

Stable isotope evidence for trophic niche partitioning in a South African savanna rodent community

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Abstract Species' partitioning of resources remains one of the most integral components for understanding community assembly. Analysis of stable carbon and nitrogen isotopes in animal tissues has the potential to help resolve patterns of partitioning because these proxies represent the individual's diet and trophic niche, respectively. Using free-ranging rodents in a southern African savanna as a model community, we find that syntopic species within habitats occupy distinct isotope niches. Moreover, species with strongly overlapping isotope niches did not overlap in their spatial distribution patterns, suggesting an underlying effect of competitive exclusion. Niche conservatism appears to characterize the behaviour of most species in our sample – with little or no observed changes across habitats – with the exception of one species, *Mastomys coucha*. This species displayed a generalist distribution, being found in similar abundances across a variety of habitats. This spatial pattern was coupled with a generalist isotope niche that shifted across habitats, likely in response to changes in species composition over the same spatial gradient. The case for *M. coucha* supports contentions that past competition effects played a significant evolutionary role in shaping community structures of today, including the absence of strong interspecific niche overlaps within particular habitats. Our study highlights the value of stable isotope approaches to help resolve key questions in community ecology, and moreover introduces novel analytical approaches to quantifying isotope niche breadths and niche overlaps that are easily comparable with traditional metrics [Current Zoology 61 (3): 397–441, 2015].

Keywords Competition, Diet, Niche breadth, Niche overlap, Sterkfontein Valley

Discussions about whether animal communities are distinctly structured or assembled more-or-less randomly rely heavily on whether or not component species partition the available resource(s). Such trophic partitioning would occur largely, but not exclusively, because of competition for resources between species (Diamond, 1986; Pianka, 1986). Competition theory predicts there is a limit to how similar the niches occupied by co-existing species can be before one is excluded from the system (MacArthur and Levins, 1967). In other words, it is predicted that no two species can occupy identical niches in the same time and place (Hutchinson, 1959).

Evidence for partitioning of trophic niches has come from numerous studies of diet and habitat use in free-ranging conditions (reviewed in Chesson, 2000).

Removal experiments, which track changes in population behaviour and dynamics in the absence of presumed competitors, have also been useful for revealing effects of competition on species' niches (Hairston, 1989; Thompson and Fox, 1993). By contrast, some field studies have found little or no evidence for trophic niche partitioning in a variety of systems (Luiselli, 2008; Amori and Luiselli, 2011), and theory about trophic partitioning and structured ecological communities is not universally accepted (Schoener, 1984; Hubbell, 2001). It is possible that in many cases there are more species co-existing within certain assemblages or communities than the number of niches available, and hence extensive niche overlap between species could be expected. Neutral theory, for example, is based on this premise, and predicts that communities are not struc-

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tured but are randomly assembled in terms of species composition (Hubbell, 2001).

Among mammals, rodents have proven to be good models for studies of community structure and trophic niche partitioning, with several accounts reporting evidence for distinct trophic structure (Bowers and Brown, 1982; Kelt et al., 1999; Abu Baker and Patterson, 2011; Fox, 2011). Rodent communities tend to be relatively species rich, and because these animals are relatively small-bodied, such speciose communities occur over confined spatial scales manageable for field investigations. Niche differences in rodent species have been extensively studied, particularly in desert and other semi-arid environments where differences in habitat utilization, behavioural patterns, and even anatomical features linked with trophic ecology, have been reported (Brown et al., 1994; Kinahan and Pillay, 2008; Morris et al., 2008; Shenbrot et al., 2010; Abu Baker and Brown, 2012). Dietary niche partitioning can also be expected amongst taxa within rodent communities, but this niche axis is harder to quantify as it generally requires sacrifice of animals and the subsequent analyses of gut content or gut morphology (Perrin and Curtis, 1980; Kinahan and Pillay, 2008). In larger animals, dietary niches can be quantified through non-invasive field observations, although this is a very labour-intensive approach.

Stable isotope analysis (SIA), an alternative approach to quantifying dietary niches of free-ranging animals, is widely used in contemporary ecological studies (reviewed in Crawford et al., 2008). The premise of SIA is that the ratios of heavy to light stable isotopes in consumer tissues record the isotopic compositions of their diets. Further, isotopes of different elements represent different aspects of the trophic niche. For example, stable carbon isotope ratios ($^{13}\text{C}/^{12}\text{C}$) vary with diet (the well-known distinction between C_3 dicot from C_4 grass biomass consumption is easily the strongest example; Cerling and Harris, 1999), whereas stable nitrogen isotope ratios ($^{15}\text{N}/^{14}\text{N}$) vary with trophic position as well as with nutritional and environmental stress factors (DeNiro and Epstein, 1978; Ambrose, 1991). Thus, SIA of consumer tissues is a proxy for measuring trophic niches in multidimensional niche space (Newsome et al., 2007), and has been successfully used to identify patterns of intra- and interspecific niche partitioning in a variety of systems (e.g. Codron et al., 2011; Fernández et al., 2011) including modern rodent communities (Mauffrey and Catzeflis, 2003; Baugh et al., 2004; Dammhahn et al., 2013; Symes et al., 2013), and those recovered from the fossil record (Kimura et al., 2013). So far,

however, most investigations have been limited to only a few species within a single habitat. The scarcity of observations recording patterns across habitats limits current understanding of ecological mechanisms that may drive isotope niche differentiation in rodent communities. Southern African rodents consume a variety of foods including insects and other arthropods, seeds, foliage of both dicots and grasses, plant roots and stems (Skinner and Smithers, 1990; Happold, 2013). Many of these items are expected to differ in isotope composition especially plant foods of C_3 dicot and C_4 grass origin (Codron et al., 2005). In addition, isotope compositions of plant foods in southern African savannas do not vary substantially across habitats (Codron et al., 2005), meaning that comparisons of animal isotope compositions across habitats in this biozone are unlikely to be affected by baseline variations and so dietary and trophic niche shifts should be easily traceable.

The aim of this study was to determine whether species occurring in rodent communities of the savanna biome partition stable isotope niches similarly across habitats, as a proxy for gaining insights into trophic niche partitioning and competitive effects across habitats. We analysed stable carbon and nitrogen isotope ratios in rodent hair from three habitat types within the South African savanna biome (open grassveld, woodland savanna, and marshes or "vlei" areas). We test the hypothesis that syntopic species have distinct isotope niches, i.e. that species' averages and/or variability differ. If partitioning occurs, we expect to find interspecific differences in stable isotope compositions of species within habitats, especially when resources are limiting, such as during the dry season of the South African savanna. In addition, we test the hypothesis that species' isotope niches differ between habitats, including across seasons. A comparison of within-species isotope compositions across habitat types illuminates whether interspecific exploitation competition is a potential mechanism generating species-level isotopic differences; if competition is occurring, we expect that species' isotope niches change across habitats in response to changes in species composition (Rosenzweig, 1981; Codron et al., 2011).

1 Materials and Methods

1.1 Study area and field collections

The study was carried out in the Cradle Game Reserve, located in the Cradle of Humankind World Heritage Site in the Sterkfontein Valley, approximately 50 km northwest of Johannesburg, Gauteng Province, South Africa. The Sterkfontein Valley lies within the Rocky

Highveld Grassland vegetation type of the South African Grassland Biome (Low and Rebelo, 1996). This vegetation type is a transitional habitat including elements of the high inland plateau grasslands and the lower inland plateau “bushveld” savanna. The region lies at altitudes between 1,500 and 1,600 m above sea level. The area includes the southern slopes of the Magaliesburg mountain range, the ridges of the Witwatersrand complex, and the dolomite plains of Gauteng and the North-West Province (Low and Rebelo, 1996). Geology includes dolomite, shale, sandstone, breccia, granite, quartzite, and andesite/basalt rock formations underlying a mostly coarse, sandy and shallow soil layer (summarized in Copeland et al., 2011). The vegetation type is a largely fire-maintained grassland, with woody elements distributed heterogeneously according to the prevailing frost regime (Low and Rebelo, 1996). Common tree species include *Acacia caffra*, *Searsia leptodictya*, *S. pyroides*, *S. rigida*, *S. magaliesmontana*, *S. zeyheri*, *Ehretia rigida*, *Maytenus heterophylla*, *Euclea crispa*, *Zanthoxylum capense*, *Dombeya rotundifolia*, *Protea caffra*, *Celtis africana*, *Ziziphus mucronata*, *Combretum molle*, *Olea europaea* subsp. *africana*, and *Grewia occidentalis*. Other dicot flora include forbs like *Sphenostylis angustifolia*, *Acrotome hispida*, *Senecio venosus*, *S. coronatus*, *Indigofera comosa*, *Xerophyta retinervis*, *Vernonia oligocephala*, the fern *Cheilanthes hirta*, and the succulent *Crassula lanceolata*. Grassland vegetation is restricted to exposed sites along the undulating landscape, especially on crests of rocky hills and

ridges (Low and Rebelo, 1996). Characteristic grass species include *Trachypogon spicatus*, *Diheteropogon amplexans*, *Andropogon schirensis*, *Loudetia simplex*, *Panicum natalense*, *Bewisia biflora*, *Digitaria* spp., and *Sporobolus pectinatus*. Climate is variable, with annual temperatures ranging from -12°C to +39°C, and a summer rainfall regime (October to March) of 650 to 750 mm. The period from April to September is characteristically dry.

We collected rodents from the Cradle Reserve during one wet season month (7–23 January 2011; ca. middle of the growing season, when adult mice are expected to be reproductively active), and one dry season month (4–12 and 19–28 May 2011; early non-growing season, when mice are less reproductively active). Initially, we selected seven sites for sampling, representing three broadly similar habitat types within the reserve: open grassveld, woodland savanna, and marsh (“vlei”) habitats (Table 1). In the dry season, four additional sites were sampled, in order to increase coverage in this period when rodent abundances in South African savannas and grasslands are expected to be at or near their annual peak (Avenant, 2011). A total of 100 rodent traps per day were placed at each site (see below), so that our total sampling effort covered 11,900 and 20,900 trap nights for the wet and dry seasons, respectively.

We conducted surveys of the vegetation at each site to classify habitats. We conducted step-point line transects over 250 m, recording vegetation data at 5 m intervals. At each interval, a 1 × 1 m² square grid was

Table 1 Characteristics of vegetation at the 11 sites from where rodents were captured for this study

Site name	Sampling month (s)	Vegetation types (%)				Canopy cover (%)
		Grasses	Forbs	Sedges / reeds	Trees	
<i>Open grassveld habitats</i>						
Bloedveld	Jan. & May 2011	80	15	0	5	15
Chateau Lawn	Jan. & May 2011	70	20	5	5	5
Kimberley	Jan. & May 2011	35	55	5	5	5
Lower kudu	May 2011	65	15	0	20	15
Rock Ridge	May 2011	60	30	0	10	5
<i>Wooded habitats</i>						
Chapel Wood	Jan. & May 2011	50	10	0	40	65
DOW	May 2011	55	20	0	25	25
Kudu Hill	Jan. & May 2011	5	10	0	85	70
Tick River	Jan. & May 2011	30	25	5	40	55
<i>Vlei areas (marshes)</i>						
Little Marsh	May 2011	45	15	20	20	30
Pieter's Vlei	Jan. & May 2011	55	10	30	5	5

Sites are divided into open grassveld, woodland savanna, and vlei/marsh habitats. DOW = dolomitic open woodland.

placed on the ground, from which a visual estimate of the percentage of tree canopy, grass cover, and forb cover was made. We also recorded the nearest grass, forb and tree (including its height) species within a 3-meter radius of each step-point. These vegetation data are presented in Table 1 in order to validate the distinction of three habitat types across our sampling sites.

Rodents were trapped using both box and snap traps. The traps were laid out along the same trajectory as the vegetation transects. For live trapping, 50 well-ventilated Sherman-like stainless steel box traps ($7.6 \times 7.6 \times 25.4 \text{ cm}^3$) were spaced 5 meters apart along a single 245-meter line transect (following Avenant, 2011, and see references therein). The traps were baited with a mixture of peanut butter, rolled oats, sunflower oil and a yeast-based spread (Bovril[®]). Each trap was checked for successful trappings and re-baited at dawn and dusk on consecutive days throughout the sampling period, in order to consistently sample diurnal and nocturnal small mammal species (Avenant, 2011). Captured specimens were identified, sexed, measured (total length, hind foot length, and tail length all in mm), weighed (grams), and marked with fur pattern clippings dorsally behind the shoulder to ensure identification of re-trapped individuals. Clipped hair samples were retained for stable isotope analysis. A second 245-meter line transect of 50 snap traps (spaced and baited in the same way as the live traps) was placed parallel to the line of box traps, but at least 50 m away. Snap traps were handmade at the National Museum in Bloemfontein, South Africa. Previously, these have proven to be as effective, if not more so, than the larger Sherman and PVC live traps, when both the number of individuals and the number of species caught is considered (N. Avenant, pers. obs.). Specimens captured in the snap traps were identified, sexed, and had fur clippings removed before being frozen for later analyses, and inclusion in the National Museum Mammal Collection.

1.2 Analytical methods

In total, 159 individuals, representing 10 rodent species, were collected across the two sampling seasons (Table 2). Details of trapping success, richness and diversity patterns will be published elsewhere. Hair samples of 140 individuals were subjected to stable carbon and nitrogen isotope analysis (see Table 2 for proveniences of individuals analyzed). Trophic, dietary, and other ecological information on the species captured are presented in Table 3. Most species sampled are omnivorous and granivorous, and therefore have overlapping trophic and dietary niches, with the exception of

Otomys spp. which are purely herbivorous. In addition, most species' body sizes are similar, in particular three of the best-sampled taxa in this study (*Micaelamys natalensis*, *Rhabdomys pumilio*, and *Mastomys coucha*) which have almost identical mean body masses (Table 3; see data in Smith et al., 2003). The sample is therefore well-suited to investigating competition as a driver of niche separation in this community.

Each hair sample was cleaned with ethanol, and approximately 1 mg was weighed into Costech 3.5x5 mm pressed tin capsules. Samples were analysed for $^{13}\text{C}/^{12}\text{C}$ and $^{15}\text{N}/^{14}\text{N}$ isotope ratios at the University of California Davis, using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Samples were combusted at 1000°C in a reactor packed with chromium oxide and silvered copper oxide. Following combustion, oxides were removed in a reduction reactor (reduced copper at 650°C), and the resultant CO_2 and N_2 gases separated on a Carbosieve GC column (65°C, 65 mL/min) before entering the stable light isotope mass spectrometer. Stable isotope ratios are presented in delta (δ) notation in part per thousand (‰) relative to the VPDB (Vienna PeeDee Belemnite) and atmospheric N_2 standards, respectively. Analytical precision, based on repeated measurements of laboratory standards (approximately one of each standard for every ten samples), was less than 0.2‰ and 0.3‰ for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively.

To test hypotheses related to trophic niche separation, we compared both the average and variability in stable isotope compositions of species within particular habitats and within each season. Because of the small and uneven sample sizes in many cases, we used non-parametric tests to compare medians across species. Species medians were compared using the Kruskal-Wallis test with multiple comparisons (Siegel and Castellan, 1988) where necessary, and species within each of the three habitat types were compared using the same test or the Mann-Whitney test if only two taxa were represented within a habitat. To compare isotopic niche variability, we compared the 25th–75th interquartile ranges (IQR) between species pairs. We calculated the ratio between the IQRs of each pair, and then conducted permutations tests by randomly mixing the data for all individuals of both taxa and comparing the randomized IQR ratio with the observed ratio. Monte Carlo simulations were then used to compute the probability of a difference between the observed and randomized ratios: significance was accepted if $P_{\text{obs}} > P_{\text{randomized}}$ was less than 0.05 over

Table 2 Abundance data for rodents sampled in the different habitat types during the wet and dry season in Cradle Nature Reserve

Species	Bloed-veld	Chapel wood	Chateau lawn	DOW	Kimberley burn	Kudu hill	Little Marsh	Lower kudu	Pieter's vlei	Rock ridge	Tick River	Total
Dry season captures: <i>n</i> (<i>n</i> analyzed for stable isotope composition)												
<i>Dendromys mystacalis</i>	-	-	-	-	-	-	1(1)	1(0)	1(1)	-	1(1)	4(3)
<i>Gerbilliscus leucogaster</i>	-	-	-	-	9(9)	-	-	-	-	-	-	9(9)
<i>Lemniscomys rosalia</i>	-	-	-	1(1)	-	-	-	-	-	-	-	1(1)
<i>Mastomys coucha</i>	-	-	1(1)	-	1(1)	-	8(7)	-	3(2)	-	5(5)	18(16)
<i>Micaelamys namaquensis</i>	2(2)	1(1)	-	-	-	13(13)	-	3(3)	-	17(17)	-	36(36)
<i>Mus indutus</i>	-	-	-	-	-	-	2(1)	-	-	-	-	2(1)
<i>Otomys angolensis</i>	-	-	-	-	-	-	-	1(1)	-	-	-	1(1)
<i>Otomys irroratus</i>	-	-	-	-	-	-	6(5)	-	3(3)	-	-	9(8)
<i>Rhabdomys pumilio</i>	-	-	5(3)	-	-	-	2(2)	-	24(22)	-	1(1)	32(28)
<i>Steatomys pratensis</i>	-	-	-	-	-	-	1(1)	-	-	-	-	1(1)
Total												113(104)
Wet season captures: <i>n</i> (<i>n</i> analyzed for stable isotope composition)												
<i>Mastomys coucha</i>	-	-	-	-	-	1(1)	-	-	-	-	-	1(1)
<i>Micaelamys namaquensis</i>	5(4)	-	-	-	-	6(5)	-	-	-	-	-	11(9)
<i>Otomys angolensis</i>	1(1)	-	-	-	-	-	-	-	-	-	-	1(1)
<i>Otomys irroratus</i>	-	-	-	-	-	-	-	-	10(9)	-	-	10(9)
<i>Rhabdomys pumilio</i>	-	-	13(8)	-	-	-	-	-	10(8)	-	-	23(16)
Total												46(36)

Number of specimens capture are shown, with the number of specimens analyzed for hair stable isotope ratios shown in parentheses.

Table 3 Average body mass, behavioural habits, and ecological information for rodent species collected from the Cradle Nature Reserve, Gauteng, South Africa

Species	Body mass (g)	Active hours	Behaviour	Diet	Habitat preference	Nesting behaviour	Reproduction
<i>Dendromus mystacalis</i>	7.6	Nocturnal	Terrestrial; partially arboreal	Omnivorous, mainly insects	Grassland, especially rank vegetation and high course grasses	Ball-shaped nests during early wet season (in low bushes or in trees)	Summer months, peaking between January and March
<i>Gerbilliscus leucogaster</i>	69.9	Nocturnal	Terrestrial	Omnivorous	Sandy soils	Excavate burrows in sandy soils, termitaria or tree roots	Year-round, peaking in February and March
<i>Lemniscomys rosalia</i>	49.5	Diurnal	Terrestrial	Omnivorous, mainly herbivorous	Grassland specialist	Burrows	Between September and March
<i>Mastomys coucha</i>	43.5	Nocturnal	Terrestrial	Omnivorous, can become cannibalistic	Wide habitat tolerance, excluding very arid regions	Burrows under logs, roots of fallen trees, or rocks	Peaking during the wet season (October to March)
<i>Micaelamys namaquensis</i>	48.8	Nocturnal	Terrestrial; partially arboreal; communal	Omnivorous	Rocky outcrops and hills	Rock crevices, fallen logs, holes in trees, piles of debris, grass tufts	Between September and May, peaking in March and April. Unstable population cycles, associated with high mortality and high reproductive potential.
<i>Mus indutus</i>	6.2	Nocturnal	Terrestrial	Omnivorous, can become cannibalistic	Wide tolerance, from arid shrub savannas to well-watered areas	Shallow burrows, rocks, crevices, or logs	Year-round
<i>Otomys angoniensis</i>	191.5	Predominantly diurnal, partially nocturnal	Terrestrial	100% herbivorous	Savanna woodland and grasslands, often associated with wetlands or rivers	Domed nests of shredded vegetation; well-defined runs extending from nests to feeding grounds	Warm, wet summer months (September to March)
<i>Otomys irroratus</i>	101.8	Diurnal	Terrestrial, can be semi-aquatic	100% herbivorous	Grasslands, preferring moist habitats associated with damp soils in wetlands and along rivers	Burrows, mainly those of other species	Between August and May
<i>Rhabdomys pumilio</i>	40.7	Crepuscular	Terrestrial	Omnivorous	Grasslands, but wide tolerance range provided there is grass cover	Burrows	Year-round, peaking between September and April
<i>Sitomys pratensis</i>	25.0	Nocturnal	Terrestrial	Omnivorous granivores	Sandy substrates, river fringes, and wetlands	Burrows sloping downwards to a chamber ~250mm below the surface, filled with shredded vegetation	Warm, wet summer months (October to May)

Body mass is mean body mass for species reported in Smith et al. (2003); Behavioural and ecological information are summarized in Skinner and Smithers (1990) and Happold (2013).

1,000 permutations. In addition to these permutations tests, we computed isotope niche breadths of species. For this purpose, $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ were binned in 1.0‰ increments – as a widely-assumed minimum level of analytical precision associated with biological isotope data (Hayes, 1982) and the number of individuals in each bin was recorded. Modifying the bin size, for example four bins separated by quartiles, did not affect the patterns emerging from subsequent analyses. Niche breadths (B) were calculated using Levins' (1968) measure

$$B = \frac{1}{\sum p_i^2}$$

where p_i is the relative proportion of individuals in isotope bin i . This measure was then standardized from 0 to 1 following

$$B_A = \frac{B-1}{n-1}$$

where n is the total number of isotope bins available. B and B_A are more traditional measures of niche breadth used in ecology, thus comparison between them and the basic descriptives of stable isotope data (e.g. IQRs) potentially allows more direct comparisons between stable isotopes and traditional approaches. Similarly, patterns in differences between species' $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ averages (medians in this study) as described above could potentially be compared against traditional niche overlap indices. Hence, we also calculated average niche overlaps within each habitat type using Pianka's (1986) index of overlap between species j and k :

$$O_{jk} = \frac{\sum p_{ij} p_{ik}}{\sqrt{\sum p_{ij}^2 \sum p_{ik}^2}}$$

where p_i is the relative proportion of individuals in bin i . A result of 0 represents zero niche overlap, and 1 represents complete overlap.

The statistical approaches described above were used not only to compare stable isotope niches among species within habitats, but also for comparing changes in species' niches across habitats - the latter potentially revealing competition effects as discussed in the Introduction. In all cases, however, dry and wet season data were treated separately, and only those data groups for which $n \geq 4$ were used in statistical hypothesis testing. Isotope data for taxa that are less-well represented in our sample are presented in the Results simply for completeness.

2 Results

Rodents had a wide range of $\delta^{13}\text{C}_{\text{hair}}$ values, from -24.4 to -10.4‰, indicating that the group consumes food items across the whole $\text{C}_3\text{-C}_4$ spectrum of terrestrial vegetation in savanna habitats. In the dry season, $\delta^{13}\text{C}$ values differed significantly across taxa ($H_{4,97} = 36.594$; $P < 0.0001$). The lowest average $\delta^{13}\text{C}$ values were recorded for the Namaqua rock mouse *Micaelamys namaquensis* (median = -22.7‰; 25th-75th interquartile range (IQR) = -23.4‰ to -21.7‰; $n = 36$) and the striped mouse *Rhabdomys pumilio* (-22.4‰; IQR = -23.6‰ to -21.4‰; $n = 28$). The multimammate mouse *Mastomys coucha* (-17.8‰; IQR = -19.5‰ to -13.3‰;



Fig. 1 Map of South Africa showing geographical location of the Cradle Nature Reserve in Gauteng Province, and location of sampling sites from where vegetation data were recorded and rodents trapped

Site key: KB = Kimberley; BV = Bloedveld; LK = Lower Kudu; KH = Kudu Hill; RR = Rock Ridge; CW = Chapel Wood; DOW = DOW (dolomite open woodland); LM = Little Marsh; PV = Pieter's Vlei; CL = Chateau Lawn; TR = Tick River.

$n = 16$) and the bushveld gerbil *Gerbilliscus leucogaster* (-17.4‰; IQR = -17.5‰ to -17.4‰; $n = 9$) had significantly higher $\delta^{13}\text{C}$ values than *M. namaquensis* and *R. pumilio* ($P < 0.0001$ to < 0.01). The vlei rat, *Otomys irroratus*, had intermediate $\delta^{13}\text{C}$ values (-18.6‰; IQR = -20.2‰ to -17.0‰; $n = 8$), lower than those for *M. coucha* ($P = 0.056$), but not different from the other taxa ($P = 0.330$ to 1.000). Species with fewer samples displayed $\delta^{13}\text{C}$ values ranging from -21.6‰ (single-striped rock mouse, *Lemniscomys rosalia*, $n = 1$) to -10.4‰ (fat mouse *Steatomys pratensis*, $n = 1$). In the wet season, rodents typically had narrower $\delta^{13}\text{C}$ ranges than in the dry season, and showed no differences across species ($H_{2,34} = 3.295$; $P = 0.193$). Medians for *M. namaquensis*, *R. pumilio*, and *O. irroratus* were all similar (-21.5‰, IQR = -22.1‰ to -20.5‰, $n = 9$; -22.1‰, IQR = -22.4‰ to -21.7‰, $n = 16$; -22.2‰, IQR = -22.4‰ to -21.9‰, $n = 9$). Only one *M. coucha* specimen was trapped in this period and had a similar $\delta^{13}\text{C}$ value (-22.2‰) to the other rodents, whereas a single *O. an-*

goniensis (Angoni vlei rat) specimen was ^{13}C -enriched (-13.5‰) relative to the others.

Rodent $\delta^{15}\text{N}_{\text{hair}}$ values also ranged widely, from 2.4 to 16.9‰ (Fig. 2). There were significant $\delta^{15}\text{N}$ differences across taxa in both the dry ($H_{4,97} = 38.103$; $P < 0.0001$) and wet seasons ($H_{2,34} = 18.686$; $P < 0.001$). The highest dry season $\delta^{15}\text{N}$ values were found in *G. leucogaster* (8.2‰; IQR = 7.6‰ to 8.3‰) and *M. coucha* (6.8‰; IQR = 6.5‰ to 8.9‰), which were significantly higher ($P < 0.0001$ to < 0.001) than those of *M. namaquensis* (5.3‰; IQR = 4.8‰ to 5.7‰) and *R. pumilio* (4.7‰; IQR = 3.7‰ to 6.5‰). *Otomys irroratus* was again intermediate (6.2‰; IQR = 5.7‰ to 7.1‰), and not significantly different from other taxa ($P = 0.165$ to 1.000). In the wet season, *M. namaquensis* (5.3‰; IQR = 3.8‰ to 5.4‰) and *O. irroratus* (5.7‰; IQR = 5.5‰ to 6.3‰) had higher $\delta^{15}\text{N}$ values than *R. pumilio* (3.0‰; IQR = 2.3 to 4.2‰; $P = 0.052$ and < 0.0001 , respectively).

These species differences provide some evidence for

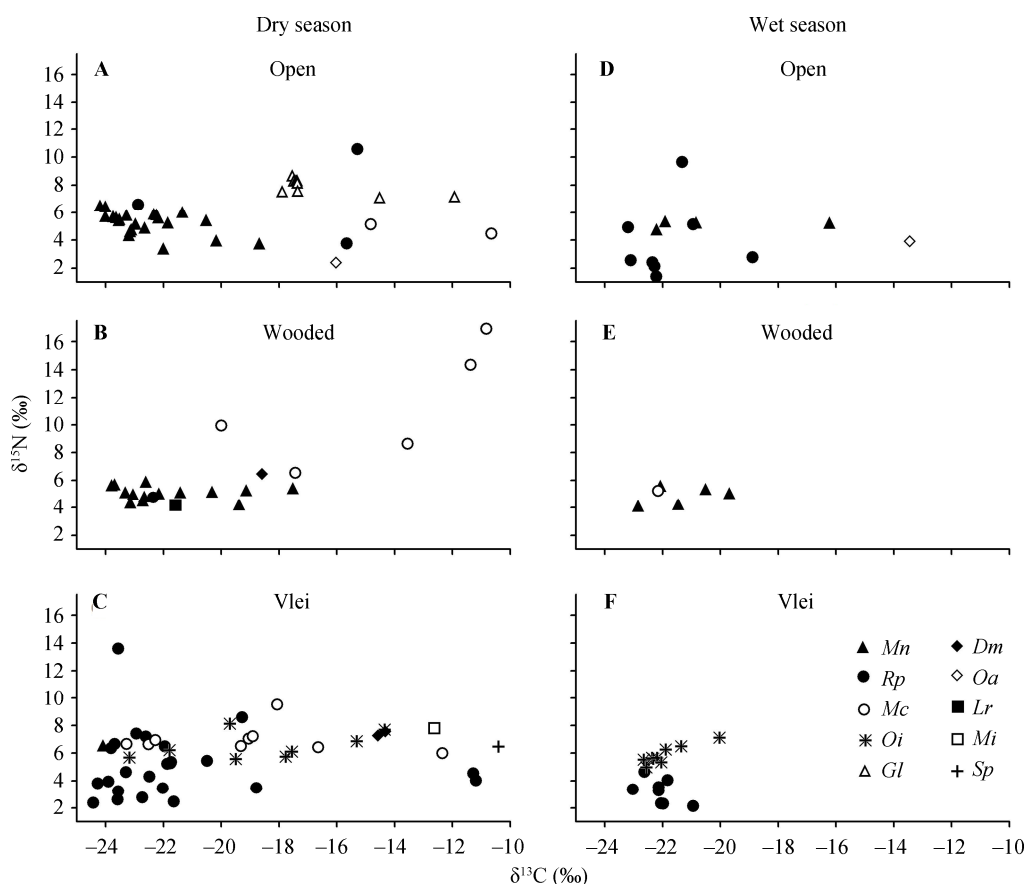


Fig. 2 Hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of ten rodent taxa included in this study

The whole dataset is presented here, regardless of how many specimens are represented by each taxon. The dataset is separated into three habitat types (open grassveld, woodland savanna, and vlei areas/marshes) and across two seasons (dry = May 2011; wet/rainy = January 2011). Taxa are indicated in the legend: *Mn* = *Micaelamys namaquensis*; *Rp* = *Rhabdomys pumilio*; *Mc* = *Mastomys coucha*; *Oi* = *Otomys irroratus*; *Gl* = *Gerbilliscus leucogaster*; *Dm* = *Dendromus mystacalis*; *Oa* = *Otomys angoniensis*; *Lr* = *Lemniscomys rosalia*; *Mi* = *Mus indutus*; *Sp* = *Steatomys pratensis*.

trophic niche separation amongst rodents, but a more relevant question is whether such separation occurs within particular habitats; i.e. between syntopic individuals of different species. In our data, there are significant differences in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values amongst the dominant species within each habitat type, at least during the dry season (differences were much smaller, or even negligible, in the wet season). In open grassveld, *M. namaquensis* had lower medians than *G. leucogaster* (Mann-Whitney $P < 0.0001$ for both isotopes; Fig. 2A; Table 4). In woodland habitats, *M. namaquensis* had lower median $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values than *M. coucha* ($P < 0.01$; Fig. 2B; Table 4). Consequently, the level of isotope niche overlap in these two habitat types was low (0.00 to 0.05; Table 4). *Micaelamys namaquensis* also typically had a larger IQR and broader isotopic niche breadth (B_A) than *G. leucogaster* in grasslands, but lower niche breadth compared with *M. coucha* in woodlands (Table 4). In the vlei areas, average isotopic niche overlap was higher than in other habitats (0.47 and 0.34 for $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$, respectively), mainly because only two out of the three dominant species differed significantly in isotopic composition (Fig. 2C). *Rhabdomys pumilio* had lower $\delta^{13}\text{C}$ values, and a narrower isotope niche breadth (IQR and B_A) than *O. irroratus*, but only differed significantly from *M. coucha* in $\delta^{15}\text{N}$ (the former having a lower median, but broader niche breadth).

In the wet season, there was no evidence for isotopic differences between taxa within habitats ($P = 0.089$ to 0.923 ; Figs 2D & E), and thus there was higher isotopic niche overlap than was found for the dry season (0.53 to 0.98). The one exception was that in the vlei, *R. pumilio* had a lower $\delta^{15}\text{N}$ median ($P < 0.001$) and broader niche breadth (P for IQR ratios = 0.005) than *O. irroratus* (Fig. 2F), and the two species showed little niche overlap (0.07).

Our next objective was to determine whether species' isotopic niches change across habitats. In general, such changes were rare. *Micaelamys namaquensis* showed no significant changes in $\delta^{13}\text{C}$ medians or niche breadths across habitats and seasons, nor in median $\delta^{15}\text{N}$ values ($P = 0.070$ to 0.472 ; Table 5). The $\delta^{15}\text{N}$ niche breadths differed across seasons for this species, but only significantly in the open grassveld where it was isotopically less diverse in the wet season. *Rhabdomys pumilio* also did not differ in $\delta^{13}\text{C}$ medians across habitats ($P = 0.677$), although it did show a significantly narrower $\delta^{13}\text{C}$ niche breadth in the vlei habitat during the wet season ($P < 0.01$). The $\delta^{15}\text{N}$ niche breadths of this species did not change across habitats, and although $\delta^{15}\text{N}$ medians did show a significant habitat effect ($P = 0.028$), no differences occurred across habitats in the same season, or within the same habitat across seasons (Table 5). *Mastomys coucha*, despite the small sample size for this taxon, showed significantly higher $\delta^{13}\text{C}$ and

Table 4 Within-habitat comparisons of species' stable isotope characteristics

Habitat	Taxon	n	$\delta^{13}\text{C}$ (‰)				$\delta^{15}\text{N}$ (‰)			
			median	IQR	B_A	O	median	IQR	B_A	O
Open grassveld, dry season	<i>Micaelamys namaquensis</i>	22	-23.04 ^a	1.5 ^a	0.23	0.00	5.49 ^a	0.99 ^a	0.13	0.02
	<i>Gerbilliscus leucogaster</i>	9	-17.38 ^b	0.13 ^b	0.12		8.17 ^b	0.78 ^a	0.06	
Wooded, dry season	<i>Micaelamys namaquensis</i>	14	-22.64 ^a	2.53 ^a	0.22	0.05	5.12 ^a	0.54 ^a	0.07	0.00
	<i>Mastomys coucha</i>	5	-13.56 ^b	6.07 ^a	0.18		9.94 ^b	5.72 ^b	0.25	
Vlei, dry season	<i>Rhabdomys pumilio</i>	24	-22.55 ^a	1.85 ^a	0.23	0.47	4.59 ^a	2.93 ^a	0.30	0.34
	<i>Mastomys coucha</i>	9	-19.06 ^{ab}	4.21 ^b	0.27		6.68 ^b	0.55 ^b	0.06	
	<i>Otomys irroratus</i>	8	-18.63 ^b	3.23 ^{ab}	0.39		6.16 ^{ab}	1.34 ^{ab}	0.07	
Open grassveld, wet season	<i>Micaelamys namaquensis</i>	4	-21.38 ^a	2.3 ^a	0.12	0.77	5.26 ^a	0.16 ^a	0.00	0.53
	<i>Rhabdomys pumilio</i>	8	-22.26 ^a	1.32 ^a	0.18		2.67 ^a	2.64 ^a	0.22	
Wooded, wet season	<i>Micaelamys namaquensis</i>	5	-21.46	1.57	0.18	-	5.08	1.12	0.11	-
Vlei, wet season	<i>Rhabdomys pumilio</i>	8	-22.09 ^a	0.31 ^a	0.08	0.98	3.32 ^a	1.35 ^a	0.16	0.07
	<i>Otomys irroratus</i>	9	-22.19 ^a	0.47 ^b	0.12		5.66 ^b	0.74 ^b	0.06	

Statistically homogeneous taxa within habitats are indicated with the same superscript letters; IQR = interquartile range; B_A = standardized isotopic niche breadth; O = mean isotopic niche overlap between the dominant taxa at each habitat. Interquartile ranges (IQR) are averages derived from a randomization procedure. Only the most dominant species in each habitat are included ($n \geq 4$, where n is the number of specimens analyzed for stable isotope compositions).

$\delta^{15}\text{N}$ medians in the woodland compared to the vlei (dry season only; $n = 5$ and 9 , respectively; $P < 0.01$ and 0.039). The $\delta^{13}\text{C}$ niche breadths did not differ across habitats for this species ($P = 0.306$), but its $\delta^{15}\text{N}$ niche breadth was wider in the woodland than in the vlei, and this difference approached statistical significance ($P = 0.050$). *Otomys irroratus* (which only occurred in the vlei areas), showed a change in its $\delta^{13}\text{C}$ niche, from a higher median with broader breadth in the dry season to lower values in the wet season ($P = 0.016$ and 0.015 , respectively).

A general trend emerging from the above was that, especially in vlei habitats, isotopic niche breadths were narrower in the wet than the dry season. A potential confounding effect here could be that whereas rodents were trapped at two vlei habitats during the dry season (Little Marsh and Pieter's Vlei), only one of these was sampled during the wet season (Pieter's Vlei). Dry season data for these two habitats are plotted in Fig. 3, which shows that for *R. pumilio* at least, the absence of wet season sampling at Little Marsh cannot account for the differences in isotope niche breadths between dry and wet seasons, as there was no evident difference in this species' isotope compositions between the two vlei habitats (Fig. 3). For *O. irroratus*, however, all ^{13}C -enriched individuals came from Little Marsh (-19.5‰ to -14.3‰ , $n=5$), whereas individuals from Pieter's Vlei were relatively ^{13}C -depleted (-23.2‰ to -19.7‰ , $n=3$). Hence, sampling bias may explain the narrower wet season $\delta^{13}\text{C}$ niche breadth found for *O. irroratus*. Interestingly, *M. coucha* was also collected from both vlei

habitats, and data for this taxon contrast the pattern observed in *O. irroratus*, in that all ^{13}C -depleted *M. coucha* individuals are from Little Marsh (-23.3‰ to -18.1‰ , $n=7$), whereas data for Pieter's Vlei are more ^{13}C -enriched (-16.6‰ to -12.4‰ , $n=2$).

3 Discussion

In this study we described and compared the stable isotope niches of a variety of sympatric rodent taxa from three southern African savanna habitat types. Results provide evidence for trophic niche separation amongst the dominant (most abundant) taxa found within each habitat. This is strengthened by the *post hoc* observation that species with strongly overlapping isotope niche breadths, for example *M. namaquensis* and *R. pumilio*, were not found in high abundances together in the same habitat. This implies that while trophic niche partitioning was occurring within each habitat type, partitioning in these communities also occurred along the habitat utilization axis. However, species' isotope niches remained largely unchanged across habitats (with the exception of *M. coucha*, and the narrowing of isotope niche breadths generally from the dry to the wet season), suggesting that differences in community composition did not influence trophic behaviour. Lower niche overlap in the dry than the wet season could imply that interspecific competition drives niche partitioning during periods of low resource availability, but the lack of niche shifting across habitats suggests the pattern is merely the result of broader niche breadths during these times. Hence, interspecific competition does not appear

Table 5 Across-habitat, and across-season, comparisons of species' stable isotope characteristics

Taxon	Habitat	<i>n</i>	$\delta^{13}\text{C}$ (‰)			$\delta^{15}\text{N}$ (‰)		
			median	IQR	B_A	median	IQR	B_A
<i>Micaelamys namaquensis</i>	Open grassveld, dry season	22	-23.04 ^a	1.50 ^a	0.23	5.49 ^a	0.99 ^a	0.13
	Open grassveld, wet season	4	-21.38 ^a	2.30 ^a	0.12	5.26 ^a	0.16 ^{bc}	0.00
	Wooded, dry season	14	-22.64 ^a	2.53 ^a	0.22	5.12 ^a	0.54 ^{ab}	0.07
	Wooded, wet season	5	-21.46 ^a	1.57 ^a	0.18	5.08 ^a	1.12 ^{ac}	0.11
<i>Rhabdomys pumilio</i>	Open grassveld, wet season	8	-22.26 ^a	1.32 ^a	0.18	2.67 ^a	2.64 ^a	0.22
	Vlei, dry season	24	-22.55 ^a	1.85 ^a	0.23	4.59 ^b	2.93 ^a	0.30
	Vlei, wet season	8	-22.09 ^a	0.31 ^b	0.08	3.32 ^{ab}	1.35 ^a	0.16
<i>Mastomys Coucha</i>	Wooded, dry season	5	-13.56 ^a	6.07 ^a	0.18	9.94 ^a	5.72 ^a	0.25
	Vlei, dry season	9	-19.06 ^b	4.21 ^a	0.27	6.68 ^b	0.55 ^b	0.06
<i>Otomys Irroratus</i>	Vlei, dry season	8	-18.63 ^a	3.23 ^a	0.39	6.16 ^a	1.34 ^a	0.07
	Vlei, wet season	9	-22.19 ^b	0.47 ^b	0.12	5.66 ^a	0.74 ^a	0.06

Statistically homogeneous habitats/seasons for each species are indicated with the same superscript letters; IQR=interquartile range; B_A =standardized isotopic niche breadth.

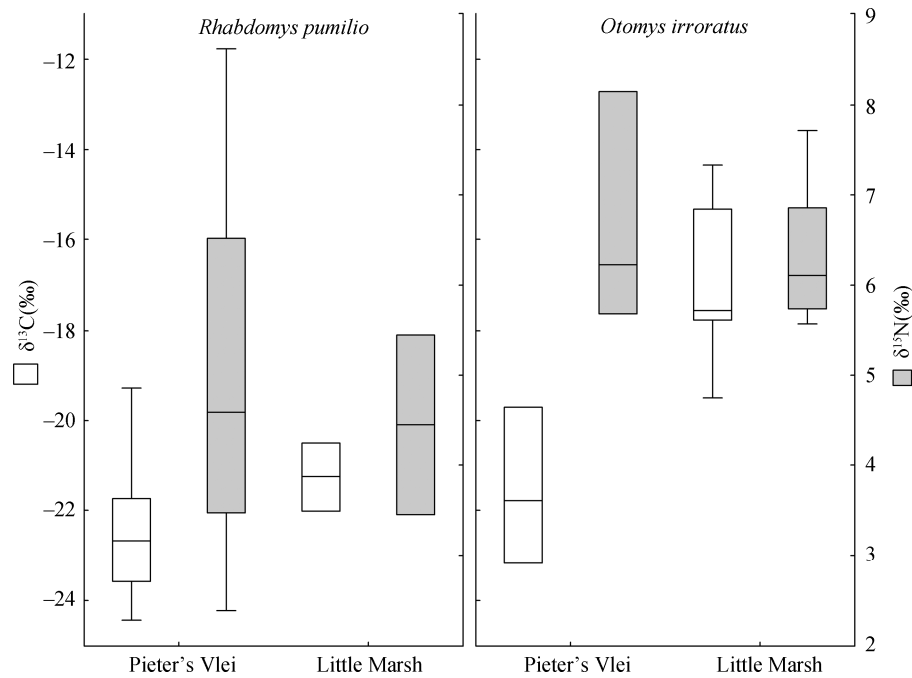


Fig. 3 Hair $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values of the two most dominant rodent taxa from the two vlei habitat sites (dry season data only). In the plots, horizontal lines depict medians, boxes are 25th-75th interquartile ranges, and whiskers are non-outlier ranges (3σ).

to be the major factor causing patterns of trophic differentiation in this community. However, the result could also indicate that competition is avoided by species with overlapping niches selecting different habitats. This behaviour could reflect a result of past competition (Diamond, 1986). However, accurate testing of such an hypothesis requires knowledge of past trophic interactions, which is potentially obtainable through stable isotope analyses (cf. Codron et al., 2008) provided that appropriate historical or fossil assemblages can be located.

A limitation of this study is that, within any one habitat type, only two to three species were sufficiently represented for detailed investigation of differences in stable isotope niches. Similarly, our sampling protocol does not entail experimental removals, and cannot investigate events in the past. Hence we cannot directly link emerging patterns with competitive effects. We cannot, therefore, make robust conclusions about the degree of structuring of communities at this scale. Sufficient data from the full array of species that occur within each habitat throughout the seasonal cycle are needed to determine whether non-random patterns of trophic differentiation persist for the respective communities. However, given our extensive sampling effort (see Methods) it may be that other species simply occur only at very low abundances within our sampling sites.

Our finding that species used distinct trophic niches within habitat types is in broad agreement with models

of structured communities (Pianka, 1986) and with studies that have shown such structure for rodents based on traditional approaches to diet and habitat use (e.g. Bowers and Brown, 1982; Kelt et al., 1999). A similar trend has been found in stable isotope studies of small mammal communities in other systems across the globe (Mauffrey and Catzeflis, 2003; Baugh et al., 2004; Bergstrom, 2013; Dammhahn et al., 2013; Symes et al., 2013). However, a recent study of rodent community compositions, based on presence/absence and relative abundance data, across an array of southern African savanna habitat types found no evidence for structure (Rautenbach et al., 2014). These authors ascribed the evidently random composition of assemblages to high diversity and availability of resources. Our results show that, in fact, resource utilization patterns of particular rodent species can be conservative across habitats, and therefore we would not expect variability in resource abundances to be a major driver of taxonomic composition. If anything, the rarity of overlapping niches within habitats during the dry season suggests that structure should be evident along habitat gradients within rodent communities. At present, the discrepancy between our findings and those of Rautenbach et al. (2014) is not easily explained. A larger sample representative of the full array of species' isotope niches, combined with diversity indices, is needed to make definitive statements about community structure.

Given that rodents are widely regarded as generalist

feeders (Delaney, 1986; Dearing et al., 2000; Happold, 2013), the isotope evidence presented here that species trophic niches are conservative across habitats - despite their generally broad isotope niche breadths overall - is unexpected. *Mastomys coucha* was an exception: this species showed significant shifts in both the stable carbon and nitrogen isotope niche axes across woodland and vlei habitats. *Mastomys coucha* has been described as an indicator of low ecological integrity where they dominate the small mammal community composition. They are generalist and opportunist omnivores, consuming a variety of plant and animal resources, and are even reported to display cannibalistic behaviour under conditions of extreme resource limitation (Avenant, 2011; Happold, 2013). This species' dietary flexibility explains the observed shifts in isotope niches across habitats, and these shifts seem to enable a diverse distribution across habitats: in vlei habitats, *M. coucha* occupied an isotopic niche similar to that of *M. namaquensis* elsewhere, but in wooded habitats where these two species co-occur, *M. coucha* shifted its niche, avoiding overlap. In this respect, *M. coucha* is the only taxon sampled here for which the data suggest competition is having an effect on these systems, and further points to the potential that such effects may have been substantial in the past.

The conservative nature of species' isotope niches, i.e. relative stasis across habitats, as revealed in this study allows us to make inferences about the dietary behaviour of each species. For example, both *M. namaquensis* and *R. pumilio* generally occurred around the low end of the $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ axes at both habitats in which they were abundant (open grassland and woodland habitats, and open grassland and vlei habitats, respectively). Therefore, in these habitats, both species appear to be predominantly C_3 -feeders, but their low $\delta^{15}\text{N}$ values are at odds with expectations from the literature - both species are described as omnivores, consuming both plant and animal matter regularly (Happold, 2013, and references therein), and should therefore occur at a higher trophic level than their respective $\delta^{15}\text{N}_{\text{hair}}$ values suggest. Moreover, *O. irroratus*, described in the literature as a herbivore (Happold, 2013, and references therein), had higher $\delta^{15}\text{N}_{\text{hair}}$ values, and occupied a significantly higher position than *R. pumilio* on the $\delta^{15}\text{N}$ axis of vlei habitats. Whether there are foraging peculiarities specific to our study area, or whether the described $\delta^{15}\text{N}$ axes represent factors other than trophic position, is unclear, but future planned comparisons between our data with analyses of stomach contents, as well as with iso-

tope data of plant materials collected from each transect, should be able to resolve this issue. Climate is another potential confounding factor for $\delta^{15}\text{N}$ interpretations, as arid-adapted mammals are often expected to display patterns of ^{15}N -enrichment (Ambrose, 1991). *Otomys irroratus* has a longer large intestine than its desert-dwelling congeners, even after accounting for body size and phylogenetic affiliations (Lovegrove, 2010), a trait which has been linked with enhanced water retention in rodents (Jackson and Spinks, 1998). Further study mechanistically linking digestive tract features with nitrogen pathways in rodents is needed to test this possibility. The primarily C_3 -based component of the diets of *M. namaquensis* and *R. pumilio* also requires some discussion, as grass seeds (most of which are C_4 in our study region), are expected to contribute significantly to the diets of both species (Skinner and Smithers, 1990; Happold, 2013). While the stable carbon isotope niche breadths for both species do indicate substantial contributions of C_4 resources, these inputs were less than C_4 inputs for co-occurring *G. leucogaster* and *O. irroratus*, respectively. For *R. pumilio*, predominantly C_3 diets, i.e. diets excluding grass-based resources, have been described for some populations (Rowe-Rowe, 1986; and see discussion below).

One of our predictions was that species' isotope niche breadths would show significant changes across habitats, depending on changes in species composition. Species' niche breadths are expected to become compressed (MacArthur and Levins, 1967), or to expand (if the species' have secondary niches they can exploit without experiencing reduced fitness; Rosenzweig, 1981), in the presence of abundant competitors. The prevailing trend in the dynamics of species isotope niche breadths we found was a general expansion from the wet to the dry season. This pattern has previously been found on Sub-Antarctic Marion Island, where house mice *Mus musculus* increased the variety and diversity of prey during the colder winter as energy requirements increased, while prey availability decreased; similarly, this pattern was also observed under laboratory conditions, when they even fed on non-preferred prey such as the slug *Deroceras caruanae* during this time, but showed no interest during summer (Smith et al., 2002). The same limiting effect seems also to apply to animal assemblages in the temperate zone, with competition effects being more pronounced during dry seasons (Gordon and Illius, 1989). In our study, rodent densities were expected to remain high at the end of the reproductive season, while energy requirements were already

increasing as temperatures dropped (Avenant, 2011). We therefore infer that this is the case for our sample, and hence that rodents were forced to forage more broadly during the dry season in order to obtain their resources. This also means that the primarily C_3 niches of *R. pumilio* and *O. irroratus* in the wet season likely represent their preferred dietary ranges, and that expansions to include more C_4 in the dry season are a secondary niche state. This is likely because the majority of southern African savanna grasses drop seed in the late wet season (e.g. van Oudtshoorn, 2006), which may have led to an increased relative abundance in the seed bank in the early dry season. There is some independent evidence which also suggests an avoidance of grasses (which are the primary C_4 source in our study area): in the Drakensberg, a montane savanna/grassland environment located approximately 400 km to the southeast of our study area, diets of *R. pumilio* comprised more parts of dicot plants and various insects in the wet season than in the dry (Rowe-Rowe, 1986). While a number of large mammalian herbivores have been found to be predominantly C_4 feeders (e.g. Cerling and Harris, 1999), early studies had predicted that C_4 resources should be largely excluded from the diets of many animal species based on the lower nutritional value and digestibility of C_4 compared to C_3 foliage (Caswell et al., 1973). However, comparative nutritional data for C_3 versus C_4 seeds (a major dietary component for the species included here), are lacking.

Apart from differences in average values (medians) between species, the observed seasonal change in isotope niche breadths is one of the key results of this study. Accordingly, we advocate that future studies pay special attention not only to species averages, but also to the degree of isotopic variability that occurs in each species, habitat, and season. Traditional approaches in ecology include deliberate attempts to quantify not only the preferred niche states of animals, but also their niche breadths (Levins, 1968; Pianka, 1986; Begon et al., 2006). In cases where researchers have attempted to quantify stable isotope niche breadths, approaches have been based mostly on general descriptive statistics such as maximum–minimum ranges or standard deviations, or non-parametric measures (the IQR) as used here. However, we also used an approach that is quantitatively similar to traditional niche breadth metrics, by separating niches along an incremental “binned” axis. Thus, we were able to quantify niche breadths and calculate niche overlaps in a way comparable to other ecological techniques, and results were in broad agreement

to those obtained from descriptive statistics. Given the increasing awareness that trophic niches within species and even within populations are variable, and that this variability has important ecological and evolutionary consequences (Bolnick et al., 2011), further development of non-invasive approaches such as ours that use stable isotope data to fully quantify trophic niche distributions within populations, will be important for exploiting the potential of stable isotope analysis to answer cryptic questions in evolutionary ecology.

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References

- Abu Baker M, Patterson BD, 2011. Patterns in the local assembly of Egyptian rodent faunas: Co-occurrence and nestedness. *J. Arid Environ.* 75: 14–19.
- Abu Baker MA, Brown JS, 2012. Patch use behaviour of *Elephantulus myurus* and *Micaelamys namaquensis*: The role of diet, foraging substrates and escape substrates. *Afr. J. Ecol.* 50: 167–175.
- Ambrose SH, 1991. Effects of diet, climate and physiology on nitrogen isotope abundances in terrestrial foodwebs. *J. Archaeol. Sci.* 18: 293–317.
- Amori G, Luiselli L, 2011. Small mammal community structure in West Africa: A meta-analysis using null models. *Afr. J. Ecol.* 49: 418–430.
- Avenant NL, 2011. The potential utility of rodents and other small mammals as indicators of ecosystem integrity of South African grasslands. *Wildl. Res.* 38: 626–639.
- Baugh AT, West AG, Rickart EA, Cerling TE, Ehleringer JR et al., 2004. Stable isotope ratios ($\delta^{15}\text{N}$ and $\delta^{13}\text{C}$) of syntopic shrews (*Sorex*). *Southwest. Nat.* 49: 493–500.
- Begon M, Townsend CR, Harper JL, 2006. *Ecology: From Individuals to Ecosystems*. 4th edn. Oxford: Blackwell Publishing.
- Bergstrom BJ, 2013. Would East African savanna rodents inhibit woody encroachment? Evidence from stable isotopes and microhistological analysis of feces. *J. Mammal.* 94: 436–447.
- Bolnick DI, Amarasekare P, Araújo MS, Bürger R, Levine JM et al., 2011. Why intraspecific trait variation matters in community ecology. *Trends Ecol. Evol.* 26: 183–192.
- Bowers MA, Brown JH, 1982. Body size and coexistence in desert rodents: Chance or community structure? *Ecology* 63: 391–400.
- Brown JS, Kotler BP, Mitchell WA, 1994. Foraging theory, patch use, and the structure of a Negev Desert granivore community. *Ecology* 75: 2286–2300.
- Caswell H, Reed F, Stephenson SN, Werner PA, 1973. Photosyn-

- thetic pathways and selective herbivory: A hypothesis. *Am. Nat.* 107: 465–479.
- Cerling TE, Harris JM, 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, Brink JS, Rossouw L, Clauss M, 2008. The evolution of ecological specialization in southern African ungulates: Competition or physical environmental turnover? *Oikos* 117: 344–353.
- Codron D, Hull J, Brink JS, Codron J, Ward D et al., 2011. Influence of competition on niche dynamics of syntopic grazing ungulates: Contrasting the predictions of habitat selection models using stable isotope analysis. *Evol. Ecol. Res.* 13: 217–235.
- Codron J, Codron D, Lee-Thorp JA, Sponheimer M, Bond WJ 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.
- Copeland SR, Sponheimer M, de Ruiter DJ, Lee-Thorp JA, Codron D et al., 2011. Strontium isotope evidence for landscape use by early hominins. *Nature* 474: 76–79.
- Crawford K, McDonald RA, Bearhop S, 2008. Applications of stable isotope techniques to the ecology of mammals. *Mammal Rev.* 38: 87–107.
- Dammhahn M, Soarimalala V, Goodman SM, 2013. Trophic niche differentiation and microhabitat utilization in a species-rich montane forest small mammal community of Eastern Madagascar. *Biotropica* 45: 111–118.
- Dearing MD, Mangione AM, Karasov WH, 2000. Diet breadth of mammalian herbivores: Nutrient versus detoxification constraints. *Oecologia* 123: 397–405.
- Delaney ML, 1986. Ecology of small rodents in Africa. *Mammal Rev.* 16: 1–41.
- DeNiro MJ, Epstein S, 1978. Influence of diet on the distribution of Carbon isotopes in animals. *Geochim. Cosmochim. Acta.* 42: 495–506.
- Diamond J, 1986. Evolution of ecological segregation in the New Guinea montane avifauna. In: Diamond J, Case TJ ed. *Community Ecology*. New York: Harper and Row, 99–125.
- Fernández R, García-Tiscar S, Santos MB, López A, Martínez-Cedeira JA et al., 2011. Stable isotope analysis in two sympatric populations of bottlenose dolphins *Tursiops truncatus*: evidence of resource partitioning? *Mar. Biol. (Berl.)* 158: 1043–1055.
- Fox BJ, 2011. Review of small mammal trophic structure in drylands: Resource availability, use, and disturbance. *J. Mammal.* 92: 1179–1192.
- Gordon IJ, Illius AW, 1989. Resource partitioning by ungulates on the Isle of Rhum. *Oecologia* 79: 383–389.
- Hairston NGS, 1989. *Ecological experiments: Purpose, design, and execution*. New York: Cambridge University Press.
- Happold DCD, 2013. *Mammals of Africa. Volume III: Rodents, Hares and Rabbits*. London: Bloomsbury Publishing.
- Hayes JM, 1982. Fractionation et al.: An introduction to isotopic measurements and terminology. *Spectra*. 8: 3–8.
- Hubbell SP, 2001. *The Unified Neutral Theory of Biodiversity and Biogeography*. Princeton: Princeton University Press.
- Hutchinson GE, 1959. Homage to Santa Rosalia, or why are there so many kinds of animals? *Am. Nat.* XCIII (870): 137–145.
- Jackson TP, Spinks AC, 1998. Gut morphology of the Otomyine rodents: An arid-mesic comparison. *S. Afr. J. Zool.* 33: 236–240.
- Kelt DA, Rogovin K, Shenbrot G, Brown JH, 1999. Patterns in the structure of Asian and North American desert small mammal communities. *J. Biogeogr.* 26: 825–841.
- Kimura Y, Jacobs LL, Cerling TE, Uno KT, Ferguson KM et al., 2013. Fossil mice and rats show isotopic evidence of niche partitioning and change in dental ecomorphology related to dietary shift in Late Miocene of Pakistan. *PLoS ONE*. 8: e69308.
- Kinahan AA, Pillay N, 2008. Does differential exploitation of folivory promote coexistence in an African savanna granivorous rodent community? *J. Mammal.* 89: 132–137.
- Levins R, 1968. *Evolution in changing environments*. Princeton: Princeton University Press.
- Lovegrove BG, 2010. The allometry of rodent intestines. *J. Comp. Physiol. B Biochem. Syst. Environ. Physiol.* 180: 741–755.
- Low AB, Rebelo AG, 1996. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria, South Africa: Department of Environmental Affairs and Tourism.
- Luiselli L, 2008. Do lizard communities partition the trophic niche? A worldwide meta-analysis using null models. *Oikos* 117: 321–330.
- MacArthur RH, Levins R, 1967. The limiting similarity, convergence, and divergence of coexisting species. *Am. Nat.* 101: 377–385.
- Mauffrey J-F, Catzefflis F, 2003. Ecological and isotopic discrimination of syntopic rodents in a Neotropical rain forest of French Guiana. *J. Trop. Ecol.* 19: 209–214.
- Morris DW, Clark RG, Boyce MS, 2008. Habitat and habitat selection: Theory, tests, and implications. *Isr. J. Ecol. Evol.* 54: 287–294.
- Newsome SD, Martinez del Rio C, Bearhop S, Phillips DL, 2007. A niche for isotopic ecology. *Front. Ecol. Environ.* 5: 429–436.
- Perrin MR, Curtis BA, 1980. Comparative morphology of the digestive system of 19 species of South African myomorph rodents in relation to diet evolution. *S. Afr. J. Zool.* 15: 22–33.
- Pianka ER, 1986. *Ecology and Natural History of Desert Lizards*. Princeton: Princeton University Press.
- Rautenbach A, Dickerson T, Schoeman MC, 2014. Diversity of rodent and shrew assemblages in different vegetation types of the savannah biome in South Africa: No evidence for nested subsets or competition. *Afr. J. Ecol.* 52: 30–40.
- Rosenzweig ML, 1981. A theory of habitat selection. *Ecology*. 62: 327–335.
- Rowe-Rowe DT, 1986. Stomach contents of small mammals from the Drakensberg, South Africa. *S. Afr. J. Wildl. Res.* 16: 32–35.
- Schoener TW, 1984. Counters to the claims of Walter et al. on the evolutionary significance of competition. *Oikos* 43: 248–251.
- Shenbrot G, Krasnov B, Burdellov S, 2010. Long-term study of population dynamics and habitat selection of rodents in the Negev Desert. *J. Mammal.* 91: 776–786.
- Siegel S, Castellan NJ, 1988. *Nonparametric Statistics for the Behavioral Sciences*. 2nd edn. New York: McGraw-Hill.
- Skinner JD, Smithers RHN, 1990. *The Mammals of the Southern*

- African Subregion. 2nd edn. Pretoria: University of Pretoria.
- Smith FA, Lyons K, Morgan Ernest SK, Jones KE, Kaufman DM et al., 2003. Body mass of Late Quaternary mammals. *Ecology* 84: 3403 (Ecological Archives: E3084–3094).
- Smith VR, Avenant NL, Chown SL, 2002. The diet and impact of house mice on a sub-Antarctic island. *Polar Biol.* 25: 703–715.
- Symes CT, Wilson JW, Woodborne SM, Shaikh ZS, Scantlebury M, 2013. Resource partitioning of sympatric small mammals in an African forest-grassland vegetation mosaic. *Austral Ecol.* 38: 721–729.
- Thompson P, Fox BJ, 1993. Asymmetric competition in Australian heathland rodents: A reciprocal removal experiment demonstrating the influence of size-class structure. *Oikos* 67: 264–278.
- van Oudtshoorn F, 2006. Guide to Grasses of Southern Africa. Pretoria, South Africa: Briza publishing.