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Reviewed work(s):
Published by: Society for the Study of Amphibians and Reptiles
Stable URL: http://www.jstor.org/stable/1564695
Accessed: 24/05/2012 13:06
Notes on the Feeding Behavior and Caudal Luring by Juvenile *Alsophis portoricensis* (Serpentes: Colubridae)

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Caudal luring, the waving or wriggling of a conspicuously colored tail by an otherwise cryptically colored snake in the presence of prey (Heatwole and Davison, 1976), has been reported for species of viperid, elapid, and boid snakes (Neill, 1960; Heatwole and Davison, 1976; Murphy et al., 1978) and recently for the colubrid snakes *Tropidodryas striaticeps* (Sazima and Puorto, 1993) and *Alsophis dorsalis* (Greene, pers. comm.). This behavior has been documented most frequently for juvenile crotaline vipers (Neill, 1960). Caudal luring may function by luring a potential prey to striking distance (Neill, 1960; Greene and Campbell, 1972; Heatwole and Davison, 1976) and/or distracting the prey’s attention, thereby facilitating close approach of the predator’s head to within striking distance (Greene and Campbell, 1972; Murray et al., 1991; Sazima and Puorto, 1993).

With the exception of *Acanthophis antarcticus laevis* (Carpenter et al., 1978), caudal luring has been documented exclusively in snakes that bear a conspicuously colored tail. Conspicuously colored tails and luring behavior are exhibited mostly by juveniles, and in most cases both are lost before adulthood (Heatwole and Davison, 1976). A lack of ontogenetic diet change was associated with retention of caudal luring by adult *Bothrops bilineatus* (Greene and Campbell, 1972), *Cerastes vipera* (Heatwole and Davison, 1976), *Acanthophis a. antarcticus* and *Acanthophis a. laevis* (Carpenter et al., 1978), and *Sistrurus miliarius barbouri* (Jackson and Martin, 1980).

*A. portoricensis* is the larger of two colubrids that inhabit the Puerto Rican Bank. It is largely a ground-dwelling, diurnal snake that uses mainly visual cues to locate prey. Here we report the use of caudal luring by juveniles of this species. This is the third known case of caudal luring for a colubrid and the second report for *Alsophis*.

We observed 12 feeding episodes by four juvenile *Alsophis portoricensis* within two months after they hatched in the laboratory (body mass [BM] 1.5–2.1 g). Each individual was presented with three different prey species: two species of lizards, *Anolis cristatellus* (Polychriidae) and *Sphaerodactylus macrolepis* (Gekkonidae), and the frog *Leptodactylus albilabris* (Leptodactylidae). Snakes were weighed (BM ± 0.1 g) immediately after each trial, and prey were measured (snout-vent length [SVL] to nearest mm) and weighed (BM ± 0.1 g) prior to the feeding trials. Feeding trials were conducted in the snake cage (40 cm long × 30 cm high × 20 cm wide) with a soil substrate. Prey was introduced by hand into the snake cage. Both the snakes and the lizards were maintained at a temperature of 25–27 C. Using a stop watch and an audio tape recorder, we recorded all behaviors exhibited by the snakes and the prey during each feeding episode.

Caudal luring was exhibited on three of the 12 feeding trials by two of the four individuals. Of the two individuals that lured, one did so when presented with *Anolis cristatellus* and *Sphaerodactylus macrolepis*, and the other when presented with *S. macrolepis*. None of the snakes lured when presented with *Leptodactylus albilabris*. The first episode of caudal luring was recorded on 31 August 1992. *Alsophis* (BM 2.1 g) began to exhibit caudal luring 300 sec after the *A. cristatellus* (SVL 20 mm, BM 0.3 g) was introduced into the cage. The snake continued twitching its tail in a waving fashion while maintaining the rest of its body immobile for the next 150 sec. During this period, the prey oriented toward the twitching tail of the snake and fixated on it; at 460 sec the lizard moved toward the snake, and the snake attacked it.

On 4 September 1992, one *Sphaerodactylus macrolepis* was offered to each snake. An *Alsophis* (BM 2.1 g) began to flick its tongue 40 sec after the prey (SVL 25 mm, BM 0.4 g) was introduced into the cage. The snake remained immobile for the next 300 sec while the lizard was moving around the cage. 600 sec after the snake began to twitch its tail while remaining immobile, and the prey responded by orienting toward the snake’s twitching tail, and began to move toward it. The lizard kept moving toward the twitching tail and was grabbed by the snake at 790 sec. The snake finished swallowing it at 990 sec. The other *Alsophis* (BM 1.7 g) began to flick its tongue 90 sec after the *S. macrolepis* (SVL 28 mm, BM 0.6 g) was introduced into the cage, while the prey remained immobile. At 900 sec after introduction, the snake began to twitch its tail, which lasted for the next 95 sec. However, the lizard did not react to the twitching tail. At 1200 sec, the snake attacked and grabbed the lizard, and finished swallowing it at 1940 sec. The other two *Alsophis* individuals (BM 1.5 g and 1.8 g) did not exhibit caudal luring to any of the prey. Caudal luring was never exhibited before the prey was introduced into the cage or after the snake finished eating it.

Although two of the four juvenile *Alsophis portoricensis* never exhibited caudal luring, they subdue their prey in the same manner as those that did lure. In all feeding episodes, when presented with *Leptodactylus* or *Sphaerodactylus*, the snake seized and swal-
lowed them directly without envenomating them, but when presented with Anolis, the snake subdued the prey with venom before swallowing it. The variation in the use of venom to subdue prey seems to be in response to the lack of strong retaliation presented by Leptodactylus and Sphaerodactylus compared with the strong retaliation employed by Anolis when handled by Alsophis (Leal and Rodriguez-Robles, unpub.). Retaliatory power, along with visual and chemical stimuli, may be used as clues by A. portoricensis to assess prey and to "decide" if it will envenomate or not (Rodriguez-Robles and Leal, 1993). Variation in the use of venom to subdue prey also has been reported for adult A. portoricensis (Rodriguez-Robles and Leal, 1993).

Alsophis portoricensis exhibited caudal luring from a loosely coiled or looped posture in which the tail was in the same direction as the snake’s head. The snakes never exhibited the vertical positioning of the tail that has been reported in Bothrops bilineatus (Greene and Campbell, 1972), Vipera russelli (Henderson, 1970), and Tropidodryas striaticeps (Sazima and Puorto, 1993). Instead, with the body immobile and the tail horizontal, A. portoricensis twitched its tail spasmodically. The tail undulated vertically with the tip sometimes curling into a U-shape, and there were occasional rotations through nearly 360° about the longitudinal axis. This movement is similar to that described for Sistrurus miliarius barbouri (Jackson and Martin, 1980) and Bothrops jararacussu (Sazima, 1991).

Although caudal luring has been associated with a combination of a conspicuously colored tail and its movements (Neill, 1960; Heatwole and Davison, 1976), the observation that Alsophis portoricensis is able to attract prey by the movement of an inconspiciously colored tail indicates that the movement of the tail itself is sufficient as a lure. The use of an inconspicuously colored tail as a lure also has been suggested for Acanthophis antarcticus laevis (Carpenter et al., 1978). In the inferred S. miliaris (Pough, 1988), because the prey was not in the cage of the snake and there was no observation of prey being attracted by the snake’s tail.

Many snakes twitch or vibrate their tails in response to a threat (Greene, 1973), but we never observed juvenile Alsophis portoricensis moving their tail when approached or handled by a person. Instead the snakes spread their neck and occasionally emitted a short hiss, a behavior which is commonly exhibited by adults. Nonetheless, adult A. portoricensis may rarely exhibit erratic movement of the tail when handled (J. A. Rodriguez-Robles, pers. comm.).

Although caudal luring is an ambush hunting technique compatible with a sit-and-wait foraging strategy, it is possible that juvenile Alsophis portoricensis also forage actively. There seem to be no literature reports of foraging by A. portoricensis, although based on its size, shape, and diurnal activity, the species is assumed to be an active forager (Henderson and Sajdak, 1986; Henderson and Crother, 1989). Sazima and Puorto (1993) also suggested a combination of sit-and-wait and active foraging for the colubrid Tropidodryas striaticeps.

Heatwole and Davison (1976) proposed that ontogenetic changes in diet may account for the lack of caudal luring in adult colubrine snakes. We suggest that different predation pressures on juvenile and adult Alsophis portoricensis may account for the presence of caudal luring in juveniles. The small size of hatchlings probably exposes them to greater predation pressure than adults, and the sit-and-wait foraging strategy may reduce predation risk (Huey and Pianka, 1981). Caudal luring is a way by which these small, diurnal, surface-feeding juveniles may lessen predation. After hundreds of hours observing A. portoricensis feeding in captivity by ourselves and J. Rodriguez-Robles (pers. comm.), we have not observed caudal luring by adults. We conclude that caudal luring is a juvenile behavior in A. portoricensis.

That two juvenile Alsophis portoricensis did not use caudal luring, although they did feed, indicates that variation exists in hunting behavior. Variability in luring tendencies also has been observed in juvenile Agkistrodon contortrix (Fitch, 1960), Bothrops jararaca (Sazima, 1991), and Tropidodryas striaticeps (Sazima and Puorto, 1993). Individual variation in use of caudal luring may be a response to differences in hunger level at the time that the prey was presented (Greene and Campbell, 1972; Murray et al., 1991; Chiszar et al., 1990).

Acknowledgments.—We thank J. A. Rodriguez-Robles, and I. Sazima for helpfully scrutinizing the manuscript. The Department of Natural Resources of Puerto Rico provided permits for the collection of all specimens. This research was partially supported by a grant from the Fondo Institucional para la Investigación, University of Puerto Rico, to R. Thomas.

Literature Cited


Accepted: 28 October 1993.

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**Analysis of Some Long-standing Controversies Concerning the Pectoral Girdle of *Atelopus* (Bufonidae) Using Ontogenetic Studies**

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In the history of anuran systematics, the genus *Atelopus* has been the protagonist in many controversies concerning pectoral girdle characters. Some long-lasting controversies include: (1) whether the girdle developmental pattern in *Atelopus* differs from those of firmisternal and arciferal taxa (Noble, 1926; Griffiths, 1963); (2) whether the posterior plate-like structure in *Atelopus* corresponds to epicoracoidal horns or the sternum (Griffiths, 1963; McDiarmid, 1971; Tyson, 1987); and (3) whether the sternum (if present) is fused to, or discrete from, the rest of the girdle (McDiarmid, 1971; Tyson, 1987).

These controversies are still unresolved. The power of developmental studies for analyzing these controversies has not been yet fully recognized. For example, even though many arguments revolve around developmental issues, no developmental study of the pectoral girdle of *Atelopus* has been made. Developmental studies can also provide detailed information about morphological structure by, for example, showing that a structure is the result of the fusion of two or more elements.

I investigated the development of the pectoral girdle in *Atelopus* to examine these and other related controversies, and to shed light on some related and persistent misconceptions on this specific topic. My study was based mainly on one species (*Atelopus farci*), but four other species of *Atelopus* were also examined to help resolve these crucial issues.

I studied preserved tadpoles and juveniles of *Atelopus farci* (lot ICN [Instituto de Ciencias Naturales, Universidad Nacional de Colombia] 15853), *Atelopus nicefori*, *Atelopus ebenoides marininki* (lot IND-AN 4477), *Atelopus ignescens* (lots KU 131940, 180275, 180276), and *Atelopus subornatus* (lots ICN 15828, 15820). Table 1 gives stages of development (Gosner, 1960) and the number of individuals examined per stage.

Histological cross sections (10 ×) were prepared using the paraffin method of Weesner (1960). Surgipath infiltration and embedding paraffin were used. Specimens were placed in alcoholic Bouins at least 24 h before infiltration. Froglets were placed in EDTA for 24 h to decalcify and then transferred to Bouins. Sections were stained with Masson’s trichrome (Weesner, 1960).

Only the stages of development relevant to important systematically-related conflicts are described. Results can be divided into three primary observations.

First, from stage 42 to froglet, a slight overlap (due to growth of both halves) can be seen at the coracoid level (Fig. 1B). In many individuals, the epicoracoids are also overlapping; however they do not expand forming blades but rather remain rounded (Fig. 1A). No overlap was observed in the two individuals of *A. nicefori* (stages 42 and 44). In the adult stage of *Atelopus*, the two halves are fused all along the girdle.

Second, from stage 36, the postero medial tips of the coracoids extend posteriorly, forming two short pro-

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**Table 1. Stages and individuals per stage studied in each of five species of Atelopus. Abbreviations:**

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