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Predatory Behavior of the Snail-Eating Snake *Pareas carinatus* (Boie, 1828) (Squamata: Pareidae): An Ethogram Study

PATCHARA DANAISAWADI[1,2], TAKAHIRO ASAMI[3], HIDETOSHI OTA[4], CHIRASAK SUTCHARIT[2] AND SOMSAK PANHA[2*]

[1] *Biological Science Program, Department of Biology, Faculty of Science, Chulalongkorn University, Bangkok 10330, THAILAND*
[2] *Animal Systematics Research Unit, Department of Biology, Chulalongkorn University, Bangkok 10330, THAILAND*
[3] *Department of Biology, Shinshu University, Matsumoto 390-8621, JAPAN*
[4] *Institute of Natural and Environmental Sciences, University of Hyogo, and Museum of Nature and Human Activities, Hyogo 669-1546, JAPAN*
* Corresponding author. Somsak Panha (somsak.pan@chula.ac.th)
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ABSTRACT.– We examined predatory behavior of the keeled-scaled snail-eating snake *Pareas carinatus* on three types of terrestrial gastropods, the fully shelled dextral snail *Cryptozona siamensis*, the semi-slug *Durgella* sp. with the substantially reduced shell, and the slug *Semperula siamensis* with no shell, by observations in captivity. We devised an ethogram to describe the snakes' characteristic behaviors toward the putative standard prey *Cryptozona siamensis*. In three predatory phases, the snake displayed 15 serial behaviors, which could be classified into nine categories of function. After the snake fixed the eyes onto given prey, the snake took a longer time before striking but a shorter time to finish feeding on the semi-slug than on the snail. The snake stared but did not strike at the slug, and flicked the tongue more times before it discontinued staring than before striking at the snail or semi-slug. This suggests that the snake *P. carinatus* does not prey on a slug. Our results provide the ethological basis to investigate the ecology and evolution of predatory behavior in snail-eating snakes.

KEY WORDS: Predation, prey distinction, prey recognition, semi-slug, slug, snail

INTRODUCTION

Dietary specialization occurs in many groups of vertebrates. In snakes, some groups consume a wide variety of animals including both endotherms and ectotherms, and both vertebrates and invertebrates, whereas others, often being referred to as dietary specialists, utilize much limited groups and even at particular life-stages of animals (Zug, 1993). Because of limb degeneration in early stages of their evolution, snakes depend almost entirely on the structure of remaining portions of body (i.e., jaw apparatus, trunk, etc.), and the way of their use in capture and subsequent handling of prey (Cundall and Greene, 2000). Generalist snakes exhibit variable feeding behaviors depending on prey types and contexts of prey encounter (Mori, 1991; Mehta, 2003). With respect to those snakes that are known as dietary specialists, however, the extent of behavioral flexibility in response to similar but actually more or less different types of prey remains to be studied.

Many members of the snake family Pareidae (family name often spelled as Pareatidae, but in error: see Savage [2015]) and Dipsadidae have been recognized as specialists that feed on snails (Pough, 1983; Greene, 1997; Cundell and Greene, 2000; Vitt and Caldwell, 2008). They have specific characters for arboreal life with modified feeding devices such as long slender body, oversize head, short snout, movable eyes and flexible mandibles (Sazima, 1989; Vitt and Caldwell, 2008). Although these snakes are known as specific snail-eaters, their feeding patterns and dietary specializations are poorly known. Götz (2002) reported the feeding behavior, number of mandibular movement and extraction time of *Pareas carinatus* by experiment in captivity with European ground-dwelling snails.

Except for *Asthenodipsas leavis*, snakes of the family Pareidae so far examined anatomically have asymmetric mandibular teeth with variation in number and size (Hoso et al., 2007; 2010). Feeding experiment with *Pareas iwasakii*, which exhibits the strongest asymmetry in the number of mandibular teeth, indicated that the snake strikes prey by tilting the head leftward regardless of prey's coiling direction and fails in capturing counterclockwise-coiled (sinistral) snails more frequently than clockwise-coiled (dextral) snails. When the snake captures a snail, feeding on dextral prey completes faster with fewer mandibular retractions than feeding on sinistral prey. These suggest that dental asymmetry has evolved for predation on the dextral majority in snails.

However, Danaisawadi et al. (2015) found by feeding experiment that *P. carinatus* completes similar feeding processes on the dextral and on the sinistral. Moreover, *P. carinatus* struck either leftward or rightward regardless of prey's coiling direction. There are several reports on snail-eating snakes with weak mandibular teeth asymmetry, for example, *Aplopletura boa* and *Asthenodipsas* spp., which feed on diverse prey such as slugs and/or small lizards (Stuebing and Inger, 1999; Lim, 2009; Das, 2010; Cox et al., 2010). It is possible that the strength of dental asymmetry may be associated with specialization in snail predation.

In this study we examined the predatory behavior of *P. carinatus* by feeding experiments with pulmonate prey candidates that coexist with this snake. We constructed the ethogram of predation by defining every behavioral step that is distinguishable from one another. We compared behavioral responses of the snake to prey candidates that largely differ in the relative size and sheltering effect of the shell. Here we show the predatory ethogram of *P. carinatus* on snails and the prey-dependence of temporal pattern of predatory behavior.

MATERIALS AND METHODS

Predation experiment

We used five adult females of *P. carinatus* (51-72 cm in snout-vent length), all collected from Chanthaburi, eastern Thailand. For experiment, each snake was placed in a terrarium (30 x 45 x 25 cm) in which a wood bar of 30 cm length and 2 cm diameter was fixed horizontally at a 10 cm height from the bottom. As prey candidates, we used 16 adult snails of *Cryptozona siamensis*, ten adult semi-slugs of *Durgella* sp. and five adult slugs of *Semperula siamensis*. Here we call a fully shelled pulmonate a snail, a pulmonate with the largely-reduced shell a semi-slug, and a pulmonate with no shell a slug. These three species of pulmonates co-occur with *P. carinatus*. Each snake was conditioned with no food for three days before each predation trial (hereafter called experiment), which began at 21:00. We first placed a snail and let it crawl 100 mm ahead of a snake perching on the horizontal bar. We

TABLE 1. The number of prey candidates presented to each snake.

Snake no.	No. individuals presented to the snake		
	Snail	Semi-slug	Slug
1	1	2	0
2	3	1	1
3	7	1	0
4	4	1	2
5	1	4	2

randomized the combination of individuals between the snake and prey candidate (Table 1). All experiments were conducted in the laboratory at 25 to 28°C under the illuminance of 100 lux. Behavioral responses of each snake were recorded with a video camera (Nikon Coolpix P100, VDO mode HD).

Analysis of predation behavior

We compared video records of predation experiment and extracted behavioral steps that the snake commonly displayed among experiment with the same type of prey candidate. We constructed the ethogram to describe the standard predatory behavior according to the results with the putative standard prey *Cryptozona siamensis*. We inferred a major function of each distinguishable behavioral display and grouped those displays into functional categories, which we indicated in capital letters.

To compare time budgets for predation, we examined differences in time lengths of the three predatory phases between the cases with the snail and the semi-slug by using the general linear mixed models (GLMMs). We also tested differences in the numbers of tongue flicks before strike, and of mandibular retractions and gapes after feeding, and differences in the frequencies of those behaviors, by GLMMs.

RESULTS

The snake began to stare at a prey candidate immediately when the latter was placed in front of the snake. The snake successfully preyed on a snail or a semi-slug provided in each experiment. In these cases with the snail or semi-slug, the snake performed closely similar behaviors for predation in sequence, which we described into the ethogram below in text, a table and figures.

On the other hand, the snake struck at none of the five slugs, although it fixed the eyes onto the slug in each case. In two of the five experiments with the slugs, the snake approached but moved away from each slug as soon as the snake touched the slug with the tongue. In the other three experiments, the snake even did not approach the slug.

The snake flicked the tongue more times toward the slug than toward the snail or semi-slug ($p = 0.026$), while the number of tongue flicks did not differ between the cases with the snail and semi-slug ($p= 0.39$) (Table 2). The snake, however, did not exhibit a behavior of strong breath to any of the five slugs, although the snake performed this behavior to every snail.

TABLE 2. Mean ± s.e. of numbers and frequencies (per second) of tongue-flicks before strike and of mandibular retractions and gapes after feeding.

	Tongue-flick		Mandibular retraction		Gape	
	No.	**Freq.**	**No.**	**Freq.**	**No.**	**Freq.**
Snail (n = 16) *Cryptozona siamensis*	1.1 ± 0.6	0.02 ± 0.01	10.9 ± 2.5	0.05 ± 0.01	7.7 ± 0.8	0.06 ± 0.01
Semi-slug (n = 10) *Durgella* sp.	1.6 ± 0.7	0.01 ± 0.01	36.9 ± 2.9	0.40 ± 0.9	24.6 ± 2.5	0.29 ± 0.09
Slug (n = 5) *Semplerula siamensis*	9.4 ± 4.2	1.7 ± 0.8	-	-	-	-

Three sequential phases can be recognized in predatory behaviors that resulted in successful extraction of the prey's soft-body from the shell (Table 3, Fig. 1). The first is a pre-capture phase from the moment of fixing the eyes at the prey candidate to the stage of pointing the head closely to the shell aperture. The second is a feeding phase from the moment of strike to the end of feeding, which was defined as the moment of dropping of the shell. The third is a post-feeding phase from the stage of retracting the mandibles alternately to the end of characteristic behavioral displays. After this, the snake becomes inactive sitting on the substrate with no particular motions.

We recognized 15 behavioral displays which were visually distinguishable during the three phases. We classified these displays into nine categories of function inferred (Table 3). The snake performs some of these displays not in a determined sequence but alternately in many cases. Thus, we diagramed a typical sequence of these behaviors in a flow chart (Fig. 1).

1. Pre-capture phase

The snake displays seven different behaviors in this initial phase. Major functions of these behaviors are hypothetically DETECTION, APPROACH and INVESTIGATE.

DETECTION: The snake begins two behavioral displays, eye-fix and tongue-flick, immediately after the prey candidate is placed in front of them (Fig. 2A). This suggests that these displays result from noticing the presence of potential prey. Subsequently the snake breathes by inflating and deflating its trunk strongly and frequently. The snake uses its eyes for vision and flicks its tongue for vomeronasal olfaction. Thus, the three displays, eye-fix, tongue-flick and strong-breath probably function for the snake to detect prey.

APPROACH: The snake begins to approach to the prey candidate only after the latter fully protrudes the soft body. After the three behavioral displays of the category DETECTION, the snake does not necessarily approach the prey candidate. This suggests that the snake decides not to approach when the snake does not obtain a positive sign by performing the preceding displays.

INVESTIGATE: Behavioral displays of this functional category occur after the snake approach the prey candidate. The snake displays neck-arch by moving the head closer down to the prey candidate and raising the anterior body part behind the head, which shapes an arch (Fig. 2B). Then,

TABLE 3. Predatory ethogram of the keeled-scaled snail-eating snake *Pareas carinatus*.

Predatory phase	Functional category	Behavioral display	Description
Pre-capture	DETECTION	Eye fix	Stares at the prey candidate
		Tongue flick	Protrudes and withdraws the tongue
		Strong breath	Inflates and deflates the trunk strongly and frequently
	APPROACH	Approach	Creeps to the prey candidate
	INVESTIGATE	Neck arch	Raises the anterior body part and pulling the head down to the prey
		Head tilt	Turns the head leftward or rightward
		Head-point	Directs the head down to the aperture
Feeding	CAPTURE	Strike	Strikes at the prey
		Handle	Seizes and lifts the prey up from substrate by inserting the lower jaws into the shell aperture and placing the upper jaws onto the ventral outer surface of the shell.
	EXTRACTION	Mandibular retraction	Retracts left and right lower jaws alternately.
	SWALLOW	Swallow	Transports the prey's soft body to the esophagus.
Post-feeding	SHELL-DROP	Shell-drop	Drops the shell.
	MUSCULAR RECOVERY	Mandibular retraction	Retracts left and right lower jaws alternately.
	MOUTH CLEANING	Gape	Opens the mouth widely.
		Mouth-rub	Rubs the mouthparts onto a hard substrate.

toward the snail, the snake tilts the head leftward or rightward and pursues the head-point display by directing the head to face and point the shell aperture further closely (Fig. 2B). These suggest that the snake investigates where and how to strike at the prey. The snake tilted the head rightward toward five of the 10 semi-slugs, but struck the other semi-slugs without tilting the head.

2. Feeding phase

Four behavioral displays, which occur to feed on the preys' soft body, can be classified into the following three categories.

CAPTURE: The snake strikes and captures the prey. The snake captures the snail and the semi-slug by different manners. When preying on the snail, the snake locates the shell aperture by facing closely and then strikes. At the moment of strike, the snake handles the prey to insert the mandibles into the aperture and to lean the upper jaws against the ventral outer surface of the aperture (Fig. 2C). On the other hand, the snake captures the semi-slug by holding the mid body near the reduced shell with jaws and mandibles.

EXTRACTION: While feeding on the prey's soft body, the snake alternately retracts the mandibles. These retractions of mandibles probably function to extract the soft body from the shell.

SWALLOW: While retracting the mandibles, the snake moves the anterior trunk zigzag in the air without creeping. During this action, a swollen part of the trunk, at which the prey's soft body is obviously located, moves rearward from the throat. This behavior may indicate that the snake transports the food from the mouth to the digestive tract.

3. Post-feeding phase

SHELL-DROP: The snake drops the shell without holding with the jaws, while continuing mandibular retractions.

MUSCULAR RECOVERY and/or MOUTH CLEANING: The snake continues to retract the left and right mandibles alternately, in a closely similar manner to mandibular retractions during feeding. There should be no need of extracting the soft body or feeding in this phase unless some part remains in the mouth. However, the snake consistently repeats retracting the mandibles after preying on a snail or semi-slug. Mandibular retractions therefore must be necessary, presumably to recover the conditions of mouthparts. One possibility is to recover muscular conditions for mandible operation. The other is to remove mucus and/or soft body remains inside the mouth.

After feeding on the semi-slug, the snake pursued 3.4 times as many mandibular retractions as after feeding on the snail (p = 0.001) (Table 2). Mandibular retraction after

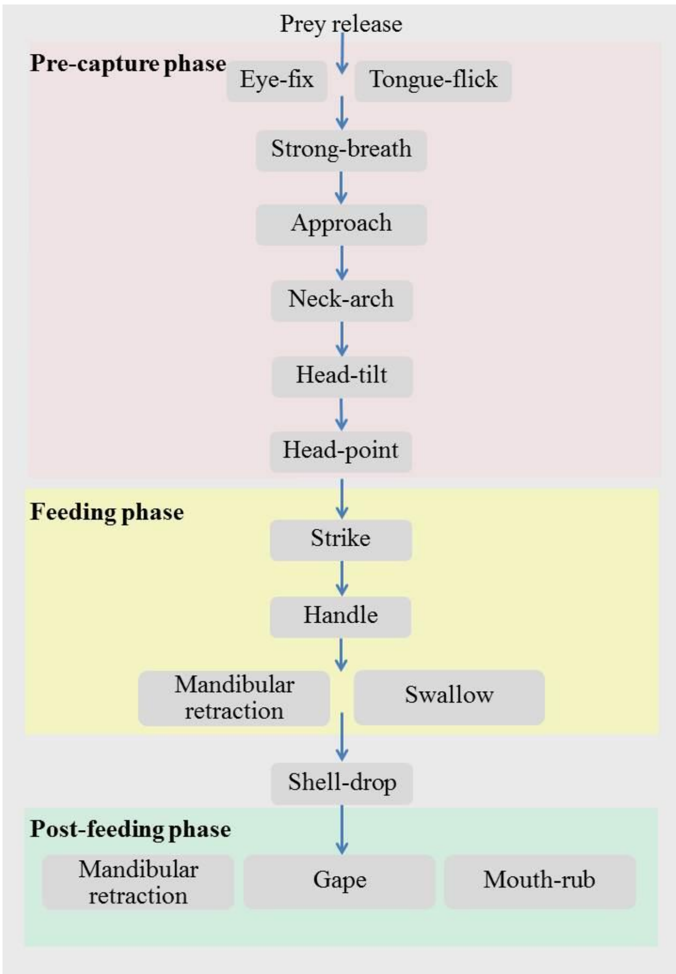

FIGURE 1. Flow chart of predatory behavior of the keeled-scaled snail-eating snake *Pareas carinatus*.

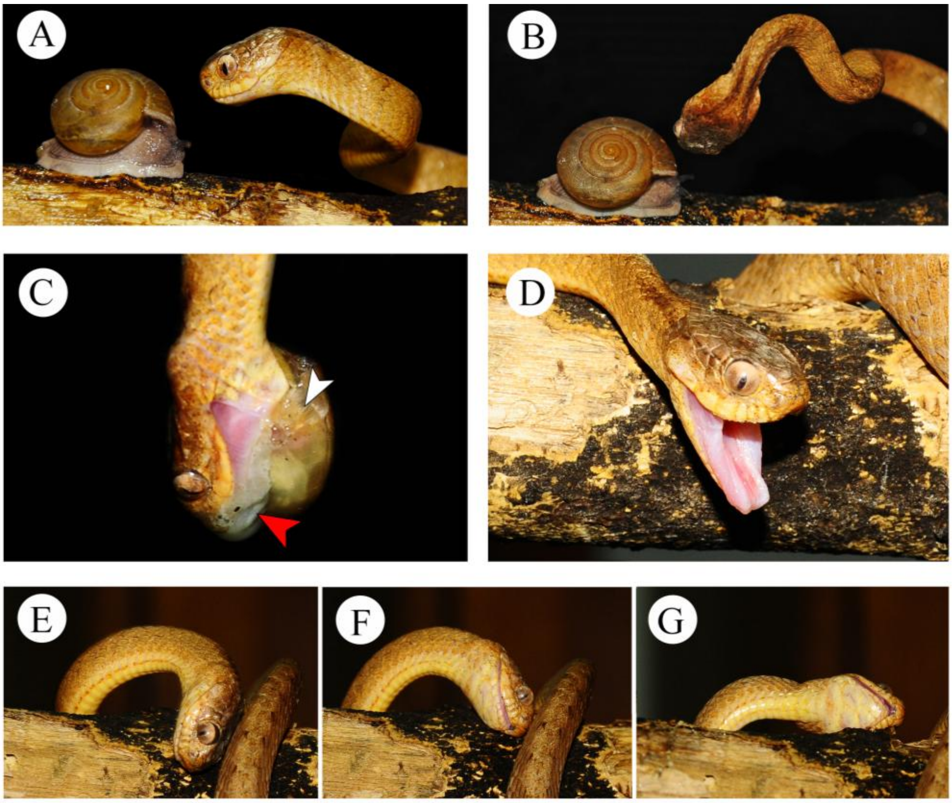

FIGURE 2. Typical behavioral displays of *Paras carinatus* in predation on a snail. (A) Eye-fix. (B) Neck-arch and head-tilt. (C) Feeding by inserting the mandibles into the shell aperture. The white arrow indicates the inserted left mandible which is visible through the shell. The red arrow indicates an excessive amount of mucus coming out to the upper mouthparts and face. (D) Gape. (E)-(G) Sequential steps of mouth-rub.

feeding on the semi-slug was also eight times as frequent as that after feeding on the snail ($p = 0.002$).

The snake also consistently displays two other behaviors that are characteristic to the post-feeding phase. One is gaping for several seconds (Fig. 2D). The other is rubbing the mouth (Fig. 2E-G). The snake opens the mouth widely at least once or multiple times between or at the end of mandibular retractions. This behavior may function to remove mucus remains inside the mouth and/or for muscular recovery. The snake tilts the head and rubs their mouth and chin with the available substrate several times (Fig. 2E-G). After this behavior, an excessive remain of mucus outside the mouthpart disappears (Fig. 3). This supports the present hypothesis that the mouth-rubbing behavior functions for removing mucus remains.

In average, gapes after feeding on the semi-slug were 3.2 times as many as those after feeding on the snail ($p = 0.001$) (Table 2). Gape frequency in the case of the semi-slug was also 4.8 times as high as that in the case of the snail ($p = 0.003$).

4. Prey-dependence of temporal pattern

The pre-capture phase in predation on the semi-slug was 3.3 times as long as that on the snail ($p < 0.001$) (Table 4). There was no difference between time lengths

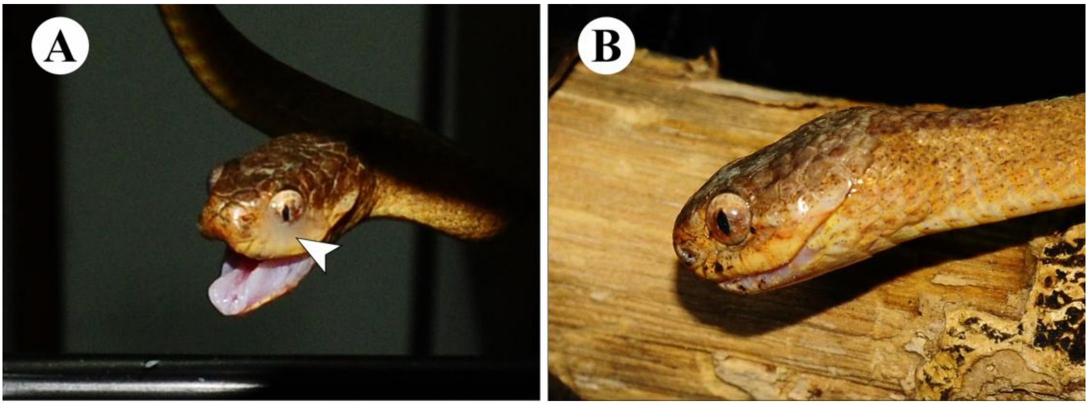

FIGURE 3. Removal of mucus remains by mouth-rub behavior. (A) Before mouth- rub. A mass of mucus remains on the left upper jaw. (B) After mouth-rub. No mucus remains visible on the same snake.

from fixing of the eyes to striking at the snail and to averting the eyes from the slug, although the latter was not necessarily approached ($p = 0.33$). On the other hand, the snake finished feeding on the semi-slug's body after strike 13 times as fast as feeding on the snail's body ($p < 0.001$). During the feeding phase, the snake performed a smaller number of mandibular retractions ($p < 0.001$) when preying on the semi-slug than on the snail. The time lengths of the post-feeding phase in predations of the snail and semi-slug did not significantly differ from each other ($p = 0.14$).

The total time length over the three phases for predation was longer with the snail than that with the semi-slug ($p < 0.04$) (Table 4). The proportions of time consumption for the three phases depended on the prey type as follows. The proportion for the pre-capture phase was larger with the semi-slug (59.7%) than with the snail (14.5%) ($p < 0.002$) (Fig. 4). The relative length of the feeding phase was, however, smaller with the semi-slug (4.4%) than with the snail (45.5%) ($p < 0.01$). The proportions of the post-feeding phase in time length were not significantly different between these prey types ($p = 0.22$).

DISCUSSION

This study disclosed that *Pareas carinatus* achieves diverse behaviors in sequence for specialized predation on terrestrial pulmonates, exclusive of the present slug species. This paper described 15 discrete displays of behavior in the three predatory phases. We found that the snake performs behaviors of mandibular retraction, gape and mouth-rub with no exception, while no longer feeding after dropping the shell.

TABLE 4. Mean ± s.e. of time length (sec.) of each predatory phase.

Prey type	Predatory phase			Total
	Pre-capture	Feeding	Post-feeding	
Snail	67.1 ± 10.0	210.1 ± 48.0	184.3 ± 31.4	462.3 ± 104.4
Semi-slug	220.8 ± 31.8	16.1 ± 1.5	132.9 ± 24.7	400.0 ± 51.6
Slug	67.0 ± 43.7	-	-	-

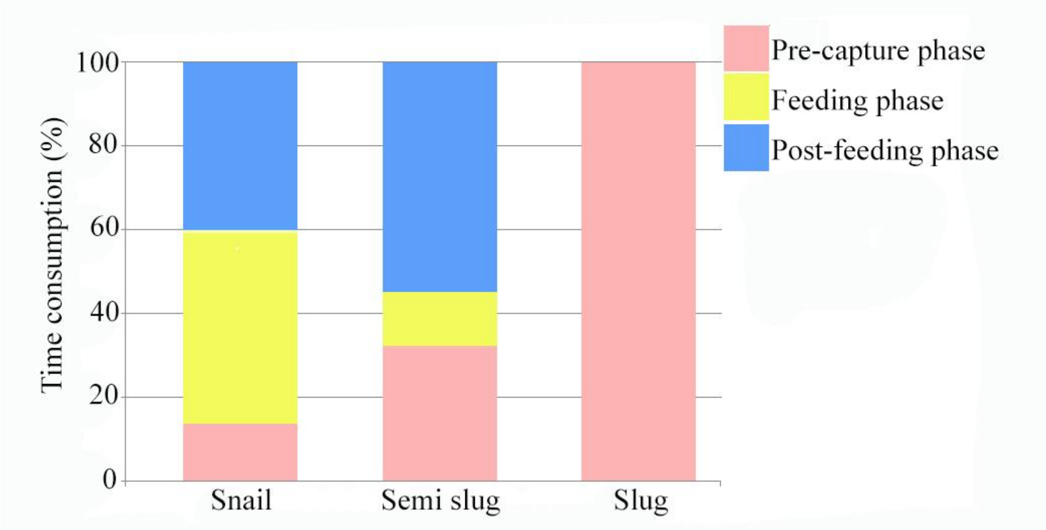

FIGURE 4. Prey-type dependence of temporal pattern of predatory behavior.

Our results suggest that the snake changes its predatory behavior by recognizing the present three types of pulmonates: snail, semi-slug and slug. The snake captured the semi-slug by striking down from the above of the prey in five of the total of 10 experiments. In these cases, the snake did not tilt the head before striking. The snake never showed this type of capturing manner to the snail prey. Thus, the snake changes behavioral manners to capture depending on the prey type.

Once the snake struck after the extended pre-capture phase, the snake finished feeding on the semi-slug one order of magnitude faster than feeding on the snail. The reduced shell of the present semi-slug only covers a small area of the dorsal surface and should not require specialized soft-body extraction unlike the shell of the present snail. These suggest that it is physically simpler or easier to eat the semi-slug's body than the snail's body. After feeding, however, the semi-slug required mandibular retractions and gapes more times and more frequently than the snail.

The snake necessarily pursues mandibular retractions and gapes after dropping the shell. For these actions in the post-feeding phase, the snake spends around 40% of the entire time for predation. This indicates the importance and necessity of mandibular retractions and gapes after feeding. Various functions of similar gaping behaviors have been inferred to be for stretching the mandibles (Sazima, 1989), facilitating vomerolfaction (Graves and Duvall, 1983) and examining mucus remains in the mouth (Cunningham and Burghardt, 1999). If the post-feeding behaviors (mandibular retraction and gape) are for stretching or reconditioning of the mandibles, easier prey would require these actions fewer times. In the present study, however, the snake retracted the mandibles and gaped after feeding on the semi-slug far more times and frequently than after feeding on the snail, despite the remarkably prompt completion of semi-slug feeding. Thus, post-feeding mandibular retractions and gapes may play a major role for removing mucus remains from the mouthpart. However, it is crucially important to consider possible confusion of gaping with yawning (Cunningham and Burghardt, 1999). Our results indicate the importance of further investigation on the function of the post-feeding behaviors.

The South American snail-eating snake *Dipsas indica* preys on a snail *Drymaerus interpunctus* and a slug *Sarasinula linguaeformis* (Sazima, 1989). In contrast, the present snake *P. carinatus* struck none of the five slugs presented. The snake approached two of these slugs and tilted the head, but did not proceed for the further steps of predation. Slugs and semi-slugs in general expose their soft bodies with no shell or only the reduced shell. Instead of forming the shell, slugs secrete sticky mucus (Smith, 2007) for physical protection, with defensive chemical compounds in some species, against predators (e.g. Pakarinen, 1994; see Luchtel and Deyrup-Olsen, 2001 for review). Our results suggest that *P. carinatus* does not prey on the present slug species by distinguishing from the present semi-slug and snail species. There may be an ecological reason for this snake not to strike or prey on slugs. Our results present an empirical basis to investigate why and how the snake avoids the present shell-less slug.

This study compared behavioral responses of the snake to three types of pulmonate gastropods to obtain a basis that is necessary to design further experiments to answer explicit questions of ecology and evolution on interactions between specialized snail-eating snakes and their prey. The present study provided a crucial ground to test each of confounding effects of species, phylogeny, structure, odor, behavior, and size of prey candidates to identify the causes of the present predator's responses by conducting experiments in necessary designs.

Arboreal and ground-dwelling snakes may differ in feeding techniques from each other. Ground-dwelling dipsadids in the genera *Sibon* and *Tropidodipsas* drag the prey against a rock and twist their heads to pull the soft body out of the shell (Sheehy, 2012). On the other hand, *Dipsas indica*, a semi-arboreal species, usually coils around the snail and holds the shell against the snake's trunk to extract the snail's soft body (Sazima, 1989), whereas snakes of the arboreal genus *Sibynomorphus* extract the snail body chiefly by mandibular actions (Peters, 1960; Sheehy, 2012). Our results show that the present arboreal species *P. carinatus* also captures the snail and extracts the soft body primarily by means of mandibular retractions as well as arboreal *P. iwasakii* (Hoso et al., 2007). This pattern suggests that similarities in predation behavior between South American dipsadids and Southeast Asian pareids may have resulted from convergent evolution.

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