

Ambush Site Selection by a Green Bamboo Pit Viper: Relation to Prey Abundance and Comparison between Juveniles and Adults

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Selecting ambush sites where prey abundance is high is vital for the foraging success of sit-and-wait predators. Ideal ambush sites, however, could vary due to different prey characteristics and intra-specific competition. We examined whether different life stages of a sit-and-wait predator, *Trimeresurus stejnegeri*, select different ambush sites, based on the observations of ambush sites of juvenile and adult snakes in three water habitats (lentic, lotic, and temporary pools) in Taiwan throughout the year. Snake stomach contents were compared between life stages in each habitat. Correlations between the monthly number of snakes observed and that of each frog species were analyzed for each habitat. Adult snakes mainly used lentic water as ambush sites and rarely used temporary pools, whereas juvenile snakes used all three habitats with a similar frequency. No clear ontogenetic diet shift was found from juveniles to adults. A high percentage of snakes from lentic water habitats had stomachs containing prey, suggesting this habitat is a better site for foraging by both juveniles and adults. Overall, our study highlights that habitat use and behavior of each prey animal and intraspecific competition as well as prey abundance should be taken into consideration when we investigate the factors that affect ambush site selection by predators.

Key words: Active period, Competition, Taiwan, *Trimeresurus stejnegeri*, Water habitats

BACKGROUND

Maximizing energy intake is the main goal of the foraging strategies of predators (Krebs 1977). To increase foraging success, predators need to consider different characteristics among prey species (Hussemann et al. 2003). Characteristics of prey, such as size, abundance, palatability, anti-predator tactics, and habitat use, overall affect predators in selecting suitable prey (Luiselli 2006; Sansom et al. 2009). Generally, prey in large size or high abundance is preferred by predators (Brooks and Dodson 1965; Downes 2002; Watanabe et al. 2014) because selecting foraging sites with large

prey or high prey abundance could result in advantages such as better body condition (Madsen and Shine 1996), higher reproductive success (Dawson and Bortolotti 2000), and larger clutch size (Strong et al. 2004).

Maximizing energy intake is also an important factor for sit-and-wait predators when they determine ambush sites (González-Bernal et al. 2011; Eberhart and Ruby 2019). Many sit-and-wait predators use high concentrations of prey scents as a clue to determine ambushing sites (Roth et al. 1999; Clark 2004; Labra 2007; Jurcak and Moore 2018). Because of the low mobility of sit-and-wait predators, selecting ambushing sites where long active periods of prey are expected is

advantageous to increase foraging efficiency (Santos et al. 2008; Foster et al. 2013).

Settling down in ideal foraging sites, however, often leads to competition when conspecific individuals share the same food resource (Schradin et al. 2010). Predator needs to balance energy gain against the energy loss caused by competition with other individuals (Sih 1980; Vincent et al. 2004; Guo et al. 2014). Eventually, individuals with low competitive ability and cannot obtain enough food are forced to search for alternative prey or foraging sites (Shine et al. 2002; Ernande and Dieckmann 2004). This indicated that competition could be indirectly obtained based on the comparison of the diet content or habitat use among individuals (Luiselli 2006; Riccialdelli et al. 2013).

In reptiles, individuals with larger body sizes usually have an advantage in resource partitioning (Calsbeek and Cox 2010), forcing smaller individuals to adopt different foraging tactics and avoid competition for the same food resource (Bonaccorso et al. 2007). *Agkistrodon piscivorus*, a semi-aquatic sit-and-wait snake, shows an ontogenetic diet shift due to different microhabitat selections between adults and juveniles (Eskew et al. 2009). *Gloydus shedaoensis*, a sit-and-wait snake that preys on migrating birds, shows that adults and juveniles select different habitats in foraging the same type of prey (Shine et al. 2002). Snakes are ideal subjects for examining habitat differentiation among life stages because body size is largely correlated with age (Madsen and Shine 2000) and is the main factor determining diet composition and competitive advantage (Shine et al. 2002; Eskew et al. 2009; Székely et al. 2020).

Trimeresurus stejnegeri (green bamboo pit viper) is a common sit-and-wait, arboreal snake often inhabiting the low elevational areas of Taiwan (Tsai and Tu 2000; Lin et al. 2007). Frogs constitute most of its diet (Creer et al. 2002). Previous research has focused on its prey-handling behavior (Tsai 2007), reproduction (Tsai and Tu 2000), and metabolism (Tsai et al. 2008). Here, we examine the possibility of different foraging tactics used by adult and juvenile *T. stejnegeri*. Specifically, our questions are: 1) whether *T. stejnegeri* targets specific breeding sites of frogs as ambush sites and 2) whether prey species and ambush sites differ between adult and juvenile snakes. We hypothesized that 1) *T. stejnegeri* selects ambush sites based on frog abundance and 2) adult and juvenile snakes select different water habitats or differ in their active period.

MATERIALS AND METHODS

Study site

The study site was in a lowland secondary forest with some grassland in Chongguang, Xiulin Township, Hualien County, Taiwan (23°54'11.4"N, 121°29'43.4"E). Hualien is warm and humid with an average annual temperature of 23.7°C and annual rainfall of 1755 mm (Central Weather Bureau, <https://e-service.cwb.gov.tw/HistoryDataQuery/MonthDataController.do?command=viewMain&station=C0T870&stname=%25E9%25AF%2589%25E9%25AD%259A%25E6%25BD%25AD&d atepicker=2014-02>). Frequent rain and several artificial ponds create suitable breeding sites for anurans. In Chongguang, fourteen anuran species are recorded to breed in three types of habitats: lotic water, lentic water, and temporary pools. The whole trail was covered by dense vegetation, therefore, we considered vegetation showed homogeneity surrounding most of the water habitats. Temporary pools were defined as water bodies lasting for less than 3 months (Summers et al. 2007). The rough trail frequently creates several small pools after the rain. Most of the area of the temporary pools was less than 0.04 m² scattered randomly in different sections of the trail. Some frog species used this type of water habitat, which the pool often dried out within few weeks. The overall area of the study site was 4044 m². It had a walking trail of approximately 3 m width and 1410 m length (Fig. 1). A small stream runs along the middle section of the trail. We randomly selected three stream sections with a width less than 3 m as lotic water, three artificial ponds as lentic water, and six sections of the trail as temporary pools. The total search areas of each of these three habitats were 143 ± 49.87 m² (lotic water, *n* = 3), 105 ± 39.69 m² (lentic water, *n* = 3), and 550 ± 138.17 m² (temporary pools, *n* = 6).

Survey design

We surveyed a total of 109 nights (18:00 to 24:00) from February 2014 to March 2016. Each month, we surveyed for at least two nights every two weeks. We walked slowly along the trail route to look for anurans and snakes within each water habitat. All the surveys were done by the same author. Trail was surveyed twice per night: walking in and walking back. Types of microhabitats included ground, grass, water, trees, and rocks. The microhabitats were scanned evenly and thoroughly on both sides of the trail. The search range was from ground level to 6 m in height. We counted the number of frogs and *T. stejnegeri* in each water habitat. Each frog was identified to species. To avoid duplicate counting of the same frog individual, we recorded the

occurrence of frogs only when walking in, unless a new frog species or snake individual was found during a return trip on the same night. The life stage (juvenile or adult) of *T. stejnegeri* was recorded based on snout-vent length (SVL). If SVL was > 370 mm, we classified the snake as an adult, otherwise, we classified it as a juvenile (Creer et al. 2002). Snout-vent length of adult and juvenile snakes in Chongguang, measurements collected until 2022, which adult was normally distributed, and juvenile was not by Kolmogorov Smirnov test (Adult: $n = 122, p = 0.169, \text{Mean} \pm \text{SD}: 463.1 \pm 51.8 \text{ mm}$; Juvenile: $n = 97, p = 0.027, 278.4 \pm 48.3 \text{ mm}$). This indicated adult male and female snakes did not show huge variance in body size, and juveniles and adults did not overlap in their mean body size (Fig. 2). Therefore, SVL 370 mm was considered as a threshold in determining whether body size affects the ambushing site selection between juvenile and adult snakes. We did not mark snake individuals during the survey, however, we marked the location next to the snake to prevent duplicate counting of the snake.

To examine whether juvenile and adult snakes selected anuran species of different sizes, we captured at least seven individuals of the seven most common anuran species in the study sites (see RESULTS) and measured their SVL and tibia length. The measurement of tibia length was based on Waters et al. (2016). All captured frogs were released at their capture site after the measurements.

Diet examination

Original data of stomach contents used in this study are a part of those presented by Yang and Mori

(2021). Here, we show the frequency of each prey species for juveniles and adults separately in each water habitat. The percentage of stomach contents was calculated as the number of individuals containing stomach contents divided by the total number of captured snakes. To examine whether juveniles and adults overlap prey size, we compared the tibia length of anuran individuals found as stomach contents between them using the Mann-Whitney test. Only the anuran individuals that retained complete tibia were included in this analysis.

Data analysis

To eradicate the effect of survey area among different water habitats, we used simple linear regression to compare the relation between survey area and number of individuals. We used the total number of frogs and *T. stejnegeri* among different water habitats to examine whether larger survey areas increase the encounter rate of individuals. Seasonal difference in habitat use by each anuran species and *T. stejnegeri* was analyzed using the Chi-squared test. Habitat use of adult and juvenile *T. stejnegeri* was analyzed separately. The season was divided into spring (March to May), summer (June to August), fall (September to November), and winter (December to February). Repeated measure analysis of variance (ANOVA) with multiple comparisons using Bonferroni correction was used to compare the total number of *T. stejnegeri* encountered each month among the three water habitats. We summed the number of snakes encountered in each habitat in each month separately for juveniles and adults to calculate monthly total numbers. The monthly total

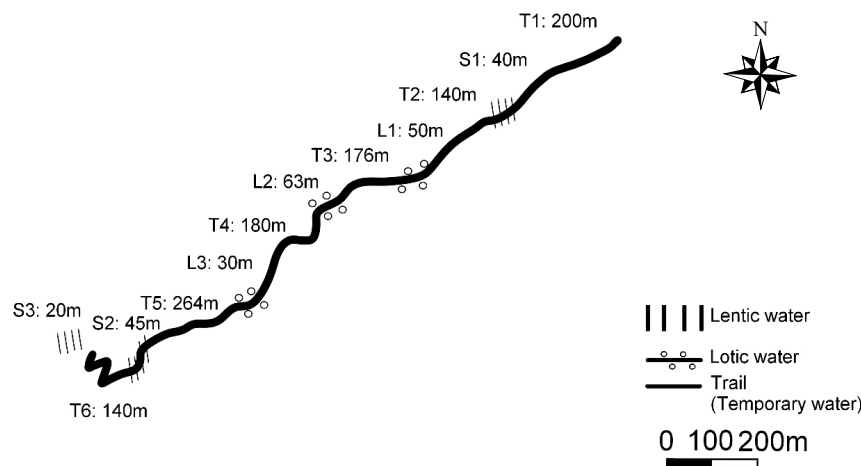


Fig. 1. Simplified map of water habitats along the survey route in Chongguang, Xiulin Township, Hualien County, Taiwan, showing relative locations of six temporary pools (T1–T6), three lentic water sites (S1–S3), and three lotic water sites (L1–L3). Map was modified using the Free and Open Source QGIS (<https://tile.openstreetmap.org/{z}/{x}/{y}.png>).

number of each common anuran species was calculated in the same way as snakes. We then examined monthly numbers between each anuran species and snakes by simple linear regression. If the data was non-parametric, we used the Spearman rank correlation. Statistical significance was set at 0.05. All analyses were conducted using SPSS 14.0.

RESULTS

Frog activity

We recorded 14 anuran species. The seven most encountered anuran species were *Buergeria otai* (3078 times), *Bufo bankorensis* (717 times), *Polypedates braueri* (645 times), *Zhangixalus moltrechti* (602 times), *Hylarana latouchii* (398 times), *Buergeria robusta* (346 times), and *Odorrana swinhoana* (202 times). The remaining seven species each was encountered less than 50 times, and thus, they were not considered as common species. The body size of the common species from large to small was: *O. swinhoana* (mean SVL \pm SD: 56.4 ± 2.8 mm; tibia length: 28.7 ± 4 mm; $n = 7$), *Bf. bankorensis* (SVL: 50.4 ± 16.2 mm; tibia length: 18.5 ± 4 mm; $n = 7$), *Br. robusta* (SVL: 50.0 ± 5.2 mm; tibia length: 22.7 ± 2.6 mm; $n = 7$), *P. braueri* (SVL: 47.7 ± 5.2 mm; tibia length: 23.0 ± 2 mm; $n = 10$), *Z. moltrechti* (SVL: 43.8 ± 4.8 mm; tibia length: 18.5 ± 2.4 mm; $n = 9$), *H. latouchii* (SVL: 41.9 ± 6.6 mm; tibia length: 22.7 ± 4.2 mm; $n = 7$), and *Br. otai* (SVL: 28.7 ± 2.6 mm; tibia length: 16.4 ± 3.2 mm; $n = 29$).

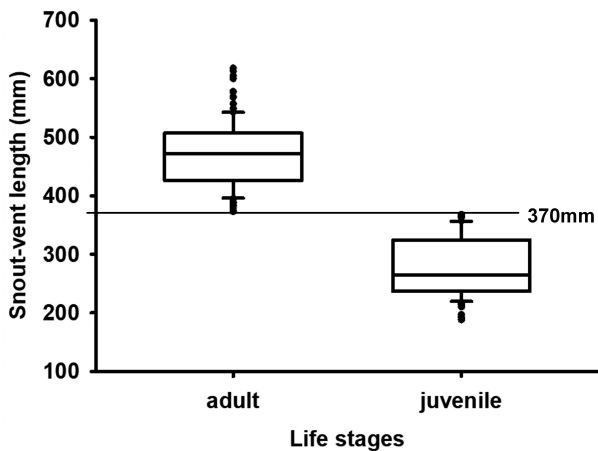


Fig. 2. Snout-vent length of *Trimeresurus stejnegeri* between adult snakes and juvenile snakes. Solid horizontal lines within boxes represent the median. Edges of the boxes represent 25% and 75% quartiles. Whiskers represent 10th and 90th percentiles. Black dots represent outliers. The horizontal line indicated cut-off point between adult snakes and juvenile snakes described in this study.

Survey area did not affect the number of individuals encountered in different water habitats. The total number of frogs ($n = 12$, $r = 0.442$, $r^2 = 0.195$, $p = 0.150$) and *T. stejnegeri* ($n = 12$, $r = 0.55$, $r^2 = 0.303$, $p = 0.064$) both did not show correlation with the survey area.

Frequency distribution of habitat use differed among these frog species ($\chi^2 = 3962.8$, $d.f. = 12$, $p < 0.001$) (Fig. 3). *Buergeria otai* was recorded as the most abundant species in temporary pools and lotic water. *Polypedates braueri* was recorded as the most abundant species in lentic water. In each habitat, seasonal activity patterns varied with species (Fig. 4). In temporary pools and lotic water, the dominant species, *Br. otai*, was active in spring and summer, but the number of frogs decreased after fall. In lentic water, the dominant species, *P. braueri*, was active in spring and summer, and the number of frogs decreased in fall. On the other hand, two other dominant species, *H. latouchii*, and *Z. moltrechti*, remained active after summer in lentic water.

Diet

A total of 279 *T. stejnegeri* that were collected between 2017 and 2019 were examined. Of these, 27 snakes had contents in their stomachs, with 21 containing a total of five frog species (Table 1), and six containing squamata species (adult: $n = 4$; juvenile: $n = 2$). The highest percentage of stomach contents was found in the lentic water in both life stages. The stomach contents of the juveniles included all the above five frog species except for *Br. otai*. Adults contained all five frog species except for *Microhyla fissipes*.

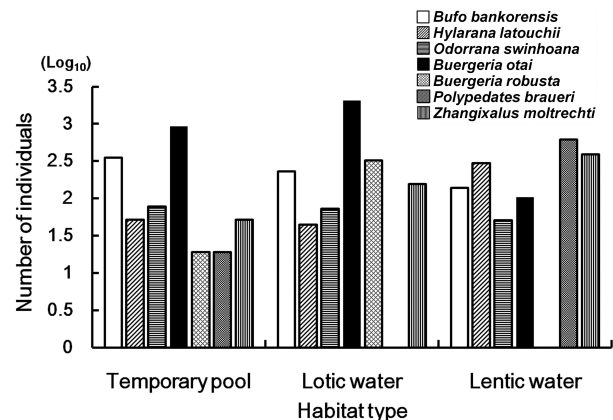


Fig. 3. Total number of the seven most common anuran species encountered in each of the three habitats.

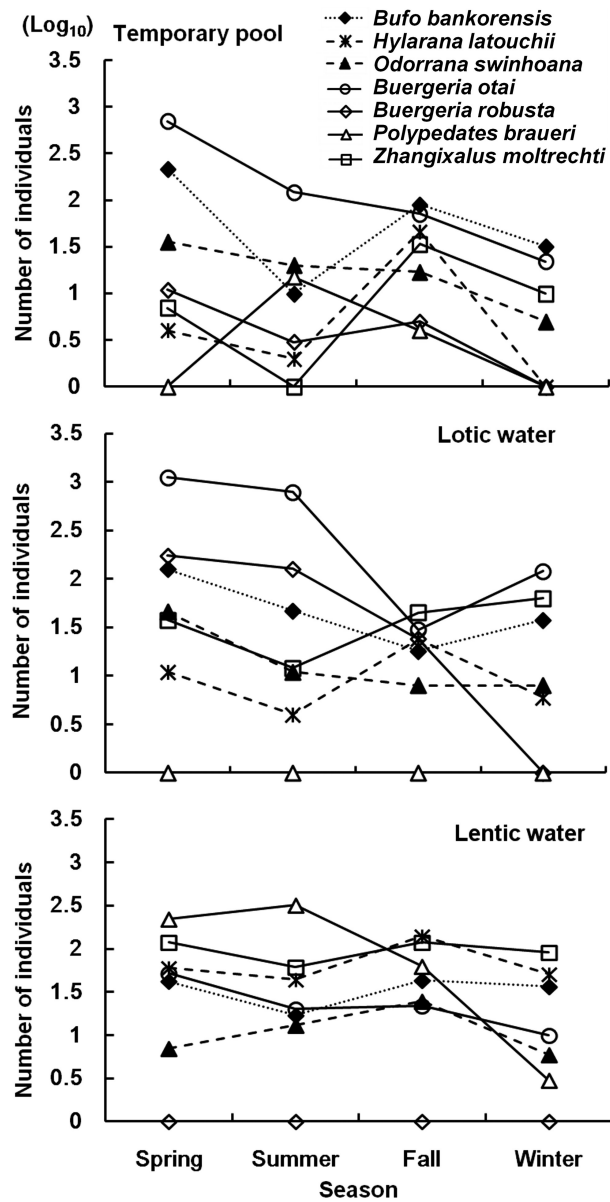


Fig. 4. Seasonal changes of the total number of common anuran species in three habitats. Data from 2014 to 2016 were combined.

Of all the frogs recovered from the stomach contents, only three were females. A significant difference was detected in the tibia length of consumed frogs between juvenile and adult snakes, however, the tibia length of the consumed frogs between juveniles and adults indicated that there was an overlap in prey size ($U = 5.00, p = 0.013$; adults, tibia length: 24.7 ± 7 mm; juveniles, tibia length: 15.1 ± 4.6 mm).

Ambush site

Juvenile and adult *T. stejnegeri* were encountered 187 and 232 times, respectively. The frequency distribution of encountered snakes among habitats was different between juveniles and adults ($\chi^2 = 53.9, d.f. = 2, p < 0.001$) (Fig. 5). Juveniles showed no significant differences in the occurrence among the lentic water, lotic water, and temporary pools (ANOVA: $F = 0.125; d.f. = 2, 33; p = 0.883$). In adults, the occurrence was significantly different among the habitats (ANOVA: $F = 12.372; d.f. = 2, 33; p = 0.005$). Adults were most frequently observed in the lentic water (60.8%), and a significant difference was detected between lentic water and temporary pools ($t = 3.52, d.f. = 11,$

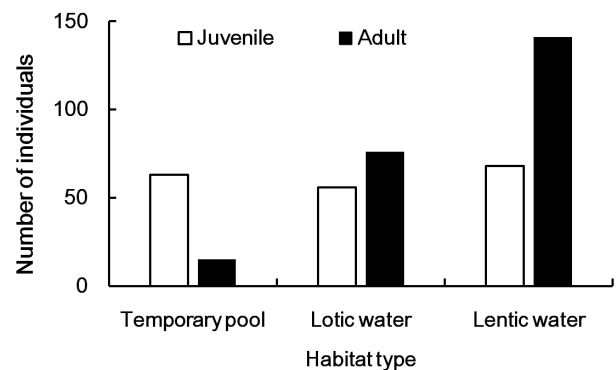


Fig. 5. Total number of juvenile and adult *Trimeresurus stejnegeri* encountered in three habitats.

Table 1. Stomach contents of juveniles and adults of *Trimeresurus stejnegeri* collected in three water habitats. Only amphibian prey was shown in this table and numerals indicate the number of snake individuals

Stomach content	Temporary pool		Lotic water		Lentic water	
	Juvenile	Adult	Juvenile	Adult	Juvenile	Adult
None	33	48	33	77	35	58
<i>Microhyla fissipes</i>	0	0	0	0	4	0
<i>Odorrana swinhoana</i>	1	1	0	3	1	0
<i>Buergeria otai</i>	0	0	0	2	0	0
<i>Polypedates braueri</i>	0	0	0	0	2	5
<i>Zhangixalus moltrechti</i>	0	0	0	0	1	1
Percentage of snakes that had stomach contents	2.94	2.04	0	6.1	18.6	9.38

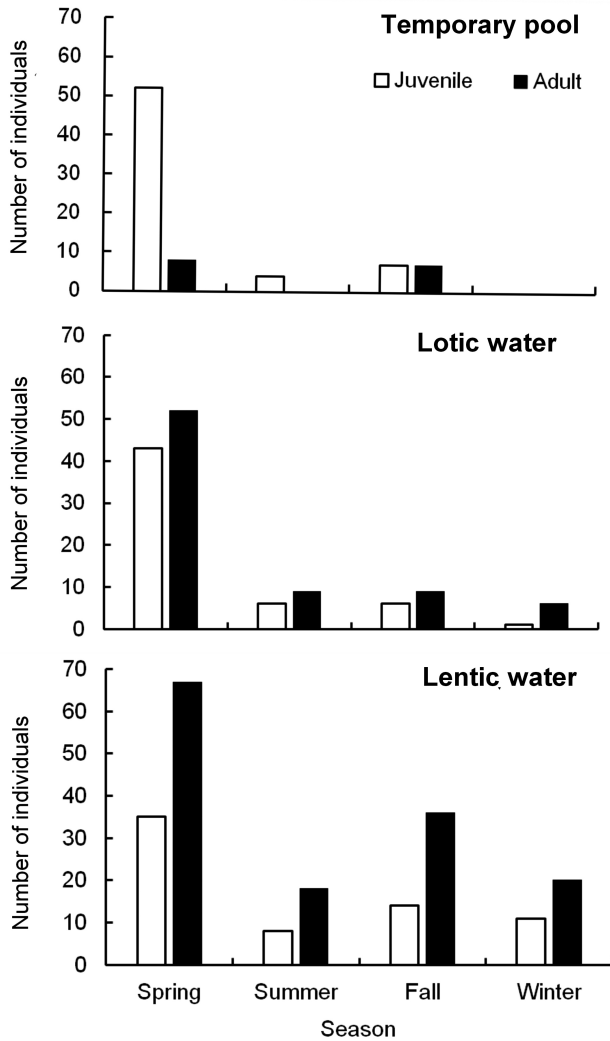


Fig. 6. Total number of *Trimeresurus stejnegeri* observed in each season in three habitats.

$p = 0.014$). Seasonal change in the use of temporary pools was significantly different between juveniles and adults ($\chi^2 = 10.8, d.f. = 2, p = 0.004$; Fig. 6). Juveniles dominated in temporary pools, but only a total of 15 adults were recorded there. No significant differences were found in the occurrence frequency between juveniles and adults in both lotic ($\chi^2 = 2.7, d.f. = 3, p = 0.448$) and lentic water sites ($\chi^2 = 0.8, d.f. = 3, p = 0.855$). In these sites, both adults and juveniles were most active during spring, with adults being more frequently observed than juveniles.

Monthly number of individuals

The monthly total number of snakes encountered showed a significantly positive correlation with that of only some anuran species (Table 2, Fig. 7), and the patterns varied among anuran species and water habitats. Four out of the seven common anuran species showed significant correlations with snakes. In the temporary pools, both life stages of the snake were positively correlated with the number of *Bf. bankorensis* and only juveniles showed a positive correlation with the two species of *Buergeria*. In the lotic water, frog species that showed a positive correlation were different between juveniles and adults. In the lentic water, both life stages showed a significant correlation with the number of *Br. otai* and *Z. moltrechti*.

DISCUSSION

Overall, our results demonstrated that *T. stejnegeri* targets specific breeding sites of frogs as ambush sites, however, abundant anurans are not necessarily

Table 2. Correlation analysis between the number of *Trimeresurus stejnegeri* (juveniles or adults) observed each month and that of each of the seven most common frog species for three types of habitats. Spearman rank correlation was used when the data was non-parametric. No correlation analysis was made for *Buergeria robusta* in the lentic water and *Polypedates braueri* in the lotic water because no frog was observed. Significance is indicated as * when $p < 0.05$ and ** when $p < 0.01$.

Frog species	Temporary pool (n = 12)						Lotic water (n = 12)						Lentic water (n = 12)					
	Juvenile			Adult			Juvenile			Adult			Juvenile			Adult		
	r	R ²	p	r _s	p	r	R ²	p	r	R ²	p	r	R ²	p	r	R ²	p	
<i>Bufo bankorensis</i>	0.92	0.846	0.03*	0.73	0.007**	0.68	0.462	0.015*	0.267	0.071	0.401	0.478	0.229	0.116	0.398	0.158	0.2	
<i>Hylarana latouchii</i>	0.068	0.005	0.835	0.573	0.052	0.143	0.0205	0.657	0.096	0.009	0.766	0.05	0.00246	0.878	0.024	0.001	0.942	
<i>Odorrana swinhoana</i>	0.223	0.05	0.486	0.023	0.942	0.172	0.03	0.593	0.158	0.025	0.624	0.022	0.001	0.945	0.275	0.0755	0.388	
<i>Buergeria otai</i>	0.943	0.89	< 0.001**	0.156	0.628	0.567	0.322	0.055	0.729	0.532	0.007**	0.753	0.568	0.005*	0.746	0.556	0.005*	
<i>Buergeria robusta</i>	0.743	0.552	0.006**	0.226	0.481	0.55	0.302	0.064	0.773	0.597	0.003**	-	-	-	-	-	-	
<i>Polypedates braueri</i>	0.162	0.0262	0.615	0.254	0.426	-	-	-	-	-	-	0.101	0.0101	0.755	0.16	0.0256	0.62	
<i>Zhangixalus moltrechti</i>	0.014	0.0002	0.965	0.416	0.179	0.108	0.012	0.738	0.085	0.007	0.793	0.764	0.584	0.004*	0.586	0.343	0.045*	

exploited as prey items by *T. stejnegeri* (Table 1). No apparent ontogenetic diet shift was discovered between juvenile and adult snakes. Nevertheless, different life stages of the snakes showed different trends in selecting ambush sites (Fig. 5). Aside from prey abundance, synchronizing the active periods with the prey in the same habitat is crucial for predators to maximize energy gain (Foster et al. 2013). With different breeding periods and breeding sites among different frog species, it is necessary to examine the relationship between frog and snake one by one to examine how the snake determines the ideal ambushing site based on the prey availability. We suggested the main factors triggering such differences were prey abundance, active periods, and predator avoidance tactics.

Prey species that had a positive correlation with the snake showed high abundance and overlaps in the active period with the snake. In temporary pools and lotic water, snakes were most active in spring, when *Br. otai* was the dominant species in both water habitats. The number of *Br. otai* in both water habitats was at

least three times larger than any other prey species in spring. Therefore, selecting ambush sites based on the breeding site of *Br. otai* may increase the foraging rate of the snake.

Snakes were able to adjust their active period based on different frog breeding seasons that occurred among different habitats. In lentic water, *T. stejnegeri* was more active in spring and fall than in summer and winter, which corresponds to the seasonal activity pattern of *Z. moltrechti*. Although *P. braueri* was also abundant during spring, the number of *P. braueri* decreased from fall, which could be the reason why this frog was not correlated with the abundance of *T. stejnegeri*. Both *Z. moltrechti* and *P. braueri* were preferred and eaten by the snake (Yang and Mori 2021). Active periods of frog species covering all year round could provide stable food resources for *T. stejnegeri* ambushing in lentic water.

Our study, however, showed that ambush site selection does not merely depend on prey abundance but predator avoidance tactics also affect the selection

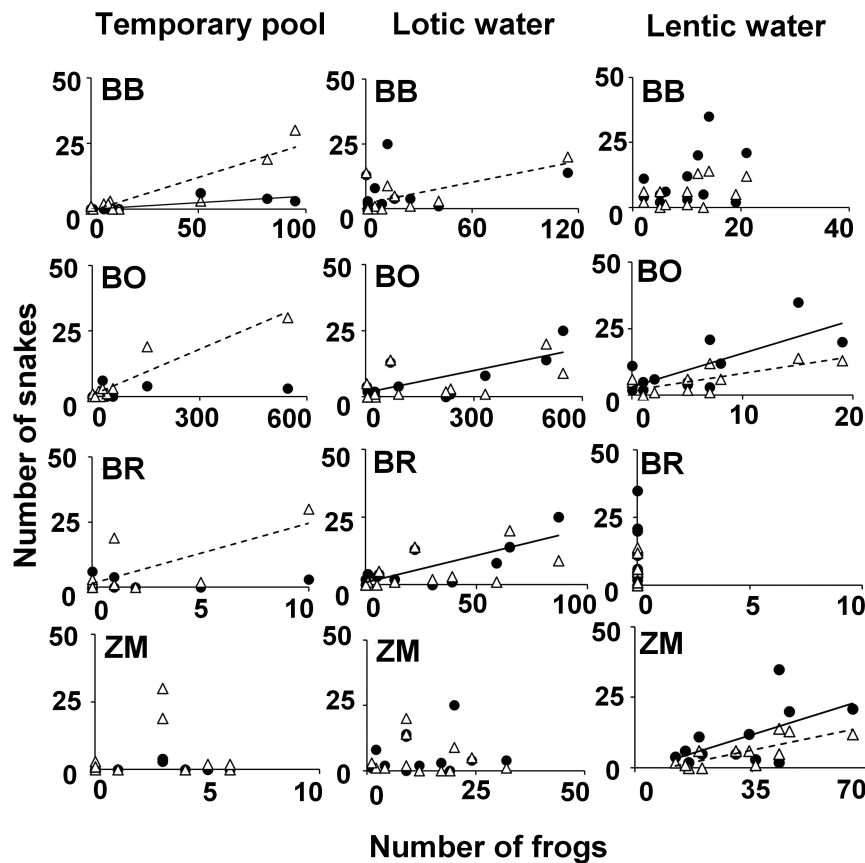


Fig. 7. Relationship of the number of adults (closed circles) or juveniles (open triangles) of *Trimeresurus stejnegeri* with the number of each of four common anuran species: *Bufo bankorensis* (BB), *Buergeria otai* (BO), *Buergeria robusta* (BR), and *Zhangixalus moltrechti* (ZM). Each point represents the total number of individuals encountered each month based on a survey from 2014-2016. Significant regression lines are shown by solid lines (adults) and dotted lines (juveniles). Note that the scale of the X-axis varies with anuran species and habitat type.

(Husseman et al. 2003). The six species, *Bf. bankorensis*, *M. fissipes*, *H. latouchii*, *O. swinhoana*, *Br. robusta*, and *P. braueri*, are considered to be selected (or avoided) under effects of factors other than the abundance. Yang and Mori (2021) demonstrated that *T. stejnegeri* shows little interest in the chemical stimulus of *Bf. bankorensis*. The result of Mohammadi et al. (2016) implies that *T. stejnegeri* is not able to physiologically resist bufadienolides secreted from toad's skin, which suggests that predation of *Bf. bankorensis* is fatal for *T. stejnegeri*. Thus, the positive correlation between the number of *Bf. bankorensis* and that of *T. stejnegeri* would be a correlation due to the presence of other preferred prey species.

Although *T. stejnegeri* shows high interest in the chemical stimulus of *H. latouchii* (Yang and Mori 2021), the stomach contents suggested that *H. latouchii* was not common prey. Given that *H. latouchii* is relatively common and especially abundant in lentic water year-round, *T. stejnegeri* should have high encounter rates with this frog. The absence of *H. latouchii* in the stomach contents suggests that *H. latouchii* could be toxic or indigestible to *T. stejnegeri*. We suggest that this frog uses skin secretion as a predator avoidance tactic and further research is required.

Odorrana swinhoana and *P. braueri* were rather common food items of *T. stejnegeri*, but both species did not show a positive correlation with *T. stejnegeri*. In contrast to *P. braueri* which was dominant in the lentic water, *O. swinhoana* maintained a similar pattern of occurrence in all water habitats and was not recorded as dominant species in any season. Among the frog species eaten by *T. stejnegeri*, *O. swinhoana* was the largest in SVL, which will provide relatively high energy to the snake.

Although positively correlated in abundance with both life stages of the snake, *Br. robusta* was not found in the stomach contents. *Buergeria robusta* is similar to *Br. otai* in the active period and morphology but is bigger in body size (Huang et al. 2001). Since these two *Buergeria* species both appeared in the lotic water and temporary pools, the similar active pattern to *Br. otai* could cause *Br. robusta* having a positive correlation with the snake (pseudocorrelation). Considering that the body size of *Br. robusta* is similar to *P. braueri*, the most dominant prey species, *T. stejnegeri* should also be able to swallow the former. Furthermore, Yang and Mori (2021) demonstrated that the snake shows the same level of interest in the chemical stimulus of *Br. otai* and *Br. robusta*. Probably *Br. robusta* may possess some effective predator avoidance tactics different from *Br. otai*, but further research is required to reveal them.

To maximize energy intake, sit-and-wait predators often consume a variety of prey animals whenever they

pass close to the ambush site (Glaudas et al. 2019). *Microhyla fissipes*, which was recorded as the least encountered frog among the 14 anuran species, were also consumed by *T. stejnegeri*. Of the 16 *M. fissipes* recorded during the census, three were found in the temporary pools and the remaining was observed in the lentic water. *Microhyla fissipes* is an explosive breeder aggregating in water habitats during heavy rain and maintains activity for only a few days (Lee et al. 2016). This breeding mode would greatly reduce constant encounters with *T. stejnegeri* throughout the year, but allow the snake opportunistically capture frogs during the explosive breeding.

The low percentage of stomach contents found in *T. stejnegeri* may be due to the arboreal snakes having a faster-digesting rate compared to the terrestrial snakes (Creer et al. 2002). In addition, frogs, with no claws, fur, or scales, may be considered as easy prey compared to other fauna (Santos et al. 2000; Eskew et al. 2009). Nevertheless, we discovered that the percentage of other fauna foraged by the snake was relatively low. This suggested that *T. stejnegeri* majorly fed on frogs. Although a high percentage of empty stomachs were found in snakes, foraging tactics among adult and juvenile snakes still could be compared based on stomach contents and the abundance of different frog species within different water habitats.

Trimeresurus stejnegeri in our study site did not show obvious differences in prey species between the life stages but showed differences in habitat use. Nevertheless, different foraging rates among different frog species suggest *T. stejnegeri* is favored in some species. In addition, *O. swinhoana* was the only prey species in both life stages collected in the temporary pools, and no snake had the dominant species, *Br. otai*. Although the number of *Br. otai* observed in the temporary pools was high, the total survey area of the temporary pools was the largest compared with other habitats. Thus, *Br. otai* scattered over the pools, making the snake difficult to target the prey. On the other hand, the finding that no stomach content was found in juveniles ambushing in the lotic water indicated that adult snakes may have occupied most of the ideal ambushing sites in this habitat. Based on the high occurrence of juveniles ambushing in the temporary pools, we suggest that juvenile snakes opportunistically use food resources in the temporary pools to avoid competing with adult snakes in other water habitats.

As a working hypothesis, we proposed that places with abundant food resources year-round are ideal ambush sites for both life stages of *T. stejnegeri*. However, our result demonstrated that sites with high prey abundance are not necessarily selected as ambush sites for the sit-and-wait predator. *Trimeresurus*

stejnegeri was able to integrate characteristics of prey species in determining ambush sites that provide high benefits. Although both life stages seem to favor the same ambush site and frog species, the different ambushing patterns and prey composition suggest the occurrence of intraspecific competition.

Some tropical Asian snakes partitioned ambush sites when two species possess similar niches (Luiselli 2006). Moreover, physical combat has been found in viperids even in *Trimeresurus* snakes (Shine 1978; Strine et al. 2018; Barnes et al. 2020). In a pit viper, larger individuals, *i.e.*, adult snakes, possess an advantage in occupying ideal ambush sites (Shine et al. 2002). Therefore, ambush site partition among life stages could be a potential reason to prevent competition. Ideal ambush sites, however, could also determine by thermoregulation, predation risk, and other factors aside from prey availability (Sih 1980; Barnes et al. 2020). Future work is required to examine whether there is any difference in microhabitat use and ambush period between juveniles and adults of *T. stejnegeri* when co-occurring within the same foraging site.

CONCLUSIONS

Prey abundance and characteristics should be considered simultaneously when examining the ambush site of *Trimeresurus stejnegeri*. The stomach contents of the snake suggested that frogs with high abundance were not necessarily foraged by the snake. Active season, predator avoidance tactics, and abundance of frogs could overall affect the snake in foraging. In addition, the selection of different ambushing sites by juvenile and adult *T. stejnegeri* without ontogenetic diet shift suggested that intraspecific competition may occur in sit-and-wait snakes.

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