

Habitat influences diet overlap in aquatic snake assemblages

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Abstract

Competition for prey is thought to be important in structuring snake assemblages. However, due in part to the secretive behavior and low detectability of many snake species, this generalization is based on a limited number of studies, most of which focus on a single study site. We examined differences in diet composition, trophic niche overlap, site occupancy and detectability of five sympatric aquatic snake species between two different habitat types in the Southeastern US, replicated at the landscape scale: permanent wetlands with fishes ($n = 13$) and isolated, often ephemeral wetlands without fishes ($n = 10$). We collected >3700 prey items from snakes and compared diet composition among snake species to examine niche breadth and overlap, correcting for relative availability of prey captured independently in the same wetlands. We evaluated evidence for competitive exclusion by estimating the probability of co-occupancy for pairs of snake species in each habitat type using occupancy modeling. In wetlands with fishes, niche overlap was low, suggesting resource partitioning. Conversely, in wetlands without fishes, niche overlap was high, with most species feeding on larval or paedomorphic ambystomatid salamanders, but competitive exclusion did not occur. We suggest that high co-occupancy of aquatic snakes in wetlands without fishes despite the apparent lack of resource partitioning is due to a combination of seasonally high abundance of high quality amphibian prey, unique aspects of predator physiology and stochastic abiotic processes that prevent these systems from reaching equilibrium. Our results demonstrate that snake diets can be highly context (e.g. habitat)-specific. Studies should consider other factors in addition to competition for prey when attempting to understand snake population and community dynamics.

Introduction

When resources are limited, consumers are thought to reduce interspecific competition by partitioning (Pianka, 1974). By occupying discrete niche space (e.g. by feeding on different types or sizes of prey), individuals of each consumer species within a community minimize competitive interactions with heterospecifics. Theoretically, this permits a greater number of syntopic consumers to occupy the same trophic level (MacArthur, 1970). An increase in the number of competitors or a decrease in the availability of resources can lead to a reduction in niche overlap due to increased partitioning of resources over evolutionary time (Hardin, 1960). Although competition for prey is only one of several interacting factors contributing to resource partitioning (Toft, 1985), it is considered a key factor in structuring many species assemblages (e.g. Luiselli, 2006c).

Of the evolutionary radiations of tetrapods, snakes are unusual in being exclusively carnivorous. Despite gape limita-

tion, many species have a wide diet breadth, by virtue of highly kinetic jaws that allow them to eat large prey relative to their body size. Snake assemblages typically consist of many species of both specialists and generalists, and often include many similar, often related, species feeding at similar trophic levels (Luiselli, 2006a). Several reviews have concluded that exploitative competition for food is the most important force in structuring snake assemblages (Arnold, 1972; Schoener, 1977; Toft, 1985). Data from either field or museum studies form the basis for generalizations about the composition of snake diets and the structure of snake assemblages (Toft, 1985). Although many excellent studies on snake diets exist, field studies often focus on a single study site (e.g. Luiselli, 2006b), whereas studies based on museum specimens generally integrate records over large spatial and temporal scales, without replication (e.g. Henderson, Dixon & Soini, 1978). Thus, little is known about spatiotemporal variation in snake diets, or the effects thereof on the structure of snake assemblages. Both Luiselli (2006c) and Gibbons & Dorcas (2004)

recommended that scientists study populations of the same snake species living in different environmental contexts in order to better understand the causes and consequences of interpopulation variation in diet.

Niches are hyperdimensional indices that describe resource use by a species (Hutchinson, 1957). According to the competitive exclusion principle (Gause, 1934; Hardin, 1960), no two species can occupy the same niche in the same environment over long time scales. Diet overlap is one type of niche overlap, a proportion that describes the shared use of food resources between two species (Pianka, 1973, 1974). Studies of resource partitioning in snakes have often shown a low degree of diet overlap among species (e.g. Gregory, 1978; Glodek & Voris, 1982; Luiselli, 2006c), suggesting that interspecific competition is an important force in structuring snake assemblages. North American aquatic snake assemblages have been cited as a particularly strong case of resource partitioning (e.g. Mushinsky & Hebrard, 1977; Camp, Sprewell & Powders, 1980; Luiselli, 2006c) because sympatric species often feed almost exclusively on different types of prey. However, these generalizations are based on a surprisingly small number of studies, and little is known about how variation in prey communities, habitat or abiotic conditions affects competition, niche overlap, and emergent community structure in snakes.

We compared diet composition and occupancy of aquatic snakes between two habitat types in the Southeastern US. Replicated at the landscape scale, these were permanent wetlands with fishes ($n = 13$) and semi-permanent wetlands without fishes ($n = 10$). We compared diet breadth and niche overlap between snake species in each type of wetland, in relation to prey availability. By examining a broad diversity of aquatic ecosystems, we challenge the generalization that competition for prey is a universally important force in structuring aquatic snake assemblages.

Methods

Study site and prey sampling

To obtain robust sample sizes of diets of multiple snake species at a large number of study sites, we amassed snake captures from a large number of snake studies conducted on the US Department of Energy's Savannah River Site, South Carolina, US, between 2002 and 2010. We sampled aquatic snakes at 23 wetlands (Supporting Information Appendix S1) located within 28 km of one another (mean inter-wetland distance = 14.8 km), 13 of which were permanent enough to support fishes. The remaining 10 wetlands were isolated, ephemeral and not inhabited by fishes. All 23 wetlands contained areas of open water and areas of submerged and emergent herbaceous aquatic vegetation, except for ephemeral wetlands when they were seasonally dry.

We sampled aquatic snakes using aquatic funnel (minnow) traps (Willson, Winne & Fedewa, 2005). We set between 30 and 465 unbaited traps each night for a total of approximately 95 000 trap-nights. We checked each trap once daily for snakes, typically in the morning. We also included data for a limited number of snakes captured opportunistically by hand

or under cover objects. We collected data on prey availability at a subset of wetlands ($n = 20$) in summer 2006 by counting the number of prey captured in all minnow traps on the first day of sampling at each wetland. We divided prey items into seven categories: (1) larval and paedomorphic ambystomatid salamanders (predominantly *Ambystoma talpoideum*, with a limited number of *Amb. opacum*, *Amb. maculatum* and *Amb. tigrinum*); (2) giant aquatic salamanders (*Siren* spp. and *Amphiuma means*); (3) adult anurans (*Lithobates* spp., *Anaxyrus* spp., *Hyla* spp., *Pseudacris* spp. and *Acris* spp.); (4) larval anurans (tadpoles of the same five genera); (5) fishes; (6) crayfishes; (7) soft-bodied invertebrates (leeches and worms). To calculate prey availability, we corrected for sampling effort (number of trap-nights per wetland) and the average mass of prey items in each category. Because the data were not normally distributed, we used a Mann-Whitney rank sum test to compare total prey biomass between wetland types. We also compared species evenness using Shannon's equitability index (E_H).

Snake species

We assessed diets of the five most abundant aquatic snake species: eastern mud snakes (*Farancia abacura*), banded watersnakes (*Nerodia fasciata*), Florida green water snakes (*N. floridana*), glossy crayfish snakes (*Regina rigida*) and black swamp snakes (*Seminatrix pygaea*). *Nerodia* spp. regularly leave the water for non-reproductive purposes (Gibbons & Dorcas, 2004), whereas the other three species are almost entirely aquatic. Snakes in our study range in size from *F. abacura* [maximum total length (TL) to 207 cm] to *S. pygaea* (TL to 56 cm). Some species are traditionally thought to be dietary specialists (e.g. *Farancia*, *Regina*) whereas others are considered generalists (e.g. *N. fasciata*). For more details see Ernst & Ernst (2003) and Gibbons & Dorcas (2004).

Diet assessment

We returned trapped snakes to the laboratory, where we obtained morphological and diet data, after which all snakes were marked by heat-branding ventral scales with a medical cautery unit (Winne *et al.*, 2006) and released at their capture location. We obtained prey items by palpation of the gut to force regurgitation. We did not force recaptured snakes to regurgitate if recaptures were less than one month apart. At each wetland, we tallied prey items eaten by each species, using the seven categories described above (Supporting Information Appendix S2). For each snake species, we calculated the average proportion of the diet consisting of each prey category, using wetland as the sampling unit. We only included wetlands for which we recorded at least one prey item from that snake species.

Calculation of resource use

We used niche overlap indices to compare dietary resource use among snake species in wetlands with and without fishes.

Niche overlap indices range from zero (complete dissimilarity in resource use between two species) to one (complete overlap in resource use). We calculated the Pianka (1973) index of dietary niche overlap among four of the species using EcoSim 7.72 (Gotelli & Entsminger, 2012). No *R. rigida* were captured in wetlands without fishes, so they were not included in the niche overlap analyses.

We compared the difference in pairwise overlap indices between the two habitat types by modeling the probability that observed niche overlaps were different from those expected by chance (average niche overlap of 1000 simulated assemblages for each pair of species). Assemblages were simulated using a Monte Carlo randomization algorithm that assigned resource use values to each species within a community. We tested two algorithms: one that relaxed niche breadth (random equiprobable specialization) and retained zero states (preventing species that did not use a certain dietary resource in the field from doing so in simulations) and one that retained niche breadth (simulated specialization equal to the observed value), but reshuffled zero states (randomly varied the particular resources that were used). These correspond to Lawlor's (1980) RA2 (relaxed niche breadth) and RA3 (retained niche breadth) randomization algorithms, respectively. For further details, see Lawlor (1980), Winemiller & Pianka (1990) and the EcoSim manual.

We modeled resource states as either equiprobable or non-equiprobable, using effort- and biomass-corrected prey availability data to inform the model in the latter case. For the RA3 algorithm, we excluded fishes as a possible resource in wetlands without fishes by using the hard zeroes 'secret option' (i.e. in simulations we allowed snake species to feed on resources they had not fed on in nature, except for fishes in fishless wetlands). The RA3 algorithm tends to overestimate niche overlap if the equiprobability assumption is not met, because more abundant resources will be used by all species even if niche segregation occurs. Thus, niche overlap indices generated under the equiprobability assumption were evaluated only to determine which species were most similar (i.e. as relative measures), instead of as true measures of niche overlap (Laurent & Kingsbury, 2003).

Estimation of co-occurrence

High interspecific competition for limited resources can alter species occupancy via competitive exclusion. We examined interspecific interactions among seven species of snake, including two for which we had insufficient prey data to analyse diet: rainbow snakes (*F. erythrogramma*) and cottonmouths (*Agkistrodon piscivorus*). For each pairwise comparison of seven snake species, we used a subset of the data from 2006 collected with a sampling structure conducive to occupancy modeling (20 wetlands, each sampled for five consecutive nights; Durso, Willson & Winne, 2011) to model the probability of co-occurrence and the detection probabilities using program PRESENCE (Hines, 2006). We used a two-species model (MacKenzie, Bailey & Nichols, 2004) that estimated site occupancy (ψ), single-species detection probability (p), two-species detection probability (r) and probability of

co-occurrence (ϕ). The parameter for two-species detection probability (r) was estimated as three separate quantities: the detection probability of Species A given that Species B was not present (r_A), the detection probability of Species A given that Species B was present and detected (r_{BA}), and the detection probability of Species A given that Species B was present, but not detected (r_{Ba}).

Results

Prey availability

Total prey availability was similar between wetlands with and without fishes whether prey abundance data were raw (i.e. effort-corrected counts; Mann–Whitney $U = 19$, $P = 0.20$, Fig. 1a) or corrected for biomass (Mann–Whitney $U = 23$, $P = 0.90$, Fig. 1b). Only one prey type was absent from each wetland type in our samples: *Ambystoma* from wetlands with fishes, and fishes from wetlands without fishes. Shannon's equitability (E_H) was 0.43 for wetlands with fishes and 0.56 for wetlands without fishes.

Snake diets

We collected a total of 3772 diet items from over 7500 snakes of five species (Supporting Information Appendix S2).

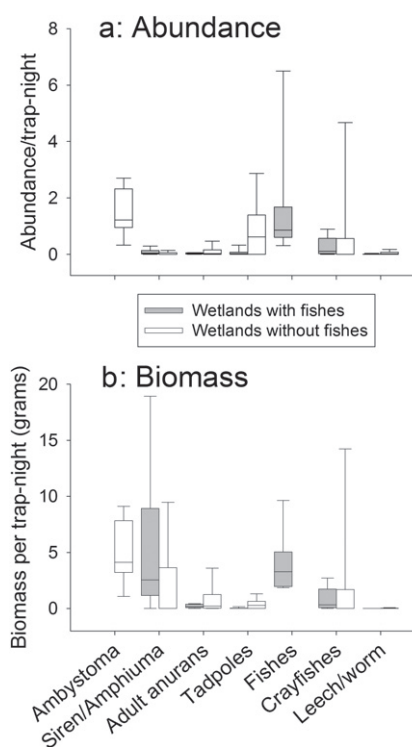


Figure 1 Prey category (a) abundance and (b) biomass in wetlands with fishes (shaded boxes) and wetlands without fishes (hollow boxes) in South Carolina, USA. Shannon's equitability (E_H) was 0.43 for wetlands with fishes and 0.56 for wetlands without fishes.

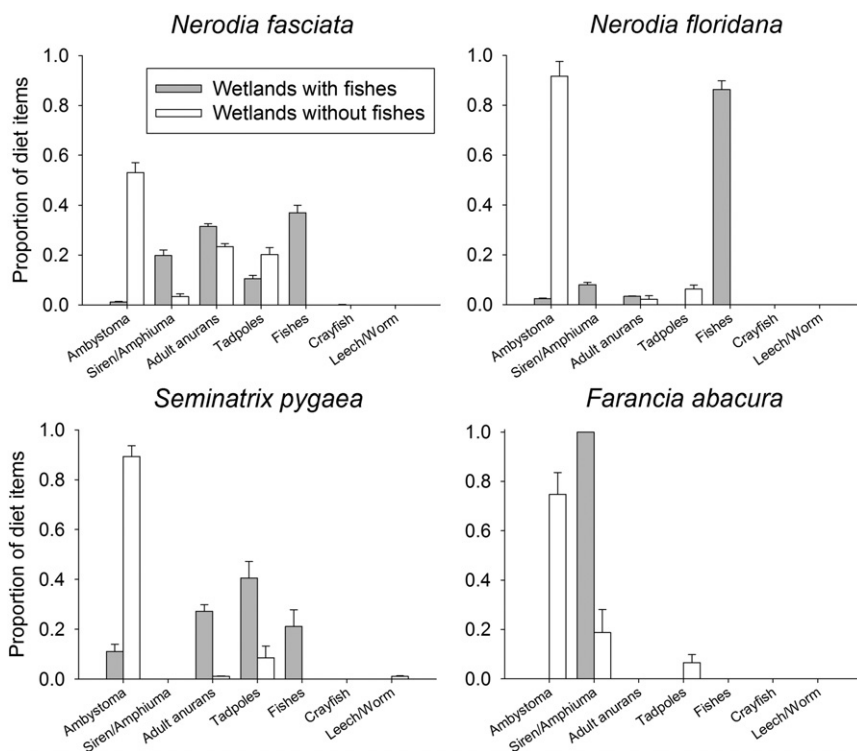


Figure 2 Differences in diet composition of four aquatic snake species between wetlands with fishes (shaded bars) and wetlands without fishes (hollow bars) in South Carolina, USA. Values are means among wetlands \pm 1 SE and are not corrected for differences in prey biomass.

Approximately 41% of snakes that we examined contained recently ingested prey. No *R. rigida* were captured in wetlands without fishes. Diets of the four focal snake species varied substantially between habitat types (Fig. 2). In wetlands with fishes, the diet of each snake species was predominantly made up of a different prey category. *Farancia abacura* consumed only giant aquatic salamanders. *Seminatrix pygaea* consumed mostly tadpoles, fishes and adult anurans, but also ate proportionally more larval salamanders than any other species. *Nerodia floridana* consumed >80% fishes, while *N. fasciata* fed broadly on fishes, adult anurans, giant aquatic salamanders and tadpoles. *Regina rigida* consumed only crayfishes in wetlands with fishes. In wetlands without fishes, all snake species fed predominantly (53–92% of prey items) on larval or paedomorphic salamanders (*Ambystoma*). No aquatic snake species preyed on other snakes, except for *Ag. piscivorus*, from which we recorded too few prey items to analyse. However, a more intensive study employing different capture methods at one fishless wetland suggested that *Ag. piscivorus* also feeds heavily on *Ambystoma* in those habitats (Eskew, Willson & Winne, 2009).

Niche overlap

Under the assumption of equiprobable resources, mean niche overlap was 39% in wetlands with fishes. This was not significantly different from the simulated assemblages, regardless of the randomization algorithm used ($P \geq 0.21$, Table 1a). Overlap in wetlands without fishes was much higher (mean = 93%) and was significantly higher than that in the

simulated assemblages regardless of the randomization algorithm used ($P \leq 0.001$, Table 1a). Niche overlap between all of the six species pairs (excluding *R. rigida*) increased (mean increase = 55%) from wetlands with fishes to wetlands without fishes (Fig. 3a).

When resource availability was specified using biomass-corrected field data on prey relative abundance, mean niche overlap was 30% in wetlands with fishes, which was either significantly lower than or not significantly different from that in the simulated assemblages, depending on the randomization algorithm used ($P = 0.02$ for RA2; Table 1b). Niche overlap in wetlands without fishes (mean = 57%) was higher than, but not significantly different from simulated assemblages regardless of the randomization algorithm used. Between four of the six pairs of species, niche overlap increased from wetlands with fishes to wetlands without fishes (mean increase = 60%; Fig. 3b).

Occupancy

Occupancy did not differ between wetland types with the exception of *R. rigida*, which we only detected in wetlands with fishes (Durso *et al.*, 2011). Probability of co-occurrence (ϕ) was not significantly different from 1 for most species pairs, indicating that occupancy did not decline based on presence of potential competitors (Table 2). Co-occurrence probabilities significantly greater than 1 were estimated between *R. rigida* and three other species (*N. floridana*, *F. abacura* and *S. pygaea*), indicating that these species co-occurred with *R. rigida* with greater frequency than expected. Estimates of

Table 1 Pianka niche overlap index (EcoSim 7.72 output) with a) equiprobable and b) biomass-corrected resource states within an assemblage of four species of aquatic snake from the Savannah River Site, South Carolina, USA^a

Habitat type	Observed overlap	Expected overlap \pm variance	P (observed \geq expected)	P (observed \leq expected)	Niche breadth	Zero states	Randomization algorithm
(a) Equiprobable resource states							
Wetlands with fishes	0.389	0.44 \pm 0.004	0.78	0.21	relaxed	retained	RA2
		0.30 \pm 0.01	0.19	0.81	retained	reshuffled	RA3
Wetlands without fishes	0.934	0.60 \pm 0.01	<0.001***	>0.99	relaxed	retained	RA2
		0.27 \pm 0.016	0.001**	0.99	retained	reshuffled	RA3
(b) Biomass-corrected resource states							
Wetlands with fishes	0.306	0.44 \pm 0.004	0.98	0.02*	relaxed	retained	RA2
		0.24 \pm 0.015	0.24	0.76	retained	reshuffled	RA3
Wetlands without fishes	0.572	0.61 \pm 0.01	0.63	0.37	relaxed	retained	RA2
		0.34 \pm 0.01	0.08	0.92	retained	reshuffled	RA3

^aRandomization algorithms after Winemiller & Pianka (1990). Simulated assemblages were restricted from feeding on fishes in wetlands without fishes using the hard zeroes option of the RA3 algorithm. Asterisks (*) = significant at $\alpha = 0.05$, (**) = highly significant, (***) = very highly significant.

detection probability for Species A were never significantly different in the presence of Species B (Table 3).

Discussion

Although many studies have investigated snake diets, ours is the first spatially replicated study to examine diet overlap among sympatric snake species across multiple habitat types. Regardless of the model algorithm and resource states used, we found that snake species exhibited low dietary niche overlap in wetlands with fishes, consistent with trophic niche partitioning observed in aquatic snake assemblages in other permanent aquatic habitats in North America (e.g. Mushinsky & Hebrard, 1977; Kofron, 1978; Mushinsky, Hebrard & Vodopich, 1982; Himes, 2003). This high level of niche partitioning is consistent with the idea that competition among snake species is strong in these assemblages. We also found that snake diet composition and level of specialization in these habitats was mostly consistent with generalizations made in the literature. This agreement between our results and the published literature makes sense, given that most studies to date have taken place in long hydroperiod aquatic ecosystems, such as rivers and swamps (Gibbons & Dorcas, 2004).

In contrast to our results from wetlands with fishes, all snake species in wetlands without fishes exhibited high dietary niche overlap by feeding predominantly on paedomorphic and larval *Ambystoma*, despite greater prey evenness in these wetlands. Shifts in dietary niche overlap between wetland types occurred without changes to snake species occupancy (with the exception of *R. rigida*, which did not occupy wetlands without fishes), indicating that competitive exclusion did not occur (Table 2). Moreover, there appeared not to be strong effects of occupancy by heterospecifics on detectability, which has been interpreted as a proxy for species abundance (Table 3; MacKenzie & Kendall, 2002; Durso *et al.*, 2011).

There are several possible (but not mutually-exclusive) hypotheses for the lack of diet partitioning by snakes in wetlands without fishes. Competitive interactions might be

relaxed in wetlands without fishes because these habitats support relatively abundant prey resources (e.g. Gibbons *et al.*, 2006; Willson *et al.*, 2010). Other studies have found empirical support for low competition in snake assemblages due to high resource abundance (e.g. Kephart, 1982; Reichenbach & Dalrymple, 1986). Many amphibian species breed primarily in fishless wetlands to avoid depredation, where their influence on energy and nutrient dynamics can be substantial (e.g. Istock, 1967; Seale, 1980; Deutschman & Peterka, 1988). Additionally, certain characteristics of salamanders, such as their elongate shape and short handling time, make them highly accessible prey for aquatic snakes (Willson & Hopkins, 2011), which might reduce the need for snakes to partition prey resources when feeding on salamanders. However, across all wetlands in our study, *Ambystoma* did not comprise more biomass than the total prey biomass available in wetlands with fishes (Fig. 1b), nor are ambystomatids more nutritious than fishes (Willson & Hopkins, 2011), so these explanations alone are unlikely to explain the substantial increase in niche overlap of snake assemblages between wetlands with and without fishes.

Prey phenology might also influence predator competitive dynamics. Although our systematic long-term surveys found similar prey biomass in both wetland types, seasonal pulses of breeding amphibians in isolated wetlands represent a temporary but extraordinary abundance of resources (Willson *et al.*, 2010). When resources are abundant, competition may be especially weak, resulting in periodic patterns of nearly complete niche overlap among several syntopic predator taxa (Luiselli, 2006b; Willson *et al.*, 2010). Critically, the low energetic requirements of snakes (Pough, 1980; McCue, 2007) and their highly plastic rates of growth and reproduction (e.g. Ford & Seigel, 1989; Bonnet *et al.*, 2001) allow them to persist through periods of resource scarcity when amphibians are not breeding, reducing the potential for competitive exclusion during those times. This unusual situation calls into question the consistent importance of competition in structuring aquatic snake assemblages (Toft, 1985). In temperate climates,

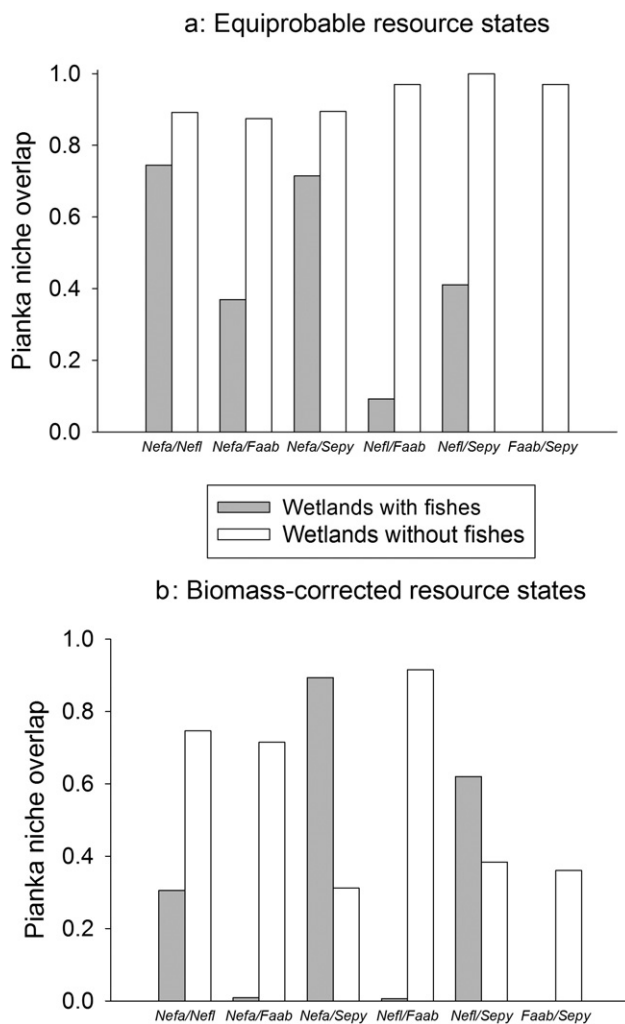


Figure 3 Observed Pianka niche overlap values between six pairs of four species of aquatic snake in wetlands with fishes (shaded bars) and wetlands without fishes (hollow bars), using (a) equiprobable and (b) effort- and biomass-corrected data for prey availability. Scientific names are abbreviated: Nefa = *Nerodia fasciata*, Neft = *Nerodia floridana*, Faab = *Farancia abacura* and Septy = *Seminatrix pygaea*.

the especially low energy requirements, rapid digestive assimilation and high energy storage capacity of snakes (Secor & Diamond, 1998) suggest that they might represent an exceptionally strong case of non-competitive utilization of seasonally fluctuating common food resources.

Finally, competition and snake community structure in isolated wetlands may be regulated not by bottom-up effects of prey availability but rather by either stochastic abiotic processes or by top-down effects of predators. Because the hydroperiod of ephemeral wetlands is fluctuating and unpredictable (Sharitz, 2003), prolonged prey shortages during droughts might shrink snake populations via emigration and death such that they never reach densities where prey resources become limiting (Madsen & Shine, 2000; Willson *et al.*, 2006). Long-term studies at one isolated wetland in our study support this hypothesis; periodic extreme droughts cause dramatic declines in several aquatic snake species at this location (Seigel, Gibbons & Lynch, 1995; Willson *et al.*, 2006), recovery from which can take years (Winne, 2008). Changes to niche overlap in snake assemblages also occur in response to abiotic factors in swamps and lotic systems (Luiselli, 2006b; Hampton & Ford, 2007). Although we did not investigate top-down effects, these are probably relatively consistent across wetlands in our system, where snakes are among the top predators.

Our findings from wetlands without fishes strongly contradict certain general assumptions about aquatic snake diets. Especially surprising is the evidence that some species thought to be dietary specialists feed more broadly than previously thought. For example, *F. abacura*, which are thought to feed almost exclusively on giant salamanders (*Siren* and *Amphiuma*), fed heavily on *Ambystoma* in wetlands without fishes, despite giant salamanders being relatively common in those habitats. Although our sample sizes for *F. erythrogramma*, which are thought to specialize on eels (Neill, 1964; Gibbons, Coker & Murphy, 1977), were too small to include this species in our analyses, we also observed this species feeding heavily on *Ambystoma* at one fishless wetland site. In contrast, *R. rigida* did not display such dietary variation, suggesting that they are strict specialists that rely upon a diet of crayfishes. This species was notably absent from wetlands without fishes, in part because their probability of site occupancy in this area is more

Table 2 Probability of co-occurrence (ϕ) \pm 1 SE for pairs of seven species of aquatic snakes in South Carolina, USA. A co-occurrence probability of 1 indicates that the two species are randomly distributed with respect to one another^a

	<i>Nerodia floridana</i>	<i>Farancia abacura</i>	<i>Seminatrix pygaea</i>	<i>Regina rigida</i>	<i>Farancia erythrogramma</i>	<i>Agkistrodon piscivorus</i>
<i>Nerodia fasciata</i>	1.05 \pm 0.05	0.95 \pm 0.05	1.05 \pm 0.05	1.05 \pm 0.05	1.03 \pm 0.06	0.98 \pm 0.02
<i>Nerodia floridana</i>		1.25 \pm 0.41	1.45 \pm 0.39	2.83* \pm 0.86	1.78 \pm 0.56	1.06 \pm 0.54
<i>Farancia abacura</i>			1.09 \pm 0.3	1.76* \pm 0.36	–	0.89 \pm 0.19
<i>Seminatrix pygaea</i>				2.25* \pm 0.66	1.51 \pm 0.48	0.57 \pm 0.41
<i>Regina rigida</i>					–	1.82 \pm 1.24
<i>Farancia erythrogramma</i>						0.91 \pm 0.18

^aCo-occurrence probabilities significantly different from 1 are indicated with an asterisk (*). Probability of co-occurrence could not be estimated for some species pairs.

Table 3 Influence of occupancy by Species A on detection probability of Species B (pB) \pm 1 SE. Similar values of pB for cases where Species A was detected (unshaded rows) and not detected (shaded rows) indicate little influence of Species A on the abundance of Species B

Species A	Species B	<i>Nerodia floridana</i>	<i>Farancia abacura</i>	<i>Seminatrix pygaea</i>	<i>Regina rigida</i>	<i>Farancia erythrogramma</i>	<i>Agkistrodon piscivorus</i>
<i>Nerodia fasciata</i>		0.50 \pm 0.10	0.49 \pm 0.09	0.62 \pm 0.09	–	0.15 \pm 0.12	0.08 \pm 0.04
		0.66 \pm 0.20	0.39 \pm 0.12	0.37 \pm 0.17	–	0.05 \pm 0.05	0.08 \pm 0.06
<i>Nerodia floridana</i>			0.37 \pm 0.12	0.39 \pm 0.16	0.65 \pm 0.29	–	0.11 \pm 0.10
			0.54 \pm 0.17	0.70 \pm 0.16	0.41 \pm 0.19	–	0.06 \pm 0.06
<i>Farancia abacura</i>				0.24 \pm 0.13	–	–	0.13 \pm 0.11
				0.35 \pm 0.20	–	–	0.08 \pm 0.05
<i>Seminatrix pygaea</i>					–	–	–
					–	–	–
<i>Regina rigida</i>						–	0.20 \pm 0.18
						–	0.20 \pm 0.18
<i>Farancia erythrogramma</i>							–
							–

Detection probability could not be estimated for some species pairs.

strongly related to proximity to floodplain habitats than to abundance of their preferred prey (Durso *et al.*, 2011).

Our finding that semi-aquatic snake species in wetlands without fishes exhibit high niche overlap without evidence of competitive exclusion challenges the generalization that competition is always a strong force structuring snake assemblages. Instead, we suspect that snake community structure in some habitats is influenced by stochastic processes such as wetland hydroperiod and that the energetically efficient lifestyle of snakes may make them less prone to competitive exclusion than other taxa. Spatially replicated, long-term studies of snake assemblages in other ecosystems are needed to fully understand factors that drive snake population and community dynamics.

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Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

Appendix S1. Map of study sites.

Appendix S2. Counts of prey items recorded in the diets of five species of aquatic snakes at 23 wetlands located on the Savannah River Site, South Carolina, USA, between 2002 and 2010.