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Reproductive Biology and Food Habits of Horned Adders, *Bitis caudalis* (Viperidae), from Southern Africa

RICHARD SHINE, WILLIAM R. BRANCH, PETER S. HARLOW, AND JONATHAN K. WEBB

Horned adders (*Bitis caudalis*) are small heavy-bodied viperid snakes widely distributed across a range of habitat types in southern Africa. Measurement and dissection of 580 preserved specimens in museum collections provided information on morphology, food habits, and reproductive biology of this species. In particular, it enabled us to assess the effects of sex and habitat type (arid to mesic) on adult body sizes and shapes, dietary composition, and reproductive output. Female horned adders mature at larger sizes than do males and grow much larger. At the same snout-vent length, females have larger heads and shorter tails than do males. Arid-zone snakes are longer and thinner than conspecifics from more mesic areas and have longer tails and larger heads. Horned adders feed primarily on lizards (especially lacertids, skinks, and geckos) but also take other small vertebrates. Dietary composition varies according to the snake's body size, sex, and geographic location: endothermic prey are taken mostly by larger snakes; by females rather than males; and by arid-zone rather than mesic-habitat snakes. Most prey are small relative to predator size, especially in large snakes. Litter sizes (3-19 offspring) increase with maternal body size, with no significant geographic differences in this relationship. However, reproductive frequency (as inferred from the proportion of adult females that were reproductive when collected) was significantly higher in mesic-habitat snakes (> 50%) than in their arid-zone relatives (15%). Habitat-associated differences in resource availability may have affected traits such as body size and shape, degree of dietary specialization, growth rates and female reproductive frequencies.

PROBABLY it is true that most species with wide geographic ranges display associated geographical heterogeneity in attributes such as body sizes, morphology, food habits, and reproductive biology (e.g., Fitch, 1970; Ralls and Harvey, 1985; Seigel and Ford, 1987). However, the ways in which local conditions induce such modifications remain unclear for most types of animals in most types of habitats. Local adaptation of organisms to their immediate environment can produce such a matching, but so can phenotypically plastic responses of individual organisms (e.g., Ballinger, 1983). For example, laboratory experiments reveal that local conditions of food availability, climate, and predator density can stimulate substantial shifts in a species' morphology, behavior, growth rates, and reproductive output (e.g., Ford and Seigel, 1989; Van Damme et al., 1990). These kinds of studies have forced a general reassessment of the role of adaptation, as compared with direct environmental effects, in producing geographic heterogeneity of life-history traits (e.g., Ballinger, 1983; James and Whitford, 1994; Via et al., 1995). This reassessment has also reinforced the value of descriptive studies on intraspecific variation, because such studies provide the raw material for more detailed work. Nonetheless, in-

formation of this kind remains fragmentary for most kinds of organisms. Despite an increasing interest in squamate ecology, the life-history traits of snakes in areas other than Europe, North America, and Australia have remained almost unstudied (e.g., see Seigel and Collins, 1993).

In this paper, we provide data on the morphology, reproductive biology, and food habits of a small viperid snake that is widely distributed across southern Africa. In its morphology and general behavior, the horned adder (*Bitis caudalis*) is strongly convergent with a number of other snake species from arid-zone regions in other parts of the world. Most of these taxa (such as the north-African viperine *Cerastes cerastes* and the Australian elapid *Acanthophis pyrrhus*) have attracted very little scientific study, although one crotaline species (the sidewinder *Crotalus cerastes*) has been the subject of intensive work (e.g., Brown and Lillywhite, 1992; Secor and Nagy, 1994). Because of their wide geographic distribution, ranging from the hyper-arid western coast of Namibia to the mesic savannah of the Limpopo River (Branch, 1988), horned adders offer an ideal opportunity to examine habitat-associated intraspecific variation in ecological traits.

MATERIALS AND METHODS

We measured and dissected all available preserved specimens ($n = 580$) of *B. caudalis* in the collections of the Transvaal Museum (Pretoria, Republic of South Africa), the Port Elizabeth Museum (Port Elizabeth, RSA), the Natural History Museum of Zimbabwe (Bulawayo), and the State Museum of Namibia and the Directorate of Wildlife Conservation (both in Windhoek, Namibia). For each specimen, we first measured snout-vent length (SVL), tail length (TL), head length (along mandible, from the snout to the retroarticular process), and head width (across the widest part of the head). The specimen was then weighed (if adjudged to be sufficiently well preserved that the mass measure would be reliable) and opened with a midventral incision to reveal the gonads and alimentary tract. Sex and reproductive status were determined by visual inspection. Males were regarded as mature if they had turgid testes and/or thickened white efferent ducts; females were classed as mature if they had oviductal eggs, thickened muscular oviducts, and/or enlarged vitellogenic ovarian follicles. Additional details of reproduction were abstracted from published literature.

Prey items were removed from the snake's alimentary tract for later identification. The mass of the prey item at the time of its ingestion was estimated by comparing the item to intact conspecifics of various sizes from a museum collection. This was not possible for many of the mammalian prey items, which generally consisted of fur in the snake's rectum. Information on the date and location of the specimen's collection were obtained from museum registers.

For analysis, we divided specimens into three groups, according to their geographic location. We used a map of long-term average annual rainfall (Branch, 1988) to divide the range of *B. caudalis* into xeric (< 125 mm annual rainfall), intermediate (125–500 mm), and mesic (> 500 mm) areas. In practice, this translates into a broadly east-west division, separating western (Namibian coastal and near-coastal) populations from snakes inhabiting more mesic eastern areas (Fig. 1). Although geographic variation occurs in both scalation and coloration within *B. caudalis* (e.g., Haacke, 1975; Branch, 1988), no detailed analyses of geographic variation have been reported. Formal recognition of intraspecific variation is restricted to the description of a western race (*B. c. paucisquamata* Mertens, 1955) that was later shown to be a junior synonym of the closely related taxon *B. schneideri* (Haacke, 1975). No other races have been proposed. In support of morphological

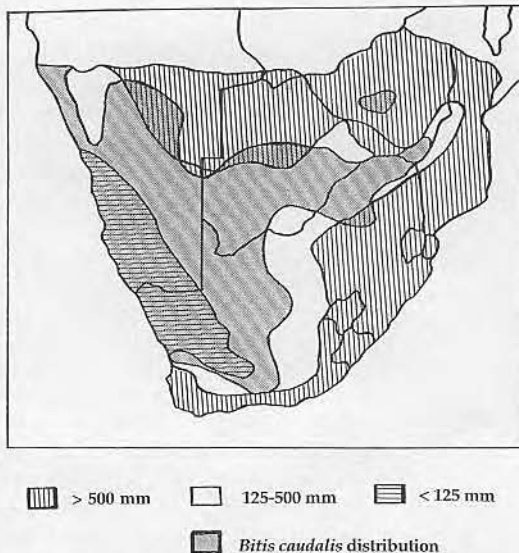


Fig. 1. Geographic distribution of horned adders in southern Africa, with climatic divisions (ranges in mean annual precipitation) used for analyses in this paper. Species distribution and precipitation maps from Branch (1988).

data, immunological studies suggest a close relationship between *B. caudalis* and two other sand-dwelling snakes from the western arid region (*B. peringueyi* and *B. schneideri*; Hermann and Joger, 1997).

Statistical analyses were performed on an Apple PowerMacintosh 6100/66 using the software programs Statview 4.5 (Abacus Concepts, Berkeley, CA, 1991, unpubl.) and SuperAnova 1.11 (Abacus Concepts, Berkeley, CA, 1995, unpubl.). Prior to analysis, data were checked for homoscedasticity of variances. Data on raw body masses were natural log-transformed to meet the assumptions of linearity. Yate's correction was applied to contingency-table analyses where appropriate. In the text, we present mean values ± 1 standard deviation.

RESULTS

Sex ratios, body sizes, and sexual dimorphism.—Male and female snakes were collected in approximately equal numbers in all three areas (Table 1). In each of these areas, however, female horned adders mature at a larger body size than do conspecific males and grow to much larger sizes. Hence, mean adult SVLs were significantly larger for females than for males (Table 1). SVLs also varied among the three areas examined, with the snakes being largest in arid regions and smallest in mesic areas. A two-factor

TABLE 1. SAMPLE SIZES, BODY SIZES, AND SEXUAL SIZE DIMORPHISM OF ADULT HORNED ADDERS, *Bitis caudalis*, FROM XERIC, INTERMEDIATE, AND MESIC PARTS OF THE SPECIES' RANGE IN SOUTHERN AFRICA. Table shows mean values, with SD in parentheses.

	Rainfall		
	Xeric	Intermediate	Mesic
Adult females			
Sample size for SVLs	43	130	22
Mean SVL (mm)	347.02 (51.04)	336.97 (40.11)	312.14 (34.21)
Range of SVLs	274–484	245–474	250–400
Sample size for masses	14	54	11
Mean body mass (g)	41.36 (21.25)	61.21 (29.00)	44.89 (15.12)
Range of body masses	22.0–95.0	28.0–160.0	25.1–65.0
Adult males			
Sample size for SVLs	41	125	21
Mean SVL (mm)	276.15 (42.06)	262.20 (45.20)	252.33 (42.89)
Range of SVLs	215–400	190–385	202–343
Sample size for masses	9	69	12
Mean body mass (g)	27.87 (11.49)	26.73 (16.17)	25.82 (11.96)
Range of body masses	14.0–50.0	8.1–92.0	10.7–55.0

ANOVA with sex and habitat type as the factors, confirmed that mean adult SVLs differed between the sexes ($F_{1,376} = 143.73$, $P < 0.0001$) and among the three areas ($F_{2,376} = 6.62$, $P < 0.002$), but the degree of sexual dimorphism in adult SVLs was similar in the three areas (interaction $F_{2,376} = 0.56$, $P = 0.57$).

Surprisingly, analyses based on body mass

rather than length gave a different result (Table 1). Mean adult body mass in males was significantly lower than in females (using \ln mass: $F_{1,163} = 36.50$, $P < 0.001$). Overall body masses of snakes from the three areas did not differ significantly ($F_{2,163} = 1.53$, $P = 0.22$), but there was a significant interaction between sex and locality ($F_{2,163} = 3.58$, $P < 0.04$). The discrepancy between these results is due to a difference in body shape (mass relative to length) among snakes from the three different areas. Arid-zone snakes were thinner-bodied than their mesic conspecifics, with intermediate-habitat snakes intermediate in this respect (one-factor ANCOVA with area as the factor, SVL as the covariate, and \ln mass as the dependent variable: heterogeneity of slopes $F_{2,213} = 0.26$, $P = 0.77$; intercepts $F_{2,215} = 7.37$, $P < 0.001$; see also Fig. 2D). Thus, arid-zone snakes are longer, but not heavier, than conspecifics from more mesic regions.

Males and females differ in body proportions as well as absolute body sizes. At the same snout-vent length, male horned adders have smaller heads than females (one-factor ANCOVA with sex as the factor, SVL as the covariate and head size as the dependent variable: for head length, slopes $F_{1,213} = 0.15$, $P = 0.70$; intercepts $F_{2,214} = 13.32$, $P < 0.001$; for head width, slopes $F_{1,197} = 3.29$, $P = 0.07$; intercepts $F_{1,198} = 4.93$, $P < 0.03$; see Fig. 2B). However, the general shape of the head (width relative to length) does not differ between the two sexes (one-factor ANCOVA with sex as the factor, head length as the covariate and head width as

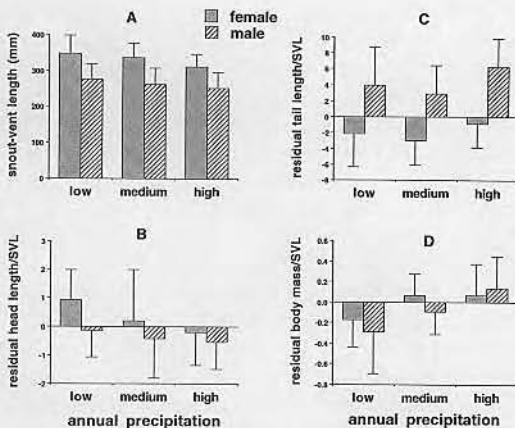


Fig. 2. Effects of sex and geographic location (rainfall-defined habitat type) on morphological traits in horned adders. Histograms show mean values for traits and associated standard deviations. For graphs (B), (C), and (D), the dependent variable is the residual score from the general linear regression of the relevant trait (head length, tail length, or \ln body mass) against snout-vent length. See text for statistical analyses of these trends, using ANCOVA rather than residual scores; the Figure shows residuals to more clearly illustrate the sources of significant effects.

the dependent variable: slopes $F_{1,196} = 3.42$, $P = 0.07$; intercepts $F_{1,197} = 0.29$, $P = 0.59$). Adult males are also more slender bodied than are females (one-factor ANCOVA with sex as the factor, SVL as the covariate and \ln body mass as the dependent variable: slopes $F_{1,165} = 0.40$, $P = 0.53$; intercepts $F_{1,166} = 6.62$, $P < 0.012$) and have significantly longer tails than do females of the same body length (one-factor ANCOVA with sex as the factor, SVL as the covariate and tail length as the dependent variable: slopes $F_{1,214} = 0.43$, $P = 0.51$; intercepts $F_{1,215} = 193.18$, $P < 0.0001$; see Fig. 2C). Geographic variation is also evident in these traits but is less marked than the sex difference. For example, arid-zone snakes tend to have larger heads relative to SVL (heterogeneity of slopes test with sex as the factor, SVL as the covariate and head length as the dependent variable: $F_{2,223} = 3.41$, $P < 0.04$), whereas snakes from mesic areas have longer tails relative to SVL (one-factor ANCOVA with area as the factor, SVL as the covariate, and tail length as the dependent variable: slopes $F_{2,220} = 2.82$, $P = 0.06$; intercepts $F_{2,222} = 7.74$, $P < 0.001$; see Fig. 2C).

Reproductive biology.—Our data confirm that horned adders are viviparous, with females producing a litter of 3–19 (mean = 8.17 ± 3.87) offspring in late summer. Although we have no direct measures of offspring sizes, we can estimate this parameter from the body sizes of the smallest preserved specimens because neonates comprise a substantial proportion of the population in the period immediately after parturition and are often collected in large numbers. To examine habitat-associated variation in offspring sizes, we compared body sizes of the smallest 20% of juvenile snakes from each of the three rainfall areas, using a one-factor ANOVA with rainfall area as the factor. The mean body sizes of “neonates” identified in this way differed significantly among the three areas ($F_{2,35} = 9.51$, $P < 0.001$), being largest in the intermediate habitat (130.86 ± 14.63 mm SVL, $n = 21$), intermediate in the arid zone (119.85 ± 3.39 , $n = 13$), and smallest in the mesic habitat (104.25 ± 15.00 , $n = 4$; all differences significant with Tukey-Kramer posthoc tests). Although sample sizes for this test are small and the method of identifying neonates is imprecise, this among-location difference is not likely to be a result of sampling error. If this had been the case, we would have expected unusually small specimens to have been overrepresented in the largest sample (that of intermediate-habitat snakes), yielding a result opposite to the one we obtained.

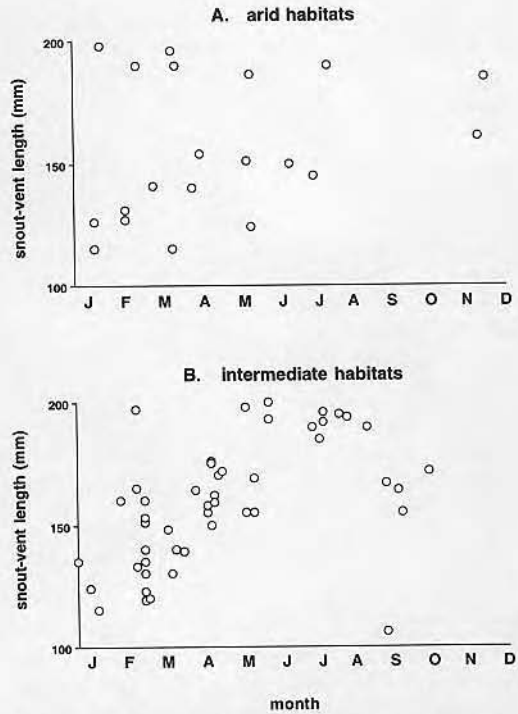


Fig. 3. Seasonal distributions of body sizes of juvenile horned adders from (A) arid (< 125 mm annual precipitation) and (B) intermediate rainfall (125–500 mm) parts of the species' range.

We also examined seasonal patterns of body-size distributions of specimens for which we could obtain dates of collection. Such distributions can suggest growth trajectories of neonates, so long as reproduction is highly synchronized within the population (e.g., Shine, 1978a) but must be interpreted with caution (e.g., Vitt, 1983). Sample sizes for the mesic-area snakes were too low for analysis, but inspection of the sizes of juvenile snakes collected at different times of year in the other habitat zones revealed a consistent pattern of very small specimens in midsummer (January) and progressively larger individuals in late summer and autumn. Inferred growth rates in the first year of life were substantially lower in the arid-zone snakes than in their intermediate-habitat counterparts. From Figure 3A, we infer that arid-zone snakes grow from birth (at around 120 mm) to about 150–160 mm by the end of the first growing season (June). In contrast, the larger neonates from intermediate habitats attain sizes of around 180 mm by this time (Fig. 3B).

Litter sizes were significantly correlated with maternal body sizes ($n = 58$, $r = 0.65$, $P < 0.0001$). This relationship did not differ between snakes from the three different habitat

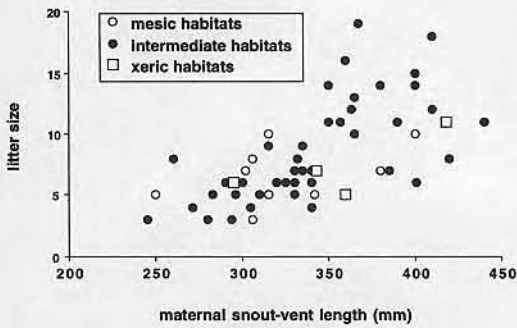


Fig. 4. Litter sizes of horned adders as a function of maternal body size (SVL), with data shown separately for females from different parts of the species' range.

zones (one-factor ANCOVA with area as the factor, maternal SVL as the covariate, and litter size as the dependent variable: slopes $F_{2,52} = 1.02$, $P = 0.37$; intercepts $F_{2,54} = 0.91$, $P = 0.41$; see Fig. 4). Many adult females in museum collections were nonreproductive, suggesting that females may reproduce on a less-than-annual schedule. Because reproductive cycles are relatively synchronous in the highly seasonal climates experienced by *B. caudalis*, we were able to estimate reproductive frequency from the proportion of adult-size females that were reproductive during summer. This proportion did not vary with body size among adult females (comparing mean SVL of reproductive versus nonreproductive adult females: unpaired $t_{121} = 1.03$, $P = 0.31$) but differed among the three areas. The proportions of reproductive animals were higher in the mesic area (eight of 15, 53%) and the intermediate habitat (46 of 75, 61%) than in the arid zone (five of 33, 15%; $\chi^2 = 19.78$, 2 df, $P < 0.001$).

Food habits.—Horned adders feed primarily upon lizards, especially gekkonids, lacertids and scincids (Table 2). However, the alimentary tracts also contained other types of lizards, as well as mammals, birds, and frogs. A snake inside one specimen provides the first record of cannibalism for this species. The lizards consumed by horned adders cover a wide taxonomic range and include both diurnally and nocturnally active taxa.

The composition of the diet varied geographically and differed between the sexes. Perhaps the most important division is between ectothermic prey (reptiles and amphibians) versus endothermic prey (mammals and birds) because these two groups differ in mean body sizes, activity levels, and other traits likely to influence their vulnerability to predators (e.g.,

TABLE 2. PREY ITEMS IDENTIFIED FROM THE ALIMENTARY TRACTS OF HORNED ADDERS FROM THREE HABITAT TYPES (XERIC, INTERMEDIATE, AND MESIC) IN SOUTHERN AFRICA. See text for definition of habitat types.

Prey type	Number of prey recorded		
	Xeric	Intermediate	Mesic
Amphibians			
unidentified	1	1	0
<i>Breviceps</i> sp.	0	1	0
Lizards			
unidentified	1	1	1
Agamidae			
<i>Agama</i> sp.	0	5	0
Cordylidae			
<i>Cordylus</i> sp.	0	1	0
Gekkonidae			
unidentified	1	2	0
<i>Colopus wahlbergi</i>	0	8	0
<i>Kaokogeto vanzyli</i>	0	2	0
<i>Pachydactylus</i> sp.	2	0	0
<i>Pachydactylus laevigatus</i>	1	2	0
<i>Pachydactylus punctatus</i>	3	0	0
<i>Ptenopus garrulus</i>	1	5	0
<i>Rhoptropus afer</i>	0	1	0
Lacertidae			
unidentified	3	1	0
<i>Heliobolus lugubris</i>	1	18	1
<i>Ichnotropis squamulosa</i>	0	1	0
<i>Meroles</i> sp.	1	0	0
<i>Meroles reticulatus</i>	0	1	0
<i>Nucras tessellata</i>	2	0	0
<i>Pedioplanis gaerdesi</i>	0	1	0
<i>Pedioplanis lineoocellata</i>	0	4	0
<i>Pedioplanis namaquensis</i>	0	1	0
Scincidae			
unidentified	1	8	2
Lygosomatinae	0	6	2
<i>Mabuya</i> sp.	3	9	0
<i>Mabuya quinqueaeniata</i>	0	1	0
<i>Mabuya spilogaster</i>	0	3	0
<i>Mabuya striata</i>	0	0	1
<i>Mabuya variegata</i>	3	1	1
Snakes			
Viperidae			
<i>Bitis caudalis</i>	1	0	0
Birds			
unidentified	2	1	1
Mammals			
unidentified	9	11	2
baby rodents	2	0	0
gerbil (<i>Tatera</i> sp.)	2	0	0
<i>Tatera leucogaster</i>	2	0	0
<i>Mus minutoides</i>	0	1	0

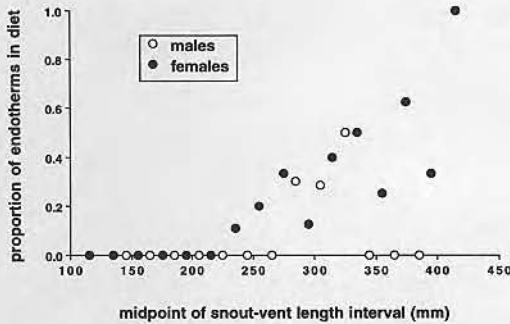


Fig. 5. Shift in composition of the diet (proportion of endothermic prey) with increasing body size in horned adders. Body sizes are divided into 20-mm SVL size classes. In both sexes, larger snakes take a higher proportion of endothermic prey (mostly mammals) and a concomitantly lower proportion of ectothermic prey (mostly lizards). See text for statistical analyses.

Pough, 1980). Female horned adders took a significantly higher proportion of endothermic prey than did males ($\chi^2 = 5.86$, 1 df, $P < 0.02$), and snakes from arid regions also fed on endotherms to a greater degree than did snakes from more mesic areas ($\chi^2 = 11.23$, 2 df, $P < 0.005$). Both of these trends may relate to absolute body size. Perhaps because of gape-limitation, endothermic prey were never taken by small snakes, and the relative importance of endotherms in the diet increased markedly in larger snakes (Fig. 5). Thus, part of the reason that female horned adders took more endotherms than did males is likely to be the larger body sizes of females. However, even at the same body lengths, females fed to a greater degree on endothermic prey (see Fig. 5; heterogeneity of slopes test with sex as the factor, SVL as the covariate, and the proportion of endothermic prey as the dependent variable: $F_{1,25} = 6.23$, $P < 0.02$).

Most of the prey items we recovered from horned adders were relatively small. Larger snakes took larger prey (regression of SVL vs prey mass: $r = 0.23$, $n = 47$, $P < 0.04$), but the mass of the prey item relative to snake mass declined in larger snakes (Fig. 6). These relationships between snake size and prey size were similar in both sexes and in all three areas (ANCOVAs, $P > 0.25$ for all effects of sex, rainfall area, and their interaction).

Frequency of feeding (as judged by the proportion of snakes containing prey) showed no clear patterns. The proportions of snakes containing identifiable prey did not differ among areas ($\chi^2 = 3.94$, 2 df, $P = 0.14$) or between sexes ($\chi^2 = 1.06$, 1 df, $P = 0.30$), nor among

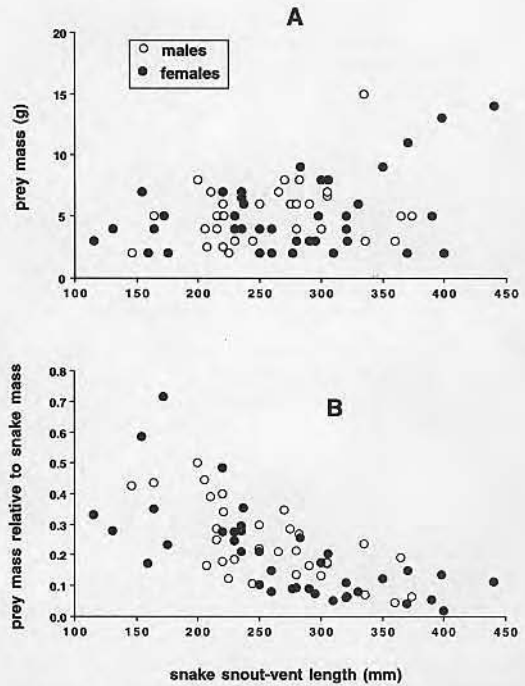


Fig. 6. Larger horned adders consume larger prey (A), but prey mass relative to predator mass declines in larger snakes (B). Note, however, that mass estimates were unavailable for most mammalian prey items.

areas within each sex (χ^2 with 2 df = 4.61 for males, 1.77 for females, $P > 0.10$). Similarly, proportions of fed to unfed snakes did not differ significantly among nine SVL categories (each spanning 40 mm; $\chi^2 = 13.35$, 8 df, $P = 0.10$).

DISCUSSION

Horned adders are locally abundant in many areas of southern Africa, and their general biology has accordingly been the subject of many published statements. However, the vast majority of these have consisted of brief notes in field guides and the like, without quantification or detail. Our study is the first to provide a large dataset, based on specimens from across much of the geographic range inhabited by *B. caudalis*. Hence, we are able to judge the accuracy of previous statements as well as to examine several aspects of the biology of horned adders not accessible to earlier workers.

In general, our data are consistent with earlier observations. For example, several authors have previously noted that horned adders are viviparous, producing a single brood of 4–19 offspring (e.g., Broadley, 1983; Branch, 1988;

Marais, 1992). Well-fed captive females may produce even larger litters (e.g., to 27 neonates in a female from central Namibia; Douglas, 1981). Sizes at birth inferred in our study are also consistent with reports from captive snakes, in terms of absolute sizes as well as patterns of geographic variation in this trait. Captive-born neonates from xeric habitat appear to be larger (e.g., for two litters from Swarkop River, central Namibia, mean offspring TLs of 147 and 136 mm; Douglas, 1981) than those from snakes collected in more mesic habitats (e.g., mean TLs of neonates in five litters = 104 mm, 116 mm, 112 mm, 124 mm, 124 mm; Haagner, 1987, pers. comm.). The seasonal timing of reproduction also fits with earlier reports. Copulation in captive snakes from mesic environments (and housed in southern Africa) has been reported in April and July (Akester, 1983), May and September (Jacobsen, 1986), and July and October (D. Morgan, pers. comm.). Douglas (1981) recorded copulation in October for Namibian captives (xeric habitat). Captive horned adders from mesic habitats have given birth in September (Jacobsen, 1986); November–December (Akester, 1983), October–January (D. Morgan, pers. comm.), and January (Haagner, 1987). The single record of birth to a female from an intermediate habitat (Tsane, Botswana) occurred in late December (Haacke, in Fitz-Simons, 1970). Birth in captive snakes from xeric habitats occurred in December (Jacobsen, 1986) and January (Douglas, 1981). No consistent geographic variation is apparent from these reports.

Previous authors have also noted that the diet consists mostly of lizards, with occasional other small vertebrate prey. The most extensive previous analysis of *B. caudalis* diets was Broadley's (1972) report on a sample of 54 prey items from the central Kalahari. The specimens from this important series were included in our study, where the more detailed analysis provided additional information. The only previous report of geographic variation in ecological traits within *B. caudalis*, to our knowledge, is Patterson's (1991) comment that captive specimens from arid regions readily fed on mice as well as lizards, whereas captives from more mesic areas took only lizards. This observation is supported by our own data, which show a significantly higher incidence of endothermic prey in the alimentary tracts of arid-zone specimens (Table 2).

Our more extensive dataset allows us to document the existence of variation in several traits within *B. caudalis* and to tease apart some of the correlates of that variation. In particular, we can

look at the effects of sex and geographic variation on body sizes, body shapes, reproductive output, and dietary composition. The general pattern is that these traits are influenced by both factors (i.e., sex and location) but with only minor interaction between the two.

First, we consider the effects of sex on the morphology and ecology of horned adders. Sex differences are pronounced in size, shape, and trophic ecology: females grow larger than males; have larger heads and shorter tails at the same SVL; and feed on a higher proportion of endotherms. The degree of sexual dimorphism in mean adult SVL is similar across the three habitat types and is more extreme than is found in most other snakes. Using the techniques of Lovich and Gibbons (1992), the calculated indices of sexual size dimorphism from the SVL data in Table 1 are 1.256 (xeric), 1.285 (intermediate), and 1.237 (mesic). By comparison, a recent review of sexual size dimorphism in snakes provided data for 367 species, only 29 of which were more highly dimorphic than the most dimorphic population of *B. caudalis* (Shine, 1994; 49 species were more dimorphic than the least-dimorphic population of *B. caudalis*). Hence, *B. caudalis* ranks among the highest 15% of snake species with regard to this index.

These differences in body proportions are reflected in scalation. Mertens (1955) noted that females had higher midbody scale row counts (25–27; males 23–27) in Namibian horned adders. Broadley (1972) noted a similar sexual dimorphism in midbody scale counts in Botswana snakes (males with 25–29 rows, usually 27; vs females with 27–31 scale rows, usually 29). He also documented a moderate sexual dimorphism in ventral counts (120–141 in males, 134–153 in females) and a more obvious one in subcaudal counts (27–40 in males, 18–34 in females). Haacke (1975) noted similar sexual dimorphism in ventral and subcaudal counts of horned adders from Great and Little Namaqualand. He indicated that there was regional variation in ventral counts, with the highest range limits occurring in the southwestern region (where the species' range overlaps that of *B. schneideri* and *B. xeropaga*), and lower limits occurring in Angola, the Kalahari, and Transvaal (Haacke, 1975).

The largest recorded specimen (Haacke, 1995) is an exceptionally large female from the eastern water carrier in Namibia that measured 600 mm (548 + 52 mm, SVL + tail, respectively) after six years in captivity. The largest wild-caught female is one of 523 mm (486 + 37 mm) from central Namibia. Only a single male,

408 mm (372 + 36 mm) from Luderitz in coastal Namibia, has exceeded 400 mm TL [Haacke, 1995; who showed that the recorded maximum size of 459 mm (417 + 45 mm) for a snake from southern Namibia (Broadley, 1983) was based on a female]. Jacobsen (1989) records a maximum snout-vent size of 292 mm and 330 mm, for Transvaal males and females, respectively. Comparable maximum total lengths for Zimbabwe snakes are 301 mm and 432 mm, respectively (Broadley and Cock, 1986).

The marked divergence in mean adult body sizes between the sexes is surprising because male horned adders engage in physical combat bouts during the mating season (Akester, 1983). This behavior is typically (but not universally) associated with larger body size in males than in females, presumably because the combat bouts result in sexual selection for larger body size in males (Shine, 1978b, 1994). Larger body size in females than in males in such a species may reflect strong selection for larger body size in females (perhaps because of enhanced fecundity; see Fig. 3) or selection for earlier maturation in males than in females (Madsen and Shine, 1995). In keeping with the general phylogenetic conservatism in mating systems and sexual size dimorphism in snakes, most or all other *Bitis* species appear to share the traits of male-male combat and female-larger size dimorphism (e.g., Fitch, 1981; Broadley, 1983). Tail-size divergence between the sexes is also widespread in other snakes and probably occurs in all *Bitis* species (Broadley, 1983; Branch, 1988).

It is more difficult to interpret the divergence between male and female horned adders in head sizes relative to body length. This divergence is unlikely to reflect adaptation to male-male combat (as has been inferred for dimorphic head sizes in lizards; e.g., Vitt and Cooper, 1985), because males rarely bite each other during combat bouts (Akester, 1983); and in any case, it is females that have the larger heads. Instead, head-size divergence in snakes is likely to reflect sex-specific adaptations to dietary differences (Shine, 1991). In keeping with this interpretation, female horned adders depend on mammalian prey to a greater degree than do males. This dietary difference is partly a result of the sex difference in body sizes but also reflects a divergence in dietary composition even at the same body size. That is, females take a higher proportion of endothermic prey even when comparison is restricted to same-sized snakes (Fig. 5). Although our data do not reveal any difference in prey size relative to predator size in the two sexes (Fig. 6), it is probable that

data on prey masses for mammalian prey would change this conclusion. Sex divergence in relative head sizes is widespread in snakes, including species that resemble *B. caudalis* in general body shape and in the direction of sexual dimorphism in both head sizes and body sizes (e.g., *Crotalus cerastes*, *Acanthophis antarcticus*, *Porthidium yucatanicum*; Klauber, 1956; Shine, 1991; McCoy and Censky, 1992). The dietary divergence between male and female horned adders also offers a possible clue to the otherwise puzzling sex difference in general color: males are more brightly patterned than females (e.g., Broadley, 1983; Branch, 1988). Such differences have been described in relatively few snake species and may reflect adaptations to subtle sex differences in foraging biology and thus habitat use (Shine, 1993) or to the increased activity (and hence, vulnerability to predation) of adult males during the breeding season (Shine and Madsen, 1994). Sex differences in habitat use and/or activity patterns may in turn favor divergent adaptations of color pattern.

The general reproductive biology of *B. caudalis* appears to be similar to that of other small snakes, with the exception that litter sizes are unusually high, and reproductive frequencies of adult females are unusually low. A strong increase in litter size with maternal body size (as in Fig. 4) is common (perhaps ubiquitous) in snakes, but litter sizes for *B. caudalis* are higher than for most similar-sized viperids (for comparative data, see tabulations by Seigel and Ford, 1987). This phenomenon probably reflects the thickset build of *B. caudalis* (allowing a high relative clutch mass; Vitt and Congdon, 1978) combined with the small size of neonates (so that many can be fitted into the maternal body cavity). The small size at birth may plausibly be linked to the adders' dependence on relatively small prey. Horned adders are born at about the same time that sympatric lizards hatch from their eggs, so that hatchling lizards may be important prey for the newborn snakes (Douglas, 1981; Branch, 1988). In terms of sizes at birth and litter sizes, horned adders fit well with general allometric patterns within the African species of the genus *Bitis*. Thus, for both of these variables, *caudalis* resemble similar-sized congeners (e.g., *atropos*, *cornuta*, *xeropaga*), exceed the smaller taxa (e.g., *peringueyi*, *schneideri*), and fall well below the three massive species (*arietans*, *gabonica*, and *nasicornis*; e.g., Broadley, 1983; Branch, 1988).

Less-than-annual reproduction by females is widespread in snakes and seems to be particularly common in ambush predators (Seigel and

Ford, 1987; Shine, 1980; Webb, 1996). Presumably, the prolonged immobility characteristic of ambush predators enhances their survival but reduces rates of prey capture. In keeping with this hypothesis, female horned adders from arid regions (where the snakes are thinner and grow more slowly, presumably because of lesser prey availability) reproduce less often than do conspecifics from more mesic habitats. Similar geographic variation in reproductive frequencies has been documented within other wide-ranging snake species, mostly in relation to the length of the activity season (e.g., for reviews, see Bull and Shine, 1979; Seigel and Ford, 1987). It seems equally likely that female reproductive frequencies will vary geographically within snake species that span a range of habitats differing in prey availability (which may often correlate with the degree of aridity). The only previous report of this effect, to our knowledge, is a brief statement that a viperid species of North African deserts (*Echis colorata*) displays higher reproductive frequencies close to an oasis than in more arid regions (Mendelssohn, 1965). The clear trend for female horned adders to modify reproductive frequency rather than output per litter is consistent with the hypothesis that reproduction involves significant "costs" that are independent of litter size (Bull and Shine, 1979). Under such circumstances, natural selection should favor females that delay reproduction until they can produce as large a litter as possible, rather than reproducing more frequently with small litters (e.g., Naulleau and Bonnet, 1996; Shine and Madsen, 1997).

The general dietary composition of *B. caudalis* (Table 2) may also shed light on the foraging tactics used by these snakes, as well as on patterns of prey availability. For example, the lack of nocturnal prey items in snakes collected from mesic habitats may reflect the scarcity of terrestrial nocturnal geckos in this habitat. These animals are much more common in xeric habitats (W. R. Branch, pers. obs.), where they comprise a high proportion of the diet (Table 2). Similarly, the high proportion of mammals in the diet of xeric-habitat snakes may reflect a greater dependency on nocturnal activity, because of very high daytime temperatures. This inference is supported by the relative scarcity of (diurnally active) lacertid lizards in the guts of xeric-habitat snakes, despite the abundance of these lizards in the deserts and the willingness of Namib horned adders to take lacertid prey in captivity (Hoffman, 1988).

The absence of invertebrate prey in these small vipers may seem surprising but is consistent with data on congeneric taxa. Although

many small viperid species from Europe and northern Africa take invertebrates either as a major component of their diet (e.g., *Vipera ursinii*; Steward, 1971; Baron, 1992; Agrimi and Luiselli, 1992) or as a frequent supplement (e.g., *Echis pyramidum*; Gasperetti, 1988), no invertebrate has been recorded as a primary food item in any *Bitis* species. The absence of invertebrates from *Bitis* diets does not reflect any shortage of available prey. For example, tenebrionid beetles are abundant in the western arid region of southern Africa (Koch, 1962) and form a major food component of many lizards in the region (e.g., *Chamaeleo namaquensis*; Buggage, 1973). Predation on invertebrates characterizes only a limited set of snake lineages, and the absence of invertebrates from the diet has been identified as a significant puzzle for other snake groups as well (e.g., Shine, 1977).

Many authors have described how horned adders lie in ambush at the edges of bushes with only their eyes and tail-tips emerging from the sand. Diurnally active prey (such as scincid and lacertid lizards) may be attracted by caudal luring, whereas nocturnal geckos and mammals may be captured as the snakes search actively for prey at night (e.g., Broadley, 1983; Branch, 1988). However, we know of no definite records of active searching by horned adders, and observational work on this topic would be of great interest. The shift in prey types and sizes with snake size (Figs. 5–6) presumably reflects gape-limitation, with larger (especially mammalian) prey being taken only by larger snakes, by the sex with the larger body size and the larger head relative to SVL (i.e., females), and in the area where snakes grow largest (i.e., arid habitats). A similar ontogenetic shift in dietary composition (from reptilian to mammalian prey) has been reported in many species of snakes, including gape-limited ambush predators (Shine and Slip, 1990; Webb, 1996). As noted above, the apparent trend for relative prey size to decline with snake size (Fig. 6B) is based almost entirely on lizard prey and may not hold true if body masses of mammalian prey were known. Large snakes continue to take even very small prey items (Fig. 6A), as is commonly true in snakes (Arnold, 1993).

Morphological and ecological shifts among geographic locations (habitat types) may reflect phylogenetic history as well as local adaptation and, hence, are more difficult to interpret than are shifts occurring with sex or body size within a single population. In the case of *B. caudalis*, we speculate that lowered prey availability in the arid zone (as evidenced by lower juvenile growth rates and thinner snakes with lower re-

productive frequencies) has favored more generalized food habits, because dietary specialization is most likely to evolve in areas of high prey availability (Pyke et al., 1977). The increased importance of relatively large mammalian prey has thus favored the evolution of larger snakes with large heads relative to body size (for a similar interpretation for island populations of European adders, see Forsman, 1991). Nonetheless, it remains possible that many of the differences that we have documented among locations reflect phenotypic plasticity rather than adaptation. Experimental studies show that direct environmental effects can induce major shifts in mean adult body sizes, the degree of sexual size dimorphism, and reproductive output (e.g., Ford and Seigel, 1989; Madsen and Shine, 1993). The role of descriptive studies such as our own is simply to document variation and patterns of covariation in morphological and ecological traits to identify potential explanations for such patterns. Rigorous tests of these ideas will require far more detailed studies, with a focus on living animals rather than on museum specimens.

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