



Seasonal variation in terrestrial resource subsidies influences trophic niche width and overlap in two aquatic snake species: a stable isotope approach

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Quantifying diet is essential for understanding the functional role of species with regard to energy processing, transfer, and storage within ecosystems. Recently, variance structure in the stable isotope composition of consumer tissues has been touted as a robust tool for quantifying trophic niche width, a task that has previously proven difficult due to bias in direct dietary analyses and difficulties in integrating diet composition over time. We used carbon and nitrogen stable isotope analyses to examine trophic niche width of two sympatric aquatic snakes, banded watersnakes *Nerodia fasciata* and black swamp snakes *Seminatrix pygaea* inhabiting an isolated wetland where seasonal migrations of amphibian prey cause dramatic shifts in resource availability. Specifically, we characterized snake and prey isotope compositions through time, space, and ontogeny and examined isotope values in relation to prey availability and snake diets assessed by gut content analysis. We determined that prey cluster into functional groups based on similarity of isotopic composition and seasonal availability. Isotope variance structure indicated that the trophic niche width of the banded watersnake was broader (more generalist) than that of the black swamp snake. Banded watersnakes also exhibited seasonal variation in isotope composition, suggesting seasonal diet shifts that track amphibian prey availability. Conversely, black swamp snakes exhibited little seasonal variation but displayed strong ontogenetic shifts in carbon and nitrogen isotope composition that closely paralleled ontogenetic shifts in their primary prey, paedomorphic mole salamanders *Ambystoma talpoideum*. Although niche dimensions are often treated as static, our results demonstrate that seasonal shifts in niche dimensions can lead to changes in niche overlap between sympatric species. Such short-term fluctuations in niche overlap can influence competitive interactions and consequently the composition and dynamics of communities and ecosystems.

Historically, ecological niche theory has been one of the most pervasive and controversial concepts in ecology. Despite its initial appeal, difficulties in defining, quantifying and testing niche theory caused the concept to fall into disuse in the 1980s and 1990s (Chase and Leibold 2003). Recently, recognition of the magnitude and diversity of effects that human activities are having on the environment has prompted increased interest in ecosystem ecology, particularly in understanding the role that individual species play in ecosystems (Grimm 1995, Tilman et al. 1997, Vanni et al. 2002). Quantifying the role of species within a system involves assessing both the requirements of species from the system and the impacts of species on the system, concepts directly related to the classical Grinnellian (Grinnell 1917) and Eltonian (Elton 1927) views of the ecological niche, respectively (Chase and Leibold 2003). Indeed, the applicability of classical niche theory to modern population, community, and ecosystem ecology has been recognized, and efforts to consolidate niche theory and revise it into a theoretically sound, quantitatively useful, and

applicable theory across multiple levels of biological organization are underway (Chase and Leibold 2003, Newsome et al. 2007).

Among the most important contributions of individual species to ecosystems is their role in energy use, storage, and transfer within the system (Heitschmidt et al. 1996, Lyons et al. 2005). Thus, assessing the functional role of a species depends in large part on quantifying its trophic niche width, which represents the richness and evenness of resources consumed (Bearhop et al. 2004). Interspecific niche overlap is often interpreted in light of potential competition and competitive exclusion or resource partitioning is often inferred from low incidence of niche overlap (Gause 1934, Pianka 1972). Traditionally, trophic niche characteristics have been described by either examining diet at one particular place and time or by pooling samples such that niche dimensions represent an integration of dietary information over large temporal or spatial scales (Luiselli 2006a). Such lumping or splitting of dietary information precludes the evaluation of

niche dynamics including spatial or temporal niche shifts. Although the dynamic nature of the trophic niche has been recognized in some taxa (Nieder 1997, Roy and Thomas 2003), the consequences of spatial and temporal variation in resource availability on niche characteristics of sympatric species remain poorly understood, particularly in herpetofauna (Luiselli 2006a).

Despite the apparent utility of the trophic niche as a tool for assessing community and food web structure, assessing diet composition for many species has proven difficult (Bearhop et al. 2004, Newsome et al. 2007). Direct dietary analyses, such as gut content or fecal analysis, often incur bias due to difficulty in accurately measuring relative abundance of prey taxa or failure to account for variation in digestibility and assimilation rates, potentially resulting in over- or under-representation of certain food items (Bearhop et al. 1999, 2004, Votier et al. 2003). Recently, the examination of stable isotope composition (reported as $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values) of consumer tissues has been touted as a robust tool for quantifying trophic niche width (Bearhop et al. 2004, Newsome et al. 2007). Indeed, Newsome et al. (2007) suggested that an organism's 'isotopic niche', its range of stable isotope values expressed in δ -space, is comparable to Hutchinson's (1957) n-dimensional hypervolume representation of the niche. Because the isotopic composition of consumer tissues reflects assimilated diet in predictable ways, isotopic variation within a consumer population can be used to examine niche characteristics through space and time (Bearhop et al. 2004). For example, Inger et al. (2006) used stable isotopes to assess seasonal shifts in diet (from marine angiosperms to terrestrial grasses) and habitat use of wintering geese in Ireland. However, in order to use stable isotopes to draw meaningful inferences about consumer trophic niche dimensions, it is necessary to quantify spatial and temporal variation in prey availability and isotopic composition (Bearhop et al. 2004). Specifically, stable isotope composition can only be used as a measure of a consumer's trophic niche if prey taxa are distinct in isotope composition and show little intraspecific variation through time and space (Bearhop et al. 2004). Consequently, despite the theoretical advantages of using stable isotopes to assess niche dimensions, few studies have characterized suitable study systems or employed the sampling designs necessary to implement this powerful tool effectively.

Typically, isolated freshwater wetlands dry periodically and lack fish, yielding simplified food webs often dominated by amphibians and reptiles (Gibbons et al. 2006). These systems provide an ideal opportunity to use stable isotopes to evaluate consumer trophic niches. Because amphibians receive source carbon from both terrestrial and aquatic plants, amphibian prey taxa are likely to vary widely in their carbon isotope composition. Moreover, amphibian-dominated systems exhibit dramatic shifts in resource availability as terrestrial adults of different species undertake seasonal breeding migrations to wetlands. Subsequently, their larvae grow within the wetland, and most species eventually metamorphose and emigrate into the surrounding uplands. In this study, we examine the diets of two sympatric aquatic predators inhabiting an isolated, fishless wetland in South Carolina; a suspected generalist predator (the banded watersnake *Nerodia fasciata*) and a species thought to specialize

on aquatic salamanders (the black swamp snake *Seminatrix pygaea*). We evaluate the effects of seasonal variation in amphibian prey availability on snake trophic niche dimensions and explore the ability of stable isotopes to reveal patterns of resource use. Specifically, we assess the isotope variance structure in our system as it relates to variation in snake and prey isotope profiles through time, space, and ontogeny. We subsequently use trophic niche width and patterns of niche overlap to infer how fluctuating resource availability affects the potential for competitive interactions between the two species. Finally, we assess the fit between our isotope analyses and traditional gut content analyses in evaluating resource use by consumers and make recommendations about using stable isotopes as trophic niche indicators.

Material and methods

Study site

Ellenton Bay is an isolated Carolina bay freshwater wetland on the Dept of Energy's Savannah River Site in the Upper Coastal Plain of South Carolina, USA. Although water levels are extremely variable (Willson et al. 2006, Winne et al. 2006b), the bay typically holds water year-round and covers approximately 10 ha when full. The water is generally shallow (< 1 m deep during 2003–2006) and is dominated by relatively uniform expanses of emergent grasses (predominantly *Panicum* sp.) with smaller patches of water lilies *Nymphaea odorata* and water-shields *Brasenia schreberi*. Because Ellenton Bay dries periodically, it is currently devoid of fish, crayfish, and large aquatic salamanders (*Siren* sp. and *Amphiuma means*), making it a relatively uncomplicated aquatic ecosystem in which amphibians are the major vertebrate prey taxa and aquatic snakes are the major vertebrate predators (Willson et al. 2006, Winne et al. 2006b).

Study species

The banded watersnake *Nerodia fasciata* and black swamp snake *Seminatrix pygaea* are natricine watersnakes native to the southeastern United States and are the most abundant snakes at Ellenton Bay. The black swamp snake is considered the smallest semi-aquatic snake in North America (maximum total length 555 mm) and is highly aquatic, seldom leaving the aquatic habitat or basking above water (Gibbons and Dorcas 2004, Winne et al. 2006b). The banded watersnake is larger (maximum total length 1588 mm) and can be observed along wetland margins or basking on emergent vegetation (Gibbons and Dorcas 2004). Both species are viviparous and give birth in July and August in our region. Although the banded watersnake is ubiquitous in the southeast, occurring in virtually all aquatic habitats, the black swamp snake is generally uncommon and patchily distributed outside of peninsular Florida. Dense populations of black swamp snakes can occur, however, in isolated, heavily-vegetated wetlands (Gibbons and Dorcas 2004, Winne et al. 2005). Both banded watersnakes and black swamp snakes are known to consume a variety of aquatic prey, with a preference for fish and amphibians (Gibbons and Dorcas 2004). Although no published study has compared the diets of these

two species where they occur in sympatry, both species feed largely on aquatic life stages of the mole salamander *Ambystoma talpoideum* at Ellenton Bay. Banded watersnakes, however, also include adult anurans and tadpoles in their diet, particularly in the spring months.

Snake sampling

We sampled snakes at Ellenton Bay monthly from June–October 2005 and March–May 2006 and divided this study period into four biologically-relevant time periods (seasons) for all analyses: spring (March–April), early summer (May–June), late summer (July–August), and fall (September–October). We sampled snakes using plastic minnow traps, which is the most effective way to sample secretive semi-aquatic snakes in heavily-vegetated aquatic habitats in the southeast (Willson et al. 2005, 2008, Winne 2005). For 5–10 days each month we set 465 traps approximately 2 m apart in a continuous transect (~1 km long) around the periphery of the wetland. Although traps were not intentionally baited, incidental captures of aquatic prey resulted in ‘natural baiting’ (Winne 2005). We checked traps daily for snakes and recorded each snake’s capture location to within 20 m. At the laboratory, we recorded sex, snout–vent length (SVL, nearest mm), and body mass (nearest 0.01 g) of each snake captured. We then individually marked each snake by branding ventral scales (Winne et al. 2006a) before releasing it at its capture location on the day of capture. For comparison with our stable isotope analyses, we also assessed snake diets through traditional gut content analysis. We identified recently-ingested prey items by forced regurgitation (Fitch 1987) and adjusted diet proportions to account for differences in prey mass by multiplying the number of prey items (grouped by genus or life-stage: *Ambystoma talpoideum*, adult *Hyla* sp., adult *Rana* sp., *Acris* sp., newly-metamorphosed *Rana* sp. and tadpoles) recorded in snake’s diets by the mean mass of prey within each group.

Snakes used for isotope analyses were selected to represent all size classes, both sexes, and an even spatial distribution around the wetland. However, because of differences in catchability among size classes (Willson et al. 2008), size distributions for black swamp snakes were not uniform between sampling periods. During each season we collected ventral scale clips from approximately 20 individuals of each snake species. Scale clips consisted of one to four ventral scales from the mid-body of the snake; however, tail clips were taken for some very small individuals. Scale clips have been shown to reflect isotopic composition of diet in snakes relatively soon (ca 15 days) after a diet switch (Pilgrim 2005). Preliminary analyses have shown that scale clips and tail clips from the same individual do not differ substantially in isotopic composition (~ 0.20‰ difference; Pilgrim unpubl.).

Prey sampling

Although 24 amphibian species are known to occur at Ellenton Bay (Gibbons and Semlitsch 1991), most either exist at such low densities or enter the aquatic habitat so infrequently that they are likely only occasionally encountered by snakes. To conservatively identify all potentially important prey taxa, we examined a database of 2795 diet

records for banded watersnakes and black swamp snakes at Ellenton Bay from 2003–2006 (Willson and Winne unpubl.) and recorded any prey species that had been documented as a prey item more than once. The resulting list of six prey species accounted for > 99% of the snake prey records: pedomorphic *Ambystoma talpoideum* (mole salamander), *Rana sphenoccephala* (southern leopard frog), *R. clamitans* (bronze frog), *R. catesbeiana* (bullfrog), *Hyla gratiosa* (barking treefrog) and *Acris gryllus* (southern cricket frog). Based on taxonomic affinity, and similarity of seasonal availability and isotopic composition, we qualitatively grouped these prey taxa into six intuitive prey functional groups (aquatic salamanders, adult ranid frogs, adult cricket frogs, adult treefrogs, recently-metamorphosed anurans, and tadpoles) for subsequent analyses.

We assessed seasonal availability of aquatic amphibian species/life stages (aquatic salamanders and tadpoles) while sampling for snakes. During each sampling interval, we deployed 15 aquatic funnel traps, spaced equally around the perimeter of the wetland, as ‘prey traps’. All prey captured in these traps were recorded daily and all trap contents were subsequently removed to avoid re-counting individuals the following day. Any traps containing snakes or large predaceous beetles (e.g. Belostomatidae or Dytiscidae) were excluded from the analysis. We classified aquatic prey groups as ‘available’ during a given season if capture rates in aquatic funnel traps exceeded 0.5 animals per trap per night during that season.

We assessed seasonal availability of adult and newly-metamorphosed anurans (ranid frogs, cricket frogs, treefrogs and anuran metamorphs) using captures in a terrestrial drift fence with pitfall and funnel traps that completely encircled Ellenton Bay from 1 Feb 2003–31 Jan 2004 (Gibbons et al. 2006). Although logistical difficulties prohibited us from operating the drift fence during years when snakes were sampled, these data represent general seasonal patterns of amphibian breeding activity, which are highly conserved across years (Blaustein et al. 2001). To determine seasonal availability, we calculated the proportion of captures of each anuran prey group within each season and classified groups as available within a season if captures for a group during that season exceeded 10% of total captures for that group across the year. Although our thresholds for judging availability of amphibian prey are subjective, they are conservative-prey taxa were only judged to be ‘unavailable’ during seasons when capture rates were extremely low. Additionally, shifting these thresholds would not affect our primary conclusion from these analyses, that richness and abundance of amphibian prey is highest in the spring and early summer.

To assess stable isotope composition of prey, we collected whole-body samples bi-monthly. In all seasons we collected prey samples one month prior to snake samples to allow for turnover time of snake scale tissue. For each bi-monthly sample we collected a minimum of ten salamanders and approximately five individuals from each other prey group available within the wetland during that season. When possible, prey items were collected from locations evenly spaced around the wetland. We fasted all prey items for 2–5 days to ensure that gut contents were voided prior to stable isotope analyses. In addition, we recorded body length (SVL) and mass of each captured prey item.

Stable isotope analyses

We dried snake scale clips in an oven (> 48 h at 40–50°C) and prey samples in a freeze drier until they reached a stable dry mass (5–14 days). Because snakes thoroughly digest nearly all components of their prey and little is known about isotopic routing in snakes, we did not lipid extract samples. We homogenized dried prey items using a cryogrinder and packaged ~1 mg of each sample (ground prey item or snake scale) into individual 3.5 × 5 mm tin capsules. We determined carbon and nitrogen isotope ratios of samples using an isotope ratio mass spectrometer at the Savannah River Ecology Laboratory. We report stable carbon and nitrogen isotope compositions of samples in conventional delta notation (Ehleringer and Osmond 1989, Ehleringer and Rundel 1989), per mill (‰) units. We used laboratory standards to calibrate samples to international standards (PDB and atmospheric air) for carbon and nitrogen, respectively.

Statistical analyses

Young snakes are known to display residual maternal isotope signatures (Pilgrim 2007). Likely reflecting this phenomenon, following parturition in the late summer and fall several of the smallest snakes of each species displayed obviously elevated isotope values, approximating those of large females. Thus, to avoid confounding diet-derived isotope signals with maternal signals we excluded those individuals – the seven smallest black swamp snakes (< 200 mm SVL) and 12 smallest banded watersnakes (< 280 mm SVL) – from analyses. We tested for ontogenetic shifts in isotopic composition within each snake species and prey group using linear regressions of isotope values on SVL. For taxa (prey or snake) that did not exhibit significant ontogenetic shifts, we used analyses of variance (ANOVA) to compare isotope values among groups (i.e. spatial location, season). For taxa that displayed significant ontogenetic shifts in isotope ratios, we used analyses of covariance (ANCOVA), with SVL as the covariate. We tested for spatial variation in isotopic composition for the three prey groups (salamanders, ranid frogs and cricket frogs) for which we had sufficient spatial distribution and sample size to subdivide samples within the wetland. We systematically divided the wetland into five equal sections and used ANOVA or ANCOVA to test for differences in isotope values among sections.

Isotopic mixing models (Phillips 2001, Harvey et al. 2002, Phillips et al. 2005, Carleton et al. 2008) have recently gained popularity as quantitative tools for explicitly translating consumer isotopic composition into diet. Although the mixing model approach is well-suited for investigations seeking to quantify the proportional contributions of multiple prey types to consumer diets, most mixing models assume that the consumers are in isotopic equilibrium with their diets, and model performance varies greatly depending on the trophic shift values used to parameterize the model. Because we suspect that snake tissues in this system are seldom in isotopic equilibrium with diet and data on trophic shift values for snake tissues are limited (but see Pilgrim 2005, 2007, Fisk et al. 2009) we did not take a mixing model approach in this study. Alternatively, we adopt the approach of Bearhop et al. (2004) and use patterns of variation in stable isotope

composition to gain insight on trophic niche characteristics for the two snake species.

We assessed overall trophic niche width of black swamp snakes and banded watersnakes by comparing variance of isotope values for each species, pooled across all seasons, using Levene's test for homogeneity of variances, and assessed seasonal variation by comparing isotope values among seasons for each snake species using ANOVA or ANCOVA. We recognized statistical significance at $\alpha = 0.05$ and performed all statistical analyses using SAS (ver. 9, SAS Institute 2000) or the STATISTICA for Windows software package (StatSoft 1998). We examined all data prior to each analysis and if statistical assumptions were not met we used appropriate non-parametric tests. Specifically, due to unequal variance among treatments, we used a Kruskal–Wallace test in lieu of ANOVA for analyses of spatial variation in $\delta^{13}\text{C}$ of salamanders and when comparing $\delta^{15}\text{N}$ in the two snake species, and used a Scheirer–Ray–Hare test (non-parametric ANCOVA; Petraitis et al. 2001) in lieu of ANCOVA when examining seasonal variation in $\delta^{15}\text{N}$ for both snake species.

Results

Snake gut content analyses

Gut content analysis suggested that both snake species prey predominantly on larval and paedomorphic *Ambystoma talpoideum* (mole salamanders) at Ellenton Bay (Fig. 1). The diet of black swamp snakes, particularly, was comprised nearly exclusively of salamanders. Banded watersnakes consumed some other amphibians, including adult anurans and tadpoles, and consumed these alternative amphibian prey types most frequently in the spring (Fig. 1).

Prey availability and isotope composition

Availability of prey groups varied dramatically across seasons (Fig. 2). Some groups were abundant year-round (e.g. salamanders, Fig. 2a; ranid frogs, Fig. 2b), while other groups were available during some seasons, but were virtually absent during other seasons (e.g. tadpoles, Fig. 2a; treefrogs, Fig. 2b). Generally, prey richness was high in the spring and early summer (Fig. 2). This was primarily due to spring arrival of breeding anurans (e.g. treefrogs and cricket frogs) and the presence of their larvae (tadpoles) in the aquatic habitat. In contrast, prey richness was low in the summer and fall, when the primary available prey was salamanders (Fig. 2). Although available year-round, abundance of ranid frogs peaked in the fall (Fig. 2).

To use isotope composition of consumer tissues as a meaningful measure of trophic niche width, prey must differ isotopically from each other and isotope signatures of prey must remain relatively stable over time (Bearhop et al. 2004). Plots of $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values for all prey sampled ($n = 128$) revealed that the six amphibian functional groups were isotopically distinct (Fig. 3). Tadpoles were most depleted in ^{13}C , whereas the more terrestrial adult anurans (ranid frogs, cricket frogs and treefrogs) were most enriched in ^{13}C . Adult anurans separated along the $\delta^{15}\text{N}$ axis, potentially reflecting variation in trophic position; the larger ranid

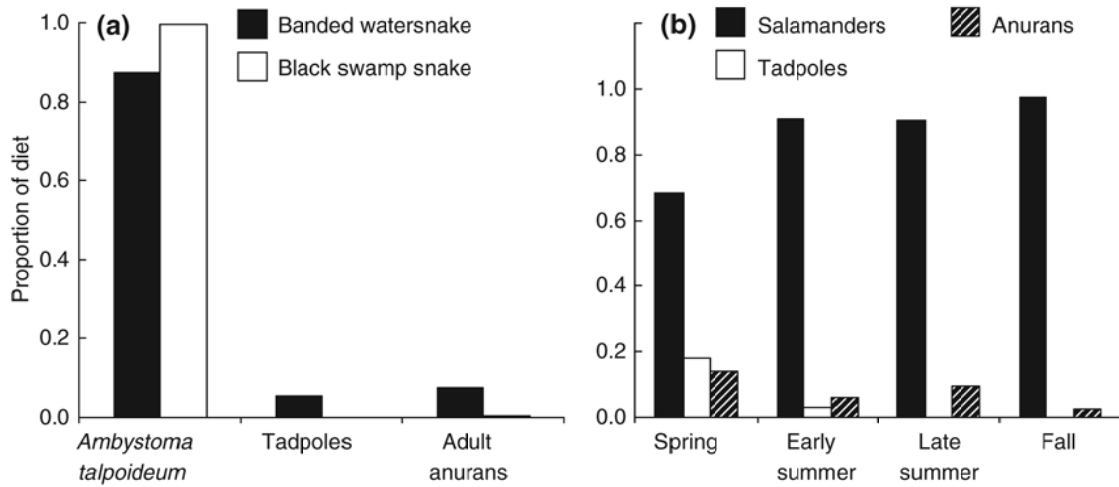


Figure 1. Diet composition of banded watersnakes and black swamp snakes at Ellenton Bay from May 2005 to April 2006 based on gut-content analysis. Overall diet composition for banded watersnakes and black swamp snakes (a) was derived from a total of 1504 and 518 diet items, respectively, adjusted to account for differences in prey mass. Seasonal diet composition for banded watersnakes (b) demonstrates seasonal diet shifts in this species.

frogs were enriched in ^{15}N relative to smaller treefrogs and cricket frogs.

The isotopic composition of prey functional groups showed little change across seasons, relative to one-another (Fig. 4). For example, ranid frogs showed relatively high isotope values in all seasons, whereas tadpoles showed low isotope values whenever they were available. Prey groups that were available year-round (e.g. salamanders and ranid frogs) exhibited little seasonal variation in isotope values, whereas those that showed some seasonal shifts were only present

within the wetland for short periods (e.g. tadpoles and treefrogs). Thus, most temporal variation in the overall isotope profile of prey at Ellenton Bay was due to seasonal changes in prey availability rather than shifts in isotopic composition within prey taxa.

Salamanders exhibited a strong positive ontogenetic shift in nitrogen isotope composition ($r^2 = 0.501$; $p < 0.001$), suggesting that larger salamanders may feed at a higher trophic level than smaller salamanders, and a trend towards ontogenetic depletion in carbon isotope values ($r^2 = 0.034$;

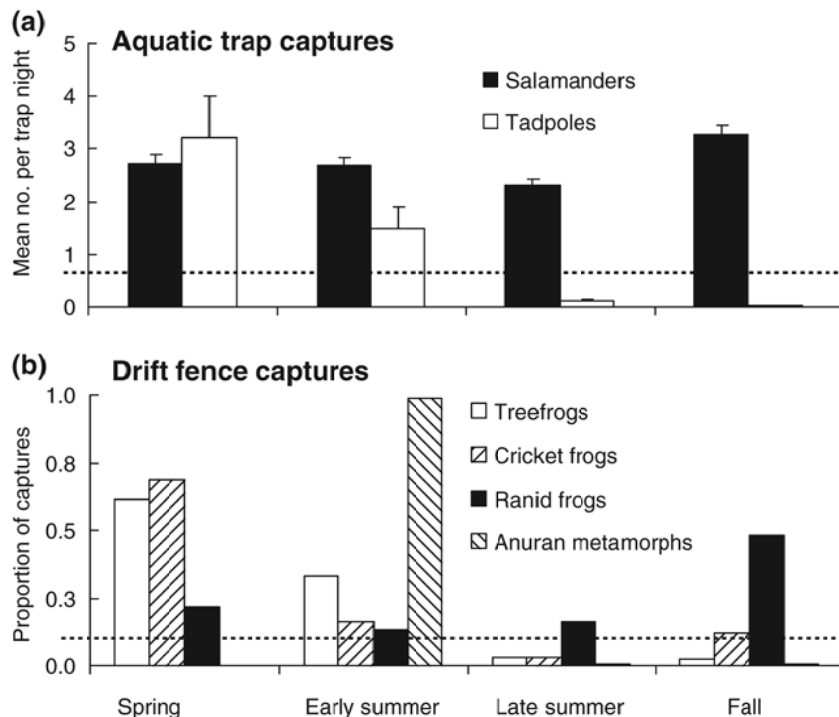


Figure 2. Seasonal availability of amphibian prey at Ellenton Bay including (a) fully aquatic groups (salamanders and tadpoles) and (b) migratory adult and metamorphic anurans. Bars in (b) represent the proportion of individuals within each prey taxon that were captured in a given season. Dashed lines represent thresholds above which prey were judged as available during a given season.

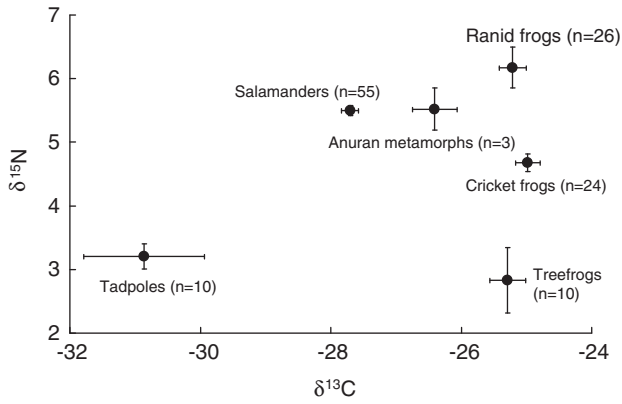


Figure 3. Average $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values (± 1 SE) of amphibian prey captured at Ellenton Bay in 2005 and 2006. Prey were grouped into six functional groups based on similarity of isotopic composition and seasonal availability.

$p = 0.096$). We did not detect any other significant ontogenetic shifts in prey isotope values (all $p > 0.05$). We found no spatial variation in isotopic composition of salamanders ($\delta^{13}\text{C}$, Kruskal–Wallace test, $H_{4,55} = 5.43$, $p = 0.246$; $\delta^{15}\text{N}$, ANCOVA, $F_{4,49} = 1.42$, $p = 0.242$), adult ranid frogs ($\delta^{13}\text{C}$, ANOVA, $F_{4,49} = 0.27$, $p = 0.894$; $\delta^{15}\text{N}$, ANOVA, $F_{4,21} = 1.07$, $p = 0.394$), or adult cricket frogs ($\delta^{13}\text{C}$, ANCOVA, $F_{4,18} = 0.69$, $p = 0.611$, one outlier excluded; $\delta^{15}\text{N}$, ANOVA, $F_{4,19} = 1.24$, $p = 0.329$). Thus, prey location within the wetland was not an important source of variation in prey isotopic composition at Ellenton Bay.

Variation in snake isotope composition

Overall, mean isotope values were similar for banded watersnakes (-26.0‰ $\delta^{13}\text{C}$ and 7.5‰ $\delta^{15}\text{N}$) and black swamp snakes (-26.2‰ $\delta^{13}\text{C}$ and 7.4‰ $\delta^{15}\text{N}$; Fig. 5). These values were slightly enriched in both ^{13}C and ^{15}N compared to mean isotope values of salamanders (Fig. 4). Although mean isotope values were not statistically different between banded watersnakes and black swamp snakes (Kruskal–Wallace test: $\delta^{15}\text{N}$, $\chi^2 = 1.90$, $p = 0.17$; $\delta^{13}\text{C}$, $\chi^2 = 1.15$, $p = 0.28$), the species displayed strong differences in isotopic variance (Levene’s test for homogeneity of variances: $\delta^{15}\text{N}$, $F_{1,172} = 41.10$, $p < 0.01$; $\delta^{13}\text{C}$, $F_{1,172} = 21.53$, $p < 0.01$). Specifically, although the range of $\delta^{15}\text{N}$ values exhibited by the two snake species was similar (5 to 9‰), banded watersnakes displayed a much broader range of $\delta^{13}\text{C}$ values (-28.5 to -23.5‰) than black swamp snakes (-27.5 to -25‰). Thus, overall, stable isotope composition suggests that banded watersnakes have a broader trophic niche than black swamp snakes (Fig. 5).

Banded watersnakes exhibited no ontogenetic shift in carbon isotope composition (Fig. 6a; $r^2 = 0.01$; $p = 0.579$) but displayed a slight positive ontogenetic shift in nitrogen isotope values (Fig. 6b; $r^2 = 0.45$; $p = 0.034$). The more specialized black swamp snakes displayed highly significant ontogenetic shifts in both carbon (Fig. 6c; $r^2 = 0.15$; $p < 0.001$) and nitrogen (Fig. 6d; $r^2 = 0.78$; $p < 0.001$) isotope values, with larger individuals depleted in ^{13}C and enriched in ^{15}N relative to smaller individuals. R^2 values demonstrate that for black swamp snakes, 78% of the variation in nitrogen isotope composition was explained by body

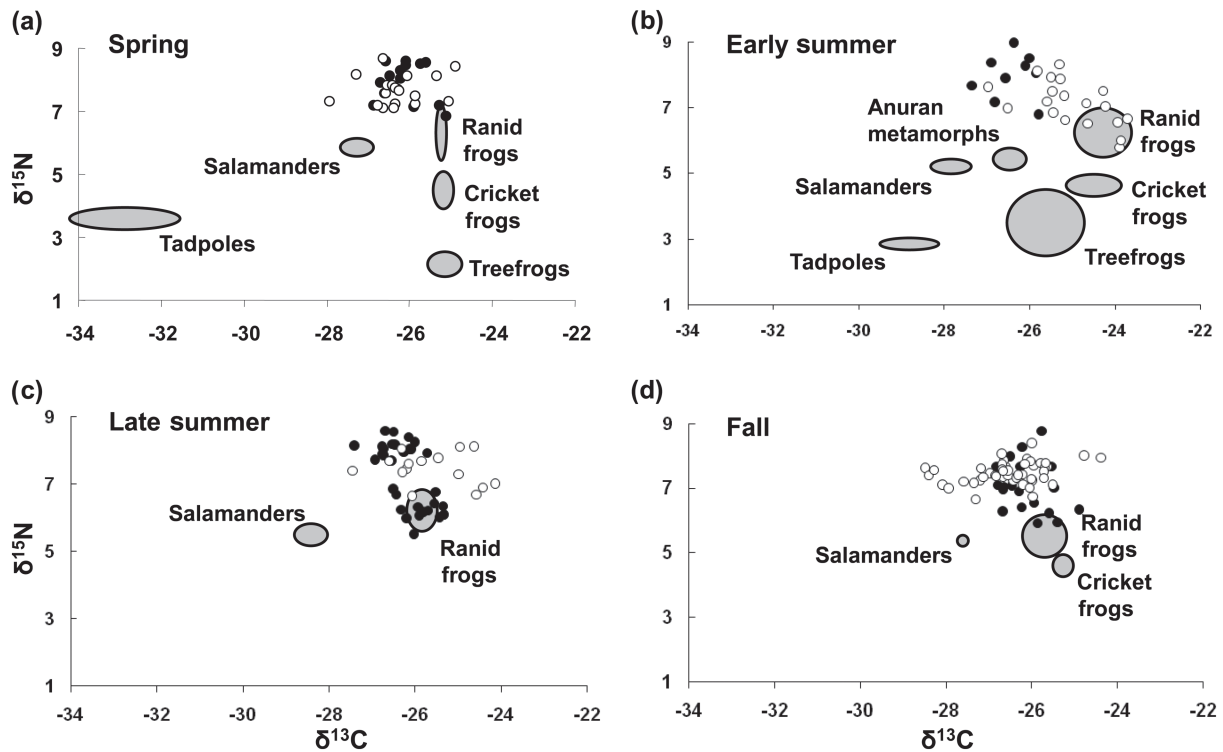


Figure 4. Seasonal shifts in isotopic composition of amphibian prey (shaded bubbles) and snakes (● black swamp snakes, ○ banded watersnakes) at Ellenton Bay. Shaded bubbles represent mean (± 1 SE) prey isotope values. Note that isotope values of prey groups are similar across seasons, thus shifts in overall seasonal isotope profiles are a result of shifts in availability, not shifts in isotope values within prey groups.

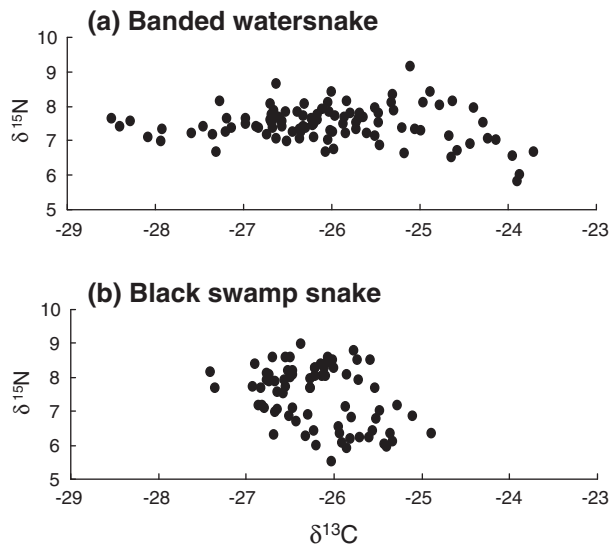


Figure 5. Overall trophic niche breadth of (a) banded watersnakes and (b) black swamp snakes at Ellenton Bay as indicated by carbon and nitrogen isotope composition.

size (SVL), compared to only 45% for banded watersnakes. The ontogenetic shifts in black swamp snakes generally paralleled those seen in salamanders (Fig. 6e–f), but were enriched slightly in both ^{13}C and ^{15}N (Fig. 6c–f).

Black swamp snakes exhibited no significant seasonal variation in carbon (Fig. 6c; ANCOVA, $F_{3,70} = 1.38$, $p = 0.256$) or nitrogen (Fig. 6d; Scheirer–Ray–Hare test, $F_{3,91} = 0.49$, $p = 0.693$) isotope values. The more generalist banded watersnakes exhibited significant seasonal variation in carbon values (Fig. 6a; ANOVA, $F_{3,94} = 15.41$, $p < 0.001$) but not in nitrogen isotope values (Fig. 6b; Scheirer–Ray–Hare test, $F_{3,94} = 0.47$, $p = 0.701$). The strongest seasonal shift in banded watersnake isotope values occurred between spring and early summer, when snakes showed strong enrichment in ^{13}C and a trend towards depletion in ^{15}N (Fig. 7). This shift occurred concomitant with availability of adult anurans, particularly treefrogs, which are enriched in ^{13}C and depleted in ^{15}N relative to other prey taxa (Fig. 4). Following early summer, banded watersnakes showed gradual depletion in ^{13}C through the late summer and fall (Fig. 7).

Seasonal shifts in prey consumption by banded watersnake resulted in shifts in overlap of isotope values between the two snake species (Fig. 4). In fall and spring the range of isotope values exhibited by banded watersnakes nearly completely encompassed those of black swamp snakes, whereas in summer the species exhibited reduced overlap in isotope values (Fig. 4).

Discussion

Stable isotopes have been proposed as useful tools for examining consumer trophic niches (Bearhop et al. 2004, Newsome et al. 2007), but their use requires relatively simplified food webs with prey sources that differ in isotopic composition. Additionally, researchers must account for (or exclude) variation in isotopic composition within prey taxa

across time and space. Recent studies have demonstrated that spatial variation in the isotopic composition of prey taxa can occur on relatively small spatial scales (e.g. < 1 km; Pilgrim 2005), seriously complicating the use of stable isotopes as diet indicators. Because we did not detect spatial variation or strong temporal variation in prey isotopic composition within our small, well-defined study site, we were able to exclude the confounding effects of spatial and temporal heterogeneity in baseline isotope sources from our analyses. Thus, this system offered an ideal opportunity to explore the ability of stable isotopes to reveal patterns of resource use and trophic niche characteristics of sympatric predators in response to seasonally-fluctuating prey resources.

The black swamp snake (a dietary specialist)

Although black swamp snakes are known to feed on a variety of aquatic prey (Gibbons and Dorcas 2004), gut content analysis suggested that they feed primarily on larval and paedomorphic mole salamanders at Ellenton Bay (Fig. 1). The low variance we observed in black swamp snake isotope values supports this conclusion, suggesting that this species exhibits a more specialized diet than banded watersnakes at Ellenton Bay. Black swamp snakes displayed strong ontogenetic shifts in $\delta^{15}\text{N}$ and $\delta^{13}\text{C}$ values with high r^2 values, indicating that much of the isotopic variation in black swamp snakes was attributable to ontogenetic shifts in isotope ratios. Ontogenetic shifts in black swamp snakes paralleled salamander ontogenetic shifts, but were isotopically heavier, likely representing trophic enrichment (i.e. preferential incorporation of heavy diet isotopes into consumer tissues; Eggers and Jones 2000). Thus, a logical explanation for the presence of an ontogenetic shift in black swamp snake isotope values is an ontogenetic shift in the size of salamanders consumed. Snakes are well-known to be gape-limited predators and ontogenetic shifts in prey size have been demonstrated in many species (Mushinsky 1987, Arnold 1993), including some dietary specialists (Voris and Moffett 1981, Godley et al. 1984). Due to the small body size of black swamp snakes, small individuals are likely gape-limited in the size of salamanders that they can consume, with only the largest snakes able to ingest full-grown salamanders. A specialized diet of salamanders also is consistent with the lack of seasonal variation in black swamp snake isotope values, as salamanders are one of the few prey taxa that are abundant at Ellenton Bay year-round. Finally, the ontogenetic shifts we observed in black swamp snakes reiterate the importance of considering multiple sources of isotopic variation in stable isotope diet studies. In species that exhibit strong within-year shifts in demography (e.g. through seasonal reproduction), diet-related seasonal shifts in isotope composition can become confounded with seasonal shifts in isotope composition due to demography if demographic variation is not accounted for during analyses.

The banded watersnake (a dietary generalist)

Banded watersnakes are well-known to consume a variety of aquatic and semi-aquatic prey (Gibbons and Dorcas 2004) and displayed the most diverse diet of five sympatric natracine watersnake species in Louisiana (Mushinsky and

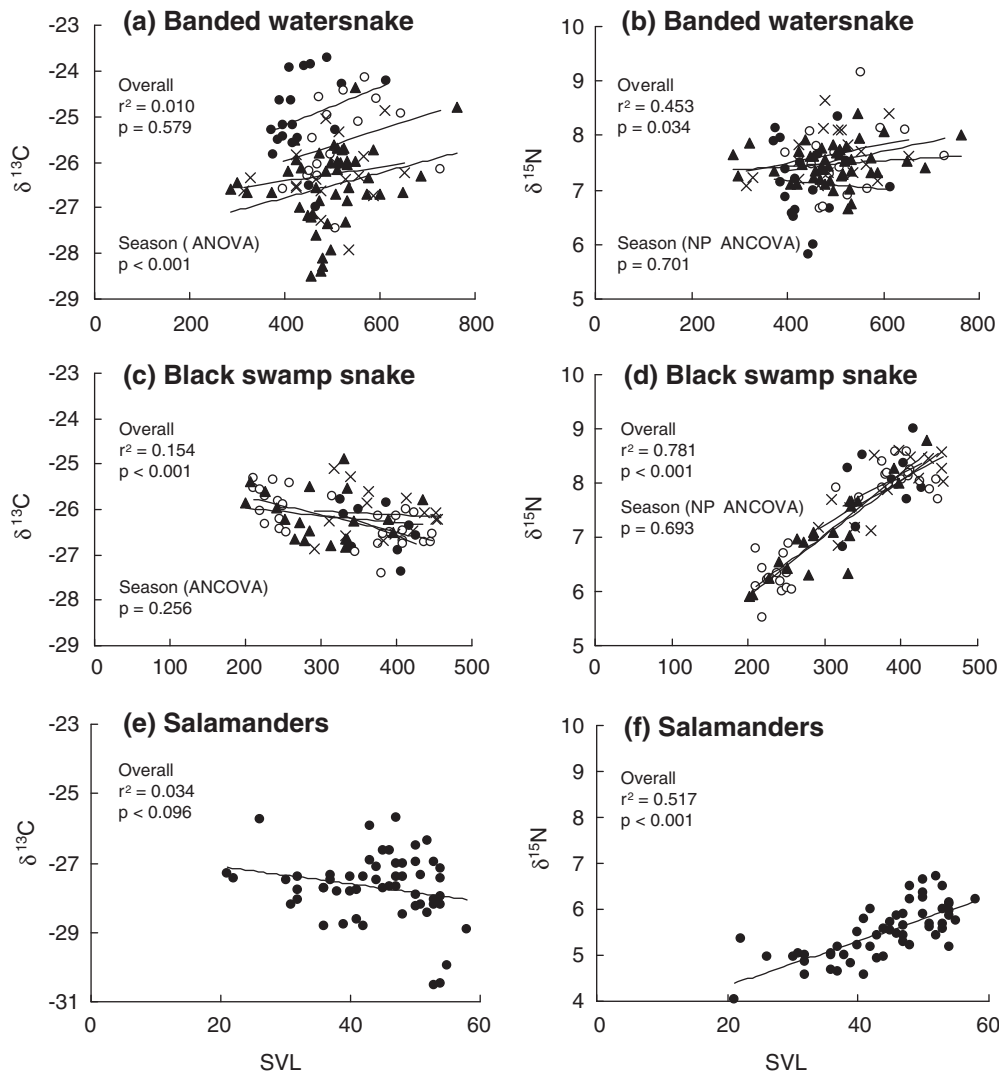


Figure 6. Ontogenetic and seasonal shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values for banded watersnakes (a and b) and black swamp snakes (c and d). Symbols in (a–d) denote seasons: (X) spring, (●) early summer, (○) late summer, (▲) fall. Ontogenetic shifts in aquatic salamanders (e and f) are provided for comparison with black swamp snakes. Seasonal shifts in $\delta^{13}\text{C}$ and $\delta^{15}\text{N}$ values were evaluated using ANOVA, ANCOVA, or non-parametric ANCOVA (Scheirer–Ray–Hare test).

Hebrard 1977). Gut content analyses suggested that banded watersnakes at Ellenton Bay feed primarily on aquatic salamanders but also consume tadpoles and adult anurans (Fig. 1). The results of our stable isotope analyses generally support this conclusion by demonstrating that banded watersnakes have a broader (more generalist) trophic niche than black swamp snakes with little ontogenetic variation in isotope values. Moreover, our isotope analyses revealed that unlike black swamp snakes, banded watersnakes showed strong seasonal shifts in isotope composition. The most notable shifts in watersnakes occurred between spring and early summer. Between these seasons, banded watersnakes tissues displayed an enrichment in ^{13}C and a trend towards depletion in ^{15}N . This pattern is consistent with banded watersnakes feeding on seasonally-available treefrogs and cricket frogs (which are enriched in ^{13}C and depleted in ^{15}N relative to other prey) in the spring. Although gut content analysis suggested that banded watersnakes also feed on tadpoles in the spring and

early summer, our stable isotope analyses do not support this conclusion. Tadpoles are depleted in both ^{13}C and ^{15}N relative to other prey. The only time period when watersnakes displayed simultaneous depletions in both ^{13}C and ^{15}N was between late summer and fall (Fig. 7), when tadpoles are rare within the wetland (Fig. 2). Thus, the patterns of stable isotope composition suggest that our gut content analysis over-represented tadpoles and potentially under-represented treefrogs within snake diets. This bias likely reflects the fact that the gut content analysis was based on recently-ingested prey taken from snakes captured in aquatic traps. Snakes may have consumed larger numbers of aquatic tadpoles and smaller numbers of terrestrial/arboreal treefrogs within aquatic traps than they would have while at large within the wetland.

Interestingly, despite the fact that we sampled prey one month prior to snakes within seasons, isotopic shifts still appeared to be lagged relative to prey. After exhibiting the

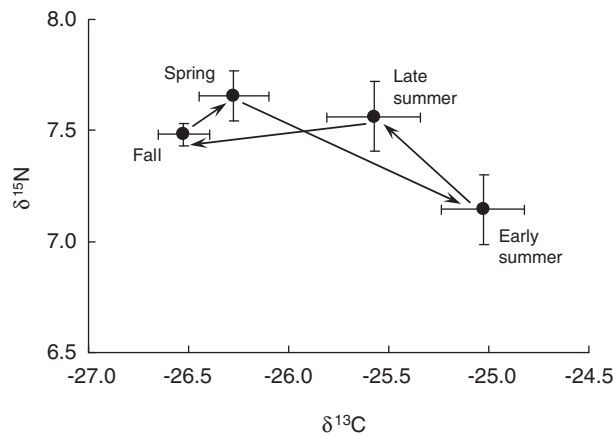


Figure 7. Seasonal shifts (arrows) in mean carbon and nitrogen isotope values (± 1 SE) for banded watersnakes at Ellenton Bay. Note that the most notable shifts occurred between spring and early summer, when banded watersnakes tissues displayed enrichment in ^{13}C and a trend towards depletion in ^{15}N . This pattern is consistent with feeding on seasonally-available treefrogs and cricket frogs (which are enriched in ^{13}C and depleted in ^{15}N relative to other prey) in the spring.

highest $\delta^{13}\text{C}$ values in the early summer, banded watersnakes exhibited gradual depletion in ^{13}C through the late summer and fall. This lag corroborates evidence that although snake scale tissue can register diet isotopic composition on relatively short time scales (ca 15 days, Pilgrim 2005), substantially longer amounts of time may be necessary for scale tissue to equilibrate with diet (e.g. 1.5–5.5 months, Pilgrim 2005). The lagged, short-term shifts we observed in snake isotope values suggest that isotopic mixing models (Phillips 2001, Phillips et al. 2005), which assume consumer tissue is in isotopic equilibrium with diet, should be used with caution, especially when attempting to use isotopes to assess diet over short time-scales.

Seasonal shifts in diet have been observed in other snake species and may allow generalist species to capitalize on seasonally abundant or particularly energy rich prey types during periods of high energetic demand. For example, during spring, female viperine snakes *Natrix maura* switch diets from fish to frogs, which are more abundant and are higher in energy content than other prey types (Santos et al. 2000). Because the timing of this dietary shift coincides with vitellogenesis, prey switching is presumably a strategy that offsets costs of reproduction in viperine snakes (Santos et al. 2000). Although our results suggest that the timing of diet shifts in banded watersnakes largely reflected seasonal prey availability, the inclusion of large adult anurans during the spring months may be important for fueling reproduction as this corresponds with the timing of vitellogenesis for this species (Willson and Winne unpubl.).

Effects of seasonal variation in resource availability on niche overlap

The role of interspecific competition in structuring snake communities remains unresolved (Reichenbach and Dalrymple 1980), but limited interspecific dietary overlap in many snake

communities has prompted some researchers to conclude that snakes, particularly temperate aquatic species, partition prey resources (Mushinsky 1987, Luiselli 2006b). A recent review suggests that among snake communities, temperate aquatic snakes have particularly low dietary overlap but differ only subtly in habitat use (Luiselli 2006b). However, few studies have examined diet overlap between sympatric snake species within ecosystems with strong temporal variation in prey availability. Our results suggest that seasonal prey availability may be extremely important in shaping food webs. At Ellenton Bay, seasonal movements of amphibian prey caused shifts in the trophic niche of the generalist banded watersnake, leading to seasonal shifts in niche overlap that ranged from complete overlap between the species to only partial overlap. Thus, in situations where resources are limiting for much of the year, brief seasonal resource pulses could alter the potential for competitive interactions by reducing niche overlap between potential competitors. This, in turn, may promote community complexity by relaxing competitive exclusion during some seasons (Hutchinson 1959).

As an example, consider competitive interactions among Darwin's finches (*Geospiza*) in the presence and absence of resource pulses driven by the El Niño cycle. Competitive interactions among species of Darwin's finches are thought to limit the number of species present on smaller islands within the Galapagos archipelago (Abbot et al. 1977). However, enhanced productivity resulting from the El Niño events relaxes interspecific competition for seed resources (Boag and Grant 1984a) and has allowed at least one species to successfully establish a breeding population on an island where it previously existed only as an immigrant (Boag and Grant 1984b, Gibbs and Grant 1987, Grant and Grant 1995). Although short term pulses of high productivity can promote species richness in the short term, in order for resource pulses to promote community complexity in the long term, species must be able to persist between pulses when resources become scarce and competitive interactions escalate. Such situations may be particularly advantageous for ectotherms. Because of their exceptionally low metabolic costs (Pough 1980), ectotherms can survive long periods when food is scarce (or competition is high) and efficiently convert resources into biomass during short periods of high productivity. Thus, for ectotherms, short periods of relaxed competition due to seasonal prey abundance or seasonal availability of alternative prey taxa may allow individuals and/or species to persist within the community. For example, several large snake species persist at extremely high densities on small islands by gorging on seasonally-abundant migrating birds (Sun et al. 2001, Boback 2005).

Implications for niche assessment

Evaluation of an organism's trophic niche can provide valuable insight into a species' role within its community and ecosystem (Chase and Leibold 2003). Unfortunately, because diet is generally examined either at one specific location and time or samples are pooled across wide geographic and temporal scales, niche dimensions often represent either instantaneous snapshots or averages over space and time, respectively (Luiselli 2006a). Stable isotopes have been proposed as useful niche indicators because isotopic composition

represents an integration of diet over time and isotope analyses do not suffer from many of the biases inherent in traditional gut or fecal content analyses (Bearhop et al. 2004). The characteristics of our study site and species allowed us to use a combination of traditional gut content analysis and stable isotope techniques to examine the trophic niches of banded watersnakes and black swamp snakes over differing spatial and temporal scales. In general, the two methods yielded similar conclusions (i.e. that both species feed largely on salamanders, but banded watersnakes consume some seasonally-available adult anurans during the spring). However, our isotope analyses suggested that the gut content analysis may have over-represented tadpoles as diet items in banded watersnakes, likely due to consumption of tadpoles by snakes within aquatic traps. Thus, a combination of the two methods was necessary to produce a comprehensive understanding of diet in these snake species. Additionally, our conclusions about niche dimensions, position, and overlap between species were dependent on the scale at which data were assessed. When samples were pooled, banded watersnakes displayed broader niche width than black swamp snakes and the niches of the two species overlapped nearly completely. However, when samples were assessed within seasons, we found that niche overlap during some seasons was minimal. Thus, when assessing niche dimensions, and especially in interspecific comparisons, careful delineation of the temporal and spatial scale across which the niche is being assessed can be critical.

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