

SEASONAL EFFECTS ON DIETARY RESOURCE UTILIZATION OF SYNTOPIC WATERSNAKES

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Abstract.—Patterns of species coexistence in seasonally dynamic ecosystems have long been of interest to ecologists. Freshwater ecosystems containing several ecologically similar, semiaquatic snake species have been a particular focus. Coexistence of syntopic, closely related snakes in aquatic habitats is typically understood through the lens of competition, and snakes often partition diet, potentially preventing competitive exclusion. Recent evidence suggests, however, that temporal changes, particularly seasonal fluctuations in prey item abundances, might promote the coexistence of similar semiaquatic snakes even in the absence of substantial dietary partitioning. To better understand the role of seasonal effects on freshwater snake coexistence, we investigated dietary patterns within an assemblage of syntopic watersnakes (*Nerodia* spp.). By analyzing the gut contents of Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes, we quantified the effects of snake species, body size, sex, and temporal factors on watersnake dietary patterns. Plain-bellied Watersnakes predominantly were anurophagous, while Diamond-backed and Common watersnakes primarily were piscivorous; however, seasonal variation in abundance of prey items influenced both the prey types watersnakes consumed and dietary overlap among these species. Seasonal prey pulses likely reduced competition among watersnakes, increasing the potential for coexistence of similar snake species. Assessing temporal variation in prey can lead to a more complete understanding of semiaquatic snake assemblage structure. Future research should further investigate the influence of seasonality on the coexistence of ecologically similar species in variable freshwater systems.

Key Words.—coexistence; dietary overlap; freshwater; Natricinae; *Nerodia*; prey fluctuation; resource partitioning; temporal variation

INTRODUCTION

Ecologists have long been interested in understanding how apparently similar species can coexist (MacArthur 1958; Schoener 1974; Pianka 1986). Many freshwater snake assemblages include semiaquatic species (Laurent and Kingsbury 2003; Karns et al. 2010; Carvalho Teixeira et al. 2017; Luiselli et al. 2020), sometimes occurring at high densities (Godley 1980; Luiselli 2006a; Willson and Winne 2016; King et al. 2018). These sympatric, potentially syntopic snakes often are closely related and might predate similar prey items, such as amphibians, fishes, and invertebrates (Kofron 1978; Byrd et al. 1998; Himes 2003b; Ford and Lancaster 2007).

The coexistence of similar semiaquatic snake species has previously been understood in the context of interspecific competition (Camp et al. 1980; Mushinsky 2001; Himes 2003b; Scali 2011). From this perspective, syntopic species might coexist in locations where there is potential for resource partitioning, thereby reducing competition

and preventing competitive exclusion. Although previous research has shown that semiaquatic snake assemblages might partition microhabitats (Hebrard and Mushinsky 1978; Keck 1998; Laurent and Kingsbury 2003; Luiselli 2006b), including thermal resources (Mushinsky et al. 1980; Tanaka and Ota 2002), diet partitioning is more often documented between semiaquatic snake species (reviewed by Luiselli 2006b). Diet also varies intraspecifically, as a function of sex (Mushinsky et al. 1982; King 1993; Luiselli et al. 2007) and life-history stage. As gape-limited predators, semiaquatic snakes ontogenetically shift prey size and taxa consumed (Mushinsky and Lotz 1980; Mushinsky et al. 1982; Plummer and Goy 1984; Vincent et al. 2007), further facilitating intra- and interspecific coexistence.

Temporal fluctuations in prey resources also might allow ecologically similar semiaquatic snakes to coexist, potentially eliminating the need for persistent diet partitioning (Luiselli 2006a; Carvalho Teixeira et al. 2017). Freshwater systems are highly dynamic, and seasonal hydrological fluctuations likely influence the prey resources available to semiaquatic



FIGURE 1. Watersnakes (*Nerodia* spp.) found at Hardy Slough Tract of the Sloughs Wildlife Management Area, Henderson County, Kentucky, USA. (A) Plain-bellied Watersnake (*Nerodia erythrogaster*), (B) Female Diamond-backed Watersnake (*N. rhombifer*) with 17 neonates, (C) Common Watersnake (*N. sipedon*). (A and B photographed by Micah Perkins; C photographed by Eric Clark).

snakes (Silvano et al. 2000; Gibbons et al. 2006; Willson et al. 2006; Shine and Wall 2007; Piatti et al. 2019). Seasonal pulses might result in increased prey abundances such that interspecific competition is temporarily reduced (Willson et al. 2010; Durso et al. 2013). In this manner, semiaquatic snake species might exhibit increased dietary overlap during times of increased prey abundance and partition their diets only during times of reduced prey availability (Luiselli 2006a; Hampton and Ford 2007; Carvalho Teixeira et al. 2017).

Herein, we describe how seasonal prey pulses affect dietary resource utilization and overlap in three syntopic natricines. We investigated dietary patterns of Plain-bellied Watersnakes (*Nerodia erythrogaster*), Diamond-backed Watersnakes (*N. rhombifer*), and Common Watersnakes (*N. sipedon*; Fig. 1). These congeners are frequently found using similar microhabitats in or near waterbodies (Tucker 1995; Burbrink et al. 1998; Laurent and Kingsbury 2003; Marshall 2008). *Nerodia* species primarily prey on fishes and amphibians, but the proportion of these taxa in their diet differs among species (Mushinsky and Hebrard 1977; Kofron 1978; Plummer and Goy 1984; Himes 2003b). Although both species are piscivorous as juveniles, feeding on small fishes such as cyprinids, Plain-bellied Watersnakes ontogenetically shift to a diet primarily comprised of anurans (i.e., ranid frogs; Preston 1970; Mushinsky and Hebrard 1977; Kofron 1978; Roe et al. 2004), and adult Diamond-backed Watersnakes predate larger fishes, such as catfish (Hess and Klimstra 1975; Kofron 1978; Savitzky 1989). Common Watersnakes feed on a variety of amphibian and fish taxa, the proportion of which often varies among populations (King 1986; Lacy 1995; Himes 2003a; Gibbons and Dorcas 2004; Roe et al. 2004). Because of their significant variation in diet, these watersnake species provide an ideal system in which to examine

seasonal fluctuations in diet and dietary overlap. We examined how snake body size, sex, and temporal changes in prey abundance affect dietary patterns in watersnakes. We expected that each of these factors would influence watersnake diets, potentially reducing interspecific competition during certain time periods and allowing these similar snakes to coexist.

MATERIALS AND METHODS

Study area.—We surveyed watersnakes 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; Fig. 2). The site is primarily managed for wintering waterfowl by the Kentucky Department of Fish and Wildlife Resources. Hardy Slough Tract is 2 km southeast of the Ohio River and contains moist soil units (shallow wetlands delineated by a levee system), scrub-shrub wetlands, and palustrine forest. Dominant plant species include 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*).

Field data collection.—We conducted surveys from April to September in 2013 and 2014. To maximize sample size during three individual seasons, we used a variety of methods to capture snakes, including hand capture, cover boards, stand-alone aquatic funnel traps, and drift-fence/funnel-trap arrays (terrestrial and aquatic; Fitzgerald 2012). For each captured watersnake, we measured snout-vent length (SVL) and determined sex by cloacal probing. To identify any recaptures, our primary marking method was subcutaneous PIT (Passive Integrated Transponder) tags (Gibbons and Andrews 2004) combined with marking watersnakes

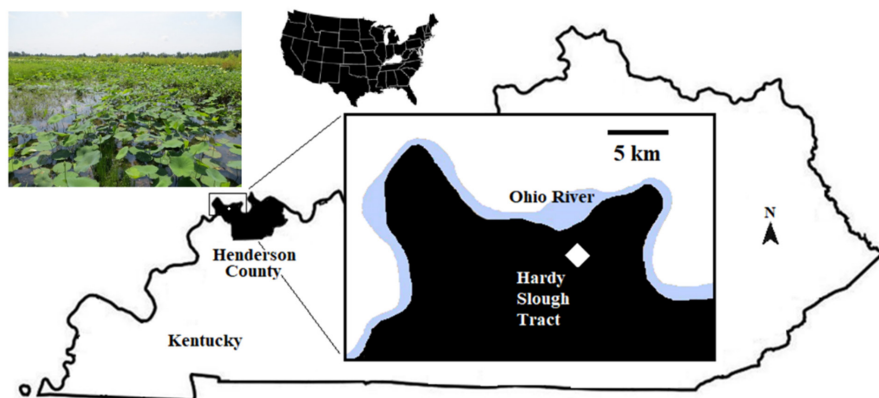


FIGURE 2. Hardy Slough Tract of the Sloughs Wildlife Management Area, Henderson County, Kentucky, USA. Photograph at top left of figure depicts a shallow wetland with water lilies (*Nuphar* sp.) in the foreground, Black Willows (*Salix nigra*) in the middle ground and palustrine forest in the background. (Photographed by Micah Perkins).

with unique ventral scale-clip patterns (Plummer and Ferner 2012). Including a secondary external marking method is often recommended in addition to PIT tagging (Roark and Dorcas 2000; Gibbons and Andrews 2004). To determine watersnake dietary patterns, we gently palpated gut contents until snakes regurgitated (Kofron 1978; Fitch 2001). We identified snake gut contents to the narrowest taxon possible, and for amphibians, we also recorded the life-history stage. We released each snake at its capture location.

We determined prey availability by sampling potential prey items (i.e., amphibians, fishes, crayfishes) weekly, using a combination of methods designed for various habitats, prey types, and prey sizes (Fitzgerald 2012; Hubert et al. 2012). We deployed traps for 48 h (two consecutive days and nights) each week and checked traps every 24 h. To assess potential aquatic prey items, we used stand-alone funnel traps, hoop traps, and drift fence-funnel trap arrays (Hubert et al. 2012). The upper 25% of the aquatic funnel traps remained above water to prevent drowning animals contained within them. To assess potential terrestrial prey items, we used drift-fence/funnel-trap arrays with pit-fall traps, i.e., 5-gallon buckets buried so that the top of the rim was flush with the ground (Fitzgerald 2012). We built drift fences with silt fencing and wooden stakes. We categorized captured anurans as tadpoles, metamorphs (tadpoles with well-defined legs and other emerging adult traits), froglets (recently metamorphosed frogs with no tadpole traits), or adults (McDiarmid and Altig 1999). We determined the number of prey-trapping nights (the number of traps multiplied by the number of days the traps were deployed) for aquatic and terrestrial prey.

Data analyses.—Because changes in amphibian life-history stages have been used to determine seasons in prior snake foraging studies (Hirai 2004; Willson et al. 2010), we defined three ecologically relevant seasons using changes in anuran capture rates at four different life-history stages (tadpole, metamorph, froglet, and frog). Spring began in April and ended when the number of captured tadpoles and metamorphs decreased by 90% from peak values; by this definition, Spring was 1 April to 29 May in 2013 and 1 April to 27 May in 2014. Early Summer began immediately thereafter and ended when the capture rate of froglets declined by 90% from peak values; Early Summer thus was 30 May to 23 July in 2013 and 28 May to 24 July in 2014. Late Summer began immediately thereafter and ran through the end of September in both sampling years.

To investigate the importance of prey types across seasons in watersnake diets, we calculated an Index of Relative Importance (IRI; Pinkas et al. 1971; Hart et al. 2002) using six prey categories: crayfish, fishes, lesser siren, ambystomatid salamanders, tadpole/metamorph anurans, and froglet/adult anurans. The IRI integrates number of prey items, their volume, and their frequency of occurrence, providing a less biased estimate of importance for each prey type than any single measure would provide. We estimated IRI using the equation:

$$IRI_i = (\%N_i + \%V_i) \times (\%F_i)$$

For each *i*th prey category, *N_i*, *V_i*, and *F_i* are the percentages of prey number, volume, and frequency of occurrence, respectively, in the gut contents for all individuals of a watersnake species. For each

TABLE 1. Potential prey items captured during aquatic and terrestrial surveys and their abundance in the gut contents of all captured Plain-bellied (*N. erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes. Bold values indicate total abundance for each prey group. The symbol — = no potential prey observed. For Fishes and Anurans, prey group total does not match the sum of prey species because some individual prey were not identified to species due to advanced digestion.

Group	Species or Family	Watersnake species		
		Plain-bellied	Diamond-backed	Common
Fishes		37	44	85
	Spotted Gar (<i>Lepisosteus oculatus</i>)	—	3	—
	Bowfin (<i>Amia calva</i>)	19	13	14
	Pugnose Minnow (<i>Opsopoeodus emiliae</i>)	—	—	—
	Pirate Perch (<i>Aphredoderus sayanus</i>)	2	7	11
	Redfin Pickerel (<i>Esox americanus</i>)	4	11	22
	Mosquitofish (<i>Gambusia affinis</i>)	11	1	12
	Smallmouth Bass (<i>Micropterus dolomieu</i>)	—	—	—
	Warmouth (<i>Lepomis gulosus</i>)	—	—	1
	Flier (<i>Centrarchus macropterus</i>)	—	—	1
	Banded Pygmy Sunfish (<i>Elassoma zonatum</i>)	—	—	—
Salamanders		2	3	3
	Lesser Siren (<i>Siren intermedia</i>)	1	2	1
	Small-mouthed Salamander (<i>Ambystoma texanum</i>)	1	1	2
	Eastern Tiger Salamander (<i>Ambystoma tigrinum</i>)	—	—	—
	Central Newt (<i>Notophthalmus viridescens</i>)	—	—	—
Anurans (tadpole/metamorph, froglet/adult)		43, 53	10, 4	9, 23
	Fowler's Toad (<i>Anaxyrus fowleri</i>)	—, —	—, —	—, —
	Eastern Cricket Frog (<i>Acris crepitans</i>)	—, 1	—, —	—, —
	Green Treefrog (<i>Hyla cinerea</i>)	—, —	—, —	—, —
	Cope's Gray Treefrog (<i>Hyla chrysoscelis</i>)	—, —	—, —	—, —
	Bird-voiced Treefrog (<i>Hyla avivoca</i>)	—, —	—, —	—, —
	Southern Leopard Frog (<i>Lithobates sphenoccephalus</i>)	41, 44	5, 2	1, 16
	Green Frog (<i>Lithobates clamitans</i>)	—, —	—, —	—, —
	Bullfrog (<i>Lithobates catesbeianus</i>)	—, 5	2, 2	3, 7
Invertebrates		1	—	1
	Crayfish (Family Cambaridae)	1	—	1

watersnake species, prey category percentages (% IRI) must sum to 100, and increased percentage values indicate greater dietary importance (Pinkas et al. 1971; Franks and VanderKooy 2000; Vaudo and Heithaus 2011). To compare IRI values for various prey categories among watersnake species, we calculated the proportion of a given prey category in the overall diet (% IRI; Cortés 1997; Kinney et al. 2011) for each snake species, using the equation:

$$\% \text{IRI}_i = 100 \times (\text{IRI}_i / \sum \text{IRI}_i)$$

To quantify the importance of specific factors and their interaction affecting the probability that

watersnakes foraged on a particular prey type, we modeled watersnake diets using logistic regressions (Hosmer and Lemeshow 2000) and identified candidate models using information theoretic methods (Burnham and Anderson 2002). We estimated the probability that watersnakes consumed a particular prey type, using the predefined prey categories of fishes, tadpole/metamorph anurans, and froglet/adult anurans. We did not include crayfish, lesser sirens, and ambystomatid salamanders because they totaled only 3% of all snake gut contents. The response variable was the presence or absence of a particular diet item (0 = absent, 1 = present). To understand overall dietary trends for watersnakes, we modeled all

TABLE 2. Sample size (n), mean (\pm standard error), and range of snout-vent length (SVL; mm) for captured Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes. For Plain-bellied and Diamond-backed watersnakes, the total number does not match the sum of male and female snakes because the sex of one neonate was unknown.

Species	n	Mean	Range
Plain-bellied	150	605.6 \pm 15.5	252 – 984
Female	84	640.2 \pm 23.1	276 – 984
Male	65	566.3 \pm 17.3	319 – 880
Diamond-backed	126	542.2 \pm 17.2	213 – 1027
Female	73	579.3 \pm 26.8	213 – 1027
Male	52	496.0 \pm 18.0	282 – 718
Common	186	496.0 \pm 9.6	207 – 794
Female	96	553.6 \pm 6.8	271 – 794
Male	90	434.5 \pm 5.0	207 – 601

three watersnake species together, using species, sex, SVL, and season as predictor variables and year as a random effect. Seasons were converted to numeric values for analysis (1 = Spring, 2 = Early Summer, 3 = Late Summer). We built 20 *a priori* candidate models using a global model, relevant interactions, and higher order functions (i.e., quadratic and cubic). We determined goodness of fit for the global model by visually inspecting predicted values versus residuals (Burnham and Anderson 2002; Mazerolle 2006). We then analyzed watersnake species separately, incorporating all predictor variables but species (13 *a priori* models). Using second-order Akaike Information Criterion (AIC corrected for small sample sizes), we identified the most parsimonious models, i.e., those models with $\Delta AIC \leq 2$ (Anderson et al. 2000; Burnham and Anderson 2002). Using these competitive models, we determined predictor variable importance by calculating parameter estimates, unconditional errors, and Akaike weights (w_i ; Burnham and Anderson 2002; Giam and Olden 2016). For those models in which season was an important predictor for a particular prey category, we plotted the estimated probability for that category to be included in the diet against Julian date to further investigate seasonal effects.

Finally, to examine watersnake dietary overlap across seasons, we calculated Proportional Similarity Indices (PSIs), where $PSI = 1 - 0.5 \times \sum |p_{ij} - q_{ij}|$ (Schoener 1968; Lanszki et al. 1999). The PSI comparing two watersnake species in a given season is the sum of the differences of the particular prey

TABLE 3. Proportional Similarity Indices (PSI) comparing prey groups found in *Nerodia* gut contents across seasons. PSIs are shown for all possible species pairings of Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) Watersnakes.

Season	Plain-bellied / Diamond-backed	Plain-bellied / Common	Diamond-backed / Common
Spring	0.70	0.42	0.58
Early Summer	0.38	0.63	0.54
Late Summer	0.30	0.30	0.82

percentages in the diets of the two species. PSI values range from 0 to 1, with a value of 0 indicating no overlap in diet and a value of 1 indicating complete overlap. We performed the PSI analysis on the taxonomic groups of ingested prey. We used SAS software Version 9.0 to perform our modeling comparison statistical analyses (SAS Institute, Cary, North Carolina, USA).

RESULTS

We sampled aquatic prey over 446 trap nights in 2013 and 918 in 2014, and terrestrial prey over 589 trap nights in 2013 and 886 in 2014. We captured and recorded prey items, including fishes, amphibians, and crayfish (Table 1). The mean number of tadpoles/metamorph anurans captured per trap night increased during Spring (2.13 individuals/trap night; Fig. 3) but was lower during Early Summer (0.06 individuals/trap night) and Late Summer (0.04 individuals/trap night). Froglets were absent during Spring, frequently captured during Early Summer (3.44 individuals/trap night), and greatly reduced in abundance during Late Summer (0.20 individuals/trap night). Adult frogs were captured at low rates during all seasons (0.02, 0.02, and 0.09 individuals/trap night during Spring, Early Summer, and Late Summer, respectively). During Spring 2013, aquatic traps resulted in an increased mean number of fishes per trap night, the result of a single trap capturing a large Bowfin (*Amia calva*) brood (n = 170) during early Spring.

We captured 462 individual watersnakes (150 Plain-bellied, 126 Diamond-backed, and 186 Common watersnakes). We obtained gut contents from 27 Plain-bellied, 11 Diamond-backed, and 22 Common watersnakes during 2013 and from 36 Plain-bellied, 28 Diamond-backed, and 52 Common watersnakes during 2014 (Table 2). Indices of relative importance (IRI) indicated that the importance of dietary items for each watersnake species varied by season (Fig.

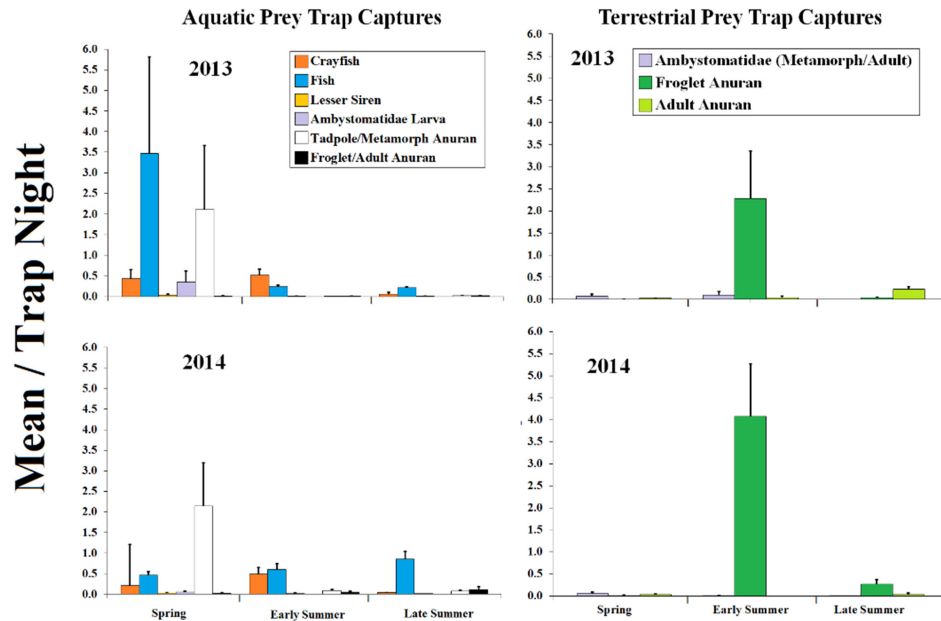


FIGURE 3. Mean number of potential aquatic and terrestrial prey items captured per trap night by season during 2013 and 2014. Error bars represent ± 1 standard error.

4). Tadpole/metamorph anurans were important dietary items during Spring for Plain-bellied (IRI = 31.7) and Diamond-backed watersnakes (IRI = 19.6). Froglet/adult anurans were important prey during Spring (IRI = 53.6), Early Summer (IRI = 79.4), and Late Summer (IRI = 95.4) for Plain-bellied Watersnakes, and during Early Summer for Common Watersnakes (IRI = 35.9). Fishes were important prey throughout the three seasons for both Diamond-backed (Spring IRI = 74.4, Early Summer IRI = 93.2, Late Summer IRI = 97.0) and Common (Spring IRI = 80.0, Early Summer IRI = 63.2, Late Summer IRI = 97.8) watersnakes, with both species predominantly foraging on fishes during Late Summer.

The Logistic Regression Analyses indicated that factors such as snake species, size, and sex as well as seasonal patterns of prey abundance influenced the probability that watersnakes predated a particular prey type. Snake species and season influenced the probability that watersnake gut contents contained fishes (Appendix Table 1). The probabilities (\pm standard error) of Diamond-backed (0.73 ± 0.09) and Common (0.70 ± 0.09) watersnakes predated fishes were similar, but Plain-bellied Watersnakes were less likely to feed on fishes (0.20 ± 0.07). As the seasons advanced, fishes became increasingly important while tadpole/metamorph anurans became decreasingly important in watersnake gut contents. Plain-bellied Watersnakes were more likely (0.67

± 0.09) to feed on froglet/adult anurans than Common (0.27 ± 0.12) or Diamond-backed (0.11 ± 0.06) watersnakes. Plain-bellied Watersnakes also were more likely to consume froglet/adult anurans as seasons progressed (Appendix Table 2). The probability of consuming fish prey decreased with snake size for Plain-bellied Watersnakes until snakes reached larger sizes (645 mm SVL; Fig. 5). Female Diamond-backed Watersnakes were more likely to be piscivorous than were males (Appendix Table 3). Common and Diamond-backed watersnakes were more likely to consume fishes as seasons progressed (Fig. 6, Appendix Tables 3 and 4). Tadpoles and metamorph anurans were less important in the diets of Plain-bellied and Diamond-backed watersnakes as seasons progressed, consistent with decreased abundances of these prey items during those times. Season influenced the number of froglets/adult anurans preyed upon by Common Watersnakes, with predation rates peaking during Early Summer and sharply declining during Late Summer.

Proportional similarity indices revealed dietary differences between species pairs (Table 3). Plain-bellied and Diamond-backed watersnakes had increased dietary overlap during Spring (PSI = 0.70), and Plain-bellied and Common watersnakes had increased overlap (PSI = 0.63) during Early Summer. During Late Summer, Diamond-backed and Common watersnakes had increased overlap (PSI = 0.82) when

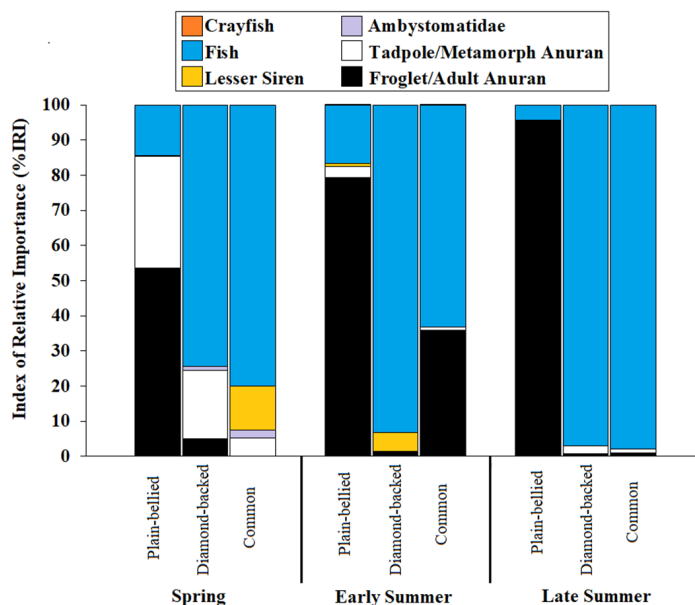


FIGURE 4. The Index of Relative Importance (%IRI) for crayfish, fishes, Lesser Siren (*Siren intermedia*), Ambystomatid salamanders, tadpole/metamorph anurans, and froglet/adult anurans based on the gut contents of Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes across seasons.

compared to both syntopic congeners (PSI = 0.30 for other pairings).

DISCUSSION

Although gut content studies provide only short-term dietary information and have limitations (see Durso et al. 2022), our study demonstrated nuanced and complex dietary patterns in three co-occurring species of *Nerodia*. The diets of Plain-bellied, Diamond-backed, and Common watersnakes overlapped in that they all fed primarily on fishes and amphibians; however, we found clear differences across snake species within these prey groups. Snake size, sex, and temporal effects also influenced watersnake diets. The observed dietary differences within and among *Nerodia* species might be associated with reduced intra- and interspecific competition, allowing these syntopic congeners to co-exist.

Consistent with prior studies (Mushinsky and Hebrard 1977; Mushinsky et al. 1982; Byrd et al. 1988; Himes 2003b; Roe et al. 2004), Plain-bellied Watersnakes primarily fed on froglet/adult anurans, whereas Diamond-backed and Common watersnakes primarily were piscivorous across all seasons (Spring, Early Summer, and Late Summer). Ontogenetic shifts within *Nerodia* might have reduced the number of conspecifics foraging on similar resources. Female

Diamond-backed Watersnakes were more likely than conspecific males to feed on fishes. Juvenile Plain-bellied Watersnakes fed upon fishes more frequently than adults, as previous studies also observed in both the field (Mushinsky et al. 1982) and the laboratory (Mushinsky and Lotz 1980). Our finding that large Plain-bellied Watersnakes preyed on fishes might reflect a preference not of taxon, but of selecting the largest prey available (Mushinsky et al. 1982).

Seasonal fluctuations in prey resources also influenced patterns of dietary overlap. During Spring, Plain-bellied and Diamond-backed watersnakes exhibited increased dietary overlap, perhaps because

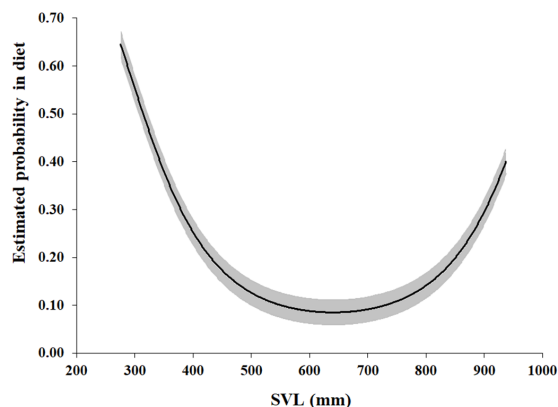


FIGURE 5. Estimated probability (shaded area: 95% confidence) by snake snout-vent length (SVL) that Plain-bellied Watersnake (*Nerodia erythrogaster*) gut contents contain fishes.

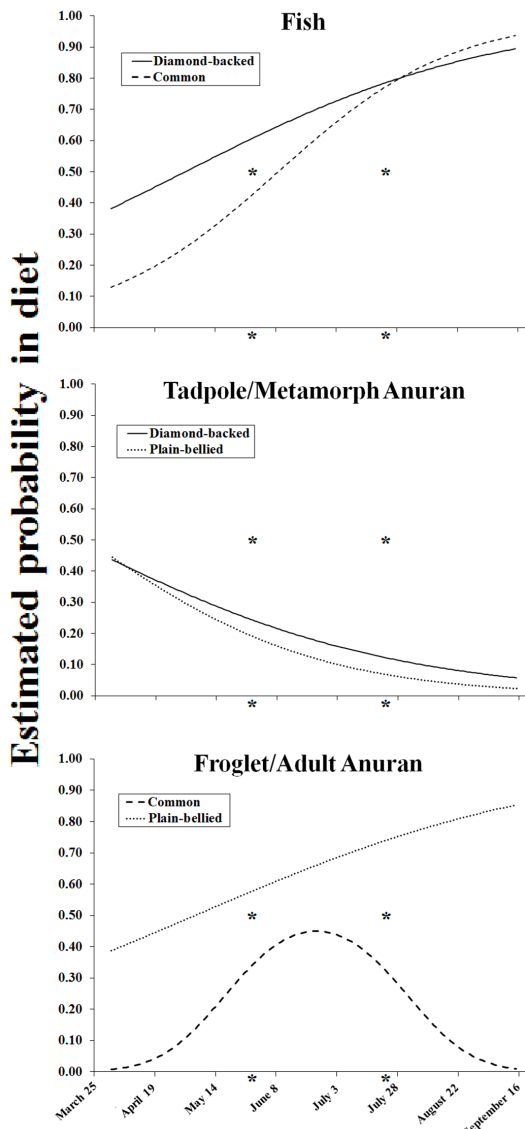


FIGURE 6. Estimated probability that snake gut contents contain a particular prey item (fishes, tadpole/metamorph anurans, or froglet/adult anurans) by date for Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes. Asterisks (*) indicate change in seasons.

these species responded to pulses of tadpoles/metamorphs. During this season, both species had a 44% probability of gut contents containing tadpole or metamorph anurans. Similarly, in Early Summer, Plain-bellied and Common watersnakes had the greatest dietary overlap, with both species responding to increased abundances of froglets. The probabilities that the gut contents of Plain-bellied and Common watersnakes contained froglet/adult anurans during that season were 66% and 45%, respectively.

Common Watersnakes select prey according to their abundance and availability (Carbone 1993; King et al. 1999; Roe et al. 2004; King et al. 2006; Perkins and Eason 2018), and consistent with our predictions, this opportunistic predator responded positively to elevated numbers of froglets during Early Summer. Contrary to our predictions, Common Watersnakes did not increase consumption of tadpole/metamorph anurans when they were abundant during Spring. This could be the result of differences in prey specialization compared to other Common Watersnake populations (Carbone 1993; King et al. 1999; Roe et al. 2004; King et al. 2006; Perkins and Eason 2018). Plain-bellied Watersnakes, the most terrestrial of these watersnakes (Keck 1998; Roe et al. 2004), responded to an increased abundance of froglet/adult anurans during Early and Late Summer, when anurans might disperse into adjacent uplands (Roe et al. 2003, 2004).

Diamond-backed and Common watersnakes exhibited increased dietary overlap during Late Summer, with both species feeding almost exclusively on fishes. The probabilities that gut contents contained fishes during Late Summer ranged between 79–90% and 78–94% for Diamond-backed and Common watersnakes, respectively. After increases in the abundances of anurans during Spring and Early Summer, watersnakes might partition their diets in subsequent seasons when prey abundances are reduced (Luiselli 2006a; Hampton and Ford 2007; Carvalho Teixeira et al. 2017). We did not observe this pattern during Late Summer. Although the diet of Plain-bellied Watersnakes differed greatly from the diets of the other two watersnakes, both Diamond-backed and Common watersnakes primarily foraged on fishes during Late Summer. Selection of fishes could be the result of reduced anuran prey or low water levels concentrating fish populations during Late Summer. Water levels were lower during Late Summer in our study area (U.S. Geological Survey. 2020. National Water Information System data. Available from <https://waterdata.usgs.gov/nwis/> [Accessed 19 May 2023]). Diamond-backed and Common watersnakes might be able to tolerate increased dietary overlap during one season for two reasons. First, their response to the seasonal pulses of increased prey biomass during Spring or Early Summer could have resulted in the storage of excess energy, such that during Late Summer, the snakes could reduce their metabolisms in response to decreased prey abundances (Willson et al. 2010). Furthermore, limited prey resources or increased

dietary overlap occurring during a single season might be of little consequence for watersnakes, as not feeding for 15 d may only be what Webb et al. (2017) called a mild period of food deprivation.

Season likely influenced assemblage structure and coexistence between watersnakes. The aquatic areas inhabited by watersnakes are seasonally dynamic, resulting in changes of prey abundance that influenced the dietary overlap and coexistence of watersnakes in several ways. Seasonal effects likely facilitated coexistence by reducing the number of individual watersnakes foraging on similar resources during a given season. Seasonal factors also increased dietary overlap of select watersnake pairs because of temporal prey pulses, which when combined with decreased metabolic requirements, might reduce competition that would otherwise lead to competitive exclusion (Willson et al. 2010; Durso et al. 2013). It is also possible that watersnake population densities did not reach levels that would limit prey resources in spite of seasonal hydrological changes (Durso et al. 2013).

We examined a dynamic system of watersnake foraging and identified factors that are potentially facilitating the coexistence of ecologically similar watersnakes. Seasonal changes in prey abundance are likely as important as dietary differences and flexibility within and among watersnake species, structuring the overall semiaquatic snake assemblage. To further understand the importance of seasonal effects and their interaction with other variables influencing semiaquatic snake assemblages, future studies should incorporate dynamic aquatic and terrestrial habitats to assess and incorporate the diversity of prey populations. Our results suggest that seasonality is an important factor influencing assemblage structure, food web dynamics, and coexistence of similar freshwater semiaquatic snake species. We suggest that future studies consider the ecological consequences of seasonality and the concomitant structuring of freshwater systems.

Acknowledgments.—We thank Lauren Beard, Joel Martin, Brandon Newton, Joey Guinto, Eric Clark, Matt Alschbach, David Perkins, Isaac Perkins, Rozalynne Perkins, Jenny Perkins, and Zack Humphrey for assistance in field data collection. We also thank Kentucky Department of Fish and Wildlife Resources for research site access. This research was funded by University of Louisville, Watershed Studies Institute (Murray State University), Greater Cincinnati Herpetological Society, Chicago

Herpetological Society, Kentucky Society of Natural History, and The Kentucky Chapter of The Wildlife Society. Specimen collection was authorized under Kentucky Department of Fish and Wildlife Resources collection permits SC1311140 and SC1411177. We followed all University of Louisville Institutional Animal Care Use Committee guidelines (IACUC Protocol: #13037) for all animal capture, handling, and processing activities.

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Perkins and Eason.—Seasonal variation in watersnake diets.



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APPENDIX TABLE 1. Logistic Regression models ($\Delta AIC_c \leq 2$) assessing the probability snake gut contents contained a particular prey item (fishes, tadpole/metamorph anurans, or froglet/adult anurans) for three watersnake species: Plain-bellied (*Nerodia erythrogaster*), Diamond-backed (*N. rhombifer*), and Common (*N. sipedon*) watersnakes.

Logistic Regression Model ^a	K_i	AIC_c	ΔAIC_c	w_i	Predictor Variable	Estimate	SE	Σw_i ^b
Probability of fish								
Snake species, season	3	192.48	0.00	0.707	Snake species (Plain-bellied)	-2.2387	0.4206	0.999
					Season	0.4292	0.2293	0.707
Probability of tadpole/metamorph anuran								
Season	2	133.41	0.00	0.332	Season	-0.4898	0.2768	0.689
Season, sex	3	135.33	1.92	0.127	SVL	0.0004	0.0007	0.352
Season, SVL	3	135.35	1.94	0.126	Sex (Female)	0.1240	0.2141	0.250
Probability of froglet/adult anuran								
Snake species	2	191.61	0.00	0.410	Snake species (Plain-bellied)	1.7033	0.3949	0.999
Snake species, SVL	3	193.02	1.41	0.203	SVL	-0.0003	0.0004	0.296

^a K_i = number of model parameters. AIC_c = Akaike information criterion corrected for small sample size. ΔAIC_c = distance of model from the most competitive model ($AIC_c - \min AIC_c$). w_i = the estimated probability of being the most competitive model (Akaike weight).

^b Σw_i = sum of Akaike weights indicating predictor variable importance with higher values having more support.

APPENDIX TABLE 2. Logistic regression models ($\Delta AIC_c \leq 2$) assessing the probability that the gut contents of Plain-bellied Watersnakes (*Nerodia erythrogaster*) contained a particular prey item (fishes, tadpole/metamorph anurans, or froglet/adult anurans).

Logistic Regression Model ^a	K_i	AIC_c	ΔAIC_c	w_i	Predictor Variable	Estimate	SE	Σw_i ^b
Probability of fish								
SVL, SVL*SVL, sex	4	59.86	0.00	0.463	SVL	-0.0189	0.0112	0.733
					Sex (Male)	1.0162	0.7585	0.710
					SVL*SVL	$1.5 \cdot 10^{-5}$	$6.7 \cdot 10^{-6}$	0.553
Probability of tadpole/metamorph anuran								
Season	2	45.03	0.00	0.252	Season	-0.3955	0.3483	0.661
Sex	2	46.67	1.64	0.111	SVL	0.0032	0.0034	0.370
SVL	2	46.77	1.74	0.106	Sex (Male)	0.2174	0.5081	0.346
Sex, season	3	46.86	1.83	0.101				
Probability of froglet/adult anuran								
Season	2	77.95	0.00	0.270	Season	0.3379	0.2611	0.746
Season, sex	3	79.74	1.79	0.110	Sex (Female)	0.4706	0.5213	0.305

^a K_i = number of model parameters. AIC_c = Akaike information criterion corrected for small sample size. ΔAIC_c = distance of model from the most competitive model ($AIC_c - \min AIC_c$). w_i = the estimated probability of being the most competitive model (Akaike weight).

^b Σw_i = sum of Akaike weights indicating predictor variable importance with higher values having more support.

APPENDIX TABLE 3. Logistic regression models ($\Delta AIC_c \leq 2$) assessing the probability that the gut contents of Diamond-backed Watersnakes (*Nerodia rhombifer*) contained a particular prey item (fishes, tadpole/metamorph anurans, or froglet/adult anurans).

Logistic Regression Model ^a	K_i	AIC_c	ΔAIC_c	w_i	Predictor Variable	Estimate	SE	Σw_i ^b
Probability of fish								
Sex	2	44.98	0.00	0.233	Sex (Female)	0.7947	0.6241	0.623
Season	2	45.12	0.14	0.217	Season	0.4803	0.3963	0.567
Sex, season	3	45.25	0.27	0.203	SVL	-0.0002	0.0010	0.276
Sex, SVL	3	46.95	1.97	0.087				
Probability of tadpole/metamorph anuran								
Season	2	35.26	0.00	0.300	Season	-0.4516	0.4227	0.648
SVL	2	36.02	0.76	0.205	SVL	0.0039	0.0042	0.492
Sex	2	37.15	1.89	0.117	Sex (Male)	0.0267	0.3742	0.386
Probability of froglet/adult anuran								
SVL, SVL*SVL, sex	4	26.95	0.00	0.325	SVL	-0.0297	0.0187	0.721
SVL, Sex*SVL, sex, season	5	27.41	0.46	0.259	Sex (Male)	6.8069	6.9108	0.685
					SVL*SVL	$1.9 \cdot 10^{-5}$	$1.1 \cdot 10^{-5}$	0.376
					Season	-0.0827	0.4445	0.373
					Sex*SVL	-0.0010	0.0219	0.259

^a K_i = number of model parameters. AIC_c = Akaike information criterion corrected for small sample size. ΔAIC_c = distance of model from the most competitive model ($AIC_c - \min AIC_c$). w_i = the estimated probability of being the most competitive model (Akaike weight).

^b Σw_i = sum of Akaike weights indicating predictor variable importance with higher values having more support.

APPENDIX TABLE 4. Logistic regression models ($\Delta AIC_c \leq 2$) assessing the probability that the gut contents of Common Watersnakes (*Nerodia sipedon*) contained a particular prey item (fishes, tadpole/metamorph anurans, or froglet/adult anurans).

Logistic Regression Model ^a	K_i	AIC_c	ΔAIC_c	w_i	Predictor Variable	Estimate	SE	Σw_i ^b
Probability of fish								
Season	2	81.52	0.00	0.479	Season	1.2331	0.4545	0.960
SVL, season	3	83.22	1.70	0.205	SVL	0.0004	0.0009	0.311
Sex, season	3	83.40	1.88	0.187	Sex (Female)	0.0775	0.2279	0.288
Probability of tadpole/metamorph anuran								
Sex	2	60.80	0.00	0.244	SVL	0.0022	0.0037	0.463
Season	2	60.82	0.02	0.241	Sex (Female)	0.3546	0.5176	0.450
SVL	2	61.89	1.09	0.141	Season	-0.2275	0.2539	0.401
SVL, sex	3	62.65	1.85	0.100				
Probability of froglet/adult anuran								
Season, season*season	3	70.56	0.00	0.996	Season	47.3962	0.9271	0.998
					Season*season	-9.9682	0.0435	0.996

^a K_i = number of model parameters. AIC_c = Akaike information criterion corrected for small sample size. ΔAIC_c = distance of model from the most competitive model ($AIC_c - \min AIC_c$). w_i = the estimated probability of being the most competitive model (Akaike weight).

^b Σw_i = sum of Akaike weights indicating predictor variable importance with higher values having more support.