

## The Effects of Prey Species Presence on Pygmy Rattlesnake (*Sistrurus miliarius*) Foraging Behaviors

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**Abstract** - We investigated *Sistrurus miliarius* (Pygmy Rattlesnake) foraging in field behavior trials by filming rattlesnakes found in typical foraging postures and randomly exposing each snake to 1 of 3 prey-stimulus treatments: frog, anole, or control. Treatment snakes were presented with a prey item tethered away from the snake using dental floss, while control snakes were exposed to a similarly placed piece of floss with no attached prey. We observed 3 instances of caudal luring and found that Pygmy Rattlesnakes tongue-flicked and respired at significantly higher rates if they relocated during the trial. There was no statistically significant effect of prey type on relocation or respiration rate. Our research provides an adaptable methodological framework for studying foraging behavior in free-ranging predators using introduced, responsive prey.

### Introduction

To combat low prey-encounter rates, ambush-foraging snakes have developed a variety of behaviors to maximize the likelihood of encountering and capturing prey. These behaviors include using chemical cues left by potential prey to select optimal foraging sites (Roth et al. 1999), positioning and repositioning the body inconspicuously and in an ideal position to strike, minimizing movement to maintain crypsis, and using luring behaviors to attract prey (Clark 2004, Greene and Campbell 1971). When prey is detected, some snakes attempt to increase foraging success by using behaviors specific to the encountered prey species (Downes and Shine 1998, Glaudas and Alexander 2017, Greenlees et al. 2005, Wasko et al. 2014, Webb et al. 2010). Similar to using chemosensory cues during ambush-site selection, some snakes may be using visual or chemosensory cues to identify prey before engaging in behaviors specific to certain prey types, like luring behaviors (Downes and Shine 1998, Hagman et al. 2008, Reiserer 2002, Roth et al. 1999).

Caudal luring consists of moving the tail, often conspicuous in color or shape, in a motion that mimics a moving animal to attract potential prey while the rest of the body remains motionless (Hagman et al. 2008, Heatwole and Davison 1976, Jackson and Martin 1980, Neill 1960, Rabatsky and Waterman 2005). As with any other ambush predation strategy, the efficacy of caudal luring relies on the ability of the predator to maintain crypsis by minimizing movement in the rest of the body (Greene and Campbell 1971). Although common in juvenile vipers, caudal luring has been documented less frequently in adults as ontogenetic shifts in diet

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occur (Heatwole and Davison 1976, Jackson and Martin 1980). However, some snake species, including *Sistrurus miliarius* (L.) (Pygmy Rattlesnake), experience less-pronounced shifts in diet composition and continue to exhibit caudal luring behavior throughout their lives (da Fonseca et al. 2019, Glaudas and Alexander 2017, Heatwole and Davison 1976, Jackson and Martin 1980).

The Pygmy Rattlesnake is a small crotaline found in the eastern United States from North Carolina south throughout peninsular Florida and as far west as eastern Texas. It is an ambush predator that feeds primarily on anurans and lizards, although its diet varies geographically (Gibbs and Mackessy 2009). Previous foraging studies on Pygmy Rattlesnakes have focused on the use of caudal luring and variation in its predatory behaviors depending upon different prey species in captive settings (Farrell et al. 2011, Jackson and Martin 1980, Rabatsky and Waterman 2005, Roth et al. 1999). Pygmy Rattlesnakes exhibit different predatory behaviors in the presence of *Scincella lateralis* (Say) (Little Brown Skink) versus the presence of *Scolopendra viridis* Say (Giant Centipede) (Farrell et al. 2018), but little research has been performed to examine interactions with 2 of their most common prey species, *Anolis carolinensis* (Voigt) (Green Anole, hereafter also anole) and *Hyla cinerea* (Schneider) (Green Treefrog, hereafter also treefrog).

As ambush predators, Pygmy Rattlesnakes choose foraging sites based on chemosensory cues and wait for prey to pass within range before striking, minimizing movement after foraging-site selection (Jackson and Martin 1980, Roth et al. 1999). Additionally, juveniles have been observed using caudal luring during lab studies (Farrell et al. 2018, Rabatsky and Waterman 2005). We studied Pygmy Rattlesnake foraging behaviors by manipulating prey presence and recording in-situ video trials of snakes in ambush-foraging positions to understand how Pygmy Rattlesnakes alter their behaviors in the presence of prey and determine if they behave differently depending upon prey type. We hypothesized that in the presence of prey Pygmy Rattlesnakes would (1) be less likely to leave their foraging sites, (2) minimize movement by reducing tongue-flicking and respiration rates, and (3) caudal lure more frequently than when prey was absent.

### Field-site Description

We conducted this study at Lake Woodruff Wildlife National Refuge, an 8700-ha conservation area along the eastern floodplain of the St. Johns River in Volusia County, FL. Our sampling took place within a section of this area composed of semideciduous mesic hammock surrounded by freshwater marsh. Pygmy Rattlesnakes are abundant at this site, and the herpetofaunal community has been studied in detail (Farrell et al. 2011, May et al. 1996).

### Methods

#### Field study

We performed field video trials from 6 September 2014 to 22 January 2015 during daylight hours when the temperature was above 17 °C. We located Pygmy

Rattlesnakes using visual searches and performed trials using only snakes that were found in typical foraging coils and not those found moving or under cover. Once we found a suitable snake, we randomly determined which of the 3 treatments (anole, treefrog, or no-prey control) the snake would receive. We tethered a wild-caught treefrog or anole to a naturally occurring structure (a branch, grass clump, etc.) ~1 m away from the snake on a 0.5-m-long dental floss tether lightly tied anterior to the hind legs for the frog and anole treatments, or used a 0.5-m piece of dental floss with no prey attached as the control treatment. Wild-caught prey items were short-term captive animals from the same site where trials were conducted. We used prey items for 1 or several trials each, with the exact number dependent upon possible time between trials and the condition of the prey animals, and subsequently released them. Prey items were originally placed outside of the snake's striking range but retained the freedom to move closer and often remained active throughout trials. The only prey item mortality occurred due to a predation attempt by a free-ranging *Thamnophis saurita* (L.) (Eastern Ribbonsnake) while a trial was in progress. We positioned a video camera (Sony HDR-CX330, Frame Rate: 30 FPS; Tokyo, Japan) to clearly view the entire snake, hit record, and then left the area. After the 40-min trial period ended, we retrieved the camera, measured total length of each snake using a squeezebox, and took close-up pictures of each snake's dorsal pattern to allow us to identify individual snakes and prevent the use of any individual in multiple trials. We were not able to measure or photograph snakes that fled unless they were discovered moving in the immediate vicinity of the trial location. The high density of snakes in this site reduced the probability of resampling an individual that fled before its individual dorsal pattern was recorded.

### Data analyses

We videotaped a total of 20 anole trials, 20 treefrog trials, and 20 control trials using Pygmy Rattlesnakes identified using individual dorsal patterns to avoid resampling individuals, although the identities of some snakes that fled were not recorded (SVL min–max = 19–43 cm). We analyzed the video by viewing it in its entirety or until the snake exited the field of view (relocated). We measured tongue-flicking rate, respiration rate (body compression was visible during exhalation), and caudal luring. We defined caudal luring as the sustained conspicuous movement of the tail (usually in a wriggling motion) while the rest of the body remained still. We determined that a snake had left its foraging site if it exited the video field of view and did not return during the trial period. We measured respiration rate and tongue flicking-rate by reviewing mins 10:00–15:00 from each video (to give the snake a period of time to recover from the initial disturbance we caused), counting the number of tongue flicks and visible inhalations taken, and calculating the per min rate. We determined if the frequency of behaviors differed among the 3 treatment groups using 3 x 2 Fisher's exact tests (Freeman and Halton 1951) for both caudal luring and relocating, and one-way ANOVAs for mean tongue-flicking and respiration rates. Statistical analyses were performed in the program SPSS® (Version 22.0; IBM Corp. 2013).

**Results**

We observed caudal luring in 3 of 60 total trials: in 2 anole trials and 1 treefrog trial. Two of these snakes (total length = 41.0 and 43.0 cm) were over minimum reproductive size (38 cm total length for females; Farrell et al. 1995) and were clearly mature snakes, while 1 (total length = 30 cm) was under the minimum reproductive size. There was no significant difference in the frequency of caudal luring between treatments ( $P = 0.76$ ). There also were no statistically significant differences in mean tongue-flicking rate ( $P = 0.29$ ) or mean respiration rate ( $P = 0.36$ ) between treatments (Table 1). Pygmy Rattlesnakes were not significantly more likely to relocate during treefrog (5 of 20 relocated) or control (6 of 20 relocated) trials than during anole trials (1 of 20 relocated) ( $P = 0.12$ ), although the results suggest a possible trend (Fig. 1). We found that snakes that relocated during a trial had a mean respiration rate almost 3x higher than snakes that did not relocate (Table 2). Snakes that relocated tongue-flicked at a mean rate of 3.7 tongue flicks/min, whereas snakes that did not relocate had a mean tongue flicking rate of 0.022

Table 1. Means, with standard errors in parentheses, of respiration rate (breaths/min) and tongue-flicking rate (flicks/min) in control, anole, and frog treatments.

Treatment	Respiration rate	Tongue-flicking rate
Control	11.45 (2.33)	1.18 (0.80)
Anole	8.33 (1.71)	0.02 (0.02)
Treefrog	12.41 (2.52)	1.11(0.63)

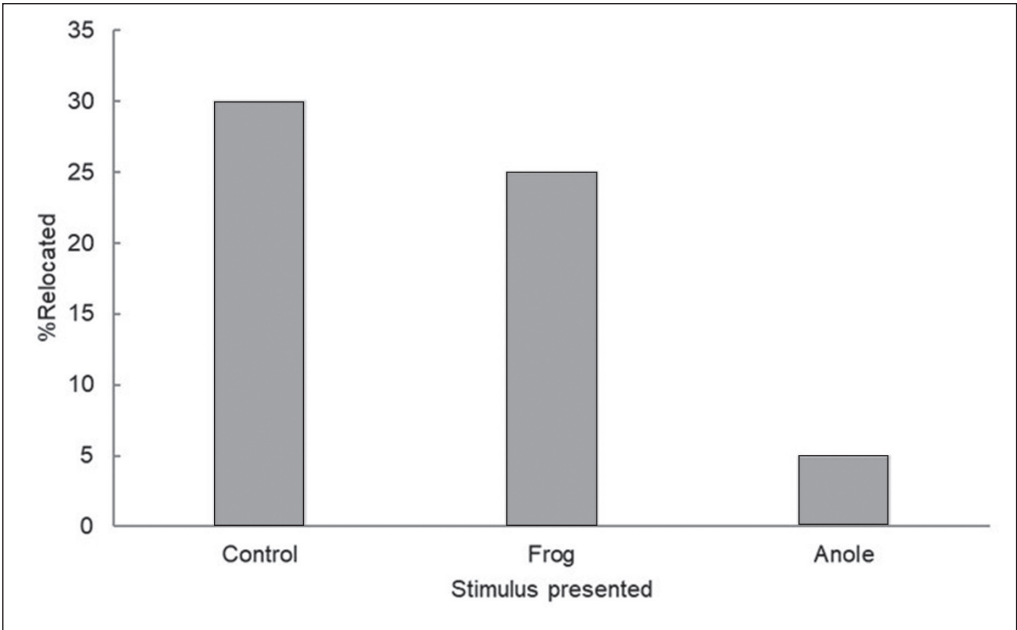


Figure 1. Percentage of snakes that relocated during trials for each treatment, showing no significant difference between trials ( $P = 0.12$ ).

tongue flicks/min (Table 2). Snakes that did relocate had significantly higher mean respiration rates ( $P < 0.001$ ) and mean tongue-flicking rates ( $P < 0.001$ ) than snakes that did not relocate during a trial.

**Discussion**

Because ambush predators need to maintain crypsis to avoid detection by nearby prey, we hypothesized that the presence of prey would reduce respiration rate and tongue-flicking, but our findings do not support these hypotheses. However, snakes that relocated during trials had higher mean tongue-flicking and respiration rates. We attribute this difference to stress induced by our disturbance, which caused relocating snakes to identify potential threats and seek new foraging or shelter sites by tongue-flicking to gain chemosensory cues. No longer concerned with maintaining crypsis for foraging, relocating snakes tongue-flicked and respired freely regardless of prey presence to gain as much information as possible about their surroundings (Clark 2004, Roth et al. 1999, Webb et al. 2010). Snakes that did not relocate continued to minimize movement perhaps to reduce the likelihood of detection by the introduced prey item and thereby increase foraging success.

Although there was no significant difference, there was a trend towards Pygmy Rattlesnakes relocating less often during anole trials compared to treefrog or control trials. This could suggest that Pygmy Rattlesnakes recognized anoles as a preferred prey type and remained inconspicuous to increase their chances of a successful strike. This trend could alternatively reflect diel shifts in prey preference, as our trials occurred during the day. Given that Green Treefrogs are largely nocturnal while Green Anoles are primarily diurnal, a Green Anole might be more likely to enter the snake’s strike range during a daytime trial. However, this hypothesis is not addressed in our study and requires further investigation.

No relocating Pygmy Rattlesnake ever attempted to approach a prey item, and it appears that Pygmy Rattlesnakes generally will not abandon ambush tactics in favor of active-predation behaviors simply because a prey item has remained just out of striking range. Farrell et al. (2018) did find that Pygmy Rattlesnakes occasionally engaged in active foraging in feeding trials using skinks in a laboratory setting, but this occurred only if the prey was introduced while the snake was already active or after a long period of unsuccessful ambush foraging. Ernst and Ernst (2011) reported a Pygmy Rattlesnake actively stalking and striking a Green Anole; however, our observations suggest that active foraging in the wild is rare.

While uncommon, we did observe 2 mature Pygmy Rattlesnakes (~5% of all mature snakes observed) caudal luring in the field, in 1 treefrog trial and 1 anole

Table 2. Means, with standard errors in parentheses, of respiration rate (breaths/min) and tongue-flicking rate (flicks/min) in snakes that relocated or remained coiled during trials.

Relocated	Respiration rate	Tongue-flicking rate
Yes	21.31 (2.49)	3.70 (1.32)
No	7.42 (0.97)	0.02 (0.01)

trial. The caudal luring we observed could be a result of individual variation in ontogenetic persistence of luring behavior or it may be relatively common among adults. Additionally, potential sources of latent heterogeneity leading to differences in behavior are numerous, ranging from the time since an individual's last meal to subtle details of prey or snake positioning. Our trials did not document common use of caudal luring behaviors among adult Pygmy Rattlesnakes, but we were limited in the duration of trials, the prey species used, and the number of trials. The 40-min trials we used likely did not capture the breadth of possible Pygmy Rattlesnake responses to prey presence, and studies with the capabilities to film individuals for long periods have recorded a much wider variety of behaviors (Clark et al. 2016).

Finally, while performing this study, we developed an effective, novel method of manipulating prey presence in the field without major disturbance to the predator. We know of no other experiment on snakes that relied on finding individuals in their foraging sites and introducing live prey items for extended periods to study behavioral responses (but see Goode et al. 1990 for similar observations on a single snake). This method could be adapted for use with many other ambush foragers, particularly vipers and boids, to develop a more detailed understanding of the impact of prey presence and prey species identity on foraging behaviors.

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