An investigation into the composition, complexity and functioning of snake communities in the mangroves of south-eastern Nigeria

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Abstract

The structure of the snake community was studied between 1996 and 2000 on a transect in the mangrove ecological zone of southern Nigeria, West Africa. In three major habitats, both taxonomical diversity and frequency of observations in relation to sampling effort were investigated. In general terms, the complexity of the snake community appeared less than in other habitats of the same geographic region (i.e. swamp forest and forest–plantation mosaics). In fact, only eighteen species were recorded, whereas 43 species are known to inhabit neighbouring habitats. A Principal Component Analysis allowed arrangement of the various species into two main groups in relation to the habitats of capture: (1) a group of species of rainforest biota (i.e. *Toxicodryas blandingii*, *Thelotornis kirtlandii*, *Thrasops flavigularis*, *Rhamnophis aethiopissa*, *Gastropyxis smaragdina*, *Grayia smythii*, *Pseudohaje goldii*, *Python sebae*), and (2) a group of species that, at least in Niger Delta, are typically linked to altered habitats, including derived savannas, plantations and suburbia (i.e. *Psammophis cf. phillipsi*, *Philothamnus cf. nitidus*, *Hapsidophrys lineatus*, *Crotaphopeltis hotamboeia*, *Boaedon lineatus*, *Naja nigricollis*, *Python regius*). The community structure in terms of food habits and body sizes appeared similar to those of other snake assemblages from different habitats of southern Nigeria. The conservation implications of our results are also discussed.

Key words: snakes, community, mangroves, Niger Delta, Nigeria

Résumé

On a étudié entre 1996 et 2000 la structure de la communauté des serpents dans un transect de la zone écologique de mangroves du sud du Nigeria, en Afrique de l'Ouest. On a étudié, dans trois habitats importants, la diversité taxonomique et la fréquence des observations par rapport à l'importance des échantillonnages. En termes généraux, la communauté des serpents y semblait moins complexe que dans d'autres habitats de la même région géographique (c.-à-d. la forêt marécageuse et une mosaïque de plantations forestières). En fait, on n'a rapporté que 18 espèces, alors qu'on sait que 43 espèces vivent dans les habitats voisins. Une Analyse du Composant Principal a permis de ranger les différentes espèces en deux groupes principaux, liés aux habitats où se sont faites les captures : (1) un groupe avec les espèces des biotes de forêt pluviale (*Toxicodryas blandingii, Thelotornis kirtlandii, Thrasops flavigularis, Rhamnophis aethiopissa, Gastropyxis smaragdina, Grayia smythii, Pseudohaje goldii, Python sebae*) et (2) un groupe d'espèces qui, au moins dans le delta du Niger, sont typiquement liées à des habitats dégradés, y compris des savanes dérivées, des plantations et des faubourgs urbains (*Psammophis phillipsi, Philothamnus cf. nitidus, Hapsidophrys lineatus, Crotaphopeltis hotamboeia, Boaedon lineatus, Naja nigricollis, Python regius*). La structure de la communauté, en ce qui concerne les habitudes alimentaires et la taille corporelle, était semblable à celle des autres groupes de serpents dans différents habitats du sud du Nigeria. On discute de l'implication de nos résultats pour la conservation.

Introduction

Nigeria houses the largest mangrove formations in the whole of Africa, and the Niger Delta region in southern

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Nigeria houses over 60% of the country's mangrove surface (Singh, Moffat & Linden, 1995). Ecologically speaking, the mangrove marshes and creeks of southern Nigeria are crucial sites for biodiversity, because they house a peculiar and sometimes endemic fauna (e.g. see Oates *et al.*, 1992; Tooze, 1995; Politano, 1998), or the few remnant populations of very endangered species (e.g. see Dore, undated).

Nevertheless, large sectors of these mangrove formations are currently under serious threat from oil-related industry and exploration activities (which are concentrated mainly in this geographic area, see De Montclos, 1994; Singh *et al.*, 1995; Politano, 1998), and, especially in Calabar, Oron, Bonny and Port Harcourt, from the exotic *Nypa* palm (Dore, undated). In particular, use of explosives by seismic teams, coupled with gas flaring, and construction of canals and pipelines, have been dramatically perturbating this crucial habitat for biodiversity.

Ecological studies on the vertebrate communities of the Nigerian mangroves are still at an embryonic stage (Powell, 1993, 1996; Politano, 1998), and, with regard to herpetofauna communities, the only data reported come from Akani, Luiselli & Politano (1999b). In the present paper we report some quantitative data on the communities of snakes of this habitat type, with emphasis on their taxonomic composition and functional organization. Some conservation implications are also discussed.

Study area and methods

Data were collected at the mangrove area south-west of Port Harcourt (Rivers State), and especially along a nearly linear transect, approximately 20 km long, situated between the rivers Nun and Brass, in the Niger Delta (southern Nigeria). The whole transect was situated inside the mangrove ecological zone (Singh *et al.*, 1995; Politano, 1998).

The study area was surveyed during several field research periods conducted from September 1996 to May 2000. Snake fauna composition and abundance were sampled by means of different surveying procedures: (i) time constrained random searching, (ii) pitfalls with drift fences and cover objects (aluminium sheets, wood pieces, rubbish and dusters) checked every day, (iii) basket traps with no return valves, set amongst barricades (approximately 1 m high) along river banks, for the capture of semi-aquatic species (*cf.* Akani & Luiselli, 2002), and (iv) examination of specimens brought to us by local people. The combination of these four methods allowed us to obtain a general qualitative picture of the structure and composition of the snake community at the study area, whereas the application of method (i) gave quantitative data on the snake fauna abundance, and permitted quantitative comparisons with similar studies from other Afrotropical environments (e.g. see Akani *et al.*, 1999a, 1999b; Andreone & Luiselli, 2000 and references therein).

Field trips were conducted under every weather conditions, including sunny, cloudy and wet days. Quantitative surveys were done at 34 days, in dry season (for a total of 13 348 min, i.e. 222.5 h) as well as in wet season (7935 min, i.e. 133 h). A total of 21 323 min (355.5 h) was spent in searching for snakes in the quantitative part of this study, i.e. excluding from this count the time spent in visiting traps and cover objects, the time spent in the field outside of the time-constrained sampling sessions and the time spent by villagers collecting animals. The field research lasted mainly from 08:00 to 18:00 PM, but night searches were done when possible. Research was suspended when it was raining heavily, and during night hours when we did not have any security assistance from 'Mobile Police' personnel. Random routes to locate snakes were followed throughout every macro-habitat type available in the study area. The total field effort was nearly identical in the three habitat types. Based on previous vegetation studies by our institution's experts (Aquater, 1998), three micro-habitat types were defined at the study area: (1) pristine arboreal mangrove (PAM), (2) secondary 'shrub' mangrove (SSM), (3) heavily altered mangrove (HAM). More vegetation details of these habitats are presented in Aquater (1998). SSM was found mainly along the pipeline of an oil tracing, and HAM was especially developed around human riverine villages. Every possible effort was made to maintain a constant surveying effort in each of the three macro-habitat types available. Given the very complicated structure of the mangrove habitat, we surveyed the various portions of the study area both by walking and by entering into inaccessible sites with canoes of indigenous design.

When seen, snakes were captured by hand, measured for snout-vent-length (SVL, to the nearest ±1 cm), and then individually marked by ventral scale clipping. With regards to the specimens that were brought to us by local people, interviews with the hunters were conducted in order to learn more about the precise sites of capture and the macro-habitat where the given snake was captured.

As already said, to measure snake abundance, we calculated the effort in the field (number of minutes spent in searching for snakes in each day and in each study period), then we divided the total number of snakes observed each day by the number of minutes spent in the field each day. Snake specimens that were just sighted but escaped before being identified were removed from the analyses.

Taxonomy and nomenclature

The taxonomic status of some snake species is still unresolved (e.g. *Psammophis cf. phillipsi, Philothamnus* spp., *Crotaphopeltis hotamboeia, Naja nigricollis*), and possibly will undergo modification and revision by systematic herpetologists in the near future. While waiting for these revisions, for practical reasons, we have followed the nomenclature given by Meirte (1992) and Chippaux (1999). Concerning *Psammophis*, our specimens were assigned to the species *phillipsi* based on several meristic and morphological characteristics, despite this they had a divided cloacal scale.

Analyses

The snake community was defined, as in Andreone & Luiselli (2000), in terms of 'habits', 'food habits' and 'body sizes', and also the classification criteria for each species followed the same source. Habits, food habits and body sizes were determined on the basis of our previous researches on conspecifics from other sites of southern Nigeria or from the same study area, when possible (e.g. see Luiselli, Akani & Capizzi, 1998). For some cases, the attribution of a given species to a precise guild may be questionable. For instance, *Naja melanoleuca* was attributed to the 'terrestrial' guild because most of its specimens were encountered on land, although fish may represent important food items for it (Luiselli & Angelici, 2000), thus it certainly exhibits some tendency to semi-aquatic habits. Similarly, *Pseudohaje goldii* was considered arboreal in the present study on the basis of (i) previous literature accounts (e.g. Spawls & Branch, 1997; Chippaux, 1999) and (ii) our personal experiences of most specimens found while climbed on trees, although it is known to feed frequently upon fish (Pauwels, David & Lenglet, 1999), thus exhibiting a certain tendency toward semi-aquatic habits as well.

Statistical analyses were made with SPSS and STATISTICA (both versions for Windows) computer packages. All tests were two tailed, and alpha was set at 5%. Factor Analysis (Principal Component Analysis, PCA) was used to classify the various species in terms of their similarity as to their micro-habitat uses within the mangrove study area. Standard VARIMAX rotation of the data (Focardi, 1993) was applied to the PCA model. Data matrix was log-transformed prior to applying any analysis.

Results

Field effort and snake abundance

Considering only snakes found in the field during our standardized routes (for a total of 21 323 min of sampling), a total of 160 snake records were done. The mean frequency of observations of snakes was 0.00750 specimens min^{-1} (i.e. 0.45 specimens h^{-1}). The mean frequency of observations of snakes was significantly higher in wet season than in dry season ($x = 0.00884$ specimens min^{-1} versus 0.00539 specimens min^{-1}; $P < 0.0001$ at Student's *t*-test, with 32 df). The daily field effort was significantly correlated with the daily number of observed snakes ($r = 0.64$, $n = 34$, $P < 0.0001$; regression equation: snakes $day^{-1} = -2.614 + 0.0116 \times$ daily effort; see Fig. 1).

Composition of the snake-fauna in terms of 'habits'

The snake-fauna composition at the study area was established on the basis of 160 specimens captured during our standardized time-constrained routes (see above), 47 specimens found in traps and during other qualitative trips, and 24 additional specimens brought to us by local people. The plot of discovery of new species in relation to the numbers of sighted specimens against the field effort (Fig. 2) clearly shows that the plateau phase is reached, thus testifying that the fauna was adequately sampled. In this plot, the 47 specimens found in traps and during other qualitative trips are not computed because of the relatively not-quantifiable nature of this latter data-set.

The list of snake specimens found in each of the three mangrove macro-habitats is presented in Table 1. In total, eighteen species were recorded, most of them (50%) were arboreal (Table 1). Terrestrial species (22.2%), terrestrial-arboreal species (11.1%), semi-aquatic species (11.1%), and the very generalist species (5.6%) accounted for lesser percentages of the whole snake diversity.

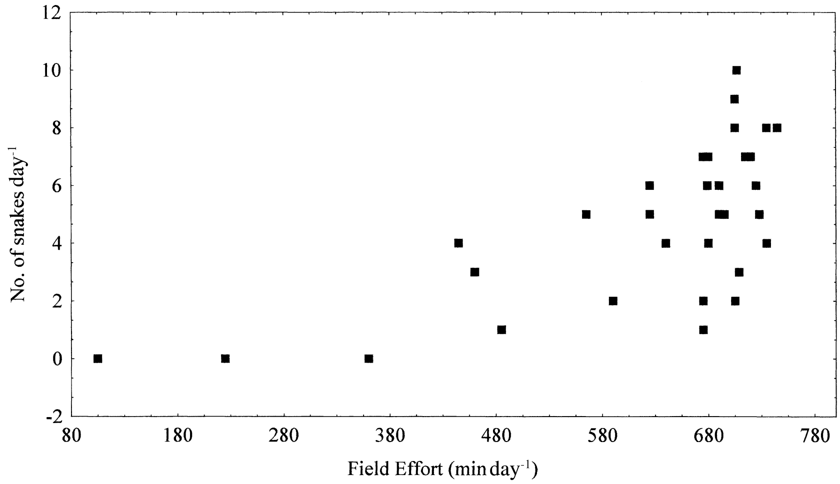

Fig 1 Relationships between daily field effort (number of minutes spent in the field during each day of research) and daily number of observed snakes at the study area. For statistical details, see text

Computing the various species into a PCA model (VARIMAX rotated, and after deleting *Philothamnus* sp., *Naja melanoleuca* and *Dendroaspis jamesoni* from the analyses due to too few data; $\log_{10}$det. Correl. Matrix = −15.231; eigenvalues = 8.2259 (51.4% of explained variance), 4.9101 (30.7% of explained variance)), it resulted that the various species were clearly split into two distinct groups (Fig. 3):

1 a group constituted by *Toxicodryas blandingii*, *Thelotornis kirtlandii*, *Thrasops flavigularis*, *Rhamnophis aethiopissa*, *Gastropyxis smaragdina*, *Grayia smythii*, *Pseudohaje goldii*, *Python sebae*;
2 a group constituted by *Psammophis cf. phillipsi*, *Hapsidophrys lineatus*, *Crotaphopeltis hotamboeia*, *Boaedon lineatus*, *Naja nigricollis*, *Python regius*.

Group 1 included species that are mainly linked to rainforest biota (Akani *et al.*, 1999b), whereas group 2 included species that, at least in Niger Delta, are typically linked to altered habitats, including derived savannas, plantations and suburbia (Akani *et al.*, 1999b; Luiselli &

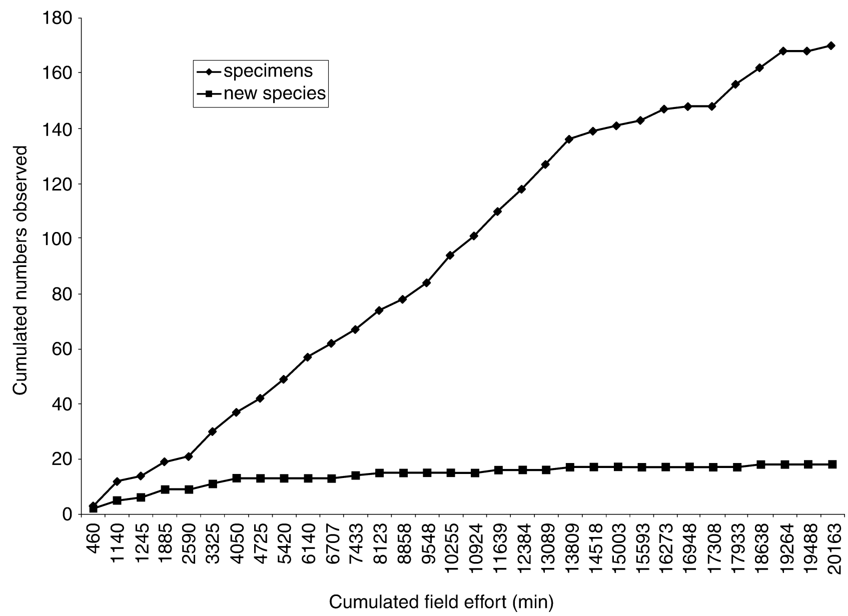

Fig 2 Plot of discovery of new species (in relation to the numbers of sighted specimens) against the field effort (expressed in minutes) at the study area. Note that the plateau phase is reached, which testifies that the fauna was adequately sampled

Table 1 Numbers of snake specimens found in each of the three mangrove macro-habitats in south-eastern Nigeria. In a few cases (e.g. *Rhamnophis aethiopissa*), the total sample sighted does not correspond to the sum of specimens found in three macro-habitats, because there were some specimens, captured by local people at the study area, whose macro-habitats of capture were not known. Symbols: PAM = pristine arboreal mangrove; SSM = secondary 'shrub' mangrove; HAM = heavily altered mangrove; HB = habits; FH = food habits; BS = body size; T = terrestrial; A = arboreal; Aq = semi-aquatic; T/A = terrestrial/arboreal; L = lizards; B = birds; F = frogs; M = mammals; Fi = fish; Eg = bird eggs

Species	Total sample sighted	PAM	SSM	HAM	HB	FH	BS (mm)
Psammophis cf. phillipsi	32	0	9	24	T	L	800–1800
Thelotornis kirtlandii	30	21	7	2	A	L	900–1200
Toxicodryas blandingii	13	10	2	1	A	L, B	1500–2800
Rhamnophis aethiopissa	6	2	2	1	A	L, F	800–1200
Thrasops flavigularis	8	3	5	0	A	B, M	1300–2000
Gastropyxis smaragdina	15	9	3	3	A	L, F	1000–1300
Hapsidophrys lineatus	4	0	2	2	A	L, F	1000–1200
Philothamnus cf. *nitidus*	2	1	1	0	A	L, F	600–800
Grayia smythii	4	1	3	0	Aq	F, Fi	1000–1600
Boaedon lineatus	7	0	0	7	T	M	400–800
Dasypeltis fasciata	4	0	1	3	T/A	Eg	600–1000
Crotaphopeltis hotamboeia	4	0	1	3	Aq	F	500–800
Dendroaspis jamesoni	1	0	0	1	A	B, M	1800–3200
Pseudohaje goldii	10	6	0	3	A	B, F, Fi, M	1500–2500
Naja melanoleuca	2	1	1	0	T	F, Fi, M	1800–3500
Naja nigricollis	13	2	5	6	T	L, M	1500–2300
Python sebae	21	11	6	3	T/A/Aq	M	Over 4000
Python regius	7	2	2	5	T/A	B, M	800–1300

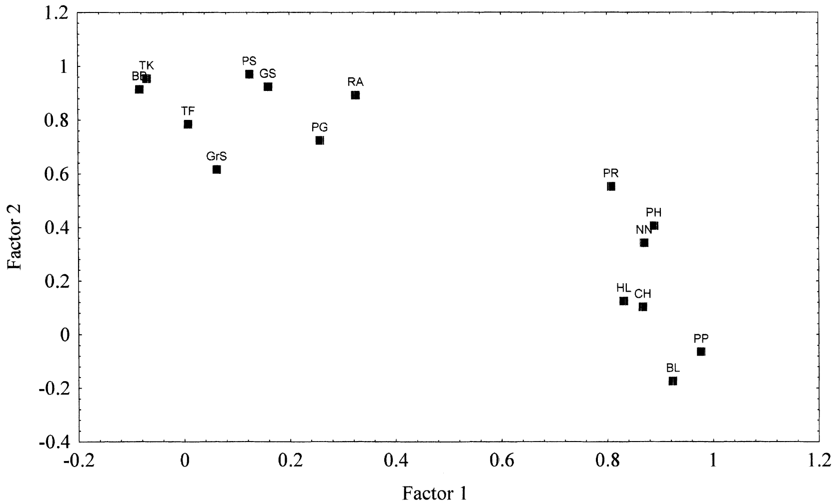

Fig 3 Two-dimensional plot of scores for individual species of snakes on factors using a standardized VARIMAX rotation model PCA. Abbreviations: PS = *Python sebae*, PR = *Python regius*, PP = *Psammophis cf. phillipsi*, TK = *Thelotornis kirtlandii*, BB = *Toxicodryas* (*Boiga*) *blandingii*, RA = *Rhamnophis* (*Thrasops*) *aethiopissa*, TF = *Thrasops flavigularis*, GS = *Gastropyxis smaragdina*, BL = *Boaedon lineatum*, DF = *Dasypeltis fasciata*, GrS = *Grayia smythii*, HL = *Hapsidophrys lineatus*, CH = *Crotaphopeltis hotamboeia*, NN = *Naja nigricollis* and PG = *Pseudohaje goldii*

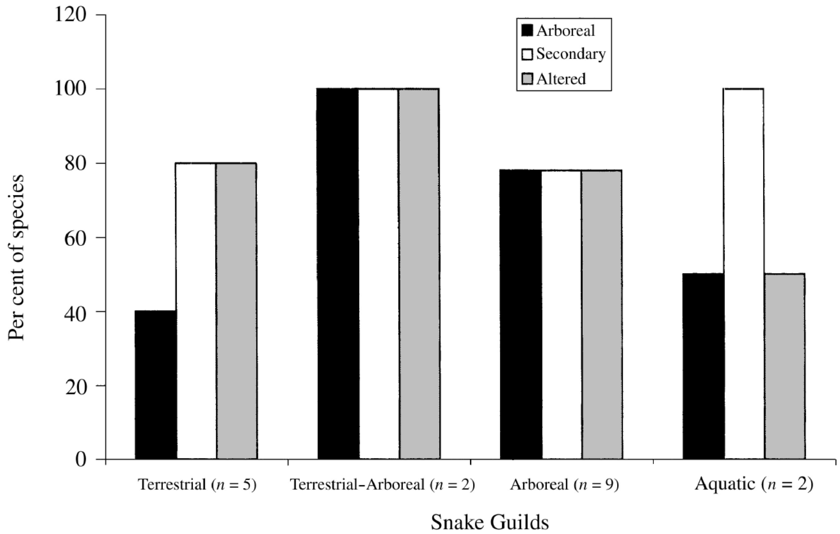

Fig 4 Per cent distribution of the various snake guilds in relation to micro-habitat types in the mangrove formations of south-eastern Nigeria. For more details, see text

Angelici, 2000). Species of group 1 were associated mainly with micro-habitat PAM, and species of group 2 with micro-habitats SSM and HAM.

When we extend our attention to micro-habitat utilization in relation to snake guild (Fig. 4), it appears that terrestrial species tended to be mainly concentrated in secondary or strongly altered mangroves (micro-habitats SSM and HAM), terrestrial-arboreal and arboreal species inhabited all the three micro-habitats available, and semi-aquatic species inhabited mainly secondary mangroves (SSM), although the distributions of the three snake guilds were not significantly different (χ^2 with df = 2, $P > 0.06$).

Composition of the snake-fauna in terms of 'food habits'

The assemblage of snakes in the mangrove habitat comprised species preying upon a wide range of different organisms. Eight species preyed on lizards and/or frogs, eight species upon mammals, five species upon birds, three upon fish and one upon bird eggs (Table 1).

Composition of the snake-fauna in terms of 'body size'

The composition of the snake-fauna of Nigerian mangroves was, in terms of body size distributions, generally similar to that observed in other major habitats of the same geographic region, i.e. dryland, swamp-rainforests and the forest–plantation mosaic (*cf.* Andreone & Luiselli, 2000). In particular, it consisted of species ranging from a small size (e.g. *Crotaphopeltis hotamboeia*) to a giant size (*Python sebae*), with most species being of average size (80–130 cm).

Discussion

A first main evidence of our study is that the specific diversity of the snake-fauna of mangroves was relatively less than that observed in other major vegetation zones of the same geographic region. For instance, only 18 species were found in mangroves, although the total number of snake species recorded by us in the Niger Delta was 43 (37 cited in Akani *et al.*, 1999b; plus other six recorded after publication of that paper). This relative scarcity of specific diversity of mangrove habitats seems to be attributable especially to the total lack of subterranean species and of species closely adapted to life on forest litter (e.g. *Typhlops* spp., *Rhinotyphlops* spp., *Atractaspis* spp., *Calabaria reinhardtii*, *Bitis* spp., etc), which are widespread in forests and forest–plantation mosaics of the same geographic region (e.g. see Akani *et al.*, 1999a, 1999b; Andreone & Luiselli, 2000). Conversely, the diversity of the species that are good climbers and swimmers is nearly identical to that observed in other vegetation zones of the same geographic region (e.g. see Akani *et al.*, 1999a, 1999b; Andreone & Luiselli, 2000). Nevertheless, some minor differences are noteworthy even with regard to these other species. For instance, in the mangrove habitats we observed frequently some species (e.g. *Pseudohaje goldii*, *Thelotornis kirtlandii*) that were rarely found in other habitats, including rainforests and forest–plantation mosaics (Akani *et al.*, 1999a; Andreone &

Luiselli, 2000). Nevertheless, some of the apparently most common species in mangroves were also common and widespread in other habitats (e.g. *Psammophis cf. phillipsi*, *Toxicodryas blandingii*, *Naja nigricollis; cf.* Akani *et al.*, 1999a; Andreone & Luiselli, 2000). The African rock python (*Python sebae*), which is widespread but in decline throughout the study region due to intense hunting for food and leather by local people (Akani *et al.*, 1999b), was however observed very frequently in the mangrove habitats. It probably depends on the semi-aquatic habits of this giant snake, which in southern Nigeria uses rivers and creeks as dispersal corridors to penetrate even suburban habitats (Luiselli, Angelici & Akani, 2001). In any case, the relative frequency of *Python sebae* in this habitat type deserves careful conservation attention, because this species is vulnerable (Akani *et al.*, 1998), and thus mangrove formations may constitute important refuges for this species.

Based on the distribution of the snake guilds in relation to micro-habitats, it is likely that the terrestrial species that are known to be well adapted to altered habitats in southern Nigeria (e.g. *Naja nigricollis*, see Luiselli & Angelici, 2000; *Psammophis cf. phillipsi*, *Boaedon lineatus*, *Python regius*, etc, see Akani *et al.*, 1999b) are especially favoured by the progressive destruction of pristine mangrove formations, and are therefore likely to extend their distribution ranges towards the oceanic coasts of Nigeria in the near future.

We observed significantly more snake specimens during the wet season than during the dry season. Does it reflect a true ecological pattern of snake activity or merely a observational bias? The mangrove habitat is, in fact, very variable either seasonally or diurnally as far as 'catchability' of snakes is concerned (mainly due to the effects of tidal oscillations, *cf.* Politano, 1998), and so an effect of the observational bias could not be *a priori* excluded. However, experimental trials employing imitation snakes to assess the accuracy of visual surveying (*cf.* Taylor & Winder, 1997) indicated that, to a human observer, snakes are more readily observed (i.e. catchable) during low tidal phases and during dry season phases. Thus, we could exclude that the higher wet season abundance of snakes is an observational bias, and are led to conclude that it reflects a real ecological pattern. Because of this differential 'catchability', it is likely that the seasonal incidence of snakes in wet season versus dry season is even greater than was observed. The seasonal variations in mangrove snake abundance (more specimens found in wet season) are likely to depend on species-specific phenologies rather than on general ecological factors of these vegetation formations. In fact, activity peaks during the wetter months have already been recorded in at least some snake species of southern Nigeria and also in other habitats (i.e. rainforest and forest–plantation mosaic) (e.g. see Luiselli & Angelici, 2000; Luiselli, 2001).

In terms of ecosystem functioning, it is obvious that, after the disappearing of the leopard, *Panthera pardus* from this area (Angelici, Grimod & Politano, 1999), *Python sebae* should be the top-chain predator of the mangroves of southern Nigeria, together with the Nile crocodile (*Crocodylus niloticus*) which, although rare, is still found in the mangrove creeks and marshes of this geographic region (Dore, undated).

In general terms, the conservation priorities for mangrove snake communities should be the same as those already highlighted for swamp forest and derived savanna habitats of southern Nigeria (Akani *et al.*, 1999a). In particular, it will be absolutely necessary to avoid opening of new canals or pipelines, because the great majority of snakes are found in the mosaics of small creeks that are largely impenetrable at the present time, but that can be easily destroyed with new road access for boats and people. Moreover, special attention should be given to the arboreal mangroves, which still house a rich diversity of snake species with a complicated trophic structure (including species foraging on fish, on frogs, on birds, on lizards, and on large mammals) that will need further careful research in the years to come.

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