

No Divergence of Habitat Selection between Male and Female Arboreal Snakes, *Trimeresurus s. stejnegeri*

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Ming-Chung Tu, Shiuang Wang and Yu-Chun Lin (2000) No divergence of habitat selection between male and female arboreal snakes, *Trimeresurus s. stejnegeri*. *Zoological Studies* 39(2): 91-98. Sexual dimorphism in body size is a common phenomenon among animals, and possibly allows the sexes to exploit different habitats. In snakes, low body mass is valuable for arboreal life because it enables the exploitation of a wider range of habitats. Therefore, we would predict that larger and heavier female arboreal snakes, *Trimeresurus s. stejnegeri*, may use thicker or lower branches than males. We visited 2 field-sampling sites and 1 outdoor enclosure regularly to check the micro-habitats that were used by adult *T. s. stejnegeri*. Totally 872 observations of 202 mature snakes were recorded from August 1996 to October 1997. The results contradicted our expectation. No difference in habitat selection between females and males was found in the measured parameters. Limited differences in size between the sexes and the physical structure of plants may account for this negative result. All snakes perched on thinner twigs more frequently than thicker branches. Twigs of diameter larger than 2 cm were rarely used by snakes. We found a significant vertical movement between day and night by the individuals in all 3 locations. Snakes in the outdoor enclosure showed a greater tendency to perch on higher branches than did those in the field. In the field, more than 93% of snakes were found at a height of less than 4 m. However, less than 64% of snakes were found within 4 m of the ground in the outdoor enclosure.

Key words: Habitat, Sex, Arboreal, Snake, Pitviper.

For most snake species, females grow larger than conspecific males (Shine 1986 1993). The primary causes for sexual dimorphism in body size may be due to selection for fecundity or ecological requirements (Shine 1986 1989). Whatever the causes, differences in body size may further allow the sexes to exploit different habitats and hence reduce competition between sexes. The underlying theoretical basis for differential habitat selection between sexes seems clear. Nevertheless, divergent habitat selection is frequently found only between gravid females and that of other members of the population, but not between adult nongravid female and male snakes (Shine 1991, Reinert 1993). The fact that snakes are secretive and difficult to locate in the field may contribute to the overall lack of information.

To adapt to life in trees, arboreal snakes have

adopted many strategies based on behavior (Fleishman 1985), physiology (Seymour and Lillywhite 1976, Lillywhite 1988), and morphology (Vitt and Vangilder 1983). Low body mass is an advantage for arboreal life because it permits snakes to better utilize tree habitats. Consequently, the traits of attenuated body shape, small body size, and short intervals between feeding and defecation are usually found in arboreal species (Vitt and Vangilder 1983, Guyer and Donnelly 1990, Lillywhite and Henderson 1993).

Since body mass is an important feature for tree-dwelling life, it may be easier to find divergent habitat selection between sexes in arboreal habitats. Female racers, *Coluber constrictor*, that have markedly larger and stouter bodies than males use arboreal habitats less frequently than males do (Fitch and Shirer 1971). Similarly, for certain snakes, the smaller sex will use more slender twigs in arboreal

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habitats (Shine 1991).

The Chinese green tree viper (*Trimeresurus s. stejnegeri*) is one of the most abundant snakes in Taiwan. A relatively smaller body size than in most other vipers on this island enables them to frequently use arboreal habitats. As with most other snakes, adult females of *T. s. stejnegeri* not only grow longer but possess heavier bodies at equal snout-vent length (SVL) compared to males (Tsai and Tu 1998). Therefore, we predicted that female tree vipers would use lower or thicker branches than males.

MATERIALS AND METHODS

Study sites

We selected 2 field sampling stations based on high local abundance of *Trimeresurus s. stejnegeri*. The first was located in the Fushan Forest site in northeastern Taiwan. King and Hsia (1997) described this site, within which there is a shallow and narrow artificial pond approximately 210 m long and 30 m wide. Snakes could be found in trees, shrubs, and on a small path that surround this pond. At the southwestern side of this pond is a small hill with undisturbed forest. At the opposite side of the pond, the terrain is flat and has been replanted with short grass and a few trees.

The second field site was in Tsaochiao Village (Miaoli County) in northwestern Taiwan. Cultivated land and small hills are the dominant landscape features. A small ditch about 3 m wide and 1.8 m deep runs between the edge of a hill and a small road. The other side of the road is occupied mainly by a paddy field. A forest with limited disturbance is on the hill, which is often steep at the edge where it meets the ditch. Shallow water, usually less than 0.3 m deep slowly flowed in the ditch. At certain parts of the ditch, trees, bamboo, or shrubs on the sides connect to form a canopy. We usually found snakes on trees or shrubs of the hillside. Sometimes, they could be found in the ditch, on the small road, or in the paddy field.

We also constructed an outdoor enclosure (10 x 8 m) enclosed by 4 metal walls at the Taipei City Zoo. Each wall was 2 m high, on which a 0.3-m-wide metal plate extending toward the inside of the enclosure prevented snakes from escaping. Two trees (12 m and 8.5 m high) were located near the northwestern corner of the enclosure; their branches neither extended outside the enclosure nor connected with branches of trees surrounding the outside of this enclosure. A few shrubs and ferns, usually shorter

than 2 m, were within the enclosure. We made a small pond, approximately 6 m x 4 m, in the center of the enclosure to maintain a water supply and for frogs that were food for the snakes. We caught a few species of frogs from the field and put them in the pond monthly. Some of the frogs (*Rana kuhlii*, *R. latouchi*, and *Rhacophorus taibeianus*) bred successfully in the enclosure. A few lizards (*Platyplacopus kuehnei*, *Takydromus formosanus*, and *Sphenomorphus indicus*), also potential prey for the snakes, were found in the enclosure. To observe snakes that perched on the tall tree, we built a 5-m tower under the tallest tree.

Sampling and measurements

We visited field sites monthly mostly at night to look for tree vipers as thoroughly as possible. Since *T. s. stejnegeri* is nocturnal, it is more difficult to find the snakes in the day. However, if ground dwellers are the main prey of these snakes, we may bias measurements of their perch height (PH) toward the lower end by sampling only at night. Consequently, for the first 6 mo, we also checked for snakes during daylight to detect differences in PH between sexes in their non-active period. Also, we could determine if vertical movement occurred between day and night in the same individual. When a snake was located, the PH, number of twigs (TN) in contact with the snake, and the diameter of each twig (DET) were measured. Since the sum of all twigs may contribute more directly to physical support of a snake, the diameter of total twigs (DTT) was also included in the analysis. When the twigs were too high to reach, we estimated their diameters by using a slide caliper to measure nearby twigs of similar size. We used temperature and relative humidity data loggers (Stow Away XT1, Stow Away RH, Onset Computer Corporation, Pocasset, MA, USA) to monitor air temperature (TA) and relative humidity (RH) 20 cm above the ground and 6 m high in trees in the outdoor enclosure. From April to August 1997, data were collected every 24 min. Due to logger malfunction, we collected only 2 complete data sets during May and August. We also used a Mikromec logger (MM418-H, HP 101 air probe, Technetics, Langemarckstr, Freiburg, Germany) to measure air temperature and relative humidity near each snake. After calibration, an 8-m extension cord was connected to the air probe, which was then attached to an extensible measuring staff. With this staff and an aluminum ladder, we could reach up to 12 m above the ground. We also measured SVL, tail length (TL), and body mass of snakes. We used only data from adult

snakes in this report. We followed the criteria of Tsai and Tu (1998) in which the minimum SVLs of adult male and female snakes were 37 and 43 cm, respectively, to separate adult snakes from immature snakes. Normally, a red stripe is found only on the lateral side of male but not female *T. s. stejnegeri* (Mao 1962, Tsai and Tu 1998). We could visually identify their sexes easily. Before a snake was released, we implanted a passive integrated transponder (DIT tag, 12 mm) to mark each snake. A mini-tracker (AVID, Norco, CA, USA) was used to read the identification number of each snake.

From October 1996 to October 1997, totally 26 (21 females, 5 males) snakes were kept in the outdoor enclosure. During any given week, the most we kept was 17 (12 females, 5 males) and the least was 10 (7 females, 3 males). We marked each snake with a microchip and collected data in the same manner that was used at field sites. We began to collect data weekly after snakes had been in the enclosure for more than a week. Data from 2 female snakes that died within 2 mo of placement in the enclosure were disregarded. Five snakes died after more than 4 mo, and 9 snakes disappeared after more than 3 mo in the enclosure. We also disregarded 1 mo of data collected from these 14 snakes before they died or disappeared. Ten snakes survived until the end of the experiment.

Statistics

We used two-way ANOVA (Sigma Stat software, Jandel Corp., CA, USA) to test for differences between sexes or localities in each measured parameter such as PH, TN, DET, DTT, TA, and RH. When significant differences were found, we used Student Newman Keuls' all pairwise multiple comparison to test the significance level of different groups. Because the observation frequency of each individual was different, we took the average value of each individual for the above analysis. This may have prevented the habitat preference of certain individuals, that were recorded many more times than others, from biasing the result. We used a paired *t*-test to test if PH of the same individual differed between day and night. We used Student's *t*-test to check for differences of TA and RH between the ground and the trees in the outdoor enclosure.

RESULTS

We marked 64 adult females and 138 males on which a total of 872 observations were recorded.

Mature females were larger than adult males (Fig. 1). The average SVLs of female and male snakes were 49.5 and 48.9 cm, while the body weights of female and male snakes were 47.8 and 40.2 g, respectively. In the field, especially at the Tsaochiao site, the number of individuals and observations were biased strongly toward males. The cause of this skew in sex ratio is under investigation. No significant differences ($p > 0.05$) in any habitat parameter were found between female and male snakes. There were significant differences ($p < 0.05$) in PH, TN, RH, and TA between different localities. In either day or night, PH from the outdoor enclosure was significantly greater than that from both field sites, while RH from the Fushan field site was significantly greater than that from the 2 other localities. TN from the outdoor enclosure was significantly more than that from both field sites during the night. Air temperature varied significantly among the 3 localities in a more complex way (Table 1). There was no significant interaction between sex and site for any of the measured parameters ($p > 0.1$) except RH at night. Although there was a significant interaction between sex and RH of a site during the night, its significant level is low ($p = 0.046$). When analyzing the difference of PH between day and night, we found a significant ($p < 0.05$) vertical movement from individuals in all 3 locations (Table 2). However, the direction of movement was different among sites. In the outdoor enclosure and at the Fushan site, snakes moved toward the ground at night. At the Tsaochiao site, snakes shifted upwards during the night (Table 2). At night, the average observation frequency of Chinese green tree vipers that stayed on the ground from 3 locations was 23.2%, while the most frequent perch height

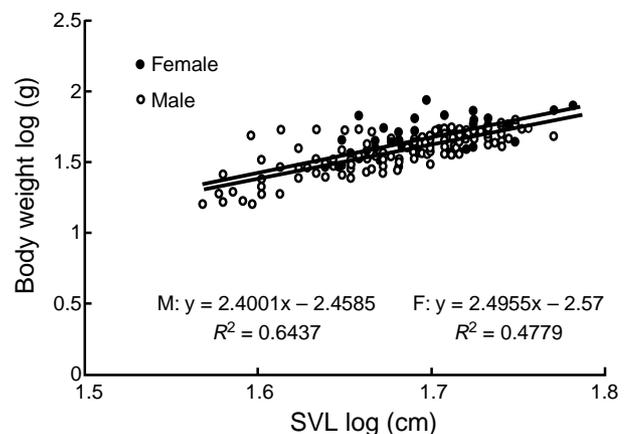


Fig. 1. Relationship between snout-vent length (SVL) and body weight of adult Chinese green tree vipers, *Trimeresurus s. stejnegeri*.

ranged between 0.01 and 1 m in all 3 locations, with an average observation frequency of 30.8%. More than 93% of snakes in the field, but only 64% of those in the outdoor enclosure were found within 4 m of the ground (Fig. 2). Snakes perched frequently on smaller-diameter twigs. The dominant twig diameter used by snakes was < 1 cm. The frequency of DET less than 1 cm was above 74%. As DET increased to 2 cm, the cumulative frequency exceeded 90% in all 3 locations (Fig. 3). Because most snakes (60%-70%) perched on only 1 or 2 twigs, the frequency pattern of DTT was similar to that of DET. More than 90% of snakes perched on twigs with DTT < 3 cm in all 3 locations. Air temperature increased during the day and decreased at night, whereas RH fluctuated in the opposite way. Generally, TA and RH near the ground were significantly greater than values in trees ($p < 0.05$). During the day, the discrepancies between ground and tree locations increased, especially for RH (Table 3).

DISCUSSION

Although arboreal snakes would appear to be good candidates for investigations of differential habitat selection between sexes, we did not find this difference in Chinese green tree vipers. The small

discrepancy in size between females and males may have contributed partially to this negative result. If it were true, it would be easier to find divergent habitat selection between gravid female and male snakes or between juvenile and adult snakes in an arboreal habitat. Some larger viperids are arboreal in juvenile stages but abandon this habitat when mature (Lillywhite and Henderson 1993). Further investigation may reveal if the extent of the difference in body size is important for divergence in arboreal habitat selection.

No correlations between body size and perch height (Henderson 1974) or twig diameter (Rodda 1992) were found in other studies. The prediction

Table 2. Comparison of perch height of Chinese green tree vipers, *Trimeresurus s. stejnegeri* from individuals at day and night from 3 sampling locations

Perch height (cm)	Fushan		Tsaochao		Taipei City Zoo	
	Day	Night	Day	Night	Day	Night
N	8	8	26	26	188	188
Mean	302	156	114	193	490	433
Min.	65	0	0	0	0	0
Max.	497	337	456	664	1,170	1,097
SD	152	109	122	169	383	385
p value	< 0.05		< 0.05		< 0.05	

Table 1. Perch height, number of perch twigs, diameter of perch twig, microhabitat air temperature, and relative humidity of Chinese green tree vipers, *Trimeresurus s. stejnegeri* from 3 sampling locations in Taiwan

		Perch height (cm)		Number of perch twigs	Diameter of perch twig (cm)		Air temperature (°C)		Relative humidity (%)	
		Night	Day		each twig	total twigs	Night	Day	Night	Day
				Night	Day	Night	Night	Night	Day	Night
Fushan	N	77	14	48	44	44	54	14	54	14
	Mean	112 ^b	210 ^b	1.7 ^b	1.1	1.5	19.0 ^b	22.0 ^a	95.5 ^a	88.6 ^a
	Min.	0	0	1.0	0.2	0.2	15.5	17.5	73.6	70.0
	Max.	500	497	4.0	9.9	9.9	24.8	3.8	100.0	97.2
	SD	122	145	0.8	1.6	1.7	2.5	28.5	3.6	9.8
Tsaochiao	N	99	28	66	64	64	94	29	88	29
	Mean	120 ^b	123 ^b	1.8 ^b	1.0	1.5	21.1 ^a	22.2 ^a	92.1 ^b	73.8 ^b
	Min.	0	0	1.0	0.2	0.3	11.9	13.3	75.4	31.6
	Max.	727	550	0.9	5.8	5.8	28.3	31.5	98.5	99.0
	SD	142	138	5.0	1.0	1.2	4.4	5.6	5.0	17.1
Taipei City Zoo	N	26	16	26	25	25	26	16	26	16
	Mean	342 ^a	469 ^a	2.8 ^a	0.8	1.4	19.7 ^{a,b}	18.2 ^b	90.8 ^b	75.6 ^b
	Min.	88	73	1.8	0.4	0.8	15.6	16.3	89.1	59.8
	Max.	751	822	7.8	1.3	2.0	24.5	23.7	93.1	84.1
	SD	35	211	0.2	0.3	0.4	3.1	1.7	1.1	4.9

Different superscript letters (^{a,b}) on mean values denote a significant difference between localities ($p < 0.05$) by Student Newman Keuls' all pairwise multiple comparison.

that heavier arboreal snakes may perch lower and/or on thicker twigs would be true if the twigs become more slender and the weight-bearing capacity of the twigs decreased with increasing height. Although the above conditions are generally true for a single plant, in the entire habitat, the situation becomes much more complex. For example, small branches that grow from the base of a plant and short bushes create many slender twigs near the ground. Consequently, in any given environment, a negative cor-

relation between height and twig diameter may not exist. This lack of correlation may explain the phenomenon that, although tree vipers perch frequently on smaller branches as do many other arboreal snakes (Plummer 1981, Goldsmith 1984), their PH can still remain at the lower end (Fig. 2). Furthermore, for small arboreal snakes such as *T. s. stejnegeri*, if the weight-bearing capacity of most small branches surpass their mass, we would not be able to see a discrepancy between sexes in PH and DET

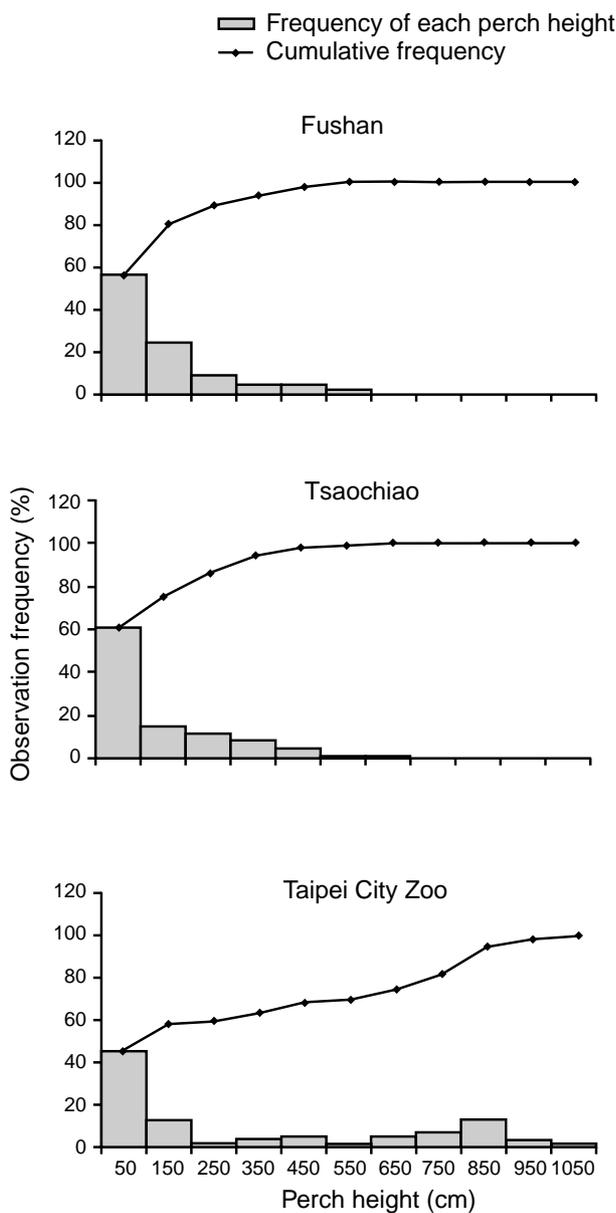


Fig. 2. Observation and cumulative frequency of each perch height of Chinese green tree vipers, *Trimeresurus s. stejnegeri*, from 3 sampling locations in Taiwan.

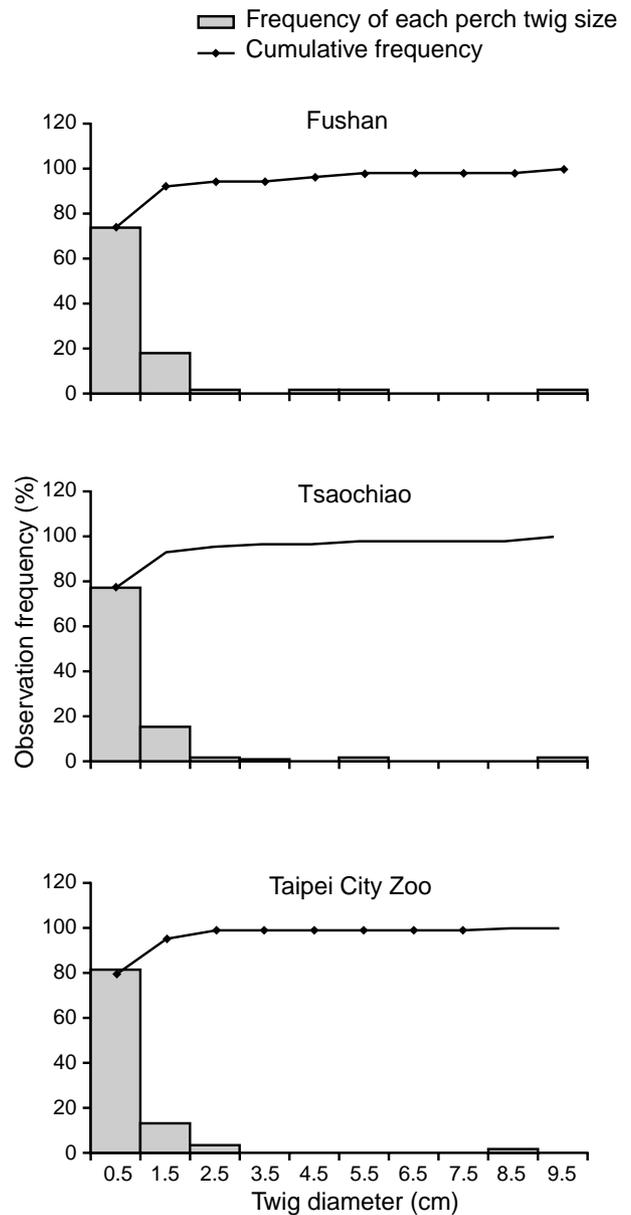


Fig. 3. Observation and cumulative frequency of different sizes of twigs used by Chinese green tree vipers, *Trimeresurus s. stejnegeri*, from 3 sampling locations in Taiwan.

or DTT due to the weight factor.

Because the size difference within either gender was larger than that between sexes, we pooled the data of both sexes and analyzed the correlation between body weight and the 3 variables (PH, DET, and DTT) in 3 different sampling locations. No significant correlation ($p > 0.05$) was found in either field station for any of the 3 variables (Table 4). In the outdoor enclosure, body weight was significantly positively correlated with DTT ($p < 0.05$) but not with DET ($p = 0.495$). Furthermore, we found a positive correlation ($p = 0.003$) between body weight and PH in the outdoor enclosure (Table 4). Nevertheless, the slope was only 0.005, which means that when weight increases by 1 g, the perch height increases by 0.005 cm. Thus, heavier snakes could perch on slightly higher twigs than lighter snakes by using a larger diameter of total twigs. The correlation resulting from the outdoor enclosure or both field sites suggests that body weight of *T. s. stejnegeri* does not influence their PH, DET, or DTT.

Lillywhite and Henderson (1993) pointed out that foliage structure, microclimate, and prey availability may all interact to affect foraging and perch height of arboreal snakes. Although the air temperature and relative humidity near the ground were normally higher than those in trees, the magnitude of the difference was limited (Table 3). Limited vertical thermal gradients in forests have also been reported in earlier studies (Lillywhite and Henderson 1993). Differences in RH between the forest floor and in trees became smaller at night (Table 3). The entire

forest space may be vapor saturated during the night (Lillywhite and Henderson 1993). This explains why the mean relative humidity of snakes' micro-habitats at night was above 90% (Table 1). At night, a limited divergence of micro-habitat TA and RH was available from which the different sexes could choose. Nevertheless, during the day even when the range of RH increased, we still did not observe a difference between the sexes in the relative humidity of their micro-habitats. The RH of snakes' micro-habitats was related to location. Therefore, RH collected from Fushan, known for its wet weather most of the year (Lin et al. 1996, King and Hsia 1997), was greater than those of the other 2 localities during

Table 4. Relationship between body weight (x) of *Trimeresurus s. stejnegeri* and 3 different variables (y) of perch height (PH), diameter of each perch twig (DET), and diameter of total twigs (DTT) in 3 sampling locations in Taiwan

		N	Regression equation	r^2	p
Fushan	PH	82	$y = 1.389x + 45.67$	0.025	0.156
	DET	45	$y = 0.016x + 0.47$	0.018	0.380
	DTT	45	$y = 0.025x + 0.42$	0.040	0.191
Tsaochiao	PH	151	$y = -0.501x + 148.42$	0.002	0.620
	DET	86	$y = -0.0004x + 1.01$	0.00001	0.976
	DTT	86	$y = 0.008x + 1.13$	0.006	0.497
Taipei City Zoo	PH	597	$y = 0.005x + 46.24$	0.017	0.003
	DET	287	$y = 0.002x + 0.65$	0.001	0.495
	DTT	287	$y = 0.009x + 1.02$	0.015	0.039

Table 3. Air temperature and relative humidity in trees (6 m above ground) and near the ground (20 cm above ground) in the outdoor enclosure during May and August 1997

	Air temperature (°C)				Relative humidity (%)			
	May		August		May		August	
	tree	ground	tree	ground	tree	ground	tree	ground
Day 0600-1800								
N	900	900	900	900	900	900	900	870
Mean	25.4	25.8	27.4	28.0	83.9	88.7	86.5	91.9
Min.	17.6	18.1	22.3	23.1	37.1	41.7	49.9	52.6
Max.	36.7	38.1	37.1	38.2	100.0	100.0	100.0	100.0
SD	3.9	4.7	2.9	3.0	15.9	14.0	14.3	11.9
p value	< 0.05		< 0.001		< 0.001		< 0.001	
Night 1800-0600								
N	900	900	900	900	900	900	900	883
Mean	21.6	21.6	25.0	25.2	96.2	97.6	97.5	98.8
Min.	17.1	17.3	22.3	23.3	61.9	71.1	60.4	56.3
Max.	27.6	27.0	34.0	28.6	100.0	100.0	100.0	100.0
SD	3.8	1.9	1.8	0.9	7.0	4.4	5.8	5.3
p value	< 0.05		< 0.001		< 0.001		< 0.001	

both day and night.

At night we frequently observed tree vipers perched on twigs with their heads pointed downward and close to the ground. It appeared as if they were waiting for prey to pass by. Occasionally, we saw dead frogs such as *Rana latouchi* in the snakes' mouths. Lee and Lue (1996) reported that *T. s. stejnegeri* feed on frogs, lizards, birds, and rats. We also observed them eating the tree frog, *Chirixalus idiotocus*. There was no indication that the snakes must restrict their feeding to be close to the ground. However, if prey availability is greater on the ground, the snakes may have a greater tendency to stay near the ground during their foraging times. If this is true, we may bias our results by sampling only during the night. During the daytime, when tree vipers are resting and habitat choice is not affected by their food availability, it may be easier to find male snakes perched on higher branches. However, our data do not support such a conclusion.

During the daytime, the snakes may utilize higher perches as safer retreats (Henderson 1974). We found that snakes at Fushan and in the outdoor enclosure moved to higher branches during the day. However, contrary to expectations, snakes in Tsao-chiao showed an opposite movement. One possible explanation for this is the special topography at Tsao-chiao. The hill is often steep, in places with a slope of 90°, and densely covered with short bushes. In the day, snakes retreat to the bases of bushes where they can hide better than on higher exposed bushes. Vertical movement has also been observed in other arboreal snakes between active and non-active periods (Henderson 1974, Henderson and Nickerson 1977).

In the outdoor enclosure, either male or female snakes may perch almost at the tops of trees. We observed snakes in the outdoor enclosure perched on higher twigs than those at both field sites. Food availability was an unlikely factor inducing tree vipers in the outdoor enclosure to perch on higher branches. Tree frogs (e.g., *C. idiotocus*) were less abundant than ground-dwelling frogs in the outdoor enclosure. Individual variation did not account for the difference between the outdoor enclosure and the field sites. We checked whether certain individuals in the outdoor enclosure tended to use higher branches. We found that 1 female nearly always (92.3% of the observations) perched on branches higher than 5 m. Other snakes frequently moved up and down. At night it was easy to see the light green-yellow belly of the snakes by flashlight even when they perched higher than 10 m if the foliage was not too dense. Nevertheless, it is generally much harder

to locate snakes when they perch high in trees (Lillywhite and Henderson 1993). Relatively higher snake density in the outdoor enclosure and/or other factors may also be responsible for the observation that the tree vipers in the outdoor enclosure perched on higher branches.

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赤尾青竹絲 (*Trimeresurus s. stejnegeri*) 兩性之微棲地選擇探討

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動物的兩性在體型上有差異，這樣的差異有助於兩性選擇不同的棲地環境，以降低種內的競爭壓力。體重是蛇類適應樹棲生活的重要因素，因為較輕的體重可以讓牠們使用較廣泛的樹上環境。赤尾青竹絲 (*Trimeresurus s. stejnegeri*) 是樹棲蛇類，其雌蛇比雄蛇大且重，因此我們推測雌蛇的棲息高度可能較雄蛇為低，或者雌蛇棲息的枝徑會較雄蛇為粗。我們定期在二個野外樣區和一個戶外圈養場內，觀察記錄牠們的微棲地資料，如離地高、枝徑、枝條數、溫度和濕度等，從 1996 年 8 月到隔年 10 月共觀察 202 隻性成熟的赤尾青竹絲，最多並記錄到 872 次的離地高資料，結果和我們的預期不吻合，兩性在所有測量的微棲地介質都沒有顯著的差異。兩性的體型差異不夠大，以及棲息植物的枝條結構，可能是導致此負面結果的原因。

關鍵詞：微棲地選擇，兩性差異，樹棲，蛇，響尾蛇亞科。

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