Foraging Behaviors of Watersnakes (*Nerodia*) and Garter-snakes (*Thamnophis*) at a Drying Pond in Southern Kansas

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Abstract - *Nerodia* (North American Watersnakes) use various feeding methods to acquire prey. At night, methods include tactile or open-mouth senses as a substitute for visual cues. Herein we describe unreported feeding behaviors for *Nerodia erythrogaster* (Forster) (Plain-bellied Watersnake). We also describe other observations of snakes feeding on fish at a drying pond. In August 2022, Plain-bellied Watersnakes fed on the water's surface with mouths open at night. In September 2022, we observed Plain-bellied Watersnakes foraging with a half-circle loop behind the head, using it to detect fish as a corral while actively swimming underwater. The change in foraging strategy likely was associated with increased fish density and decrease in water volume. We also documented 3 species of snakes consuming *Gambusia affinis* (Baird and Girard) (Western Mosquitofish) at this pond. These observations increase our understanding of foraging behaviors of snakes in the Great Plains.

Introduction

In North America, *Nerodia* spp. Baird and Girard (North American Watersnakes) fill many aquatic niches across most of the eastern United States from the Atlantic Ocean to the Great Plains (Gibbons and Dorcas 2004). Watersnakes use various feeding methods to capture prey in water, which mostly include fish and anurans (Gibbons and Dorcas 2004). One commonly noted behavior is residing underwater with tails anchored to underwater substrates (Brown 1958, Byrd et al. 1988, Conant 1969, Gillingham and Rush 1974, Kofron 1978). Another frequent behavior is directly attacking prey using visual cues (Clark 1949, Diener 1957, Evans 1942, Greene et al. 1994, Raney and Roecker 1947). Other infrequent behaviors also have been recorded, generally during daylight hours. For example, Kennedy (1964) observed *Nerodia* probing crevices with its head in a hunting manner. Preston (1970) recorded 2 instances where snakes ambushed prey from below while hiding beneath submerged plant material. Additionally, Stoner (1941) observed an individual writhing in water, potentially to disturb prey items from the muddy substrate before subduing them.

Prey detection at night can potentially complicate the feeding behaviors of visually and chemically orientated Watersnakes. In the dark, detection of prey through visual stimuli is difficult (Brown 1958). Although chemoreception underwater is known in various Watersnakes via tongue-flicking behaviors (Waters and Burghardt 2013, Ryerson and Schwenk 2022), how this might be connected to foraging on actively swimming prey is unclear. However, to facilitate hunting during the night, *Nerodia* use tactile responses as the primary method of prey detection in water (Brown 1958). Two methods commonly cited in literature are open-mouthed underwater foraging (Clark 1949, Conant 1969, Drummond 1979, Evans 1942, Mushinsky and Hebrard 1977) as well as tactile touching along the side of the body to detect prey items, noted as encircling (Kofron and Dixon 1980, Mushinsky and Hebrard 1977).

Nerodia erythrogaster (Forster) (Plain-bellied Watersnake) is a common species distributed across the southeastern United States from the Atlantic Coast to western Texas

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and southeastern New Mexico (Ernst and Ernst 2003, Gibbons and Dorcas 2004, McCranie 1990). Despite its widespread distribution, limited publications have described the foraging behaviors for this species to capture prey items (Byrd et al. 1988, Diener 1957, Evans 1942, Gillingham and Rush 1974, Mushinsky and Hebrard 1977, Preston 1970). In August and September 2022, we observed 2 previously unreported feeding behaviors for *N. erythrogaster*, both occurring at night at a drying pond in southern Kansas. Herein, we also report on prey items and interactions of 3 snake species (Plain-bellied Watersnake, *Thamnophis proximus* (Say) (Western Ribbonsnake), and *Nerodia rhombifer* (Hallowell) (Diamond-backed Watersnake) feeding in the same pond simultaneously.

Methods

Our opportunistic observations were made by visual observations in late summer at a small pond at the Z Bar Ranch, 1 km north and 1.8 km west of Aetna, Barber County, Kansas. All observations were from the edge of this small pond within only meters of snakes, which were unphased by the white lights used to observe them. Observations were made during the first couple of hours after sunset. The pond was within 1.1 km of the Salt Fork of the Arkansas River and about 250 m from Mule Creek. Small, wooded patches of deciduous trees occurred near this pond and along the 2 waterways. Much of the area consisted of prairie dominated by *Schizachyrium scoparium* (Michx.) Nash (Little Bluestem) within the Gypsum Hills of northwestern Oklahoma and south-central Kansas. The area contains red rock buttes, mesas, and escarpments capped with a layer of gypsum from the Permian Blaine Formation (Gould 1905).

During the summer of 2022, the weather was consistently hot with little precipitation in the region. This caused ponds, lakes, and waterways to dry. In early March 2022, the diameter of the pond was about 18 m, with water filling the entire shallow basin. On 12 August 2022, the diameter of the pond decreased to about 12 m and was reduced in depth. On 24 September 2022, the diameter was further reduced to about 8 m and the pond was shallower at <0.5 m in depth. Reduction in water volume was likely associated with both evaporation of impounded water and the lowering of groundwater. For example, by 13 August 2022, Mule Creek was completely dry with no water in the active channel. On this same day, the Salt Fork of the Arkansas River was a trickle. Returning to the study site in late January 2023, the entire pond was full of water and Mule Creek and the Salt Fork were once again flowing across their entire active channels even though the area had not received much precipitation since September. During observations in August and September, water visibility was low, and we did not walk through water or disturb foraging snakes.

Results

On 12 August 2022, immediately after sunset, we observed 4 adult Plain-bellied Watersnakes foraging, swimming atop the water surface with open mouths. Snakes captured *Gambusia affinis* (Baird and Girard) (Western Mosquitofish) from the water's surface for >90 min, with all individuals using the same foraging technique. Snakes swam moderately slowly on the surface using undulatory motion until a fish contacted the snake's mouth, at which time the tactile sensation elicited a snapping response of its jaws to capture the fish. Snakes would occasionally pause or rest, but most of the time individuals were actively foraging. Only a single species of snake was observed during this evening, the Plain-bellied Watersnake. We also observed a single *Acris blanchardi* Harper (Blanchard's Cricket Frog) and 3 *Lithobates blairi* (Mecham, Littlejohn, Oldham, Brown, and Brown) (Plains Leopard Frog) along the edge of the pond. Throughout our observations, watersnakes did not attempt to prey upon these anurans.

On returning to the pond on 24 September 2022, we again observed adult Plain-bellied Watersnakes foraging for Western Mosquitofish (Fig. 1). We arrived at dusk and observed Plain-bellied Watersnakes foraging underwater by making a half loop with a short segment of their body immediately behind their head (Fig. 2). The head was held parallel to the looped section of the body. All individuals with this half-circle loop appeared to use it to detect fish by tactile sensation like a small corral while actively swimming in figure eights downward under in the murky water. Although we observed 4 Plain-bellied Watersnakes upon arrival at the pond, 3 additional individuals arrived during the next hour. All 7 individuals foraged in the same manner.

On 24 September, we observed 2 additional species of snakes foraging on the dense aggregation of Western Mosquitofish in the shallow drying pond. A single Western Ribbonsnake foraged on fish (Fig. 3) throughout the entire observation period by swimming in an undulatory motion at the water's surface with its mouth closed. Additionally, a single Diamond-backed Watersnake arrived in the dark to feed. This snake also foraged underwater but without the half-circle loop used by Plain-bellied Watersnakes. The 3 species of snakes showed no aggressive behaviors towards one another and occasionally were observed touching and resting on each other (Fig. 4 and 5). All *Nerodia* were observed consuming Western Mosquitofish while in water (Fig. 1), whereas the Western Ribbonsnake occasionally consumed fish on the mud near the edge of the water (Fig. 3).

Figure. 1. A Plain-bellied Watersnake feeds on a Western Mosquitofish in a pond in Barber County, Kansas (photo by Keith Geluso).

Discussion

Our observation of open-mouth foraging behavior by Plain-bellied Watersnakes while on the water's surface was similar to behaviors noted by Evans (1942) where this same species foraged with mouth open at night but only underwater. One explanation for this difference is that the Plain-bellied Watersnakes we observed fed on Western Mosquitofish that tend to congregate in the uppermost strata of the water column, or in shallow waters (Meffe and Snelson 1989). Optimal foraging models suggest that species tend to forage in a manner to maximize rewards and minimize costs while acquiring prey in environments with patchy resources (Charnov 1976). In August, when fish likely aggregated more densely

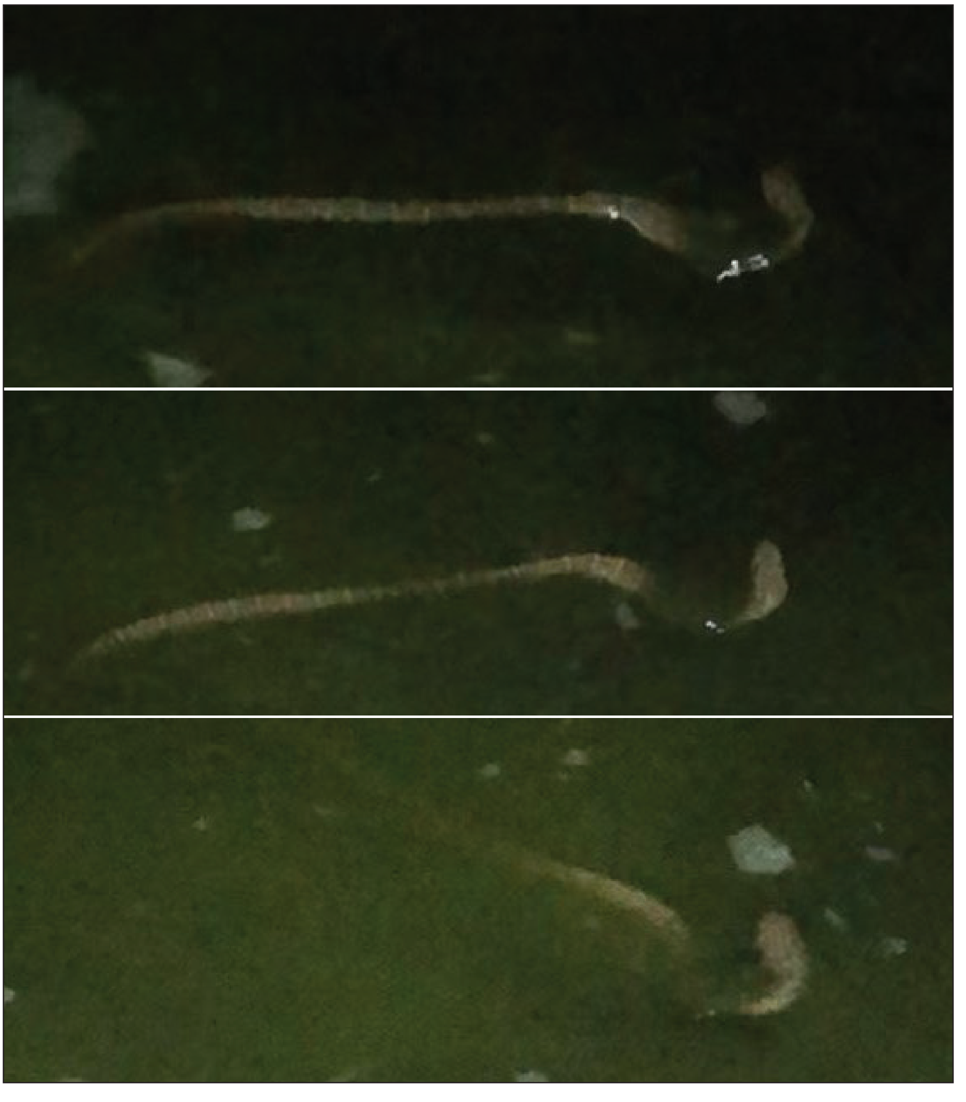

Figure 2. Multiple Plain-bellied Watersnakes displaying a foraging behavior involving a sharp bending at the neck while foraging for Western Mosquitofish at a pond in Barber County, Kansas (photos by Keith Geluso).

Figure 3. A Western Ribbonsnake feeding on a Western Mosquitofish at a pond in Barber County, Kansas (photo by Keith Geluso).

Figure 4. A Western Ribbonsnake rests on a Plain-bellied Watersnake that is feeding on a Western Mosquitofish at a pond in Barber County, Kansas (photo by Keith Geluso).

at the surface of the pond, the most profitable methodology to capture these prey appeared to reside and forage at the water's surface. Evans (1942) did not state which fish species the snakes foraged upon in his study except that "schools of minnows or other small fish" were in the area. The open-mouth foraging documented with Plain-bellied Watersnakes was likely related to the lack of visual stimuli in water at night and the high density of prey near the water's surface. Our observations are interesting, as Plain-bellied Watersnakes generally do not prey upon small fish as adults. This species generally feeds on small fish only when young, with larger and older individuals shifting their diets to anurans (Mushinsky et al. 1982).

Upon returning to the same pond in September, we observed a different foraging behavior exhibited by Plain-bellied Watersnakes feeding upon Western Mosquitofish. To our knowledge, this represented another undescribed method to capture prey for *Nerodia*. Here individuals appeared to sweep through the water with a distinct narrow half loop behind the head to detect prey. The behavior observed in Plain-bellied Watersnakes somewhat resembled behavior in Diamond-backed Watersnakes where individuals completely encircle a fish after the fish contacts the snake's body (Kofron and Dixon 1980). Those authors reported that snakes would move through water with a normal undulating movement and when a fish touched the side of the snake's body, the snake would encircle and trap the fish before eating it. Mushinsky and Hebrard (1977) also observed snakes trapping fish with their bodies, though the specific method the snakes used was not mentioned. The behaviors we observed differed from those recorded behaviors, as our snakes did not create a full circle with their bodies, but instead created a half loop near the head, likely for detecting but not for trapping or capturing the fish.

Figure 5. Two Plain-bellied Watersnakes displaying no aggression toward one another as they move about in a pond in Barber County, Kansas. Several Western Mosquitofish are visible at the surface of the water (photo by Keith Geluso).

Western Mosquitofish are small prey compared to prey items shown in diagrams of snakes encircling fish (Bowers 1966, Kofron and Dixon 1980). Thus, the partial looping behavior that we observed might reflect the difference in prey size compared to previous observations. We suspect that Plain-bellied Watersnakes used partial looping to detect but not trap fish, whereas other snakes use encirclement to both trap and capture larger prey. The partial loop formed behind the head of Plain-bellied Watersnakes (Fig. 2) appeared most like the posturing of another aquatic snake, *Erpeton tentaculatum* Lacépède (Tentacled Snake), from southeast Asia (Catania 2009). Tentacled Snakes also form a half loop "J-shaped posture" behind the head that triggers the snake to strike once the fish touches inside the concave loop. For Tentacled Snakes, individuals remain motionless in this position waiting for fish to contact the loop, whereas Plain-bellied Watersnakes used the loop in murky water, apparently in a sweeping fashion to detect fish.

During our study, we observed a temporal change in foraging behaviors of Plain-bellied Watersnakes between August and September 2022. In August we observed the open-mouth surface feeding, whereas in September we observed the side to side sweeping of a half loop underwater to detect fish by tactile cues. One plausible explanation for this change is that when the pond's volume decreased from 12 m to 8 m, it resulted in a higher concentration of Western Mosquitofish in the pond, including below the surface. We observed only a few dead fish in September, and the water still supported a high density of fish. Western Mosquitofish are durable, able to withstand high and low salinities (Meffe and Snelson 1989), hot temperatures (Otto 1973, 1974; see Meffe and Snelson 1989), and breathe atmospheric oxygen when water oxygen levels are low (Cech et al. 1985). With the pond depth and volume decreasing and the overall number of mosquitofish likely remaining high, using the underwater half loop behind the head likely was more energetically efficient, maximizing foraging efforts, with high prey densities throughout the shallow water.

Western Mosquitofish were previously observed in diets of Plain-bellied Watersnakes, Diamond-backed Watersnakes, and Western Ribbonsnakes in the United States (Ernst and Ernst 2003). For example, Western Mosquitofish have been reported in diets of Plain-bellied Watersnakes in Louisiana (Mushinsky and Hebrard 1977), in diets of Diamond-backed Watersnakes in Louisiana (Kofron 1978, Mushinsky and Hebrard 1977) and Texas (Bowers 1966), and in diets of Western Ribbonsnakes in Texas (Clark 1974, Fouquette 1954), but to our knowledge, no literature previously documented the consumption of Western Mosquitofish by these species in Kansas. Many papers cited within Ernst and Ernst (2003) and Gibbons and Dorcas (2004) on diets of these snakes were older references. We postulate that our observations on lack of Western Mosquitofish in diets of snakes in southern Kansas, in part, is a result of Western Mosquitofish expanding their range in southern Kansas in more recent times (Brown 1987). Previous literature stated that Western Mosquitofish were once rare in Kansas (Cross 1954).

Nerodia are known to occasionally form aggregations in areas with high prey densities, and we did not observe any aggressive behaviors between snakes in the limited space of the pond in September. Others have noted aggregations of multiple species of snakes in a limited area when fish were concentrated in drying bayou inlets (Mushinsky and Hebrard 1977) or at a culvert at a flooded field (Gillingham and Rush 1974). Interspecific and intraspecific interactions were common between snakes at our pond (Fig. 4). The abundance of food resources likely limited aggression between individuals. Other studies demonstrate that intraspecific aggression is reduced with increased food availability (Ducey and Heuer 1991, Hodge et al. 2009). Our study adds to the body of literature on foraging techniques of snakes in the Great Plains and demonstrates predators switch foraging strategies in response to changing environments and prey availability.

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