Ecology of cobras from southern Africa

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Abstract

Large slender-bodied snakes that forage actively for a generalized array of small vertebrates are conspicuous elements of the terrestrial snake fauna of most continents; the venomous elapid species fill this role in much of Asia, Africa and Australia. Our dissections of eight species of cobras from southern Africa *Aspidelaps, Hemachatus, Naja; Serpentes and Elapidae* (total of 1290 specimens) provide extensive data on sexual dimorphism, reproductive biology and food habits. Females grow larger than males in *Aspidelaps lubricus* and *Naja nigricincta*, but (perhaps reflecting selection on male body size due to male–male combat) males grow as large as females in *Naja anchietae, Naja melanoleuca, Naja mossambica, Naja nivea* and *Hemachatus haemachatus*, and males grow larger than females in *Naja annulifera*. Overall, the degree of male size superiority is higher in species with a larger absolute mean adult body size. Male cobras typically have larger heads and longer tails than conspecific females. Fecundity increases with maternal body size, and is higher in the viviparous rhinkals *H. haemachatus* than in the oviparous *Naja* species studied. Diets are broad in all eight species, comprising a wide variety of amphibians, reptiles, mammals and (less often) birds. Ontogenetic (size-related) shifts in dietary composition (amphibian to reptile to mammal) are significant within some taxa (*N. annulifera, N. nigricincta*) but absent in others (notably *N. nivea*, the most arid-adapted species). Overall, despite substantial interspecific variation among the eight study species, strong parallels are evident between the cobras of southern Africa and their ecological counterparts in other continents.

Introduction

Recent decades have seen a rapid proliferation of scientific research on the ecology of snakes (Seigel & Collins, 1993; Shine & Bonnet, 2000; Beaupre, 2002); generating a remarkable increase in our knowledge at two levels. First, detailed and intensive studies on a few 'model species', most notably North American garter snakes (Mason, 1993; Shine, Langkilde & Mason, 2003a) and European vipers (Madsen et al., 1993; Luiselli, 1995; Bonnet et al., 2001) have provided more sophisticated insights into ecological processes within these populations. Thus, basic ecological parameters such as mating systems, spatial ecology and so forth are now relatively well understood for at least some snake populations and lineages. Second, the geographic and phylogenetic base of studies has expanded enormously. Until a few years ago, research on snake ecology was strongly biased towards cool-climate North American and northern European taxa (Parker & Plummer, 1987; Fitch, 1999). In recent years, however, tropical snakes have attracted intense scrutiny in Africa (Luiselli & Angelici, 1998; Luiselli, Angelici & Akani,

2000), the West Indies (Henderson, 1993), Australia (Brown & Shine, 2005; Brown, Shine & Madsen, 2005) and South America (Almeido-Santos et al., 1999; Almeida-Santos & Salomão, 2002; Martins, Marques & Sazima, 2002). Importantly, many of the focal species for these studies belong to phylogenetic lineages only distantly related to the 'model organisms' of earlier studies. Strong phylogenetic conservatism in ecological traits (Shine, 1989) allied to plasticity in response to local environmental conditions (Seigel & Ford, 1991; Madsen & Shine, 1999) mean that this increased breadth both phylogenetically and ecologically puts us in a much stronger position to detect generalities in ecological patterns.

Nonetheless, many major lineages of snakes remain poorly known. Perhaps surprisingly, this tends to be true for some of the snake taxa that are most familiar to the general public, and that feature most heavily in television documentaries and zoo collections – that is, large and highly venomous species. Although spectacular, such animals rarely occur in densities and in places that facilitate the logistics of field study. Perhaps one of the best examples of

such a high-profile but poorly studied lineage involves the cobras and their allies (*Aspidelaps, Naja, Hemachatus, Ophiophagus*, etc.). Although species of the genus *Naja* are abundant over much of Asia and Africa, and are significant both for human welfare (as common causes of snakebite) and for economic issues (via commercial exploitation: Jenkins & Broad, 1994; Boeadi *et al.*, 1998), their taxonomy has been clarified only recently (Wüster & Broadley, 2003; Broadley & Wüster, 2004; Broadley & Baldwin, 2006). Apart from some basic information obtained from harvested specimens (Boeadi *et al.*, 1998), the only detailed ecological data on cobras come from extensive field studies conducted by Luiselli and his colleagues on Nigerian species (Luiselli & Angelici, 2000; Luiselli *et al.*, 2002a). Given the strong differences in climate and vegetation types between Nigeria and southern Africa, as well as the differences in snake species composition, it is also clearly of interest to document the basic biology of cobra radiation within southern Africa.

Although the work of Luiselli's team proves that field-based research on live African elapids is indeed possible, the logistical difficulties are immense. Another way to quickly accumulate important basic ecological data is through examination of preserved specimens in museum collections, and this approach has proven highly successful for groups that are otherwise very difficult to study (Shine 1987, 1989). In turn, such information constitutes a solid empirical basis for detecting overall patterns in traits such as sexual dimorphism, reproductive biology and dietary habits, for comparison with other datasets and ultimately for framing and testing hypotheses about the evolutionary and ecological processes that have shaped the ecology of snakes on a global scale.

Study species

Recent molecular studies provide strong evidence for monophyly of the genus *Naja*, for sister-group status between *Naja, Hemachatus* and *Aspidelaps*, and on phylogenetic relationships among these taxa (Keogh, 1998; Slowinski & Keogh, 2000; J. S. Keogh, unpubl. data). We examined eight species within this clade, as follows:

(1) The coral shield cobra (Broadley & Baldwin, 2006; previously called the coral snake) *Aspidelaps lubricus* is a relatively small (up to 70 cm) nocturnal stout-bodied burrowing taxon from south-western Africa.

(2) The rhinkal *Hemachatus haemachatus* is also relatively stocky, but larger (up to 1.2 m), and can spit venom as well as bite; this is the only viviparous species among our sample and is found in south-eastern Africa. Its diel activity varies geographically and seasonally, and in the Highveld grasslands it is mainly diurnal (Alexander, 1996). However, it is more nocturnal in Zimbabwe miombo woodland (Broadley & Cock, 1975) and Eastern Cape coastal fynbos (W. R. Branch, unpubl. obs.).

(3) Regarded as conspecific until recently, the snouted Anchieta's cobra *Naja anchietae* is restricted to south-western Africa whereas the snouted cobra *Naja annulifera*

occurs in the south-east (Broadley & Wüster, 2004). Both are large (up to >2 m) mainly crepuscular oviparous snakes found over a broad range of habitats.

(4) The forest cobra *Naja melanoleuca* is also very large (up to >2.5 m), but is mainly diurnal and restricted to more mesic, often riparian habitats with relatively thick vegetation. A number of cryptic sibling species are subsumed under *N. melanoleuca*, but only one taxon is found in southern Africa (D. G. Broadley & W. Wüster, pers. comm.).

(5) The spitting cobras *Naja mossambica* and *Naja nigricincta* are medium-sized (<2 m) savannah species, with geographically disjunct distributions. The Mozambique spitting cobra or m'fezi, *N. mossambica*, is widely distributed through south-eastern Africa whereas the western barred spitting cobra *N. nigricincta* is restricted to south-western areas. Both these spitting cobras are primarily nocturnal, closely related and have hybridized in captivity (Marais & Liebenberg, 1980). The status of *Naja woodi* remains problematic. Broadley (1974) treated it and *N. nigricincta* as southern races of *Naja nigricollis*. However, Branch (1998) considered *N. nigricincta* to be a valid species with *N. woodi* treated conservatively as a southern race, although it is predominantly diurnal in contrast to the nocturnal habits of *N. nigricincta*. This taxonomic confusion does not affect our analysis, however, as we studied only typical *N. nigricincta* from northern Namibia.

(6) The smaller (up to 1.5 m) Cape cobra *Naja nivea* penetrates further south than any of its congeners, and is common in relatively arid karroid regions. This species is mainly diurnal, although it may become crepuscular in summer in the northern parts of its range (Branch, 1998).

Methods

We measured and dissected preserved specimens of the above eight elapid species from southern Africa (south of the 17°S latitude, corresponding to the northern borders of Namibia, Botswana and Zimbabwe) in the collections of the Northern Flagship Institute (formerly the Transvaal Museum) and Bayworld (incorporating the Port Elizabeth Museum) in the Republic of South Africa, the State Museum of Namibia and the Directorate of Wildlife Conservation (both in Windhoek, Namibia), the National Museum of Bloemfontein and the South African Museum, Cape Town. Identification of all specimens was verified (by W. R. B.) at the time that we gathered ecological and morphological data, and has been updated with respect to subsequent taxonomic changes. For most animals we recorded snout–vent length (SVL), tail length, head length (from the posterior margin of the lower jaw to the tip of the snout), head width (at the widest point) and eye diameter. The specimen was opened with a mid-ventral incision, and any prey items in the alimentary canal (including the hindgut) were removed for later identification. Sex and reproductive status of the snakes were determined by visual inspection of the gonads. Males were considered mature if they had enlarged, turgid testes and/or white, thickened efferent ducts

(indicating the presence of sperm). Females were classed as mature if they had thick muscular oviducts, vitellogenic ovarian follicles and/or oviductal eggs or embryos. Damage to some specimens during collection meant that our sample sizes varied among traits as well as among species; for example, we frequently were unable to obtain reliable measures of some head dimensions.

Because of geographic variation in collection methods for the snakes that we examined, our sample is poorly suited for analyses of traits such as the proportions of animals that contained prey items in their alimentary tracts or that were in reproductive condition. Some collection methods (such as roadkills, a common source of South African snakes) are likely to produce recently fed or reproductive adult animals, whereas others (especially specimens that drowned in the Otjiwarongo Canal of Namibia) involve snakes of a wide size range that are likely to have been trapped for weeks prior to collection and thus contain neither food nor eggs. Accordingly, we do not present analyses of such traits.

Results

Sample sizes, age structure and sex ratio

We obtained data on a total of 1290 snakes, with sample sizes smallest for *N. melanoleuca* ($n = 48$) and largest for *H. haemachatus* ($n = 237$). The relative proportions of adult versus juvenile specimens varied significantly among the eight study species for both sexes (males: $\chi^2 = 89.47$, 7 d.f., $P < 0.0001$; females: $\chi^2 = 27.55$, 7 d.f., $P < 0.0003$). The primary difference was between the 'spitters' *N. mossambica* and *N. nigricincta* (in which juveniles outnumbered adults) compared with all other species (in which adults outnumbered juveniles). Despite this variation, there was a clear overall pattern for the proportion of juvenile animals to be higher in females than in conspecific males (true in all species; paired $t = 3.97$, 7 d.f., $P < 0.005$).

Sex ratios did not show significant interspecific variation among adults ($\chi^2 = 7.81$, 7 d.f., $P = 0.35$) but varied among juveniles ($\chi^2 = 15.05$, 7 d.f., $P < 0.04$). Among adults, males consistently outnumbered females in museum collections (true in all species; mean = 65% male, against a null of 50%, $t = 6.59$, 7 d.f., $P < 0.0003$). Samples of juvenile snakes were close to 50% male (mean = 49%, $t = 0.38$, 7 d.f., $P = 0.72$). Accordingly, the proportion of males was higher among adults than in conspecific juveniles (true in all species; paired $t = 4.05$, 7 d.f., $P < 0.005$).

Sexual dimorphism

We examined possible sex differences in body size at maturation, mean adult body size, maximum body size and body proportions. The first three traits are of interest because they interact: for example, males might exceed females in mean adult SVL because they either (1) mature larger, and reach the same maximum size, or (2) mature at the same size or smaller, but eventually grow larger. Using mean adult SVL as a measure of body size, sexual size

dimorphism was minor for most of the taxa (Fig. 1a) and statistically significant only for *A. lubricus*, where females attained larger mean adult sizes than did conspecific males (Table 1). However, this apparent monomorphism obscures variation in minimum and maximum body sizes of adult animals of each sex. If analysis is restricted to the largest 20% of adult specimens of each sex, females averaged significantly larger than males in *N. nigricincta* as well as *A. lubricus* whereas the reverse was true in *N. annulifera* (Fig. 1b, Table 1). Minimum sizes at sexual maturation were significantly lower in males than in females for *A. lubricus* and *H. haemachatus* and close to significance in *N. melanoleuca* ($P = 0.06$; Table 1).

Returning to sexual dimorphism in mean adult body sizes (the variable calculated in most previous studies), the index of sexual size dimorphism (SSD) as proposed by Gibbons & Lovich (1990) ranged from $+0.22$ in *A. lubricus* to -0.08 in *N. anchietae* (i.e. from females 22% longer than males, through to males 8% longer than females). In an
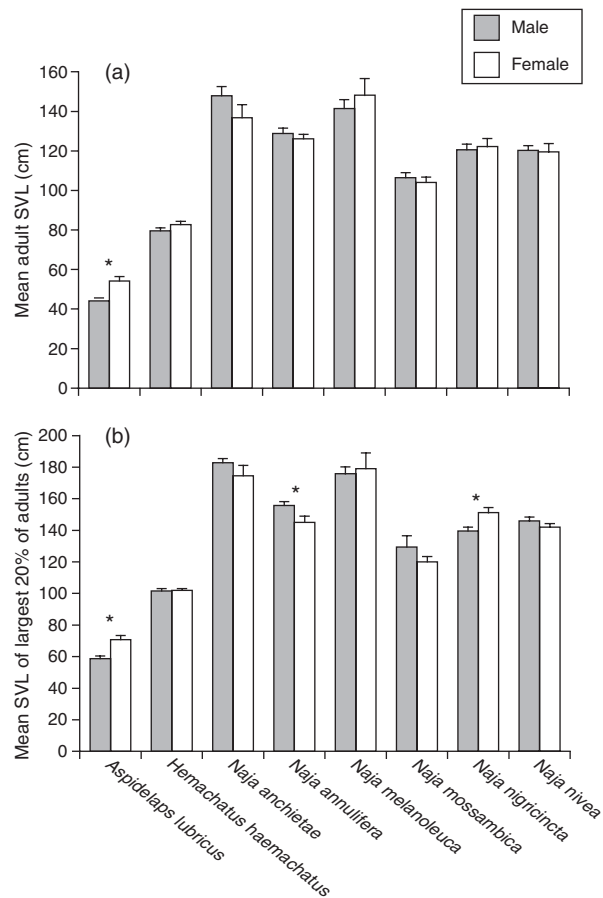

Figure 1 Sexual size dimorphism in adult specimens of African elapid snakes using snout–vent length (SVL) as a measure of body size. The upper graph (a) is based on mean adult SVL, whereas the lower graph (b) is based on the largest 20% of adults of each sex. The histograms show mean values and one standard error. Asterisks show statistically significant ($P < 0.05$) differences between the sexes.

Table 1 Sex differences in body sizes and proportions in the elapid snake species examined in our study

Trait	Covariate	Species	Heterogeneity of slopes test			Analysis of variance or covariance		
			F	d.f.	P	F	d.f.	P
Mean adult SVL	–	*Aspidelaps lubricus*	–	–	–	16.29	1,64	**0.0001**
		Hemachatus haemachatus				1.74	1,144	0.19
		Naja anchietae				1.83	1,43	0.18
		Naja annulifera				0.53	1,81	0.47
		Naja melanoleuca				0.52	1,30	0.48
		Naja mossambica				0.34	1,52	0.56
		Naja nigricincta				0.11	1,46	0.74
		Naja nivea				0.02	1,96	0.88
Mean SVL of the largest 20% of adults of each sex	–	*A. lubricus*				15.94	1,11	**0.002**
		H. haemachatus				0.03	1,28	0.86
		N. anchietae				2.00	1,7	0.20
		N. annulifera				5.72	1,14	**0.03**
		N. melanoleuca				0.13	1,4	0.73
		N. mossambica				0.89	1,9	0.37
		N. nigricincta				7.87	1,10	**0.02**
		N. nivea				1.16	1,20	0.29
Mean SVL of the smallest 20% of adults of each sex	–	*A. lubricus*				163.21	1,11	**0.0001**
		H. haemachatus				33.96	1,28	**0.0001**
		N. anchietae				0.39	1,4	0.55
		N. annulifera				1.38	1,14	0.26
		N. melanoleuca				7.01	1,4	0.06
		N. mossambica				2.19	1,9	0.17
		N. nigricincta				0.01	1,10	0.94
		N. nivea				0.08	1,20	0.79
Head length	SVL	*A. lubricus*	2.69	1,85	0.10	8.06	1,86	**0.006**
		H. haemachatus	9.41	1,210	**0.002**	–	–	–
		N. anchietae	0.10	1,58	0.75	4.61	1,59	**0.04**
		N. annulifera	2.71	1,8	0.14	3.01	1,9	0.12
		N. melanoleuca	1.65	1,44	0.21	2.19	1,45	0.15
		N. mossambica	3.24	1,120	0.07	11.53	1,121	**0.001**
		N. nigricincta	1.70	1,93	0.20	7.68	1,94	**0.007**
		N. nivea	7.14	1,127	**0.009**	–	–	–
Tail length	SVL	*A. lubricus*	3.95	1,85	**0.05**	–	–	–
		H. haemachatus	5.55	1,221	**0.02**	–	–	–
		N. anchietae	11.25	1,49	**0.002**			
		N. annulifera	0.002	1,107	0.97	0.71	1,108	0.40
		N. melanoleuca	0.36	1,39	0.55	0.42	1,40	0.52
		N. mossambica	0.72	1,122	0.40	1.72	1,123	0.19
		N. nigricincta	2.56	1,90	0.11	7.21	1,91	**0.009**
		N. nivea	0.44	1,122	0.51	6.24	1,123	**0.015**
Head width	Head length	*A. lubricus*	5.86	1,81	**0.02**	–	–	–
		H. haemachatus	0.02	1,208	0.88	1.90	1,209	0.17
		N. anchietae	2.81	1,57	0.10	3.34	1,58	0.07
		N. annulifera	0.36	1,8	0.57	2.97	1,9	0.12
		N. melanoleuca	0.28	1,44	0.60	0.21	1,45	0.65
		N. mossambica	4.38	1,117	**0.04**	–	–	–
		N. nigricincta	0.25	1,86	0.62	0.89	1,87	0.35
		N. nivea	0.84	1,127	0.36	0.81	1,128	0.37
Eye diameter	Head length	*A. lubricus*	1.13	1,86	0.29	1.84	1,87	0.18
		H. haemachatus	1.22	1,209	0.27	1.03	1,210	0.31
		N. anchietae	6.38	1,45	**0.03**			
		N. annulifera	2.64	1,5	0.17	0.02	1,6	0.89
		N. melanoleuca	0.30	1,43	0.59	0.09	1,44	0.76
		N. mossambica	0.14	1,103	0.75	0.87	1,104	0.35
		N. nigricincta	1.69	1,86	0.20	0.13	1,87	0.72
		N. nivea	0.96	1,127	0.33	0.10	1,128	0.75

This table shows the results of tests for sex differences in (1) mean adult snout–vent length (SVL), (2) mean SVLs for the largest 20% of adult individuals of each sex and (3) body proportions relative to SVL. The first two sets of tests are based on one-way ANOVA with sex as the factor, whereas the third set of tests (those that include a covariate in the second column) comprises analysis of heterogeneity of slopes, followed by single-factor analysis of covariance if (and only if) slopes did not differ significantly. Some variables could not be measured reliably for some specimens (due to damage, tail loss, etc.); hence sample sizes differ among traits. Boldface font refers to a significant ($P < 0.05$) difference between adult males and females.

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interspecific regression, mean adult SVL (i.e. average of male plus female values) was negatively related to this index of SSD ($n = 8$, $r = -0.79$, $P < 0.02$). However, this result was largely due to a single species, *A. lubricus*; deletion of data for this taxon removed the statistical significance of the regression ($n = 7$, $r = -0.35$, $P = 0.45$).

The sexes may differ in bodily proportions even at identical body sizes. ANCOVA revealed several cases of this kind. For example, female *A. lubricus* (which grow larger than conspecific males) have smaller heads relative to SVL and shorter tails relative to SVL than do males. Head shape also differs between the sexes, with males exhibiting significantly narrower heads relative to length (see Table 1). Males of most of our study species have longer heads than do females at the same SVL (*A. lubricus, H. haemachatus, N. anchietae, N. mossambica, N. nigricincta* and *N. nivea*: Table 1) and relatively longer tails in males than in females occur in five of the eight species also (*A. lubricus, H. haemachatus, N. anchietae, N. nigricincta* and *N. nivea*: Table 1). The other variables that we measured revealed sexual dimorphism only in a minority of species (Table 1). Overall, then, male and female cobras generally attained similar adult body sizes, but males typically had longer tails and larger heads than did females at the same body length.

Reproduction

Shelled eggs *in utero* confirmed oviparity as the reproductive mode of all the study species except for the viviparous *H. haemachatus*. However, we found relatively few reproductive females, and thus sample sizes for fecundity estimates are low. Figure 2 shows that fecundity increased with maternal SVL overall, but that *Hemachatus* produces a greater number of offspring than do *Aspidelaps* or *Naja* (interaction SVL × genus, $F_{2,15} = 1.50$, $P = 0.26$; after deleting the non-significant interaction term, ANCOVA $F_{2,17} = 5.17$, $P < 0.02$).
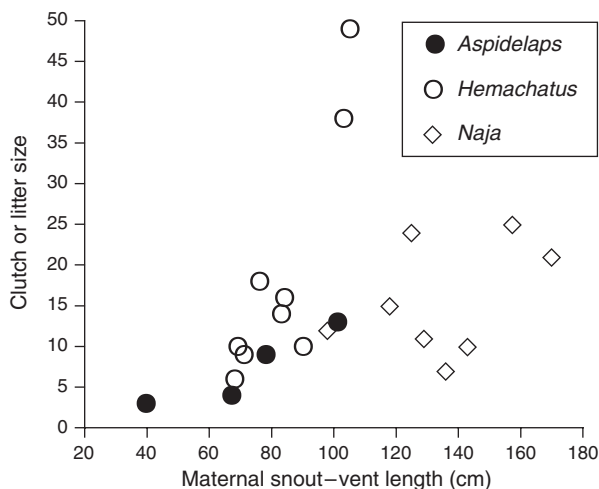

Figure 2 Fecundity of African elapid snakes as a function of maternal body size (snout–vent length) and genus.

Despite the scarcity of reproductive females in our sample, clear seasonality was evident in the reproductive cycle. Of 19 adult female snakes containing enlarged ovarian follicles (>11 mm diameter) or oviductal eggs and with known collection dates, almost all were from warmer months of the year (two in August, three in September, five in October, three in November, two in December, four in January). Seasonal distributions of these animals thus differed from those of non-reproductive adult females, because the latter were collected over a broader period ($\chi^2 = 27.01$, 12 d.f., $P < 0.008$).

Diet

Overall, these elapid species have very generalized diets. The most specialized taxon in this respect was *H. haemachatus* (80% amphibians; see Fig. 3), but the dietary sample from all other species included at least two major prey types each comprising 20% or more of dietary items (Fig. 3). Broad patterns in the relative proportions of each major prey type were similar among the three 'spitter' species (*H. haemachatus, N. mossambica, N. nigricincta*) and *N. nivea*, with the same relative rankings of prey types in all four elapid species (i.e. amphibians, then reptiles, then mammals, then birds: Fig. 3). Overall, amphibians were the most common prey items, and bufonid anurans were the most frequently recorded type of amphibian (Table 2). Nonetheless, a wide variety of other vertebrates was recorded, ranging from domestic chickens through to other cobras, varanid lizards and even a tortoise (Table 2). No single prey taxon, except perhaps toads, stands out as unusually common. For quantitative analysis of interspecific differences, we thus focused on prey type at a very broad level (i.e. amphibian, reptile, mammal or bird). Multiple logistic regression with prey type as the dependent variable and potential predictors of diet (the predator's species, body size and sex) as independent variables showed that dietary composition differed significantly among the eight elapid species ($\chi^2 = 58.61$, 21 d.f., $P < 0.0001$) and as a function of predator body size (using SVL as a measure of snake size; $\chi^2 = 13.55$, 3 d.f., $P < 0.004$). However, diet was not significantly affected by the sex of the predator ($\chi^2 = 2.79$, 3 d.f., $P = 0.43$).

Although we were unable to determine prey size for most of the items listed in Table 2, it is clear that most belong to species that are relatively small compared with the predator that consumed them. This is true, for example, of most geckos, skinks and anurans that were taken (Table 2). Occasionally, however, the snakes contained very large prey. For example, some of the varanids and snakes consumed were large relative to the snakes that had consumed them (e.g. *Varanus albigularis* of 35 cm SVL in *N. annulifera* of 166 cm SVL; *Bitis arietans* of 80 cm SVL in *N. anchietae* of 182 cm SVL).

Because of significant interspecific differences in diet (above and Fig. 3), we examined the datasets separately by species, again using major prey type as the dependent variable. Sample sizes of prey items from *A. lubricus* and
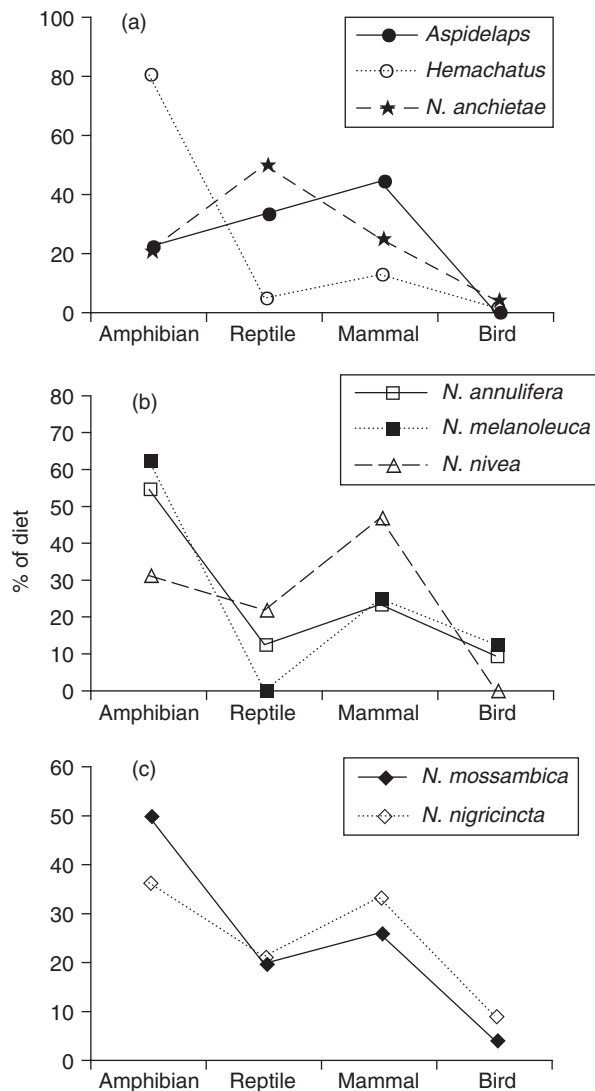
Figure 3 Interspecific variation in dietary composition of African elapids split into three groups: (a) *Aspidelaps lubricus, Hemachatus haemachatus, Naja anchietae*; (b) the non-spitting cobras *Naja annulifera, Naja melanoleuca* and *Naja nivea*; (c) the spitting cobras *Naja mossambica* and *Naja nigricincta*. The points show the proportion of all recorded dietary items consisting of each major prey group.

N. melanoleuca were too low for separate analysis in this way. Supporting the earlier combined analysis, logistic regressions suggest that sex did not affect diet composition within any of the species (all $P > 0.13$). In contrast, a snake's body length (SVL) affected its feeding habits significantly in *N. annulifera* ($\chi^2 = 11.07$, 3 d.f., $P < 0.015$) and *N. nigricincta* ($\chi^2 = 9.50$, 3 d.f., $P < 0.024$), but not in *H. haemachatus* ($\chi^2 = 5.68$, 3 d.f., $P = 0.13$), *N. anchietae* ($\chi^2 = 2.81$, 3 d.f., $P = 0.43$), *N. mossambica* ($\chi^2 = 5.89$, 3 d.f., $P = 0.12$) or *N. nivea* ($\chi^2 = 0.06$, 3 d.f., $P > 0.99$). Figure 4 shows that patterns nonetheless were broadly similar, with ectothermic prey (amphibians and reptiles) more commonly found inside

smaller snakes whereas endotherms were found inside larger animals. The Cape cobra *N. nivea* is a notable exception to this generality, however, with no hint of a size-related (ontogenetic) shift in dietary habits (Fig. 4).

Discussion

Our dissections of museum specimens provide the most extensive quantitative data yet available on ecological traits of cobra species from southern Africa, but broadly support previous reports based on smaller datasets. The overall picture that emerges is of a lineage encompassing significant ecological diversity, but within a fairly circumscribed (lineage-wide) set of attributes. For example, all the species that we studied forage actively for a diverse array of small vertebrates, but dietary composition nonetheless varies interspecifically within this general conservatism. Similarly, despite an overall similarity in sexual dimorphism (relatively modest sex-based divergence in mean adult body sizes, at least in the larger species), we nonetheless see significant interspecific variation in the degree of size dimorphism as well as in other aspects of reproductive biology (such as mode of reproduction and fecundity). Below, we consider in turn each of the traits that we measured.

The relative numbers of adult versus juvenile specimens within museum collections may well reflect biases in methods of collection rather than underlying interspecific variation in population age structures. Most strikingly, samples of the two nocturnal spitting cobras *N. mossambica* and *N. nigricincta* were dominated by juveniles whereas adults predominated for all other species. Further studies are warranted to discern the reason for this pattern, which may relate to the ability of 'spitters' like *N. nigricincta* to utilize highly disturbed habitats (Luiselli, Angelici & Akani, 2002*b*), and thus be encountered when they enter human dwellings. Even small snakes can be seen and collected under such conditions, whereas samples from roadkills and field-based collecting may be less likely to detect secretive and cryptic juveniles. Ontogenetic shifts from diurnal to nocturnal activity may also be involved (Broadley, 1974). High proportions of juvenile specimens in museum collections of Australian brownsnakes *Pseudonaja textilis* may likewise reflect the abundance of this species in anthropogenically disturbed habitats (Shine, 1989, 1994*a*).

Similarly, general patterns in sex ratios within museum collections may relate to sex differences in behaviour rather than to underlying deviations from parity in the numbers of males and females in natural populations. For example, samples of all the species that we examined showed a male-biased sex ratio among adults but not among juveniles. Differential mortality of adult females offers a possible explanation, but it is more likely that females are more cryptic and difficult to collect whereas adult males (especially during the mating season) are encountered more frequently, for two reasons. First, they travel longer distances during mate searching (Gibbons & Semlitsch, 1987; Gregory, Macartney & Larsen, 1987; Aldridge & Brown, 1995; Bonnet, Naulleau & Shine, 1999); and second,

Table 2 Prey items recorded from alimentary tracts of African elapids

Prey item	Aspidelaps lubricus	Hemachatus haemachatus	Naja anchietae	Naja annulifera	Naja melanoleuca	Naja mossambica	Naja nigricincta	Naja nivea
Bird species		1			1	3	3	
Passerine chicks			1	4		2		
Chicken eggs				4				
Mammal species	3	8	6	14	2	29	8	11
Rodentia							3	6
Otomys sp.				1				
Rhabdomus pumileo								1
Reptile species								
Lizard sp.		2				1		6
Agamidae				1				
Gekkonidae								
Chondrodactylus bibronii							1	
Chondrodactylus turneri			1					
Pachydactylus mariquensis	1							
Gerrhosauridae								
Gerrhosaurus sp.			1					
Lacertidae	2							
Ichnotropis squamulosa						1		
Scincidae							1	
Trachylepis sp.								1
Trachylepis capensis		1				2		
Trachylepis striata						1		
Trachylepis varia						1		
Varanidae								
Varanus albigularis				2			1	
Snake sp.			2	1				
Colubridae						2	3	
Lamprophis capensis fuliginosus							1	
Lycophidion capense						2		
Psammophis jallae			1					
Psammophis leightoni			1					
Pseudaspis cana			2					
Elapidae								
N. nigricincta			1					
Viperidae								
Bitis arietans			1	1		1		
Tortoise sp.								
Testudinidae								
Kinyxis sp.						1		
Amphibian species	1	44	3	19	5	39	13	8
Bufonidae	1	2		8		18		
Amietophrynus gutturalis				4		5		2
Amietophrynus rangeri		3		1				
Schismaderma carens						2		
Vandijkophrynus gariepensis								2
Hyperoliidae								
Kassina maculata				1				
Ranidae								
Ranid tadpoles			4					
Total no. of items	8	61	24	61	8	110	34	35

This table shows the number of snakes containing prey of each type (e.g. 'bird species' = birds, but species unknown). Multiple prey items per snake were rare, so that the total numbers of prey items of each type are very similar to these values based on numbers of snakes containing each type of prey.
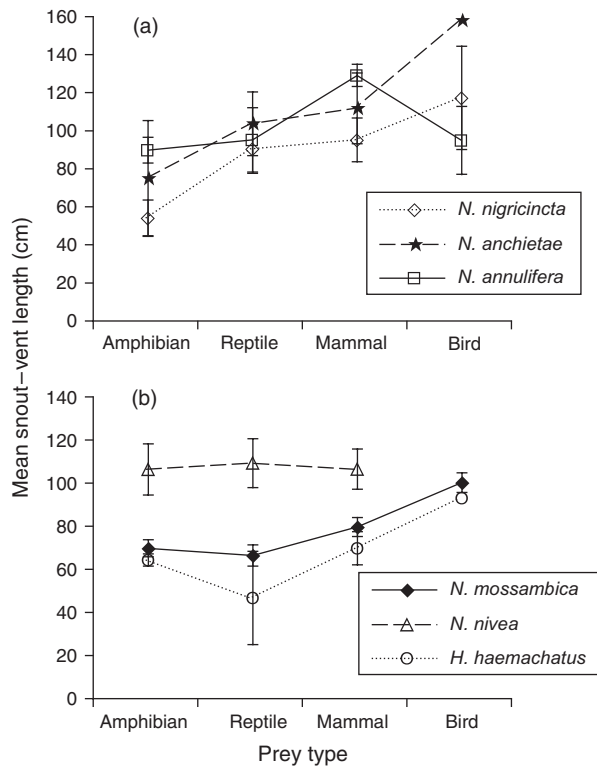
Figure 4 Intraspecific shifts in dietary habits within cobra species as a function of body size of the predator. The graphs show mean snout–vent lengths and associated standard errors for the specimens recorded to contain prey of each major type. The upper graph (a) shows *Naja anchietae*, *Naja annulifera* and *Naja nigricincta*, whereas the lower graph (b) shows *Naja mossambica*, *Naja nivea* and *Hemachatus haemachatus*.

reproduction can reduce vigilance in male snakes such that they allow closer approach by predators and motor vehicles (Brown & Shine, 2004).

In terms of SSD, coral snakes *A. lubricus* differed from the seven other study species. As in the congeneric *Aspidelaps scutatus* (Shine *et al.*, 1996), female *A. lubricus* mature at larger sizes than conspecific males, grow to larger maximum sizes and hence average larger mean adult body sizes (Fig. 1, Table 1). In contrast, SSD is modest in the other seven taxa, albeit with statistically significant interspecific variation, and with a general allometry whereby the relative size superiority of males is greatest in species with larger mean body size in absolute terms. The SSD divergence between *Aspidelaps* and the other taxa does not relate in any obvious way to mating systems. Male–male combat has been reported in *A. lubricus* (Mavromichalis & Bloem, 1997) and is widespread within Asian *Naja* (including *Naja oxiana*, *Naja sputatrix* and *Naja 'tripudians'* from Malaysia and India: Carpenter, 1986; Shine, 1994b). However, although male–male combat is known for at least two African cobra species [*Naja annulifera* (as *Naja haje*: Carpenter, 1986) and *N. melanoleuca*, Branch, 1998], this behaviour has never

been reported in the rhinkals or in some of the other widespread South African cobras (e.g. *N. mossambica*, *N. nigricincta*, *N. anchietae*, *Naja pallida*). Observations of captive cobras also hint that combat may take a different form than in many other snakes, with vigorous wrestling and biting involving females as well as males, and occurring between males in the absence of females (R. Shine, W. R. Branch & P. S. Harlow, pers. obs. for *N. annulifera*). Phylogenetic analyses have revealed a strong functional link between the occurrence of male–male combat and SSD in snakes: females typically attain larger adult body sizes than males in the absence of male–male combat, but males grow to similar sizes as (or larger than) females in taxa where males engage in physical combat bouts during the mating season (Shine, 1978, 1994b).

Published literature on SSD in cobras is largely consistent with our own data, showing relatively minor sex differences in mean adult body size (*Naja naja* – Shine, 1994b; *Naja sputatrix* – Boeadi *et al.*, 1998; *N. melanoleuca* and *N. nigricollis* – Luiselli, 2002; Luiselli *et al.*, 2002b). The trend for SSD to correlate interspecifically with mean absolute adult body size also mirrors a general pattern seen in many other kinds of organisms, including snakes (for animals in general, Reiss, 1989; for elapids, see Shine, 1994a). Variation in SSD among cobras might reflect multiple factors, including interspecific variation in sex-specific adult mortality rates (and thus age distributions), in the intensity of fecundity selection in females (Shine, 1994a), in ecologically based divergence between the sexes (Shine, 1991) or in the degree to which success in combat enhances individual fitness in males or even in females. Even if combat occurs in all species and is largely restricted to males, it may influence male mating success more in some taxa than others and, hence, constitutes a more or less powerful selective force on male body size. The same kind of variation may occur even among populations within a single species or in a single population through time. For example, annual (prey-resource-induced) variation in the proportion of reproductive female adders *Vipera berus* in a small Swedish population generates equivalent variation in the importance of male–male combat, and hence of male body size, in determining male mating success (Madsen & Shine, 1992).

In most of the eight elapid species that we studied, adult males and females differed in body shape, not simply body size. Males typically had larger heads and longer tails than did conspecific females at the same body length (Table 1). Longer tails in males than in females are commonly but not universally reported in snakes and may reflect a variety of selective forces, such as the need for extra space to accommodate the hemipenes (King, 1987) or advantages in tail-wrestling competitions with rival males during group courtship (Shine *et al.*, 1999). Sex differences in head size are similarly widespread but not universal in snakes, and tend to be phylogenetically conservative (Shine, 1991). A study of the Asian cobra *N. sputatrix* (Boeadi *et al.*, 1998) documented larger relative head size in males, as seen in most of our study species. Surprisingly, however, Luiselli *et al.* (2002a) reported that head sizes increased more rapidly with body

size in female than in male *N. melanoleuca* from Nigeria, in contrast to the pattern we found. Closer inspection of their paper suggests that this apparent paradox may be due to a simple mistaken interpretation; their data (table 1 of Luiselli *et al.*, 2002*a*) actually show a higher slope in males (0.025) than in females (0.016), similar to the general pattern in other cobra species. As Luiselli *et al.* (2002*a*) note, such a sex divergence in relative head size (regardless of the direction of the dimorphism) is difficult to reconcile with the hypothesis that sex divergence in head sizes evolves as an adaptation to sex differences in prey type or prey size. Neither our own study nor that of Luiselli *et al.* (2002*a*) suggests that male and female cobras differ in feeding habits (although interestingly, the closely related *A. scutatus* may do so – Shine *et al.*, 1996). Also, the general reliance of cobras on relatively small prey makes it less likely that selection will favour sexual dimorphism in traits (such as head size) because of their influence on maximal ingestible prey size (Luiselli *et al.*, 2002*a*).

Why, then, do male cobras generally have larger heads than do conspecific females of the same body length? Luiselli *et al.* (2002*a*) suggest that male mate choice for larger-headed females may be important, but we doubt this explanation because (1) females in their sample actually appear to have smaller not larger heads, and (2) although male snakes may indeed exert mate choice, they appear to rely upon pheromonal rather than visual cues to do so (Shine *et al.*, 2002, 2003*b*, 2004; but see Rivas & Burghardt, 2001). Instead, we suggest that the larger heads of males may function in male–male rivalry, as is commonly inferred for lizards (Vitt & Cooper, 1985). Unlike most other venomous snakes, male cobras bite each other vigorously during combat bouts (*Naja oxiana* – Kudrjavtsev & Mamet, 1989; *N. annulifera* – R. Shine & W. R. Branch, pers. obs. on captive specimens, 1994; P. Harlow, pers. obs. on captive specimens, 2001).

In other respects, most of our results for reproductive biology and food habits mirror previous reports, and show many of the same features revealed by earlier work. For example, although tortoises are presumably taken very rarely by snakes of any kind, there is a previous record of a large *N. annulifera* eating two leopard tortoises *Geochelone pardalis* (Mackie, 1994). The patterns revealed by our work are similar in many respects to those from Luiselli *et al.*'s pioneering studies on Nigerian elapids. This is true not only for generalities (such as a dependence upon a phylogenetically diverse array of small vertebrates) but also for interspecific and intraspecific variation. For example, Luiselli & Angelici (2000) and Luiselli *et al.* (2002*b*) noted ontogenetic shifts in dietary habits in *N. melanoleuca* and *N. nigricollis*. Although the specific prey types differed between the two studies – for example, fishes were commonly taken by Nigerian animals but were not recorded in our southern African snakes – the same patterns are evident in the two studies. Interestingly, however, one species in our sample (*N. nivea*) took similar prey types throughout ontogeny.

We obtained relatively little information on reproductive biology, but our data broadly support earlier statements. For example, the restriction of vitellogenesis and pregnancy to relatively warm months of the year is consistent with previous studies on a wide range of other snake species from temperate-zone habitats (Seigel & Ford, 1987). In turn, this conservatism may reflect the requirement for relatively high temperatures during embryogenesis (Shine, 1985). The most obvious interspecific divergence in our sample involves the much greater fecundity of the viviparous rhinkals *H. haemachatus* than any of the oviparous cobras (*Naja*). We doubt that there is any functional relationship between the divergence in reproductive mode and fecundity, in that comparisons of closely related oviparous and viviparous reptile species (and in some cases, populations within a species) do not reveal any consistent relationship between reproductive mode and fecundity (Shine, 1987; Qualls & Shine, 1995). Instead, the unusually high fecundity of *Hemachatus* may relate partly to the stocky build of females (thus providing more abdominal space for the litter: Du, Ji & Shine, 2005) and other undetected species-specific selection pressures on fecundity and offspring size (Rohr, 1997).

Overall, the expanding database on cobra ecology reveals some striking similarities and convergences between these snakes and their ecological analogues on other continents. Broad similarities in body shape, coloration and foraging biology are evident between cobras and the large colubrid generalist-feeders of North America (*Pituophis melanoleucus*, *Masticophis flagellum*), South America (*Drymarchon corais*, *Spilotes pullatus*) and southern Europe (*Coluber viridiflavus*, *Elaphe quatorlineata*). However, the closest similarities may lie with large terrestrial elapids in Australia, notably of the genera *Pseudechis* and *Pseudonaja*. In both Africa and Australia, these large active foragers fall within a range of body sizes larger than the majority of confamilial taxa, but smaller than sympatric mammal-specialists (*Dendroaspis polylepis* in Africa, *Oxyuranus scutellatus* in Australia). Notably, both adaptive radiations encompass substantial interspecific variation within a general framework of ecological conservatism in traits such as foraging mode, broad dietary habits and dependence on relatively small prey items. In both cobras and the Australian *Pseudechis–Pseudonaja* radiation, some species are diurnal whereas others are nocturnal or crepuscular; some are viviparous whereas others are oviparous; some produce large clutches of small offspring whereas others produce small clutches of large offspring; some are semi-fossorial whereas others are surface active; and some are restricted to relatively mesic habitats whereas others extend into very arid areas. This parallel diversity provides exciting opportunities for further comparative analyses.

Acknowledgements

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