically difficult for large animals, we have shown that stable isotope analysis can reveal cases where niche shifts are the result of exploitation competition.

The $\delta^{13}C$ niche dynamics we observed most likely reflect shifts in relative use of $C_3$ (dicots and possibly sedges) and $C_4$ (grass) resources across populations. Previous research has focused on grass height, and grass quality (e.g. leaf:stem ratios) as axes for resource partitioning amongst grazing ungulates (Arsenault and Owen-Smith, 2008; Bell, 1971; Codron et al., 2008b; Kleynhans et al., 2011; Murray and Brown, 1993; Murray and Illius, 2000). Our result demonstrates that partitioning of the grass/browse axis can occur in some systems.

The $^{13}C$-enriched signal for black wildebeest at GNR, and the narrow range of $\delta^{13}C$ values here, indicates that this population utilized $C_4$ items almost exclusively. By contrast, the wide $\delta^{13}C$ niche breadth of blue wildebeest at GNR almost certainly indicates substantial $C_3$ browse intake by some individuals (comprising no more than $\sim 20 – 30\%$ of the whole diet). Confounding factors such as differences in animal-diet $^{13}C$ discrimination (Martínez del Rio et al., 2009) should be relatively small between these two closely-related species, as they appear to be for ungulates in general (Sponheimer et al., 2003a). Our analyses accounted for interhabitat variability in plant isotope composition, and even intrahabitat variability (which, in South African savannas, is usually $< 2\%$ (Codron et al., 2005)) cannot explain faecal $\delta^{13}C$ values of blue wildebeest at the most $^{13}C$-depleted end of the scale. Based on previous research on faecal $\delta^{13}C$ distributions in southern African habitats (Codron et al., 2009; Codron et al., 2007), we are confident that values $< -15.5\%o$ are unlikely to occur without significant $C_3$ inputs to diet.

Around 22\% of blue wildebeest faecal specimens collected at GNR had $\delta^{13}C$ values in this range, whereas no specimens from allopatric populations of this species were so depleted in $^{13}C$. These
observations support the interpretation that the dietary niche of blue wildebeest expanded in sympatry, with the most likely ‘secondary’ resource being C₃ browse (shrubs, forbs, or trees).

The difference in faecal δ¹⁵N values between the two species could indicate additional partitioning of the resource, if local C₄ grasses (the dominant resource in all wildebeest diets) varied systematically in ¹⁵N composition. Then, black wildebeest were likely consuming more grasses that use the NAD-ME or PCK photosynthetic sub-pathways, as these are often ¹⁵N-enriched relative to NADP-ME grasses in southern African savannas (Codron et al., 2009; Codron et al., 2005). The former group comprises more species of panicoids and chloridoids, whereas the latter comprise more tall, fibrous andropogonoid species (Sage et al., 1999). Given that both wildebeest species are preferentially short-grass grazers (Brink, 2005; Skinner and Smithers, 1990), a shift to higher rates of tall-grass grazing in blue wildebeest could further indicate it was using a secondary resource. However, although statistical evidence, based on isotope mixing models, for an NAD/PCK vs NADP dichotomy in herbivore faecal δ¹⁵N values has been presented (Codron and Codron, 2009), such an interpretation for the present study must be considered speculative. In addition, numerous other climatic and ecophysiological factors do influence herbivore ¹⁵N-abundance distributions (Ambrose, 1991; Sponheimer et al., 2003b), albeit physiological differences between such closely-related species are probably small.

Mechanisms of Co-existence

Results reflect niche compression in black wildebeest, especially along the δ¹³C (C₃ browsing/C₄ grazing) dietary axis, at GNR. However, we do not believe this is consistent with the niche compression hypothesis of MacArthur and Pianka (1966). For one, while the δ¹⁵N niche of black wildebeest was also ‘compressed’ relative to that of blue wildebeest, this pattern
was general and not restricted to the sympatric populations only. Second, the dietary (isotopic) niches of both species were virtually identical across the whole range of habitats studied here, indicating that preferences were not distinct, as implied by the compression theory (Rosenzweig, 1981). This theory also does not explain the expansion of the blue wildebeest $\delta^{13}C$ niche in sympathy, and under the compression hypothesis the asymmetric result for GNR would cast blue wildebeest as the superior competitor (see Fig. 2b). Yet, the grassland biome is optimal habitat for black wildebeest, but sub-optimal for blue wildebeest, which are more commonly found in tree/grass savannas (Brink, 2005; Skinner and Smithers, 1990). South African grasslands represent only the southern margin of the blue wildebeest distribution in Africa, where the species was largely replaced by black wildebeest since their divergence c. 1 million years ago (Brink, 2005; Codron et al., 2008a). Thus, we would expect black wildebeest to be the dominant competitor in these habitats.

Further evidence for black wildebeest dominance can be drawn from our data. Grasses at GNR had lower $\%N$ (lower quality) than grasses at the other reserves, but only blue wildebeest showed lower faecal $\%N$ values in this reserve compared to other habitats. This implies that blue wildebeest in sympathy used diets of poorer nutritional value compared with populations of this species elsewhere, whereas black wildebeest maintained similar levels of faecal $\%N$ throughout. Thus, at GNR, black wildebeest likely forced blue wildebeest to forage outside the preferred dietary niche space, which is consistent with predictions of shared preference community structure drawn from isoleg theory (Fig. 1b, and see especially Fig. 2d). Also, wider variation in oral and dental morphology of blue wildebeest (Brink, 2005; Codron and Brink, 2007) means this species should be more tolerant to a wider diversity of dietary niches, and so more likely to utilize secondary resources efficiently.
A similar pattern of niche dynamics was found several decades ago by Holmes (1961). He studied experimentally-manipulated densities of two helminth species parasitizing the small intestine of the definitive host (rats). In single infections, both species preferred the anterior parts of the small intestine as attachment site, but in concurrent infections one species, *Moniliformis dubius* (acanthocephalan), appeared to force the other, *Hymenolepis diminuta* (cestode), to occupy less-preferred posterior attachment sites. Pimm (1985) studied hummingbird behaviour using feeders of two different concentrations of sucrose. Both the blue throated hummingbird (*Lampornis clamenciae*) and black chinned hummingbird (*Archilochus alexandri*) preferred feeders with high sucrose concentrations, but black chinned hummingbirds used both feeder types at high densities of their own, or the blue throated, species.

One area in which our data could appear inconsistent with shared preference structure, and more consistent with the niche compression hypothesis, is that allopatric populations of black wildebeest used a broad $\delta^{13}$C niche breadth. Niche reduction at GNR is not an explicit prediction of isoleg theory, if black wildebeest are considered the dominant competitor. But, the theory is based on the ideal-free distribution (IFD) which does, in fact, allow for the dominant species to use preferred and secondary niches, even in allopatry, and even at densities below its isoleg. This could happen, for example, with any increase in density of the dominant species. In Holmes’ (1961) study, both the subordinate cestode and dominant acanthocephalan expanded attachment size niches with increasing densities of their own species, in line with predictions of the IFD (Fretwell and Lucas, 1970). In Pimm’s (1985) experiments, he found that even the [dominant] blue throated species accepted feeders with the low sucrose concentration as its density increased (but it never used only this feeder type).
Studies of niche partitioning in ungulates have also revealed that some species have expanded dietary niche ranges, suggesting a possible mechanism for co-existence with more restricted taxa (Gordon and Illius, 1989; Stewart et al., 2003). It is, however, difficult to to draw analogies between those studies with our results, because the former compared species with different forging styles (browsers, grazers, and mixed-feeders), whereas we focused on grazers only. Nevertheless, Gordon and Illius (1989) did hypothesize that any ungulate assemblages may partition the resource in this way, with dominants excluding subordinates so that the latter use a wider variety of resources. They predicted that under limiting conditions, larger species would react first to expand their niche ranges, because their lower metabolic requirements (relative to small species) would make them more tolerant to less-preferred, low quality, forages. Our result for niche expansion in blue wildebeest supports their idea, since they (mean mass of females c. 180 kg) are almost 50% larger than black wildebeest (mean mass of females c. 130 kg) (Skinner and Smithers, 1990).

Conclusion

Most approaches to grazer community structure expect niche compressions. We suggest that shared preference structure may be quite common in this guild. For example, Dickman (1986) found that ‘apparent’ compressions were not general to all species in a guild of grazing macropods. He suggested that the niche compression hypothesis would not apply to assemblages in which one species is markedly dominant, and/or generalist feeding niches are prevalent. In light of our results, Dickman’s (1986) study seems easily interpretable in terms of some species expanding their niches according to rules of density-dependent habitat selection theory. Actually, specific strategies of using dynamic niches depending on the environmental/ecological context
(e.g. with and without competition) could even help explain grazer co-existence when overall
niche ranges overlap.

Of course, the niche compression hypothesis, isoleg theory, and other habitat selection
models (e.g. Morris, 1988; Wasserberg et al., 2007) are explicitly density-dependent. We were
not able to gather sufficient demographic data to test hypotheses related to density-dependence in
this study. For example, black wildebeest at MM and SNR may have used relatively broad
dietary niches if they occurred at very high densities there (which could indicate reduced
population performance due to competition from blue wildebeest). Habitat heterogeneity could
also play a role, if environments at SNR and MM were such that the black wildebeest isoleg was
different from that at GNR (shifted to the left on the x-axis of Fig. 1b). Then, the black
wildebeest dietary niche would have been broader at SNR and MM even at (relatively) low
densities. Linking population and demographic data to niche dynamics would lead to a better
understanding of the interspecies interaction. Such a study would test the hypothesis that density-
fitness functions are stable across contexts, and thus enforce the evolutionary value of adaptive
trophic strategies in these taxa (cf. Valdovinos et al., 2010). Conversely, niche shifts (whether by
compression of by expansion) could have negative consequences for population dynamics,
adding another problem (besides hybridization) for conservation authorities and ranch managers
wanting to justify stocking of both species in confined spaces.

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References


Statsoft_Inc. 2007. STATISTICA Version 8.0 (data analysis software system).


Table 1. Sampling details and vegetation data (mean ± 1 SD) for reserves included in this study.

<table>
<thead>
<tr>
<th>Region</th>
<th>Month/ year</th>
<th>Wildebeest species</th>
<th>C₄ grass</th>
<th>C₃ tree and forb foliage</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>n</td>
<td>δ¹³C (‰/oo)</td>
</tr>
<tr>
<td>Gariep (GNR) *</td>
<td>06/08</td>
<td>Both</td>
<td>15</td>
<td>-13.5±0.56</td>
</tr>
<tr>
<td></td>
<td>05/06</td>
<td></td>
<td>-</td>
<td>-</td>
</tr>
<tr>
<td>Maria Moroka (MM) @</td>
<td>06/08</td>
<td>Black only</td>
<td>23</td>
<td>-13.4±0.54</td>
</tr>
<tr>
<td>Soetdoring (SNR) #</td>
<td>06/08</td>
<td>Black only</td>
<td>13</td>
<td>-14.0±0.65</td>
</tr>
<tr>
<td>Northern Basalt Plains (NBP)</td>
<td>06/04 &amp; 05/05</td>
<td>Blue only</td>
<td>43</td>
<td>-13.2±0.75</td>
</tr>
<tr>
<td>Hans Merensky (HM)</td>
<td>06/04 &amp; 05/05</td>
<td>Blue only</td>
<td>12</td>
<td>-13.6±0.55</td>
</tr>
</tbody>
</table>

* data collected in this study; @ data from Codron and Brink (2007); # data from Codron et al. (2007); n = number of observations (individual plants sampled)
Table 2. Faecal stable isotope data, and %N (mean ± 1 SD) for the wildebeest populations included in this study.

<table>
<thead>
<tr>
<th>Population (reserve)</th>
<th>n</th>
<th>$\delta^{13}$C (‰)</th>
<th>$\delta^{15}$N (‰)</th>
<th>%N</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Black wildebeest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gariep (GNR)</td>
<td>35</td>
<td>-14.9 ± 0.25</td>
<td>5.1 ± 0.53</td>
<td>1.1 ± 0.21</td>
</tr>
<tr>
<td>Maria Moroka (MM)</td>
<td>14</td>
<td>-14.0 ± 0.40</td>
<td>3.7 ± 0.60</td>
<td>1.0 ± 0.18</td>
</tr>
<tr>
<td>Soetdoring (SNR)</td>
<td>11</td>
<td>-16.1 ± 0.56</td>
<td>5.3 ± 0.34</td>
<td>1.0 ± 0.15</td>
</tr>
<tr>
<td>Overall</td>
<td>60</td>
<td>-14.9 ± 0.75</td>
<td>4.8 ± 0.82</td>
<td>1.1 ± 0.20</td>
</tr>
<tr>
<td><strong>Blue wildebeest</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Gariep (GNR)</td>
<td>36</td>
<td>-15.2 ± 0.73</td>
<td>4.2 ± 0.93</td>
<td>1.2 ± 0.25</td>
</tr>
<tr>
<td>Northern Basalt Plains (NBP)</td>
<td>15</td>
<td>-14.6 ± 0.42</td>
<td>4.5 ± 0.42</td>
<td>1.5 ± 0.27</td>
</tr>
<tr>
<td>Hans Merensky (HM)</td>
<td>20</td>
<td>-14.4 ± 0.88</td>
<td>4.2 ± 0.70</td>
<td>1.3 ± 0.12</td>
</tr>
<tr>
<td>Overall</td>
<td>71</td>
<td>-14.8 ± 0.79</td>
<td>4.3 ± 0.79</td>
<td>1.3 ± 0.26</td>
</tr>
</tbody>
</table>

$n =$ number of observations (individual faecal samples)
Figure Legends

**Figure 1.** Density-dependent habitat selection by two competing species with distinct (a) and shared (b) preferences, explained using isoleg theory. In (a) species 1 prefers niche A, species 2 prefers niche B. The species select different habitats at low densities \((N)\), but to the right and above their respective isolegs (solid line = species 1, dotted line = species 2) their niches expand to include the secondary habitat C. When density of the competitor increases, i.e. above and to the right of the respective isolegs, the species again select different habitats. In (b), species 1 is the dominant (D) competitor, and species 2 is the subordinate (S). Both species prefer habitat A, but with an increase in density of D, species S expands its niche to include secondary habitat B (to the right of dashed isoleg, the subordinate only uses its secondary habitat). In most of the range species D uses its preferred habitat, and may include its secondary habitat C, but to the right of its isoleg even D is forced to include both its primary and secondary habitats. Adapted from Rosenzweig and Abramsky (1986; see also Tregenza, 1995; Ward and Seely, 1996).

**Figure 2.** Conceptualized stable isotope niche dynamics under the niche compression (distinct preference system) and niche expansion (shared preference system) hypotheses (adapted from Fig. 1). Allopatric populations use similar niches (a), but in sympatry competition leads to reduced – i.e. niche compression (b, c), or broader – i.e. expansion (d, e), isotope niche breadths along a continuous resource use axis. In b) and d), the outcome is asymmetric because one species is competitively dominant (solid lines) and the other subordinate (dashed lines), whereas in c) equilibrium is reached when both species become more selective. Grey areas in d) and e) indicate secondary isotope niche spaces of the two species: due to the asymmetric interaction,
niche expansion is one-tailed, causing a niche shift (change in mean along the $x$-axis). At very high densities both species could utilize only their secondary niche range, and the outcome would be indistinguishable from (c).

**Figure 3.** Map of South Africa with grassland (dark shading) and savanna (light shading) biomes, and reserves sampled (GNR = Gariep Dam Nature Reserve, both wildebeest species; MM = Maria Moroka Reserve and SNR = Soetdoring Nature Reserve, black wildebeest only; NBP = Northern Basalt Plains, Kruger National Park and HM = Hans Merensky Nature Reserve, blue wildebeest only). White areas comprise other biomes.

**Figure 4.** Comparative distributions of faecal data in a) $\delta^{13}$C niche space, b) $\delta^{15}$N niche space, and c) $%N$ between the two wildebeest species. Plots on the left represent data for all populations (reserves), plots on the right represent sympatric populations (GNR) only. Isotope niche space ($x$-axes in a and b) is derived from a mixing model that accounts for regional differences in plant isotope composition: higher values indicate increasing similarity to $C_4$ grass values. Curves are fitted normal distributions.

**Figure 5.** Comparative distributions of faecal data in a) $\delta^{13}$C niche space, b) $\delta^{15}$N niche space, and c) $%N$ between populations of each species living sympatrically (GNR, black bars) and allopatrically (grey bars). Plots on the left are black wildebeest populations, plots on the right are blue wildebeest populations. Isotope niche space ($x$-axes in a and b) is derived from a mixing model that accounts for regional differences in plant isotope composition: higher values indicate increasing similarity to $C_4$ grass values. Curves are fitted normal distributions.
Fig. 1

a) distinct preferences

b) shared preferences

N₂

N₁

N₅

N₄
Fig. 2

- **a**: Allopatric populations
- **b**: Asymmetric compression (1 species is dominant)
- **c**: Symmetric compression
- **d**: Expansion of subordinate (at low densities)
- **e**: Expansion of both (at high densities)
Fig. 3
Fig. 4

(a) All populations
(b) Sympatric populations (GNR)

frequency

$\delta^{13}$C niche

$\delta^{15}$N niche

%N
Fig. 5

- Black wildebeest
  - GNR
  - MM
  - SNR
- Blue wildebeest
  - GNR
  - NBP
  - HM

**Frequency**

- Black wildebeest
- Blue wildebeest