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### Feeding Envenomation by *Arrhyton exiguum* (Serpentes: Colubridae)

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During ophidian evolution, two major specializations for immobilizing prey have arisen, constriction and envenomation. Both methods presumably reduce the risk of the prey escaping or injuring the snake while struggling (Gans, 1961; Shine and Schwaner, 1985). Venom may also facilitate digestion (Thomas and Pough, 1979; Rodríguez-Robles and Thomas, 1992), and a few other functions have been suggested (Kardong, 1982). Both digestion and prey immobilization may be enhanced, although in species of *Thamnophis* that have toxic oral secretions (Jansen and Foehring, 1983) prey are not held until immobilized (Gregory et al., 1980). Kardong (1982) has argued cogently that an oral secretion may be toxic but should not be considered a venom, unless it is used to kill prey. Toward understanding the evolution of oral secretions, it is of interest to know what combinations of effects and functions exist among different species of colubrids.

*Arrhyton exiguum* Cope is a small, Puerto Rican bank colubrid; it has Duvernoy's glands and an enlarged, ungrooved, blade-like tooth at the rear of each maxilla (opisthomegadont dentition of Anthony fide Edmund, 1968), similar to the larger *Alsophis portoricensis* that also inhabits the Puerto Rico region. The maxillae of both species have two postdiastemal sockets, but modally only one fang is emplaced. Thomas and Prieto-Hernández (1985) and Rodríguez-Robles (1992) reported on the effect of venom on the prey of *Alsophis portoricensis*. Thomas and Prieto-Hernández (1985) observed feeding of *A. portoricensis* and autopsied prey that was envenomated but not ingested. They concluded that *Alsophis portoricensis* seizes and holds large prey (*Anolis cristatellus* and *Ameiva exsul*) in a stationary bite punctuated by hard "embedding" bites, but does not begin swallowing until the prey is dead or immobilized. The venom is hemorrhagic and lizards die after respiratory distress, showing gaping and labored, spasmodic breathing that appears to result from asphyxia due to bleeding into the lungs. Time to apparent death is on the order of 15-20 min (900-1200 sec), sometimes longer in larger prey.

Because of the similarity in dentition, we expected that *Arrhyton exiguum* would have a mode of feeding and venom use similar to that of *Alsophis portoricensis*. Although *A. exiguum* has been reported to feed on a variety of small or easily-subdued prey, such as *Eleutherodactylus* eggs and young (47.4%) and *Sphaerodactylus* (10.5%), *Anolis* comprise a substantial amount of its diet (42.1%; Schwartz and Henderson, 1991). In the *Alsophis* study, Thomas and Prieto-Hernández (1985) challenged snakes with relatively large and dangerous prey. We followed the same procedure here and report for the first time feeding sequences that demonstrate envenomation of prey by *Arrhyton exiguum*.

TABLE 1. Size and evidence of envenomation exhibited by *Anolis* during feeding episodes. Signs: Sw, swallowing; G, gaping; Sp, spasmodic breathing movements; B, blood in mouth. T1, time (sec) after seizure of first sign of envenomation; T2, time (sec) of apparent death (time of flaccid immobility beyond which no further movement occurred).

	Size and envenomation signs			
	SVL (mm)	Signs	T1	T2
<i>A. stratulus</i>	50	Sw, Sp, G, B	743	1528
<i>A. pulchellus</i>	50	Sw, Sp, G	1120	1340
<i>A. cristatellus</i>	45	Sw, Sp, G	—	1226
<i>A. cristatellus</i>	45	Sw, Sp, G	—	1320
<i>A. cristatellus</i>	ca. 40	Sw, G	1320	2760
<i>A. cristatellus</i>	43	Sw, Sp, G, B	840	1927
<i>A. cristatellus</i>	40	Sw, Sp, G, B	472	1800

We observed seven feeding episodes by two adult snakes, summarized in Table 1. The episodes are presented in order of occurrence, the first five feedings by snake A, ca. 280 mm snout-vent length (SVL), and the last two by snake B, 268 mm SVL. In all feedings, after the snake held the lizard for a time, we observed a similar sequence: swallowing, gaping, and spasmodic breathing movements of the thorax; these signs were repeated at intervals until immobility.

Eating anoles of the size reported here would be difficult or impossible for *A. exiguum* if the snakes did not have means of immobilizing the prey, because the anoles defended themselves vigorously. In four feedings the anoles bit the snake on the side of the head after being seized. In the other two feedings the snake grasped the anole by the head or neck, so a biting defense was impossible. When first seized during the first feeding, the anole immediately seized snake A by the snout, severely deforming it. The snake could not get a grip allowing use of the maxillary fangs until, after 120 sec of impasse, it wrenched away, damaging some scales, and seized the lizard anew. In all feedings the lizards made pronounced swallowing movements before or at the time they gaped and breathed spasmodically; immobilization (apparent death) ensued quickly. Swallowing was the first sign, apparently occurring when blood begins to exit the glottis from bleeding in the lungs. Swallowing, gaping, and spasmodic breathing occurred repeatedly until apparent death. Autopsy of the anole from feeding 3 showed bloody froth in the lungs, trachea, and the back of the throat, and blood in the stomach (presumably swallowed since there was none in other parts of the digestive tract). The same hemorrhagic effects were observed during feeding by *Alsophis portoricensis* by Thomas and Prieto-Hernández (1985).

In all feedings, while maintaining a static hold on the lizard, the snake periodically bit down forcefully. These "embedding" bites are evidently efforts to inject more venom (Jansen and Foehring, 1983), but they might allow the snake to assess the responsiveness of the lizard, thereby providing cues for the initiation of swallowing. Thomas and Prieto-Hernández (1985) and Rodríguez-Robles (1992) also reported

"embedding" bites in *Alsophis portoricensis*. In all feedings, once the lizard was immobile the snake lifted it off the ground and carried it around the cage before beginning to swallow, a behavior also exhibited frequently by *Alsophis portoricensis* (pers. obs., and J. A. Rodríguez-Robles, pers. comm.). We conclude that immobilization of prey is one function of venom in *Arrhyton exiguum*. Presumably, it also helps in accelerating the digestion rate, as it does in *A. portoricensis* (Rodríguez-Robles and Thomas, 1992).

Kardong (1982:110) has argued that most colubrids with toxic oral secretions, such as *Alsophis portoricensis* (by implication, since he cited Heatwole and Banuchi, 1966) "do not use their oral secretions to rapidly kill prey as do truly venomous snakes possessing fangs"; therefore their Duvernoy's gland secretions should not be categorized as venoms. However, observations on *Alsophis portoricensis* (Thomas and Prieto-Hernández, 1985; Rodríguez-Robles and Leal, unpubl. obs.) and *Arrhyton exiguum* (Leal, unpubl. obs.) are relevant. Both species swallow inoffensive prey directly but employ embedding bites on difficult prey and wait until the prey is immobile (apparently dead) before swallowing, suggesting that the oral secretion is used by the snake as a venom to subdue the prey. The critical feature is not the time that the secretion takes to kill or immobilize the prey, but its use by the snake to facilitate the subduing process. This implies that toxicity is selectively favored.

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### Body Size and Age Assessment among Advertising Male Chorus Frogs

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Calling males in breeding choruses of *Pseudacris maculata* and *P. triseriata* are often flanked by one or two smaller, non-calling males (J. Platz, pers. obs.). It is often assumed that larger individuals are older because amphibians have indeterminate growth. If the body size-age correlation is true, then the inference from our original observations above is that satellite males should be younger than calling males. Skeletochronology as a technique for determining age has in the last decade or so been successfully applied to a limited number of anuran taxa: Hemelaar and Van Gelder (1980) and more recently Höglund and Säterberg (1989) for *Bufo bufo*; Lykens and Forester (1987) for *P. crucifer*; Leclair and Castanet (1987) for *Rana pipiens*; and Gibbons and McCarthy (1984) for *R. temporaria*. The present study was undertaken to determine if skeletochronology techniques could be applied to male chorus frogs, and if so, to determine whether body size is correlated with age well enough to allow aging of males based on snout-vent length (SVL), thus avoiding the need to kill individuals. This work is part of a larger ongoing project involving a similar assessment of the body size-age relationship between calling males and attending satellites.

All specimens were calling males collected in April and May of 1980. Locales included two species (populations 1-4 represent the Boreal chorus frog, *Pseudacris maculata*, and 5-6 the Western chorus frog, *P. triseriata*) as follows: South Dakota, (1) Marsh Lake, Hamlin County, (2) Springfield, Bon Homme Co.; Nebraska, (3) Dodge Park, Omaha, Douglas Co., (4) Cozad, Dawson, Co., (5) Ogallala, Keith Co.; Kansas, (6) Arkansas City, Cowley Co. Individuals were preserved in 10% formalin and transferred to 40% iso-

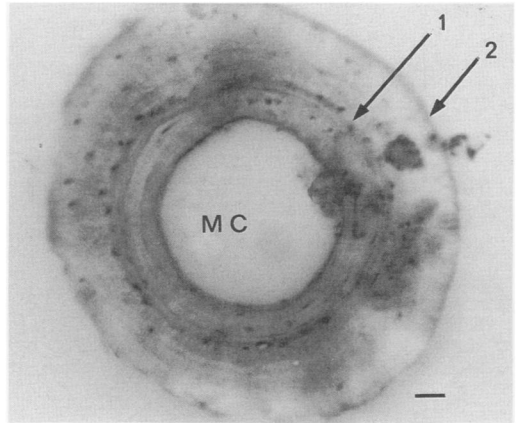


FIG. 1. Representative stained cross section of the femur of a two year old male *P. triseriata* (no. 8650). Arrows indicate lines of arrested growth; MC = medullary cavity. Note that RL 1 is a double line. Scale bar represents 20  $\mu$ m.

propyl alcohol and stored until sectioned. SVLs were obtained to the nearest 0.01 mm with dial calipers. Bone sectioning and staining procedures followed Hemelaar and Van Gelder (1980) with the exception of their use of 70% ethanol for temporary storage of bone samples. Femurs were removed from the frogs and decalcified in 5% nitric acid for 3 h and left in water overnight. The diaphysis was cut from each femur and sectioned on a Spencer model 880 freeze microtome. A series of mid-diaphyseal sections 15 to 20 microns thick were mounted on glass slides treated with an albumen-glycerin preparation, containing equal proportions of egg white and glycerin with thymol added. All preparations were then stained in Cabisco's Delafield hematoxylin for 15 min and washed in tap water for an equivalent period. Stained slides were examined and photographed at 125 $\times$  under a compound light microscope.

Stained sections (Fig. 1) showed a series of narrow, concentric, hematoxylinophilic rings separated by wider zones of paler background material. The narrower, dark-staining rings are interpreted to be the result of climatically-imposed winter periods of arrested growth or "resting lines" (RL). Intervening, broader, pale zones are interpreted to represent active bone deposition during one growing season. Because this is an annual phenomenon, a wide zone and subsequent RL are interpreted to represent one year. On occasion (Fig. 1) a pair of very closely spaced dark concentric rings occurred. According to Klevezal and Kleinenberg (1967), double lines are caused by interruptions in hibernation and therefore we regarded these as equivalent to one season. Because all frogs were collected in April and May, the outer bone perimeter was counted as an RL for bone growth, which is consistent with observations by Smirina (1972) indicating that renewed bone growth starts only after the reproductive season is over. Limited attempts to section the penultimate phalanx of the second digit of the hind foot as an alternative method failed to produce good sections using the present freeze technique.