Stable isotope analysis of diet confirms niche separation of two sympatric species of Namib Desert lizard

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Abstract

We used stable isotopes of carbon and nitrogen to study the trophic niche of two species of insectivorous lizards, the Husab sand lizard Pedioplanis husabensis and Bradfield’s Namib day gecko living sympatrically in the Namib Desert. We measured the $\delta^{13}$C and $\delta^{15}$N ratios in lizard blood tissues with different turnover times (whole blood, red blood cells and plasma) to investigate lizard diet in different seasons. We also measured the $\delta^{13}$C and $\delta^{15}$N ratios in available arthropod prey and plant tissues on the site, to identify the avenues of nutrient movement between lizards and their prey. Through the use of stable isotope mixing models, we found that the two lizard species relied on a largely non-overlapping but seasonally variable array of arthropods: P. husabensis primarily fed on termites, beetles and wasps, while R. bradfieldi fed mainly on ants, wasps and hemipterans. Nutrients originating from C₃ plants were proportionally higher for R. bradfieldi than for P. husabensis during autumn and late autumn/early winter, although not summer. Contrary to the few available data estimating the trophic transfer of nutrients in ectotherms in mixed C₃ and C₄/crassulacean acid metabolism (CAM) plant landscapes, we found that our lizard species primarily acquired nutrients that originated from C₄/CAM plants. This work adds an important dimension to the general lack of studies using stable isotope analyses to estimate lizard niche partitioning and resource use.

Key words: Namib Desert, niche partitioning, Pedioplanis, Rhoptropus, stable isotopes

Introduction

For all species there exists a particular set of biotic and abiotic conditions that bound their existence, which may be thought of as the species’ niche (Hutchinson 1957). Species niches can be characterized by habitat
requirements, geographical distribution, thermal niches or other dimensions, which may not be independent of each other. Resource use is one niche dimension that is widely studied because the resources that organisms use play an important role in determining species diversity, and may allow different species within a similar feeding guild to coexist in the same habitat (Simberloff & Dayan 1991). Within the same feeding guild, a species may be a resource specialist or a resource generalist (Futuyma & Moreno 1988). Habitats usually will be able to support a greater number of specialist species that consume non-overlapping resources than generalist species that overlap in their resource consumption (Roughgarden 1974). This is due to competitive exclusion, the theory that two similar species are unable to coexist with one another unless there is some level of divergence in how they use resources (Hardin 1960; Pianka 1974). Indeed, a basic premise of community ecology is that the coexistence of otherwise similar species within a feeding guild may be accomplished by the use of distinct resources (MacArthur 1958; Bowers & Brown 1982).

Research on lizard community structure and function has been important for characterizing the concept of the species niche, as well as understanding how different species coexist (e.g., Schoener 1977; Pianka 1986). Arid ecosystems in particular may be ideal places to examine species niche partitioning because in such environments lizard diversity is often high, it can be relatively easy to secure large samples of individual lizards (Pianka 1986), and limited resources have the potential to intensify competition (MacArthur & Levins 1967). For example, despite the low availability of plant resources, the Namib Desert is home to a diverse lizard fauna with high levels of endemism (Robinson & Cunningham 1978; Murray & Schramm 1987; Herrmann & Branch 2013), and, as with other hot deserts, high lizard biomass may represent an important component of the food web in this ecosystem (Pianka 1986). However, few studies to date have examined resource partitioning and trophic dynamics within the Namib lizard fauna (Robinson & Cunningham 1978; Murray & Schramm 1987; Murray et al. 2016).

The use of stable isotopes, particularly carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) stable isotopes, is an effective and minimally invasive way to quantify the spatial and temporal patterns of consumer resource partitioning (Gannes et al. 1997; Boecklen et al. 2011). Because tissue $\delta^{15}N$ increases by approximately 3.0‰, on average, across each trophic level within a food web, $\delta^{15}N$ may be used as an indication of an organism’s trophic level (DeNiro & Epstein 1981; Peterson & Fry 1987). Conversely, tissue $\delta^{13}C$ changes very little (approximately 0–1.0‰), on average, across trophic levels within a food web; consequently, $\delta^{13}C$ may be used to trace carbon sources (DeNiro & Epstein 1978; Peterson & Fry 1987). During photosynthesis plants discriminate against carbon dioxide molecules containing the $^{13}C$ isotope. However, due to differences in the enzymes responsible for carboxylation, plants which use the $C_3$ photosynthetic pathway (e.g., trees and most forbs) have significantly lower $^{13}C$ values compared to plants that use either the $C_4$ (e.g. many grasses) or crassulacean acid metabolism (CAM; many succulents) photosynthetic pathway. These differences lead to $C_3$ plants having a lower $\delta^{13}C$ ratio compared to $C_4$/CAM plants (Ehleringer et al. 1986, 1997). $C_4$ and $C_4$/CAM plants also have important structural differences (e.g. $C_4$ plants are characterized by Kranz anatomy, which includes the presence of thick-walled bundle sheath cells), which influence their nutritional profitability to consumers, and may have distinct growth responses to seasonal patterns of precipitation and climate (Ode et al. 1980; Schulze et al. 1996; Barbehenn et al. 2004a,b; Muldavin et al. 2008). Consequently, ecosystem primary productivity can be divided into distinct resource compartments based on plant photosynthetic pathways.

Importantly, the physiological differences between $C_3$ and $C_4$/CAM plants mean that they are likely to be affected differently under current projections of climate change and enhanced atmospheric CO$_2$ levels (IPCC 2014). For example, higher CO$_2$ levels may improve $C_3$ plant nutrient and water use efficiency, and favor plants with high demands for woody structural tissue, such as trees, compared to herbaceous plants, such as grasses (most of which are $C_4$ in arid regions; Drake et al. 1997; Bond et al. 2003). However, warmer and drier climatic conditions would tend to favor $C_4$/CAM plants (Bond et al. 2003). From a consumer’s perspective these differences matter because many animals selectively forage on either $C_3$, or $C_4$/CAM plants, and the nutritional quality of these plant groups is not the same (Ehleringer et al. 2002; Barbehenn et al. 2004a,b). Furthermore, enhanced CO$_2$ levels may translate into negative consumer effects due to lower plant tissue nitrogen content and higher carbon to nitrogen ratios (Ehleringer et al. 2002).

Here we investigate and compare the resource partitioning of 2 sympatric and similarly-sized species
of insectivorous Namib lizards. The Husab sand lizard, *Pedioplanis husabensis* Berger-Dell’Mour & Mayer, 1989, is a 2.5–3.0-g lacertid lizard endemic to rocky substrates in the west-central Namib Desert between the ephemeral Swakop and Khan Rivers (Berger-Dell’Mour & Mayer 1989). Bradfield’s Namib day gecko, *Rhoptropus bradfieldi* Hewitt, 1935, is a 3.0–4.0-g rock-dwelling diurnal gecko endemic to the Namib Desert (Branch 1998). We examine the trophic niches for each of these lizard species by analyzing the carbon and nitrogen stable isotope ratios in plant tissues, available arthropod prey and lizard tissues. Because *P. husabensis* and *R. bradfieldi* differ in their foraging strategy and habitat use (Murray et al. 2014, 2015), we predict that there will be significant differences between their trophic niches, evidenced by different tissue isotope values.

**Materials and Methods**

**Study site**

Our study site is along the dry Swakop River, Namibia, at Hildenhof, approximately 40 km east of Swakopmund (22°42.049′S, 14°54.890′E; 210 m; see Murray et al. [2014, 2015] for further details) in the Namib Desert. The dry riverbed vegetation is characterized by a riparian woodland consisting of scattered trees and shrubs including *Vachellia erioloba* (camelthorn), *Tamarix usneoides* (tamarisk), *Faidherbia albida* (ana tree), *Euclea pseudebenus* (wild ebony) and *Salvadora persica* (mustard bush), growing in and along the edges of the sandy riverbed (Cowlishaw & Davies 1997). Adjacent to the riverbed are bare rocky slopes sparsely-covered with small shrubs such as *Arthraeriuia leubnitziae* (pencil bush) and *Sesuvium sesuvoides* (desert pink). A narrow zone of more densely-spaced shrubs such as *Zygophyllum stapfii* (dollar bush), *Lycium* sp. and *Salsola* sp. (salt bush) is situated on the silty substrates where the rocky slopes meet the river channel. Perennial grasses make up a small proportion of plant cover and generally are restricted to the edges of the river channel (I. Murray, personal observation). The study site is in a hyper-arid system with mean annual precipitation of approximately 25 mm, and 25–50 fog days per year may be expected based on data from other similar sites (Olivier 1995; Haensler et al. 2011; Eckardt et al. 2013). After sporadic precipitation events, such as one during April 2013, annual grasses such as *Stipagrostis* sp. were also evident.

**Lizard tissue collection**

We captured lizards during austral summer (December 2012–January 2013) and austral autumn (May 2013) using noose poles. We took blood samples (approximately 50 μL) from the infraorbital sinus with heparinized capillary tubes before releasing the lizards unharmed (Murray et al. 2014). All procedures were approved by the University of the Witwatersrand’s Animal Ethics Screening Committee (clearance certificate number 2012/50/03) and were in accordance with the Namibian Ministry of Environment and Tourism Research/Collecting Permit 1744/2012.

We collected whole blood from adult lizards of both species between December 2012 and January 2013 (austral summer), and in May 2013 (austral autumn/early winter). Blood was sampled from 21 male and 5 female *P. husabensis* and 13 male and 8 female *R. bradfieldi* during austral summer, and 17 male and 26 female *P. husabensis* and 7 male and 11 female *R. bradfieldi* in austral autumn.

We centrifuged the blood samples collected in autumn to separate out the plasma and red blood cells (RBC). Plasma was not available for the blood that we collected during summer because we used the plasma water for the determination of field metabolic rates (Murray et al. 2014, 2015). We air-dried RBC and loaded approximately 0.4 mg of RBC and dried whole blood into 4 × 6-mm tin cups (Costech Analytical Technologies, California, USA; #041070). In addition, we pipetted approximately 15 μL of plasma into 4 × 6-mm tin cups immediately after centrifuging and air-dried the samples before folding the tin cups for analysis. We did not extract lipids from the blood samples because blood contains too little lipid to confound analyses (Bearhop et al. 2000). Due to small blood volumes, several of the *R. bradfieldi* samples did not yield large enough nitrogen peaks to be analyzed by isotope ratio mass spectrometry, resulting in fewer nitrogen isotope ratios being reported than carbon ratios. For several additional samples we did not have sufficient RBC sample masses to run either carbon or nitrogen. We lost several plasma samples in the mass spectrometer.

In small insectivorous lizards, plasma has a carbon retention time (the average amount of time a carbon atom is retained in tissue and a means to estimate tissue-specific turnover times; Martínez del Rio & Anderson-Sprecher 2008) of 25 days while RBC have a carbon retention time of 61 days (Warne et al. 2010b). Because
plasma and RBC have different biological turnover rates, their isotope ratios reflect dietary history over both short (plasma) and long (RBC) periods (Boecklen et al. 2011). Consequently, plasma from blood collected in May reflected diet in late autumn/early winter, and RBC from blood collected in May reflected diet during autumn. Although plasma was unavailable for blood collected in summer, the use of whole blood is well established in the published literature (e.g. Boecklen et al. 2011) for estimating diet. The carbon retention time for whole blood is unknown for lizards, but because it is likely to have a retention time between that of plasma (25 days) and RBC (61 days), with RBC largely driving whole blood carbon retention times (Flaherty et al. 2010; Warne et al. 2010b), we can confidently make the assumption that isotope ratios in whole blood collected in summer reflect early summer diet.

**Characterization of plant and arthropod resources**

We collected tissue from 30 plant species on the site during May 2013, which represented a majority of the species growing during our lizard sampling activity. We sampled multiple leaves and stems from 3 to 5 randomly selected plants of each species and stored them in paper envelopes. The plant tissues were dried in an oven at 55°C and samples were homogenized with a clean mortar and pestle to create a homogenate for each species. We analyzed the carbon and nitrogen stable isotope ratios for each species using aliquots (approximately 1 mg) of the dried homogenate.

We sampled arthropods from areas where lizards were active and foraging during May 2013 by walking through the habitat and hand capturing arthropods (beetles, ants, termites and spiders) and sweeping vegetation with a net (flies, bees, wasps, true bugs, as well as some beetles and spiders). We made a concerted effort to sample ants and termites (identified as key components of lizard diet; Murray et al. 2016) in the same microhabitats where we saw lizards. Arthropods were kept cool (approximately 15°C) in vials for 1–3 days, a period in which we assumed that all gut contents were metabolized, and then frozen (approximately −4°C) for storage. We acknowledge the potential difficulties involved with inferring lizard consumption of arthropods in summer based on the tissue isotope ratios of arthropods collected during late autumn/early winter. However, for the primary prey items that lizards feed on, such as termites and ants, the long periods of time required for growth and development means that any diet switches in those arthropods could take several months to be reflected in the arthropod tissue isotope ratios (termites [Watson 1973]; ants [Mooney & Tillberg 2005; Straka & Feldhaar 2007; Menke et al. 2010]). We identified arthropods to the species level where possible, and otherwise to the order, family or genus level, using references for southern African arthropods (Scholtz & Holm 1985; Marsh 1986; Uys 2002; Picker et al. 2004). As with plant samples, we dried arthropods in an oven and homogenized individuals before loading them in 4 × 6-mm tin capsules.

**Stable isotope analyses**

We analyzed all of our tissue samples for carbon (δ13C) and nitrogen (δ15N) stable isotope ratios using a continuous flow isotope ratio mass spectrometer (Delta V Plus, ThermoFinnigan, Bremen, Germany) connected to an Elemental Analyzer (Flash EA 1112 series, ThermoFinnigan, Bremen, Germany) in the University of Pretoria Isotope Ratio Mass Spectrometry Laboratory. The instrumental precision of these measurements was ± 0.1‰ SD based on repeated measurements of internal laboratory standards. All sample runs included a laboratory standard (Merck Gel δ13C = −20.57‰; δ15N = 6.8‰) and blank after each set of 12 unknowns. Isotope concentrations are reported in delta notation (δ) in parts per thousand (%): δX = (Rsample/Rstandard − 1) * 1000. Rsample and Rstandard represent the ratio of heavy to light isotopes (13C/12C or 15N/14N) for the sample and standard. The results are normalized to the international standards air for δ15N and Vienna Pee Dee Belemnite for δ13C.

When carbon and nitrogen stable isotope ratios in consumer tissue are analyzed, there is often an offset between the diet and the tissue termed the diet-to-tissue discrimination factor (Δ). Diet-to-tissue discrimination factors may significantly differ according to diet quality, growth rates, tissue or species (Caut et al. 2008; Caut et al. 2009; Boecklen et al. 2011). Determining discrimination factors requires time and labor-intensive feeding trials, which have not been carried out for all species (Gannes et al. 1997; Martinez del Rio & Carleton 2012). Consequently, we used the mean Δδ13C (0.4‰; 91 studies) and the mean Δδ15N (2.3‰, 65 studies) determined for poikilotherm tissue diet-to-tissue discrimination factors during controlled feeding trials to adjust our lizard tissue δ13C and δ15N values (McCutchan et al. 2003). We assumed that all lizard tissues analyzed would have similar discrimination factors.

**Data analyses: Tissue stable isotope ratios**
We tested for sex-related differences in tissue stable isotope ratios for both species using 2-sample t-tests. Plasma and RBC samples from individual lizards are not independent, so we used repeated measures linear mixed effects models to compare the carbon and nitrogen isotope ratios between species across seasons. We used an unstructured repeated covariance type, and modeled species, season and the species*season interaction as fixed effects and individual lizard as a random effect. We conducted post hoc comparisons using a Bonferroni correction. We used 2-sample t-tests to compare the seasonal incorporation of arthropods feeding on C₄/CAM plant resources by the two lizard species.

Data analyses: Isotopic niche metrics

To compare seasonal changes in lizard dietary niches (using different tissues to estimate seasonal dietary changes), we used the Stable Isotope Bayesian Ellipses in R (SIBER) package to calculate the standard ellipse area corrected for small sample sizes (SEAₐ) as well as the area of overlap for the summer, autumn and late autumn/early winter dietary niches (Jackson et al. 2011). SEAₐ is a proxy for the trophic niche, and is the bivariate standard deviation of the stable isotope ratios (e.g. carbon and nitrogen) characterizing a group of consumers; SEAₐ thus represents the core isotopic niche for each lizard species. We also describe the area of the convex hull (TA), and the associated Layman niche metrics estimating additional measurements of species niche structure calculated using the package Stable Isotope Analyses in R (SIAR), for comparative purposes. The TA (the smallest surface that encompasses all of the carbon and nitrogen stable isotope ratios for individuals of a species in a bivariate plot) is a geometric approach that may be used to estimate consumer dietary niche breadth, although TA is more sensitive to sample size than SEAₐ, and fails to take into account uncertainty within a dataset (Layman et al. 2007; Parnell et al. 2010; Jackson et al. 2011). Layman niche metrics further characterize diet spacing patterns between individuals in a population, and include the mean distance to centroid (CD), the mean nearest neighbor distance (MNND) and the standard deviation of the mean nearest neighbor distance (SDNND; Layman et al. 2007). For example, high values of MNND would indicate a more diverse trophic niche, while high SDNND indicates a high degree of unevenness in the spacing of the individual lizards in bivariate isotopic space (Layman et al. 2007).

Data analyses: Mixing models

We estimated the extent to which lizards used arthropods dependent on C₄/CAM versus C₃ plant resources with a 2-end point mixing model (Martinez del Rio & Wolf 2005):

\[
\delta^{13}C_{\text{tissue}} = p(\delta^{13}C_{\text{C₄/CAM}}) + (1-p)(\delta^{13}C_{\text{C₃}}) + \Delta;
\]

where “tissue” is either lizard plasma, whole blood or RBC; \(p\) is the fraction of C₄/CAM plant resources assimilated in lizard tissue; and \(D\) is the carbon discrimination factor (0.4‰, McCutchan et al. 2003). The subscripts “C₃” and “C₄/CAM” represent the carbon isotope ratios of C₃ and C₄/CAM plant photosynthetic pathways, respectively.

We estimated the proportional contribution of arthropod prey groups to lizard tissues using the Bayesian Stable Isotope Sourcing Using Sampling (SISUS; Erhardt & Bedrick 2013) software which provides a significant advantage over other stable isotope mixing models because SISUS allows for the variability of stable isotope ratios in diet categories, as well as accounts for uncertainty in stable isotope discrimination factors (Erhardt & Bedrick 2013). We identified potential prey based on those groups that we have found previously in lizard fecal pellets (Murray et al. 2016). We used SigmaPlot 8.0 (Systat Software, San Jose, CA, USA), Microsoft Excel 2007 (Microsoft, Redmond, WA, USA), IBM SPSS 21.0 (SPSS, Chicago, IL, USA) and R 2.15.2 (R Development Core Team 2009) for all analyses. For all analyses, significance was accepted at \(P < 0.05\) and values are reported as mean ± SD.

Results

C₃ plants and C₄/CAM plants growing on the site had non-overlapping carbon isotope ratios, a critical observation allowing the sources of the nutrients assimilated by insectivorous lizards to be traced back to the plant functional groups consumed by their prey (Fig. 1). Mean carbon isotope ratios were \(-26.2\% ± 0.4\%\) (range, \(-30.3\%\) to \(-23.7\%\); \(n = 16\) species) in C₃ plant tissues and \(-14.5\% ± 0.3\%\) (range, \(-16.4\%\) to \(-13.0\%\); \(n = 14\) species) in C₄/CAM plant tissues. Plant tissue nitrogen ratios were 12.0% ± 1.0% in C₃ plants (range, 7.4‰ to 18.4‰) and 10.4‰ ± 0.9‰ in C₄/CAM plants (range, 6.8‰ to 19.3‰).
**Figure 1** Mean (± SD) δ¹⁵N and δ¹³C ratios for seasonal diet as estimated from plasma (late autumn/early winter), whole blood (WB; summer) and RBC (autumn) from the Husab sand lizard (Pehu, *Pedioplanis husabensis*) and Bradfield’s Namib day gecko (Rhbr, *Rhoptropus bradfieldi*). Blood tissue carbon and nitrogen isotope ratios are plotted relative to the δ¹⁵N and δ¹³C tissue values for individual species of plants belonging to different functional groups (30 species; C₃ shrubs/trees, C₄ grasses, C₄ shrubs and crassulacean acid metabolism [CAM] succulents) available on the site. Lizard blood tissue δ¹⁵N (2.3‰) and δ¹³C (0.4‰) ratios have been adjusted by subtracting the appropriate diet-tissue-discrimination factors determined for poikilotherms (McCutchan *et al.* 2003).

**Table 1** Mean (± SD) δ¹⁵N and δ¹³C ratios of potential prey items collected during May 2013 for the Husab sand lizard (*Pedioplanis husabensis*) and Bradfield’s Namib day gecko (*Rhoptropus bradfieldi*) along the dry Swakop River bed in the Namib Desert, Namibia

<table>
<thead>
<tr>
<th>Prey category</th>
<th>n</th>
<th>Mean δ¹³C (‰)</th>
<th>Mean δ¹⁵N (‰)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>12</td>
<td>−17.9 ± 2.3</td>
<td>18.3 ± 2.4</td>
</tr>
<tr>
<td>Insecta</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Psammodes/Physosterna/Zophosis/Scarabidae (beetles1)</td>
<td>14</td>
<td>−14.9 ± 1.9</td>
<td>17.2 ± 3.8</td>
</tr>
<tr>
<td>Somaticus/Gonocephalum/Stenocara (beetles2)</td>
<td>19</td>
<td>−20.1 ± 3.2</td>
<td>15.2 ± 3.4</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>2</td>
<td>−21.9 ± 0.9</td>
<td>13.4 ± 3.3</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ants</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lepisiota capensis</td>
<td>4</td>
<td>−19.5 ± 2.2</td>
<td>16.7 ± 1.6</td>
</tr>
<tr>
<td>Pheidole sp.</td>
<td>3</td>
<td>−15.3 ± 0.3</td>
<td>14.9 ± 0.1</td>
</tr>
<tr>
<td>Camponotus sp.</td>
<td>2</td>
<td>−13.3 ± 0.3</td>
<td>14.5 ± 1.5</td>
</tr>
<tr>
<td>Bees</td>
<td>4</td>
<td>−17.8 ± 4.6</td>
<td>14.8 ± 3.9</td>
</tr>
<tr>
<td>Wasps</td>
<td>3</td>
<td>−18.7 ± 5.0</td>
<td>8.8 ± 3.6</td>
</tr>
<tr>
<td>Isoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trinervitermes sp.</td>
<td>6</td>
<td>−17.1 ± 0.3</td>
<td>5.8 ± 0.2</td>
</tr>
<tr>
<td>Hodotermes mossambicus</td>
<td>8</td>
<td>−18.6 ± 0.5</td>
<td>7.3 ± 0.6</td>
</tr>
<tr>
<td>Psammotermes allocerus/Amitermes sp.</td>
<td>16</td>
<td>−16.1 ± 0.8</td>
<td>11.8 ± 1.0</td>
</tr>
</tbody>
</table>

Based on similar tissue isotope ratios the beetle genera *Somaticus, Gonocephalum* and *Stenocara* were combined into the category “beetles2,” and the genera *Psammodes, Physosterna, Zophosis* and *Scarabidae* were combined into the category “beetles1.” Sample sizes (n) indicate the numbers of individuals sampled with the exception of the small ant *Lepisiota capensis* in which case each sample was a homogenate of 4 individual ants from a single nest.
The potential arthropod prey groups of lizards occupied largely non-overlapping domains in carbon and nitrogen isotope niche space (Table 1). For example, mean δ13C ranged from −21.9‰ ± 0.9‰ in hemipteran insects to −13.3‰ ± 0.3‰ in ants in the genus Camponotus (Table 1). Arthropod prey groups also occupied a diversity of trophic levels, as evidenced by their tissue δ15N, which ranged from 18.3‰ ± 2.4‰ in spiders to 5.8‰ ± 0.2‰ in termites of the genus Trinervitermes. There also was significant variation in tissue nitrogen and carbon isotope ratios for different arthropod genera within the same order, apparent, for example, in the distinct and non-overlapping δ13C and δ15N ratios for genera of termites and ants (Table 1). The distinct isotope ratios of the lizards’ potential prey allowed unambiguous identification of their diets.

There were no sex-related differences in blood carbon and nitrogen isotope ratios for both P. husabensis (RBC δ15N, t41 = −0.22; P = 0.829; RBC δ13C, t41 = −0.55; P = 0.582; plasma δ15N, t21 = 0.32; P = 0.752; plasma δ13C, t21 = 0.49; P = 0.631; whole blood δ15N, t5 = 1.98; P = 0.105; whole blood δ13C, t6 = 1.39; P = 0.215) and R. bradfieldi (RBC δ15N, t13 = −0.01; P = 0.996; RBC δ13C, t14 = −1.89; P = 0.08; plasma δ15N, t7 = −1.63; P = 0.148; plasma δ13C, t16 = 0.10; P = 0.920; whole blood δ15N, t18 = −0.3; P = 0.767; whole blood δ13C, t20 = −1.25; P = 0.238), so we combined male and female values for both species (Table 2). On average blood δ15N did not differ between lizard species (F1,82.091 = 0.009; P = 0.925), but there was a significant difference between seasons (F2,67.392 = 21.170; P = 0.000) with the δ15N ratio reflecting the late autumn/early winter dietary niche (plasma) significantly higher than those reflecting autumn (RBC) but not summer (whole blood) dietary niches. The interaction between species and season also was significant (F2,67.392 = 6.554; P = 0.003; Table 2). Across seasons the tissue δ15N ratios increased similarly for P. husabensis, while for R. bradfieldi the δ15N ratios were similar in summer and late autumn/early winter but declined in the autumn dietary niche (Table 2).

Table 2 Mean (± SD) δ15N and δ13C ratios for austral summer dietary niches (November–January as estimated from whole blood), autumn dietary niches (March–May as estimated from red blood cells), and late autumn/early winter dietary niches (April–May, as estimated from plasma) for the Husab sand lizard (Pedioplanis husabensis) and Bradfield’s Namib day gecko (Rhoptropus bradfieldi).

<table>
<thead>
<tr>
<th>Isotope ratio</th>
<th>Summer</th>
<th>Autumn</th>
<th>Late autumn/early winter</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Pedioplanis husabensis</td>
<td>Rhoptropus bradfieldi</td>
<td>Pedioplanis husabensis</td>
</tr>
<tr>
<td>Mean δ13C (%)</td>
<td>−17.0 ± 1.2 (n = 27)</td>
<td>−16.7 ± 1.5 (n = 21)</td>
<td>−16.0 ± 0.7 (n = 43)</td>
</tr>
<tr>
<td>Mean δ15N (%)</td>
<td>10.8 ± 2.7 (n = 26)</td>
<td>13.0 ± 1.0* (n = 21)</td>
<td>12.2 ± 2.7 (n = 43)</td>
</tr>
</tbody>
</table>

Sample sizes (n) indicate the number of individual lizards from which samples were analyzed. *Significant inter-species difference (95% confidence interval estimates; P < 0.05).
Blood $\delta^{13}C$ ratios were on average significantly lower in *R. bradfieldi* than in *P. husabensis* ($F_{1,103.760} = 21.494; P < 0.001$). In addition, $\delta^{13}C$ ratios reflecting late autumn/early winter diet (plasma) were significantly lower than the $\delta^{13}C$ ratios reflecting both autumn (RBC) and summer (whole blood) diet ($F_{2,60.412} = 161.763; P < 0.001$). The interaction between species and season again was significant ($F_{2,60.412} = 23.812; P < 0.001$; Table 2). For *P. husabensis*, tissue $\delta^{13}C$ ratios reflecting both the summer and late autumn/early winter dietary niches were lower than those reflecting the autumn dietary niche (Table 2). In *R. bradfieldi* the $\delta^{13}C$ ratios remained the same for both the summer and autumn dietary niches, but were significantly lower for the late autumn/early winter dietary niche (Table 2).

In addition to the species differences in seasonal dietary niches, *P. husabensis* assimilated significantly more nutrients from arthropods that fed primarily upon C$_4$ or CAM plants than *R. bradfieldi* during autumn (2 sample $t$-test; $t_{50} = 3.91; P = 0.000$) and late autumn/early winter (2 sample $t$-test; $t_{60} = 8.78; P = 0.000$) but not summer (2 sample $t$-test; $t_{60} = -1.30; P = 0.201$; Fig. 2). During summer *R. bradfieldi* and *P. husabensis* both derived approximately 75% of their diet from arthropods that consumed C$_4$/CAM plants. However, compared to *P. husabensis*, during autumn and late autumn/early winter *R. bradfieldi* sourced 10–20% fewer resources from arthropods feeding on C$_4$/CAM plants (Fig. 2).

More evidence for the significant differences in the isotopic niches between *R. bradfieldi* and *P. husabensis* was that both the SEA, and TA of *P. husabensis*’s dietary niche were larger than those of *R. bradfieldi* across all seasons (Table 3, Fig. 3). During the summer and late autumn/early winter, the dietary niche for *R. bradfieldi* was more than twice that for *P. husabensis* than for *R. bradfieldi*, while during autumn *P. husabensis*’s dietary niche was only slightly greater than that of *R. bradfieldi* (Table 3). There was also considerable seasonal overlap in the summer, autumn and late autumn/early winter SEAs for *P. husabensis*, while the dietary niche for *R. bradfieldi* was spatially distinct across these seasons (Fig. 3). The niches of the two species overlapped in summer such that the area of that overlap occupied approximately half of the total niche area in *R. bradfieldi*, but only one-fifth of *P. husabensis*’s summer niche area (Table 3). During autumn, the overlap in the lizards’ dietary niches took up a similar proportion of the total area of the autumn dietary niche in both species (Table 3). However, during late autumn/early winter there was almost no overlap in the dietary niches of *R. bradfieldi* and *P. husabensis* (Table 3). Furthermore, in all seasons the CD was greater for *P. husabensis* relative to *R. bradfieldi*, while the MNND and SDNND were either similar in size or greater for *R. bradfieldi* compared to *P. husabensis* (Table 3).

Analysis of the whole blood isotope ratios indicated that the summer diet of *P. husabensis* was 63% termites,
Table 3 Calculated niche metrics based on the $\delta^{15}$N and $\delta^{13}$C ratios during austral summer as estimated from whole blood, austral autumn as estimated from red blood cells and austral late autumn/early winter as estimated from plasma in the Husab sand lizard (*Pedioplanis husabensis*) and Bradfield’s Namib day gecko (*Rhoptropus bradfieldi*).

<table>
<thead>
<tr>
<th>Niche metric</th>
<th>Summer</th>
<th>Autumn</th>
<th>Late autumn/Early winter</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pedioplanis husabensis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhoptropus bradfieldi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Standard ellipse area</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>SEAc</td>
<td>10.4</td>
<td>4.0</td>
<td>5.8</td>
</tr>
<tr>
<td>Area of overlap</td>
<td>2.3</td>
<td>2.0</td>
<td>0</td>
</tr>
<tr>
<td>Layman niche metrics</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>TA</td>
<td>27.0</td>
<td>12.1</td>
<td>21.7</td>
</tr>
<tr>
<td>CD</td>
<td>2.6</td>
<td>1.5</td>
<td>2.4</td>
</tr>
<tr>
<td>MNND</td>
<td>0.73</td>
<td>0.63</td>
<td>0.44</td>
</tr>
<tr>
<td>SDNND</td>
<td>0.43</td>
<td>0.54</td>
<td>0.29</td>
</tr>
</tbody>
</table>

Niche metrics are based on standard ellipse areas corrected for small sample sizes (SEA,) and the inter-species overlap between seasonal SEA, as well as the Layman niche metrics area of the convex hull (TA), distance to centroid (CD), mean nearest neighbor distance (MNND), and the standard deviation of the mean nearest neighbor distance (SDNND).

Table 4 The relative contribution of arthropod prey groups to the diet of sympatric Bradfield’s Namib day geckos (*Rhoptropus bradfieldi*) and Husab sand lizards (*Pedioplanis husabensis*), as calculated (mean ± SD) by the software Stable Isotope Sourcing Using Sampling (SISUS) using carbon and nitrogen isotopes.

<table>
<thead>
<tr>
<th>Prey category</th>
<th>Summer diet</th>
<th>Autumn diet</th>
<th>Late autumn/early winter diet</th>
</tr>
</thead>
<tbody>
<tr>
<td>Pedioplanis husabensis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Rhoptropus bradfieldi</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Arachnida</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Araneae</td>
<td>0.05 ± 0.04</td>
<td>0.04 ± 0.03</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>Coleoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Psammodes/Physosterna/Zophosis/Scarabidae (beetles1)</td>
<td>0.15 ± 0.08</td>
<td>0.07 ± 0.06</td>
<td>0.44 ± 0.07</td>
</tr>
<tr>
<td>Somaticus/Gonocephalum/Stenocara (beetles2)</td>
<td>0.08 ± 0.06</td>
<td>—</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>Hemiptera</td>
<td>—</td>
<td>0.05 ± 0.04</td>
<td>—</td>
</tr>
<tr>
<td>Hymenoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ants</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Camponotus sp.</td>
<td>—</td>
<td>0.21 ± 0.10</td>
<td>—</td>
</tr>
<tr>
<td>Pheidole sp.</td>
<td>—</td>
<td>0.13 ± 0.10</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>Lepisiota capensis</td>
<td>—</td>
<td>0.04 ± 0.03</td>
<td>—</td>
</tr>
<tr>
<td>Bees</td>
<td>0.06 ± 0.05</td>
<td>0.07 ± 0.06</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>Wasps</td>
<td>0.08 ± 0.06</td>
<td>0.35 ± 0.04</td>
<td>0.01 ± 0.01</td>
</tr>
<tr>
<td>Isoptera</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Trinervitermes sp.</td>
<td>0.29 ± 0.10</td>
<td>—</td>
<td>0.32 ± 0.07</td>
</tr>
<tr>
<td>Psammotermes allocerus/Amitermes sp.</td>
<td>0.25 ± 0.16</td>
<td>—</td>
<td>0.18 ± 0.16</td>
</tr>
<tr>
<td>Hodotermes mossambicus</td>
<td>0.09 ± 0.07</td>
<td>—</td>
<td>0.02 ± 0.01</td>
</tr>
</tbody>
</table>

—, not included in the diet, based upon prior gut content analyses (Murray et al. 2016).
wasps, 17% ants and 7% bees) but with considerable contributions from hemipterans (40%) and a low proportion of spiders and beetles (Table 4).

Discussion

The insectivorous lizards *P. husabensis* and *R. bradfieldi* occurred within an isotopically-diverse landscape of C₃ and C₄/CAM plants (Fig. 1), and, consequently, had an isotopically-distinct prey base of arthropods available to them (Table 1). That isotopic diversity allowed us to assess changes in lizard resource use over time. There was considerable variation between the two species in arthropod resource use (Fig. 3, Table 4). Although both lizard species showed some degree of seasonal variation in arthropod prey use, the dietary composition of the two lizard species did not overlap in its major constituents (Table 4). *P. husabensis* fed predominantly on termites and beetles, while *R. bradfieldi* fed predominantly on ants, wasps and hemipteran insects. Furthermore, despite the presence of considerable C₃ plant biomass in their immediate habitat, these two insectivorous lizard species showed a preference for arthropods dependent on C₄/CAM plants (Fig. 2).

Overall, the δ¹⁵N ratios for lizard tissues were similar, implying that *R. bradfieldi* and *P. husabensis* fed at the same trophic level, although the lower δ¹⁵N ratios for *P. husabensis* in summer may reflect its high consumption of termites with their relatively low tissue δ¹⁵N ratios at this time of year. However, when we examined δ¹⁵N values in conjunction with δ¹³C values seasonally, we found notable differences between *P. husabensis*’s and *R. bradfieldi*’s dietary niche (Table 2). For example, *P. husabensis* always had a larger dietary niche (TA and SEAₐ) than did *R. bradfieldi* occupying the same habitat (Fig. 3; Table 3). Depending on the season, the TA of *P. husabensis* was 2.2–3.1 times larger than the corresponding TA in *R. bradfieldi*. The TA incorporates data from all individuals, including outliers that may be critical to capturing the population’s or species’ complete trophic spectrum (Layman *et al.* 2012); however, it is a metric that is sensitive to sample size (Jackson *et al.* 2011), and we sampled fewer *R. bradfieldi* than *P. husabensis* (Table 2). The SEAₐ is a metric which characterizes the niche far more robustly given a limited sample size, and the SEAₐ results echoed those yielded from the TA analysis: SEAₐ for *P. husabensis* was 1.3–2.6 times larger than that of *R. bradfieldi* (Table 3). In addition to having a larger isotopic niche, there was a higher degree of trophic diversity among individual *P. husabensis* relative to *R. bradfieldi*, as evidenced by the higher CD (Table 3), but the higher SDNND and MNND for *R. bradfieldi* in autumn and late autumn/early winter indicated that individuals of this species had less redundancy in the trophic niche than did individuals of *P. husabensis* (Layman *et al.* 2007; Table 3). These niche differences reflect the consumption of distinct arthropod prey items and probably result from differences in foraging strategies between the two lizard species.

*Pedioplanis husabensis* uses an active foraging strategy and moves widely through its habitat (Murray *et al.* 2014). In contrast, *R. bradfieldi* uses a sit-and-wait foraging strategy in which it ambushes its prey from an immobile and exposed position (Murray *et al.* 2015). Relative to sit-and-wait foraging lizards, actively-foraging lizards are likely to have larger territories and move over greater distances through a diversity of habitats (Pianka 1986; Vitt *et al.* 2003). While we lack data on home range size and the spatial length of daily movements in *P. husabensis* and *R. bradfieldi*, data from other communities of insectivorous desert lizards indicate that the hourly distances moved by active foraging lizards are 4 to 4.5 times the distances (Anderson & Karasov 1981; Huey & Pianka 1981) and the home ranges 4 times larger (Anderson & Karasov 1981) than those of sympatric sit-and-wait foraging lizards. As lizards forage over greater distances they are likely to encounter a greater degree of habitat heterogeneity. Because landscape heterogeneity is positively correlated with arthropod diversity (Liu *et al.* 2013), it is likely that more widely foraging lizards may come into contact with a more diverse assortment of prey and, thus, have a larger trophic niche, as we found for *P. husabensis*. Because actively-foraging lizards use visual and chemosensory means to locate prey above and below ground, they are also capable of feeding on a greater array of potential prey, such as subterranean insect larvae and immobile insect pupae that are not available to sit-and-wait foraging lizards (Pianka 1986; Vitt *et al.* 2003). Therefore, the consequences of foraging actively may contribute to the larger trophic niche of *P. husabensis*.

Compared to *P. husabensis*, the variable and non-overlapping seasonal SEAₐs for *R. bradfieldi* may be related to a sit-and-wait predator foraging opportunistically during a particular time of year (Fig. 3). The reduced trophic redundancy and increased “unevenness” characterizing *R. bradfieldi* in isotopic
space during autumn and late autumn/early winter (high MNND and SDNND; Table 3) implies that *R. bradfieldi* show a less uniform pattern of resource use. This pattern could be due to individual geckos encountering a relatively heterogeneous variety of arthropods during sit-and-wait foraging bouts. In contrast, individuals of the actively-foraging *P. husabensis* can target distinct prey resources, specifically making its dietary niche more uniform. We acknowledge that we cannot be sure that the isotopically-distinct SEA found seasonally for *R. bradfieldi* are the result of the inclusion of different types of arthropod prey in the diet; the diets of the arthropods themselves may have varied seasonally, and we did not collect arthropod samples during summer. Further data collection would be required to better address this question.

From the perspective of individual consumers, the relative importance of the C3 versus C4 components of plant primary productivity varies by species, season and habitat (Magnusson et al. 1999; Warne et al. 2010a). In addition, C4 plant production represents an important component of food web nutrients, particularly in arid ecosystems (Ehleringer et al. 1997; Still et al. 2003). There are relatively few studies estimating the transfer of C3 versus C4-derived nutrients to higher-level consumers, such as lizards in a nutritional landscape containing both C3 and C4 plants (Magnusson et al. 1999, 2001; Warne et al. 2010a). However, the available data indicate that lizards continue to acquire considerable amounts of nutrients from prey that feed on C3 plant resources even when appreciable proportions of total primary productivity stem from C4 plants (Magnusson et al. 1999, 2001; Smith et al. 2002; Warne et al. 2010a). However, contrary to other published studies, our lizards included a large proportion of arthropods that consumed resources derived from C4 CAM plants.

While we cannot distinguish between the carbon isotope ratios of C4 and CAM plants on our study site, CAM plants were a minor component of the landscape and were represented chiefly by scattered and isolated succulents, while perennial and annual C4 grasses and the C4 shrub *Salsola* sp. were conspicuous and regular components of the landscape (I Murray, personal observation). Some Namib Desert plants are capable of facultatively switching between C3 and CAM photosynthesis depending on water stress (e.g. Winter et al. 1978), and insect use of these resources could lead to a misinterpretation of insectivore use of plant resources based on tissue stable isotope ratios. However, these plants were relatively minor components of the local flora (e.g. *Mesembryanthemum guericheanum*; represented by several widely scattered small individuals). Consequently, an enriched carbon isotope ratio in insectivores here is likely to represent significant use of C4 plants.

*Pedioplanis husabensis* obtained more than 70% of its nutrients from arthropods that sourced most of their carbon from C4 plants in all seasons that we studied, as did *R. bradfieldi* in summer and autumn. During late autumn/early winter, however, *R. bradfieldi* preyed almost equally on arthropods dependent on C4 plants (Fig. 2). For *P. husabensis*, we believe that its consumption of termites brought about its tight linkage to C4 plants. The termite genera that it fed upon are known to feed largely on C4 grasses (e.g. *Hodotermes, Psammotermes* and *Trinervitermes*; De Visser et al. 2008; Symes & Woodborne 2011), and our carbon isotope analyses of individual termites supported this assertion (Table 1). However, we are unable to distinguish isotopically between termites feeding on C4 grasses and on woody C4 shrubs such *Salsola* sp. that occurred on the site, which means that the importance of C4 grasses to the arthropods making up *P. husabensis*’s dietary niche may be overestimated. In an entirely different system, consumption of termites also was considered to underlie flow of C4 grass-derived nutrients into lizard and frog tissues (Magnusson et al. 1999, 2001).

Compared to *P. husabensis*, *R. bradfieldi* fed to a greater extent on arthropods that used C3 plant biomass (Figs. 2 and 3). During late autumn/early winter in particular, *R. bradfieldi* acquired nutrients from arthropods that used significantly more C3 plant-derived resources than did *P. husabensis*, incorporating up to 54% of its carbon from C3 plant resources (Fig. 2). We surmise that the late autumn/early winter dietary niche of *R. bradfieldi* reflected incorporation of arthropods using C3 plant production available after recent precipitation (Noy-Meir 1973, 1974; Polis 1997). As a sit-and-wait forager *R. bradfieldi* is likely to feed largely on more mobile arthropods that are active during its diurnal activity period (Pianka 1986). Indeed, the SISUS mixing model results showed its diet to be made up of mobile and diurnally-active insects like ants, wasps and hemipterans (Table 4). The ecology of these arthropod groups also enables them to transfer this C3 plant biomass to *R. bradfieldi* effectively. For example,
hemipterans make up a large part of the total available arthropod biomass after rare desert precipitation events (Polis 1991), and many small wasps feed on C3 flower pollen or are predators on insects that feed on C1 plant production (Scholtz & Holm 1985; Picker et al. 2004).

Our previous work documenting the diet of P. husabensis and R. bradfieldi during May of 2013 using fecal pellet analyses generally supports our estimates of diet composition based on the SISUS mixing model results (Murray et al. 2016). These fecal pellet analyses showed that the diet of P. husabensis was dominated numerically by termites (71%) and that of R. bradfieldi by ants (87%; Murray et al. 2016). However, we note that the mixing model results and the fecal pellet analyses do not align perfectly such that, in some seasons, P. husabensis and R. bradfieldi incorporated fewer nutrients from termites and ants than the fecal pellet analysis implied (Table 4). These contrasting results are perhaps not surprising given the very short periods over which fecal pellet analyses survey diet (days) relative to the period over which the mixing model results based on body tissues do (1–2 months), as well as the fact that the fecal pellet diet analyses estimated prey items and not proportional contribution to diet. We further acknowledge that diet reconstructions estimated from isotope mixing models may give false-positive results even if the items are not included in the diet and it may be difficult to include coverage of all possible dietary items. In addition, here we have employed blood only, and left unexplored the differential routing of prey macronutrients and their associated stable isotope ratios to different tissues (Podlesak et al. 2006; Voigt et al. 2008).

Recent models imply that climate change in the Namib Desert could result in a mean annual increase of up to 3°C and a reduction in annual precipitation by up to 22%, with coastal regions of the Namib Desert likely experiencing less pronounced change (Thuiller et al. 2006). In this xeric environment the potential benefits that increased atmospheric CO2 levels may have for plant photosynthetic efficiency elsewhere are not likely to be capable of compensating for warmer and drier conditions. C3 plant biomass is projected to decrease significantly in parts of the Namib Desert, while C4 plant biomass is likely to change to a much lesser extent in the Namib Desert (Thuiller et al. 2006). However, modeling the impacts of climate change in the Namib Desert is made more complex due to the significant role that fog-derived moisture plays in this system (Henschel & Seely 2008). The number of days that fog occurs may increase slightly in the coastal Namib Desert, but decrease by 23–39% further inland (Haensler et al. 2011).

While we do not know how reliant on fog moisture versus precipitation the C4/CAM plants are that fed the arthropods that the lizards preyed on, most of the C3 plants in the dry riverbed are reliant upon ground water, and evidence exists suggesting that some riverbed trees (e.g. Vachellia erioloba and Faidherbia albida) may already be experiencing significant water stress from reduced ground water availability (Schachtschneider & February 2010). Furthermore, most of the primary productivity on the gravel plains of the Namib Desert is from annual C4 grasses that grow in response to rainfall (Henschel et al. 2005). While the effects of reduced precipitation, warmer temperatures and higher atmospheric CO2 levels could potentially lead to losses of C4/CAM plant biomass and reductions in plant nutritional quality, lizards in this study occupy dry riverbed habitat at the juxtaposition of a C3 riparian woodland plant community and a C4/CAM desert plant community. Their potential resource use flexibility, coupled with this habitat juxtaposition, may allow enhanced consumer resilience despite negative climate change impacts to particular plant groups.

We describe and compare the movement of nutrients from the C3 and C4/CAM photosynthetic pathways of primary productivity into two secondary consumers (lizards) in the Namib Desert. We show that two sympatric species of insectivores consume isotopically distinct arthropod resources, and that despite the very high available biomass of C3 plants in the adjacent riparian plant community, these two lizard species both rely heavily on a food web based on C4/CAM-based plant resources. Although the amount of flexibility that these lizards and their arthropod prey have in their dietary ecology is unknown, we think it possible that any potential negative impacts that climate change may have on the availability or nutritional quality of C3 versus C4/CAM plants in this system may be partially buffered by the food web flexibility provided by the adjacent plant community types. Our findings highlight the importance of understanding how environmental change may impact different plant functional groups when considering ecosystem-level implications of climate change for consumer populations. Expanding the temporal, spatial and consumer scope of tissue stable isotope analyses may be particularly useful for better understanding food web dynamics in the Namib Desert.
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References


