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its high permeability), a slug-eating snake need not use maxillary and mandibular protractions or maintain a prolonged grip (which would be disadvantageous when dealing with mucous-producing prey). As shown by our bioassays, the liberation of mucous appeared to be less intense when slugs received Duvernoy's extracts. Thus, we hypothesize the role of the secretion of Duvernoy's glands as paralyzing, whereas the role of the secretions from the other two glands may act in unison to initiate the digestive process.

The presence of both proteolytic and toxic secretions in the saliva of snakes apparently supports the idea that secretions from oral glands initially had a non-toxic role but presently aid in both prey handling and ingestion (Gans, 1978; Kardong, 1979).

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LITERATURE CITED

- ALCOCK, A., AND L. ROGERS. 1902. On the toxic properties of the saliva of certain non-poisonous colubrines. Proc. Royal Soc. London 1902:446-454.
- AMARAL, A. 1924. Contribuição à biologia dos ophidios brasileiros (habitats, hábitos e alimentação). Coll. Trab. Inst. Butantan 2:177-181.
- ———. 1933. Mecanismo e gênero de alimentação das serpentes do Brazil. Boletim Biológico (Nov. Ser.) I(1):2-4.
- CHAYKIN, S. 1966. Biochemistry Laboratory Techniques. John Wiley, New York.
- GANS, C. 1978. Reptilian venoms: some evolutionary considerations. In C. Gans and K. Gans (eds.), Biology of the Reptilia, Vol. 8, pp. 1–42. Academic Press, London.
- GREENE, H. W., AND G. M. BURGHARDT. 1978. Behavior and phylogeny: constriction in ancient and modern snakes. Science 200:74-77.
- HOGE, A. R., I. L. LAPORTA, AND S. R. W. L. ROMANO HOGE. 1978/79. Notes on Sibynomorphus mikani (Schlegel, 1837). Mem. Inst. Butantan 42/43:175– 178.
- KARDONG, K. V. 1979. "Protovipers" and the evolution of snake fangs. Evolution 33:433-443.
- KOCHVA, E. 1987. The origin of snakes and evolution of the venom apparatus. Toxicon 25:65–106.
- LAPORTA-FERREIRA, I. L. 1985. Fisioecologia da serpente moluscófaga *Sibynomorphus neuwiedi* (Colubridae, Dipsadinae). Doctoral Diss., Inst. Biocienc. Univ. Sáo Paulo, Brazil.
- , AND M. G. SALOMÃO. 1991. Morphology, physiology and toxicology of the oral glands of a tropical cochleophagous snake, *Sibynomorphus neuwiedi* (Colubridae, Dipsadinae). Zool. Anz. 227(3/ 4):198-208.
- LOMONTE, B., AND J. M. GUTIERREZ. 1983. La actividad proteolítica de los venenos des serpientes de Costa Rica sobre la caseína. Rev. Biol. Trop. 31:37-40.
- LOWRY, O. H., N. J. ROSENBROUGH, A. L. FARR, AND R. J. RANDALL. 1951. Protein measurement with folin phenol reagent. J. Biol. Chem. 193:265-275.
- PETERS, J. A. 1960. The snakes of the subfamily Dipsadinae. Misc. Publ. Zool. Univ. Michigan 144:1– 224.

- SALOMÃO, M. G. 1991. Estrutura e secreção das glândulas de Duvernoy de Sibynomorphus mikani (Colubridae, Dipsadinae) e Philodryas olfersii (Colubridae, Xenodontinae) e das glândulas de veneno de Bothrops jararaca (Viperidae, Crotalinae) e Micrurus frontalis (Elapidae, Elapinae) e a influência dos estados de alimentação e jejum. Thesis, Inst. Biocienc. Univ. Sao Paulo-Brazil.
- SAVITZKY, A. H. 1980. The role of venom delivery strategies in snake evolution. Evolution 34:1194– 1204.
- SAZIMA, I. 1989. Feeding behavior of the snail-eating snake, Dipsas indica. J. Herpetol. 23:464–468.
- TAUB, A. M. 1965. The labial glands of the Colubridae. Amer. Zool. 5:296.
- . 1967. Comparative histological studies on Duvernoy's gland of colubrid snakes. Bull. Amer. Mus. Nat. Hist. 138:1-50.

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Life History Characteristics of Nerodia clarkii compressicauda at Placido Bayou, Florida

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The mangrove salt marsh snake, Nerodia clarkii compressicauda (after Lawson et al., 1991), inhabits estuarine mangrove forests dominated by the red mangrove, Rhizophora mangle, on Cuba and along the coasts of pennisular Florida (Dunson, 1979; Zug and Dunson, 1979; Hebrard, 1981). Adult snakes range in size from 38 to 76 cm snout-vent length (SVL) (Conant and Collins, 1991) and exhibit highly variable body coloration. Most common is the "green-morph" typified by dark olive green color with brown bandings, but "red-morph" snakes have also been observed. The latter, rarer of the two color morphs is usually dark, rust-red in color, with alternating lighter and darker bands, or is uniformly a dark reddish-orange. Mangrove salt marsh snakes mate during the early spring, and young are born in mid to late summer (Ashton and Ashton, 1984). Neill (1965) recorded brief observations of mangrove salt marsh snake foraging behavior, and Miller (1985) and Miller and Mushinsky (1990) reported that these snakes feed exclusively on fish. Aside from measurements of those snakes captured in these latter two studies, however, little morphometric data are available for this subspecies. This study presents additional measurements of head and body size of adult mangrove salt marsh snakes collected at Placido Bayou, Florida, and neonates born in captivity. Also, I report the frequency of green-

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FIG. 1. Snout-vent length (SVL) correlated with gape index for mangrove salt marsh snakes (*Nerodia clarkii compressicauda*) collected at Placido Bayou or born in captivity between 25 June 1990 and 16 October 1991. $r_s = 0.871$.

morph and red-morph snakes as well as the frequency of injury among snakes collected at Placido Bayou.

Miller and Mushinsky (1990) reported a strong correlation between head size and SVL in this subspecies. As the maximal size of prey which a snake is capable of ingesting is often dictated by head dimensions (Pough and Groves, 1983; Mushinsky, 1987), I further substantiate the estimate of gape index (GI; sensu Miller and Mushinsky, 1990) for Nerodia clarkii compressicauda. Gape index is an ecologically-significant parameter because, though GI is believed to underestimate maximum prey size for N. c. compressicauda (Miller and Mushinsky, 1990), the size of prey which an individual is capable of ingesting should

TABLE 1. Morphometric measurements for neonate, and adult mangrove salt marsh snakes (*Nerodia clarkii compressicauda*) born in captivity or collected at Placido Bayou between 25 June 1990 and 16 October 1991. Reported values represent means \pm one standard deviation. (SVL = snout-vent length; JW = jaw width; JL = jaw length; GI = gape index).

Charac- teristic	Neonates (N)	Adults (N)
Mass (g)	4.5 ± 0.2 (80)	211.4 ± 13.5 (27)
SVL (mm)	158.9 ± 1.3 (78)	$570.2 \pm 11.4 (42)$
JW (mm)	$8.3 \pm 0.1 (77)$	22.0 ± 0.5 (42)
JL (mm)	$13.0 \pm 0.1 (77)$	30.0 ± 0.5 (42)
GI	68.7 ± 0.4 (77)	165.5 ± 2.9 (42)

be positively related to snake size. Having large heads, larger snakes should have an easier time obtaining a sufficient amount of prey to survive when compared to smaller snakes, because larger snakes can ingest a wider range of prey size (both small and large prey) than that which is available to small snakes (only small prey).

I caught snakes inhabiting peripheral regions of *Rhizophora mangle* overwash and fringe forests (Snedaker, 1989) at Placido Bayou (Pinellas County, Florida) between 25 June and 4 August 1990, and 8 May and 16 October 1991. Snakes were caught by hand, and measured for the following characteristics: SVL (mm), mass (g), jaw width (mm), and jaw length (mm). I followed procedures outlined in Miller and Mushinsky (1990) to calculate each snake's gape index.

TABLE 2. A comparison of morphometric measurements between green-morph and red-morph adult mangrove salt marsh snakes (*Nerodia clarkii compressicauda*) collected at Placido Bayou or born in captivity between 25 June 1990 and 16 October 1991. See Table 1 for explanation of characteristics.

Charac- teristic	Green-morph (N)	Red-morph (N)
Mass (g)	213.0 ± 15.1 (23)	$202.1 \pm 32.4 (4)$
SVL (mm)	572.7 ± 12.2 (37)	551.4 ± 32.5 (5)
JW (mm)	22.0 ± 0.5 (37)	22.2 ± 0.6 (5)
JL (mm)	30.0 ± 0.6 (37)	30.0 ± 1.4 (5)
GI	165.4 ± 3.2 (37)	166.0 ± 6.5 (5)

Briefly, this technique treats jaw length and jaw width as the length and width diameters of an ellipse, and presumes that the area defined by an ellipse having those dimensions represents the maximal cross-sectional area of snake gape (i.e., the maximal prey size). Thus, gape index is calculated as:

$$GI = 2\pi ((JL^2 + JW^2)/2)^{0.5}$$
[1]

I recorded the color, any evidence of injury (including tail loss), and measurements described previously for each snake caught. Gravid females (determined by palping for presence of young) were returned to the lab, housed in 37.9 L aquaria at 28-30 C, and exposed to an ambient light cycle. Newborn snakes were measured for the characteristics described above within 24 h of parturition. Adult females and young maintained in captivity were released at Placido Bayou at the conclusion of the study. Other snakes collected were used in another study, ensuring that no snake was measured more than once.

Data for each of the morphometric parameters examined were not normally distributed, even following attempted transformations. Therefore, Kruskal-Wallis tests ($\alpha = 0.05$) were used to compare distributions of mass, length, and head dimension measurements. Comparisons of the measured characteristics by sex were not made because very few males were caught at Placido Bayou (see below), and determination of sex at time of parturition in the lab was unreliable.

All but two of the 42 adult mangrove salt marsh snakes collected at Placido Bayou were initially sighted perched in the peripheral branches of mangroves; the other two were caught while swimming in the water immediately adjacent to the mangroves. Six (14.3%) individuals were male, and 36 (85.7%) were female. Five (11.9%) individuals were red-morph and 37 (88.1%) were green-morph; there were no redmorph males collected at Placido Bayou. Selection of warmer microhabitats (peripheral areas of the mangrove canopy, exposed to direct sunlight) by gravid females may account for the higher abundance of female snakes caught in this study. Preference for warmer microhabitats has been previously reported for ovoviviparous natricines (Osgood, 1970).

Eight (22.2%) of the female snakes collected were gravid, yielding between five and 19 young per clutch (mean = 10.8 ± 1.9). I did not anticipate parturition in all gravid females, and did not record their mass immediately prior to giving birth. Thus, relative clutch mass (Seigel and Fitch, 1984) is not reported in this study. Two of the gravid females were red-morph: Of the five offspring from one of those females, one was also red-morph while three were green-morph, and the fifth neonate exhibited an alternating banding pattern of red-morph and green-morph coloration. The other red-morph female gave birth to 15 offspring: nine were red-morph, four were green-morph and two had the mixed banding pattern. The six remaining gravid females were of the green-morph, and gave birth to all green-morph offspring.

Eighteen (43%) of the captured snakes had one or a combination of three types of injuries: scars on the body or tail, cysts on the body, or tail loss. Of those snakes with injuries, three (14.3%) had scars on the body, one (4.8%) had scars on both the body and the tail, six (28.6%) had some amount of tail loss, and 13 (61.9%) had some combination of body and/or tail scars and tail loss. Cysts were present on three (7%) of the captured snakes, but these injuries were assumed not to have resulted from encounters with predators.

Table 1 lists the morphometric characteristics measured from adult mangrove salt marsh snakes collected from Placido Bayou, and the neonates obtained from the eight gravid females. Among adult snakes, there were no differences in these characteristics between green- and red-morphs (P > 0.05; Table 2). Spearman's rank correlation indicated a positive relationship (P < 0.01; $\mathbf{r}_s = 0.871$) between SVL and GI for all snakes measured (Fig. 1). Though both were significant (P < 0.01), the correlation between SVL and GI was more variable among only neonate snakes ($\mathbf{r}_s = 0.541$), compared to adult snakes ($\mathbf{r}_s = 0.898$).

There were no differences between the morphometric characteristics of green-morph and red-morph snakes (P > 0.05), though lack of statistical difference is not likely attributable to the small red-morphs sample size. Green-morph snakes appeared slightly longer and heavier than red-morph snakes, but mean GI values for both color morphs differed by only 0.6. Little evidence is available to suggest why red-morph snakes are rare in natural populations, and why a conspicuous color pattern persists in this subspecies. Red-morph neonates were obtained from only redmorph females in this study however, indicating that there is some genetic component to coloration in this subspecies. One hypothesis is that mortality due to predation may be much greater for red-morph than for green-morph individuals. Using recent wounds as an indicator of incidence of predation, Mushinsky and Miller (1993) suggest that sub-adult water snake encounters with predators (such as racoons and wading birds) are frequent events, rarely survived by the snake. The incidence of injury to mangrove salt marsh snakes reported here (43% of individuals caught at the study site, though wounds were not necessarily recent) indicates that predation is also widespread in this population. Being more conspicuous than greenmorph individuals, red-morph snakes may be more susceptible to predation, and therefore rarer in the population.

Gape index in Nerodia clarkii compressicauda is a function of body size, suggesting that snake size restricts the size of ingestible prey. This restriction is especially critical for neonate individuals, which must ingest prey at a faster relative rate than adults in order to increase in size as well as maintain daily metabolic demands. Furthermore, as smaller snakes are limited in the size of prey which they can ingest, they have a narrower prey base available, compared to adult snakes. In other words, adult snakes can ingest both small and large prey, while small snakes must forage for only small prey. Previous studies (Miller, 1985; Miller and Mushinsky, 1990) have demonstrated that small mangrove salt marsh snakes ingest relatively larger prey than large snakes. Small snakes probably experience greater selective pressure to perform well as predators than adult snakes, because their opportunities for encountering prey which they are capable of ingesting are less frequent.

Head size appears to be more variable among neonate mangrove salt marsh snakes than in adults, accounting for the difference in the correlation coefficients for these variables measured for the two groups of snakes. Shine and Crews (1988) report that males have smaller heads than females among neonate Thamnophis. The same relationship may be valid for newborn mangrove salt marsh snakes; however, validity of this hypothesis awaits measurements of neonates whose sex is determined. If predation on young mangrove salt marsh snakes approaches the levels reported in previous studies (Mushinsky and Miller, 1993), there may be selective pressure for increased head size in neonate females, because young snakes with larger heads may not forage as often as those with smaller heads, thus reducing their risk of predation. Further research should examine if snakes born with larger heads experience higher survivorship rates when compared to smaller-head neonates, because the former are capable of ingesting a wider size range of prey.

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LITERATURE CITED

- ASHTON, R. E., JR., AND P. S. ASHTON. 1984. Handbook of Reptiles and Amphibians of Florida: 1. The Snakes. Windward Publishing, Inc., Miami, Florida.
- CONANT, R., AND J. T. COLLINS. 1991. A Field Guide to Reptiles and Amphibians: Eastern and Central North America, 3rd ed. Houghton Mifflin Company, Boston, Massachusetts.
- DUNSON, W. A. 1979. Occurrence of partially striped forms of the mangrove snake Nerodia fasciata compressicauda Kennicott, and comments on the status of N. f. tæniata Cope. Florida Sci. 42:102-112.
- HEBRARD, J. J. 1981. A large collection of brackish water snakes from the central Atlantic coast of Florida. Copeia 1981:886-889.
- LAWSON, R., A. J. MEIER, P. G. FRANK, AND P. E. MOLER. 1991. Allozyme variation and systematics of the Nerodia fasciata-Nerodia clarkii complex of water snakes (Serpentes: Colubridæ). Copeia 1991:638-659.
- MILLER, D. E. 1985. Prey selection during ontogeny of the mangrove water snake, Nerodia fasciata compressicauda. M.S. Thesis, Univ. of South Florida, Tampa.
- , AND H. R. MUSHINSKY. 1990. Foraging ecology and prey size in the mangrove water snake Nerodia fasciata compressicauda. Copeia 1990:1099– 1106.
- MUSHINSKY, H. R. 1987. Foraging ecology. *In* R. A. Seigel, J. T. Collins, and S. S. Novak (eds.), Snakes: Ecology and Evolutionary Biology, pp. 302–334. Macmillan Publ. Co., New York.
 - ——, AND D. E. MILLER. 1993. Predation on water snakes: ontogenetic and interspecific considerations. Copeia 1993:660-665.
- NEILL, W. T. 1965. Notes on aquatic snakes, *Natrix* and *Tretanorhinus* in Cuba. Herpetologica 21:62– 63, 66.

- OSGOOD, D. W. 1970. Thermoregulation in water snakes studied by telemetry. Copeia 1970:568-571.
- POUGH, F. H., AND J. D. GROVES. 1983. Specializations of the body form and food habits of snakes. Amer. Zool. 23:443–454.
- SEIGEL, R. A., AND H. S. FITCH. 1984. Ecological patterns of relative clutch mass in snakes. Oecolocia (Berlin). 61:293-301.
- SHINE, R., AND D. CREWS. 1988. Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. Evolution 42:1105-1110.
- SNEDAKER, S. C. 1989. Overview of ecology of mangroves and information needs for Florida Bay. Bull. Mar. Sci. 44:341–347.
- ZUG, D. A., AND W. A. DUNSON. 1979. Salinity preference in fresh water and estuarine snakes (Nerodia sipedon and N. fasciata). Florida Sci. 42:1-8.

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The Atypical Tadpole of the Dendrobatid Frog, Colostethus chalcopis, from Martinique, French Antilles

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The well-known herpetofauna of Martinique, French Antilles, includes only three anurans: Bufo marinus, Eleutherodactylus johnstonei, and E. martinicensis (Schwartz and Henderson, 1991). Several searches by the senior author during 1990–1992 resulted in the discovery of the dendrobatid Colostethus chalcopis (Kaiser et al., 1994). In the summer of 1992, six tadpoles were reared from a terrestrial egg mass collected near calling males of C. chalcopis. Based on number of eggs, egg pigmentation, deposition site, and developmental mode, these eggs could not have been laid by B. marinus (many small, darkly pigmented eggs in strings in lentic water which develop into exotrophic tadpoles) or by Eleutherodactylus spp. (few large non-pigmented, terrestrial eggs which develop directly). Based on tadpole morphology, general breeding biology, presence of adult C. chalcopis, and assuming the absence of any unknown taxa, we assign these eggs to C. chalcopis, even though the death of the larvae prevented examination of post-metamorphic material. These free-living, nidicolous larvae (fide Altig and Johnston, 1989) differ from all known tadpoles of the genus Colostethus as presently diagnosed (e.g., Lynch, 1982; Frost, 1985; Myers et al., 1991; Kaiser et al., 1994).

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