

# Foraging ecology of the mangrove salt marsh snake, *Nerodia clarkii compressicauda*: effects of vegetational density

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**Abstract.** The mangrove salt marsh snake (*Nerodia clarkii compressicauda* Baird and Girard) may experience varying levels of foraging success because the prop roots of the red mangrove (*Rhizophora mangle* L.) have a six-fold variation in density. Adult female *N. c. compressicauda* were allowed to forage for 24 h on a known density of prey in an enclosed habitat simulating one of four experimental prop root densities. Snake behaviors were recorded during the first hour of each trial, and the number of prey ingested was determined at the conclusion of the trial period. Individuals had the greatest success at the root density most often encountered in their habitat. More time was spent in the water than atop roots; but individuals were less likely to forage in the water at low root densities, suggesting that they, like their prey, may be afforded protection from avian and mammalian predation by the mangrove forest canopy. Mangrove salt marsh snakes spent the majority of time resting motionless and appeared to be opportunistic predators, attempting to ingest prey only during chance encounters.

## Introduction

Several studies have focussed on how the structural heterogeneity of a habitat affects a predator's ability to capture prey (Savino and Stein, 1982; Nelson and Bonsdorff, 1990; Heck and Crowder, 1991). While early studies suggested the existence of structural complexity thresholds below or above which predation rates were hindered (Nelson, 1979; Heck and Orth, 1980), recent findings suggested that prey capture rate is a monotonically decreasing function of increasing habitat complexity (Nelson and Bond-sdorff, 1990). Generally, increased structural complexity of a habitat decreases foraging success (reviewed by Heck and Crowder, 1991), indicating that predators should forage in areas relatively devoid of habitat structure. We follow Heck and Crowder (1991) and Royama (1970) in defining increased foraging success as an increase in the food intake per unit time by the predator.

The mangrove salt marsh snake, *Nerodia clarkii compressicauda* Baird and Girard (Lawson et al., 1991), inhabits estuarine forests dominated by the red mangrove, *Rhizophora mangle* L., along the coasts of Cuba and peninsular Florida (Conant and Collins, 1991).

While snakes of the Genus *Nerodia* employ a variety of foraging behaviors (Mushinsky and Hebrard, 1977; Kofron and Dixon, 1980), most accounts of *N. c. compressicauda* are anecdotal (Neill, 1965; Miller, 1985). This subspecies is known to feed exclusively on fish (Miller and Mushinsky, 1990). Observations of *N. c. compressicauda* predatory behavior (Neill, 1965) suggest that they may use foraging techniques among mangrove prop roots similar to those described for other water snakes.

A stable supply of prey is usually available in habitats of optimal complexity, where levels of foraging success are highest (Crowder and Cooper, 1982). For example, small estuarine fish often use prop roots of the red mangrove as a primary refuge from predators including larger fish, snakes, and birds (Thayer et al., 1987). Mangrove salt marsh snakes forage among *R. mangle* prop roots (Neill, 1965; Miller, 1985), where mean fish community biomass can be 19 times greater than in open areas adjacent to mangrove forests (Thayer et al., 1987). A refuge, therefore, affords protection from predation for the prey while concentrating the food resource of the predator (Kitching, 1986; Murdoch and Bence, 1987), even though the structural complexity presented by a refuge may hinder predation by obscuring prey from the predator. Foraging behavior may change from that of an ambush predator in dense vegetation to one of actively pursuing prey in lower vegetational densities in order to maintain a constant capture rate (Savino and Stein, 1982).

This study addresses the following questions related to mangrove salt marsh snake foraging ecology: (1) Do snakes experience increased foraging success at a particular density of *Rhizophora* prop roots (possibly optimal)? Do any behaviors (possibly related to foraging success) occur more or less often at certain densities? (3) Do snakes forage preferentially in the water, or from a perch atop prop roots? (4) Without regard for structural complexity, how much time do snakes actually spend foraging?

## Materials and methods

As predator size has been shown to influence predator-prey interactions (Heck and Crowder, 1991), we used only adult female mangrove salt marsh snakes exceeding 500 mm snout-vent length (SVL) (Miller and Mushinsky, 1990). Mangrove salt marsh snakes found along peripheral red mangrove forests in Placido Bayou, Pinellas County, Florida (N27°49', W82°38'), were caught by hand, and SVL (mm) and mass (g) determined. Individuals were returned to the lab, housed separately in 27.8 litre aquaria at 28-30°C, and exposed to an ambient light cycle. Conspicuously gravid individuals were not used.

Because an observer's presence may affect predatory performance (Savino and Stein, 1982; Drummond, 1983), we ensured that each mangrove salt marsh snake would feed in our presence by feeding each individual five sheepshead minnows (*Cyprinodon variegatus* Lacépède) every ten days until beginning the experiment. We chose *C. variegatus* because it was found most often in stomachs of palpated mangrove salt marsh snakes (Miller and Mushinsky, 1990). We ensured that all individuals were morphologically capable of eating all available fish by standardizing fish size between 15 and 22.5 mm

standard depth (Miller, 1985). This size class of *C. variegatus* was also used exclusively in the foraging trials, however mean prey size per treatment was not fixed. Collected *C. variegatus* were kept in aquaria equipped with a sponge aerator, filter, and daily supply of flake fish food.

We constructed simulated *Rhizophora mangle* forests in circular wading pools 2.4 m in diameter and 0.46 m deep (cf. Savino and Stein, 1982; Nelson and Bonsdorff, 1990). Characteristics used in constructing the simulated habitat for foraging trials include prop root density, diameter, and dispersion. Density of *C. variegatus* was predetermined to equal that of the four fish species most frequently ingested by adult mangrove salt marsh snakes (Miller and Mushinsky, 1990). Field densities of any one of the four species were considered to be too low to allow us to draw conclusions on mangrove salt marsh snake foraging behavior. Physical properties of Placido Bayou which we felt were important for properly simulating the habitat—salinity, pH, dissolved oxygen content of the water, and the light intensity underneath the mangrove canopy—were also measured, and (unless otherwise stated) mean ambient values were simulated in each of the pools. Mullin (1992) described the methods used to measure all simulated hydro-physical characteristics.

Pools contained a 20 cm deep base of masonry sand and enough de-ionized tap water (approximately 1635 liters) to approximate the low tide water level of 4 to 6 cm depth of water above the sand layer. Instant Ocean was added (Zug and Dunson, 1979) until water salinity was between 26 and 33 ppt, similar to the range recorded in the field. To prevent fouling, the upper several cm of sand turned over between trials, and the water was drained and replaced periodically.

We maintained all pools at the Botanical Gardens of the University of South Florida, at ambient temperature and photoperiod. Mean levels of dissolved oxygen at low tide ( $5.4 \pm 1$  S.E. of  $0.3 \text{ ml l}^{-1}$ ;  $n = 26$ ) and pH ( $7.1 \pm 0.1$ ;  $n = 24$ ) were maintained within each pool. A charcoal fiberglass-mesh screen lid was secured to each pool, and corrugated fiberglass panelling sheltered all pools overhead. The combination of the corrugated fiberglass and screen lids reduced the intensity of direct midday sunlight to the mean light meter readings taken at mid-day under the mangrove canopy at Placido Bayou ( $2134.2 \pm 216.2 \text{ lux}$ ;  $n = 35$ ).

Prop root density measurements were obtained at randomly-selected sites along the periphery of red mangrove forests (Mullin, 1992). Based on recorded mean root density at Placido Bayou ( $29.9 \pm 12.3 \text{ roots m}^{-2}$ ;  $n = 35$ ), we chose four treatments at which foraging success was examined: 0, 15, 30 (“natural”), and 45 roots  $\text{m}^{-2}$ . We divided the distribution of root diameters measured in the field into three even groups, using the mean diameter of each group to establish size class of roots used in the simulated environments. For the foraging trials, we used three diameters of polyvinyl chloride (PVC) pipe that most closely approximated the mean values of the three groups: 1.9, 2.9, and 3.8 cm. Because prop roots were randomly distributed in Placido Bayou (Pielou, 1959), we could change the spatial arrangement of roots between trials at the same density (Poole, 1974), such that mangrove salt marsh snakes were not exposed to the same structural configuration in successive trials.

We placed 32 *C. variegatus* in each pool (8.4 fish m<sup>-2</sup>) to reflect the maximal natural density of prey species (see Mullin, 1992, for methods used to sample estuarine fish). Trials were conducted between 3 June and 25 October 1991. At least five days prior to the start of each trial, we embedded PVC pipes, painted to resemble red mangrove prop roots, vertically into the sand layer at the random sites leaving 20 cm of exposed pipe. We constructed a perch for the mangrove salt marsh snake (from painted PVC pipe) in the center of each pool. Prior to testing, each individual was not fed and was allowed to acclimate to the simulated habitat for at least ten and five days, respectively. We conducted 41 trials (10 at each density and an extra trial at mean ambient root density) with 25 mangrove salt marsh snakes. Individuals were tested three or fewer times; no individual was tested twice at the same treatment density. We assumed that prior experience at one root density did not significantly alter performance during subsequent trials at different treatment densities.

We removed each individual from the enclosure following acclimatization to determine mass (to the nearest 0.1 g). While the individual was out of the pool, 32 *C. variegatus* were added to the enclosure. After 15 min, we returned the mangrove salt marsh snake to the enclosure and initiated the trial. During the first hour of each trial, one of us (SJM) timed and recorded all behaviors to the nearest second. Behaviors of mangrove salt marsh snake fall into two categories—those occurring in the water and those occurring atop the roots or the perch with at least 50 percent of the snake's body out of the water (table 1). After the 24 h trial, we removed the mangrove salt marsh snake and determined its mass. We then caught and counted fish remaining in the enclosure and returned them to aquaria. If fewer than 32 fish were removed, we palpated the snake to confirm the presence of ingested prey.

For all timed behavioral data, we used an arcsin-square root transformation to correct for normality. All other analyses are non-parametric; the level of significance for all statistical tests was  $\alpha \leq 0.05$ . To confirm that ingestion of fish corresponded to an increase in snake mass, we correlated number of fish caught during a trial with the change in mass using Spearman's rank correlation. We determined if an individual's foraging success was influenced by changes in habitat structural complexity by using a Kruskal-Wallis test to compare the number of prey ingested at the four root densities (Steel and Torrie, 1980).

Comparisons of percent time spent performing particular behaviors as a function of root density were made using one-way analyses of variance (ANOVA). We then used a Student-Newman-Keul's (SNK) test to determine which behaviors were performed more often among all treatment densities of prop roots. To reduce confounding effects during the latter multiple comparison test, those behaviors occurring in the water (cumulatively referred to as TOTALDOWN) were tested independently of those occurring atop the roots (cumulatively referred to as TOTALPERCH) (Steel and Torrie, 1980). We also summed times performing each behavior across all treatment densities, and used Kruskal-Wallis tests to determine if individuals perform certain behaviors more often regardless of root density.

**Table 1.** Descriptions of abbreviations or codes used to designate observed behaviors performed by *Nerodia clarkii compressicauda* during the first hour of each trial.

Abbreviation/ Code	Description
RIW (resting in water)	No movement in the water.
SLS (slow search)	Forward progression in the water and tongue-flicking greater than 1 flick per 2 sec.
STS (stationary search)	Tongue-flicking greater than 1 flick per 2 sec, but at least 50% of body was stationary in the water.
SSW (slow swim)	Forward progression without using tongue.
FSW (fast swim)	Quick movement through the water, without using tongue.
DIVE	Head entirely immersed under water (may have exhibited any behaviour other than STRIKE or INGEST, and still be classified as DIVE).
STRIKE	Attempting to catch a fish.
INGEST	Swallowing a fish after successful capture.
TOTALDOWN	Sum of the time spent performing RIW, SLS, STS, SSW, FSW, DIVE, STRIKE, and INGEST.
RIP (resting in perch)	No movement atop perch or roots.
STSIP (stationary search in perch)	Tongue-flicking greater than 1 flick per 2 sec, but at least 50% of body was stationary atop perch or roots.
ASCEND	Climbing up into the perch or roots.
DESCEND	Lowering body from perch or roots into the water.
PERCHSTRIKE	Striking from the perch into the water while attempting to catch a fish.
TOTALPERCH	Sum of the time spent performing RIP, STSIP, ASCEND, DESCEND, and PERCHSTRIKE.

## Results

Mangrove salt marsh snakes used in the trials ranged in SVL from 506 to 675 mm (mean =  $570 \pm 20$  mm), and in mass from 124.2 to 338.5 g (mean =  $208.3 \pm 16.2$  g). Individuals ingested between zero and eight fish during the 24 h trials. Change in mass was positively correlated with the number of prey ingested ( $r_s = 0.51$ ,  $p < 0.001$ ). Although the trend was for more fish to be caught at 30 roots  $m^{-2}$  than at any other treatment (table 2), the number of prey caught per unit time did not differ among treatments ( $p = 0.32$ ;  $df = 3$ ). Few behaviors were performed more often at any one treatment density of roots (table 3). Mangrove salt marsh snakes spent more time ingesting fish at 30 roots  $m^{-2}$  ( $p = 0.04$ ;  $df = 3$ ), and more time performing a stationary search from the perch at root densities of 0 and 15 roots  $m^{-2}$  ( $p = 0.04$ ;  $df = 3$ ).

Most behavioral trends were consistent regardless of root density (table 2). Individuals spent more time in the water than perched atop roots ( $p < 0.001$ ). Of the time spent atop either the roots or perch, individuals spent more time resting than performing any other behavior ( $p < 0.001$ ). Similarly, in the water, mangrove salt marsh snakes spent more of

**Table 2.** Number of *Cyprinodon variegatus* caught by, and change in mass of, adult female *Nerodia clarkii compressicauda* during a 24 h trial (mean  $\pm$  one standard error) at four root densities between 3 June and 25 October 1991.

Root density (no. m <sup>-2</sup> )	(n)	Number of fish caught	Change in mass (g)
0	10	0.2 $\pm$ 0.1	-1.0 $\pm$ 0.6
15	10	1.4 $\pm$ 0.7	1.3 $\pm$ 1.9
30	11	1.6 $\pm$ 0.8	2.2 $\pm$ 1.9
45	10	1.2 $\pm$ 0.4	0.8 $\pm$ 2.3

**Table 3.** Percent of 1 h which adult female *Nerodia clarkii compressicauda* spent performing particular behaviors (mean  $\pm$  one standard error) at different root densities in trials between 3 June and 25 October 1991. See table 1 for an explanation of behaviour abbreviations/codes. Letters designate behaviors performed more often regardless of root density (a), at specific root densities (b), or within a group of certain behaviors (c).

Behavior	Root Density (No. m <sup>-2</sup> )			
	0 (n = 10)	15 (n = 10)	30 (n = 11)	45 (n = 10)
RIW	47.3 $\pm$ 11.9 <sup>a</sup>	47.8 $\pm$ 11.3 <sup>a</sup>	75.7 $\pm$ 5.6 <sup>a</sup>	59.9 $\pm$ 10.0 <sup>a</sup>
SLS	9.5 $\pm$ 3.9	8.5 $\pm$ 3.1	7.4 $\pm$ 2.0	12.4 $\pm$ 4.2
STS	6.5 $\pm$ 4.5	6.4 $\pm$ 3.5	5.1 $\pm$ 1.2	5.0 $\pm$ 1.0
SSW	<0.1	<0.1	0.1 $\pm$ 0.1	0.7 $\pm$ 0.4
FSW	<0.1	<0.1	<0.1	0.1 $\pm$ 0.1
DIVE	1.2 $\pm$ 1.0	0.4 $\pm$ 0.2	6.5 $\pm$ 2.9	2.2 $\pm$ 0.7
STRIKE	<0.1	0.3 $\pm$ 0.2	0.3 $\pm$ 0.2	0.1 $\pm$ 0.03
INGEST	0.0	0.0	0.5 $\pm$ 0.3 <sup>b</sup>	0.0
TOTALDOWN	64.5 $\pm$ 13.3 <sup>a</sup>	63.3 $\pm$ 13.2 <sup>a</sup>	95.6 $\pm$ 4.3 <sup>a</sup>	80.4 $\pm$ 12.2 <sup>a</sup>
RIP	26.6 $\pm$ 10.7 <sup>c</sup>	30.0 $\pm$ 11.2 <sup>c</sup>	3.2 $\pm$ 3.2 <sup>c</sup>	15.4 $\pm$ 9.8 <sup>c</sup>
STSIP	7.3 $\pm$ 2.8 <sup>b</sup>	5.3 $\pm$ 2.8 <sup>b</sup>	0.9 $\pm$ 0.9	3.1 $\pm$ 1.8
ASCEND	1.5 $\pm$ 0.5	1.3 $\pm$ 0.5	0.4 $\pm$ 0.3	1.0 $\pm$ 0.8
DESCEND	<0.1	<0.1	0.0	0.2 $\pm$ 0.1
PERCHSTRIKE	<0.1	0.0	0.0	0.0
TOTALPERCH	35.5 $\pm$ 13.3	36.7 $\pm$ 13.2	4.5 $\pm$ 4.3	19.6 $\pm$ 12.2

their time resting than performing any other behavior ( $p < 0.001$ ). Among non-resting behaviors in the water, individuals spent more time performing slow search and stationary search regardless of root density ( $p < 0.05$ ). When considering all behaviors, mangrove salt marsh snakes spent more time resting in water than they did performing any other behavior ( $p < 0.001$ ).

## Discussion

Because of the limited number of prey selected from those available in their habitat (Miller, 1985), *Nerodia clarkii compressicauda* may be considered a foraging specialist (Drummond, 1983). Such predators use chemosensory (Burghardt, 1970), visual (Drummond, 1985), and tactile (Jayne et al., 1988) cues (perhaps more than one simul-

taneously) to identify and facilitate prey capture. Mangrove salt marsh snakes appear to respond most to tactile cues, as they often remain motionless until ripples in the water, generated by fish swimming within approximately six cm of, or in direct contact with, the snakes' bodies, appeared to trigger predatory behavior (either a strike or search behavior). Similar to behavior recorded in the aquatic homalopsinid snake, *Cerberus rynchops* (Jayne et al., 1988), predatory behaviors of mangrove salt marsh snakes usually continued following an unsuccessful attempt to capture prey. For example, following an unsuccessful capture attempt, individuals sometimes submerged and touched their snouts to, or tongue-flicked along, the sand perhaps in an attempt to capture prey hidden in the upper layers of the sand. In contrast to other aquatic specialists which have the ability to distinguish among underwater objects (Drummond, 1985; Schaeffel and Mathis, 1991), vision appears to be minimally important to the foraging success of *N. c. compressicauda*.

Mangrove salt marsh snakes exhibited a trend of successfully capturing more prey per unit time at the root density encountered most often in Placido Bayou ( $\approx 30$  roots  $m^{-2}$ ). This trend is consistent with earlier findings (Nelson, 1979; Heck and Orth, 1980), and suggests that the best opportunity for foraging success occurs at an optimal level of structural complexity, below or above which predators will not capture as many prey. Our results contradict the idea that foraging success increases with decreasing habitat structural complexity (Nelson and Bonsdorff, 1990). The magnitude of within-treatment variance in our study was sufficiently high to limit statistical verification of the relations between root density and foraging success. Incorporating body mass into our analyses as a covariate (possibly reducing these variances) however, also failed to yield significant results.

Our experimental design likely limited our findings regarding mangrove salt marsh snake foraging success as a function of root density. During trials, individuals were observed unsuccessfully attempting to capture prey. As mangrove salt marsh snakes forage infrequently (Miller and Mushinsky, 1990), successful ingestion of fish may be stochastic in nature. Had we allowed each trial to proceed for a longer period of time, the total number of stochastic predatory events would likely increase. Additionally, prey encounter rates may vary according to time of day (Crowder and Cooper, 1982), such that increasing the trial length may allow snakes to spend more time foraging at preferred times of day. A second and perhaps more significant factor attributing to little difference in foraging success among root densities was the high prey density. Preliminary trials indicated that a fish density simulating the mean ambient density obtained from samples at Placido Bayou (the equivalent of having five fish in the pool) was insufficient to stimulate foraging by the snakes. Exposure to the maximum recorded prey density, however, may have diminished the effects of varying root density on foraging success or predatory behaviors as prey were overly abundant.

Several general tendencies for mangrove salt marsh snake foraging behavior can be inferred from our data. Root density influences both the individual's level of foraging success and predatory behaviors performed during the first hour of trials at each

treatment. Although mangrove salt marsh snakes spent more time resting (either in the water or atop roots) than performing other behaviours, they rested less at 30 roots  $m^{-2}$  than at other densities. Individuals also spent more time ingesting fish at this level of structural complexity, confirming the apparent increase in foraging behavior at mean ambient root density. Mangrove salt marsh snakes may have remained atop the roots or perched for longer time periods at low root densities to avoid open water areas where protective cover from avian and mammalian predation is absent. If this species avoids predation by remaining in the protective cover *Rhizophora mangle* stands, then encounter rates for fish species seeking refuge among red mangrove prop roots (Thayer et al., 1987) will be higher than for open-water prey. Similar foraging postures have been noted for other snake species (Jones and Whitford, 1989).

When evaluating the results of this study, several points relative to the experimental design should be noted. It enabled the direct observation of the effects of known conditions of habitat structural complexity on foraging success. While preferred, such documentation in the field is logistically prohibitive, meaning that many variables in this system must be either removed or assumed to be of little consequence to predator-prey interactions. However, constructing a simulated habitat for the observation of snake foraging ecology allows experimental manipulation of known variables, such that any factors influencing the predator's behaviors or foraging success can be easily identified. Replicate testing of the effects of structural heterogeneity on foraging success should include levels of complexity intermediate to, and in excess of, those examined in our study, and should further document the behavior of both predator and prey species over longer time intervals.

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