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Variation in number of ventral scales in snakes: effects on body size, growth rate and survival in the adder, *Vipera berus*

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(With 3 figures in the text)

The relationship between number of ventral scales, correlating with number of body vertebrae, and body size of adders, *Vipera berus*, was investigated using captive-born young and wild-caught adults (snout–vent length >400 mm) from six populations in eastern Sweden. Females had significantly more ventral scales, and were larger, than males in all populations. Among adult individuals, snout–vent length was highly positively correlated with the number of ventral scales when differences due to sex and locality were controlled for. The same pattern was true for new-born individuals when differences due to litter and sex were controlled for. The influence of number of ventral scales on survival and growth rate as possible causes of this positive correlation was examined. Mean number of ventral scales was lower in new-born snakes than in adults, indicating selection against individuals with a low scale count. Since this selection appears to take place in the early juvenile phase, it is inadequate to explain the relationship between adult body size and number of ventral scales. However, individuals with many ventral scales had significantly higher growth rates than individuals with few ventrals. This suggests that individuals with many ventral scales enjoy a higher growth rate and therefore are able to reach a larger size than their conspecifics of the same age with few ventral scales. This would explain the positive relationship between body size and ventral scale number observed in new-born and adult snakes.

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Introduction

The number of ventral scales has often been used in the literature for the identification of snakes, since it shows great variation among species and higher taxa (e.g. Boulenger, 1913). Yet there is a substantial amount of variation in number of ventral scales also within species (Klauber, 1943; Marx & Rabb, 1965; Kerfoot, 1970), both between sexes (e.g. Inger, 1943; Campbell & Armstrong, 1979; Grobman, 1984; Thorpe, 1989), among different populations (e.g. Schwartz, 1976; Grobman, 1984; Nilson & Andrén, 1986; Arnold, 1988) and among individuals (Klauber, 1945). Some indications of the possible causes of this variation have emerged. For example, Fox (1948), Fox, Gordon & Fox (1961) and Osgood (1978) have shown that exposure to low temperatures during embryonic development results in a decrease in the number of scales and an increase in the variability in scale number in garter snakes (*Thamnophis* spp.). Duplication of vertebrae is also known to result in an increase in ventral scale numbers (W. King, 1959; Clark & Callison, 1967; Plummer, 1980). On the other hand, the number of ventral scales and vertebrae does not change during ontogeny (Klauber, 1945; Arnold, 1988) and has been shown to exhibit moderate to high heritability (Beatson, 1976; Arnold, 1988).

The ventral scales are connected to the ribs by the costocutaneous musculature (Kerfoot, 1970), and the vertebrae, ribs, muscles and ventral scales are all part of a functional complex involved in locomotion (Gans, 1962). The usual condition among snakes is a ratio of one ventral scale to one vertebra (e.g. Ruthven & Thompson, 1913; Kramer, 1961; Alexander & Gans, 1966; Voris, 1975), although some primitive snakes deviate from this ratio (Bellairs & Underwood, 1951; Gans & Taub, 1965). Consequently, in *Vipera*, the number of ventral scales has been shown to correlate with number of vertebrae (Kramer, 1961).

Although intraspecific variation in number of ventral scales (and thus of vertebrae) has been frequently shown, only few papers have considered the ecological importance of this variation. Some indications of its ecological significance have emerged though, following two general lines. First, there seems to be a positive association between body size and number of ventral scales. This has been demonstrated at different levels. A positive relationship between number of ventral scales and body size across species of the genus *Vipera* has been shown (Saint Girons, 1978), and according to data from Saint Girons (1978) and Nilson & Andrén (1986), the same pattern exists also at the subspecific level within some species of *Vipera*. Further, in species of *Vipera* which show sexual size dimorphism, the larger sex tends to have a larger number of ventral scales (Saint Girons, 1978). In spite of the fact that snakes have indeterminate growth (Andrews, 1982), a positive relationship between body size and number of ventral scales has also been documented among individuals within populations (Klauber, 1945, but see Voris, 1975), even among juvenile snakes (Klauber, 1945; Arnold & Bennett, 1988). Secondly, recent studies have demonstrated an association between number of ventral scales and locomotor performance (Arnold & Bennett, 1988). Jayne & Bennett (1990) also showed that both locomotor performance and body size were related to differential survival of individuals in *Thamnophis sirtalis*, where individuals with high performance and large body size enjoyed higher survival. Since the number of ventral scales has been shown to affect both these characters, it may have profound effects on survival. Some studies have also demonstrated a higher mean number of ventral scales and/or a smaller variance in adults than in juvenile snakes, indicating directional and/or stabilizing selection against low number of ventral scales (Linsdale, 1936; Stuart, 1941; Dunn, 1942; Inger, 1943; Beatson, 1976, but see Klauber, 1945). Given heritable variation within a population, scale number has therefore the potential for undergoing evolutionary change in response to selection.

In this paper, we examine the relationship between number of ventral scales and body size in the adder (*Vipera berus*). We will address the following questions: (1) How much variation exists in number of ventral scales and body size within and among different adder populations? (2) Is there a positive relationship between number of ventral scales and body size among individuals within populations, between sexes and among different populations? (3) If such a relationship exists at the individual level, does this result from a positive relationship between number of ventral scales and individual growth rate, or can it be explained in terms of differential survival of individuals with different numbers of ventral scales?

Materials and methods

We present data from 2 mainland (V and U) and 4 insular (A, I, R and F) populations of adders where V stands for Västmanland; U: Uppsala; A: Ängskär; I: Infredeln, R: Röder and F: Svenska högarna. Data from locality V derive from Bernström (1943); all other data were collected by the authors.

For each snake, we recorded date of capture, sex, snout–vent length (SVL) to the nearest 5 mm, number of ventral scales (excluding the anal scale but including anomalous scales) and number of anomalous ventral scales. All snakes were individually marked by branding on different combinations of ventral scales, and subsequently released at the place of capture. A number of wild-caught pregnant females were held in an outdoor enclosure in Uppsala until parturition, and the same data were gathered from the new-born young as from wild-caught snakes.

Since growth rate decreases with age and size in snakes (Andrews, 1982), studies of body size or growth will inevitably be affected by age-dependent size variation. In order to reduce the influence of such confounding age effects, our analyses only include adult individuals. Since it is not possible to age snakes in the field, we restricted our analyses to individuals with a SVL above 400 mm, unless otherwise stated. That is the approximate size at which adders reach sexual maturity (Phelps, 1989).

The relationship between number of ventral scales and SVL was examined by analysis of covariance, using SVL as the dependent variable and number of ventral scales as a covariate (i.e. a continuous independent variable). Because SVL differed between sexes and localities, sex and locality were also included in the model as independent variables. Since also the number of ventral scales differs between sexes, it was standardized to a mean of zero and a standard deviation of one for each sex in both new-born and wild-caught adders.

Data on growth rates were obtained in a mark–recapture study on localities A and I in 1986 to 1990. Growth rate was calculated as the increment in SVL between captures divided by the time, in days, between captures. Periods of hibernation and non-feeding were excluded from the calculations and were set to 16 September–31 May for males and 16 September–15 May for females. The longer non-feeding period of males, as compared to females, depends on the fact that males usually do not feed before mating in spring, whereas females do. Since growth rate changes with size we calculated relative growth rate as the residuals from the linear regression of growth rate on SVL at first capture. The relationship between number of ventral scales and relative growth rate was then analysed by a linear regression.

In order to test for possible effects of anomalous ventral scales on growth rate, we compared mean relative growth rates between individuals with and without scale anomalies. Relative growth rate was here calculated as the residuals from the multiple regression of growth rate on SVL and number of ventral scales. The residuals will thus represent a measure of growth rate independent of size and number of ventral scales in relation to other individuals in the sample.

Results

Variation in number of ventral scales and body size

Between sexes

Mean SVL and mean number of ventral scales for male and female adders from the six localities are given in Table I. Both characters exhibited pronounced sexual dimorphism. Females were larger ($F_{1,287} = 54{\cdot}3$; $P < 0{\cdot}0001$) and had a higher number of ventral scales ($F_{1,287} = 141{\cdot}0$; $P < 0{\cdot}0001$) than males. There was a significant interaction between sex and locality ($F_{5,287} = 2{\cdot}7$;

TABLE I

Mean snout–vent length (SVL, mm) and mean number of ventral scales for male and female ***V. berus*** *over 400 mm SVL at six localities*

Sex	Locality	*n*	SVL (S.D.)	Scales (S.D.)
M	A	37	494 (48·8)	144·8 (2·3)
	I	33	517 (64·2)	145·5 (2·6)
	R	11	499 (42·1)	144·5 (1·8)
	F	14	496 (50·6)	145·8 (3·4)
	U	17	451 (38·8)	144·9 (2·7)
	V	57	466 (37·9)	144·2 (2·3)
F	A	32	525 (61·9)	148·5 (2·7)
	I	18	592 (66·7)	149·1 (2·8)
	R	22	546 (74·5)	150·6 (3·2)
	F	26	519 (59·8)	149·2 (2·7)
	U	4	546 (67·3)	149·8 (1·0)
	V	28	544 (52·7)	149·0 (2·6)

$P=0{\cdot}0221$), showing that the degree of sexual size dimorphism varied among localities. The size advantage of females varied from 5–21% and was largest at locality U and smallest at locality F. By contrast, the degree of sexual dimorphism in number of ventral scales did not vary among localities ($F_{5,287}=1{\cdot}5$; $P=0{\cdot}19$).

Among localities

Body size and number of ventral scales also varied among localities, as seen in Table I. The variation in SVL was highly significant ($F_{5,287}=5{\cdot}9$; $P<0{\cdot}0001$), while that of number of ventral scales was not ($F_{5,287}=1{\cdot}2$; $P=0{\cdot}29$). In males, the difference between the largest and the smallest population mean SVL was 66 mm, whereas in females this difference was 73 mm. The difference between the highest and the lowest population mean number of ventral scales was 1·6 and 2·2, respectively.

Number of ventral scales in relation to body size

Previous studies have indicated a positive relationship between number of ventral scales (and vertebrae) and body size at different levels (Klauber, 1945; Saint Girons, 1978; Arnold & Bennett, 1988). Here we test for such a relationship in the adder at the level of individuals, sexes and populations.

Among individuals

Among adults there was a clear positive relationship between body size and number of ventral scales within sexes and populations. Number of ventral scales accounted for a significant amount of the variation in SVL when differences due to sex and locality were controlled for ($P=0{\cdot}0003$, Table II). Just to visualize this result we show the regression lines of SVL on number of ventral scales for each sex and locality in Fig. 1. Only three of the 11 regression lines were significant (locality R: males, $b=17{\cdot}9$, $P=0{\cdot}006$, $n=11$; locality F: males, $b=8{\cdot}3$, $P=0{\cdot}04$, $n=14$; females,

TABLE II

Results from analysis of covariance treating snout–vent length (SVL) as dependent variable, standardized number of ventral scales as covariate and sex and locality as independent variables. Data from adult adders (SVL > 400 mm). The model was highly significant; $F = 7{\cdot}18$; $r^2 = 0{\cdot}38$; $P = 0{\cdot}0001$; $n = 299$. The other interaction terms were not significant

Source	*d.f.*	F	*P*
Locality	5	6·3	0·0001
Sex	1	40·6	0·0001
Scales	1	13·1	0·0003
Sex∗Scales	1	4·0	0·0461

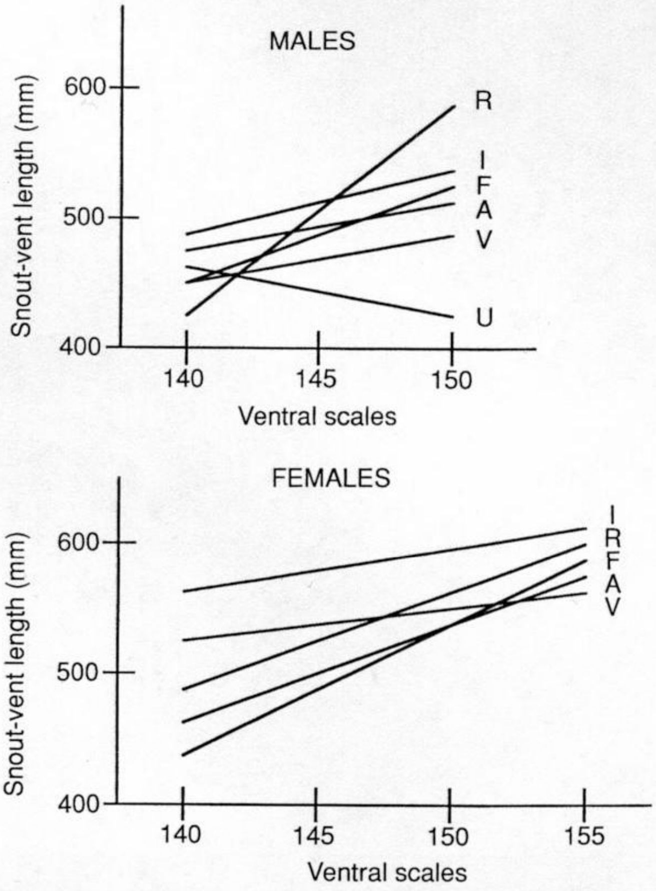

FIG. 1. Regression lines for the relationship between number of ventral scales and snout–vent length for adult individuals (SVL > 400 mm) in six adder populations. Females at locality U excluded due to low sample size.

TABLE III

Results from analysis of covariance treating snout–vent length as dependent variable, litter and sex as independent variables and standardized number of ventral scales as covariate. Data from new-born adders. The model was highly significant ($F=6{\cdot}25$; $r^2=0{\cdot}86$; $\mathbf{P}=0{\cdot}0001$; $\mathbf{n}=72$). No interaction term was significant

Source	*d.f.*	F	*P*
Litter	9	8·9	0·0001
Sex	1	0·004	0·9511
Scales	1	4·7	0·0365

$b=9{\cdot}6$, $P=0{\cdot}03$, $n=26$), but more importantly, 10 out of them were positive. This distribution of negative slopes differs significantly from random (Binomial test; $P=0{\cdot}012$). Also, among captive-born neonates there was a significant positive relationship between number of ventral scales and SVL, when differences due to sex and litter were controlled for ($P=0{\cdot}0365$, Table III). Thus, these analyses show that individuals with many ventral scales are larger than those with few already at birth as well as later in life when they have reached sexual maturity.

The significant interaction term Sex∗Scales ($P=0{\cdot}0461$) in Table II shows that SVL increases with number of ventral scales at different rates in males and females as illustrated in Fig. 2. Both SVL and number of ventral scales were standardized to a mean of zero and a standard deviation of one for each locality and sex in order to allow pooling of data from all five localities. It is clear from Fig. 2 that females increase more in SVL per additional scale than do males.

As an additional test for the relationship between number of ventral scales and body size among

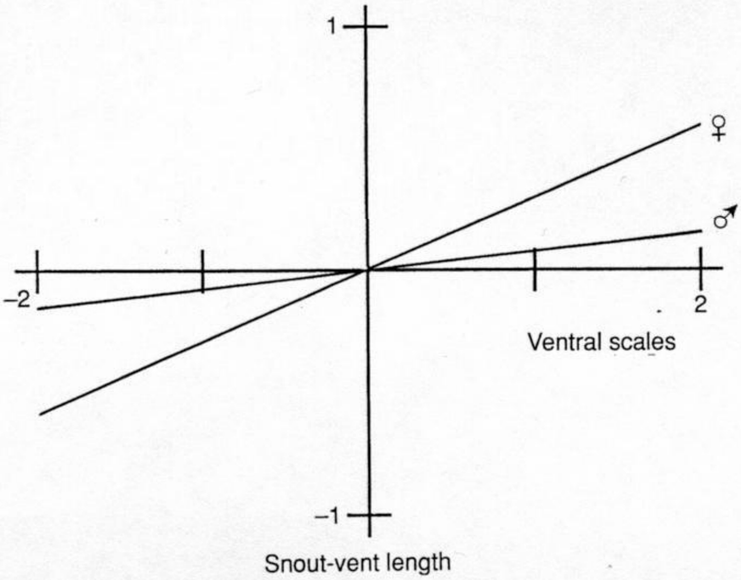

FIG. 2. Relationship between number of ventral scales and snout-vent length in male and female adders. The number of ventral scales and snout-vent length were standardized to a mean of zero and a standard deviation of one for each sex and locality to allow pooling of data. The equations were: for females; $y=0{\cdot}293x$, and for males; $y=0{\cdot}153x$.

the adults, we selected the five largest individuals of each sex from each locality and compared their number of ventral scales with the mean of the series. By this method each of the five largest specimens is given separate recognition and it is possible to determine whether the largest individuals have more ventral scales than expected by chance. Thirty-six of the 55 largest individuals (females at locality U excluded owing to inadequate sample size) had ventral scale counts above the mean. This differs significantly from a random distribution (Binomial test: $P < 0{\cdot}031$), again showing that there is a positive relationship between number of ventral scales and body size at the individual level.

Between sexes

Our results showing sexual dimorphism in both SVL and number of ventral scales, with females being the larger sex and having a larger number of ventral scales, conforms to the pattern suggested by Saint Girons (1978) that the larger sex possesses the larger number of ventral scales.

Among populations

Since there was a strong positive correlation between number of ventral scales and SVL among individuals within populations, we wanted to see whether this relationship might exist also at the level of populations. It apparently does not. There was no significant correlation between mean number of ventral scales and mean body size among localities, in either males or in females (males: $r = 0{\cdot}49$, $P = 0{\cdot}33$, $n = 6$; females: $r = 0{\cdot}20$, $P = 0{\cdot}83$, $n = 6$). Thus, although number of ventral scales is highly positively correlated with body size at the individual level, it does not explain body size variation at the population level.

Number of ventral scales in relation to growth rate

Since body size increases with number of ventral scales at the individual level, we also wanted to examine the mechanism behind this pattern. One possibility could be that the larger size of individuals with many ventral scales is caused by a higher growth rate. To evaluate this hypothesis, data on 39 males and 22 females from locality A, and 24 males and 11 females from locality I, were subjected to four separate linear regressions of growth rate on SVL. The residuals from these regressions represent a measure of relative growth rate and were subsequently examined in relation to a standardized number of ventral scales. (Ventral scale number was standardized to a mean of zero within sexes since males and females differ in scale counts.) There was a significantly positive (although rather weak) relationship between the standardized number of ventral scales and relative growth rate (Fig. 3).

Anomalous ventral scales are often associated with abnormal vertebrae and/or ribs such as fusions or duplications, and a previous study indicated a negative effect of such anomalies on individual growth rate (Arnold, 1988). The presence of anomalous ventral scales did not, however, influence growth rate of the individuals in our sample (Table IV). Mean relative growth rate of individuals with and without anomalies was not significantly different in any of the four comparisons, and the sign of the difference showed no consistency among groups.

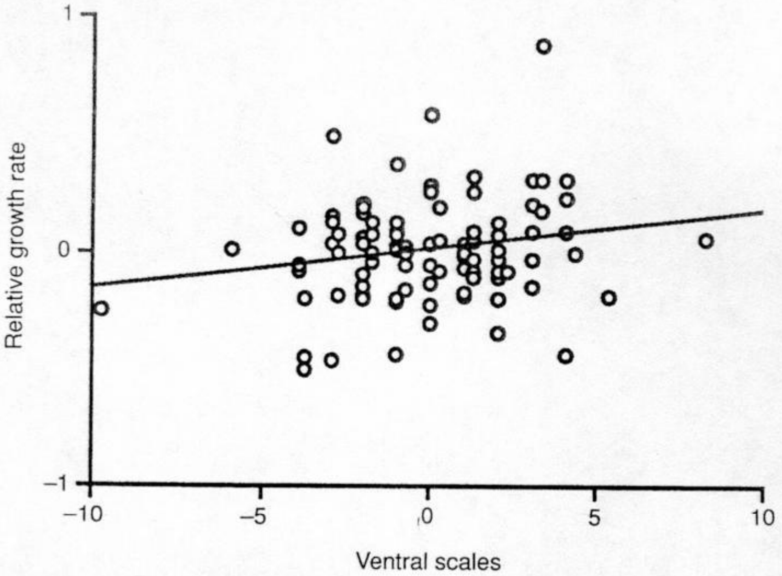

FIG. 3. Graph showing the relationship between standardized number of ventral scales and relative growth rate (RGR) for 96 adders from localities A and I. Number of ventral scales was standardized to a mean of zero for males and females separately. RGR was calculated at each locality as the residuals from the linear regression growth rate (mm/day) on snout–vent length at first capture, thus representing growth rate independent of initial size. The regression was significant ($y=0{\cdot}020x$; $r^2=0{\cdot}053$; $P=0{\cdot}023$). Note that 10 observations are hidden.

TABLE IV

Mean relative growth rate of adders with one or more anomalous ventral scale vs. individuals without anomalous scales. Mean relative growth rate was calculated as the residuals from the multiple regression of growth rate (mm/day) on snout–vent length and number of ventral scales on each locality and sex separately. Z denotes statistics of the Mann–Whitney U-test

Locality	Sex	Anomalous scales Yes/No	*n*	Mean relative growth rate	S.D.	Z	*P*
A	M	Yes	12	0·016	0·23	−0·18	0·86
		No	22	−0·009	0·22		
	F	Yes	7	−0·057	0·11	−0·44	0·66
		No	13	0·030	0·50		
I	M	Yes	9	0·009	0·19	−0·19	0·85
		No	11	−0·007	0·17		
	F	Yes	2	−0·222	0·05	−1·67	0·10
		No	6	0·074	0·21		

Number of ventral scales in relation to survival

The positive correlation between scale counts and SVL among adults could also be due to individuals with many ventral scales living longer and thus attaining larger body size. If the number of ventral scales influences survival of individuals, one would expect the distribution of ventral scale counts to differ between young and old individuals within a population. Directional selection favouring either high or low numbers would tend both to change the mean and to reduce

TABLE V

Means and variances (S2) for the number of ventral scales in juvenile/subadults (snout–vent length $\leqslant$ 400 mm) and adult (snout–vent length > 400 mm) adders in six populations with tests of differences in means and variances. Z denotes statistics of the Mann–Whitney U-test. No juvenile/subadult females in locality U were found

Sex	Loc.	Juv./Sub. Adult	*n*	Mean (Range)	Z	*P*	S^2	F	*P*
M	A	J/S	22	144·0 (141–148)	1·68	0·09	3·9	1·37	>0·20
		A	37	144·8 (140–149)			5·6		
	I	J/S	5	145·6 (144–147)	0·07	0·94	1·3	4·91	>0·05
		A	33	145·5 (139–150)			6·5		
	R	J/S	3	144·3 (142–146)	0·25	0·81	4·3	1·30	>0·50
		A	11	144·5 (143–147)			3·3		
	F	J/S	5	144·0 (140–146)	0·70	0·48	6·5	1·75	>0·50
		A	14	145·8 (141–152)			11·4		
	V	J/S	12	144·1 (141–148)	0·39	0·70	5·2	1·02	>0·50
		A	57	144·2 (139–149)			5·1		
	U	J/S	3	144·0 (143–145)	0·59	0·55	1·0	7·34	>0·10
		A	17	144·9 (141–149)			7·4		
F	A	J/S	14	147·7 (145–152)	1·32	0·18	3·8	1·95	>0·10
		A	32	148·5 (139–154)			7·4		
	I	J/S	9	149·7 (146–153)	0·22	0·83	7·3	1·08	>0·50
		A	18	149·1 (146–157)			7·9		
	R	J/S	2	148·5 (147–150)	0·95	0·34	4·5	2·31	>0·50
		A	22	150·6 (145–158)			10·4		
	F	J/S	4	150·0 (147–153)	0·65	0·52	6·7	1·06	>0·50
		A	26	149·2 (145–157)			7·1		
	V	J/S	4	147·8 (145–151)	1·04	0·30	7·6	1·18	>0·50
		A	28	149·0 (143–152)			6·6		
	U	A	4	149·3 (149–151)			0·9		

the variance, while disruptive selection, favouring the extremes, would increase the variance (e.g. Endler, 1986). We compared means, ranges and variances in number of ventral scales between wild-caught individuals classified as juveniles/subadults (SVL $\leqslant$ 40 mm) or adults (SVL > 400 mm) for the six populations separately. By using all individuals of a wide range of sizes, it is likely that those classified as adults are, indeed, older than those classified as juveniles/subadults. The results are given in Table V. Mean number of ventral scales did not differ significantly between the two groups in any of the populations but was slightly higher in adults in eight out of 11 comparisons. Adults also showed the same or a larger range in all 11 comparisons but this was probably due to the larger number of adult individuals sampled. The total range in ventral scale counts was 140–153 among juveniles/subadults and 139–158 among adults. There were no significant differences in variance between the two age categories, although it was slightly larger in the adult group in eight out of the 11 cases. Thus, these data do not indicate that differences in number of ventral scales might influence survival of individuals. However, it is possible that the young wild-caught adders had already been exposed to selection. We therefore compared mean number of ventral scales between captive-born neonates not exposed to selection with wild-caught adults. New-born females at localities I and R and new-born males at locality R had a significantly smaller mean number of ventral scales than adults from the same localities (Table VI), suggesting selection

TABLE VI

Comparison between new-born (New) adders and wild-caught adults (Ad. SVL > 400 mm) from three localities with tests of differences in means and variances. Z denotes statistics of the Mann–Whitney U-test

Sex	Loc.	New/Ad.	*n*	Mean (Range)	Z	*P*	S^2	F	*P*
M	A	N	21	144·1 (140–150)	1·22	0·22	7·6	1·35	>0·20
		A	37	144·8 (140–149)			5·6		
	I	N	5	143·4 (141–145)	1·79	0·07	3·3	1·97	>0·20
		A	33	145·5 (139–150)			6·5		
	R	N	18	142·6 (139–146)	2·16	0·03	3·3	1·19	>0·50
		A	11	144·5 (143–147)			3·3		
F	A	N	18	148·2 (144–151)	0·41	0·68	4·1	1·80	>0·10
		A	32	148·5 (139–154)			7·4		
	I	N	5	145·2 (142–147)	2·56	0·01	4·7	1·68	>0·50
		A	18	149·1 (146–157)			7·9		
	R	N	14	148·1 (143–151)	2·09	0·04	6·4	1·63	>0·20
		A	22	150·6 (145–158)			10·4		

against low scale counts. These results, therefore, indicate that individuals with many ventral scales may have higher survival and that this selection takes place in the early juvenile stage.

Discussion

Number of ventral scales and body size

Adders vary considerably both in number of ventral scales and in body size among individuals, sexes and populations. Females were both significantly larger and had a higher number of ventral scales than males at all localities. Mean SVL also varied significantly among localities, as did the degree of sexual dimorphism (see also Forsman, 1991). By contrast, no significant variation among localities could be demonstrated in mean number of ventral scales or in the degree of sexual dimorphism in number of ventral scales.

There are some indications in the literature of a positive relationship between body size and number of ventral scales among individuals within a population. Thus, Arnold & Bennett (1988) reported a positive correlation ($r = 0{\cdot}28$; $P < 0{\cdot}01$) for new-born *Thamnophis radix*, whereas Voris (1975) found no such correlation for different species of sea snakes (although with a small sample size). Klauber (1945) made a thorough investigation of possible relationships between ventral scale counts and body size in several species of snakes. Although his results were negative in some cases, the overall result suggested that larger individuals have more ventral scales than smaller ones. In an analysis of broods of five species (genera *Elaphe*, *Natrix*, *Thamnophis* and *Crotalus*), separated by sex and locality, 12 out of 15 correlations between body size and number of ventral scales were positive, although none was significant. Klauber pointed out that any such correlation may not become apparent until some time after birth when the snakes have had time to grow, thus implying that snakes with many ventral scales may grow faster. He therefore made an additional test for this relationship. In seven species of the genera *Adelphicos*, *Diadophis*, *Geophis*, *Phyllorhynchus*, *Sonora* and *Toluca* he selected the five largest individuals of each sex and compared their number of ventral scales with the mean of the series. Altogether 53 out of 70 specimens were above the means, representing a probability of less than 0·0001. Klauber's results are thus in agreement with ours, according to which 36 out of the 55 largest individuals ($P=0{\cdot}031$) had scale counts exceeding the mean. This suggests that individuals with a large number of ventral scales attain a larger asymptotic body size. This was further confirmed by an analysis of covariance. Among adults we found a strong positive relationship between number of ventral scales and body size when differences due to sex and locality were controlled for (Table II; Figs 1 and 2). This was also the case among new-born snakes (Table III). As the number of ventral scales does not change during an individual's lifespan, body size must be influenced, at least partly, by the number of ventral scales, rather than the opposite.

Snakes enjoy several advantages by having a large body size. For example, large size is usually favoured in terms of increased reproductive output, such as larger clutch or litter sizes in females (e.g. Fitch, 1970), and in terms of increased competitive ability in males (e.g. Shine, 1978; Andrén & Nilson, 1981; Madsen, 1988). Thus, given a relationship between body size and number of ventral scales, selection for larger body size may be expected to result in a correlated response in the number of ventral scales.

Previous studies have shown that there is a positive relationship between the number of ventral scales and body size also at the interspecific and intersexual levels. Thus, Saint Girons (1978) showed that among some European species of the genus *Vipera*, species with more ventral scales usually attain a larger body size. Also, between the sexes of these species, Saint Girons (1978) demonstrated a positive relationship between ventral scale count and body size.

Among the six localities in this study, mean body size, but not mean number of ventral scales, varied significantly. There was, however, no correlation between mean number of ventral scales and mean body size among localities. Thus, number of ventral scales does not seem to influence body size variation at the population level. Instead, other factors are probably more important in determining body size at the population level (e.g. Case, 1978; Andrews, 1982; Plummer, 1987; Shine, 1987; R. B. King, 1989; Schwaner & Sarre, 1990; Forsman, 1991).

We thus conclude that body size of adult individuals clearly increases with number of ventral scales within populations but not among populations. The question then is: what is the mechanism behind such a positive association at the individual level? We evaluate two different mechanisms that may cause such a pattern: (1) that a higher number of ventral scales is associated with a higher growth rate, or (2) that many ventral scales improve the probability of survival and thus of a long life and big size.

Number of ventral scales and growth rate

Arnold (1988) examined the relationship between number of ventral and subcaudal scales (and thus number of body and tail vertebrae) and individual growth rate in a population of *Thamnophis elegans*. In females, individuals with intermediate numbers of ventral and subcaudal scales grew at the fastest rate, whereas in males no correlation was observed between growth rate and scale number. As neither ventral nor subcaudal scale numbers alone could explain individual variation in growth rate, he concluded that, at least for the females, several different combinations of the two scale characters may permit the same high growth rate.

We found a significant positive relationship between number of ventral scales and relative growth rate (Fig. 3), showing that, irrespective of size, individuals with many ventral scales grew faster than those with few. The reason why individuals with many ventral scales and vertebrae will grow faster and reach a larger body size might be that each vertebra, with its attached tissues and ventral scale, grows at the same rate and to a fixed size in all snakes. Given this, a snake with many vertebrae will have an overall higher growth rate and larger size than one with few vertebrae of the same age. Body size would thus be a function of number of vertebrae *per se*. This notion is supported by the analysis of SVL among new-born individuals (Table III). Since these are of the same age, the larger size of individuals with many ventral scales (and vertebrae) must be a consequence of their having higher growth rates.

Furthermore, Arnold (1988) showed that in male *T. elegans* the number of anomalous ventral scales (and presumably abnormal vertebrae) was a statistically significant negative predictor of growth rate. This is not in agreement with our results, though. We found no effect of anomalous ventral scales on individual growth rate, neither in males nor in females (Table IV). However, as the proportion of individuals with scale anomalies is larger among snakes with few scales than among those with many (Merilä, Forsman & Lindell, 1992), it is possible that the higher incidence of anomalous scales may contribute to the lower growth rate of individuals with few ventral scales.

Number of ventral scales and survival

Another possibility is that the positive relationship between body size and number of ventral scales may be a consequence of individuals with many ventral scales enjoying a higher survival and hence a longer growing period. Some evidence supporting this has appeared in the literature. For example, Linsdale (1936) reported that, in *Chilomeniscus stramineus*, the lowest numbers of ventral scales were found only in the smallest and youngest individuals. Similarly, Stuart (1941) concluded that, in *Dryadophis boddaerti*, individuals with few vertebrae did not live to reach maturity. Inger (1943) showed that, in *Thamnophis radix*, both adult males and adult females possessed a significantly larger mean number of ventral scales, as well as a lower correlation of variability (CV), than did juveniles, and inferred differential survival among individuals differing in number of ventral scales. Inger concluded that the difference between the cohorts was the result of an early elimination of individuals with particularly low ventral scale counts. The mechanism for this was not clear, but Inger suggested that low scale numbers may be associated with some physiological deficiencies. We have data offering some support to this view. In our adder populations, anomalous ventral scales are more frequent among individuals with few ventral scales than among individuals with many (Merilä *et al.*, 1992). Thus, it is possible that individuals with few ventral scales also suffer from the correlated disadvantage of having many anomalous ventral scales.

CV-values for ventral scale numbers have also been shown to be consistently lower than for other scale characters (Klauber, 1943, 1945; Campbell & Armstrong, 1979; Kminiak & Kaluz, 1983). Kminiak & Kaluz (1983) reported a CV for subcaudal scale numbers of 5·1 and 5·9% for male and female *V. berus*, respectively, whereas the corresponding values for ventral scale numbers were 2·5% in both sexes. This may indicate that selection is more intense on ventral scales or body vertebrae than on subcaudal scales or tail vertebrae. This suggestion was further supported by Arnold (1988), who concluded that the higher total number of vertebrae (both body and tail vertebrae) in inland populations of *T. elegans*, compared to coastal populations, has evolved primarily by selection of body vertebrae rather than of tail vertebrae.

Further evidence supporting the idea of differential survival among individuals with different numbers of ventral scales comes from Beatson (1976), Arnold & Bennett (1988) and Jayne & Bennett (1990). Beatson (1976) noted the same mean number of ventral scales but a significantly lower variance among one-year-old *Natrix sipedon* than in new-born snakes, inferring early stabilizing selection on ventral scale numbers. Also, in an experiment using new-born *T. radix*, Arnold & Bennett (1988) showed that the number of body and tail vertebrae influenced locomotor performance. Number of body vertebrae alone did not explain any variation in performance, but the combination of body and tail vertebrae significantly did so. The best locomotor performance was achieved by two classes of snakes; those with high numbers of body and tail vertebrae and those with low numbers of body and tail vertebrae. In addition, Jayne & Bennett (1990) showed that both locomotor performance and body size affected survival of juvenile *T. sirtalis fitchi*. Individuals with high locomotor performance and large body size survived their first winter better than others. Since the number of ventral scales has been shown to influence both body size and locomotor performance, it may affect the probability of survival too.

Although we do not know if these results are applicable to the adder, it is clear that if Arnold & Bennett's (1988) suggestion of disruptive selection on number of ventral scales is valid also for the adder, selection should cause higher variance in adult than in juvenile/subadult snakes. We failed to find any significant difference in either means or in variances between age cohorts among wild-caught adders, although adults showed somewhat higher variance in eight out of 11 cases (Table V). Our sample included only a few really young snakes, though, and the individuals classified as juveniles/subadults may not represent the true scale count distribution among new-born adders. A comparison between wild-caught adults and young born in captivity, on the other hand, suggested directional selection against low scale counts since three out of six comparisons showed significantly larger mean scale number among the adults (Table VI). This conforms to the results obtained by Linsdale (1936), Stuart (1941) and Inger (1943). However, this selective process will not cause a positive correlation between scale counts and body size among adult individuals if the selection takes place early in life. Only if some selection occurs also after the individuals have reached maturity can such a positive association be achieved. Since we found no difference in means between the wild-caught juveniles/subadults and adults we find such a difference among adults unlikely. Yet, it is possible that there is strong selection against low scale counts early in life, but when the snakes reach sexual maturity the variants with few scales are no longer present in the population. A longitudinal study of a large number of new-born, free-living snakes would be the best way to address this issue.

Conclusions

Our aim was to examine the relationship between number of ventral scales and body size of adders, both among individuals within populations and among different populations. We conclude that the number of ventral scales is highly positively correlated with body size among both adult and new-born individuals within populations, but not among population means. To evaluate two possible hypotheses about the causes of this pattern, we also investigated whether the number of ventral scales *per se* might be related to variation in growth rate and/or survival. Our results showed a significant positive relationship between number of ventral scales and growth rate. There was also some indication of differential survival associated with individual variation in ventral scale numbers. However, this selection appeared to take place early in life and therefore may be insufficient for generating the demonstrated positive association between scale counts and body size among the adults. We therefore suggest that the larger size of individuals with many ventral scales is caused primarily by an overall higher growth rate. Finally, we want to stress that this does not necessarily mean that number of ventral scales and body vertebrae is very important in determining body size in snakes, but we point out that it is a previously largely unrecognized trait influencing body size.

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REFERENCES

Alexander, A. A. & Gans, C. (1966). The pattern of dermal-vertebral correlation in snakes and amphibians. *Zool. Meded., Leiden* **41:** 171–190.

Andrén, C. & Nilson, G. (1981). Reproductive success and risk of predation in normal and melanistic morphs of the adder, *Vipera berus. Biol. J. Linn. Soc.* **15:** 235–246.

Andrews, R. M. (1982). Patterns of growth in reptiles. In *Biology of the Reptilia* **13:** 273–320. Gans, C. & Pough, F. H. (Eds). London: Academic Press.

Arnold, S. J. (1988). Quantitative genetics and selection in natural populations: Microevolution of vertebral numbers in the garter snake *Thamnophis elegans*. In *Proceedings of the second international conference on quantitative genetics*: 619–636. Weir, B. S., Goodman, M. M., Eisen, E. J. & Namkong, G. (Eds). Sunderland, Massachusetts: Sinauer Associates, Inc. Publishers.

Arnold, S. J. & Bennett, A. F. (1988). Behavioural variation in natural populations. V. Morphological correlates of locomotion in the garter snake *Thamnophis radix. Biol. J. Linn. Soc.* **34:** 175–190.

Beatson, R. R. (1976). Environmental and genetical correlates of disruptive coloration in the water snake, *Natrix s. sipedon. Evolution* **30:** 241–252.

Bellairs, A. d'A. & Underwood, G. (1951). The origin of snakes. *Biol. Rev.* **26:** 193–237.

Bernström, J. (1943). Till kännedom om huggormen *Vipera berus berus* (L.). *Göteborgs K. Vetensk.-o. VitterhSamh Handl.* (B) No. 10: 2–43. (meddelanden från Göteborgs Musei Zoologiska Avdelning 103).

Boulenger, G. A. (1913). *The snakes of Europe*. London: Methuen & Co.

Campbell, J. A. & Armstrong, B. L. (1979). Geographic variation in the Mexican pygmy rattlesnake, *Sistrurus ravus*, with the description of a new subspecies. *Herpetologica* **35:** 304–317.

Case, T. J. (1978). A general explanation for insular body size trends in terrestrial vertebrates. *Ecology* **59:** 1–18.

Clark, D. R. & Callison, G. L. (1967). Vertebral and scute anomalies in a racer, *Coluber constrictor*. *Copeia* **1967:** 862–864.

Dunn, E. R. (1942). Survival value of varietal characters in snakes. *Am. Nat.* **76:** 104–109.

Endler, J. A. (1986). *Natural selection in the wild*. Princeton, New Jersey: Princeton University Press.

Fitch, H. S. (1970). Reproductive cycles in lizards and snakes. *Univ. Kans. Publs Mus. nat. Hist.* **52:** 1–247.

Forsman, A. (1991). Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *J. Anim. Ecol.* **60:** 253–267.

Fox, W. (1948). Effect of temperature on development of scutellation in the garter snake, *Thamnophis elegans atratus. Copeia* **1948:** 252–262.

Fox, W., Gordon, C. & Fox, M. H. (1961). Morphological effects of low temperatures during the embryonic development of the garter snake, *Thamnophis elegans*. *Zoologica* **46:** 57–71.

Gans, C. (1962). Terrestrial locomotion without limbs. *Am. Zool.* **2:** 167–182.

Gans, C. & Taub, A. (1965). Segmental correlation between integument and vertebral column in typhloids (Reptilia, Squamata). *Copeia* **1965:** 107–108.

Grobman, A. B. (1984). Scutellation variation in *Opheodrys aestivus*. *Bull. Fla St. Mus. biol. Sci.* **29:** 153–170.

Inger, R. F. (1943). Further notes on differential selection of variant juvenile snakes. *Am. Nat.* **77:** 87–90.

Jayne, B. C. & Bennett, A. F. (1990). Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44:** 1204–1229.

Kerfoot, W. C. (1970). The effect of functional changes upon the variability of lizard and snake body scale numbers. *Copeia* **1970:** 252–260.

King, R. B. (1989). Body size variation among island and mainland snake populations. *Herpetologica* **45:** 84–88.

King, W. (1959). Vertebra duplication, an osteological anomaly widespread in snakes. *Herpetologica* **15:** 87–88.

Klauber, L. M. (1943). The correlation of variability within and between rattlesnake populations. *Copeia* **1943:** 115–121.

Klauber, L. M. (1945). Herpetological correlations. 1. Correlations in homogeneous populations. *Bull. zool. Soc. S. Diego* No. 21: 5–101.

Kminiak, M. & Kaluz, S. (1983). Evaluation of sexual dimorphism in snakes (Ophidia, Squamata) based on external morphological characters. *Folia zoologica* **32:** 259–270.

Kramer, E. (1961). Variation, Sexualdimorphismus, Wachstum und Taxonomie von *Vipera ursinii* (Bonaparte, 1835) und *Vipera kaznakovi* Nikolskij, 1909. *Rev suisse Zool.* **68:** 627–725.

Linsdale, J. (1936). Variation in the dotted burrowing snake, *Chilomeniscus stramineus*. *Copeia* **1936:** 232–234.

Madsen, T. (1988). Reproductive success, mortality and sexual size dimorphism in the adder, *Vipera berus*. *Holarctic Ecol.* **11:** 77–80.

Marx, H. & Rabb, G. B. (1965). Relationships and zoogeography of the viperine snakes (Family Viperidae). *Fieldiana Zool.* **44:** 161–206.

Merilä, J., Forsman, A. & Lindell, L. E. (1992). High frequency of ventral scale anomalies in *Vipera berus* populations. *Copeia* **1992** (In press).

Nilson, G. & Andrén, C. (1986). The mountain vipers of the middle east—the *Vipera xanthina* complex (Reptilia, Viperidae). *Bonn. zool. Monogr.* No. 20: 1–90.

Osgood, D. W. (1978). Effect of temperature on the development of meristic characters in *Natrix fasciata*. *Copeia* **1978:** 33–47.

Phelps, T. (1989). *Poisonous snakes*. London: Blandford Press.

Plummer, M. V. (1980). Ventral scute anomalies in a population of *Opheodrys aestivus*. *J. Herpet.* **14:** 199.

Plummer, M. V. (1987). Geographic variation in body size of green snakes (*Opheodrys aestivus*). *Copeia* **1987:** 483–485.

Ruthven, A. G. & Thompson, C. (1913). The variation in the number of vertebrae and ventral scutes in two snakes of the genus *Regina*. *Am. Nat.* **47:** 625–632.

Saint Girons, H. (1978). Morphologie externe. comparée et systématique des vipères d'Europe (Reptilia, Viperidae). *Rev. suisse Zool.* **85:** 565–595.

Schwaner, T. D. & Sarre, S. D. (1990). Body size and sexual dimorphism in mainland and island tiger snakes. *J. Herpet.* **24:** 320–322.

Schwartz, A. (1976). Variation in the Hispaniolan colubrid snake *Uromacer frenatus* Günther (Reptilia, Serpentes, Colubridae). *J. Herpet.* **10:** 319–327.

Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia* **33:** 269–278.

Shine, R. (1987). Intraspecific variation in thermoregulation, movements, and habitat utilization by Australian black snakes, *Pseudechis porphyriacus* (Elapidae). *J. Herpet.* **21:** 165–177.

Stuart, L. C. (1941). Studies of neotropical Colubrinae. VIII. A revision of the genus *Dryadophis* Stuart, 1939. *Misc. Publs Mus. Zool. Univ. Mich.* No. 49: 1–106.

Thorpe, R. S. (1989). Pattern and function of sexual dimorphism: A biometric study of character variation in the grass snake (*Natrix natrix*, Colubridae) due to sex and its interaction with geography. *Copeia* **1989:** 53–62.

Voris, H. K. (1975). Dermal scale-vertebra relationships in sea snakes (Hydrophiidae). *Copeia* **1975:** 746–755.