POPULATION ECOLOGY – ORIGINAL RESEARCH

Foraging strategies of individual silky pocket mice over a boom–bust cycle in a stochastic dryland ecosystem

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Abstract

Small mammals use multiple foraging strategies to compensate for fluctuating resource quality in stochastic environments. These strategies may lead to increased dietary overlap when competition for resources is strong. To quantify temporal contributions of high (C_3) versus low quality (C_4) resources in diets of silky pocket mice (*Perognathus flavus*), we used stable carbon isotope ($\delta^{13}C$) analysis of 1391 plasma samples collected over 2 years. Of these, 695 samples were from 170 individuals sampled ≥ 3 times across seasons or years, allowing us to assess changes in dietary breadth at the population and individual levels across a boom–bust population cycle. In 2014, the *P. flavus* population increased to 412 captures compared to 8 captures in prior and subsequent years, while populations of co-occurring small mammals remained stable. As intraspecific competition increased, the population-wide dietary niche of *P. flavus* did not change, but individual specialization increased significantly. During this period, ~ 27% (41/151) of individuals sampled specialized on C_3 resources, which were abundant during the spring and previous fall seasons. Most of the remaining individuals were C_3–C_4 generalists (64%) (96/151), and only 9% (14/151) specialized on C_4 resources. In 2015, *P. flavus* population density and resource availability declined, individual dietary breadth expanded (84% generalists), no C_3 specialists were found, and specialization on C_4 resources increased (16%). Our results demonstrate a high degree of inter-individual plasticity in *P. flavus* foraging strategies, which has implications for how this species will respond to environmental change that is predicted to decrease C_3 resources in the future.

Keywords Generalists · Intraspecific competition · Niche variation hypothesis · *Perognathus flavus* · Specialists

Introduction

Collectively, individual foraging strategies govern population-wide niche width (Bolnick et al. 2007). Foraging strategies may differ among individuals in a population in response to four primary causes: changes in resource quality and quantity (Bolnick et al. 2003; Araújo et al. 2011;

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Rosenblatt et al. 2015), inter- and intraspecific competition (Araújo et al. 2009), predation risk (Kotler et al. 1994), and phenotypic (morphological or physiological) variation (Roughgarden 1972; Agashe and Bolnick 2010; Maldonado et al. 2019). The Niche Variation Hypothesis (Van Valen 1965) originally proposed that the increase in population niche width in island birds in comparison to mainland counterparts could, in principle, be achieved by an increase in food diversity as a result of ecological release from interspecific competition and from adaptive genetic differences to different microenvironments (Van Valen 1965; Smith and Skúlason 1996; Wilson 1998; Bell 2007). In this scenario, the population total niche width (TNW) expands through an increase in among-individual variation as a consequence of functional trade-offs that constrain the breadth of individual niches. Thus, individuals become more specialized by foraging on a narrower subset of preferred resources relative to those consumed by the population as a whole, a condition known as individual specialization (IS). Alternatively, the increase in population TNW can result from all individuals

increasing their own niche width by additionally foraging on a novel high-value resource, which ultimately yields a generalist population composed of generalist individuals (Araújo et al. 2011). According to optimal foraging theory, however, when animals are constrained by intraspecific competition in the use of a common optimal resource, individuals begin to feed on alternative resources leading to an expansion of population TNW, which can be achieved via a decrease in the within-individual component of dietary variation (Svanbäck and Bolnick 2005, 2007).

Initial examinations of levels of IS in natural populations were based on measurements of morphological differences among individuals; however, Bolnick et al. (2007) argued that behavioral responses, such as foraging behavior, may occur in the absence of morphological variation. In addition, measurements of IS have primarily occurred in environments where resource availability across space and time is relatively stable (Bolnick et al. 2003; Araújo et al. 2011). Desert ecosystems, on the other hand, are characterized by high seasonal and annual variability in precipitation (Sala et al. 2012; Collins et al. 2014) resulting in highly variable resource quantity and quality (e.g., nitrogen content) over short timescales. In response to resource variability, population sizes of small mammals typically persist at low densities during times of scarcity and erupt periodically in response to increased resource availability (Yates et al. 2002; Thibault et al. 2010; Dickman et al. 2011; Meserve et al. 2011). Despite the initial positive impact on survival and reproduction, high consumer population densities may have negative consequences on future population size because of potentially strong intraspecific competition for food and/or space (Lima et al. 2008; Kelt 2011; Previtali et al. 2009). It has been reported that to survive in a landscape characterized by variable resource availability and associated increases in inter- and intraspecific competition (Hart et al. 2016), small mammals use a variety of strategies including dietary flexibility, internal fat stores, short periods of torpor, and/or seed caches (Hoffmeister 1986; Vander Wall 1990; Kelt 2011). Nevertheless, previous studies fail to address how individual and population foraging choices of key consumers are affected by resource variability often encountered in stochastic environments (McCluney et al. 2012; Meserve et al. 2011; Letnic and Dickman 2010).

Much of the American Southwest experiences annual bimodal precipitation (Notaro et al. 2010) resulting in two seasonal pulses of net primary production that use either the C_3 or C_4 photosynthetic pathway. Cooler temperatures and winter/spring rains favor the production of C_3 plants (Xia et al. 2010), while higher temperatures and monsoon rains fuel a second pulse of production dominated by C_4 grasses (Muldavin et al. 2008; Rudgers et al. 2018). C_3 and C_4 plants differ in both their stable carbon isotope composition (Farquhar et al. 1982) and nutritional quality. C_3 plants produce larger seeds and have higher nitrogen contents in both leaves and seeds than C_4 plants (Guo et al. 2000; Guo 2003; Hope and Parmenter 2007; Orr et al. 2015). Since herbaceous forb production is strongly correlated with seasonal rainfall (Xia et al. 2010; Mulhouse et al. 2017) and models predict drier and more variable future climates (Cook et al. 2015), future precipitation patterns will likely decrease the biomass of C_3 forbs, reducing the availability of this high-quality forage. Understanding how consumers utilize both high- and low-quality forage as resource availability changes will provide valuable insight into how consumer populations will respond to more variable climates predicted for the future and associated rapid shifts in resource variability.

Our field site in the northern Chihuahuan Desert harbors a diverse assemblage of small mammal species with a wide range of life-history strategies in terms of reproduction, foraging behavior, and resource requirements (Ernest et al. 2000; Fox 2011; Kelt 2011). The silky pocket mouse (Heteromyidae: *Perognathus flavus*) is a small (6–12 g) larder hoarder that forages throughout the year excluding short (< 72 h) weather-induced periods of torpor during winter (Wolff and Bateman 1978). In 2014, *P. flavus* experienced a population explosion (boom) at our field site when C_3 plant production was high relative to overall plant biomass. Perhaps more importantly, this population boom followed a rainy year (2013) with exceptionally high C_3 and C_4 forb production. In 2015, *P. flavus* population size returned to pre-boom levels during a year with average or low C_3 plant production. This scenario provides an ideal opportunity to analyze how individual niches, population TNW, and IS vary in response to changes in both the presence of high-quality resources and intraspecific competition.

Here, we combined an extensive stable carbon isotope ($\delta^{13}C$)-based dataset on the diet of an abundant desert primary consumer with local estimates of resource quantity and quality. We measured $\delta^{13}C$ values of *P. flavus* blood plasma samples during 2014 and 2015 to quantify niche metrics in both years, including population TNW, the between-individual (BIC) and within-individual components (WIC), and the prevalence of IS (Roughgarden 1972). In addition, to track the contribution of C_3 versus C_4 primary production to individual diets across this 2-year boom–bust population cycle, we used stable isotope mixing models to determine if individual mice were differentially specializing on a subset of available C_3 or C_4 resources. We predicted that *P. flavus* would have a larger TNW in 2014 because of increased availability of high-quality C_3 resources relative to total plant biomass, and potential use of C_4 forbs produced and cached during the previous (2013) fall season. The increase in TNW was predicted to be accompanied by a decrease in the WIC to avoid intraspecific competition caused by the *P. flavus* population boom observed in this year that should result in a higher prevalence of IS.

Methods

Study site

Fieldwork was conducted across an ecotone between black grama (*Bouteloua eriopoda*)-dominated C_4 grassland and creosote bush (*Larrea tridentata*)-dominated C_3 shrubland on the Sevilleta National Wildlife Refuge (SNWR: 34°20′N, 106°43′W), Socorro County, New Mexico, USA. Mean annual precipitation at this site is ~ 250 mm, more than half (~ 150 mm) of which falls during the summer monsoon during July–September (Notaro et al. 2010; Petrie et al. 2014). Seasonal precipitation was measured using a nearby (0.7 km) meteorological station maintained by the Sevilleta Long-Term Ecological Research (LTER) program (Moore 2016). The most common small mammal species at this site include members in the New World rodent families Heteromyidae (*P. flavus, Dipodomys ordii*, *D. spectabilis,* and *D. merriami*) and Cricetidae (*Onychomys arenicola*, *Peromyscus leucopus*, *P. maniculatus, P. truei, Reithrodontomys megalotis,* and *Neotoma albigula*). We used net primary productivity (NPP) data measured semi-annually in May and October each year starting in 2004 at a mixed grass/shrub site < 1 km from our 200-m diameter small mammal trapping webs (http://sev.lternet.edu/data/sev-185) as a proxy for C_3 and C_4 seed availability based on the positive correlation between size and fecundity in herbaceous plants (Aarssen and Taylor 1992; Meserve et al. 2003).

Small mammals were trapped monthly from March to October 2014 and March to November 2015 over three consecutive nights closest to the new moon. For endotherms the size of *P. flavus*, blood plasma completely turns over in ~ 3–4 weeks (Tsahar et al. 2008; Martínez Del Rio et al. 2009), thus monthly sampling and isotopic analyses provide a near-continuous record of diet. A total of 290 Sherman live traps was set on two adjacent trapping webs (Parmenter et al. 2003) baited with rolled oats, peanut butter, and heat-treated millet. All trapped mice were identified to species. For individual identification, a pit tag (BioMark HPT8; Boise, ID) was injected subcutaneously in each animal. All animal trapping and processing protocols were approved by the UNM Institutional Animal Care and Use Committee (IACUC #13-100970-MC).

To place this boom–bust cycle in a broader context, we quantified long-term population dynamics of the small mammal community at this site using trapping data (Newsome 2018) collected by the Sevilleta LTER program starting in 2004 in black grama grassland and creosote shrubland sites that are located < 3 km from our study site combined with long-term measures of net primary production of grasses and forbs at these sites.

Sample collection and stable isotope analysis

A ~ 50 μL blood sample was obtained from each mouse by slipping a heparinized microcapillary tube behind the eye to puncture the retro-orbital sinus. Tubes of blood were capped and placed on ice for transport to the laboratory where they were centrifuged at 10,000 rpm for 5 min to separate plasma from red blood cells. A total of 14,210 trap nights over 2 years resulted in 1391 plasma samples from 695 individual *P. flavus*. Of these samples, 170 individuals (151 in 2014 and 19 in 2015) were captured during three or more monthly trapping bouts within a year.

The leaves and seeds of abundant plants on the trapping webs were collected throughout the year for stable isotope and elemental concentration analysis. Plant samples were placed in coin envelopes in the field and dried at 40 °C for at least 48 h in the laboratory. Carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope analyses were conducted at the University of New Mexico Center for Stable Isotopes (Albuquerque, NM, USA). Nitrogen analyses were conducted only on plant tissues to assess resource quality, whereas $\delta^{13}C$ analyses were used to determine plant photosynthetic pathway as well as isotopic diets (hereafter "diets") of individual *P. flavus*. Approximately 0.5–0.6 mg of plasma and ~ 3–5 mg of plant material was sealed in tin capsules and $\delta^{13}C$ and $\delta^{15}N$ values were measured with a Costech ECS 4010 Elemental Analyzer (Valencia, CA, USA) coupled to a Thermo Scientific Delta V Plus isotope ratio mass spectrometer (Bremen, Germany). Carbon isotope values were referenced against international standards of Vienna Pee-Dee Belemnite (VPDB) and atmospheric N_2 for nitrogen. Measured isotope values were calibrated against an international reference material (USGS-40) using internal reference standards run alongside plasma and plant samples to correct for instrument drift within and between runs. Repeated within-run measurement of these reference materials yielded an analytical precision ($\pm$ SD) of $\pm$ 0.2‰ for $\delta^{13}C$ and $\delta^{15}N$ values. Isotope values are reported in delta (δ) notation as parts per mil (‰): $\delta = (R_{sample}/R_{standard} - 1) \times 1000$, where R_{sample} and $R_{standard}$ are the relative ratios of the heavy and light isotopes ($^{13}C/^{12}C$ or $^{15}N/^{14}N$) in a sample and standard, respectively.

Data analysis

To estimate the degree of individual specialization (IS) of each population we used the approach outlined in Roughgarden (1972), which defines two elements of the niche, within and between individual components, that when summed are equal to the population or total niche width (TNW). The within-individual component (WIC) reflects the average of resource variability utilized by individuals, while the between-individual component (BIC) represents the between-individual variation in average resource use.

Thus, we estimate TNW as the variance in δ^{13}C values of blood plasma of all individuals that comprise the population; WIC as the mean of the variance of δ^{13}C values of plasma samples from each individual, and BIC as the variance of the mean of δ^{13}C values of plasma samples of each individual. The degree of IS is reflected in the WIC/TNW ratio. Relatively low WIC/TNW ratios closer to zero indicate greater prevalence of IS in a population, and as ratios approach one, individuals become more generalist and consume a higher proportion of the resources utilized by the entire population. To estimate IS, TNW, WIC, and BIC we used individuals for which we have ≥ 3 plasma samples collected in a given year (2014 or 2015). To avoid variance bias due to uneven sample size because we had many more captures in 2014 ($n = 151$ individuals) than in 2015 ($n = 19$), the reported niche metrics are average estimates obtained from 10,000 populations constructed with a Monte Carlo procedure that randomly sampled 19 individuals (with replacement) from the original populations to mimic the 2015 sample size. The metrics used to estimate WIC/TNW ratio uses the diet of the entire population as a proxy for resource availability; individual diets are compared with those from the population instead of with the environment, and thus, estimates of the abundance of resources available in the environment are not required (Bolnick et al. 2002).

To test the statistical significance of IS within a single population against a null model, in which IS was generated by individuals stochastically sampled from the population niche constructed by the undifferentiated pool of all individual diets, we used a nonparametric Monte Carlo procedure of 10,000 replicates to obtain p values for IS (Zaccarelli et al. 2013). Finally, statistical differences in TNW, niche components (WIC and BIC), and the degree of IS between years were evaluated with a Monte Carlo permutation procedure; to obtain p values for this procedure, the observed difference in the means between years was compared to the randomly assembled mean differences generated through 10,000 permutations. All statistical analyses were performed using the boot package (Canty and Ripley 2017; Davison and Hinkley 1997) in R (v3.5.2; R Development Core Team 2018).

The proportion of C_3 versus C_4 resources in the diets of individual *P. flavus* was estimated with the Stable Isotope Analysis in R (SIAR; Parnell et al. 2010). This mixing model was applied to plasma samples collected from 170 mice processed three or more times over spring and fall in either 2014 or 2015. Using a two source and one isotope Bayesian mixing model, we estimated the proportion of assimilated carbon in *P. flavus* plasma that was derived from C_3 versus C_4 resources using isotope data from plants collected on our trapping webs. We used a mean ($\pm$SD) δ^{13}C trophic discrimination factor ($\Delta^{13}C_{plasma-diet}$) of 1.0 ± 0.3‰ based on controlled feeding experiments on mammals (Caut et al. 2009; Kurle et al. 2013). Given the large difference

in δ^{13}C values between C_3 and C_4 plants at our study site (12-14‰), subtle variation in trophic discrimination factors on the order of 0.5–1.0‰ do not greatly influence mixing model results.

On average, *P. flavus* diets had higher percent C_3 values in spring when C_3 forbs were setting seed in this system, and potentially higher percent C_4 values during the monsoon when environmental conditions favor C_4 (grass) production (one-way ANOVA across months, $F_{16,676} = 5.464$, $p < 0.0001$). To reduce the influence of this seasonal trend in our data, we applied a correction factor each month, which we calculated as the percent difference between monthly mean C_3 values and the annual C_3 mean value (Online Appendix 1). This correction allowed us to determine which individuals specialized on C_3 versus C_4 resources relative to the rest of the *P. flavus* population in a given year. To classify individuals as C_3 or C_4 specialists or generalists, we first defined the expected maximum niche width as the mean percent C_3 dietary contribution to all individuals $\pm$ one standard deviation each year. Individuals with mean diets within one standard deviation of the population mean percent C_3 were considered generalists; these individuals consumed a mixture of C_3 and C_4 forage in quantities representing the mean annual diet for all mice in a particular year. Individuals with mean diets greater than one standard deviation from the population mean percent C_3 were determined to be either C_3 or C_4 specialists. These individuals consistently consumed relatively high amounts of C_3 or C_4 forage throughout the trapping year, even as the availability of these resources changed seasonally.

To quantify consumer biomass and assess the relative degree of intraspecific competition in *P. flavus* between years, we compared via ANOVA the total small mammal population mass (g) for the entire small mammal community in our long-term trapping dataset between 2014 and 2015 with and without *P. flavus* biomass. Results are expressed as mean $\pm$ standard deviation (SD) throughout.

Results

Long-term trapping data show that *P. flavus* has exhibited multiple population boom–bust cycles since 2004, the largest of which occurred in 2014 (Fig. 1). At our trapping site, the abundance of *P. flavus* in March 2014 was 51.1 times higher than in March 2015 (412 versus 8 captures). During 2014–15, abundances of Cricetids remained relatively constant while all other Heteromyids exhibited smaller fluctuations in population size (Fig. 1c). We found no significant difference (ANOVA, $F_{1,7} = 0.18$, $p = 0.69$) in the combined mass of the small mammal community between 2014 and 2015 when *P. flavus* were excluded; however, there was a significant difference (ANOVA, $F_{1,7} = 22.3$, $p = 0.002$)

Fig. 1 **a** Precipitation (mm) binned by season. Spring season bins (S) include total precipitation measured from October through May while monsoon season bins (M) include total precipitation measured from June through September. **b** Net primary production (g/m^2) measured semi-annually at a mixed grassland/shrubland site within < 0.3 km of our trapping webs. **c** Rodent abundance at the Sevilleta LTER creosote and black grama core sites which are located < 1 km from our trapping webs. Abundance is calculated as the total number of individuals caught per species, divided by the number of trap nights for each trapping bout. Abundances of *P. flavus*, other heteromyids and cricetids were averaged across the two core sites to illustrate population trends. Inset shows rodent abundance in 2014 and 2015 from the trapping webs used for this study
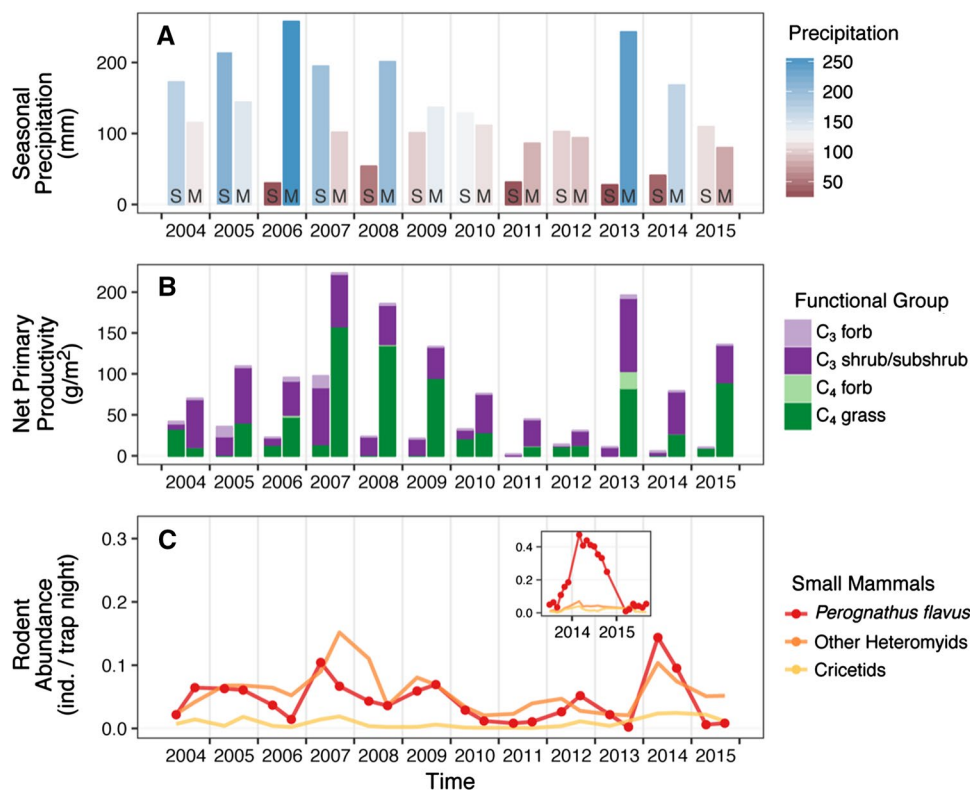
in total community mass with *P. flavus* included (Online Appendix 2).

The 2014 population spike, like a similar spike in 2007, occurred after a monsoon season with above average rainfall (Fig. 1a). The 2013 monsoon season was 162% above average (234 mm of rainfall) following a dry spring (27.8 mm) that was 72.2% below mean annual precipitation (Fig. 1a). In response to abundant monsoon precipitation, forb production increased tenfold from spring to fall of 2013 (10.8–115.4 g/m^2), including a large increase in fall C_4 forbs (Fig. 1b). This high net primary production (NPP) resulted in a large volume of standing biomass in 2014, a year with average precipitation and plant production, but one in which C_3 production represented a higher proportion of overall NPP than in 2015 (Fig. 1b). In 2015, below-average spring and monsoon precipitation resulted in decreased primary production and a lower proportion of C_3 production relative to total plant biomass (Fig. 1b).

Based on analysis of 622 plant samples collected on our trapping webs, mean weight percent nitrogen, a proxy for nutritional quality, was significantly higher on average in leaves ($2.79 \pm 0.14\%$) and seeds ($3.3 \pm 0.16\%$) of C_3 plants compared to leaves ($1.64 \pm 0.18\%$) and seeds ($2.09 \pm 0.2\%$) of C_4 plants (leaves: $F = 25.4$, seeds: $F = 22.6$, $df = 1,32$, $p < 0.0001$). As a consequence, C_3 plants also had significantly lower C:N ratios, a commonly used proxy for nutritional quality, in their leaves (17.0 ± 1.8) and seeds

(16.1 ± 4.6) in comparison to the leaves (34.4 ± 2.5) and seeds (25.4 ± 9.2) of C_4 plants (leaves: $F = 28.4$, seeds: 22.8, $df = 1,32$; $p < 0.0001$). $\delta^{13}C$ analysis of leaf and seeds from sixteen C_3 forb, five C_3 sub-shrub, seven C_4 forb, and nine C_4 grass species resulted in strong differentiation in carbon between C_3 and C_4 plants, providing well-separated endpoints from which we could estimate consumer resource use with mixing models. Mean $\delta^{13}C$ values of C_3 and C_4 plants were $-26.6 \pm 1.8\%$ and $-14.4 \pm 0.8\%$, respectively.

Perognathus flavus exhibited significant differences in population niche components (WIC and BIC) and the levels of IS between years (Table 1). Estimates of WIC ($p = 0.03$), BIC ($p = 0.017$) and IS ($p = 0.002$) were significantly different in 2014 versus 2015, while TNW ($p = 0.44$) was similar between years. Overall, the *P. flavus* population in 2014 ($p = 0.001$) was comprised of more individual specialists, whereas in 2015 ($p = 0.879$) the population was comprised of more generalist individuals (Fig. 2; Table 1).

Mixing models show that during the population boom in 2014, the average *P. flavus* diet consisted of $54.2 \pm 9.5\%$ C_3 resources. Sixty-four percent of individuals had mean dietary %C_3 within this range, classifying them as generalists. In contrast, 27% of mean individual dietary %C_3 values were one standard deviation above the mean classifying them as C_3 specialists and 9% of individuals had mean %C_3 values one standard deviation below the mean classifying them as C_4 specialists. In 2015, a year of relatively low availability

Table 1 Samples sizes (*n*), within-individual component (WIC), between-individual component (BIC), total isotopic niche width (TNW) and individual specialization index (IS) of *P. flavus* in 2014 and 2015

Year	*n*	WIC	BIC	TNW	IS
2014	151	1.79[a]	2.60[a]	4.38[a]	0.41[a]
2015	19	3.33[b]	0.87[b]	4.04[a]	0.82[b]

In the first year (2014), abundant C3 resources were available and population density of *P. flavus* increased, whereas both resource availability and *P. flavus* population density declined in 2015. Units for WIC, BIC and TNW are in ‰². Note that sample size in 2014 represents the total number of individuals used in the analysis; however, for the estimation of niche metrics via a Monte Carlo resampling procedure, we used a sample size of 19 individuals (with replacement) to mimic the sample size in 2015. Different superscript letters denote significant differences (WIC: $p = 0.03$, BIC: $p = 0.017$, IS: $p = 0.002$) among populations
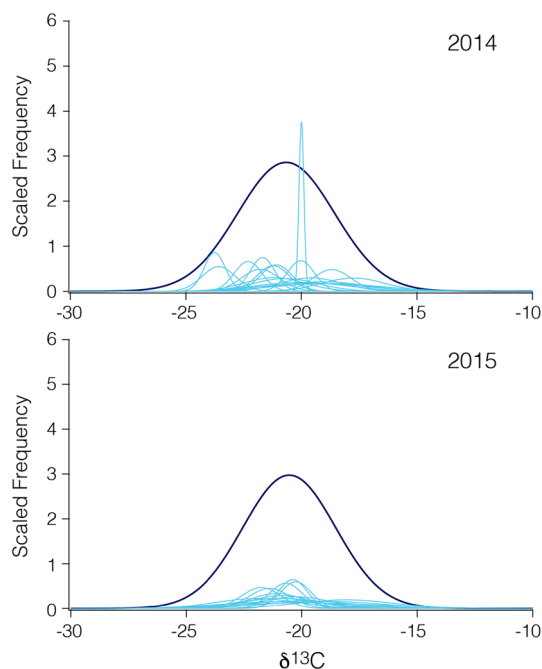

Fig. 2 Individual specialization of representative *P. flavus* population in 2014 and 2015. Lighter curves correspond to normal functions N (μ_t, σ_t) with a unitary area, where μ_t and σ_t are the mean and standard deviations of blood plasma $\delta^{13}C$ values that represent the individual niches. Bold curves correspond to the normal function N (μ_t, σ_t), where μ_t, σ_t are the mean and standard deviations of blood plasma $\delta^{13}C$ values of all individuals in the population, which represents the population isotopic niche width (TNW). For visual clarity, population (bold) curves were scaled to an area equal to 15

of high-quality C3 resources and a large decline in population numbers (Fig. 1), the mean *P. flavus* diet consisted of 57.6 ± 13.2% C3 resources, while 16% of the *P. flavus* population were C4 specialists, 84% were generalists, and there were no C3 specialists. Overall, individual C3 specialists had

less variable diets than either generalists or C4 specialists (Fig. 3), whereas C4 specialists had the highest variability in resource use.

Discussion

Desert ecosystems often support diverse and dynamic small mammal populations in spite of low and unpredictable resources associated with high inter-annual variation in climate. In these environments, it is expected that consumers use a variety of foraging strategies, which may quickly change with seasonal or inter-annual variation in resource quantity and/or quality. Here we used estimates of net primary production (Meserve et al. 2003; Smiley et al. 2015; Lehmann et al. 2015), plant tissue elemental concentrations, and isotope-based measurements of diet composition to examine individual and population-level niche metrics in a Heteromyid rodent over a 2-year boom–bust population cycle. Contrary to our prediction, we found that population total niche width (TNW) of *P. flavus* was the same in 2014 and 2015, 2 years that differed dramatically in population density and high-quality C3 resource availability. As predicted, we did find that greater intraspecific competition along with higher resource availability in 2014 yielded an increase in individual specialization relative to the following year (2015) when *P. flavus* population numbers returned to normal levels.

In agreement with our predictions, *P. flavus* consumed a greater proportion of more nutritious seeds of C3 resources in 2014. However, because the total population niche width in 2014 was not significantly higher than in 2015, the greater degree of IS on high-quality C3 resources was not related to an expansion of population-level diet variation. This finding contrasts with expectations based on the Niche Variation Hypothesis (Van Valen 1965). Foraging on a highly nutritious subset of available resources has been shown to improve individual fitness in raptors (Terraube et al. 2014), sea otters (Tinker et al. 2008), penguins (Lescroël et al. 2010), and a variety of other taxa (Agashe and Bolnick 2010; Araújo et al. 2008; Tinker et al. 2008; Bison et al. 2015; Bolnick et al. 2010; Costa et al. 2008; Svanbäck and Bolick 2007; Frédérich et al. 2010; Warne et al. 2010). While C3 perennial shrubs such as *L. tridentata*, *Gutierrezia sarothrae*, and *Krascheninnikovia lanata* account for a large portion of primary production and standing biomass at our study site (Fig. 1b), the *P. flavus* population boom in 2014 followed abundant monsoon rains in 2013 that tripled C4 forb production in the fall of this year, and doubled C3 forb production in the spring of 2014. Both leaves and seeds of C3 and C4 forbs have a higher nitrogen content than C4 grasses, so a higher quantity of high-quality C3 resources was available to *P. flavus* in 2014 in comparison to 2015.
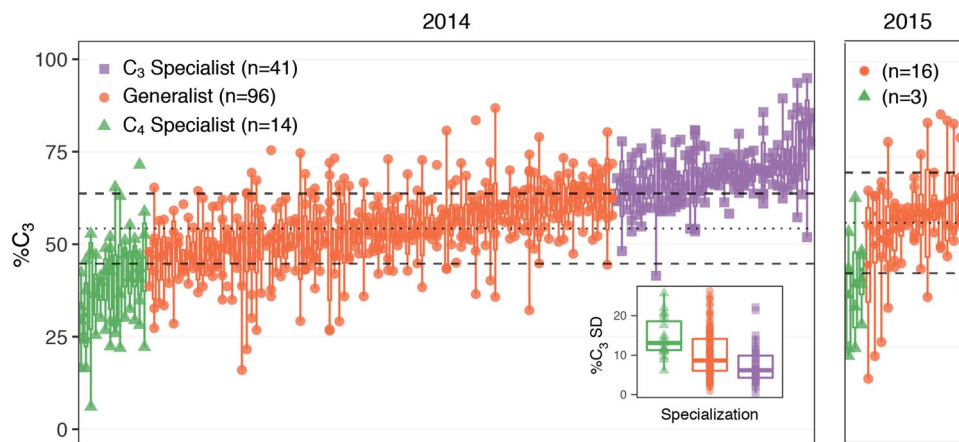
Fig. 3 Individual foraging strategies of *P. flavus* in 2014 and 2015. Black dotted lines indicate the mean %C_3 in the diet of all *P. flavus* captured each year, while dashed lines indicate the mean individual foraging width each year. Each box plot represents the range of monthly %C_3 values recorded for individual *P. flavus* captured at least three and up to eight times that year. Individual generalists (orange symbols) fall within one standard deviation of the mean diet, while C_3 (purple symbols) and C_4 (green symbols) specialists fall one standard deviation above or below the yearly mean, respectively. Inset shows the correlation between the standard deviation in % C_3 in diet of each individual, grouped by diet specialization (C_3/C_4 specialist or generalist) (color figure online)

In 2014, when the *P. flavus* population was at its peak, we observed three fairly distinct dietary strategies. Of 151 mice, 27% specialized on the higher quality C_3 forage, while 64% were generalists that consumed a mixed C_3–C_4 diet. Only 9% specialized on C_4 resources (Fig. 3). In 2015, a decrease in C_3 resources relative to total plant biomass and scarcity of C_4 forbs resulted in a change in foraging strategies used by *P. flavus* in comparison to the prior year. We observed a complete loss of strict C_3 specialists, a modest increase in C_4 specialists (16%) and a large majority of consumers (84%) using a generalist foraging strategy.

During the *P. flavus* population boom–bust cycle, the abundance of co-occurring small mammal species remained constant (Fig. 1d, Online Appendix 2). Herbivore pressure on the landscape increased as primary and secondary production had to support a 21% increase in small mammal community biomass in the form of *P. flavus* at the peak of the population boom, resulting in an increase in intra- relative to inter-specific competition. *P. flavus* showed higher levels of IS in 2014 in comparison to 2015 (Fig. 2), which was achieved by a significant reduction of the WIC, likely related to an increase in intraspecific competition (Roughgarden 1972; Bolnick et al. 2003). In addition, the observed inter-annual patterns in niche metrics (Table 1) does not conform to the Niche Variation Hypothesis, which posits that increases in a population's TNW occurs via increases in the between-individual component (BIC) of diet because the WIC is restricted by functional trade-offs among individuals (Bolnick et al. 2003; Maldonado et al. 2019). The WIC in 2015 was ~ 1.5 times larger than that observed in 2014 even though the population TNW was similar in both years, suggesting that individuals can readily increase their

niche width and are not constrained by functional trade-offs. Thus, the reduction in WIC observed in 2014 is likely driven by intraspecific competition and the need for individuals to minimize niche overlap with conspecifics. Overall, our results evidence a strong connection between temporal variation in resource availability, intraspecific competition, and individual diet specialization in stochastic resource-limited ecosystems.

Previous studies show that IS can vary over short timescales in response to seasonality in tropical environments that typically include a wet season characterized by high resource abundance followed by a dry season when resources may be limiting. Such conditions produce temporal variation in both intraspecific competition and the relative availability of high-quality foods that are amenable to studying the ecological causes of IS (Araújo and Gonzaga 2007; Herrera et al. 2008; Costa-Pereira et al. 2017). We argue that stochastic and often resource-limited aridland environments that experience larger temporal variation in both resource quantity/quality and consumer population size than tropical ecosystems provide an even better setting to examine the ecological factors that promote and maintain foraging strategies at both the individual and population level. But to our knowledge, surprisingly no data exist on individual- or population-level variation in the diets of aridland small mammals between seasons or years. The high degree of foraging plasticity in small mammals observed here across two consecutive years in response to changes in population density and resource quantity/quality has not been reported from other ecosystems. Although our analysis included only one boom–bust cycle we believe that our results are generalizable because past boom–bust cycles occurred following

similar climatic events. Overall, our results and those from tropical environments highlight the potentially strong but unresolved connection between temporal resource availability and IS.

We acknowledge that using the relative proportion of C_3 versus C_4 resources consumed by individual mice over time is a coarse index of diet specialization based on the use of plant functional groups; however, our approach does offer some advantages over existing techniques. Other direct (e.g., observation) or indirect (e.g., gut content analysis or scat DNA metabarcoding) dietary proxies may offer more taxonomic resolution of the food consumed; however, none of these approaches provide a time-integrated measure of diet composition. Furthermore, our strategy of using isotope data for individuals that were recaptured several times to generate a longitudinal dietary record for an individual nocturnal consumer is impossible via observation or gut content analysis, and extremely difficult via scat DNA metabarcoding. As such, we suggest that the most integrative approach for studying resource use at the population or individual level would be to use a combination of isotope analysis of a sequentially sampled tissue such as blood plasma with a rapid isotopic incorporation rate (Martínez Del Rio et al. 2009) coupled with scat DNA metabarcoding (e.g., Kartzinel et al. 2015; Soininen et al. 2014) to identify the composition of plant species and/or functional groups—C_3 forbs, C_3 shrubs, C_4 forbs, or C_4 grasses—consumed by individual animals over time.

Finally, since herbaceous forb production is strongly correlated with seasonal rainfall (Xia et al. 2010; Mulhouse et al. 2017) and models predict drier and more variable future climates (Cook et al. 2015), future precipitation patterns will likely decrease the biomass of C_3 forbs in aridland systems throughout the American Southwest, reducing the availability of this high-quality forage. Thus, understanding how consumers utilize both high- and low-quality forage as resource availability changes will provide valuable insight into how consumer populations will respond to more variable climates predicted for the future and associated rapid shifts in resource variability. Our results suggest that a combination of dietary generalism and specialization among individuals represents a successful strategy for population persistence in stochastic resource-limited ecosystems because segments of the population will experience reproductive success under different resource scenarios (Woo et al. 2008).

Compliance with ethical standards

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