Zoological Studies **46**(5): 631-637 (2007)

Zoological Studies

When Prey Acts as a Lever: Prey-Handling Behavior of the Chinese Green Tree Viper, *Trimeresurus stejnegeri stejnegeri* (Viperidae: Crotalinae)

Tein-Shun Tsai

Department of Life Science, National Taiwan Normal University, 88 Ting-Chow Rd., Sec. 4, Taipei 116, Taiwan
Tel: 886-2-29333149. Fax: 886-2-29312904. E-mail:t43013@ntnu.edu.tw

(Accepted April 12, 2006)

Tein-Shun Tsai (2007) When prey acts as a lever: prey-handling behavior of the Chinese green tree viper, *Trimeresurus stejnegeri stejnegeri* (Viperidae: Crotalinae). *Zoological Studies* **46**(5): 631-637. Snakes may use tongue flicking and snout touching to locate the head-end of immobilized prey, but tongue use is limited when snakes are holding prey after a strike. In this condition, how can they differentiate the anterior and posterior ends of the prey so that they still ingest their prey mainly from the anterior end? To answer the question, I analyzed the prey-handling behavior of *Trimeresurus stejnegeri stejnegeri* (Viperidae: Crotalinae) in the laboratory. Following the capture of a prey, *T. s. stejnegeri* lifted the prey from the ground. The prey thus hung in the air, with the body tilted, like a lever with the fulcrum at the site of the bite. In most cases, the snake gradually maneuvered its jaw to the higher end of the prey and began ingesting it. As an adaptation for arboreal feeding, the direction of prey ingestion in *T. s. stejnegeri* depended largely on the location of the initial bite site, under the proposed action of gravity. A significantly greater proportion of frogs (42.1%) were struck in the posterior region than mice (9.6%). The ratio of prey ingested from the anterior to the posterior ends was 54: 19 for mice and 24: 14 for frogs. http://zoolstud.sinica.edu.tw/Journals/46.5/631.pdf

Key words: Arboreal pit viper, Feeding behavior, Ingestion direction, Gravity.

Numerous lineages of snakes, including colubrids, viperids, and boids, have independently evolved arboreal habits (Lillywhite and Henderson 1993). Many general questions related to arboreality and the constraints or opportunities of arboreal habits have been addressed in recent years (Lillywhite and Smits 1992, Lillywhite and Henderson 1993). Arboreal snakes may remain immobile most of the time, be cryptically colored (brown or green), and often have narrowed skulls and large eyes in order to feed successfully and avoid predation. Further adaptations, such as a short pulmonary vasculature, high arterial blood pressure, short defecation time, and caudal prehension for stabilization, may help the snakes counter the effects of gravity in discontinuous substrata (Greene 1992, Lillywhite and Henderson 1993).

Few studies have focused on the feeding behaviors of arboreal snakes. The effect of gravity may restrict prey size when feeding from twigs; it is necessary for arboreal snakes to choose smaller prey. Arboreal snakes that are not constrictors may be forced to hold prey, and grasping dangerous and struggling prey may outweigh the disadvantages of releasing it and not being able to relocate it in an arboreal environment (Murphy and Campbell 1987, Campbell and Solorzano 1992). Chinese green tree vipers (*Trimeresurus stejnegeri stejnegeri*) (Viperidae: Crotalinae) are nocturnal and feed mainly on frogs in the field, although they are known to include lizards, birds, rodents, and shrews in their diet (Pope 1935, Mao 1970, Zhao and Adler 1993, Creer et al. 2002). Campbell and Solorzano (1992) mention that arboreal species such as *Bothriechis* spp. almost invariably seize and hold their prey following a strike. I found this to be the case with Chinese green tree vipers in both the field and laboratory. Unlike arboreal boids, no constriction behavior was observed during feeding episodes in Chinese green tree vipers.

Capturing prey at a position close to its head could decrease the risk of prey retaliation (Mehta 2003). If ingestion is attempted tail-first, the direction of scales, limbs, or feathers may impede swallowing (Campbell and Solorzano 1992). For these reasons, most snakes ingest prey from the anterior end (Murphy and Campbell 1987, Brown and Lillywhite 1992, Campbell and Solorzano 1992). Snakes may use tongue flicking (chemosensory cues) and snout touching (thigmosensory cues) to locate the head-end of immobilized prey (Campbell and Solorzano 1992, Savitzky 1992, Sazima 1992). For *T. s. stejnegeri* and other arboreal pit vipers, the prey-holding behavior makes inspection of the anterior end of the prey using these methods impossible. Under this condition, I want to know how they differentiate the ingestion direction and whether the snakes still ingest their prey mainly from the anterior end while in an arboreal environment.

MATERIALS AND METHODS

Adult *T. s. stejnegeri* (size range, 20.1-107.1 cm) were captured from Taipei, Miaoli, Hualien, and Pingtung Counties in Taiwan, and maintained in the laboratory on a 12: 12 h L: D photoperiod at 20-25°C. Snakes were individually housed in plastic boxes (of either 20 x 13 x 14 or 28 x 17 x 18 cm), fed mice every month, and provided with water ad libitum. Fluorescent lighting provided illumination during the day. Each plastic box contained wood chip bedding, a water cup, twigs, and a shelter. Prey used in this study included mice (*Mus musculus*; at 2.7%-54.1% of a snake's mass; relative prey size) and frogs (*Rana limnocharis*; at 4.0%-24.9% of a snake's mass).

Each trial began with the introduction of a single, live prey into the original box housing the snake or into another test box (28 x 17 x 18 cm) specifically designed for video recording. The room temperature was set to 21-24°C. All feeding behaviors of the snakes were recorded using a camera and a video recorder (Panasonic, Japan), as well as by visual observations, for at least 35 min. The capture position, direction of ingestion, and prey-handling tactics were observed and recorded for each feeding episode. To determine the center of gravity of prey, I grasped different regions (head, shoulders, waist, and hips) of the back of a prey with forceps, and checked which end of the hanging prey body was higher. When both ends of the prey body were at the same level, the grasped region was closest to the center of gravity (Fig. 1).

Capture positions were classified into 4 regions; anterior (head or neck), mid-anterior (shoulders, forelimbs, or thorax), mid-posterior (abdomen or waist), and posterior (hips, hindlimbs, or tail). The prey was enclosed in a small cup beneath the cover of the box and was released into the box at the start of the experiment. Each snake was subjected to only 1 trial. Data analysis was performed with the JMP (SAS Institute, Cary, NC, USA) statistical software. The log-likelihood ratio test (*G*-test), with Yates correction if needed, was used to assess (1) the frequency difference between anterior-first and posterior-first prey ingestion, (2) the frequency difference of prey struck on the posterior region, and (3) the frequency difference of anterior-first and posterior-first prey ingestion among different prey size groups. Testing for trends among proportions is a more-powerful procedure than is the hypothesis test of differences among proportions (Zar 1999). To test whether there was a linear increase in the frequency of head-first ingestion as the captured position was nearer the anterior end, I calculated and assessed the Chi-squared value of the linear trend (X_t^2) (Zar 1999; pp. 565-568). Differences were considered significant at $p < 0.05$. Data are presented as the mean ± standard error (SE).

RESULTS

Mostly, Chinese green tree vipers held onto their prey after a strike, but exceptions to this occurred when the prey was large and struggled violently. I found that 11 snakes released a mouse after capture; 81.8% of these mice ($n = 9$) weighed more than 33% of the snake's body mass. Following the death of the released mouse, the snake would inspect the mouse body, sometimes used its snout to touch it, and recaptured it. Eight (72.7%) of these recaptured mice were ingested from the anterior end.

The center of gravity of prey was close to the waist region in both prey types. When I grasped the prey in the waist region, both ends of prey body were at the same level (Fig. 1). When the grasping point was anterior to the center of gravity, such as head or shoulders, the anterior end of prey body was higher (Fig. 1). When the grasping point was posterior to the center of gravity, such as the hip region, the posterior end of the prey body was higher (Fig. 1). Similar results existed in real situations when snakes fed on prey (Fig. 2). After striking, a snake would withdrew to a branch with its head angled downward, and lifted the prey from the ground. The prey was hung with the body tilted like a lever with the fulcrum at the site of the bite. When the prey ceased struggling, the snake

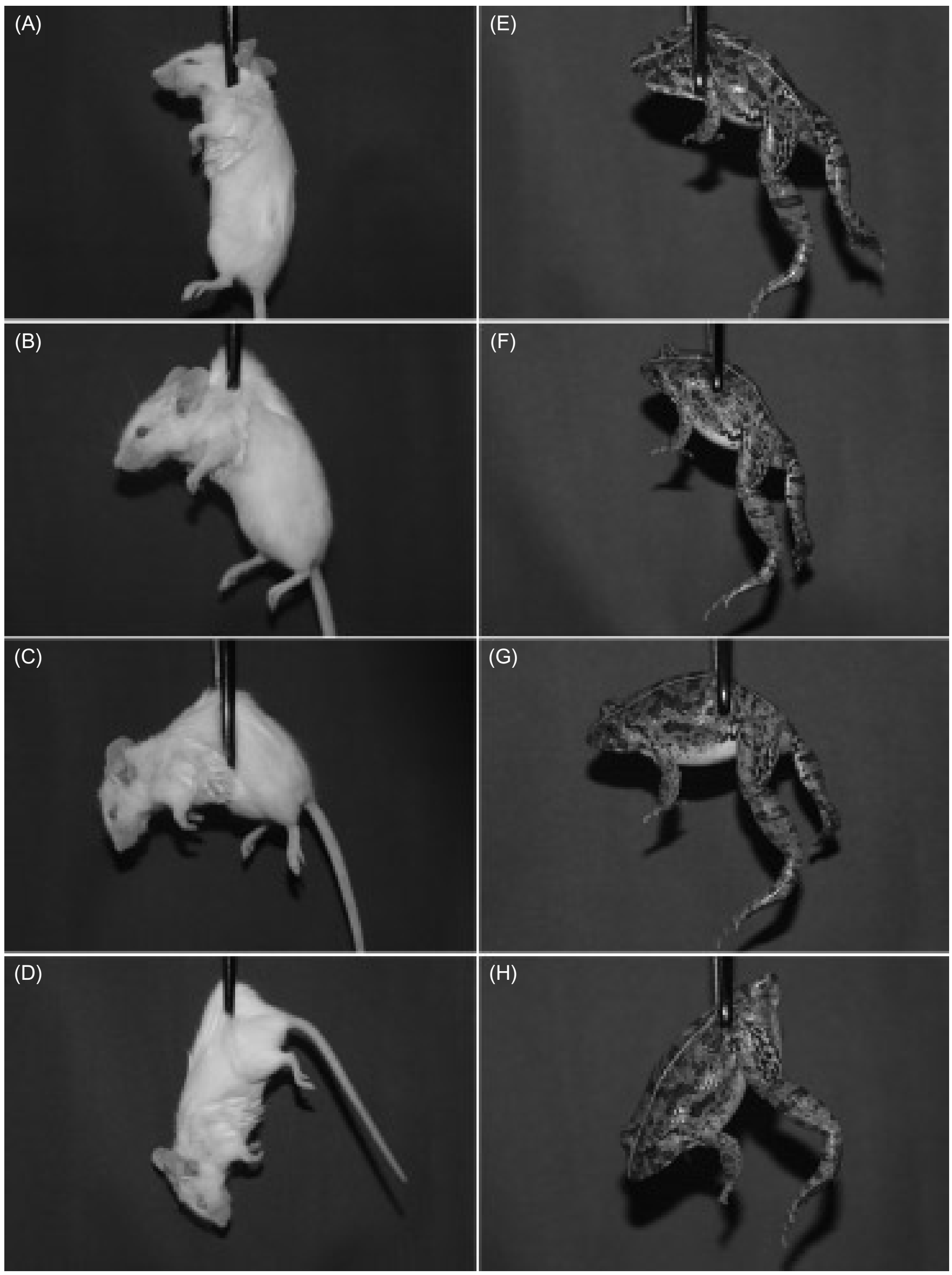

Fig. 1. Graphic illustration of the leverage involved in hanging prey items, when the prey was grasped in different body regions with forceps. The prey included mice (*Mus musculus*, 20.7 g; A-D) and frogs (*Rana limnocharis*, 11.7 g; E-H). The grasped regions included the head (A, E), shoulders (B, F), waist (C, G), and hips (D, H). The hanging prey body acted like a lever. When the grasped region was anterior to the center of gravity of the prey, such as the head and shoulder region, the anterior end of prey body was higher. When the grasped region was posterior to the center of gravity, such as the hip region, the posterior end of the prey was higher. When the grasped region was close to the center of gravity, such as the waist region, both ends of the prey body were at the same level.

would gradually maneuver its jaw to the higher end of the prey body and began ingesting it. I found that the proportion of anterior-first ingestion increased as the capture position was closer to the anterior end, and vice versa (Table 1) (X_t^2 = 33.51, *d.f.* = 1, $p < 0.0001$ for mice and X_t^2 = 23.44, *d.f.* = 1, $p < 0.0001$ for frogs). When a snake captured a mouse in the mid-posterior region, close to the center of gravity, the ingestion end ratio was close to 50: 50. However, frogs caught in the mid-posterior region were ingested anterior-end first (Table 1). I also observed that frogs would jump violently or stretch their hind legs forward, in an effort to push the snake's head away, for a long time after the strike if bitten forward of the posterior region. All prey were ingested from either end of the body, rather than the middle region.

Fewer than 10% of mice were struck in the posterior region (Table 1) and a significantly higher proportion was ingested from the anterior end (Table 2). Up to 42% of frogs were struck in the posterior region (Table 1), and the frequencies of anterior and posterior end ingestion did not significantly differ (Table 2). Compared to mice, a significantly higher proportion of frogs was struck in the posterior region (*G* = 13.55, *d.f.* = 1, *p* = 0.0002). Although an increase in prey size produced an increase in anterior-first ingestion (Table 3), no significant effect was found (*G* = 3.60, *d.f.* = 2, *p* = 0.17). A single attack was frequently sufficient for a snake to successfully capture a prey. The proportion of snakes that attacked prey more than once before a successful capture was 19.2% (14/73) when fed mice and 7.8% (3/38) when fed frogs.

DISCUSSION

Feeding adaptations have made important

Table 1. Frequencies of prey capture positions and the proportion of head-first ingestion when feeding on different types of prey (mice or frogs)

Prey type	Capture position[a]	*n*	Proportion of head-first ingestion
Mouse			
(*n* = 73; RPS[b] = 18.7% ± 1.4%)	Anterior	34	97.06%
	Mid-anterior	12	91.70%
	Mid-posterior	20	50.00%
	Posterior	7	0%
Frog			
(*n* = 38; RPS = 13.0% ± 0.9%)	Anterior	11	100.00%
	Mid-anterior	6	100.00%
	Mid-posterior	5	100.00%
	Posterior	16	12.50%

[a]Capture positions were classified into 4 regions; anterior (head or neck), mid-anterior (shoulders, forelimbs, or thorax), mid-posterior (abdomen or waist), and posterior (hips, hindlimbs, or tail). [b]RPS, relative prey size (mean ± standard error). Relative prey size = (weight of prey / weight of snake) x 100%

Table 2. Comparisons of ingestion positions when feeding on different types of prey

Prey type	Ingestion position		Log-likelihood ratio test (with Yates correction)[a]
	Anterior	Posterior	
Mouse (*n* = 73)	54 (20.0% ± 1.7%)[b]	19 (14.9% ± 2.4%)	*G* = 16.46, *p* < 0.0001
Frog (*n* = 38)	24 (12.0% ± 1.0%)	14 (14.6% ± 1.6%)	*G* = 2.15, *p* = 0.14

[a]To test the significance of the frequencies of anterior and posterior ingestion from equality.
[b]Numbers within parentheses are the relative prey sizes (mean ± standard error).

contributions to the evolutionary success of snakes (Mori 1994). Various morphological and behavioral specializations for feeding have been recognized in snakes. Two important methods of immobilizing prey, constriction and venom injection, have arisen in ophidian evolution (Shine 1985). Some snakes adopt both techniques, but the former has never been observed in viperids (Shine 1985). Arboreal vipers are forced to hold their prey after capturing it, a prey-handling behavior that may be adapted to non-constricting, terrestrial snakes with fangs. There are 2 factors that poten-

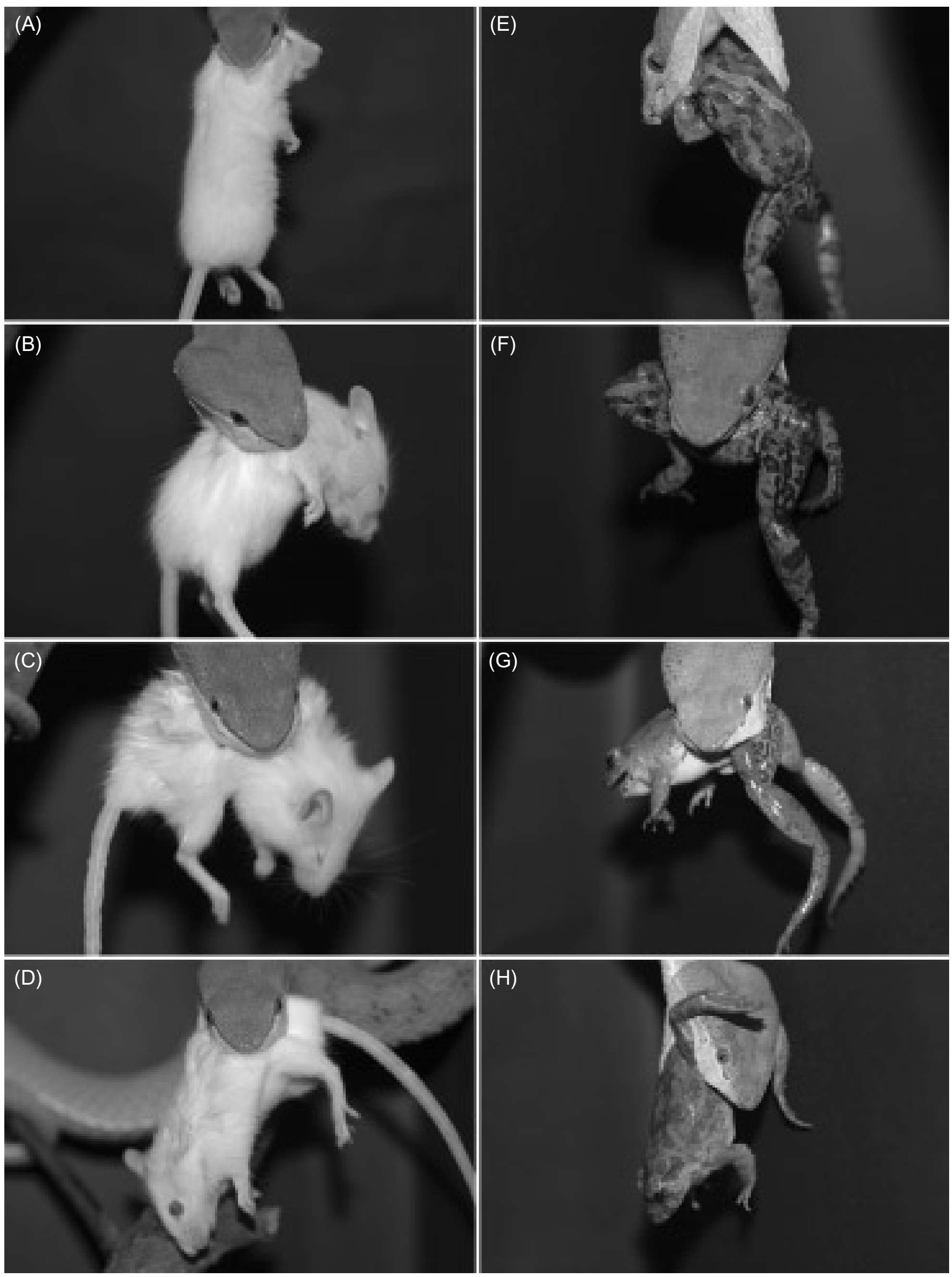

Fig. 2. Graphic illustration of the leverage which occurred in real situations, when snakes held their prey at different body regions. The prey included mice (*Mus musculus*; A-D) and frogs (*Rana limnocharis*; E-H). The captured regions included the head (A, E), shoulders (B, F), waist (C, G), and hips (D, H). The body weight ratios (in g/g) of prey/snake in (A) through (H) were 13.0/73.7, 10.1/75.2, 12.8/140.7, 10.5/94.9, 5.9/93.0, 9.4/148.9, 11.0/158.3, and 11.8/168.3, respectively. The hanging prey body acted like a lever, and the leverage was similar to that described in figure 1.

tially cause these snakes to hold on to their prey. First, the prey is small in size or exhibits little or no aggressive behavior. For example, the cottonmouth snake (*Agkistrodon piscivorous*) presents post-strike retention in fish, which lack claws and teeth with which to harm the attacking snake (Savitzky 1992). Other snakes, such as the coral snake (*Micrurus fulvius*), also feed on small, less-aggressive prey (e.g., small terrestrial snakes, elongate lizards, or amphisbaenians) and are able to retain them after a strike (Mushinsky 1987). Juvenile snakes also tend to exhibit greater retention of prey following a strike (Campbell and Solorzano 1992, Sazima 1992), while adults will release and trail larger prey (e.g., mammals). The relative prey size, rather than prey type, appears to determine which feeding strategy is adopted (Brown and Lillywhite 1992). The 2nd factor is ease with which the prey can be relocated after release. Desert sidewinders have a tendency to seize and hold prey until the struggle ceases, before releasing it for swallowing (Brown and Lillywhite 1992). This is due to the extremely cursorial behavior of desert mammals and lizards, which unless killed on the spot can probably run some distance; it would be difficult for desert sidewinders to relocate their prey. Another disadvantage is the hot substrate, which makes it impossible for a snake to follow its prey out into the open. The release and re-gripping maneuver of some venomous, piscivorous snakes seems to be unique, with the snake taking advantage of the buoyancy and inertia of its prey (Mori 1998). For Chinese green tree vipers, the relatively small size and lack of aggression of prey and the difficulty of relocating prey from their high arboreal positions could all be factors affecting the retention of prey following a strike. In most cases in the laboratory, snakes were unable to hold prey when its relative size exceeded 33% of the snake's own body mass. However, whether this is also true in the field requires further verification.

Snakes may use visual, infrared, chemical, and/or tactile cues in the feeding process (Murphy and Campbell 1987, Ford and Burghardt 1993, Young and Morain 2002, Young 2003). It is possible that snakes may use chemosensory and tactile cues, such as the direction of the hair or scales and the shape of snout and skull, to determine the direction of ingestion (Cock Buning 1983, Mushinsky 1987, Mehta 2003). The effect of gravity on the ingestion direction has not been proposed before this study. Under the action of gravity, the hanging prey acts like a lever with the fulcrum at the bite site. The end further from the bite site hangs lower, therefore making it more energy-efficient for the snake to maneuver its jaw to the higher end. This explains why there was a relationship between the location of the bite and the end of the prey which was ingested. When the strike site was located near the center of gravity, it was more difficult for the snake to determine the higher end of the prey, and it spent a longer time deciding on the ingestion direction (Tsai, unpubl. data). If energy efficiency is a critical factor, it might be common for other arboreal pit viper species to ingest prey from the higher end. Violation to the above rule of deciding the ingestion direction in this study occurred with frogs caught in the mid-posterior region, close to their center of gravity, which were ingested anterior-first. One possible explanation for this is the stout resistance put up by captured frogs. They sometimes jumped violently or stretched their hind legs forward in an effort to push the snake's head away for long periods of time after the strike if bitten forward of the posterior region, so frogs were usually not ingested posterior-first.

Anterior-first ingestion in piscivorous snakes seems to be more obligatory and independent of prey size, while the direction of ingestion is generally facultative and dependent on prey size for snakes feeding on lizards, rodents, frogs, and snakes (Mori 1998). Generally, larger prey tends to be ingested anterior-first (Mori 1994, Mehta 2003). This tendency occurred in *T. s. stejnegeri*, when feeding on mice. However, this trend was not found to be statistically significant, possibly owing to the small prey size used (median, 15.8% relative prey size). Rattlesnakes (*Crotalus*) struck rodents behind the head or shoulder region in over 70% of trials, and the mice died faster as a result (Kardong 1982). A similar behavior seemed to occur in *T. s. stejnegeri* when feeding on mice, but not when feeding on frogs.

Table 3. Comparisons of ingestion positions among different prey (mouse) size groups

Ingestion position	Relative prey (mouse) size		
	< 10%	10%-20%	> 20%
Anterior	9	25	20
Posterior	7	8	4

Acknowledgments: I thank C.C. Lin, S.M. Huang, T.W. Lee, W.H. Liao, H.C. Su, W. Chen, S.P.

Huang, and T.W. Shiau for assistance with field and laboratory work. In particular, I thank my graduate adviser, Dr. M.C. Tu, for providing comments that improved the manuscript. Additional thanks go to Dr. S.H. Chen for offering additional laboratory space, Dr. Y. Hsu for instructions in statistics, and T.L. Gorton, D.A. Pike, and A.K.S. Tan for proofreading the manuscript. My gratitude also goes to the Academic Paper Editing Clinic, at National Taiwan Normal University.

REFERENCES

Brown TW, HB Lillywhite. 1992. Autecology of the Mojave desert sidewinder, *Crotalus cerastes cerastes*, at Kelso Dunes, Mojave Desert, California, USA. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 279-308.

Campbell JA, A Solorzano. 1992. The distribution, variation, and natural history of the middle American montane pitviper, *Porthidium godmani*. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 223-250.

Cock Buning T de. 1983. Thermal sensitivity as a specialization for prey capture and feeding in snakes. Am. Zool. **23:** 363-375.

Creer S, WH Chou, A Malhotra, RS Thorpe. 2002. Offshore insular variation in the diet of the Taiwanese bamboo viper *Trimeresurus stejnegeri* (Schmidt). Zool. Sci. **19:** 907-913

Ford NB, GM Burghardt. 1993. Perceptual mechanisms and the behavioral ecology of snakes. *In* RA Seigel, JT Collins, eds. Snakes: ecology and behavior. New York: McGraw-Hill, pp. 117-164.

Greene HW. 1992. The ecological and behavioral context for pitviper evolution. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 107-117.

Kardong KV. 1982. Comparative study of changes in prey capture behavior of the cottonmouth (*Agkistrodon piscivorus*) and Egyptian cobra (*Naja haje*). Copeia **1982:** 337-343.

Lillywhite HB, RW Henderson. 1993. Behavioral and functional ecology of arboreal snakes. *In* RA Seigel, JT Collins, eds. Snakes: ecology and behavior. New York: McGraw-Hill, pp. 1-48.

Lillywhite HB, AW Smits. 1992. The cardiovascular adaptations of viperid snakes. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 143-153.

Mao SH. 1970. Food of the common venomous snakes of Taiwan. Herpetologica **26:** 45-48.

Mehta RS. 2003. Prey-handling behavior of hatchling *Elaphe helena* (Colubridae). Herpetologica **59:** 469-474.

Mori A. 1994. Prey-handling behaviour of newly hatched snakes in two species of the genus *Elaphe* with comparison to adult behaviour. Ethology **97:** 198-214.

Mori A. 1998. Prey-handling behavior of three species of homalopsine snakes: features associated with piscivory and Duvernoy's glands. J. Herpetol. **32:** 40-50.

Murphy JB, JA Campbell. 1987. Captive maintenance. *In* RA Seigel, JT Collins, SS Novak, eds. Snakes: ecology and evolutionary biology. New York: Macmillan, pp. 165-181.

Mushinsky HR. 1987. Foraging ecology. *In* RA Seigel, JT Collins, SS Novak, eds. Snakes: ecology and evolutionary biology. New York: Macmillan, pp. 302-334.

Pope CH. 1935. The reptiles of China, turtles, crocodilians, snakes, lizards. Natural History of Central Asia, Vol. 10. New York: American Museum of Natural History.

Savitzky BAC. 1992. Laboratory studies on piscivory in an opportunistic pitviper, the cottonmouth, *Agkistrodon piscivorus*. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 347-368.

Sazima I. 1992. Natural history of the jararaca pitviper, *Bothrops jaracaca*, in southeastern Brazil. *In* JA Campbell, ED Brodie Jr, eds. Biology of the pitvipers. Tyler, TX: Selva Press, pp. 199-216.

Shine R. 1985. Prey constriction by venomous snakes: a review, and new data on Australian species. Copeia **1985:** 1067-1071.

Young BA. 2003. Snake bioacoustics: toward a richer understanding of the behavioral ecology of snakes. Q. Rev. Biol. **78:** 303-325.

Young BA, M Morain. 2002. The use of ground-borne vibrations for prey localization in the Saharan sand vipers (*Cerastes*). J. Exp. Biol. **205:** 661-665.

Zar JH. 1999. Biostatistical analysis. 4th ed. Upper Saddle River, NJ: Prentice-Hall.

Zhao EM, K Adler. 1993. Herpetology of China. Society for the Study of Amphibian and Reptiles. Oxford, OH: Oxford Press.