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Use of Experimental Enclosures to Examine Foraging Success in Water Snakes: A Case Study

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Vegetation structure is an important component of habitat that may affect the outcome of a predator-prey interaction. Studies of fish have focused on how habitat structure affects a predator's ability to capture prey (Crowder and Cooper, 1982; Savino and Stein, 1982; Nelson and Bonsdorff, 1990). Collectively, the results indicate either that thresholds of structural complexity exist, below or above which predation rates are hindered (Nelson, 1979; Heck and Orth, 1980), or that prey capture rate decreases monotonically as habitat complexity increases (Nelson and Bonsdorff, 1990). Generally, a stable supply of prey is available in habitats of optimal complexity, where foraging success (prey captured per unit time) is highest (Royama, 1970; Heck and Crowder, 1991). Foraging behavior may change from that of an ambush predator in dense vegetation to that of active pursuit in lower vegetation densities in order to maintain a constant capture rate (Savino and Stein, 1982). Here, we present a protocol for experimentally examining the effects of varying structural complexity on predator-prey interactions using a snake as the predator. We test our methods by observing the mangrove salt marsh snake, *Nerodia clarkii compressicauda* (Lawson et al., 1991), foraging in an environment which simulates field conditions.

Mangrove salt marsh snakes prey on fish (Miller and Mushinsky, 1990) inhabiting estuarine forests dominated by the red mangrove, *Rhizophora mangle*. Although they vary in density and diameter (see below), emergent mangrove prop roots provide a relatively uniform habitat structure which can be easily manipulated in an artificial setting, making this predator-prey system ideal for studying the effects of varying complexity on foraging success. Fish inhabiting estuarine forests often use red mangrove prop roots as a primary refuge from predators including larger fish, snakes, and birds (Thayer et al., 1987; Mullin, 1995). Although the structural complexity presented by prop roots may hinder predation by obscuring prey from mangrove salt marsh snakes, such structural complexity also concentrates the food resource for the predator (sensu Murdoch and Bence, 1987). In addition to discussing the merits and logistical considerations of manipulating physical variables within an artificial habitat, we address three questions related to

predator-prey interactions of the mangrove salt marsh snake: (1) Do snakes experience increased foraging success at a certain density of red mangrove prop roots? (2) Is predatory behavior influenced by the density of prop roots? (3) Is prop root density a factor in microhabitat selection by foraging snakes?

We constructed simulated red mangrove forests in circular wading pools 2.4 m in diameter and 0.46 m deep (cf. Savino and Stein, 1982; Nelson and Bonsdorff, 1990). Use of circular pools minimized any edge effects that may influence prey or predator behavior (Krebs, 1989). All pools were maintained at the Botanical Gardens of the University of South Florida, at ambient temperature and photoperiod (Fig. 1).

Characteristics used in constructing the simulated red mangrove forest for foraging trials included prop root density, diameter, and dispersion. Prop root density measurements were obtained at randomly-selected sites along the periphery of red mangrove fringe and overwash (Snedaker, 1989) forests of Placido Bayou, Pinellas County, Florida (27°49'N, 82°38'W). Interior forest sites were inaccessible to us (either to observe foraging snakes or to measure prop roots), and thus not sampled. Based on the recorded mean (\pm one standard error) prop root density at Placido Bayou (29.9 ± 12.3 roots m^{-2} ; $N = 35$), we chose four treatments to use in the mangrove salt marsh snake foraging trials: 0, 15, 30 ("natural"), and 45 roots m^{-2} . Three size classes of roots were established from the mean of each third of the distribution of prop root diameters measured in the field. The proportion of simulated roots in each size class was held constant across all treatment densities. Because prop roots were randomly distributed in Placido Bayou (Pielou, 1959), we altered spatial arrangement of roots between trials of the same density (Poole, 1974), so that individuals were not exposed to the same structural configuration in successive foraging trials.

Certain physical properties of Placido Bayou, which we believed were important for properly simulating the mangrove forest habitat, were also measured. Mean ambient values for pH (7.1 ± 0.1 ; $N = 24$) and dissolved oxygen content of the water (5.4 ± 0.3 ml L^{-1} ; $N = 26$) at low tide, and the light intensity below the mangrove canopy (2134.2 ± 216.2 lux; $N = 35$) were simulated in each of the pools. The methods used to measure all simulated hydrophysical characteristics are described elsewhere (Mullin, 1995). Each pool contained a 20 cm deep base of masonry sand and enough deionized tap water (≈ 1635 L) to approximate the low tide water depth (4 to 6 cm) above the sand layer. Logistical considerations prohibited simulating tidal fluctuations in the water level, so we chose a shallow depth on the basis of observing mangrove salt marsh snakes in the field foraging only during low tide. PVC pipes, painted to resemble red mangrove prop roots, were embedded vertically into the sand layer at random sites leaving 20 cm of exposed pipe. We also provided a perch (of painted PVC pipes) for individuals in the center of each pool.

Instant Ocean was added until water salinity was between 26 and 33 ppt, similar to the range recorded at Placido Bayou. To prevent fouling, the upper layer

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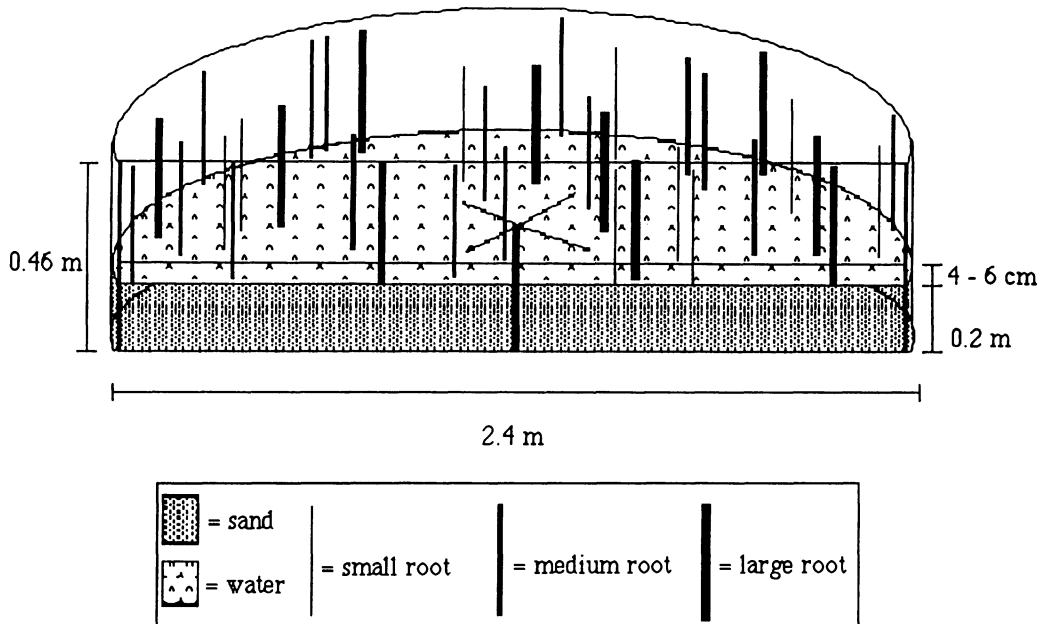


FIG. 1. Diagram of an oblique cross-section of an experimental enclosure simulating a red mangrove (*Rhizophora mangle*) prop root habitat of 15 roots m^{-2} . The center structure apparent in the sand layer represents the base of the perch provided in the center of the pool.

(≈ 6 cm) of sand was turned over between trials, and the water was drained and replaced periodically. A charcoal fiberglass-mesh screen lid was secured to cover each pool, preventing escape of either predator or prey, and corrugated fiberglass paneling provided overhead shelter for all pools. The combination of the corrugated fiberglass and screen covers reduced the intensity of direct midday sunlight to the mean light meter readings taken at mid-day under the mangrove canopy, and prevented rain from diluting the salinity within the pools. All materials representing physical structure within the simulated habitats were inert, thereby minimizing their interference with vomeronasal cues from prey.

Because an observer's presence may affect predatory performance (Savino and Stein, 1982; Drummond, 1983), we conditioned mangrove salt marsh snakes to feed in our presence by feeding individuals five sheepshead minnows (*Cyprinodon variegatus*) every ten days until beginning the foraging trials. We used *C. variegatus* throughout the study because it was found most often in stomachs of adult snakes (Miller and Mushinsky, 1990). We ensured that all snakes were morphologically capable of eating all available fish by standardizing fish size to 15–22.5 mm standard depth. Mean size of *C. variegatus* in each treatment of the foraging trials was not fixed.

Foraging trials were conducted between 3 June and 25 October 1991, within the activity season of this subspecies (pers. obs.). We conducted 41 trials with 25 mangrove salt marsh snakes. Individuals were tested three or fewer times; no individual was tested twice at the same treatment density, and if tested more than once at differing densities, use of the individual in a particular treatment was random. This experimental

design violates certain assumptions concerning independent data (Hurlbert, 1984); however availability of snakes was limited and, preliminary trials revealed that prior experience at one root density did not alter performance during subsequent trials at different treatment densities (paired t-test; $df = 12$, $t = 0.55$, $P = 0.59$).

Individual mangrove salt marsh snakes were not fed for 10 d prior to testing and, within that time period, were acclimatized to the simulated habitat for five days. To reduce confounding effects of predator size and gender on predator-prey interactions (Heck and Crowder, 1991), we used only adult female individuals exceeding 500 mm snout-vent length (Miller and Mushinsky, 1990) in the foraging trials. Mangrove salt marsh snakes were obtained from red mangrove forests at Placido Bayou, housed individually in 37.8 L aquaria at 28–30 C, and exposed to an ambient photoperiod. Snakes giving birth after capture were not used, as recent post-partum condition may affect behavior (Gibbons and Semlitsch, 1987).

Immediately preceding each trial, the individual's mass was determined (± 0.1 g). With the test animal out of the pool, 32 *C. variegatus* were added to the enclosure to reflect the maximum natural density (8.4 fish m^{-2}) of four preferred prey species (Miller and Mushinsky, 1990) inhabiting red mangrove overwash forests (see Mullin, 1995, for methods used to sample fish). Field densities of a single prey species in overwash forests were considered to be too low to allow us to draw conclusions on mangrove salt marsh snake foraging behavior.

After 15 min of acclimating the fish, we returned the mangrove salt marsh snake to the pool and initiated the trial. During the first hour of each trial, one

TABLE 1. 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 ⁻²)	(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

observer (SJM) timed and recorded all behaviors to the nearest second. Behaviors of mangrove salt marsh snakes fell into two categories—those occurring in the water, and those occurring atop the roots or the perch with at least 50% of the snake's body out of the water (for a detailed description of behaviors, see Mullin and Mushinsky, 1995). Searching behaviors were designated as those during which the individual's tongue-flick rate equaled or exceeded one flick per 2 sec. After the 24 h trial, we removed the 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 found, the snake was palpated to confirm the presence of ingested prey as boluses in the stomach.

Arcsin-square root transformations were applied to all timed behavioral data to obtain normal distributions ($P \leq 0.04$). To confirm that ingestion of fish corresponded to an increase in snake mass, we correlated the number of fish caught during a trial with the change in mass using Spearman's rank correlation. We determined whether snake 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). All statistical tests were computed using Statistical Analysis Systems software (SAS Institute, 1990) at a significance level of $\alpha \leq 0.05$.

Individual snakes ingested between 0 and 8 fish during the 24 h trials. Change in mass was correlated positively with the number of prey ingested ($r_s = 0.51$, $P < 0.001$). More fish were caught at 30 roots m⁻² than at any other treatment, though differences in the number of prey caught per unit time among treatments were not statistically significant (Table 1). Few behaviors were performed more often at any one particular treatment density of roots (Mullin and Mushinsky, 1995). Of the eight behaviors described for snakes in the water, individuals spent more time ingesting fish at 30 roots m⁻² (0.5 \pm 0.3% of 1 h; $P < 0.05$). Among the five behaviors described for snakes on top of either roots or perch, more time was spent performing a stationary search from the perch at root densities of 0 and 15 roots m⁻² (7.3 \pm 2.8% and 5.3 \pm 2.8%, respectively; $P < 0.05$).

The durations of some behaviors were consistent regardless of root density. Mangrove salt marsh snakes 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, individuals spent more of their time resting than performing any other behavior ($P < 0.001$).

The magnitude of within-treatment variance in our study was sufficiently high to limit statistical verification of the effects of root density on foraging success. The trend of mangrove salt marsh snakes capturing more prey per unit time at the root density encountered most often in the natural habitat (≈ 30 roots m⁻²), however, is consistent with some previous studies (Nelson, 1979; Heck and Orth, 1980). While field observations indicate that foraging opportunity may be equal among all root densities (Mullin, 1995, pers. obs.), perhaps predatory success does not increase monotonically with structural complexity of the habitat. A *post hoc* analysis indicated that the test comparing number of prey ingested in the different treatments had a power of 0.28 (following Cohen, 1977; $\alpha \leq 0.05$, $u = 3$, $f = 0.29$), suggesting a high probability of committing a Type II error. Establishing a value for power of 0.80 for this same comparison would necessitate 34 trials at each treatment level of root density (Cohen, 1977).

Mangrove salt marsh snakes are foraging specialists (*sensu* Drummond, 1983) and appear to readily respond to both vomeronasal and tactile cues. Ripples generated by fish swimming within 6 cm of an individual's body triggered predatory behavior (either a strike or search behavior). Similar to other species (Jayne et al., 1988), mangrove salt marsh snakes followed an unsuccessful capture attempt with more predatory behavior. After a missed strike, individuals often 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. Sheepshead minnows occasionally buried themselves in the substrate (possibly a predator-avoidance behavior) with surprising speed and efficiency (pers. obs.). When buried, the tip of the mouth and one eye were usually the only parts of the fish protruding above the sand. The escape behavior of prey should be considered in future studies, when choosing among several potential prey species.

The enclosures used in this study were relatively simple and inexpensive (approximately \$125 each) to construct, and once erected, relatively maintenance free for the duration of the study. As Instant Ocean was the most expensive item, a similar study involving a fresh-water semi-aquatic species of snake would be less costly to perform. The deep sand layer used in this study to support PVC pipes can be reduced or eliminated, thus increasing water depth, or allowing the use of other forms of habitat structure (e.g., artificial or harvested macrophytes). These enclosures would therefore lend themselves well not only to future interspecific comparisons of snake foraging ecology, but also to further examinations of behavioral response to different structural components of a snake's habitat.

Our experimental design probably limited our findings regarding mangrove salt marsh snake foraging

success as a function of root density. During the trials, numerous individuals were observed unsuccessfully attempting to capture prey. As these snakes forage infrequently (Miller and Mushinsky, 1990), successful ingestion of fish may be rare in a 24 h period. Had we allowed foraging to continue for 72 h for example, the total number of predatory events likely would 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. Perhaps a more significant factor contributing to little difference in foraging success among root densities was the high prey density. Preliminary trials indicated that mangrove salt marsh snakes were not stimulated to forage in enclosures having a fish density matching the mean ambient level recorded at Placido Bayou (the equivalent of five fish in the pool). We did not assess a minimum prey density that would motivate foraging; however, exposure to the maximum recorded prey density may have diminished the effects of varying root density on foraging success or predatory behaviors as prey were overly abundant.

When evaluating the results of this study, several points relative to the experimental design should be noted. Constructing a simulated habitat to study foraging ecology allows experimental manipulation of known variables, such that any factor influencing the predator's behaviors or foraging success can be identified. While preferred, documentation of laboratory findings in the field is often logistically prohibitive, meaning that many variables in this system must be either ignored or assumed to be of little consequence to predator-prey interactions. Particular attention should be paid to accurate measurement (Yezerinac et al., 1992) of the environmental variable(s) of interest, so that results reflect foraging responses presumed to occur in the natural setting.

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***Cerrophidion godmani* in Costa Rica: A Case of Extremely Low Allozyme Variation?**

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Phenotypic variation among snake populations has been quantified extensively using morphological characters (Auffenberg, 1955; King, 1988), and the biological and biochemical differences between venom toxins (Jiménez-Porras, 1964; Gutiérrez et al., 1980; Aragón and Gubensek, 1981). Unfortunately, genetic diversity at the intraspecific level is available only for a few species (Sattler and Guttman, 1976; Rose and Selcer, 1989; Wilkinson et al., 1991), and is usually inferred using allozyme polymorphisms. Allozyme data, though not reflecting a truly unbiased sampling of the genome, can serve as an estimate of variability among structural loci.

Low allozymic variation has been reported in some snake populations, and these studies have shown the existence of uncoupled rates of evolution between morphological and allozymic characters (Gartside et al., 1977; Murphy and Ottley, 1980). Here I report another example of low allozyme variation, this time in Costa Rican populations of the viper, *Cerrophidion godmani*.

Cerrophidion godmani is a small pitviper that occurs in the Central American highlands, disjunctly distributed from southeastern Oaxaca, Mexico, to the southeastern portion of the Cordillera de Talamanca in Chiriquí, Panamá (Campbell and Solórzano, 1992). In Lower Central America, this species occurs above 1500 m in two regions: the Cordillera Volcánica Cen-

tral (CVC) and the Cordillera de Talamanca (CT). The purpose of this study was to estimate genetic variability and to look for evidence of geographic variation among populations inhabiting the different physiographic regions in Costa Rica.

Specimens of *C. godmani* were collected between 1991 and 1992, and transported to the Instituto Clodomiro Picado, Universidad de Costa Rica. Locality, snout-vent length (SVL), and sex were determined for each individual. A total of 148 adults of both sexes, all over 35 cm in SVL, were studied. Most samples came from grassland areas surrounded by oak forest. Localities examined (Fig. 1) and sample sizes are: CVC-Las Nubes de Coronado (20), Cascajal (21), Rancho Redondo (19), San Ramón de Tres Ríos (15), Ochomogo (16); CT-El Empalme (22), Piedra Alta (22), and Capellades de Cartago (13). The snakes were kept in captivity for antivenom production.

A 1 ml blood sample was obtained by clipping the distal tip of the tail. Erythrocytes were separated from other blood components, washed three times in saline solution, and hemolyzed with 0.1% sodium citrate. Horizontal starch gel electrophoresis follows Murphy et al. (1990). Enzymes systems and electrophoretic conditions are listed in Table 1.

To quantify venom variation, venom was pooled for individuals from a particular locality. Venom was centrifuged at low speed at 4 C for 15 min to remove cells and debris and stored at –20 C. Protein concentrations of liquid venom samples were determined by the Coomassie Blue method (Spector, 1978). Protein electrophoresis (SDS-Page) was conducted under both reducing and nonreducing conditions on 12% polyacrylamide gels. Proteins were stained with Coomassie Blue r-250.

Of the 15 loci examined (Table 1), none exhibited within-locality polymorphism, nor was there any detectable variation among localities. Similarly, no geographic variation was found in the mobility patterns of venom proteins. Because several electrophoretic conditions were applied to each enzyme system (Table 1), it seems unlikely that the results can be attributed to a failure in allozyme resolution.

Heterozygosity estimates are affected severely by number of loci sampled (Nei and Roychoudhury, 1974; Gorman and Renzi, 1979) and it has been demonstrated that the number of individuals used for estimating heterozygosity and genetic distance can be very small if a large number of loci are studied (Nei, 1978). Although the possibility of error due to the small number of loci used in this study cannot be dismissed, other causes may explain these results.

Werman (1992) presented data that also suggested low polymorphism in *C. godmani* allozymes. He employed 26 loci from 20 different enzyme systems while analyzing the phylogenetic relations among members of the genus *Bothrops* (sensu lato). He failed to find any allozymic variation in a sample of fourteen individuals of *C. godmani* from Costa Rica, except for the Phosphogluconate dehydrogenase (Pgdh) locus. Three alleles were found in this locus but Pgdh was excluded from his analysis because it was too variable among and within other taxa to be of use phylogenetically (Werman, pers. comm.).

Reduced allelic variability has been reported among other vertebrates (Nadler et al., 1967; Bonnell and Se-

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