

SEXUAL SIZE DIMORPHISM IN EASTERN SLOW-WORM (*Anguis fragilis colchica*, REPTILIA: ANGUIDAE)

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The direction and magnitude of inter-sexual differences in body and head size in one eastern slow-worm (*A. f. colchica*) population were investigated. We compared morphological measures of 92 male and 127 female adult *A. f. colchica* from a single population. In line with our expectations, we found that females were generally larger, but males had larger relative head size. At similar growth rate a disproportionate increase of head size in males and respectively of body size in females are pointed. The sexual difference in relative head size increased with the size (a proxy for age) of the animals. Our results fits well to the general theory, especially when studies of the reproductive biology of the species — reporting vigorous male-male combats, the presence of copulatory bites, and showing that female fecundity is size dependent — is taken into account. However, considering this generalist species, another common hypothesis suspecting dietary divergence between sexes behind sexual differences in relative head size is not likely to represent a strong evolutionary pressure in this case.

Keywords: *Anguis fragilis colchica*, growth, sexual size dimorphism.

INTRODUCTION

Sexual dimorphism is a complex trait and theoretically might be the consequence of adaptive, exaptive selection, nonadaptive genetic influences random genetic drift, as well as environmental variables or can be a result of phenotypic plasticity (e.g., Shine 1990). When studying the evolution of sexual dimorphism it is crucial to consider that the direction and the degree of sexual dimorphism is often the result of different selective forces acting separately on females and males (Tomović et al., 2002). For instance, dimorphism in size and color may be a product of intraspecific competition, mate choice, or both. Large size or bright coloration may confer advantages to males in male-male contests (e.g., Vitt and Cooper, 1985; Cooper and Vitt, 1989; Fairbairn, 1997, Baird et al., 2003; Gvoždík and Van Damme, 2003), or in cases when it promotes ability to forcibly inseminate

females (e.g., Birkhead et al., 1985). Females may show mating preferences for males with exaggerated traits, due their fitness state signal (e.g., Johnson et al., 1993) and they generally prefer larger males (Cooper and Vitt, 1993; Censky, 1997). In other cases, even though large size may be selected for in both sexes, females may grow larger because young females allocate more of their available energy to egg production (e.g., Cooper and Vitt, 1989; Fairbairn, 1997; Anderson and Vitt, 1990). Dimorphic structures associated with prey capture and feeding (e.g., jaw and head size) may also evolve owing to sexual differences in the use of food resources (e.g., Perry, 1996; Shine et al., 2002).

Sexual size dimorphism (SSD) is widespread among different lizard taxa, mostly found in head characters and/or in trunk-tail ratio and/or in overall size (e.g., Anderson and Vitt, 1990; Baird et al., 2003; McCoy et al., 2003; Gvoždík and Van Damme, 2003). Similarly, SSD was found in a legless anguid lizard, the slow-worm *Anguis fragilis* (Linnaeus 1758) too. Previous studies have shown that in *A. fragilis*: (i) at the same body size, adult male exhibit larger head (pileus) than adult female (Wermuth, 1950; Dely, 1972, 1974, 1981; Günther and Völkl, 1996), (ii) at similar growth rate the head size of male has a positive allometry regarding to body size (Wermuth, 1950; reviewed in Dely, 1981), and respectively

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(iii) the female *A. fragilis* develop a longer body (Wermuth, 1950; reviewed in Dely, 1981). In these studies, dealing mostly with the distribution and the taxonomy of *A. fragilis* subspecies (see cited in Dely, 1981) the examined specimens belonged to different populations (and subspecies) from a wide area and in most cases represented a small number of specimens from the same population.

The aim of this study was to examine the direction and magnitude of intersexual differences in body and head size in one eastern slow-worm (*A. f. colchica* Nordmann, 1840) population, lying in the western part of the subspecies distribution area. We predicted that the expected and well documented sexual difference in relative head size and body length is not a constant phenomenon, but increases with size.

MATERIAL AND METHODS

Data Collection

The legless lizard, *A. fragilis* is found over almost the whole mainland Europe (Cabela 1997). Two subspecies have been described, *A. f. fragilis* and *A. f. colchica*, based on morphological characteristics: generally *A. f. fragilis* inhabits Western and Central Europe, while *A. f. colchica* is found in Eastern Europe and non-European areas (e.g., Dely, 1981). The investigated population belongs to *A. f. colchica* (Sos, unpublished data).

Morphological data were collected during 2001–2004 from a single population in Rupea, Braşov County, Romania, located in the south-western part of Transylvania, at about 451 m a.s.l. Our sample included 219 individuals (92 males and 127 females). Sex was determined by the presence or absence of the hemi-penis and by using the sexual coloration of males and other clues (e.g., gravid states of females). Adults were classified as those individuals with a snout-vent length (SVL) greater than 120 mm (following e.g., Smith, 1990). For each individual, eight morphometric measures were recorded: SVL (measured from the tip of the snout to the vent); L.cap.1, head length 1 (from the tip of the snout to the edge of the mouth), L.cap.2, head length 2 (from the tip of the snout to the ear opening), L.nas., nose-eye distance (from the tip of the snout to the anterior edge of the eye); Lt.cap., head width (across the head, between the corners of the mouth); Alt.par., parietale height (from the edge of mouth to the top of the head); L.pil., pileus length (from the tip of the snout to the dorsal edge of the occipital scale); Lt.pil., pileus width (between the farthest edge of the parietale scales). As the ratio of indi-

viduals with intact tail was low (below 25%), the use of tail length had to be rejected.

A. f. colchica inhabit the undisturbed parts of cemetery, and are usually found in or near to the bushy patches using coverboards or other natural covers. The preferred headquarters are represented by the organic dumps. In parallel a study on thermoeology of the species was performed (Sos, unpublished data). To avoid the repeated measurements of the same individuals, scale counts on the head, head patterns, tail condition, color, scars or other injuries, and practically all individual-specific clues were recorded. Unfortunately, other marking techniques have failed in long-period marking in this species (review in Riddell, 1996).

Data Analysis

First, we tested for sexual difference in SVL with the aid of a General Linear Model (ANOVA) with sex as fixed factor and SVL as the dependent variable. Data was pooled across years.

Correlations between the head characters were tested with Pearson's correlation. As the characters strongly correlated (see *Results*) separate univariate analyses would have been redundant. To overcome this problem, we applied principal component analysis (PCA) to collapse the seven original head size variables into a smaller number of independent variables. We had only one informative principal component (PC; see *Results*). We analyzed sexual differences in that PC using a General Linear Model (ANCOVA) with sex as fixed factor, the PC scores as dependent variable and SVL as a covariate. Statistical analyses were performed by statistical package STATISTICA 6.1 for Windows (StatSoft Inc., Tulsa, Oklahoma).

RESULTS

SVL of males was shorter than that of females ($F_{[1,217]} = 24.89$, $p < 0.001$; Table 1). All the measured head dimensions were positively correlated ($R > 0.46$, $p < 0.05$).

In comparison with females, male *A. fragilis* had bigger heads (Table 1). 67% of the total variance could be explained by the first PC (PC 1), while the second PC explained only 9% of the total variance (Table 3). We excluded the second PC following Kaiser's criteria (it has lower eigenvalue than one). All morphometric characters had strong positive loadings on the first PC, indicating that this PC could be interpreted as general size measure (Table 2). PC 1 scores differed significantly between sexes ($F_{1,215} = 15.65$, $p < 0.001$), were correlated

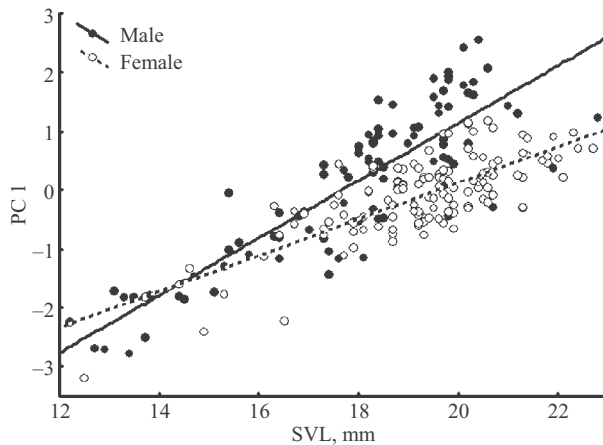


Fig. 1. Relationship between head size (the first principal component scores) and body size (SVL) in male and female *Anguis fragilis colchica*. Note that the principal component scores were multiplied with -1 , in order to clarify the figure (all the correlations with the original variables were negative).

with SVL ($F_{1,215} = 448.93, p < 0.001$) and the SVL \times PC 1 correlation differed between sexes ($F_{1,215} = 25.68, p < 0.001$; Fig. 1), thus in growth the male develop a larger head size, while the females develop a larger body size (e.g., see differences between sexes in mouth length, i.e., L.cap.1, and mouth width, i.e., Lt.cap., fitted in Figs. 2 and 3).

DISCUSSION

Both intra-sexual competition and mate choice can result in dimorphism in size and coloration in lizards (e.g., Vitt and Cooper, 1985; Censky, 1997; McCoy et al., 2003; Molina-Borja, 2003). Other studies on lizards

TABLE 1. Descriptive Statistics of Eighth Morphometric Characters of Both Sex in *Anguis fragilis colchica*

Character	Males		Females	
	$x \pm$ S.D.	min – max	$x \pm$ S.D.	min – max
SVL	17.92 \pm 2.29	12.2 – 22.8	19.28 \pm 1.75	12.5 – 22.7
L.cap.1	0.91 \pm 0.13	0.62 – 1.30	0.89 \pm 0.08	0.64 – 1.10
L.cap.2	1.45 \pm 0.18	0.82 – 1.78	1.44 \pm 0.11	1.07 – 1.83
L.nas.	0.51 \pm 0.07	0.34 – 0.67	0.50 \pm 0.04	0.36 – 0.62
Lt.cap.	0.80 \pm 0.10	0.57 – 1.10	0.77 \pm 0.05	0.58 – 0.93
Alt.par.	0.43 \pm 0.04	0.30 – 0.52	0.42 \pm 0.03	0.29 – 0.51
L.pil.	1.34 \pm 1.58	0.96 – 1.58	1.32 \pm 0.08	1.02 – 1.50
Lt.pil.	0.64 \pm 0.06	0.39 – 0.81	0.63 \pm 0.48	0.48 – 0.78

Note. Means (x), standard deviations (S.D.), and minimum – maximum ranges (min – max) are shown. Estimates are based on 92 male and 127 female individuals. For abbreviations see text.

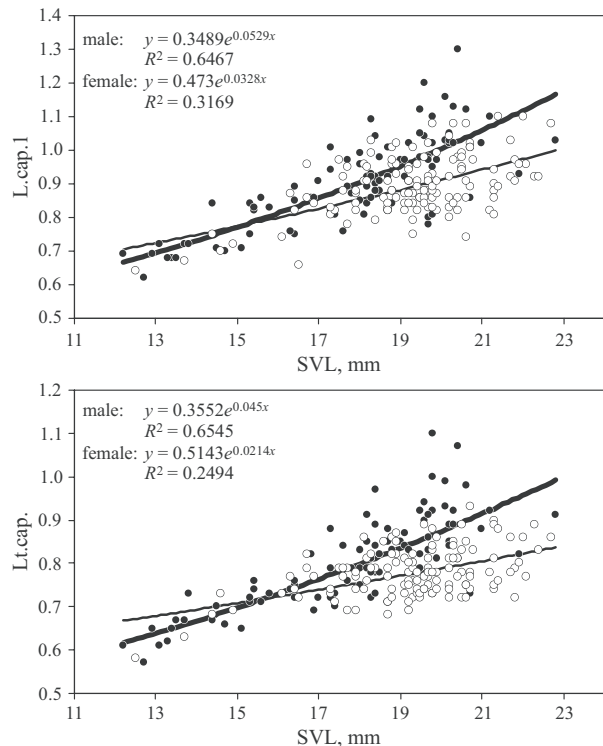


Fig. 2. Relationship of mouth length (L.cap.1; upper) and mouth width (Lt.cap.; lower) to SVL in male (black point and bold regression line) and female (white point and thin regression line) *Anguis fragilis colchica*. The regression lines are fitted on exponential equations.

have provided evidence that sexual dimorphism is related to sexual differences in energy allocation to growth (e.g., Mouton et al., 1999) and differences in food resource partitioning (e.g., Powell and Russell, 1985).

In the studied eastern slow-worm (*A. f. colchica*) population males exhibit larger head size, than females of similar size, a fact that was also previously pointed

TABLE 2. Factor Loadings of Analyzed Morphometric Characters in *Anguis fragilis colchica* on Principal Components 1 and 2

Character	PC 1	PC 2
L.cap.1	-0.854	0.117
L.cap.2	-0.870	-0.293
L.nas.	-0.780	-0.510
Lt.cap.	-0.826	0.268
Alt.par.	-0.754	0.360
L.pil.	-0.888	-0.159
Lt.pil.	-0.765	0.263
Eigenvalue	4.724	0.654
% of variability	67.490	9.392

Note. For abbreviations see text.

out for the species (e.g., Wermuth, 1950; Dely, 1972, 1974, 1981; Günther and Völkl, 1996). At similar growth rate, the head/SVL relationship indicates a disproportionate increase of head size in males and respectively of body size in females, as partially was pointed in literature (e.g., Wermuth, 1950; Dely, 1981). Sexual dimorphism in *A. f. colchica* could result from different selection pressure acting on each sex. Three potential evolutionary mechanisms have been invoked to explain the sexual dimorphism in *A. f. colchica*: (i) sexual selection acting in mate acquisition in both sexes, (ii) ontogenetic change of allometry to improve reproductive output in females, and (iii) natural selection acting in features that reduce food competition between sexes.

Sexual differences in head dimensions have been reported in numerous reptile species (Vitt and Cooper, 1985; Cooper and Vitt, 1989; Thorpe, 1989; Fairbairn, 1997; Gvoždík and Boukal, 1998; Tomović et al., 2002; Baird et al., 2003; Gvoždík and Van Damme, 2003; McCoy et al., 2003). In species with males having larger head size and where male-male combat does occur, this dimorphism has been attributed to sexual selection and the role of head structures in combat bouts (Vitt, 1983). Surprisingly, the occurrence of an aggressive display behavior in *A. fragilis* was relatively recently reported (Malkmus 1995). This was shortly later confirmed by Capula et al. (1998) and interpreted as combat behavior between males in mating period. Their results based on a studies made on an alpine *A. f. fragilis* populations indicated that body sizes of males defeated during combats were always lower than those of the winner (as in other reptile species too, e.g., Luiselli 1993), and respectively the mean length of the males courting and successfully mating with females was significantly higher than the mean length of the male *A. fragilis* occurring in the study area. As suggested by Capula et al. (1998), the access to reproductive females is probably almost monopolized by the larger males in the population, as in such high densities (>80 individuals/ha) the establishment of hierarchical rather than territorial social structures could be favored.

In Capula et al. (1998) only considered the SVL of males and the head size importance in *A. fragilis* male-male combat was not questioned, although during combat males bite each other vigorously and for prolonged times (10 – 30 min or even longer; Capula et al., 1998). It is concluded that differences in head and body size, through their effect on bite force capacity, may affect prey selection, either directly, or via handling efficiency in some species (Verwajen et al., 2002). Thus the musculature of head (thus the force of the jaws) and the jaw size (beside body size and stronghold) in *A. fragilis*

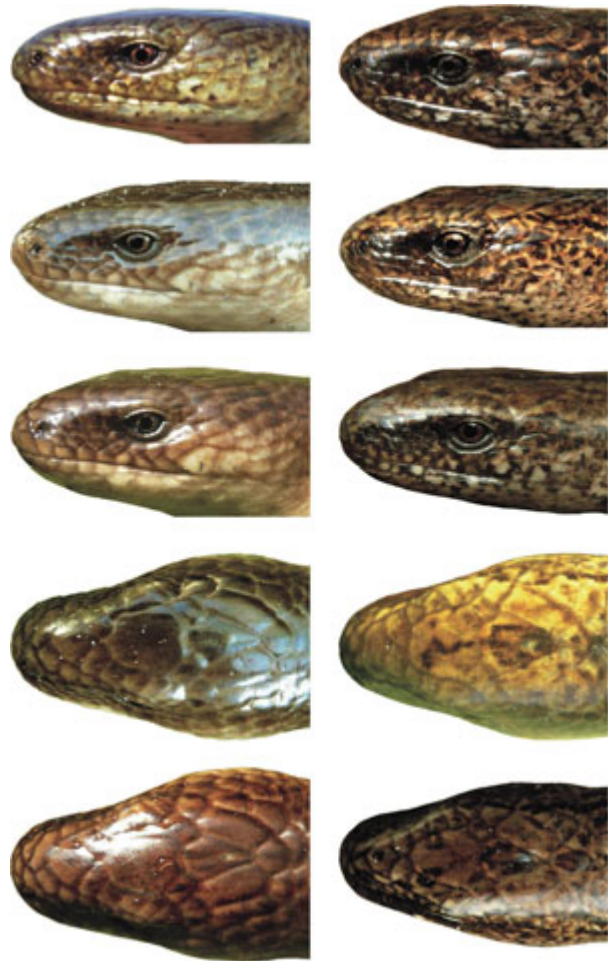


Fig. 3. *Anguis fragilis colchica* samples from Rupea, Romania (first column males, second column females).

probably play an important role in these contests (e.g., see differences in mouth length and width between sexes in Fig. 1). These features are important during mating attempt also, when the male bites the female (usually her anterior body parts, either head or neck) and tries to oppose his vent to that of the female, apparently forcing the mating (as pointed in other species too, e.g., Birkhead et al., 1985). Correspondingly in *Zootoca vivipara* males with larger heads succeeded in grasping a female faster than males with smaller heads. It follows that head size in *Z. vivipara*, and highly probably in *A. fragilis* too, may affect male reproductive success both through intrasexual competition (fighting ability) and through intersexual selection (grasping ability; Gvoždík and Van Damme, 2003). This suggests that sexual selection may be the cause for the sexual dimorphism in head size in these lizard species. The importance of the head size and

jaws power in *A. f. colchica* is increased by the presence of easy recognized bite marks (due its dentition peculiarities) in both sexes far after mating period (Sos, personal observation).

In numerous reptile (especially snake) species exhibiting male-male combat, females attain a larger body size compared to males (e.g., Tomović et al., 2002). Shine (1978) suggested that intrasexual selection did not have result in larger body size in males compared to conspecific females. Larger body size of females could readily be attributable to fecundity selection, since it has been reported that reproductive success of females is depending on body size, with larger females producing larger and/or more frequent litters (Madsen and Shine, 1994), thus females allocate relatively more energy to the growth of reproductively significant morphological characters after reaching maturity than to characters less directly tied to reproductive success (Cooper and Vitt, 1989). *A. fragilis* could be included in this model, as (i) in most cases, in alpine or northern *A. f. fragilis* females reproduce in alternate years (Patterson 1983, Capula et al., 1998) and it seems that female reproductive frequency essentially depends on energy availability (Patterson 1983), and respectively (ii) according to Capula et al. (1992) a positive linear correlation between clutch size and female SVL was found in an alpine population of *A. f. fragilis* population. This model could be reflected in the greater body length attained by adult females in *A. f. colchica* too, selected for ability to increase space in the body cavity for the brood (e.g., Thorpe, 1989), coincident with a reduction in the rate of head-size increase, although studies concerning reproductive pattern in lowland areas are not performed yet. Similar growth particularities have been reported also in one other anguid lizard, *Barisia monticola* (Vial and Stewart, 1989) and in some Western Australian dragon lizards (Agamidae; Thompson and Withers, 2005). According to Thompson and Withers (2005), this inconsistency is problematic when linking morphological characteristics with performance traits, use of space, or preferred habitat for species, and they recommend, in accordance with our opinion, that male and female lizards with similar differentiated growth to be treated separately in morphological analyses. In the subspecies differentiation of *A. fragilis*, the different ratios use in pooled data, without considering the gender (e.g., Grillitsch and Cabela, 1990), is possibly inadequate. However this is untested yet.

In several reptile species (e.g., in *Vipera ammodytes*; Tomović et al., 2002) the females had higher values of head width and the shape of the head as well as the size differed between sexes. These results are in accordance

to inter-sexual dietary divergence theory (Camilleri and Shine, 1990). According to Luiselli et al. (1994), *A. f. fragilis* are rather generalist predators that use several of the most available prey resource (of adequate size) in the environment, as dietary composition are different in different habitats. Thus in *A. fragilis*, a possible resource partitioning, still unquestioned, could be a cause or just the consequence of sexual size differences (Vitt and Cooper, 1985). In concordance, the male *A. fragilis*, due its larger head size, is able to swallow larger food items than a female at similar body size. The fact that, Luiselli et al. (1994) discovered a juvenile *Salamandra atra* in the stomach content of one male *A. f. fragilis*, and respectively, remains of a small mammals was found in an freshly killed large *A. f. colchica* male's carcass in Cheile Râmeșului (Cluj County) in summer 2007 (Sos, personal observation), is not surprising. However in *Lacerta agilis* the high food overlap between sexes do not support the hypothesis that food is a factor forcing the evolution of sexual dimorphism in this species (Gvoždík and Boukal, 1998).

In conclusion, the sexual size differences in *A. fragilis*, according to recent results of the ecology of this species, could be related to the sexual selection for larger head in males because of its potential role in its reproductive behavior, due to the observed combats and copulatory bites in mating period, and respectively to the fecundity selection for larger body size in females, since the reproductive success of females is depending on body size, as larger females give birth to larger and/or higher number of offsprings. According to Capula et al. (1998), in males an intra-sexual selection for larger body size is obvious, as the larger male "always" win in the male-male contests. The existence of sexual differences in use of food resources as consequence of inter-sexual competition, which could be other possible cause of sexual differences in head size in *A. f. colchica* must be questioned in further studies.

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