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Ecological data of Nigerian *Crotaphopeltis hotamboeia* (Colubridae) populations

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We present field ecological data for the snake *Crotaphopeltis hotamboeia* (Colubridae) from southern Nigeria. Adult sex-ratio was close to equal, and females attained significantly larger body size than males (on average 470 mm versus 400 mm SVL). Annual above-ground activity peaked during the wet months. A preponderance of snakes were captured in agricultural lands (plantations and farmlands), whereas few snakes were captured in both mangroves and mature forests. Anurans accounted for over 70% of the total prey items; lizards (Scincidae and Agamidae) were also frequently preyed upon. The food niche breadth and diet composition was similar between sexes. There was no apparent ontogenetic dietary change in this species.

Key words: Crotaphopeltis hotamboeia, ecology, Nigeria, phenology, snake

INTRODUCTION

Wide areas of West Africa are characterized by landscape with extended deforestation, with sites once occupied by lowland rainforest or swamp forest currently transformed into a myriad of farms, plantations, towns and derived savannahs with remnant fragments of original forest (e.g., De Montclos, 1984; Gornitz, 1985; Ndukwu et al., 2010). In this altered landscape, several typical forest species can become locally extirpated, due to direct habitat loss as well as hunting (e.g., Fa, 2009; Harrison, 2011). However, there is a relatively small number of adaptable species which profit from deforestation due to predator pressure relaxation (e.g., Liu et al., 2003). These species can reach high densities in altered habitats.

One of the most abundant species of West African snakes in altered environments is *Crotaphopeltis hotamboeia* (Fig. 1), a small-sized (up to 885 mm long; Broadley & Cock, 1975), oviparous, mild venomous, rear-fanged colubrid that shows remarkable displays (Sapwell, 1969) and is responsible of many cases of slight envenomation in southern Nigeria (Akani et al., unpublished data). *Crotaphopeltis hotamboeia* is characterized by a broad head and by blackish, grayish, brownish or olive-green dorsal colouration usually with white lips (Spawls et al., 2006). This snake is considered to be mainly nocturnal and terrestrial, active in damp areas and usually hiding by day under ground cover (Spawls et al., 2006). It feeds mostly on anuran amphibians (Keogh et al., 2000).

In this paper we describe basic ecological aspects of *C. hotamboeia* which, although abundant in highly altered environments, has remained previously understudied in Western Africa (but see Butler & Reid, 1986; 1990).

MATERIALS AND METHODS

Study Area

Data given here were collected from September 1996 to September 2011, during both standardized long-term surveys (e.g., Reading et al., 2010) and opportunistic observations. The data were collected from several localities, notably the Port Harcourt region in the eastern

Fig. 1. Adult *Crotaphopeltis hotamboeia* from the surroundings of Uyo, Akwa Ibom State, Nigeria. Photo: Edem A. Eniang.

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branch of the River Niger Delta (Rivers State), the Uyo area in Akwa-Ibom State and the Calabar area in Cross River State. These three main regions are situated 50–150 km apart. All areas, ranging 0–500 m a.s.l., are characterized by a tropical climate, with a dry season occurring from October to March and a wet season from April to September. The study areas are densely populated, with patches of rainforest and swamp forest interspersed among plantations. Mangroves are found along the coastal areas with brackish water channels and rivers.

Protocol and statistical analyses

Snakes were searched for under all weather conditions during the day and at night, although a stronger field effort was conducted between 0800 and 1800 hours. For this paper, we collated data originated from both standardized surveys and opportunistic catches, hence we could not quantify the field effort performed in each month and in each habitat type. However, possible biases should be low because (i) the data were collected during a long time (15 years) of continued field research, (ii) all available habitats for snakes were carefully surveyed during this long period, and (iii) a high number of snake individuals belonging to over 40 species (some thousands of animals captured; e.g., Luiselli, 2005) was encountered in the various habitat types.

Snakes were captured by hand, pitfall traps with drift fences and by placing flat objects on the ground and checking what was hiding below them each day. The captured snake individuals were sexed, measured for snout-vent length (SVL, precision 2 mm) and individually marked by ventral scale clipping. Meteorological conditions, hour of the day, habitat of capture and eventual food ingested were also recorded. Food items were obtained by forcing the snake to regurgitate the ingested bolus. Several individuals were also found as dead on the road (DOR) or killed by farmers. These dead individuals were dissected to obtain food items. In addition, we also measured and dissected snake specimens which were stored in several Nigerian institutions (hospitals, secondary schools and university collections).

For evaluating sexual size dimorphism, we excluded all immature individuals. As a threshold adult size value, we considered 29.5 cm SVL for females and 24 cm SVL for males; this is, respectively, the size of the smallest female with thickened muscular oviducts, indicating sexual maturity, and the minimum size of a sexually mature male in a large sample of southern African conspecifics (Keogh et al., 2000). Prey items were identified to the lowest taxon possible. Prey items were recovered only once from each captured individual, thus avoiding pseudoreplication.

Food niche breadth was estimated using Levin's index (B) (1968) and its standardized form (B_A) (Hurlbert, 1978):

$$B = \frac{1}{\left[\sum_{i}^{n} p_{ji}^{2}\right]} \qquad B_A = \frac{(B-1)}{(n-1)}$$

where p_{ji} is the proportion of species j using prey i and n is the number of food categories found.

Prey niche overlap between sexes was calculated applying Pianka's (1973) index:

$$O_{xy} = \frac{\sum_{i=1}^{n} p_{xi} p_{yi}}{\left(\sum_{i=1}^{n} p_{xi^2} \sum_{i=1}^{n} p_{yi^2}\right)^{1/2}}$$

where p_{xi} is the proportional utilization of prey i by form x and p_{yi} the proportional utilization of prey i by form y. Both indexes range from 0 (no prey in common in the diet spectrum) to 1 (same diet spectrum).

Because the evaluation and comparison of niche overlap indexes are affected by the limitation of arbitrary cut-offs (Feinsinger et al., 1981), we compared the observed overlap values to an appropriate null model. The distribution of the null model was created using the software Ecosim (version 7.0; Gotelli & Entsminger, 2011) running two simulations each with 30,000 randomized replications of the data. The simulations were generated using two randomization algorithms: RA2 (Niche breadth relaxed/Zero States retained) whereby every cell in the matrix is replaced with a randomly chosen, uniforming number between zero and one but maintaining the zero structure in the matrix; and RA3 (the 'scrambled-zeros' randomization algorithm proposed by Winemiller & Pianka, 1990) whereby the entries in each row of the utilization matrix were randomly reshuffled for each iteration retaining the niche breadth of each species but randomizing which particular resource states are utilized. Due to the objective limits in assessing food availability in a complex environment, resource availability was assumed as equiprobable. Statistical significance was determined by comparing the observed overlap value to the null distribution; an observed value greater than 95% of the simulated values indicates significant overlap at the $p<0.05$ level (Winemiller & Pianka, 1990).

We used parametric tests when the variables were normally distributed; otherwise, nonparametric tests were used (e.g., χ^2 test). For analyses of habitat, seasonality, food habits and body size, the individual identity of each snake was considered, i.e. pseudoreplication was avoided. Body size differences between males and females were analyzed by student *t*-tests. Seasonal and inter-habitat differences in the frequency of encountered snakes were analyzed by χ^2 tests. Data were processed by Statistica version 8.0, with all tests being two-tailed and alpha set at 5%.

RESULTS

Our sample consisted of 136 adult males and 147 adult females; adult sex-ratio (0.92:1) did not depart significantly from equality (χ^2=0.427, df=1, p=0.501). Females attained significantly larger body size than males ($\text{mean}_{\text{males}=124}$=387.8mm, SD_{males}=67.5; $\text{mean}_{\text{females}=147}$=469.7mm, SD_{Ds}=80.3; df=281, t=9.22, p<0.0001, t-test).

Table 1. List of prey items recovered from captured *Crotaphopeltis hotamboeia* snakes.

Prey type	males	females	undetermined
Lizards			
Agama agama	7	9	2
Mabuya sp.	4	9	0
Panaspis togoensis	2	1	0
lizard clutches	0	0	1
Anurans			
Bufo maculatus (small)	17	23	0
Phrynobatrachus sp.	31	26	0
Hyperolius sp.	6	2	0
Frogs (undetermined)	8	3	0
Amphibian clutches	3	3	0
arthropods	2	0	1
Total	78	76	4

Snakes were observed more frequently during the wet months (Fig. 2), with highly significant differences between wet seasons versus dry season counts (χ^2 test, df=1, p<0.0001).

A sample of 377 snake individuals with habitat type recorded showed that there was an uneven use of the various habitat types (χ^2=269.1, df=7, p=0.0001), with a preponderance of snakes captured in agricultural lands (plantations and farmlands, Fig. 3). More specifically, these snakes apparently avoided mangroves and mature forests (less than 1% of individuals were captured in each of these habitat types).

A total of 160 prey items were recorded from handled snakes (Table 1). The bulk of the diet consisted of anurans (72.5 % of the total items or 76.25 % if we include clutches), mostly adults of small sized species (i.e. *Phrynobatrachus* and *Hyperolius*) but also newly metamorphosed toads and even frog clutches. Despite being terrestrial, *C. hotamboeia* preyed upon both terrestrial and arboreal frogs (*Hyperolius* spp.). These snakes also fed frequently upon lizards (21.25% of the total items or 21.88% if we include clutches), both Scincidae and Agamidae being equally consumed (Table 1). Food niche breadth (B_A) did not show remarkable intersexual differences (total=0.427, males=0.433, females=0.451). The application of Pianka's index showed a diffuse overlap between sexes in the dietary spectrum (O=0.95). The observed intersexual overlap value was significantly higher than the mean values obtained from simulations using both the RA2 (mean of simulated indices=0.721, variance=0.01) and RA3 (mean of simulated indices=0.480, variance=0.03) algorithms (for all tests p<0.01). Trophic niche overlap between adults and juveniles was also very high (O=0.89).

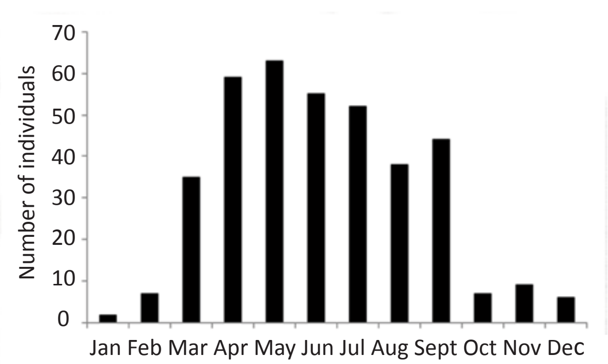

Fig. 2. Snake annual phenology. The snake observations peaked during wet season (April–September).

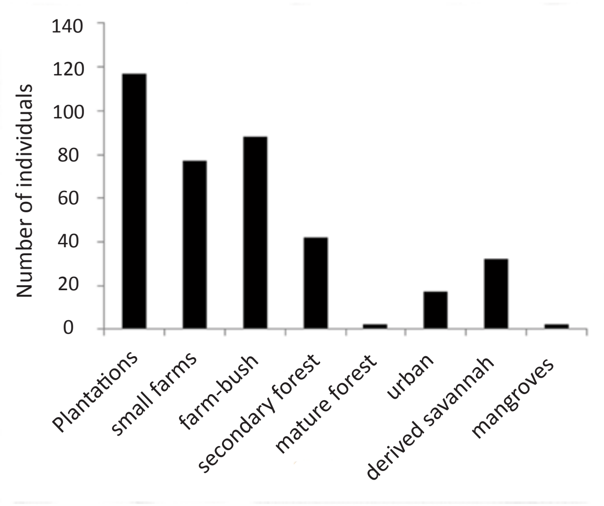

Fig. 3. Habitat type of capture of 377 individuals of *Crotaphopeltis hotamboeia*.

DISCUSSION

Data presented here considerably improves the knowledge on the natural history of West African *C. hotamboeia* populations, including comparisons with South African populations which have been carefully studied (Keogh et al., 2000).

Our morphometric data showed that females were clearly larger than males, consistent with what was observed in southern African conspecifics (Keogh et al., 2000). Body sizes (both mean and maximum) observed in our populations were also similar to those recorded in Southern Africa (Keogh et al., 2000) and elsewhere (Chippaux, 2001; Chirio & LeBreton, 2007). The two sexes were distinctly similar in terms of food composition. This is unexpected as in other snake species with significant sexual size dimorphism also the diet composition significantly diverged between sexes (Shine, 1986; 1991; 1994). There was also no apparent ontogenetic dietary change in terms of taxonomic food composition, the same as conspecifics from southern Africa (Keogh et al., 2000).

The above-ground activity of Nigerian *C. hotamboeia* populations was uneven, with highest activity peaks recorded in the wet season, and especially between April and July. Overall, this pattern is consistent with studies on other snake species from the forest region of southern Nigeria, which demonstrated that activity peaks at the onset of the wet season are usual. Indeed, this pattern has been demonstrated in such diverse species, among others, as *Bitis gabonica* and *Bitis nasicornis* (Luiselli, 2006), or *Naja melanoleuca* and *Naja nigricollis* (Luiselli & Angelici, 2000). During the onset period of the wet season, *C. hotamboeia* individuals were frequently observed close to small ponds transitorily formed by strong tropical rainfall. It is likely that these snakes search for amphibian prey after rainfall and around these temporary ponds, since small to moderately sized anurans were often found as prey of these colubrid snakes (see also Keogh et al., 2000). Qualitative data from earlier literature also suggested that humid habitats are particularly favoured by this species (e.g., Chirio & LeBreton, 2007). Above-ground activity decreased significantly by dry season (minimum activity recorded in January); however, this species apparently did not estivate, as at least two individuals were encountered in each month of the year. The absence of a dry season diapause is consistent with data available for other sympatric snake species. Snakes do not aestivate in the dry months in southern Nigeria, including also those species which are typical savannah inhabitants (e.g., the spitting cobra *Naja nigricollis*, see Luiselli, 2001; 2002).

Our habitat and dietary data clearly showed that *C. hotamboeia* is a highly adaptable species with a wide range of habitats inhabited and a variety of different prey types being eaten. Farm-bush and plantations appeared as the preferred habitats, whereas mature forests and mangroves were inhabited very rarely. Although we did not record precise effort times spent in each habitat type, we exclude that the observed patterns may depend merely on differential survey efforts across habitats. Indeed, we spent remarkably more time doing surveys in forest and mangrove habitats than in agricultural lands (Akani et al., unpublished), but the snake sightings were clearly dominant in the latter habitat type. Overall, our data clearly confirmed previous anecdotal observations in showing that this is one of the snake species most adapted to the now widespread human-made habitats of West Africa, after the large-scale loss of rainforests and swamp forests (e.g., Chippaux, 2001; Chirio & LeBreton, 2007). In this regard, Chirio & LeBreton (2007) suggested that *C. hotamboeia* can be considered a good biological indicator for the status of a rainforest, with high frequencies of individuals of this species at a site indicating low conservation status of the given rainforest patches. Unfortunately these authors did not report quantitative details for this assertion, and hence it would be interesting to test this hypothesis with *ad hoc* field studies in the future.

Our unpublished observations indicated that, within the altered habitats, this species lives mainly under leaf litter and is mostly active in the night and spends most of the time resting under leaf litter, pieces of wood and small boulders. We also frequently observed this species around garbage dumps and generally dirty environments, and it frequently hides under old and abandoned items like sacks, cement bags, old basins and plastic wares, including abandoned tyres. Individuals of *C. hotamboeia* were not easily encountered in open areas and bushes. In the altered habitats of southern Nigeria, *C. hotamboeia* is one of the most abundant species, together with *Lamprophis* spp., *Psammophis phillipsii, Toxicodryas blandingii, Naja nigricollis* and *Causus maculatus* (Akani et al., unpublished data). Compared to these other species, some of which may be potential competitors, *C. hotamboeia* showed quite catholic dietary habits, including frogs (dominant prey type), frog eggs, lizards and arthropods. Among the snake species commonly inhabiting farmland and plantations, *C. hotamboeia* is possibly the one showing the widest dietary spectrum. Indeed, house snakes of the genus *Lamprophis* are specialized in feeding upon small mammals and lizards (Chippaux, 2001; Akani et al., 2008), *Toxicodryas blandingii* on birds and lizards (Luiselli et al., 1998), *P. phillipsii* on lizards (with small mammals as secondary prey, see Akani et al., 2003; Luiselli et al., 2004), *N. nigricollis* on lizards and rodents (although being also generalist forager; see Luiselli & Angelici, 2000; Luiselli et al., 2002) and *C. maculatus* feeding especially on frogs (Chippaux, 2001; Ineich et al., 2006). It is likely that the wide dietary spectrum of *C. hotamboeia* may facilitate its colonization of altered habitats, where relying on some specific prey types (for instance frogs) may expose the predator to relatively long periods of food shortage. However, since there are no data analyzing the availability of potential prey types for snakes along the various months, this hypothesis still needs verification.

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REFERENCES

Akani, G.C., Eniang, E.A., Ekpo, L.J., Angelici, F.M. & Luiselli, L. (2003). Food habits of the snake *Psammophis phillipsi* from the continuous rainforest region of Southern Nigeria (West Africa). *Journal of Herpetology* 37, 208–211.

Akani, G.C., Luiselli, L., Eniang, E.A. & Rugiero, L. (2008). Life in the tropical suburbs: food type partitioning among sympatric African house snakes of the genus *Lamprophis* (Colubridae). *Italian Journal of Zoology* 75, 395–399.

Broadley, D.G. & Cock, E.V. (1975). *Snakes of Rhodesia*. Salisbury, Longman Rhodesia, 221 pp.

Butler, J.A. & Reid, J. (1986). Habitat preferences of snakes in the Southern Cross River State, Nigeria. In: *Studies in Herpetology*, Rocek, Z., ed., p. 483–488. Charles University, Prague.

Butler, J.A. & Reid, J. (1990). Records of snakes from Nigeria. *Nigerian Field* 55, 19–40.

Chippaux, J.P. (2001). *Les Serpents de l'Afrique Occidentale et Centrale*. IRD Editions, Paris.

Chirio, L. & LeBreton, M. (2007). *Atlas des reptiles du Cameroun.*

IRD Editions, Paris.

De Montclos, M.A. (1984). *Le Nigéria.* Kurthala, Paris.

Fa, J.E. (2009). Impacts of hunting on mammals in African tropical moist forests: a review and synthesis. *Mammal Review* 39, 231–264.

Feinsinger, P., Spears, E.E. & Poole, R.W. (1981). A simple measure of niche breadth. *Ecology* 62, 27–32.

Gornitz, V. (1985). A survey of anthropogenic vegetation changes in West Africa during the last century – climatic implications. *Climatic Change* 7, 285–325.

Gotelli, N.J. & Entsminger, G.L. (2011). *EcoSim: Null models software for ecology*. Version 7. Acquired Intelligence Inc. & Kesey–Bear. Jericho, VT 05465. http://garyentsminger.com/ecosim.htm

Harrison, R.D. (2011). Emptying the Forest: Hunting and the Extirpation of Wildlife from Tropical Nature Reserves. *Bioscience* 61, 919–924.

Hurlbert, S.H. (1978). The measurement of niche overlap and some relatives. *Ecology* 59, 67–77.

Ineich, I., Bonnet, X., Shine, R., Shine, T., Brischoux, F., Lebreton, M. & Chirio, L. (2006). What, if anything, is a "typical" viper? Biological attributes of basal viperid snakes (genus *Causus* Wagler, 1830). *Biological Journal of the Linnean Society* 89, 575–588.

Keogh, J.S., Branch, W.R. & Shine, R. (2000). Feeding ecology, reproduction and sexual dimorphism in the colubrid snake *Crotaphopeltis hotamboeia* in southern Africa. *African Journal of Herpetology* 49, 129–137.

Levins, R. (1968). *Evolution in Changing Environments: Some Theoretical Explorations.* Princeton, Princeton University Press.

Liu, W., Xiao, D. & Yi, Y. (2003). Relaxation oscillations in a class of predator–prey systems. *Journal of Differential Equations* 188, 306–331.

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. (2002). Life–history correlates of suboptimal adaptation to rainforest biota by spitting cobras, *Naja nigricollis*, in southern Nigeria: comparative evidences with sympatric forest cobras, *Naja melanoleuca*. *Revue d'Ecologie (Terre et Vie)* 57, 123–133.

Luiselli, L. (2005). Snakes don't shrink but 'shrinkage' is an almost inevitable outcome of measurement error by the experimenters. *Oikos* 110, 199–202.

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.

Luiselli, L., Akani, G.C. & Angelici, F.M. (2002). Comparative feeding strategies and dietary plasticity of the sympatric cobras *Naja melanoleuca* and *Naja nigricollis*, in three diverging Afrotropical habitats. *Canadian Journal of Zoology* 80, 55–63.

Luiselli, L., Akani, G.C., Angelici, F.M., Eniang, E.A., Ude, L. & Politano, E. (2004). Local distribution, habitat use, and diet of two supposed 'species' of the *Psammophis 'phillipsi'* complex (Serpentes: Colubridae), sympatric in southern Nigeria. *Amphibia–Reptilia* 25, 415–423.

Luiselli, L., Akani, G.C. & Barieenee, I.F. (1998). Observations on habitat, reproduction and feeding of *Boiga blandingii* (Colubridae) in south–eastern Nigeria. *Amphibia–Reptilia* 19, 430–436.

Luiselli, L. & Angelici, F.M. (2000). Ecological relationships in two Afrotropical cobra species (*Naja melanoleuca* and *Naja nigricollis*). *Canadian Journal of Zoology* 78, 191–198.

Ndukwu, B.N., Idigbor, C.M., Onwudike, S.U. & Chukwum, M.C. (2010). Evaluation of the effects of selected agricultural land utilization types on soil properties in Nando, Southeastern Nigeria. *International Journal of Sustainable Agriculture* 2, 34–38.

Pianka, E.R. (1973). The structure of lizard communities. *Annual Review of Ecology and Systematics* 4, 53–74.

Reading, C.J., Luiselli, L.M., Akani, G.C., Bonnet, X., Amori, G., Ballouard, J.M., Filippi, E., Naulleau, G., Pearson, D. & Rugiero, L. (2010). Are snake populations in widespread decline? *Biology Letters* 6, 777–780.

Sapwell, J. (1969). An unusual defensive display by a West African snake, *Crotaphopeltis hotamboeia hotamboeia* (Laurenti). *Herpetologica* 25, 314–315.

Shine, R. (1986). Sexual differences in morphology and niche utilization in an aquatic snake, *Acrochordus arafurae*. *Oecologia* 69, 260–267.

Shine, R. (1991). Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* 138, 103–122.

Shine, R. (1994). Sexual size dimorphism in snakes revisited. *Copeia* 1994, 326–346.

Spawls, S., Howell, K. & Drewes, R.C. (2006). *Pocket Guide to the Reptiles and Amphibians of East Africa*. A & C Black, London.

Winemiller, K. O. & Pianka, E. R. (1990). Organization in natural assemblages of desert lizards and tropical fishes. *Ecological Monographs* 60, 27–55.

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