

# Interspecific relationships between two species of sympatric Afrotropical water snake in relation to a seasonally fluctuating food resource

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**Abstract:** In this paper, the ecological relationships and the resource partitioning patterns in a two-species system of sympatric aquatic snakes (*Grayia smythii* and *Afronatrix anoscopus*) from a riverine forest area in southern Nigeria, West Africa, were tested. The monthly availability of their food resources in the field, and the monthly variation in the feeding relationships between these snakes and their preys, were also studied. Food items of 1245 snakes, i.e. 554 *Grayia smythii*, and 691 *Afronatrix anoscopus*, were examined. The mean body length of *Grayia smythii* was significantly larger than that of *Afronatrix anoscopus* in any interspecific comparison, i.e. males versus males, females versus females, and females versus males; however, in both species the females attained significantly larger body sizes than the males. 676 prey items were obtained from the stomachs of *Afronatrix anoscopus*, and 390 from those of *Grayia smythii*. Both species of snake exhibited an increased activity in the open during the wet months, and this increased activity was positively correlated to the higher abundance of prey during the wet season. In both species the diet consisted of a great variety of different amphibian and fish species. Direct interference competition was not observed. The month-by-month dietary patterns exhibited by the two snake species were similar. Mean prey size was significantly larger in the larger species, and the difference in prey size between the two snake species increased during the dry season, i.e. during the period of reduced prey availability. The monthly availability of the three main food types for these snakes varied, and were significantly more abundant during the wet season (April–September). A positive relationship between prey availability and prey use by snakes strongly suggests that the two snake species are predatory generalists, utilizing prey in relation to their abundance in the field.

**Key Words:** Africa, *Afronatrix anoscopus*, ecological relationships, *Grayia smythii*, Nigeria, prey availability, prey size, prey type, resource utilization, water snakes

## INTRODUCTION

The study of ecological relationships among sympatric species is still a major issue in the ecology of natural communities (both of vertebrates and invertebrates) (Hanski 1987, Krijger *et al.* 2001, Ray & Sunquist 2001, Shorrocks 1990). Hence, it is not surprising that numerous studies have been devoted to examining the dynamics of coexistence of closely related sympatric species (Bronmark *et al.* 1991, Connell 1983, Gurevitch *et al.* 1992) as well as distantly related species which share few phenotypic similarities (Capizzi & Luiselli 1996, Hurlbert *et al.* 1986, Mokany & Shine 2003).

Snakes have been studied quite extensively in these terms (Luiselli & Angelici 2000, Luiselli *et al.* 2002, Toft 1985), and water snakes have been especially well

studied (Vitt 1987). Studies on the coexistence ecology of sympatric water snakes have proliferated in temperate regions of both North America and Europe (Luiselli & Rugiero 1991, Mushinsky & Hebrard 1977, Mushinsky & Lotz 1980, Mushinsky *et al.* 1982) but not in tropical regions, despite the fact that the tropics house the most diverse and abundant snake fauna of the world. Among the few exceptions, there was a study of sympatric marsh snakes (genus *Natriciteres*: Colubridae) from southern Nigeria (Luiselli 2003). In this study, it was demonstrated that the presence of a potential competitor for food may produce a shift in the diet composition of the target snake species, with a result that, where species are sympatric, there is a partitioning of food resources between the two predator species and a reduction in the diversity of prey taken by the target species (Luiselli 2003). Similarly, studies conducted in North America and Europe have demonstrated that food resource partitioning is an important mechanism for the coexistence of freshwater

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snake communities (Himes 2003a, 2003b; Kofron 1978, Luiselli & Rugiero 1991, Mushinsky & Hebrard 1977, Mushinsky & Lotz 1980, Mushinsky *et al.* 1982, Vitt & Vangilder 1983). Furthermore, another important aspect to study is whether a given species (or a given guild of potential competitors) use a given prey source in relation to its availability in the environment or not. This issue has been investigated in the field of several vertebrate communities (Capizzi & Luiselli 1996, Morin 1983, Ray & Sunquist 2001), but it has never been investigated in snake communities from tropical Africa. Hence, these communities remain among the poorest known in terms of how they utilize available food resources (Luiselli & Angelici 2000, Luiselli *et al.* 1998, 2002). This is an important shortcoming concerning our understanding of these predator guilds, which often occur in surprisingly high biomass (Luiselli *et al.* 2005a), and may strongly influence the population dynamics of their preys (Barbault 1977, 1984, 1987, 1991).

My long-term studies of snake community ecology conducted in a riverine forest in south-eastern Nigeria (see Luiselli 2005) have revealed that two aquatic fish- and amphibian-eating species (*Afonatrix anoscopus* (Cope, 1861) and *Grayia smythii* (Leach, 1818) (synonymized with *smithii* in some studies) are very abundant in the study area, and the present paper specifically attempts to answer the following questions:

- (1) Do these sympatric species of snakes use the same food resources?
- (2) Is there any interference competition between the species, i.e. does one of the two species prey on its potential competitor?
- (3) Are there quantitative temporal interspecific differences in the dietary habits?
- (4) Are there interspecific differences in prey size?
- (5) Are there temporal differences in the food resource availability for snakes?
- (6) What is the response of the two snake species to the temporal differences in food resource availability? That is, do the snakes feed on their prey in relation to its relative availability in the field or not?
- (7) Is the interspecific difference in prey size higher in periods of prey shortage than in periods of prey abundance? That is, can the predators adjust their prey-size preferences in relation to the availability of their prey in the field?

## MATERIALS AND METHODS

### Study area

This study was conducted between September 1996 and May 2004 at a swamp rain forest (about 44.5 ha) around Eket, Akwa-Ibom State (04°50'N, 07°59'E; about 10 m

asl), characterized by a moist rain-forest patch along the banks of the River Quo-Ibo (Kwa-Ibo). The area consists of water bodies of different shape and nature, such as freshwater creeks, ponds, and marshes. Detailed description of the study area is given in Luiselli *et al.* (2005b). The study area has a tropical climate with a wet season from April to September, and relatively constant monthly temperatures throughout the year (mean monthly range between 29 and 32 °C). Daily air temperatures ranged between 27 and 34 °C, and averaged  $30.6 \pm 3.7$  °C (N = 188).

### Protocol

Fieldwork was conducted during all months of the year. Ten searching days per month, every year, were spent in the field throughout the whole study period, and each day in the field lasted for 6–9 h. The constant field effort allowed me to ensure that (1) the number of snakes found in each month, and (2) the number and category of prey items, did not depend on differential field effort across months, but reflected true patterns.

Fieldwork was conducted along transects, and snakes were captured by hand, often when under cover, and by using pitfall traps with drift fences, and fish traps (more details of the experimental design and the size of traps are given in Luiselli *et al.* 2005b). An identical number of trap-days was used in every month throughout the study period, in order to avoid sampling biases due to differential field effort across months. It is possible that, occasionally, snakes may have opportunistically fed on trapped fishes when they were also trapped. However, in several instances (1) fishes and snakes were found together inside traps and the stomachs of the snakes were sometimes empty under these circumstances; (2) the stomach of a trapped snake contained a meal in advanced digestion state whereas the trap was just recently set, and (3) the stomach of the trapped snake contained fish species of different types from those actually trapped in adjacent traps.

Snout–vent length (SVL, to the nearest 5 mm) and mass (to nearest 0.1 g) were recorded and the snakes were individually marked by ventral scale clipping for future identification. Snakes were palpated abdominally, until regurgitation of ingested food occurred. In addition, specimens found dead during surveys (e.g. snakes killed by farmers and by fishermen, squashed along the roads, etc.) were dissected to identify stomach contents. Prey items were identified to the lowest taxon possible, and weighed (to nearest 0.1 g) when recently ingested (i.e. not yet digested).

In *Afonatrix anoscopus*, specimens shorter than 270 mm SVL were considered subadults, based on the smallest size of reproductive females (i.e. females with

**Table 1.** Summary of the dietary data collected from juveniles, males and females of *Afonatrix anoscopus* (Aa) and *Grayia smythii* (Gs), in southern Nigeria. Numbers indicate the total number of prey items. The number of specimens which have eaten a particular prey item are indicated in parentheses (some specimens contained more than a single prey item in a category).

Prey type	Aa Juveniles	Aa Males	Aa Females	Gs Juveniles	Gs Males	Gs Females
<b>Amphibians</b>						
<i>Silurana tropicalis</i>	38 (32)	60 (46)	71 (60)	26 (14)	66 (44)	23 (16)
<i>Phrynobatrachus auritus</i>	11 (7)	21 (8)	18 (9)			
<i>Bufo maculatus</i> (froglets)		7 (5)	7 (7)	8 (3)	11 (3)	3 (1)
<i>Bufo maculatus</i> (adults)		1 (1)	1 (1)		3 (3)	9 (7)
<i>Hylarana albolabris</i>		2 (2)			1 (1)	
<i>Ptychadena</i> sp.	1 (1)	26 (25)	20 (17)	6 (6)	24 (21)	45 (37)
<i>Aubria subsigillata</i>			1 (1)			
<i>Afrivalus</i> sp.		1 (1)				
Tadpoles	72 (29)	118 (37)	96 (32)	31 (17)	29 (11)	21 (7)
<b>Fish</b>						
<i>Periophthalmus</i> sp.		3 (3)	4 (4)	1 (1)	3 (2)	4 (4)
Cyprinidae sp.		27 (25)	14 (12)	3 (2)	8 (6)	9 (8)
Cyclidae sp.		8 (5)	7 (7)	2 (2)	4 (4)	6 (6)
<i>Tilapia</i> sp.		1 (1)	3 (3)	5 (5)	3 (2)	6 (4)
<i>Clarias</i> sp.	2 (2)	8 (6)	9 (7)	3 (3)	3 (3)	3 (2)
Unidentified spp.	4 (3)	9 (9)	5 (5)	4 (3)	8 (5)	9 (7)
Total prey items	128	292	256	89	163	138

eggs) and the smallest size of males observed while mating in the field (see Luiselli & Akani 2002, Luiselli *et al.* 2003). In *Grayia smythii*, specimens shorter than 600 mm SVL were considered subadults (Luiselli & Akani 2002). Sex of subadults is not indicated here because several specimens were impossible to sex correctly (via the relative numbers of subcaudals), unlike most other snake species.

Monthly availability was assessed for three main prey categories for both species (see Table 1): (1) frogs of the species *Silurana tropicalis* Gray, 1864 (Pipidae), (2) frogs of the genus *Ptychadena* (Ranidae), and (3) anuran tadpoles. The monthly variation in availability of other prey (mainly fish) was not assessed because of logistic difficulties. The temporal abundance of frogs (both *Silurana* and *Ptychadena*) was assessed by a combination of techniques. A 10-d survey was conducted during each month across the study period. Each day, three independent observers spent 6 h actively searching for frogs (3 h daylight/3 h night, using headlamps). Secretive individuals were sought in their refuges (e.g. under logs/rocks, beneath bark, in leaf litter, soil and leaf axils). In addition, a second collecting method consisted of plastic pitfall bucket traps (c. 250 mm deep, 290 mm top internal diameter, 220 mm bottom internal diameter). Handles were removed, and drainage holes were made and then the buckets were sunk into the ground, 25 m apart, along a drift fence on either side of creeks. The fence (c. 50 cm high and 350 m long) was made from plastic sheeting stapled to thin wooden stakes. The fence bottom was buried 50–80 mm into the ground and positioned to run across the top of each pitfall trap. The pitfalls were checked each morning and evening, and the frogs were individually marked by toe-clipping for future identification. Temporal occurrences of anuran

tadpoles (all species combined) were examined using a standardized procedure. A monthly total of 450 dip net trials were done. When captured, tadpoles were put into a clean tank, and counted.

Food niche breadth of juveniles, adult males and adult females of both species has been quantified using the Simpson (1949) diversity index:

$$B = 1 / \sum pi^2$$

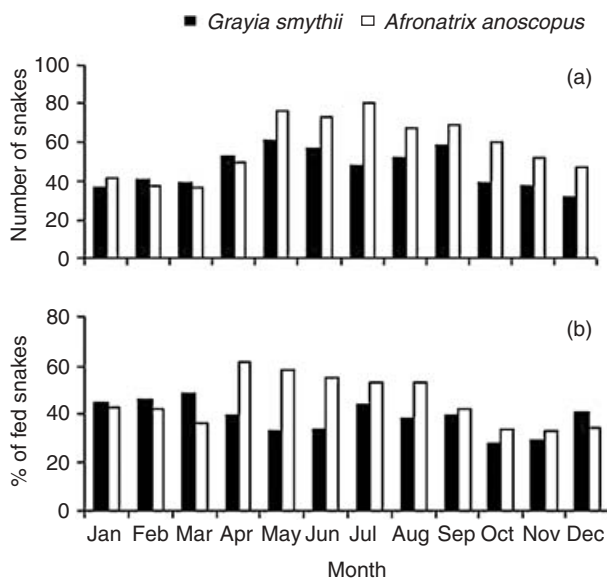
where B = the breadth and  $pi$  = the frequency of utilization of the  $i$ th category.

For calculating the similarity in dietary types use of the various categories of individuals (juveniles, males and females) of both species, the overlap index of Pianka (1986) was calculated. Pianka's formula for species  $j$  and  $k$ , with resource utilizations  $p1i$  and  $p2i$ , is:

$$O_{j,k} = O_{k,j} = \frac{\sum p2i \times p1i}{\sqrt{\sum (p2i^2 \times p1i^2)}}$$

In this formula the values range from 0 (no similarity) to 1 (absolute identity).

Statistical analyses were performed using (two-tailed,  $\alpha = 0.05$ ) STATISTICA (version 6.0, for Windows). In the text, values are presented as the mean  $\pm$  SD. To avoid pseudo-replication of data, food data were recorded only once from each individual. Data on the diet composition of the two species from the various years were pooled after having verified (by  $\chi^2$  tests) that there were no significant inter-annual differences in the prey items of both species. The same applies also for data on monthly activity intensity and per cent of fed specimens. For simplicity, when indicating significant results of statistical tests, three significant figures are given (i.e.  $P < 0.05$ , 0.01, 0.001).



**Figure 1.** Monthly numbers of water snakes examined (a); and monthly frequency of fed individuals (b) in two species of water snake at the study area in southern Nigeria.

## RESULTS

### Snake body size and total sample sizes

In total, 1245 snakes were captured, 554 were *Grayia smythii* (62 subadults, 248 adult males and 244 adult females), and 691 were *Afronatrix anoscopus* (68 subadults, 306 adult males and 317 adult females). There was a significant reversed sexual size dimorphism in both species: in *Afronatrix anoscopus* the mean male SVL was  $358 \pm 42$  mm ( $n = 306$ ), and the mean female SVL was  $413 \pm 82$  mm ( $n = 317$ ) (inter-sample difference:  $t = -4.21$ ,  $df = 621$ ,  $P < 0.001$ ); in *Grayia smythii* the mean male SVL was  $699 \pm 183$  mm ( $n = 248$ ), and the mean female SVL was  $867 \pm 206$  mm ( $n = 244$ ) (inter-sample difference:  $t = -7.32$ ,  $df = 552$ ,  $P < 0.001$ ). The mean SVL of *Grayia smythii* was significantly higher than that of *Afronatrix anoscopus* in any interspecific comparison, i.e. males vs. males, females vs. females, and females vs. males (in all cases, at least  $P < 0.001$  from t-tests).

### Temporal patterns of activity intensity and per cent of fed snakes

The temporal distribution of captures of both species differed significantly from the null hypothesis of an equal monthly distribution across the whole year (*Grayia smythii*:  $\chi^2 = 23.0$ ,  $df = 11$ ,  $P < 0.05$ ; Figure 1a; *Afronatrix anoscopus*:  $\chi^2 = 46.5$ ,  $df = 11$ ,  $P < 0.001$ ; Figure 1b). Both species were more abundant than expected in the wet months (April–September) (*Grayia*

*smythii*:  $\chi^2 = 12.1$ ,  $df = 5$ ,  $P < 0.05$ ; *Afronatrix anoscopus*:  $\chi^2 = 24.9$ ,  $df = 5$ ,  $P < 0.001$ ).

The proportion of *Grayia smythii* and *Afronatrix anoscopus* containing prey was 38.4% and 46.6% respectively, and differed significantly between the two species ( $\chi^2$  test,  $df = 1$ ,  $P < 0.01$ ). The monthly proportion of *Grayia smythii* containing prey did not differ significantly from the null hypothesis of an equal monthly frequency of fed snakes across the whole year ( $\chi^2 = 12.7$ ,  $df = 11$ ,  $P = 0.315$ ), whereas the temporal proportion of *Afronatrix anoscopus* containing prey peaked during the wet months ( $\chi^2 = 12.5$ ,  $df = 5$ ,  $P < 0.05$ ) and consequently reduced feeding activity was recorded during the dry months ( $\chi^2 = 13.5$ ,  $df = 5$ ,  $P < 0.05$ , Figure 1b). The monthly proportion of fed snakes was similar in the two species during the dry season (September–March), whereas the frequency of fed specimens was significantly higher in *Afronatrix anoscopus* than in *Grayia smythii* during the wet season (April, May, June, July, and August;  $\chi^2$  test,  $df = 1$ , in all cases at least  $P < 0.05$ ).

### Overall diet analysis

The overall diet composition (all months combined) of the two sexes of *Afronatrix anoscopus* and *Grayia smythii* is given in Table 1. Among the 322 individuals of *Afronatrix anoscopus* which contained identifiable food in the stomach, 44 were subadults, 146 were males and 132 were females. Among the 213 individuals of *Grayia smythii* which contained identifiable prey, 39 were subadults, 84 were males and 90 were females.

*Afronatrix anoscopus.* From *Afronatrix anoscopus*, a total of 676 prey items were obtained (Table 1). The diet of subadults consisted almost exclusively of small-sized *Silurana tropicalis* (29.7% of the total prey items,  $n = 128$ ) and anuran tadpoles (56.2%), and the majority of the fed specimens contained multiple prey items of the latter prey type. The diet of both adult males and adult females consisted of a wide variety of amphibians and fish. In males the main prey type was anuran tadpoles. Larger prey items (frogs of the genus *Ptychadena*) accounted for a relatively low per cent of prey items (8.9% of the total), but were eaten by a relatively high number of specimens (17.1% of the total). Hence, many males had multiple small prey items or single large prey items. Female diet was also based essentially on two prey types (i.e. *Silurana tropicalis* and tadpoles), although they fed on a great variety of amphibian taxa. Food niche breadth was much higher in adults ( $B = 4.4$ ) than in juveniles ( $B = 2.4$ ), and was similar between adult males ( $B = 4.5$ ) and adult females ( $B = 4.3$ ).

*Grayia smythii.* A total of 390 prey items were obtained from *Grayia smythii* (Table 1). The diet of subadults

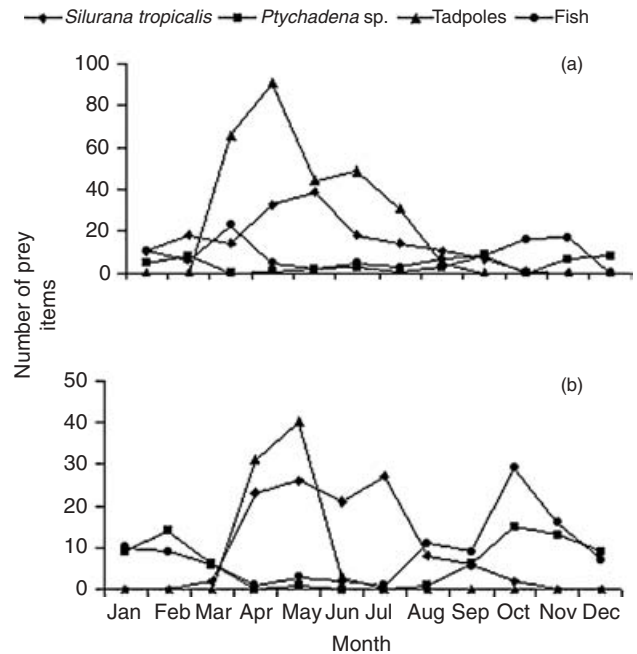
**Table 2.** Values of Pianka overlap measure on pairwise comparisons of diet composition of the various categories of snakes at the study area in southern Nigeria. Symbols: Aa, *Afronatrix anoscopus*; Gs, *Grayia smythii*.

	Aa males	Aa females	Gs juveniles	Gs males	Gs females
Aa juveniles	0.97	0.97	0.93	0.73	0.52
Aa males	****	0.98	0.94	0.77	0.67
Aa females		****	0.97	0.85	0.68
Gs juveniles			****	0.89	0.67
Gs males				****	0.77

consisted mainly of anuran tadpoles (34.8% of the prey items,  $n = 89$ ) and of *Silurana tropicalis* (29.2% of the prey items), and most specimens contained multiple items of both these prey. Adults of both sexes were primarily frog-eating, but also preyed on fish frequently. Males fed mainly on three prey types: *Silurana tropicalis* (accounting for 40.5% of the total prey items, and eaten by 52.4% of the fed individuals), *Ptychadena* sp. (14.7% of the prey items, and eaten by 25% of the snakes), and tadpoles (17.8% of the prey items, and eaten by 13.1% of the individuals). Females fed mainly upon *Ptychadena* spp. (32.6% of the prey items, and eaten by 41.1% of the fed specimens) and *Silurana tropicalis* (16.7% of the prey items, and eaten by 17.8% of the fed specimens). Compared to males, the females fed significantly more frequently (contingency table analysis,  $\chi^2 = 23.7$ ,  $P < 0.01$ ) upon adult toads (*Bufo* spp.) and significantly less frequently ( $\chi^2 = 11.8$ ,  $P < 0.05$ ) on anuran tadpoles (Table 1). Food niche breadth was slightly higher in adults ( $B = 5.1$ ) than in juveniles ( $B = 4.4$ ), and was higher in adult females ( $B = 5.7$ ) than in adult males ( $B = 4.4$ ).

**Interspecific comparisons in prey types.** Overall, both species were mainly frog-eating but also included fish in their diet (Table 1). However, *Grayia smythii* preyed upon fish significantly more often than *Afronatrix anoscopus* ( $\chi^2 = 10.0$ ,  $df = 1$ ,  $P < 0.01$ , calculated on the total number of prey items). This pattern also emerged when considering the proportion of fed specimens containing at least one fish item, which was 19.2% in *Afronatrix anoscopus* (total  $n = 322$  individuals) and 27.8% in *Grayia smythii* ( $n = 213$  individuals) ( $\chi^2 = 4.22$ ,  $df = 1$ ,  $P < 0.05$ ).

Overall, the diet composition of the two species was very similar, as shown by the high niche overlap values calculated for all the categories of individuals (juveniles, males, females) of both species (Table 2). It is noteworthy that there were very high food niche overlap values between juvenile *Grayia smythii* and adults (both sexes) of *Afronatrix anoscopus* ( $O > 0.9$  in all cases; see Table 2), i.e. between the two different species when their mean body size difference was removed from the analyses. Adult *Afronatrix anoscopus* and juvenile *Grayia smythii* were also identical in terms of dietary diversity ( $B = 4.4$  in both



**Figure 2.** Numbers of the main prey items found month-by-month in snake stomachs at the study area in southern Nigeria. *Afronatrix anoscopus* (a); *Grayia smythii* (b).

species). No case of cannibalism was recorded in either species.

**Interspecific comparisons in prey sizes.** A total of 238 prey items of *Afronatrix anoscopus* and 184 prey items of *Grayia smythii* were weighed. The mean size (in g) of the prey eaten by *Afronatrix anoscopus* ( $6.8 \pm 3.4$  g) was significantly smaller than the mean prey eaten by *Grayia smythii* ( $9.6 \pm 5.9$  g) (inter-sample difference:  $t = 2.71$ ,  $df = 420$ ,  $P < 0.001$ ), this being in agreement with the smaller body size of the former snake species versus the latter.

The larger individuals of both species selected against smaller prey sizes, as the minimum prey size increased directly with snake size (*Afronatrix anoscopus*,  $r_s = 0.36$ ,  $n = 164$ ,  $P < 0.01$ ; *Grayia smythii*,  $r_s = 0.38$ ,  $n = 152$ ,  $P < 0.01$ ). The differences between regression lines were not significant between *Afronatrix anoscopus* and *Grayia smythii* (ANCOVA on slopes:  $F_{1,113} = 0.29$ ,  $P > 0.7$ ).

### Temporal variation in diet composition

In order to avoid a risk of biased results due to small sample sizes, in this analysis only the four main prey types recorded in the two snake species, i.e. *Silurana tropicalis*, *Ptychadena* sp., anuran tadpoles, and all fish combined, were included.

With regard to *Afronatrix anoscopus* (Figure 2a), the main patterns were that (1) *Silurana tropicalis* was not

consumed at a constant rate across the year ( $\chi^2 = 120$ ,  $df = 11$ ,  $P < 0.001$ ), but was preyed upon particularly in April ( $\chi^2 = 26.7$ ,  $P < 0.001$ ) and in May ( $\chi^2 = 46$ ,  $P < 0.001$ ); (2) anuran tadpoles were taken almost exclusively during the wet months ( $\chi^2 = 468$ ,  $df = 11$ ,  $P < 0.001$ ), with peaks in March, April, May and June (in all cases at least  $P < 0.01$  compared to all the other months in pairwise comparisons); (3) *Ptychadena* spp. were not consumed at a constant rate through the year, but they were eaten significantly more often during the dry months ( $\chi^2 = 31.4$ ,  $df = 11$ ,  $P < 0.001$ ); and (4) fish were not consumed at a constant rate through the year ( $\chi^2 = 20.3$ ,  $df = 11$ ,  $P < 0.001$ ), but tended to be preyed upon particularly in the dry months, and with the most significant peak in March ( $\chi^2 = 23.7$ ,  $P < 0.001$ ).

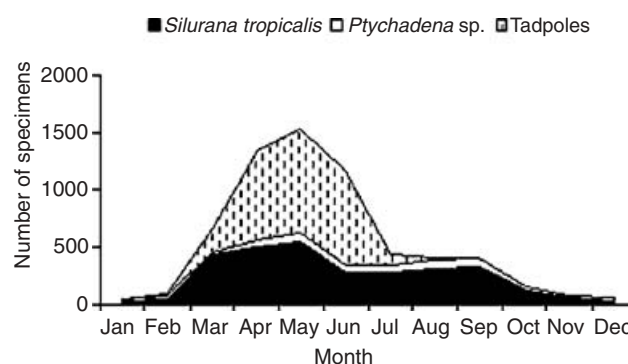
With regard to *Grayia smythii* (Figure 2b), the main patterns were that (1) *Silurana tropicalis* was not consumed at a constant rate through the year ( $\chi^2 = 144$ ,  $df = 11$ ,  $P < 0.001$ ), but almost exclusively during the wet months (peaks, all significant at  $P < 0.001$ , from April to July); (2) anuran tadpoles were not consumed constantly through the year ( $\chi^2 = 343$ ,  $df = 11$ ,  $P < 0.001$ ), but almost only in April and May (for both months,  $P < 0.001$  in all pairwise comparisons with every other month); (3) *Ptychadena* spp. were not taken constantly through the year ( $\chi^2 = 59.9$ ,  $df = 11$ ,  $P < 0.001$ ), but they were eaten mainly during the dry months (most significant peaks in February, October and November); and (4) fish were not taken constantly through the year ( $\chi^2 = 78.3$ ,  $df = 11$ ,  $P < 0.001$ ), but mainly during the dry months and with the greatest peak in October ( $\chi^2 = 47.7$ ,  $P < 0.001$ ).

The monthly dietary patterns were similar between species, but in *Grayia smythii* tadpoles and fish were prominent prey types during short periods (respectively, the early phases of the wet and of the dry seasons), whereas these prey types were more uniformly consumed by *Afronatrix anoscopus* (Figure 2).

### Food resource availability at the study area

The cumulative number of *Silurana tropicalis*, *Ptychadena* sp. and anuran tadpoles, captured per month is given in Figure 3. There were very strong seasonal patterns in the captures of all the three prey types, all being significantly more abundant during the wet season (April to September). Indeed, the cumulative number of all the potential prey captured strongly suggest that prey biomass increased during the wet season compared with the dry season (one-way ANOVA,  $F_{1,34} = 10.1$ ,  $P < 0.01$ ).

In both snake species, above-ground activity (expressed as per cent of individuals found in the open in relation to the total sample observed; cf. Figure 1a) was positively correlated to the relative monthly number of prey (in all cases, i.e. for both snake species and for all the three prey



**Figure 3.** Month-by-month resource availability in the field of three types of prey at the study area in southern Nigeria.

**Table 3.** Means ( $\pm$  SD) of the availability of the three prey types (i.e. number of specimens captured) at the study area in southern Nigeria during the wet and the dry season. Note that wet season extended from April to September. For all three prey types, the differences between seasons were statistically significant (at least  $P < 0.05$  by one-way ANOVA).

Prey type	Dry season	Wet season
<i>Silurana tropicalis</i>	115 $\pm$ 161	373 $\pm$ 121
<i>Ptychadena</i> sp.	23.2 $\pm$ 6.9	69.3 $\pm$ 4
Tadpoles	37.7 $\pm$ 75.6	437 $\pm$ 433

types surveyed,  $r > 0.51$ ,  $P < 0.05$ ). This suggests that snakes were more active in the wet season than in the dry season because prey were more abundant (Table 3).

In *Afronatrix anoscopus* the per cent of fed snakes peaked significantly during the wet months (Figure 1b), and was significantly correlated to the food resource availability (for all the three prey types surveyed,  $r > 0.55$ ,  $n = 12$ ,  $P < 0.05$ ). However, in *Grayia smythii* the proportion of snakes containing prey did not vary significantly through the year (Figure 1b), and, hence, was not correlated with prey abundance (for all the three prey types surveyed,  $r < 0.27$ ,  $n = 12$ ,  $P > 0.05$ ).

### Relationships between prey availability and prey consumption

To determine whether the monthly increase in consumption of a given prey type by *Afronatrix anoscopus* corresponded to an increase in the frequency of consumption of the same prey type by *Grayia smythii*, the numbers of prey items of each food category eaten by *Afronatrix* in each month were compared with the corresponding number of prey items of the same food category eaten by *Grayia* in the same month. This analysis revealed significant linear correlation between the two species ( $r = 0.51$ , adjusted  $r^2 = 0.24$ ; ANOVA,  $F_{1,46} = 16.1$ ,  $P < 0.01$ ). In order to analyse whether the two snake species used the available food resources (*Silurana tropicalis*, *Ptychadena* sp. and tadpoles) in relation to

**Table 4.** Results of the linear regression model applied to the relationships between the relative frequency of occurrence of each prey type (expressed as the number of food items; dependent variable) in the snake stomachs in each month and the frequency of occurrence of the same food type in the field (expressed as the number of items collected during quantitative surveys) during the same month (independent variable).

Type of prey	r	Adjusted r <sup>2</sup>	F (df = 1,10)	P value
<i>Afronatrix anoscopus</i>				
<i>Silurana tropicalis</i>	0.74	0.56	12.5	0.01
<i>Ptychadena</i> sp.	0.27	0.21	0.8	0.40
Tadpoles	0.77	0.55	14.6	0.01
<i>Grayia smythii</i>				
<i>Silurana tropicalis</i>	0.70	0.45	9.9	0.01
<i>Ptychadena</i> sp.	0.78	0.57	15.3	0.01
Tadpoles	0.81	0.62	18.8	0.01

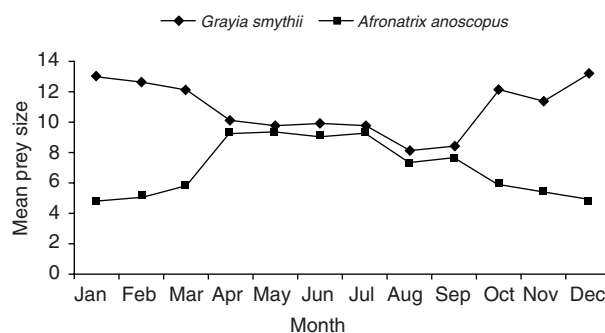
their monthly availability in the field, the occurrence of each prey type (expressed as the number of food items; dependent variable) in the snake stomachs in each month was compared to the occurrence of the same food type in the field (expressed as the number of items collected during my quantitative surveys) during the same month (independent variable). Apart from *Ptychadena* spp. obtained from *Afronatrix anoscopus* and number recorded in the field, all other relationships between prey availability and prey use by snakes were statistically significant (Table 4), which indicates that the two snake species were predatory opportunists, foraging on their preferred prey in relation to their relative availability in the field.

#### Relationships between food resource availability and prey size

The mean prey size of both snake species varied significantly across months (one-way ANOVA: for *Afronatrix anoscopus*:  $F_{11,628} = 48.7$ ,  $P < 0.001$ ; for *Grayia smythii*:  $F_{11,321} = 25.7$ ,  $P < 0.001$ ), and furthermore the mean prey size of *Afronatrix anoscopus* was significantly smaller than that of *Grayia smythii* in all months ( $P < 0.01$ ). The greatest interspecific differences in mean prey size occurred during the dry season months (Figure 4), i.e. during periods of prey shortage availability.

#### DISCUSSION

This study demonstrates that both *Afronatrix anoscopus* and *Grayia smythii* have similar diet composition, with a few species of frogs (*Silurana tropicalis* and *Ptychadena* sp.) and tadpoles being the principal prey components. In both species, some intersexual variation in diet and some differences between diets of adults and subadults were detected, but, overall, these differences were relatively small and based more on the prey size than on the prey type.



**Figure 4.** Month-by-month variation in mean prey size of *Afronatrix anoscopus* and *Grayia smythii* at the study area in southern Nigeria. In all months, t-tests for independent samples showed statistical significance (at least  $P < 0.01$ ).

The two snake species studied here also showed an ontogenetic change in diet composition, with diet diversity increasing with body size, and hence adults (especially the adult females of *Grayia smythii*) having a broader dietary spectrum than juveniles. This pattern is widespread in snakes (e.g. the viperids *Bitis gabonica* and *Bitis nasicornis*, Luiselli & Akani 2003). However, there are also species where the opposite pattern seems to be true (e.g. Brito 2004 for *Vipera latastei*, Santos & Llorente 1998 for *Natrix maura*). In other species of aquatic snake (e.g. *Nerodia rhombifera* from North America), the smaller specimens have less diverse diets than intermediate- and large-size specimens, but more diverse diets than very large specimens (Gibbons & Dorcas 2004, Plummer & Goy 1984).

Both snake species tended to select against smaller prey items (although foraging on relatively small fish and amphibian species). The same pattern (ontogenetic shift in lower size limit, sensu Arnold 1993) has already been observed in other species of piscivorous aquatic snakes (Jayne *et al.* 1988, Plummer & Goy 1984, Santos & Llorente 1998). This pattern has been classified by Arnold (1993) as 'enigmatic', and may to some extent depend on statistical artefacts (Arnold 1993).

The two species diverged considerably in terms of body size, with *Afronatrix anoscopus* being much smaller than *Grayia smythii*. Such a difference likely drives many other ecological divergences, notably in prey size. In fact, little competition would be expected between two species which are quite different in size (Pianka 1986). Of course, the overlap in body sizes owing to growth patterns (juvenile *Grayia smythii* may be similar in size compared with *Afronatrix anoscopus*) provide an interesting opportunity to test the effect of size (see below).

Similarity in prey composition is usually an important prerequisite for interspecific competition in snakes (Toft 1985). In the case of this study, it is evident that (1) the two species had a high overall similarity in prey type composition, and that (2) this similarity was

especially evident between *Grayia smythii* juveniles and *Afronatrix anoscopus* adults (both males and females, as revealed by the very high values of Pianka's overlap index and the very similar values of Simpson's diversity index found). Hence, it may be concluded that these latter categories of individuals are those which appear to be the more likely competitors, also given that their body sizes overlapped widely.

No evidence of interference competition of one species on the other was found, contrary to what happens in other guilds (terrestrial and arboreal) of Nigerian rainforest snakes (Luiselli *et al.* 1998).

The consumption of the major prey items by both snake species was clearly not constant through the year, but varied significantly with the season, with some types of prey (chiefly, the frog *Silurana tropicalis* and the anuran tadpoles) being consumed mainly during the wet months and other prey types (frogs of the genus *Ptychadena* and fish) during the dry months (Figure 2). With some minor differences, these overall patterns were seen clearly in both snake species, and strongly suggest that both species depended on the seasonal availability of these prey.

My study supports the general finding that in snakes there is a positive relationship between prey size and predator size (Arnold 1993). Indeed, *Afronatrix* being smaller consumed smaller prey compared with the larger *Grayia*. In terms of guild structure and community ecology theory, different prey size has already been suggested as facilitating coexistence of potential competitors feeding on the same limited food resource, especially when the two competitors also differ significantly in terms of their body size (Neale & Sacks 2001, Schoener 1982). Hence, the results of this study also support the theoretical expectations.

The present study showed that the availability of the major prey types (amphibians and fish) increased during the wet season. This pattern depended on the fact that lowland forests that are seasonally inundated are sometimes amongst the most productive habitats in the world (Molles *et al.* 1998). The huge nutrient input occurring during flood pulses supports large numbers of invertebrates, fish, and amphibians, that in turn serve as the base for these highly productive ecosystems (Ostfeld & Keesing 2000, Ross & Baker 1983, Turner *et al.* 1994). Both snake species consumed the various prey types in relation to their seasonal availability in the environment, and, hence, they can be considered as opportunists.

A consequence of the seasonal prey abundance is that, if the two snake species compete for food, such competition should be more pronounced during the dry season, with reduced prey abundance. Thus, we would expect to detect changes in the feeding ecology of these snakes during this part of the year. Indeed, although both species were opportunist predators that foraged mainly in

relation to prey availability, they partitioned the limited food resource during the dry season by foraging on prey organisms of similar type but of very different size (Figure 4). This suggests that increased competition may result in an adjustment of prey-size preferences in relation to the relative abundance of food. Of course, this scenario must be tested experimentally before being accepted, but the natural history data presented here strongly suggest that the above-mentioned pattern does occur in this system.

The type of prey eaten by these snakes differed slightly between months. How did these snakes manage to adjust their prey-size preferences during the period of depressed resource availability? During the period of high prey availability (i.e. the wet months), individuals of both species tended to be more active in the open, thus suggesting an increased foraging activity in this period (see also Madsen & Shine 1996, 2000). Hence, as expected, the frequency of fed specimens was higher during the period of high food availability in *Afronatrix anoscopus*. However, surprisingly, in *Grayia smythii* the proportion of fed individuals was similar during the dry and the wet seasons, suggesting that snakes may be equally successful at finding prey although their activity is reduced. This apparently counterintuitive result may be due to the snakes utilizing some alternative prey, the abundance and spatial distribution of which was not examined in this study (fish). Indeed, fish were eaten more frequently by *Grayia smythii* than by *Afronatrix anoscopus*, especially during the dry season. During the dry months there is less surface of potential habitat inundated (Luiselli *et al.* 2005b), and hence the snakes may move less because their foraging habitat is smaller. As a consequence, if their prey is more concentrated (as seems the case; Luiselli, unpubl. data), their predatory efforts may be facilitated, thus explaining the constant proportions of fed specimens despite the reduction in activity intensity.

What are the ecological and behavioural mechanisms that may facilitate the snakes in adjusting their food size preferences in relation to food availability? I suggest that the diel activity patterns may partly explain this ability. During the dry season, *Afronatrix anoscopus* is more nocturnal than *Grayia smythii*, whereas both species are diurnal during the wet season (Luiselli, submitted). So, it is possible that *Afronatrix* may find particularly small, and *Grayia smythii* particularly large prey during the dry season, because of this different diel activity pattern, as their prey types exhibited different diel activity patterns in relation to their own body size (age).

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## LITERATURE CITED

- ARNOLD, S. J. 1993. Foraging theory and prey-size-predator-size relations in snakes. Pp. 87–115 in Seigel, R. A. & Collins, J. T. (eds). *Snakes – ecology & behavior*. McGraw-Hill, New York.
- BARBAULT, R. 1977. Structure and dynamique d'une hérapécénose de Lamto (Cote d'Ivoire). *Géologie et Ecologie Tropicale* 1:309–334.
- BARBAULT, R. 1984. Stratégies de reproduction et démographie de quelques amphibiens anoues tropicaux. *Oikos* 43:77–87.
- BARBAULT, R. 1987. Pression de predation et évolution des stratégies démographiques en zone tropicale: le cas des lézards et des amphibiens. *Revue de Zoologie Africaine* 101:301–327.
- BARBAULT, R. 1991. Ecological constraints and community dynamics: linking community patterns to organismal ecology. The case of tropical herpetofaunas. *Acta Oecologica* 12:139–163.
- BRITO, J. C. 2004. Feeding ecology of *Vipera latastei* in northern Portugal: ontogenetic shifts, prey size and seasonal variations. *Herpetological Journal* 14:13–19.
- BRONMARK, C., RUNDLE, S. D. & ERLANDSSON, A. 1991. Interactions between freshwater snails and tadpoles: competition and facilitation. *Oecologia* 87:8–18.
- CAPIZZI, D. & LUISELLI, L. 1996. Feeding relationships and competitive interactions between phylogenetically unrelated predators (owls and snakes). *Acta Oecologica* 17:265–284.
- CONNELL, J. H. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122:661–696.
- GIBBONS, J. W. & DORCAS, M. E. 2004. *North American watersnakes*. University of Oklahoma Press, Norman. 438 pp.
- GUREVITCH, J., MORROW, L. L., WALLACE, A. & WALSH, J. S. 1992. A meta-analysis of competition in field experiments. *American Naturalist* 140:539–572.
- HANSKI, I. 1987. Colonization of ephemeral habitats. Pp.155–185 in Gray, A. J., Crawley, M. J. & Edwards, P. J. (eds.). *Colonization, succession and stability*. Blackwell Science, Oxford.
- HIMES, J. G. 2003a. Intra- and interspecific competition among the water snakes *Nerodia sipedon* and *Nerodia rhombifer*. *Journal of Herpetology* 37:126–131.
- HIMES, J. G. 2003b. Diet composition of *Nerodia sipedon* (Serpentes: Colubridae) and its dietary overlap with, and chemical recognition of *Agkistrodon piscivorus* (Serpentes: Viperidae). *Amphibia-Reptilia* 24:181–188.
- HURLBERT, S. H., LOAYZA, W. & MORENO, T. 1986. Fish-flamingo-plankton interactions in Peruvian Andes. *Limnology and Oceanography* 31:457–468.
- KOFRON, C. P. 1978. Foods and habitats of aquatic snakes (Reptilia, Serpentes) in a Louisiana swamp. *Journal of Herpetology* 12:543–554.
- KRIJGER, C. L., PETERS, Y. C. & SEVENSTER, J. C. 2001. Competitive ability of neotropical *Drosophila* predicted from larval development times. *Oikos* 92:325–332.
- JAYNE, B. C., VORIS, H. K. & HEANG, K. B. 1988. Diet, feeding behavior, growth, and numbers of a population of *Cerberus rynchops* (Serpentes: Homalopsinae) in Malaysia. *Fieldiana* 50:1–15.
- LUISELLI, L. 2003. Do snakes exhibit shifts in feeding ecology associated with the presence or absence of potential competitors? A case study from tropical Africa. *Canadian Journal of Zoology* 81:228–236.
- 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. & AKANI, G. C. 2002. Is thermoregulation really unimportant for tropical reptiles? Comparative study in four sympatric snake species from Africa. *Acta Oecologica* 23:59–68.
- LUISELLI, L. & AKANI, G. C. 2003. Diet of sympatric Gaboon vipers (*Bitis gabonica*) and Nose-horned vipers (*Bitis nasicornis*) in southern Nigeria. *African Journal of Herpetology* 52:101–106.
- 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.
- LUISELLI, L. & RUGIERO, L. 1991. Food niche partitioning by water snakes (genus *Natrix*) at a freshwater environment in central Italy. *Journal of Freshwater Ecology* 6:439–444.
- LUISELLI, L., AKANI, G. C. & CAPIZZI, D. 1998. Food resource partitioning of a community of snakes in a swamp rainforest of south-eastern Nigeria. *Journal of Zoology, London* 246:125–133.
- LUISELLI, L., ANGELICI, F. M. & AKANI, G. C. 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., POLITANO, E., UDE, L. & WARIBOKO, S. M. 2003. Diet of the semi-aquatic snake, *Afonatrix anoscopus* (Colubridae) in southern Nigeria. *African Journal of Herpetology* 52:123–126.
- LUISELLI, L., AKANI, G. C., RUGIERO, L. & POLITANO, E. 2005a. Relationships between body size, population abundance and niche characteristics in the communities of snakes from three habitats in southern Nigeria. *Journal of Zoology, London* 265:207–213.
- LUISELLI, L., AKANI, G. C., ANGELICI, F. M., UDE, L. & WARIBOKO, S. M. 2005b. Seasonal variation in habitat use in sympatric Afrotropical semi-aquatic snakes, *Grayia smythii* and *Afonatrix anoscopus* (Colubridae). *Amphibia-Reptilia* 26:372–376.
- MADSEN, T. & SHINE, R. 1996. Seasonal migrations of predators and prey: pythons and rats in tropical Australia. *Ecology* 77:149–156.

- MADSEN, T. & SHINE, R. 2000. Rain, fish and snakes: climatically driven population dynamics of Arafura filesnakes in tropical Australia. *Oecologia* 124:208–215.
- MOKANY, A. & SHINE, R. 2003. Competition between tadpoles and mosquito larvae. *Oecologia* 135:615–620.
- MOLLES, M. C., CRAWFORD, C. S., ELLIS, L. M., VALETT, H. M. & DAHM, C. N. 1998. Managed flooding for riparian ecosystem restoration. *Bioscience* 48:749–756.
- MORIN, P. J. 1983. Predation, competition, and the composition of larval anuran guilds. *Ecological Monographs* 53:119–138.
- MUSHINSKY, H. R. & HEBRARD, J. J. 1977. Food partitioning by five species of water snakes in Louisiana. *Herpetologica* 33:162–166.
- MUSHINSKY, H. R. & LOTZ, K. H. 1980. Chemoreceptive responses of two sympatric water snakes to extracts of commonly ingested prey species: ontogenetic and ecological considerations. *Journal of Chemical Ecology* 6:523–535.
- MUSHINSKY, H. R., HEBRARD, J. J. & VODOPICH, D. S. 1982. Ontogeny of water snake foraging ecology. *Ecology* 63:1624–1629.
- NEALE, J. C. C. & SACKS, B. N. 2001. Resource utilization and interspecific relations of sympatric bobcats and coyotes. *Oikos* 94:236–248.
- OSTFELD, R. S. & KEESING, F. 2000. Pulsed resources and community dynamics of consumers in terrestrial ecosystems. *Trends in Ecology and Evolution* 15:232–237.
- PIANKA, E. R. 1986. *The ecology and natural history of the desert lizards*. Princeton University Press, Princeton.
- PLUMMER, M. V. & GOY, J. M. 1984. Ontogenetic dietary shift of water snakes (*Nerodia rhombifera*) in a fish hatchery. *Copeia* 1984:550–552.
- RAY, J. C. & SUNQUIST, M. E. 2001. Trophic relations in a community of African rainforest carnivores. *Oecologia* 127:395–408.
- ROSS, S. T. & BAKER, J. A. 1983. The response of fishes to periodic spring floods in a southeastern stream. *American Midland Naturalist* 109:1–14.
- SANTOS, X. & LLORENTE, G. A. 1998. Sexual and size-related differences in the diet of the snake *Natrix maura* from the Ebro Delta, Spain. *Herpetological Journal* 8:161–165.
- SCHOENER, T. W. 1982. The controversy over interspecific competition. *American Scientist* 70:586–595.
- SHORROCKS, B. 1990. Coexistence in a patchy environment. Pp.91–106 in Shorrocks, B. & Swingland, I. S. (eds.). *Living in a patchy environment*. Oxford University Press, Oxford.
- SIMPSON, E. H. 1949. The measure of diversity. *Nature* 163:688.
- TOFT, C. A. 1985. Resource partitioning in amphibians and reptiles. *Copeia* 1985:1–21.
- TURNER, T. F., TREXLER, J. C., MILLER, G. L. & TOYER, K. E. 1994. Temporal and spatial dynamics of larval and juvenile fish abundance in a temperate floodplain river. *Copeia* 1994:174–183.
- VITT, L. J. 1987. Communities. Pp.335–365 in Seigel, R. A., Collins, J. S. & Novak, S. S. (eds.). *Snakes: ecology and evolutionary biology*. MacMillan, New York.
- VITT, L. J. & VANGILDER, L. D. 1983. Ecology of a snake community in north-eastern Brazil. *Amphibia-Reptilia* 4:273–296.