

Monsoon does matter: annual activity patterns in a snake assemblage from Bangladesh

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During the last decades annual activity patterns of temperate snake species have received considerably more attention than those of tropical snakes. In this study, we document the monthly activity patterns of a species-rich assemblage of snakes from a tropical forest-plantation mosaic in Bangladesh based on specimens collected by a systematic road kill survey for 14 months, and relate them to the climatic characteristics of the study area with special reference to monsoon regimes. We recorded 503 Dead-On-Road (DOR) snakes, belonging to 30 different species, with a mean DOR/km rate of 0.247. Overall, snake activity was uneven throughout the year, being particularly intense during July, August and October, and significantly reduced in December, January and February. Five out of nine species with considerably robust sample sizes showed consistently uneven monthly activity patterns. Monsoon seasonality deeply influenced the phenology of several Asian-tropical snakes, with some species being active especially at the middle or end of the monsoon period while others are active throughout the monsoon period.

Keywords: Asia, Bangladesh, monsoon, road-kills, seasonal activity, Serpentes

INTRODUCTION

A considerable body of evidence has shown that temperate zone snakes may exhibit two distinct patterns of species-specific annual activity, i.e. a unimodal pattern with a single peak between late spring and late summer, or a bimodal pattern with peaks in spring (generally confined to the mating season) and autumn (coinciding with the emergence of juveniles, for a review see Gibbons & Semlitsch, 1989). The activity patterns of tropical snakes have received considerably less attention, although it has been hypothesized that they may exhibit a polymodal activity pattern in response to wet-dry cycles (Gibbons & Semlitsch, 1989). Studies on African tropical snakes have shown a strong relationship between rainfall and activity, with peaks occurring at the onset of the wet seasons and continuing to increase throughout wet months (e.g., Akani et al., 2002). This general pattern has been confirmed in both mainly savannah species, for instance *Naja nigricollis* (Luiselli, 2001) and *Crotaphopeltis hotamboeia* (Eniang et al., 2013), and mainly forest-dwelling species such as *Naja melanoleuca* (Luiselli, 2001), *Bitis gabonica* and *Bitis nasicornis* (Luiselli, 2006; Akani et al., 2013). Moreover, the seasonal incidence of humans getting bitten by snakes (a proxy of snake activity intensity) showed that

in agricultural landscapes in Bangladesh and African savannah, snake bites occur more frequently in the wet season (pattern observed in Bangladesh, Mali, Burkina Faso, Nigeria, Ivory Coast, Cameroon, Ghana and Benin; see Chippaux, 2006; Rahman et al., 2010). Whilst there are studies on seasonal activity patterns on an entire tropical snake assemblage from the Neotropics (e.g., Marques et al., 2001), to the best of our knowledge, no such studies have been conducted in tropical Asia. Such information could be crucial to document not only the

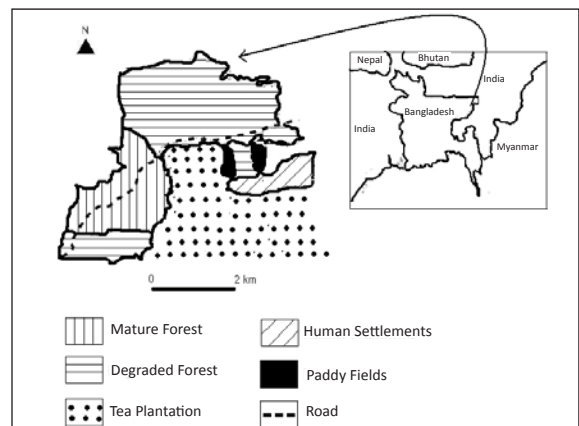


Fig. 1. Map of the study area, showing the position of the road surveyed for DOR snakes during this study.

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main assemblage pattern (for instance, higher numbers of snakes active in wet season), but also the degree of variation which occurs across species inhabiting the same study site. In this study, we document the monthly activity patterns of a species-rich assemblage of snakes from a tropical forest-plantation mosaic in Bangladesh. More specifically, we address the following key questions: (i) Are the monthly activity patterns of snakes polymodal, unimodal, bimodal or even variable across months? (ii) Are there any relationships between rainfall, temperature and activity intensity of snakes in the study area?

MATERIALS AND METHODS

Study area

Field work was carried out in Lawachara National Park (LNP) and its adjacent areas (Fig. 1). LNP is situated in Maulavibazar District in the north-east of Bangladesh and is characterized by an undulating landscape, with slopes and hillocks at an average altitude range of roughly 10–80 m a.s.l. (Nature Conservation Management, 2003). LNP is a 1250-ha mixed-evergreen forest-most of whose original forest cover has been altered or substantially removed, by rotation, with only some small, remnant patches of primary forest left inside the park (Nature Conservation Management, 2003). In between the forest habitat there are shrubs, bushes, bamboo plantations and open patches caused by human disturbance.

The forest is surrounded by human modified habitats on all sides, such as tea plantations, with patches of agricultural lands, human settlements, modified vegetation for betel leaf (*Piper betle*), native bamboo plantations (*Bambusa tulda*, *B. polymorpha*, *B. longispiculata*, etc.) and monoculture forest plantations (e.g., *Tectona grandis*, *Aquilaria crassna*, *Eucalyptus* sp., *Acacia* sp., etc). Numerous streams run through the forest and the tea plantations, and there are several man-made

Table 1. Summarized data on the monthly number of field days and relative index of sampling effort used to build the monthly expected number of DOR snakes. Note that the values reported for July and August refer to the pooled number of field days for July 2011 and 2012, and August 2011 and 2012. For more details, see the text.

| | Number of days in the field | Relative monthly sampling effort index |
|-------|--------------------------------|---|
| Jan | 18 | 0.061 |
| Feb | 18 | 0.061 |
| Mar | 24 | 0.082 |
| Apr | 25 | 0.085 |
| May | 16 | 0.054 |
| Jun | 23 | 0.078 |
| Jul | 30 | 0.102 |
| Aug | 50 | 0.17 |
| Sep | 15 | 0.051 |
| Oct | 25 | 0.085 |
| Nov | 27 | 0.092 |
| Dec | 23 | 0.078 |
| TOTAL | 294 | |

perennial and seasonally inundated ponds in the tea plantation and the surrounding villages. For a detailed description of different habitat types see Rahman et al. (2013). LNP falls within the monsoon climatic zone, with average annual rainfall of ~3000 mm, of which 80% falls from June to September and July–August is the peak of the monsoon. October to March is dry with the first rainfall usually arriving in April. The annual mean diurnal temperature ranges from 27°C (June–September) to 16°C (January).

Temperature and rainfall data were collected from Sreemongol weather station, Bangladesh Meteorological Department, located 8 km from the study site.

Protocol

Annual patterns of snake activity were assessed by Dead-on-Road (DOR) surveys. We assumed that there should be a linear relationship between intensity of above-ground activity in snakes and their risk of being killed along the road (Bonnet et al., 1999; Meek, 2009). However, with regard to this, it should be mentioned that this assumption may have some limitations. Indeed, DOR numbers certainly indicate the specimens which are more often found (and killed) on an open surface, i.e. on the roads, but nearly nothing can be said concerning other activities (mating, basking, etc.).

DOR specimens were collected along a 7 km segment of the Sreemongol-Komgolgonj road which dissects LNP. Half of the road passes along moderately dense forest habitat and the remaining 3.5 km separates human-modified habitat, with tea plantations on one side and highly degraded plantation forest in the other. The survey was conducted by walking daily (almost every day) during the survey days, from July 11, 2011 to August 31, 2012, totalling 2058 km throughout 294 road survey days. Although we realize that our study lacks spatial replicates and that sampling in at least two spatially independent locations might support the robustness of the results, we were logistically impeded to perform this type of study.

Surveys were conducted from 1600–1900 hours during spring and summer months (April to August) and from 1300–1600 hours during the autumn and winter months (September to March) by one surveyor walking slowly on the road. Snakes were identified to species level following the taxonomic keys provided by Whitaker and Captain (2004) and Das (2010). 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 level all DOR specimens potentially belonging either to *Ramphotyphlops braminus* or to *Typhlops* spp. Therefore, for analysis, we classified them as Typhlopidae. Once inspected, all DORs were moved off the road to avoid double counts of the same individuals in different days.

Statistical analyses

To evaluate whether each of the species were observed with a similar frequency of occurrence throughout the various months, the records were grouped into monthly intervals (from the first to the last day of each month). We then determined the relative sampling effort per

month interval by dividing the number of days spent in the field in each month by the total number of days in the field during the entire research period (Table 1). Using a null hypothesis of equal distribution frequency among months, we subsequently generated the expected number of DOR snakes each month by multiplying the total number of snakes found during the study by the relative sampling effort for each monthly interval. Finally, observed and expected values were compared

by a χ^2 test. For analyses at the species level, and based on the histogram distribution of the records, we only considered those species which were recorded at least 11 times during the course of our study (i.e. on average at least once per month during the study period, in order to exclude those species occurring too scarcely in the sample). A logistic regression (Quasi-Newton method, with 50 as maximum number of iterations and convergence criterion at 0.0001) was applied to analyze

Table 2. Summary of the DOR snake records throughout the study period. Note that from this table we excluded the snake species which are known to occur in this study area but that were never recorded as DOR (e.g., *Python molurus bivittatus*; see Rahman et al., 2013). Overall, four species were never recorded as DOR but were observed in the study area (Rahman et al., 2013). Unidentified specimens were not considered in the analyses.

| | July | Aug | Sep | Oct | Nov | Dec | Jan | Feb | Mar | Apr | May | Jun | July | Aug | Total |
|---|------|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|-----|------|-----|-------|
| TYPHLOPHIDAE | | | | | | | | | | | | | | | 126 |
| <i>Ramphotyphlops</i> <i>braminus</i> and <i>Typhlops</i> <i>spp.</i> | 5 | 16 | 12 | 19 | 4 | 1 | 0 | 0 | 6 | 16 | 6 | 0 | 18 | 23 | 126 |
| COLUBRIDAE | | | | | | | | | | | | | | | 316 |
| <i>Ahaetulla prasina</i> | 0 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 2 | 1 | 0 | 1 | 0 | 0 | 7 |
| <i>Amphiesma stolatum</i> | 2 | 6 | 0 | 0 | 2 | 0 | 0 | 1 | 1 | 1 | 0 | 1 | 1 | 6 | 21 |
| <i>Blythia reticulata</i> | 2 | 1 | 0 | 0 | 4 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 0 | 9 |
| <i>Boiga gokool</i> | 1 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 1 | 2 | 1 | 0 | 0 | 1 | 8 |
| <i>Boiga ochracea</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Boiga siamensis</i> | 0 | 0 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 2 | 1 | 1 | 0 | 0 | 8 |
| <i>Chrysopelea ornata</i> | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| <i>Coelognathus radiatus</i> | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 | 0 | 0 | 0 | 0 | 3 |
| <i>Dendrelaphis pictus</i> | 2 | 0 | 0 | 3 | 5 | 2 | 0 | 0 | 7 | 7 | 4 | 2 | 1 | 5 | 38 |
| <i>Lycodon aulicus</i> | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 1 | 0 | 2 | 1 | 0 | 2 | 7 |
| <i>Lycodon jara</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 1 | 0 | 0 | 0 | 3 |
| <i>Lycodon zawi</i> | 0 | 0 | 0 | 6 | 3 | 3 | 0 | 0 | 2 | 1 | 1 | 0 | 0 | 1 | 17 |
| <i>Oligodon albocinctus</i> | 2 | 2 | 0 | 2 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 8 |
| <i>Oligodon cyclurus</i> | 1 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 3 |
| <i>Oligodon dorsalis</i> | 1 | 3 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 | 0 | 1 | 0 | 9 |
| <i>Oreocryptophis</i> <i>porphyracea</i> | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 2 |
| <i>Pareas monticola</i> | 0 | 3 | 0 | 1 | 3 | 1 | 0 | 0 | 1 | 4 | 2 | 0 | 3 | 3 | 21 |
| <i>Ptyas mucosa</i> | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 3 |
| <i>Psammodynastes</i> <i>pulverulentus</i> | 4 | 10 | 6 | 13 | 3 | 0 | 0 | 0 | 1 | 3 | 1 | 4 | 5 | 7 | 57 |
| <i>Rhabdophis</i> <i>himalayanus</i> | 2 | 2 | 1 | 4 | 4 | 2 | 0 | 0 | 2 | 4 | 3 | 6 | 3 | 1 | 34 |
| <i>Rhabdophis</i> <i>subminiatus</i> | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 4 | 2 | 3 | 0 | 10 |
| <i>Sibynophis collaris</i> | 0 | 3 | 0 | 0 | 2 | 1 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 9 |
| <i>Xenochrophis piscator</i> | 0 | 1 | 2 | 2 | 1 | 0 | 1 | 0 | 2 | 4 | 9 | 7 | 5 | 2 | 36 |
| ELAPIDAE | | | | | | | | | | | | | | | 14 |
| <i>Sinomicrurus</i> <i>maclellandi</i> | 0 | 1 | 0 | 2 | 0 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 4 |
| <i>Bungarus fasciatus</i> | 1 | 1 | 1 | 1 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 5 |
| <i>Bungarus niger</i> | 0 | 0 | 1 | 1 | 0 | 0 | 0 | 0 | 0 | 1 | 0 | 0 | 0 | 1 | 4 |
| <i>Naja kaouthia</i> | 0 | 0 | 1 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 0 | 1 |
| VIPERIDAE | | | | | | | | | | | | | | | 25 |
| <i>Cryptelytrops</i> <i>albolabris</i> | 0 | 3 | 2 | 6 | 5 | 0 | 0 | 0 | 1 | 3 | 0 | 2 | 1 | 2 | 25 |
| Unidentified | 2 | 2 | 3 | 5 | 3 | 4 | 0 | 0 | 1 | 1 | 1 | 0 | 0 | 0 | 22 |
| TOTAL | 26 | 56 | 33 | 70 | 41 | 17 | 2 | 4 | 33 | 56 | 41 | 27 | 42 | 55 | 503 |

whether the sample size for each species influenced the probability of a species to exhibit an uneven monthly activity pattern (score 1=uneven pattern; score 0=even pattern). Statistical analyses were performed with Statistica v.11.0 software. Non-normal variables were log-transformed before applying parametric tests.

Shortcomings of this study

We wish to stress that our data might have been partially affected by the scavenging activity of golden jackals (*Canis aureus*) which often patrol roads at night to feed on road-kill animals, including snakes. This scavenging activity may have resulted in several snakes being removed from the road at night. Also, the national park visitors and the local residents were occasionally observed removing specimens from the road. Hence, it is possible that several snakes had already been eaten or removed from the road when the surveys were undertaken, thus resulting in a diminished sample size. Furthermore, the probability of crossing road by snakes can vary from species to species (Andrews & Gibbons, 2005), and thus several of the species may have been underrepresented in our sample.

RESULTS

Overall, we recorded 503 DORs, belonging to 30 different species, with a mean of 0.247 DOR/km (Table 2). For the analyses, however, we considered 29 ‘species’ categories, given that Typhlopidae included two species (see Materials and Methods). Unidentified specimens, although reported in Table 2, were not included in the analyses. The observed monthly number of all the species recorded deviated significantly from an even distribution ($\chi^2=112.3$; $df=11$; $p<0.0001$), thus showing that snake activity was skewed throughout the year, being particularly intense in July, August and October, whereas being low in December, January and February (Fig. 2A). During the rest of the year, we did not observe any significant differences between the monthly observed and expected DORs. In five out of nine species with sufficient sample size to conduct robust analyses, there were uneven monthly activity patterns (Fig. 2B–F). An uneven monthly activity pattern occurred in (i) Typhlopidae ($\chi^2=76.3$; $df=11$; $p<0.0001$), with activity peaks in July and August, and reduced activity in November to February (Fig. 2B); (ii) *Amphiesma stolatum* ($\chi^2=28.3$; $df=11$; $p<0.005$), with an activity peak

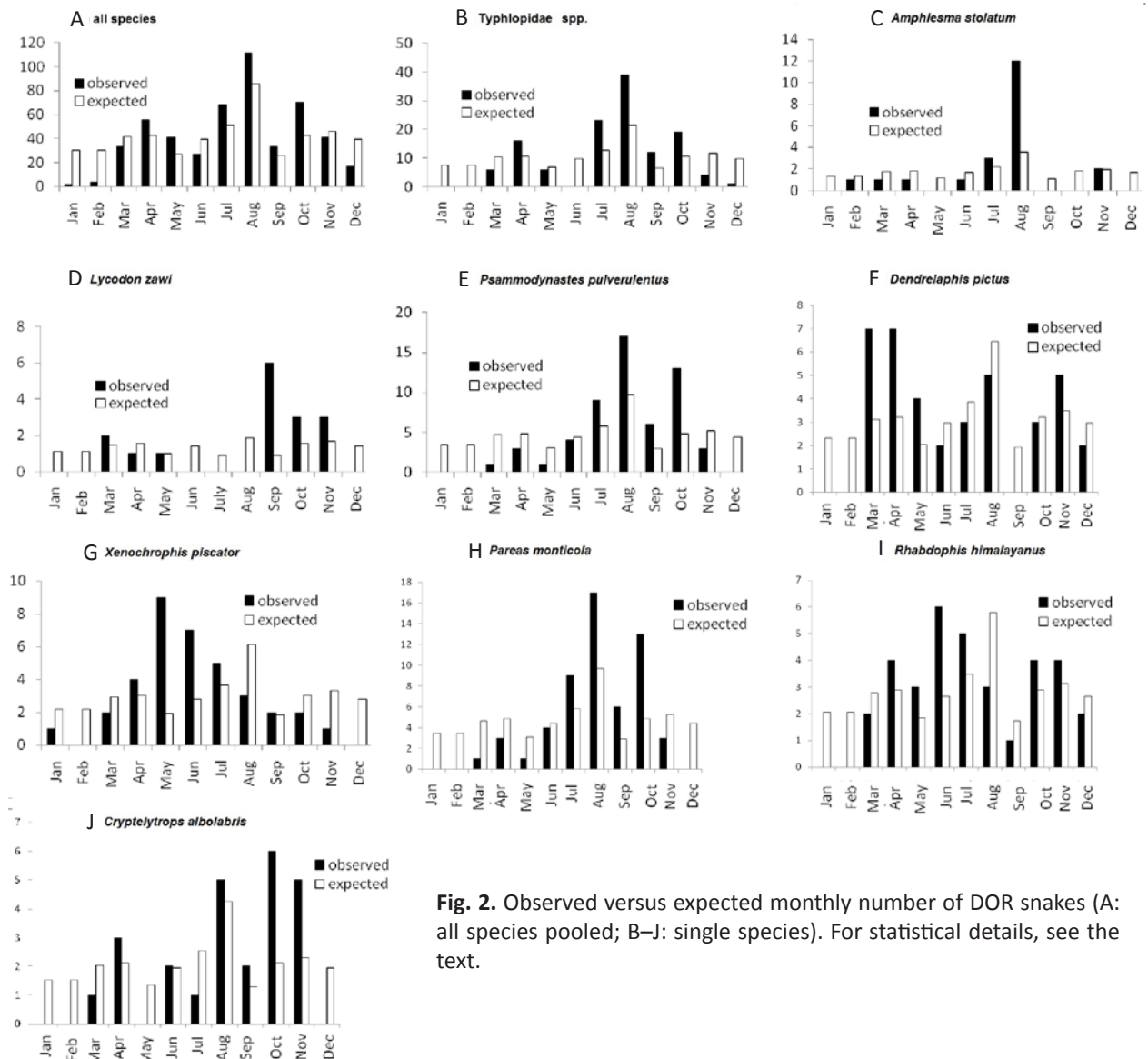


Fig. 2. Observed versus expected monthly number of DOR snakes (A: all species pooled; B–J: single species). For statistical details, see the text.

in August (Fig. 2C); (iii) *Lycodon zawi* ($\chi^2=38.4$; $df=11$; $p<0.0001$), with activity peak in September (Fig. 2D); (iv) *Psammodynastes pulverulentus* ($\chi^2=41.7$; $df=11$; $p<0.0001$), with a prolonged activity peak in July to October and reduced activity in December to March (Fig. 2E); (v) *Xenochrophis piscator* ($\chi^2=42.3$; $df=11$; $p<0.0001$), with an activity peak in May to June and reduced activity in August, and in November to February (Fig. 2F). Interestingly, Typhlopidae and *A. stolatum* were active mainly during the central phase of the monsoon, *L. zawi* during the final phase and *P. pulverulentus* during the whole of the monsoon period. When relating the activity patterns to monsoon seasonality (June, July, August and September), the activity pattern of four out of the five species occurred during the monsoon, the only exception being the semi-aquatic *X. piscator*.

Conversely, monthly activity was even in *Dendrelaphis pictus* ($\chi^2=19.5$; $df=11$; $p=0.054$; Fig. 2G), *Pareas monticola* ($\chi^2=12.2$; $df=11$; $p=0.349$; Fig. 2H), *Rhabdophis himalayanus* ($\chi^2=12.9$; $df=11$; $p=0.299$; Fig. 2I), and *Cryptelytrops albolabris* ($\chi^2=17.6$; $df=11$; $p=0.061$; Fig. 2J). A logistic regression analysis revealed that species' sample size did not influence the probability of uncovering an uneven monthly activity pattern in that species ($-2\log$ (likelihood) of the model=11.062, $-2\log$ (likelihood) of the intercept=12.36; $\chi^2=1.30$; $df=1$; $p=0.254$), that is: even activity patterns were not due to an insufficient sample size but were real patterns.

The (log) mean monthly temperature positively influenced the (log) monthly number of DORs (considering all species pooled) ($r^2=0.530$; $n=12$; $p<0.001$). Moreover, the (log) mean monthly rainfall was significantly positively correlated to the (log) number of monthly DORs ($r=0.698$; $r^2=0.487$; $n=12$, $p<0.03$).

DISCUSSION

Road mortalities may provide insights into activity for some species which are highly active above-ground (e.g., Bonnet et al., 1999), but perhaps not in others. Due to this, the difficulty for researchers is deciding where they do and where they do not. Sentinel predators, for instance, may have very low activity patterns during certain months and move greater distances during others - but both types of movement can be classed as active. A typical example of this spacing pattern behaviour has been observed, for instance, in the tropical viper *Bitis gabonica*, which shows very limited movements during most of its active cycle (Angelici et al., 2000). However, that can disperse considerably during the mating period (especially the males), with a higher risk of road mortality during these unusually longer displacements as a consequence (Akani et al., 2002). Thus, it is likely that in our study there are both highly-active species (Bonnet et al., 1999) and sentinel ambush predators (Angelici et al., 2000). Unfortunately, the current knowledge of the ecology and life-history strategies of the snake species in Bangladesh is so scarce that we cannot anticipate which of the studied species conform with the former pattern and which to the latter pattern. Certainly, it is likely that *Python molurus* can mirror the sentinel ambushing

pattern. *Python molurus* were often reported to cross roads at nights in our study site, and their large size probably led the vehicle drivers to avoid running over them, which would explain why no DOR specimens of *P. molurus* were found during our study period. Highly active species, such as, *P. korros*, are one of the most commonly found species in the study area (Rahman et al., 2013), however they were rarely found dead on the road. The most likely explanation could be that the probability of snake crossing the road could vary from species to species, with *P. korros* probably avoiding this.

All the species recorded in the present study showed a strong reduction in activity from December to February, i.e. during the colder period of the year when the mean monthly temperature ranges between 16 and 18°C. Some species, such as for instance Typhlopidae spp., *Lycodon zawi* and *Psammodynastes pulverulentus*, were in fact not observed during the colder part of the year. The effect of ambient temperatures on snake activity was strongly supported by the significant association between snake activity and mean monthly temperatures, as was also true for rainfall. Indeed, if we exclude the significant reduction of snake activity during the coldest months of the year, three major activity patterns, two of them directly linked to rainfall patterns, were observed: (i) species displaying an even activity across the year; (ii) species with a single peak of activity coinciding with the monsoon (June to September); and (iii) species with a single peak of activity, well distinct from the monsoon phase.

Prey abundance and availability is probably one of the main factors affecting the snakes' activity patterns (Marques et al., 2001). With regards to *Amphiesma stolatum*, observations from Tetulia, Panchagarh in north-west Bangladesh indicate that they are very active in June-July and many of the road killed *A. stolatum* encountered were gravid (SMAR, unpublished information). Frogs are one of most important prey resources for the majority of the snake species in our study (e.g., Das, 2010). Therefore the high activity of frog-eating snakes such as *Amphiesma stolatum* during the monsoon is likely attributable to an increase in both the number and availability of frogs. Most of the temporal ponds and streams in our study site dry out completely by the end of December and remain dry until the first rains of the monsoon. Therefore, frogs are rarely active during the drier parts of the year. However, some amphibians such as toads of the genus *Duttaphrynus* are seen throughout the year, and these amphibians most likely substitute an important prey resource for *Rhabdophis subminiatus* (SCR, unpublished observations), and most likely explains why this species did not display a monsoon-related seasonal activity pattern.

The activity peaks of Typhlopidae occurred in July and August, during the peak of the monsoon. However, the increased activity during the monsoon was most likely not caused by increased prey availability. Typhlopidae are fossorial and during the wettest part of the year their underground shelters often become temporarily inundated by heavy rains forcing the snakes above ground.

Another important factor affecting temporal variation in snake activity had frequently been linked to reproduction (e.g., Gibbons & Semlitsch, 1989; Bonnet et al., 1999; Akani et al., 2002), when males become particularly active in search of receptive females, and females to find suitable sites for oviposition (e.g., Madsen, 1984, 1987; Gibbons & Semlitsch, 1989). In our study site, we observed a bimodal pattern of reproduction in: i) some oviparous snakes laying eggs during the dry season (December–March) and newborns emerging in the early monsoon (e.g., *Xenochrophis piscator*), and ii) other oviparous snakes laying eggs in the monsoon and newborns emerging during the late monsoon (*Naja kaouthia*, *Lycodon zawi*, *Rhabdophis himalayanus* and *Dendrelaphis pictus*, SCR, unpublished observations). In the semi-aquatic (*Xenochrophis piscator*), the peaks of observation were recorded prior to the onset of the monsoon, which can most likely be explained by the reproductive cycle: *Xenochrophis piscator* breeds during December–March (SCR, personal observation; Whitaker & Captain, 2004) and large numbers of hatchlings were seen during the early monsoon.

We suggest that more detailed long term studies must be undertaken in order to gain a more rigorous understanding of the annual activity pattern of tropical snakes in this region. However, our study provided firm evidence that (i) monsoon seasonality deeply influences the phenology of several Asian-tropical snakes, and that (ii) temperature and rainfall regimes due to monsoons influence snake activity patterns similar to those exerted by the onset of the rainy season in other tropical regions (for instance in West Africa and southeastern Brazil, see Akani et al., 2002, 2013; Marques et al., 2001).

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REFERENCES

- Akani, G.C., Ebere, N., Franco, D., Eniang, E.A., et al. (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* 19, 1–8.
- Akani, G.C., Eyo, E., Odegbune, E., Eniang, E.A. & Luiselli, L. (2002). Ecological patterns of anthropogenic mortality of suburban snakes in an African tropical region. *Israel Journal of Zoology* 48, 1–11.
- Angelici, F.M., Effah, C., Inyang, M.A. & Luiselli, L. (2000). A preliminary radiotracking study of movements, activity patterns and habitat use of free-ranging Gaboon vipers, *Bitis gabonica*. *Revue d'Ecologie (Terre et Vie)* 55, 45–55.
- Andrews, K.M. & Gibbons, J.W. (2005). How do highways influence snake movement? Behavioral responses to roads and vehicles. *Copeia* 2005, 772–782.
- Bonnet, X., Naulleau, G. & Shine, R. (1999). The dangers of leaving home: dispersal and mortality in snakes. *Biological Conservation* 89, 39–50.
- Chippaux, J.-P. (2006). *Snake Venoms and Envenomations*. Krieger Publishing Company, Malabar, FL.
- Das, I. (2010). *A Field Guide to the Reptiles of Southeast Asia*. New Holland Publishers, Cape Town.
- Eniang, E.A., Akani, G.C., Rugiero, L., Vignoli, L. & Luiselli, L. (2013). Ecological data of Nigerian *Crotaphopeltis hotamboeia* (Colubridae) populations. *Herpetological Journal* 23, 5–9.
- Gibbons, J.W. & Semlitsch, R.D. (1989). Activity patterns. In: *Snakes, ecology and evolutionary biology*, pp. 396–421. Seigel, R.A., Collins, J.T., Novak, S.S. (eds). MacMillan, New York.
- Luiselli, L. (2001). The ghost of a recent invasion in the reduced feeding rates of spitting cobras during the dry season in a rainforest region of tropical Africa? *Acta Oecologica* 22, 311–314.
- Luiselli, L. (2006). Site occupancy and density of sympatric Gaboon viper (*Bitis gabonica*) and nose-horned viper (*Bitis nasicornis*). *Journal of Tropical Ecology* 22, 555–564.
- Madsen, T. (1984). Movements, home range size and habitat use of radio-tracked grass snakes (*Natrix natrix*) in southern Sweden. *Copeia* 1984, 707–713.
- Madsen, T. (1987). Cost of reproduction and female life-history tactics in a population of grass snakes, *Natrix natrix*, in southern Sweden. *Oikos* 49, 129–132.
- Marques, O.A.V., Eterovic, A. & Whaldener, E. (2001). Seasonal activity of snakes in the Atlantic forest in southeastern Brazil. *Amphibia-Reptilia* 22, 103–111.
- Meek, R. (2009). Patterns of reptile road-kills in the Vendée region of western France. *Herpetological Journal* 19, 135–142.
- Nature Conservation Management. (2003). *Secondary Data Collection for Pilot Protected Areas: Lawachara National Park*. Co-Management of Tropical Forest Resources of Bangladesh, USAID, Dhaka, pp. 57.
- Rahman, R., Faiz, M.A., Selim, S., Rahman, B. & Basher, A. (2010). Annual incidence of snake bite in rural Bangladesh. *PLoS Neglected Tropical Diseases* 4, e860.
- Rahman, S.C., Rashid, S.M.A., Das, K., Luiselli, L. (2013). Composition and structure of a snake assemblage in an altered tropical forest-plantation mosaic in Bangladesh. *Amphibia-Reptilia* 34, 41–50.
- Whitaker, R. & Captain, A. (2004). *Snakes of India: the Field Guide*. Draco Books, New Delhi.

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