Evolutionary Ecology Research, 2011, **13**: 217–235

Effect of competition on niche dynamics of syntopic grazing ungulates: contrasting the predictions of habitat selection models using stable isotope analysis

Daryl Codron[1,2], John Hull[2], James S. Brink[3,4], Jacqui Codron[2],
David Ward[2] and Marcus Clauss[1]

[1]*Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Zurich, Switzerland,* [2]*School of Biological and Conservation Sciences, University of KwaZulu-Natal, Scottsville, South Africa,* [3]*Florisbad Quaternary Research, National Museum, Bloemfontein, South Africa and* [4]*Centre for Environmental Management, Faculty of Natural and Agricultural Sciences, University of the Free State, Bloemfontein, South Africa*

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 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 $\delta^{13}C$ 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 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

---

Correspondence: D. Codron, Clinic for Zoo Animals, Exotic Pets and Wildlife, Vetsuisse Faculty, University of Zurich, Winterthurerstr. 260, CH-8057 Zurich, Switzerland. e-mail: darylcodron@gmail.com

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

Inter-specific 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 proportion 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 modelled using 'isolegs', lines in state space representing equal choice among 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 species 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; Sinclair, 1985; Murray and Brown, 1993; Prins and Olff, 1998). Although resource partitioning has been shown along dietary (feeding height, forage quality) and spatial niche axes (Bell, 1971; Jarman, 1974; Murray and Brown, 1993; Murray and Illius, 2000; Cromsigt and Olff, 2006; Codron *et al.*, 2008b; Kleynhans *et al.*, 2011), extensive niche overlap is a persistent feature of these systems (Arsenault and Owen-Smith, 2008). Simulation models of exploitation competition

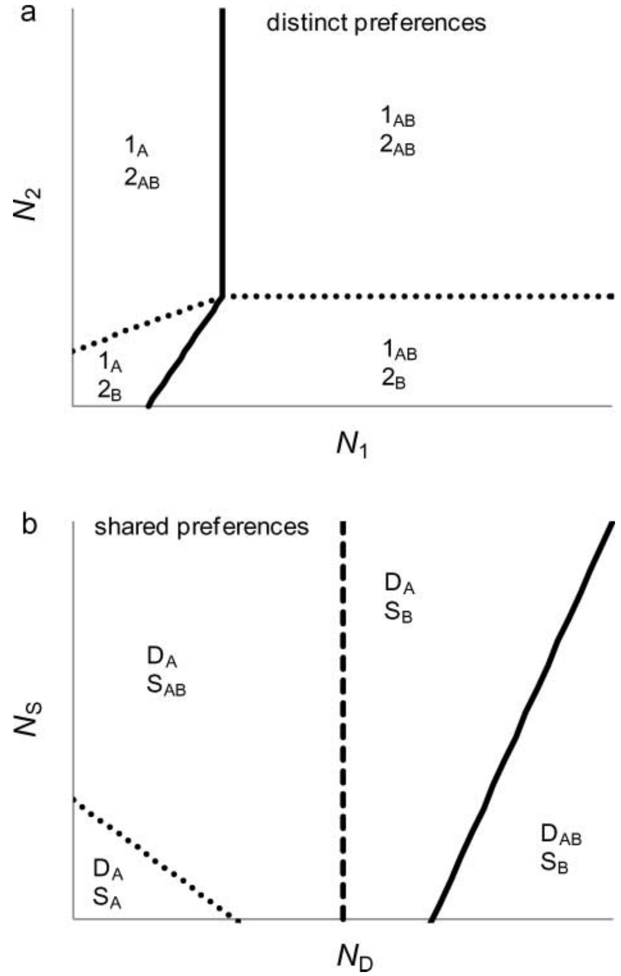

Fig. 1. Density-dependent habitat selection by two competing species with distinct (a) and shared (b) preferences, modelled using isoleg theory. In (a) species 1 prefers habitat A, species 2 prefers habitat B. The species select different habitats at low densities (N_i). But to the right of N_1's isoleg (solid line) and above N_2's isoleg (dashed line), their respective niches expand to include their secondary habitat (B). In contrast, in (b), species 1 is the dominant (D) competitor, and species 2 is the subordinate (S). S has two isolegs (dotted and dashed lines); D has one (solid line). Both species prefer habitat A and use it exclusively when both are at low densities. But both may use B if certain density conditions are met. To the right of its isoleg, even D is forced to include both habitats A and B. With N_D greater than S's isoleg threshold (the dashed line), S uses B (the secondary habitat) exclusively. Adapted from Rosenzweig and Abramsky (1986; see also Tregenza, 1995; Ward and Seely, 1996).

generally converge on exclusion, or at best unstable co-existence, as the most likely outcome in the absence of a spatially heterogeneous resource (Murray and Illius, 1996; Murray and Baird, 2008; 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 among grazers have explicitly contrasted niche dynamics under the compression versus 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 and Seely, 1996; Ward, 2009), such as 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 (Holt, 1987; Gordon and Illius, 1989). In grazers, resource partitioning is most often studied by field observations of diet, from which 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 (Newsome *et al.*, 2007; Crawford *et al.*, 2008; Michaud *et al.*, 2008; Codron *et al.*, 2009; 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 $^{13}C/^{12}C$ ratios track differential consumption of ^{13}C-depleted C_3 (trees, shrubs, forbs) versus ^{13}C-enriched C_4 (mainly grass) foods, as well as other aspects of habitat use such as relative openness and proximity to water (Vogel, 1978; Tieszen *et al.*, 1979; Cerling and Harris, 1999; Codron *et al.*, 2007). Herbivore $^{15}N/^{14}N$ ratios also reflect trophic behaviour 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; Sponheimer *et al.*, 2003b; Robbins *et al.*, 2010).

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 (Van Zyl, 1965; Skinner and Smithers, 1990; Murray and Illius, 2000; Helm, 2006). 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, personal communication). 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 wildebeests partition the stable isotope axes (Codron and Brink, 2007). Herein we investigate whether this partitioning is due to resource competition. We do so 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 (Gordon and Illius, 1989; Arsenault and Owen-Smith, 2008). We contrast predictions of the niche compression hypothesis with those of niche expansion in a shared preference system. We anticipated that niche compression would lead to narrower isotope distributions along a continuous axis of one or both species in sympatry (Figs. 2b, c), whereas niche expansion would manifest itself 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, whereas black wildebeest only inhabit the other two reserves. The grassland biome is typically a homogeneous, open landscape, with mostly high grass productivity and little or no tree cover (Mucina and Rutherford, 2006). The 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). The topography is mainly flat, but the grasslands extend eastwards over the escarpment, where altitude rises as high as ~2500 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 analyser (Carlo Erba, Milan, Italy), and introducing the resultant CO_2 and N_2 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 N_2 standards for $\delta^{13}C$ and $\delta^{15}N$, respectively. Standard deviations of repeated measures of laboratory standards (Merck Gel, lentil, and chocolate powder) were less than 0.1‰ and 0.3‰ for $\delta^{13}C$ and $\delta^{15}N$, 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

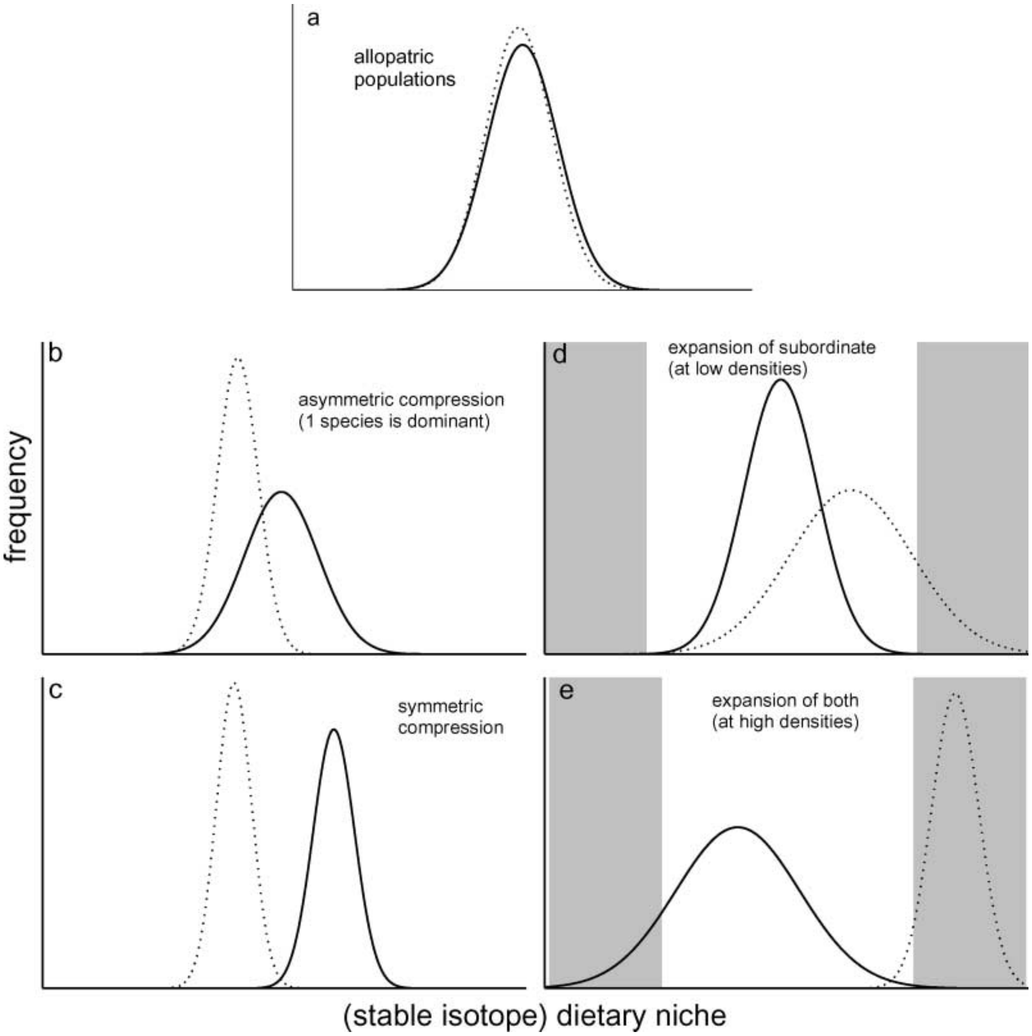

Fig. 2. Conceptualized stable isotope niche dynamics under the niche compression (distinct preference system) and niche expansion (shared preference system) hypotheses (adapted from Fig. 1). Allopatric populations use similar niches (a), but in sympatry competition leads to reduced (i.e. niche compression: 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).

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 (i.e. ~400 mm of rainfall per annum), open grassland

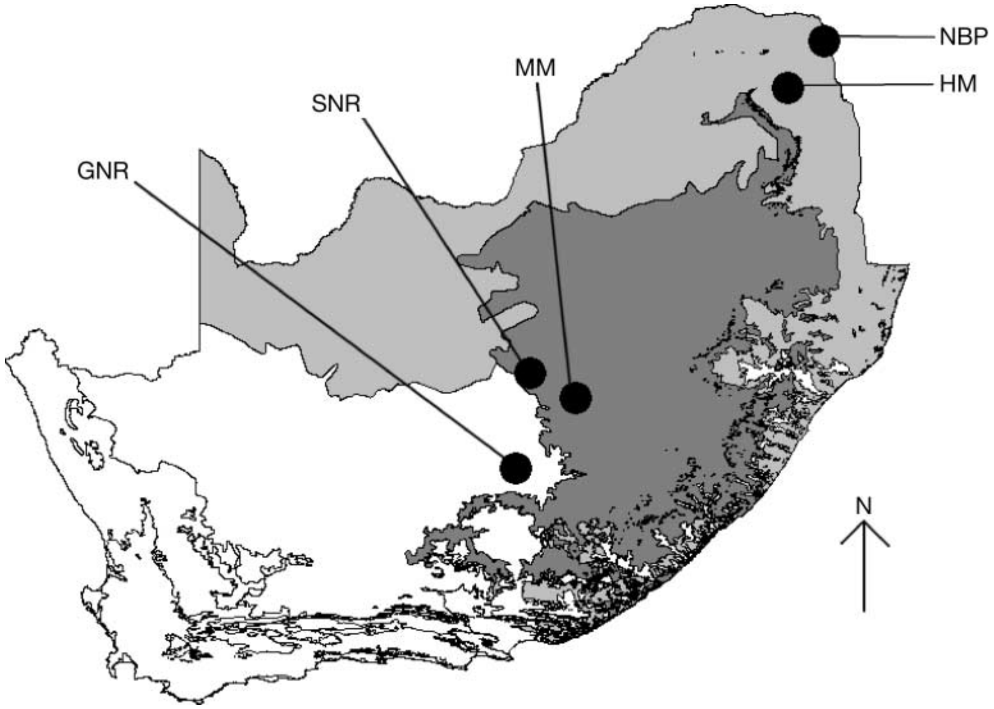

Fig. 3. Map of South Africa with grassland (dark shading) and savanna (light shading) biomes, and reserves sampled (GNR = Gariep Dam Nature Reserve, both wildebeest species; MM = Maria Moroka Reserve and SNR = Soetdoring Nature Reserve, black wildebeest only; NBP = Northern Basalt Plains, Kruger National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

permeated with a network of seasonal pans (Grant *et al.*, 2002), and is thus comparable to habitats in the grassland biome. The HM reserve 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 $\delta^{13}C$ values, $\delta^{15}N$ values, and %N as continuous dependent variables, and 'Reserve' or 'Species' as categorical factors. Data were compared using one-way analysis of variance (ANOVA), or the non-parametric Kruskal-Wallis alternative when residuals were not normally distributed (plant $\delta^{15}N$ and %N). For plant data, multiple comparisons tests were performed with Tukey's HSD. For faeces we used Dunnett's *post hoc t*-test 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 v.8.0 (Statsoft Inc., 2007).

Table 1. Sampling details and vegetation data (mean ± 1 standard deviation) for reserves included in the study

			C_4 grass				C_3 tree and forb foliage			
Region	Date	Wildebeest species	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%N	*n*	$\delta^{13}C$ (‰)	$\delta^{15}N$ (‰)	%N
GNR	June 2008*	Both	15	−13.5 ± 0.56	2.6 ± 1.99	0.6 ± 0.27	12	−27.5 ± 1.28	5.1 ± 2.79	1.2 ± 0.47
	May 2006⁺		—	—	—	—	—	—	—	—
MM	June 2008*	Black	23	−13.4 ± 0.54	1.2 ± 1.78	0.5 ± 0.19	2	−26.7 ± 1.12	3.6 ± 6.36	1.0 ± 0.42
SNR	June 2008*	Black	13	−14.0 ± 0.65	2.0 ± 1.72	0.9 ± 0.49	10	−25.9 ± 0.97	3.7 ± 1.87	1.9 ± 0.74
NBP	June 2004 & May 2005#	Blue	43	−13.2 ± 0.75	4.6 ± 1.58	1.4 ± 0.85	34	−26.5 ± 1.17	6.1 ± 1.67	2.2 ± 0.68
HM	June 2004 & May 2005#	Blue	12	−13.6 ± 0.55	2.6 ± 0.39	1.1 ± 0.43	12	−26.9 ± 0.97	3.3 ± 0.61	2.0 ± 0.33

Note: GNR = Gariep Dam Nature Reserve, MM = Maria Moroka Park, SNR = Soetdoring Nature Reserve, NBP = Northern Basalt Plains, HM = Hans Merensky Nature Reserve. *n* = Number of observations (individual plants sampled).

* Data collected in the present study. ⁺ Data from Codron and Brink (2007). # Data from Codron *et al*. (2007).

Variation in stable isotope composition of dietary baselines influences consumer isotope compositions, which blurs the relationship between ecological and isotopic niches (Post, 2002; Codron *et al.*, 2007). 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 δ^{15}N data) values for local C_4 (grass) and C_3 (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 on which the highest values correspond most closely to values for C_4 vegetation. We used these estimates of 'δ niche space' as dependent variables in our analyses because they account for regional variations in plant δ^{13}C and δ^{15}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^{13}C values consistent with C_4 vegetation (−15.0‰ to −11.7‰, $n = 106$) and values for tree and forb foliage were all consistent with C_3 vegetation (−29.7‰ to −24.3‰, $n = 70$). Plant δ^{13}C values did not differ by much between habitats, although significant differences were found between SNR and NBP for C_4 grass (mean difference = 0.8‰; Tukey's $P = 0.002$), and between GNR and SNR for C_3 foliage (mean difference = 1.6‰; Tukey's $P = 0.011$; Table 1). Variance in δ^{13}C values for both plant groups did not differ between regions (Levene's $P = 0.898$ for C_4 and 0.967 for C_3).

Plant δ^{15}N differed across regions, in that values for C_4 grass were ~2.0‰ to 3.5‰ higher at NBP compared with the other reserves ($H_{4,106} = 50.146$; $P < 0.05$), and values for C_3 foliage were ~2.5‰ higher at NBP compared with SNR and HM ($H_{4,70} = 24.299$; $P = 0.013$ 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 $P < 0.0001$, 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

The δ^{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 standard deviations 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 δ^{13}C niche space were almost identical (Dunnett's $P = 0.842$; $F_{70,59} = 1.325$, $P = 0.134$; Fig. 4a). A δ^{13}C niche shift was manifest, however, in the sympatric populations at GNR. Here, black wildebeest had, on average, larger values (more strongly

Table 2. Faecal stable isotope data, and %N (mean ± 1 standard deviation) for the wildebeest populations included in this study

Population (reserve)	*n*	δ^{13}C (‰)	δ^{15}N (‰)	%N
Black wildebeest				
GNR	35	−14.9 ± 0.25	5.1 ± 0.53	1.1 ± 0.21
MM	14	−14.0 ± 0.40	3.7 ± 0.60	1.0 ± 0.18
SNR	11	−16.1 ± 0.56	5.3 ± 0.34	1.0 ± 0.15
Overall	60	−14.9 ± 0.75	4.8 ± 0.82	1.1 ± 0.20
Blue wildebeest				
GNR	36	−15.2 ± 0.73	4.2 ± 0.93	1.2 ± 0.25
NBP	15	−14.6 ± 0.42	4.5 ± 0.42	1.5 ± 0.27
HM	20	−14.4 ± 0.88	4.2 ± 0.70	1.3 ± 0.12
Overall	71	−14.8 ± 0.79	4.3 ± 0.79	1.3 ± 0.26

Note: GNR = Gariep Dam Nature Reserve, MM = Maria Moroka Park, SNR = Soetdoring Nature Reserve, NBP = Northern Basalt Plains, HM = Hans Merensky Nature Reserve. *n* = Number of observations (faecal piles sampled).

C_4; Dunnett's $P = 0.028$), but a smaller niche variance than blue wildebeest ($F_{35,34} = 8.323$, $P < 0.0001$).

Mean faecal δ^{15}N for black wildebeest was greater than for blue wildebeest, both overall (mean difference = 0.5‰; Dunnett's $P < 0.001$) and in sympatry at GNR (mean difference = 0.9‰; Dunnett's $P < 0.001$). However, after accounting for regional differences in plant δ^{15}N, the overall difference did not persist (Dunnett's $P = 0.186$; Fig. 4b), and the situation among sympatric populations became reversed, i.e. the estimated δ^{15}N niche of black wildebeest was *narr*ower than that of blue wildebeest (Dunnett's $P < 0.0001$), whereas blue wildebeest values were more similar to those of local C_4 grass. Variance in faecal δ^{15}N for the two species was similar ($F_{70,59} = 1.074$, $P = 0.385$), but after controlling for plant variations, we still found that black wildebeest had a narrower δ^{15}N niche breadth than blue wildebeest (s.d. = 0.61 and 1.09, respectively; $F_{70,59} = 3.169$, $P < 0.0001$). At GNR, however, variance in δ^{15}N 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 than that of blue wildebeest (Dunnett'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 (Dunnett's $P = 0.632$; $F_{35,34} = 1.326$, $P = 0.206$; Fig. 4c).

Niche dynamics across populations

Mean faecal δ^{13}C values of black wildebeest differed between the three populations studied (Dunnett's $P < 0.0001$ for all comparisons; Table 2). The sample with the most positive values in δ^{13}C niche space (most similar to C_4 plants) was at MM, while the SNR population utilized the least positive δ^{13}C niche space, and the GNR sample had an intermediate range of values (Fig. 5a). Also, 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 δ^{13}C niche variance of MM and SNR were not different ($F_{10,13} = 1.962$, $P = 0.127$).

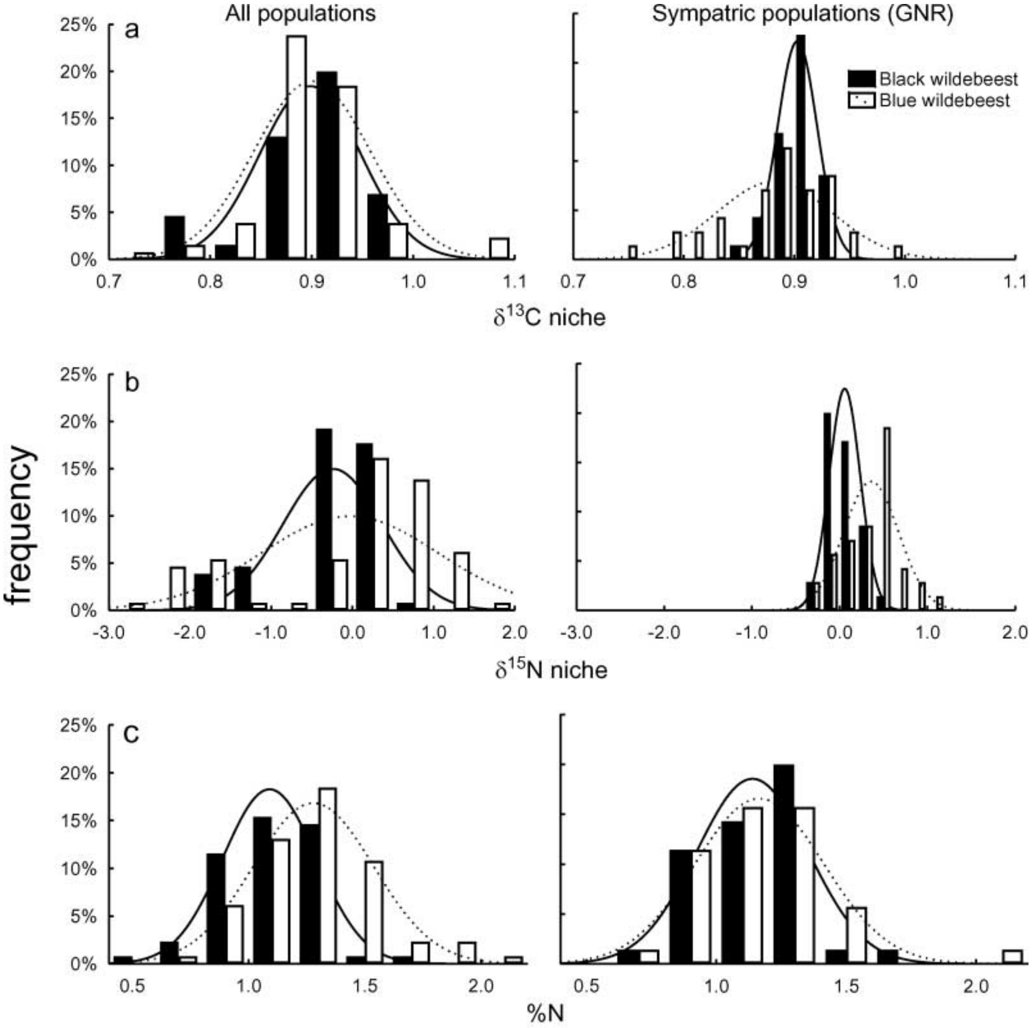

Fig. 4. Comparative distributions of faecal data in (a) $\delta^{13}C$ niche space, (b) $\delta^{15}N$ niche space, and (c) %N between the two wildebeest species. Plots on the left represent data for all populations (reserves), plots on the right represent sympatric populations (GNR) only. Isotope niche 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.

Faecal $\delta^{15}N$ 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 $\delta^{15}N$ niche was lower at SNR compared with the other two reserves (Dunnett's $P < 0.0001$; Fig. 5b), suggesting the former result was likely due to the low grass $\delta^{15}N$ values at MM (see Table 1). There were no significant differences in $\delta^{15}N$ 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 standard deviations, 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).

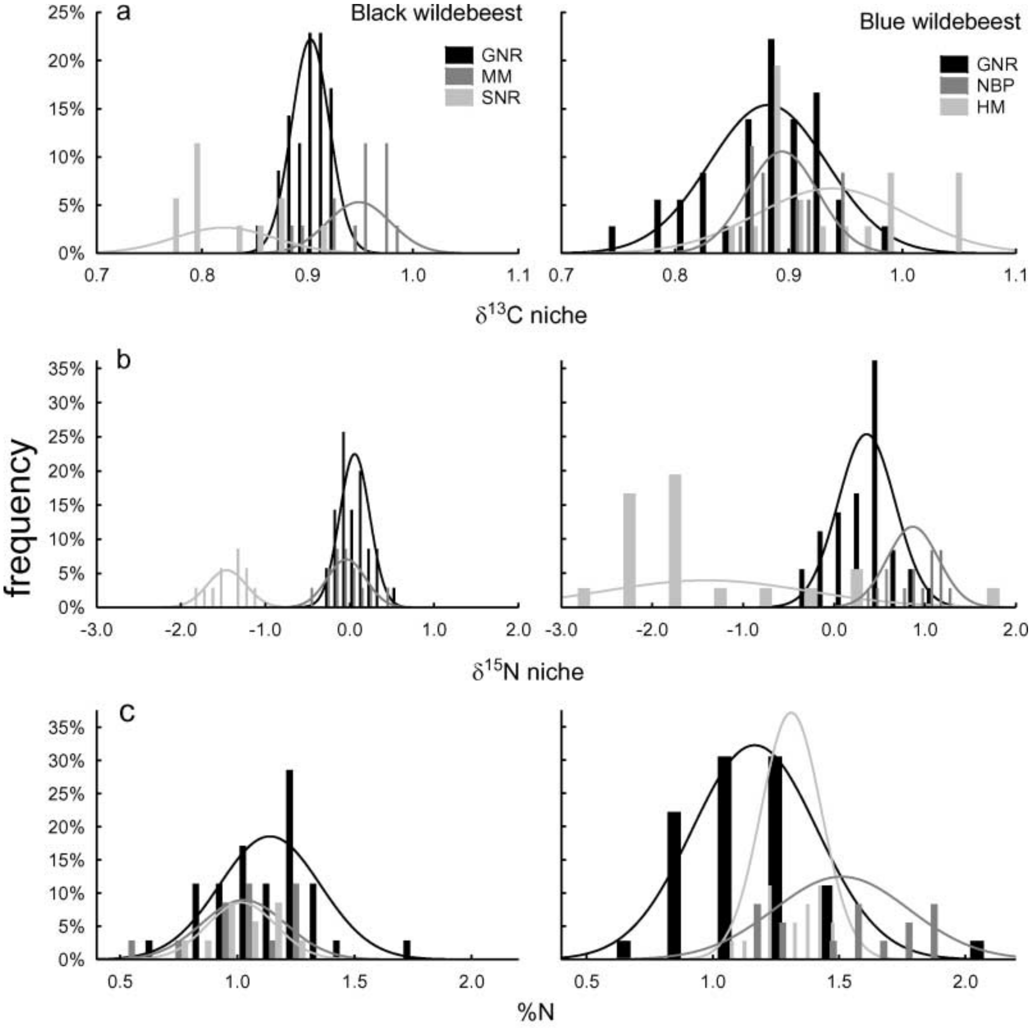

Fig. 5. Comparative distributions of faecal data in (a) $\delta^{13}C$ niche space, (b) $\delta^{15}N$ niche space, and (c) %N between populations of each species living sympatrically (GNR, black bars) and allopatrically (grey bars). Plots on the left are black wildebeest populations, plots on the right 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.

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 we accounted 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 we did find differences 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 that 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. Results also showed that the isotopic niches of both species at GNR differed from those of their allopatric conspecifics, indicating that inter-specific competition was an important driver of niche dynamics. Black wildebeest at GNR had a narrower faecal $\delta^{13}C$ niche breadth compared with the two allopatric populations of this species, whereas the $\delta^{13}C$ niche breadth of blue wildebeest at GNR was wider than that of the allopatric population from the NBP, but not from HM.

The relatively small sample sizes ($n < 20$ in some reserves) of our study might be a limitation, but the pattern of isotopic niche overlap with partitioning emerging in sympatry appears quite robust, especially for the $\delta^{13}C$ data. For instance, data for the sympatric populations reflect similar trends over two study years (2006 and 2008). Furthermore, 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 versus 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' and '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 results demonstrate 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) that are logistically difficult for large animals, we have shown that stable isotope analysis can reveal cases where niche shifts result from 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-to-stem ratios) as axes for resource partitioning among grazing ungulates (Bell, 1971; Murray and Brown, 1993; Murray and Illius, 2000; Arsenault and Owen-Smith, 2008; Codron *et al.*, 2008b; Kleynhans *et al.*, 2011). Our results demonstrate 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 δ^{13}C values here indicate that this population utilized C_4 items almost exclusively. By contrast, the wide δ^{13}C niche breadth of blue wildebeest at GNR almost certainly indicates substantial C_3 browse intake by some individuals (comprising no more than about 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 inter-habitat variability in plant isotope composition. Even intra-habitat variability [which, in South African savannas, is usually <2‰ (Codron *et al.*, 2005)] cannot explain faecal δ^{13}C values of blue wildebeest at the most ^{13}C-depleted end of the scale. Based on previous research on faecal δ^{13}C distributions in southern African habitats (Codron *et al.*, 2007, 2009), we are confident that values less than −15.5‰ are unlikely to occur without significant C_3 inputs to diet. Approximately 22% of blue wildebeest faecal specimens collected at GNR had δ^{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 C_3 browse (shrubs, forbs, or trees).

The difference in faecal δ^{15}N values between the two species could indicate additional partitioning of the resource if local C_4 grasses (the dominant resource in all wildebeest diets) varied systematically in ^{15}N composition. In that case, black wildebeest were likely consuming more grasses that use the NAD-ME or PCK photosynthetic sub-pathways, as these are often ^{15}N-enriched relative to NADP-ME grasses in southern African savannas (Codron *et al.*, 2005; Codron *et al.*, 2009). The former group comprises more species of panicoids and chloridoids, whereas the latter comprises more tall, fibrous andropogonoid species (Sage *et al.*, 1999). Given that both wildebeest species are preferentially short-grass grazers (Skinner and Smithers, 1990; Brink, 2005), 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 versus NADP dichotomy in herbivore faecal δ^{15}N 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 eco-physiological factors do influence herbivore ^{15}N-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 δ^{13}C (C_3 browsing/C_4 grazing) dietary axis, at GNR. However, we do not believe this is consistent with the niche compression hypothesis of MacArthur and Pianka (1966). First, while the δ^{15}N 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 hypothesis (Rosenzweig, 1981). This theory also does not explain the expansion of the blue wildebeest δ^{13}C niche in sympatry, 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 (Skinner and Smithers, 1990; Brink, 2005). South African grasslands represent only the southern margin of the blue wildebeest distribution in Africa. Here, blue wildebeest have largely replaced black wildebeest since they diverged ~1 million years ago (Brink, 2005; Codron *et al.*, 2008a). Thus, we would expect black wildebeest to be the dominant competitor in these habitats.

Our data provide further evidence for black wildebeest dominance. 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 with other habitats. This implies that blue wildebeest in sympatry 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.

The shared-preference pattern of niche dynamics is known in other systems. For example, Holmes (1961) 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 their attachment site, but in concurrent infections one species, *Monilformis dubius* (acanthocephalan), appeared to force the other, *Hymenolepis diminuta* (cestode), to occupy less-preferred posterior attachment sites. Pimm *et al.* (1985) studied hummingbird behaviour using feeders of two different concentrations of sucrose. Both the blue-throated hummingbird (*Lampornis clemenciae*) and black-chinned hummingbird (*Archilochus alexandri*) preferred feeders with high sucrose concentrations, but black-chinned hummingbirds used both feeder types at high densities of either species. Ziv *et al.* (1995) discovered a shared preference in two species of competing psammophilic gerbils. Fuerthermore, Rosenzweig (1987, 1991) discussed the general applicability of the concept to plant and animal competition.

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 δ^{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 site niches with increasing densities of their own species, in line with predictions of the IFD (Fretwell and Lucas, 1970). Pimm *et al.* (1985) showed that even the dominant blue-throated species accepted feeders with the low sucrose concentration at high blue-throated densities (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 difficult, however, to draw analogies between those studies with our results, because the former compared species with different foraging styles (browsers, grazers, and mixed-feeders), whereas we focused on grazers only. Nevertheless, Gordon and Illius (1989) did hypothesize that 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 ~180 kg) are almost 50% larger than black wildebeest (mean mass of females ~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. Indeed, 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 or 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.

ACKNOWLEDGEMENTS

We thank Savvas Vrahmis, Peter Calverley, Garreth Champion, Stuart Dunlop, Jeff Hean, and the management of the various nature reserves for their assistance with this work, John Lanham and Ian Newton for stable isotope analysis, Jürgen Streich for statistical advice, and Michael Rosenzweig for comments on an earlier version of the manuscript. Funding was provided by the National Research Foundation, the University of KwaZulu-Natal, and the Palaeontological Scientific Research Trust, South Africa; the European Union (Marie-Curie PIIF-GA-2009-236670) and the Swiss National Fund (IZ32Z0-125787). This work was approved by the Animal Ethics Sub-Committee of the University of KwaZulu-Natal.

REFERENCES

Ambrose, S.H. 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *J. Archaeol. Sci.*, **18**: 293–317.

Arsenault, R. and Owen-Smith, N. 2008. Resource partitioning by grass height among grazing ungulates does not follow body size relation. *Oikos*, **117**: 1711–1717.

Bell, R.H.V. 1971. A grazing ecosystem in the Serengeti. *Sci. Am.*, **225**: 86–93.

Brink, J.S. 2005. The evolution of the black wildebeest, *Connochaetes gnou*, and modern large mammal faunas in central Southern Africa. PhD thesis, Stellenbosch University.

Cerling, T.E. and Harris, J.M. 1999. Carbon isotope fractionation between diet and bioapatite in ungulate mammals and implications for ecological and paleoecological studies. *Oecologia*, **120**: 347–363.

Chesson, P. 2000. Mechanisms of maintenance of species diversity. *Annu. Rev. Ecol. Syst.*, **31**: 343–366.

Codron, D. and Brink, J. 2007. Trophic ecology of two savanna grazers, blue wildebeest *Connochaetes taurinus* and black wildebeest *Connochaetes gnou*. *Eur. J. Wildl. Res.*, **53**: 90–99.

Codron, D. and Codron, J. 2009. Reliability of $\delta^{13}C$ and $\delta^{15}N$ in faeces for reconstructing savanna herbivore diet. *Mammal. Biol.*, **74**: 36–48.

Codron, D., Lee-Thorp, J.A., Sponheimer, M. and Codron, J. 2007. Stable carbon isotope reconstruction of ungulate diet changes through the seasonal cycle. *S. Afr. J. Wildl. Res.*, **37**: 117–125.

Codron, D., Brink, J.S., Rossouw, L. and Clauss, M. 2008a. The evolution of ecological specialization in southern African ungulates: Competition or physical environmental turnover? *Oikos*, **117**: 344–353.

Codron, D., Brink, J.S., Rossouw, L., Clauss, M., Codron, J., Lee-Thorp, J.A. *et al.* 2008b. Functional differentiation of African grazing ruminants: An example of specialized adaptations to very small changes in diet. *Biol. J. Linn. Soc.*, **94**: 755–764.

Codron, D., Codron, J., Lee-Thorp, J.A., Sponheimer, M., Grant, C.C. and Brink, J.S. 2009. Stable isotope evidence for nutritional stress, competition, and loss of functional habitat as factors limiting recovery of rare antelope in southern Africa. *J. Arid Environ.*, **73**: 449–457.

Codron, J., Codron, D., Lee-Thorp, J.A., Sponheimer, M., Bond, W.J., De Ruiter, D. *et al.* 2005. Taxonomic, anatomical, and spatio-temporal variations in the stable carbon and nitrogen isotopic compositions of plants from an African savanna. *J. Archaeol. Sci.*, **32**: 1757–1772.

Crawford, K., McDonald, R.A. and Bearhop, S. 2008. Applications of stable isotope techniques to the ecology of mammals. *Mammal Rev.*, **38**: 87–107.

Cromsigt, J.P.G.M. and Olff, H. 2006. Resource partitioning among savanna grazers mediated by local heterogeneity: an experimental approach. *Ecology*, **87**: 1532–1541.

Dickman, C.R. 1986. Niche compression: Two tests of an hypothesis using narrowly sympatric predator species. *Austral Ecol.*, **11**: 121–134.

Farnsworth, K.D., Focardi, S. and Beecham, J.A. 2002. Grassland–herbivore interactions: how do grazers coexist? *Am. Nat.*, **159**: 24–39.

Fretwell, S.D. and Lucas, H.L.J. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheor.*, **19**: 16–36.

Gordon, I.J. and Illius, A.W. 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia*, **79**: 383–389.

Grant, C.C., Davidson, T., Funston, P.J. and Pienaar, D.J. 2002. Challenges faced in the conservation of rare antelope: A case study on the northern basalt plains of the Kruger National Park. *Koedoe*, **45**: 45–66.

Helm, C.V. 2006. Ecological separation of the black and blue wildebeest on Ezemvelo Nature Reserve in the highveld grasslands of South Africa. MSc dissertation, University of Pretoria.

Holecheck, J.L., Vavre, M. and Pieper, R.D. 1982. Methods for determining the nutritive quality of range ruminant diets: a review. *J. Anim. Sci.*, **54**: 363–376.

Holmes, J.C. 1961. Effects of concurrent infections on *Hymenolepis diminuta* (Cestoda) and *Moniliformis dubius* (Acanthocephala). I. General effects and comparison with crowding. *J. Parasitol.*, **47**: 209–216.

Holt, R.D. 1987. On the relation between niche overlap and competition: the effect of incommensurable niche dimensions. *Oikos*, **48**: 110–114.

Janecke, B.B., du Preez, P.J. and Venter, H.J.T. 2003. Vegetation ecology of the pans (playas) of Soetdoring Nature Reserve, Free State Province. *S. Afr. J. Bot.*, **69**: 401–409.

Jarman, P.J. 1974. The social organization of antelope in relation to their ecology. *Behaviour*, **48**: 215–266.

Kleynhans, E.J., Jolles, A.E., Bos, M.R.E. and Olff, H. 2011. Resource partitioning along multiple niche dimensions in differently sized African savanna grazers. *Oikos*, **120**: 591–600.

MacArthur, R.H. and Pianka, E.R. 1966. An optimal use of a patchy environment. *Am. Nat.*, **100**: 603–609.

Martínez del Rio, C., Wolf, N., Carleton, S.A. and Gannes, L.Z. 2009. Isotopic ecology ten years after a call for more laboratory experiments. *Biol. Rev.*, **84**: 91–111.

Michaud, W.K., Power, M. and Kinnison, M.T. 2008. Trophically mediated divergence of Arctic charr (*Salvelinus alpinus* L.) populations in contemporary time. *Evol. Ecol. Res.*, **10**: 1051–1066.

Morris, D.W. 1988. Habitat-dependent population regulation and community structure. *Evol. Ecol.*, **2**: 253–269.

Mucina, L. and Rutherford, M.C. 2006. *The Vegetation of South Africa, Lesotho and Swaziland*, Vol. 19. Pretoria: South Africa National Biodiversity Institute.

Murray, M.G. and Baird, D.R. 2008. Resource-ratio theory applied to large herbivores. *Ecology*, **89**: 1445–1456.

Murray, M.G. and Brown, D. 1993. Niche separation of grazing ungulates in the Serengeti: an experimental test. *J. Anim. Ecol.*, **62**: 380–389.

Murray, M.G. and Illius, A.W. 1996. Multispecies grazing in the Serengeti. In *The Ecology and Management of Grazing Systems* (J. Hodgson and A.W. Illius, eds.), pp. 247–272. Wallingford, UK: CAB International.

Murray, M.G. and Illius, A.W. 2000. Vegetation modification and resource competition in grazing ungulates. *Oikos*, **89**: 501–508.

Mysterud, A. 2000. Diet overlap among ruminants in Fennoscandia. *Oecologia*, **124**: 130–137.

Newsome, S.D., Martinez del Rio, C., Bearhop, S. and Phillips, D.L. 2007. A niche for isotopic ecology. *Front. Ecol. Environ.*, **5**: 429–436.

Pimm, S.L., Rosenzweig, M.L. and Mitchell, W. 1985. Competition and food selection: field tests of a theory. *Ecology*, **66**: 798–807.

Post, D.M. 2002. Using stable isotopes to estimate trophic position: models, methods, and assumptions. *Ecology*, **83**: 703–718.

Prins, H.H.T. and Olff, H. 1998. Species-richness of African grazer assemblages: towards a functional explanation. In *Dynamics of Tropical Communities* (D.M. Newbery, H.H.T. Prins and N. Brown, eds.), pp. 449–490. Oxford: Blackwell Science.

Robbins, C., Felicetti, L. and Florin, S. 2010. The impact of protein quality on stable nitrogen isotope ratio discrimination and assimilated diet estimation. *Oecologia*, **162**: 571–579.

Rosenzweig, M.L. 1981. A theory of habitat selection. *Ecology*, **62**: 327–335.

Rosenzweig, M.L. 1987. Community organization from the point of view of habitat selectors. In *Organization of Communities: Past and Present* (J.H.R. Gee and B.J. Giller, eds.), pp. 469–490. British Ecological Society Symposium #27. Oxford: Blackwell Science.

Rosenzweig, M.L. 1991. Habitat selection and population interactions: the search for mechanism. In *Habitat Selection Symposium* (G. Orians, ed.). *Am. Nat.*, **137**: S5–S28.

Rosenzweig, M.L. and Abramsky, Z. 1986. Centrifugal community organization. *Oikos*, **46**: 339–348.

Sage, R.F., Li, M. and Monson, R.K. 1999. The taxonomic distribution of C_4 photosynthesis. In *C4 Plant Biology* (R.F. Sage and R.K. Monson, eds.), pp. 551–584. San Diego, CA: Academic Press.

Schoener, T.W. 1983. Field experiments on interspecific competition. *Am. Nat.*, **122**: 240–285.

Sinclair, A.R.E. 1985. Does interspecific competition or predation shape the African ungulate community? *J. Anim. Ecol.*, **54**: 899–918.

Sinclair, A.R.E., Fryxell, J.M. and Caughley, G. 2006. *Wildlife Ecology, Conservation, and Management*, 2nd edn. Malden, MA: Blackwell Publishing.

Skead, C.J. 1980. *The Western and Northern Cape*, Vol. 1. Cape Town: Department of Nature and Environmental Conservation of the Provincial Administration of the Cape of Good Hope.

Skinner, J.D. and Smithers, R.H.N. 1990. *The Mammals of the Southern African Subregion* (2nd edn.). Pretoria: University of Pretoria.

Sponheimer, M., Robinson, T., Ayliffe, L., Passey, B., Roeder, B., Shipley, L. *et al.* 2003a. An experimental study of carbon-isotope fractionation between diet, hair, and feces of mammalian herbivores. *Can. J. Zool.*, **81**: 871–876.

Sponheimer, M., Robinson, T., Ayliffe, L., Roeder, B., Hammer, J., Passey, B. *et al.* 2003b. Nitrogen isotopes in mammalian herbivores: hair $d^{15}N$ values from a controlled feeding study. *Int. J. Osteoarchaeol.*, **13**: 80–87.

Statsoft Inc. 2007. *STATISTICA*, Version 8.0 (data analysis software system). www.statsoft.com. Tulsa, OK: Statsoft Inc.

Stewart, K.M., Bowyer, R.T., Kie, J.G., Dick, B.L. and Ben-David, M. 2003. Niche partitioning among mule deer, elk, and cattle: do stable isotopes reflect dietary niche? *Ecoscience*, **10**: 297–302.

Tieszen, L., Hein, D., Qvortrup, D., Troughton, J. and Imbamba, S. 1979. Use of $d^{13}C$ values to determine vegetation selectivity in east African herbivores. *Oecologia*, **37**: 351–359.

Tregenza, T. 1995. Building on the ideal free distribution. *Adv. Ecol. Res.*, **26**: 253–302.

Valdovinos, F.S., Ramos-Jiliberto, R., Garay-Narváez, L., Urbani, P. and Dunne, J.A. 2010. Consequences of adaptive behaviour for the structure and dynamics of food webs. *Ecol. Lett.*, **13**: 1546–1559.

Van Zyl, J.H.M. 1965. The vegetation of the S.A. Lombard Nature Reserve and its utilization by certain antelope. *Zool. Africana*, **1**: 55–71.

Vogel, J.C. 1978. Isotopic assessment of the dietary habits of ungulates. *S. Afr. J. Sci.*, **74**: 298–301.

Ward, D. 2009. *The Biology of Deserts*. Oxford: Oxford University Press.

Ward, D. and Seely, M.K. 1996. Competition and habitat selection in Namib desert tenebrionid beetles. *Evol. Ecol.*, **10**: 341–359.

Wasserberg, G., Kotler, B.P., Morris, D.W. and Abramsky, Z. 2007. A field test of the centrifugal community organization model using psammophilic gerbils in Israel's southern coastal plain. *Evol. Ecol. Res.*, **9**: 299–311.

York, H.A. and Billings, S.A. 2009. Stable-isotope analysis of diets of short-tailed fruit bats (Chiroptera: Phyllostomidae: *Carollia*). *J. Mammal.*, **90**: 1469–1477.

Ziv, Y., Kotler, B.P., Abramsky, Z. and Rosenzweig, M.L. 1995. Foraging efficiencies of competing rodents: why do gerbils exhibit shared-preference habitat selection? *Oikos*, **73**: 260–268.