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FEEDING TECHNIQUE OF JUVENILE *TROPIDODRYAS STRIATICEPS*: PROBABLE CAUDAL LURING IN A COLUBRID SNAKE.—Caudal luring, the wriggling movements of a conspicuous tail tip made by an otherwise cryptically colored snake in the presence of prey, has been reported for several species of Boidae, Viperidae, and Elapidae (reviews in Neill, 1960; Pough, 1988). We are not aware of any record of this behavior among Colubridae, and here we report and comment on caudal luring, feeding behavior, and diet of *Tropidodryas striaticeps*, a neotropical colubrid snake.

Tropidodryas striaticeps and *T. serra*, the two recognized species, are semiarboreal, apparently diurnal snakes from the Atlantic Forest of southeastern Brazil, preying on lizards, birds, and rodents (Müller, 1970; Thomas and Dixon, 1977). Their dorsal color pattern varies from greenish gray to yellowish brown, with darker oblong and angular blotches resulting in a cryptic pattern (Fig. 1). The tail of juveniles is whitish to yellowish and has flared scales (Thomas and Dixon, 1977; see also Fig. 1). Based on the appearance of the tail of juveniles, caudal luring behavior was suspected for *Tropidodryas* (Sazima, 1992).

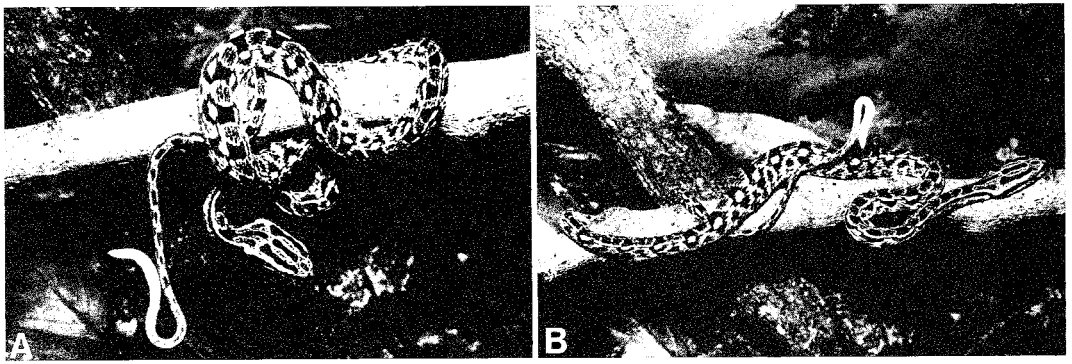

Fig. 1. Caudal luring in juvenile *Tropidodryas striaticeps*. (A) Female performing caudal luring in presence of frog prey (not visible on picture); the swollen appearance of the whitish tail is due to flared scales (246 mm SVL, specimen ZUEC 1005). (B) Same individual performing caudal luring in absence of prey, shortly after eating a treefrog (perceived as a bulge at snake's midbody) on this branch.

Materials and methods.—Four juvenile females *T. striaticeps* (225–283 mm SVL; 3.5–5.5 g) were caught in the Atlantic Forest at the localities of Itaquaquecetuba, Santana de Parnaíba, and São Luís de Paraitinga, State of São Paulo, southeastern Brazil. One juvenile male (241 mm SVL, 3.8 g) came from the outskirts of the city of São Paulo, from an area of degraded Atlantic Forest. The snakes were maintained in 70 × 30 × 30 cm glass terraria with branches, leaf litter, and live plants from sites similar to those where the animals were caught. After acclimation (5–18 days), the snakes spent most of the time (60–70%) coiled on branches or on the ground and were then tested for their ability to lure potential prey.

Small lizards (20–50 mm SVL), the gekkonids *Gymnodactylus darwini* and *Hemidactylus mabouia*, and frogs (20–35 mm SVL), the hylids *Hyla berthalutzae* and *H. minuta*, and the leptodactylid *Adenomera marmorata*, all sympatric with *T. striaticeps*, were presented and/or offered to the snakes. Prey was placed in a glass vial or a transparent plastic bag directly into the terrarium, 10–30 cm from the coiled snake. In some trials, prey was released behind an opaque glass plate making a temporary compartment within the snake's terrarium; after prey's acclimation the plate was removed. Part of our procedure was similar to that of Chiszar et al. (1990), especially their experiments 1 and 6. However, because we had only one snake available at a time and replicates were not always feasible, we adopted a predominantly qualitative, descriptive approach emphasizing the diverse aspects of the caudal luring and its probable relations to *T. striaticeps* feeding habits.

Prey items were examined from gut contents of four juveniles (210–330 mm SVL) and eight adult *T. striaticeps* (600–900 mm SVL) housed at the Instituto Butantan, São Paulo (IB). Vouchers are preserved at the Universidade Estadual de Campinas (ZUEC 1005) and the Instituto Butantan (IB 40389). We also examined gut contents from two juveniles (370 and 410 mm SVL) and five adults (605–1055 mm) of *T. serra*.

Results and discussion.—Caudal luring was displayed by juvenile *T. striaticeps* upon notice of potential prey moving around (one snake performed caudal luring movements in absence of visible prey, shortly after successful luring episodes). The snakes usually lured from a coiled posture on a branch (Fig. 1A), but luring from partly coiled or "sprawled" postures occurred as well (Fig. 1B). Caudal luring episodes were observed during midmorning (0900–1030 h, n = 4) and late afternoon (1600–1700 h, n = 4) but mostly at twilight (1830–1930 h, n = 8) and even at night (~2200 h, n = 3) under subdued room lights. Luring at twilight or "clear" nights may indicate occasional night activity (see nocturnal gekkonid and frog prey); alternatively, night luring may be an artifact due to captivity (see Chiszar et al., 1990). Snakes also stalked or pursued prey without luring (n = 6), and one female (283 mm SVL and 5.5 g) was never observed to lure; however, it caught no lizards and was successful with less active frog prey only (see Sazima, 1991 for similar variable hunting behavior in juveniles of the viperid, *Bothrops jararaca*).

One well-documented and timed luring sequence (Fig. 2) was chosen to illustrate this behavior in *T. striaticeps* (see also Figs. 1, 3). The sequence began with the snake stealthily raising its tail to an almost erect posture, its tip per-

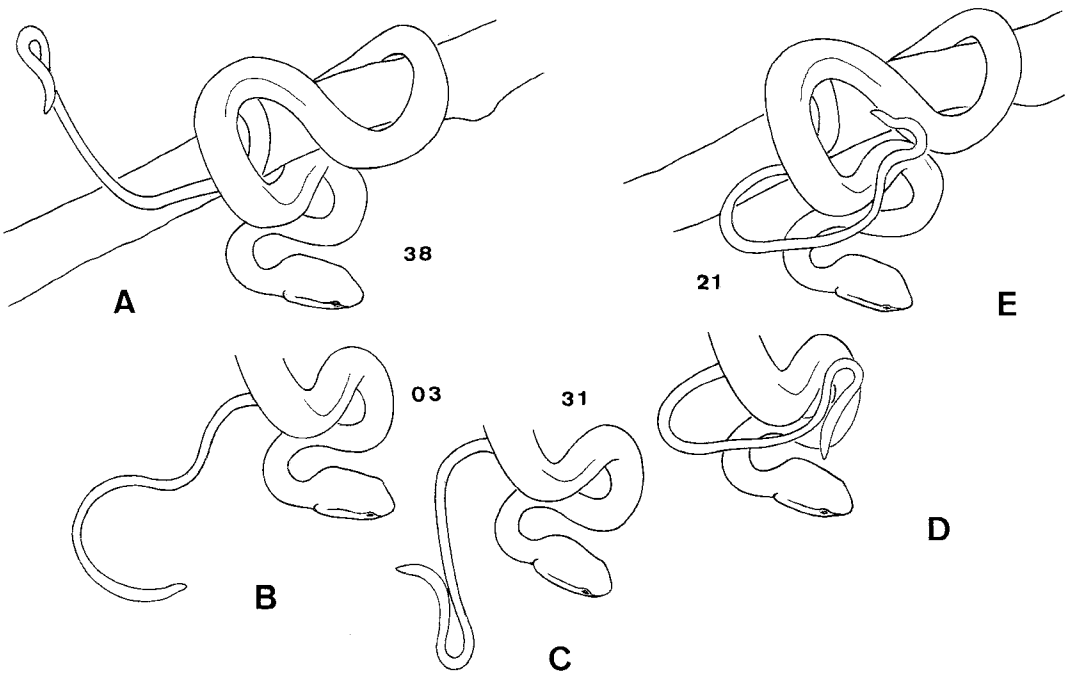

Fig. 2. Caudal luring in juvenile *Tropidodryas striaticeps*. (A–E) Postures of tail and amplitude of caudal movements during one luring sequence; after posture D or E, wriggling tail returns to posture A and new sequence begins. Numbers are seconds spent at each of figured tail positions while tail tip moved continuously (last two positions grouped as one due to minor differences in tail tip postures). Same specimen as in Fig. 1; drawn from timed seriate photographs.

forming horizontal or vertical undulations that progressed along the tail tip, concomitant to partial rotations around the longer axis of tail (Figs. 2–3). After a series of undulations to one direction, the tail tip turned to the opposite side and continued waving (Figs. 2E–D, 3). Then the snake slowly lowered its tail to a hanging posture (Fig. 2C), the tail tip waving to one then the other side. When the tail was gradually raised again by the snake, the tail tip now waved close to the snake's head (Fig. 2D–E). After a while, the snake moved the tail back to the initial erect posture (Fig. 2A), continuing to undulate the tail tip. From this erect tail posture, a new sequence along a swinging path (Fig. 2) started. The described sequence lasted 144 sec, and whole luring episodes (several sequences) lasted up to 20–30 min.

Caudal luring in *T. striaticeps* involves simultaneous postures and movements performed by the proximal and middle parts (erect and hanging postures, swinging path), and the terminal portion of the tail (undulations and rotations). The whitish, swollen appearance and the wriggling movements of the tail bear a close similarity to an insect larva. Sometimes while luring, the snake moved its head toward prey by stealthily stretching the neck, maintaining its position on a branch (Fig. 3). In such instances, besides acting as a lure, the moving tail could perhaps additionally distract the prey's attention from the approaching snake (see Greene and Campbell, 1972 for additional comments on this possibility).

Three acclimated lizards were seen to approach and try to grab the tail tip of a luring *T. striaticeps*, and two of them (one *Gymnodactylus* and one *Hemidactylus*) were seized by the snake. The luring role of caudal movements was particularly illustrated by one of these instances: the smallest *Tropidodryas* tried to catch a *Hemidactylus* with no success for four consecutive days, using visually guided pursuits interspersed with short and sporadic episodes of caudal movements while coiled. The lizard even moved toward the snake during luring sequences but stopped as the snake's tail movements ceased and easily evaded pursuit (wariness is characteristic of this lizard). On the fifth day, the snake engaged in several successive luring episodes interspersed with periods of immobility for about three hours. The lizard slowly approached the snake but always stopped when the snake ended a luring sequence. After about

50 min of this "approach-stop," the lizard was close enough to make a short lunge toward the wriggling tail, being immediately seized and constricted by the snake.

Shortly after swallowing a lizard prey, one snake raised its tail and performed a luring episode briefer (2–3 min) than those displayed in the presence of visible prey. This snake was seen a few days later on the same branch, again performing a brief luring episode after eating a treefrog at this site (Fig. 1B). Presumably this brief luring at a profitable hunting place probes for the presence of additional prey (see Chiszar et al., 1990, for a similar suggestion for the elapid *Acanthophis antarcticus*).

Frogs and small lizards (up to 30 mm SVL) were seized and swallowed directly by juvenile *T. striaticeps*, whereas larger lizards were constricted. Coiling around prey was anterior, dorsal, and either dextral or sinistral (cf. Greene and Burghardt, 1978; Heinrich and Klaassen, 1985). Adult snakes constrict rodents, a prey probably also subdued with use of venom (pers. obs.). Constriction and envenomation of rodents is known for at least three species of *Philodryas* (Vitt, 1980; pers. obs.), a genus related to *Tropidodryas* (Thomas and Dixon, 1977).

Three juvenile *T. striaticeps* contained lizards (two *H. mabouia* and one unidentified gymnophthalmid), and one had remains of a hylid frog. Four adults contained akodontine rats, three contained rodent hair, and one had passerine bird feathers in its gut. Additionally, we found lizards in two juveniles and rodents in four adults of *T. serra* (one young adult contained lizard remains). These findings indicate an ontogenetic dietary change in *Tropidodryas* comparable to those reported for species of *Bothrops* and some other viperids (Mushinsky, 1987; Sazima, 1992). Tail tip of adult *Tropidodryas* is suffused with darker, cryptic colors, and flared scales are retained to a certain extent by *T. striaticeps* only (Thomas and Dixon, 1977); it seems unlikely that adults lure extensively if at all.

Although caudal luring and type of prey of juvenile *Tropidodryas* are consistent with ambush hunting, these snakes probably also forage actively both as juveniles and adults. In the forest at Ubatuba, São Paulo, on 13 Oct. 1990 from 1250–1340 h, one of us (IS) followed an adult female *T. serra* (850 mm SVL) which moved on the ground and entered several rocky crevices and holes in an apparent foraging pattern. Upon capture, the snake disgorged a freshly killed akodontine rat and another one probably eaten some hours earlier. Although some rats may be attracted to a caudal lure (Sazima, 1991), a better hunting tactic for a diurnal snake may be active searching in potential rodent retreats.

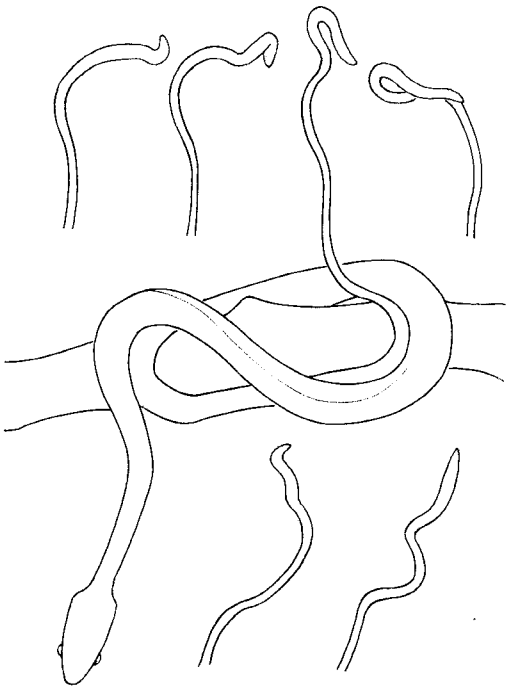

Fig. 3. Movements of tail tip by a juvenile *Tropidodryas striaticeps* while luring. Undulations along tail tip and simultaneous partial rotations along the long axis of tail (upper), and undulations only (lower). Same specimen as in Fig. 1; drawn from seriate photographs.

The African colubrid *Hemirhagerris nototaenia*, an arboreal snake with cryptic color pattern, feeds on lizards and frogs and has a long tail with orange to pink tip (Branch, 1988). Based on these attributes, we suggest that *H. nototaenia* may employ caudal luring to attract prey. H. W. Greene (pers. comm.) noted that another colubrid, *Alsophis dorsalis* from the Galapagos Islands, wriggles its tail to attract lizard prey. We think that the apparent rarity of caudal luring among colubrid snakes is likely related to their foraging mode, because active searching seems the rule among colubrids and elapids, whereas ambush hunting predominates among boids and viperids (Shine, 1980; Mushinsky, 1987). *Acanthophis antarcticus*, the only elapid known to use a caudal lure, is a cryptically colored ambush hunter convergent to viperids (Carpenter et al., 1978; Shine, 1980) as also seems, to a certain extent, to be the case for the colubrid *Tropidodryas* (see below).

Tropidodryas serra and *T. striaticeps* were suggested to mimic the pitviper *Bothrops jararaca* (Sazima, 1992) due to their similarity to this

viper both in external appearance and defensive behavior. However, cryptic color and caudal luring are attributes clearly related to each other (see Pough, 1988 for several examples), and, not by coincidence, both characters are present in *Tropidodryas* and *Bothrops*. The convergence between the two species of *Tropidodryas* and *B. jararaca* extends further to ontogenetic changes in tail coloration and diet (Thomas and Dixon, 1977; Sazima, 1991, 1992; pers. obs.). Thus we now think that the similarities between these two colubrids and a sympatric viperid may better be viewed as resulting from the combination of selective pressures due to both predators and prey (see Gans, 1986 for this view).

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