

Food Habits of the Taiwanese Mountain Pitviper, *Trimeresurus gracilis*

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Chia-Fan Lin and Ming-Chung Tu (2008) Food habits of the Taiwanese mountain pitviper, *Trimeresurus gracilis*. *Zoological Studies* 47(6): 697-703. We studied the food habits of the Taiwanese mountain pit viper, *Trimeresurus gracilis*, by checking gut contents and conducting feeding trials. In total, the stomach contents of 160 snakes were checked. The stomachs of only 27 (16.9%) snakes contained prey items, and most (88.5%) of the prey items had been swallowed head-first. The prey-predator mass ratios ranged 0.08-0.81, and prey mass was positively correlated with snake snout-vent length. An ontogenetic diet shift from ectothermic to endothermic prey was evident: only ectotherms (lizards, 91.7% and amphibians, 8.3%) were found in the guts of yearlings, whereas mammals (rodents and shrews) represented 68.1% of gut contents of adults. Additionally, adult females and males presented different diets. Females preyed mostly on rodents (45.5%), whereas males preyed mostly on shrews (59.3%). Consistent with the gut content analysis, in feeding trials, neonates preferred lizards and frogs whereas adults preferred mice. Invertebrate prey was always ignored in the feeding trials and was considered to be secondary prey. <http://zoolstud.sinica.edu.tw/Journals/47.6/697.pdf>

Key words: Snake, Diet, Gut content, Food, Ontogenetic diet shift.

Determining the food habits of a particular species is a fundamental issue in understanding its ecology (Litvaitis 2000). On the basis of dietary information, we can understand the relationship between prey and predator and the feeding niche of a species within an ecosystem. Dietary information is essential for understanding foraging behaviors (Lind and Welsh 1994), habitat use (Reinert 1993), reproductive strategies (Shine and Madsen 1997), migration activities (Forsman and Lindell 1997), predator-prey co-evolution (Downes and Shine 1998), and behavioral genetics (Arnold 1981). Data on diet is essential to wildlife management, especially for threatened and endangered species (Litvaitis 2000, Holycross and Mackessy 2002).

Interspecific variations in diet have been found in snakes (Rodriguez-Robles et al. 1999a), and in many species, diet varies geographically (Daltry et al. 1998, De Queiroz et al. 2001, Creer et al. 2002), seasonally (Houston and Shine 1993,

Santo et al. 2000, Hirai 2004), between the sexes (Houston and Shine 1993, Su et al. 2005), or among age classes (Cobb 2004). Ontogenetic shifts in prey types are a recurrent pattern in many snake families (Kjaergaard 1981, Schulz 1996, De Queiroz et al. 2001, Valdujo et al. 2002); for example, crotalines and viperines commonly switch from ectotherms to endotherms as they mature (Greene 1997, Holycross and Mackessy 2002, Martins et al. 2002).

The diets of many Taiwanese snakes have been reported (Mou 1970, Lee and Lue 1996, Creer et al. 2002, Su et al. 2005). Despite the increasing number of studies, most of them only report a list of prey items yet lack greater detail of food habits, especially ontogenetic and sexual divergences in the diets.

The Taiwanese mountain pit-viper (*Trimeresurus gracilis*) is a small venomous snake endemic to Taiwan. It is found underneath

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rocks in low scrub vegetation at elevations above 2000 m in mountainous areas (Wang and Wang 1956, Keegan and Matsui 1964). In this study, we focused on the feeding ecology to reveal the diet composition, prey preference, and ontogenetic and sexual dietary divergences of *T. gracilis*.

MATERIAL AND METHODS

Snake collecting, measurement, and maintenance

This work was approved (approval no 93009) by the Animal Care and Use Committee of the National Taiwan Normal University, and we adhered to the laws. The snakes were released to the original site of capture after the experiments. From 2002 to 2005, we collected live *T. gracilis* in Yushan and Taroko National Parks and Taipingshan, Kuanwu, and Tahsuehshan Forest Recreation Areas. Museum specimens were from the High Mountain Museum, Alishan and the National Museum of Natural Science, Taichung, and some individuals were also collected which had been killed on provincial highways 18, 21, and 20 near areas where we collected live snakes. For each snake, we recorded the locality, snout-vent length (SVL, using measuring tape to the nearest 0.1 cm), sex (using a sexual probe), and body mass (using a scale to the nearest 0.1 g). According to SVL, we classified snakes into the 3 categories of yearlings, subadults, and adults. A yearling's SVL of ≤ 22 cm was the maximal length of 1-yr-old snakes born in the lab. The SVLs of adult male and female snakes were the minimum sexual mature length from our accumulated data, at ≥ 30 and 37 cm respectively. The SVL of subadults was located between that of yearlings and adults (22-30 cm for males; 22-37 cm for females). After checking for the presence of stomach contents (see below), snakes were housed in individual plastic containers (27 x 18 x 16 cm for adults and 20 x 17 x 11 cm for neonates) with shelter and water ad libitum for subsequent feces collection.

Prey items

We investigated prey items by checking both live and dead snakes. For live snakes, as soon as they were captured in the field, we palpated the belly to detect ingested prey items. If any food remains were present in the stomach, we

forced the snake to regurgitate by gently pushing them towards the snake's mouth. Snakes were then brought back to the laboratory to collect their feces. We dissected dead specimens to obtain the stomach contents and fecal samples. We recorded prey number, length, weight, and the direction of ingestion in the stomach. Prey length was measured by calipers to the nearest 0.1 mm, and prey weight was measured on an electronic scale to the nearest 0.1 g after being blotted dry with a paper towel. Both stomach contents and feces were preserved in 75% alcohol. The total mass of partially digested prey items was estimated using linear regressions for the relationships of body parts of complete specimens of the same species (Perrin and Bodbijn 2001). Amphibian remains were identified to the lowest taxonomic level using morphological characters. Lizard remains were identified to species from whole remains or scales, by which means the 3 species of resident lizards can easily be distinguished. Mammal remains were identified to order, and to species when possible, by checking characteristics of hair medulla and dentition.

Feeding trials

Eight adult snakes were starved for 1 mo, and 11 neonates were starved for 2 wk before offering each prey item. We sequentially offered each snake one of 6 types of prey in random order: a small mammal (*Mus musculus*), lizard (*Sphenomorphus taiwanensis*), frog (*Buergeria japonicus*), annelid (*Perionyx excavatus*), arachnid (*Brachytripes portentosus*), and mollusk (*Philomycus bilineata*). Each prey was offered 1 time. We put each individual prey item into a snake's cage and checked to see if it had been consumed after 72 h. If the prey had not been ingested, it was removed and a different type of prey was placed in the cage and left for another 72 h. These sequential offerings continued until 1 prey item was ingested. When a prey was ingested, we waited 1 mo for adults and 2 wk for neonates before offering a new prey type. The feeding trial of each snake was completed when all 6 types had been offered.

Statistics analysis

We used Pearson Chi-square tests with Yates' correction to determine if there was a significant difference in the direction of ingestion. We used a Spearman rank correlation to determine if there

was a significant positive correlation between prey mass and snake SVL. An ontogenetic shift in the diet was evidenced by comparing snake size with the type of prey consumed (endothermic vs. ectothermic) (Rodriguez-Robles et al. 1999a). For this, a Kruskal-Wallis test was performed using prey type as the factor and body size as the variable; we used pair-wise comparisons for post-hoc testing.

To gather more information, we combined stomach contents with fecal remains. We conservatively recorded the number of prey items. If the same prey was in the stomach contents and fecal remains, we counted it as 1 item. We restricted the contingency table to the different mammalian taxa (rodents and shrews) and used Fisher's exact test to determine whether male and female snakes preyed on different mammalian prey. In the feeding trials, we used Fisher's exact test to determine whether adult and neonate snakes preyed on different prey types. All statistical tests were performed using JMP 5.01 (SAS Institute, Cary, NC, USA). Means are followed by the standard error. All tests were

2-tailed, and the significance level was set to $p = 0.05$.

RESULTS

Food habits

In total, 169 snakes (160 live snakes, 5 road kills, and 4 museum specimens) were examined, of which 9 individuals were not checked for stomach contents but their feces was collected. We collected 28 stomach contents from 160 snakes, of which only 27 (16.9%) individuals contained prey items. We examined 169 snakes and obtained fecal remains from 93 individuals, of which only 62 (36.7%) snakes contained feces. Prey items are summarized in table 1. Each snake had a single stomach content, except for 1 snake which had ingested 2 lizards. Of the 26 stomach contents for which the direction of ingestion could be determined, 23 (88.5%) items had been swallowed head-first ($\chi^2 = 13.88$, $p < 0.001$). The 3 prey items ingested tail-first were all relatively small

Table 1. Prey items recorded in the stomach and fecal remains of live, museum, and road kill specimens of *Trimeresurus gracilis* ($n = 169$) in Taiwan

Prey taxon	<i>Trimeresurus gracilis</i>	
	Stomach contents	Fecal remains
	$n = 27$	$n = 62$
Arthropoda (secondary ingestion)	0	27
Amphibia		
Caudata		
<i>Hynobius arisanensis</i>	5	0
Reptilia		
Squamata		
<i>Eumeces elegans</i>	0	1
<i>Sphenomorphus taiwanensis</i>	11	14
<i>Takydromus hsuhsanensis</i>	6	9
Mammalia		
Rodentia		
<i>Apodemus semotus</i>	1	1
<i>Eothenomys melanogaster</i>	1	1
<i>Volemys kikuchii</i>	2	1
Unidentified species	0	7
Insectivora		
<i>Soriculus fumidus</i>	1	3
Unidentified species	0	24
Unidentified prey category	1	5
Total	28	93

items: a shrew (*Soriculus fumidus* of 4.4 g) eaten by a female (SVL of 39.7 cm), and 2 salamanders (*Hynobius arisanensis* of 1.3 and 3.2 g) eaten by 2 neonates (SVLs of 17.7 and 21.5 cm). The prey-predator mass ratio of these 3 cases were all < 0.1 ; in all the others, it ranged 0.084-0.807 (mean \pm S.E. = 0.396 ± 0.058 , $n = 16$). There was a significant positive correlation between prey mass and predator snout-vent length (Spearman Rho = 0.6824, $p = 0.0036$, $n = 16$) (Fig. 1). The snout-vent length of snakes that consumed mammal (SVL of 42.1 ± 3.3 cm, $n = 5$), lizard (SVL of 22.6 ± 1.3 cm, $n = 16$), and amphibian (SVL of 22.12 ± 1.9 cm, $n = 6$) prey significantly differed (Kruskal-Wallis test, $p = 0.0027$) (Fig. 2). The SVL of snakes that consumed amphibians did not differ from that of snakes that consumed lizards, but snakes that consumed mammals were significantly larger than those that consumed lizards and amphibians (Pair-wise comparison, $p < 0.01$).

We combined stomach contents with fecal remains, but excluded 5 unidentified fecal items and 27 arthropod items, and results revealed an ontogenetic dietary shift (Fig. 3). We found that lizards were the main prey of yearlings, comprising 91.7% of their diet. None of the yearlings preyed on mammals (rodents or shrews). Shrews were the main prey of subadults (75.0%) and adults (47.7%). None of the subadults preyed on rodents, which comprised 20.5% of the adult diet. Together, rodents and shrews comprised 68.1% of the food items of adults. Amphibians were absent from the adult diet, and lizards comprised only 30.4% of items. Among adult snakes, males had preyed on 2 (7.4 %) rodents, 16 (59.3%) shrews, and 9 (33.3 %) lizards. Females had ingested 5 (45.5%) rodents, 4 (36.4%) shrews, and 2 (18.2%) lizards. Females preyed more on rodents than did males (Fisher's exact test, $p = 0.0235$), thus showing a significant difference in the dietary composition between sexes.

Feeding trials

Neonates used in the feeding trials ($n = 11$) had an average SVL of 192 ± 2.4 mm and mass of 4.7 ± 0.1 g. Adults ($n = 8$) had an average SVL of 400 ± 2.3 mm and mass of 64.3 ± 18 g. All neonates ate frogs and lizards, and only 1 neonate ingested a mouse. All adults ate mice, 2 preyed on frogs, and 3 on lizards. Neonates ingested more ectothermic prey than did adults (Fisher's exact test, $p = 0.0003$). Both neonates and adults ignored slugs, earthworms, and crickets (Fig. 4).

DISCUSSION

Our experiments clearly show that invertebrates are secondary prey items of *T. gracilis*: (1) no snake preyed on any of the invertebrates during the feeding trials; (2) we found no invertebrate prey in the stomach contents; and (3) in fecal remains, invertebrates always appeared with shrews or lizards that mainly feed on invertebrates. The same conclusion was reached by Creer et al. (2002), studying *T. s. stejnegeri*, which was determined to feed mainly on amphibians.

Lee (1996) reported that salamanders and rodents were food items of *T. gracilis*. Our findings indicated that *T. gracilis* not only feeds on salamanders and rodents, but also includes shrews, lizards, and frogs. The generalist diet of *T. gracilis*, based on small mammals, amphibians, and lizards, is similar to those of other congeneric vipers (Mori and Moriguchi 1988, Saviozzi 1997). Because *T. gracilis* takes various types of prey, it should be considered a generalist predator.

The frequency of prey found in the stomach of ambush snakes is usually low, for example, 8.1% in *Acanthophis antarcticus* (Shine 1980), 13%-15.4% in *T. s. stejnegeri* (Mao 1970, Creer 2002), 15.0% in *Crotalus viridis* (Shine 1986), and 16.1% in *C. horridus* (Clark 2002). On the other hand, active foragers have higher feeding frequencies even in temperate areas: 26%-63% in *Thamnophis sirtalis*, 41% in *Nerodia rhombifera* (Shine 1986), 23%-70% in 5 Australian elapids, and 35%-81% in some species of Hydrophiidae. In our study, 27 stomachs (16.9%) of the 160 *T. gracilis* examined contained prey items, suggesting that this species is an ambush forager. However, the body shape of *T. gracilis* is unlike a typical ambush viper, which normally has a short, thick body. In addition to being an ambusher, limited prey availability and/or low energy requirements can also explain a low proportion of prey in snakes (Mushinsky 1987).

Trimeresurus gracilis showed an ontogenetic shift in its diet. Juveniles consumed a large proportion of lizards and switched to shrews as they grew, while larger size classes fed on larger rodents such as *Apodemus semotus*. Ontogenetic dietary shifts from ectotherms to endotherms have been reported in many species (Henderson 1993, Rodriguez-Robles et al. 1999b, Shine et al. 1998, Luiselli and Capula 1997, Shine 1980), and it is very common among viperids (Greene 1992, 1997, Holycross and Mackessy 2002). Martins (2002) showed that almost all of the 22 species

of *Bothrops* exhibit ontogenetic dietary shifts, except for 4 species that have specialized diets. Similarly, six of 8 European vipers switch their diets from lizards to mammals as they grow (Saint Girons 1980). An ontogenetic dietary shift might result from shifts in habitat use (Lind and Welsh 1994) or gape size (Forsman and Lindell 1993). Our results revealed that amphibian prey became less common in adults (Fig. 3), which suggests that adult snakes might use habitats away from wet areas, whereas subadult and yearling snakes might visit wet areas more frequently. A study of their habitat selection might show whether this is

true. As gape-limited predators, larger snakes can swallow larger prey (King 2002). Although gape size might not limit young snakes from ingesting a newborn endotherm, strong parental care by endotherms may prevent this from happening. Avoiding newborn endotherms may prevent young snakes from being attacked by aggressive parents in the wild. Our feeding trials suggested that this might be the case for *T. gracilis*. Even though the mammals provided were small enough for neonate snakes to swallow, they still preferred frogs and lizards to mammals.

Prey size increases with snake size, and

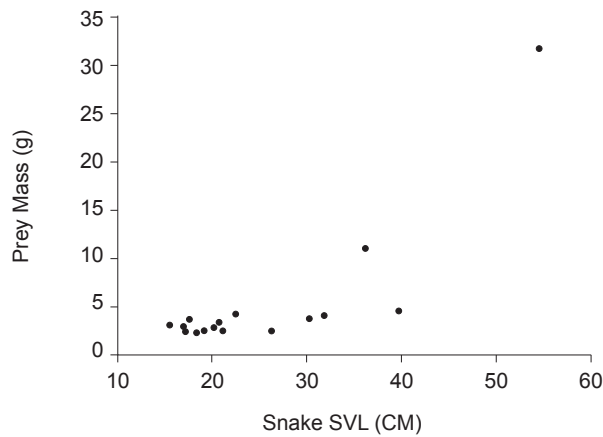


Fig. 1. Relationship between prey mass and snake snout-vent length (SVL) of *Trimeresurus gracilis* ($n = 16$) from Taiwan.

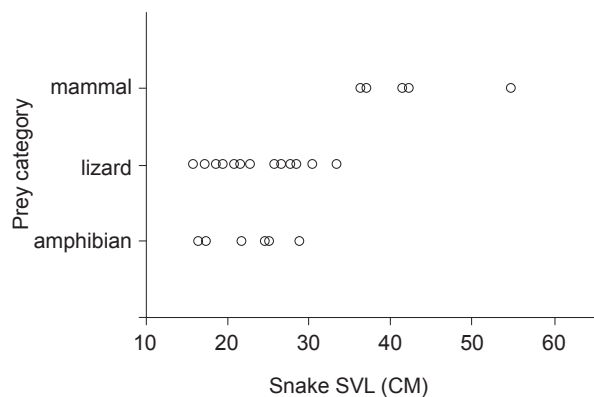


Fig. 2. Relationship between prey type and snake snout-vent length (SVL) of *Trimeresurus gracilis* ($n = 27$, prey items = 28) from Taiwan.

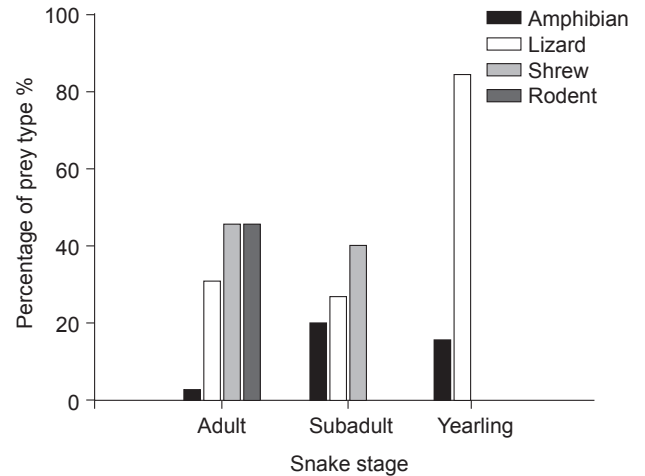


Fig. 3. Relative frequencies (%) of each prey type in the diet composition of adults ($n = 97$), subadults ($n = 28$), and yearlings ($n = 44$) of *Trimeresurus gracilis* in Taiwan.

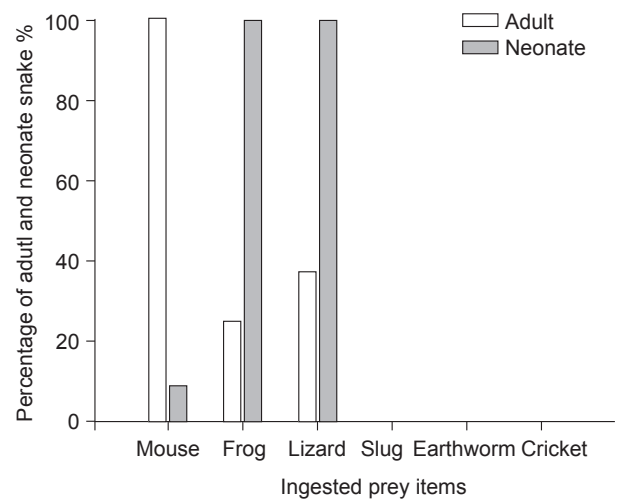


Fig. 4. Percentages of adult ($n = 8$) and neonate ($n = 11$) *Trimeresurus gracilis* that had ingested each type of prey in the feeding trials.

in mountainous areas of Taiwan, rodents (SVL of 7.4-18.6 cm) are generally larger than shrews (SVL of 6.0-10.8 cm) (Chyi 1998). Stomach contents and fecal remains in our samples revealed that females fed on a higher proportion of rodents, whereas males rarely preyed on those animals. Dietary divergence between the sexes has been reported in snake populations with significant sexual size dimorphism (Santo et al. 2000, Nogueira et al. 2003), especially in head size (Shine 1991). Mature *T. gracilis* females are significantly larger than mature males in body mass (*t*-test, $p < 0.0001$), SVL (*t*-test, $p < 0.0001$), and head size (one-factor ANCOVA, sex: factor, SVL: covariate, head length, $F_{1,100} = 151.8$, $p = 0.014$, head width, $F_{1,100} = 80.59$, $p = 0.026$) (more-detailed data will be published soon). The dietary divergence between sexes in *T. gracilis* might be due to their sexual size dimorphism, as in other vipers (Shine et al. 1998, Nogueira et al. 2003).

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