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Sexual size dimorphism and natural history traits are correlated with intersexual dietary divergence in royal pythons (*Python regius*) from the rainforests of southeastern Nigeria

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ABSTRACT

Food habits of the royal python (Python regius) were studied in some localities of southeastern Nigeria by means both of faeces analysis and forced regurgitation of living individuals. Female pythons were significantly longer than the males. Both sexes preyed exclusively upon birds and mammals, but there were significant intersexual differences in terms of dietary composition. Males preyed more frequently upon birds (70.2% of the total number of prey items) whereas females preyed more frequently upon mammals (66.7% of the total number of prey items). There was an apparent ontogenetic change in the diet of both sexes: specimens shorter than 70 cm total length preyed almost exclusively upon small sized birds (nestlings and immature), whereas the longer specimens (> 100 cm total length) preyed almost entirely upon small mammals. We suggest that the two sexes are different in terms of their main natural history traits (males being more arboreal than females), and that this behavioural difference can explain the observed intersexual differences in dietary composition.

KEY WORDS: *Python regius* - Snakes - Feeding habits - Sexual size dimorphism - Afrotropical region - Rainforests - Nigeria.

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INTRODUCTION

There are very few species of snakes in sub-Saharan Africa which have been well described from the ecological point of view (Shine et al., 1996a, b). Despite the notoriety of old world Booidea, their ecology and behaviour in native habitat are poorly known (Starin & Burghardt, 1992). Snakes of the genus Python are widespread across sub-Saharan Africa. In the rainforests of central Africa (Gulf of Guinea), two species of Python can be found, and they often occur in sympatric conditions: the African rock python, P. sebae, and the royal python, P. regius (Butler & Reid, 1986, 1990). Available information on the ecology and natural history of these species, including their food habits, is extremely scarce and anecdotal (Spawls & Branch, 1997), despite these snakes being conspicuous organisms in several Afrotropical ecosystems; thus, the study of their ecology has particular relevance for understanding the ecological mechanisms regulating these ecosystems.

The present paper reports detailed information, based on the analysis both of faecal pellets and regurgitated ingesta, on the diet of the royal or ball python *P. regius*, from the rainforests of southeastern Nigeria. Emphasis is placed on whether there are significant differences in dietary composition between sexes, and, if so, whether these differences can be attributed to intersexual differences in mean body sizes or in spatial niche (habitat) utilization.

MATERIALS AND METHODS

Study area and species

The field study was carried out mainly during the wet season of 1997, i.e. from early Jule to late September, with some additional information in September-October 1996, April-May, and November 1997, in some localities of southeastern Nigeria (Abarikpo, Rivers State, 05°08' N latitude, 06°37' E longitude; Rumuji, Rivers State, 04°57' N latitude, 06°46' E longitude; Orubiri, Rivers State, 04°42' N latitude, 07°01' E longitude; Eket-Mobil station surroundings, Akwa-Ibom State, 04°50' N latitude, 07°59' E longitude, Itu surroundings, Calabar, Cross River State). These localities are characterized by (1) permanently flooded swamp rainforest patches surrounded by cultivations of cassava and oil palms, and (2) dryland rainforest patches. The swamps are dominated by *Elaeis* sp. and dicotyledonous trees. The study area lies within the Guinea-Congolian rainforest (White, 1983) and the Equatorial climatic zone (Chi-Bonnardel, 1973). The climate is typical for a tropical sub-Saharan country, with well-marked dry and wet seasons and with relatively little monthly fluctuation in maximum and minimum temperatures (White, 1983). The dry season extends from November to April, whereas the wet season goes from May to October, with the highest rainfall peak during July. Mean monthly maximum temperatures range between 27° and 34° C, while minima vary between 22° and 24° C. This region is one of the wettest in the world, with an average yearly rainfall of 3146 mm (data from the Department of Geography, University

Python regius is a species widespread and locally abundant in southeastern Nigeria. We found it especially in bushy and dryland rainforest patches, but occasionally even in permanently flooded swamp-forest patches, along creak and river banks, and in suburban areas.

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Methods

Field trips were conducted both on sunny and rainy days. Each day, the field research lasted approximately from 8 a.m. to 6 p.m. Random routes to locate snakes were followed throughout every macrohabitat type available in each study area. When seen, snakes were captured by hand. The handled snakes were sexed by analysing the morphology of the tail, and measured for snoutvent length (SVL, to the nearest ± 0.5 cm) and tail length (tL, to the nearest 0.5 cm), and then individually marked by ventral scale-clipping. In addition, pitfall traps were used in each macrohabitat type. The pitfalls were examined on each day of research. Snakes were captured by drift fences, and by placing flat objects on the ground and checking under them each day. The animals captured by local people, and those traded in bush-meat markets of local people, were also examined (Akani et al., 1998).

Stomach contents and faecal pellets were collected by gentle palpation of the snake abdomen until regurgitation or defaecation occurred. No specimen was killed or injured during the study. The prey items were identified to the lowest taxon possible. After examination, the snakes were forced to re-ingest the disgorged prey. When the snake did not re-ingest it, the item was placed in 75% ethanol. After laboratory examination, all the remains of the faecal pellet were also preserved in 75% ethanol for further examination. Several other dietary records were given us from Prof. Godfrey Akani of the Port Harcourt University.

Statistical analyses were carried out on an SPSS (version for Windows) computer package. All tests were two-tailed, and α was set at 5%.

RESULTS

A total of 29 *Python regius* males and 33 females was examined for food intake. The apparent sex-ratio was not significantly skewed from equality (binomial test: P > 0.7). The males were shorter than females (males: x = 82.71 cm (SD: 13.69 cm); females: x = 97.70 cm (SD: 16.22 cm), and the intersexual difference attained statistical significance (one-way ANOVA: P < 0.001).

Since some specimens were recaptured several times, the total numbers of snakes processed for any food items in the stomach were 38 males and 49 females. Identifiable prey items were obtained from faeces of 36 males (94.7% of the processed animals) and 42 females (85.71% of the processed specimens), while only 11 males (28.94% of the processed animals) and 12 females (28.57% of the processed animals) had prey in their stomachs. These frequencies differed significantly (in all comparisons, P < 0.001 in χ^2 test), thus indicating that to obtain a large number of food items in ecological studies on African pythons it is much more convenient to examine faeces than stomach contents. For similar conclusions on free-ranging snakes from elsewhere, see Capizzi & Luiselli (1997). However, comparing the proportions of food items found both in faeces and stomachs, there were no statistically significant differences (in all comparisons, P > 0.6 in χ^2 test), thus indicating that the feeding rates were in fact similar between sexes. Pooling the food items found both in stomachs and faeces, 47 prey items were collected from the males and 54 prey items from the females. The summary of the dietary data recorded during the present study is presented in Table I. Although the diet of both males and fe-

TABLE I - Food composition of male and female Python regius from southeastern Nigeria.

Prey Type	Males		Females	
	Ns	Nf	Ns	Nf
	··········			
Birds				
Turtus sp.	1	-	-	-
Columbidae (ND)	-	6	-	-
Psittacus erithacus juv.	2	-	-	-
Meropidae (ND)	-	1	-	-
Sylviidae (ND)	-	2	-	-
Nectarinia sp.	2	-	-	-
Sturnidae (ND)	-	1	-	-
Ploceus sp.	2	-	-	-
Birds (ND)	-	16	1	17
Mammals				
Crocidura sp.	1	-	-	-
Epomophorus sp.	-	-	2	-
Megaloglossus woermanni	-	-	1	-
Cricetomys gambianus	•	-	1	-
Praomys tullbergi	-	-	3	-
Muridae (ND)	-	-	-	5
Lemniscomys striatus	2	-	3	-
Protoxerus stangeri	-	-	1	-
Galagoides demidoff	1	-	-	-
Mammals (ND)	-	10	-	20

Nf, faeces contents; Ns, stomach contents; ND, species not determined.

males consisted only of birds and mammals, there were significant differences between sexes (P < 0.001 at χ^2 test): the males preyed more frequently upon birds (70.2% of the total number of prey items) than upon mammals (29.8% of the total number of prey items), whereas the females preyed more frequently upon mammals (66.7% of the total number of prey items) than upon birds (33.3% of the total number of prey items). There was an apparent ontogenetic change in the diet of both sexes: specimens shorter than 70 cm total length preyed almost exclusively upon small-sized birds (nestlings and immature), whereas the longer specimens (> 100 cm total length) preyed almost entirely upon small mammals.

DISCUSSION

Our data indicate that royal pythons from southeastern Nigeria show a reversed sexual size dimorphism, with the females significantly longer than the males. This data mirrors available information on other Booidea, including species such as *Candoia carinata* (Shine, 1994), *Charina bottae, Eryx conicus, Eryx johni, Lichanura roseofusca* (Smith, 1943; Shine, 1978), and *Eunectes murinus* (Calle *et al.*, 1994), whereas the sexu-

al size dimorphism of Nigerian Calabaria reinbardti, sympatric to royal pythons, was a lesser one (Akani et al., unpublished data). However, the surprising topic of our study does not deal with the sexual size dimorphism in royal pythons, but with the dietary (and perhaps niche) differences which are correlated with this significant sexual size dimorphism. Although in both sexes the diet consisted exclusively of mammals and birds, as in other African Booidea species studied to date (Starin & Burghardt, 1992), the intriguing difference between sexes consisted in the prevalence of birds versus mammals in the smaller sex (male) and in that of mammals versus birds in the larger one (female). We suggest that these differences in dietary composition depend on a major arboreality of males in comparison with females. Factors in favour of this hypothesis are: (i) males were found climbing on trees more frequently than females (14 specimens versus 2 specimens); and (ii) the presence in the males' diet of a higher number of arboreal prey, including birds, squirrels, and Galagoides demidoff. In this context, it is however worthnoting that arboreality and bird-eating are not always correlated events in snakes (Shine, 1983; Luiselli & Rugiero, 1993; Angelici & Luiselli, 1998). Interesting cases of sexual size differences accompanied with diet composition differences have already been recorded in snakes, including e.g. Acrochordus arafurae (Shine, 1986; Houston & Shine, 1993), Nerodia rhombifera (Manjarrez & Macias-Garcia, 1991), Telescopus fallax (Shine, 1991), Coronella austriaca (Luiselli et al., 1996), Natrix natrix (Luiselli et al., 1997), Laticauda colubrina (Shine, 1991), and Trimeresurus borneensis (named T. wiroti in Shine, 1991). An ecological situation similar on the whole to that described here (i.e., with the larger sex living on the ground and the smaller sex in the trees) was observed in Telescopus fallax and Trimeresurus borneensis (Shine, 1991). According to Shine (1995), intersexual differences in body sizes brought about by fecundity selection for larger females or sexual selection for larger males may then be reinforced (or opposed) by natural selection working on foraging abilities of the two sexes, and the same pattern of reinforcement of an original sexually selected difference may apply to other sex-specific foraging morphologies.

With regard to the prey eaten by royal pythons, it may be noted that all the mammalian species, except *Galagoides demidoff*, are widespread and relatively abundant in the forest ecosystems of the studied region (Angelici, unpublished data). Thus, it is likely that opportunism represents an intrinsic trait of the predatory behaviour of these snakes.

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