

Correspondence

Tail-first ingestion of prey by the false coral snake, *Erythrolamprus aesculapii*: Does it know where the tail is?

HENRIQUE B. BRAZ & OTAVIO A. V. MARQUES

Laboratório de Ecologia e Evolução, Instituto Butantan, Avenida Vital Brazil, 1500, CEP 05503-900, São Paulo, Brasil

Corresponding author: HENRIQUE B. BRAZ, e-mail: h.braz@hotmail.com

Manuscript received: 9 June 2014

Accepted: 8 January 2015 by ARNE SCHULZE

Many snakes tend to swallow their prey head first, particularly when the prey is large (LOOP & BAILEY 1972, GREENE 1976, MORI 1991). This behaviour can reduce the resistance offered by the limbs and body covering of the prey (e.g., fur, feathers), and consequently may reduce the overall feeding time (DE QUEIROZ & DE QUEIROZ 1987). Reduction of total prey-handling time may be advantageous because it decreases the period in which snakes are more vulnerable to predators (GREENE 1976, DE QUEIROZ & DE QUEIROZ 1987). Head-first ingestion also might be advantageous to ophiophagous snakes, mainly because it decreases the resistance from posteriorly projecting overlapping ventral scales (see GREENE 1976). Actually, many ophiophagous snakes ingest their prey head first (GREENE 1976, 1997, URDANETA et al. 2004). This is true even for snake species that occasionally predate upon other snakes (PINTO & LEMA 2002, JACKSON et al. 2004). However, unlike most snake-eating species, the ophiophagous coral snakes of the genus *Erythrolamprus* usually swallow their prey tail first (GREENE 1976, 1997, MARQUES & PUERTO 1994, HARTMANN et al. 2009). The occurrence of such behaviour is hypothesized to be a consequence of the way in which *Erythrolamprus* handles its prey (MARQUES & PUERTO 1994). In a study on the predatory behaviour of *Erythrolamprus aesculapii*, MARQUES & PUERTO (1994) noted that individuals repeatedly weakened their bite after seizing prey, allowing small escape movements of the captured prey. As the seized prey snake usually tries to flee forward, *E. aesculapii* individuals slowly reach the prey's caudal region and then start ingesting it, usually while the prey is still alive (MARQUES & PUERTO 1994). This handling behaviour led MARQUES & PUERTO (1994) to suggest that tail-first ingestion in *Erythrolamprus* is a result of a combination of weakening its hold and the for-

ward-force exerted by the prey in a quest to escape. This assumption implies that tail-first ingestion in *Erythrolamprus* has only mechanistic causes, excluding the possibility that it intentionally searches for the prey's tail. However, additional observations made after the study by MARQUES & PUERTO (1994) have shown that during prey-handling, *E. aesculapii* individuals (in addition to weakening the hold) also make "jaw-walking" movements along the prey's body (H. B. BRAZ & O. A. V. MARQUES pers. obs.), suggesting that they intentionally search for the prey's posterior end. If *E. aesculapii* ingests its prey tail first only as a consequence of the prey's escape force, then we could predict that by offering it motionless prey we might find differences in the direction of ingestion. Here, we test this prediction by offering, under laboratory conditions, dead prey (i.e., motionless prey) to *E. aesculapii* and comparing the frequency of head-first versus tail-first ingestions.

Our test subjects were eight adult wild-caught *E. aesculapii* (five females and three males; snout-vent lengths: 565–925 mm) housed individually in plastic cages (SanRemo, Brazil, 975; 564 × 385 × 371 mm for larger individuals, and SanRemo, Brazil, 965; 400 × 270 × 362 mm for smaller ones), each containing a piece of corrugated cardboard as a bottom substrate and a water bowl. The room temperature averaged $24 \pm 2^\circ\text{C}$, and each terrarium was exposed to the natural photoperiod. As prey, we used newly dead diposid snakes belonging to different species as follows: *Oxyrhopus guibei* (n = 11), *Philodryas patagoniensis* (n = 2), *Sibynomorphus mikanii* (n = 4), *Tomodon dorsatus* (n = 8), and *Xenodon newwiedii* (n = 1). Most of these species are part of the natural diet of *E. aesculapii* (GREENE 1976, MARQUES & PUERTO 1994). All snakes (predator and prey) were brought to the Instituto Butantan by ordinary citi-

zens, and had been collected from several localities in the surroundings of São Paulo city, southeastern Brazil (23°11' to 24°16' S, 45°53' to 47°27' W; datum WGS84). Prey items were measured (to the nearest millimetre) and weighed (to the nearest 0.1 g). Ratio of prey total length to predator SVL ranged from 0.22 to 0.65. Twenty-six feeding trials were performed. Prey items were offered during daytime, i.e., during the period in which false coral snakes are active (MARQUES et al. 2004). For each trial, we placed a prey item in the cage at a distance of about 10–20 cm from the resident *E. aesculapii* individual. Prey items were left unanimated, leaving the predator to discover it on its own. The following information was recorded: (i) prey acceptance; (ii) capture position, i.e., the part of the prey's body first seized by the false coral snake (for that, three equally sized regions were predefined; regions I, II, or III, starting from the head); and (iii) direction of ingestion (head-first or tail-first). If the false coral snake did not respond to the presence of a prey item within 15 minutes, the prey item was removed from the cage. We used chi-squared analyses to test for differences in the frequencies of the body region of the captured prey seized first and in the direction of ingestion.

Food items were accepted in 84.6% (n = 22) of the trials. Ignored prey items included *T. dorsatus* (n = 2), *O. guibeii* (n = 1), and *S. mikani* (n = 1). Capture position (Fig. 1A) was not significantly different across trials (36%, 41%, and 23% in regions I, II, and III, respectively; $\chi^2 = 1.18$; df = 2; P = 0.55). After prey capture, *E. aesculapii* individuals moved their jaws along the prey's body until they reached one end of the prey's body (Figs. 1B, C). The frequency of tail-first ingestion (77.3%; n = 17 occurrences) was significantly higher than head-first ingestion ($\chi^2 = 6.55$; df = 1; P = 0.01).

In qualitative terms, the observed feeding behaviour of *E. aesculapii* on dead prey was similar to that previously reported for live prey. All three phases of the predatory behaviour of *E. aesculapii* (seizing, handling, and ingesting) described by MARQUES & PUERTO (1994) were also observed. In addition, the behaviour during each phase was similar to their previous descriptions. For example, as observed with live prey (MARQUES & PUERTO 1994), *E. aesculapii* seized dead prey indistinctly along the prey item's body.

Our results do not support the hypothesis that *Erythrolamprus* ingests its prey tail first only as consequence of prey's escape force. We found that even when handling motionless prey, *E. aesculapii* individuals continued to search for the posterior end of the prey, and ingesting it tail first, as observed for live prey. Behavioural repertoires of snakes are innate but greatly affected by experience (FUCHS & BURGHARDT 1971, ARNOLD 1978, MORI 1993, WATERS & BURGHARDT 2005). In the present study, we used only adult wild-caught *E. aesculapii*, which certainly had repeatedly made experiences with live prey snakes in nature before. The continued tail-first ingestion of dead prey by *E. aesculapii* indicates that this strategy could perhaps have been incorporated in its food acquisition repertoire due to previous experiences with live prey. However, the observation that *E. aesculapii* also executes “jaw-walking” move-

ments along the prey's body and the data presented here, taken together, suggest that another mechanism is used as a cue for tail-first ingestion. Detection of the direction of overlapping ventral scales has been suggested as a mecha-

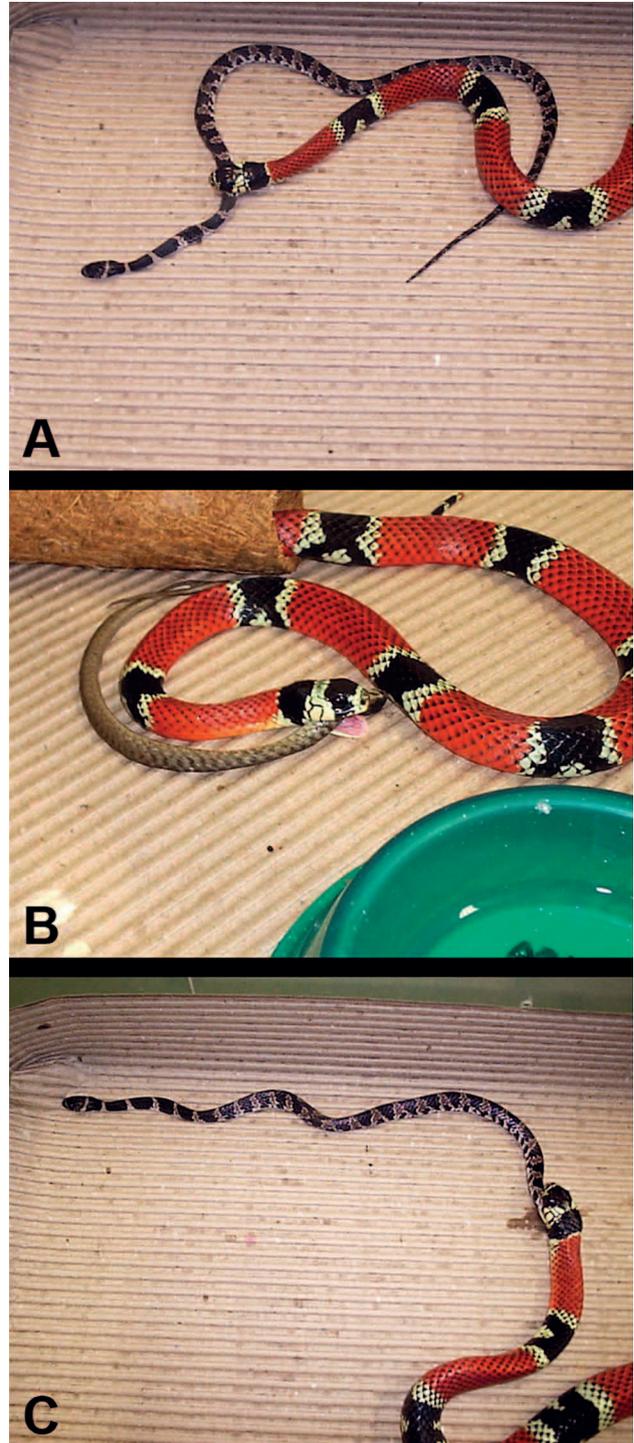


Figure 1. Behavioural sequence of *Erythrolamprus aesculapii* feeding on dead prey items: A) Seizing a *Sibynomorphus mikani*; B) handling a *Tomodon dorsatus*; and C) beginning of the ingestion of an *S. mikani*.

nism used by ophiophagous snakes to locate the head of the prey (GREENE 1976). Although this is the opposite end of the ingestion observed in *E. aesculapii*, it is likely that scale overlaps of the prey's body also plays an important role in the ingestion habits of this species.

Although scale overlap may serve as a pointer for *Erythrolamprus* to detect the prey's tail, the ultimate causes of tail-first ingestion remain unclear. This is an intriguing question, given the advantages and the commonly observed action of ingesting prey head first (LOOP & BAILEY 1972, GREENE 1976, 1997, MORI, 1991, JACKSON et al. 2004). Most ophiophagous snakes kill their prey before ingestion. For example, the ophiophagous coral snakes (*Micrurus* spp.) and king cobras (*Ophiophagus hannah*) maintain their bite until venom action causes prey movements to cease; then they use the direction of the prey's overlapping ventral scales to "jaw-walk" toward its head (GREENE 1976, 1997). The king snake *Lampropeltis getula* includes snakes in its diet, and these are first subdued by constriction, and then swallowed head first (JACKSON et al. 2004). Species of *Erythrolamprus* are rear-fanged, and their Duvernoy's glands produce potentially harmful and toxic secretions (LEMOINE & RODRÍGUEZ-ACOSTA 2003). When seizing prey, *E. aesculapii* will firmly hold the prey for a certain period, probably to inject its venom into the prey (MARQUES & PUERTO 1994). Despite this, ingestion usually begins, and is completed, while the prey is still alive and moving (MARQUES & PUERTO 1994; H. B. BRAZ pers. obs.), suggesting that its toxic secretion is not sufficiently potent to kill the prey. We propose that the origin of tail-first ingestion in *Erythrolamprus* may be related to its incapability to kill prey prior to ingesting it. Tail-first ingestion in *Erythrolamprus* may have been selected as the easiest and fastest way to consume an elongated live prey item. Nevertheless, tail-first ingestion of live prey by *Erythrolamprus* may entail the risk of injuries to the predator because prey's head remains free to strike back. The maintenance of this feeding habit may be feasible only in cases of harmless or slightly aggressive prey. A survey of food items consumed by *Erythrolamprus* published in the literature (BEEBE 1946, GREENE 1976, 1997, DUELLMAN 1978, SAZIMA & ABE 1991, MARQUES & PUERTO 1994, MARTINS & OLIVEIRA 1998, RIVAS-FUENMAYOR 2002, HARTMANN et al. 2009, BERNARDE & ABE 2010, SANTOS & VAZ-SILVA 2012) seems to support this hypothesis. The vast majority of prey species consumed by *Erythrolamprus* (e.g., *Atractus*, *Dipsas*, *Echianthera*, *Liophis*, *Oxyrhopus*, *Sibynomorphus*, and *Tantilla* spp.; which account for more than 80% of food items) are harmless (aglyphous and/or rarely strike when handled, see MARTINS & OLIVEIRA 1998, MARQUES et al. 2004 for descriptions of the defensive repertoire of such species). On the other hand, highly venomous (e.g., newborn *Bothrops* spp.), opisthoglyphous, and/or aggressive sympatric snakes (e.g., *Philodryas* spp., *Thamnodynastes* spp.), common in nature (MARTINS & OLIVEIRA 1998, MARQUES et al. 2004), are rarely consumed by *Erythrolamprus*. The hypothesis of prey selectivity (harmless vs. aggressive/venomous) in *Erythrolamprus* needs to be tested in further studies.

Acknowledgements

We thank M. F. D. FURTADO for allowing us to use the Laboratory of Herpetology for carrying out the experiments, S. R. TRAVAGLIA-CARDOSO for sharing observation on her unpublished work on feeding behaviour, and A. F. D. FONSECA for revising our English draft manuscript. This study was supported by FAPESP (Fundação de Amparo à Pesquisa do Estado de São Paulo). O. A. V. MARQUES benefited from a scholarship from CNPq (Conselho Nacional de Desenvolvimento Científico e Tecnológico). Animals were maintained under approval of the Butantan Institute Ethics Committee for Animal Use (CEUAIB 482/08).

References

- ARNOLD, S. J. (1978): Some effects of early experience on feeding responses in the common garter snake, *Thamnophis sirtalis*. – *Animal Behaviour*, **26**: 455–462.
- BEEBE, W. (1946): Field notes on the snakes of Kartabo, British Guiana and Karipito, Venezuela. – *Zoologica*, **31**: 11–52.
- BERNARDE, P. S. & A. S. ABE (2010): Hábitos alimentares de serpentes em Espigão do Oeste, Rondônia, Brasil. – *Biota Neotropica*, **10**: 167–173.
- DE QUEIROZ, A. & K. DE QUEIROZ (1987): Prey handling behavior of *Eumeces gilberti* with comments on headfirst ingestion in squamates. – *Journal of Herpetology*, **21**: 57–63.
- DUELLMAN, W. E. (1978): The biology of an equatorial herpetofauna in Amazonian Ecuador. – University of Kansas Museum of Natural History, Miscellaneous Publication, **65**: 1–352.
- FUCHS, J. L. & G. M. BURGHARDT (1971): Effects of early feeding experience on the responses of garter snakes to food chemicals. – *Learning and Motivation*, **2**: 271–279.
- GREENE, H. W. (1976): Scale overlap, a directional sign stimulus for prey ingestion by ophiophagous snakes. – *Zeitschrift für Tierpsychologie*, **41**: 113–120.
- GREENE, H. W. (1997): Snakes: the evolution of mystery in nature. – University of California Press, Berkeley, California, United States of America.
- HARTMANN, P. A., M. T. HARTMANN & M. MARTINS (2009): Ecologia e história natural de uma taxocenose de serpentes no Núcleo Santa Virgínia do Parque Estadual da Serra do Mar, no sudeste do Brasil. – *Biota Neotropica*, **9**: 173–184.
- JACKSON, K., N. J. KLEY & E. L. BRAINERD (2004): How snakes eat snakes: the biomechanical challenges of ophiophagy for the California kingsnake, *Lampropeltis getula californiae* (Serpentes: Colubridae). – *Zoology*, **107**: 191–200.
- LEMOINE, K. & A. RODRÍGUEZ-ACOSTA (2003): Haemorrhagic, proteolytic and neurotoxic activities produced by Duvernoy's gland secretion from the false coral snake (*Erythrolamprus bizona* Jan 1863) (Serpentes: Colubridae). – *Revista Científica, FCV-LUZ*, **13**: 371–377.
- LOOP, M. S. & L. G. BAILEY (1972): The effect of relative prey size on the ingestion behavior of rodent-eating snakes. – *Psychonomic Science*, **28**: 167–169.
- MARQUES, O. A. V. & G. PUERTO (1994): Dieta e comportamento alimentar de *Erythrolamprus aesculapii*, uma serpente ofiófaga. – *Revista Brasileira de Biologia*, **54**: 253–259.
- MARQUES, O. A. V., A. ETEROVIC & I. SAZIMA (2004): Snakes of the Brazilian Atlantic Forest – An illustrated field guide for the Serra do Mar range. – Holos. Ribeirão Preto, São Paulo, Brasil.

- MARTINS, M. & M. E. OLIVEIRA (1998): Natural history of snakes in forests in the Manaus region, Central Amazonia, Brazil. – *Herpetological Natural History*, **6**: 78–150.
- MORI, A. (1991): Effects of prey size and type on prey-handling behavior in *Elaphe quadrivirgata*. – *Journal of Herpetology*, **25**: 160–166.
- MORI, A. (1993): Prey handling behaviour of neonatal rat snakes, *Elaphe taeniura* and *E. dione* (Colubridae). – *Japanese Journal of Herpetology*, **15**: 59–63.
- PINTO, C. C. & T. LEMA (2002): Comportamento alimentar e dieta de serpentes, gêneros *Boiruna* e *Clelia* (Serpentes, Colubridae). – *Iheringia, Série Zoologia*, **92**: 9–19.
- RIVAS-FUENMAYOR, G. (2002): *Erythrolamprus aesculapii* (Coral-patterned Snake). Diet. – *Herpetological Review*, **33**: 140.
- SANTOS, D. L. & W. VAZ-SILVA (2012): Predation of *Phimophis guerrini* and *Ameiva ameiva* by *Erythrolamprus aesculapii* (Snake: Colubridae). – *Herpetology Notes*, **5**: 495–496.
- SAZIMA, I. & A. S. ABE (1991): Habits of five Brazilian snakes with coral-snake pattern, including a summary of defensive tactics. – *Studies on Neotropical Fauna and Environment*, **26**: 159–164.
- URDANETA, A. H., F. BOLAÑOS & J. M. GUTIÉRREZ (2004): Feeding behavior of coral snake *Micrurus nigrocinctus* (Serpentes: Elapidae) on its natural prey in captivity. – *Comparative Biochemistry and Physiology, Part C*, **138**: 485–492.
- WATERS, R. M. & G. M. BURGHARDT (2005): The interaction of food motivation and experience in the ontogeny of chemoreception in crayfish snakes. – *Animal Behaviour*, **69**: 363–374.