

Composition and structure of a snake assemblage in an altered tropical forest-plantation mosaic in Bangladesh

Shahriar Caesar Rahman^{1,2,3}, S.M.A. Rashid², Kanai Das³, Luca Luiselli^{4,*}

Abstract. Despite the growing trends in quantitative field studies on tropical snake assemblages around the world, Asian tropical snake assemblages have remained less profoundly studied. A snake assemblage in an altered tropical forest-plantation mosaic in Bangladesh was studied for six months. Data were collected on the species composition and their relative frequency of occurrence. On the basis of these data, some major patterns highlighted by earlier studies on tropical snake ecology were tested. More specifically, we tested, the existence of: (1) non-random habitat niche partitioning, (2) the energetic equivalence rule, and (3) different mean body sizes among snake guilds, with distinctly smaller body sizes being expected among the subterranean species. A total of 374 specimens belonging to 34 different species were collected. High mean habitat niche overlap among species was observed, and there was no apparent non-random niche partitioning by snakes either considering all species together or dividing them by guild. The 'energetic equivalence rule' was verified, with larger species being less abundant than smaller species. Body sizes differed significantly across species' habits, with subterranean species being not only significantly smaller but also revealing the least interspecific variation, and terrestrial/arboreal species showing the greatest interspecific variation. Overall, tropical Asian snake assemblages seem to be similar to tropical African snake assemblages in terms of their general organization.

Keywords: agro-forest, body size, energetic equivalence rule, habitat use, habits, resource partitioning.

Introduction

Understanding the organization and the mechanisms regulating the assemblages of living organisms are among the ultimate aims of community ecology (e.g., Schoener, 1974; Gotelli, 2000, 2001). A major research theme in recent community ecology has been whether ecological communities have a non-random structure and, if so, what are the causes explaining this structure (Gotelli and Graves, 1996; Gotelli, 2000, 2001). In several cases, non-random community structure was likely the outcome of interspecific competition (Gotelli, 2000, 2001). Interspecific competition has traditionally been viewed as one of the strongest shaping forces

determining the structure of living communities (e.g. Pianka, 1986; Gotelli, 2000, 2001; Poulin, 2006), although the prominence and relative importance of this force has also been questioned (e.g. Bradley and Bradley, 1985; Ricklefs, 2008). Several studies, both empirical and theoretical, suggested that interspecific competition should be more intense in tropical than in non-tropical communities (Rhode, 1992; Luiselli, 2008; Vignoli and Luiselli, 2012), and that diversification of body sizes among potential competitors may minimize the strength of interspecific competition (e.g. Pianka, 1986). The links between intensity of competition and diversification in body size among potential co-existing competitors are also complicated by (1) the trend for larger species to exhibit lower abundances than smaller co-occurring species according to the 'energetic equivalence rule' (Cotgreave, 1993; Blackburn and Gaston, 1999) and (2) the tendency for species inhabiting different types of microhabitats to evolve different body sizes (for instance to better exploit foraging microhabitats, see Dickman, 1988), so that body size differences between potential com-

1 - School of Environmental Science and Management, Independent University, Bashundhara, Dhaka, 1229, Bangladesh

2 - Lawachara Snake Research and Conservation Project, Maulavibazar, Bangladesh

3 - Centre for Advanced Research in Natural Resources & Management (CARINAM), Dhaka, 1207, Bangladesh

4 - Centre of Environmental Studies Demetra, via Olona 7, 00198 Rome, Italy

*Corresponding author; e-mail: lucamlu@tin.it

petitors may be an outcome of different niches at fine spatial scales rather than a direct outcome of interspecific competition (Bowers and Brown, 1982; Dickman, 1988). Because of all of these suites of complications, it is always difficult to analyze patterns of community composition and structure and to resolve the main causes producing the observed patterns (Gotelli, 2000, 2001; Poulin, 2006).

Traditionally, field studies on community composition and structure have been taxonomically strongly biased, especially in tropical regions, where most research has focused on birds and lizards (e.g. Pianka, 1986; Terborgh et al., 1990). However, the incomplete knowledge we have on different taxonomic groups may prevent from stressing firm conclusions and a fuller understanding on community ecology patterns. In the last few decades, new model organisms have entered into community ecology scene, including e.g. cestodes (Friggens and Brown, 2005), insects (e.g. Field, 1992; Solida et al., 2011), tropical fishes (Winemiller and Pianka, 1990), and snakes (e.g. Guyer and Donnelly, 1990; Cadle and Greene, 1993; Franca et al., 2008).

Quantitative field studies of snake assemblages have greatly expanded in number and scope during the past 20 years (Luiselli, 2006a, 2006b and references therein), after a long period of time in which these animals were neglected in terms of community ecology studies (but see Barbault, 1971; Mushinsky and Hebrard, 1977a, 1977b). Available studies documented such disparate aspects as species composition within particular sites (Orlov, 1995, 1997), diversity and rarity patterns (Akani et al., 1999; Luiselli, 2006a), and the role of resource partitioning and interspecific competition as a key factor in the ecology of these assemblages (Kadowaki, 1996; Luiselli et al., 1998; Laurent and Kingsbury, 2003; Luiselli, 2006b). In recent years, studies of tropical snake assemblages have grown tremendously, particularly in Africa and South America (for quantitative reviews, see Luiselli, 2006a, 2006b, 2008). On the other hand, Asian tropical snake assemblages

have remained less profoundly investigated, although some studies, mainly with taxonomic emphasis, are available (Orlov, 1995, 1997; Rooijen, 2009; Karns et al., 2010; Karunaratna and Amarasinghe, 2011). In general, studies on snake assemblages have showed that competition is much stronger in tropical than in temperate snake assemblages (thus confirming expectations from the general theory), and the intensity of this process fluctuates throughout the year being most intense during periods of low food availability (= dry seasons) (Luiselli, 2006b, 2006c, 2008).

Our aims with this study are to test the occurrence of some major patterns which were highlighted by earlier studies on tropical snake community ecology (Luiselli, 2006a, 2006b, 2008), by using a snake assemblage from a tea plantation/altered forest habitat in Bangladesh. More specifically, we examine a series of relevant hypotheses. Firstly, we hypothesize that snake species in our Asian-tropical assemblage non-randomly partition the habitat resource as a consequence of interspecific competition. This hypothesis is based on the fact that (i) interspecific competition plays often an important role in structuring snake communities with even cases of character displacements (for a review, see Luiselli, 2006a) and (ii) spatial resource partitioning is frequently observed in reptile communities (Toft, 1982; Pianka, 1986). Moreover, contrary to what happens in most vertebrate assemblages around the world (e.g., Pianka, 1986; Caro and Stoner, 2003), tropical snakes usually partition the food resource (prey type and/or prey size) more clearly than the habitat resource (Luiselli, 2006b, 2008). Thus, testing the generality of this pattern with additional tropical cases of study may be noteworthy. Secondly, we hypothesize that a species' relative abundance should be influenced by its body size, that is: larger-bodied species should be less abundant than smaller-bodied species. This is an important theoretical question in ecology studies, because the 'energetic equivalence rule' predicts that the amount of energy con-

sumed by a species is independent of its body size because larger species have lower population densities (Cotgreave, 1993; Blackburn and Gaston, 1999). Indeed, previous snake studies conducted in tropical Africa confirmed the 'energetic equivalence rule' (Luiselli et al., 2005; Luiselli, 2006a) but there are doubts about the general applicability of this rule to all systems (Damuth, 1981; Blackburn and Gaston, 1999). Thirdly, we hypothesize that the snake body sizes were influenced by a species' habits, that is: there should be detectable differences in mean body sizes among guilds inhabiting arboreal, terrestrial, semi-aquatic and subterranean niches, with subterranean snakes being much smaller than those inhabiting other niches (Halliday and Adler, 2002).

Materials and methods

Study area

The field work was carried out in Lawachara National Park (LNP) and its adjacent areas (fig. 1). LNP, situated in Maulavibazar District in the north-east of Bangladesh, is a 1250-ha mixed-evergreen forest. Most of park's original forest cover has been altered or substantially removed by rotation, with only some small remnant patches of primary forest still left (NACOM, 2003). The overall tree density

in this site is 528.5/ha (Muzzafar et al., 2007). In-between the forest habitat, there are landscapes modified by human disturbances, including patches of agricultural lands, human settlements, modified vegetation for betel leaf (*Piper betle*), tea plantation, native bamboo plantation (*Bambusa tulda*, *Bambusa polymorpha*, *Bambusa longispiculata*, etc.), and monoculture plantation forest (e.g. *Tectona grandis*, *Aquilaria crassna*, *Eucalyptus* sp., *Acacia* sp., etc.). Numerous streams passed through the forest and the tea plantations, and there are several man-made perennial and seasonally inundated ponds in the tea plantation and the surrounding village settlements.

This area falls within the monsoon climatic zone, with average annual rainfall of ~3000 mm (most of which falls during June-September), and annual diurnal temperature ranging from 27°C (June-September) to 16°C (January). The area is undulating with slopes and hillocks and the average altitude range of roughly 10-80 m a.s.l. (NACOM, 2003).

We attributed each snake record to a given category of habitat, based on the characteristics of the site where it was collected. We catalogued five different habitat types: (1) Mature Forest: this is the core natural area of LNP a plantation forest from 1920s-1950s with deciduous trees mixed with smaller evergreen trees and bamboos, and several sandy seasonal streams. The canopy cover includes *Artocarpus chapalasha*, *Tectona grandis*, *Dipterocarpus turbinatus*, *Elaeocarpus floribundaas*, *Dillenia pentagyna*, *Castanopsis tribuloides*, etc.; (2) Degraded Secondary Forest: this is the plantation forest from 1950s-2008. The tree species of this forest are similar to those of the mature forest, but the forest is highly degraded as its forest cover has been cleared or anthropogenically modified for betel vine (*Piper betle*) plantation, with extensive growth of woody climbers and patches of bamboo clumps with sandy seasonal streams;

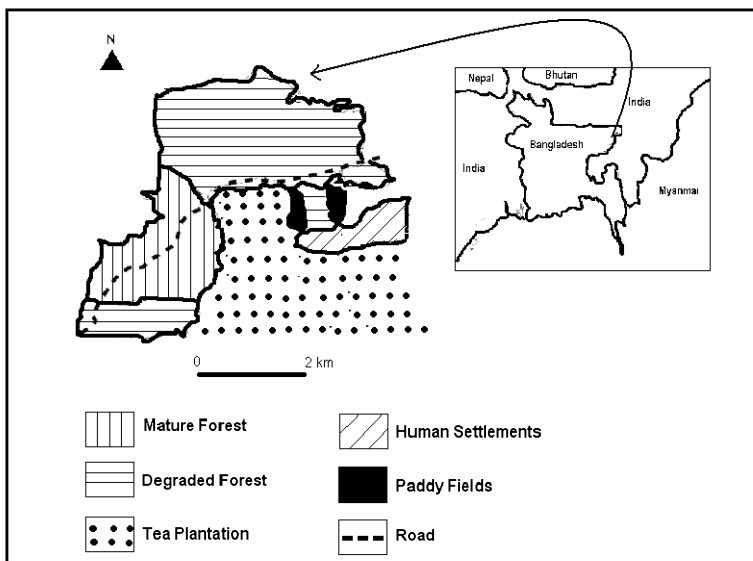


Figure 1. Map of the study area.

(3) Tea Plantation: this is dense tea plantation (*Camelia* sp.) with sparsely planted mature trees (*Albizia saman*, *Eucalyptus* sp., *Acacia* sp.) providing shade for the tea plants; (4) Paddy Fields: open seasonally flooded rice field adjacent to the village, tea plantation and degraded forest and (5) Village Habitat: these are the human settlements embedded in the matrix of tea plantation, degraded forest and the paddy fields with small patches of home garden and shrubs. There are several permanent and seasonal ponds in it.

Field protocol

Field work was conducted from 14 May 2011 to 18 November 2011, i.e. during wet (June-September) and dry seasons (October-November) and for a total of 138 field days. Conducting field surveys during both wet and dry seasons is important because tropical snake communities can show remarkable interseasonal variation in probability of encounter due to variable phenology (e.g., Luiselli, 2006d; Akani et al., 2013; Eniang et al., 2013). For instance, some species are more nocturnal and/or less above-ground active in dry season, thus lowering their probability of encountering (Akani et al., 1999).

We used three standard field methods for tropical snake studies (Akani et al., 1999), i.e. (1) road-killed individuals (death-on-road, DOR) encountered during standardized road surveys, (2) specimens opportunistically collected (OC), and (3) individuals encountered during visual-encounter surveys (VES).

In VES, snakes were actively searched for using time-constrained searches in standardized routes throughout available habitats. We used two different routes in the natural habitat and three different routes in the human modified habitat to minimize any sampling bias. In the natural habitat, one route was on a sandy seasonal stream bed and the other route was on the existing forest trail constructed by the forest department. In the human modified habitat, one of the routes was along a sandy stream bed while the other two was on existing trails. A total of 1543 man-hours were spent for VES survey in five different habitat types, with all habitats surveyed for an almost identical time. Suitable spots like, logs, mammal burrow, leaf litter etc. were also checked. Field survey was conducted in standardized routes from approximately 9.00 h to 17.00 h, during both wet and sunny days. One to four surveyors walked the area in standard pace visually examining the area. However, field-work was suspended during heavy showers. Night surveys were conducted in the open forest habitat only occasionally because of security reasons. More specifically, less than 15% of total time was employed for nocturnal VES, from 18.00 h to 21.00 h. Many tropical snake species are nocturnal and therefore very limited night survey effort might under-represent the nocturnal species. However, we examined specimens killed by people at nights and also collected road killed specimens, thus reducing under-representation of nocturnal species. When seen, snakes were captured by hand or tongs, measured for snout-vent length (SVL) and tail length (TL) to the nearest 1 cm, and then individually marked by ventral scale-clipping. Snake specimens that were just sighted but that escaped before being identified

were not included in the analyses. DOR specimens were collected along a 7-km segment of Sreemongol-Komgolgonj road that cut through the LNP. 3.5 km of this road segment passes along the moderately dense forest habitat and the rest dissects the human-modified habitat, with tea plantation on one side and the highly degraded, plantation forest in the other. DOR survey was conducted by walking at least once a day from July 11, 2011 to November 11, 2011, totalling 728 km. Survey time was typically from 16.00 h to 19.00 h. Since the survey was conducted almost daily, the majority of the DOR specimens were identifiable to species level. However, due to their small size and similar morphology, we were not able to discriminate to species all DOR specimens which were potentially belonging either to *Ramphotyphlops braminus* or to *Typhlops* spp. Therefore, for analysis, we classified them as Typhlopidae. DOR snakes were measured (total length, TL) using a measuring tape. After identification of the species, all DORs were taken out of the road to avoid double counts in following days. For OC, both live and dead (killed by people) snakes were collected opportunistically from plantation workers and local villagers from May 14 to November 18, 2011. Detailed data were collected from each captured individuals following the same protocol for the VES captured individuals.

Statistical analyses

Relationships between snake body sizes (using maximum body length as obtained from Das, 2010; Whitaker and Captain, 2007) and number of recorded specimens were assessed by Pearson's correlation coefficient (after log-transformation of the variables). The effects of a species' habits (as grouping variable) on snake body sizes were assessed by Kruskal-Wallis ANOVA. Habitat niche analyses were independently performed both on the total number of species and at the guild level by dividing the snake species into five guilds. We used five categories of habits/guilds: 1 = subfossorial, 2 = terrestrial, 3 = arboreal, 4 = terrestrial/arboreal, and 5 = semiaquatic.

Cluster analyses (UPGMA with single linkage and Euclidean distances) were used to classify the species in terms of their relative dissimilarity as for habitat type use (Luiselli et al., 1998). In these analyses, we entered the species abundance data, with all seasons, method of capture, sex, and age pooled. Branching measurements were after 40 bootstraps.

To evaluate whether the frequency distributions of the various species among habitat types were structured randomly, we contrasted the data matrix with random "pseudo-communities" generated by Monte Carlo simulations (Gotelli and Entsminger, 2011; Vignoli and Luiselli, 2012). We calculated Pianka's (1986) overlap index on the percentages of snakes recorded by each habitat type for each pair of snake species. Then, we randomized the original species utilization matrices by shuffling the original values among resource states according to two randomization algorithms, RA2 and RA3 (Gotelli and Graves, 1996). RA2 tests for structure in the generalist-specialist nature of the resource utilization matrix by conserving guild structure, but destroying observed niche breadth (Gotelli and Graves, 1996). RA3 tests for guild structure by conserving niche

breadth for each species, but destroying guild structure manifested by the resource utilization matrix's zero structure (Gotelli and Graves, 1996). For each pair of species, 30,000 random Monte Carlo permutations were generated. Niche overlap values were calculated for each of these randomly generated matrices, and species-pair and community-summary statistics were computed. Actual overlap values were then compared to the distributions of expected values. Structure was assumed when $P_{(obs \leq exp)} = 0.05$ (Gotelli and Graves, 1996). We performed separate sets of analysis for all species entered without any guild separation, and for species sorted by guild.

Pseudo-replication of data was avoided because the counted individuals were either road-killed or individually marked. Only one data point per individual was used, and all DOR records were used to calculate abundances. Fossorial snakes were likely more difficult to encounter than were those in the other habitats studied and this fact may have introduced some uncontrolled bias in the outcomes of our results.

We used EcoSim software (Acquired Intelligence Corp., Kelsey-Bear; <http://www.uvm.edu/biology/Faculty/Gotelli/Gotelli.html>) to calculate overlap indices and generate Monte Carlo simulations. All other analyses were conducted using SPSS (SPSS 11.0 for Windows) and Statistica (Statistica 6.4 for Windows); all tests were two-tailed with alpha set at 0.05.

Results

In total, 374 snake specimens belonging to 34 different species were collected after pooling individuals obtained with the three survey methods, but 11 of them were in too poor condition and hence remained unidentified (see Supplementary Appendix 1). There were two singletons (*Boiga cyanea* and *Lycodon jara*).

Distribution of snake species across habitat types

An UPGMA dendrogram showed the presence of complicated clusters, with at least five close clusters (<20% in the Euclidean distance; coph. corr. = 0.965) (fig. 2): (1) a four-species cluster (*Boiga ochracea*, *Ptyas mucosa*, *Oligodon cyclurus*, *Bungarus fasciatus*) consisting of taxa which were observed nearly only in degraded forest; (2) a three-species cluster (*Ahaetulla prasina*, *Boiga siamensis*, *Naja*



Figure 2. UPGMA dendrogram (single linkage with Euclidean distances) showing dissimilarity among sympatric snake species in terms of habitat type utilization. Branching measurement is with 40 bootstraps.

kaouthia) formed by taxa occurring in both degraded forest and tea plantation; (3) a four-species cluster (*Blythia reticulata*, *Oligodon albocinctus*, *Oligodon dorsalis*, *Sibynophis collaris*) consisting of forest taxa predominantly found in mature forest but also in degraded forest; (4) a cluster formed by *Enhydris enhydris* and *Xenochrophis piscator* which are linked to ponds, lakes and flooded wetlands; and (5) a cluster formed by *Boiga cyanea* and *Oreocryptophis porphyracea* which are exclusively mature forest specialists.

Assemblage composition: do snakes non-randomly partition the habitat resource?

Absence of non-random structure was always confirmed, either considering all species together or dividing them by guild, both using RA2 and RA3 (Appendix 2). However, the semi-aquatic guild was not considered in the analyses by guild because there was only one species assigned to this guild (Appendix 1).

Assemblage composition: are larger species least abundant than smaller species?

Natural history attributes of the snake species recorded at the study area showed that there

was a great interspecific variation in body size (with lengths ranging from about 25 cm to over 7 m; Appendix 1). There was a marginally significant (but weak) negative relationship between (log) snake body size and (log) relative abundance (i.e., number of recorded individuals) ($r = -0.34$, $r^2 = 0.12$, $P = 0.05$) (fig. 3A). However, if we remove the outliers from the plot (i.e. Typhlopidae and *Python molurus bivittatus*), the negative relationship between body size and abundance was not significant ($r = -0.21$, $r^2 = 0.04$, $P = 0.277$; fig. 3B).

Assemblage composition: were snake body sizes influenced by a species' habit?

The snake species varied remarkably in terms of diel pattern, habit and diet (Appendix 1). 52.9% of the species (i.e. 18 out of 34) were terrestrial, 7 (20.6%) arboreal, 3 (8.8%) terrestrial/arboreal, 3 (8.8%) subterranean and 2 (5.9%) aquatic/terrestrial. Snake body size differed significantly across species' habit (Kruskal-Wallis ANOVA, $\chi^2 = 11.6$, $df = 4$, $P = 0.021$), with subterranean species being not only significantly smaller but also revealing the lowest interspecific variation, and terrestrial/arboreal showing the greatest interspecific

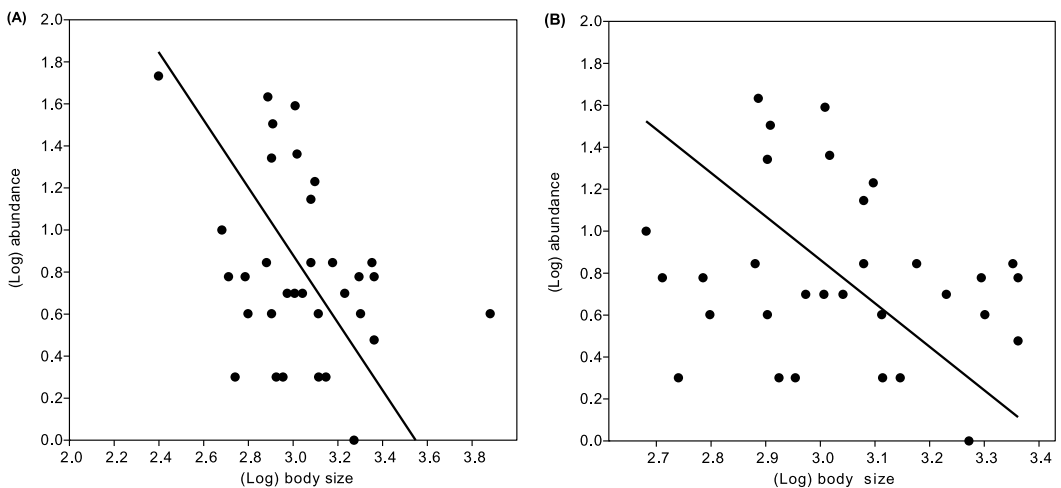


Figure 3. Relationship between (log) snake mean body size and (log) number of recorded individuals. All individuals recorded with the three methods are pooled for this analysis. (A) with the outliers (Typhlopidae and *Python molurus*) in the graph; (B) without the outliers in the graph.

variation. When we removed *Python molurus bivittatus* (an outlier for body size) from the analyses, the body size differences among snake species exhibiting different categories of habit still remained statistically significant (Kruskal-Wallis ANOVA, $\chi^2 = 13.2$, $df = 4$, $P < 0.02$).

Discussion

Do snakes non-randomly partition the habitat resource?

Our null models revealed no non-random niche-partitioning patterns for habitat types by sympatric snakes at our study area, even when the null model analyses were performed by guild. These patterns are apparently consistent with available literature: indeed, through an overall re-analysis of available data on snake communities worldwide, Luiselli (2006b) showed that these reptiles do not usually partition the habitat niche, but the food niche. This general pattern is especially typical of tropical snake assemblages, and has been consistently detected in forest-plantation mosaics of tropical Africa (Luiselli, 2006b, 2008). Thus, apparently, tropical Asian snake assemblages seem to be similar to tropical African snake assemblages in terms of their general organization. Further studies should however extend this finding before our conclusion can be definitely accepted.

In our study case, and contrary to the classical interpretation (Gotelli and Graves, 1996), it is also possible that the observed high overlap in habitat means that (recent) species competition for resources is very high but co-occurring species have not yet partitioned the available resources, because we are looking at human modified ecosystems (forest-plantation mosaic) that have only relatively recently (in evolutionary terms) been disturbed. To fully answer this, however, we would ideally need historical data including pre-/post alteration species composition data which are not available. Phylogenetic data that would provide information on evolutionary trajectories may also be use-

ful to analyze competition versus deep evolutionary ecological divergence (e.g. Cadle and Greene, 1993), but it is unfortunate that no such data are available for all the species forming our study assemblage. In absence of more informative historical data, it is more cautionary to accept the traditional view, i.e. that higher than expected overlap means no competition (Gotelli and Graves, 1996; Gotelli, 2000, 2001). Nonetheless, Steen (2010) and Steen et al. (2012) provided evidence that interspecific interactions influence snake assemblage structure and habitat use. Thus, data coming from both Luiselli (2003, 2006b) and Steen et al. (2007, 2012), suggest that interspecific interaction mechanisms do shape the organization of natural assemblages of snakes to even a greater extent than other studies of resource overlap and partitioning have suggested, especially when dealing with assemblages of species from temperate regions (e.g., Lelièvre et al., 2012).

Concerning the habitat preferences of snakes, our study showed that no species was really an habitat specialist, as all species were more or less able also to inhabit altered forest habitats and plantations. Given the absence of mature forest specialists, we suggest that the snake communities of unaltered mature forests of Bangladesh may be quite different in terms of species composition compared to that studied here.

Are larger species least abundant than smaller species?

The type of relationships between snake size and relative species abundances (= numbers of animals recorded during this study) confirms, although at a marginally significant and poorly predictive level, the general rule of a negative association between population abundance and body size in snakes (Luiselli et al., 2005; Luiselli, 2006a). The same type of negative relationships was also documented in other animal groups (e.g., insects and mammals; see Ulrich, 2001a, 2001b; Harcourt, 2002), and although there has been no consensus on a sin-

gle and comprehensive theory about that relationship (Damuth, 1981), it has been considered a necessary byproduct of the 'energetic equivalence rule' (Cotgreave, 1993; Blackburn and Gaston, 1999). The pattern of a negative relationship between absolute body size and abundance in snakes is also noteworthy because, as ectotherms, most snake species consume relatively little biomass. Hence if prey availability is one factor limiting the abundance of large endothermic carnivores (as supposed by theory; Spencer, 2000), we might in fact not expect the abundance of large snakes to be limited in the same way. However, field data on snakes (e.g. Luiselli et al., 2005; Luiselli, 2006a; this study) revealed similar patterns as those highlighted in endothermic predators as well (Cotgreave, 1993; Blackburn and Gaston, 1999). However, in our study we dealt with several species of snakes which differed considerably each from another in terms of behavior and life-history (Whitaker and Captain, 2007), with probably very different species-specific detectability for researchers. Hence, our data probably are not an exact description, but just a reliable approximation, of the true snake community structure. It is likely that, given the lesser detectability of small and elusive subterranean species (Typhlopidae) compared to larger above-ground active species (i.e. Colubridae, Elapidae and Viperidae), the counts for Typhlopidae were under-evaluated. Thus, it is likely that the negative relationship between population abundance and body size would be strengthened in our studied population if detectability was taken into account.

Were snake body sizes influenced by a species' habits?

Our study confirmed that, as expected, the subterranean snake guild included not only the smaller species, but also those showing the least interspecific variation in terms of body size. This pattern likely depends on environmental constraints, because it is certainly easier for small and earthworm-shaped snakes to move inside burrows and galleries. However, this pat-

tern is also noteworthy in terms of its attributes to community ecology research. Indeed, several theoretical and empirical studies revealed that competitive interactions are more intense when body size differences among sympatric species are negligible (Pianka, 1986). Thus, based on the results presented here, we predict that competition intensity should be higher among species within the subterranean guilds than among species belonging to other guilds. Because, unfortunately there is no available study on the assemblage structure of subterranean tropical snakes, we could not conclude firmly about this issue.

Overall, the tropical Asian snake assemblage studied in this article is consistent with African snake assemblages from comparable habitats (Luiselli et al., 2005; Luiselli, 2008) because of (1) an apparent congruence with expectations from the energetic equivalence rule and (2) the apparent absence of non-random habitat resource partitioning.

Acknowledgements. The project was financially supported by Rudolf G. Arndt, Pomona, New Jersey, USA, The Ori-
anne Society, USA and Eni Environmental Department, Italy. We acknowledge the support of Forest Department of Bangladesh, Integrated Protected Area Co-Management Committee of Lawachara National Park and the authority of Fulbari Tea Estate. We also acknowledge Wahid Islam, Rupa Dutta and Animesh Ghose for their assistance in the field, and Dr Giuliano Milana for his help with drawing the dendrogram. The fieldwork was conducted under the Forest Department of Bangladesh research permit #2M-47/11 given to Centre for Advanced Research in Natural Resources & Management (CARINAM).

References

- Akani, G.C., Barieene, I.F., Capizzi, D., Luiselli, L. (1999): Snake communities of moist rainforest and derived savanna sites of Nigeria: biodiversity patterns and conservation priorities. *Biodiv. Conserv.* **8**: 629-642.
- Akani, G.C., Ebere, N., Franco, D., Eniang, E.A., Petrozzi, F., Politano, E., Luiselli, L. (2013): Correlation between annual activity patterns of venomous snakes and rural people in the Niger Delta, southern Nigeria. *Journal of Venomous Animals and Toxins including Tropical Diseases*, in press.

- Barbault, R. (1971): Les peuplements d'ophidiens des savannes de Lamto, Cote d'Ivoire. Ann. Univ. Abidjan Ser. E Ecol. **4**: 133-194.
- Blackburn, T.M., Gaston, K.J. (1999): The relationship between animal abundance and body size in natural animal assemblages. J. Anim. Ecol. **62**: 519-528.
- Bowers, M.A., Brown, J.H. (1982): Body size and coexistence in desert rodents: chance or community structure? Ecology **63**: 391-400.
- Bowman, J., Forbes, G., Dilworth, T. (2000a): The spatial scale of variability in small-mammal populations. Ecology **23**: 328-334.
- Bowman, J., Forbes, G., Dilworth, T. (2000b): Landscape context and small-mammal abundance in a managed forest. For. Ecol. Manag. **140**: 253-259.
- Bowman, J., Forbes, G., Dilworth, T. (2001): The spatial scale component of variation in small-mammal abundance measured at three scales. Can. J. Zool. **79**: 137-144.
- Bradley, R.A., Bradley, D.W. (1985): Do non-random patterns of species in niche space imply competition? Oikos **45**: 443-445.
- Cadle, J.E., Greene, H.W. (1993): Phylogenetic patterns, biogeography and the ecological structure of Neotropical snake assemblages. In: Species Diversity in Ecological Communities. Historical and Geographical Perspectives, p. 281-293. Ricklefs, R.E., Schluter, D., Eds, University of Chicago Press, Chicago.
- Caro, T.M., Stoner, C.J. (2003): The potential for interspecific competition among African carnivores. Biol. Cons. **110**: 67-75.
- Cotgreave, P. (1993): The relationship between body size and population abundance in animals. Trends Ecol. Evol. **8**: 244-248.
- Da Silva, J. (1993): The snakes from Samuel Hydroelectric Power Plant and vicinity, Rondonia, Brazil. Herp. Nat. Hist. **1**: 37-86.
- Damuth, J. (1981): Population density and body size in mammals. Nature **290**: 699-700.
- Das, I. (2010): A Field Guide to the Reptiles of the South-east Asia. New Holland Publishers, Cape Town.
- Dickman, C.R. (1988): Body size, prey size, and community structure in insectivorous mammals. Ecology **69**: 569-580.
- Eniang, E.A., Akani, G.C., Rugiero, L., Vignoli, L., Luiselli, L. (2013): Ecological data of Nigerian *Crotaphopeltis hotamboeia* (Colubridae) populations. Herpetol. J. **23**: 5-9.
- Field, J. (1992): Guild structure in solitary spider-hunting wasps (Hymenoptera: Pompilidae) compared with null model predictions. Ecol. Entomol. **17**: 198-208.
- Franca, F.G.R., Mesquita, D.O., Nogueira, C.C., Araújo, A.F.B. (2008): Phylogeny and ecology determine morphological structure in a snake assemblage in the Central Brazilian Cerrado. Copeia **2008**: 23-38.
- Frigens, M.H., Brown, J.H. (2005): Niche partitioning in the cestode communities of two elasmobranchs. Oikos **108**: 76-84.
- Gotelli, N.J. (2000): Null model analysis of species co-occurrence patterns. Ecology **81**: 2606-2621.
- Gotelli, N.J. (2001): Research frontiers in null model analysis. Global Ecology and Biogeography Letters **10**: 337-343.
- Gotelli, N.J., Entsminger, G.L. (2011): EcoSim: null modeling software for ecology, v.7.0. Acquired Intelligence Inc. and Keesey-Bear, Jericho. <http://garyentsminger.com/ecosim/index.htm>
- Gotelli, N.J., Graves, G.R. (1996): Null Models in Ecology. Smithsonian Institution Press, Washington, D.C.
- Guyer, C., Donnelly, M.A. (1990): Length-mass relationships among an assemblage of tropical snakes in Costa Rica. Journal of Tropical Ecology **6**: 65-76.
- Halliday, T., Adler, K. (2002): The New Encyclopedia of Reptiles and Amphibians. Oxford University Press, Oxford.
- Harcourt, A.H. (2002): Rarity, speciation and extinction in primates. J. Biogeogr. **29**: 445-456.
- Kadowaki, S. (1996): Ecology of a Japanese snake community: resource use patterns of the three sympatric snakes, *Rhabdophis tigrinus*, *Elaphe quadrivirgata*, and *Agkistrodon b. blomhoffii*. Bull. Tsukuba Univ. **12**: 77-148.
- Karns, D.R., Murphy, J.C., Voris, H.K. (2010): Semi-aquatic snake communities of the central plain region of Thailand. Trop. Nat. Hist. **10**: 1-25.
- Karunarathna, D.M.S., Amarasinghe, T.A.A. (2011): Reptile diversity of a fragmented lowland rain forest patch in Kukulugala, Ratnapura district, Sri Lanka. Taprobonica **2**: 2.
- Laurent, E.J., Kingsbury, B.A. (2003): Habitat separation among three species of water snakes in northwestern Kentucky. J. Herp. **37**: 229-235.
- Lelièvre, H., Legagneux, P., Blouin-Demers, G., Bonnet, X., Lourdaï, O. (2012): Trophic niche overlap in two syntopic colubrid snakes (*Hierophis viridiflavus* and *Zamenis longissimus*) with contrasted lifestyles. Amphibia-Reptilia **33**: 37-44.
- Luiselli, L. (2006a): Testing hypotheses on the ecological patterns of rarity using a novel model of study: snake communities worldwide. Web Ecol. **6**: 44-58.
- Luiselli, L. (2006b): Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos **114**: 193-211.
- Luiselli, L. (2006c): Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource. J. Trop. Ecol. **22**: 91-100.
- Luiselli, L. (2006d): Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). J. Trop. Ecol. **22**: 555-564.
- Luiselli, L. (2008): Community ecology of African reptiles: Historical perspective and a meta-analysis using null models. Afr. J. Ecol. **46**: 384-394.
- Luiselli, L., Akani, G.C., Capizzi, D. (1998): Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. J. Zool., Lond. **246**: 125-133.
- Luiselli, L., Akani, G.C., Rugiero, L., Politano, E. (2005): Relationships between body size, population abundance and niche characteristics in the communities of snakes from three habitats in southern Nigeria. J. Zool., Lond. **265**: 207-213.

- Mushinsky, H.R., Hebrard, J.J. (1977a): Food partitioning by five species of water snakes in Louisiana. *Herpetologica* **33**: 162-166.
- Mushinsky, H.R., Hebrard, J.J. (1977b): The use of time by sympatric water snakes. *Can. J. Zool.* **55**: 1545-1550.
- Muzaffar, S.B., Islam, M.A., Feeroz, M.M., Kabir, M., Begum, S., Hasan, M.K. (2007): Habitat characteristics of the endangered Hoolock Gibbons (*Hoolock hoolock*) of Bangladesh: the role of plant species richness. *Biotropica* **39**: 539-545.
- Nature Conservation Management (NACOM) (2003): Secondary Data Collection for Pilot Protected Areas: Lawachara National Park. Co-Management of Tropical Forest Resources of Bangladesh, USAID, Dhaka, pp. 57.
- Orlov, N.L. (1995): Rare snakes of the mountainous forests of northern Indochina. *Russ. J. Herp.* **2**: 179-183.
- Orlov, N.L. (1997): Viperid snakes (Viperidae Bonaparte, 1840) of Tam-Dao mountain ridge (Vinh-Phu and Bac-Thai Provinces, Vietnam). *Russ. J. Herp.* **4**: 64-74.
- Pianka, E.R. (1986): *The Ecology and Natural History of Desert Lizards*. Princeton University Press, Princeton.
- Poulin, R. (2006): *Evolutionary Ecology of Parasites*. Princeton University Press, Princeton.
- Ricklefs, R.E. (2008): Disintegration of the ecological community. *Am. Nat.* **172**: 741-750.
- Rohde, K. (1992): Latitudinal gradients in species diversity: the search for the primary cause. *Oikos* **65**: 514-527.
- Rooijen, J.V. (2009): Estimating the snake species richness of the Santubong Peninsula (Borneo) in two different ways. *Contr. Zool.* **78**: 141-147.
- Schoener, T.W. (1974): Resource partitioning in ecological communities. *Science* **185**: 27-39.
- Solida, L., Celant, A., Luiselli, L., Grasso, D., Mori, A., Fanfani, A. (2011): Competition for foraging resources and coexistence of two syntopic species of *Messor* harvester ants in Mediterranean grassland. *Ecol. Entomol.* **36**: 409-416.
- Spencer, M. (2000): Are predators rare? *Oikos* **89**: 115-122.
- Steen, D.A. (2010): Snakes in the grass: secretive natural histories defy both conventional and progressive statistics. *Herpetol. Conserv. Biol.* **5**: 183-188.
- Steen, D.A., McClure, C.J.W., Brock, J.C., Rudolph, D.C., Pierce, J.B., Lee, J.R., Humphries, W.J., Gregory, B.B., Sutton, W.B., Smith, L.L., Baxley, D.L., Stevenson, D.J., Guyer, C. (2012): Landscape-level influences of terrestrial snake occupancy within the southeastern United States. *Ecol. Applic.* **22**: 1084-1097.
- Steen, D.A., Smith, L.L., Conner, L.M., Brock, J.C., Hoss, S.K. (2007): Habitat use of sympatric rattlesnake species within the Gulf Coastal Plain. *J. Wildl. Manag.* **71**: 759-764.
- Terborgh, J., Robinson, S.K., Parker, T.A., Munn, C.A., Pierpont, N. (1990): Structure and organization of an Amazonian forest bird community. *Ecol. Monogr.* **60**: 213-238.
- Ulrich, W. (2001a): Ecological characteristics of rare species: the case of parasitic Hymenoptera. *Pol. J. Ecol.* **49**: 379-389.
- Ulrich, W. (2001b): Relative abundance distributions of species: the need to have a new look at them. *Pol. J. Ecol.* **49**: 391-405.
- Vignoli, L., Luiselli, L. (2012): Dietary relationships among coexisting anuran amphibians: a worldwide quantitative review. *Oecologia* **169**: 499-509.
- Whitaker, R., Captain, A. (2007): *Snakes of India: the Field Guide*. Draco Books, New Delhi.
- Winemiller, K.O., Pianka, E.R. (1990): Organization in natural assemblages of desert lizards and tropical fishes. *Ecol. Monogr.* **60**: 27-55.

Submitted: October 13, 2012. Final revision received: December 19, 2012. Accepted: December 19, 2012.

Associated Editor: Sylvain Ursenbacher.