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Diurnal Retreat Site Selection by the Arboreal Chinese Green Tree Viper (*Trimeresurus s. stejnegeri*) as Influenced by Temperature

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Hwa-Ching Lin, Hsin-Yi Hung, Kuang-Yang Lue, and Ming-Chung Tu (2007) Diurnal retreat site selection by the arboreal Chinese green tree viper (*Trimeresurus s. stejnegeri*) as influenced by temperature. *Zoological Studies* **46**(2): 216-226. We investigated the role of vegetation cover, prey availability, and air temperature on the selection of a retreat site by the Chinese green tree viper (*Trimeresurus s. stejnegeri*), a nocturnal, arboreal sit-and-wait predator. We manipulated the vegetation structure and distance to the prey source, and monitored the microhabitat temperature within the test enclosures. The results indicated that the height of the daytime perch sites was influenced by the ambient temperature. Snakes perched on lower layers of vegetation seeking cooler conditions when the ambient temperature within the enclosure was high. In addition, when the ambient temperature rose above 25°C, tree vipers retreated into denser vegetation, which provided significantly lower temperatures due to shading. In contrast, tree vipers in low-temperature environments exhibited no preference for vegetation structures in terms of density, except for an apparent avoidance of vegetation with bare branches and no leaves. The distance to the prey source did not appear to have any significant influence on the green tree viper's selection of a retreat site; this could be attributed to the fact that these snakes hunt both terrestrial targets and arboreal species. Our study demonstrated that temperature is the most important factor influencing retreat site selection by Chinese tree vipers. The temporal variations and seasonal differences in the space utilization patterns may have been attempts to satisfy their thermoregulation needs.
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Key words: Microhabitat selection, Temperature, Retreat site, Snake, Vegetation density.

Habitat selection by snakes is influenced by complex biotic and abiotic factors (reviewed in Reinert 1993), of which the availability of suitable retreat sites is a critical determinant (Shah et al. 2004). Many nocturnal lizards and snakes spend long periods concealed in their diurnal retreat sites (Huey et al. 1989, Webb et al. 2004). Research on the selection of retreat sites by snakes is conducive to understanding their habitat utilization behaviors and needs (Shah et al. 2004). Furthermore, it is a less-demanding undertaking than attempting to describe the entire environment of an actively moving animal (Webb and Shine 1998b, Shah et al. 2004).

Safety or predator avoidance is considered the most critical factor that determines how a reptile chooses its retreat sites or microhabitats (Downes and Shine 1998, Theodoratus and Chiszar 2000, Downes 2001, Blouin-Demers and Weatherhead 2002, Stapley 2003). With respect to arboreal lizards and snakes that do not normally hide in holes or crevices, the selection of a dense vegetative structure can provide cover and protection from predators (Lillywhite and Henderson 1993, Mullin and Cooper 2000, Fitzgerald et al. 2003, Pringle et al. 2003, Reaney and Whiting 2003, Shah et al. 2004). Therefore, the complexity and density of the vegetative structure should be an important determinant in an arboreal reptile's selection of retreat sites.

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Prey acquisition and foraging requirements are other important cues for snakes when selecting retreat sites. This is especially true for sit-and-wait predators, since a poor choice may significantly affect their hunting efficiencies (Downes 1999). This has been supported by studies which show that reptiles prefer habitats with high prey abundance (Houston and Shine 1994, Mullin and Cooper 2000, Theodoratus and Chiszar 2000, Blouin-Demers and Weatherhead 2002, Shine and Sun 2002, Shine et al. 2002, Heard et al. 2004, Tsairi and Bouskila 2004). For example, the odors of small mammal prey (chemical cues) played an important role in the microhabitat selection of timber rattlesnakes (*Crotalus horridus*) in long-term studies (Reinert et al. 1984, Reinert 1993).

Additionally, temperature is a basic factor that influences the choice of retreat sites for many reptiles (Dial 1978, Huey et al. 1989, Webb and Shine 1998b, Kearney 2002, Pringle et al. 2003). The body temperature of ectoderms can influence their physiology, and ecological and behavioral performances (Huey and Kingsolver 1989, Brodie and Russell 1999, Shine et al. 2000). Reptiles rely on specific components of their habitat to maintain an appropriate body temperature (Christian et al. 1983, Kearney 2002, Heard et al. 2004). Webb et al. (2004) reported that both the broad-headed snake (*Hoplocephalus bungaroides*) and common small-eyed snake (*Cryptophis nigrescens*) used substrate temperature as a cue to choosing among potential retreat sites. Suitable retreat sites should not only provide refuge, but also fulfill thermoregulation requirements during inactive periods.

Although predator avoidance, prey availability, and thermoregulation needs are the 3 key factors that appear to have major influences over a snake's selection of retreat site, the complex correlations among factors make it difficult to pin down any specific causal determinant (Shah et al. 2004). It has been demonstrated that some reptiles use multiple cues in making decisions regarding retreat site selection (Reinert 1993, Webb and Shine 1997b, Downes and Shine 1998, Downes 1999, Theodoratus and Chiszar 2000, Fitzgerald et al. 2002, Fitzgerald et al. 2003, Stapley 2003, Shah et al. 2004). For example, a snake's choice of certain microhabitats often represents a compromise between predation risk and resource acquisition (Downes 2001). Heard et al. (2004) discovered that habitats providing both favorable physical structure and prey availability were more attractive to the inland carpet python (*Morelia spilota metcalfei*) than habitats with only high prey availability. Thick-tailed geckos (*Nephrurus millii*) displayed a strong preference for retreat sites which offered the dual advantages of enhanced thermoregulation and predator avoidance (Shah et al. 2004).

However, relative to lizard, bird, and mammal taxa, the role of proximate cues in influencing the retreat site selection of snakes is not as well understood (Huey et al. 1989, Webb and Shine 1997b, Heard et al. 2004, Webb et al. 2004, Fitzgerald et al. 2005). This may be attributable to the inherent difficulties of quantifying and manipulating the attributes and the range of habitats used by creatures with a propensity to conceal themselves in their surroundings such as snakes (Shah et al. 2004). Therefore, a controlled laboratory manipulation or field enclosure is probably more suitable for investigating the cues used by such creatures in selecting retreat sites (Downes and Shine 1998, Webb and Shine 1998b, Shah et al. 2004).

The Chinese green tree viper (*Trimeresurus s. stejnegeri*) is one of the most common snakes in Taiwan and an excellent model for studying retreat site selection. This serpent is a sit-and-wait predator with nocturnal and arboreal tendencies (Tu et al. 2000). Green tree vipers often retreat into vegetation during daytime hours, then move to ambush sites at dusk (Tu et al. 2000, Xiao 2000). They usually spend several days (sometimes up to 2 wk) around the same ambush site waiting for prey (H. Lin, unpubl. obs.). Although several factors influencing microhabitat selection by green tree vipers in the field have been suggested (Tu et al. 2000), further investigations are required to reach unambiguous conclusions.

We used an experimental approach to investigate the role of prey availability and vegetation density with respect to diurnal retreat site selection by the Chinese green tree viper in outdoor enclosures. We addressed 2 basic questions: (1) Do green tree vipers tend to retreat to locations closer to the source of prey? and (2) Do green tree vipers tend to select retreat sites with denser vegetation for safety's sake? In order to take into consideration air temperature, we conducted further investigations into a 3rd question: Does the selection of retreat site under different ambient temperatures fluctuate with seasonal changes?

MATERIALS AND METHODS

Outdoor enclosures

Two outdoor enclosures (12.0 m long, 2.4 m wide, and 3.0 m tall) were constructed using stainless steel pillars and mesh at the Taipei Zoo, Taiwan. The top of each enclosure was covered with opaque plastic plates and enclosed on all sides with black shade nets. The floors were made of smooth concrete. Twelve sets of fluorescent lights, each with three 40-W lamps, were installed at 45 cm intervals, and were controlled by timers which turned the lights on at 07:00 and off at 17:30 each day.

Each enclosure was partitioned into 2 sections: a vegetation area (10.0 m long and 2.4 m wide) and a smaller foraging area (2.0 m long and 2.4 m wide) (Fig. 1A). Within the vegetation area, horticultural pots of *Schefflera arboricola* were provided as potential retreat sites for the vipers. The foliage and branch structure of *S. arboricola* are similar to those of *S. odorata*, one of the most common plants in which green tree vipers retreat in the field (H. Lin, unpubl. obs.). Each *S. arboricola* plant was 1.3-1.4 m tall, and formed a tree-crown about 0.7 m in diameter. We used potted plants to allow easy manipulation and control of the vegetative cover and shade. After each trial, the leaves and branches of each plant were sprayed with ethanol (Tsai and Tu 2005) and rinsed with fresh water for 10 min in order to remove the scent of snakes from the vegetation.

A square water pool (1.5 (1.5 m) with a water depth of 5-10 cm was placed at the center of the foraging area. Paddy frogs (*Rana l. limnocharis*), a common prey of green tree vipers in the field (Mao 1970), were provided in the foraging area as food for the snakes during the prey availability experiments. Pebbles and aquatic plants were provided to shelter the paddy frogs. A perching log (2.5 m long and 10 cm in diameter) was positioned above the water to provide an ambush-site for the vipers (Fig. 1A). The paddy frogs were fed meal worms and crickets daily. In order to effectively confine the frogs within the foraging area, a vertical stainless steel wall with a smooth surface (0.9 m tall and 1 mm thick) was installed between the foraging and vegetation sections. Two 2-cm-diameter ropes were placed between the log above the pool and plants adjacent to the stainless steel partition, to allow the vipers to travel between the foraging and vegetation areas (Fig. 1B).

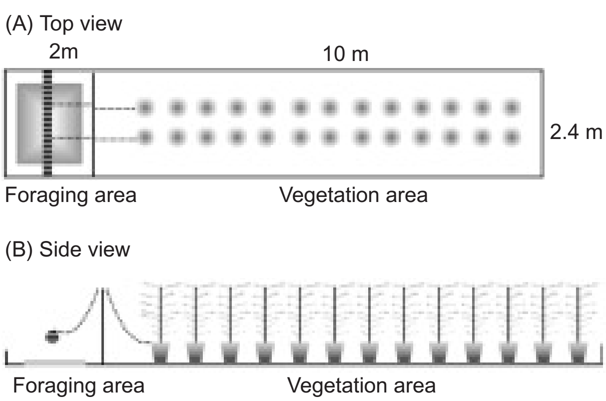

Fig. 1. Arrangement of the foraging and vegetation areas in the outdoor enclosures. ▬ represents the log; ▭ represents the water pool (foraging area); ● represents pots of *Schefflera arboricola* (shelter vegetation); and ----- represents the climbing ropes. (A) Top view. (B) Side view.

Collection and housing of the snakes

We collected 186 Chinese tree vipers, from northern Taiwan, including areas around Wulai, Sanchih, Yuanshan, Tsaochiao, and Nuannuan. Only adult males, characterized by a snout-vent length exceeding 37 cm (Tsai and Tu 2000), were included in this study in order to avoid any experimental bias due to juvenile-adult or female-male interactions or the influence of gravid females. We housed the snakes in a single room at the Taipei Zoo. Each individual snake was marked with a unique number on the dorsal scales using a water-resistant marker for identification purposes. Tree vipers tend not to interact in an antagonistic or repellent manner; in fact, they generally ignore each other's presence even when they are in physical contact or in ambush positions on the same or adjacent sites in the field or laboratory (H. Lin, unpubl. obs.). Therefore, the vipers were housed in groups of 5 in commercial aluminum netted cages (50 cm long, 50 cm wide, and 75 cm tall). Each cage was covered with a paper substrate and contained a pot of *S. arboricola* and a small water dish. Snakes were fed paddy frogs every 10 days, and supplied with water ad libitum. Lighting in the room was adjusted to match the appropriate photoperiod in the outdoor enclosures. Each snake was tested only once, and released back to their exact capture locations after the experimental trials were completed.

Data collection

For each trial, we released 5-10 vipers into the vegetation area during the late afternoon. In order to eliminate experimental bias from possible differences in thermoregulation requirements between the tree vipers in postprandial and preprandial states (Tsai and Tu 2005), snakes in a postprandial state were not immediately released into the enclosures for the experimental trials. A preliminary study showed that none of the snakes perched themselves completely on the plants until the 3rd day after being released into an enclosure. Therefore, we began data collection on the 3rd day. During the daytime, we entered the enclosures and for each experimental trial, we recorded the time, ambient temperature, vipers' motion, posture, location, perch site, and perch height within the enclosures. Postures were categorized as follows: (1) when a viper was stationary and coiled with its head in the center, or laid its head on its body, it was deemed as being in a "resting" position; and (2) when a viper was stationary with its neck and fore body positioned in a sigmoid shape, and its head pointed downward, it was deemed as bring in a "foraging" position. In order to compare differences in temperature between different strata of vegetation as well as different vegetation densities, we recorded the data at shaded air temperatures in the upper (130 cm height), middle (80 cm height), and lower strata (28 cm height) of the vegetation using data loggers (Dickson TK120) every 2 h during the experiments conducted in 2005.

Activity patterns

We established activity patterns for 9 green tree vipers in Aug. 2002. Two columns of 14 pots of *S. arboricola* were positioned at intervals of 30 cm within the vegetation area. Within the foraging area, 15 paddy frogs were maintained in the pool to enhance prey availability and provide a choice for retreat site selection of the vipers. We observed the activities and behavior of the green tree vipers every 2 h over a 24 h period.

Prey availability

We studied the role of prey availability and perch site selection of 48 green tree vipers between Nov. 2002 and Oct. 2005. Vegetation areas were subdivided into 2 plots: C1 (beside the foraging area) and C2 (away from the foraging area). Two columns of 7 *S. arboricola* pots were positioned at 30 cm intervals within each plot. To ensure ample prey availability, we maintained the paddy frog population at a 3: 2 ratio to the tree viper population within the enclosures. Vipers were randomly released in plot C1 or C2 during each trial. Each viper's preferred retreat site, C1 vs. C2, was determined based on a Chi-square test.

Vegetation density

Between Aug. 2002 and Nov. 2005, we studied the effects of vegetation density and structure on retreat site selection by 129 green tree vipers. We placed 8 *S. arboricola* pots in a single row within the vegetation area, and manipulated the percentage of vegetation coverage by changing the distance between the pots and foliage. The average relative coverage (ARC) of each treatment was calculated. The ARC is the mean illumination from the upper (130 cm height), middle (80 cm height), and lower (28 cm height) strata of each plant divided by the concurrent illumination of the open area without shade within the enclosure. Illumination was measured with Lutron illumination readers (Lutron Lx-101).

We established 4 levels of vegetation density: (1) dense (D), with a pot interval of 15 cm (mean ± SD: ARC = 0.14 ± 0.09, n = 24); (2) medium (M), with a pot interval of 30 cm (mean ± SD: ARC = 0.23 ± 0.14, n = 24); (3) loose (L), with a pot interval of 45 cm (mean ± SD: ARC = 0.31 ± 0.19, n = 24); and (4) foliage stripped (F), with a pot interval of 45 cm and all foliage stripped from the plants (mean ± SD: ARC = 0.53 ± 0.17, n = 24). The vegetation area was evenly divided into 2 longitudinal halves each with a different vegetation density. We performed 3 pairwise comparisons of vegetation densities: L vs. M, M vs. D, and L vs. F, and made the comparisons in a random order. The position of the row of each vegetation density was randomly replaced after each experimental trial. Vipers were also randomly released in each row with a different vegetation density for each trial. The distribution of the retreat sites selected by the snakes was compared with tests involving vipers that preferred retreating into denser vegetation. Therefore, to distinguish the effects of different ambient temperatures in the enclosures, we divided the vipers' distribution data into 2 categories: hot season with an ambient temperature of > 25°C and cool season with an ambient temperature of < 25°C.

RESULTS

Activity patterns

Movements of the green tree vipers mainly occurred at night (Fig. 2A). Activities began after 18:00 and reached a peak at 02:00. During this activity peak, over 40% of individual snakes moved to the foraging area (Fig. 2B). By 06:00, the vipers had gradually ceased all movement. Observations made during the night showed that all of the stationary vipers were in a foraging position. During the daytime, all of the vipers would perch within the vegetation area, most of which (89%) were in a resting position. Only 11% of the individual snakes were observed in a foraging position during the daytime. A secondary peak of activity occurred between 12:00 and 16:00 when the vipers moved vertically to lower layers of vegetation. This behavior was coincident with a rise in the ambient temperature within the test enclosures after midday (Fig. 2A).

Prey availability

The selection of retreat sites in the vegetation area did not appear to be influenced by the distance to the food source. The frequency of green tree vipers in C1 (beside the foraging area) versus C2 (away from the foraging area) were similar (Chi-square test: C1 = 27, C2 = 21, x^2 = 0.75, df = 1, p = 0.386). The snakes did not exhibit a significant preference for retreating into areas closer to the food source.

Perch height and temperature

The activity pattern indicated that green tree vipers tended to move to lower layers of vegetation after 12:00, when the ambient temperature increased (Fig. 2A). To further investigate the relationship between perch height and ambient temperature, we pooled data from the activity pattern (n = 9) and prey availability experiments (n = 43, excluding 5 individual snakes which were disqualified because they were on the ground under the vegetation during the recording visits) with the same vegetation arrangement. A significant inverse relationship was found (Fig. 3). Vipers tended to stay on the lower stratum of vegetation when the ambient temperature was high. The concurrent shaded temperatures significantly differed among the 3 strata in the hot season (Table 1A). In particular, when vipers moved from a high to a low stratum at 13:00, the shaded temperature within the bottom strata was significantly lower than those of the upper and middle strata (ANOVA, Scheffe's test, mean ± SD: upper stratum = 30.72 ± 0.72°C A, middle stratum = 30.26 ± 0.68°C A, lower stratum = 27.04 ± 3.09°C B, F = 6.882, p = 0.008). However, no significant differences in the shaded temperature between the lower and upper

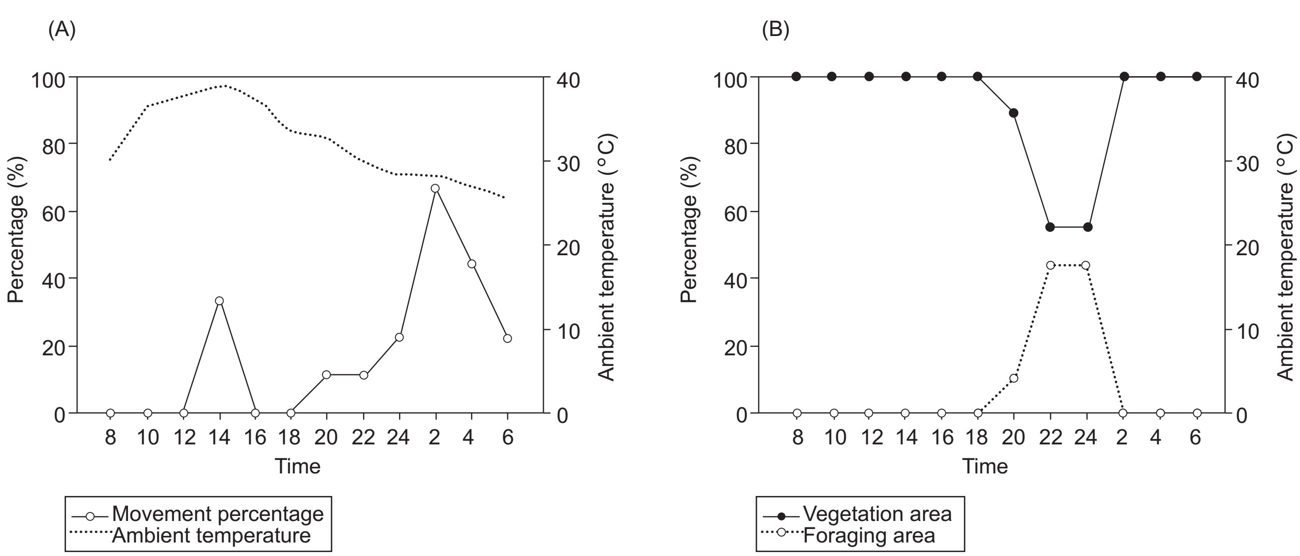

Fig. 2. (A) Activity pattern of green tree vipers and the ambient temperature within the enclosure during a 24 h period. Movement percentage = (Moving individuals/Total no. of vipers) x 100% (n = 9). (B) Percentage of individual snakes remaining in the foraging area or in the vegetation area during a 24-hour period. Percentage = (Number of individuals in the foraging or vegetation area/Total no. of vipers) x 100% (n = 9). Lights in the enclosures were turned on from 07:30 to 17:30 (as indicated by the white area).

strata were detected during the cool season (mean ± SD: upper stratum = 20.79 ± 2.88°C, middle stratum = 20.79 ± 2.88°C, lower stratum = 20.70 ± 2.76°C, $F = 0.001$, $p = 0.999$) (Table 1B).

Vegetation density and temperature

Fifty-seven green tree vipers were studied to determine their preference of retreat sites in vegetation of densities L and M, respectively. Overall, vipers significantly preferred retreating into the medium rather than the low vegetation density (Chi-square test: L = 19, M = 38, $x^2 = 6.333$, df = 1, $p = 0.011$). However, the preference was significant only during the hot season ($p = 0.012$) and not during the cool season (Fig. 4A). Shaded temperature was significantly lower from 09:00 to 15:00 at density M than density L during the hot season (paired t-test, mean ± SD: M = 29.72 ± 1.99°C, L = 30.36 ± 2.06°C, $n = 27$, $t = 5.728$, $p < 0.001$). During the cool season, there was no difference in shaded temperatures between the 2 types of vegetation density (paired *t*-test, mean ± SD: M = 18.28 ± 2.44°C, L = 18.23 ± 2.48°C, $n = 27$, $t = -1.12$, $p = 0.273$).

Fifty-two green tree vipers were tested to determine their preference of retreat sites between vegetation densities M and D, but we found no significant difference in the snakes' selections of retreat sites attributable to differences in vegetation density (Chi-square test: M = 23, D = 29, $x^2 = 0.692$, df = 1, $p = 0.405$) in either the hot or cool season (Fig. 4B). However, the shaded temperature in vegetation density D was significantly lower than that in vegetation density M during both the hot (paired t-test, mean ± SD: D = 25.83 ± 1.61°C, M = 26.61 ± 1.74°C, $n = 27$, $t = -9.536$, $p < 0.001$) and cool (paired *t*-test, mean ± SD: M = 19.63 ± 1.14°C, D = 19.48 ± 1.21°C, $n = 27$, $t = -3.29$, $p = 0.004$) seasons.

In order to further investigate the correlation between retreat site selection and ambient temperature, we pooled data samples from the 3rd, 4th,

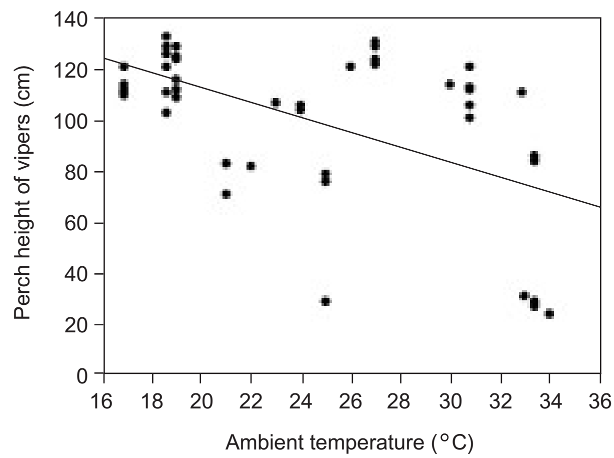

Fig. 3. Correlation between perch height of green tree vipers and ambient temperature within the enclosure ($n = 52$, *** $p < 0.001$, $R = -0.542$).

Table 1. Analyses of the effects of time and stratum on shaded temperatures. (A) Hot season (21-23 Aug. and 28-30 Sept. 2005, $n = 72$). (B) Cool season (12-14 Oct. and 10-12 Dec. 2005, $n = 72$)

(A) Hot season

Source	df	*F*-ratio	*p*
Time[1]	3	7.361	< 0.001***
Stratum[2]	2	13.861	< 0.001***
Time x Stratum	6	0.820	0.559
Error	60		

(B) Cool season

Source	df	*F*-ratio	*p*
Time[1]	3	0.148	0.930
Stratum[2]	2	0.002	0.998
Time x Stratum	6	0.000	1.000
Error	60		

Two-way ANOVA. [1]Categories of the variable, Time, are 09:00, 11:00, 13:00, and 15:00. [2]Categories of the variable, Stratum, are upper (height = 130 cm), middle (height = 80 cm), and lower (height = 28 cm). *** $p \le 0.001$.

and 5th morning visits during the hot season and cool season. For vegetation densities L and M, there was a significant correlation between the frequency at which snakes remained in the M type vegetation cover and ambient temperatures (correlation analyses: $p = 0.004$, $R = 0.539$, Fig. 5A). In comparing vegetation densities M and D, there was also a significant correlation between the frequency of the snakes perched in vegetation density D and the ambient temperature (correlation analyses: $p = 0.001$, $R = 0.627$, Fig. 5B). Our observations indicate that under high ambient temperatures, green tree vipers consistently chose shaded areas with lower temperatures, i.e., M instead of L, and D instead of M.

Between Oct. and Nov. 2005, 20 green tree vipers were tested for selection of retreat sites in vegetation densities L and F. The results showed that all vipers selected vegetation density L, and none retreated in vegetation density F (Chi-square test: L = 20, F = 0, $x^2 = 20$, df = 1, $p < 0.0001$). There was no significant difference in shaded temperatures within the vegetation between F and L (paired *t*-test, mean ± SD: F = 21.99 ± 1.31°C, L = 22.01 ± 1.27°C, $n = 27$, $t = -0.247$, $p = 0.807$).

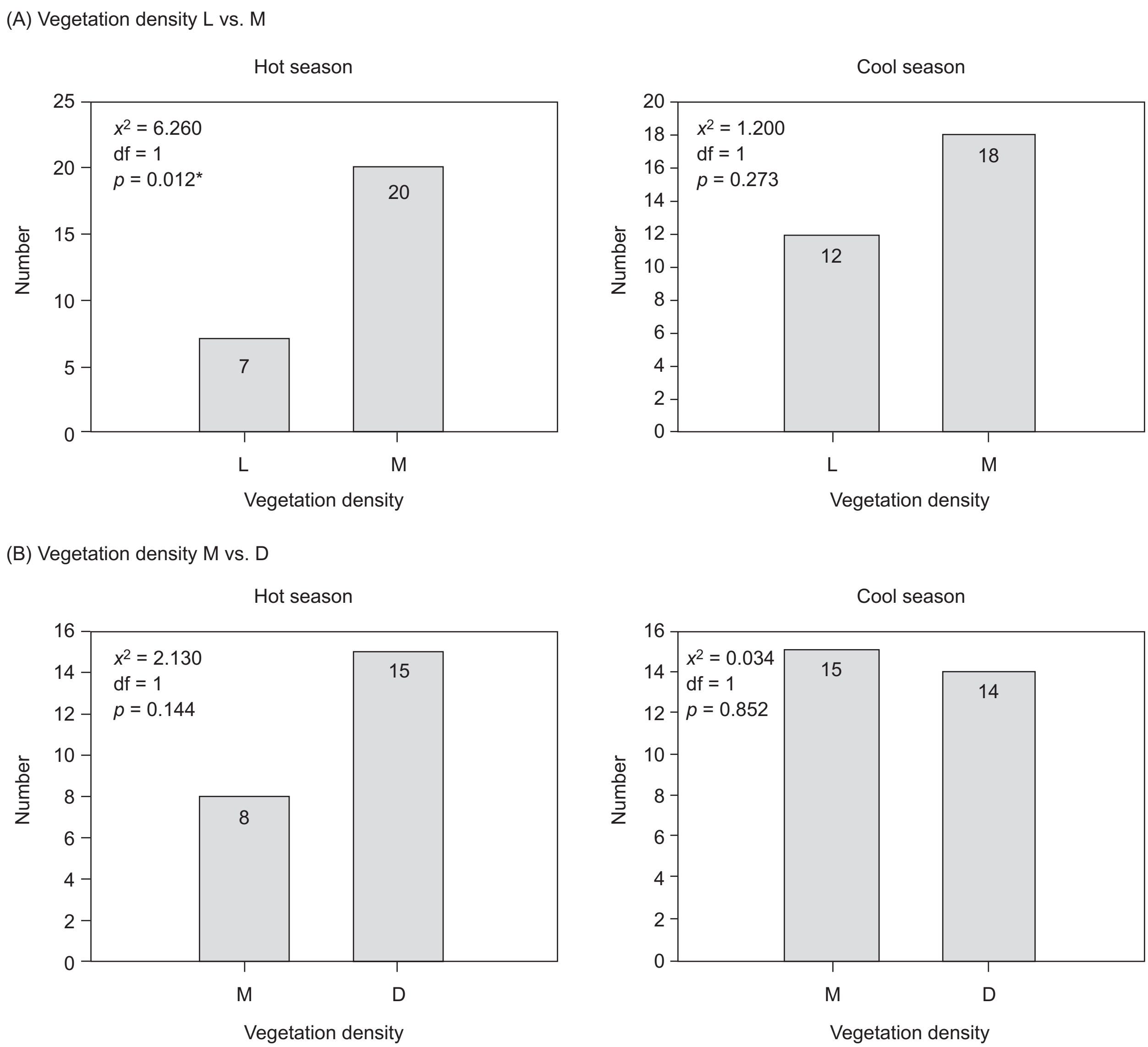

Fig. 4. Number of green tree vipers selecting different vegetation densities in the hot and cool seasons (by Chi-square test). Vegetation densities were divided into 3 categories: D (dense, with a pot interval of 15 cm), M (medium, with a pot interval of 30 cm), and L (loose, with a pot interval of 45 cm). (A) Comparison between vegetation densities L and M. (B) Comparison between vegetation densities M and D.

DISCUSSION

An animal's choice of a retreat site reflects a set of decisions that give priority to certain factors over others (Downes and Shine 1998). We discovered that relative to vegetation density and/or prey availability, available thermal conditions appeared to be the most significant temporal cue influencing retreat site selection by the green tree viper. According to previous studies, reptiles within retreats often adjust their posture or position to exploit thermal gradients in order to regulate their body temperature (Losos 1987, Huey et al. 1989, Kearney and Predavec 2000). Vertical movements of green tree vipers in the enclosures appeared to be adjustments in position to achieve optimal thermal regulation. The crown vegetation canopy provides a wide range of temperatures due to solar radiation and radiative cooling (Lillywhite and Henderson 1993). Although the tops of our enclosures were not transparent, solar radiation could still pass through. The screening effect provided by the plant leaves resulted in lower temperature within the lower strata of the vertical vegetation structure, which helped form a distinctive thermal gradient. We observed a positive correlation between a snake's perch height in the tree and its body temperature (Fitzgerald et al. 2003). Green tree vipers may utilize this temperature gradient to accommodate variations in their thermal needs. Snakes tended to move vertically between the upper and bottom strata to achieve optimum thermoregulation in the daytime. At high ambient temperatures, vipers tended to remain in the lower stratum of the vegetation, where temperatures were lower. This phenomenon was especially obvious when the ambient temperature was higher than 28°C. Tsai and Tu (2005) discovered that the preferred fasting temperature of Chinese tree vipers in the laboratory was 20.3-24.3°C. Therefore, we believe that the vipers tend to move towards the lower stratum of vegetation in order to reach their preferred temperature for achieving thermal regulation when the ambient temperature is high.

The types of vegetation density selected by green tree vipers as retreat sites are also influenced by temperature cues; moreover, the physical environment within a habitat structure may influence the thermal attributes and microclimate of a reptile's selected habitat (Christian et al. 1983, Huey et al. 1989, Pringle et al. 2003, Heard et al. 2004, Tsairi and Bouskila 2004, Webb et al. 2004). When the ambient temperature was higher than 25°C, tree vipers preferred to retreat into denser vegetation (Figs. 4A, 5), which provides significantly lower shaded temperatures. In contrast, when the ambient temperature in the enclosures dropped to below 25°C, vipers did not appear to have a consistent preference for retreating into denser vegetation, apart from an apparent distaste for vegetation with only bare branches and little or no foliage. This may be attributable to the fact that there is either no perceivable distinction in the

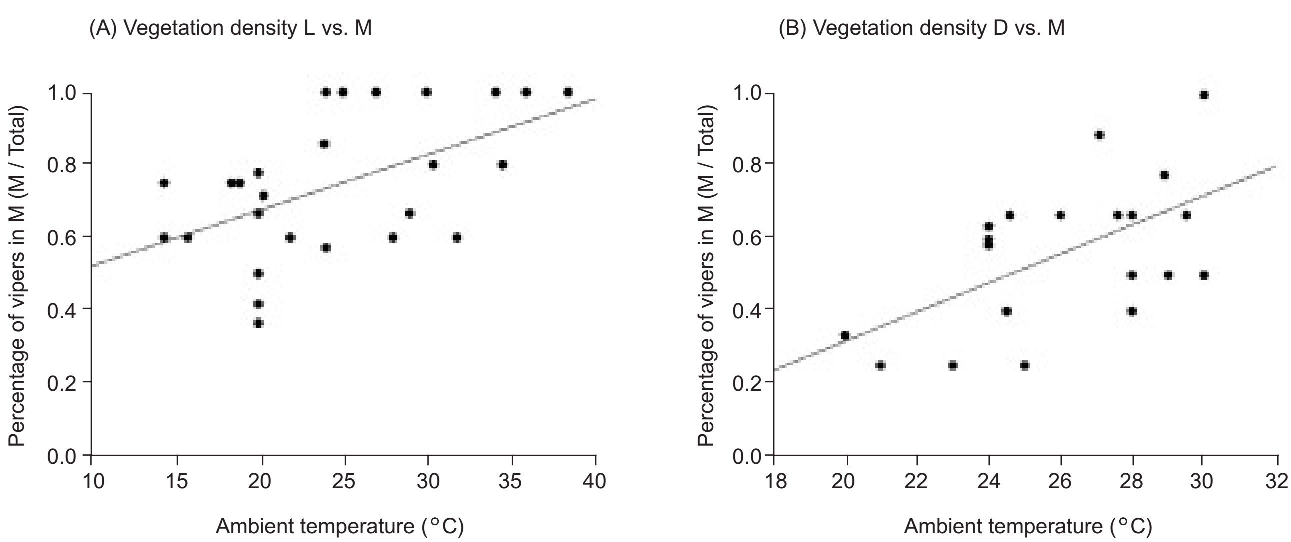

Fig. 5. Correlation between the percentage of green tree viper's perch selection in different vegetation densities and the ambient temperature regimes. Vegetation densities were divided into 3 categories: D (dense, with a pot interval of 15 cm), M (medium, with a pot interval of 30 cm), and L (loose, with a pot interval of 45 cm). (A) Comparison between vegetation densities L and M (correlation: n = 27, ** p = 0.004, R = 0.539). (B) Comparison between vegetation densities M and D (correlation, n = 24, *** p = 0.001, R = 0.627).

shaded temperatures between sparse and dense vegetation, or the difference between the shaded temperature and the green tree vipers' preferred temperature (20.3-24.3°C) was insignificant.

Nocturnal reptiles spend a large portion of their time sequestered in diurnal retreat sites where thermal conditions strongly impact their long-term fitness (Huey et al. 1989, Kearney and Predavec 2000, Webb et al. 2004). Thermal requirements and exploitation of microclimates are the overriding determinants of temporal variations or seasonal differences in the space utilization patterns of some reptiles (Christian et al. 1983, Kearney 2002, Heard et al. 2004). For example, the Galapagos land iguana (*Conolophus pallidus*) exploits the warmer microclimate provided by cliffs, which allow the iguana to maximize the duration it is able to maintain a constant body temperature during the cool season (Christian et al. 1983). Webb et al. (2004) also proposed that the influence of temporally variable cues such as substrate temperature, may be particularly significant for habitat selection by both the broad-headed snake and the common small-eyed snake (Webb et al. 2004). Our study showed that temporal thermal conditions had significant influences on retreat site selection by green tree vipers, and we suggest that daily and seasonal differences in space utilization patterns (perch height and vegetation density) may be for the purpose of satisfying their thermoregulation needs.

Small ectotherms appear to select their retreat sites with the objective of enhancing fitness (Webb and Shine 1998a, Mullin and Cooper 2000, Downes 2001, Shah et al. 2004). Tree vipers did not appear to have a consistent preference for retreating into denser vegetation. In the field, we also discovered that some green tree vipers at perch heights of < 2 m from the ground would frequently retreat upwards into trees, bushes, or ferns with sparser vegetation. Which leads us to an important question: Why don't green tree vipers prefer to retreat into the denser, and presumably "safer", vegetation structure? There are few known diurnally visual predators of the green tree viper, but the Crested Serpent Eagle (*Spilornis cheela*) is among the known predators (Lin 2005). One possible explanation may be that because diurnal raptors fly in the sky, they cannot easily discover green tree vipers that are resting in the mid-layer of the canopy or within the lower shrubs and ferns of a forest during the day, even in retreats with sparse vegetation. Additionally, cryptic (camouflage) coloration and immobilization are very important protective mechanisms that help arboreal reptiles avoid or minimize the risk of being attacked by potential predators (Clark and Gillingham 1990, Lillywhite and Henderson 1993). Tree vipers' arboreal behavior, linked with their green coloration and sedentary seclusion within branches and foliage, enhances their protection as they may go unnoticed by predators even as they rest in the upper canopy of vegetation structures during the day. Based on observations of 2 nesting pairs of Crested Serpent Eagles during their entire brooding period, of the 65 recorded instances where snakes were taken as food for their chicks, only 2 episodes involved green tree vipers (Lin 2005). This is a very low frequency of predation considering the green tree viper's abundance in the Taipei area.

Enhancing their foraging advantage may be another reason why green tree vipers tend not to retreat into denser vegetation. A snake's habitat selection of a particular structural complexity may reflect a compromise between protection from predators and the snake's visual ability to pursue its own prey (Mullin and Cooper 2000). Visual cues may be an important factor in a snake's orientation for obtaining prey (reviewed in Ford and Burghardt 1993, Shine and Sun 2002). The complexity of the vegetative structure may affect the ability of a snake to visually detect and pursue its prey (Mullin et al. 1998). A clear and bright line-of-sight is necessary for the capture of prey (Mullin and Cooper 2000, Shine and Sun 2002, Shine et al. 2002). Green tree vipers primarily feed on frogs, lizards of the Agamidae, birds, and rodents (Mao 1970, Lee and Lue 1996, Creer et al. 2002). Some of them are diurnally arboreal species such as *Japalura polygonata xanthostoma* (H. Lin, unpubl. obs.). Because green tree vipers may encounter their arboreal prey when resting in trees during the day, selecting an excessively complex or dense vegetation structure is not conducive to detecting and attacking their prey.

Although we intuitively expected that green tree vipers would prefer retreat sites closer to prey resources, our research did not support this prediction. One reason may have been due to the length of the artificial enclosure, which was insufficient when compared to physical conditions in the wild. Based on field observations of 55 vipers, the average foraging distance (defined as the average distance between retreat sites during daytime and ambushing sites on the same night) for each individual snake was 2.3 m (H. Lin, unpubl. obs.). This distance is similar to those observed for some other arboreal snakes (Henderson et al. 1977, Lillywhite and Henderson 1993, Webb and Shine 1997a, Shine and Sun 2002). However, due to the difficulty of finding snakes that are perched high up in trees, the foraging distance might be underestimated (Lillywhite and Henderson 1993, Heard et al. 2004). In this study, the vegetation we provided was an interlocking canopy that facilitated the green tree vipers' movement without descending to the ground. Therefore, it was possible that the difference in time and energy spent by green tree vipers resting in different locations of the vegetation area may have been minimal in our 10-m-long enclosures (vegetated areas). Consequently, no significant preference with respect to distance to prey resources was detected.

Furthermore, failure on the part of the green tree vipers to show a clear preference for retreating in the close proximity of the pool area (where the frogs were located) may also have been due to their ability to capture both terrestrial prey and arboreal species. Aside from diurnally arboreal prey, green tree vipers also feed upon various nocturnal tree frogs (Tu et al. 2000). A high probability for encounters with prey is an important factor in the selection of microhabitats by the desert snakes (*Echis coloratus*), but the key to predicting the future availability of prey by desert snakes appears to be related to the type of microhabitat structure where prey is likely to appear rather than the actual odor of the prey (Tsairi and Bouskila 2004). Therefore, some vipers might not use the availability or odor of paddy frogs as the sole determinant for selecting a retreat site. They may select microhabitats where arboreal lizards and/or tree frogs appear more often at their retreat sites, rather than locations closest to the provided foraging area. Nighttime movements of green tree vipers for foraging purposes were not uniformly towards the ground in the field (Tu et al. 2000). Likewise, our nighttime observations also showed that over 50% of the snakes in the enclosures elected to stay in the trees (Fig. 2B), and all of them consistently remained in the foraging position. This comparison appears to provide further support for our conclusion that the selection of a retreat site is not solely determined by the abundance of terrestrial prey.

This study demonstrates that temperature is the most important temporal cue for retreat site selection by Chinese green tree vipers. The strong correlation between temperature and retreat site selection has the benefit of allowing snakes to better control their thermoregulation while remaining concealed. The absence of a consistent preference for retreating into denser vegetation on the part of the snakes may reflect a compromise between protection from predators and acquisition of prey.

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