Feeding Behavior of the
Snail-eating Snake, *Dipsas indica*

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Dipsadinae snakes have long been recognized as specialized snail-eaters (e.g., Amaral, 1924; Dunn, 1951; Peters, 1960). Available information on feeding habits of *Dipsas*, the most speciose and specialized genus within the group, include stomach contents (Peters, 1960; Cunha and Nascimento, 1978; Kofron, 1982) and behavior of captive individuals feeding on foreign snails (Rembold, 1934; Mertens, 1952; Harris and Simmons, 1967; Gans, 1975). Here I report on the feeding
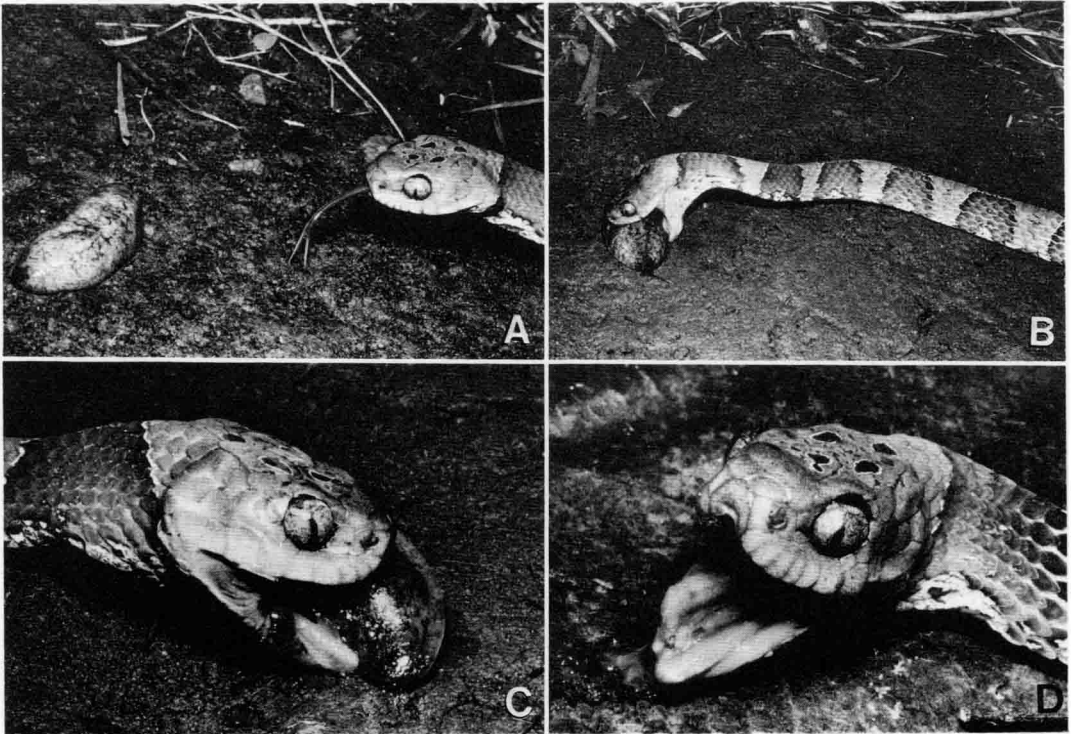
FIG. 1. *Dipsas indica* while feeding on veronicellid slugs, *Sarasinula linguaeformis*. A. Tongue-flicking close to the prey (compare orientation of snake's pupil with Fig. 2A). B. Grasping slug at midbody. C. Swallowing slug tailfirst (note course of right mandibular unit near the close phase). D. Stretching jaws after swallowing (note relative autonomy and the course of each mandibular unit).

behavior of free-living and captive individuals of *Dipsas indica*, feeding on their native prey in southeastern Brazil.

Dipsas indica was found in the Reserva Mata de Santa Genebra, a small (250 ha) remnant of subtropical, semideciduous broad-leaved forest in São Paulo, southeastern Brazil (22°49'S, 37°06'W, 640 m). A description of the study site is in Sazima (1988). Snakes were sought mainly during dusk and night (1830–2330 hr), yielding 15 specimens, all but one during the wet season (Oct–Mar), in about 700 field hours during 1986–1988 (Sazima, 1988). Foraging individuals of *D. indica* were followed on three instances and one trailing sequence was observed. Encounters between nine foraging snakes and potential prey were staged in the field, and three snakes accepted the prey. Seven snakes were observed feeding in 60 × 40 × 30 cm terraria, with soil, litter and dead branches from the study site. Descriptions are based on 63 behavior sequences (two video-taped and nine photographed), performed by three free-living and seven captive snakes feeding on 28 slugs and 35 snails. Only veronicellid slugs, and bulimulid and eulotid snails syntopic with *D. indica* were used as prey. Stomach contents of two snakes provided additional confidence about local gastropod prey. One snake (female, 695 mm SVL, tail tip broken) and 43 color transparencies are as vouchers in the Museu de História Natural, Universidade Estadual de Campinas (ZUEC 585, and unnumbered).

I found 14 individuals of *D. indica* (54–81 cm TL, unsexed) active at night, 11 of them moving on the ground and three on branches or barbed wire fence 1.5–2.0 m above ground. One snake was found during the day coiled among vines.

One individual of *D. indica* was slowly moving on a patch of bare ground when it stopped and retracted the neck region. The snake pointed the snout toward the substrate, and its tongue repeatedly touched the ground. Closer inspection of the site revealed a mucus trail, intersected by the moving *Dipsas*. The snake trailed the mucus track for about 2 m to the dense undergrowth and moved out of sight. Mucus trail following is to be expected for a snail-eating snake, as the trail covers a much larger area than the slug itself thus giving more chances to be intersected by the foraging snake. Tongue flicking response to slug mucus track, trail following and prey recognition by chemoreception were reported for slug-eating populations of *Thamnophis elegans* (Arnold, 1981).

Close to a veronicellid slug, *D. indica* flicks its tongue toward the prey (Fig, 1A), and may move the eyes. Closer to the slug the snake touches it with its tongue one to several times, and sometimes places its snout touching the ground close to the prey, moving the eyes toward prey. It then raises the head, arches the neck and forebody, lunges forward, gapes widely and grasps the slug at midbody (Fig. 1B). With a torsion of the forebody, the snake lifts the slug off the substrate and then quickly swallows the prey, usually

tailfirst. Swallowing is done by alternative advance followed by retraction of one then the opposite side of the lower jaw over the slug. During the "advance" phase (cf. Kardong, 1977), each mandible protracts in a long excursion over the prey's body (Fig. 1C). At the very beginning of the "close" phase, the dentary teeth firmly engage the prey, and the mandibular unit retracts pulling the slug inward. Thus the prey is swallowed mainly due to the mandibular long excursion followed by retraction. The mandibular unit may be projected from the mouth floor about one third of its length, and bent to one or the other side. After prey is swallowed, the snake gapes and "yawns," stretching the mandibles (Fig. 1D), and may rub its chin on the ground, especially if slime is adhered.

Medium-sized to large slugs (3–6 cm) were swallowed in 8 to 15 mandibular moves on each side, whereas on smaller slugs as few as six such moves were enough. Large slugs were swallowed in 20–45 sec and the small ones in 10 sec or less.

The behavioral similarity between Dipsas indica and the African lycodontine snake Duberria lutrix when attacking slugs is impressive (see figure in Gans, 1975). The long mandibular teeth of Dipsas, Sibynomorphus, Pareas, Contia, and other specialized slug-eaters have already been presented as an adaptation for feeding on slippery prey (Zweifel, 1954; Peters, 1960; Laporta-Ferreira et al., 1986). The teeth, together with the long excursion of the mandibular unit in Dipsas, make this snake able to quickly handle a very viscous prey.

Bulimulid and eulotid snails are approached and tongue-flicked by Dipsas in a way similar to that described for slugs. After the presumed chemorecognition, the snake gazes at the prey (Fig. 2A), moves the eyes and may change position relative to snail, sometimes still tongue-flicking. Lunging at prey, the snake gapes and tilts the head so as to grasp the snail's body with the mandible (Fig. 2B). With a head jerk, the snake lifts the snail off from the substrate, twists its neck and coils around most of the shell. This coiling may be brief and appear at the very beginning of the feeding sequence. The coil is mostly ventral with right side (cf. Greene and Burghardt, 1978), but left side may also be used (Fig. 2C), holding the shell against the body. During the coil the snake usually pushes its mandible further into the shell (Fig. 2C), moving the mandibular units sequentially. (Presumably the snail retracts upon being grabbed, also dragging the snake's mandibles into the shell.) After some mandibular movements, the snake partly uncoils, manages to accommodate the shell bracing it against the roof of the mouth, and begins to extract the snail's body. During the extraction, the mandibles move in excursions similar to those used to swallow a slug, judging from the degree of displacement noticeable for some cranial components (quadrate, articular). In some instances it is possible to perceive that about one third of the lower jaw may be placed into the shell (Fig. 2D), bent to the side and upwards. After extracting the whole snail or most of it the snake releases the shell, dragging it on the substrate.

The number of mandibular moves on each side to extract a snail varied from 16 to 25, possibly related to snail size and shell architecture. Moreover, depending on shell shape and size the snake was not always able to extract the snail whole (elongate, 1–2 cm shell length snails usually had body ruptured).

Handling time for snails ranged from 70 to 325 sec, most snails being extracted in about 120 sec.

According to the definition of snake constriction in Greene and Burghardt (1978), D. indica may be regarded as a constricting snake (when feeding on snails), and adds to the colubrid genera known to use this behavior to subdue prey (Shine and Schwaner, 1985). Alternatively, parts of this behavior of D. indica may be seen as manipulation of prey, similar to that observed for some egg-eating snakes (see Gans, 1974, and Mora, 1987). Constriction or manipulation of prey in this highly specialized, arboreal snake seems of further interest in view of the arguments advanced by Gans (1961), Greene and Burghardt (1978), and Savitzky (1980), on the origin and adaptiveness of this behavior in snakes.

Peters (1960) noted that the short head of Dipsas, and its protruding and movable eyes seem adaptive for arboreality. I would add that the same features possibly are of great help to evaluate the distance from prey and its relative position, seemingly crucial to successfully grabbing a snail. Sibynomorphus neuwiedii prefers snails over slugs (Laporta-Ferreira et al., 1986) and has more protruding eyes, and shorter and broader snout than either S. ventrimaculatus or S. mikanii (pers. obs.), the latter being a slug-eater (Laporta-Ferreira et al., 1986).

Taub (1966) noted that Dipsas has a serous gland associated with lower (instead of the more usual upper) jaw. Judging from the short time needed to deshell a snail, if indeed such glands do play a role in the extraction, their products must act quickly. As mere strength may not be enough in some instances (large or tough snails), this issue merits closer inspection.

The ability of Dipsas to make long, independent mandibular excursions, as well as the jaw "bending qualities," was anticipated by several authors (e.g., Dunn, 1951; Peters, 1960; Kofron, 1982; Savitzky, 1983) and is to be expected in a specialized snail-eater, that is well suited to handle slugs as well. For most Dipsas species, slugs predominate over snails in stomach contents (Peters, 1960; Cunha and Nascimento, 1978; but see Kofron, 1982), and unless prey availability does not allow choice I would expect a preference for slugs, among other reasons for the much shorter handling time. Dipsas possibly evolved towards specialized cochleophagy through slug-eating, gradually shifting to snails, with species such as D. brevifacies, with highly modified jaw architecture and seemingly restricted diet (Kofron, 1982), probably being one extreme of this feeding mode (see also Gans, 1972).

The jaw qualities used to feed on snails and slugs allow Dipsas to triangulate its head in a way that resembles the shape of a pit viper (see discussion on viper head mimicry in Werner, 1985, and Pough, 1988). Moreover, the dorsal color pattern, which may be viewed as arboreal crypsis, may also be regarded as mimicking the pattern of certain pit vipers, especially slender individuals of Bothrops jararaca. Populations known as D. indica bucephala have much the same range as B. jararaca (see Peters, 1960). Thus D. indica might be another unarmed, specialized feeder mimicking a dangerous snake (see Gans, 1974, and Savitzky, 1983). Defensive tactics of D. indica include some components reminiscent of B. jararaca aposematic displays, such as elevating the head and neck, s-coiling,
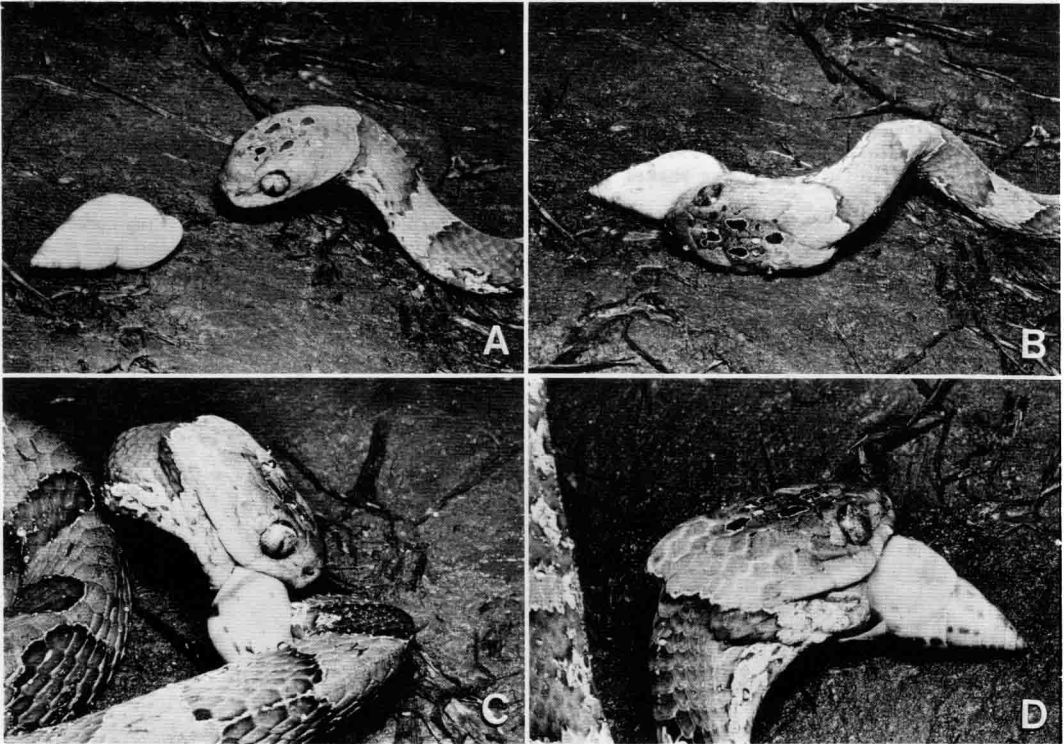
FIG. 2. *Dipsas indica* while feeding on the snail, *Drymaeus interpunctus*. A. Gazing at prey after tongue-flicks, while waiting for snail to reemerge from shell (note orientation of snake's pupil toward snail). B. Tilting head during lunge at prey, to grasp snail's body with mandible. C. Final phase of coiling around prey, while still pushing mandible into the shell. D. Extracting snail, with about one third of mandible into the shell (note part of skin from lower jaw retracted, while mandibular units work into the shell). Droplets on snake are raindrops.

and thrashing anterior part of the body as if delivering lateral, false strikes (cf. Greene, 1988, and Sazima, 1988). Indeed, the similarity of some *Dipsas* species to *Micrurus* coral snakes indicated by Kofron (1982) and Pough (1988) suggests that mimicry as a defensive strategy is widespread among the Dipsadinae.

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