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Factors Influencing Habitat Selection by Arboreal Pit Vipers

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We studied factors influencing habitat selection by two arboreal species of pit viper, namely *Trimeresurus malabaricus* (Malabar pit viper) and *T. gramineus* (Bamboo pit viper). The macrohabitat of these species was classified as forest, forest edge, or open habitat. To determine microhabitat selection, a variety of features at every other snake location were measured. Whether or not the animal was found in a tree, the tree species, its height of perch, position on the branch (distal/apical/middle), diameter of the branch, the tree canopy (thick/sparse) and vegetation of the area (thick/sparse) were recorded. Assessment of habitat was done to determine how patterns of habitat use vary seasonally. Shaded ambient (air) temperatures and humidity were recorded. Data pertaining to 90 individuals of *T. malabaricus* and 100 individuals of *T. gramineus* were recorded. *Trimeresurus malabaricus* selected home ranges that included areas with thick vegetation and were encountered at regions of higher altitude. Neither of the species was found in open habitats. Both of the species preferred diverse habitats and were spread over the entire available space during the monsoon; they did not show any preference for the perch height during different seasons. Males had a positive correlation between body mass and preferred perch diameter. The present study suggests that several factors play an important role in habitat selection by these arboreal pit vipers, thus making them highly habitat-specific.

Key words: microhabitat, macrohabitat, perch height, perch diameter, pit viper, shaded ambient temperature

INTRODUCTION

"The habitat of a species can be defined as that portion of a multi-dimensional hyperspace (defined by any number of habitat factors) that is occupied by a given species" (Whitaker, et al., 1973). There is little data on interspecific niche partitioning by snakes as compared to other vertebrate groups (Schoener, 1977; Toft, 1985). Presently, descriptions of the preferred habitat are available only for a very few species of snakes (Reinert, 1993) and therefore, snakes are not well represented in studies of habitat selection. This may be because snakes are rarely encountered in the tropics. Few studies suggest that individual snakes actively select a suitable portion of their environment, which is influenced by biotic and abiotic factors (Reinert, 1984; Weatherhead and Charland, 1985; Burger and Zappalorti, 1988; Weatherhead and Prior, 1992; Reinert, 1993). Although some species are specialized to exploit a narrow range of habitat, most species sporadically utilize an extensive range (Heatwole, 1977). Hence, it is very important to know and understand the probable reasons for such wide variation in habitat selection amongst various species of snakes. Many snake species are decreasing in abundance, and habitat loss is considered to be a major causal factor. Hence, it is important for species conservation efforts to understand a snake's habitat ecology (Dodd, 1987; Mittermeier et al., 1992; Wilson, 1992; Dodd, 1993; Reinert, 1993; Losos et al., 1995; Fahrig, 1997; Gibbons et al., 2000; Fahrig, 2002).

Pit vipers belong to the family Viperidae and subfamily Crotalinae, which is represented by 21 genera. *Trimeresurus malabaricus* and *T. gramineus* are arboreal in nature, have restricted distribution, and are habitat specific; abiotic factors within the habitat, such as seasonal changes in temperature and humidity, influence the distribution of these snakes (Sawant et al., 2010). Very limited information is available on the ecology of these snakes (Tu et al., 2000; Oliveira and Martins, 2001; Shine and Sun, 2002; Valdujo et al., 2002; Lin et al., 2007; Eskew et al., 2009) and the studies of their spatial ecology have never been conducted. Because habitat destruction may lead to extinction of these species it is crucial to identify the factors that influence their habitat in order to conserve these species. Hence, this study will describe the habitat of *T. malabaricus* and *T. gramineus* and the factors that influence their habitat selection.

MATERIALS AND METHODS

The fieldwork was conducted in five protected areas of Goa, India, viz., Mhadei Wildlife Sanctuary (208 km^2), Bhagwan Mahaveer Wildlife Sanctuary and National Park (241 km^2), Bondla Wildlife Sanctuary (8 km^2), Netravali Wildlife Sanctuary (211 km^2) and Cotigao Wildlife Sanctuary (85 km^2) from June 2005 to January 2009. Two arboreal pit viper species, *T. malabaricus and T. gramineus*, were chosen for the present study. Pit vipers can be relatively easily captured using visual encounter survey due to their ambush predation habits. The detailed survey method is as described elsewhere (Sawant et al., 2010).

The macro-habitat was classified as forest, forest edge, or open habitat. Forest edge was defined as any location, 15 m from

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where forest met open habitat (e.g., fields and rocky outcrop) (Blouin-Demers and Weatherhead, 2001). To determine microhabitat selection, a variety of features at every other snake location were measured, classified and noted. Whether or not it was in a tree, the tree species, its height of perch, the position on the branch (distal/apical/middle), the diameter of the branch, the tree canopy (thick/sparse) and the vegetation of the area (thick/sparse) was recorded. Seasonal shifts in habitat use are a consistent feature of the ecology of many snake species (Reinert, 1993) as well as other types of reptiles (Paulissen, 1988). Activity cycles also appear to be seasonal among diverse animal taxa in the tropics. Thus, assessment of habitat was done to examine seasonal habitat use; hence, the analysis also involves seasonal (summer: March to May; monsoon: June to October; and winter: November to February) comparisons of snake-selected sites.

Whenever a snake was sighted, the hygrothermal profile of the habitat was recorded. Shaded ambient (air) temperatures and humidity were recorded following the methodology of Shine et al. (2005), with a few modifications. The shaded temperature and humidity at different heights above the ground were recorded using a thermometer. The temperature was recorded on the ground up to the point where the snake was located with a distance of 30 cm between two readings and up to 60 cm above the point where the snake was located. This data was recorded to know whether snakes will select their location based on their thermal preference i.e., whether there is association between height and temperature during summer and monsoon seasons.

All the calculations i.e. one-way ANOVA, two-way ANOVA, correlation coefficient, and plotting of graphs were carried out using the Microsoft Excel Software 2007. Differences of $P < 0.05$ were regarded as statistically significant. All the figures were represented as mean ± SE (Standard Error).

RESULTS

Habitat assessment

Data pertaining to 90 individuals of *T. malabaricus* and 100 individuals of *T. gramineus* were recorded. *Trimeresurus malabaricus* selected locations that included areas with thick vegetation. Amongst the 90 individuals of *T. malabaricus*, 87.78% were encountered in forest habitat, whereas, the remaining 12.22% were present in forest edge habitats. Neither of the species was found in open habitats. Only 12.22% of *T. malabaricus* that preferred forest edge habitat were encountered at regions of higher altitude (above 700 m). In contrast, amongst the 100 individuals of *T. gramineus*, 40% were encountered in the forest habitat, whereas 60% were observed in the forest edge habitat. One-way ANOVA between correlation of each species and the preferred habitat (forest, forest edge, and open) showed that the habitat utilization by *T. malabaricus* varied significantly ($P = 0.006$, df = 2, $F_{2,\,12} = 7.74$), whereas *T. gramineus* showed an insignificant pattern of habitat use ($P = 0.14$, df = 2, $F_{2,\,12} = 2.36$). Both species of pit vipers preferred diverse types of habitat and individuals were spread over the entire available space during the monsoon, whereas, they were restricted to cool and moist places during winter and summer. The temperature and humidity varied during different seasons (Table 1).

Table 1. Variation in range of temperature and humidity in different seasons.

Seasons	Temperature	Humidity
Summer	28–35°C	51–79%
Monsoon	21–28°C	88–98%
Winter	18–33°C	65–85%

Habitat preference differed in males and females of *T. malabaricus* whereas in *T. gramineus* it was observed that both sexes were encountered in forest edge habitats (Table 2). For differences between sexes, one-way ANOVA analysis showed that the preference of habitat types by *T. malabaricus* varied significantly, [males ($P = 0.033$, df = 1, $F_{1,\,8} = 6.53$) and females ($P = 0.039$, df = 1, $F_{1,\,8} = 6.03$)], whereas, there was no difference in the preference for habitat types by both sexes of *T. gramineus* ($P > 0.05$). *Trimeresurus malabaricus* and *T. gramineus* were observed mostly on vegetation and rarely on ground. Amongst the individuals of *T. malabaricus* encountered during the present study 86% ($n = 77$) were encountered on vegetation while 14% ($n = 13$) were found on the ground (three were found while crossing a road [at night] and 10 were found on rocks near a water body). All three individuals of *T. malabaricus* encountered while crossing the road were males and were encountered during the monsoon; 70% of the individuals encountered on rocks were females. It was observed that 64% of the individuals encountered on vegetation were females and 36% were males. Also 69% of the total individuals were sighted in the areas having thick tree canopy cover, while 31% were encountered in areas having sparse tree canopy cover.

Table 2. Number of individuals of *T. malabaricus* and *T. gramineus* found in different types of habitat.

Species	Forest Habitat			Edge Habitat			Open Habitat		
	M	F	N	M	F	N	M	F	N
T. malabaricus	30	49	79	4	7	11	0	0	0
T. gramineus	16	24	43	31	29	57	0	0	0

M = Male, F = Female , N = Total number of individuals

Of 100 *T. gramineus* encountered during the study, 94% ($n = 94$) were encountered in the vegetation whereas, 6% ($n = 6$) were encountered on the ground while crossing the road at night. It was observed that five of six (83%) individuals encountered while crossing the roads were males, whereas 55% of the individuals encountered in vegetation were females and 45% were males. Of all individuals sighted in vegetation, 34% were sighted in areas having thick tree canopy cover, while 66% were encountered in areas having sparse tree canopy cover. The tree canopy cover structure differed in different seasons. However, both arboreal pit vipers utilized only those regions having thick tree canopy cover. The arboreal pit vipers exhibited no preference for vegetation structure at low ambient temperature (monsoon), except for an apparent avoidance of vegetation with bare branches and no leaves. However, during summer they were distributed in the regions with thick tree canopy and thick vegetation.

The tree species utilized by *T. malabaricus* and *T. gramineus* are given in Table 3. One-way ANOVA showed no significant differences ($P > 0.05$) between tree species utilization when compared between *T. malabaricus* and *T. gramineus* and also when compared between males and females of each species separately.

Perch height

Amongst pit vipers observed in vegetation, the mean perch height for *T. malabaricus* was 1.56 ± 0.07 m (mean ±

Table 3. List of floral species used for perch by *T. malabaricus* and *T. gramineus.*

Floral species	*T. malabaricus*	*T. gramineus*
Bamboosa bambos		√
Calicopteris floribunda	√	√
Careya arborea	√	
Carvia callosa	√	√
Catunaregum spinarum	√	√
Dalbergia latifolia	√	√
Dendrocalamus strictus		√
Duranta species		√
Eupatorium odoratum	√	√
Grewia species (Unidentified)		√
Grewia tiliaefolia		√
helicteris isora	√	√
Leea indica	√	√
Melastoma malabatricum	√	
Mussaenda glabrata	√	√
Psychotria dalzelli	√	
Strychnos nuxvomica,		√
Tabernamonatana hyneana		√
Terminalia paniculata		√
Woodfordia fruticosa	√	√

Table 4. The mean perch height ± SE and mean perch diameter ± SE attained by males and females of *T. malabaricus* and *T. gramineus.*

Species		Mean Perch height (meters)	Mean Perch Diameter (milimeters)
T. malabaricus	M	1.57 ± 0.11	38.4 ± 2.26
	F	1.56 ± 0.08	46.7 ± 2.54
T. gramineus	M	1.51 ± 0.08	35.71 ± 1.73
	F	1.50 ± 0.08	42.85 ± 2.06

Table 5. The number of individuals of arboreal pit viper species occupying different regions on the branch.

Species	Distal			Middle			Apical		
	M	F	N	M	F	N	M	F	N
T. malabaricus	4	2	6	7	10	17	17	37	54
T. gramineus	7	2	9	24	31	55	11	19	30

M = male, F = female, N = totla number of individuals

SE) and ranged from 0.60 to 3.35 m. One-way ANOVA showed no significant difference ($P > 0.05$) in perch height between male and female *T. malabaricus* (Table 4). There was a positive correlation between body length and perch height attained by males ($r = 0.02$, $P > 0.05$) as well as females ($r = 0.102$, $P > 0.05$) of *T. malabaricus*. The mean perch height for *T. gramineus* was 1.48 ± 0.06 m (mean ± SE) and ranged from 0.54 to 3.04 m. One-way ANOVA showed no significant difference ($P > 0.05$) in perch height between male and female *T. gramineus* (Table 4). There was a positive correlation between body length and perch height attained by males ($r = 0.027$, $P > 0.05$) and females ($r = 0.108$, $P > 0.05$) of *T. gramineus.* The arboreal pit vipers did not show any preference for perch height during different seasons.

Perch diameter

Amongst pit vipers encountered in vegetation the mean perch diameter (diameter of the branch) utilized by *T. malabaricus* ($n = 50$) was 42.5 ± 1.78 mm (mean ± SE) and ranged from 21 to 67 mm. One-way ANOVA showed significant difference ($P = 0.019$, df = 1, $F_{1,\,48} = 5.83$) in perch diameter used by male and female *T. malabaricus* (Table 4). There was a positive correlation between body mass and perch diameter preferred when tested for males ($r = 0.74$, $P = 0.001$) and females ($r = 0.71$, $P = 0.001$). The mean perch diameter for *T. gramineus* ($n = 70$) was 39.28 ± 1.40 mm (mean ± SE) and ranged from 19.8 to 62.1 mm. Analysis of variance (one-way ANOVA) showed significant difference ($P = 0.008$, df = 1, $F_{1,68} = 7.32$) in perch diameter used by male and female *T. gramineus* (Table 4). There was a positive correlation between body mass and perch diameter preferred when tested for males ($r = 0.17$, $P > 0.05$) and females ($r = 0.18$, $P > 0.05$).

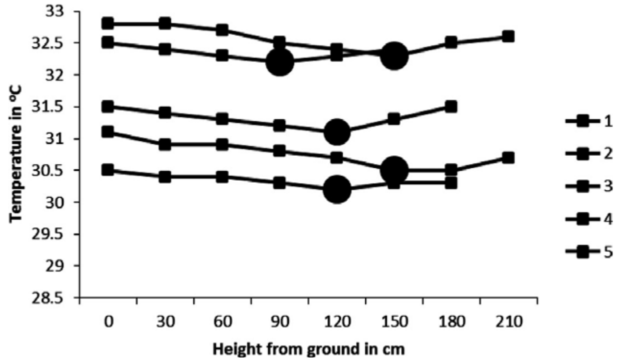

Fig. 1. Graph showing the location of arboreal pit viper and the shaded ambient temperature at different heights from the ground during summer (● represents the perch height at which the pit viper was located).

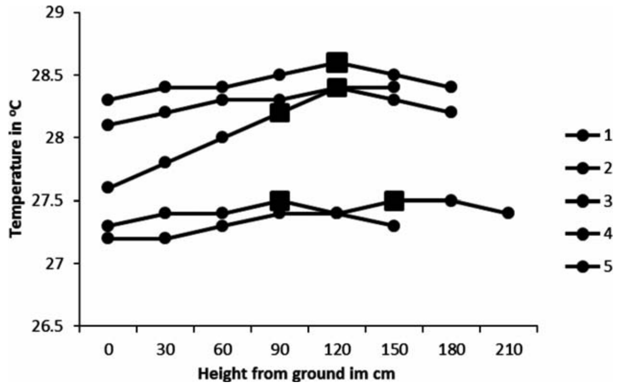

Fig. 2. Graph showing the location of arboreal pit viper and the shaded ambient temperature at different heights from the ground during monsoon (■ represents the perch height at which the pit viper was located).

Location on the branches where arboreal pit vipers were found

The location on the branches where *T. malabaricus* and *T. gramineus* were found differed. We observed that *T. malabaricus* mostly preferred distal position on the branches followed by middle and apical. In contrast, *T. gramineus* mostly preferred middle branch segments, followed by apical and distal. The arboreal pit vipers did not show any preference for the position on branch during different seasons. Two-way ANOVA showed a significant ($P = 0.01$, df = 2, $F =$

10.74) difference in the utilization of branch position by each species of arboreal pit viper. Preference for position on the branches differed when compared between males and females of each species (Table 5).

Thermal profile

A thermal profile was taken at five occasions in summer and five occasions in monsoon to get an impression of the association between thermal regimes and snake locations. The ambient temperature at a height of every 30 cm from the ground up to the position of pit viper declined during summer ($n = 5$; two *T. malabaricus* and three *T. gramineus*), whereas, it elevated during monsoon ($n = 5$; three *T. malabaricus* and two *T. gramineus*). On all five sampling occasions during summer the ambient temperature was generally found to be high and averaged about 0.42°C, higher on the ground than at the position where pit vipers were located on the trees. We also noted that in summer the ambient temperature at 60 cm above the point where pit viper was located on the tree was high with an average of 0.24°C higher than the ambient temperature at the position of pit viper (Fig. 1). On all five sampling occasions during monsoon the ambient temperature was generally found to be low and averaged about 0.3°C, lower on the ground than at the position where pit vipers were located on the trees. It was also noted that the ambient temperature at 60 cm above the point where pit viper was located on the tree was low, with an average about 0.18°C lower than the ambient temperature at the position of pit viper (Fig. 2).

DISCUSSION

Terrestrial and arboreal habitats differ greatly in the types and amount of food availability, susceptibility to predators, and physical factors such as temperature and humidity. As a consequence of these differences, many species have become highly specialized for either terrestrial or arboreal life and rarely inhabit alternative habitat (Plummer, 1981; Luiselli et al., 2000; Vilt et al., 2000). Identifying habitats that are used selectively is the first step in determining a species' critical habitat. Habitat selection occurs at different spatial scales. At the landscape level, animals select the most suitable habitats (i.e. forest, field, wetlands) and then, within habitats, select microhabitats that fulfill their requirements (Cody, 1985; Orians and Wittenberger, 1991). The habitat composition within both species of pit vipers' home range differed from habitat composition within the total study areas. *Trimeresurus malabaricus* predominantly occupied tropical evergreen forest and rarely used moist deciduous forest. *T. gramineus* were observed largely in wet bamboo brakes, tropical semi evergreen, and moist deciduous forest (see Sawant et al., 2010).

At the macrohabitat scale, the locations of both pit viper species differed. Their home range was restricted to forest and forest edge habitat, thus, avoiding open habitats. *T. malabaricus* had higher encounter rates in forests than forest edges thus, showing preference for thick vegetation, selecting a home range in forest habitat. ANOVA showed a significant difference in habitat (forest and forest edge) utilization by *T. malabaricus*, whereas the habitat use by *T. gramineus* did not differ significantly between forest and forest edge. Martins et al. (2001) stated that, most species of *Bothrops* and *Trimeresurus* are found in forests. Unfavorable ranges of habitat types can occur even within a small area, and animals use this diversity in multifaceted ways. The organism's 'choice' of particular habitat features apparently relates to advantages and disadvantages linked with each option (Krebs and McCleery, 1984). The forest edge is located at the boundary of the coolest habitat (forests) that is always shaded and the warmest habitats (open habitats) that receive full solar radiation, thus, snakes in forest edges always have access both to protection from the forest and to the warmest possible habitats (open habitats). Weatherhead and Charland (1985) proposed that snakes might prefer edges because increased solar radiation allows snakes to bask to increase body temperatures. Presumably, edges also facilitate thermoregulation as they provide simultaneous access to open sunny habitats that help to increase body temperatures and shaded forests, which serve to decrease body temperatures. Carfagno and Weatherhead (2006) reported intraspecific and interspecific variation in use of forest and forest edge habitat by snakes to occur as a result of thermoregulatory needs. Thus, a higher diversity in macrohabitat use in pit vipers may be associated with inhabiting structurally more intricate habitats, such as tropical forests. However, when the preference for the habitat was tested for males and females of each species separately it showed insignificant pattern of habitat use, suggesting that habitat utilization does not differ between sexes.

The study also revealed that the pit vipers do not show any change in habitat preference during different seasons. Reinert (1993) suggested that the need to locate essential resources such as food, shelter, and gestation sites, influence habitat selection by snakes.

There was no great difference observed between the temperature and humidity between the study areas. However, the microhabitat use varied seasonally in both the species, during monsoon they were found in all the transects, whereas, in summer and winter they were observed in transects having water bodies in the vicinity and thick vegetation The individuals of both the species were encountered in the regions having cool climate (segments of the transects with lower temperature and higher humidity) suggesting that the species prefer cool and moist places and thus are hygrophilic in nature. Daltry et al. (1998) reported a similar observation in *Calloselasma rhodostoma*, a pit viper which typically remains motionless in areas with dense cover of undergrowth.

Trimeresurus malabaricus and *T. gramineus* remain camouflaged in the thick canopy of the trees. Amongst the individuals of *T. malabaricus* encountered in the vegetation, most were sighted in the areas having thick tree canopy cover, while amongst the individuals of *T. gramineus* encountered in vegetation only few were sighted in areas having thick tree canopy cover. Furthermore the arboreal pit vipers exhibited no preference for vegetation structure at low ambient temperature (monsoon), except for avoiding vegetation with bare branches and no leaves. However, during summer they were distributed in regions with thick tree canopy and thick vegetation. We observed that tree species utilization did not differ significantly between the two arboreal species or between the two sexes of both species. Meik et al. (2002) suggested that type of vegetation can have a significant impact upon habitat availability for ectotherms by affecting the thermal characteristics of probable habitats. The types of vegetation selected by pit vipers as retreat sites are also influenced by temperature cues; moreover, the physical environment within a habitat structure may influence the thermal attributes and microclimate of a reptile's selected habitat (Christian et al., 1983; Huey et al., 1989; Pringle et al., 2003; Heard et al., 2004; Tsairi and Bouskila, 2004; Webb et al., 2004). This explains the difference in encounter rate of the two arboreal species in thick and sparse vegetation. Janzen (1976) suggested that vegetation cover plays a crucial role in concealing snakes from predators. Thus, arboreal snakes may be selecting the thick vegetation as a defense approach; however data pertaining to predator density affecting the habitat selection by arboreal pit vipers is sparse, therefore this possibility cannot be assessed formally.

Individuals of the arboreal species were also encountered while crossing the roads during night hours; this could be due to the thigmothermic reaction to warm surfaces, such as asphalt roads at night as observed in nocturnal crotalines (Klauber, 1972). Since the arboreal species were found crossing the roads during the monsoon, this excursion to the ground could be driven by the availability of prey, especially frogs, which represent easy and abundant prey available during the monsoon season on roads. The findings also suggest that since all the individuals of *T. malabaricus* and five of six *T. gramineus* sighted on the roads were males, the search for a mate could also result in such excursions. Shine et al. (2004) suggested that pheromonal trail-following may result in males traveling further and longer to locate females. *Trimeresurus malabaricus* was also found in the rock crevices near water bodies; this may be mainly due to their hygrophilic nature (discussed above).

Amongst the arboreal pit vipers the mean perch height did not differ significantly. The mean perch height for *T. malabaricus* was 1.56 ± 0.61 m (ranged from 0.60 to 3.35 m) and that of *T. gramineus* was 1.48 ± 0.55 m (ranged from 0.54 to 3.04 m) this could help avoiding the avian predators as very high perch heights have the risk of predations whereas low perch height may affect thermoregulation. The males and females of both the species showed no significant difference between the perch heights. Although the data indicate no significant differences in perch height between the two species and between the sexes of the two species, the vertical heights used by pit vipers showed a positive but not significant correlation with body length, except for males of *T. malabaricus* which showed a negative correlation. This may have been due to constraints on the available vegetative height in the forest. These findings supported the hypothesis that the hygrothermal profile i.e. ambient temperature and humidity may affect perch height selection during dry and wet seasons, this findings augments that of Shine et al. (2005). During the dry seasons, attaining higher perches may help to avoid higher ambient temperatures close to ground level. Heatwole (1970) suggested that arid zone lizards seek higher perches in hotter weather to avoid high temperatures on the ground, whereas during monsoon higher perch heights may be attained for basking. However, this result is primarily based on data of five individuals during both dry and wet seasons, and more intensive study is required to confirm it. There was however a significant difference in perch diameter used by males and females of both the species, which also showed a positive but an insignificant correlation between body mass and perch diameter, suggesting that arboreal pit vipers select twigs/branches depending on their body mass. Thus, heavier arboreal snakes may prefer lower branches (perch height) if the twigs become more slender towards the apex of the tree and the weight-carrying capacity of the twig decreases. These assumptions depend on the type of tree species and the habitat composition. However, no correlation between body size and perch height (Henderson, 1974) and body mass and twig diameter (Rodda, 1992; Tu et al., 2000) were found in other studies. The analysis of the regions of the branch (distal, apical, and middle) inhabited by the arboreal snakes showed that the regions inhabited by the arboreal pit vipers differed significantly; *T. malabaricus* occupied the distal region of the branch followed by middle and apical, whereas, *T. gramineus* was found to prefer middle regions on the branch, followed by middle and distal. The preference for distal position by *T. malabaricus* may be mainly to conceal with the branch color, whereas the preference by *T. gramineus* for middle and apical regions on the branch helps to conceal amongst the foliage and thus helps the snakes both to avoid predation and to capture prey. However, few individuals of *T. malabaricus* on middle and apical region of the branch and of *T. gramineus* on distal region of the branch were encountered. These encounters are possibly due to the presence of prey, such as arboreal agamids, which are concealed within the branches and small birds, usually bird nests, in the apical regions of branches, but the type of vegetation (bare branches, i.e. branches without leaves and thick bushes) will also determine the location of the snake on the branch.

The findings of the present study, thus suggest that several patterns (i.e. hygrothermal profile, positive correlation of body length with perch height, positive correlation of body mass with perch diameter and regions of branches utilized, vegetation structure) play an important role in habitat selection by these arboreal pit vipers. As these species are very precise in their habitat selection, these abiotic factors will play a vital role not only in their survival but also in their distribution. Many species are decreasing in abundance and habitat loss is considered as one of the major reason. Thus, habitats that provide the necessary physical environment for their survival should be protected in order to conserve these species.

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