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Is sexual size dimorphism in relative head size correlated with intersexual dietary divergence in West African forest cobras, *Naja melanoleuca*?

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Abstract

Sex-biased differences in dietary habits of snakes are often linked to pronounced sexual size dimorphism in absolute body size or in relative head size. We studied the food habits of free-ranging forest cobras (*Naja melanoleuca*) in southern Nigeria to find whether any intersexual dietary divergence is present in this species, and measured both museum vouchers and free-ranging specimens to find whether any intersexual divergence in relative head size is present. We demonstrated that: (1) head sizes increases more rapidly with SVL in females than in males, with a result that, at the same body length, the females tended to have significantly larger heads; (2) males and females were nearly identical in dietary habits, both if we consider prey size or prey type; (3) both sexes tended to prey upon relatively little sized preys. It is concluded that traditional evolutionary scenarios for explaining sexual dimorphism and food niche divergence are hardly valid in this case, and we need to look for entirely different hypotheses (e.g. linked to the sexual preference of males for females with larger heads).

Contents

Introduction

It is widely accepted that a potentially important source of variation in dietary habits of a given predator is its gender, and it has been suggested that niche divergence may contribute substantially to the evolution of sexual dimorphism (e.g. see Darwin, 1871; Slatkin, 1984; Shine, 1986; Camilleri & Shine, 1990; Houston & Shine, 1993). With regard to snakes, it has been recently highlighted that intersexual divergence in dietary habits is strongly linked to pronounced sexual size dimorphism in absolute body size or in head sizes (e.g. see Shine, 1986; Camilleri & Shine, 1990; Houston & Shine, 1993), given that both these conditions are widespread among snakes (Shine, 1991). Moreover, it has been also observed that large-headed specimens could ingest larger prey, and that the snakes' net energy gain rose steeply with body size and with swallowing capacity, which depends on relative head size (Forsman, 1992). And, apparently as a consequence of it, snake populations inhabiting areas with larger preys may tend to have larger heads than conspecifics inhabiting areas with smaller preys (Werner, 1994). Nevertheless, and despite the claimed generality of the above-mentioned patterns, the case studies have been so far very few, but interpretation of these patterns is hindered by the paucity of information on sex differences in snake diet. Therefore, we absolutely need much more species added to these case studies before accepting the generality of these phenomena.

In this paper we study the intersexual dietary divergence in relation to relative head size sexual dimorphism in the forest cobra, *Naja melanoleuca*. We carried out our study in a region (southern Nigeria) where this species has been carefully studied, and where its diet is very well known from a quantitative point of view (Luiselli *et al*, 1998; Luiselli & Angelici, 2000; Luiselli *et al.*, 2002).

Since forest cobras are often so large (> 2 m in length) and highly dangerous (their bites may easily kill adult people) from preventing precise measurements of head size in the field, we examined whether there is any significant difference in relative head size between sexes by using also several museum vouchers (stored at the California Academy of Sciences at San Francisco [CAS], and at the Zoological Museum at Copenhagen [ZMUC]), whereas the dietary data are entirely relative to free-ranging specimens inspected for any food item in the stomach.

Materials and methods

The following vouchers, all from Nigeria or, in additional cases, from other countries of West Africa, were measured for snout-vent length (SVL, to the nearest 1 mm) and head length (HL, to the nearest 1 mm): CAS 104584, 16956, 136118, 103119, 147664, 103276, 121002, 154799, 103278, 103277, 16981, 16982, 7298, ZMUC 6529, 6527, 6528, 6526, 655, 6541, 65511, 6539. In addition, the same measurements were taken from 13 unnumbered specimens stored at the Institute Demetra (Roma, Italy), at the Cross River National Park (Akampka and Butatong, Nigeria), at the University of Calabar (Nigeria), at the University of Uyo (Nigeria), at the University of Abraka (Nigeria), and at the Department of Biological Sciences, Rivers State University of Port Harcourt (Nigeria). When possible, we recorded the same measures from free-ranging specimens, captured between September 1996 and September 2000 in southern Nigeria (for the surveyed areas, see Luiselli & Angelici, 2000).

Cobras were captured by hands with the aid of sticks, or by pitfall traps with drift fences, or by traps used by local people to capture frogs and fish. The captured snakes were sexed, measured, and palpated in the abdomen until regurgitation of ingested food or defecation occurred. Specimens found already dead (road-killed or macheted by farmers, or preserved in local collections; for a list of them see Luiselli and Angelici 2000) were dissected in order to obtain diet data. No specimens were killed or damaged for the purposes of this study. Prey items were identified to the lowest taxon possible. The mass of the prey item at the time of its ingestion was estimated, when possible, by comparing the item to intact conspecifics of various sizes from the authors' personal collection, or measuring the fresh biomass in perfectly preserved items.

Statistical analyses were performed with all tests two-tailed and a set at 5%. Data on raw body masses of both snakes and their prey were natural log-transformed to meet the assumptions of linearity. In the text, we present mean values ± 1 standard deviation.

Results

Head size sexual dimorphism

Including both museum vouchers and specimens measured alive in the field, we recorded SVL and HL of 42 males, 40 females, and 7 unsexable juveniles. As predictable, SVL and HL were significantly correlated in the three groups (Table 1), although the relationships relative to juveniles was just within the significance level (P = 0.0487). It probably depended on the fact that there was much more homogeneity in the body sizes of this group of specimens (range of SVL: 445 - 540 mm) than in the ranges of body sizes of both males (775 - 2370 mm) and females (867 - 2332 mm), other than important differences in the sizes of the three samples. Slopes of the regressions deviated significantly from 0 in both males (F = 9.613, P = 0.0211) and females (F = 90.53, P = 0.0002). Analysis of Covariance revealed that the ordinate-intercepts of the regressions relative to males and females were significantly different, and that the slope of the females was higher than that of the males (F = 3.71, DFn = 2, DFd = 84, P = 0.04). It indicated that head size increases more rapidly with SVL in females than in males, i.e. at the same body length, the females had generally larger heads than the males. However, it should be reminded that the

Table I. Statistical results of the regressions of (ln-transformed) snout-vent length (mm) against (ln-transformed) head length (mm) in the sample studied of *Naja melanoleuca* from West Africa

	MALES $N = 42$	FEMALES $N = 40$	JUVENILES $N = 7$
Slope	0.025 ± 0.008	0.0156 ± 0.001	0.0106 ± 0.011
Y-intercept	- 8.35 ± 13.89	11.39 ± 2.51	13.18 ± 5.36
r^2	0.6157	0.9477	0.1795
P	< 0.0001	< 0.0001	< 0.05

r-squared values relative to males is low, which suggests that this pattern, although statistically significant, is not particularly marked.

Food habits

In terms of taxonomical dietary composition (see Table 2 for a list of preys), both sexes preyed mainly upon mammals, fish, and frogs. Contingency table analysis revealed that the taxonomical composition of the diet of the two sexes was very similar ($P > 0.8$).

The mean prey mass/predator mass ratio was similar in the two sexes (0.197 in males [$N = 25$] versus 0.201 in females [$N = 21$]) ($P = 0.45$ at two tailed *t* test with df = 44). In both sexes there was a significant positive relationship between ln-transformed prey mass and ln-transformed predator mass (in all cases, adjusted $r^2 > 0.4$, $P < 0.0001$). Analysis of Covariance revealed that the regression line of males did not differ significantly from that of females (Heterogeneity of slopes: $F = 0.4318$, $P = 0.443$; heterogeneity of y-intercepts: $F = 0.4133$, $P = 0.521$), thus showing that the type of relationship between predator size and prey size was indeed similar between sexes.

Table II. Prey eaten by *Naja melanoleuca* specimens in south-eastern Nigeria. Only data for males and females are presented in this table.

Prey item	Males	Females
Mammals		
Mus musculoides	2	1
Lemniscomys striatus	6	13
Rattus rattus	1	2
Dendromus sp.	1	-
Lophuromys sp.	1	1
Funisciurus sp.	1	1
Rodentia undetermined	15	10
Crocidura sp.	2	-
Birds		
Undetermined Passerine	2	4
Chicken eggs and pulli	1	1
Reptiles		
Psammophis sp.	1	-
Natriciteres sp.	-	1
Mochlus fernandii	-	1
Amphibians		
Ptychadena sp. adults	2	1
Ptychadena sp. (tadpoles)	4	4
Hoplobatrachus occipitalis	1	-
Ranidae undetermined	9	9
Bufo sp. (adults)	1	2
Bufo sp. (tadpoles)	1	3
Fish		
Periophtalmus sp.	18	18
Cyprinidae indet.	3	2
Fish undetermined	4	4
TOTAL	76	78

Discussion

This study demonstrates that in *Naja melanoleuca*, although females tend to have larger heads than males at the same body size (being not larger in terms of absolute body size, see Luiselli & Angelici, 2000; Luiselli et al., 2002), the two sexes are nearly identical as for dietary habits, both if we consider prey type or prey size. Thus, this study presents some evidence that pronounced sexual dimorphism in head size does not always reflect the presence of any important dietary divergence in snakes, and that the generality of previous conclusions (e.g. see Shine, 1986) should always be tested for before accepting it with unknown species.

With regard to the studied case, it is difficult to devise any plausible evolutionary scenario for the observed pattern of a significant intersexual divergence in relative head size but not in dietary habits. Traditional theory (e.g. see Houston & Shine, 1993) suggests that sexual size dimorphism in snakes result either from trophic niche divergence, or from sexual selection (respectively, through selection of larger litter sizes (and thus body sizes) of females, or larger body sizes of males (to win more sexual combats). But, with regard to *Naja melanoleuca,* the problem seems a lot more complex. In this species, both the occurrence of male-male combats during the mating season (dry season, from December to February) and the usual positive relationships between female size and litter size have been observed (Luiselli & Angelici, 2000). Moreover, *Naja melanoleuca* is an elapid, and superiority based on absolute size is a common pattern of ritual combats among male elapids (e.g. see Shine *et al.,* 1981). Thus, the lack of a significant sexual dimorphism in absolute body size (Luiselli & Angelici, 2000; Luiselli et al., 2002) is likely dependent on the equilibrium in the interaction of two antagonist evolutive forces: sexual selection towards larger males (to win more combats), and natural selection towards larger females (to produce larger litters). Shine (1978) has observed the same pattern in several snake species with concurrently occurring male-male combats and positive relationships between female size and litter size.

But, why do females have larger heads than males at the same body length? Given that the snakes swallow the whole prey, the simplest solution would be that females have larger heads in order to swallow larger preys. But, in fact, they preyed upon organisms of size nearly identical as that of prey eaten by males (Luiselli et al., 2002), and moreover both sexes preyed upon very little prey in comparison to their own body size (Luiselli et al., 2002). Therefore, we doubt whether this simple solution may be true in the case studied. A possible alternative explanation for the observed pattern is that the larger head of females is a "ghost" of a past condition, i.e. it reflects an adaptation towards eating on larger prey that is not longer occurring at the present time. However, this hypothesis is not testable on the basis of the data in our hands. As alternative, we suggest that larger head size in females may be a result of the selection via male choice of mating. In other snakes (e.g., *Natrix natrix,* see Luiselli, 1996), the males mate preferably with the largest female available, when a choice is possible. We suggest that male cobras may choose the female with the largest head, although our hypothesis is still entirely tentative and is going to be tested by us in the years to come, with a specifically designed experimental procedure.

In any case, it is evident that cobras may be very useful models to study the ecological attributes of sexual dimorphism, as well as many other aspects of snake ecology (e.g. see Luiselli & Angelici, 2000; Luiselli, 2001, 2002).

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