Northern Watersnake Selection of Fish Prey in Western Kentucky

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Abstract: Watersnakes serve a variety of important roles in aquatic ecosystems with many species being of conservation interest. The northern watersnake (*Nerodia sipedon*) has some populations of concern, but is found in a wide variety of aquatic habitats throughout North America. Although previous studies have examined the diet of this typically piscivorous species, research has not addressed whether the northern watersnake is preferentially selecting particular fish as prey. In this study, we sampled snake stomach contents and used Chesson's alpha selection index (α_i) to investigate whether northern watersnakes are eating fish families in proportion to their availability or are preferentially selecting or avoiding specific fish families. At the Sloughs Wildlife Management Area in western Kentucky, the northern watersnake fed on fish from six families in 2013 ($n=15$) and 2014 ($n=36$). Five of those fish families were eaten in proportion to their availability but avoided pirate perch (*Aphredoderus sayanus*), the lone member of the family Aphredoderidae. This is the first study testing prey preferences in the northern watersnake.

Key words: northern watersnake, *Nerodia sipedon*, diet selection, fish family, pirate perch

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Many watersnakes are of conservation concern and can potentially be used as indicators to understand harmful human impacts on wetland habitats (Gibbons and Dorcas 2004). Watersnakes serve important roles in aquatic and adjacent terrestrial systems. Their position in aquatic food webs is complex, with ontogenetic dietary changes and watersnakes being both predator and prey of fishes and frogs (Harding 1997, Gibbons and Dorcas 2004). However, watersnakes often are incorrectly maligned as dangerous to humans and have been historically labeled as significant predators of sport fish (Harding 1997, Gibbons and Dorcas 2004).

One watersnake species similarly misconstrued as venomous and affecting sport fish populations is the northern watersnake (*Nerodia sipedon*) (Harding 1997, PFBC 2016). Although some populations are of conservation concern (Harding 1997, King et al. 2006), the northern watersnake, an aquatic habitat generalist, has the largest range of any watersnake in North America (Ernst and Ernst 2003, Gibbons and Dorcas 2004). Not surprisingly, this species has the most diverse diet of any northern American watersnake, preying on fishes, amphibians, arthropods, mollusks, annelids, and even small mammals (Ernst and Ernst 2003, Gibbons and Dorcas 2004).

Although a generalist species in regards to habitat and diet, previous studies suggest dietary differences across northern watersnake populations may be the result of differences in prey availability (Ernst and Ernst 2003, Bowen 2004). For example, as amphibian populations declined, one northern watersnake population in Michigan shifted from a heavily amphibian-based diet to feeding only on fishes (Meyer 1992, Carbone 1993). Similarly, a population of the northern subspecies, the Lake Erie watersnake (*N. s. insularum*), altered its feeding patterns over one to two snake generations, changing the proportions of amphibians versus fishes in its diet according to relative prey abundance (King et al. 1999, King et al. 2006).

Fishes probably are the northern watersnake's most common prey (Ernst and Ernst 2003, Himes 2003, Gibbons and Dorcas 2004). From previous research, northern watersnake diet comprised of fishes ranged from 48%–92% but was generally greater than 50% (48%, Roe et al. 2004; 65%, this study; 78%, Zelnick 1966; 90%, Lacy 1995; and 92%, King 1986). Dix (1968) showed that a northern watersnake population in Maryland had an innate preference for fish, with 80% of individuals selecting fish over anurans and earthworms. Nonetheless, previous research has not tested whether northern watersnakes eat fishes in proportion to their availability compared to other taxa, as Gibbons and Dorcas (2004) and Roe et al. (2004) hypothesized, nor whether they instead prefer or avoid specific fishes.

Watersnake consumption of fish can be influenced by factors other than fish species. As watersnakes increase in size, smaller prey often decrease in their diet (Plummer and Goy 1984, Bowen 2004) with watersnake size correlating with prey size (King 1993). The foraging and ingestion by gape-limited predators is also affected by prey shape including prey height and width (Voris and Voris 1983, Vincent et al. 2006). With these in mind, fishes of various sizes and shapes may be important in prey preference or avoidance. Our study investigated whether northern watersnakes

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select or avoid particular fish families in proportion to their relative abundance. Our work also addresses fish size and shape influencing the inclusion in diet having implications on populations of interest to fisheries management.

Study Area

Our study area was a 100-ha section of the Sloughs Wildlife Management Area (Henderson County, Kentucky), which is managed by the Kentucky Department of Fish and Wildlife Resources. This section is located 2 km southeast of the Ohio River and is known as Hardy Slough/Muddy Slough located in the interior low plateau physiographic province. Habitat types include moist soil units, scrub-shrub wetlands, and palustrine forest. Dominant plants are water primrose (*Ludwigia* sp.), smartweed (*Polygonum* sp.), water lily (*Nuphar* sp.) cattail (*Typha* sp.), buttonbush (*Cephalanthus occidentalis*), black willow (*Salix nigra*) and hackberry (*Celtis occidentalis*). The study period was divided into spring (April–May), early summer (June–July) and late summer (August–September) in 2013 and 2014. These temporal sub-units relate to the availability of different anuran life stages, which may affect overall watersnake prey availability among these three periods.

Methods

We captured northern watersnakes using a variety of methods including hand capture, cover board placement, stand-alone aquatic funnel traps, and drift fence arrays (terrestrial and aquatic) with funnel traps. For each captured watersnake, we measured snout-vent length (SVL) and used cloacal probing to determine sex. We marked snakes with both subcutaneous pit tags (Gibbons and Andrews 2004) and ventral scale-clip patterns (Plummer and Ferner 2012) to identify recaptures. In order to determine snake diet, we used gentle palpation to force northern watersnakes to regurgitate gut contents (Kofron 1978, Fitch 2001). Our study was part of a larger research project on watersnake diet in which we recorded crayfish, salamanders, and anurans in watersnake gut contents. We measured the standard length of fishes found in snake gut contents and identified fishes only to family because partial digestion of some prey items prevented more specific identification. Each snake was released at its capture location. All animal capture, handling and processing activities were approved by the University of Louisville Institutional Animal Care and Use Committee (IACUC Protocol: #13037).

For each of the three seasons in 2013 and 2014, we calculated the proportion of each fish family in the diet of northern watersnakes by summing the number of fishes in a given family across all snake stomach contents in a season over the total number of fishes found in all snakes for that season. For snake diet, this resulted in fish family proportions for each season and a mean proportion for all fish families over the two-year study.

To determine prey availability over two years at the study area, we placed an average of 36.3 (SD = 16.4) aquatic funnel traps which likely provide a credible estimate of available prey (Roe et al. 2004, Willson et al. 2010). We opened these traps for two days and nights (~48 hours) each week in each of the three seasons in 2013 and 2014, and we removed fishes from traps after day 1 and at the end of each 48-hour sampling period. Each trap had 25% of the trap above the waterline to prevent the drowning of non-target animals. We calculated trap nights per season as the number of traps multiplied by the number of days each trap was out for a given season, but if a snake was found in a given prey trap, that trap was not included in the count of trap nights and any prey in the trap were similarly ignored. We identified captured fishes to family and measured standard length, body depth, and body width of each fish. To determine seasonal prey availability for fish families, we first calculated the mean number of fishes that were captured per trap night. For each season within each year, we then summed those means and divided that sum by the sum of the total mean number of fishes captured per trap night for that season.

We used Chesson's alpha selection index ($\alpha_i = (r_i/n_i)/\Sigma(r_j/n_j)$) to determine whether snakes were preferentially selecting or avoiding particular fish families (Chesson 1978, Lawson et al. 1998). Chesson's alpha values were determined for each fish family for each season in 2013 and 2014, and those values were then used to determine a mean Chesson's alpha for each family over the two-year study (Pattinson et al. 2003). Chesson's alpha selection index values were scaled from negative one to positive one ($(\alpha_i/(\alpha_i + \Sigma_j{\neq}_i\ \alpha_i/(m-1)) \cdot 2) - 1$), with zero indicating no selection, positive values indicating selection and negative values indicating avoidance (Chesson 1983). To assess whether any selection or avoidance was significant, we calculated 95% confidence intervals for each scaled Chesson's alpha selection index value for each fish family (Pattinson et al. 2003).

To further investigate how fish size and shape influenced northern watersnake diet, we used general linear models (SAS Institute 2000) to examine the relationship of snake size (SVL) with both fish size (standard length) and ratio of fish body width to body depth for fishes in northern watersnake diet. As some individual watersnakes ($n = 15$) had more than one fish in their gut contents, we used median fish metrics found in individual snake gut contents for these analyses. We also used a general linear model to determine whether standard fish length was related to the ratio of fish body width to body depth. In this model, we tested slopes to determine differences between northern watersnake diet and captured available prey.

Results

In 2013, 72 individual northern watersnakes were captured, with 15 having fishes in regurgitated gut contents. These 15 snakes had a mean SVL of 557 mm (SE = 35.27; range 327–729 mm). In 2014, 114 new individuals were captured, with a total of 36 snakes having fishes in gut contents. These 36 snakes had a mean SVL of 525 mm (SE = 21.01; range 275–794 mm). In 2014, there were also eight recaptures from 2013 but recaptured individuals with gut contents in 2014 did not have fish in their guts in 2013. A total of three individuals were caught twice within years (one in 2013 and two in 2014) and regurgitated fishes both times. In all three individuals, fishes in the two gut content samples were from different families. These diet data from the recaptures were included in the analyses.

Over 1,364 trap nights, we captured fishes belonging to eight fish families, with 349 fishes captured in 2013 and 592 fishes captured in 2014 (Table 1). Amiidae and Centrarchidae were the most abundant fish families among the available prey. Fishes belonging to six different families were found in the gut contents of northern watersnakes. Esocidae and Amiidae together comprised 37.4% of available prey but 54.3% of snake diet, with members of both families present in higher mean proportions in snake diet than in the fishes available in the habitat (Figure 1). Aphredoderidae, Poeciliidae and Centrarchidae all had lower proportions in snake diet than in the prey population, whereas Cyprinidae was nearly equal for snake diet (6.0%) and prey availability (5.6%).

Scaled Chesson's alpha selection values were above zero for fishes in Amiidae and Esocidae, but 95% confidence intervals included zero and thereby indicated that watersnakes were not preferentially selecting prey from these families (Figure 2). Scaled Chesson's alpha selection values for Cyprinidae, Poeciliidae, and Centrarchidae were below zero, but again the 95% confidence intervals included zero, indicating no significant avoidance of these groups by watersnakes. However, northern watersnakes significantly avoided Aphredoderidae.

Esocidae was the only fish family that had a longer average standard length in snake diet (94.5 mm) than in captured available prey (90.0 mm), but this difference was not significant ($F = 0.45$, df = 1,60; $P = 0.51$). Except for Elassomatidae, that was not found in snake gut contents, the two families of Aphredoderidae and Poeciliidae had the smallest average length of the potentially available fishes in this study, and fish in those two families also had the shortest average standard lengths of the prey in snake gut contents. As northern watersnakes increased in size, they fed on larger fish ($F = 9.22$, df = 1,45; $P = 0.004$, $r^2 = 0.17$) but did not drop smaller

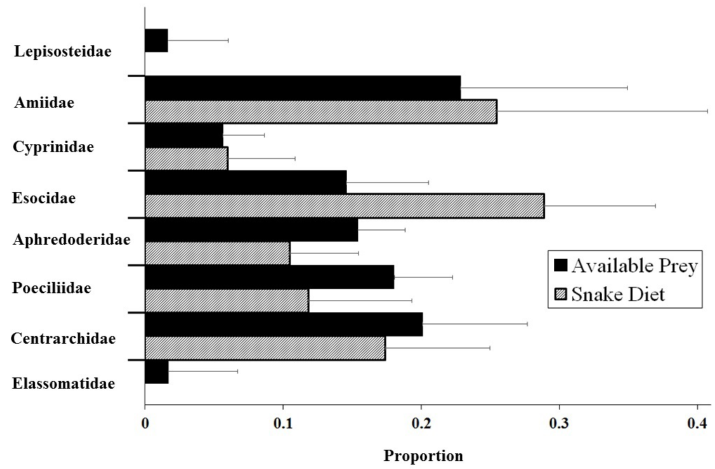

Figure 1. Mean proportions of available prey (number per trap night) and snake diet (prey number in gut contents) of northern watersnakes (*Nerodia sipedon*) for eight fish families at Sloughs Wildlife Management Area, Henderson County, Kentucky, 2013 and 2014. Error bars indicate SE.

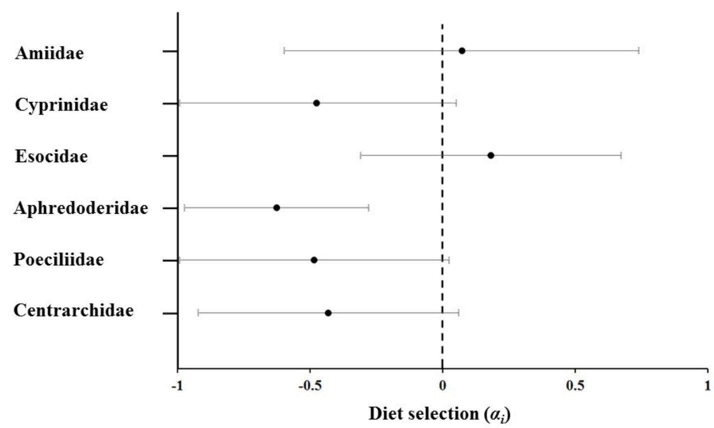

Figure 2. Northern watersnake (*Nerodia sipedon*) diet selection for six fish families indicated by scaled Chesson's alpha selection index (α_i) at Sloughs Wildlife Management Area, Henderson County, Kentucky, 2013 and 2014. Error bars indicate 95% confidence intervals.

Table 1. Mean standard length, percentage, and mean number of fish per trap night for eight fish families found in northern watersnake (*Nerodia sipedon*) diet and captured available prey at Sloughs Wildlife Management Area, Henderson County, Kentucky, 2013 and 2014.

	Snake diet			Available prey			
Fish family	*n*	Mean standard length mm (SE)	Percent in diet	*n*	Mean standard length mm (SE)	Percent available prey	Mean fish per trap night (SE)
Lepisosteidae	0	–	0	13	364.5 (49.0)	1.7	0.006 (0.004)
Amiidae	6	86.1 (11.1)	25.4	32	162.9 (20.8)	22.8	0.430 (0.364)
Cyprinidae	8	50.6 (5.8)	6.0	18	62.9 (4.4)	5.6	0.041 (0.026)
Esocidae	21	94.5 (5.3)	28.9	41	90.0 (4.0)	14.6	0.061 (0.010)
Aphredoderidae	11	32.2 (1.2)	10.5	33	51.1 (3.1)	15.4	0.083 (0.028)
Poeciliidae	11	35.6 (1.0)	11.8	19	36.7 (0.78)	18.1	0.172 (0.105)
Centrarchidae	13	47.7 (5.6)	17.4	63	64.9 (3.8)	20.1	0.145 (0.053)
Elassomatidae	0	–	0	3	31.2 (1.3)	1.7	0.009 (0.009)

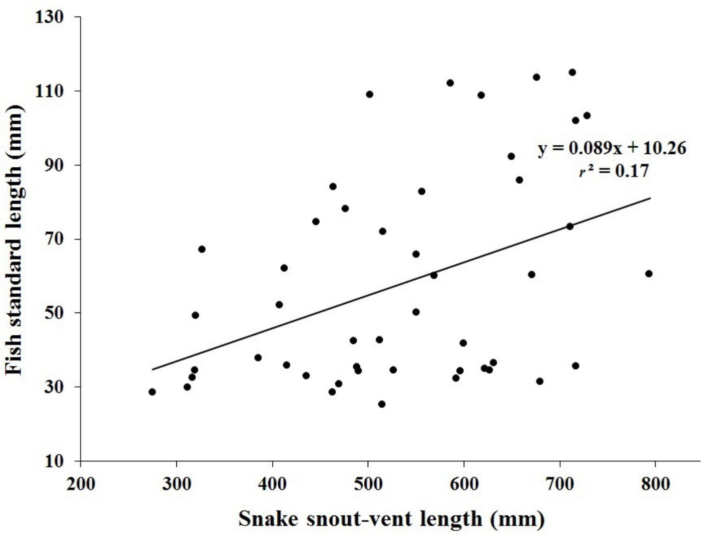

Figure 3. Median fish standard length (mm) in northern watersnake (*Nerodia sipedon*) diet regressed against snake snout-vent length (mm) at Sloughs Wildlife Management Area, Henderson County, Kentucky, 2013 and 2014.

fish from their diets (Figure 3). Snake size (SVL) was not related to the ratio of fish body width to body depth in northern watersnake diet ($F = 0.03$, df = 1,45; $P = 0.871$, $r^2 = 0.001$).

Fish body shape does play a role in determining the size of fish that an individual snake is capable of swallowing. Fishes in Amiidae and Esocidae had the longest average standard lengths of the fishes found in snake gut contents, and mean ratios of body width to body depth for Amiidae (mean = 0.86; SE = 0.02) and Esocidae (mean = 0.76; SE = 0.02) were closer to 1 than were those ratios in the other four fish families (mean ratio range: 0.38–0.59) found in available prey. The general linear model was significant ($F = 4.30$, df = 3,8; $P = 0.044$, $R^2 = 0.617$) with longer standard length fishes in snake stomach contents having higher ratios of body width to body depth than did shorter fishes in stomach contents ($F = 11.94$, df = 1,8; $P = 0.009$). This indicated that larger fish had more tubular shapes. However, fishes found in snake diet and captured available prey had similar relationships between fish standard length and the width to depth ratio ($F = 0.93$, df = 1,8; $P = 0.364$).

Discussion

Previous research has suggested that northern watersnakes might not preferentially prey on specific species, instead consuming fishes at the rate at which they encounter them (Gibbons and Dorcas 2004, Roe et al. 2004). Our study provides an initial test for this hypothesis and demonstrates that northern watersnakes did not preferentially select their fish prey from any particular family, instead taking prey from most fish families in proportion to their relative abundance. Fishes in the two least common fish families at the study site, Lepisosteidae and Elassomatidae, were not included in the diet of northern watersnakes.

Northern watersnakes, however, did prey on the family Aphredoderidae significantly less frequently than expected based on its relative abundance. The pirate perch (*Aphredoderus sayanus*) is the sole species in this family, and among congeners of the northern watersnake, the pirate perch has previously only been recorded in the diet of banded (*N. fasciata*) and brown (*N. taxispilota*) watersnakes (Ernst and Ernst 2003, Gibbons and Dorcas 2004). Aphredoderidae in this study had the smallest average standard length of the six fish families eaten by northern watersnakes. Aphredoderidae was similar in availability (15.4%) to the fish family most often preyed upon by northern watersnakes, Esocidae (14.6%).

Resetarits and Binckley (2013) demonstrated that the pirate perch uses chemical masking to increase foraging success and possibly to avoid predation. Langford et al. (2011) found that eastern ribbon snakes (*Thamnophis sauritus*) did not eat pirate perch even though pirate perch were very abundant. Northern watersnakes use both olfaction and vision when foraging (Drummond 1985, Balent and Andreadis 1998), and although northern watersnakes can successfully forage using only chemical cues (Gove and Burghardt 1975), prey capture success increases when northern watersnakes use both olfaction and vision (Drummond 1979). The pirate perch forages mostly at night (Froese and Pauly 2016), and Ernst and Ernst (2003) indicated that times from 1800 to 2400 hours may be particularly important for northern watersnake foraging but that easily captured prey will be taken during the day. The northern watersnake may therefore be at a disadvantage for encountering and capturing pirate perch if the fish is foraging at night when visual cues are reduced and there are few or no chemical cues to reveal the presence of the pirate perch. Future research will need to determine if the pirate perch's chemical camouflage can shield it from detection by northern watersnakes.

Fishes in the families Esocidae and Amiidae likely play an important role in northern watersnake diet even though they were not preferentially selected by northern watersnakes. Together, they constituted over 50% of the prey items taken in this study. Further, the proportions of Esocidae and Amiidae in the snake diet were greater than available proportions and mean selection indices were greater than zero. Fishes in these two fish families also had the largest mean standard lengths of the fish families in the snake diet, suggesting these two groups provide a significant proportion of the calories consumed by the watersnakes at this site. Members of the Esocidae family have previously been reported as northern watersnake prey (Ernst and Ernst 2003, Gibbons and Dorcas 2004). In this study, Esocidae was the fifth most abundant fish family but had the highest selection index and formed the largest proportion of the northern watersnake diet. Amiidae had not been previously recorded as being northern watersnake prey (Ernst and Ernst 2003, Gibbons and Dorcas 2004), but it was the most abundant available fish in this study. Local northern watersnakes may have shifted their diets to include this prey, given that watersnakes are known to adjust their diet to include abundant prey types (Roe et al. 2004, King et al. 2006).

Snake foraging for prey is affected by fish size (Voris and Voris 1983), with some snake species dropping smaller prey from their diets as the snakes increase in size (Plummer and Goy 1984, Arnold 2001, Bowen 2004). Although the size of predated fish did increase significantly with snake size in our study population, larger northern watersnakes still fed on a wide range of fish sizes (Figure 3). Given that northern watersnakes generally feed on what they encounter, abundant smaller fish may be eaten along with larger fish by larger snakes. Northern watersnakes did not appear to select prey by size, at least within the fish families on which they fed.

Fish shape is also known to affect snake prey selection (Voris and Voris 1983), and the body shape of the fishes in the Esocidae and Amiidae families may have facilitated the capture and consumption of relatively large individuals by the watersnakes. Fishes in these families had ratios of body width to depth closer to one than did fishes in the other families. Members of these two families have very similar shapes, with Esocidae being saggitiform (arrow-like) and Amiidae cylindrical. These two fish families were on average the largest fish by length eaten by northern watersnakes in our study, suggesting that northern watersnakes and other gape-limited predators may more easily ingest fish species that have a relatively circular cross-section compared to fishes that are more laterally or dorso-ventrally flattened. In banded watersnakes, prey with greater height or width required more skull movements to ingest, and they caused difficulties with prey movement through the snake digestive tract (Vincent et al. 2006). Not surprisingly, and similar to the northern watersnake in our study, juvenile banded watersnakes tend to eat primarily fusiform fishes (Mushinsky et al. 1982, Vincent et al. 2007) or tubular-bodied salamanders over tall, narrow Centrarchidae fishes (Willson and Hopkins 2011). If larger fish are tubular in shape, such as Esocidae and Amiidae, they may be easier to swallow and may be particularly important for larger northern watersnakes because these snakes may feed primarily on large prey (King 1993, Bowen 2004). Although northern watersnakes in this study did not feed disproportionately on tubular-shaped fish or increase consumption of such prey as snake size increased, larger fish with more tubular shapes may be important for foraging northern watersnakes in part because of their relatively high caloric value.

The northern watersnake has a diverse diet across its distribution and dietary flexibility even within populations. In general, we predict that northern watersnakes eat fishes according to their abundance and availability in the habitat unless ecological or behavioral factors alter the probability of some fish being encountered and captured. The ubiquitous northern watersnake likely has an important role in a variety of aquatic ecosystems. While we did not directly study impacts of watersnakes on sport fish, this opportunistic feeder will likely eat fish according to their availability rather than preferentially selecting certain fishes of management interest. If larger cylindrical shapes are indeed selected for, sport fish from the sunfish family (Centrarchidae) with laterally flattened, deeper bodies could be less selected. Also, northern watersnakes could potentially benefit sport fish by reducing overpopulation and feeding on unhealthy fish (Harding 1997). However, more research is needed to determine the effects of watersnake predation and possibly competition involving game fish populations.

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