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Is there any interspecific competition between dwarf crocodiles (*Osteolaemus tetraspis*) and Nile monitors (*Varanus niloticus ornatus*) in the swamps of central Africa? A study from south-eastern Nigeria

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Abstract

Aspects of coexistence between the dwarf crocodile *Osteolaemus tetraspis* and the Nile monitor lizard *Varanus niloticus* were studied in swamp rain forests of south-eastern Nigeria, central Africa. Crocodiles were significantly smaller than monitor lizards. There was no significant sexual size dimorphism in the examined sample of *Varanus*, whereas the female size exceeded the male size in *Osteolaemus*. The food niche breadth was narrower in young than in adults of both species, and *V. niloticus* showed a narrower niche breadth than *O. tetraspis*. Crabs constituted the main prey type category for both species, whereas vertebrates were more rarely preyed upon. The diet composition of males and females was similar in *V. niloticus*, but it was different in *O. tetraspis*. The general diet composition of the two species was similar (78.2% of overlap), and even the habitats where these two species were found were similar. These interspecific similarities suggest that *O. tetraspis* and *V. niloticus* could be potential competitors in the freshwater ecosystems of the Nigerian rainforest. However, it is suggested that the main prey type for these species (crabs) is not limited in the environment, which may minimize interspecific competition. Interference competition can also occur between these species, as suggested by one case of direct predation of the one species (*V. niloticus*) towards the other species (*O. tetraspis*). A case of cannibalism was observed in *V. niloticus*. This could indicate that intraspecific competition can be important for regulating the dynamics of monitor populations in the rainforests of south-eastern Nigeria.

Key words: *Osteolaemus tetraspis*, *Varanus niloticus ornatus*, interspecific competition, Nigeria

INTRODUCTION

Monitor lizards (Varanidae) and crocodiles (Crocodylidae) are frequently found in the same places, often along marshes, creeks, lakes and swamps, in either Asia or Africa. In Asia, for instance, the monitor *Varanus salvador* is often found in the same places as the crocodiles *Crocodylus palustris* and *C. porosus*, whereas in sub-saharan Africa a similar coexistence occurs between the Nile monitor *Varanus niloticus* and the crocodiles *C. niloticus* and *Osteolaemus tetraspis*. The ecological relationships between sympatric monitors and crocodiles are poorly understood, but it is well known that adult crocodiles can forage on monitors and that monitors can forage on both eggs and juveniles of crocodiles (see e.g. Cott, 1961). Apart from such cases of direct predation, when varanid lizards cohabit with large sized-crocodiles (i. e. *C. niloticus*, *C. porosus*, and *C. palustris*) it seems very unlikely that a true interspecific competition could occur, because (1) the size differences between monitors and crocodiles are great, (2) competition tends to be reduced when there exist relevant size differences between potential competitors (see e.g. Pianka, 1973, 1986; Ricklefs, 1973), and (3) the large crocodiles forage in the water, unlike the varanids, which typically forage on the ground. Even competition between young *C. niloticus* and *O. tetraspis* or *V. niloticus* is unlikely to occur, since *C. niloticus* is much more aquatic than the two other species in the places where they live in close sympatry (e.g. Cott, 1961). However, in the rainforests of central-western Africa there is an interesting case of coexistence between a varanid lizard (the Nile monitor *Varanus niloticus ornatus*) and the dwarf crocodile *Osteolaemus tetraspis*, which are respectively the largest and most aquatic of the African varanids and the smallest and least aquatic of the African crocodilids. This case of coexistence is particularly interesting from an ecological point of view because both the taxa (1) average approximately the

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same size (adult length from 1 to 1.8 m), and (2) inhabit the same environmental types, i.e. marshes and swamps surrounded by forest patches. Thus, these two taxa seem to present the basic characteristics for being considered as potential competitors.

In this paper we present data on the food habits and habitat characteristics of sympatric Nile monitors and dwarf crocodiles in swamp forests of southeastern Nigeria, and discuss whether these taxa are in fact competitors for some resources in the environment.

MATERIALS AND METHODS

Study area

The field study was carried out mainly from early June to late September 1997, but additional data were collected in September–October 1996, March–May 1997, and October–November 1997, mainly in two localities of south-eastern Nigeria: vicinities of Eket, Akwa-Ibom state, 04°50′ N latitude, 07°59′ E longitude (area A); surroundings of Elem-Sangama, Rivers State, 04°40′ N latitude, 06°40′ E longitude (area B), characterized by permanently flooded swamp rainforest patches, surrounded by cultivations of cassava and oil palms, growing along the courses of the black-water rivers Kwa-Ibo (area A) and Orashi (area B). The 2 study areas are similar in terms of environmental characteristics and faunistic composition, but the extent of the forest was considerably wider in area A than in area B (Luiselli *et al.*, unpubl. data). The swamps were dominated by *Elaeis* sp. and dicotyledonous trees. The study area is located within the Guinea-Congolian rainforest (White, 1983) and lies within the Equatorial climatic zone (Von Chi-Bonnardel, 1973). The climate of the study area is typical for a tropical sub-Saharan country, with well-marked dry and wet seasons and relatively little monthly fluctuation in maximum and minimum temperatures (White, 1983). The dry season extends from November to April, and the wet season from May to October, with the highest rainfall peak during July. Mean monthly maximum temperatures ranged between 27 and 34 °C, while minima varied between 22 and 24 °C. This region is one of the wettest in the world, with an average yearly rainfall of more than 3000 mm (data from the Department of Geography, University of Calabar).

Methods

Food data presented in this study were collected by dissection of dead specimens of both *V. niloticus ornatus* and *O. tetraspis*, but no specimen of any species was killed specifically for the purposes of this research. All the examined specimens were killed by local people, and traded in local bush-meat markets. Each specimen found in these bush-meat markets was sexed, measured for snout–vent length (SVL, to the nearest 5 mm), and dissected. The contents of the stomach were removed, placed in 75% alcohol, and later identified to the lowest taxon possible.

Observations of activity patterns and macrohabitats of these 2 species were also done, contextually to other studies of snakes and lizard ecology (Luiselli *et al.*, in press). Field trips were conducted on either sunny or rainy days. Each day, the field research lasted approx. from 08:00 to 18:00, but occasionally later in the evening. Random routes to locate animals were conducted throughout every macrohabitat type available in each study area. Time of observation (Lagos time) and habitat of sighting of each lizard and crocodile specimen were also recorded. Habitats available in the study area were divided into the following categories: surroundings of swamps in the primary forest (habitat A), surroundings of swamps in the secondary forest (habitat B), banks of the river creeks (habitat C), bushy boundary strip surrounding the forest (habitat D), and former cultivations actually recolonized by vegetation (habitat E). No crocodile or monitor lizard was seen in actual cultivations or in urban areas.

All statistical analyses were done with a SPSS (version for Windows) computer package. All tests were 2-tailed, and alpha was set at 5%. In the text the means are followed by ± 1 SD. Normality in the distribution of the variables was checked by using the Kolmogorov–Smirnov test. When we failed to obtain a normal distribution of data, non-parametric tests were then used. Niche breadths for numerical data were calculated with Simpson's (1949) measure of niche breadth, and niche overlap between species was assessed with Pianka's (1986) symmetric equation, with values ranging from 0 (no overlap) to 1 (total overlap).

RESULTS

Body sizes of monitors and crocodiles

Body sizes of the monitors and crocodiles examined in this study are presented in Fig. 1. Considering only adult specimens, monitor length exceeded significantly that of crocodiles (one-way ANOVA: $F_{1,29}$ = 62.03, $P<0.000001$). Mean body length did not differ significantly between males and females in *V. niloticus* (males: 139.4 16.7 cm (SD); females: 133.4 ± 17.9 cm; one-way ANOVA: $F_{1,11}=0.034$, P = 0.57), but the females were significantly larger than the males in *O. tetraspis* (males: 101.2 ± 4.5; females: 108.6 ± 5.9 cm; one-way ANOVA: $F_{1,16}=9.28$, $P=0.008$).

Intraspecific diet variations

Varanus niloticus

The summary of the dietary data collected in this study is presented in Table 1. Unidentified prey remains are excluded from the table. Adults preyed on a wide

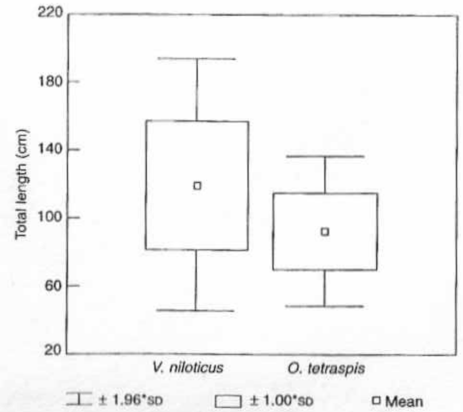

Fig. 1. Box and whisker plot showing mean total length (and dispersion measures) of sympatric *Osteolaemus tetraspis* and *Varanus niloticus* in south-eastern Nigeria. For statistical details, see text.

Table 1. Food habits of *Varanus niloticus* in the study area

	Juveniles	Females	Males
Gastropoda	1	7	1
Malacostraca	7	10	22
Araneae	0	2	1
Scorpiones	0	0	1
Coleoptera	1	1	5
Rhynchota	0	0	1
Boiga blandingi	0	0	1
Varanus niloticus	0	0	1
Osteolaemus tetraspis	0	0	1
Rodentia	0	1	2
Total	9	21	36

variety of organisms, and crabs were the most important prey type in terms of frequency of occurrence (56.1%). Crabs of indeterminate genus were found in all the adults examined in this study. Vertebrates were rarely prey, but this species proved to feed on both smaller conspecifics (1.75% of the total number of prey items) and young *Osteolaemus* (1.75%). However, vertebrates constituted over 10% of the total number of prey found in monitor stomachs. The juveniles fed only upon invertebrates, essentially crabs (77.8% of the total number of prey items).

The diet composition of males and females was significantly different ($\chi^2=78.85$, d.f. = 9, $P<0.00001$), whereas there were no statistically significant differences between juveniles and adult males ($\chi^2=4.709$, d.f. = 9, $P=0.86$), or between juveniles and adult females ($\chi^2=12.551$, d.f. = 9, $P=0.18$). The food niche breadth of juvenile specimens was narrower than that of the adults (B = 1.58 *vs* 2.83), and this difference attained statistical significance ($P<0.001$, Mantel test). The food

Table 2. Food habits of *Osteolaemus tetraspis* in the study area

	Juveniles	Females	Males
Gastropoda	2	4	7
Malacostraca	5	2	11
Pisces	1	2	4
Amphibia	3	3	5
Rodentia	0	0	4
Fruit	0	0	1
Total	11	11	33

niche breadth was similar in the adults of both sexes (males: B = 2.49; *vs* females: 2.85; differences unsignificant at Mantel test).

Osteolaemus tetraspis

The feeding data collected during this study are presented in Table 2. Unidentified prey remains are excluded from the table. The diet of the adults consisted mainly of crabs (29.5%) and gastropods (25%). Vertebrates (essentially fish and adult frogs) accounted for about 40% of the total number of prey items. The juvenile crocodiles fed essentially upon crabs (45.5%), and vertebrates accounted for 36.4% of the total diet.

The differences in terms of dietary composition were minor, between males and females ($\chi^2=8.69$, d.f. = 5, $P=0.11$), between juveniles and adult males ($\chi^2=3.68$, d.f. = 5, $P=0.6$), or between juveniles and adult females ($\chi^2=6.00$, d.f. = 5, $P=0.31$). The food niche breadth of juvenile specimens was narrower than that of the adults (B = 3.10 *vs* 4.72), and the difference was statistically significant ($P<0.01$, Mantel test). The food niche breadth was wider in males than in females (B = 4.71 *vs* 3.77), and the intersexual difference fell just short of statistical significance ($P=0.063$, Mantel test).

Interspecific diet variations

In general, the food composition of the two species was relatively similar (78.2% of overlap). Crabs and amphibians represented the two main food type categories preyed on by both the species. However, the food niche breadth was considerably wider in *O. tetraspis* than in *V. niloticus* (B = 7.38 *vs* 2.83; interspecific difference: $P<0.0001$, Mantel test). Moreover, the proportion of vertebrates eaten was significantly higher in *O. tetraspis* than in *V. niloticus* (2 × 2 contingency table, $\chi^2=7.86$, d.f. = 1, $P=0.005$).

Habitat characteristics

Assessment of habitat characteristics of sympatric *O. tetraspis* and *V. niloticus* was based on 32 sightings of *Osteolaemus* and 30 sightings of *Varanus* (Fig. 2). Some specimens examined for food were excluded from this

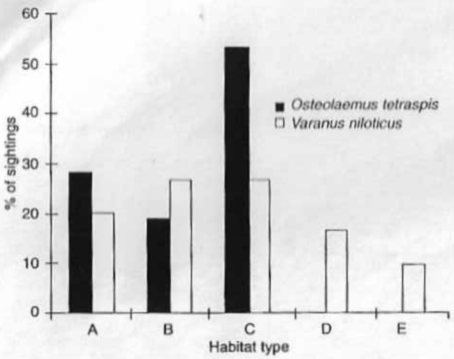

Fig. 2. Habitat characteristics of sympatric *Osteolaemus tetraspis* and *Varanus niloticus* in south-eastern Nigeria. For details on the habitat type associated with symbol (from A to E); see Methods.

number because it was not always easy to understand the habitat of capture on the basis of the information coming from hunters and local people. Dwarf crocodiles were sighted essentially in habitat type C (53.1% of the total number of sightings), whereas monitor lizards were found mainly in habitat types B and C (26.7% of the total number of sightings). In general, *V. niloticus* individuals were found in a wider range of habitat types than *O. tetraspis*, which is to be expected if we consider that this species can move even towards dry environments, contrary to the dwarf crocodile which is strictly bounded to freshwater ecosystems. However, there were no significant differences in the frequency of observation of the two study species in the various habitat types (Mann–Whitney *U*-test, $U = 12.00$, $Z = -0.104$, $P = 0.92$).

DISCUSSION

Our study provided evidence that the composition of the diet of dwarf crocodiles and Nile monitor lizards is relatively similar in the swamps of south-eastern Nigeria. Crabs constituted the main prey type for both the species, whereas other invertebrates and small-sized vertebrates were preyed upon less frequently. A single instance of cannibalism was recorded in Nile monitors, which also fed occasionally upon dwarf crocodiles. With regard to crabs, it should be noticed that these crustaceans are extremely abundant along the banks of creeks, rivers, ponds, and swamps, of the rain forests of south-eastern Nigeria, where they probably represent an unlimited food resource which is crucial for a wide variety of predators. In fact, crabs provide food not only for dwarf crocodiles and monitors, but also for other reptiles, birds, and carnivorous mammals. For instance, with regard to the study areas, crabs were found in the stomachs of young Nile crocodiles *Crocodylus niloticus*, in the faeces of genets, mongooses, and otters, and were also eaten by some raptors (Luiselli *et al.*, pers. obs).

At an intraspecific level, in both the study species the juveniles showed a narrower food niche breadth than the adults. This result is to be expected, as reduced body size could place a constraint over the variety of prey types they can capture and swallow. Compared with other varanids of similar size (see e.g. Cowles, 1930; Shine, 1986a), Nigerian *V. niloticus* preyed on vertebrates less frequently, and the same is true also for *O. tetraspis* in comparison with other small crocodile species or the young of larger species (see e.g. Taylor, 1979; Magnusson, Silva & Lima, 1987; Thorbjarnarson, 1993; Santos *et al.*, 1996). We suggest that the great abundance of crabs can explain even these 'uncommon' foraging habits in our study species. An unexpected result of our study is that remarkable intersexual dietary differences emerged in the species showing no obvious sexual size dimorphism (*V. niloticus*), but not in the species showing a significant sexual size dimorphism (*O. tetraspis*). In fact, it is well known that remarkable intersexual differences in food habits are usually found in species where one sex is much larger than the other, and/or with remarkable differences in habitat characteristics (Shine 1986b; Houston & Shine 1993).

Our study demonstrated that both dwarf crocodiles and Nile monitors are found especially along forested creek banks, but also in the swamps and ponds of the permanently flooded swamp–rain-forest patches. The fact that they live in the same habitats is well known to local hunters, who capture both these species, exactly in the same spots, by placing home-made traps at the borders of the swamps.

The general similarity in food habits and habitat characteristics between dwarf crocodiles and Nile monitors suggests that these species could be potential competitors in the freshwater ecosystems of the Nigerian rainforest. Interference competition can also occur between these species, as suggested by the case of direct predation of the one species (*V. niloticus*) on the other (*O. tetraspis*). Two factors could minimize interspecific competition between these two species: (1) the size differences existing between them (cf. Ricklefs, 1973), and (2) the fact that their major food source (crabs) is probably non-limited, and thus can substain a diversified community of predators in these tropical ecosystems.

With regard to predation, an omnipresent phenomenon in nature, which is a key factor in regulating the population dynamics of many tropical communities (cf. Barbault, 1974, 1977, 1991; Luiselli *et al.*, in prep.), monitors and dwarf crocodiles are possibly not subject to it, because serious potential predators are greatly reduced in numbers (e.g. *Python sebae*, *Crocodylus niloticus*, etc). For instance, dwarf crocodiles and Nile monitors were never preyed upon by any of the 22 snake species examined by us in the same study areas of this research (Luiselli *et al.*, in press); nevertheless, young specimens of both *Osteolaemus* and *Varanus* could be preyed on by herons, kingfishers, birds of prey, and

even large freshwater chelonians like *Trionyx triunguis*. Humans, who frequently capture both dwarf crocodiles and monitor lizards with simple noose traps, for food or skins (Akani *et al.*, 1998), probably represent the major source of predation for these species.

Since it is likely that competition between *O. tetraspis* and *V. niloticus* could occur in other swamps of central and west Africa, it would be interesting in the future to study the variation of competition intensity between these species in various freshwater biotopes, and to establish whether young Nile crocodiles could really be competitors with both *Osteolaemus* and *Varanus*, or whether their highly aquatic habits serve to separate their niche from that of the other two species. These future studies have, however, to be planned in such a way that no killing of specimens has to be done, since these animals are already under heavy pressure from killing for food, trade, etc., even in the Nigerian territory (Akani *et al.*, 1998).

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