
**Effects of sex and season [\(breeding and non-breeding\)](#) on ~~ambush~~
microhabitat selection in Stejneger's bamboo pitviper
(*Viridovipera stejnegeri*)**

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Abstract

Habitat quality and availability are crucial for the survival and reproduction of animal species.
Intraspecific and seasonal differences in habitat selection reflect adaptations to changing
biological requirements and environmental factors. [To investigate the effects of season](#)

(breeding and non-breeding) and sex on microhabitat selection in snakes, here we employed field surveys to analyze microhabitat selection data for Stejneger's bamboo pitviper (*Viridovipera stejnegeri*) across different sexes and seasons. In this study, we surveyed and analyzed sexual and seasonal differences (breeding and non-breeding) in ambush microhabitat selection in Stejneger's bamboo pitviper (*Viridovipera stejnegeri*). Results indicated that although no significant differences were observed between groups, marked differences in certain microhabitat factors were noted. Specifically: 1) Non-breeding season females (NBF) displayed distinct differences in altitude, slope position, distance from roads compared to other groups. 2) Temperature exerted a lesser effect on non-breeding season individuals compared to breeding season individuals. Additionally, distance from roads only significantly impacted breeding season males, not females. 3) Regarding sexual differences, males and females differed in slope position and distance from residential sites, reflecting their distinct ecological requirements. Regarding seasons, differences in habitat selection between breeding and non-breeding seasons were primarily related to temperature, reflecting indicating behavioral changes linked to seasons. 4) Non-breeding season females NBF exhibited the narrowest microhabitat niche width and the least microhabitat niche overlap with other groups, potentially due to their pronounced foraging requirements, which compel them to explore limited habitats with higher human disturbance but richer food sources. This study contributes novel insights into the habitat selection behaviors of snakes, emphasizing the complexity of ecological niche adaptation.

Keywords: Microhabitat selection, Ecology, Snakes, Pitviper, Ambush, Sexual differences, Seasonal differences, *Viridovipera stejnegeri*

INTRODUCTION

Habitat selection is the process through which animals actively choose geographical spaces that best meet their needs for predator avoidance, reproduction, and survival. Animal habitat selection is not only influenced by evolutionary and behavioral factors but

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also by changes in habitat quality and availability, crucial determinants of animal population survival (Ortega & Pérez-Mellado, 2016; Zhang, 2020b; Zhang et al., 2023). Studying the variations in habitat selection and its influencing factors contributes to our understanding of the life histories and behavioral patterns of species (Shenbrot ~~et al.~~, 2014).

Intraspecific differences in habitat selection are common (Zhao et al., 2023), often arising due to the diverse requirements of different wild populations ~~within a species~~ (Ficetola et al., 2013). For example, adult and juvenile European cave salamanders (*Hydromantes strinatii*) exhibit varied habitat preferences due to differences in risk-taking strategies (foraging and predator avoidance trade-offs; Ficetola et al., 2013). Another potential driver is intraspecific competition for resources such as food, water, and shelter, as observed in the sand lizard (*Lacerta agilis bosnica*; Popova et al., 2020) and Chinese giant salamander (*Andrias davidianus*; Zhao et al., 2023). Seasonal variations in habitat selection are also evident across multiple animal taxa, with animals adapting their habitat use in response to periodic changes in environmental factors (Rozen-Rechels et al., 2019). Therefore, habitat selection patterns fluctuate with seasonal shifts in habitat quality and availability, as well as with changes in biological behaviors and requirements (Michel et al., 2018; Bista et al., 2022~~3~~), as evidenced by various species, including the lesser prairie-chicken (*Tympanuchus pallidicinctus*; Lawrence et al., 2022).

Seasonal ~~(seasons of the year)~~ and sexual differences in habitat selection have been confirmed in certain species of snakes. For example, the bullsnake (*Pituophis catenifer sayi*) selects different burrow habitats in response to seasonal changes in temperature and humidity (Johnson, 2021). Similarly, the canebrake rattlesnake (*Crotalus horridus*) exhibits season-based changes in habitat selection, linked to foraging, reproduction, and hibernation activities (Waldron et al., 2006). Studies on seasonal (breeding and non-breeding) differences in microhabitat selection are relatively scarce. At present, however, nocturnal arboreal snakes have been less studied due to their elusive nature and challenging habitats, which complicates data collection (Fraga et al., 2013). As such, further research is required to verify seasonal ~~(breeding and non-breeding)~~ and sexual differences in habitat selection among nocturnal

79 arboreal snake species.

80 Existing methods for surveying snake habitat selection typically include: fixed-distance
81 transect or quadrat methods, and comparisons between presence points and pseudo-absence
82 points (Zhang et al., 2020b). However, due to the cryptic nature of snakes, detecting
83 individuals is often the most challenging issue. Additionally, the limited density of snakes
84 results in insufficient data for statistical analysis, making repeated sampling one of the
85 primary reasons for data deviation. Subjectivity in sampling is also a significant factor
86 contributing to data discrepancies. Recently, Mizsei et al. developed an R script that processes
87 images of quadrats, effectively mitigating this issue (Mizsei et al., 2024).

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88 The nocturnal arboreal Stejneger's bamboo pitviper (*Viridovipera stejnegeri*, Squamata,
89 Viperidae) is widely distributed in southern China and Vietnam (Guo et al., 2022). This
90 species primarily resides in rocky cliffs and vegetated areas near mountain streams, creeks,
91 and other wet environments, subsisting mainly on frogs, but also consuming lizards and small
92 rodents (Creer et al., 2002). The reproductive mode of this species is ovoviviparity, typically
93 giving birth to 5-8 neonates in August, with the offspring measuring approximately 250 mm
94 in total length (Zhao, 2006). Previous research has indicated that the species showed no

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95 significant differences in vegetation-based habitat selection between males and females (Tu et
96 al., 2000). ~~Furthermore, our observations of ambush microhabitat selection in *V. stejnegeri*~~
97 ~~suggest no marked differences in occurrence probability across different sexes and seasons.~~
98 ~~Therefore~~Based on these observations, we hypothesize that there are no significant seasonal
99 or sexual differences in ambush microhabitat selection of *V. stejnegeri*. This study aims to
100 analyze habitat preferences among groups, differences in habitat factor selection among
101 groups, overall differences between groups.~~This study aimed to validate our hypothesis~~ and
102 explore potential explanations for our findings.

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104 MATERIALS AND METHODS

105 Study area

106 Data were collected in Huangshan City, Anhui Province, eastern China (117°23'–118°55'E,

29°24'–30°24'N; Fig. 1), [the study area covers 25 square kilometers](#). The region is characterized by a subtropical monsoon climate with abundant heat and moisture. Annual average temperature ranges from 15.5 to 16.4 °C, and average annual precipitation ranges from 1 395 to 1 702 mm, predominantly falling from May to August [\(summer\), with reduced rainfall from September to November \(autumn\), although it does not reach an extreme level of aridity \(The People's Government of Anhui Province, 2023\)](#). The vegetation is primarily composed of subtropical evergreen broad-leaved forests, [the understory is primarily composed of perennial herbs \(Poaceae and Urticaceae\) and ferns, with minimal variation in vegetation diversity between seasons which harbor rich biodiversity \(Huangshan Municipal Government, 2023\)](#).

Data acquisition and variable [assignment of categories](#)division

Data were collected during two periods, June–July 2023 and September–October 2023, from approximately 20:00 to 24:00. [We extensively searched for *V. stejnegeri* in the survey area, and manually collected snakes](#). Each located snake was injected with an independent electronic tag (EM4305; wnLikes, Shenzhen, China), and its unique identification number, latitude and longitude coordinates, and sex were recorded. At each sampling location, a 4 × 4 m quadrat was established [\(Strine et al., 2018\)](#). Within these quadrats, 13 habitat factors were measured, with detailed descriptions and measurement methods provided in Appendix 1. [A total of 92 snakes were collected \(females = 34, males = 58\), all snakes were released after data collection. The data were obtained only at the time of the first collection.](#)

Sex identification was performed via cloacal probing by gently pressing the region located 5 cm below the vent at the tail towards the anterior direction of the cloaca using the thumb. The detection of an everted hemipenis was used to determine the sex of the individual. [Existing research indicated that *V. stejnegeri* typically given birth in August \(Huang, 1980; Huang et al., 2015\). Therefore, ~~Data~~ data collected between June and July were designated as breeding season data, while data from September to October were considered non-breeding season data \[\\(Huang, 1980; Huang et al., 2015\\)\]\(#\). During each survey period, ArcGIS v10.8 was](#)

used to randomly generate 50 pseudo-absence points within the survey area, excluding unsuitable habitats for *V. stejnegeri* such as highways, open water bodies, and cliffs, as well as and points with the presence of *V. stejnegeri* within a 50-meter radius (Mizsei et al., 2024) areas within 50 m of snake presence. The remaining points served as pseudo-absence points for measuring the aforementioned habitat factors (Zhang, 2020b). All animal procedures were carried out in accordance with and approved by the Animal Care and Use Committee at Yibin University (animal protocol number: YBU2020007). We also adhered to the ARROW (Animals in Research: Reporting On Wildlife) guidelines.

Data processing and analysis

~~A total of 62 habitat data points were collected during the breeding season and 30 during the non-breeding season. Additionally, 50 control data points from different seasons were collected for comparison.~~ The collected data were categorized into four groups based on season and sex: breeding season males (BM), breeding season females (BF), non-breeding season males (NBM), and non-breeding season females (NBF).

Before starting data analysis, we checked and removed all extreme outliers and used the chain equation multivariate interpolation method to impute missing values. And all data were logarithmically processed before analysis to improve normality. All data were tested for normality and homogeneity of variance.

To analyze the habitat selection preferences of *V. stejnegeri* for each habitat factor, the Vanderploeg (W_i) and Scavia (E_i) selection indices were calculated (Vanderploeg & Scavia, 1979):

$$W_i = \frac{r_i}{p_i} / \sum \left(\frac{r_i}{p_i} \right)$$
$$E_i = (W_i - \frac{1}{n}) / (W_i + \frac{1}{n})$$

Where r_i denotes the number of quadrats selected by *V. stejnegeri* with characteristics i ; p_i denotes the total number of quadrats in the environment with characteristics i ; and n refers to the level or category number of a particular habitat factor. E_i ranges from -1 to 1 , with $E_i = 1$ indicating strong preference, $0.1 < E_i < 1$ indicating selection, $-0.1 < E_i < 0.1$ indicating

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random selection, $-1 < E_i < -0.1$ indicating [avoidance/escape](#), and $E_i = -1$ indicating no selection.

To analyze the importance of habitat factors for each group, factor autocorrelation analysis was performed to exclude highly correlated factors (see Appendix 3). Random forest models were then constructed using the habitat data for each group as well as the [pseudo-absence point control](#) data. [We used viper presence/pseudo-absence as the dependent variable and employed the R package “randomForest” to construct random forest models.](#) [employing](#) the mean decrease Gini index to evaluate the importance of each factor (Zhang *et al.*, 2020a).

Multiple linear models were used to analyze the interactive effects of season and sex on various factors. For factors showing significant effects, *post hoc* multiple comparisons ([Least significant difference, LSD](#)) were conducted among the four groups, while for factors without significant effects, differential analyses were restricted to within either seasonal or sexual groups. Prior to within-group analyses, tests for normality and homogeneity of variance were conducted on continuous variables. Continuous variables that met the assumptions of normality and homogeneity of variance were analyzed using one-way analysis of variance (ANOVA), while those that did not meet these criteria were analyzed using the Mann-Whitney U test. Discrete variables were examined using chi-square tests to identify differences within groups. [We also calculated the mean and standard deviation within each group.](#) Furthermore, partial dependence plots were employed to visually depict the relationship between habitat factors and predicted probability of occurrence for each group, as determined from the random forest models (Hastie *et al.*, 2005).

To analyze overall differences and associations in [ambush](#) microhabitat selection among groups, the microhabitat niche width Levins index (B) for each group was calculated using the *spaa* package in R (R Development Core Team, 2018):

$$B = \frac{1}{\sum_{j=1}^R (P_j)^2}$$

Where P_j represents the proportion of individuals found at sampling point j and R denotes the total number of sampling points (Simpson, 1949). Subsequently, microhabitat niche overlap

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191 between groups was quantified using the Levins index (O_{ik}):

192
$$O_{ik} = \frac{\sum_{j=1}^R P_{ij} P_{kj}}{\sum_{j=1}^R (P_{ij})^2}$$

193 Where P_{ij} and P_{kj} represent the abundance of groups i and k at sampling point j , respectively,
194 and R is the total number of sampling points (Levins, 1968).

195 Principal component analysis (PCA) was conducted to determine the eigenvalues of each
196 principal component (PC). PCA scatter plots were created using the PCs with the highest
197 eigenvalues as axes. The distribution of points within 95% confidence ellipses for different
198 groups on the scatter plot was analyzed to assess whether significant differences existed
199 among the groups. To further validate the results, permutational multivariate analysis of
200 variance (PERMANOVA) (ADONIS) was conducted using the *vegan* package in R, with the
201 degree of overlap among groups in the graphical representations assessed to determine
202 whether significant differences existed (R Development Core Team, 2018).

203 All analyses were conducted with a confidence level of 0.05. Data analysis was
204 performed using R v4.2.3, and graphs were plotted using R v4.2.3 and Origin 2022 (R
205 Development Core Team, 2018).

206

207 **RESULTS**

208 **Microhabitat preferences and factor importance among groups**

209 A total of 62 presence points were collected during the breeding season (males = 43, females
210 = 19) and 30 during the non-breeding season (males = 15, females = 15), all snakes are adults.

211 The Vanderploeg (W_i) and Scavia (E_i) selection indices revealed no significant
212 differences among the four groups in their preferences for factors such as temperature,
213 humidity, vegetation height, vegetation coverage, slope, distance from water, distance from
214 residential sites, landscape habitat, and vegetation type. However, compared to other the
215 groups, NBF displayed a preference for lower altitudes and slopes, and for locations furthest
216 from roads. Additionally, all groups showed either no preference or extremely weak
217 preference for “aspect” factor, leading to its exclusion in subsequent analyses (Fig. 2).

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The mean decrease Gini index identified the key factors influencing habitat selection. For the BM group, important factors included humidity, temperature, distance from water, and distance from roads. The BF group was influenced by humidity, temperature, and distance from water, while the NBM and NBF groups were influenced by humidity and distance from water (Fig. 3).

Seasonal ([breeding and non-breeding](#)) and sexual differences

Multiple linear model analyses revealed that, apart from altitude, there were no significant interactions between sex and season for other factors (Appendix 2).

Mann-Whitney U and chi-square tests demonstrated significant differences between males and females only in distance from residential sites (M vs F: 414.98 ± 170.96 vs 338.65 ± 148.48 ; $P = 0.026$) and slope position (F vs M: mid-slope position vs down-slope position; $P = 0.0045$; Table 1). Seasonal [differences](#) analyses only indicated a significant difference in temperature preference (M vs F: 21.95 ± 0.81 vs 23.71 ± 0.84 ; $P < 0.001$; Table [12](#)), with no significant differences in preferences for other factors. Specific differences among groups are illustrated in Fig. 4.

Multiple comparisons [analysis](#) revealed that the altitudes selected by NBF differed significantly from those selected by NBM ($P < 0.001$), BM ($P = 0.001$), and BF ($P = 0.009$). However, there were no significant differences in altitude selection among NBM, BM, and BF. Partial dependence plots indicated that NBF selected lower altitudes than the other groups, with a narrower range of altitude preferences ([NBF: \$190.73 \pm 19.06\$, BM: \$212.09 \pm 15.91\$, NBM: \$211.42 \pm 17.63\$, BF: \$208.40 \pm 22.77\$](#) , Fig. 4A).

Overall differences in microhabitat selection among different groups

Microhabitat niche analysis indicated that the microhabitat niche widths varied among the different groups, with NBM exhibiting the largest (2.935) and NBF the smallest (1.895). As shown in Table 2, the greatest microhabitat niche overlap was found between NBM and BF (98.63%), while the smallest overlap was found between NBF and BM (53.86%).

The PCA plot indicated no significant differences among the four groups (Fig. 5), supported by ADONIS analysis (Fig. 6).

DISCUSSION

Sexual and seasonal (breeding and non-breeding) differences in habitat selection have been extensively documented across various animal taxa (Ficetola et al., 2013; Popova et al., 2020; Zhao et al., 2023). Sexual differences are usually driven by varying needs between the sexes or intense intersexual competition. Seasonal differences typically relate to changes in the availability or quality of resources, as well as shifts in animal behavior and requirements throughout the year. In this study, sexual and seasonal differences in ambush microhabitat selection in *V. stejnegeri* were explored. The findings showed that although there were no pronounced overall differences among the groups, there were specific differences in preferences for certain factors, thereby not supporting our hypothesis and contradicting corroborating previous research (Tu et al., 2000). While the earlier study by Tu et al. (2000) examined sexual differences in vegetation utilization characteristics, it did not explore other factors or seasonal differences. As such, our research provides a more comprehensive analysis, contributing to a deeper understanding of the life activities of this species.

Vanderploeg (W_i) and Scavia (E_i) selection indices revealed differences in preferences for altitude, slope position, and distance from roads between NBF and the other groups, possibly due to the stronger foraging needs of these individuals. Notably, females often experience significant energy depletion after reproductive activities, prompting them to select habitats with higher predation success rates (Harvey & Weatherhead, 2010). In the study area, the non-breeding season coincides with the dry season, during which potential food sources for *V. stejnegeri*, such as frogs, tend to congregate in downstream areas with sufficient water and significant human (agricultural) disturbances. Therefore, NBF displayed a preference for downhill positions and lower altitudes, possibly taking risks to meet higher foraging requirements. This behavior is consistent with the results obtained from multiple comparison

analyses and random forest model predictions (Fig. 4). Similar risk-taking strategies driven by foraging demands have also been observed in other species, such as *Hydromantes strinatii* (Ficetola et al., 2013) and *Trimeresurus macrops* (Strine et al., 2018), although these studies did not differentiate between various groups within the species. The differentiation among groups in our study provides a basis for further discussions on the varied impacts of human disturbances on different snake groups.

Regarding factor importance, the influence of temperature on **ambush** microhabitat selection for non-breeding season individuals was relatively minor compared to that of breeding season individuals (Fig. 3). This may stem from slightly higher nighttime average temperatures during the non-breeding season compared to the breeding season in the study area (23.71 ± 0.84 vs 21.95 ± 0.81). Therefore, it easier for snakes to find habitats with suitable temperatures during the non-breeding season. Nocturnal snakes typically require less precise thermoregulation and often adopt a passive thermoregulation strategy (Vitt et al., 1997). In the non-breeding season, higher environmental temperatures facilitate thermoregulation in *V. stejnegeri*, thereby reducing the impact of temperature on microhabitat selection compared to the breeding season. Additionally, proximity to roads, typically associated with shelter due to roadside crevices serving as ideal hides for snakes (Shew et al., 2012), showed an unexpected pattern in our study. Notably, shelters proved more crucial resource for males than females during the breeding season, contrasting with trends observed in northern pine snakes (*Pituophis melanoleucus-m. melanoleucus*; Gerald et al., 2006) and northern Mexican gartersnakes (*Thamnophis eques megalops*; Sprague & Bateman, 2018). One possible explanation is that, similar to eastern brown snakes (*Pseudonaja textilis*; Whitaker et al., 2003), males exhibit strong territorial behavior towards shelters during the breeding season. Alternatively, NBF may select trees away from roads as shelters to minimize human disturbance, which is consistent with the findings of Strine et al. (2018). Additionally, roads typically have higher nighttime temperatures, so the distance from roads may also be related to the competition among males for thermal resources.

Minimal seasonal and sexual variation in microhabitat selection was detected in *V.*

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302 *stejnegeri*, with only a few habitat factors showing differences. Significant sexual differences
303 were only found in slope position and distance from residential sites, likely due to ~~the~~
304 differ~~ent~~ing reproductive needs of males and females. Males expanding their habitat range can
305 increase encounter rates with females and reduce intrasexual reproductive competition,
306 thereby enhancing mating opportunities (*Shew et al., 2012*). In contrast, females require stable
307 and suitable habitats for reproductive activities, as reported in other species such as Chinese
308 giant salamanders (*Zhao et al., 2023*). Significant differences in temperature preferences
309 between the breeding season and non-breeding season were also detected for *V. stejnegeri*,
310 while other factors remained consistent, aligning with the findings from factor importance
311 analysis.

312 In terms of microhabitat niche analysis, NBF exhibited the narrowest microhabitat niche
313 width and lowest microhabitat niche overlap compared to the other groups. This pattern is
314 potentially due to the strong foraging demands of these females, leading them to forage in
315 limited habitats with higher human disturbance but richer food resources. Overall, the PCA
316 and ADONIS results showed no significant differences among the groups. However, a notable
317 limitation is that all females surveyed were either non-pregnant or in early pregnancy
318 (undeveloped eggs; Survey: June, Birthing: August), preventing a comparison of microhabitat
319 selection preferences between pregnant and non-pregnant females. Although this limitation
320 has been acknowledged in previous research (*Shew et al., 2012*), many studies have
321 documented significant differences in habitat selection between pregnant and non-pregnant
322 females (e.g., *Blouin-Demers and Weatherhead, 2001; Harvey and Weatherhead, 2006; Crane*
323 *and Greene, 2008*). Furthermore, despite our efforts to collect relevant microhabitat data,
324 many factors influencing **ambush** microhabitat selection, such as the significant influence of
325 canopy height observed in *T. macrops* (*Barnes et al., 2023*), were not collected. These
326 unexplored factors could lead to noticeable differences among groups, potentially resulting in
327 ecological niche divergence. Therefore, more comprehensive data collection is required in our
328 future research.

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CONCLUSIONS

This study investigated sexual and seasonal (breeding and non-breeding) differences in ambush-microhabitat selection of *V. stejnegeri*. While no significant overall differences were observed among groups, certain microhabitat factors did show variations. Specifically, NBF differed from the other groups in terms of preference for altitude, slope position, and distance from roads. Regarding factor importance, temperature had a lesser effect on non-breeding season individuals compared to breeding season individuals. Furthermore, distance from roads significantly influenced BM but not BF. Regarding sexual differences, males and females varied in preferences for slope position and distance from residential sites, reflecting differing requirements between the sexes. Seasonally, the primary differences in habitat selection between the breeding and non-breeding seasons were in temperature, influenced by seasonal behavioral changes. Regarding microhabitat niches, NBF exhibited the narrowest microhabitat niche width and lowest microhabitat niche overlap with the other groups. We speculate that this is due to the strong foraging requirements of these females, leading them to venture into limited habitats with higher human disturbances but richer food sources. Overall, this study offers new insights into the habitat selection of snakes, thus enhancing our understanding of their ecological preferences.

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