



Rejection of non-adaptive hypotheses for intraspecific variation in trophic morphology in gape-limited predators

ANDERS FORSMAN

Department of Zoology, Uppsala University, Villavägen 9, S-752 36 Uppsala, Sweden

RICHARD SHINE

Zoology A08, School of Biological Sciences, Sydney University, NSW 2006, Australia

Received 21 November 1996; accepted for publication 28 February 1997

Recent studies have interpreted intraspecific divergence in relative head sizes in snakes as evidence for adaptation of the trophic apparatus in gape-limited predators to local prey size. However, such variation might also arise from non-adaptive processes (such as allometry, correlated response, genetic drift, or non-adaptive phenotypic plasticity). We test predictions from these alternative hypotheses using data on the allometric relationship between head size and body size in two wide-ranging snake species: eight populations of adders (*Vipera berus*) and 30 populations of common gartersnakes (*Thamnophis sirtalis*). Our data enable strong rejection of the alternative (non-adaptive) hypotheses, because the relationship between head and body size differed significantly among populations, the geographic distance separating pairs of populations explained less than 1.5% of their divergence in allometric coefficients, and the within-population allometric coefficients were higher than the among-population coefficients in each species. In addition, the geographical variability of allometric coefficients in females did not parallel that in males, suggesting that allometric coefficients have evolved independently in the two sexes. Phenotypic plasticity also cannot explain the data, because laboratory studies show that the allometric relationship between head size and body size is relatively insensitive to differing growth rates. We conclude that the intraspecific head size divergence in these snakes is better explained by spatially heterogeneous selection to optimize prey handling ability, than by non-adaptive processes.

© 1997 The Linnean Society of London

ADDITIONAL KEY WORDS:—allometry – correlated response – divergence – evolution – feeding habits – geographic variation – phenotypic plasticity – snakes.

CONTENTS

Introduction	210
Material and methods	211
Study species	211

Correspondence to Dr Anders Forsman. E-mail: Anders.Forsman@zoologi.uu.se

Data acquisition	212
Allometric coefficients	212
Results	213
General	213
Allometric coefficients	214
Discussion	216
Acknowledgements	221
References	221

INTRODUCTION

The morphology of the trophic apparatus (jaws, teeth, beak, etc.) of predators varies enormously among species, and is clearly related to the characteristics of their prey. This matching of form to function has been generally interpreted as evidence for adaptation of trophic morphology to enhance the ability of predators to capture, overpower and consume their prey (e.g. Hespeneide, 1973; Toft, 1980; Pough & Groves, 1983; Grant, 1986; Benkman, 1989; Wainright, 1991; Dayan *et al.*, 1992; Schluter & McPhail, 1992). This inference is entirely plausible for broad comparisons at high taxonomic levels, because the complexity of the morphological modifications, and their clear functional utility in prey-handling, is difficult to understand without invoking some kind of functional (adaptive) modification of trophic morphology. However, this inference is weaker when the attributes involved differ primarily in size rather than shape, and where the variation occurs within a single species. In such cases, intraspecific (geographic or sexual) differences in the size of trophic structures might result from processes (such as correlated response, genetic drift or phenotypic plasticity) unrelated to adaptation for foraging efficiency.

Head-size variation in snakes provides an ideal model system in which to investigate this question. Because they must swallow prey items entire, snakes are gape-limited predators (Pough & Groves, 1983; Shine, 1991a; Forsman & Lindell, 1993). Therefore, natural selection to optimise prey-handling ability has been invoked to explain divergence in head size among populations of wide-ranging species (e.g. Forsman, 1991, 1996a; Shine, 1991b; Grudzien *et al.*, 1992) and between the sexes within single populations (Shine, 1991b, 1993, Houston & Shine, 1993). In both cases, the primary evidence to support the adaptationist hypothesis is a correlation between the trophic divergence and prey characteristics (size and species): snakes with larger heads eat larger prey (reviewed in Arnold, 1993). Adaptation, however, is an onerous concept with many underlying assumptions, and should not be invoked if the same phenomenon is consistent with simpler explanations (Williams, 1966). In this case, at least three such alternatives offer feasible explanations for generating geographic variation in head size relative to body size in snakes:

- (1) Head size divergence among populations may arise as a correlated response to geographic differences in overall body size, combined with allometry of trophic structures (Lande, 1979; Atchley, Rutledge & Cowley, 1982; Price & Langen, 1992).
- (2) Head size relative to body size may diverge in adjacent populations because of stochastic (non-adaptive) processes such as genetic drift and founder effects (e.g. Bohren, Hill & Robertson, 1966; Lande, 1979).
- (3) Geographic differences in ecological conditions (e.g. incubation temperatures,

food supply) may induce different developmental pathways, and hence modify the relationship between head size and body size (Cock, 1966; Gould, 1966; Blouin & Loeb, 1991; Shine & Harlow, 1996).

Although these hypotheses might plausibly explain geographic differences in head size of snakes, they do not predict any correlation between prey size and predator head size. However, given underlying geographic variation in trophic morphology of a gape-limited predator, it is not difficult to devise hypotheses that would predict such a correlation. For example, concordant geographic variation in prey size and snake head size might arise simply because of direct physical consequences, if all snakes eat the largest prey that they can swallow. Alternatively, such a correlation might arise due to adaptations of the prey rather than the predator (if prey are under intense selection to grow to a size too large for the local predators to swallow).

Fortunately, these hypotheses generate predictions that differ from those generated by the hypothesis that intraspecific head-size divergence reflects adaptation of the predator:

- (1) If the geographic variation is due to correlated response to body-size evolution, we expect the allometric relationship linking head size to body size to be similar among populations, and to be similar to the overall (among-population) allometric relationship between these two variables (Lande, 1979; Lofsvold, 1988).
- (2) If the divergence is due to drift, we expect that adjacent populations would be most similar to each other in the relationship between head size and body size, under the assumption that adjacent populations share a more recent ancestor than do populations separated by greater distances.
- (3) If local conditions induce different developmental pathways, we might expect similarity among adjacent populations (as above) if physical conditions (such as temperature and moisture) are the important factors. If local food supply (and hence, growth rates) are more important, we would predict that experimental manipulation of food supply would substantially modify the form of the head size-body size relationship.

Below, we test predictions from these alternative hypotheses, using data on the allometric relationship linking head size to body size in two geographically wide-ranging snake species.

MATERIAL AND METHODS

Study species

We used data on two species of snakes, chosen because of their wide geographic distributions, the availability of published information on their ecology and morphology, and our own existing data sets on geographic variation in head and body sizes in these taxa. The two species differ substantially in phylogenetic position, geographic distribution, body form, and trophic relationships. One species, the adder (*Vipera berus*) is a small (to 75 cm snout-vent length, or SVL) venomous viperid snake widely distributed through Europe (Arnold & Burton, 1978). Adult adders feed primarily upon small mammals, but juveniles feed also on frogs and lizards (Prestt, 1971; Kjaergaard, 1981). The common garter snake (*Thamnophis sirtalis*), in contrast,

is a nonvenomous colubrid species found over most of North America (Fitch, 1965). It is much more slender-bodied than the adder, and feeds on a much wider diversity of prey types. Local populations of gartersnakes have been reported to specialize on prey types such as small mammals, fishes, earthworms and frogs; dietary composition may differ strongly even between populations separated by only a few kilometers (Fitch, 1965; Kephart, 1982). Females grow larger than males in both adders and common gartersnakes (Fitch, 1965; Prestt, 1971). Head sizes relative to body size are similar in male and female adders, but female gartersnakes have larger heads than conspecific males of the same body length (Shine & Crews, 1988, Shine, 1991b; Forsman, 1991, 1996b).

Data acquisition

Data on individual gender, head size and snout-vent length (henceforth SVL) were obtained from eight populations of the European adder *Vipera berus* (L.) inhabiting different groups of islands off the Swedish east coast in the Baltic Sea, and from 30 populations of the North American garter snake *Thamnophis sirtalis* (Tables 1 and 2). All *V. berus* specimens used in this study were live animals captured, marked and released during 1988 to 1991. All *T. sirtalis* specimens were preserved snakes in the collections of the following museums: the Carnegie Museum of Natural History, Chicago Field Museum, University of California Museum of Vertebrate Zoology, California Academy of Sciences, Louisiana State University Museum of Zoology, University of Texas Memorial Museum, University of Kansas Museum of Natural History and U.S. Fish and Wildlife Service Natural History Collection. Wherever possible, we relied upon large series of adult specimens from single populations (i.e., small geographic areas). All *V. berus* were measured by A.F. and all *T. sirtalis* by R.S.

Allometric coefficients

To test whether morphological divergence can be explained by neutral rather than adaptive models of evolution, we compare the slope of the within-population allometric relationship between head and body size (within-population allometry) with the among-population allometric relationship (evolutionary allometry). We expect a close resemblance between within-population and evolutionary allometries if morphological divergence results primarily from drift or correlated responses (Lande, 1979, Lofsvold, 1988). Conversely, we expect within-population allometries to vary among populations and to deviate from the evolutionary allometry if morphological divergence is caused largely by spatially heterogeneous selection (Zeng, 1988; Riska, 1989; Arnold, 1992).

Bivariate allometry coefficients were calculated from least-squares linear regressions of head length on SVL. Prior to analyses, both variables were standardized to a mean of zero within each locality and sex. Within-population allometric coefficients were estimated from separate regression coefficients within each locality. This was done separately for the two sexes. Within-population allometric coefficients were subjected to analyses of covariance to test for effects of sex (over all pooled localities) and localities (over pooled sexes unless there was significant heterogeneity of

slopes between sexes). Evolutionary (among-population) allometric coefficients were estimated from regressions through the locality means, and their 95% confidence intervals were estimated using bootstrap.

Finally, we tested whether the divergence in within-population allometries among pairs of localities could be accurately predicted by the geographic distance separating them. For this purpose we constructed a matrix of geographic distances between the populations and compared this with a matrix of allometric slope distances. The elements in these matrices are not independent, nor can they be assumed to be normally distributed. We therefore estimated the association between elements in the two matrices, and determined the significance of the correlation by comparison with the randomization distribution (3000 permutations) using Mantel's (1967) randomization test (see also Manly, 1991).

Our approach is based on the assumption that phenotypic correlations between head size and body size are similar to the underlying genetic correlations. Unfortunately, we do not have the data necessary to test this assumption. However, several studies have found that there are marked similarities between the genetic and phenotypic covariance patterns, such that estimates of phenotypic correlations may, in general, be suitable substitutes for the genetic correlations, at least for coarser kinds of comparisons and predictions made here (e.g. Roff & Mosseau, 1987; Cheverud, 1988; Roff, 1995; Schluter, 1996). One potential shortcoming of our phenotypic-for-genetic substitution is that if the phenotypic regression slopes are affected by environmental factors, then for selection solely on body size and the correlated response of another character, there is no necessary congruence between the pattern of adult phenotypic variation within populations and the course of evolution (Lande, 1979: 404). We do not believe this to be a serious problem with the current study, however, because experimental evidence suggest that the allometric relationship between head size and body size in snakes is relatively insensitive to environmental factors such as food and temperature (Arnold & Peterson, 1989; Forsman, 1996b).

RESULTS

General

We obtained morphological data on 442 *Vipera berus* and 1154 *Thamnophis sirtalis*. Mean values of SVL and head size for the eight populations of *V. berus* and 30 populations of *T. sirtalis* are presented in Tables 1 and 2, respectively. Overall, we found that both species showed geographic and sexual variation in body as well as head size. Thus, two-factor ANOVAs revealed significant variation in SVLs of *V. berus* among the eight populations (SVL, $F_{7,433} = 2.73$, $P < 0.01$; Head size, $F_{7,433} = 2.44$, $P < 0.05$) and between the two sexes (SVL, $F_{1,433} = 40.67$, $P < 0.0001$; Head size $F_{1,433} = 32.66$, $P < 0.0001$). Females were larger and had larger heads than males in all populations (Table 1), and the degree of sexual size dimorphism did not vary significantly among populations in either character (Effect of interaction, SVL, $F_{7,426} = 1.69$, $P = 0.11$; Head size, $F_{7,426} = 1.43$, $P = 0.19$). A similar overall pattern was evident in *T. sirtalis*, with both characters varying significantly among the 30 populations (SVL, $F_{29,1123} = 10.21$, $P < 0.0001$; Head size, $F_{29,1123} = 8.59$, $P < 0.0001$).

and between the two sexes (SVL, $F_{1,1123} = 186.68$, $P < 0.0001$; Head size, $F_{1,1123} = 336.95$, $P < 0.0001$), and with no variation among populations in the degree of sexual dimorphism (Effect of interaction, SVL, $F_{29,1094} = 0.82$, $P = 0.74$; Head size, $F_{29,1094} = 0.93$, $P = 0.58$).

Allometric coefficients

Vipera berus

Within-population allometric slope coefficients did not differ significantly between male and female *Vipera berus*; this was true both when data from all localities were pooled ($F_{1,438} = 2.75$, $P = 0.10$) and when each locality was analysed separately (all $P > 0.05$) (Table 1). The direction of the difference between sexes in allometric coefficients was not consistent among the eight localities (Table 1). Within-population allometric coefficients did not vary significantly among the eight localities (ANCOVA, pooled sexes, effect of interaction, $F_{7,426} = 0.73$, $P = 0.65$, Fig. 1). A common within-population allometric coefficient was therefore calculated for the combined sexes, yielding an estimate of 0.0284 (95% confidence interval = 0.0283–0.0285).

Geographic distance accounted for no more than 0.07% (pooled sexes) of the observed non-significant divergence in within-population allometries among pairs of populations.

The evolutionary allometric coefficients estimated from regressions through the locality means were very similar for male (0.0211) and female (0.0199) *Vipera berus* (Table 1). The common evolutionary coefficient for the combined sexes was 0.0191 (95% confidence interval = 0.0102–0.0255), a value significantly lower than the common within-population allometric coefficient. Also, all but one of the within-population allometric values were larger than the evolutionary allometric value (Table 1 Fig. 1).

Thamnophis sirtalis

Thamnophis sirtalis showed significant heterogeneity of the within-population allometric coefficients between the two sexes (ANCOVA, effect of interaction, $F_{1,1150} = 33.25$, $P < 0.0001$). The within-population allometric coefficient for the combined localities was significantly higher for females (0.0424, 95% confidence interval = 0.0416–0.0432) than for males (0.0382, 0.0373–0.0391). This greater allometric value for females was evident in 23 of the 30 localities, with the difference being statistically significant in 3 cases (Table 2). Both sexes showed significant heterogeneity of within-population allometric coefficients among localities (Females: $F_{29,601} = 2.46$, $P < 0.0001$; Males: $F_{29,433} = 1.86$, $P < 0.01$) (Table 2, Fig. 2). Interestingly, this variability among populations was not parallel in males and females (Pearson correlation, $r = 0.32$, $n = 30$ localities, $P = 0.08$, the power of this analyses was 0.43: Cohen, 1988).

Somewhat surprisingly, Mantel's tests revealed that the divergence in within-population allometric coefficients among localities could not be accurately predicted by the geographic distance separating them ($r^2 = 1.4\%$ in females and 0.4% in males) (Fig. 3).

Because within-population allometry differed between sexes, we calculated evolutionary allometric coefficients for *Thamnophis sirtalis* separately for males and females. As for the common within-population allometries, the evolutionary allometric value

TABLE 1. Geographical and sexual variation in head size, snout-vent length and head allometry in *Vipera berus*. Before calculating allometric coefficients (slopes) data were standardized to mean zero within localities and sexes. *P* denotes results from test for heterogeneity of slopes between sexes

Locality	Females			Males			<i>P</i>	
	<i>n</i>	Head length (mm)	Snout-vent length (mm)	Slope	<i>n</i>	Head length (mm)		Snout-vent length (mm)
Ångskär	68	23.0	487.4	0.029	74	22.0	450.5	ns
In-Fredeln	33	23.7	513.3	0.027	41	22.3	479.9	ns
Svenska Högarna	61	23.9	505.4	0.027	42	22.8	461.8	0.061
Uppsala	7	24.1	545.7	0.022	23	21.0	445.4	ns
Kärringboskär	9	24.4	553.9	0.019	7	21.5	440.0	ns
Norrpada	10	24.4	560.0	0.039	15	23.3	502.0	ns
Röder	21	24.5	528.1	0.027	11	22.6	463.6	ns
Hamnskär	10	25.4	591.1	0.027	10	21.7	453.0	ns

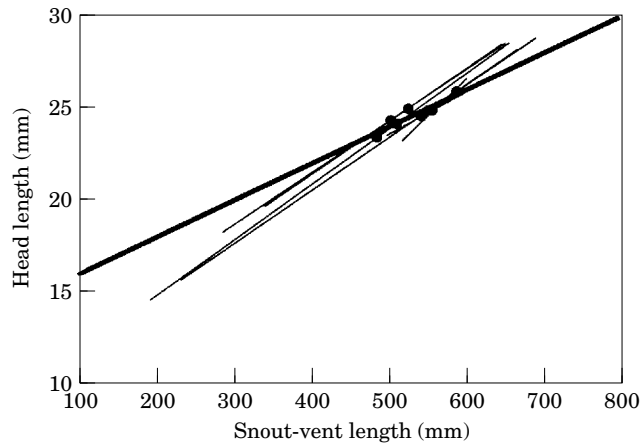


Figure 1. Within- (thin lines) and among- (thick line extended to axes) population allometric relationships between head size and body size in adders, *Vipera berus*. The figure is based on data from eight different populations. Data for the two sexes are pooled.

for females (0.0337, 95% confidence interval = 0.0247–0.0435) was 10% higher than that for males (0.0306, 0.0252–0.0376). For both sexes, the evolutionary allometric coefficient was lower than the common within-population coefficient. Nearly all of the within-population allometric values were larger than the evolutionary allometric value (females 30 of 30; males 27 of 30), and in 24 of 60 cases (females 11, males 13) they were outside the 95% confidence interval of the evolutionary allometric coefficient (Table 2, Fig. 2).

DISCUSSION

Our results provide strong support for the inference that intraspecific variation in relative head sizes in two snake species (*Vipera berus* and *Thamnophis sirtalis*) has arisen through some process of active divergence, with modifications occurring to different degrees in different areas and (within *T. sirtalis*) independently in each sex. This pattern is consistent with an adaptationist hypothesis (i.e. head sizes relative to body size have evolved to enhance foraging success in these snakes) but is difficult to reconcile with alternative hypotheses focusing on the roles of correlated response, drift, and phenotypic plasticity.

(1) *Correlated response*. If geographic divergence in relative head sizes was due to correlated response to selection on absolute body size, we would expect a general similarity among populations with respect to the within-population allometric coefficient. This prediction is clearly falsified: populations displayed very different allometric relationships, and the among-population relationship diverged significantly from the within-population relationships (Figs 1 and 2).

(2) *Genetic drift*. Stochastic processes would be expected to generate a pattern whereby geographically contiguous populations would display similar allometries between body size and head size, with a gradual divergence to snakes from more geographically distant areas. Our analyses falsify this prediction, with geographic distance between

TABLE 2. Geographical and sexual variation in head size, snout-vent length and head allometry in *Thamnophis sirtalis*. Before calculating allometric coefficients (slopes) data were standardized to mean zero within localities and sexes. *P* denotes results from test for heterogeneity of slopes between sexes.

Locality	Females				Males				<i>P</i>
	<i>n</i>	Head length (mm)	Snout-vent length (mm)	Slope	<i>n</i>	Head length (mm)	Snout-vent length (mm)	Slope	
CAN, BC	19	27.0	575.1	0.039	17	22.1	496.2	0.038	ns
CAN, Alberta	7	23.0	564.0	0.038	8	20.6	502.0	0.037	ns
CAN, Manitoba	19	19.9	488.5	0.034	19	16.3	406.2	0.031	ns
CAN, Ontario	25	24.4	499.5	0.043	12	20.3	438.8	0.034	ns
California	26	25.7	521.3	0.044	19	18.7	395.4	0.030	0.035
Colorado	21	25.6	555.6	0.043	28	21.9	489.0	0.042	ns
Florida	28	29.5	588.5	0.039	21	23.7	494.9	0.036	ns
Idaho	9	23.0	487.7	0.042	6	20.4	456.0	0.045	ns
Indiana	27	23.6	459.5	0.048	23	20.6	432.1	0.041	ns
Iowa	26	24.9	534.3	0.040	23	18.9	410.9	0.039	ns
Kansas	35	24.3	483.1	0.042	30	18.4	380.3	0.035	0.0004*
Kentucky	34	22.7	408.1	0.043	25	15.3	268.4	0.037	0.0001*
Massachusetts	26	22.8	451.8	0.050	15	18.4	384.0	0.036	0.056
Michigan	27	26.2	536.6	0.044	21	20.6	429.8	0.037	ns
Maine	31	22.4	454.3	0.034	14	18.4	388.4	0.040	ns
Missouri	26	28.4	577.2	0.044	15	20.9	452.3	0.042	ns
Minnesota	15	23.2	493.4	0.042	13	17.3	391.7	0.039	ns
North Carolina	25	25.9	479.1	0.050	12	19.9	377.6	0.051	ns
Nebraska	9	27.7	644.8	0.039	4	21.6	513.5	0.022	ns
New Hampshire	20	22.5	445.2	0.045	14	17.5	354.6	0.041	ns
New Mexico	10	25.9	544.7	0.048	12	20.0	437.2	0.043	0.068
New York	28	22.5	440.5	0.043	19	17.6	352.9	0.035	ns
Ohio	23	23.6	462.3	0.046	24	19.6	413.3	0.042	ns
Oregon	19	25.6	539.9	0.038	19	21.0	447.2	0.038	ns
Pennsylvania	27	23.4	433.8	0.050	23	19.4	383.4	0.040	0.0182
South Dakota	6	22.1	477.7	0.041	4	18.4	428.2	0.048	ns
Texas	24	30.0	625.8	0.042	18	23.3	511.6	0.038	0.0165
Virginia	20	27.7	538.9	0.042	12	19.9	394.8	0.045	ns
Washington	27	22.5	480.1	0.048	12	17.8	388.2	0.036	0.0001*
Wisconsin	22	21.3	439.3	0.042	11	19.4	411.1	0.044	ns

* denotes that the difference is significant after correction for multiple comparisons ($\alpha = 0.05/30$).

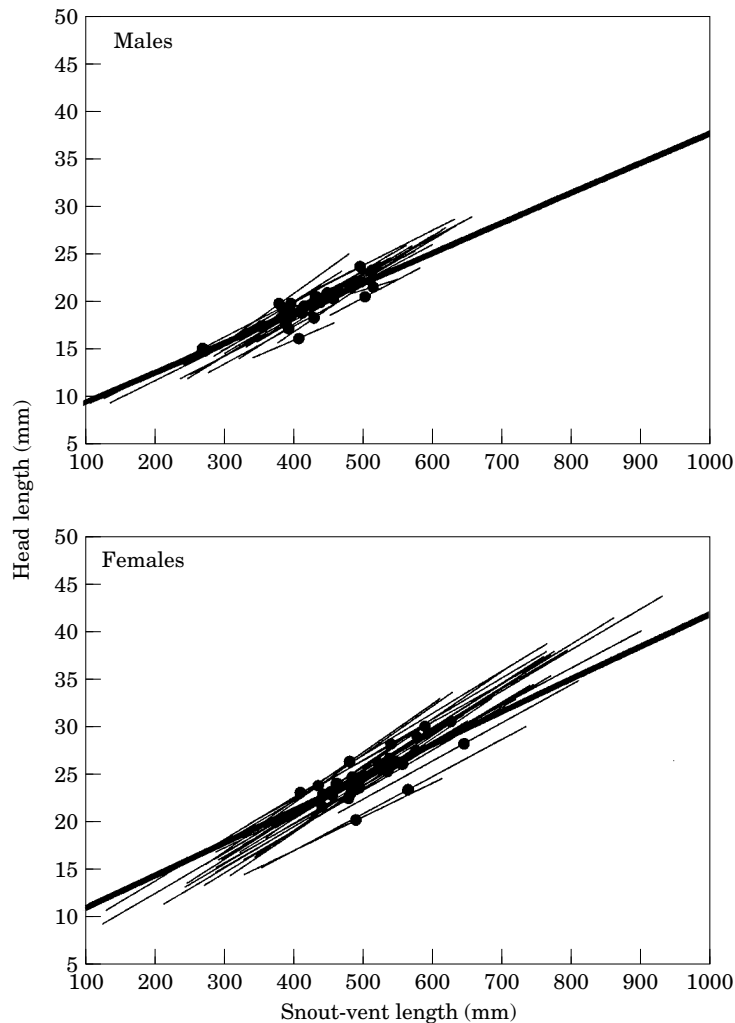


Figure 2. Within- (thin lines) and among- (thick lines extended to axes) population allometric relationships between head size and body size in male (top) and female (bottom) gartersnakes, *Thamnophis sirtalis*. The figure is based on data for 30 different populations.

populations explaining less than 1.5% of the intraspecific divergence in allometric coefficients (Fig. 3).

(3) *Phenotypic plasticity*. Phenotypic plasticity of overall growth rate in snakes in response to changing resource levels is well documented (e.g. Barnett & Schwaner, 1985; Madsen & Shine, 1993; Forsman, 1996b). If the observed geographic variation in head size relative to body size resulted from modifications to developmental pathways directly induced by local environmental conditions, we would expect to see similarities between adjacent populations (as above) and considerable flexibility in the relationship between these two variables within a single population. Instead, there is little such consistency between adjacent populations (see above), and experimental manipulations show that relative head size is relatively insensitive to

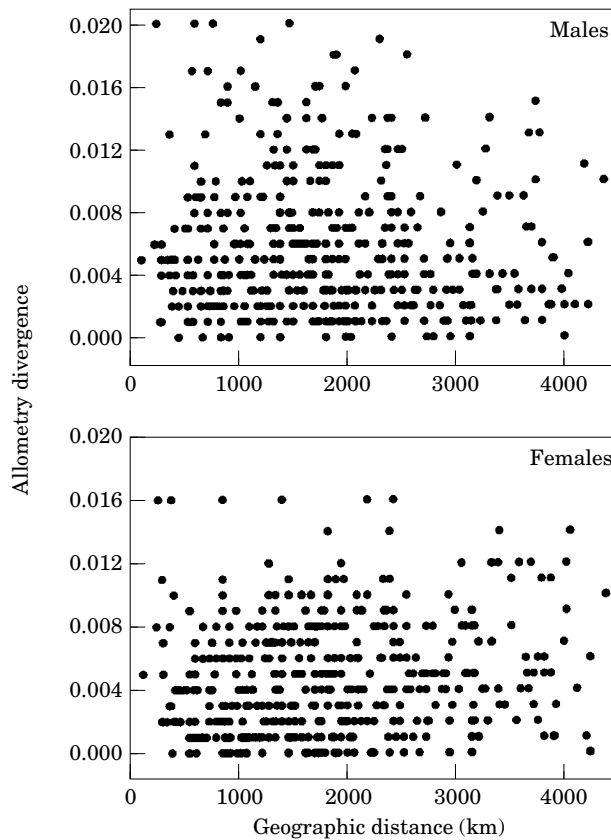


Figure 3. The divergence in within-population allometric relationships between head size and body size, compared to the geographic distance separating pairs of populations in male (top) and female (bottom) gartersnakes, *Thamnophis sirtalis*. The figure is based on data for 30 populations, yielding 435 pairwise comparisons.

differences in growth rates (Forsman, 1996b for *Vipera berus*; Arnold & Peterson, 1989 for *Thamnophis sirtalis*). Also, sex differences in relative head size are evident at birth in *T. sirtalis* (Shine & Crews, 1988).

Our data also enable us to falsify the hypothesis that correlations between prey size and predator trophic morphology (relative head size) reflect adaptation of the prey rather than the predator. In the case of common gartersnakes, the wide diversity of prey types eaten in different (even adjacent) populations means that any consistent matching between prey size and predator size must reflect adaptation of the snakes rather than their prey (for example, it is clearly nonsensical to posit that mice are larger than worms because of selection to overcome a local gape-limited predator). In the case of adders, the variation among populations in head size relative to body size parallels the variation in body size of available prey (Forsman, 1991). Furthermore, feeding experiments performed with captive adders show that variation in swallowing capacity among snakes of the same body size is related to individual variation in relative head size, and several fitness-related characters (body condition,

growth rate, and survival) correlate positively with relative head size within natural populations (Forsman, 1991, 1994; Forsman & Lindell, 1993).

These patterns are consistent with the hypothesis that the relative dimensions of the trophic apparatus in gape-limited predators evolve as adaptations to the size of locally available prey species. Also, our analyses revealed that the geographic variation of allometric coefficients in females was not related to the variation in males. This pattern supports the inference that male-female divergence in head size relative to body size reflects independent adaptations to foraging in each sex, rather than selection for sex divergence (Shine, 1991b, 1993).

Despite an overall similarity in our results for these two species, important differences were also apparent. These may reflect the substantial ecological differences between the two species. For example, we found no significant heterogeneity of allometric coefficients among sexes or populations in adders (*Vipera berus*), whereas within gartersnakes (*T. sirtalis*), the within-population allometric coefficient was significantly higher for females than for males, and both sexes showed significant heterogeneity of allometric coefficients among populations. The greater conservatism of adders in this respect might be due to the smaller geographic range over which we sampled them, or to the less diverse diet of this taxon than of *T. sirtalis* (Fitch, 1965; Prestt, 1971; Kjaergaard, 1981; Kephart, 1982). Also, most of the adder populations included in this study are relatively young (the islands emerged from the sea some 5000–7000 years ago) and have had less time available for evolutionary change, compared to our populations of garter snakes. Despite the more recent origin of our adder populations, however, the magnitude of the difference between evolutionary and within-population allometric coefficients was greater in *V. berus* (49%) than in *T. sirtalis* (25%).

Our results suggest that evolution of trophic morphology in these snakes has not occurred entirely along the genetic lines of least resistance (Schluter, 1994, 1996). The simplest way for average head size to increase or decrease in response to selection for greater or smaller swallowing capacity would involve a change in overall body size, with head size simply diverging along a slope determined by the additive genetic regression between head size and body size (Lande, 1979; Lofsvold, 1988). The variability (within *Thamnophis*) among populations in allometric relationships, and the deviation (in both species) of the common within-population allometries from the evolutionary allometries, does not accord with such a scenario. Thus, although genetic constraints may have retarded the rate of evolutionary change (Lande, 1980; Arnold, 1992), they clearly have not altogether prevented modifications of trophic morphology in these organisms. Instead, the sexual and spatial variation in head size relative to body size suggests that both characters have been subjected to directional selection (Price & Langen, 1992). Given the tight linkage between snake head size and prey-handling ability, geographic variation in the size of available prey will plausibly induce directional selection for increased or decreased head size in different areas. However, body size in snakes is correlated with many aspects of performance other than swallowing capacity. These aspects include thermoregulation, male mating success, female fecundity, and survival (Stevenson, 1985; Jayne & Bennett, 1990; Duvall, Shuett & Arnold, 1993; Forsman, 1993; Madsen & Shine, 1994). Hence, selection on body-size in relation to these other abilities may oppose selection on head size (for efficient prey-handling). Such conflicting selection pressures on head size and body size probably offer the best explanation for the geographical and sexual divergence in head size relative to body size seen in so many species of

snakes (e.g. Klauber, 1938; Forsman, 1991; Shine, 1991b, 1993; Grudzien *et al.*, 1992), and other kinds of gape-limited predators (e.g. Wilson, 1953; Malmquist, 1985; Benkman, 1989; Shine, 1989; Snorrason *et al.*, 1994).

ACKNOWLEDGEMENTS

We thank S. Arnold, E. Ranta and S. Ulfstrand for helpful comments on the manuscript. The study was funded by grants from Olle & Signhild Engkvists Stiftelser and the Swedish Natural Science Research Council (to AF), and the Australian Research Council (RS).

REFERENCES

- Arnold EN, Burton JA. 1978.** *A Field Guide to the Reptiles and Amphibians of Britain and Europe*. London: Collins.
- Arnold SJ. 1992.** Constraints on phenotypic evolution. *American Naturalist* **140**: Supplement 85–107.
- Arnold SJ. 1993.** Foraging theory and prey size-predator size relations in snakes. In: Seigel RA, Collins JT, eds. *Snakes: Ecology and Behavior*. New York: McGraw-Hill, 87–115.
- Arnold SJ, Peterson CR. 1989.** A test for temperature effects on the ontogeny of shape in the garter snake *Thamnophis sirtalis*. *Physiological Zoology* **62**: 1316–1333.
- Atchley WR, Rutledge JJ, Cowley DE. 1982.** A multivariate statistical analysis of direct and correlated response to selection in rats. *Evolution* **36**: 677–698.
- Barnett B, Schwaner TD. 1985.** Growth in captive born tiger snakes (*Notechis ater serventyi*) from Chappell island: implications for field and laboratory study. *Transactions from the Royal Society of South Australia* **109**: 31–36.
- Benkman CW. 1989.** On the evolution and ecology of island populations of crossbills. *Evolution* **43**: 1324–1330.
- Blouin MS, Loeb MLG. 1991.** Effects of environmentally induced development-rate variation on head and limb morphology in the green tree frog, *Hyla cinerea*. *American Naturalist* **138**: 717–728.
- Bohren BB, Hill WG, Robertson A. 1966.** Some observations on asymmetrical correlated responses to selection. *Genetical Research* **7**: 44–57.
- Cheverud JM. 1988.** A comparison of genetic and phenotypic correlations. *Evolution* **42**: 958–968.
- Cock AG. 1966.** Genetical aspects of metrical growth and form in animals. *Quarterly Review of Biology* **41**: 131–190.
- Cohen J. 1988.** *Statistical Power Analysis for the Behavioral Sciences*, 2nd ed. Hillsdale, New Jersey: Lawrence Erlbaum Associates.
- Dayan T, Simberloff D, Tchernov E, Yom-Tov Y. 1992.** Canine carnassials: Character displacement in the wolves, jackals and foxes of Israel. *Biological Journal of the Linnean Society* **45**: 315–331.
- Duvall D, Schuett GW, Arnold SJ. 1993.** Ecology and Evolution of snake mating systems. In: Seigel RA, Collins JT, eds. *Snakes: Ecology and Behavior*. New York: McGraw-Hill, 165–193.
- Fitch HS. 1965.** An ecological study of the garter snake, *Thamnophis sirtalis*. *University of Kansas Publications from the Museum of Natural History* **15**: 493–564.
- Forsman A. 1991.** Adaptive variation in head size in *Vipera berus* L. populations. *Biological Journal of the Linnean Society* **43**: 281–296.
- Forsman A. 1993.** Survival in relation to body size and growth rate in the adder, *Vipera berus*. *Journal of Animal Ecology* **62**: 647–655.
- Forsman A. 1994.** Growth rate and survival in relation to relative head size in *Vipera berus*. *Journal of Herpetology* **28**: 231–238.
- Forsman A. 1996a.** Body size and net energy gain in gape-limited predators: a model. *Journal of Herpetology* **30**: 307–319.
- Forsman A. 1996b.** An experimental test for food effects on head size allometry in juvenile snakes. *Evolution* **50**: 2536–2542.

- Forsman A, Lindell LE. 1993.** The advantage of a big head: swallowing performance in adders, *Vipera berus* (L.). *Functional Ecology* **7**: 183–189.
- Gould SJ. 1966.** Allometry and size in ontogeny and phylogeny. *Biological Review* **41**: 587–680.
- Grant PR. 1986.** *Ecology and Evolution of Darwin's Finches*. Princeton, NJ: Princeton University Press.
- Grudzien TA, Huebner BJ, Cvetkovic A, Joswiak GR. 1992.** Multivariate analysis of head shape in *Thamnophis sirtalis sirtalis* (Serpentes: Colubridae) among island and mainland populations from northeastern Lake Michigan. *American Midland Naturalist* **127**: 339–347.
- Hespenheide HA. 1973.** Ecological inferences from morphological data. *Annual Review of Ecology and Systematics* **4**: 213–229.
- Houston D, Shine R. 1993.** Sexual dimorphism and niche divergence: feeding habits of the Arafura filesnake. *Journal of Animal Ecology* **62**: 737–749.
- Jayne BC, Bennett AF. 1990.** Selection on locomotor performance capacity in a natural population of garter snakes. *Evolution* **44**: 1204–1229.
- Kephart DG. 1982.** Microgeographic variation in the diets of of garter snakes. *Oecologia (Berl.)* **52**: 287–291.
- Kjaergaard J. 1981.** A new method for examination of stomach content in live snakes and some information on feeding habits in common viper (*Vipera berus*) in Denmark. *Natura Jutlandica* **19**: 45–48.
- Klauber LM. 1938.** A statistical study of the rattlesnakes, V. Head dimensions. *San Diego Society for Natural History* **4**: 1–53.
- Lande R. 1979.** Quantitative genetic analysis of multivariate evolution, applied to brain: body size allometry. *Evolution* **33**: 402–416.
- Lande R. 1980.** Genetic variation and phenotypic evolution during allopatric speciation. *American Naturalist* **116**: 463–479.
- Lofsvold D. 1988.** Quantitative genetics of morphological differentiation in *Peromyscus*. II. Analyses of selection and drift. *Evolution* **42**: 54–67.
- Madsen T, Shine R. 1993.** Phenotypic plasticity in body sizes and sexual size dimorphism in European grass snakes. *Evolution* **47**: 321–325.
- Madsen T, Shine R. 1994.** Components of lifetime reproductive success in adders, *Vipera berus*. *Journal of Animal Ecology* **63**: 561–568.
- Malmquist MG. 1985.** Character displacement and biogeography of the pygmy shrew in northern Europe. *Ecology* **66**: 372–377.
- Manly BFJ. 1991.** *Randomization and Monte Carlo Methods in Biology*. London: Chapman and Hall.
- Mantel N. 1967.** The detection of disease clustering and a generalized regression approach. *Cancer Research* **27**: 209–220.
- Pough FH, Groves JD. 1983.** Specializations of the body form and food habits of snakes. *American Zoologist* **23**: 442–454.
- Prestt I. 1971.** An ecological study of the viper *Vipera berus* in southern Britain. *Journal of Zoology* **164**: 373–418.
- Price T, Langen T. 1992.** Evolution of correlated characters. *Trends in Ecology and Evolution* **7**: 307–310.
- Riska B. 1989.** Composite traits, selection response, and evolution. *Evolution* **43**: 1172–1191.
- Roff DA. 1995.** The estimation of genetic correlations from phenotypic correlations: a test of Cheverud's conjecture. *Heredity* **74**: 481–490.
- Roff DA, Mosseau TA. 1987.** Quantitative genetics and fitness: lessons from *Drosophila*. *Heredity* **58**: 103–118.
- Schluter D. 1994.** Adaptive radiation along “Genetic lines of least resistance”. *Journal of Ornithology* **135**: 357.
- Schluter D. 1996.** Adaptive radiation along genetic lines of least resistance. *Evolution*, **50**: 1766–1774.
- Schluter D, McPhail JD. 1992.** Ecological character displacement and speciation in sticklebacks. *American Naturalist* **140**: 85–108.
- Shine R. 1989.** Ecological causes for the evolution of sexual dimorphism: a review of the evidence. *Quarterly Review of Biology* **64**: 419–464.
- Shine R. 1991a.** Why do large snakes eat larger prey items? *Functional Ecology* **5**: 493–502.
- Shine R. 1991b.** Intersexual dietary divergence and the evolution of sexual dimorphism in snakes. *American Naturalist* **138**: 103–122.
- Shine R. 1993.** Sexual dimorphism in snakes. In: Seigel RA, Collins JT, eds. *Snakes: Ecology and Behavior*. New York: McGraw Hill 49–86.
- Shine R, Crews D. 1988.** Why male garter snakes have small heads: the evolution and endocrine control of sexual dimorphism. *Evolution* **42**: 1105–1110.

- Shine R, Harlow P. 1996.** Maternal manipulation of offspring phenotypes via nest-site selection in an oviparous lizard. *Ecology*. **77**: 1808–1817.
- Snorrason SS, Skulason S, Jonsson B, Malmquist HJ, Jonasson PM, Sandlund OT, Lindem T. 1994.** Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): Morphological divergence and ontogenetic niche shifts. *Biological Journal of the Linnean Society* **52**: 1–18.
- Stevenson RD. 1985.** Body size and limits to the daily range of body temperatures in terrestrial ectotherms. *American Naturalist*. **125**: 102–117.
- Toft CA. 1980.** Feeding ecology of thirteen sympatric species of anurans in a seasonal tropical environment. *Oecologia* **45**: 131–141.
- Wainright PC. 1991.** Ecomorphology: experimental functional anatomy for ecological problems. *American Zoologist* **31**: 680–693.
- Williams GC. 1966.** *Adaptation and Natural Selection*. Princeton, NJ: Princeton Monographs.
- Wilson EO. 1953.** The origin and evolution of polymorphism in ants. *Quarterly Review of Biology* **28**: 136–156.
- Zeng ZB. 1988.** Long-term correlated response, interpopulation covariation, and interspecific allometry. *Evolution* **42**: 363–374.