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Adaptive variation in head size in *Vipera berus* L. populations

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To prove that predators are morphologically adapted to the size of their prey one has to demonstrate that the morphological variation in the trophic apparatus is related to the prey size distribution and that the variation in the trait has some effect on individual fitness. I have studied geographic variation in relative head length (RHL) of adders, *Vipera berus*, on the Swedish mainland and on groups of islands in the Baltic Sea, and the relationship between RHL and physical condition, a character related to fitness. I also examined the relationship between RHL and sex and colour morph. Relative head length of adders was smallest on the mainland and increased on the islands with increasing body size of the main prey, *Microtus agrestis*, suggesting stabilizing selection for head size within each population. There was no difference in RHL between sexes or colour morphs. However, physical condition was positively correlated with RHL, indicating directional selection for larger heads. The observed pattern is interpreted as an evolutionary response to the geographic variation in body size of the main prey species and the smaller number of alternative prey species available on islands.

KEY WORDS—*Vipera berus* – relative head size – morphological variation – geographic variation – insular populations – stabilizing selection – directional selection – sexual monomorphism – prey size limited predator – physical condition.

CONTENTS

INTRODUCTION

In many groups of animals a strong positive correlation has been found between the size of a predator and its prey (Wilson, 1975). In animals with

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determinate growth such as mammals this relationship emerges from interspecific comparisons of predators and their prey (Rosenzweig, 1966; Gittleman, 1985; Vézina, 1985). In snakes, with indeterminate growth and extraordinarily large variation in adult body size, the same correlation has been found when comparing individuals within a population (Beavers, 1976; Voris & Moffett, 1981; Reynolds & Scott, 1982; Henderson & Schwartz, 1986, but see Shine, 1987). Furthermore, intraspecific geographic variation in predator body size has been shown to follow prey size distribution both in mammals (Simms, 1979; Erlinge, 1987) and snakes (Schwaner, 1985; Forsman, 1991).

For prey-size-limited predators such as snakes, which swallow their prey in one piece, the morphology of the trophic apparatus represents a physical constraint on the maximum size of prey it is possible to ingest. Thus, small snakes or snakes with small heads cannot utilize the same food resources as large snakes or snakes with large heads. Ontogenetic dietary shifts in adders, *Vipera berus*, have been demonstrated by Kjaergaard (1981), who showed that juvenile snakes fed on lizards while adults fed on small mammals. Water snakes, *Nerodia*, show similar dietary shifts (Mushinsky, Hebrard & Vodopich, 1982; Plummer & Goy, 1984). As a result of different adaptations of the trophic apparatus the ability to utilize relatively large prey also differs between snake species and families. In a comparative study of snake families Pough & Groves (1983) showed that compared with elapid and boid snakes viperid snakes have stouter bodies, larger heads and longer jaws, i.e. characters that facilitate the swallowing of large prey. If natural selection is operating on head size, one would expect to find differences in relative head size also between populations of snakes utilizing prey of different sizes.

The reason is that the number of potential prey items increases with maximum ingestible prey size, i.e. head size in snakes. Thus, snakes with large heads will have higher foraging success and fitness than snakes with small heads. One would expect this difference to be most pronounced when prey is a limiting resource, that is when prey density is low. Presumably there are also costs constraining relative head size. In a stable situation there should be an optimal relative head size determined in part by prey size distribution.

If males and females compete for food, disruptive selection may result in sexual dimorphism in the trophic apparatus if there is a wide range of prey species and/or prey sizes. Sexual dimorphism in morphological characters as well as in foraging behaviour and diets has been demonstrated in birds (Selander, 1966, 1972) and mammals (Erlinge, 1981; Moors, 1980). For species with indeterminate growth such a difference is harder to imagine since the sexes will be overlapping in adult body size. It has, however, been documented in a few snake species, namely in the filesnake *Acrochordus arafurae* (Shine, 1986) and the watersnakes *Nerodia rhombifera* and *N. cyclopion* (Mushinsky *et al.*, 1982). In these cases adult males and females preyed on different prey species.

To test whether predators are adapted morphologically to prey size one must study geographic variation in an ecologically relevant character such as trophic apparatus, that is, *relative head size* in snakes, in relation to prey size distribution, rather than body size variation which is more likely to be influenced by other factors, e.g. competition, predation or abiotic variables. But, even if the expected positive correlation between geographic variation in relative head size and prey size is found, no firm conclusion can be drawn about the mechanism involved, for autocorrelations or founder effects may be responsible for the pattern observed. Individual variation of the trait must be shown to have some effect on fitness or on a character related to fitness for a causal connection to be indicated. In a situation of stabilizing selection there should be a negative correlation between the absolute distance from the mean relative head length and fitness. In an unstable situation where selection is directional there should be a positive (selection for larger heads) or negative (selection for smaller heads) correlation between relative head size and fitness.

I have studied geographic variation in relative head length of adders, *Vipera berus*, from seven localities with different prey size distributions (Ebenhard, 1988; Ebenhard & Forsman, unpublished) to see if adders are adapted morphologically to the size of their prey. The study was conducted on the Swedish mainland and on six groups of islands in the Baltic Sea. A positive relationship between mean relative head length of the snakes and prey body size was expected between localities. I also examined whether adders are sexually dimorphic with respect to relative head length. The dimorphism was expected to be most pronounced on the mainland locality where prey diversity is highest. I also analysed the effect of individual variation in relative head size on physical condition, measured as relative body mass. This was to determine whether selection is stabilizing or directional, under the reasonable assumption of condition being an approximation of an individual's probability of survival and producing offspring, i.e. of fitness. Male adders in poor condition are known to have a delayed spring sloughing and no reproductive success (Andrén, 1982), while longer and heavier males are superior in rivalry combats over females which gives them a higher chance of mating (Andrén & Nilson, 1981; Madsen, 1988). Furthermore, the distance at which adders in poor condition flee from a potential approaching predator has been shown to be shorter than for adders in good condition (Andrén 1982) suggesting predation to be higher on malnutritioned individuals.

On islands in the Baltic adders occur in two colour morphs, viz. melanistic and pale grey with a dark zig-zag pattern (Forsman & Ås, 1987), with different growth rates (Madsen & Stille, 1988). If variation in relative head length is caused by constant rate of head growth and varying rates of body growth, differences in the proportions of colour morphs may be responsible for geographic variation in relative head length. To determine if this was the case I compared relative head length between melanistic and zig-zag patterned snakes and tested for differences in relative head length among localities after the variation due to colour morph had been accounted for.

MATERIALS AND METHODS

Data on snakes

Data were gathered from one locality in central Sweden (Uppsala = U, 59°50′N, 17°40′E) on 29 March–10 April, and from four groups of islands in the Stockholm archipelago (K, N, A, and F) off the Swedish east coast on 6 May–15 June in 1988. Locality A was visited on several occasions during the study period. The other three insular localities were visited on one occasion, each visit lasting 2–3 days. In spring 1989 adders were captured on two additional island

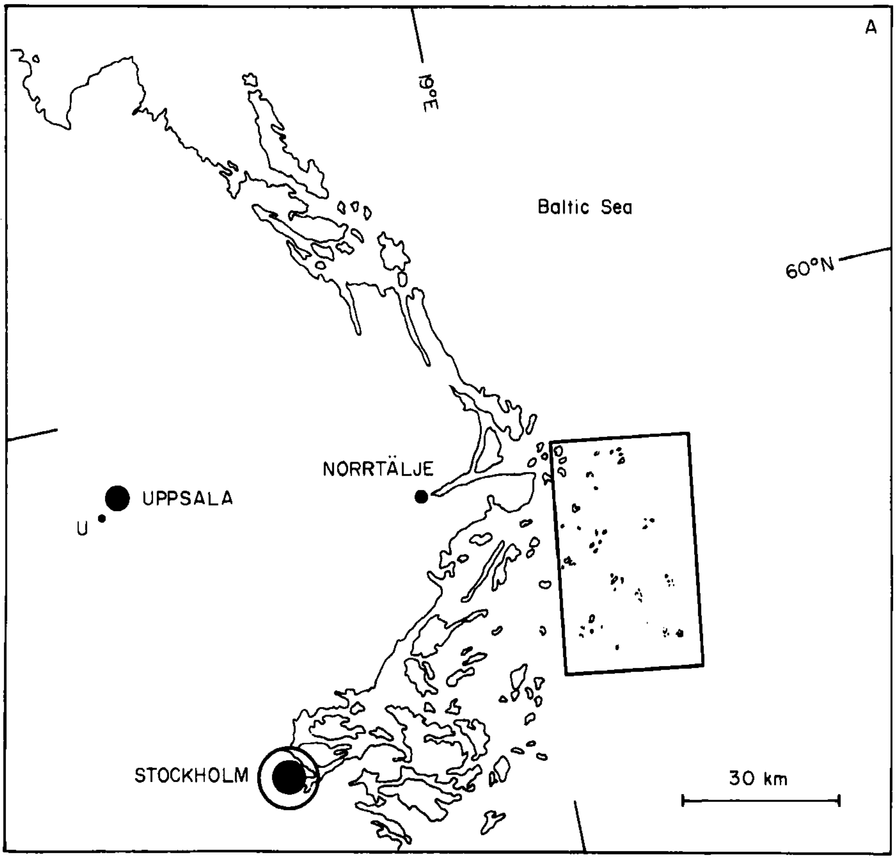
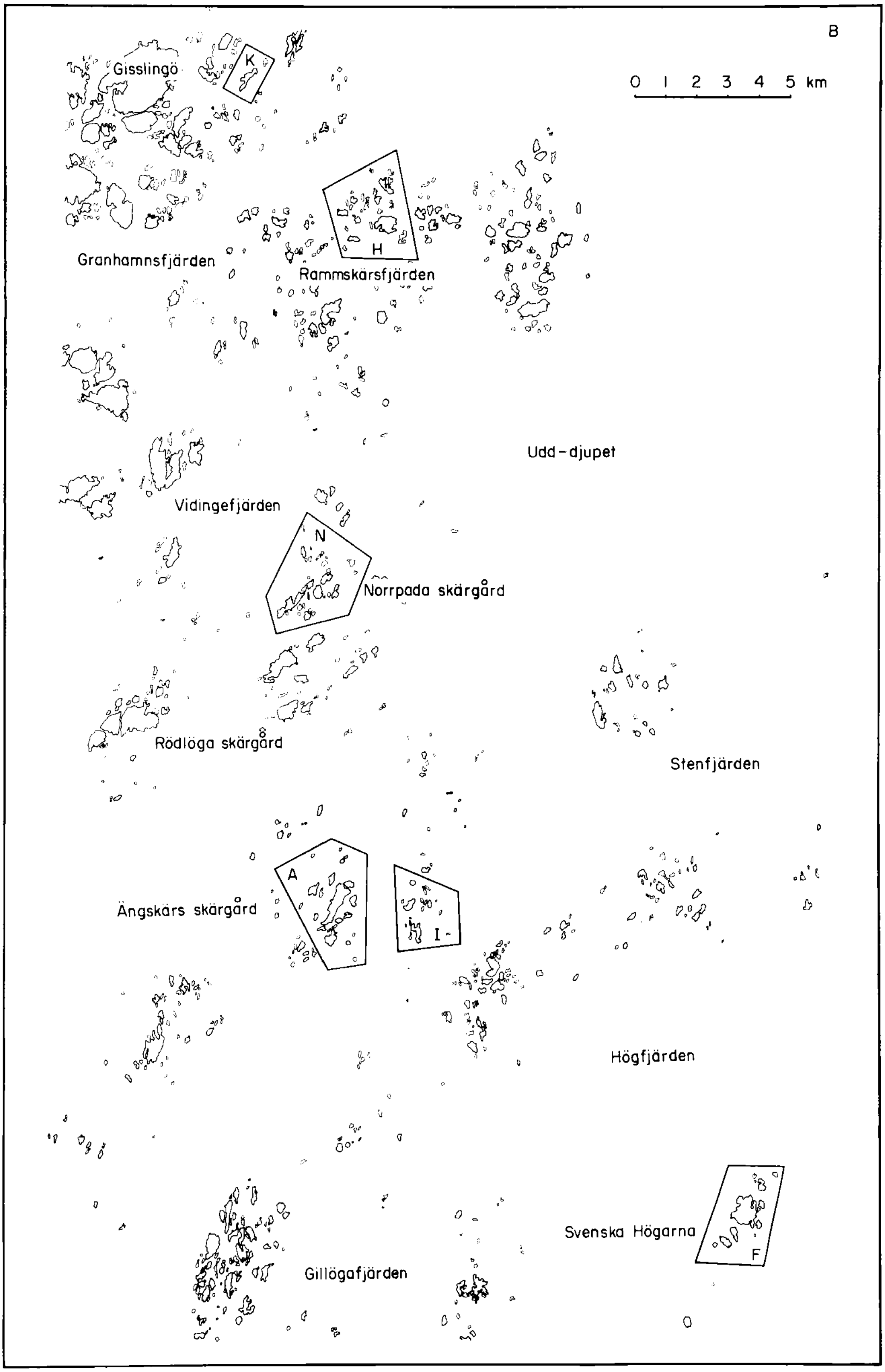


Figure 1. The study area. Mainland locality U = Uppsala (map A). The six island groups in the Baltic Sea (map B). K = Kärringboskär, H = Inre Hamnskär, N = Norrpada, A = Ängskär, I = In-Fredeln, F = Svenska Högarna.

groups, I and H. Figure 1 is a map of the study area. For each group of islands distance to mainland was measured as a straight line from the centre of each island group to the nearest mainland.

The following information was taken for each individual: sex; colour morph (black or grey); body mass; snout–vent length (SVL) and head length measured with digital calipers, to the nearest 0.1 mm, from tip of snout to posterior end of mandible, i.e. essentially length of the lower jaw.

In order to compare snakes of different sex, colour morph and locality, measurements of individual relative head length (RHL), compensating for differences in body size, were needed. This was achieved by calculating the residuals from the common regression equation of head length on SVL. The residuals thus represent the deviations from the mean head length for each given body length. Likewise, the residuals from the common regression equation (males only) of 1 g mass on SVL were used as measurements of individual physical condition (COND). COND measured as relative body mass may vary over time. Observations from localities N, K and F were made over a short time period during which COND could not have changed much. Localities U and A were visited at longer time intervals, and COND scores of snakes from these


B
0 1 2 3 4 5 km
Gisslingö
K
H
Granhamnsfjärden
Rammskärsfjärden
Udd-djupet
Vidingefjärden
N
Norrpada skärgård
Rödlöga skärgård
Stenfjärden
A
I
Ängskärs skärgård
Högfjärden
Svenska Högarna
F
Gillögafjärden

localities therefore might depend on when they were captured, making it more difficult to detect relationships between RHL and COND. Females were not included since their weight varies greatly with reproductive status. Snakes from I and H were not included since they were captured after the mating season and thus had started feeding.

Data on prey density and prey species distribution

Adders feed mainly on small rodents, and the species dominating the diet reflect their relative availability in the area (Pielowski, 1962; Pomianowska-Pilipiuk, 1974; Sebela, 1980). In September 1987, field voles (*Microtus agrestis*), by far the most common rodent in the archipelago (Ebenhard & Forsman, personal observations), were captured at two localities, N and F. Snap traps, baited with dried apricots, and live traps (Ugglan Special), baited with oats and carrots, were used in the same proportions at both localities. Trapping was carried out during 7 consecutive days and nights with about 20 traps per ha. The data reflect the relative field vole densities at the two sites in the year preceding that during which the snake data were collected.

The distribution of potential vertebrate prey species among the different localities is given in Table 1. Field voles, *Microtus agrestis*, and frogs, *Rana* spp., have been observed and/or trapped at all localities. Common shrews, *Sorex araneus*, are present at the mainland site and the three least isolated insular localities. Pygmy shrews, *S. minutus*, bank voles, *Clethrionomys glareolus*, wood mice, *Apodemus* spp., and lizards, *Lacerta vivipara*, are present at the mainland site but have not been observed or trapped at the insular localities, even though all localities have been visited on several occasions during 1983 and 1989.

Data on prey size

An earlier study of body size patterns of insular field voles, *Microtus agrestis*, on eight localities on the mainland and in the Stockholm archipelago (including U, H, N, A and F) revealed that insular voles in general were larger than mainland voles and that voles on more isolated islands/groups of islands generally were larger than those on less isolated islands (Ebenhard, 1988; Ebenhard & Forsman, unpublished). In a principal component analysis of ten morphometric characters (body length and nine different skull characters) the first component,

TABLE 1. Distribution of potential adder vertebrate prey species for one mainland locality and six groups of islands in the Baltic Sea

	Locality						
	U	K	H	N	A	I	F
Microtus agrestis	+	+	+	+	+	+	+
Rana spp.	+	+	+	+	+	+	+
Sorex araneus	+	+	+	+			
Sorex minutus	+						
Clethrionomys glareolus	+						
Apodemus spp.	+						
Lacerta vivipara	+						

TABLE 2. Geographic and sexual variation in snout–vent length (mm) and head length (mm) in adders, *Vipera berus*, on one mainland locality (U) and in six groups of islands (I, H, N, K, A, F). N = Sample size

		Males					Females			
		Snout–vent length		Head length			Snout–vent length		Head length	
Locality	N	Mean	SD	Mean	SD	N	Mean	SD	Mean	SD
U	17	448	29.3	21.11	0.82	4	562	37.5	24.20	1.48
I	21	512	65.4	23.19	1.94	13	592	67.4	25.26	2.10
H	10	453	40.3	21.74	1.17	10	591	55.8	25.38	1.94
N	15	502	39.9	23.27	1.16	10	560	27.1	24.35	1.26
K	6	441	60.3	21.68	2.42	1	470		22.80	
A	46	461	76.9	22.27	2.33	36	498	97.7	23.47	3.02
F	22	446	64.9	22.42	2.39	26	496	74.0	23.47	2.31

explaining 76% of the variance, represented overall body size. The mean scores on this size-descriptive component are given in Table 4 for field voles from five of the localities. I have no data on vole size for localities I and K. The difference in body size between mainland and insular field voles is genetically determined (Ebenhard, 1990).

RESULTS

Variation in body size

A total of 237 (100 females, 137 males) adders were captured at the seven localities. Their mean body lengths and head lengths are given in Table 2. Females were larger than males at all localities. Furthermore, mean body size of both sexes varied between localities. To see whether the differences were significant the effects of sex, locality and, in addition, colour morph on body size (SVL) were investigated by analysis of variance. The result showed significant differences between groups ($F_{24,212} = 4.08$, $P = 0.0001$). Snout–vent length differed significantly between sex and localities ($F_{1,212} = 26.33$, $P = 0.0001$; $F_{6,212} = 4.54$, $P = 0.0002$). However, there was no significant difference in body size between colour morphs ($F_{1,212} = 1.06$, n.s.). None of the possible interactions was significant.

The mean SVL of adders from different localities were not significantly correlated with local body size of the field voles (Spearman rank correlation, females: $N = 5$, $r_s = -0.90$, n.s. = males: $N = 5$, $r_s = -0.10$, n.s.).

Variation in relative head size

Head length (HL) was regressed on snout–vent length (SVL) for males and females separately but with all localities pooled. The regression equations were:

females: $N = 100$, $\mathrm{HL} = 0.266\mathrm{SVL} + 99.9$, $R^2 = 0.84$, $P < 0.0001$.

males: $N = 137$, $\mathrm{HL} = 0.286\mathrm{SVL} + 89.4$, $R^2 = 0.85$; $P < 0.0001$.

There was no significant sexual difference in the relationship between head length and SVL when all localities were analysed together (between slopes:

TABLE 3. Results from the analysis of variance of relative head length of adders, *Vipera berus*, between sexes, localities (LOC), and colour morphs (CM).

Source	d.f.	F-value	*P*
LOC	6	4.77	0.0001
CM	1	3.24	0.0734
SEX	1	0.24	0.6255
SEX*LOC	6	1.44	0.2003
LOC*CM	5	0.77	0.5699
SEX*CM	1	0.19	0.6666
SEX*LOC*CM	4	1.04	0.3890

$F_{1,233} = 1.74$, n.s.; between adjusted means: $F_{1,234} = 0.06$, n.s.). Since the body size of the adders' main prey differs between localities (Table 4), as does the number of alternative prey species (Table 1), the opportunity for differential niche utilization by the sexes and thus the likelihood of evolution of sexual dimorphism in head size also differs between localities and should be greatest where the number of prey species is highest or the variation in prey size most pronounced. Therefore, males and females were compared for each locality separately. At none of the localities, however, was there a significant difference in relative head length between sexes, nor even a consistent tendency in any particular direction.

Differences in relative head length (RHL), when measured as the residual from the common regression line of head length on SVL, between sexes, localities and colour morphs were investigated in an analysis of variance (Table 3). There were no differences in RHL between sexes or colour morphs. However, relative head length differed significantly between localities. Among the five localities for which I have data on prey size, mean relative head length of adders was positively correlated with field vole body size (Spearman rank correlation, $N = 5$, $r_s = 1$, $P = 0.02$, Table 4, Fig. 2). There was no correlation between relative head length and distance from mainland ($N = 6$, $r_s = 0.26$, n.s.).

TABLE 4. Mean relative head lengths of adders, *Vipera berus*, from seven localities and their distance (km) to mainland. Means with the same letter are not significantly different (Student-Newman-Keuls). N = Sample size. Prey size = principal component scores representing overall body size of field voles, *Microtus agrestis* (Data from Ebenhard & Forsman, unpublished)

Locality	N	Distance (km)	Relative head length mean				Field vole body size
U	21	0	−6.98	A			−1.75
I	34	25.1	−4.24	A	B		
H	20	13.4	−2.79	A	B		−0.16
N	25	14.7	−2.22	A	B		1.31
K	7	10.0	1.27		B	C	
A	82	22.7	1.88		B	C	1.67
F	48	39.6	4.98			C	2.17

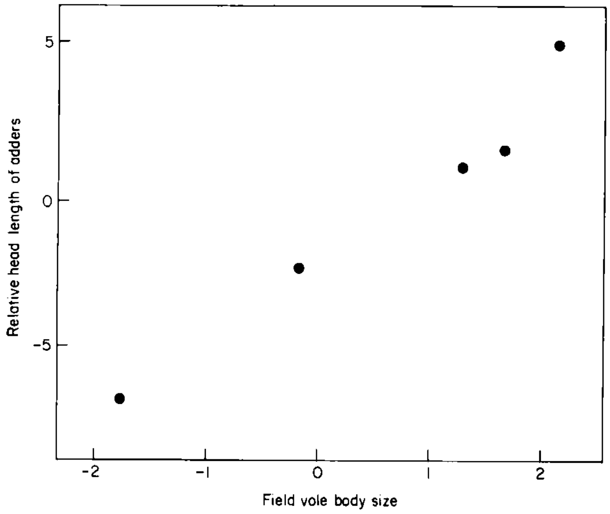


Figure 2. Relationship between geographic variation in mean relative head length of adders, *Vipera berus*, and mean body size (principal component scores) of field voles, *Microtus agrestis*, from five localities.

Relationship between head size and physical condition

Does it matter to the individual adder whether it has a large or small head? To answer that question directly one would have to compare hunting success, growth rates and survival between individuals with differently sized heads. In the absence of such information I examined the relationship between relative head length and individual physical condition COND, defined as the residuals from the regression equation of 1 g mass on SVL ($N = 103$, males, 1 g mass $= 0.0024\text{SVL}+0.70$, $R^2 = 0.81$, $P < 0.0001$). COND thus represents nutritional

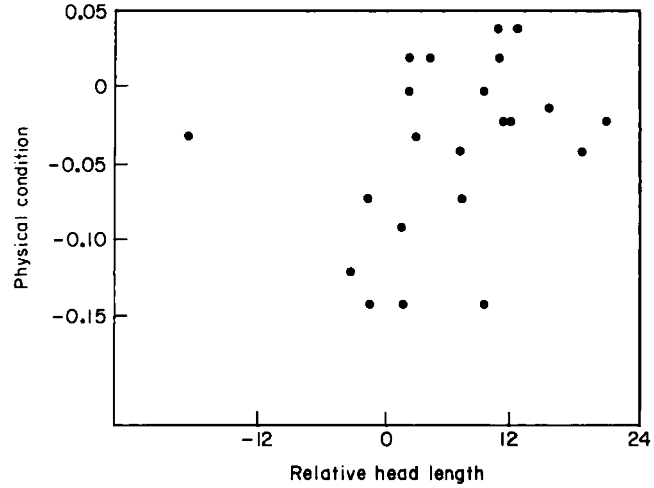


Figure 3. Relationship between physical condition and relative head length in male adders. *Vipera berus*, from locality F. $N = 22$, $r_s = 0.46$, $P < 0.05$.

TABLE 5. Spearman rank correlation coefficients between physical condition and relative head length in male adders, *Vipera berus*, from five localities. N = Sample size. Combining probability test (Fisher, 1954: section 21.1)

Locality	N	r_s	P
U	17	0.22	0.39
N	15	0.25	0.37
K	5	0.60	0.29
A	38	0.21	0.21
F	22	0.46	0.03
	# of tests		
All	5	$-2\Sigma\ln P = 23.41$	0.01

status. The relationship between RHL and COND was investigated using Spearman rank correlation analysis for each locality, except H and I. In one locality, namely F, a significant positive correlation between relative head length and physical condition was found ($N = 22$, $r_s = 0.46$, $P < 0.05$, Fig. 3), while the other localities showed positive but non-significant correlations in the same direction (Table 5). The probability of obtaining five positive correlations out of five by chance alone is 3.1%. Furthermore, combining the one-tailed probabilities from these five correlations (Fisher, 1954) produced a significant overall positive correlation between RHL and physical condition (Table 5).

Prey density

The advantage of having a relatively large head may be a function of prey density, because if prey availability is high even snakes with small heads will encounter enough ingestible prey items to survive. However, when prey density is low, prey encounters will become less frequent and it becomes more important to be able to ingest as many of the prey items encountered as possible, i.e. to have a large head. Thus, one would expect the strongest relationship between relative head size and physical condition on localities or in years with low prey densities. Therefore, relative prey density was measured at two localities in September 1987. A total of 75 and 14 field voles were captured on the two island localities N and F, respectively. The numbers of voles captured/trap · ha are given for each of the two groups of islands in Table 6. Prey density was significantly lower at F than N (Mann–Whitney U-test; $U = 0$, $P = 0.022$).

TABLE 6. Number of field voles, *Microtus agrestis*, captured/trap · ha for each of the two island localities N and F during 7 days and nights in September 1987. F had significantly lower prey densities than N. Mann–Whitney U-test: U = 0, $P = 0.022$

	Island number								
Locality	1	2	3	4	5	6	7	8	Mean
N	0.06	0.15	0.30	0.30	0.55	1.47	2.56	4.17	1.20
F	0.0002	0.04							0.02

DISCUSSION

Between-sex comparison

Is the adder's sexual dimorphism in body size and/or in relative head size large enough to permit differential niche utilization of the two sexes?

A sexual dimorphism in body size of adders as documented in this study with females being the slightly larger sex has been reported earlier (e.g. Andrén, 1986; Kminiak & Kaluz, 1983; Madsen, 1988). The most likely explanation for this dimorphism is that reproductive success is more strongly coupled to body size in females than males even though males engage in sexual combats over females. Patterns of variation in sexual size dimorphism in these populations is discussed in more detail elsewhere (Forsman, 1991).

There was no significant difference in relative head size between males and females, and the difference was inconsistent between the seven localities. Sexual differences in diet and relative head size have been documented in snake species where males and females are more dissimilar in size. Mean male to female size ratio for *Vipera berus* in this study was 89% whereas the corresponding ratio for *Acrochordus arafurae* was 78% (data from Shine, 1986), for *Thamnophis sirtalis* 83% (data from Shine & Crews, 1988) and for the genus *Nerodia* 81% (Fitch, 1981). The opportunity for niche differentiation and evolution of sexual dimorphism in relative head size may primarily relate to the number of prey species and abundance of each prey. There is, however, no support for that suggestion in the present study. There was no significant difference in relative head size between males and females on the mainland even though the number of potential prey species is highest there. Thus, there are no indications that sexual segregation in terms of food utilization is an important element in the evolution of the sexual size dimorphism in the adder (see also Forsman, 1991).

Morphometric variation in relation to prey size

Does the geographic variation in adder body size and/or relative head size coincide with the geographic variation in prey size? There were significant differences in adder body size between the localities included in the present study. However, these differences were not as one would expect from the variation in prey size among localities. If the body size of adders at different localities were adapted to local prey size, then mean body size should be smallest on the mainland locality, where prey were smallest, and increase with prey size on the insular localities. This was not the case. On the contrary there was a negative relationship between mean snake SVL and field vole body size, although it was not significant. There are two possible explanations. First, sampling intensity differed between localities, and the five sample means may not reflect the actual body size means in the populations. The purpose of this study, however, was not to compare body size *per se* among populations but relative head size. Second, some of the insular adder populations are small, and stochastic events, e.g. food shortage, bad weather, high mortality during hibernation or failed reproduction in some years, may have caused large and abrupt demographic changes in different directions at the different sites. If one wants to test whether body size of predators with indeterminate growth is adapted to prey size one should only include the largest individuals in the calculations of means, as such an approach will be less sensitive to differences in age structure among populations. Schwaner (1985) calculated mean snout–vent length of the ten largest black snakes, *Notechis ater*, from different islands and found these means to be positively correlated with local prey size. There is a positive relationship between the geographic variation in body size of adders and field voles among the localities comprised in the present study when only the five largest individuals of each sex from each locality are included (Forsman, 1991). This indicates that body size of adders is partly determined by prey size, although other factors are also important.

The geographic variation in relative head length of adders reported here can be more readily interpreted. Heads were smallest in relation to body size on the mainland, where the size of the main prey, i.e. *Microtus agrestis*, is smallest and the number of alternative prey species, all of which are smaller than *Microtus agrestis*, is highest. Across the islands, the relative head size of the adder increased with the overall size parameter of field voles and reached a maximum at the most distant locality, as does body size of the field vole. Thus, the fit between the geographic variation in snake relative head size and prey size distribution is very good (Fig. 2).

Stabilizing or directional selection?

Viperid snakes in general can ingest prey items weighing up to 40% of their own body mass (Pough & Groves, 1983). The body mass of an adder with an SVL of 450 mm is roughly 60–70 g. The range of field vole body weights from the mainland locality is 3–60 g with a mean of 30 g. The corresponding values for insular voles is 3–100 g and a mean of about 40 g, with some variation among localities (Forsman, 1991). Obviously, only very large adders will be capable of swallowing the largest prey items.

Given the increase in maximum ingestible prey size (MIP) with head size in snakes (Reynolds & Scott, 1982) the advantages of relatively large head size can easily be imagined. The proportion of individuals in a prey population constituting potential prey items to a snake increases with its head length but only up to the point where MIP equals the largest prey item in the population. A snake with a head size corresponding to this MIP would gain no further advantage in terms of foraging success by growing an even larger head.

The number of encounters, per unit of time, with ingestible prey items will be lower for snakes with small heads than for snakes with large heads. Consequently, large-headed snakes should have higher foraging success and higher growth rates. During periods with low prey densities they should also have higher survival because energy intake, per unit of time, will decrease below minimum critical levels at an earlier stage for a small-headed snake than for a large-headed snake, given that they are of the same body size, i.e. have the same energetic requirements. Vole densities are known to fluctuate widely over years (Stenseth *et al.*, 1977), and this is the case also on islands in the Baltic Sea (Pokki, 1981; Ebenhard & Forsman, unpublished). In fluctuating populations of voles the decline phase is characterized by reduced birth rates and increased death rates of small juveniles (Krebs *et al.*, 1973; Myllimäki, 1977). This will decrease the proportion of small voles during periods with low densities which makes the situation for small-headed snakes even worse. The overall positive correlation between snake relative head length and physical condition (nutritional status) found in this study does indicate that adders with large heads fare better than do those with small heads. That the relationship between RHL and COND was strongest at locality F, where prey abundance in the preceding year was relatively low, at least compared to N, supports the hypothesis that the advantage of a relatively large head is partly a function of prey density.

The number of prey items needed per unit of time and thus the number of foraging bouts will decrease with increasing ingestible prey size, and thus with snake head size. Whatever risks are incurred during foraging, such as predation, these will also decrease as the size of prey taken increases and the number of foraging bouts accordingly decreases. Thus, there seem to be considerable advantages for an adder to have a large head, especially when prey availability is low.

Obviously there must also be costs or disadvantages limiting relative head size. It has been argued that a small narrow head may facilitate pursuing and taking prey in runways and crevices (Catling & Freedman, 1980). A large head may decrease manoeuvrability and striking efficiency. There is, furthermore, a risk associated with engulfing too large a prey item because the prey may swell during digestion and suffocate the snake. In addition, too large a prey may be impossible to regurgitate and as a result may cause the snake's death in case of a sudden decrease in temperature. There are reports of snakes dying as a result of trying to engulf prey exceeding their ingestive capacity (Barton, 1949; Howard, 1949; Hailey & Davies, 1986; Forsman, unpublished).

Given enough time, adders ought to evolve an optimal relative head size related to the body size of their prey. In a stable situation individuals with a head size smaller or larger than the local optimum should be selected against. The positive relationship found between relative head size and prey size between localities in the present study strongly suggest stabilizing selection to operate in these snake populations. On the other hand, since physical condition is bound to be a fitness related character, the positive correlation found between relative head length and condition means that adders with the largest relative head size have the highest fitness. This result suggests that there is directional selection for larger heads within each locality/population. Why should this be so?

Since the islands in the Baltic Sea are young (*c.* 3000 years), adders may not yet have evolved the optimal sized heads on each locality. However, Grant (1986) has shown selection to act very strongly and rapidly on the trophic apparatus, i.e. beak size and shape, in a population of Darwin's finches, *Geospiza fortis*, following a change in the size distribution of the seeds available in the local habitat. Conant (1988) provided a parallel example in the Laysan finch, *Telespyza cantans*, subsequent to its introduction to islands with different food resources.

Conceivably, a situation of an evolutionary arms race between predator and prey may be taking place where body size of the field vole increases over time, to escape predation from adders or for whatever reason. To remain successful adders would have to grow larger heads. Clearly there are constraints setting limits on such a coevolutionary process.

Yet another possibility is that within each population there is stabilizing selection for an optimal head size, increasing with local prey size. However, this pattern could be disturbed by migration of adders between localities. If an individual originating from locality N moves to locality A, its relative head size would be too small to cope with the larger prey on this locality. Such immigration of suboptimal individuals may prevent the situation from stabilizing. Actually, one male adder marked on locality A in 1987 was recaptured on locality I 2 years later. Thus, the populations are not completely genetically isolated even though the rate of migration between localities is probably very low.

An alternative explanation?

What is the proximate cause of the geographic differences in relative head lengths? Shine & Crews (1988) concluded that androgens inhibited growth of the head early during development of male *Thamnophis sirtalis* leading to sexual dimorphism in relative head size. They also discarded the alternative possibility: "any differences seen in relative jaw lengths reflect differing rates of growth of the head, rather than constant rates of head growth allied to varying rates of bodily growth". Observations from snakes brought up in captivity, however, indicate that this is a premature conclusion or at least not a general one. Differences in energy intake during the juvenile stage induce different developmental pathways. Snakes that starve as juveniles end up with short bodies and relatively large heads as adults while snakes getting plenty of food as juveniles develop longer bodies and relatively smaller heads (Göran Nilson, personal communication). Consequently, a possible alternative explanation to geographic variation in relative head length in snakes would be that geographic differences in prey availability induce different developmental pathways with geographic differences in rates of body growth but similar rates of head growth.

There are five reasons why such alternative developmental pathways probably do not explain the pattern found in the present study: (1) in contrast to what would be expected on the basis of the fact that the two colour morphs have different growth rates there was no significant difference in RHL between the two morphs when the variation between localities had been accounted for; (2) mean RHL is not correlated with mean SVL for females ($N = 7$, $r_s = -0.64$, n.s.) or males ($N = 7$, $r_s = 0.68$ n.s.). For reasons mentioned above, however, mean body length should be treated with caution; (3) alternative developmental pathways cannot explain the positive correlation found between RHL and field body size; (4) alternative developmental pathways cannot explain the positive correlation found between relative head length and physical condition; (5) snakes from the mainland locality (U) have slower growth rates than snakes from locality A (Forsman, 1991), yet they have smaller relative head size.

Conclusion

This study has shown geographic variation in relative head size of adders to be positively correlated with the geographic variation in body size of their main prey, viz. the field vole. This suggests that selection has favoured snake individuals capable of utilizing large prey items, and that the variation in relative head size of adders among localities should be interpreted as the result of an adaptation to local prey size. The pattern found among localities indicates stabilizing selection. On the other hand, the positive relationship between physical condition, a fitness related character, and relative head size suggests a potential for directional selection for larger heads within each population. Possibly the situation has not yet stabilized, and there is an ongoing evolutionary arms race between predator and prey, or else there is immigration of locally suboptimal individuals.

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