What Does the Snake Eat? Breadth, Overlap, and Non-native Prey in the Diet of Three Sympatric Natricine Snakes

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Abstract.—We investigated diet breadth and diet overlap in three sympatric snakes of similar body size: Dekay's Brownsnakes (*Storeria dekayi*), Red-bellied Snakes (*S. occipitomaculata*), and sub-adult Common Gartersnakes (*Thamnophis sirtalis*), by examining recently consumed prey (n = 388) collected from wild-caught snakes (n = 263) in northern Illinois. *Storeria occipitomaculata* were dietary specialists, feeding nearly exclusively on slugs. *Storeria dekayi* fed predominately on slugs but also consumed snails and earthworms. Sub-adult *T. sirtalis* fed predominately on earthworms but also consumed frogs and small mammals. Diet overlap was extensive between *Storeria* species but relatively low between *Storeria* and *Thamnophis*. It is noteworthy that the two most abundant prey types, slugs and earthworms, are non-native. These non-native prey occur in high numbers, which may ameliorate competitive interactions and influence grassland snake abundance and persistence regionally.

Key Words.—competition; earthworm; frog; slug; snail; *Storeria*; *Thamnophis*

Introduction

Competition can be a potent factor structuring communities and can drive local extinction of competitively inferior species or niche differentiation sufficient to allow coexistence (Hardin 1960; Pianka 1981; Pacala and Roughgarden 1985). Neither competitive exclusion nor niche differentiation, however, may occur in situations where resource availability is high enough to sustain competing species (Durso et al. 2013). High seasonal prey abundance, low predator energetic requirements, and other sources of population regulation (e.g., abiotic or top-down biotic effects) may contribute to coexistence in the absence of niche differentiation as demonstrated by coexistence with high diet overlap in some snake communities (Durso et al. 2013). This contrasts with the more general pattern seen among coexisting snakes, in which partitioning of prey is common (reviewed by Toft 1985; Luiselli 2006a).

Phylogenetically related species often share dietary characteristics (Greene 1997). Consequently, related species living in sympatry could experience greater diet overlap than more distantly related species. Additionally, species that are similar in size may consume similar prey, especially if prey size is limited by gape size, as in snakes (King 2002). We studied the diets of Dekay's Brownsnake (*Storeria dekayi*), Red-bellied Snake (*S. occipitomaculata*), and Common Gartersnake (*Thamnophis sirtalis*), three related North American natricines that sometimes occur in sympatry in northern Illinois, USA (Smith 1961). *Storeria dekayi*,

S. occipitomaculata, and younger age classes of *T. sirtalis* overlap greatly in body size. At our study sites, *S. occipitomaculata* ranged from 77–284 mm snout-vent length (SVL), *S. dekayi* ranged from 76–378 mm SVL, and sub-adult *T. sirtalis* ranged from 123–366 mm SVL (Fig. 1). All three species are known to feed on invertebrates, making diet overlap a distinct possibility (Ernst and Ernst 2003). We studied snake diets at three sites that differed in snake species composition. All three species were commonly encountered at one site, *S. dekayi* and *T. sirtalis* were commonly encountered at a second site, and only *T. sirtalis* was commonly encountered at the third. Thus, competitive interactions may differ among study sites as may prey availability. Because all three species in our study frequently consume non-native prey, we provide context by reviewing quantitative studies of consumption of non-native prey by snakes more generally.

Materials and Methods

We collected prey from wild-caught snakes at three northern Illinois, USA, study sites separated by 45–105 km: Potawatomi Woods Forest Preserve (DeKalb County), Nachusa Grasslands (Lee and Ogle County), and Goose Lake State Natural Area (Grundy County; Fig. 2). Potawatomi Woods consists of 120 ha of floodplain and upland habitat managed by the DeKalb County Forest Preserve District. We concentrated snake monitoring in 4 ha of wet sedge meadow and adjacent restored Tall-grass Prairie Savanna. We frequently encountered *S. occipitomaculata*, *S. dekayi*, and *T. sirtalis*
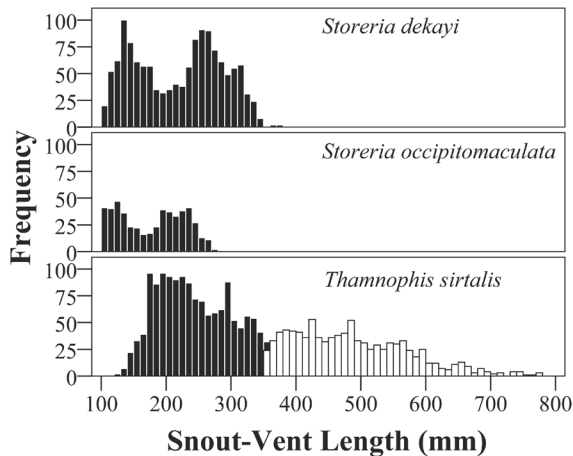
FIGURE 1. Snout-vent length of Dekay's Brownsnake (*Storeria dekayi*), Red-bellied Snake (*S. occipitomaculata*), and Common Gartersnake (*Thamnophis sirtalis*) at study sites in northern Illinois, *S. dekayi*, *S. occipitomaculata*, and sub-adult *T. sirtalis* (black histograms) overlap broadly in body size whereas adult *T. sirtalis* (white histograms) are larger.

at Potawatomi Woods. Nachusa Grasslands consists of 1,400 ha of remnant and restored Tall-grass Prairie managed by The Nature Conservancy. We concentrated snake monitoring in a chronosequence of restoration units that had previously been used for row crop agriculture. We encountered *S. dekayi* and *T. sirtalis* frequently at Nachusa Grasslands, but *S. occipitomaculata* was absent. Goose Lake Prairie consists of a about 1,000 ha remnant and restored Tall-grass Prairie and wetland complex managed by the Illinois Department of Natural Resources. We concentrated snake monitoring in five areas encompassing sand prairie, mesic prairie, and wet prairie habitats. *Thamnophis sirtalis* was numerically dominant at Goose Lake but we encountered just eight *S. dekayi* and no *S. occipitomaculata* there.

We caught snakes from under cover boards made of used conveyor belts or plywood measuring about 60 × 80 cm or 76 × 90 cm, which we placed 20 m apart in transects (n = 41 cover boards at Potawatomi Woods, 281 cover boards at Nachusa Grasslands, 200 cover boards at Goose Lake Prairie). We weighed snakes using a portable electronic balance, measured them from snout to vent, uniquely marked snakes via ventral scale clipping (Fitch 1987), and we palpated snakes for prey. If a snake was suspected to contain prey, we forced regurgitation of the meal by palpation (Fitch 1987). We stored prey in 70% ethanol for later identification and measurement. We surveyed sites every one to two weeks from mid-April to mid-October. Snakes were rarely encountered other than beneath cover boards.

We identified prey to the lowest taxonomic level possible. We patted dry complete prey items with a paper towel and weighed them on an electronic balance


FIGURE 2. The state of Illinois in the USA showing the location of Potawatomi Woods, Nachusa Grasslands, and Goose Lake Prairie. (Base map: Illinois Land Cover from Luman, D., T. Tweddale, D. Lund, and P. Willis. 2007. Illinois land cover: Champaign, Illinois State Geological Survey, scale 1:500,000. Available from http://clearinghouse.isgs.illinois.edu/data/land-cover/usda-nass-cropland-data-layer-illinois-2007. (Used by permission of the Illinois State Geological Survey).

(precision = 0.0001 g). Because our primary interest was the potential for competition among species and because prey were infrequently recovered from large individuals, we excluded *T. sirtalis* > 350 mm SVL from analysis. We characterized niche breadth for each species at each site using Levin's measure,

$$B = \frac{1}{\sum_{j=1}^{n} p_j^2},$$

where n is the number of prey types and p_j is the proportion of prey type *j* (Krebs 1999). Niche breadth (*B*) ranges from 1 (low niche breadth as when only a single prey type is consumed) to n, (higher niche breadth as when each prey type is consumed in equal proportions). We characterized niche overlap among species within sites and within species among sites using Pianka's measure,
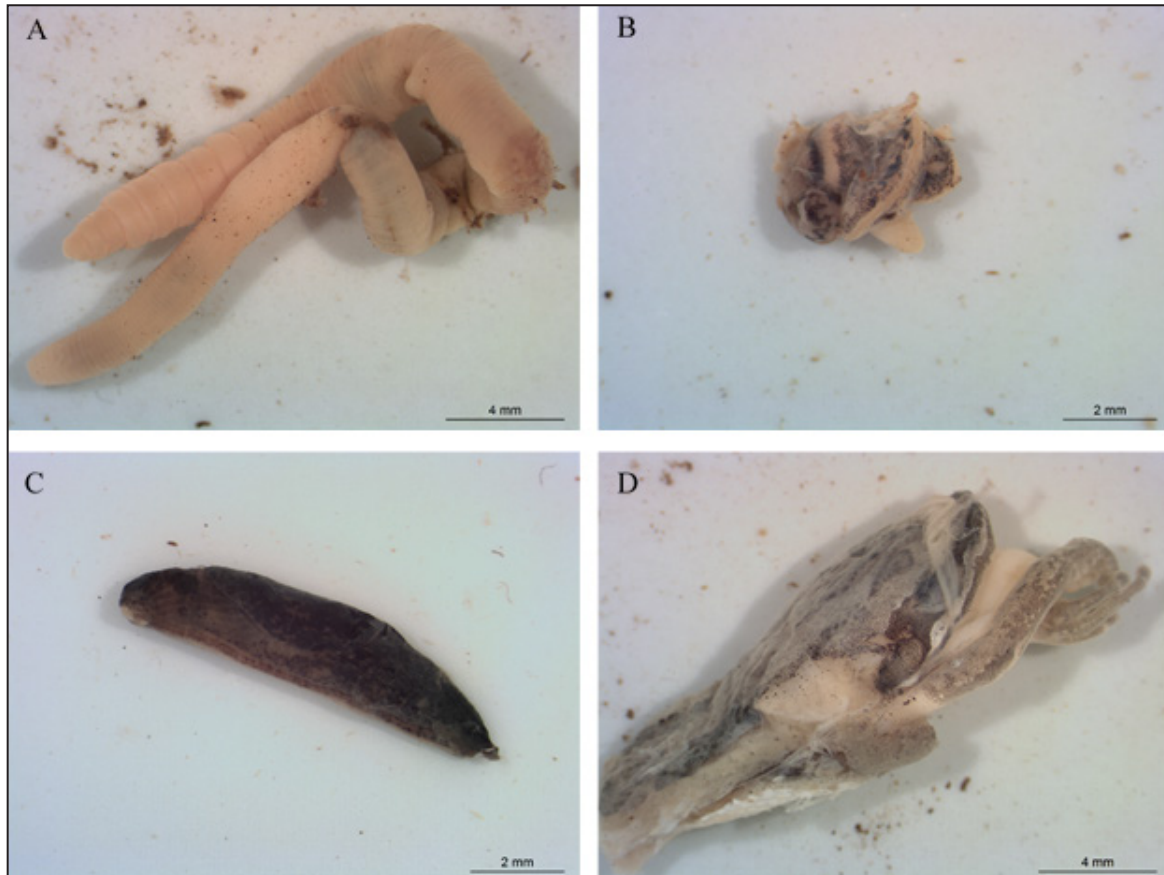
FIGURE 3. Examples of prey frequently recovered from snakes in this study; (A) earthworm (*Lumbricus* sp.), (B) snail (Phylum Mollusca, Class Gastropoda) (C) Gray Garden Slug (*Derocoras reticulatum*), (D) Boreal Chorus Frog (*Pseudacris maculata*). (Photographed by Lori Bross).

$$O_{jk} = \frac{\Sigma p_{ij} p_{ik}}{\sqrt{\Sigma p_{ij}^2 \Sigma p_{ik}^2}} \ ,$$

where p_{ij} is the proportion of prey type i consumed by species j and p_{ik} is the proportion of prey type i consumed by species k (Krebs 1999). Niche overlap (O) ranges from 0 (no overlap) to 1 (complete overlap as when both species consume the same prey in the same proportions). We computed niche breadth and niche overlap using the frequency of each prey type relative to all prey recovered and the frequency of snakes containing a given prey type relative to all snakes from which prey were recovered. To determine whether apparent differences in diet composition could be attributed to sampling error, we resampled with replacement the array of prey recovered from observed sample pairs 1,000 times and computed Pianka's measure for each of these random samples. This provided us with a distribution of random overlap values given the observed prey pool and sample size to which observed overlap values could be compared.

For intact prey, we compared the relationship between snake size and prey size using Analysis of Covariance with snake size as covariate and species as factor. Because the relationship between prey mass (our measure of prey size) and snake SVL (our measure of snake size) is expected to be curvilinear (King 2002), we transformed both snake size and prey size by taking natural logarithms after adding 1 (Zar 2010). For snakes from which multiple prey items were recovered, we included only the largest prey item to more closely approximate the relationship between snake size and maximum prey size (King 2002). Males and females overlapped broadly in SVL (*S. dekayi* males: 97–270 mm SVL, females: 94–340 mm; *S. occipitomaculata* males 102–205 mm, females: 93–268 mm, *T. sirtalis* males: 143–321 mm, females: 132–336 mm) and so sex was not included as a factor in these analyses. We characterized the scaling of snake head size to body size by Analysis of Covariance with jaw length, measured from the anterior-most point on the rostral scale to the posterior margin of the last supralabial scale, as dependent variable, SVL as covariate, and species as factor (King 2002). We transformed both jaw length and SVL by taking natural logarithms after adding 1.

TABLE 1. Diet composition of Dekay's Brownsnake (*Storeria dekayi*), Red-bellied Snake (*S. occipitomaculata*), and Common Gartersnake (*Thamnophis sirtalis*) at three northern Illinois, USA, study sites based on (A) the number of prey recovered and (B) the number of snakes containing a given prey type.

Species	Site	Slug	Snail	Worm	Mammal	Frog	Total
(A) Number of prey							
Storeria dekayi	Nachusa	110	2	5	0	0	117
	Potawatomi	26	17	6	0	0	49
S. occipitomaculata	Potawatomi	27	0	1	0	0	28
Thamnophis sirtalis	Goose Lake	0	0	27	0	11	38
	Nachusa	0	0	63	1	5	69
	Potawatomi	0	0	85	0	2	87
(B) Number of snakes							
Storeria dekayi	Nachusa	48	2	5	0	0	55
	Potawatomi	13	7	4	0	0	24
S. occipitomaculata	Potawatomi	23	0	1	0	0	24
Thamnophis sirtalis	Goose Lake	0	0	22	0	11	33
	Nachusa	0	0	50	1	5	56
	Potawatomi	0	0	69	0	2	71

RESULTS

From 2013 to 2015, we collected 388 identifiable prey from 263 snakes, 166 prey from 79 *S. dekayi*, 28 prey from 24 *S. occipitomaculata* (28 items), and 194 items from 160 sub-adult *T. sirtalis* (194 items; Table 1). Five additional prey items from four *S. dekayi* and one *T. sirtalis* could not be identified. We frequently recovered only a single prey item from an individual snake (n = 210 snakes), but multiple prey, up to a maximum of 15 (all slugs from an adult female *S. dekayi*) were sometimes recovered. Usually, when we recovered multiple prey, they were all of the same prey type but we recovered both a slug and a snail from six *S. dekayi*, a slug and an earthworm from one *S. dekayi*, and an earthworm and a frog from one *T. sirtalis*. Recaptures were infrequent and we obtained prey on two occasions from just nine snakes.

Earthworms were the most common prey recovered (n = 187), followed by slugs (n = 163), snails (n = 19), amphibians (n = 18), and mammals (n = 1; Table 1, Fig.

3). The majority of earthworms were juveniles (i.e., they lacked a clitellum) and so could not be identified to species but adult earthworms recovered from snakes or collected at our study sites consisted of members of two non-native genera, *Lumbricus* and *Apporectodea*. Slugs were identified as nonnative Gray Garden Slugs, *Derocoras reticulatum*. We were unable to identify snails (Phylum Mollusca, Class Gastropoda) recovered from snakes because they consisted of soft-body parts only. Amphibian prey consisted of post-metamorphic Boreal Chorus Frogs (*Pseudacris maculata*, n = 18), American Toads (*Anaxyrus americanus*, n = 1), and Northern Leopard Frogs (*Lithobates pipiens*, n = 1; taxonomy follows Frost et al. 2012). The single mammal recovered was a juvenile vole (*Microtus* sp.).

Patterns of diet breadth and diet overlap were similar regardless of whether measures were computed based on prey frequency or snake frequency (Table 2). Diet breadth was greatest in *S. dekayi* at Potawatomi Woods where three prey types (slugs, snails, and earthworms) were consumed in relatively similar proportions (Table

TABLE 2. Diet breadth (diagonal elements), diet overlap (off-diagonal elements) between sites within species (shaded gray), and diet overlap between species within sites (unshaded). Measures based on frequency of prey items and frequency of snakes are separated by forward slashes (/).

| Species		*T. sirtalis* Goose Lake	*T. sirtalis* Nachusa	*T. sirtalis* Potawatomi	*S. dekayi* Nachusa	*S. dekayi* Potawatomi	*S. occipitomaculata* Potawatomi
Thamnophis sirtalis	Goose Lake	1.70/1.79					
	Nachusa	0.94/0.94	1.11/1.25				
	Potawatomi	0.93/0.91	1.00/1.00	1.04/1.06			
Storeria dekayi	Nachusa		0.04/0.10		1.13/1.30		
	Potawatomi			0.18/0.26	0.84/0.89	2.39/2.47	
S. occipitomaculata	Potawatomi			0.04/0.04		0.83/0.86	1.08/1.08
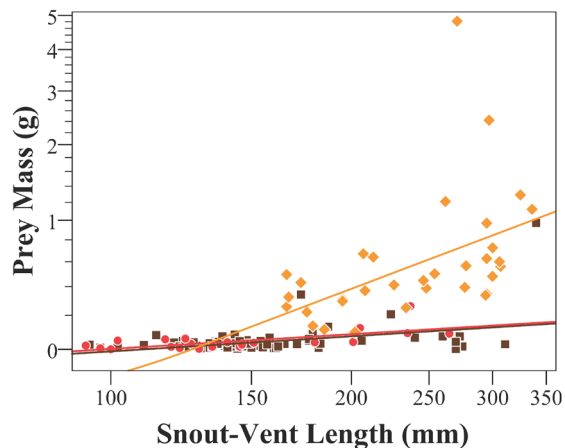
FIGURE 4. Relationship between snake size (snout-vent length) and prey size (mass) among Dekay's Brownsnake, *Storeria dekayi* (brown squares), Red-bellied Snake, *Storeria occipitomaculata* (red circles), and sub-adult Common Gartersnake, *Thamnophis sirtalis* (gold diamonds).

2). *Storeria dekayi* also consumed these three prey types at Nachusa Grasslands but slugs predominated, resulting in much lower diet breadth. Diet breadth was intermediate in sub-adult *T. sirtalis* at Goose Lake where both earthworms and amphibians were frequently consumed. Earthworms and amphibians were also consumed by sub-adult *T. sirtalis* at Nachusa Grasslands and Potawatomi Woods, but earthworms predominated, resulting in lower diet breadth. Diet breadth was also low in *S. occipitomaculata*, which, with the exception of a single earthworm, consumed only slugs (Table 2).

Diet overlap was consistently high among sites within species (Table 2). Diet overlap between *S. dekayi* and sub-adult *T. sirtalis* was intermediate at Potawatomi Woods where both species included earthworms in their diets but was low at Nachusa Grasslands where *S. dekayi* consumed mostly slugs and sub-adult *T. sirtalis* consumed mostly earthworms. Diet overlap was also low between *S. occipitomaculata* and sub-adult *T. sirtalis* at Potawatomi Woods where *S. occipitomaculata* consumed mostly slugs and sub-adult *T. sirtalis* consumed mostly earthworms. Diet overlap between *S. occipitomaculata* and *S. dekayi* was high at Potawatomi Woods where slugs were consumed frequently (*S. dekayi*) or almost exclusively (*S. occipitomaculata*; Table 2). Resampling demonstrated that observed diet overlap was significantly less than random ($P \leq 0.006$) for all sample pairs except *T. sirtalis* at Nachusa Grasslands and *T. sirtalis* at Potawatomi ($P = 0.150$ for prey frequency, $P = 0.087$ for snake frequency). In contrast to sub-adults, we recovered few prey from adult (> 350 mm SVL) *T. sirtalis*. Among 33 prey we recovered from 22 snakes were 21 earthworms, nine amphibians (eight American Toads, *Anaxyrus americanus*, and one Green Frog, *Lithobates clamitans*), and three rodents (one vole, *Microtus*, and two unidentified).

The slope of the relationship between snake size and prey size varied significantly among species (species-by-snake SVL interaction, $F_{2,121} = 8.88$, $P < 0.001$; Fig. 4). Slopes of regression lines did not differ significantly between *S. dekayi* and *S. occipitomaculata* (Tukey HSD, $P > 0.50$) but did differ significantly between *S. dekayi* and *T. sirtalis* (Tukey HSD, $P < 0.001$) and between *S. occipitomaculata* and *T. sirtalis* (Tukey HSD, $P < 0.025$). Back-transformation yielded the following allometric relationships between snake size and prey size;

Storeria dekayi: Prey Mass-1 = 0.577Snake SVL$^{0.117}$-1
S. occipitomaculata: Prey Mass-1 = 0.593Snake SVL$^{0.114}$-1
Thamnophis sirtalis: Prey Mass-1 = 0.033Snake SVL$^{0.707}$-1

The slope of the relationship between snake jaw length and SVL varied significantly among species (species-by-snake SVL interaction, $F_{2,261} = 67.533$, $P < 0.001$). Slopes of regression lines did not differ significantly between *S. dekayi* and *S. occipitomaculata* (Tukey HSD, $P > 0.50$) but did differ significantly between *S. dekayi* and *T. sirtalis* (Tukey HSD, $P < 0.001$) and *S. occipitomaculata* and *T. sirtalis* (Tukey HSD, $P < 0.001$). Back-transformation yielded the following allometric relationships between snake jaw length and SVL;

Storeria dekayi: Jaw Length-1 = 1.079Snake SVL$^{0.406}$-1
S. occipitomaculata: Jaw Length-1 = 1.098Snake SVL$^{0.387}$-1
Thamnophis sirtalis: Jaw Length-1 = 0.534Snake SVL$^{0.576}$-1

DISCUSSION

Our results clarify diet composition for *S. dekayi*, *S. occipitomaculata*, and sub-adult *T. sirtalis*, at least in this part of Illinois, USA. Our observation that the diet of *S. dekayi* consists of slugs, snails, and earthworms is consistent with other quantitative studies (Judd 1954; Hamilton and Pollock 1956; Catling and Freedman 1980; Gray 2013, 2014). In contrast, secondary sources often include additional prey taxa (insects, mites, isopods, frogs, amphibian eggs, and fish; Conant 1951; Smith 1961; Harding 1997; Trauth et al. 2004; Moriarty and Hall 2014), mostly without support (reviewed by King, In press). Similarly, the preponderance of slugs that we observed in the diet of *S. occipitomaculata* is consistent with other studies reporting slugs as the exclusive or principal prey type (Hamilton and Pollack 1956; Brown 1979a, 1979b). Furthermore, in studies in which slugs were identified to species, non-native species are common (Gilhen 1984; Gray et al. 2013; Semlitsch and Moran 1984). Reports of other prey types are limited to a field cricket (Class Insecta, Order Orthoptera; Barbour 1950), and two earthworms (Phylum Annelida) and a vole were also consumed. Although our data are limited,
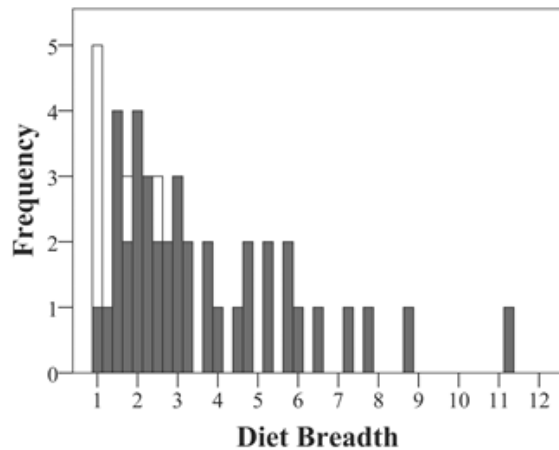
Figure 5. Diet breadths observed in this study (unfilled histogram segments) and in snakes more generally (filled histogram segments). See Appendix for species and data sources.

the diet of adult *T. sirtalis* was similar to that of sub-adults. *Thamnophis sirtalis* is often considered a dietary generalist, consuming both invertebrate (earthworms, slugs, leeches) and vertebrate (fish, amphibians, birds, mammals) prey (Arnold 1980; Ernst and Barbour 1989). Local populations or population segments (e.g., adults), however, can exhibit relatively narrow diet breadth, consuming earthworms and amphibians (Reichenbach and Dalrymple 1986) as we observed, amphibians only (Kephart 1982), or salmonid fish (Gregory and Nelson 1991) depending on local prey availability. A shift in *T. sirtalis* diet from predominantly earthworms and small anurans to larger anurans and small mammals can also occur (Fitch 1965), resulting in broader diet breadth on a population level despite narrower diet breadth within age classes.

Laboratory studies demonstrate that ingestively naïve *S. dekayi* respond more positively to slug and earthworm extracts compared to fish extracts and distilled water (Burghardt 1967) and to earthworms compared to aquatic snails or mealworms (*Tenebrio* sp.; von Achen and Rakestraw 1984). In contrast, ingestively naïve *T. sirtalis* respond more positively to earthworms, amphibians, and fish than to slugs, mice, and distilled water (Burghardt 1967). Comparable data for *S. occipitomaculata* are not available.

The range of diet breadths observed in this study (about 1.1–2.5) fall on the low end of diet breadths reported for snakes elsewhere (Fig. 5, Appendix). Diet overlap was high within species among sites (0.84–1.00 based prey number), a pattern seen in snakes generally (Luiselli 2006b); however, resampling demonstrated that, with one exception, even these high overlap values were less than expected by chance given our sample sizes. Consequently, variation in diet within species may reflect differences among sites in prey availability.

We also observed high diet overlap between sympatric *Storeria* species (0.83 based on prey number) but low overlap between sympatric *Storeria* and sub-adult *Thamnophis* (0.04–0.18 based on prey number). Thus, our study provides examples at the extremes of low (*Storeria* versus *Thamnophis*) and high (*S. dekayi* versus *S. occipitomaculata*) diet overlap in snakes generally (e.g., Gregory 1978; Henderson 1982; Capizzi et al. 1995; Luiselli et al. 1998; Carvalho Teixeira et al. 2017). *Storeria dekayi* and *S. occipitomaculata* also exhibit similar prey size-snake body size relationships. Prey size increases little with increasing body size in *Storeria* but increases more rapidly with increasing body size in *T. sirtalis*. The scaling of head dimensions to body size is also similar in *S. dekayi* and *S. occipitomaculata* with both species showing more strongly negative allometry than is seen in *T. sirtalis*.

It is noteworthy that the two most prevalent prey items recovered from snakes in this study, earthworms and slugs, are non-native species. This is not an isolated occurrence. We know of at least 19 cases involving 12 species in which non-native prey constitute a substantial portion of snake diets (Table 3) and additional incidents of snakes consuming non-native prey are commonly documented (e.g., citations in Emmons et al. 2016). In some cases, non-native species constitute more than 90% of prey consumed and have been credited with snake population recovery (King and Stanford, In press) and range expansion (Gray 2005, 2010). The potential for positive impacts of non-native species is well known but incompletely understood (Rodriguez 2006; Schlaepfer et al. 2011; Vitule et al. 2011; Pintor and Byers 2015) and noteworthy examples of non-native prey having negative impacts exist (e.g., Phillips et al 2003). Possibly, in the case of sympatric snakes, such as those that were the focus of this study, the availability of abundant non-native prey species ameliorates competitive interactions and promotes coexistence. Information on prey availability, especially before and after the arrival of non-native prey, would be useful in better understanding trophic interactions among sympatric snakes. Information on prey composition prior to the arrival of non-native prey might be obtained from examination of specimens in natural history collections.

TABLE 3. Examples of snake species for which non-native prey constitutes a significant fraction of the diet.

Snake Species	Prey species and frequency of consumption	Reference
Dinodon rufozonatum (Red-banded Snake)	*Lithobates catesbeianus* (Bullfrog): 77 of 148 prey (52%)	Li et al. 2011
Morelia spilota (Carpet Python)	*Rattus* spp. (Rat), *Mus domesticus* (House Mouse), *Columba livia* (Rock Dove), *Agapornis pullaria* (Lovebird), *Gallus domesticus* (Poultry), *Anser anser* (Goose eggs): 74 of 84 prey (88%)	Shine and Fitzgerald 1996
Natrix natrix (European Grass Snake)	*Ameiurus nebulosus* (Brown Bullhead), *Carassius gibelio* (Prussian Carp): 21 of 21 prey (100%)	Šukalo et al. 2014
	Rana ridibunda (Marsh Frog): 17 of 27 prey (63%)	Gregory and Isaac 2004
Natrix tessellate (Dice Snake)	*Salaria fluviatilis* (Freshwater Blenny): 6 of 13 prey (46%)	Dubey et. al. 2015
	Carassius gibelio (Prussian Carp): 15 of 17 prey (88%)	Acipinar et al. 2006
	Non-native fish: 5 of 8 prey (62%), 42 of 80 prey (52%)	Šukalo et al. 2014
Nerodia sipedon insularum (Lake Erie Watersnake)	*Neogobius melanostomus* (Round Goby): 298 of 322 prey (93%)	King et al. 2006
Pseudonaja affinis (Dugite)	*Mus musculus* (House Mouse): 9 of 48 prey in urban Dugites (19%); 71 of 176 prey in non-urban Dugites (40%).	Wolfe et al. 2017
	Rattus norvegicus (Brown Rat): 1 of 48 prey in urban Dugites (2%); 1 of 176 prey in non-urban Dugites (0.6%).	
	Rattus rattus (Black Rat): 2 of 48 prey in urban Dugites (4%).	
Storeria dekayi (Dekay's Brownsnake)	*Deroceras reticulatum* (Gray Garden Slug), *Lumbricus* and *Apporectodea* spp. (Earthworm): 175 of 194 prey (90%)	This study
	Earthworm: 14 of 18 snakes (78%)	Hamilton and Pollock 1956
Storeria occipitomaculata (Red-bellied Snake)	*Deroceras reticulatum* (Gray Garden Slug), *Lumbricus* and *Apporectodea* spp. (Earthworm): 28 of 28 prey (100%)	This study
	Deroceras and *Arion* (slugs): 23 of 24 prey (96%)	Gilhen 1984
Thamnophis atratus (Aquatic Gartersnake)	*Oncorhynchus mykiss* (Rainbow Trout), *Salvelinus fontinalis* (Brook Trout): >50% of 54 snakes	Pope et al. 2008
Thamnophis eques (Mexican Gartersnake)	*Eisenia* sp. (Earthworm), *Carassius auratus* (Goldfish): 66 of 130 prey (51%)	Macías García and Drummond 1988
	Gambusia affinis (Western Mosquito Fish), *Micropterus salmoides* (Largemouth Bass), *Ameiurus melas* (Black Bullhead), *Lithobates catesbeianus* (American Bullfrog):20 of 23 prey (87%)	Emmons et al. 2016
Thamnophis gigas (Giant Gartersnake)	*Lithobates catesbeianus* (American Bullfrog), Centrachid and Ictalurid fish: 102 of 168 prey (61%)	Ersan 2015
Thamnophis sirtalis (Common Gartersnake)	*Lumbricus* and *Apporectodea* spp. (Earthworm): 175 of 194 prey (90%)	This study
	Oncorhyncus (Salmon): 117 of 128 prey from hatchery sites (91%)	Gregory and Nelson 1991

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APPENDIX. Species and sources of diet breadth values included in Figure 5. Values from this study are shaded in gray. When values were calculated by us from raw diet, the source Table is listed.

Species	Diet Breadth	Source
Uromacer oxyrhynchus (Pointed Snake)	1.00	Henderson 1982 (Table 3)
Dipsas sp. (Snail Eating Snakes)	1.04	Ray et al. 2012 (Table 3)
Thamnophis sirtalis (Common Gartersnake)	1.04	This study (Potawatomi)
Storeria occipitomaculata (Red-bellied Snake)	1.08	This study (Potawatomi)
Thamnophis sirtalis (Common Gartersnake)	1.11	This study (Nachusa)
Storeria dekayi (Dekay's Brownsnake)	1.13	This study (Nachusa)
Thamnophis radix (Eastern Plains Gartersnake)	1.38	Tuttle and Gregory 2009
Thamnophis atratus (Aquatic Gartersnake)	1.44	Fitch 1941 (Table 1, Coast Gartersnake)
Oxybelis fulgidus (Green Vine Snake)	1.45	Henderson 1982 (Table 3)
Sibon argus (Argus Snail Sucker)	1.54	Ray et al. 2012 (Table 3)
Oxybelis aeneus (Mexican Vine Snake)	1.65	Henderson 1982 (Table 3)
Uromacer catesbyi (Catesby's Pointed Snake)	1.69	Henderson 1982 (Table 3)
Thamnophis sirtalis (Common Gartersnake)	1.70	This study (Goose Lake)
Sibon annulatus (Ringed Snail Sucker)	1.97	Ray et al. 2012 (Table 3)
Thamnophis ordinoides (Northwestern Gartersnake)	1.99	Gregory 1978
Thamnophis sirtalis (Common Gartersnake)	1.99	Gregory 1978
Thamnophis hammondii (Two-striped Gartersnake)	2.06	Fitch 1941 (Table 1, Southern California Garter Snake)
Thamnophis ordinoides (Northwestern Gartersnake)	2.13	Fitch 1941 (Table 1, Red-striped Garter Snake)
Thamnophis couchii (Sierra Gartersnake)	2.24	Fitch 1941 (Table 1, Moccasin Garter Snake)
Dendroaspis jamesoni (Jameson's Mamba)	2.28	Luiselli et al. 1998 (Table 3)
Storeria dekayi (Dekay's Brownsnake)	2.39	This study (Potawatomi)
Helicops hagmanni (Hagmann's Keelback)	2.49	Carvalho Teixeira et al. 2017
Natriciteres fuliginoides (Collared Marsh-Snake)	2.57	Luiselli et al. 1998 (Table 3)
Naja nigricollis (Black-necked Spitting Cobra)	2.66	Luiselli et al. 1998 (Table 3)
Afronatrix anoscopus (African Brown Water Snake)	2.67	Luiselli et al. 1998 (Table 3)
Bitis nasicornis (Rhinoceros Viper)	2.94	Luiselli et al. 1998 (Table 3)
Thamnophis couchii (Sierra Gartersnake)	3.02	Fitch 1941 (Table 1, Oregon Gray Garter Snake)
Thamnophis elegans (Terrestrial Gartersnake)	3.05	Gregory 1978
Calabaria reinhardti (Calabar Ground Python)	3.13	Luiselli et al. 1998 (Table 3)
Thamnophis sirtalis (Common Gartersnake)	3.22	Lagler and Salyer 1945 (natural waters)
Vipera aspis (Asp Viper)	3.64	Capizzi et al. 1995
Thamnophis sirtalis (Common Gartersnake)	3.74	Lagler and Salyer 1945 (fish-rearing stations)
Thamnophis elegans (Terrestrial Gartersnake)	3.88	Fitch 1941 (Table 1, Klamath Garter Snake)
Helicops polylepis (Norman's Keelback)	4.62	Carvalho Teixeira et al. 2017
Thamnophis sirtalis (Common Gartersnake)	4.79	Fitch 1941 (Table 1, Common Gartersnake)
Natrix natrix (European Grass Snake)	4.83	Hutinec and Mebert 2011
Python regius (Ball Python)	5.14	Luiselli et al. 1998 (Table 3)
Hierophis viridiflavus (Green Whip Snake)	5.18	Capizzi et al. 1995
Zamenis longissimus (Aesculapean Snake)	5.65	Capizzi et al. 1995
Elaphe quatuorlineata (Four-lined Ratsnake)	5.75	Capizzi et al. 1995
Natrix tessellata (Dice Snake)	6.08	Hutinec and Mebert 2011
Thamnophis elegans (Terrestrial Gartersnake)	6.56	Fitch 1941 (Table 1, Mountain Garter Snake)
Hierophis viridiflavus (Green Whip Snake)	7.33	Lelièvre et al. 2012
Zamenis longissimus (Aesculapean Snake)	7.79	Lelièvre et al. 2012
Thamnophis elegans (Terrestrial Gartersnake)	8.82	Fitch 1941 (Table 1, Wandering Garter Snake)
Helicops angulatus (Brown-banded Watersnake)	11.29	Carvalho Teixeira et al. 2017