

Natural History of the African Shieldnose Snake *Aspidelaps scutatus* (Serpentes, Elapidae)

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ABSTRACT.—Examination and dissection of museum specimens, combined with observations of free-ranging and captive snakes, provided original data on morphology, sexual dimorphism, feeding habits, and reproductive biology of shieldnose snakes (*Aspidelaps scutatus*) from southern Africa. These small (to 60 cm snout-vent length) stockily-built snakes are nocturnal, and often fossorial. Females mature at larger sizes than males, and attain larger maximum sizes. At the same body length, males have longer tails, and longer and wider heads, than do conspecific females. The sex divergence in head sizes and shapes may be related to dietary differences between the sexes: males contained a significantly higher proportion of anuran prey, and fewer snakes and mammals, than did conspecific females. However, sample sizes for this comparison were small. Reproduction is strongly seasonal, with mating in spring (October), oviposition in midsummer (December-January), and hatching in autumn (March). Females laid 4 to 10 eggs (mean = 7.9), with clutch size, egg size, and Relative Clutch Mass (RCM) independent of maternal body size. Offspring averaged 16 cm (5 g) and RCM averaged 0.48.

Snakes display a considerable diversity of body shapes, from thickset to extraordinarily slender, but the ecological significance of that diversity remains obscure. Correlations between body shape and other traits—such as foraging mode and reproductive output—have attracted considerable study in lizards (e.g., Vitt and Congdon, 1978; Huey and Pianka, 1981) but remain almost undocumented in snakes. There is a clear distinction between slender, fast-moving snakes that search actively for prey (e.g., *Masticophis*) and heavy-bodied sedentary snakes that ambush passing prey (e.g., *Crotalus*—Secor and Nagy, 1994). However, many species do not fit this simple dichotomy. For example, some ambush hunters are elongate (e.g., “vine snakes”—Henderson and Binder, 1980; Shine et al., 1996) whereas some “active searchers” are relatively heavy-bodied (e.g., *Austrelaps*—Shine, 1977). Even within a single species, foraging modes may differ between the sexes (e.g., Zinner, 1985; Houston and Shine, 1993) or change with time within a single foraging bout by the same individual (Rodda, 1992). The scarcity of quantitative information on foraging “tactics”, body shapes, food habits, and reproductive output in snakes precludes comparative analysis of patterns of association among these variables (see also Seigel and Fitch, 1984).

This difficulty is exacerbated by the fact that snakes show considerable phylogenetic conservatism in body shapes, food habits, and reproductive biology. For this reason, taxa that diverge from closely-related species in body shape are particularly informative about the adaptive

significance of this trait, because the ecological characteristics of these species are likely to reflect the selective pressures that favored the evolutionary change in shape. In this paper, we focus on one such species. With the exception of the marine and fossorial radiations, the majority of proteroglyphous (“elapid”) snakes are slender, elongate, and relatively fast-moving. A notable exception is the shieldnose snake, *Aspidelaps scutatus*, a relatively sluggish, thick-bodied African species. In these respects, shieldnose snakes resemble viperids rather than elapids (Broadley, 1983). We investigated the ecological correlates of this atypical body shape using information from examination of preserved museum specimens, supplemented by observations from the field, to quantify the body shape of *A. scutatus* and describe sexual dimorphism, food habits, and reproductive biology of these small snakes.

MATERIALS AND METHODS

Examination of Museum Specimens.—We examined all preserved specimens of *Aspidelaps scutatus* in the collections of the Transvaal Museum (Pretoria, South Africa), the Port Elizabeth Museum (Eastern Cape, South Africa), the State Museum of Namibia and the Directorate of Wildlife Conservation (both in Windhoek, Namibia). We measured snout-vent length (henceforth, SVL), head length (along the lower jaw, from the tip of the snout to the quadrate-articular projection at the rear of the jaw), head width (at the widest part of the head), eye diameter, midbody width, and body mass. The

TABLE 1. Morphology and sexual size dimorphism in shieldnose snakes (*Aspidelaps scutatus*) of southern Africa. Table shows ranges and mean values, with SD in parentheses. See text for sample sizes; data for SVL and mass include females from captive breeding records, whereas other variables are based only on preserved specimens. Last three columns show results from unpaired two-tailed t-tests for sexual dimorphism.

	Adult males	Adult females	Significance of sexual dimorphism		
			df	t	P
Snout-vent length (cm)	35.1 (4.98)	43.2 (8.83)	64	8.39	0.0001
SVL range	25.5-44.5	30.5-58.2			
Tail length (cm)	6.35 (1.09)	5.09 (0.55)	47	3.81	0.0004
Tail length range	4.6-8.5	3.9-5.8			
Head length (mm)	19.98 (2.14)	19.54 (1.16)	35	0.56	0.58
Head length range	17.1-24.3	17.7-20.9			
Head width (mm)	15.80 (2.62)	14.99 (1.30)	36	0.80	0.43
Head width range	10.5-19.9	12.9-16.6			
Body width (mm)	15.52 (2.94)	14.50 (1.28)	40	0.89	0.38
Body width range	11.0-21.4	12.7-16.0			
Body mass (g)	61.8 (38.8)	89.7 (50.11)	47	2.08	0.043
Body mass range	19.0-190.0	25.0-171.0			
Eye diameter (mm)	3.67 (0.45)	3.43 (0.29)	36	1.36	0.18
Eye diameter range	3.0-4.9	3.2-4.0			

specimen was then opened with a midventral incision so that we could examine the gonads and alimentary tract. Any prey items in the gut (including hindgut) were removed for later identification and measurement. Sex and reproductive condition were determined by visual inspection of the gonads. Males were classed as mature if they had enlarged turgid testes and/or thickened opaque efferent ducts (indicating the presence of sperm). Females were classed as mature if they had oviductal eggs, thickened muscular oviducts, or large vitellogenic ovarian follicles. Developing follicles and oviductal eggs were counted and measured.

Field Observations.—Additional information on reproductive biology and feeding habits was gathered by one of us (GVH) through observation of free-ranging and captive specimens at Manyeleti Nature Reserve in the Eastern Transvaal lowland from 1986 to 1991. All snakes were collected on the road between Orpen Gate (Kruger National Park) and Acornhoek. An additional record came from longterm captives at Dallas Zoo (D. M. Boyer, pers. comm.). The captive Manyeleti snakes were maintained individually after mating, and eggs were removed and weighed <24 h after oviposition. Females were weighed after oviposition, and eggs incubated at 28 to 30 C. Relative clutch mass (RCM) was calculated as clutch mass divided by the post-oviposition mass of the female. Haagner and Morgan (1992) provide details of methods, and summary data on behavior and general reproductive biology for some of the clutches described in more detail in the present paper.

RESULTS

We measured 102 preserved shieldnose snakes in museum collections, and obtained reproduc-

tive data from an additional 10 captive and wild-caught gravid females. We included these 10 reproductive females in our analyses of mean body length and body mass of adult snakes (Table 1).

Morphology.—Table 1 shows that shieldnose snakes are small (mean adult SVL <45 cm in both sexes) and heavily built (to >170 g in both sexes), and show significant sexual dimorphism. Adult females have larger mean body sizes (snout-vent length and mass) but shorter tails than conspecific males. The sexes did not differ in mean values of the other traits we measured (Table 1). Males attained sexual maturation at a smaller size than females (25 versus 30 cm SVL) and achieved smaller maximum sizes (45 versus 58 cm SVL; Table 1). In both sexes, there was a very large size range in the mass of adult animals (tenfold in males, sevenfold in females—Table 1).

We used single-factor analysis of covariance (with sex as the factor, and SVL as the covariate) to test for differences in body proportions between the sexes. At the same body length, female *Aspidelaps* had shorter tails than did males (Fig. 1; heterogeneity of slopes $F_{1,66} = 16.28$, $P < 0.0001$), and smaller heads (Fig. 1; heterogeneity of slopes for head length, $F_{1,66} = 4.41$, $P < 0.04$; for head width, $F_{1,66} = 11.27$, $P < 0.002$). The heads of males are wider, relative to head length, than are those of females (heterogeneity of slopes $F_{1,65} = 4.42$, $P < 0.04$). However, the sexes did not differ in body width relative to SVL (heterogeneity of slopes $F_{1,66} = 3.06$, $P = 0.085$; intercepts $F_{1,67} = 2.17$, $P = 0.15$) or mass relative to SVL (using ln-transformed mass to linearize the relationship: heterogeneity of slopes $F_{1,66} = 0.99$, $P = 0.32$; intercepts $F_{1,67} = 1.02$, $P = 0.35$). Relative eye size also did

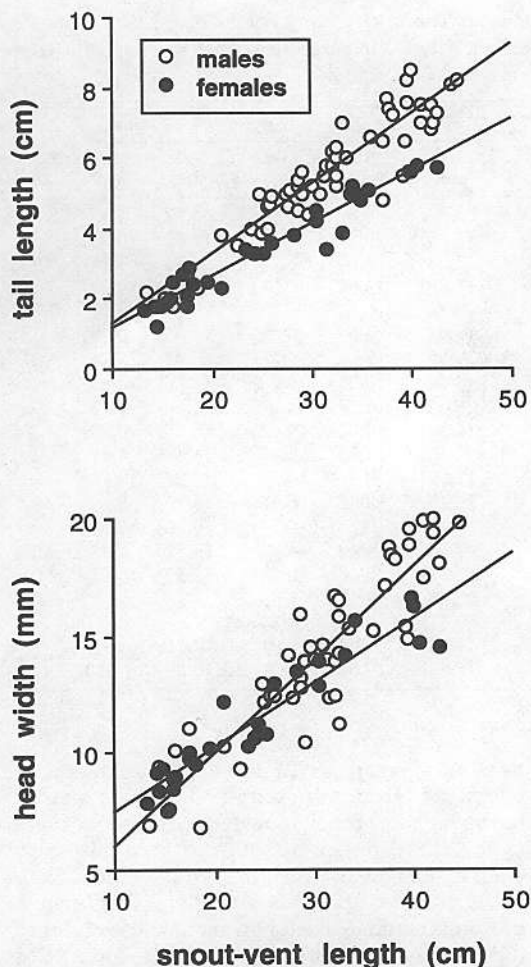


FIG. 1. Sexual dimorphism in shieldnose snakes, *Aspidelaps scutatus*. Males (circles) have relatively longer tails (upper graph) and wider heads (lower graph) than do females (dots). See text for statistical tests.

not differ between the sexes (using head length as the covariate: heterogeneity of slopes $F_{1,65} = 1.59$, $P = 0.21$; intercepts $F_{1,66} = 1.99$, $P = 0.16$). Because of the relatively larger heads and longer tails of males, the larger SVLs of female *Aspidelaps* did not result in them having larger heads or longer tails than males (Table 1).

Food Habits.—We recorded 24 prey items from shieldnose snakes, including 10 field records from Manyeleti animals. The most common prey were anurans (14 records, = 58%), snakes (five records, = 21%) and mammals (four records, = 17%: Table 2). The single record of a squamate egg may represent a secondary item, retained in the stomach after the reptile that contained it had been fully digested. To examine possible dietary differences between the sexes, we classified prey items as reptiles, amphibians or mammals and compared the relative numbers

TABLE 2. Prey items identified from alimentary tracts of shieldnose snakes, *Aspidelaps scutatus*.

Prey type	Number of snakes containing that prey type
Anurans	
Unidentified anurans	6
<i>Breviceps adspersus</i>	1
<i>Bufo garmani</i>	1
<i>Hemisus</i> sp.	1
<i>Pyxicephalus edulis</i>	2
<i>Tomopterna</i> sp.	1
<i>Tomopterna cryptotis</i>	2
Reptiles	
<i>Crotaphopeltis hotamboeia</i>	2
<i>Lycophidion capense</i>	3
Squamate egg	1
Mammals	
Unidentified sp.	4

of each prey type in each sex. Despite the small sample size in snakes of known sex (five prey in females, 11 in males), the sex difference was significant ($\chi^2 = 6.30$, $P < 0.05$). Males in our sample contained mainly anurans (6 of 11 prey) whereas this prey type was not recorded in females.

Reproductive Biology.—The seasonal timing of mating, oviposition and hatching was very consistent from year-to-year in the Manyeleti females (Table 3). Mating was recorded in springtime (October) for three pairs of snakes, with oviposition in midsummer for most clutches (late December to early January), and hatching in autumn (March: Table 3). Two additional Manyeleti snakes were observed in courtship on 15 and 16 October, and oviposition was recorded on 11 November and 21 December. One Manyeleti clutch was laid earlier than usual (11 November) and consequently hatched earlier (15 January). A very different timing of reproduction was evident in the captive snakes acclimated to Northern Hemisphere seasonal cycles (Table 3). Incubation required 61 to 82 d, with specific records (clutch means at known temperatures) of 61 and 62 d at 30°C, and 63 and 68 d at 28°C.

Clutch sizes ranged from four to ten eggs, and averaged 7.92 (SD = 2.14, $N = 11$). Clutch sizes were not significantly correlated with maternal body length ($N = 11$, $r = -0.27$, $P = 0.42$). Offspring averaged around 16 cm SVL (5 g) at hatching, with no correlation between maternal SVL and offspring dimensions (*versus* egg mass — $N = 10$, $r = 0.48$, $P = 0.16$; *versus* offspring SVL: $N = 9$, $r = -0.06$, $P = 0.87$; *versus* offspring mass — $N = 9$, $r = 0.19$; $P = 0.63$). Unsurprisingly, heavier eggs produced hatchlings that

TABLE 3. Reproduction in shieldnose snakes, *Aspidelaps scutatus*. SVL = snout-vent length (cm). Female mass was recorded post-oviposition. Table shows mean values, with SD in parentheses. * = specimen at Dallas Zoo; others at Manyeleti. # = mating recorded in field at time of collection.

Female body size		Dates			Egg sizes			Hatchlings		
SVL (cm)	Mass (g)	Mating	Oviposition	Hatching	Length (mm)	Width (mm)	Mass (g)	SVL (cm)	Mass (g)	Clutch size
48.6	64.7	—	31-Dec-93	4-Mar-94	28.3 (1.33)	18.8 (0.28)	5.91 (0.13)	16.22 (1.00)	4.85 (0.05)	7
53.0	128.0	—	31-Dec-88	3-Mar-89	32.83 (1.85)	16.80 (0.52)	6.26 (0.37)	16.14 (0.67)	5.16 (0.24)	9
52.9	—	7-Oct-88	21-Dec-88	7-Mar-89	30.24 (1.97)	18.32 (0.67)	6.41 (0.31)	15.68 (0.64)	6.01 (0.24)	8
47.1	107.8	—	8-Jan-92	—	39.92 (3.36)	17.1 (0.53)	7.36 (0.29)	17.48 (6.76)	5.96 (0.61)	5
44.8	52.9	19-Oct-88	5-Jan-89	8-Mar-89	26.45 (1.53)	16.57 (0.40)	4.59 (0.12)	15.99 (0.77)	5.13 (0.07)	9
58.2	154.6	—	11-Nov-90	15-Jan-91	32.53 (1.99)	17.85 (0.99)	6.43 (0.27)	16.4 (0.26)	4.95 (0.13)	4
55.4	142.0	4-Oct-89	14-Dec-89	1-Mar-90	31.23 (2.47)	18.08 (0.75)	6.46 (0.29)	15.77 (0.56)	5.45 (0.36)	10
51.8	—	—	29-Dec-89	3-Mar-90	29.34 (2.11)	18.42 (0.60)	6.23 (0.26)	16.52 (2.33)	4.78 (0.17)	10
47.5	146.8	25-Nov-88	9-Feb-89	—	30.75 (0.81)	18.57 (0.44)	6.38 (0.24)	—	—	9
*56.2	116.2	—	9-May-88	14-Jun-88	41.27 (1.99)	20.01 (0.64)	9.91	17.21 (0.69)	6.67 (0.30)	7

were heavier (using clutch means: $N = 9$, $r = 0.79$, $P < 0.012$) and longer ($N = 9$, $r = 0.67$, $P < 0.048$). Eggs from larger clutches tended to be smaller, but the trend fell well short of statistical significance ($N = 10$, $r = -0.31$, $P = 0.38$). RCMs averaged 0.482 (SD = 0.19, $N = 8$), and ranged from 0.17 to 0.78. RCMs were not significantly correlated with maternal SVL ($N = 8$, $r = -0.52$, $P = 0.19$), clutch size ($N = 8$, $r = 0.51$, $P = 0.20$), or egg mass ($N = 8$, $r = -0.18$, $P = 0.68$). Partial correlation analysis was also carried out using these variables, but did not reveal any significant correlations.

DISCUSSION

Our results are generally consistent with those of previous authors, but provide additional detail on the biology of shieldnose snakes. The seasonal timing of reproduction in *Aspidelaps scutatus* appears to be very consistent from year-to-year, as would be expected of a snake living in a highly seasonal temperate environment. The pattern of mating in spring, oviposition in midsummer, and hatching in autumn (Table 3) is probably typical for most snakes of southern Africa (e.g., Branch, 1988) as well as for other southern continents (Shine, 1985). Production of two clutches within a single breeding season has been recorded in a captive Manyeleti female (Haagner and Morgan, 1992).

Our data on reproductive output of *A. scutatus* support and extend the previous study of Haag-

ner and Morgan (1992). For example, the mean clutch size from our study (7.9 eggs) is similar to the mean number reported by those workers (8.3). Hatchling sizes from our study are also similar. The mean RCM that we calculated from eight clutches (0.48) is slightly lower than a previous estimate based on six of these clutches (0.54: Haagner and Morgan, 1992). This RCM is close to the average value for other snakes (0.47 for all snakes; 0.52 for oviparous species; from the review by Seigel and Fitch, 1984, after statistical correction so that clutch mass appears only in the numerator of this ratio). That the RCM for *A. scutatus* should be similar to that for other, more slender-bodied snakes is surprising in light of the correlation between body shape and RCM seen in lizards (Vitt and Congdon, 1978). Under this argument, we might expect that the heavyset build of *A. scutatus* would allow females to fit more eggs into their body cavity, and hence increase the maximum possible RCM. However, unlike the case in lizards, abdominal volume relative to maternal mass may be relatively independent of body shape among snakes (Shine, 1992).

Female shieldnose snakes are known to guard their eggs after oviposition (Haagner and Morgan, 1992), a behavior that may incur substantial costs (e.g., in reduced feeding opportunities) that are independent of the number of eggs produced. These high fecundity-independent costs of reproduction, in turn, may also favor delayed maturation in females, and hence the

evolution of sex differences in mean adult body size (Bull and Shine, 1979; Madsen and Shine, 1995). Such costs may be common, and larger body size in females than males (as seen in shieldnose snakes) is the most common situation among snakes in general. Notwithstanding this general pattern, however, elapids show more interspecific variation in the direction and degree of sexual size dimorphism than do most other snake lineages (Shine, 1978, 1994). Larger female body size is typically (but not universally) seen in snake species in which rival males do not engage in physical combat bouts during the mating season, suggesting that large body size in male snakes (relative to conspecific females) may be a sexually-selected trait that enhances male success in combat bouts (Shine 1978, 1994). In keeping with this interpretation, male-male combat has not been recorded in *A. scutatus*, and attempts to elicit the behavior in captive specimens have been unsuccessful (Haagner and Morgan, 1992). Research on raptorial birds (hawks and eagles) has attributed large female body size to selection for ability to defend the clutch (Mueller and Meyer, 1985), and the same factor may have exaggerated the degree of sexual size dimorphism present in *A. scutatus*.

Shieldnose snakes show significant sex divergence in relative body proportions, as well as in absolute size. Divergence in tail lengths is widespread in snakes, and may have evolved for a number of reasons (King, 1989). Divergence in head sizes is also widespread, but seems to be consistent with a more limited number of explanations. Although larger head size in males than in females (as seen in *A. scutatus*) is a common phenomenon in lizards, and has generally been attributed to selection to enhance biting power during male-male combat (e.g., Vitt and Cooper, 1985), this interpretation seems unlikely to apply to shieldnose snakes. Male *A. scutatus* have not been reported to fight each other (see above), and even if such bouts do occur, they are unlikely to involve biting (based on the form of the combat bouts described for related species of elapids—Shine 1994). Instead, the divergence in relative head sizes and head shapes between male and female shieldnose snakes may reflect differences in food habits between the sexes.

Despite the very small sample sizes, our data showed a significant difference in prey types between male and female *A. scutatus*. We do not know if this difference is biologically significant, perhaps due to sex differences in the times or places of activity. Such sex differences in diet may be relatively widespread in snakes, and may impose selection for differences in head size and shape between the sexes (Shine, 1991). Snakes that eat anurans (a prey type seen only

in males in our data) may be under strong selection for a wider gape, to ingest these relatively wide prey (especially since toads can inflate their bodies and hence greatly increase their cross-sectional area). Such pressures may be less intense in the larger sex (females), where prey size is lower relative to predator size, and selection on gape size may also be less intense for animals that eat elongate prey items (such as other snakes). Interestingly, the body-size dimorphism and head-size divergence in *A. scutatus* work in opposite directions (females are larger but have relatively smaller and thinner heads), with the end result that the two trends cancel each other out. Thus, there is no significant difference in mean head sizes between adult male and female shieldnose snakes (Table 1). In having relatively larger heads in males than in females, *A. scutatus* resembles confamilial species rather than snakes from other lineages: the sex with the larger head tends to be the female in most colubrid lineages, but the male in most elapids (Shine, 1991).

The prey items we identified from shieldnose snakes comprise a broad array (Table 2), supporting statements of previous workers (e.g., "lizards, other snakes, toads and small mammals"—Broadley 1983, pp. 283; "a varied diet, taking small mammals, amphibians, lizards, and even other snakes"—Branch 1988, pp. 90). Haagner and Morgan (1992) provided specific records of predation on amphibians, and Haagner (1991) reported alate termites in the stomachs of two specimens. Although there is general agreement about the catholic diet of these small snakes, the way in which they capture their prey remains unclear. Our dietary data (Table 2) do, however, permit some inferences. Shieldnose snakes are highly nocturnal in nature: the only specimen of *A. scutatus* seen active on the road at Manyeleti during daylight hours was a small male at dusk (1910 h) in midsummer (8 January 1991). All of the prey items we identified to species level were also nocturnal species (Table 2). Hence, it seems unlikely that these prey were taken by the snakes actively searching out inactive prey in their diurnal retreat sites (the most common foraging strategy of nocturnal elapids in other parts of the world—e.g., Zinner, 1971; Shine, 1981). Instead, the shieldnose snakes presumably captured active prey: either from ambush, or while both prey and predator were active. We cannot determine which of these possibilities is more likely. Detailed behavioral observations of free-ranging shieldnose snakes, or snakes in large outdoor enclosures, would be needed to resolve this question.

Finally, we turn to the topic that introduced this paper: the ecological significance of body shape in snakes. We cannot draw any firm con-

clusions, especially given our small sample sizes and the preliminary nature of this study. However, it is interesting to note that the heavyset build of *A. scutatus*—an unusual feature among proteroglyphous snakes—is associated with distinctive characteristics of trophic biology (possible ambush foraging; divergence in trophic morphology and prey types between the sexes) and reproduction (maternal egg-guarding). We cannot infer any causal connection between these morphological and ecological features, but the correlations are suggestive. Additional data are needed on other, independently-derived shifts in morphology and ecology within snake lineages, before we can explore the adaptive significance of these kinds of variations.

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