Short Communication

Allometry of head size and shape dimorphism in the grass snake (*Natrix natrix* L.)

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Abstract: This study was conducted to investigate allometry of head growth patterns in the grass snake (*Natrix natrix* (Linnaeus, 1758)). Although male and female grass snakes differ in relative head size, their head growth patterns follow similar trajectories. The sexual differences are roughly constant during ontogeny. Most head dimensions grow with negative allometry or isometry with respect to the snout–vent length except head width, which grows with positive allometry in both sexes.

Key words: Allometry, morphology, Natricinae, *Natrix*, sexual shape dimorphism

Sexual dimorphism is a common phenomenon in the animal kingdom and has been reported in numerous snake species (see Shine, 1993 for review). In most colubrids (sensu lato) females are the larger sex (Shine, 1994). Body size differences are often accompanied by body shape and scalation differences, e.g., proportionally longer male tails or longer female trunks (Thorpe, 1989; Shine, 1993; Bonnet et al., 1998), and dietary niche divergence that leads to head size and shape sexual dimorphism (Pough and Groves, 1983; Shine, 1986; Camilleri and Shine, 1990; Shine, 1991; Vincent and Herrel, 2007; but also see Luiselli et al., 2002).

In the European grass snake *Natrix natrix*, females tend to be the larger sex (Mertens, 1947; Kminiak and Kaluz, 1983; Madsen, 1983; Feriche et al., 1993; Madsen and Shine, 1993; Mertens, 1995, Gregory, 2004; Borczyk, 2007; Baier and Wiedl, 2010). It makes them more energy-consuming, as maintaining a larger body is energetically expensive. Moreover, the costs of reproduction are higher for females due to the nutritional components needed for developing eggs or embryos. Thus, one can expect females to evolve adaptations enabling them to be more effective in acquiring energy (food). Many researchers have shown that grass snake males and females differ in their food habits; however, in some populations these differences are limited only to prey size, or both prey size and type (Madsen, 1983; Filippi et al., 1996; Luiselli et al., 1997; Gregory and Isaac, 2004), but it is always the females that feed on larger prey. In the case of snakes, the prey size (and thus the prey spectrum) is limited by predator gape size (Arnold, 1993; Cundall and Greene, 2000; but see Jayne et

al., 2002 for the exception of crab-eating snakes), and in the grass snake, these dietary differences are accompanied by relatively bigger heads in females (e.g., Thorpe, 1979; Kabisch, 1999).

As there is female-biased sexual size and head-size dimorphism in the grass snake, an interesting question arises: namely, whether male and female head dimensions follow different allometric trajectories.

Forty-nine grass snakes (26 males and 23 females) from the collection of the Zoological Institute of the Russian Academy of Sciences (St. Petersburg) were measured (see Appendix). The snakes came from the Kalmykia region (Russia). The following dimensions were measured: the snout-to-vent length (SVL), head length (HL), head width (HW), head height (HH), pileus length (PLL), and mandible length (MDBL). SVL was measured to the nearest 1 mm using a string that reached along the midventral surface of the specimen from the snout to the cloaca, and all head dimensions were measured using a digital caliper to the nearest 0.01 mm.

To evaluate the overall pattern of head size and shape variation, a principal component analysis (PCA) was run on a covariance matrix. To evaluate the pattern of head growth, a regression was run on the head dimensions on the SVL. Because measurement error is present in both dependent and independent variables, the ordinary least-squares regression may produce skewed values for the allometry equations (Sokal and Rohlf, 1995). Thus, RMA regression was applied using RMA Software for Reduced Major Axis Regression, v. 1.17 (Bohonak, 2004). The confidence intervals were calculated with 1000 bootstrap

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replications. Deviations from isometry and homogeneity of slopes between the sexes were examined by inspection of the 95% confidence intervals of the slope estimates.

PCA yielded 3 axes (Table 1). ANCOVA with sex and SVL as independent variables and PC1 scores as the dependent variable showed that both sexes statistically differ when controlling for SVL and that females have larger heads ($r^2 = 0.905$, F = 20.556, P < 0.001; Figure). The characters that contribute the most to PC1 are head length and mandible length. Interestingly, the head height has a relatively low contribution to this axis (Table 2). PC2 and

PC3 also show statistically significant differences between the sexes ($r^2 = 0.1$, F = 4.721, P = 0.035 and $r^2 = 0.085$, F = 4.277, P = 0.044); however, they explain so little variation that they may be omitted in further analyses (Table 1).

Table 2 presents the slope parameters calculated for the particular characters. In the case of HL, PLL, and HW, males have higher allometric coefficients compared to females, and the reverse is true for HH and MDBL. The HL in females grows with slightly negative allometry and HW in males grows with positive allometry. Other parameters show similar growth patterns in both sexes with respect

Table 1. Variable loadings for principal component analysis of head length (HL), pileus length (PLL), head width (HW), head height (HH), and mandible length (MDBL) of *Natrix natrix* from the Kalmykia region, Russia; eigenvalues and percentage (%) of variation explained by each of the 3 axes.

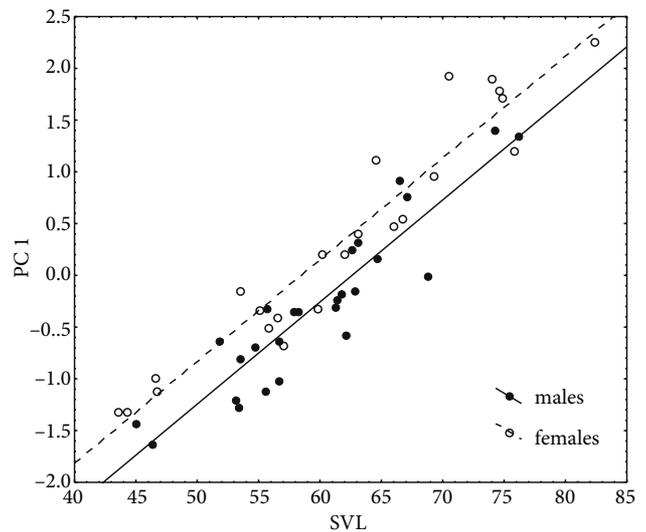|	PC1	PC2	PC3
HL	0.993	−0.025	0.057
PLL	0.894	0.422	−0.149
HW	0.909	−0.253	−0.325
HH	0.841	−0.025	0.387
MDBL	0.983	−0.059	0.146
Eigenvalue	35.344	1.711	1.459
%	90.49	4.38	3.74

Figure. Principal component scores of 5 head dimensions as a function of snout–vent length reveal that female *Natrix natrix* have proportionally bigger heads than males.

Table 2. Intercepts, slopes, and their 95% confidence intervals of RMA regression of head measurements regressed on SVL male (M) and female (F) of grass snakes (*Natrix natrix*).

Character	Sex	*a*	Intercept 95% confidence intervals		*b*	Slope 95% confidence intervals		R²
HL	M	−0.122	−0.442	0.072	0.851	0.743	1.031	0.857
	F	−0.0003	−0.209	0.152	0.792	0.710	0.915	0.911
PLL	M	−0.588	−1.270	0.079	1.047	0.669	1.431	0.714
	F	−0.018	−0.232	0.128	0.728	0.645	0.850	0.913
HW	M	−1.181	−1.703	−0.660	1.311	1.037	1.727	0.729
	F	−0.626	−1.228	−0.239	1.014	0.796	1.348	0.652
HH	M	−0.586	−1.120	−0.220	0.863	0.651	1.169	0.343
	F	−0.695	−0.992	−0.440	0.940	0.798	1.099	0.815
MDBL	M	−0.085	−0.398	0.173	0.814	0.666	0.987	0.797
	F	−0.103	−0.340	0.059	0.842	0.751	0.972	0.916

to the SVL (isometry or negative allometry). Female HW and male HH show relatively low r^2 values (0.652 and 0.343, respectively), which means that these characters are strongly variable in both sexes.

The allometric pattern of head dimensions growth is similar in both sexes, although there are some minor differences. In general, males and females follow similar head growth trajectories and the differences between the sexes are roughly the same through the ontogeny, which corresponds to previous observations (King et al., 1999). However, it has been demonstrated that although the differences between the sexes remain constant during ontogeny, the differences in maximum prey size increase (King, 2002). The only dimension that grows with positive allometry in both sexes is the head width. The head width contributes positively to gape size, and thus allows exploration of a wider prey size range. It also may be possible that a wider head provides more space for jaw musculature, and thus the snake is able to generate a more powerful bite. Grass snakes do not kill the prey by crushing with the jaws as lizards do, or by constriction or envenomation as many other snake species do, but in fact swallow their prey alive. Thus, a strong bite, which improves the snake's ability to hold actively struggling prey, usually anurans with powerful hind limbs (Filippi et al., 1996; Shylakhtin et al., 2005; Najbar and Borczyk, 2012), may be of greater importance for bigger snakes, which as a consequence of their size prey on larger and thus stronger animals. Head width is positively correlated with bite strength in lizards (Herrel et al., 2001; McBrayer, 2004; Lappin et al., 2006); however, as far as I know, there is no bite-force data for colubrid snakes.

The relative head-size dimorphism in snakes seems to be a common phenomenon in snakes, and usually the larger sex also has a relatively larger head, as documented in numerous studies including the genus *Natrix* (Mertens, 1947; Shine, 1993; Mebert, 1996, 2011). However, because of the relatively low number of published studies on the sexual differences in head growth pattern in snakes, it is hard to make generalizations. In some snake species, males and females follow the same allometric pattern and the differences between them are constant, regardless of the presence and direction of sexual size dimorphism (Forsman, 1991; Vincent et al., 2004a, 2004b; Elgee and Blouin-Demers, 2011), but in other cases there are some differences (Luiselli et al., 2002). More results regarding species with both male- and female-biased sexual dimorphism covering a wide taxonomical range are needed to make more general conclusions possible and to test the ideas about parallel or independent evolution of such dimorphism.

Appendix
Measured specimens (ZIN: Zoological Institute, Russian Academy of Sciences). Males: 13513.3-4, 14648.1, 21187.1-6, 8-9, 21188.1, 3-4, 9, 21189.1, 5, 8, 12, 21703/p-2908, 23237, 24325, 24327, 24328, 24329; Females: 4045, 10312, 21185.2-5, 21187,7, 21189.6-7, 9, 11, 13, 21188.1-2, 8, 21703/p-2906, p-2909, 23043.1, 2, 24326, 24330, 24331, 24332.

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