

RESEARCH ARTICLE

Competition shapes individual foraging and survival in a desert rodent ensemble

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Abstract

1. Intraspecific variation, including individual diet variation, can structure populations and communities, but the causes and consequences of individual foraging strategies are often unclear.
2. Interactions between competition and resources are thought to dictate foraging strategies (e.g. specialization vs. generalization), but classical paradigms such as optimal foraging and niche theory offer contrasting predictions for individual consumers. Furthermore, both paradigms assume that individual foraging strategies maximize fitness, yet this prediction is rarely tested.
3. We used repeated stable isotope measurements ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$; $N = 3,509$) and 6 years of capture–mark–recapture data to quantify the relationship between environmental variation, individual foraging and consumer fitness among four species of desert rodents. We tested the relative effects of intraspecific competition, interspecific competition, resource abundance and resource diversity on the foraging strategies of 349 individual animals, and then quantified apparent survival as function of individual foraging strategies.
4. Consistent with niche theory, individuals contracted their trophic niches and increased foraging specialization in response to both intraspecific and interspecific competition, but this effect was offset by resource availability and individuals generalized when plant biomass was high. Nevertheless, individual specialists obtained no apparent fitness benefit from trophic niche contractions as the most specialized individuals exhibited a 10% reduction in monthly survival compared to the most generalized individuals. Ultimately, this resulted in annual survival probabilities nearly 4x higher for generalists compared to specialists.
5. These results indicate that competition is the proximate driver of individual foraging strategies, and that diet-mediated fitness variation regulates population and community dynamics in stochastic resource environments. Furthermore, our findings show dietary generalism is a fitness maximizing strategy, suggesting that plastic foraging strategies may play a key role in species' ability to cope with environmental change.

KEYWORDS

Chihuahuan desert, *Dipodomys merriami*, *Dipodomys ordii*, *Dipodomys spectabilis*, heteromyid, individual specialization, *Perognathus flavus*, Sevilleta LTER

1 | INTRODUCTION

Intraspecific variation is increasingly recognized as a principal driver of ecological processes (Des Roches et al., 2018; Violle et al., 2012). Individual diet variation, in particular, can have fitness consequences that affect populations and communities (Bolnick et al., 2011; Manlick & Newsome, 2021; Thompson et al., 2012). For example, individuals often utilize different resources within a population's trophic niche (Bolnick et al., 2003), which can alter body condition (Cucherousset et al., 2011), reproductive output (Annett & Pierotti, 1999) or survival (Darimont et al., 2007). Moreover, both individual foraging and its fitness consequences can vary with ecological stressors such as competition and resource availability (Balme et al., 2020; Woo et al., 2008). Given that global change is rapidly altering environmental conditions, quantifying the causes and consequences of individual foraging dynamics is critical to understanding the role of diet variation in ecological processes.

Variation in consumer diets has traditionally been credited to fixed morphological traits or differences in age and sex, but recent empirical advances have shown that individual foraging is both flexible and a function of ecological stressors (Costa-Pereira et al., 2018; Courbin et al., 2018; Sheppard et al., 2018). Two fundamental ecological paradigms underlie predictions for individual foraging strategies: optimal foraging theory and classical niche theory. Optimal foraging theory predicts that individuals should specialize when resource availability is high, but generalize when competition increases or resources become limiting (Stephens & Krebs, 1986). Conversely, niche theory predicts that individuals should specialize when competition increases or resources become limiting to minimize resource overlap and promote coexistence (i.e. limiting similarity; MacArthur & Levins, 1967). There is empirical support for both predictions (Jesmer et al., 2020; Newsome et al., 2015), indicating that complex interactions between competition and resources ultimately determine individual foraging strategies (Costa-Pereira, Araújo, et al., 2019). For example, numerous studies have shown that intraspecific competition limits access to shared resources, leading to population-level dietary niche expansion as individuals exploit secondary prey items (Newsome et al., 2015; Svanbäck & Bolnick, 2007; Van Valen, 1965). However, interspecific competition serves as a counterbalance limiting such niche expansion (Bolnick et al., 2010; Roughgarden, 1972), while resource diversity can dictate the ability to switch between prey items (i.e. 'ecological opportunity'; Araújo et al., 2011). Furthermore, both resource abundance and resource diversity interact with competition to influence individual foraging strategies (Costa-Pereira, Araújo, et al., 2019; Svanbäck et al., 2011; Tinker et al., 2008). Quantifying the relative impacts of, and interactions between, competition and resources is therefore needed to determine whether animals forage in accordance with optimal foraging or niche theory.

Ecologists have long recognized that populations exhibit a mix of foraging strategies, and that this diet variation can have fitness consequences (Estes et al., 2003; Price, 1987; Schoener, 1971). The principle of 'adaptive foraging' proposes that individual

consumers adjust their foraging strategies and resource use to increase fitness (e.g. survival, reproduction) relative to hetero- and conspecifics (Loeuille, 2010). Both optimal foraging and niche theory assume that individual foraging strategies are indeed adaptive responses to environmental change that increase individual fitness, either via energy maximization or limiting competition, respectively (Roughgarden, 1972; Stephens & Krebs, 1986). One particular strategy, individual diet specialization, is often presumed to maximize individual fitness because it can optimize foraging behaviors (e.g. search images, handling time; Werner et al., 1981) while limiting competitive interactions (Bolnick et al., 2003; Terraube et al., 2014). Conversely, individual generalists risk being outcompeted by specialized consumers (i.e. jack-of-all-trades master of none hypothesis; MacArthur & Pianka, 1966), but may also benefit from toxin dilution (Freeland & Janzen, 1974), balanced nutrient intake (Pulliam, 1975), and reduced movement and predation risk (MacArthur & Pianka, 1966; Stephens & Krebs, 1986). Recent empirical studies have found mounting support for generalization as an optimal foraging strategy, particularly in stochastic environments (Balme et al., 2020; Costa-Pereira, Toscano, et al., 2019; Lefcheck et al., 2013), but studies directly connecting individual foraging strategies to fitness variation remain scarce.

We use longitudinal sampling of a desert mammal ensemble to quantify the causes and consequences of individual foraging strategies in four species of granivorous Heteromyid rodents. Previous studies of individual foraging have largely focused on single species (Noble et al., 2019; Sheppard et al., 2018) or have explored the impact of environmental variation across space (Costa-Pereira et al., 2018; Jesmer et al., 2020), but the interactions between ecological stressors remain considerably understudied. Furthermore, most studies have explored individual foraging in stable, productive ecosystems (e.g. nearshore marine, Newsome et al., 2009; neotropical wetlands, Costa-Pereira et al., 2018), where the impact of environmental stochasticity on different foraging strategies may be lessened. Lastly, foraging strategies like individual diet specialization are often assumed to be adaptive (i.e. increase fitness, Loeuille, 2010), but the relationship between individual foraging and fitness is rarely quantified. We address these limitations using 6 years of repeated stable isotope measurements ($\delta^{13}\text{C}$, $\delta^{15}\text{N}$; $N = 3,509$) and capture-mark-recapture data to quantify the relationship between environmental variation, individual foraging and consumer fitness in a stochastic desert ecosystem. We ask two specific questions: (a) What are the environmental drivers (e.g. competition, resources) of individual foraging strategies and how do they interact? and (b) How do individual foraging strategies (e.g. specialization vs. generalization) impact survival? We predicted that individual foraging strategies would respond most strongly to competitive interactions in accordance with classical niche theory (Noble et al., 2019), and we expected individual generalists to have higher survival than individual specialists due to resource stochasticity.

2 | MATERIALS AND METHODS

2.1 | Study site and field sampling

We sampled desert rodents at the Sevilleta National Wildlife Refuge (hereafter, Sevilleta; 34°20'N, 106°43'W; New Mexico, USA) located at the transition from northern Chihuahuan Desert to Great Plains grassland. The site is characterized by seasonal and inter-annual climate variation, including low annual precipitation (~250 mm) punctuated by late-summer monsoons that account for more than half the annual rainfall (Petrie et al., 2014). This climate stochasticity ultimately drives high inter-annual variation in both resource and consumer abundances (Ernest et al., 2000; Rudgers et al., 2018), with consequences for individual foraging dynamics (Noble et al., 2019).

We sampled animals from 2013 to 2019 following a standardized small mammal sampling protocol in association with the Sevilleta LTER program (Noble et al., 2019). Briefly, we trapped monthly (~March–November; Table S1) at two adjacent trapping webs (5.3 ha) spread across an ecotone dominated by C_4 grassland (black grama; *Bouteloua eriopoda*) in the north and C_3 shrubland (creosote bush; *Larrea tridentata*) in the south. We used 290 Sherman live traps (145/web, 10 m apart) baited for 2–4 consecutive nights ($\bar{x} = 3.12$) following the new moon for a total of 41,470 trap nights. Webs were independent, separated by ~1 km with only 30 individuals (0.01%) captured at both webs throughout the study period. Individuals were identified to species and marked with either ear tags or a passive integrated transponder (BioMark HPT8). We collected ~50 μ l of blood via retro-orbital bleeding and centrifuged at 10,000 rpm for 10 min to separate plasma and red blood cells. The most common species captured were four members of the family Heteromyidae (hereafter, heteromyids)—Merriam's kangaroo rat *Dipodomys merriami*, Ord's kangaroo rat *Dipodomys ordii*, the banner-tailed kangaroo rat *Dipodomys spectabilis* and the silky pocket mouse *Perognathus flavus*—which represented 85% of rodent biomass (Figure S1). Nearly a dozen species in family Cricetidae (hereafter, cricetids) were also captured, including grasshopper mice *Onychomys* spp., deer mice *Peromyscus* spp., harvest mice *Reithrodontomys* spp. and woodrats *Neotoma* spp. All sampling adhered to ethical guidelines (Sikes, 2016) and was approved by the University of New Mexico Animal Care and Use Committee (#19-200940-MC).

2.2 | Stable isotope analyses

Stable isotopes in animal tissues reflect the flow of energy through food webs (Layman et al., 2012). For example, carbon isotopes ($\delta^{13}\text{C}$) trace energy channels and the diversity of basal resources (e.g. C_3 vs. C_4 plants) while nitrogen isotopes ($\delta^{15}\text{N}$) reflect consumer trophic position. Thus, patterns in consumer isotope values can be used as a quantitative proxy for trophic niches known as the isotopic niche (Layman & Post, 2008; Marshall et al., 2019; Newsome et al., 2007) and can assess foraging dynamics across individuals, populations and communities (Manlick & Pauli, 2020; Manlick et al., 2019; Sheppard

et al., 2018). Furthermore, repeated isotope measurements from the same individual can quantify individual trophic niches and diet variation (Maldonado et al., 2017, 2019; Newsome et al., 2009).

We used $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ isotope analysis of blood plasma to quantify trophic niches and foraging strategies among desert rodents at the Sevilleta, and all analyses were conducted at the University of New Mexico Center for Stable Isotopes (see Supporting Information). Small mammal blood plasma has an isotopic turnover rate of ~3 weeks (Thomas & Crowther, 2015; Vander Zanden et al., 2015); thus, our monthly sampling provided a nearly continuous record of small mammal foraging in each calendar year. Moreover, our sampling straddled an ecological transition zone encompassing two distinct energy channels with significantly different $\delta^{13}\text{C}$ values: C_3 ($-26.6 \pm 1.8\text{‰}$) and C_4 plants ($-14.4 \pm 0.8\text{‰}$; Noble et al., 2019). Similarly, $\delta^{15}\text{N}$ values in C_3 plants ($3.7 \pm 0.8\text{‰}$) exceed C_4 plants ($2.6 \pm 0.9\text{‰}$) while omnivory (e.g. insectivory) can generate additional $\delta^{15}\text{N}$ differences in consumers (Post, 2002). Collectively, these patterns create an isotopic landscape that enables the quantification of trophic niches and individual foraging at the Sevilleta (Noble et al., 2019; Warne et al., 2010).

2.3 | Individual foraging strategies

We quantified individual foraging strategies annually using the relative individual niche index (RINI; Sheppard et al., 2018). This index uses repeated isotope measurements (e.g. $\delta^{13}\text{C}$, $\delta^{15}\text{N}$) to quantify the isotopic niche of each individual using standard ellipse areas corrected for sample size ($\text{SEA}_{\text{Ind}}, \text{‰}^2$), and the union of all individual ellipses then defines the total niche width (TNW; ‰^2) of the population (Sheppard et al., 2018; Table 1). Then, RINI is calculated as the proportion of the TNW an individual's trophic niche occupies (i.e. $\text{RINI} = \text{SEA}_{\text{Ind}}/\text{TNW}$) and ranges from 0 (complete specialist) to 1 (complete generalist) for each animal. This is analogous to Roughgarden's index (1974) which defines population-level specialization and generalization as the mean within-individual variation of a population divided by the TNW.

Heteromyids dominated the community, so we estimated RINI only for *D. spectabilis*, *D. merriami*, *D. ordii* and *P. flavus*. For 2013–2015 and 2017–2019, we calculated SEA_{Ind} using 95% prediction ellipses for all individuals with ≥ 3 isotope measurements ($\delta^{13}\text{C}$ and $\delta^{15}\text{N}$) in a calendar year as this is the minimum number of samples needed to calculate an ellipse. Due to incomplete sampling, 2016 was excluded from all analyses (Table S1). Importantly, RINI defines TNW only by the union of individual ellipses and is therefore sensitive to the number of individuals with a calculated SEA_{Ind} (i.e. the number of individuals with ≥ 3 isotope measurements within a year). Throughout our sampling, however, we consistently captured more individuals than we were able to calculate SEA_{Ind} for. Thus, we calculated an adjusted RINI metric that estimated TNW using the 95% prediction ellipse of all isotope measurements from a given species in each year. On average, our adjusted RINI more than doubled the amount of data used to calculate TNW and provided a

TABLE 1 Description of response and predictor variables used in Bayesian generalized mixed-effects models, including transformations, range of values and units

Response	Description	Transformations	Range	Unit
Relative Individual Niche Index (RINI)	Proportion of total isotopic niche width (TNW) occupied by an individual's isotopic niche (SEA_{ind})	Normalized, Square root	0–1	–
Predictor	Description; prediction	Transformations	Range	Unit
Intraspecific competition	Relative abundance of conspecifics; increases specialization	–	0.26–21.76	individuals web ⁻¹ night ⁻¹
Interspecific competition	Relative abundance of heterospecifics; increases specialization	–	3.52–28.88	individuals web ⁻¹ night ⁻¹
Resource abundance	Mean annual plant biomass; increases generalization	–	120.43–244.06	grams
Resource diversity	Simpson's index of plant species diversity; increases specialization	–	0.22–0.45	D
SEA_{ind}	Individual isotopic niche width (95% prediction ellipse for individuals with ≥ 3 measurements per year); decreases with specialization	Square root	0.29–12.77	‰ ²
TNW	Total isotopic niche width of population (95% prediction ellipse for all samples per species per year); increases with specialization	–	27.36–69.63	‰ ²

more conservative measure of resource use at the population level (Table S2). This population-level TNW, however, can produce an ellipse area smaller than SEA_{ind} , thereby rendering RINI estimates >1 (Sheppard et al., 2018). Accordingly, we min-max normalized all measurements from zero to one for continuity, and all RINI estimates were square root transformed to meet the assumption of normality for downstream analyses. Our adjusted RINI approach was directly compared to the original Sheppard et al. (2018) in all downstream analyses. All SEA_{ind} , TNW and RINI measurements were implemented in the R package SIBER (Jackson et al., 2011).

2.4 | Statistical analyses

An individual specialist is one whose trophic niche is smaller than the population TNW, independent of age, sex or morphology (Bolnick et al., 2003). Thus, we used a series of single-factor ANOVAs to test for differences in RINI between age (adult, sub-adult; Frey, 2007; Moses et al., 2012), sex (female, male) and species given that we did not observe any discrete morphological differences within each population. We also tested the effects of spatiotemporal variation by quantifying differences in RINI between sampling webs and across seasons. We classified animals into three seasons—spring, fall, both—defined by individuals sampled only in the pre-monsoon spring (February–June), individuals sampled only in the monsoon fall (July–November), and animals sampled across both seasons. To quantify drivers of individual foraging strategies, we then used Bayesian generalized linear mixed-effects models to analyse RINI as a function of four ecological stressors: intraspecific competition,

interspecific competition, resource abundance and resource diversity (Table 1).

We quantified intraspecific competition as the relative abundance of conspecifics experienced per individual per year. Specifically, we calculated the number of unique individuals web⁻¹ night⁻¹ for each year and assigned individuals to the web they were captured on most frequently. We similarly quantified interspecific competition as the relative abundance of heterospecifics experienced per individual, including all cricetids. We calculated the number of unique heterospecific individuals web⁻¹ night⁻¹ for each year and assigned individuals to the web they were encountered on most frequently. In 2013, *P. flavus* were not marked with unique identifiers so we estimated abundance as the number of unique traps with a *P. flavus* capture. Across the entire study period, the number of unique traps with a capture was strongly correlated with the number of unique individuals ($r = 0.86$, $p < 0.001$), indicating that trap counts provide a suitable proxy for abundance and intraspecific competition in this instance.

We quantified resource abundance and diversity using plant biomass (g) and diversity estimates from the Sevilleta LTER (Rudgers et al., 2018). Briefly, plant volume was measured for all species in spring (April–May) and fall (September–October) at 40 permanent 1 m² plots located adjacent to the trapping webs. Plant biomass was then estimated for each species allometrically using established linear regression procedures (Muldavin et al., 2008). To generate a single, annual estimate of plant biomass and diversity, we first took the maximum biomass per species so that plants present at both time points were not pseudo-replicated. We then summed all plant species biomasses to generate a single estimate of resource abundance

per year, and we estimated resource diversity using Simpson's diversity index on plant biomass.

We used Bayesian mixed models and leave-one-out model selection to quantify the response of RINI to competition, resources and their interactions. Specifically, we developed a suite of 16 a priori models to quantify RINI as a function of intraspecific competition, interspecific competition, resource abundance and resource diversity. Because standard ellipses are sensitive to sample size (Jackson et al., 2011), all models also included a measurement covariate to account for the number of isotope values used to calculate SEA_{ind} . Models included species as a random effect, and a subset of models let slope and intercept vary by species to assess species-specific responses to ecological stressors (Table S3). To optimize statistical power, we did not include individual as a random effect because only 5% of response values came from individuals with RINI estimates in multiple years, but this was included in supplementary analyses (Figure S4). Lastly, because RINI is a function of two parameters— SEA_{ind}/TNW —observed changes in foraging strategies can occur via two, non-mutually exclusive pathways: (a) individuals alter their foraging niches such that SEA_{ind} occupies a different proportion of the TNW or (b) TNW changes thereby altering the proportion of the population niche occupied by an individual. To assess the relative importance of SEA_{ind} versus TNW in determining individual foraging strategies, we used a single, additive Bayesian mixed model to quantify RINI as a function of SEA_{ind} (square root transformed) and TNW (Table 1) with a random effect of species nested within year to account for pseudo-replication. All models were implemented in the R package *RSTANARM* (Stan Development Team, 2016) and compared using expected log predictive density (ELPD) in the R package *loo* (Vehtari et al., 2017, 2019; Supporting Information). We defined significant effects as model coefficients with 95% credible intervals not overlapping zero.

2.5 | Survival models

To quantify the fitness consequences of foraging strategies, we estimated apparent monthly survival (ϕ_{month}) using capture–mark–recapture data for individuals with RINI estimates. Specifically, we used Cormack–Jolly–Seber (CJS) models implemented in program MARK (White & Burnham, 1999) using the R package *RMARK* (Laake, 2013). To develop capture histories, we condensed monthly trapping bouts into single, binary (detection/non-detection) occasions for each animal and concatenated occasions at the annual level. We censored 21 individuals with known fates (e.g. trap mortality), and tested the sensitivity of our models to age and pseudo-replication by censoring sub-adults ($N = 10$) and individuals with >1 year of captures ($N = 13$; see Supporting Information). We estimated ϕ_{month} in two steps. First, we held ϕ_{month} constant and developed five a priori models for detection probability (p) varying as function of time, year and species (Table S4). We identified the top detection model using Akaike's information criteria adjusted for small sample size (AIC_C ; Burnham & Anderson, 2002). We then

used the top detection model and developed eight a priori models for ϕ_{month} varying as function of year, species, RINI and interactions between the predictors (Table S5). Year and species were included as factors, and RINI was modelled as an individual (i.e. continuous) covariate. We tested goodness-of-fit for CJS models using program RELEASE (Burnham et al., 1987), and found no significant overdispersion ($p = 0.98$). Lastly, we identified the top model using AIC_C and converted monthly survival into annual survival probability (ϕ_{annual}) using the Delta method to calculate 95% confidence intervals (Powell, 2007).

3 | RESULTS

From 2013 to 2015 and 2017 to 2019, we captured 2,657 unique individuals (1,995 heteromyids and 667 cricetids) and generated 3,509 isotope measurements ($\delta^{13}C$, $\delta^{15}N$) for heteromyids (Figure S2). From this, we calculated 369 RINI estimates for 349 individual heteromyids, with 20 individuals presenting enough captures to estimate RINI in multiple years (Figure 1). Individuals were evenly split across webs (166 vs. 203), and nearly 70% of animals were caught across both seasons ($N = 254$) compared to only spring ($N = 44$) or fall ($N = 71$). We found no significant differences in RINI between age ($p = 0.73$) or sex ($p = 0.23$) classes, but we did observe significant differences

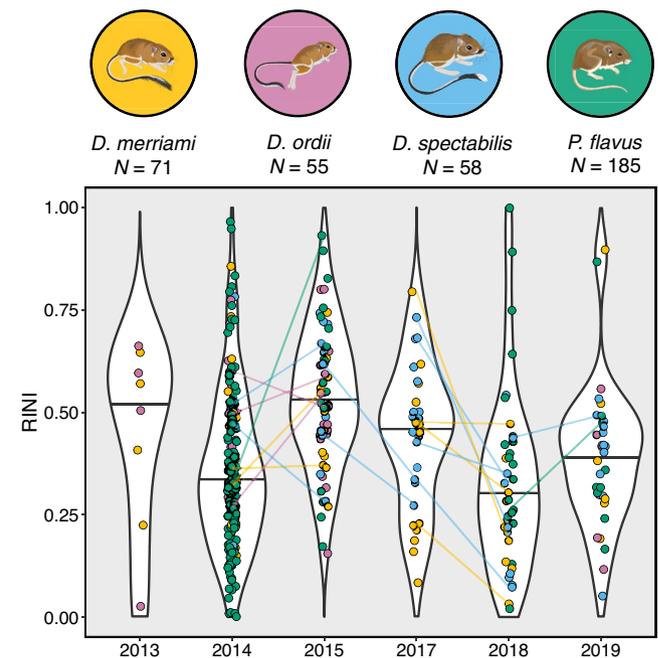


FIGURE 1 Relative individual niche index (RINI, normalized and square root transformed) of Merriam's kangaroo rat *Dipodomys merriami* (gold), Ord's Kangaroo rat *Dipodomys ordii* (violet), banner-tailed kangaroo rat *Dipodomys spectabilis* (blue) and silky pocket mice *Perognathus flavus* (green) across 6 years at the Sevilleta NWR. Violin plots indicate density of RINI estimates, ranging from specialization (0) to generalization (1). Black lines represent median RINI for the community each year, and coloured lines connect individuals across years. Illustrations by Juliana Masseloux

between species ($p = 0.02$). RINI also did not differ across webs ($p = 0.79$) but did differ by season ($p < 0.001$), with spring animals exhibiting lower RINI values than fall animals or individuals trapped across both seasons. Ultimately, we observed widespread variation in RINI at the individual, population and community levels across years (Figure 1; Figure S3).

Our adjusted RINI approach yielded similar results to the original Sheppard et al. (2018) approach (Figure S4); thus, we report only our adjusted metric hereafter. Competition was the primary driver of specialization in our system, but we found evidence that all four ecological stressors influence individual foraging. Indeed, our top model, which held >80% of the weight (Table S3), found that both intraspecific competition ($\beta = -0.44$; 95% Credible Interval [CI] = -0.26 to -0.66) and interspecific competition ($\beta = -0.71$; CI = -0.37 to -1.03) had significantly negative effects on RINI, indicating greater individual diet specialization when competition is high (Figure 2a,b). We also observed significant but contrasting effects of resource availability ($\beta = 0.30$; CI = 0.12 – 0.49) and resource diversity ($\beta = -0.12$; CI = -0.02 to -0.22) on individual foraging strategies (Figure 2c,d). Our top model identified significant interactions between competition and resources (Figure 3). First, we found that intraspecific and interspecific competition interacted ($\beta = -0.53$; CI = -0.15 to -0.92) such that RINI was minimized (i.e. high specialization) when both interspecific and intraspecific competition were high (Figure 3a). Second, we observed

a significant interaction between interspecific competition and resource abundance ($\beta = 0.41$; CI = 0.13 – 0.69) where the effect of interspecific competition was lessened (i.e. higher generalization) when plant biomass was high (Figure 3b). Lastly, the number of isotope measurements used to calculate SEA_{Ind} also had a significant influence on RINI ($\beta = 0.17$; CI = 0.08 – 0.27). We observed no significant species-specific responses (Figure S4). Lastly, we found that SEA_{Ind} and TNW had opposing effects on RINI (Figure 4), but SEA_{Ind} ($\beta = 1.15$; CI = 1.11 – 1.20) was the most proximate mechanism influencing IS, with twice the effect of TNW ($\beta = -0.41$; CI = -0.36 to -0.46). Both models exhibited high fit with posterior predictive checks accurately simulating response variables across species (Figure S5).

The most supported CJS model received nearly 70% of the weight and indicated that ϕ_{month} was best predicted by RINI (Figure 5; Table S5), while detection probability (p) was high and varied only by species (all $p \geq 0.78$, Table S4). Age and pseudo-replication had no impact on our results (Figure S6). For all species, survival was higher among the most generalized individuals (i.e. highest RINI; $\phi_{\text{month}} = 0.97$, 95% CI = 0.93 – 0.98) compared to the most specialized (i.e. lowest RINI; $\phi_{\text{month}} = 0.87$, 95% CI = 0.82 – 0.91). Compounded over the course of a year, the estimated annual survival probability of the most generalized individuals ($\phi_{\text{annual}} = 0.66$, 95% CI = 0.44 – 0.81) was nearly four times that of the most specialized ($\phi_{\text{annual}} = 0.18$, 95% CI = 0.09 – 0.31).

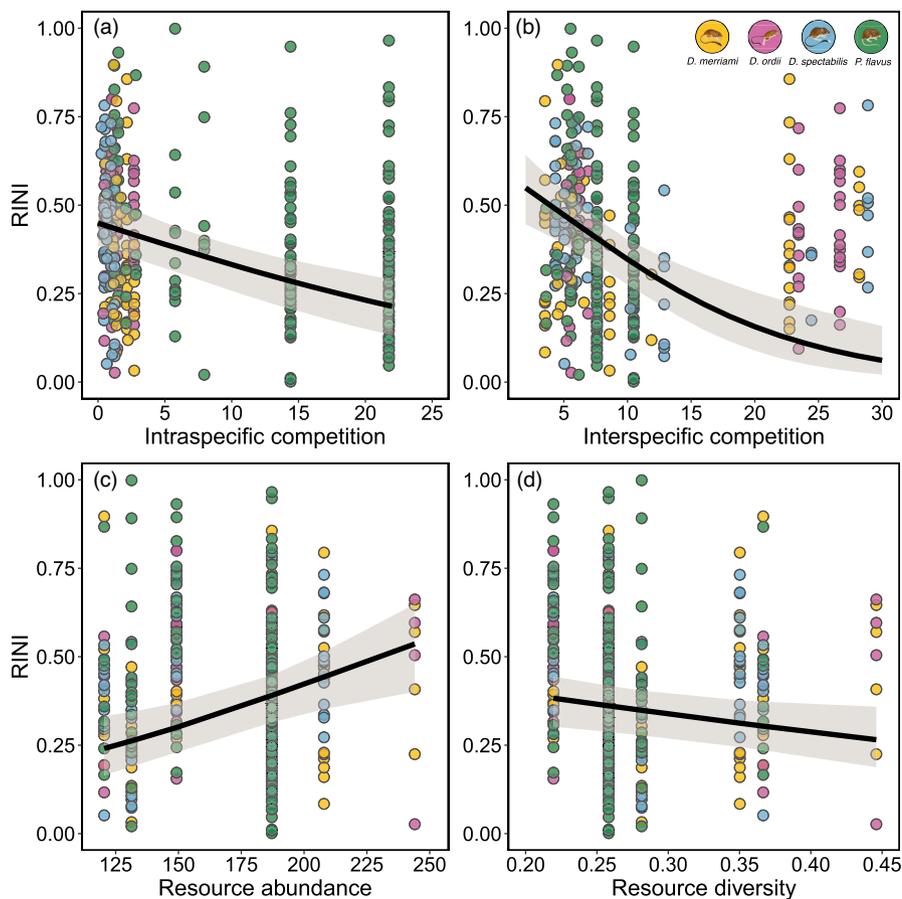


FIGURE 2 Effects of environmental drivers on individual foraging strategies (RINI; relative individual niche index, normalized and square root transformed) ranging from specialization (0) to generalization (1). (a) Median response of RINI (black line) to intraspecific competition (relative abundance of conspecifics), (b) interspecific competition (relative abundance of heterospecifics), (c) resource abundance (plant biomass [g]), and (d) resource diversity (Simpson's diversity index). Grey ribbons denote 95% credible intervals and coloured circles represent individuals

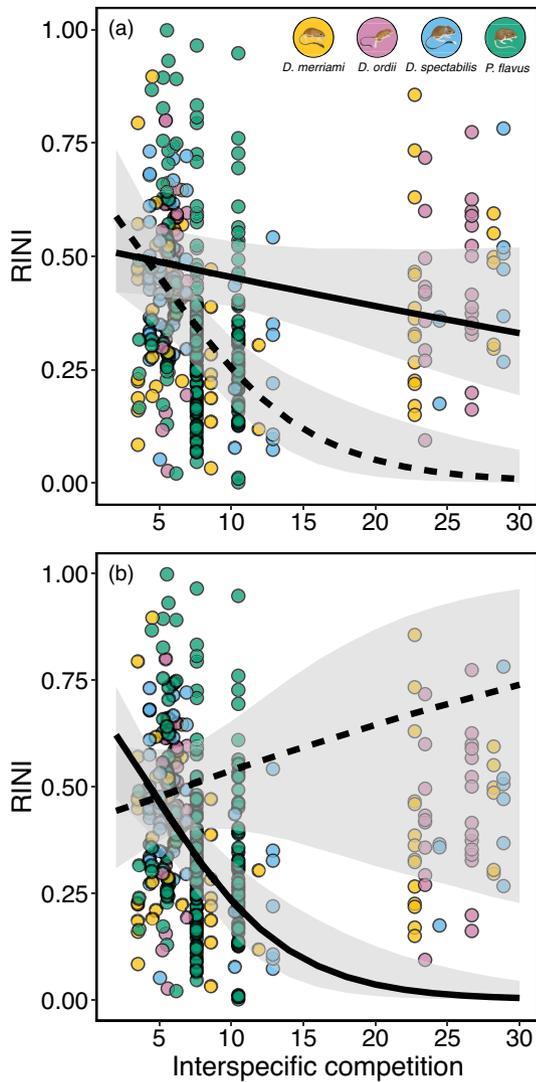


FIGURE 3 Interacting effects of environmental drivers on individual foraging strategies (RINI; relative individual niche index, normalized and square root transformed) ranging from specialization (0) to generalization (1). (a) Predicted median response of RINI to the interaction between intraspecific (conspecific density) and interspecific competition (heterospecific density). Solid black line illustrates response to interspecific competition at the lowest observed intraspecific competition, and dashed line illustrates median response to interspecific competition at the highest observed intraspecific competition. (b) Predicted median response of RINI to the interaction between resource abundance (plant biomass [g]) and interspecific competition (heterospecific density). Solid black line illustrates response to interspecific competition at the lowest observed resource abundance, and dashed line illustrates median response to interspecific competition at the highest observed resource abundance. Grey ribbons denote 95% credible intervals and coloured circles represent individuals

4 | DISCUSSION

All heteromyid species exhibited substantial inter-annual diet variation at the individual, population and community levels, and this

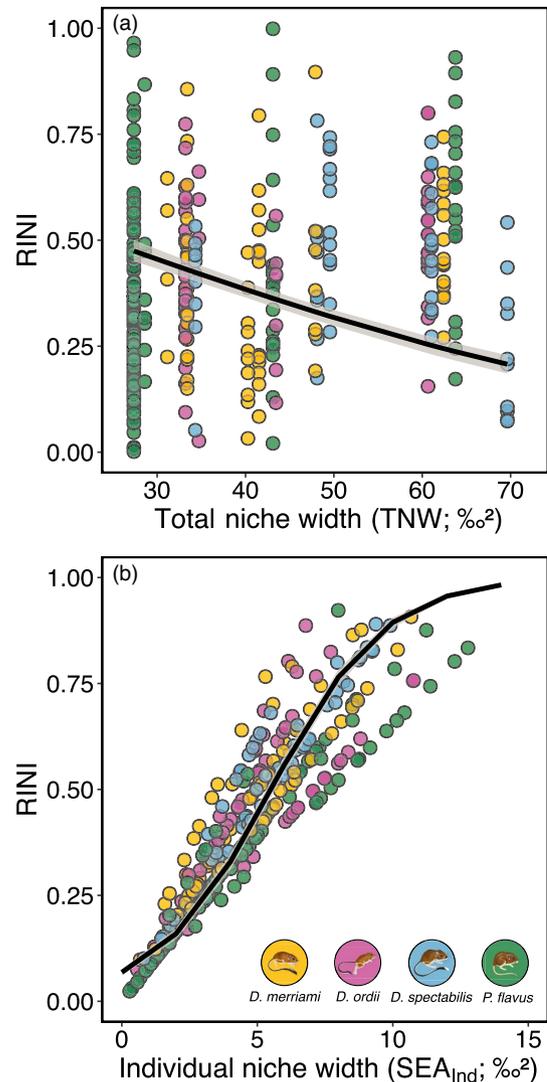


FIGURE 4 Predicted effects of (a) total niche width (TNW) and (b) individual niche width (SEA_{Ind}, square root transformed) on individual diet specialization (RINI; relative individual niche index, normalized and square root transformed), ranging from complete specialization (0) to complete generalization (1). Black lines denote median response, grey ribbons denote 95% credible intervals and coloured circles represent individuals

variation was primarily driven by contraction of trophic niches in response to interspecific and intraspecific competition (Figures 1–4). These results support our hypothesis that heteromyid rodents forage in accordance with classical niche theory and increase dietary specialization to minimize competitive overlap (Roughgarden, 1974; Van Valen, 1965). Contrary to niche theory, however, individual specialists obtained no apparent fitness benefits and instead experienced lower monthly survival than generalist foragers (Figure 5). Nevertheless, we found that high resource abundance offset the impact of competition and enabled generalization (Figure 3b), suggesting that climate-mediated resource availability ultimately drives the relationship between competition, foraging and consumer fitness.

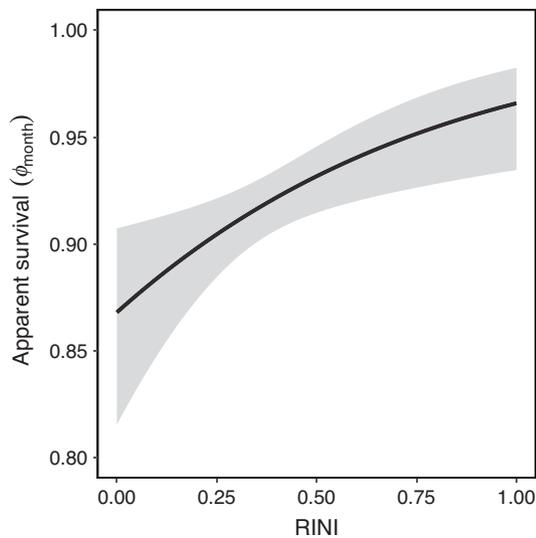


FIGURE 5 Predicted response of apparent monthly survival (ϕ_{month} ; black line) to individual foraging strategies (RINI; relative individual niche index, normalized and square root transformed) for all species, ranging from specialization (0) to generalization (1). Grey ribbon represents 95% confidence interval

Individual diet variation is now widely recognized (Bolnick et al., 2003, 2007) and the emergent theory suggests intraspecific competition, interspecific competition, resource abundance and resource diversity all mediate foraging dynamics (Araújo et al., 2011). We found support for each of these ecological stressors influencing individual diets. Consistent with niche theory and empirical studies, intraspecific competition significantly increased individual diet specialization in all heteromyid species, presumably to minimize competitive interactions with conspecifics (Noble et al., 2019; Svanbäck & Bolnick, 2007). Likewise, interspecific competition significantly increased individual specialization, as did the interaction between intraspecific and interspecific competition. This result runs contrary to the Niche Variation Hypothesis (Van Valen, 1965) which contends that interspecific competition limits TNW, thereby by restricting access to alternative resources and promoting individual generalism (Araújo et al., 2011). However, there is mixed empirical support for this prediction (Bolnick et al., 2010; Cloyd & Eason, 2016), and our findings are consistent with recent work showing interspecific competition increases specialization via contractions in individual niche width (Costa-Pereira et al., 2018). We suggest this incongruence stems from past studies neglecting the interactive effects of competition on individual diets. Indeed, we found that individual specialization was most prevalent when both interspecific and intraspecific competition were high, but specialization decreased if either form of competition was reduced. Interspecific competition has long been recognized as a driver of foraging dynamics among desert rodents (Bowers, 1982; Smigel & Rosenzweig, 1974), as have resource specializations that promote coexistence (Rosenzweig & Winakur, 1969). Thus, we posit that foraging strategies of heteromyid rodents adhere to classical niche theory across multiple levels of biological organization such that interspecific competition

limits population niche expansion and heterospecific diet overlap, while intraspecific competition promotes individual niche contractions that minimize overlap among conspecifics. This hypothesis is also supported by the significant interaction between interspecific competition and resource abundance which revealed high plant biomass alleviates the impact of interspecific competition on individual specialization. Lastly, we found significant but opposing effects of resource abundance and resource diversity on individual diets: plant abundance (i.e. biomass) increased individual generalization and plant diversity increased specialization. As noted, elevated plant abundance reduced the effects of competition and promoted generalism via individual niche expansion, whereas high plant diversity likely provides 'ecological opportunity' that promotes prey switching and dietary specialization (Araújo et al., 2011). The strength of these responses, however, may have been impacted by high species abundances during a 2014 population 'boom'—a characteristic trait of desert rodent populations (Brown & Zeng, 1989; Ernest et al., 2000; Noble et al., 2019)—though the directional effect of all environmental drivers was consistent across models (Figure S4). Though often considered independently, our results highlight the interactive effects of ecological stressors on individual foraging strategies. Future studies should consider similar approaches to assess the context dependency of these interactions.

Individual diet specialization is generally predicted to maximize individual fitness by limiting competitive overlap with conspecifics (Roughgarden, 1972). Contrary to theoretical predictions, we found that individual specialists exhibited substantially lower survival than generalists (Figure 4). This is one of the first studies to directly assess survival as a function of individual foraging strategy, but our findings are consistent with empirical assessments of other fitness proxies, particularly in stochastic resource environments. For example, Costa-Pereira, Toscano, et al. (2019) found that *Leptodactylus* frogs with specialized diets had higher parasite loads and lower reproductive investments than dietary generalists in seasonal wetlands, while Balme et al. (2020) observed fewer cubs sired by specialized male leopards *Panthera pardus* during a drought. We documented higher survival of generalists in our desert study site that exhibits considerable inter-annual resource variation (Noble et al., 2019), and over the course of our 6-year study both resource abundance and diversity varied twofold. Our results augment empirical and theoretical research indicating that individual generalization is a fitness maximizing strategy when resource availability is dynamic (Futuyma & Moreno, 1988; Woo et al., 2008). Nevertheless, we detected a wide range of foraging strategies both within and between years, despite the apparent benefits of generalization as an individual strategy. Thus, a combination of dietary generalism and specialization at the population level may represent a successful strategy in stochastic ecosystems because segments of the population will experience greater fitness under different resource scenarios (i.e. portfolio effects; Bolnick et al., 2011; Woo et al., 2008).

We propose three, non-mutually exclusive mechanisms that may regulate the relationship between consumer foraging and fitness in our system. First, generalization can increase fitness by improving

body condition (Lefcheck et al., 2013), most likely via nutrient balance or toxin dilution (Bernays et al., 1994; Hägele & Rowell-Rahier, 1999). Indeed, generalization may be particularly important for herbivores like heteromyid rodents who consume desert flora that are both low in nutrients (e.g. protein) and high in secondary metabolites (Henderson, 1990; Reichman, 1977). Furthermore, foraging and body condition likely interact with a second potential mechanism, predation risk. Predation is a fundamental driver of heteromyid rodent communities (Kotler, 1984), and mortality is highest among mobile individuals (Daly et al., 1990). Indeed, considerable research has shown that heteromyids are tethered to underground burrows and forage nocturnally in short bouts to minimize predation risk (Daly et al., 1992; Kenagy, 1973; Rosenzweig, 1974). Yet, heteromyids also compete strongly for patchy resources (Price, 1978; Reichman, 1977; Schroder, 1979) such that when competition is high or resources are low individuals are predicted to spend more time foraging above-ground (Brown & Munger, 1985). We posit that individual specialists allocate more foraging time and movement than generalists to acquire specific resources in a highly competitive landscape, ultimately leading to higher mortality via predation. This is likely exacerbated if specialized individuals also suffer from reduced body condition that enhances predation risk (Mcnamara & Houston, 1987). Lastly, specialization may not be a choice, but rather the consequence of an ideal despotic distribution where inferior competitors are relegated to risky habitats with limited access to diverse resources (Fretwell & Lucas, 1970; Harper, 1982). Indeed, heteromyids exhibit territoriality (Behrends et al., 1986; Bowers et al., 1987) and interspecific aggressions (Frye, 1983) that likely govern home ranges and access to high-quality forage, and this spatiotemporal niche partitioning can interact with predation to drive differential survival (Calsbeek & Sinervo, 2002; van den Hout et al., 2014). Ultimately, it is likely that individual behaviors, predation and spatiotemporal niche partitioning all impact the observed relationship between consumer foraging and fitness (Araújo et al., 2011), but untangling the proximate effects of these processes requires further research.

Diet-mediated fitness variation has considerable implications for population dynamics, as differential survival and reproduction are hypothesized to enable coexistence among heteromyid rodents (Brown & Munger, 1985; Brown & Zeng, 1989; Kotler, 1984). We found that survival was lower among specialists for all species, but our second-ranked model yielded slight support for differences in monthly survival between species and years ($w = 0.16$; Table S5). Similarly, a single-factor ANOVA revealed significant differences in RINI between species, random effects detected slight differences in mean RINI values between species, and a post-hoc ANOVA found a significant interaction between species and year ($p = 0.02$; Figure 1). This suggests that the average degree of specialization, and subsequently survival, varied annually among species, with likely implications for population and community dynamics. In particular, *Dipodomys* spp. exhibit unusually slow life histories for rodents, often surviving >3 years with low annual reproductive investment (~0–4 offspring per year; Waser & Jones, 1991; Zeng & Brown, 1987). Thus, even small changes in diet-mediated adult survivorship between species

may have strong effects on population growth and coexistence of competitors (Brown & Munger, 1985). Though we found individual specialization decreased survival, specialized individuals could trade this off for increased reproduction. Indeed, individual specialization has been shown to increase reproductive success (Golet et al., 2000), but this foraging strategy often coincides with higher risk (Annett & Pierotti, 1999). We did not quantify reproduction in this study, but understanding the trade-offs between foraging, survival and reproduction will be key to determining how diet-mediated fitness variation impacts population and community dynamics.

Competitively mediated individual diet specialization and its resulting fitness variation can have significant evolutionary consequences, particularly if foraging strategies are consistent and coupled with heritable phenotypic traits (Bolnick et al., 2003; Dieckmann & Doebeli, 1999). We found widespread variation in foraging strategies between individuals, with some animals even shifting strategies across years (Figure 1). However, we did not observe any discrete morphological variation tied to foraging, and increasing evidence suggests that cryptic behavioural or physiological syndromes also generate foraging variation (Maldonado et al., 2019; Toscano et al., 2016). For instance, Maldonado et al. (2019) showed that phenotypic plasticity in digestive enzymes enables increased generalization. Thus, it is possible that physiological variation may underlie the foraging patterns observed here, in which case increased survival of generalists would also represent directional selection for plastic, generalist phenotypes in a stochastic resource landscape. To understand the mechanistic links between environmental variation, foraging strategies and evolutionary feedbacks, future research must quantify the heritability of cryptic traits associated with foraging variation (e.g. behaviour, physiology), but should also focus on repeated measures of individuals to quantify the plasticity of these traits as they relate to foraging patterns and fitness variation.

We note a potential caveat to these results - individual sample sizes and timing of sampling could have impacted our results. For example, we found that individuals with more isotope measurements also had higher RINI values. This is because resource availability (e.g. C_3 vs. C_4 production) varies monthly with precipitation, so individuals captured in more months have opportunities to consume different resources (i.e. generalize). Nevertheless, our models accounted for this sampling variation and still found significant, interactive effects of competition and resources. Samples were also dispersed across distinct seasons, and we found significantly lower RINI values in spring. Thus, we reran all models post-hoc including season as a random effect. We observed nearly identical results (Figure S4), indicating that neither sample size nor temporal variation was likely to influence our findings. Yet, because generalization increased with captures, it raises the question of whether survival estimates were also affected by sample size. To assess this, we added the same measurement term from the mixed models to our top survival model. We found that the strength of the relationship between generalization and survival did decrease with the number of captures; however, the overall trend was only reduced for individuals captured ≥ 6 times, <20% of all data (Figure S7). Thus, the relationship between

individual generalism and survival appears robust. Ultimately, these results indicate that our individual-based isotope and survival models accurately captured foraging variation and its fitness consequences, but we caution future researchers to scrutinize sample sizes and temporal spacing when employing RINI or other individual-based metrics of foraging strategy.

We show that competition and resources interact to shape individual foraging strategies and fitness, consistent with classical niche theory. However, our results indicate that heteromyid consumers are ultimately limited by bottom-up processes such that high resource abundance can alleviate competitive interactions and their cascading effects on individual foraging and fitness. Like many dryland ecosystems, though, the Chihuahuan Desert climate is becoming increasingly stochastic, triggering changes in resource abundance and diversity (Collins et al., 2020; Rudgers et al., 2018). This shifting resource availability has considerable potential to affect consumers (Kazeneel et al., 2020; Noble et al., 2019), and our results indicate that diet-mediated fitness variation could be the proximate mechanism restructuring consumer communities in this rapidly changing arid ecosystem.

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CONFLICT OF INTEREST

The authors declare no conflicts of interest.

AUTHORS' CONTRIBUTIONS

All authors conceived of the study; P.J.M. and S.D.N. collected the data; P.J.M. conducted all the statistical analyses and wrote the first draft of the manuscript. All authors contributed substantially to revisions.

DATA AVAILABILITY STATEMENT

All data and R scripts are available at <https://doi.org/10.6084/m9.figshare.14378813> (Manlick et al., 2021).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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