

# 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*

Luca LUISELLI<sup>1</sup>

## RÉSUMÉ

La zone de forêt continue du sud du Nigéria héberge deux espèces de najas (*Naja melanoleuca* et *N. nigricollis*). Elle est actuellement soumise à une forte déforestation due aux activités humaines (extractions et prospections pétrolières notamment, mais aussi effets de la surpopulation). À l'évidence, jusqu'à un passé récent, l'espèce forestière (*N. melanoleuca*) était beaucoup plus commune que l'espèce savanicole (*N. nigricollis*) quand les taux de déforestation étaient bien inférieurs aux actuels. De nos jours, l'espèce savanicole est très commune et répandue, non seulement dans les zones péri-urbaines et les habitats altérés, mais aussi en vieille forêt secondaire. De plus, contrairement à l'espèce forestière, elle est particulière en ce qu'elle réduit considérablement son alimentation durant la saison sèche. Cela s'observe chez les adultes et chez les jeunes, chez les mâles et chez les femelles, et dans trois types d'habitats différents (forêt, voisinage des habitations et mosaïque forêt-plantations). Aucun lien avec la biologie de la reproduction ne peut être établi pour expliquer ce fait. L'hypothèse la plus vraisemblable est que cette particularité écologique refléterait une adaptation suboptimale de l'espèce savanicole au biome forestier et serait le « fantôme » d'une récente invasion de la zone forestière par cette espèce savanicole.

## SUMMARY

The region of continuous rainforest in southern Nigeria is inhabited by two species of cobras (*Naja melanoleuca* and *N. nigricollis*), and is nowadays subjected to devastating deforestation due to human activity (mainly oil extraction and exploration projects) and overpopulation. Evidence is presented that the forest species (*N. melanoleuca*) was much more common than the savanna species (*N. nigricollis*) in the recent past when rates of deforestation were much smaller than today. Nowadays, the savanna species is very common and widespread, not only in suburban and altered habitats, but also in mature secondary forests. Moreover, contrary to the forest species, it is peculiar in that it greatly reduces its feeding rates during the peak of the dry season. These reduced feeding rates were observed in both adults and juveniles, in both males and females, and in three different habitat types (forest, suburbs, and forest-plantation mosaic). No links with reproductive biology can be advocated to explain such a pattern. It is hypothesized that this ecological pattern reflects suboptimal adaptation of the savanna species to rainforest biota, and is a "ghost" of this species' recent invasion of the rainforest region.

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<sup>1</sup> F.I.Z.V., via Olona 7, I-00198 Rome, Italy; and Institute of Environmental Studies "Demetra", via dei Cochi 48/B, I-00133 Rome, Italy (e-mails: [lucamclu@tin.it](mailto:lucamclu@tin.it); [lucalui@iol.it](mailto:lucalui@iol.it))

## INTRODUCTION

Many animal species experience range reductions or extensions due to a complex set of dynamic events (*e.g.*, Ricklefs, 1973; Brandon, 1995; Williamson, 1996). For the ecologist, it is of particular interest to study the dynamics of adaptation that many species have experienced for extending their range. Concerning vertebrates, most case studies have been birds or mammals (*e.g.* see Moulton & Pimm, 1983; Ehlich, 1989; Pimm, 1991; Brandon, 1995; Brooke *et al.*, 1995; Case, 1996), whereas reptiles, and snakes in particular, have been less studied in this respect (but see Case & Bolger, 1991; Case *et al.*, 1994; Petren & Case, 1998; Losos & Spiller, 1999).

The tropical regions of Africa are especially prone to eventual cases of range extensions among vertebrates, as a consequence of a variety of new niches available to potential “pioneers” due to the dramatic changes of the general environmental conditions that wide regions of this continent have been experiencing in the last few decades. For instance, the opening of new access roads and the formation of savanna-like secondary vegetation in formerly forested areas may favour range extensions of species typically linked to savannas, to the detriment of those species typically linked to rainforest biota (Politano, 1998).

The above-mentioned ecological phenomenon may be particularly spread in Nigeria, which is contextually the by far most populated country of the continent (with a population well over 100 millions people), and one of the most developed, in the southernmost regions where much of the oil and gas industry is concentrated (de Montclos, 1994). Due to this over-excess of anthropization, more than 90 % of the originally forested zone has felled, and — apart of a few regions of Cross River State in the extreme south-east of the country —, the actual landscape is formed by a few fragments of rainforest islands interspersed among a sea of farmlands, cultivations, industrial and urban centres (Singh *et al.*, 1995; Politano, 1998). This massive rainforest decline has been quite a recent event, which dates back mainly to the oil industry “boom” in the 1970s (Singh *et al.*, 1995; Politano, 1998). Nonetheless, Nigeria is an important hotspot for biodiversity, especially in the south-eastern part of the country where rainforest and mangrove forest blocks are found (Singh *et al.*, 1995; Olajide & Eniang, 2000), and where several endemic taxa are found in many faunal and floral groups (Kingdon, 1990). Therefore, the recently deforested regions of southern Nigeria seem to be ideal “natural laboratories” where to test for eventual cases of range extensions and new dynamic adaptations of vertebrates to the suddenly changing environmental conditions.

A study case of special interest seems to be that of the cobras (genus *Naja*; Elapidae), which are among the largest and most venomous snakes of the African continent. Two species of cobras are found in the forested regions of southern Nigeria: the forest cobra (*Naja melanoleuca*) and the spitting cobra (*Naja nigricollis*) (Politano, 1998; Luiselli *et al.*, 1998; Luiselli & Angelici, 2000; Eniang & Luiselli, 2002). These two species are parapatric or even sympatric over a very wide area in southern Nigeria (in a belt of approximately 800 × 300 km), especially in those sites which have been just recently deforested (Luiselli & Angelici, 2000; Luiselli, 2001; and see Menzies, 1962, 1966, for similar observations in Sierra Leone). However, the width of the overlap belt observed in Nigeria is certainly much surprising, as these two species are clearly different in terms of habitat requirements: the forest cobra is mainly linked to mature forests and swamp-forests and rarely enters into very altered habitats, whereas the spitting

cobra is often found in highly disturbed habitats (including suburbs, plantations, farmlands), and is typical of savannas and open bushes (Spawls & Branch, 1997; Luiselli & Angelici, 2000). Moreover, the ranges of the two species are obviously different also at the continental scale (see maps in Spawls & Branch, 1997): the forest cobra occurs almost throughout the forests of sub-Saharan Africa, from Sierra Leone to western Kenya, south to northern Angola and Kasai (Zaire), and occurs also in isolated forest islands in Sudan, mount Kenya, and the islands of the Gulf of Guinea. On the other hand, the spitting cobra occurs in most of sub-Saharan Africa, but does not enter deeply inside the Guinea-Congo continuous rainforest belt, apart that in southern Nigeria.

Thus, an emerging question is: Why do the rainforest zone in southern Nigeria is so unusual in being inhabited by sympatric populations of these two cobra species? Aims of the present paper are:

- (1) to try to answer the above-mentioned question;
- (2) to examine whether spitting cobras could exhibit any type of suboptimal adaptation to the rainforest biota, which is known to be an unusual habitat for this species (Spawls & Branch, 1997);
- (3) to examine whether the forest cobra is still ecologically superior to the spitting cobra in this forested region, or whether it is succumbing to the competition of its congener.

To examine these three points, I use the by far largest dataset available on the ecology of free-ranging afrotropical cobras available in the literature (see also Luiselli *et al.*, 1998, 2002; Luiselli & Angelici, 2000; Luiselli, 2001).

## MATERIALS AND METHODS

### STUDY AREA

The field study was carried out from September 1996 to August 2001 (with some data recorded even in 1994 and 1995), in several localities of south-eastern Nigeria (Figure 1; for the territories surveyed see also Luiselli & Angelici, 2000, and for a detailed environmental description, see Luiselli *et al.*, 2000). The study region is tropical, with wet season from May to September, and dry season from October to April. The wettest period of the year is June-July, and the driest period between late December and February. Activity of the two cobra species peak during the wetter months of the wet season (Luiselli & Angelici, 2000).

### METHODS

Methods used to survey the study area, capture cobras, and analyse their food items, are fully detailed in Luiselli & Angelici (2000), and here I just present a brief summary of it. Data presented here were partially published in Luiselli (2001) and in Luiselli *et al.* (2002), but much original new information is added in the present paper.

Fieldwork was conducted under all climatic conditions, but with a bias towards the diurnal hours (from 8 a.m. to 6 p.m.) due to security constraints related to the prevailing unstable political situation. Field effort was almost identical in the

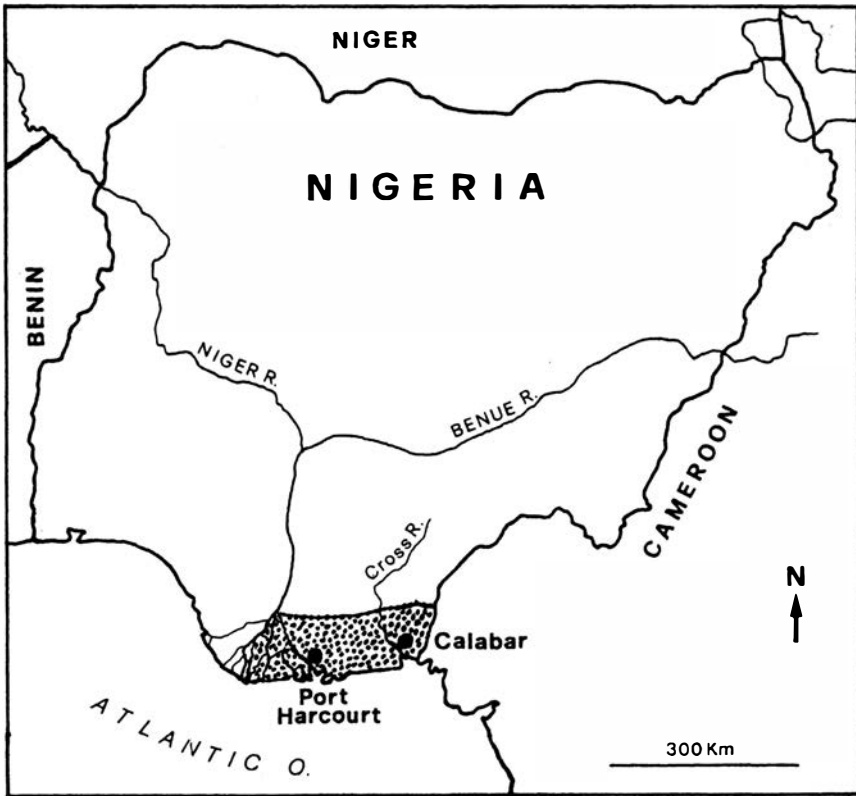


Figure 1. — Map of Nigeria, showing the study region.

wet and dry seasons: 402 field days during the wet season and 411 days during the dry season. Random routes to locate snakes were followed throughout every available macrohabitat type in each study area (see Luiselli & Angelici, 2000 for a characterization of the various study habitats). When seen, the cobras were captured by hand with the aid of sticks, but additional free-ranging specimens were captured by pitfall traps with drift fences and by traps used by local people to capture frogs and fish. The site of capture and the habitat at each capture site were recorded. The captured snakes were sexed and measured for snout-vent length (to the nearest  $\pm 1$  cm) and tail length. Then, they were palpated in the abdomen until regurgitation of ingested food or defecation occurred. No specimens were killed or damaged for the purposes of this study. Prey items were identified to the lowest taxon possible (see Luiselli *et al.*, 2002, for a list of preys).

For analysis of cobra diets in the various habitats, we divided specimens into three groups, according to their habitats of capture. We used maps (scale: 1: 10,000) of the vegetation and landscape utilization of the surveyed territory produced by the Federal Government of Nigeria and/or by Aquater S.p.A. for environmental assessment reports, to define how to assign each snake record to

any of the three groups. The three groups were: (1) cobras captured in suburbs and wide plantations or derived savannas (*i.e.* areas with < 15 % of forested territory inside a radius of 10 km around the site of capture); (2) cobras captured in the plantation-forest mosaic (*i.e.* areas with < 65 % and > 15 % of forested territory inside a radius of 10 km around the site of capture); and (3) cobras captured in mature forests (*i.e.* areas with > 65 % of forested territory inside a radius of 10 km around the site of capture). It should be mentioned that forested patches in groups (1) and (2) were secondary or at least partially altered forests, whereas those in group (3) were often undisturbed or slightly altered forests. Specimens captured in mangroves were also classified in the three groups depending on the status and surface of the mangrove formations, *i.e.* by considering mangroves exactly as a type of forest. To avoid strong bias in data collection, we have maintained as much as possible a similar field effort in each of the three habitat groups. Specimens < 100 cm total length are considered as juveniles (*cf.* Luiselli & Angelici, 2000).

Statistical analyses were performed with all tests two-tailed and  $\alpha$  set at 5 %.

## RESULTS AND DISCUSSION

### HISTORICAL ECOLOGY OF COBRAS

The literature on the distribution of African snakes is generally very preliminary, and almost nothing is known on the historical variations of the various species' ranges. Thus, it is often difficult to understand whether a given species is actually reducing or increasing its range. Nonetheless, the environments of southern Nigeria have been sufficiently explored in the recent past to make some general considerations possible, at least with regard to the two species of cobra, *Naja melanoleuca* and *Naja nigricollis*.

Based on field casualties and literature compilation, the most accurate continental description of the ranges of the two cobra species indicates that *N. melanoleuca* is widespread in the continuous rainforest and in the derived savanna regions of Nigeria, whereas *N. nigricollis* is found in Guinea savanna region, with isolated records from the rainforest region (*i.e.* Port Harcourt and Calabar) (*cf.* Spawls & Branch, 1997). In fact, these ranges are fully consistent with the known ecological distribution of the two species, that normally have very limited overlap areas at the continental scale (Spawls & Branch, 1997). In addition, the most accurate compilation of field records from Nigeria (*i.e.* Butler & Reid, 1990) was also quite consistent with the above-described patterns, giving a general impression of the presence, inside the continuous rainforest region, of a widespread species (*i.e.* *N. melanoleuca*), and of a localized species confined to few suburban areas (*i.e.* *N. nigricollis*).

This apparent scenario was strongly different from that I was looking at, when I started studying the ecology of Nigerian forest snakes in the middle of '90s. Indeed, *N. nigricollis* emerged immediately as one of the most abundant and widespread snakes, whereas *N. melanoleuca* appeared uncommon and nearly confined to mature forest blocks (*e.g.*, see Akani *et al.*, 1999). I was immediately puzzled by this contrasting evidence, also in consideration of the fact that Dr Godfrey C. Akani, an experienced herpetologist based at the Rivers State University of Science and Technology in Port Harcourt, confirmed that, just twenty

years earlier, the spitting cobra was very rare almost everywhere apart in the suburbs of Port Harcourt, whereas the forest cobra was common and widespread. Thus, I supposed to be in front of a case of range extension by one invading species (*N. nigricollis*) to the detriment of another congener (*N. melanoleuca*), probably as a result of the rapid deforestation of the study region. To collate more data on it, I tried to get as much information as possible from the available local literature, including unpublished environmental reports for industry development projects (EIA reports), and university level theses. In total, I examined for data over 50 EIA reports by industry companies working in southern Nigeria, and over 30 theses on vertebrate zoology topics. In most cases, my efforts were unfruitful, as either no mention of these snakes is done (e.g., Powell, 1993, 1996; Singh *et al.*, 1995; Isoun *et al.*, 1996), or they are mentioned without much detail (e.g., Reid, 1989; Schmitt, 1996). Nevertheless, in a EIA report for AGIP oil company (Politano, 1985), raw data are given on *all* the snakes captured in the Niger Delta over their two-year-long study period (443 specimens), with locality, and habitat of capture of the various specimens. These data are unavailable to herpetologists if not, as us, involved specifically in environmental works with this industry organization, but they are nonetheless of enormous scientific relevance, and will be in fact fully re-analysed by myself in a forthcoming paper. In any case, only two spitting cobras were captured in that study (years 1981-1982; both were collected at Rumueme, a suburb of Port Harcourt), whereas 64 forest cobras were captured, from a variety of localities and different habitats. This source was, therefore, another convincing proof of the fact that *N. nigricollis* was certainly much rarer in the recent past than nowadays, the contrary being true for *N. melanoleuca*.

SEASONAL AND HABITAT VARIATIONS IN THE PROPORTION OF COBRAS WITH PREY: ADULT VERSUS JUVENILE, AND INTER-HABITAT DIFFERENCES

The month-by-month distribution of the captures of the two cobra species is presented in Figure 2. Exactly as observed in previous studies (*cf.* Luiselli &

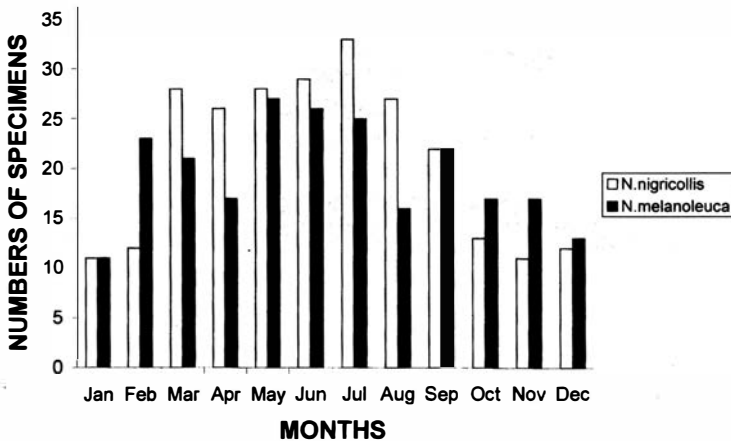


Figure 2. — Numbers of cobra specimens examined for food data, month-by-month (years 1994-2001), in southern Nigeria.

Angelici, 2000), the activity of the two species peaked in the wet months (April to September) at a statistically significant rate ( $\chi^2$  test,  $df = 1$ ,  $P < 0.001$ ). The percent of snakes with food in stomachs varied from 0 % to 85 % in *N. nigricollis* and from 52 % to 100 % in *N. melanoleuca*. Nonetheless, there were important seasonal pattern differences between these two species. In fact, in *N. melanoleuca* no significant differences between wet and dry season months emerged in terms of percent of “fed” specimens ( $\chi^2$  test,  $df = 1$ ,  $P > 0.6$ ), whereas in *N. nigricollis* there was a clear peak of feeding rates during the wet months, and a very reduced feeding activity during the dry months ( $\chi^2$  test,  $df = 1$ ,  $P < 0.0001$ ). This evidence widely supports and further extends previous data available from the same study region (see Luiselli, 2001). Indeed, the analysis of the proportion of cobra specimens with prey, with arcsin transformed data, shows that the interaction between cobra species and season was significant, with significant species-specific differences (model with species, rainy season, and interaction as effects: species:  $MS = 0.611$ ,  $F = 34.9$ ,  $P = 0.00001$ ; rainy season:  $MS = 0.713$ ,  $F = 41.4$ ,  $P = 0.0000001$ ; interaction:  $MS = 0.473$ ,  $F = 26.3$ ,  $P = 0.00004$ ).

The two sexes did not depart significantly from the above-described pattern, either in *N. nigricollis* or *N. melanoleuca* (for all comparisons,  $\chi^2$  test, at least  $P > 0.3$ ). In addition, the adults were consistent with juveniles, in both species and seasons, as for the percent of “fed” specimens is concerned (for all comparisons,  $\chi^2$  test, at least  $P > 0.1$ ).

The percentages of specimens of the two species of cobra captured in three habitat types are presented in figure 3, and the percentages of prey types in diets of adults and juveniles are presented in figure 4 (for crude data, see Luiselli *et al.*, 2002). The three habitat types were not significantly different in terms of monthly percent of fed specimens of both species (for all comparisons,  $\chi^2$  test with  $df = 2$ ,

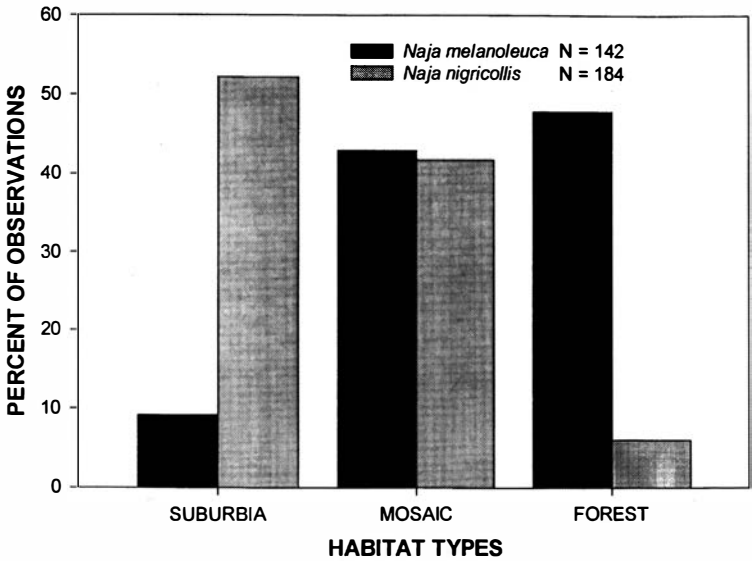


Figure 3. — Percentages of specimens of two species of cobra captured in three habitat types, as described in “Methods”.

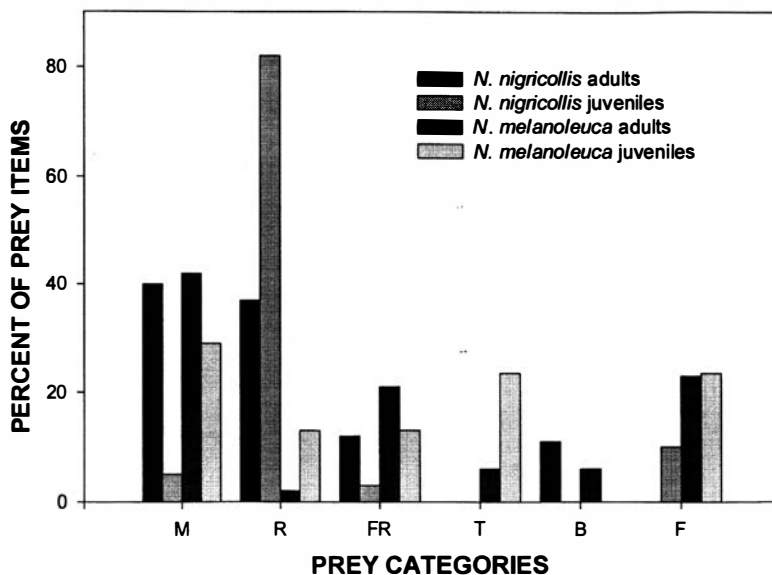


Figure 4. — Percentages of prey types in diets of adults and juveniles of two cobra species in southern Nigeria. Symbols: M = mammals, R = reptiles, FR = frogs, T = tadpoles, B = birds, F = fish.

at least  $P > 0.2$ ), although the same inter-habitat comparison was not done as for adults *versus* juveniles is concerned, due to the too little juvenile sample examined.

#### TESTING THE HYPOTHESES

The combination of (i) the different seasonal feeding patterns exhibited by the two cobra species, and (ii) the inferences on the historical ecology as emerged from the above-mentioned considerations, suggests that rainforest spitting cobras reduce feeding rates during the dry months (for general inferences on the reduction of activity during the dry season in cobras, see Luiselli & Angelici, 2000) because their behaviour is just a “ghost” of their recent past, when they were “normal” spitting cobras of dry savannas, which were constrained to aestivate during the peak of the dry season (see also Luiselli, 2001). Thus, the seasonal pattern emerging from this study may be related to the recent invasion by these cobras of the rainforest region of southern Nigeria, where they were very rare when the forest was continuous (*i.e.*, before the '70s). Therefore, this pattern may reflect a suboptimal adaptation to the newly colonized region (Luiselli, 2001).

Although the “ghost-of-the-past” hypothesis certainly deserves attention, the evidence in support of it remains indirect in the absence of experimental data. So, it seems necessary to briefly discuss eventual complications with its acceptance.

If it is accepted, obviously the seasonal anorexia of spitting cobras should be a genetically fixed character, and so such anorexia should be encoded into a



particular combination of alleles. Thus, it would be quite easy to test for the reliability of this hypothesis by analysing a good sample of spitting cobra populations throughout West and Central Africa, and it is hoped that such studies will be soon started.

In my opinion, it is difficult to accept the hypothesis that the observed pattern may depend on reproduction-linked factors, although several snake species are well known to reduce feeding rates during the mating season or the pregnancy period (*e.g.*, see Saint-Girons, 1952). Indeed, spitting cobras may have prolonged reproductive periods and multiple mating periods (Luiselli & Angelici, 2000; Luiselli *et al.*, submitted), which do not necessarily coincide with the peak of the dry season. And, last but not least, the gravid females normally eat during the pregnancy phase (Luiselli, 2001).

From this point, there are profound differences between males and females in snakes (*e.g.*, Saint-Girons, 1952), and thus it is neither scientifically correct nor easy to merge the sexes into a single explanation. In fact, there are several respective ecological or physiological reasons why female and male snakes sometimes stop feeding, although these reasons have been carefully studied only in a few species of temperate regions (and so may not apply to afro-tropical cobras). High plasma levels of testosterone often inhibit male's foraging activity, perhaps because there is a trade-off between mating and foraging behaviours in this sex. In females the situation is probably more complex (*e.g.*, see Naulleau & Fleury, 1990; Bonnet *et al.*, 2001a). Some authors suggested that gravid females cannot accommodate meals in their stomach (Vitt & Congdon, 1978; Shine, 1988; Ford & Seigel, 1989), but this hypothesis is not firmly supported by experimental evidence. For instance, female vipers (*Vipera aspis*, *Vipera berus*) are known to feed during pregnancy (Madsen & Shine, 1993), and the same is true for gravid female cobras (this study). In fact, some species exhibit obligatory anorexia during gestation (*e.g.*, *Bitis gabonica*, Akani *et al.*, unpublished) whilst other species show facultative anorexia (*Vipera aspis*, *Vipera berus*; Madsen & Shine, 1993; Bonnet *et al.*, 2001b). It is a pity that these interspecific differences in feeding patterns are still unexplainable at the present time.

However, the fact that (i) both juveniles and adults drastically reduce feeding during the peak of the dry season, and that (ii) the same pattern did not vary in the three habitat types of southern Nigeria, is another strong indication that the reproduction-linked hypothesis is to be rejected. Other hypotheses may be refuted as well (see Luiselli, 2001).

In conclusion, based on the data presented in this paper and in previous studies (Luiselli & Angelici, 2000; Luiselli, 2001; Luiselli *et al.*, 2002), it seems that *N. melanoleuca* still maintain an ecological superiority over *N. nigricollis* in pristine and secondary mature rainforests, due to some apparent suboptimal adaptations of the latter. However, the increasing rates of deforestation, together with an evident adaptability of the latter species, would suggest that in the next decades the ecological superiority of *N. melanoleuca* will be counteracted by the higher adaptability of *N. nigricollis* for altered habitats, with a likely further reduction of the former species' range, and an increase of the latter species' range. The continued monitoring of the population ecology and life-history attributes of the two species would probably permit to collate crucial data on the long-term adaptation strategies of these species to the rapidly changing afro-tropical environment.

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