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Offshore Insular Variation in the Diet of the Taiwanese Bamboo Viper *Trimeresurus stejnegeri* (Schmidt)

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ABSTRACT—Dietary data were ascertained for 229 *T. stejnegeri* (snout vent length >300mm) from 36 localities throughout the main island of Taiwan and the outlying Orchid (Lanyu) and Green (Ludau) Islands. Twenty nine percent of the snakes were devoid of any prey, and of the snakes containing prey, 43% of the cases were unidentifiable. This relatively large proportion of unidentifiable prey items (observed in the hindgut) may reflect either rapid digestion of amphibian prey and/or rapid venting of feces as an evolutionary adaptation to arboreal life. *Trimeresurus stejnegeri* appears euryphagous, taking primarily amphibians, but additionally reptilian, mammalian and insect prey. There was no discrepancy in prey composition based on comparisons of where the prey item was recorded in the digestive tract. No sexual variation in diet composition was evident, although males were more likely to contain prey than females, indicating the utilisation of different foraging strategies on similar sympatric prey items. Variation in diet composition was observed between mainland Taiwan and offshore islands, which is most likely the result of differences in prey availability.

Keywords: *Trimeresurus stejnegeri*, diet, Taiwan

INTRODUCTION

Intraspecific variation in the diet composition of non-venomous snake species has been studied at a number of levels throughout space and time. Geographic (Kephart and Arnold, 1982; Gregory and Nelson, 1991; King, 1993), ontogenetic (Mushinsky *et al.*, 1982; Wallace and Diller, 1990), sexual (Houston and Shine, 1993) and seasonal variations (García and Drummond, 1998) have been recorded and attributed to the interaction of life-history characteristics with ecological and/or environmental parameters.

Further studies have detailed the diet and trophic ecology of venomous species (Pernetta, 1977; Shine, 1977, 1987, 1989; Macartney, 1989; Wallace and Diller, 1990; Dalttry *et al.*, 1998), including East Asian members of the genus *Trimeresurus* (Koba, 1961, 1963a,b, 1979; Mori and Moriguchi, 1988; Mori *et al.*, 1989). The bamboo viper, *Trimeresurus stejnegeri* (Schmidt) is a nocturnal (Tu *et al.*, 2000) and arboreal pitviper predominately occupying riparian niches (Mao, 1993) throughout South-east and East Asia. The nominal species is currently thought to range from India and Nepal through Myanmar and SE Asia to China and Taiwan

(McDiarmid *et al.*, 1999). Although generally limited to higher altitude forests (>800m) on the continent, the snake is widespread throughout Taiwan from sea level to 1800m (Creer *et al.*, 2002). East Asian *Trimeresurus* species appear euryphagous, taking a combination of endothermic and ectothermic vertebrates, and invertebrate prey (Koba, 1961; Mori and Moriguchi, 1988; Mori *et al.*, 1989). Frog, rat and shrew remains were found in the stomachs of *T. stejnegeri* from mainland China (Pope, 1935). Within Taiwan, up to 10 species of ranid and rhacophorid frogs (including tadpoles), lizards, birds and mammals have been recorded as prey items of *T. stejnegeri* (Mao, 1970, 1993; Lee and Lue, 1996).

Many ophidian diet studies have relied on regurgitated stomach contents from live specimens (Kephart and Arnold, 1982; Gregory and Nelson, 1991; Houston and Shine, 1993; King, 1993). However, the only way to unequivocally ascertain diet composition relies upon examination of the entire digestive tract (stomach and hindgut) of autopsied or museum voucher specimens (Koba, 1961; Shine, 1977, 1989; Macartney, 1989; Wallace and Diller, 1990; Campbell and Solorzano, 1992). Some studies have summarised diet composition by only searching the stomachs of autopsied or museum specimens (Pernetta, 1977; Rodríguez-Robles *et al.*, 1999), ignoring the hindgut, which has proven an invaluable source of dietary information (Saviozzi and Zuffi, 1997;

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Daltry *et al.*, 1998). It is therefore desirable to include dietary information from both the stomach and hindgut of autopsied or museum specimens to ensure a complete picture of diet.

This study describes the diet of the bamboo viper, *Trimeresurus stejnegeri*, throughout its range in Taiwan. Diet composition is determined by analysis of both the stomach and hindgut contents. Sexual variation in diet composition is examined in addition to geographic variation in diet between the main island of Taiwan and two outlying Pacific islands.

MATERIALS AND METHODS

The contents of the digestive tracts of 229 *T. stejnegeri* (snout vent length (SVL) >300mm, male n=164, female n=65) sampled from 36 geographically widespread localities around mainland Taiwan and Orchid and Green islands (Fig. 1) were examined for remnants of ingested prey (catalogue numbers in Creer [2000] from the National Museum of Natural Science (NMNS), Taiwan, collection). They were usually sacrificed within 24 hr of capture. Although SVLs over 370mm (male) and 432mm (female) can be regarded as thresholds for sexual maturity in this species (Tsai and Tu, 1998), snakes with SVLs over 300mm were used to maximise sample size (only 3% of the snakes included in the analysis had a SVL between 300mm and the threshold SVL for sexual maturity). The snakes were individually examined by making a mid-ventral incision through the body wall from the anterior region of the stomach to the vent, thus revealing the entire digestive tract where food items would be located if present. This was then carefully scanned for stomach contents and prey items at any stage of digestion. The location of any digestive tract contents ranging from almost whole or partially digested prey items to fecal pellets was subsequently recorded. All contents were removed and preserved in industrial methylated spirit (IMS) for closer examination. Recognisable prey items were recorded to class, order, genus and species where possible. Prey biomasses were not recorded due to the advanced stages of digestion evident even in recognisable prey. Hindgut contents not identifiable by eye were resuspended in approximately 20mls of IMS in a petri dish and teased apart using forceps. The plate contents were subsequently scanned using a dissecting microscope ($\times 10$ – $\times 40$ magnification).

Keratin is highly resistant to digestion and therefore fur, claws and scales can pass through the digestive tract almost entire. Consequently, the presence of fur and/or whiskers was recorded as mammalian prey. Chitinous arthropod exoskeletons are invariably broken up due to the mechanical forces of ingestion, but additionally pass through the intestine undigested (Daltry *et al.*, 1998). Consequently, arthropods were only recorded as prey if the specimen or body fragments were either too large and/or intact to be the product of secondary ingestion of primarily ingested prey, and unaccompanied by the digested remnants of any other prey (Neill and Allen, 1956). Amphibians were recorded as prey items if recognisable, or if small arthropod body fragments were found in the hindgut without the digestive products of any other vertebrate prey (Daltry *et al.*, 1998). To further test this assumption, the stomach contents of all the partially digested amphibians with intact stomachs were scanned using the process described above to check that the diet of amphibian prey consisted primarily of small arthropods. The presence of either scales or reptilian claws with or without chitinous arthropod fragments was recorded as reptilian. Combinations of prey within a single snake were recorded according to the above criteria. If there was any uncertainty of the identification of any prey item, it was recorded as unidentifiable.

Given that *T. stejnegeri* exhibits sexual dimorphism (Tsai and Tu, 1998; Tu *et al.*, 2000), a 2-sample t-test was used to test

whether size dimorphism existed between the male and female sampled snakes. Chi-squared contingency table tests (Sokal and Rohlf, 1995) were used to statistically compare the results of the diet analyses with respect to where the prey item was found in the digestive tract, the composition of male and female diets and of snakes from different geographic regions shown in Fig. 1. The groupings were chosen according to areas with similar biogeographical history, geographical proximity and micro-environmental characteristics (thus representing homogenous ecological environments and available prey biota) whilst maximising sample size within each category. The two sample sites (site 28, Paoli, and site 12, Chufengshan) at the southern tip of Taiwan comprised only five observations of amphibian prey and could have been grouped with either the western, or east coast datasets, without biasing any statistical analysis. If significant geographic differences in prey types were found, temporal and size comparisons were further tested (2 sample t-tests) to check whether any seasonal differences of prey consumption and/or body size differences among the geographic regions were apparent. All statistical analyses were performed using Minitab version 13.1.

RESULTS

Forty six (29%) of the *T. stejnegeri* were devoid of any prey, whereas 183 (71%) had at least the remnants of some prey items in the digestive tract. Of the snakes containing prey, 79 (43%) cases were unidentifiable, but 104 (57%) cases of the contents could be assigned to a particular prey taxon or taxa. Eighty eight snakes contained solely amphibian prey, or the digested products of amphibian prey (secondary ingestion). Two snakes (site 10, Shanping, and site 20, Dong Ha Farm) contained remnants of mammalian prey. Ten snakes (sites 34, Litau n=1, 40, Orchid Island n=1, 13, Chihpen n=1, and 14 Green Island n=6) contained almost whole, or the digested fragments of reptile prey only. One snake contained the femur of a large orthopteran and reptile remains (site 24, Chaochiao). Three snakes contained both amphibian and mammalian prey products (site 34, Litau n=2, and site 40, Orchid Island n=1), and one snake contained only a single large hymenoptera (site 40, Orchid Island). No avian prey were found in the survey. Only 29 snakes (16% of the snakes found with prey) contained prey items in the stomach. Individually identifiable stomach contents ranged from a single *Rana swinhoana* to up to 6 ranid froglets. Six of the cases of identifiable stomach contents were located exclusively in the stomach. Prey types identified to order, and where possible to species, are listed in Table 1.

Secondarily ingested arthropod prey fragments comprised of leg sections, mouthparts, bodyparts, coleopteran elytra (wing cases), and wings. The subset of arthropod prey identified to order were identical to fractions of the stomach contents of the frogs found within the snakes as shown in Table 2. Furthermore, if anuran limbs, or other semi-digested body fragments of anuran prey were found in the stomach, a characteristic digested assortment of secondarily ingested arthropod prey and anuran biomatter was always located in the hindgut.

Given the strong bias towards amphibian prey in the

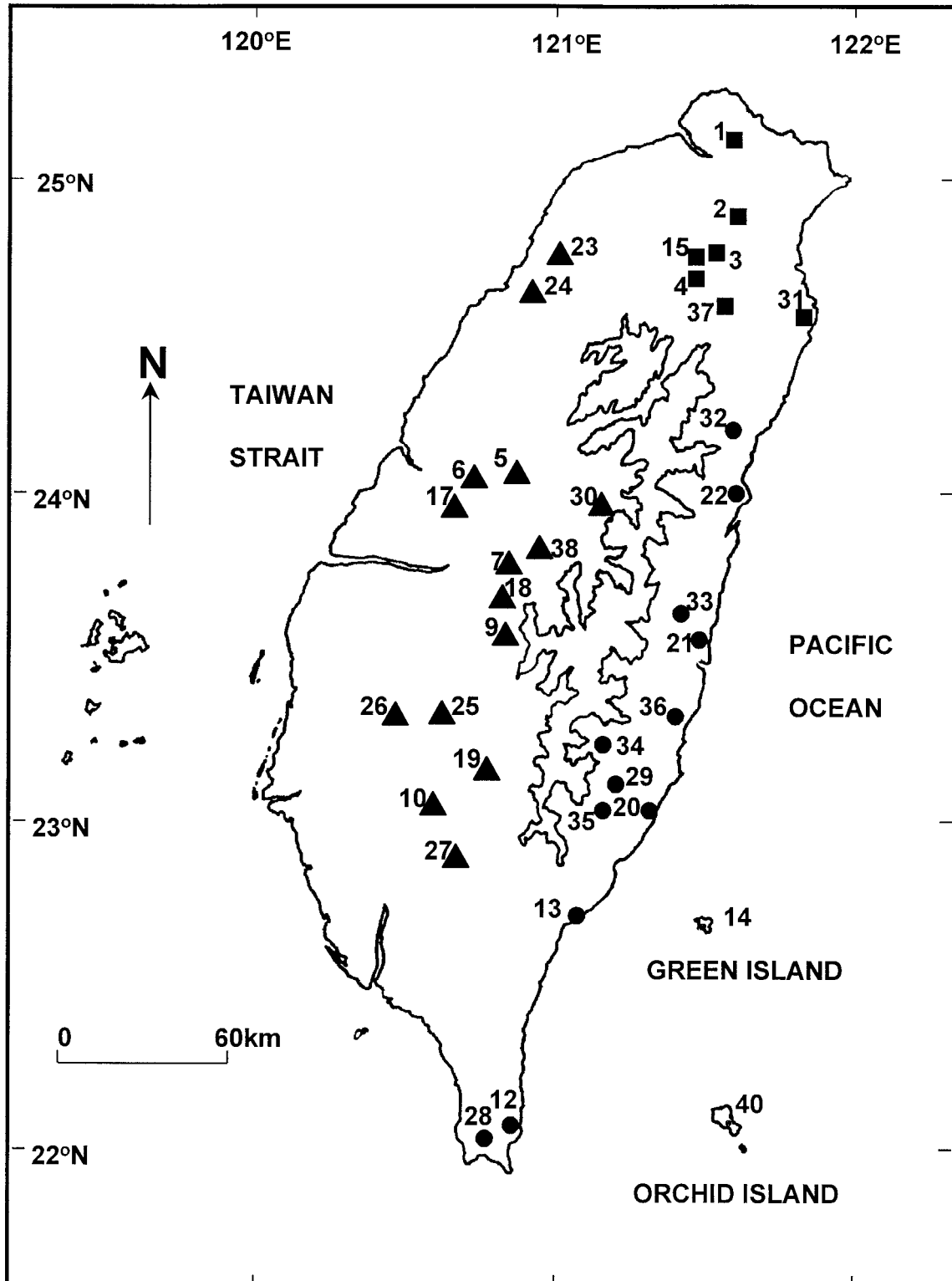


Fig. 1. Map of Taiwan showing the 36 sample locations of the 229 *T. stejnegeri*. The 2000m contour line is shown. The following symbols correspond to the groupings used in the geographical comparisons of the main island of Taiwan (Northern, Western, Eastern and Southern). Non-sequential site numbers correspond to: 1. Yangminshan, 2. Wulai, 3. Fushan, 4. Paling, 5. Pa-shen-san, 6. Takeng, 7. Chichi, 9. Hsitou, 10. Shanping, 12. Chufengshan, 13. Chihpen, 14. Green Island, 15. Tungyanshan, 17. Chutyukeng, 18. Luku, 19. Chuyunshan, 20. Dong Ha Farm, 21. Chimei, 22. Shuiyuan, 23. Hsincheng, 24. Chaochiao, 25. Sanmei, 26. Quantzelin, 27. Machia, 28. Paoli, 29. Kuanshan, 30. Wushe, 31. Suao, 32. Taroko, 33. Fuyuan, 34. Litau, 35. Chiana, 36. Antung, 37. Ming-chi, 38. Lienhwachih, 40. Orchid Island.

Table 1. Summary of identified prey items of *T. stejnegeri* (n =number of identifiable specimens found).

Class	Order	Family	Species (n)
Amphibia	Anura	Ranidae	<i>Rana swinhoana</i> (1)
			<i>Rana sauteri</i> (12)
		Rhacophoridae	<i>Rhacophorus moltrechti</i> (1)
			<i>Polypedates megacephalus</i> (1)
			<i>Buergeria robusta</i> (1)
Reptilia	Squamata	Agamidae	<i>Japalura</i> sp. (2)
Mammalia	Rodentia	Unidentified	
Insecta	Hymenoptera	Unidentified	
	Orthoptera	Unidentified	

Table 2. Summary of secondarily and primarily ingested arthropod prey found within the hindguts of *T. stejnegeri* and stomachs of *T. stejnegeri* anuran prey, respectively. All prey items were found in anuran stomachs. Prey items highlighted in bold were recorded in both snake hindguts and anuran stomachs.

Class	Order
Insecta	Hymenoptera, Bees, Wasps and Ants
	Coleoptera (Adults and Larvae),
	Beetles
	Lepidoptera (Larvae), Butterflies and
	Moths
	Hemiptera, True Bugs
	Diptera, True Flies
Arachnida	Araneae, Spiders
	Acari, Mites
Malacostraca	Isopoda

diet of *T. stejnegeri* (85% of all observations) and the small number of additional prey observations, chi-square comparisons were used to compare the abundance of amphibian prey compared to all other prey types (comprising Reptilia, Mammalia, and Insecta). There was no discrepancy in prey composition recorded based on comparisons between whether digested prey were found in both the stomach and hindgut (Amphibia 80%, $n=25$) or hindgut only (Amphibia 87%, $n=77$; $X^2=0.696$; $df=1$), or between the stomach only and hindgut only (Amphibia 83%, $n=6$; Fisher's exact test). If prey items were found in the stomach, digested prey fragments were often (80% of all observations) found throughout the hindgut.

No sexual variation was evident in the diet composition of *T. stejnegeri* throughout Taiwan (male $n=77$, female $n=31$; $X^2=0.428$; $df=1$; $P=0.428$), although sampled males were more likely to contain prey than sampled females (males $n=170$ (84%), females $n=50$ (69%); $X^2=5.377$; $df=1$; $P=0.02$). Females appeared slightly larger than males in this survey; however, no significant differences in SVL were recorded between the two sexes (male, $n=140$, mean \pm SD=497.0 \pm 59.6mm; female, $n=53$, mean \pm SD=507.4 \pm 69.0mm,

$P=0.336$). Given the homogeneity of the composition of the diets of males and females, total diet data for males and females were pooled for geographic analyses.

Based on the geographic regions summarised in Fig. 1 and Table 3, geographic variation in diet composition was observed between the whole of the main island of Taiwan and Green and Orchid Islands ($X^2=19.115$; $df=1$; $P<0.0001$). The diets of island populations of *T. stejnegeri* appear to consist of less amphibian prey, and in the case of Green Island, more reptilian prey.

The snakes from island populations were sampled predominantly in June, and this may bias the results if there is seasonal variation in diet. Therefore, another comparison of diets between the islands and the east coast and southern populations of mainland Taiwan also sampled in June was performed. These regions were chosen as they experience similar climatic regimes to Orchid and Green Islands (Lin, 1990). The test additionally showed geographic variation ($n=47$; $X^2=6.299$; $df=1$; $P=0.012$), suggesting temporal bias was not responsible for the variation in diet composition. *Trimeresurus stejnegeri* from Green and Orchid Islands was significantly larger when compared with a random sample of SVL's of snakes (equal numbers of males and females) from the main island of Taiwan (Taiwan, $n=33$, mean \pm SD=497.7 \pm 48.4mm; Islands (combined data), $n=33$, mean \pm SD=534.8 \pm 39.8mm, $P=0.001$). Geographic variation in diet was still observed when comparing the diets of "large" mainland snakes (greater than mean SVL [497.7mm]) with the diets of insular populations ($n=70$, mainland [mean \pm SD=540.4

Table 3. Number of times prey items were recorded in the dietary provinces used in the geographical comparisons shown in Fig. 1. "Other" represents pooled data for Reptilia, Mammalia and Insecta.

Geographical region	Amphibia	Other	% Frogs in diet	n
Northern	13	0	100	13
Western	33	3	91.7	36
Eastern and southern	29	5	85.3	34
Green Island	7	8	46.7	15
Orchid Island	4	3	57.1	7

± 29.1 mm], 90% amphibian, insular [mean \pm SD=534.8 \pm 39.9mm], 50% amphibian; $X^2=13.405$; $df=1$; $P<0.0001$).

DISCUSSION

Of the 229 *T. stejnegeri* studied, only 13% contained any prey matter in the stomach (2.6% exclusively in the stomach). Comparative studies have recorded stomach content frequencies as approximately 20% in the Malayan pitviper, *Caloselasma rhodostoma* (Daltry *et al.*, 1998); 35% in the European adder, *Vipera aspis* (Saviozzi and Zuffi, 1997); between 23% and 70% in a survey of Australian elapids (Shine, 1977); 32% in the sea snake, *Laticauda colubrina* (Pernetta, 1977); 18% in the rattlesnake, *Crotalus viridis oreganus* (Macartney, 1989); and 36% of all studied specimens of species of garter snake (Kephart and Arnold, 1982; King, 1993).

The retrieval and resuspension of scatological material in this study proved invaluable. The identification of the presence of five out of the eight key orders of local anuran diet (Arthropoda) found within the *T. stejnegeri* hindgut (see Table 2) without the digested fragments of reptilian, mammalian or large arthropod prey was highly indicative of amphibian ingestion. The class of prey could be identified in less than 60% of the cases where prey matter was found in the digestive tract. In comparable studies, most prey items have been readily distinguishable when found within the digestive tract (Shine, 1977; Daltry *et al.*, 1998). This may in part be the result of the high proportion of soft-bodied amphibian prey consumed by the snakes. Amphibian prey generally lack keratinous structures and therefore, if the amphibian gut and arthropod contents have already been vented by the snake (or if the amphibian gut was empty), no identifiable prey items remain in the ophidian digestive tract.

Another contributing factor to the low proportion of identifiable diet items found within the snakes may be a reflection of an evolutionary adaptation to arboreal life. Snakes exhibit large interspecific variation in gut passage times (Lillywhite *et al.*, 1998). Not to be confused with digestive rate, gut passage time is measured as the time between food consumption and defecation. In a comparative study (performed under uniform experimental conditions), exceptionally long passage times have been recorded in heavy, terrestrial species of viperids and boids, which have accumulated feces for periods of months and sometimes exceeding one year. Conversely, gut passage times for *T. stejnegeri*, are relatively fast (3.5 ± 0.4 days, $n=21$; Lillywhite *et al.* 2002), representing a common trend for arboreal species compared to terrestrial forms (Lillywhite and Henderson, 1993; Tu *et al.*, 2000). Naturally, a large body mass would be disadvantageous for a slender, arboreal species inhabiting weak, vertical substrata. Therefore, the rapid digestion and voiding of prey items would be selectively advantageous in arboreal snakes (Lillywhite *et al.*, 1998, 2002).

The diet of *T. stejnegeri* within Taiwan is dominated by

amphibian prey. However, the presence of reptilian, mammalian and insect prey suggests that the snake is euryphagous, or a dietary generalist (Schoener, 1971), feeding on a range of prey. The combination of nocturnal ranid and rhabdophorid prey alongside arboreal lizards suggests that the nocturnal *T. stejnegeri* most likely combines foraging strategies according to geographic locality, habitat and prey availability (McLaughlin, 1989; Mori *et al.*, 1992) and could be described as an opportunistic "mobile ambusher" (Greene, 1992).

Whilst *T. stejnegeri* is recognised as sexually dimorphic (Tsai and Tu, 1998), no significant differences in size and/or diet composition were apparent between the male and female snakes of the present sample. The principal cause attributed to sexual variation in diet appears to be the result of differential prey handling ability as a consequence of sexual size dimorphism (Mushinsky *et al.*, 1982; King, 1993). Therefore, in the absence of significant sexual dimorphism, as well as empirical evidence for similar habitat requirements between males and females (Tu *et al.*, 2000), the lack of sexual variation in diet composition is not unexpected. Quantitative differences (i.e. the size, or number of prey items consumed simultaneously) may occur, but were impossible to detect due to the lack of whole prey found in the survey. The greater tendency to discover males with prey items in the digestive tract compared to females may reflect different foraging strategies between the sexes.

Prey choice (Arnold, 1981), predator-prey arms races (Heatwole and Poran, 1995), ecological resource partitioning (Toft, 1985; Mushinsky, 1987), and varying prey availability (Campbell and Solorzano, 1992; Daltry *et al.*, 1998; Gregory and Nelson, 1991; King, 1993; Schwaner, 1985) have been described as causal factors of geographic variation in diet composition. However, differences in microhabitat and/or island biogeographical isolation would be the most plausible reasons for the variation in diet between the snakes inhabiting the Pacific islands and the main island of Taiwan. Although Ota (1991) classified at least Orchid Island as having a similar reptilian fauna to mainland Taiwan, the topology and microclimate of the islands are not suitable for a large percentage of the ranid frogs native to the mainland sites (Chou and Lin, 1997a). For example *Rana swinhoana* (Kam *et al.*, 1998) and *Rana sauteri* (Chou and Lin, 1997b), both identified as prey items of *T. stejnegeri*, inhabit mountainous habitats adjacent to fast running streams on the mainland, and are not recorded on Green and Orchid Islands. *Bufo spp.* on the other hand, which have not been recorded as prey of *T. stejnegeri*, were uncharacteristically prolific at certain sampling sites in Green Island. While species diversity is not necessarily correlated with the biomass of available and palatable amphibians, differences in microclimate and/or habitat form the most likely hypotheses to explain why snakes from Pacific island populations prey on amphibians less frequently than snakes from the main island of Taiwan.

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