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Characteristics of a Snake Community in the Hilly Forest of Quan Son District, Northern Vietnam

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Abstract.—**The snake communities in Asian tropical forests are relatively unknown, with most studies focusing on species lists. We investigated species composition, relative abundance, and community ecology of snakes in a mature secondary hilly forest area in the Quan Son District, northern Vietnam. To our knowledge, it is one of the few field investigations focused on snake community structure to have been undertaken within the Indo-Burma Hotspot, which is one of the most biologically important regions on the planet. We surveyed snakes along random transects in forests during two time periods (10–12 d), between 500 and 1,350 m elevation. In 361.8 h of surveys, we encountered 19 species, with a clear altitudinal separation in snake assemblages and numbers. Encounter frequencies dropped with elevation but had a peak at the intermediate elevation of 600–699 m. We therefore observed a Mid Domain Effect in our snake community in terms of both species richness and number of individuals observed. Of the 19 recorded species (including one Pythonidae, 11 Colubridae, two Elapidae, one Pseudaspididae, three Viperidae, and one Xenodermidae), 78.9% were exclusively or primarily terrestrial, 42.1% were semiarboreal, and 21% were semiaquatic (with some species belonging to two guild categories). We also present new natural history observations of snakes in the region. We discuss the importance of our findings relative to other similar studies conducted in South America and Africa, in addition to those in Vietnam and South-East Asia.**

Key Words.—community; field survey; habitat; Indo-Burma region; snakes

Introduction

Snake assemblages in Subtropical and Tropical forest regions are often species-rich (Luiselli 2006a), with the number of sympatric species varying considerably from just over 20 species in West African forests (e.g., Akani et al. 1999a,b); 53 species in a lowland rainforest in Ecuador (Duellmann 1978); 66 species in a forest reserve in Brazil (Martins and Oliveira 1998); and as many as 89 species in rainforests of Peru (Dixon and Soini 1975). Snake assemblages also represent a functionally important element of biotic communities in a given space and time (Beho et al. 1986); if snakes are found in sufficiently large numbers and biomass, they can considerably influence the population dynamics of their prey (such as lizards and amphibians; see Luiselli et al. 1998).

Quantitative community ecology studies on snake assemblages in Asian forests are scarce, although careful lists of species for well-defined study areas have already been published (Orlov 1995; Ziegler 2002), and studies have been done by Inger and Colwell (1977); Karns et al. (2005, 2010), Zug (2011), Rahman et al. (2013), and Crane et al. (2018). Inger and Colwell (1977) was certainly the most extensive study for the region, being a 10-mo-long longitudinal study conducted over both wet and dry seasons in three habitat types at a site in northeastern Thailand. These authors used quantitative litter transects and visual encounter surveys for determining relative abundances, densities, and microhabitat use, and their dataset contained hundreds of individuals. The Indo-Burma Hotspot in tropical Asia is one of the most biologically important regions on the planet (Myers et al. 2000). Similar to other vertebrate groups, reptile diversity and endemism in the Indo-Burma Hotspot are high and include a number of distinct phylogenetic lineages (more than 296 species in Vietnam; Nguyen et al. 2005). Despite this importance, knowledge of the ecology of many reptile species in the region is largely unknown, in particular for snakes. Most studies published for snakes from Vietnam are species lists (Nguyen and Ho 1996; Orlov et al. 2000; Nguyen et al. 2005; Nguyen et al. 2009) or taxonomical descriptions (Bain et al. 2006; Stuart and Bain 2005; Ziegler and Le 2005, 2006; Orlov et al. 2006), with community ecology studies being less than for Africa and South America (see Luiselli 2006a; but see Ziegler et al. 2007).

Vietnamese natural forests have been overexploited and heavily fragmented in the past few decades, and have been routinely subject to slash-and-burn agriculture and are the source of non-timber forest products, harvesting of bushmeat, and traditional medicine use and trades (e.g., Haibin and Kunming 1999). Nonetheless, there are still a few areas of mountainous forests in northern Vietnam that have escaped significant habitat disturbance and destruction by humans, where it is probable that the composition of snake communities has remained relatively undisturbed. Because these mountainous areas are hard to survey due to their terrain and inaccessibility, there have been few studies undertaken there (Ziegler et al. 2007). Thus, evaluating the community ecology of snakes in mature South-East Asian forests can provide unprecedented data on relatively undisturbed snake assemblages in subtropical and tropical forests.

In this paper, we documented the composition, relative abundance, and community ecology of snake species in a mature secondary hilly forest area in northern Vietnam. We also compare our data with those collected in other forest sites in South-East Asia and in tropical forests from other continents (Africa and South America). We also highlight the elevational pattern of the studied snake community in the light of general theory about the distribution and richness of animal communities along elevational gradients (e.g., Connolly 2005; Brehm et al. 2007).

Materials and Methods

Study area.—We studied the snake community in Hang Trình, in the Tam Thanh Commune (20°11′15″N, 104°50′29″E), Quan Son District, northern Vietnam (Fig. 1). The Tam Thanh Commune adjoins the northern

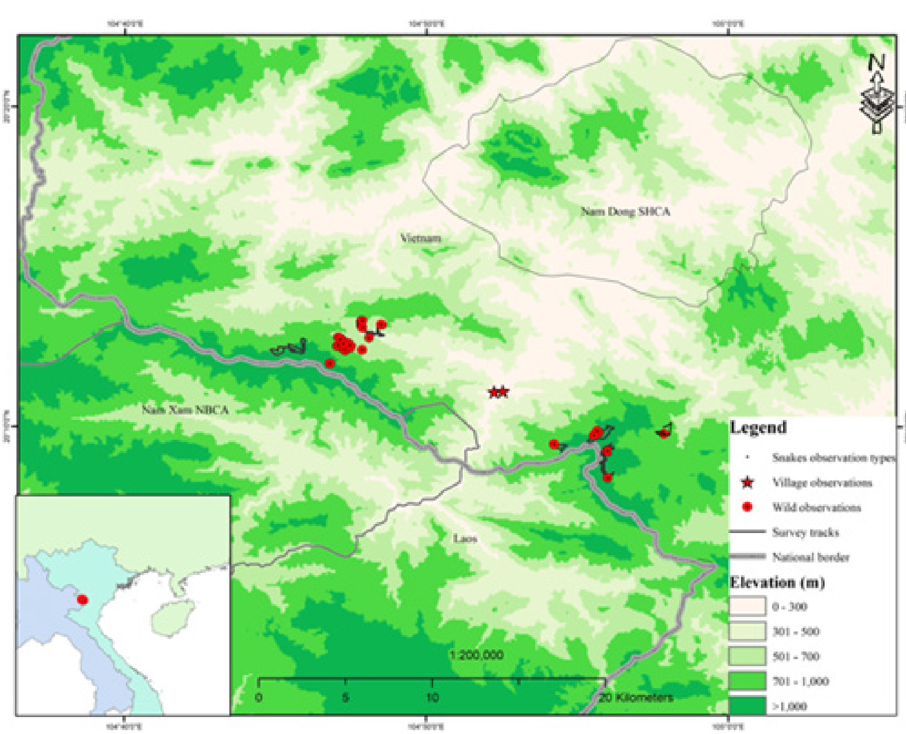

Figure 1. Map of northern Vietnam, showing the study area, the survey tracks made by the researchers, and the sites of sighting for free-ranging snakes. Roads are not included in the map.

Laos border within the northern Indochina Subtropical Moist Forests (World Wildlife Fund. 2019. Tropical and subtropical moist broadleaf forests. Southeastern Asia: China, Laos, Myanmar, Thailand, and Vietnam. World Wildlife Fund. Available from http://worldwildlife.org/ecoregions/im0137 [Accessed 8 September 2019]), dominated by evergreen and semi-evergreen forests. The climate of the region is subtropical montane, with an average temperature of 23° C, maximum temperature of 40° C from May to July and lowest temperature of 2.6° C in December. Average rainfall is 1,900 mm; the wet season is from May to October (> 1,000 mm rainfall) and the dry season from December to January. Humidity averages around 84% (http://huyenquanson.vn/gioi-thieu/dieu-kien-tu-nhien/8). The linear distances of the study area to the three nearest protected areas were about 85 km to Pu Luong Nature Reserve (NR), 75 km to Xuan Lien NR, and 65 km to Pu Hu NR.

Human activities have been responsible for some habitat modification and destruction, but in this area about 80% forest cover still remains (including mature, secondary, and plantation forests). This forest area is considered important for the conservation of biodiversity in Vietnam (Sterling and Hurley 2005). The Tam Thanh forest area (4,909.9 ha) is composed of 4,824.9 ha of natural forest and 85.0 ha of plantation forest. Within the natural forest, 59.3% consists of Evergreen and Semi-deciduous forest, 28.2% Bamboo Forest, and 12.5% Mixed Evergreen and Bamboo forests (unpubl. report). The forest in Tam Thanh Commune is managed by a local board, where regulated extraction of timber and non-timber products is allowed by the local inhabitants; however, agriculture, pollution, and poaching represent the main threats for the local biodiversity. The human population density was very low (36 persons per km2; Tam Thanh People Committee, unpubl. report).

Field surveys.—The period of highest snake activity in tropical and sub-tropical regions is the rainy season (Akani et al. 2013). Thus, we conducted two independent random walks, along distinct transects, during the rainy season, applying a time-constrained search effort (Akani et al. 1999a,b). A team of two main researchers and seven local assistants undertook snake searches between 0700 and 1700 and between 1900 and 2200 Hanoi time during each survey day. The first field survey was from 11 to 23 May 2019 at an elevation range of 500–1,000 m, the second was from 14 to 24 August 2019 at elevations ranging between 900 and 1,350 m (Fig. 1). We followed random transects (1 to 4.5 km long depending on the quality of the surveyed habitat) within which we searched for snakes. Longer transects were walked in mature forests and in sites with minimal human disturbance. Overall, we carried out 15 transects per person, with a total of 75 transects as each person walked independently from the others. We did not follow paths and forest tracks, although in some cases our random transects crossed through them. Recording of searching time was stopped when an animal was found and measured.

We recorded snake individuals that were observed during visual transects (VES) and that were in the open, but also those that were on trees, and we also turned surface cover objects, including logs, stones, and other cover. We did not set traps for aquatic snake species. We used machetes to open the transect line when needed, given the relative inaccessibility of some spots. All individual snakes found during the field surveys were examined and identified to species and were also photographed using a Nikon D800 camera with a Nikkor macro 105D 2.8 lens (Nikon, Minato, Tokyo, Japan). We recorded, if possible, length, body mass, and sex (by inspecting the cloacal area) for each individual. Length measurements were taken using a measuring tape, and snake body mass was taken using a 5 kg scale, (accuracy 1 g). We identified species using Nguyen et al. (2009), supplemented by checking the Reptile Database 2020 (http://reptile-database.reptarium.cz/advanced_search?taxon=snake&location=Vietnam&submit=Search). We released all animals captured during the field survey after sampling.

Habitat description.—We described the microhabitat characteristics within a 10 m radius of each encountered snake, using five different variables; (1) main habitat types with 1 = stream; 2 = evergreen forest, 3 = bamboo forest, and 4 = village and plantations; (2) canopy cover estimated on the basis of the percentage of sunny spots on the ground; (3) ground temperature (°C) collected by B61200-1300 infrared thermometer (Zoo Med Manufacturing, Wuhan, China); (4) ground humidity (%) collected by AR827 Hygrometer (Zoo Med Manufacturing); (5) slope angle (degrees) using a smartphone application (Angle Meter). We assigned each snake species to one of the following three ecological guilds: (1) arboreal, (2) terrestrial, or (3) aquatic (Akani et al. 1999).

Statistical analyses.—To calculate snake observation frequencies corrected for searching effort, we used the following formula:

$$S = x / (a \times b)$$

with S = snake relative frequency of observation; x = number of snakes found in a given transect; a = number of people involved in the time searching along a given transect; b = total time spent for a trip along a given transect. To determine whether the snake taxonomic composition of the study area was adequately assessed, we performed a rarefaction analysis using the total (i.e., field observed + hunter collected) snake sample. We made sample-based rarefactions (or species accumulation curve) using Mao's tau, with one standard deviation (Colwell et al. 2004). In the graphical plot, we converted standard errors to 95% confidence intervals.

We evaluated the diversity of the snake assemblage within the study forest by calculating the Dominance Index of Magurran (1988):

$$D = 1 - \text{Simpson Index}$$

In this case, the Simpson's Diversity Index is 1−*D* with *D* calculated as:

$$D = 1 - \sum_{i=1}^{s} \left(\frac{n_i(n_i - 1)}{N(N-1)} \right)$$

with n_i = number of individuals in species *i* and *N* = total number of individuals. We also calculated evenness (*e*) of Pielou (1966):

$$e = H' / \log Sn$$

with *H′* = Shannon and Weaver's Index (1948), and *Sn* = the total number of snake species observed in the study forest (Magurran 1988). The Shannon and Weaver Diversity Index (*H'*) is:

$$H' = -\sum_{i=1}^{s} p_i(\log_2 p_i)$$

with $p_i = n_i / N$; p_i is the relative abundance of species *i* in the sample. We used bootstrap analysis to generate upper and lower confidence intervals of all indices, with 9,999 random samples, each with the same total number of individuals as in each original sample (Harper 1999). We also used observed-versus-expected Chi-square Tests, using equal frequencies as expected values, to compare frequencies of occurrences among snakes in different guilds (terrestrial versus arboreal versus aquatic). Frequency of occurrence of snake species among ecological guilds and habitats was assessed by Chi-square Tests. We used Linear Regression on the proportion of observed individuals against elevation band (in 100 m intervals), with Pearson's Correlation Coefficient as a measure of correlation strength. In the text, the means are presented ± 1 standard deviation. We used PAST version 3.0 statistical software (Hammer 2012) for all tests, with alpha set at 5%.

Results

The survey team spent 361.8 h in the forest searching for snakes (194.4 h in May and 167.4 h in August). We recorded as many as 19 snake species (including one Pythonidae, 11 Colubridae, two Elapidae, one Pseudaspididae, three Viperidae, and one Xenodermidae; Fig. 2; Appendix Table 1). During the May surveys, we encountered 31 snakes of 16 species, with a frequency of 1.72 individuals/person-hour (Supplemental Information, Table S1), including one species (a Burmese Python, *Python bivittatus*) that was not seen in the wild but that was found in a village ready to be sacrificed for food.

At 500–900 m elevation, during the August surveys, the overall snake encounter rate was 0.154 individuals / person-hour, ranging from 0.086 individuals / person-hour (aquatic species) to 0.211 individuals / person-hour (terrestrial species). At 901–1,350 m elevation, we found seven snakes in the wild of seven species and three snakes of three species observed in a village (Supplemental Information, Table S1). Overall snake encounter rate for this survey was 0.042 individuals / person-hour, ranging from 0.0091 individuals / person-hour (aquatic species) to 0.111 individuals / person-hour (terrestrial species).

Of the 19 recorded species, 78.9% were exclusively or primarily terrestrial, 42.1% species were semiarboreal, and 21% were semiaquatic (with some species belonging to two guild categories). Overall, the frequencies of species in different ecological guilds significantly differed (χ^2 = 13.17, df = 2, $P < 0.050$), with terrestrial significantly greater than other categories (χ^2 = 6.78, df = 1, $P < 0.050$). We observed more snake species in forest habitats than in streams or villages (Table 1). Although the sample sizes of the various species were too small for evaluating statistical differences, some general quantitative considerations for the whole snake community can be done. Snake encounters were not homogeneously distributed across habitats (χ^2= 8.93, df = 3, $P < 0.050$), with the two types of forest (bamboo and evergreen) having significantly more observations than the other habitats, but with no significant difference between bamboo and evergreen forests (Fig. 3). The snakes were encountered in sites with high canopy cover (mean = 74.9 ± 15.2% standard deviation, median, 77.5%) at an average temperature of 25.1° ± 2.34° C (median, 25° C), and at a high humidity (91.4 ± 7.6%; median, 93.6%). Snakes were also observed at relatively moderate slope angles (21.1 ± 8.9°; median, 22°), partly because of the various arboreal species encountered. There was also a slight decrease in the percentage of encountered snakes by elevational band, with the peak of the encounters being reached at 600–699 m (slope = -3.46; intercept = 28.29; $F_{1,11}$ = 0.800, P = 0.372, r^2 = 0.161; Fig. 4).

We observed a predation event of a Burmese Python by a King Cobra (*Ophiophagus hannah*; Supplemental Information, Fig. S1). The incident was

Figure 2. Snakes observed during surveys in Quan Son District, northern Vietnam, 2019. From the top left side to the right side: (a) Vietnamese Bronzeback (*Dendrelaphis ngansonensis*), (b) Vietnam Water Snake (*Hebius chapaensis*), (c) Fusting Wolf Snake (*Lycodon futsingensis*), (d) Ruhstrat's Wolf Snake (*Lycodon ruhstrati abditus*), (e) Chinese Kukri Snake (*Oligodon chinensis*), (f) Large-eyed Bamboo Snake (*Pseudoxenodon macrops*), (g) Red-necked Keelback (*Rhabdophis subminiatus*), (h) Rhinoceros Ratsnake (*Rhynchophis boulengeri*), (i) Common Many-toothed Snake (*Sibynophis collaris*), (j) Diamond-back Water Snake (*Sinonatrix aequifasciata*), (k) Banded Krait (*Bungarus fasciatus*), (l) Common Mock Viper (*Psammodynastes pulverulentus*), (m) Brown-spotted Pit Viper (*Protobothrops mucrosquamatus*), (n) Gumprecht's Green Pit Viper (*Trimeresurus gumprechti*), (o) Big-eyed Green Pit Viper (*Trimeresurus macrops*). (Photographs a, d, e, h, k by Oanh Lo Van and all others by Olivier Le Duc).

recorded 20 May 2019 at 1240 at an elevation of 532 m, 27° C ambient temperature, and 86% humidity, in a riverine rainforest habitat. Additionally, we found a female Brown Spotted Pit Viper (*Protobothrops mucrosquamatus*; 113 cm total length) covering and protecting its eight eggs with its body (Fig. 5) while resting inside a tree hole (50 cm diameter) next to a waterfall. We also recorded a 106 cm long female Large-Eyed Bamboo Snake (*Pseudoxenodon macrops*; body mass = 186 g) that regurgitated two undetermined frogs (Supplemental Information, Fig. S1). The individual rarefaction curve revealed that taxonomic diversity of species was adequately represented by our data, although the plateau phase was not yet perfectly reached (Fig. 6). The dominance index was very low (D = 0.0717, bootstrapped range = 0.0717–0.1348), whereas the evenness index was contrastingly high (e = 0.834, bootstrapped range = 0.708–0.906).

Discussion

At Hang Trình forest, we observed a higher frequency of observed species in the terrestrial ecological guild compared to semiarboreal and semiaquatic guilds. We

Table 1. Summary of snake habitat characteristics in Quan Son District, northern Vietnam, 2019. Abbreviations are Elev. = elevation, T = temperature, H = humidity, S = slope angle, and CC = percentage of closed canopy.

Common name	Species	Elev. (m)	Habitat	T (°C)	H (%)	S (°)	CC (%)
odd-scaled snake	*Achalinus* sp.	1,004	Bamboo forest	23.5	78.2	15	
Banded Krait	*Bungarus fasciatus*	509	Village				
Nganson Bronzeback	*Dendrelaphis ngansonensis*	638	Evergreen forest				
bronzeback snake	*Dendrelaphis* sp.	1135	Bamboo forest	26.7	79.5	8	60
Vietnam Water Snake	*Hebius chapaensis*	613	Stream				
Vietnam Water Snake	*Hebius chapaensis*	948	Stream	22.2	91.0		80
Fusting Wolf Snake	*Lycodon futsingensis*	832	Village				
Fusting Wolf Snake	*Lycodon futsingensis*	1025	Stream	22.7	70.0	10	70
Ruhstrat's Wolf Snake	*Lycodon ruhstrati abditus*	1079	Stream	22.6	93.0	5	75
Chinese Kukri Snake	*Oligodon chinensis*	615	Evergreen forest				
Brown-spotted Pit Viper	*Protobothrops mucrosquamatus*	532	Evergreen forest	27.0	86.3		80
Common Mock Viper	*Psammodynastes pulverulentus*	738	Bamboo forest				
Common Mock Viper	*Psammodynastes pulverulentus*	657	Evergreen forest				
Common Mock Viper	*Psammodynastes pulverulentus*	536	Bamboo forest	32.0	68.0		
Large-eyed Bamboo Snake	*Pseudoxenodon macrops*	738	Bamboo forest				
Large-eyed Bamboo Snake	*Pseudoxenodon macrops*	608	Stream				
Red-necked Keelback	*Rhabdophis subminiatus*	643	Evergreen forest	25.0	96.0	10	75
Red-necked Keelback	*Rhabdophis subminiatus*	662	Bamboo forest	25.0	92.1		99
Red-necked keelback	*Rhabdophis subminiatus*	654	Evergreen forest	26.6	89.2	5	65
Common Many-toothed Snake	*Sibynophis collaris*	706	Evergreen forest	24.2	93-96		85
Common Many-toothed Snake	*Sibynophis collaris*	642	Bamboo forest	24.4	97.9	35	80
Common Many-toothed Snake	*Sibynophis collaris*	640	Evergreen forest	26.4	93.6	10	80
Common Many-toothed Snake	*Sibynophis collaris*	680	Bamboo forest	23.6	90.1	26	85
Diamond-back Water Snake	*Sinonatrix aequifasciata*	608	Stream	22.4	94.3		
Diamond-back Water Snake	*Sinonatrix aequifasciata*	631	Stream				
Grumprecht's Green Pit Viper	*Trimeresurus gumprechti*	698	Bamboo forest	23.4	93.0	20	
Grumprecht's Green Pit Viper	*Trimeresurus gumprechti*	644	Evergreen forest	26.2	94.5	25	70
Grumprecht's Green Pit Viper	*Trimeresurus gumprechti*	1023	Evergreen forest	24.4	82	3	30
Kramer's Pit Viper	*Trimeresurus macrops*	655	Evergreen forest	25.2	93.6	22	75
Kramer's Pit Viper	*Trimeresurus macrops*	1023	Evergreen forest	23.0	80.0	5	

think that the few semiaquatic species were because the surveyed habitat was mainly terrestrial with little time spent within streams, ponds, or other aquatic habitats. We also observed that the evenness index was very high and the dominance index was very low; both these indices would suggest that the snake community is relatively undisturbed, as these values could be expected in areas with stable habitats, for instance in relatively pristine forests (e.g., Magurran and McGill 2011). If detectability is not high and constant among species, however, it could be in part also an artifact of low detectability because if some snakes are difficult to detect, we likely missed seeing them, resulting in low dominance and high evenness. Although our statistical analyses suggested that the snake community was adequately sampled at the study area, it is well possible that we underestimated the true number of sympatric species. Indeed, there are many fossorial, arboreal (in this case, even gliding), and aquatic snake species that are easily overlooked in surveys like ours that are mainly based on VES. Thus, the rarefaction/encounter curves that are quantified in this study may be biased to terrestrial, surface active species that spend most of their time between ground level and 3–4 m above the ground, and not to the snake community as a whole. The conclusions we can draw from a rarefaction curve are suggestive but not definitive: there could be rare species that have not yet been observed even if the curve appears to converge.

We compared our list of snakes to that found in Tam Dao National Park (Orlov et al. 2000), which is only about 150 km away and is the best sampled site in

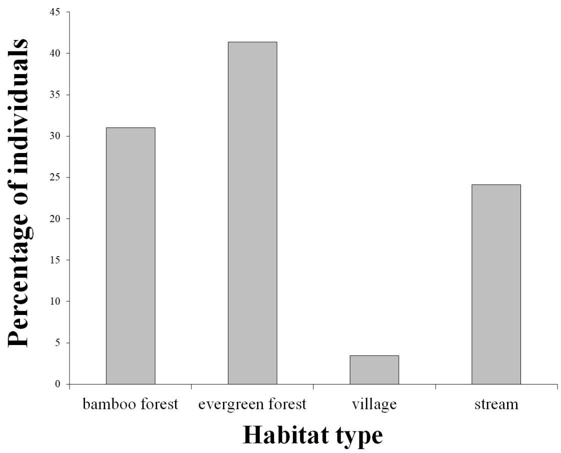

Figure 3. Percentage of the snake sightings across the four habitat types at the study area in Quan Son District, northern Vietnam, 2019.

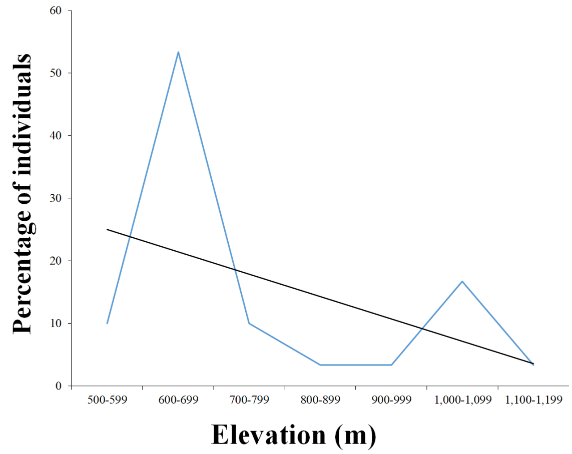

Figure 4. Elevational distribution (m) of the encountered snakes (percentage of observed individuals) at the study area in the Quan Son District, northern Vietnam, 2019. The blue line is the observed data, and the black line is a regression line.

Vietnam for snakes (Appendix Table 1). Tam Dao was a French hill resort for French colonials to escape the heat of Hanoi and was an extremely popular collecting site for natural history collectors during the colonial period (e.g., Bourret 1934, 1935). It has also been a site of many herpetological studies by Vietnamese and foreign scientists since the 1980s (Orlov et al. 2000). During 23 y of study, Orlov et al. (2000) observed 85 different species, and did not observe eight species that we found. These two areas cannot be directly compared though because: (1) they are about 150 km apart; (2) Tam Dao is much larger in size; and (3) it has been sampled much more intensely over the decades (see references in Orlov et al. 2000) than our study area. The much larger size of Tam Dao likely accounts for the much higher number of species recorded there than at our study area. The snake list at Tam Dao also includes several fossorial species, a guild that was not sufficiently represented in our surveys.

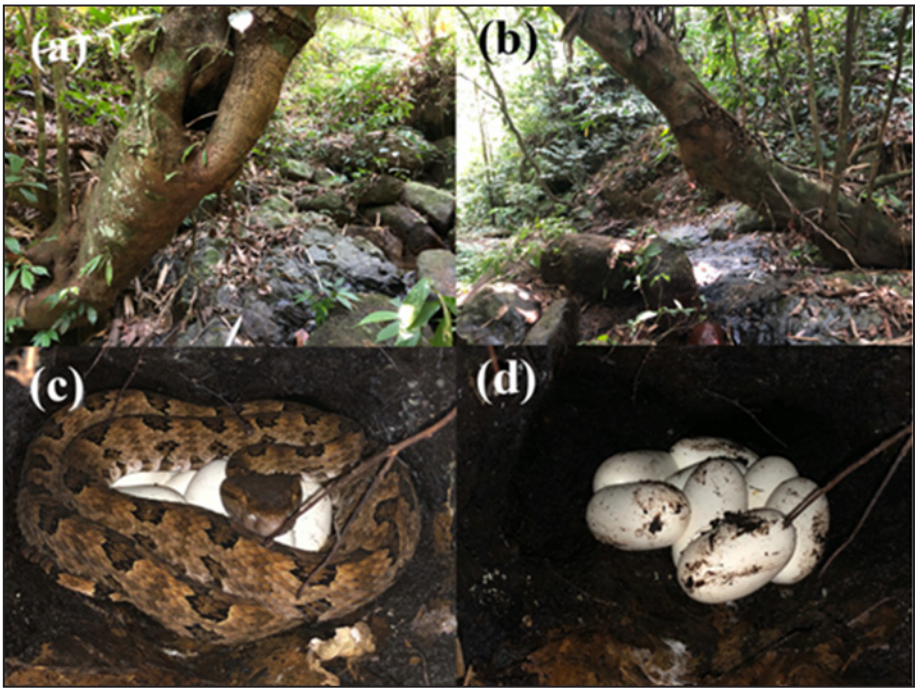

Figure 5. Female Brown Spotted Pit Viper (*Protobothrops mucrosquamatus*) with its eggs inside a tree hole in Quan Son District, northern Vietnam, 2019, and habitat characteristics of the site of sighting. (a) Tree hole. (b) position of the tree, upper the stream. (c) female *P. mucrosquamatus* covering its eggs. (d) eggs. (Photographed by Olivier Le Duc).

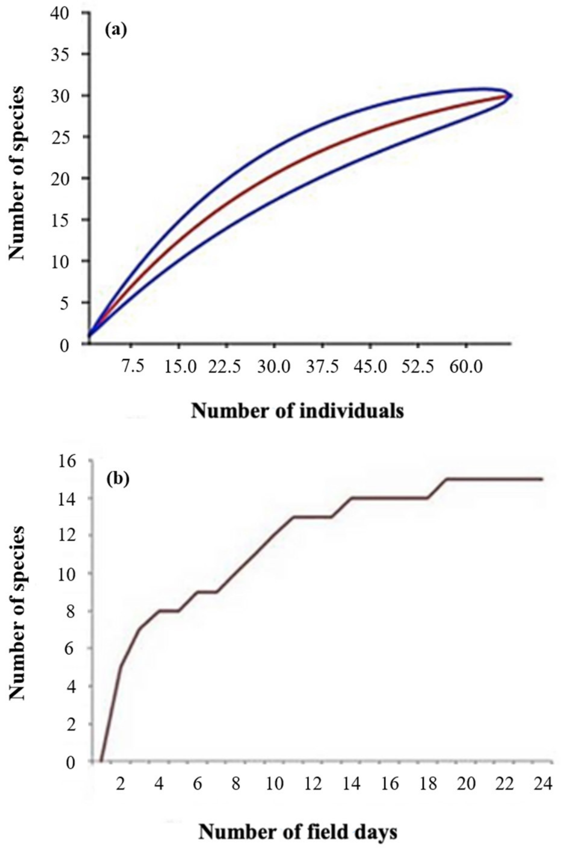

Figure 6. Individual rarefaction curve for (a) the cumulative number of observed individual snakes versus cumulative number of snake species, with the blue lines the 95% confidence interval and the red line the saturation curve, and (b) the cumulative number of days spent in the field versus cumulative number of observed snake species in Quan Son District, northern Vietnam, 2019.

Our study followed a community ecology approach, where the focus was the description of the community structure at a given small area in time, including the evaluation of the truly sympatric species (Ricklefs and Schluter 1993). Data available for Tam Dao includes all the snake species encountered in a very large area throughout several years of mostly opportunistic field research. Because of this, the number of sympatric species at Tam Dao remains unknown and it is impossible to evaluate whether the snake community at Tam Doa is comparable to our site. The same is true for the snakes of Phong Nha - Ke Bang National Park of Vietnam, where Ziegler et al. (2007) found 59 snake species in a prolonged period of research (9 y). In addition, 61 snake species were observed in the much larger region of the Son La Province (Van Pham et al. 2020), where a subgroup of 51 species were observed during 15 mo of field research (Van Pham et al. 2014), and 49 species in the Phong Na-Ke Bang National Park, Vietnam (Ziegler et al. 2004). Our data are more comparable to other Asian studies carried out at a similar spatial scale as ours: 47 species in the Sakaerat Station in Thailand (Inger and Colwell 1977); 36 in Ba Vi forests, Vietnam (Luu et al. 2020); 34 in Lawachara, Bangladesh (Rahman et al. 2013); 25 in Yen Bai, Vietnam (Le et al. 2018); 20 in Cat Ba Biosphere Reserve (Nguyen et al. 2011); 16 in Chu Mom Ray National Park, Vietnam (Jestrzemski et al. 2013); 15 in a Taiwan tropical forest (Lee 2005) and in a Thailand swampy area (Khorat; see Karns et al. 2005); 10 in Bai Tu Long National Park, Vietnam (Schmitz and Ziegler 2016), and in the Thailand flooded plains (Karns et al. 2010); and 7 in Tonle Sap Lake, Cambodia (in this latter case not a forest; Brooks et al. 2009). Data from West African forests revealed that the number of sympatric species in single forest patches is about 20 species (Akani et al. 1999a,b; Luiselli and Akani 1999), whereas in South America the number of sympatric species is much higher (e.g., Dixon and Soini 1975; Duellmann 1978). Although snake communities in south Asian forests consist of a similar number of sympatric species as in West African rainforests (e.g., Akani et al. 1999a), our study indicated that the dominance index in Vietnamese forests was much lower than in Africa, but the evenness index was much higher. These metrics suggest that the snake community in our Vietnamese study area is less altered compared to that in West African rainforests, likely because our site is less disturbed and in better ecological condition than those areas studied in West Africa (e.g. see Luiselli and Fa 2019).

Although direct comparisons of our data in Vietnam with studies from elsewhere can be complicated, there were some noteworthy similarities in the community structure that should be highlighted. In both Vietnamese and West African forests, for instance, the overall structure of the community was nearly identical, with a greater dominance in the number of terrestrial species, followed by arboreal species and a few aquatic species. This similarity is surprising given that the studied forests in West Africa were lowland and mostly seasonally flooded, whereas the Vietnamese forests are mountainous and mainly on dry land. The results of these comparisons suggest that the coexistence of many sympatric snake species in tropical areas may be constrained by interspecific competition as an important assembly force (Luiselli et al. 1998; Luiselli 2006a), allowing more terrestrial (or arboreal) species to coexist than aquatic species because of a higher possibility of minimizing competition by niche partitioning mechanisms (Luiselli 2006a). Indeed, it has already been demonstrated that tropical aquatic snakes are under high interspecific competition pressure during the dry seasons (Luiselli 2006b), and this may limit the number of sympatric species at each study area. Food resource constraints are less likely in the terrestrial habitat, where the various species may, in theory, partition their food types, with some species specializing on small mammals, others on birds, or on lizards, frogs, snakes, etc. (Luiselli et al. 1998; Luiselli 2006a). In our study area, for instance, there is a purely snake-eating species (King Cobra) that has the role of top predator, as it even eats pythons, as we found.

We observed that, at our study area, snakes tended to inhabit sites with high cover and high slope angles, i.e., sites where their detectability is low. This pattern is not unexpected given the very elusive nature of these animals, especially in tropical forests. Nonetheless, we also observed that encounter frequencies dropped with elevation but had a peak at the intermediate elevation of 600–699 m. The typical pattern observed for many different taxa and in different regions of the world is that the number of species decreases with elevation (Rohde 1982; Willig et al. 2003; Sanders 2002; Sanders and Rahbek 2012). Greater numbers of species at mid elevations is termed the Mid Domain Effect (McCain 2004; Brehm et al. 2007), which we found in our snake community in terms of both species richness and number of individuals observed.

We found only a single giant snake species, the Burmese Python (*Python molurus*). The fact that we did not find any Reticulated Pythons (*Python reticulatus*) may suggest that this species and *P. molurus* are not sympatric in the mountainous forests of Vietnam, possibly due to low resource availability. Although these two giant species are generally considered sympatric in Indonesian forests (usually with no strict field evidence; see Barker and Barker 2008, but see also Auliya 2006), we think that in Vietnam, *P. reticulatus* is likely to be confined to lower elevations as it is at the northern edge of its distribution (Nguyen et al. 2009). *Python molurus* is likely not constrained by temperatures in our study area.

Although we collected some noteworthy data, we recognize some shortcomings in our study. We were able to collect only a relatively small sample of snakes, and our surveyed area was small compared to that of surveys in other sites. Thus, any conclusion we make in our study may be affected by these shortcomings. For instance, the dominance index may appear higher at our site than other sites if one or a few species were more active above-ground and easily seen when we surveyed or if areas were not well sampled.

We recommend that future efforts evaluate in more detail the occurrence of the Mid Domain Effect in South-East Asian snake assemblages, as this pattern has not been found previously in field studies. It would also be helpful to better understand tropical snake communities by analyzing the interspecific competition potential for food and for the spatial resource among snake species and measure the resources available in the various sectors of a given study area. This would help to disentangle the reasons behind the uneven distribution of snakes among habitats and across the elevational bands in South-East Asian montane forests.

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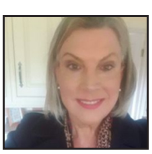
Luu Quang Vinh earned a Ph.D. and is a Senior Lecturer at the Vietnam National University of Forestry (Hanoi, Vietnam). He is active as a senior field researcher regarding herpetological research and publications. He is active as a reptile and amphibian taxonomist and ecologist. Vinh is a key expert who leads academic research in herpetology communities in Vietnam and Laos, and he has described over 20 species of reptiles and amphibians from South-East Asia. (Photographed by Lo Van Oanh).

Lo Van Oanh worked for Vietnam National University of Forestry (Hanoi, Vietnam) as a Herpetologist. He has been involved in many research projects regarding snakes, turtles, and salamanders in Vietnam and Laos. Oanh obtained a M.Sc. in Nature Resources and Environment Management with the final thesis focusing on the community of amphibians in Nam Dong Nature Reserve, Vietnam. (Photographed by Thong Van Pham).



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Appendix Table 1. Comparison between the list of snake species observed in Quan Son District, northern Vietnam, 2019, and those observed at Tam-Dao National Park (from Orlov et al. 2000).

Common name	Species	Present study	Tam-Dao
Bourret's Odd Scaled Snake	*Achalinus ater*		x
Rufous Burrowing Snake	*Achalinus rufescens*		x
Peter's Odd-Scaled Snake	*Achalinus spinalis*		x
odd-scaled snake	*Achalinus* sp.	x	
Asiane Vine Snake	*Ahaetulla prasina*		x
Mountain Keelback	*Amphiesma atemporale*		x
Tai-Young Keelback	*Amphiesma boulengeri*		x
Kuatun Keelback	*Amphiesma craspedogaster*		x
Khasi Keelback	*Amphiesma khasiensis*		x
Modest Keelback	*Amphiesma modesta*		x
Mount Omei Keelback	*Amphiesma optata*		x
Yunnan Keelback	*Amphiesma parallela*		x
Sauter's Keelback	*Amphiesma sauteri*		x
Black-Headed Burmese Viper	*Azemiops feae*		x
Brown Tree Snake	*Boiga guangsinensis*		x
Square-Headed Cat Snake	*Boiga kraepelini*		x
Many-Spotted Cat Snake	*Boiga multomaculata*		x
Banded Krait	*Bungarus fasciatus*	x	x
Many-Banded Krait	*Bungarus multicinctus*		x
Collared Reed Snake	*Calamaria pavimentata*		x
Hong Kong Dwarf Snake	*Calamaria septentrionalis*		x
Golden Tree Snake	*Chrysopelea ornata*		x
Chinese Green Snake	*Cyclophiops major*		x
Many-Banded Green Snake	*Cyclophiops multicinctus*		x
Red-Tailed Pipe Snake	*Cylindrophis ruffus*		x
Sharp-Nosed Viper	*Deinagkistrodon acutus*		x
Vietnamese Bronzeback	*Dendrelaphis ngansonensis*	x	x
bronzeback	*Dendrelaphis* sp.	x	
Yellow-Banded Big Snake	*Dinodon flavozonatum*		x
Red-Banded Snake	*Dinodon rufozonatum*		x
Bella Rat Snake	*Elaphe leonardi*		x
Mandarin Rat Snake	*Elaphe mandarina*		x
Flower Snake	*Elaphe moellendorffi*		x
Black-Banded Trinket Snake	*Elaphe porphyracea*		x
Green Bush Rat Snake	*Elaphe prasina*		x
Radiated Rat Snake	*Elaphe radiata*		x
Beauty Snake	*Elaphe taeniura*		x
Chinese Rice Paddy Snake	*Enhydris chinensis*		x
Rice Paddy Snake	*Enhydris plumbea*		x
Vietnamese Water Snake	*Hebius chapaensis*	x	
Kellogg's Coral Snake	*Hemibungarus kelloggi*		x

Appendix Table 1 (continued). Comparison between the list of snake species observed in Quan Son District, northern Vietnam, 2019, and those observed at Tam-Dao National Park (from Orlov et al. 2000).

Common name	Species	Present study	Tam-Dao
MacClelland's Coral Snake	*Hemibungarus macclellandi*		x
Banded Wolf Snake	*Lycodon fasciatus*		x
Ruhstrat's Wolf Snake	*Lycodon ruhstrati*	x	x
Mountain Wolf Snake	*Lycodon ruhstrati abditus*	x	
White-Banded Wolf Snake	*Lycodon subcinctus*		x
Chinese Cobra	*Naja atra*		x
Light-Barred Kukri Snake	*Oligodon albocinctus*		x
Chinese Kukri Sanke	*Oligodon chinensis*	x	x
Black Cross-Barred Kukri Snake	*Oligodon cinereus*		x
Cantor's Kukri Snake	*Oligodon cyclurus*		x
Eberhardt's Kukri Snake	*Oligodon eberhardti*		x
Taiwan Kukri Snake	*Oligodon formosanus*		x
Striped Kukri Snake	*Oligodon taeniatus*		x
King Cobra	*Ophiophagus hannah*	x	x
Mountain Keelback	*Opisthotropis jacobi*		x
Bicoloured Stream Snake	*Opisthotropis lateralis*		x
Mountain Pit Viper	*Ovophis tonkinensis*		x
Keeled Slug-Eating Snake	*Pareas carinatus*		x
Slug Snake	*Pareas hamptoni*		x
Mountain Slug Snake	*Pareas macularius*		x
White-Spotted Slug Snake	*Pareas margaritophorus*		x
Common Slug Snake	*Pareas monticola*		x
no common name	*Plagiopholis delacouri*		x
Chinese Mountain Snake	*Plagiopholis styani*		x
Brown Spotted Pit Viper	*Protobothrops mucrosquamatus*	x	x
Common Mock Viper	*Psammodynastes pulverulenta*	x	x
Common Bamboo Snake	*Pseudoxenodon bambusicola*		x
Chinese Bamboo Snake	*Pseudoxenodon karlschmidti*		x
Large-Eyed Bamboo Snake	*Pseudoxenodon macrops*	x	x
Chinese Rat Snake	*Ptyas korros*		x
Common Rat Snake	*Ptyas mucosus*		x
Indian Rock Python	*Python molurus*		x
Burmese Python	*Python molurus bivittatus*	x	
Angel's Keelback	*Rhabdophis angeli*		x
Bavi Keelback	*Rhabdophis callichroma*		x
Hubei Keelback	*Rhabdophis nuchalis*		x
Red-Necked Keelback	*Rhabdophis subminiata*	x	x
Rhinoceros Rat Snake	*Rhynchophis boulengeri*	x	x
Chinese Many-Tooth Snake	*Sibynophis chinensis*		x
Common Many-Tooth Snake	*Sibynophis collaris*	x	

Appendix Table 1 (continued). Comparison between the list of snake species observed in Quan Son District, northern Vietnam, 2019, and those observed at Tam-Dao National Park (from Orlov et al. 2000).

Common name	Species	Present study	Tam-Dao
Diamond-Back Water Snake	*Sinonatrix aequifasciata*	x	x
Olive Annulate Keelback	*Sinonatrix percarinata*		x
Triangle Keelback	*Sinonatrix trianguligera*		x
White-Lipped Tree Viper	*Trimeresurus albolabris*		x
Grumprecht's Green Pit Viper	*Trimeresurus gumprechti*	x	
Pope'es Tree Viper	*Trimeresurus popeiorum*		x
Large-Eyed Pit Viper	*Trimeresurus macrops*	x	
Chen's Bamboo Pit Viper	*Trimeresurus stejnegeri*		x
Striped Water Snake	*Xenochrophis flavipunctatus*		x
Sunbeam Snake	*Xenopeltis hainanensis*		x
Common Sunbeam Snake	*Xenopeltis unicolor*		x
Big-Eyed Rat Snake	*Zaocys dhumnades*		x