

Individual variation of isotopic niches in grazing and browsing desert ungulates

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Received: 13 June 2014 / Accepted: 28 April 2015 / Published online: 9 May 2015
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Abstract Ungulates often adjust their diet when food availability varies over time. However, it is poorly understood when and to what extent individuals change their diet and, if they do so, if all individuals of a population occupy distinct or similar dietary niches. In the arid Namibian Kunene Region, we studied temporal variations of individual niches in grazing gemsbok (*Oryx gazella gazella*) and predominantly browsing springbok (*Antidorcas marsupialis*). We used variation in stable C and N isotope ratios of tail hair increments as proxies to estimate individual isotopic dietary niches and their temporal plasticity. Isotopic dietary niches of populations of the two species were mutually exclusive, but similar in breadth. Isotopic niche breadth of gemsbok was better explained by within-individual variation than by between-individual variation of stable isotope ratios, indicating that gemsbok individuals were facultative specialists in using isotopically distinct local food resources. In contrast, inter- and intra-individual variations contributed similarly to the isotopic niche breadth of the

springbok population, suggesting a higher degree of individual isotopic segregation in a more generalist ungulate. In both species, between-individual variation was neither explained by changes in plant primary productivity, sex, geographical position nor by group size. Within species, individual dietary niches overlapped partially, suggesting that both populations included individuals with distinct isotopic dietary niches. Our study provides the first evidence for isotopic dietary niche segregation in individuals of two distinct desert ungulates. Similar, yet isotopically distinct dietary niches of individuals may facilitate partitioning of food resources and thus individual survival in desert ecosystems.

Keywords Resource availability · Dietary strategy · Spatial behaviour · Tail hair · Stable isotope analyses

Introduction

Mammalian herbivores such as ungulates select food resources according to various factors. For example, ungulates may choose food according to the availability of plants in space and time, endogenous digestive capabilities (du Toit 2003) and social constraints like individual ranks in a group (Appleby 1980; Côté 2000). Yet, many ungulates are also flexible in their feeding habits, for example when food abundance varies over time (Owen-Smith 2008; Lehmann et al. 2013). The dietary niche of an animal is typically defined by the overall range of food resources contributing to its diet. Since variation in primary productivity often follows precipitation patterns, and since a dietary niche of an animal species is influenced by the local quantity, quality and accessibility of available food resources (Macdonald 1983; Spalinger and Hobbs 1992; Sih and Christiansen

Communicated by Peggy Ostrom.

Electronic supplementary material The online version of this article (doi:10.1007/s00442-015-3335-1) contains supplementary material, which is available to authorized users.

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2001), dietary niches of populations are expected to expand or shrink in response to the availability of the animals' preferred food items (Codron et al. 2007; Owen-Smith et al. 2013). At the population level, such expansions or constrictions in dietary niche width have been confirmed for sable antelopes (*Hippotragus niger*) (Owen-Smith et al. 2013), zebras (*Equus quagga*) (Owen-Smith et al. 2013) and moose (*Alces alces*) (Dungan and Wright 2005). Yet, past studies neglected that the feeding ecology of local ungulate populations might result from the additive effect of individual food selection and consequently from the extent of individualized dietary niches. Accordingly, dietary niches of animals may be better inferred from the sum of individual feeding preferences within a given population (Bolnick et al. 2003, 2007). For example, individuals within a population of dietary generalists might largely overlap in their use of food resources, or each individual might be highly specialized towards a subset of food resources (Roughgarden 1972). Individual dietary specialization has been confirmed for apex marine predators (Matich et al. 2010; Kim et al. 2013) and other predatory fishes (Quevedo et al. 2009), for birds (Inger et al. 2006; Martinez del Rio et al. 2009), and for reptiles (Vander Zanden et al. 2010). Dietary specialization of individuals may be driven by seasonal and yearly or inter-habitat differences in resource availability or by energy requirements or habitat choices at specific life stages (Estes et al. 2003; Svanbäck and Persson 2004; Darimont et al. 2009). Overall, studies on individual dietary strategies of mammals are scarce and mainly limited to top predators (Urton and Hobson 2005), omnivores (Newsome et al. 2007), primates (Watts 1984; Dammhahn and Kappeler 2014) or mega-herbivores (Codron et al. 2012). Thus far, no study has considered dietary specialization in individual ungulates, and none has investigated individual specialization in antelopes of deserts.

Many desert plants differ in their stable C isotope ratios ($\delta^{13}\text{C}$) depending on their metabolic pathway of CO_2 fixation, which is either the C4 and crassulacean acid metabolism (CAM) (e.g. in grasses and succulents such as members of the family Euphorbiaceae, respectively) or the C3 (trees and shrubs) photosynthetic pathway (Bender 1971; Osmond 1978; Tieszen et al. 1979). Thus, stable C isotopes differentiate C3 and C4/CAM plants. In addition, using stable N isotope ratios ($\delta^{15}\text{N}$) of C3, C4 and CAM plants may further refine the differentiation of plants at the species levels within the aforementioned plant groups (Lehmann et al. 2013). Indeed, in a previous study, we observed that N ratios distinguished between grasses and succulent species of similar $\delta^{13}\text{C}$. We were also able to discriminate between trees and shrub species based on their $\delta^{15}\text{N}$ (Lehmann et al. 2013). Based on stable isotope ratios in metabolically active tissues (blood, liver and muscle), we showed that local populations of gemsbok (*Oryx gazella*

gazella) and springbok (*Antidorcas marsupialis*) varied in their dietary choice according to temporal changes in precipitation, (Lehmann et al. 2013). Our findings highlighted that gemsbok populations exhibit relatively flexible dietary habits (Lehmann et al. 2013), i.e. they consume a mixture of potential food plants, including more than 30 % of C3 plants during drought periods, but almost exclusively C4 and CAM plant types when food is plentiful. During drought periods, the inferred diet of gemsbok consisted of up to 25 % of *Euphorbia damarana*, an endemic CAM plant that is rich in toxic plant secondary compounds. In contrast, the studied springbok population consisted of more generalist feeders, which consumed a higher proportion of C3 than C4/CAM plants, independent of changes in environmental conditions (Lehmann et al. 2013). The ranges of such variations may therefore be used to infer the isotopic niche breadth at both individual and population levels in the two-dimensional ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) environmental isotopic space of the study site. The isotopic niche breadth therefore reflects the overall range of isotopically contrasted food resources consumed by an individual or a species. Although our previous findings provided important insights into how syntopic ungulates overcome unpredictable shortages in biomass productivity, individual isotopic niche breadths and their temporal plasticity still remained unexplored. Here, we go beyond the population-level approach and ask how isotopic variation of individual gemsbok and springbok may contribute to the isotopic dietary niches of populations.

Stable isotope ratios of incrementally growing inert tissues such as teeth (including ivory), horns, whiskers or tail hairs have been increasingly used to infer temporal changes in both dietary isotopic niches of individuals and population (Cerling et al. 2009; Newsome et al. 2009; Codron et al. 2012, 2013; Kim et al. 2013). This is because such continuously growing tissues record temporal variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ that directly reflect the range of isotopically contrasting food resources consumed over time. Specifically, we aimed to evaluate the isotopic dietary niche breadths of individual ungulates and their variation in time and position within the two-dimensional isotopic food space of our study site. We characterized the individual isotopic dietary niche breadths as the surface area enclosed within the boundaries of the 95 % confidence interval (CI) of Bayesian ellipses within the two-dimensional ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) isotopic space of the food resources (Newsome et al. 2007; del Rio et al. 2009; Flaherty and Ben-David 2010). Accordingly, we estimate the isotopic dietary niche breadth of an animal by the metric size of the area occupied in the dietary isotopic space (Newsome et al. 2007, 2012). These ellipses were calculated and drawn from the varying values of the combined $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tail hair of individual ungulates over a period of almost 2 years, encompassing

two annual cycles that differed markedly in food and water availability. We asked if individual isotopic niches varied within and between populations of generalist and facultative specialists. We also asked if and how isotopic dietary niche breadths of individuals vary in response to temporal changes in resource availability. We hypothesized that the isotopic niche breadths of springbok and gemsbok ought to differ when plant productivity changes. Yet, we are aware that a distinction between isotopic and realized niches still remains. Therefore, based on the previously observed isotopic ratios of potential food resources and their temporal variations in the arid environment of the Kunene Region of Namibia (Lehmann et al. 2013), we set the variation of isotopic values of tail hair, recorded as Bayesian ellipse areas, in relation to the realized dietary niche of individual gemsbok and springbok.

For springbok we predicted that the isotopic dietary niche breadth remains constant and thus independent of fluctuating plant primary productivity, which is consistent with our previous findings that this ungulate species is an opportunistic intermediate feeder of C3 and C4/CAM plant resources (Lehmann et al. 2013). In contrast, we predicted that individuals of gemsbok, a facultative dietary specialist species in the arid Kunene Region of Namibia (Lehmann et al. 2013), have narrow isotopic dietary niches during periods of high primary productivity but broad ones when food resources become scarce. This pattern would indicate that both ungulate species are flexible in their feeding habits, allowing animals to adjust their diets to the food availability of a heterogeneous habitat, which in the long term may enhance their survival during periods of extreme food shortage, such as during prolonged droughts. Furthermore, intra- and inter-species competition for resources may also influence habitat selection in ungulates (Hensman et al. 2013). Accordingly, high levels of individual niche variations in desert-dwelling ungulates would indirectly reflect mechanisms of habitat and resource partitioning in time and space among individuals and populations.

Materials and methods

Study site and species

Field work took place in June 2011 in the southern part of the Kunene Region of Namibia (20°12'98.3"S, 14°04'15.2"E), a 3500-km² area that is managed by the Torra Conservancy under the premise of the sustainable use of natural resources (Fig. 1). The local ecosystem consists of outcrops of basaltic mountain ranges, rocky and gravel plains, dry riverbeds and deltas formed by the ephemeral Huab and Springbok rivers. The annual precipitation usually ranges between 100 mm and 150 mm and the ambient

temperature may reach up to 50 °C during the dry season (Digital Atlas of Namibia 2002). Precipitation may vary largely in this area and therefore plant availability is mostly unpredictable. The vegetation ranges from few, scarce open grasslands with bushes to plain rocky and/or sandy desert.

Gemsbok are relatively large ungulates (body mass 180–240 kg) that have a geographical distribution from South Africa to northern Namibia and the southern parts of Botswana (Skinner and Chimimba 2005). Springbok body mass (30–44 kg) is lower than that of gemsbok. Springbok occur from the north-western part of South Africa through the Kalahari Desert into Namibia and Botswana (Skinner and Chimimba 2005). The distribution range of both species largely overlaps and includes various habitats such as savannahs, woodlands and deserts (Skinner and Chimimba 2005).

Sample collections

Sample collection was authorised by the Ministry of Environment and Tourism of Namibia (research permit nos. 1534/2010 and 1676/2012) and approved by the Institutional Committee for Ethics and Animal Welfare of the Leibniz Institute for Zoo and Wildlife Research (IZW) of Berlin (no. 2009-10-01).

Under the Namibian program of community-based natural resource management (CBNRM) [Namibia Association of CBNRM Support Organizations; NACSO 2012], conservancies are given annual quotas for population control. We collected tail hairs of springbok and gemsbok hunted by conservancy members. In total, we collected tail hairs from 16 adult gemsbok (ten males and six females) and 30 adult springbok (17 males and 13 females). As the growth rate of gemsbok and springbok tail hair is unknown, we used data from closely related species of similar body size as the best estimate. We assumed that gemsbok tail hair has a similar growth rate to that of equids and large-bodied bovid, which both average 0.7 mm day⁻¹ [domestic horse *Equus caballus* (Ayliffe et al. 2004; West et al. 2004); ponies (Dunnett and Lees 2003); and domestic cow *Bos taurus* (Schwertl et al. 2003)]. As the best proxy for the growth rate of springbok tail hair, we referred to a study on the similar-sized impala (*Aepyceros melampus*) (Saitoh et al. 1969; Sponheimer et al. 2003) that indicated a tail hair growth rate of 1 cm month⁻¹. We collected on average 35 ± 6 cm (mean ± SD) of tail hair from gemsbok individuals and 16 ± 6 cm from springbok individuals. Accordingly, we assumed that the stable isotope ratios of tail hair of both species integrated over the food consumption of a maximum of 22 months (from November 2009 to 15 June 2011, i.e. the day of the hunt).

We recorded the specific location where an animal was hunted (location), as well as the identity and size of

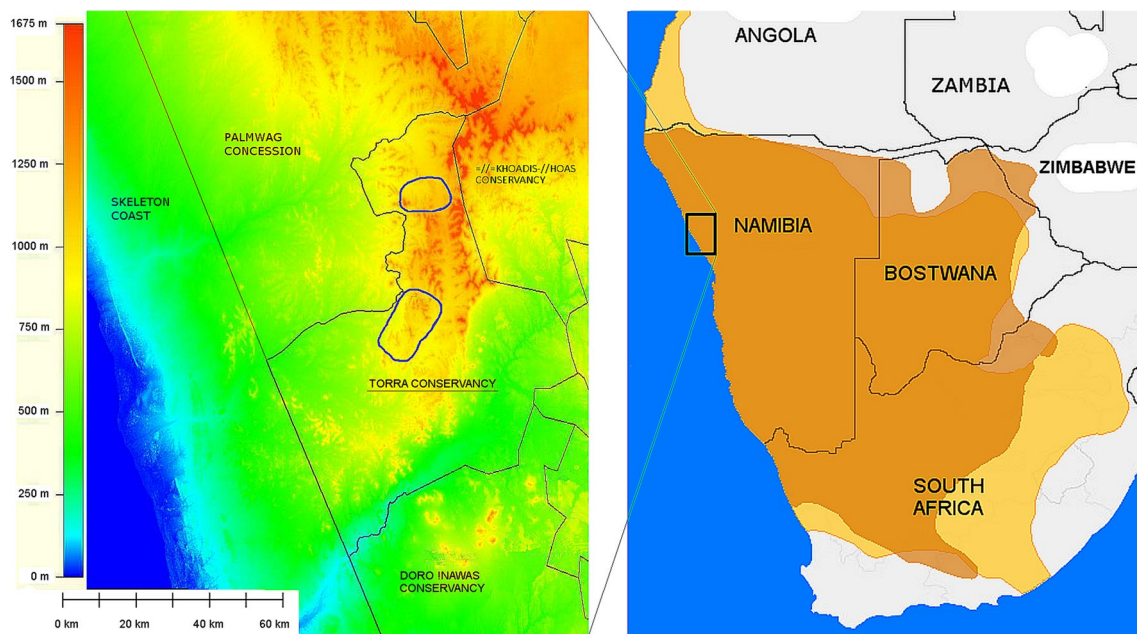


Fig. 1 Maps. Distribution ranges of gemsbok and springbok across Southern Africa (right). Springbok distribution is reported in yellow. Gemsbok distribution is represented in orange. Note that both animal distributions largely overlap. The black rectangle delimits the limits of this study in the Kunene Region of Namibia. The distribution ranges were taken from the International Union for Conservation of Nature (IUCN) [*Oryx gazelle* and *Antidorcas marsupialis* (IUCN 2014)]. The enlarged and topographic map of the study area (left) details the Torra Conservancy where this study took place. The two major locations from which our focal animals were sampled are indicated by blue circles. Both sampling areas were located within

the Etendeka mountain chain (red). Map built from topographic satellite imagery [Advanced Spaceborne Thermal Emission and Reflection Radiometer (ASTER) Global Digital Elevation Model (GDEM); a product of the Ministry of Economy, Trade, and Industry and the National Aeronautics and Space Administration (NASA); ASTER L1B data product was obtained through the online data pool at the NASA Land Processes Distributed Active Archive Center, US Geological Survey/Earth Resources Observation and Science Center, Sioux Falls, SD; https://lpdaac.usgs.gov/data_access; freely accessible]

the group from which it was collected (group identity and size). Springbok and gemsbok were harvested by game guards from two areas in the Torra Conservancy. In the western part of the conservancy, we collected samples from animals roaming around at four localities at a distance of about 8 ± 6 km (mean ± 1 SD) from each other (Euclidian distance, Table S1; Fig. 1). In addition, we collected samples from animals near Spaartwater, around 40 km north from the central position of the four other locations (Euclidian distance, Table S1; Fig. 1). These two areas are situated within the Etendeka mountain range and are similar in habitat characteristics; a set of rugged hills interlaced with open grassland, flood plains and herbaceous uplands, as well as with more wooded riverbed and drainage lines. Springbok were sampled from 12 groups of eight group sizes. Gemsbok individuals were sampled from nine distinct groups of six group sizes. The identity of groups, their respective sizes at the time of the hunt and locations are reported beside numbers and sex of individuals in Table S1. We collected mean values of the normalized difference vegetation index [NDVI; 1-month composite NDVI; National Aeronautics and Space Administration Moderate-resolution

Imaging Spectroradiometer (NASA MODIS 13B; <http://earthexplorer.usgs.gov/>)] from the Torra Conservancy as a measure of vegetation growth that corresponds to variations in plant primary productivity during the 22 months preceding the communal hunt. High NDVI values occurred after rainfall events, while low values indicated drought periods, when vegetation growth rates are minimal or null. However, since these variations in plant primary productivity are unpredictable in the arid environment of the Kunene Region, the pattern is not consistent with the conventional definition of a yearly seasonal cycle.

Our estimations of monthly rainfall in our study site were not reliable and therefore could not be used in this study. Based on discontinuous records of local precipitation and weather stations from tourist camps and neighbouring conservancies, we estimated yearly amounts of rainfall in Torra Conservancy. In 2009, rainfall occurred from February to March and October–November and amounted in total to about 60 mm. In 2010, the area received less than 80 mm of rainfall from January to March and November to December. In 2011, local habitats received more than 500 mm of rainfall with an intense rainy period between

January and April [Torra Conservancy, Damaraland Camp weather station, Namibian Weather Network (<http://www.namibiaweather.info/>)]. Since NDVI measures green vegetation, it takes into account the retention of green matter through drier periods, allowing a more accurate observation of the temporal changes in food resource availability than rainfall (Chirima et al. 2013).

All tail hairs were cleaned with water, dried in the sun and stored in plastic bags. Hair samples were shipped to the stable isotope laboratory at the IZW under the export permit number MET 85,197 (issued on 30 August 2011).

Laboratory preparation

We cut tail hairs into series of 1-cm intervals, which totalled 557 samples for gemsbok and 453 samples for springbok. Tail hair sections were obtained from a single individual hair to avoid potential signal blurring that could arise when using clumps of multiple hair strands (Remien et al. 2014). We obtained on average 34.8 ± 5.6 hair sections from each gemsbok individual and 15.1 ± 6.0 from each springbok individual. The soft tissue root of each hair was removed using a scalpel to avoid sample contamination by non-keratinous material. All samples were wiped with 96 % alcohol to remove potential oil residues and dirt that could have biased the stable C isotopic values. We did not use a 2:1 chloroform–methanol solution to further extract lipids from the hairs since the effects of lipid extraction seem to have no or little effect on $\delta^{13}\text{C}$ in lipid-poor tissues [such as keratinous materials (see Tieszen and Bouton 1989)].

All samples were then repeatedly cleansed with distilled water and dried in a drying oven (Heraeus Function Lab; Thermo Electron, Langensbold, Germany). Samples were then powdered using a mortar grinder (RETSCH milling machine). An aliquot sample of 0.3–0.4 mg of each hair section was then loaded into tin capsules (COSTECH) and combusted. The resultant gases (N_2 and CO_2) were sequentially measured in a CE 1110 elemental analyser which was connected to a Thermo Finnigan Delta Plus (Thermo Finnigan, Bremen) isotope ratio mass spectrometer via continuous flow. The sample isotope ratios were then compared with international gas standards; US Geological Survey (USGS)-24 (USGS graphite) uses the $\delta^{13}\text{C}$ of Vienna Pee Dee belemnite limestone as a reference and International Atomic Energy Agency ammonium sulphate refers to the N isotope ratio of air (Gonfiantini et al. 1995; Voigt et al. 2003). Stable isotope ratios were expressed following the δ notation with parts per mil (‰) as the unit of measurement (Slater et al. 2001). According to repeated measurements of laboratory standards, precision was always better than 0.1 ‰ (1 SD) in both elements.

Statistical analyses

Animal hair isotopic compositions

To project the compositions of tail hairs of gemsbok and springbok in an isotopic space, we required a priori estimates of isotopic trophic discrimination of the tissues of interest. Trophic discrimination of stable isotopes refers to the differences in isotopic composition between animal tissues and that of the animals' diet. Since we did not know the species-specific discrimination factors for our study species, we used discrimination factors for keratinous materials that have been observed in other ungulate species before (Cerling and Harris 1999, 2003; Sutoh et al. 1987). Accordingly, we corrected raw $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tail hair by subtraction of 3.1 ‰ (Cerling and Harris 1999) and 2.9 ‰, respectively (Sutoh et al. 1987).

To find whether the isotopic compositions of segmented tail hairs varied significantly among and within individuals of both species and among groups and locations, we performed linear mixed-effects (LME) models. To do so, we nested the identity of an individual within the group identity from which it belonged, which was nested within its original location, i.e. $\text{lmer}[\text{Carbon} \sim 1|\text{location}/\text{group identity (ID)/ID}]$.

To assess the influence of NDVI on within- and between-individual variations in isotopic concentration, we used the method described by van de Pol and Wright (2009) since NDVI values were linked to specific tail-hair sections according to the respective hair growth rate of each species. We defined two different covariates for NDVI: one provides the mean values for NDVI in each individual and one provides a proxy for temporal deviations from this mean value (NDVI-Mean_NDVI) for each measurement of an individual (hereafter, we refer to this deviation as "Residual_NDVI"). Accordingly, the regression coefficient associated with the first covariate quantifies the effect of between-individual isotopic variations of tail hairs and the one associated with the second covariate measures the effect of NDVI on within-individual variation of $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ (van de Pol and Wright 2009). Thus, to explain the inter- and intra-individual variation in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in both species, we considered Mean_NDVI, Residual_NDVI, and sex and group size as fixed factors to be included in two additional models, one for each stable isotope and species, i.e. $\text{lmer}[\text{Carbon} \sim \text{Mean_NDVI} + \text{Residual_NDVI} + \text{Sex} + \text{GroupSize} + (1|\text{Location}/\text{GroupID}/\text{ID})]$.

Each factor (Mean_NDVI, Residual_NDVI, group size, sex) was added one by one and models were compared using one-way ANOVA based on Akaike's information criterion (AIC). We then selected the model with the lowest

value of AIC, i.e. the model which explained best the isotopic variation for each species and element. We performed one model/isotope per species. The model residuals were tested for normal distribution using a $Q-Q$ plot. Model outputs provided estimates of the influence of factors in explaining the inter- and intra-individual range of stable isotope ratios of tail hairs. We used 1000 parametric bootstraps to obtain the 95 % CIs of the effects of fixed and random factors on the variation of tail hair isotopic ratios within and between individuals. All tests were performed with R (version 3.0.2) using the functions `lmer` and `confint` from the package `lme4` (version 1.0.5) (Bates et al. 2013) for LME.

To assess whether changes in food resource availability influenced the variations of springbok and gemsbok individual isotopic niches, we clustered NDVI values according to periods of high and low primary productivity; namely NDVI+ (February–June 2011 and February–May 2010) and NDVI– (June 2010–January 2011– and August 2009–January 2010).

Isotopic niches

Isotopic dietary niche metrics were calculated and plotted using stable isotope Bayesian ellipses in R (SIBER) routines (Jackson et al. 2011; Parnell and Jackson 2013) from the stable isotope analysis in R (SIAR) and companion to applied regression (CAR) packages using R (version 3.0.1). The limits of the isotopic niche were statistically defined as Bayesian standard ellipses drawn in bivariate plots ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) of the local isotopic space of plant resources. Since stable isotopes ratios of gemsbok and springbok were converted to diet coordinates, we regarded the generated ellipses as being representative of the respective isotopic dietary niche in the isotopic space of the Torra Conservancy, which is defined by the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of the food resources potentially consumed by animals. Standard ellipse area (SEA) values were corrected for small sample size (SEAc) using SIBER (Jackson et al. 2011) from the SIAR package, version 4.2, in R. We defined the 95 % CIs of these niches as the actual boundaries of individual isotopic dietary niches during the study period (see Jackson et al. 2012). We then used 1000 parametric bootstraps to create Bayesian estimations of SEAc (SEA.B), which allowed calculations of isotopic dietary niche overlaps by comparing 95 % CIs. Accordingly, we estimated isotopic niche overlap among individuals (and populations) by looking at the extent at which ellipses overlapped. Ellipses were first estimated for each individual of both gemsbok and springbok across the study period, which summed to 46 ellipses ($n = 46$ individuals). To observe the degree of individual isotopic specialization, we calculated the overlap of an individual's isotopic

dietary niche with niches of all other conspecifics. We then estimated the mean total overlap for each individual with all other conspecifics. We calculated the proportional overlap between two ellipses based on total area of the corresponding ellipses involved. Thus, we obtained the extent of total mean overlap that ranged from 0 to 100 % for each individual, with values closer to 100 % suggesting almost complete isotopic dietary niche overlap and implying that individuals of the study population occupy the exact same isotopic dietary niche. The mean isotopic compositions of females and males were calculated for each species as four ellipses, thereby allowing SIBER pair-wise comparisons between the ellipses of males and females in each species. Finally, population ellipses were also calculated, allowing isotopic niche comparisons between our two focal species. Using a pair-wise niche comparison approach based on SIBER, we calculated and compared ellipses for each sex and population for periods of NDVI+ and NDVI– to assess covariation in isotopic dietary niche breadth with plant productivity.

Results

Isotopic composition of tail hairs

The tail hair isotopic compositions of 16 gemsbok averaged -15.6 ± 1.2 ‰ for $\delta^{13}\text{C}$ (range -18.1 to -12.2 ‰; Fig. 1a) and 14.1 ± 0.8 ‰ for $\delta^{15}\text{N}$ (range 12.4–15.5 ‰; Fig. 1b). The stable isotopic compositions of tail hair analysed from 30 springbok averaged -21.8 ± 1.2 ‰ for $\delta^{13}\text{C}$ (range -24.1 to -17.3 ‰; Fig. S1C) and 13.3 ± 1.3 ‰ for $\delta^{15}\text{N}$ (range 10.4–16.3 ‰; Fig. S1D). For gemsbok, the best models explaining isotopic variations within and between individuals included Mean_NDVI and Residual_NDVI as fixed factors for both elements (Table S2.a). Our models indicated that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tail hairs significantly differed among individuals (inter-individual differences hereafter referred to as $\Delta^{13}\text{C}$ or $\Delta^{15}\text{N}$), since the estimate for the random effect (ERE; 0.5 ‰) fell within the 95 % CI (0.2–0.8 ‰) for C ($\Delta^{13}\text{C}$) and for N [$\Delta^{15}\text{N}$, ERE = 0.5 ‰, 95 % CI = (0.2–0.8 ‰)]. Our models also revealed larger variations within than between individuals for both stable isotopes ratios [$\Delta^{13}\text{C}$, ERE = 1.1 ‰, 95 % CI = (1.05–1.2 ‰); $\Delta^{15}\text{N}$, ERE = 0.8 ‰, 95 % CI = (0.7–0.8 ‰)]. $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ varied only little between gemsbok groups of the same location [$\Delta^{13}\text{C}$, ERE = 0.8 ‰, 95 % CI = (0.07–1.02 ‰); $\Delta^{15}\text{N}$, ERE = 0.6 ‰, 95 % CI = (0.02–1.04 ‰)]. In addition, our models suggested that isotope ratios varied between gemsbok individuals from different locations [$\Delta^{13}\text{C}$, ERE = 0.2 ‰, 95 % CI = (0.1–1.3 ‰); and $\Delta^{15}\text{N}$, ERE = 0.001 ‰, 95 % CI = (0.01–0.9 ‰)].

For gemsbok, our models further indicated that sex and group size did not explain $\Delta^{13}\text{C}$ and $\Delta^{15}\text{N}$. Furthermore, the model suggested that a difference in Mean_NDVI of 0.1 is equivalent to an average isotopic difference among individuals of 0.7 ‰ for C and of 1.7 ‰ for N. However, Mean_NDVI had a wide range of effects on inter-individual isotopic variations and, therefore, its impact cannot be generalized for the gemsbok population [95 % CI = (−3.9 to 5.3 ‰) for C, 95 % CI = (−1.9 to 5.7 ‰) for N], indicating that NDVI+ or NDVI− had no effect on the isotopic differences between individuals. In addition, we observed that as Residual_NDVI increased by 0.1, isotopic compositions of individual tail hairs increased by 0.1 ‰ for stable C isotopes [95 % CI = (0.04–0.2 ‰)] and by 0.09 ‰ for N isotopes [95 % CI = (0.02–0.1 ‰)], suggesting a significant effect of Residual_NDVI on isotopic composition within individuals.

For springbok, the best models explaining isotopic variations within and between individuals for both $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ included Mean_NDVI and Residual_NDVI but did not include group size and sex (Table S2.b). Both models revealed that $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ differed significantly among individuals [$\Delta^{13}\text{C}$, ERE = 0.8 ‰, 95 % CI = (0.5–1.1 ‰); $\Delta^{15}\text{N}$, ERE = 1.0 ‰, 95 % CI = (0.6–1.2 ‰)]. We also observed high isotopic variations within individuals [$\Delta^{13}\text{C}$, ERE = 1.3 ‰, 95 % CI = (1.2–1.4 ‰); $\Delta^{15}\text{N}$, ERE = 1 ‰, 95 % CI = (0.9–1.1 ‰)]. Similar to gemsbok, the isotopic composition of springbok did not vary between groups [$\Delta^{13}\text{C}$, ERE = 0.001 ‰, 95 % CI = (0.05–1.1 ‰) for C; $\Delta^{15}\text{N}$, ERE = 0.001 ‰, 95 % CI = (0.03–1.04 ‰)]. As for gemsbok, the isotopic compositions of springbok varied only little between locations [$\Delta^{13}\text{C}$, ERE = 0.07 ‰, 95 % CI = (0.01–0.7 ‰); $\Delta^{15}\text{N}$, ERE = 0.2 ‰, 95 % CI = (0.1–0.8 ‰)]. Since group size and sex were not selected as fixed parameters based on AIC, we assumed that these factors had no effect on the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tail hair sections within and between springbok individuals. Our models showed that a difference in Mean_NDVI of 0.1 is equivalent to an isotopic difference in tail hair among individuals of 0.6 ‰ in ^{13}C and of 1.5 ‰ in ^{15}N . However, Mean_NDVI had a wide range of effects on inter-individual isotopic variation and its impact can therefore not be generalized for the springbok population [95 % CI = (−0.5 to 1.8 ‰) for C; 95 % CI = (−0.2 to 1.4 ‰) for N], indicating that NDVI+ or NDVI− had no effect on the isotopic differences between springbok. Also our models revealed that as Residual_NDVI increased by 0.1, within-individual stable isotope compositions decreased by 0.2 ‰ for stable C isotopes [95 % CI = (−0.3 to −0.05 ‰)] and by 0.5 ‰ for N isotopes [95 % CI = (−0.6 to −0.4 ‰)], suggesting a significant effect of Residual_NDVI on isotopic composition within springbok individuals.

Breadth and overlap of isotopic niches

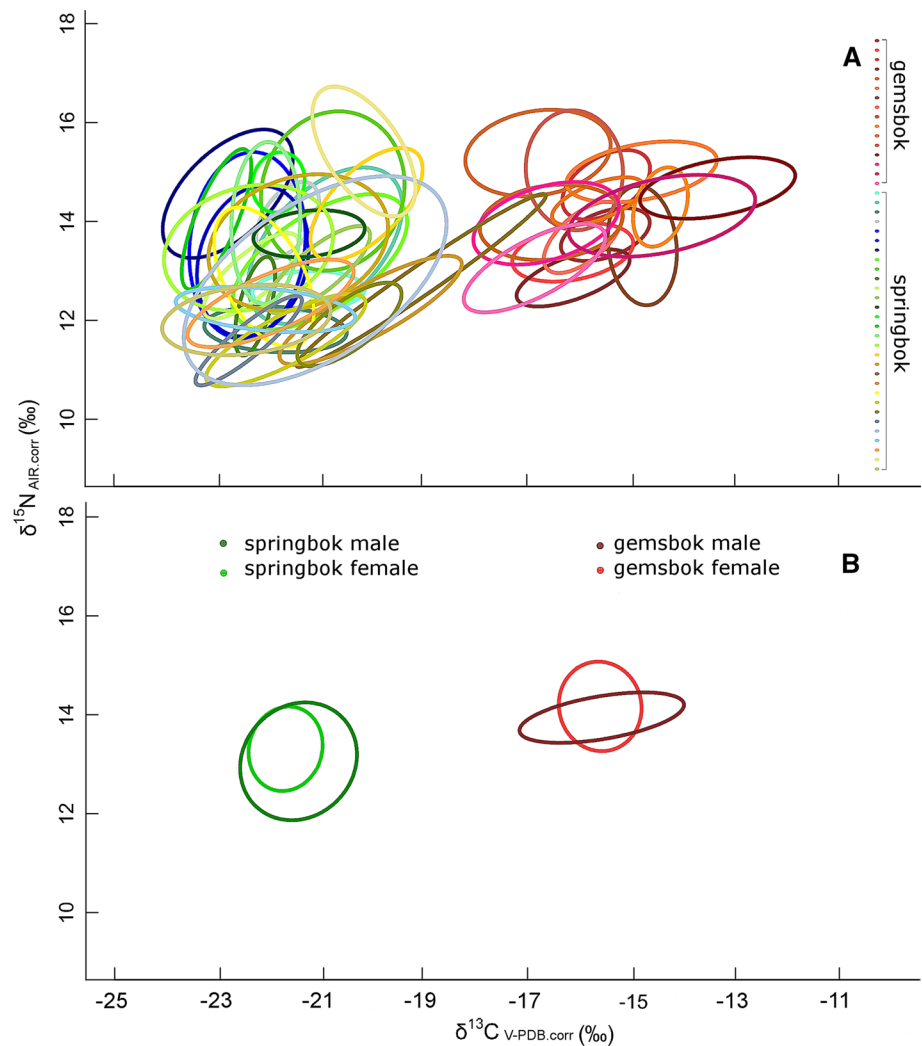
At the individual level, we observed variations in the areas of ellipses ($2.5 \pm 1 \text{ ‰}^2$; Fig. 2a) and an average overlap of $18.8 \pm 8.7 \%$ across all studied gemsbok individuals (Figs. 2a, 3a). Our results showed a similar extent of overlap between springbok individuals ($21 \pm 7.6 \%$; Fig. 2a). The sizes of the isotopic surface area occupied by springbok within the dietary isotopic space varied greatly among individuals ($3.8 \pm 2.8 \text{ ‰}^2$; Fig. 3a). On average, isotopic niches of male and female gemsbok overlapped by 55 % (Fig. 2b), with isotopic dietary niches of males being wider along the N axis than those of females. In contrast, females exhibited a broader isotopic dietary niche along the C axis than males (Fig. 2b). Male and female gemsbok showed similar isotopic dietary niche areas as defined by standard Bayesian ellipses (SEA.B; male = 2.3 ‰^2 ; female = 2.2 ‰^2 ; $p = 0.33$; Fig. 3b). In springbok, females exhibited significantly smaller isotopic dietary niches than males (females, SEA.B = 1.9 ‰^2 ; males, SEA.B = 4.2 ‰^2 ; $p = 0.041$; Figs. 2b, 3b), i.e. the isotopic niches of male springbok encompassed the isotopic niches of female springbok, yet only 43 % of male isotopic niches overlapped with the female isotopic niches (Fig. 2b).

We calculated the isotopic dietary niche of both species, using the mean $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ of tail hair increments of individuals of the respective species. Isotopic niches of the two species were completely separated at the population level (Fig. 2b), yet both isotopic niches were of similar size (gemsbok SEA.B = 2.4 ‰^2 , springbok SEA.B = 3.1 ‰^2 ; $p = 0.26$; Fig. 3c).

We further asked if changes in primary productivity, recorded here as NDVI+ and NDVI−, would affect the isotopic niches of individuals and, thus, populations of both species. Also, we asked if isotopic niche size and breadth of males and females changed in response to primary productivity. At the individual level, only five out of 16 gemsbok (31 % of individuals) showed significant decreases in isotopic niche sizes as primary productivity increased (Table S3a). Similarly, six out of 30 springbok individuals (20 % of individuals) showed decreases in isotopic niche sizes following increased primary productivity (Table S3b).

Gemsbok individuals had similar isotopic niche breadths in times of high and low primary productivity (NDVI+/NDVI−; $p = 0.5$) and isotopic niches of males and females showed a large overlap during both periods (Table 1). Springbok individuals, however, had a narrower isotopic dietary niche during the NDVI+ period than during the NDVI− period ($p = 0.018$). The overlap of isotopic niches of springbok between both periods averaged 34 % (Table 1). The isotopic dietary niche of gemsbok males did not differ in size during periods of higher plant source availability (NDVI+) from that realised during periods of lower primary

Fig. 2 Bivariate plot of stable C ($\delta^{13}\text{C}$) and N isotope ratios ($\delta^{15}\text{N}$) (mean \pm 1 SD) in tail hair of individual gemsbok and springbok. Raw isotopic data were corrected for trophic discrimination. Each Bayesian standard ellipse was calculated based on all data points of a given individual (a) or for males and females of both species separately (b). *V-PDBcorr* Corrected Vienna Pee Dee belemnite



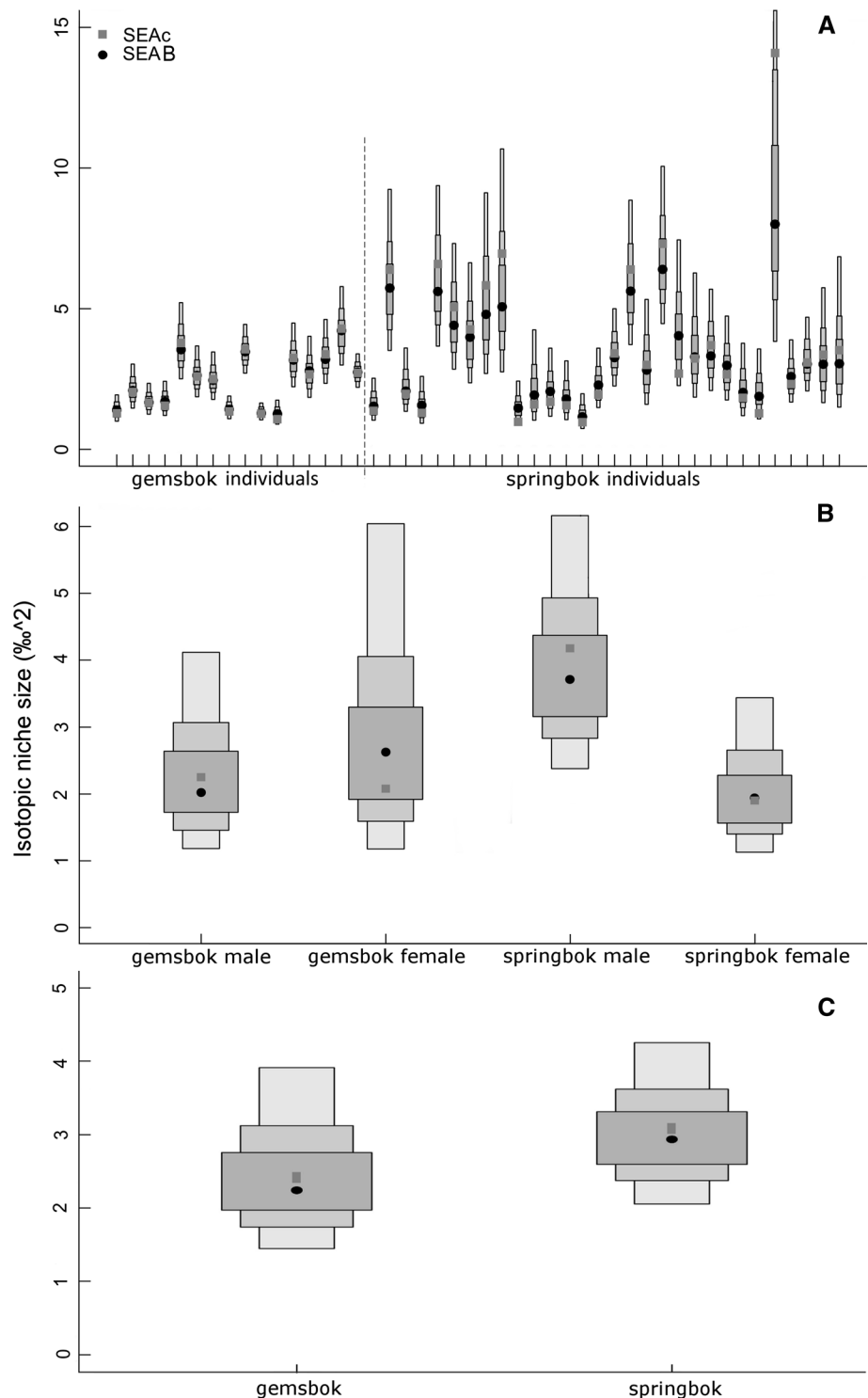
productivity (NDVI–) ($p = 0.78$; Table 2), yet the overlap was only small (Table 2). Also, males and females had similar isotopic niche sizes during periods of higher vegetation growth, i.e. during periods of NDVI+ ($p = 0.88$). Female isotopic niche breadths did not differ between periods with contrasting NDVI values ($p = 0.88$) but the overlap was large (Table 2). In contrast, niche breadth of male springbok decreased as primary productivity increased ($p = 0.032$) and overlapped only a little between periods of NDVI+ and NDVI– (Table 3). The niche breadths of female springbok were similar in times of high and low primary productivity and overlapped only a little ($p = 0.68$; Table 3). Niche breadth was larger in males than in female springbok during times of low primary productivity ($p = 0.004$; Table 3).

Discussion

We assessed the isotopic niches of individual gemsbok and springbok in the arid Kunene Region of Namibia by

measuring the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ in tail hair increments. We were interested in the variation of individual isotopic dietary niches in response to temporal changes of food availability. Our study revealed for gemsbok that within-individual variation of stable isotope ratios explained the isotopic niche breadth of the study population better than between-individual variation. In contrast, inter- and intra-individual variation in stable isotope ratios contributed equally to the isotopic niche breadth of springbok. We observed that the isotopic surface areas of study animals, characterized in our study by Bayesian ellipses, fell within the local isotopic space defined by the stable isotopic composition of the food resources that they potentially consumed. Therefore, we inferred that the limits of these ellipses reflected the extent of the isotopic dietary niche occupied by an individual. Further, we demonstrated that populations of both species consisted of individuals with distinct isotopic dietary niches. In contrast to our prediction, we found that the breadth of the gemsbok isotopic dietary niche did not

Fig. 3 Isotopic niche sizes of gemsbok and springbok individuals (**a**) of males and females of the corresponding species (**b**) and of the two species (**c**) estimated by the area of ellipses (‰^2) in two-dimensional isotopic space. *Black dots* represent the mode, *grey squares* represent the true population values. The *shaded boxes* indicate the 50, 75 and 95 % credible intervals from *dark to light grey*



differ between periods of low and high primary productivity, whereas springbok individuals reduced their isotopic dietary niche breadth during periods of high primary productivity. Lastly, we showed that isotopic dietary niches of springbok and gemsbok populations were similar in breadth but did not overlap in the isotopic space of local habitats.

Variation of isotopic niches in individual ungulates

Our study suggests non-overlapping isotopic dietary niches of individuals in the studied gemsbok and springbok population. Relatively high levels of within- and between-individual variations in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of tail hair sections, and thus a high degree of individual isotopic food

Table 1 Bayesian estimations of corrected standard ellipse areas (SEA.B) ($\%e^2$) and niche overlap (%) of populations of both species during periods of high normalized difference vegetation index (NDVI+) and low NDVI (NDVI–) primary productivity

Population	Gemsbok ($n = 16$)		Springbok ($n = 30$)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI+	2.7	77.2	3.2	52.8
NDVI–	3.0	69.7	4.9	34.8

Table 2 SEA.B areas ($\%e^2$) and niche overlap (%) of male and female gemsbok during periods of high (NDVI+) and low (NDVI–) primary productivity; for abbreviations, see Table 1

Gemsbok	Male ($n = 10$)		Female ($n = 6$)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI+	1.8	52	1.9	76.7
NDVI–	2.9	31	3.0	49

Table 3 Summary of the SEA.B areas ($\%e^2$) and niche overlap (%) of male and female springbok during periods of high (NDVI+) and low (NDVI–) primary productivity; for abbreviations, see Table 1

Springbok	Male ($n = 17$)		Female ($n = 13$)	
	Size SEA.B	Overlap	Size SEA.B	Overlap
NDVI+	3.4	54.6	2.6	32.1
NDVI–	7.0	26.7	1.9	44.0

specialization, have also been found in previous isotopic studies on e.g. carnivores (Cherel et al. 2009; Matich et al. 2010), omnivores (Newsome et al. 2009) and non-mammalian herbivores (Murray and Wolf 2013). Yet, our findings contrast with those from African mega-herbivores, namely elephants, where intra-individual isotopic variations caused by seasonal changes in plant productivity explained almost all inter-individual variation in stable C, N and O isotopes (Codron et al. 2013).

We speculate that the difference in isotopic dietary niches among individuals of desert ungulates is best explained by a combination of individual preferences for a specific food type and also by specific movements of individuals across various habitats in response to changing environmental conditions. With respect to dietary strategy, our previous study indicated that the two study species prefer distinct food resources in the Kunene Region of Namibia. This clear dietary segregation between gemsbok and springbok echoed the results of this study because the respective isotopic dietary niches of gemsbok and springbok individuals did not overlap. Furthermore, the stable isotopic compositions

of both gemsbok and springbok populations observed in the current study matched those recorded previously across a 19-month period within the entire geographical range of the Torra Conservancy (Lehmann et al. 2013). Therefore, we assume that the gemsbok sampled in this study followed the relatively flexible feeding habits demonstrated in our earlier study (Lehmann et al. 2013), where the gemsbok diet included 30 % of C3 plants and up to 25 % of *Euphorbia damarana* during drought periods, but fed almost exclusively on C4 grasses and discrete CAM plants when food was plentiful. Hence, the results of the present study suggest that the breadth of the realized dietary niche of the gemsbok population might be represented by the sum of the distinct, non-overlapping, isotopic dietary niches of individual conspecifics. We therefore conclude that individual variation in the isotopic dietary niche arises from individual specialization in gemsbok. The studied springbok population consumed a mixture of C3 and C4/CAM plants, irrespective of changes in environmental conditions (Lehmann et al. 2013). Thus, the high level of isotopic dietary niche segregation observed among individual springbok suggested that the population of this dietary generalist is in fact composed of relatively specialized individuals, similar to that found in previous studies of populations of other species, e.g. reptiles and fishes (Bolnick et al. 2007; Vander Zanden et al. 2010), mammalian predators (Newsome et al. 2009) and mammalian herbivores (McEachern et al. 2006). In both our study species, the isotopically distinct individual dietary niche may mitigate the intensity of intra-specific resource competition.

Influence of sociality, age, sex and plant primary productivity on individual use of isotopic niche

Typically, increases in NDVI values at a local scale reflect an overall increase in both C3 and C4/CAM biomasses. However, the availability of C4 plants seemed to be more related to rainfall than that of C3 plants (Lehmann et al. 2013). For example, evergreen C3 plants such as *Cyperus* sp. and *Acacia* sp. and also CAM plants, e.g. the endemic *Euphorbia damarana*, might represent the most available food resources during periods of low NDVI values; i.e. drought. *Stipagrostis* sp. (C4 grass) also persists at a relatively high density during both wet and dry periods and may therefore provide continuously available forage even during severe droughts. In our previous study, we collected 30 different plant species that included potential food resources for gemsbok and springbok in the study area. Based on $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, these plants species were grouped into 13 different food types (Lehmann et al. 2013). C3 plants biomasses was mainly present in riverbed habitats and their isotopic compositions remained constant

from drought to wetter periods, while C4 and CAM food resources mainly occurred in open-field habitats (grassland, flood plains and herbaceous uplands). In contrast to C3 plants, $\delta^{15}\text{N}$ values of some C4/CAM plant species such as *Zygophyllum simplex* (CAM) and *Eragrostis* sp. (C4) varied with the extent of drought, and thus between periods of high and low NDVI values, at the local geographic scale of the Torra Conservancy (Lehmann et al. 2013). In this study, we observed that both gemsbok and springbok move over relatively large areas (personal observation, unpublished data), which suggests, given the short distances between our collection sites, that individuals of this study were equally likely to cross the interlacing set of habitats (riverbeds, open field and hillsides) that characterized our study area. Therefore, we argue that individual ungulates of our study were subject to similar spatial and temporal variations in food plant availability and isotopic compositions. Furthermore, we did not observe any differences in isotopic compositions of the two study species between populations of the two study sites (at 40-km distance), suggesting that vegetation structures and availabilities might have been similar in both of our sampling areas.

Springbok are usually gregarious, roaming in small herds during drier periods but aggregating in much larger groups when primary productivity increases (Child and Le Riche 1969). Therefore, we expected a similar isotopic dietary niche in individuals of the same group. In contrast, our findings of relatively high isotopic dietary niche segregation of individuals during both dry and wet periods indicate that this species partitions its food resources even when grazing or browsing in a group. This is also supported by the fact that group size did not explain intra- or inter-individual isotopic variations in this study. However, group compositions may vary over time in both species following a fission–fusion pattern (Jarman 1974) and might therefore still explain some of the isotopic differences found among members of the same core group. We only considered adult individuals in our study, but were not able to include age as a factor. Therefore, we were not able to evaluate if age correlates with isotopic niche breadth. Age-related changes in dietary requirements have already been observed in other taxa, including herbivorous mammals (Lindström 1999). Therefore, some of the unexplained variation in isotopic data may be attributable to age-specific feeding habits. Also, intrinsic physiological conditions may have varied among conspecific individuals and this may have influenced their food-resource selection and spatial movements.

We observed differences between individuals of the studied gemsbok and springbok population in sex-specific isotopic niche size. We observed a twofold broader isotopic dietary niche in male springbok than in female springbok, suggesting that males included a broader range of isotopically contrasting plant resources in their diet. This might

have been caused by sex-specific differences in movement behaviour. Like other ungulates of Southern Africa, springbok and gemsbok females usually form groups, whereas males are more loosely associated with members of the same or opposite sex and have typically larger home ranges (Estes 1991; Skinner and Chimimba 2005). Possibly, springbok males utilized larger territories, thereby encountering a larger number of isotopically different food items. Male and female gemsbok did not differ in their respective absolute isotopic niche breadths, but we observed differences in isotopic locations of their niches, with females exploiting a broader range of plants with different $\delta^{13}\text{C}$ values. In contrast, males selected plants with similar $\delta^{13}\text{C}$ values but with more variable $\delta^{15}\text{N}$ values. Sex-specific differences in isotopic dietary niches may also reflect sex-specific differences in the use of local habitats. Indeed, the isotopic dietary niches of female gemsbok seem to include more C3 plants than those of males. In the Torra Conservancy, we recorded C3 plants mostly along ephemeral riverbeds, suggesting that female groups preferred this habitat. Possibly, they were capable of this preference because, as a group, they were better able to be vigilant against predators (Jarman 1974) even in dense *Colophospermum mopane* forests with large *Acacia* trees and dense bushes (e.g. *Salvadora persicata* and *Cyperus marginatus*), which lowered the visibility of predators (Thaker et al. 2011).

Accordingly, group living could enable female gemsbok to exploit other plants compared with solitary males. The latter may prefer open grassland and uplands where they can better detect and avoid predators. Additionally, the shape of the isotopic dietary niche of males, which was broad along the $\delta^{15}\text{N}$ scale but narrower along the $\delta^{13}\text{C}$ scale, may also reflect the preferential use of open habitat food types, i.e. the larger range of $\delta^{15}\text{N}$ values of the male isotopic niche is consistent with the observation of $\delta^{15}\text{N}$ variation (around 2 ‰) in the most available C4/CAM plants, such as *Stipagrostis* sp., *Eragrostis* sp., and *Zygophyllum simplex* (Lehmann et al. 2013). In summary, we conclude that the variations in isotopic compositions of males may reflect the variations in isotopic compositions of C4/CAM plants across varying environmental conditions, i.e. from drought to wetter periods. Lastly, the observed differences in isotopic dietary niche variations between males and females might also be related to sex-specific energy demands due to the allometric correlation of metabolism and body size, which might lead to both foraging and habitat segregation (reviewed by du Toit 2005). In general, female ungulates increase the selection of high-quality food resource, to enhance their digestion rate and to compensate for the physiological costs imposed by maternal care (Ruckstuhl et al. 2003). Thus, we hypothesized that the stable C isotopic variations observed in females reflect a dietary shift from C4/CAM to C3 plant

foods to fuel the high energetic costs of gestation and lactation, since C3 food resources were more available over time than C4 plants and because C3 plants contain in general more nutrients than C4 plants (Barbehenn et al. 2004). Also, females may reduce their consumption of CAM plant food resources during reproductive periods, since the high concentration of secondary plant metabolite in these plants may have adverse effects on the foetal and ontogenic development of their offspring. A dietary shift from C4/CAM to C3 plant resources may also explain some of the more pronounced intra-individual isotopic variations observed in reproductively active female gemsbok.

We predicted that the isotopic dietary niche breadth of gemsbok would decrease with increasing primary productivity. Although this trend of isotopic dietary niche reduction was observed it was only statistically significant for five individuals, representing 30 % of all gemsbok studied. For springbok, we predicted that the isotopic niche breadth would remain constant irrespective of changes in plant productivity. However, we observed a reduction in isotopic dietary niche breadth size in six individuals, representing 20 % of our springbok data set. The tail lengths of five springbok were too short to allow a statistical comparison of their respective isotopic compositions between periods of low and high plant production. Since these variations among some individuals followed fluctuations of plant primary growth that unpredictably occurred in the arid environment of the Kunene Region, the observed pattern of isotopic dietary niche constriction from drought to wetter periods is therefore not consistent with the conventional definition of a yearly (periodic) or seasonal (semi-periodic) cycle. However, these results suggest that individuals of both species exhibited different dietary tactics to cope with changes in plant productivity. Variation in the feeding habits of individuals has to be considered when investigating the impacts of food resource abundance on both distribution and dietary niches of ungulate species in desert environment (Hopcraft et al. 2012).

Conclusion

In this study, we observed high levels of dietary segregation within populations of two desert ungulate species that differed in body size and feeding habits. We showed that populations of gemsbok and springbok exhibited isotopically distinct dietary niches and argue that individually distinct isotopic niches within populations of the same species reflect dietary preference of individuals, which can also be potentially influenced by their specific spatial behaviour and intrinsic physiological requirements. The observed flexibility in the breadth of the dietary niche of desert ungulates may help to increase the survival and co-existence of individuals during adverse periods such as drought.

Moreover, we demonstrated that males and females of both species occupied distinct, albeit overlapping, isotopic niches, which may reflect sex-specific differences in habitat utilization. In conclusion, stable isotope ratios of tail hair increments indicated that isotopic dietary niches were distinct and, overall, separated from each other in individuals of gemsbok and springbok co-existing in an arid environment of the Kunene Region in Southern Africa.

Author contribution statement D. L., J. K. E., C. B. and C. C. V. developed the original idea. D. L., E. G. and C. B. established the logistics. D. L. and E. G. conducted the fieldwork. D. L. and C. C. V. analysed the samples and data. D. L., J. K. E. and C. C. V. wrote the manuscript.

Acknowledgments We would like to express our gratitude to the Ministry of Environment and Tourism of Namibia for granting us research permits (nos. 1534/2010 and 1676/2012). We are very grateful to the Torra Community-based Conservancy and its members for allowing this study to be performed on their communal territory. We thank Wilderness Safari Namibia for support in the field with logistics and field vehicle maintenance. We are thankful to the team of Damaraland Camp for assisting with logistics, especially Pascolena Florry, Maggie Vries, Efreida Hebach and Johann Cloete. We thank Anja Luckner, Karin Sörgel and Doris Fichte for preparing and analysing the samples in the stable isotope laboratory. We are grateful to Alexandre Courtiol for statistical advice. We thank Emilia Haimbili from the University of Namibia for assisting in data collection. We thank Ortwin Aschenborn, Bettina Wachter and Joerg Melzheimer for logistical advice and support in the field. We thank Norman Owen-Smith for providing useful comments. This study was approved by the Institutional Committee for Ethics and Animal Welfare of the IZW (no. 2009-10-01).

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