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Intraspecific dietary variation in niche partitioning within a community of ecologically similar snakes

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Abstract
Niche partitioning is an important mechanism for allowing ecologically similar species to coexist, contributing to biodiversity and the functioning of ecological communities. Species partition niches by taking advantage of environmental heterogeneity. However, niche partitioning and species coexistence investigations often do not include intraspecific variation or individual differences like sex and body size even though these factors can have important ecological consequences. Such intrapopulation factors can reduce the number of individuals among species that overlap in resource use and potentially facilitate coexistence. Using stable isotopes (δ^{13}C and δ^{15}N), we quantified dietary differences among three ecologically similar, sympatric watersnake species: *Nerodia erythrogaster*, *N. rhombifer* and *N. sipedon*. Additionally for each species, we determined intraspecific dietary patterns and determined how those within-species patterns may contribute to dietary niche partitioning among species. *Nerodia erythrogaster* fed more on terrestrial prey, while *N. rhombifer* fed at higher trophic levels. Females across species fed at higher trophic levels than did males, and isotopic variance differed between the sexes in *N. sipedon*. Larger watersnakes foraged at higher trophic levels and fed more on terrestrial prey. Each watersnake species had a distinct diet that overlapped to some degree with the other species' diets, but these diets varied both between sexes and among size groups within species. This inter- and intraspecific dietary variation can facilitate species coexistence by reducing the number of individuals from all species that use the same resources. Intraspecific variation can add important and nuanced layers to the evolution of species coexistence, and research on interspecific niche relationships needs to increasingly consider the effects of these intraspecific variations.

Keywords Coexistence · Dietary variation · Intraspecific · Niche partitioning · Ontogeny · Trophic level

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Introduction

Niche partitioning is an important ecological concept in part because it can reconcile theoretical and laboratory studies that demonstrate competitive exclusion (Gause 1934; Hutchinson 1961; MacArthur and Levins 1967) with field observations and studies that demonstrate widespread coexistence among ecologically similar species (MacArthur 1958; Hutchinson 1959; Hardin 1960). Interspecific niche partitioning is ubiquitous in all ecosystems and is a key component to understanding biodiversity and community structure (Schoener 1974; Pianka 1975; Hadi et al. 2012). Slight differences in morphology and behavior that can facilitate the partitioning of limited resources have evolved among closely related or ecologically similar species (Roughgarden 1976; Gittleman and Van Valkenburgh 1997; Dayan and Simberloff 2005). Species can partition dietary resources in several different ways, often taking advantage of spatial or temporal resource heterogeneity (Schoener 1968; Pianka 1973, 1975). Ecologically similar species can forage in different habitats or microhabitats (van Beest et al. 2014; Lürig et al. 2016), on different resources (Langeland et al. 1991; Vassilieva et al. 2017), or at different trophic levels (Cherel et al. 2010; Beaulieu and Sockman 2012).

Recent work has demonstrated the importance of intraspecific dietary variation and niche partitioning within species and populations (Sheppard et al. 2018; Costa-Pereira et al. 2019; Falke et al. 2020). In species that are dietary generalists, individuals often use only a subset of the dietary items used by the species as a whole (Bolnick et al. 2007; Woo et al. 2008). Intraspecific resource variation can occur between the sexes and among ontogenetic stages, morphotypes, and individuals (Sabatés and Saiz 2000; Bolnick et al. 2003; Mata et al. 2016; Egan et al. 2018). Diets can differ dramatically across ontogeny and between sexes, the most common contributors to intraspecific dietary variation. Ontogenetic niche shifts are widely documented (Olson 1996; Rudolf and Rasmussen 2013; Nakazawa 2015; Samplonius et al. 2016), and are largely driven by body size differences (Cloyed and Eason 2017; Dalponti et al. 2018). Similarly, sexual size dimorphisms often result in dietary and trophic differences between the sexes (Bearhop et al. 2006; Zalewski 2007; Voigt et al. 2018). These types of intraspecific variations in resource use reduce competition among conspecifics by decreasing the number of individuals that are competing for the same resources (Svanbäck and Bolnick 2005; Bolnick et al. 2007).

Given that intraspecific variation reduces the number of individuals that use certain resources, it can also affect interspecific niche partitioning. Among species that vary in size through ontogeny, only certain ontogenetic groups may overlap in resource use (Canavero et al. 2014; Kliemann et al. 2019); for example, smaller, younger individuals of a larger species may overlap in resource use with larger, older individuals of a smaller species (Cloyed and Eason 2017). Likewise, differential resource use between the sexes can lead to each sex overlapping in resource use with different species (Broekhuis et al. 2018). The net effect of these types of intraspecific variation is a reduction in the number of individuals from each species that overlap in resource use with other species, and thus they may facilitate species coexistence (Lichstein et al. 2007; Lasky et al. 2014; Cloyed and Eason 2017).

Here we used stable isotopes from three watersnake species, *Nerodia erythrogaster* (plain-bellied watersnake), *N. rhombifer* (diamondback watersnake), and *N. sipedon* (northern watersnake), to investigate niche partitioning among species and how intraspecific diet variation mediates that partitioning. Although there is some disagreement about the monophyly and phylogeny of the genus *Nerodia*, *N. erythrogaster* and *N. sipedon* are more closely related to one another than to *N. rhombifer* (Alfaro and Arnold 2001; McVay

et al. 2015). These watersnake species are dietary generalists with considerable overlap in diet, feeding mainly on fish and amphibians (Mushinsky and Hebrard 1977; Kofron 1978; Plummer and Goy 1984; Himes 2003). All three species often coexist, may use similar habitats and are found in or near bodies of water (Tucker 1995; Burbrink et al. 1998; Laurent and Kingsbury 2003). Watersnakes are also known to partition dietary resources intraspecifically between sexes, as females are often larger (Mushinsky et al. 1982; King 1993), and ontogenetically, as they are gape-limited predators that change their diets as they grow (Mushinsky et al. 1982; Plummer and Goy 1984). Specifically, we determined how sex, size and their interaction influenced diet, niche partitioning and species coexistence among sympatric watersnakes. We predicted that watersnake species would overlap in their dietary resources but that intraspecific variability based on snake sex and size would result in only subgroups of each species overlapping in diet use.

Methods

Research site

We performed our study at Hardy Slough Tract (37° 50′ 32.50″ N, 87° 45′ 1.91″ W), a 100-ha section within the Sloughs Wildlife Management Area (Henderson County, Kentucky, USA) that is managed primarily for wintering waterfowl by the Kentucky Department of Fish and Wildlife Resources. Hardy Slough Tract is located 2 km southeast of the Ohio River and includes moist soil units (shallow wetlands delineated by a levee system), scrub-shrub wetlands and palustrine forest. Water primrose (*Ludwigia* sp.), smartweed (*Polygonum* sp.), water lily (*Nuphar* sp.), cattail (*Typha* sp.), buttonbush (*Cephalanthus occidentalis*), black willow (*Salix nigra*) and hackberry (*Celtis occidentalis*) were the dominant plant species within Hardy Slough Tract.

Snake and prey sampling

We collected snake and prey data from April to September in 2013 and 2014 and captured snakes with a variety of methods, including hand capture, cover boards, stand-alone aquatic funnel traps and drift fence-funnel traps arrays (terrestrial and aquatic) (Fitzgerald 2012). For each captured watersnake, we measured snout-vent length (SVL) and determined sex by cloacal probing. We marked snakes using subcutaneous pit tags and unique ventral scale-clip patterns to identify recaptures (Gibbons and Andrews 2004; Plummer and Ferner 2012) and used the clipped scales for stable isotope analysis. To prevent sampling watersnakes that might retain maternal isotopic signatures, we obtained scale clips only from watersnakes ≥ 275 mm SVL. We released each snake at its capture location.

To determine prey availability and obtain prey stable isotope samples, we sampled potential snake prey (e.g., amphibians, fishes, invertebrates) weekly using a combination of traps designed for different habitats, prey types and prey sizes. Traps were open for 2 days and nights (48 h) every week during the sampling periods. For aquatic prey, we used stand-alone aquatic funnel traps, aquatic hoop traps and aquatic drift fence-funnel trap arrays (Hubert et al. 2012). The upper 25% of each aquatic funnel trap was above water to prevent the drowning of non-target animals. For terrestrial prey, we used drift fence-funnel trap arrays with pit-fall traps (5-gallon buckets) (Fitzgerald 2012). Drift fences were built with silt fencing and wooden stakes. Prey items that we captured and recorded included

amphibians, fish and crayfish. Anurans were recorded as tadpoles, metamorphs (i.e., tadpoles that had well-defined legs and thus were beginning to show adult traits), froglets (recently metamorphosed frogs with no tadpole traits) or adults (McDiarmid and Altig 1999).

Stable isotope analysis

We performed stable isotope analyses using scale clips from each individual watersnake and tissue samples obtained from a subset (20%) of captured potential prey animals. Prey samples included whole bodies of anuran tadpoles, anuran metamorphs and fishes with standard length < 50 mm (Sanderson et al. 2009; Trakimas et al. 2011); toe clips of the tip of the longest toe on a hind foot for froglets and adult frogs (Trakimas et al. 2011); a caudal fin sample (7 mm diameter) for fishes with standard length ≥ 50 mm (Sanderson et al. 2009); the distal end of salamander tails (3 mm; Milanovich and Maerz 2012); and a 3 mm sample of the uropod exoskeleton of crayfish (Hollows et al. 2002). While sampling the whole body of prey is ideal, sampling specific tissues or section of adult individuals prevented unnecessary sacrifice of animals, and the prey tissues we sampled provide information regarding their habitat use (Sanderson et al. 2009; Milanovich and Maerz 2012; Cloyed and Eason 2016, 2017).

Samples were stored in a − 80 °C freezer until they were dried in an oven for 48 h at 60 °C. Samples were then stored in plastic vials in darkness, a standard procedure for storing dry samples. We did not extract lipids because carbon to nitrogen ratios were 3.16–3.18 (Tronquart et al. 2012). We homogenized samples with mortar and pestle when necessary; samples weighed 1.24 mg ± 0.34 (mean ± SE; all means are reported ± SE) and were placed in 3.5 × 5 mm tin capsules. All stable isotope samples were analyzed for carbon ($\delta^{13}C$) and nitrogen ($\delta^{15}N$) isotope values at the University of California, Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced with a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). Stable isotope values were expressed in standard delta notation (δ) in parts per thousand (‰), where $\delta X = (R_{sample}/R_{standard} - 1) \times 1000$, with R_{sample} and $R_{standard}$ being the molar ratios of C^{13}/C^{12} and N^{15}/N^{14} of the sample and the standard reference material. The standard reference material was Vienna PeeDee Belemnite for carbon and atmospheric N_2 for nitrogen. Instrument precision was 0.07‰ for $\delta^{13}C$ and 0.13‰ for $\delta^{15}N$.

Statistical analyses

We used $\delta^{13}C$ or $\delta^{15}N$ stable isotope values to examine niche partitioning among species, between sexes and across snake sizes (< 450 mm SVL, 450–650 mm SVL, 650–850 mm SVL and > 850 mm SVL). We determined these size classes based on the size range of captured individuals across all three species, having an adequate sample size in each class, and using size divisions (200 mm increments) that would be adequate to identify potential shifts in diet. *Nerodia sipedon* was not included in the largest size class because all captured *N. sipedon* had a SVL < 850 mm. We used general linear models with $\delta^{13}C$ or $\delta^{15}N$ as a dependent variable, and watersnake species, sex, snake size classes, year and all possible interactions as independent variables. When main effects were significant, we used followup Tukey-Kramer multiple comparison tests. We also performed regression analyses comparing watersnake species, with $\delta^{13}C$ and $\delta^{15}N$ as dependent variables and SVL (mm) as the independent variable. In this study, we utilized SVL as a size class predictor variable

in some analyses and as a continuous variable in other analyses; the size classes enabled us to compare variances and group means, and the continuous variable more precisely determined the relationship of snake size with isotopic change.

We used isotopic variances (δ^{13}C and δ^{15}N) to investigate dietary niche width across species, sexes and sizes with higher variance indicating feeding across a greater number of habitats or trophic levels (Bearhop et al. 2004; Fink et al. 2012). We used Levene's test for homogeneity of variance and Tukey-type multiple comparison tests to determine differences in isotopic variances among species and between sexes (Fink et al. 2012). We investigated isotopic variance due to size only within species, so as to reduce the probability of Type I error, by dividing each species into 100-mm size classes (300–399 mm SVL, 400–499 mm SVL, etc.) and then using linear and quadratic regressions between isotopic variance and size class. When both regression types were significant or marginally significant, we used Akaike Information Criterion (AIC) values to determine which better fit the data (Burnham and Anderson 2002).

We used the Bayesian stable isotope mixing models, *Stable Isotope Analysis in R* (SIAR v4; Parnell et al. 2010) to estimate the proportions of prey (dietary groups) in consumer diets (snake species, sex, and size classes). We employed trophic discrimination factors of 0.17‰ ($\pm$ 0.03) for δ^{13}C and 2.8‰ ($\pm$ 0.11) for δ^{15}N, which were obtained from green sea turtles, *Chelonia mydas* (Seminoff et al. 2006), the most closely related reptile for which we had discrimination information for skin. All reported watersnake stable isotope results for this study have been corrected by subtracting these trophic discrimination factors from the original isotope data. Results were reported as mean proportion of each resource for each of the snake groups along with 95% credible intervals (Parnell et al. 2010). All other statistical analyses were performed using SAS software (SAS Institute 2000), and statistical tests were considered to be significant at $\alpha = 0.05$. If data did not meet assumptions for parametric analyses, we performed square root transformations on dependent variables.

Results

Analyses of isotopic ratios among and within species

We obtained stable isotope samples from 299 potential prey individuals (154 in 2013 and 145 in 2014). Stable isotope values of prey clustered into six groups: aquatic salamanders, tadpole/metamorph anurans, froglet/adult anurans, crayfish, Lepisosteidae and all other fishes. For simplicity, we will refer to the non-lepisosteid fishes as 'fishes.' The δ^{13}C and δ^{15}N residuals were both normally distributed, but Levene's test for homogeneity of variance was significant for δ^{15}N ($F_{2,330} = 5.50$, $P = 0.004$), and we accordingly used the square roots of δ^{15}N values for analyses of niche overlap.

Snake stable isotope values were obtained from 333 individuals (163 in 2013 and 170 in 2014), which included 116 *Nerodia erythrogaster*, 106 *N. rhombifer* and 111 *N. sipedon*. The general linear model on δ^{13}C values was significant ($F_{23,309} = 14.25$, $P < 0.0001$), with significant differences among species ($F_{2,309} = 103.09$, $P < 0.0001$; Fig. 1) and size classes ($F_{3,309} = 32.19$, $P < 0.0001$), but not between years ($F_{1,309} = 0.09$, $P = 0.763$), between sexes ($F_{1,309} = 0.39$, $P = 0.535$) or among interactions ($P \geq 0.10$). Tukey–Kramer multiple-comparison tests showed that in all species, δ^{13}C values increased with SVL and that *N. erythrogaster* had enriched δ^{13}C values compared to *N. rhombifer* and *N. sipedon*; there were no other differences among
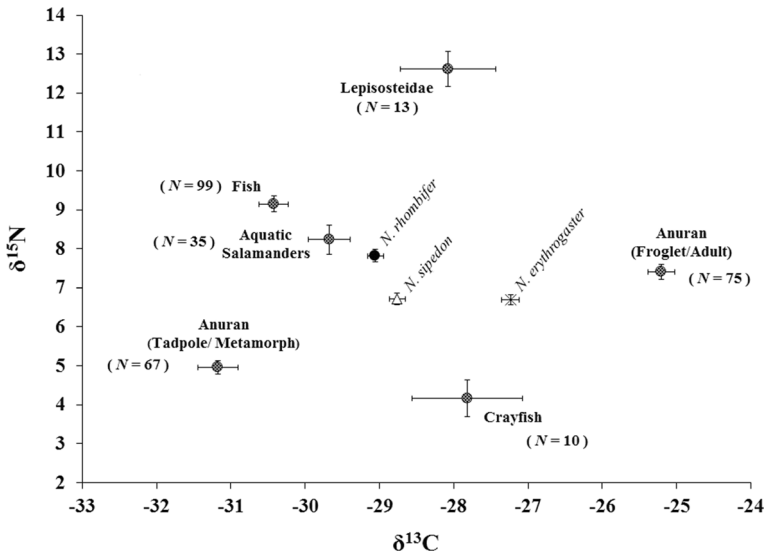
Fig. 1 Mean (± 1 SE) watersnake and prey stable isotope (δ^{13}C and δ^{15}N) values. *Nerodia erythrogaster* mean stable isotope values are indicated by cross, *N. rhombifer* by filled circle, and *N. sipedon* by triangle. Prey mean stable isotope values are indicated by crosshatch circles. *N* in parentheses refers to prey sample sizes

species. The general linear model for δ^{15}N values was also significant ($F_{23,309} = 16.74$, $P < 0.0001$), with significant differences for species ($F_{2,309} = 31.86$, $P < 0.0001$), sex ($F_{1,309} = 19.98$, $P < 0.0001$) and size classes ($F_{3,309} = 95.36$, $P < 0.0001$) but no differences in δ^{15}N values between years ($F_{1,309} = 0.04$, $P = 0.843$) or interaction effects ($P \geq 0.282$). Tukey–Kramer multiple comparison tests revealed several differences among snake groups. First, *N. rhombifer* had significantly more enriched δ^{15}N values than both *N. sipedon* and *N. erythrogaster*, with the latter two having similar δ^{15}N values. Second, female watersnakes (mean δ^{15}N $= 7.33‰ \pm 0.13$) had more enriched δ^{15}N values than males ($6.72‰ \pm 0.12$). Finally, there was no significant difference in δ^{15}N values between snakes in the two largest size classes (> 850 mm and 650–850 mm SVL), but all other size class comparisons showed significant differences, with larger snakes having more enriched δ^{15}N levels (Fig. 2).

Within species, individuals with longer SVL had more enriched δ^{13}C and δ^{15}N values (δ^{13}C: *N. erythrogaster* $F_{1,114} = 33.28$, $P < 0.0001$; *N. rhombifer* $F_{1,104} = 48.86$, $P < 0.0001$; *N. sipedon* $F_{1,109} = 26.98$, $P < 0.0001$) (δ^{15}N: *N. erythrogaster* $F_{1,114} = 122.93$, $P < 0.0001$; *N. rhombifer* $F_{1,104} = 113.54$, $P < 0.0001$; *N. sipedon* $F_{1,109} = 77.64$, $P < 0.0001$) (Fig. 3). The relationship between δ^{13}C values and SVL was similar across species ($F_{2,330} = 0.24$ $P = 0.790$). However, there was a significant interaction between SVL and watersnake species for δ^{15}N values ($F_{2,330} = 3.65$, $P = 0.027$); δ^{15}N values increased significantly more with size for *N. sipedon* compared to *N. erythrogaster* ($F_{1,330} = 7.28$, $P = 0.007$) and marginally significantly more than in *N. rhombifer* ($F_{1,330} = 3.72$, $P = 0.055$). The increasing enrichment of δ^{15}N values with SVL did not differ in *N. rhombifer* and *N. erythrogaster* ($F_{1,330} = 0.89$, $P = 0.347$).
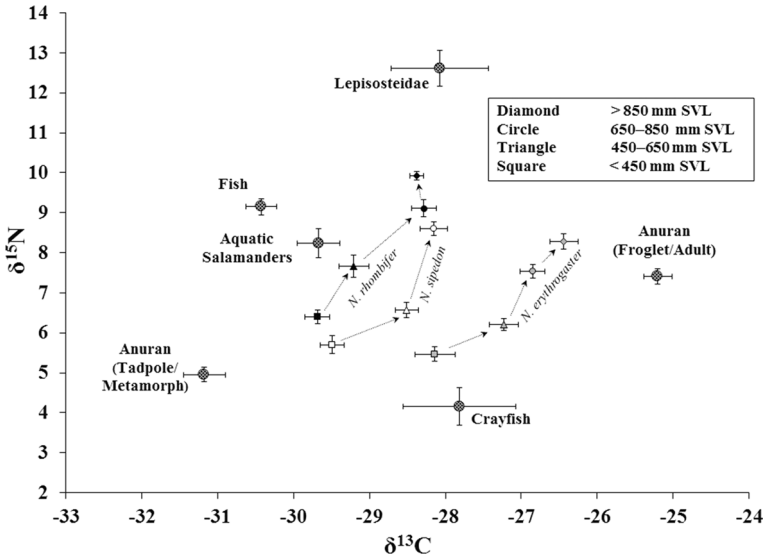
Fig. 2 Mean ($\pm$ 1 SE) watersnake and prey stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values based on snake size class. *Nerodia erythrogaster* mean stable isotope size class values are indicated by gray symbols, *N. rhombifer* by black, and *N. sipedon* by white. Arrows indicate the increase in size class for each watersnake species. SVL is snout-vent length. Prey mean stable isotope values are indicated by crosshatch circles

Isotopic variances

Isotopic variances differed among and within watersnake species, though not across all possible comparisons. There was no difference in $\delta^{13}C$ variance among species ($F_{2,330} = 2.03$, $P = 0.133$; Table 1), but $\delta^{15}N$ variance differed among species ($F_{2,330} = 5.50$, $P = 0.005$); Tukey-type multiple comparison tests demonstrated that *N. rhombifer* had a larger $\delta^{15}N$ variance than *N. erythrogaster* ($q = 3.43$, $q_{0.05,3} = 3.314$, $P < 0.05$), with no other significant differences among species. Within species, $\delta^{13}C$ variance did not differ between sexes in *N. erythrogaster* ($F_{1,114} = 0.03$, $P = 0.857$) or *N. rhombifer* ($F_{1,104} = 0.04$, $P = 0.846$), but did to some degree in *N. sipedon* ($F_{1,109} = 3.67$, $P = 0.058$) with $\delta^{13}C$ variance being greater in males. Similarly, sex did not affect $\delta^{15}N$ variance in *N. erythrogaster* ($F_{1,114} = 0.72$, $P = 0.397$) or *N. rhombifer* ($F_{1,104} = 1.67$, $P = 0.199$) but female *N. sipedon* had greater $\delta^{15}N$ variance ($F_{1,109} = 11.24$, $P = 0.001$) than male *N. sipedon*.

Isotopic variances differed among some size classes but not others. There was no significant variation in $\delta^{13}C$ values among *N. sipedon* size classes ($F_{1,3} = 1.10$, $P = 0.371$; Fig. 4), but variation decreased with size for *N. erythrogaster* ($F_{1,5} = 7.46$, $P = 0.041$) and *N. rhombifer* ($F_{1,6} = 15.94$, $P = 0.007$). The variance of $\delta^{15}N$ was not related to size class in *N. erythrogaster* ($F_{1,5} = 2.07$, $P = 0.210$) but did decrease as *N. sipedon* size class increased ($F_{1,3} = 29.55$, $P = 0.012$). For *N. rhombifer*, a quadratic regression between $\delta^{15}N$ and size was significant ($F_{2,5} = 6.10$, $P = 0.046$, $R^2 = 0.71$, AIC $= 18.14$), with a significant linear term ($F_{1,5} = 7.22$, $P = 0.044$) and a quadratic term that approached significance ($F_{1,5} = 4.99$, $P = 0.076$). The linear regression had a higher AIC value ($F_{1,6} = 1.33$, $P = 0.083$, $R^2 = 0.42$, AIC $= 21.68$) than the quadratic regression.

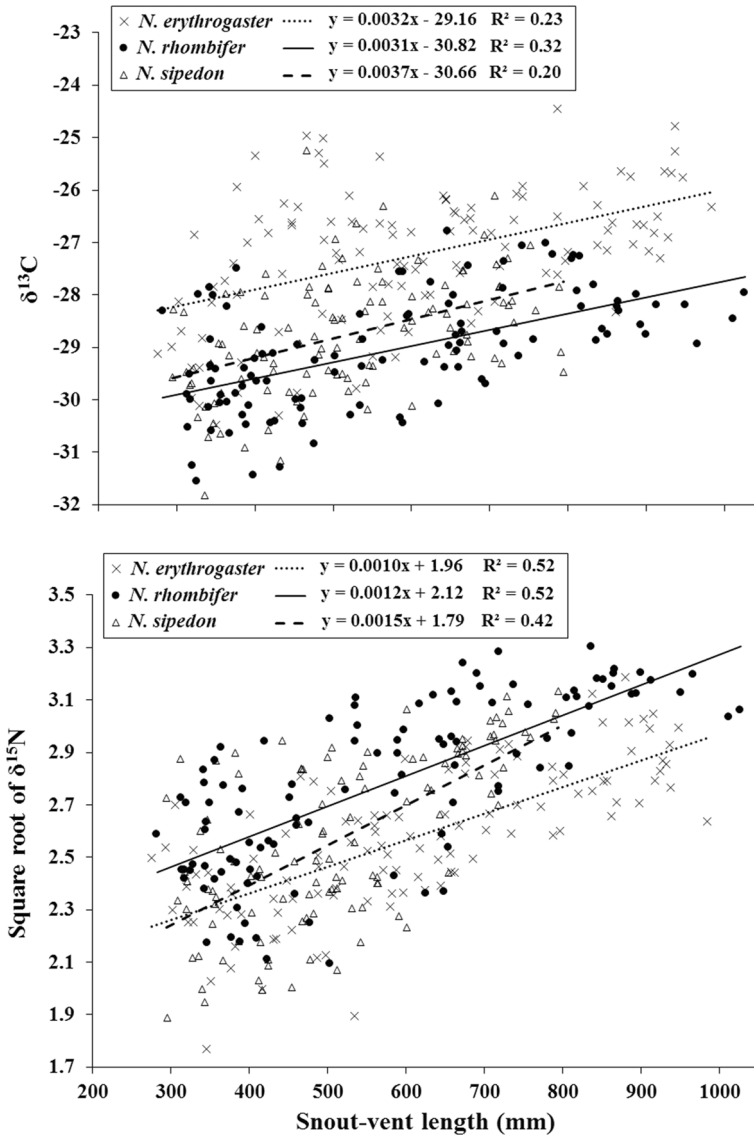**Fig. 3** Simple linear regression analyses of stable isotope ($\delta^{13}C$ and $\delta^{15}N$) values versus watersnake snout-vent length (mm). *Nerodia erythrogaster* stable isotope values are indicated by crosses, *N. rhombifer* by filled circles, and *N. sipedon* by triangles

Mixing model analysis

Mixing model results suggested only slight variation in prey proportions among snake species. Credible intervals (CI) overlapped for all prey groups among the three snake species with one exception: *N. erythrogaster* fed more on froglet/adult anurans than did *N. rhombifer* (Fig. 5). Prey proportions were not affected by watersnake sex. However,

Table 1 Stable isotope (δ^{13}C and δ^{15}N) watersnake summary statistics

Snake group	N	δ^{13}Carbon			δ^{15}Nitrogen		
		δ^{13}C	SE	s^2	δ^{15}N	SE	s^2
Nerodia erythrogaster	116	−27.23	0.12	1.65	6.69	0.13	1.91
Sex							
Female	65	−27.19	0.16	1.69	6.84	0.18	2.07
Male	51	−27.28	0.18	1.62	6.50	0.18	1.67
Size class							
<450 mm SVL	29	−28.14	0.26	2.02	5.47	0.17	0.87
450–650 mm SVL	40	−27.23	0.20	1.54	6.21	0.15	0.92
650–850 mm SVL	27	−26.85	0.17	0.75	7.53	0.18	0.88
>850 mm SVL	20	−26.44	0.19	0.70	8.29	0.19	0.73
Nerodia rhombifer	106	−29.05	0.11	1.18	7.82	0.17	3.03
Sex							
Female	59	−28.88	0.14	1.13	8.09	0.24	3.29
Male	47	−29.27	0.16	1.19	7.48	0.23	2.56
Size class							
<450 mm SVL	39	−29.69	0.16	1.00	6.40	0.17	1.18
450–650 mm SVL	28	−29.21	0.20	1.07	7.66	0.29	2.29
650–850 mm SVL	27	−28.29	0.16	0.70	9.11	0.22	1.27
>850 mm SVL	12	−28.37	0.09	0.10	9.92	0.10	0.13
Nerodia sipedon	111	−28.76	0.11	1.25	6.72	0.16	2.67
Sex							
Female	59	−28.64	0.12	0.92	7.13	0.23	3.25
Male	52	−28.90	0.18	1.62	6.26	0.18	1.65
Size class							
<450 mm SVL	37	−29.49	0.16	0.95	5.71	0.23	1.90
450–650 mm SVL	50	−28.51	0.15	1.11	6.57	0.19	1.74
650–850 mm SVL	24	−28.16	0.18	0.76	8.60	0.17	0.69

dietary groups did change with snake size (Fig. 6). For all three watersnake species, estimated proportions of crayfish and tadpole/metamorph anurans in the diet decreased with snake size, while froglet/adult anurans and Lepisosteidae became a larger component of diet as snake size increased; proportions of fish and aquatic salamanders varied little across size classes.

Although individuals from different species but in the same size class tended to eat similar prey, there were several important exceptions. Model estimates suggested that *N. rhombifer* > 650 mm in SVL tended to feed more on Lepisosteidae than did similarly sized N. *erythrogaster*, and that the smallest *N. erythrogaster* (<450 mm SVL) were predicted to feed significantly more on crayfish than did similarly sized *N. rhombifer*. *N. erythrogaster* > 450 mm in SVL fed more on froglet/adult anurans than did *N. rhombifer* in that size class; *N. erythrogaster* 650–850 mm in SVL also fed more on froglet/adult anurans than did *N. sipedon* of the same size class.
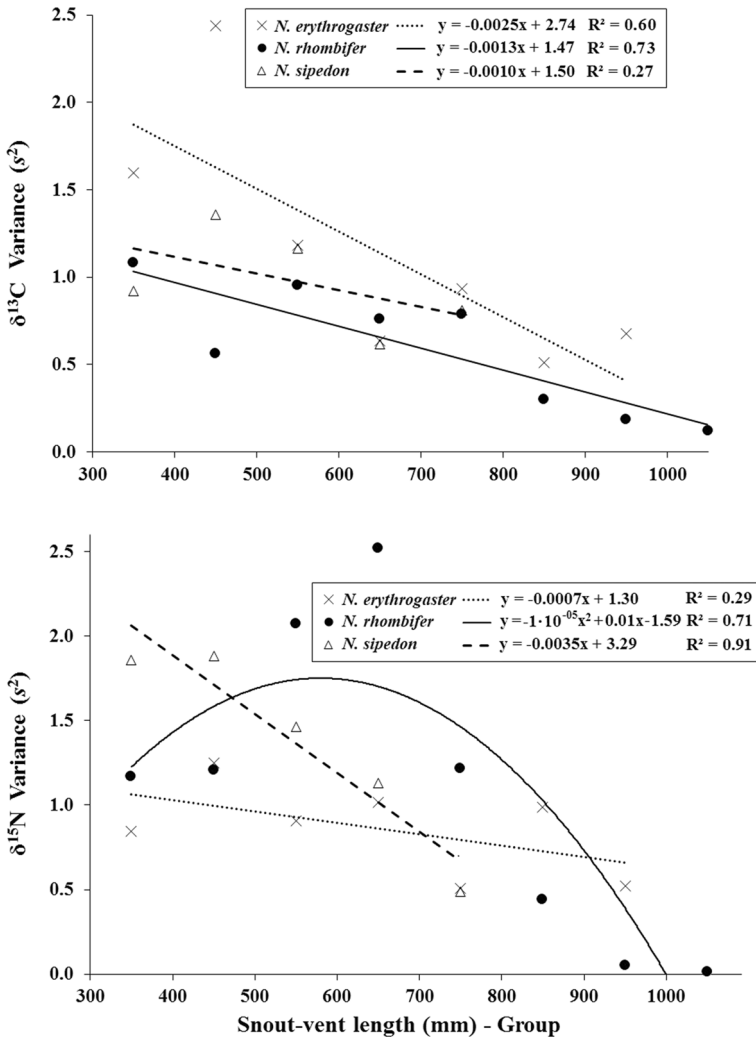
Fig. 4 Regression analyses of stable isotope ($\delta^{13}C$ and $\delta^{15}N$) variance versus watersnake snout-vent length (100-mm size class groups). *Nerodia erythrogaster* stable isotope values are indicated by crosses, *N. rhombifer* by filled circles, and *N. sipedon* by triangles

Discussion

Our stable isotope analyses revealed complex dietary relationships among sympatric *Nerodia erythrogaster, N. rhombifer* and *N. sipedon*. Although all three species may forage on similar prey, we found interspecific differences in their niches, including dissimilar isotopic values, isotopic variances, and proportional estimates of their diets. Within species, sex and size influenced diet; females and larger snakes fed at higher trophic levels and the latter consumed more terrestrial prey. This intraspecific diet variation decreased the number of individuals that shared resources and may reduce interspecific competition and facilitate

the coexistence of these three ecologically similar species. While these three similar watersnake species may often coexist (Tucker 1995; Burbrink et al. 1998; Laurent and Kingsbury 2003), their abundance may be affected by habitat use at a variety of spatial scales (Laurent and Kingsbury 2003; Roe et al. 2004; Marshall 2008). Watersnake coexistence and dietary overlap are a complicated system affected by habitat, seasonal food pulses and interspecific interactions (Laurent and Kingsbury 2003; Willson et al. 2010; Durso et al. 2013; Steen et al. 2014) but our results support the idea that observed isotopic and dietary patterns are related to niche partitioning.

Snake species varied in carbon isotopic values in ways that indicate niche partitioning along a terrestrial-aquatic habitat gradient. The enriched $\delta^{13}C$ values of *N. erythrogaster* suggest they use terrestrial habitats more frequently and consume more terrestrial prey than *N. rhombifer* and *N. sipedon* (Cloyed and Eason 2017), and mixing models estimated that *N. erythrogaster* consumed two to four times more froglets and adult frogs than *N. rhombifer* and *N. sipedon*. *Nerodia erythrogaster* may thus reduce interspecific competition with the other two snake species by feeding on terrestrial resources, which may require different foraging strategies (Bilcke et al. 2006; Hutinec and Mebert 2011). *Nerodia erythrogaster* is more terrestrial than both congenerics (Preston 1970; Laurent and Kingsbury 2003), with large home ranges (~ 16 ha.) that include scattered wetlands in a terrestrial matrix where they feed on a variety of anurans (Roe et al. 2004). Our results corroborate earlier work showing that adult anurans are a major component of *N. erythrogaster* diets (Mushinsky and Hebrard 1977; Mushinsky et al. 1982), although crayfish, which can use both terrestrial and aquatic habitats, may also form a large part of the diet according to our stable isotope study. Previous studies using gut content analyses found crayfish to be a minor dietary item for all three *Nerodia* species, in contrast to our results (Gibbons and Dorcas 2004). The depleted $\delta^{13}C$ values of *N. sipedon* and *N. rhombifer* suggest that both species consume primarily aquatic prey, i.e. tadpoles, crayfish, aquatic salamanders and fishes at our site. *Nerodia sipedon* typically prey on amphibians and fishes (Lacy 1995; Roe et al. 2004; King et al. 2006) and are found in a large variety of aquatic habitats (Gibbons and Dorcas 2004), but previous studies have found that *Nerodia rhombifer* is strongly aquatic, a forager in deeper (300 mm), open water and mostly piscivorous (Mushinsky et al. 1982; Plummer and Goy 1984; Savitsky 1989), which is different from this species' diet at our site, where it fed somewhat evenly across the six prey categories.

In addition to partitioning resources along a habitat gradient, these three species also feed at slightly different trophic levels. *Nerodia rhombifer* had enriched $\delta^{15}N$ values compared to both *N. sipedon* and *N. erythrogaster*. Lepisosteidae, other fishes and aquatic salamanders had the most enriched $\delta^{15}N$ values among the prey, and mixing model estimates suggested that these 3 prey groups comprised 54% of *N. rhombifer*'s diet but only 35% of *N. sipedon*'s diet and 19% for *N. erythrogaster*. *Nerodia sipedon* and *N. erythrogaster* were predicted to eat more crayfish, which occupy a lower trophic level. *Nerodia rhombifer* therefore fed at higher trophic levels than *N. sipedon* and *N. erythrogaster*, and the combination of partitioning both trophic level and habitats results in each species occupying unique niche space.

Within the niche space that each species occupied, individuals varied in how they used that space. Carbon and nitrogen isotopes varied with sex in *N. sipedon*, which may have important implications for dietary overlap and coexistence with congenerics. Male *N. sipedon* had marginally wider $\delta^{13}C$ variances than females and thus may have fed on a wider range of aquatic and terrestrial prey. Female *N. sipedon*, in contrast, had a significantly greater range of $\delta^{15}N$ values and therefore may have foraged on a wider range of trophic levels. Female *N. sipedon* are likely to use different habitats, especially when gravid, which

Fig. 5 Stable isotope mixing model mean proportions (δ^{13}C and δ^{15}N) with ±95% credible intervals (error ▶ bars) of each prey group for watersnake species overall and watersnake sex for *Nerodia erythrogaster*, *N. rhombifer* and *N. sipedon*

could contribute to the observed foraging differences between sexes (Brown and Weatherhead 2000; Pattishall and Cundall 2009; Neuman-Lee et al. 2013). These sex-driven differences in isotopic variance across both isotopes increase this species' overall diet breadth. Furthermore, the reduction in intraspecific competition caused by sex differences could help explain how this dietary generalist can coexist with the two larger-bodied watersnake species. Male *N. sipedon* overlap more in diet with *N. erythrogaster,* as both may consume more terrestrial prey, and female *N. sipedon* overlap more with *N. rhombifer*, which consume more fishes from higher trophic levels (Perkins and Eason 2019).

Snake diets changed with size for all three species, and these changes occurred across both habitat and trophic gradients. Snakes incorporated more terrestrial prey in their diets (enriched δ^{13}C) as they grew, suggesting that larger snakes increased their use of terrestrial habitats for foraging or their hunting of adult frogs in the water or along the water's edge (Rasmussen 2010; Trakimas et al. 2011). The shift towards terrestrial prey in larger snakes was most apparent in *N. erythrogaster*, as supported by δ^{13}C values becoming enriched as snake size increased, the sharp decrease in δ^{13}C variance in larger size classes, and the mixing model estimates. *Nerodia erythrogaster* likely fed primarily on crayfish and tadpoles/metamorphs when they were younger and on adult anurans when they were older, thus spanning larger habitat space but a smaller trophic range. Similarly, *N. sipedon* shifted towards froglets/adult anurans when snakes grew larger than 450 mm SVL, supporting a previous descriptive study (Lacy 1995). The inclusion of adult anurans in larger watersnakes' diet might be driven by an innate chemical response to these prey, as observed in *N. erythrogaster* when individuals reach 8 months in age or >500 mm SVL (Mushinsky and Lotz 1980; Mushinsky et al. 1982). With the widest trophic range, younger, smaller *N. rhombifer* fed on tadpoles/metamorph anurans at a lower trophic level and shifted to predatory fish from the highest trophic level when watersnakes were older and larger (Altig et al. 2007; Zeug and Winemiller 2008; Fletcher et al. 2015).

Larger watersnakes of all three species foraged at higher trophic levels (enriched δ^{15}N), making a trophic shift, from tadpoles and crayfish to fish, aquatic salamanders, and adult anurans as they grew. This trophic shift was strongest in *N. sipedon*, which has the broadest diet of any watersnake in North America (Ernst and Ernst 2003; Gibbons and Dorcas 2004). *Nerodia rhombifer* also shifts from smaller to larger fish as snakes increase in size (Mushinsky et al. 1982; Plummer and Goy 1984), and our work suggests that the largest *N. rhombifer* increased the amount of Lepisosteidae in their diets, which would increase their trophic position. Similarly, the switch from crayfish to adult anurans in *N. erythrogaster* accompanies a trophic shift with body size. Furthermore, large *N. rhombifer* and *N. sipedon* had little variance in δ^{15}N, suggesting they increasingly consumed resources from the highest trophic levels as they grew. Watersnake prey at these highest trophic levels are likely larger themselves, as body size is positively related to trophic level in many aquatic systems (Arim et al. 2010; Dalponti et al. 2018), and as optimal foraging theory predicts, it is probably more profitable for larger watersnakes to feed on larger prey items that occupy higher trophic levels (Costa et al. 2008).

Snake sex and size interacted to affect isotopic values and ranges. Females, which reach larger sizes than males, did not differ from males in carbon isotope values but fed at higher trophic levels across all three species. Females likely consumed more fishes, including
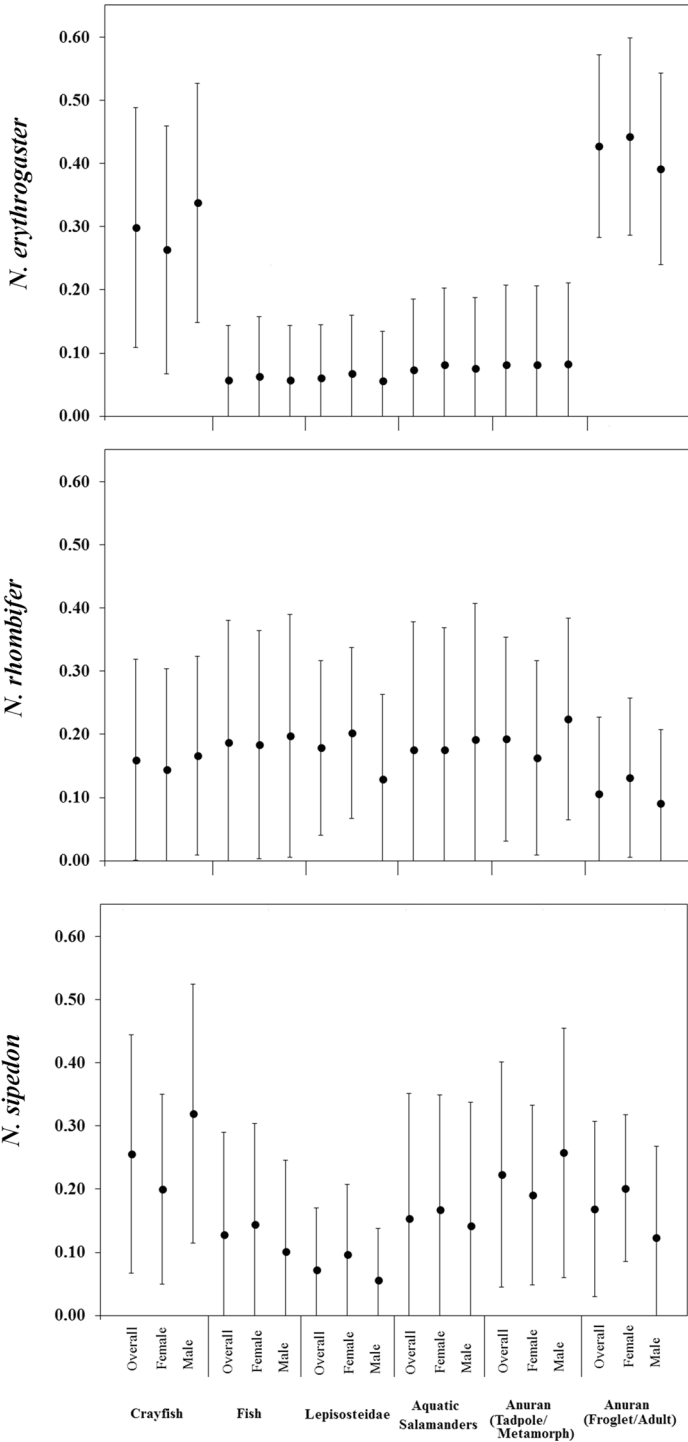
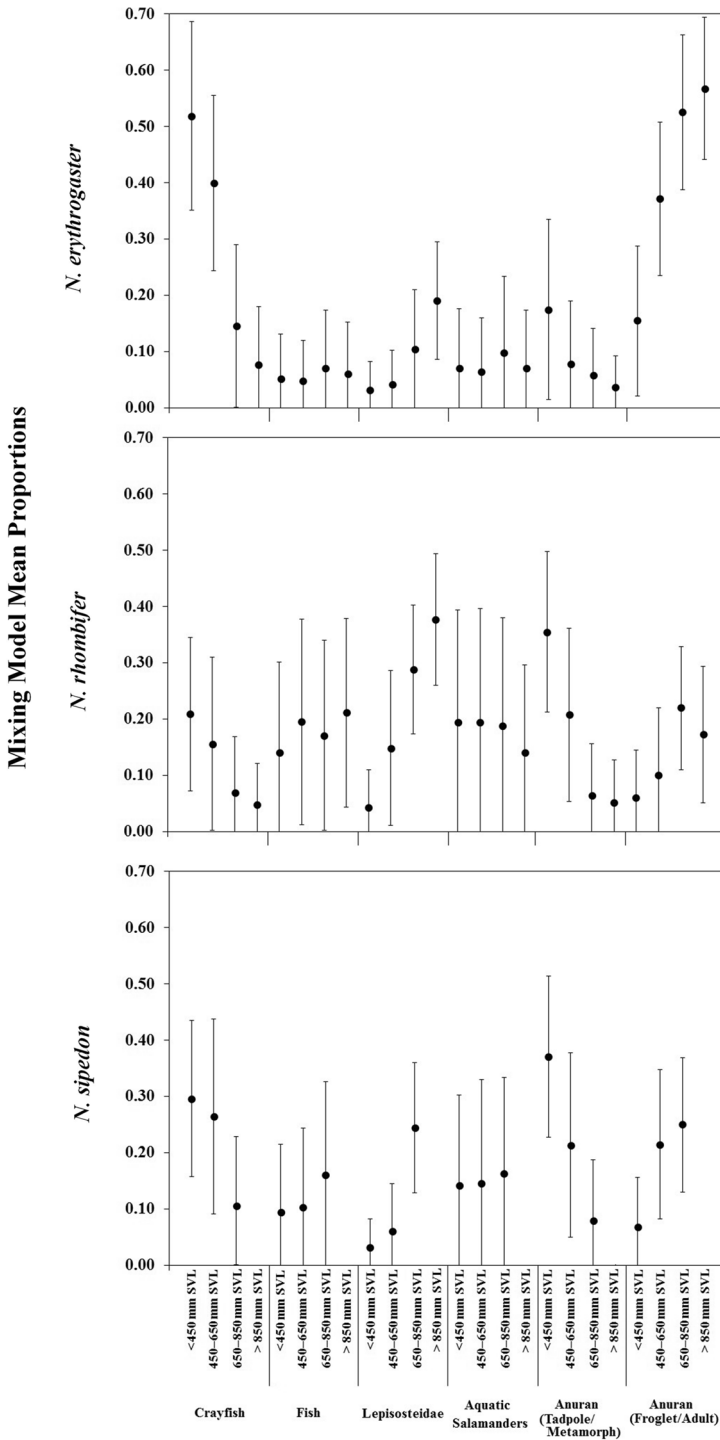**Fig. 6** Stable isotope mixing model mean proportions (δ¹³C and δ¹⁵N) with ±95% credible intervals (error bars) of each prey group across watersnake size classes for *Nerodia erythrogaster*, *N. rhombifer* and *N. sipedon*

Lepisosteidae, which had the most enriched $\delta^{15}N$ values among the prey analyzed in this study. Further, females are larger and have wider gapes that allow them to feed on fishes that are too large for males (Mushinsky et al. 1982; King 1993), and larger fishes might feed at higher trophic levels in our system (Fry et al. 1999; Jennings et al. 2001). Snakes typically drop smaller prey from their diets as they grow (e.g., Arnold 1993; Bowen 2004), and larger females may not eat smaller prey from lower trophic levels while males continue to feed on them. Sexual dimorphism affects dietary variation in many animal taxa (e.g., southern giant petrel, *Macronectes giganteus*; Forero et al. 2005; grey seal, *Halichoerus grypus*; Beck et al. 2007; ant-eating spider, *Zodarion jozefienae*; Pekár et al. 2011), and intersexual ecological differences such as those that can occur in foraging may enforce the evolution of these dimorphisms (Stephens and Wiens 2009; Hendry et al. 2014).

Our study demonstrates how intra- and interspecific variation can interact to affect relationships among evolutionarily and ecologically similar species. Although we did not measure competition directly, our results have potentially important implications for how such species coexist. Intraspecific variation can decrease competition by reducing the number of individuals that overlap in resource use, thus decreasing both intraspecific competition by widening species' niches as well as interspecific competition by ameliorating the effects of niche overlap, thereby maintaining biological diversity at multiple scales. As demonstrated in our study, generalist species with wide dietary niches, feeding on a variety of resources across trophic levels and habitats, can be the result of intraspecific dietary variation. This may be particularly significant for gape-limited, sexually dimorphic species, predisposing them to ontogenetic and sex-driven intraspecific variation (Shine and Wall 2007). Broadening of dietary niches can result in resource overlap of only certain species subgroups, as was the case in this study, with large male *N. sipedon* overlapping in diet most with large *N. erythrogaster*, large female *N. sipedon* overlapping most with mid-to-large sized *N. rhombifer* and smaller individuals of *N. sipedon* and *N. rhombifer* overlapping more with each other than they do with large conspecifics. Without considering the effects of sex, size, and their interaction on diet in this watersnake community, we would have missed nuanced aspects of how resources are partitioned both among and within species. Our results suggest how a balance between intra- and interspecific variation may evolve among ecologically similar generalist species so as to decrease the overall amount of competition rather than just intra- or interspecific competition. Future studies on resource partitioning and community structure need to consider if and when this balance facilitates coexistence and shapes the evolution and ecology of similar coexisting species.

Data availability Data from this study are available at Dyrad Digital Depository: https://doi.org/10.5061/dryad.2ngf1vhm0

Compliance with ethical standards

Conflict of interest The authors declare no conflict of interest.

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