Patterns of resource use, overlap and partitioning among three sympatric species of south Indian pitvipers

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ABSTRACT - We examined resting substrate utilization, habitat occupancy, altitudinal preference, size/age class distribution and encounter rate estimates of three, sympatric pitviper species, *Hypnale hypnale*, *Trimeresurus malabaricus* and *Trimeresurus macrolepis* in the Cardamom Hills of the Western Ghats Mountain Range, southern India and found that the resource use pattern of *Trimeresurus malabaricus* overlaps with that of *Hypnale hypnale* and *Trimeresurus macrolepis*, but *Hypnale hypnale* and *Trimeresurus macrolepis* have mutually exclusive, non-overlapping resource use patterns.

PITVIPERS in southern India are found only in hilly forest tracts (Smith, 1943; Whitaker, 1978; Das, 2002; Whitaker & Captain, 2004). The work-area of our study, Cardamom Hills (09ºN 077ºE; ≈100-2020 m ASL), is situated in the Western Ghats Mountain Range of southern India (Fig. 1). Here the habitat type is correlated with altitude, with deciduous, evergreen and montane forest types occurring correspondingly in low, middle and high altitudes (Fig. 2) (Champion & Seth, 1968). Four species of pitvipers are reported here (Whitaker & Captain, 2004). Of these, *Hypnale hypnale* (Fig. 4) is a member of the *Ancistrodon* complex while, *Trimeresurus macrolepis* (Fig. 5), *T. malabaricus* (Fig. 6) and *Tropidolaemus huttoni* are members of the *Trimeresurus* complex. *Tropidolaemus huttoni* is very rare (David & Vogel, 1998) and was not recorded in this study. Barring *T. huttoni*, the remaining three common species were investigated. *Ancistrodon* (*sensu lato*) are predominantly terrestrial taxa while *Trimeresurus* (*sensu lato*) are both arboreal and terrestrial, and the habit is more or less correlated to the dorsal coloration, i.e., green ones being more arboreal while brown ones being more terrestrial (Whitaker, 1978; David & Vogel, 1998; Gumprecht et al., 2004). These three pitviper species are frequently reported to be sympatric, with dynamic relationships of co-existence (Inger et al., 1984; Aengals, 1995; Kumar et al., 2001; Kannan et al., 2006). In a few Indian pitviper species, adults and juveniles are reported to use different resting substrates (Whitaker & Captain, 2004). Species exhibiting age-based microhabitat selection are considered as two different Occupational Taxonomic Units (Brown, 1992). Limited similarities, spatial niche segregation and character displacement are demonstrated analogous to resource-heterogeneity based niche partitioning (Christiansen et al., 1980). Given this scenario, the following questions were raised.

1. Does resting substrate preference influence pitviper sympatry?
2. Does habitat type and quality affect pitviper sympatry?
3. Will altitudinal preference allow pitvipers to be sympatric? If yes, to what extent?
4. When morphology and age-class play significant roles in resting substrate preference of pitvipers, how do these variables affect them being sympatric?
5. What is the relative abundance of these pitviper species? Are they equally abundant?

MATERIALS AND METHODS

Surveys were conducted for a period of four months from December 2007 to March 2008. Visual Encounter Surveys (VES) were used to detect the presence/apparent absence of pitvipers (Crump

Figure 1. Map of southern India showing the location of the Cardomom Hills.

Figure 2. Evergreen Forest; Natural climax vegetation type.

Figure 3. Cultivated tea plantation.

Figure 4. *Hypnale hypnale* (Merrem, 1820).

Figure 5. *Trimeresurus macrolepis* Beddome, 1862.

Figure 6. *Trimeresurus malabaricus* (Jerdon, 1854).

& Scott, 1994). Possible resting substrates such as fallen logs, rocks, branches, base of trees, and leaf-litter were examined. Surveys were conducted in both riparian and non-riparian habitats between 9.00 and 13.00 hrs. Transects were of a fixed length, determined using K & R pedometer (L.C. = 250 m). The forest path transects were 1 km long and the stream transects were 0.5 km long, as streams in Western Ghats harbour twice as much habitat diversity, herpetofaunal diversity and density as non-riparian vegetation (Ganesh et al., 2007). All forest path transects were narrow footpaths, no greater than 1 m width, that were not necessarily in a straight line. Stream transects were small river courses, with maximum stream width no greater than 3 m. The vegetation type classification follows Champion & Seth (1968). The total length of the smallest female was used to determine size/age class (Smith, 1943; Whitaker & Captain, 2004). Altitude was determined using Garmin 12 channel Global Positioning System. Encounter rate was expressed as the ratio of sighting frequency to the total distance surveyed.

RESULTS

In all, 49 sightings of pitvipers were recorded; *Hypnale hypnale* (n = 13), *Trimeresurus malabaricus* (n = 20) and *Trimeresurus macrolepis* (n = 16). The values obtained for the selected factors like resting substrate, habitat type, altitudinal range, size/age class and encounter rate estimates are shown in Table 1.

Resting Substrate

Fallen logs were mostly used by *H. hypnale* (38.4%), rocks were mostly used by *T. malabaricus*

Factors	Variables	*H. hypnale* (n = 13)	*T. malabaricus* (n = 20)	*T. macrolepis* (n = 16)
Resting Substrate	Fallen log	5*# (38.4%)	2* (10%)	0
	Rock	2* (15.3%)	11*# (55%)	0
	Branch	0	5* (25%)	16*# (100%)
	Tree base	2* (15.3%)	1* (5%)	0
	Leaf-litter	2* (15.3%)	1* (5%)	0
	Bare ground	2 (15.3%)	0	0
Habitat Type	Deciduous	6*# (46%)	3* (15%)	0
	Evergreen	4* (30.7%)	13*# (65%)	0
	Montane	0	0	7# (43.7%)
	Tea	0	0	2 (12.5%)
	Coffee	3* (23%)	3* (15%)	2* (12.5%)
	Cardamom	0	1* (5%)	5* (31.2%)
Altitude (m)	500-800	12*# (92.3%)	3* (15%)	0
	800-1000	1* (7.7%)	13*# (65%)	0
	1000-1300	0	4* (20%)	4* (25%)
	1300-1600	0	0	12# (75%)
Size/Age Class	Sub-adults	4/13; (31%)	7/20; (35%)	6/16; (37%)
	Adults	9/13; (69%)	13/20; (65%)	10/16; (63%)
	Ratio	31:69%	35:65%	37:63%
Encounter Rate Est. (km)	Paths	10/17=0.58#	6/26=0.23	13/20=0.65#
	Streams	3/8=0.38	14/13=1.07#	3/10=0.30
	Overall enc. rate	13/25=0.52	20/39=0.51	16/30=0.53

Table 1. Values of various selected factors and variables for three species of pitvipers. Numbers denote sighting frequency; * denotes overlap; # denotes maximum value.

(55%) and *T. macrolepis* exclusively used branches (100%). Overlap was observed in the resting substrate usage of *T. malabaricus* with both *H. hypnale* and *T. macrolepis*. But *H. hypnale* and *T. macrolepis* had mutually exclusive resting substrate preferences.

Habitat Type

Sighting frequencies of pitvipers were greater in pristine forests (15-65%) than in estates (5-31.2%), regardless of the species or the habitat. Deciduous and evergreen forests were occupied by *H. hypnale* and *T. malabaricus*. Montane forests and tea estates were occupied only by *T. macrolepis* (Figs. 2 and 3). Cardamom estates were occupied by *T. malabaricus* and *T. macrolepis*. Coffee estate was the only habitat occupied by all three species.

Altitude

Overlap was observed between *H. hypnale* and *T. malabaricus* in 500-1000 m and between *T. malabaricus* and *T. macrolepis* in 1000-1300 m. But there was no overlap between *H. hypnale* and *T. macrolepis*. Exclusive sightings of *T. macrolepis* were from 1300-1600 m. The altitudinal range where *T. malabaricus* was recorded (500-1300 m) also harboured the other two species.

Size/Age class

Juveniles were scarcer (31-37%) than adults (63-67%), among all three pitviper species. The least frequency of sub-adults (i.e., the highest frequency of adults) was recorded in *H. hypnale*, followed by *T. malabaricus* and *T. macrolepis*. The ratio of sighting frequencies of sub-adults: adults ranged from 31-37:63-69%.

Encounter Rate Estimates

All the species were uniformly sampled, with proportionately equal number of riparian and non riparian transects surveyed. Total distance walked was comparable with respect to the number of days surveyed for all three species. Number of transects walked for each species differed due to inevitable natural constraints like correlation between habitat type and altitudinal range. Encounter rates were also comparable for all the three species (0.52, 0.51 and 0.53 respectively). Thus, a distance-coverage of two km will yield one pitviper sighting, regardless of species, habitat, elevation and size/age class in this season, in this hill range. The species will depend on the habitat and altitude.

DISCUSSION

H. hypnale is predominantly terrestrial as inferred by our study and literature records (Smith, 1943; Whitaker & Captain, 2004). Smith (1943) reported *H. hypnale* resting on shrubs but we did not observe this behaviour. We recorded *T. macrolepis* only on branches of trees and shrubs. This species is regarded as arboreal and terrestrial (Smith, 1943; Malhotra & Davis, 1991; Whitaker & Captain, 2004). Moreover, those species of pitvipers that are primarily green in colour are said to be arboreal, while the many-coloured species like the Malabar Rock Pitviper (*T. malabaricus*) are said to be terrestrial forms (Whitaker, 1978). *T. malabaricus* was more frequently sighted in riparian habitats, as inferred by our study. The frequent arboreal tendencies of juvenile *T. malabaricus* has been widely reported (Smith, 1943; Whitaker & Captain, 2004). Our observation of all six juveniles and sub-adults on shrubs is strongly supportive to literature.

We sighted *H. hypnale* in deciduous forests, *T. malabaricus* in evergreen forests and *T. macrolepis* in montane forests, the most. Whitaker (1973) and Kumar et al. (2001) stated that montane forests were preferred by *T. macrolepis*. Aengals (1995) and Malhotra & Davis (1991) recorded *T. malabaricus* and *T. macrolepis* from Valparai and Srivilliputhur hills respectively, which are primarily montane forest habitats; while Inger et al. (1984) recorded *H. hypnale* and *T. malabaricus* from Ponmudi, an evergreen forest habitat, and found both species to be more abundant in this habitat than deciduous belts. Kumar et al. (2001) recorded all three species from Anaimalai hills, which has both evergreen and montane forests.

Whitaker & Captain (2004) mention the altitudinal range of *H. hypnale* to be 300-600 m. In the present study one individual of *H. hypnale* was seen above 800 m. Thus there are good chances for it to occur sympatricly with other higher-elevation species. Whitaker & Captain (2004) states that, both *T. macrolepis* and *T. malabaricus*

occur from 610-2134 m. But in the present study, no *T. macrolepis* was recorded below 1000 m and no *T. malabaricus* was sighted above 1300 m. It is noteworthy to mention here that this survey was undertaken from 500-1600 m, in hills covered with all the three habitat types inhabited by pitvipers. In general, literature states that, higher elevation forests (> 1000 m) were often recorded to have either or both *T. macrolepis*, *T. malabaricus* (Aengals, 1995; Kumar et al., 2001; Malhotra & Davis, 1991) and lower elevation forests (< 1000 m) were reported to have either or both, *H. hypnale*, *T. malabaricus* (Inger et al., 1984; Kannan et al., 2006). However, in one instance *H. hypnale*, *T. macrolepis* and *T. malabaricus* all coexisting in the same forest has been recorded from Andiparai (1000 m), in Anaimalai hills (Kumar et al., 2001). In the present study however, we did not observe all the three species to be syntopic. This confusing state regarding altitudinal distribution of south Indian pitvipers necessitates further field studies.

We observed fewer juveniles (31-37%) than adults (63-67%) revealing an equal and homogenous recruitment of populations. Thus our data corroborates previous findings that suggest the result of high mortality in juveniles and increased life expectancy with age is that the adult populations of snakes represent the accumulation of many years' reproduction (Porter, 1972).

Our study produced equal encounter rate estimates and hence equal relative abundance (0.51-0.53 sightings per km) equating to one sighting per 2 km. The relatively lower encounter rates in anthropogenic (5-31.2%) than pristine habitats (15-65%) is in accordance with Porter (1972) who remarked that snake populations seem to be regulated by conditions of cover, food and basking sites. The high optimal conditions found in pristine conditions support higher densities and diversities of snakes than less favourable conditions, as anthropogenic pressures will degrade its abiotic and thus its biotic content.

CONCLUSION

It is well understood that, of the three species of pitvipers studied, one is terrestrial, another is arboreal and the other both terrestrial and arboreal. Thus they differed in resting substrate usage, with a marginal overlap. It was also observed that there was an altitudinal separation in their distribution, with a marginal overlap. It is clear that all three species of pitvipers are equally abundant, as inferred from their encounter rates. Thus, theoretically these three pitviper species with different resting substrate preferences can be sympatric, although altitude is a limiting factor. They were indeed sympatric in a wider altitudinal range of 500-1300 m, the transition zone of deciduous - evergreen - montane forest types, where *T. macrolepis* was not dominant. The other two species were observed to be dominant in this altitudinal range. The sighting frequencies of the three species were relatively low in intermediary altitudinal zones where they were sympatric.

One species differed from the other two in terms of niche breadth. *T. malabaricus* is (1) both arboreal and terrestrial (vs. predominantly terrestrial *H. hypnale* and predominantly arboreal *T. macrolepis*), (2) has preference for mid-altitude zones (vs. predominantly low altitude preferring *H. hypnale* and predominantly high altitude preferring *T. macrolepis*) and (3) is primarily a riparian habitat species (vs. primarily non-riparian habitat preferring *H. hypnale* and *T. macrolepis*). Therefore *T. malabaricus* has diverged preferences thus avoiding resource-competition with *H. hypnale* and *T. macrolepis*. *H. hypnale* and *T. macrolepis*, despite being capable of occurring sympatricly with one another (due to their mutually exclusive resting substrate preferences) were observed separately because of their diverse altitudinal preferences. This was an advantage for the mid-elevation preferring *T. malabaricus*. Thus the resource use pattern of *T. malabaricus* overlaps with that of the other two species, which in turn have mutually exclusive, non-overlapping resource use patterns. This is a preliminary study and a more detailed, long-term study, involving a greater sample size of each pitviper species and increased geographical range, is needed for a better understanding of their ecology.

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