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Sexual dimorphism and allometry in the head and body size of two viperid snakes (genus *Vipera*)

Bartosz Borczyk [1,*], Przemysław Puszkiewicz [1] & Stanisław Bury [2,3]

[1]Department of Evolutionary Biology and Conservation of Vertebrates, University of Wrocław, Poland.
[2]Department of Comparative Anatomy, Institute of Zoology and Biomedical Research, Jagiellonian University Gronostajowa 9, 30-387 Cracow, Poland.
[3]NATRIX Herpetological Association, Opolska 41/1, 52-010 Wrocław, Poland.

[*]Corresponding author: bartosz.borczyk@uwr.edu.pl

Abstract. Sexual dimorphism in the size and shape of the body and head is the result of manifold selective pressures acting on organisms. In snakes, sexual size dimorphism is common and has been well-studied. However, intersexual differences in relative head size and shape have attracted far less attention. Similarly, the allometric properties of head shape and size in snakes are poorly known. Here, we analyse sexual dimorphism in two viperid species: European adder *Vipera berus* (Linnaeus, 1758) and Steppe viper *Vipera renardi* (Christoph, 1861). We measured body length, tail length and several head characteristics: head length, head width, head height, pileus length, interorbital distance and internarial distance. Our findings were that males and females of both species did not differ in body length (SVL), but that males tended to have significantly longer tails; there were also significant differences in head characteristics – males tended to have higher heads, and larger internarial and interorbital distances. The head dimensions displayed negative allometry when compared against SVL but when scaled against head length, dimensions like head height and head width exhibited positive allometry. We argue that these differences may be related to sexual selection and that the wider heads may also serve as antipredatory signal.

Keywords. Allometry, head size, head shape, morphology, sexual dimorphism.

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Introduction

Body size and shape are a result of the various selective pressures acting on organisms (e.g., Kozłowski 1992; Shine 1994). They greatly influence fundamental fitness-relevant traits, including metabolic rate, feeding performance, reproductive output, vulnerability towards predation risks and many others (e.g., Greene 1997). For example, selection for increased fecundity may favour a large abdomen in females, since larger individuals may produce more offspring (Bonnet *et al*. 2000). Pressure for feeding niche separation between males and females may lead to significant changes in overall body size and feeding structures (e.g., Camileri & Shine 1990; Shine 1991; Tomović *et al*. 2002; Borczyk 2015). Sexual

selection may favour males that are more intensively coloured, and which have larger bodies if male-male combat occurs or to enhance their mobility (Shine 1993, 1994). Apart from sexual selection, body size influences the ecology of individuals because the growth rate, food intake, energy reserve storage, defensive behaviour (e.g., flight vs fight), heat budget and other traits depend heavily on size (e.g., Cliburn 1976; Gibson & Falls 1979; Seigel & Ford 1987; Bonnet *et al*. 2000; Madsen & Shine 2002; Iraeta *et al*. 2006; Bury *et al*. 2020; Bury 2021). In snakes, interspecific variations in body size and shape are obvious and can reach extreme magnitudes, with snout-to-vent lengths ranging from ca 10 cm in *Leptotyphlops carlae* (Hedges 2008) to > 5 m in some pythons and boids (Greene 1997). However, variation at the intraspecific scale may be no less considerable, and the most striking examples of such within-species variation in both size and shape are found in sexual dimorphism (e.g., Darwin 1871). One of the most pronounced aspects of intersexual variation is size dimorphism (SSD) (Shine 1994).

Snakes are exceptional with regard to SSD, as such variation exists in the majority of species (Shine 1978, 1993, 1994). It can be directed into different trajectories: in many species SSD is female-biased, in others it is male-biased, and in yet others it may vary between populations (Bury & Zając 2020). SSD in snakes often reaches extreme magnitudes, with up to more than 2-fold differences between males and females in length and 10-fold differences in weight, e.g., in the carpet python (*Morelia spilota imbricata*) (Pearson *et al*. 2002). Several environmental pressures, not mutually exclusive, are proposed to play a major role in shaping SSD. Female-biased SSD is often linked directly with reproductive success, i.e., fecundity selection, as female size is positively correlated with fecundity, whereas male-biased SSD is attributed to sexual selection in favour of larger males in species with male-male combats (Shine 1978, 1993, 1994).

Head shape differences are mostly attributed to cranial morphology and are proposed to be driven by intersexual niche divergence associated with different diets. Trophic divergence and corresponding variations in head shape have been reported for many snake species, e.g., *Laticauda colubrina* (Shetty & Shine 2002), *Agkistrodon piscivorus* (Vincent *et al*. 2004) and *Tomodon dorsatus* (Loebens 2019). Less well recognised is the variation in head shape and head structures associated with sexual selection. The head bears structures critical for mate searching and recognition, namely, the eyes and olfactory structures. Faiman *et al*. (2018) found male-biased eye size dimorphism in viperid snakes but the reverse trend in colubrid species. In snakes, olfactory signals are believed to be primary cues in sexual behaviour, especially of males (Andrén 1982). This is reflected in the tongue, which is relatively longer and more deeply bifurcated in males (Smith *et al*. 2008) and may be associated with further modification of the head, i.e., with males having a relatively wider rostral region (bearing the olfactory structures). However, the question of sexual dimorphism in reproduction-related head dimensions is underrepresented in published studies (Saint-Girons 1957; Steward 1971; Forsman 1991a), although subtle intersexual differences have been recently reported in nasal bones in *Natrix* species (Andjelković *et al*. 2016), and in the nasal and orbital regions in two elapid species – *Aipysurus eydouxii* (Borczyk *et al*. 2021) and *Laticauda colubrina* (Borczyk 2023).

Besides the degree of sexual dimorphism (or its absence), the interesting question arises as to whether it is a product of an allometric growth pattern or whether it is manifested if both sexes follow similar (isometric) growth trajectories. For example, in some snake species, the tail grows isometrically with respect to the snout-to-vent length (SVL) in males, but with negative allometry in females, whereas in other species the reverse may be true: relative head size differences may increase with body size or be constant (Borczyk 2015), etc. Hence, the rich diversity of patterns of sexual dimorphism and growth in snakes.

Here, we investigate the patterns of sexual dimorphism in a suite of size-related traits, together with possible allometric relationships among them, with the focus on head-size variables. For our models, we selected two widely distributed viperid snake species: the adder (*Vipera berus*) and the steppe viper (*Vipera renardi*). SSD has been described in the former (e.g., Madsen & Shine 1993; Forsman 1991b; Gentilli *et al*. 2006) but not in the latter. We analyse sexual dimorphism and allometry in *Vipera berus*

and *V. renardi* based on linear measurements in order to address the following questions: (i) Do males and females differ in head proportions; specifically, do females have relatively larger heads, and do males have wider internarial distances? (ii) Does the pattern of sexual dimorphism differ between these species? (iii) Do intra- and interspecific differences result from different growth trajectories (growth allometry) or are they "set" (static allometry)?

Material and methods

Material

We measured 41 specimens of the European adder (henceforth: adder) from the collections of the Museum of Natural History of the University of Wrocław (MNHW, unnumbered specimens) (19 males and 22 females) and 38 steppe vipers from the Zoological Institute of the Russian Academy of Sciences in St Petersburg (ZIN – 20 males and 18 females) (*Vipera renardi* females: ZIN 19016/1, ZIN 19016/2, ZIN 19016/3, ZIN 19016/4, ZIN 25882, ZIN 25883, ZIN 25884, ZIN 21669/114, ZIN 21139/1, ZIN 21139/3, ZIN 21669/115, ZIN 21669/113, ZIN 22457/9, ZIN 22457/7, ZIN 22457/6, ZIN 22457/2, ZIN 21955-105, ZIN 21955-104; *Vipera renardi* males: ZIN 19016/5, ZIN 19016/6, ZIN 19016/7, ZIN 19016/8, ZIN 19061/9, ZIN 21139/2, ZIN 21139/4, ZIN 21139/5, ZIN 25880, ZIN 25881, ZIN 25885, ZIN 21669/116, ZIN 21669/117, ZIN 21669/118, ZIN 22457/8, ZIN 22457/5, ZIN 22457/3, ZIN 21955-106, ZIN 22457/1, ZIN 2212). The adders came from Lower Silesia (SW Poland), whereas the steppe vipers were collected in the Altay mountains. No live snakes were killed for this study.

Measurements

We measured the following parameters: snout-to-vent length (SVL), tail length (TL), head length (HL), head width (HW) and head height (HH), pileus length (PIL), internarial distance (INS) and interorbital

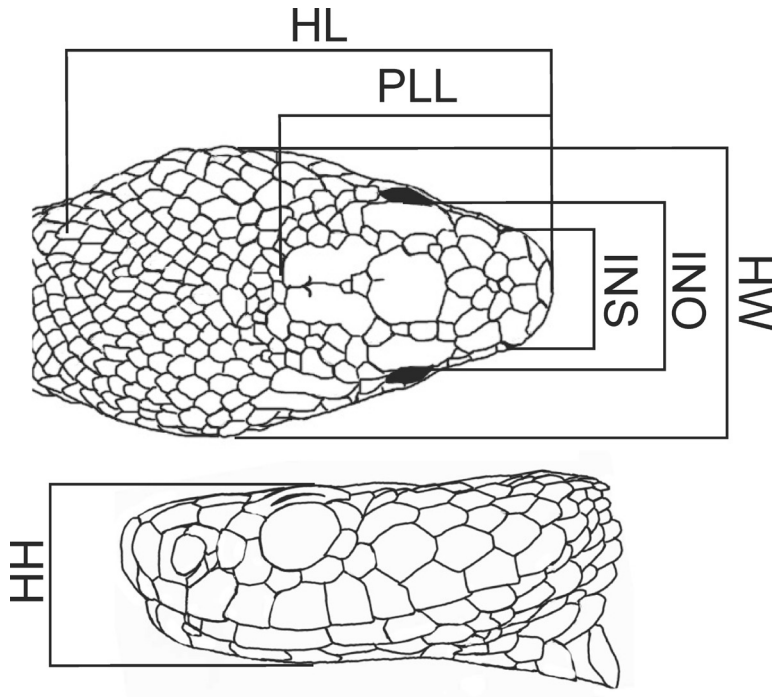


Figure 1 – Dorsal and lateral views of the head of *Vipera berus* showing the dimensions. Abbreviations: HL = head length; HW = head width; HH = head height; INS = internarial distance; INO = interorbital distance.

distance (INO) (Fig. 1). All the head measurements were made to an accuracy of 0.1 mm with digital callipers. SVL and TL were measured using string to the nearest 1 mm.

Data analysis

Sexual dimorphism in SVL and HL was analysed using the Mann-Whitney *U* test. This test was used because the distribution of SVL for *V. renardi* males did not meet the assumption of a parametric test. To evaluate the overall pattern of head size and shape variation, we ran a multivariate analysis of covariance (MANCOVA) for each of the measured characteristics, with sex as predicting variable, and SVL and HL as covariates. We used two different covariates because SVL is the sexually dimorphic distance, and scaling head characteristics against SLV may often produce skewed results (see KRATOCHVIL *et al*. 2003; BORCZYK *et al*. 2014). Prior to the analyses, we log-transformed the data in order to achieve linear relationships. We also investigated whether the samples were normally distributed, and whether the homogeneity of the slopes and variances validated the test assumptions. All the analyses were done using SPSS Statistics 20.0.0 software.

To determine whether the differences between the sexes stemmed from an allometric growth pattern or were set and constant during ontogeny, we scaled the head measurements and tail lengths against SVL, and the head measurements against HL, using two base lines, as described above. Because both dependent and independent variables are subject to measurement errors, we employed Reduced Major Axis Regression (RMA) to determine the allometric equation (SOKAL & ROHLF 1995), using RMA for JAVA ver. 1.21 software by BOHONAK & VAN DER LINDE (2004), and producing the graphs wi SPSS software. We compared the slopes to values of 1 to determine isometry or allometry in the growth pattern.

One specimen of *V. renardi* (with a broken tail) was omitted from the analysis of the TL-SVL relationships, and two males of *V. berus* and one of *V. renardi* were excluded because the positions of the jaws in the preserved specimens hampered the precise measurement of HH.

Results

Body and head size

Females of *V. berus* tended to be larger than males, although this difference was not statistically significant (Mann-Whitney *U* test, $p = 0.214$) (Table 1).

MANCOVA showed that sexual dimorphism in head dimensions was manifested in both species when corrected to both SVL and HL (Table 2).

Closer examination revealed that when scaled against SVL or HL, the sexually dimorphic characteristics for *Vipera berus* were TL (SVL covariate $F = 17.699$ $p < 0.001$; HL covariate $F = 16.039$, $p < 0.001$), HH (SVL covariate $F = 4.722$, $p = 0.036$, HL covariate $F = 5.646$, $p = 0.023$), INS (SVL covariate $F = 6.386$, $p = 0.016$, HL $F = 7.862$ covariate $p = 0.008$) and INO (SVL covariate $F = 4.743$, $p = 0.036$, HL covariate $F = 5.028$, $p = 0.031$). In *V. renardi* the sexually dimorphic trait was TL (SVL covariate $F = 115.647$, $p < 0.001$; HL covariate $F = 90.683$, $p < 0.001$). However, two distances – INS and HH – exhibited no clear pattern in *V. renardi*. When analysed with SVL as a covariate, INS differed at $F = 4.08$, $p = 0.035$, but when HL was the covariate, the differences in INS were not significant ($F = 3.481$, $p = 0.071$). Head height was not statistically significantly different when SVL was the covariate ($F = 0.417$, $p = 0.417$), but when HL was used, the difference in HH was not significant at $F = 4.099$, $p = 0.051$.

TABLE 1

Morphological characteristics of males and females of *Vipera berus* and *V. renardi*. All measurements are given in mm. Abbreviations: HH = head height; HL = head length; HW = head width; INO = interorbital distance; INS = internarial distance; PLL = pileus length; SVL = snout-to-vent length; TL = tail length.

	***V. berus* females**		***V. berus* males**		***V. renardi* females**		***V. renardi* males**	
	N	**Mean±SD**	**N**	**Mean±SD**	**N**	**Mean±SD**	**N**	**Mean±SD**
SVL	22	421.9±121.97	19	400.58±72.12	18	357.67±119.68	20	356.3±80.17
TL	22	53.00±16.37	19	62.95±12.61	18	37.00±12.13	20	46.4±15.04
HL	22	20.34±3.53	19	20.07±2.40	18	18.95±4.08	20	19.46±2.86
HW	22	13.14±2.71	19	12.85±2.02	18	12.69±3.35	20	12.24±1.86
HH	22	7.57±1.48	17	7.89±1.15	18	7.19±1.66	19	7.05±1.02
INS	22	4.78±0.87	19	4.96±0.71	18	4.15±0.83	20	4.4±0.55
INO	22	7.65±1.26	19	7.89±1.1	18	7.38±1.3	20	7.53±1.2
PLL	22	12.26±2.02	19	12.49±1.65	18	11.6±2.54	20	12.04±1.7

TABLE 2

Summary of MANCOVA analyses for sexual dimorphism in *Vipera berus* and *V. renardi*. Head length (HL) is included in the analyses with snout-vent length (SVL) as covariate.

species	**covariate**	**Wilks's λ**	**F**	**df**	**p**
V. berus	SVL	0.573	3.189	7	0.012
	HL	0.645	2.844	6	0.025
V. renardi	SVL	0.169	19.001	7	<0.001
	HL	0.236	15.092	6	<0.001

Allometry

The head dimensions were scaled with negative allometry (compared with the slopes predicted by a model of geometric similarity) with respect to SVL in both species. However, when HL was used as covariate, the remaining head dimensions displayed isometry or positive allometry. In other words, larger snakes had relatively smaller heads (in relation to SVL), but heads became relatively wider and higher in relation to HL. Moreover, in *V. berus*, males usually had steeper slopes than females when scaled against HL, whereas the opposite pattern prevailed in *V. renardi*. The tail growth patterns differed between the two species. In *V. berus*, the tail grew with positive allometry with respect to SVL and the slope was markedly steeper in females. This means that although males have relatively longer tails, the differences between the sexes decrease as the animals grow larger. In the steppe viper, the tail growth pattern was isometric with respect to SVL in both sexes; thus, the tail-to-SVL ratio was constant (Tables 3– 4, Fig. 2).

Discussion

Sexual dimorphism

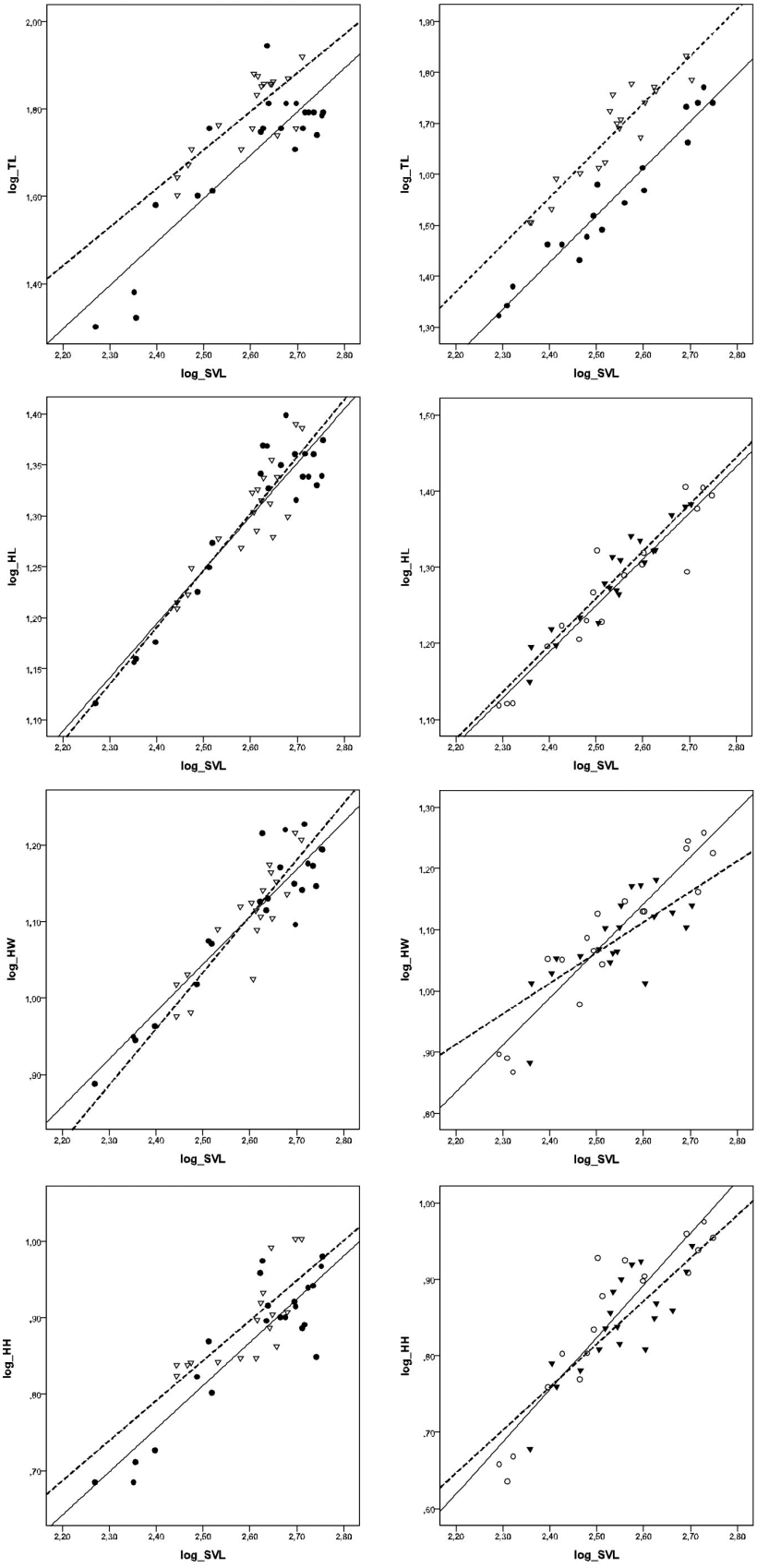
Males of *V. berus* males tend to have a bigger head height than females. This characteristic is rarely considered in studies of snake sexual dimorphism (e.g., SCALI & GENTILLI 1998; GENTILLI *et al*. 2006; TOMOVIĆ 2002). A few studies reported similar though non-significant differences, e.g., in *V. ursinii* (STRUGARIU *et al*. 2011), but sample sizes were extremely small – only six adult males and six adult females were examined. Although the feeding structures in snakes, and the head as a whole, are thought

TABLE 3

Intercepts, slopes and 95% confidence intervals of RMA-regression of head and tail measurements regressed on SVL or HL of male and female *Vipera berus*. Abbreviations: HH = head height; HL = head length; HW = head width; INS = internarial distance; INO = interorbital distance; PLL = pileus length; TL = tail length.

		Intercept	95% confidence intervals		Slope	95% confidence intervals		r^2
Baseline: SVL								
HH	F	-0.7741	-1.117	-0.4316	0.6314	0.5001	0.7627	0.8011
	M	-0.868	-1.485	-0.2514	0.6789	0.4414	0.9165	0.5957
HL	F	-0.1637	-0.4034	-0.07597	0.5627	0.4707	0.6546	0.8774
	M	-0.3214	-0.6934	-0.05063	0.6246	0.4813	0.7678	0.7991
HW	F	-0.6291	-0.9261	-0.3322	0.6674	0.5535	0.7812	0.8662
	M	-1.069	-1.595	-0.5429	0.8371	0.6345	1.04	0.7762
INS	F	-0.8595	-1.11	-0.609	0.5881	0.4921	0.6842	0.8774
	M	-1.268	-1.745	-0.7903	0.7547	0.5709	0.9385	0.7735
INO	F	-0.5093	-0.5708	0.2677	0.5326	0.4399	0.6252	0.8609
	M	-1.044	-1.473	-0.6151	0.7464	0.5812	0.9116	0.8129
TL	F	-1.265	-1.938	-0.5917	1.138	0.8798	1.396	0.7635
	M	-1.067	-1.94	-0.1933	1.101	0.7644	1.437	0.6434
PLL	F	-0.2683	-0.5773	-0.04083	0.5187	0.4002	0.6373	0.7601
	M	-0.6984	-1.226	-0.1705	0.6903	0.487	0.8936	0.6687
Baseline: HL								
HH	F	-0.5904	-0.8646	-0.3162	1.122	0.9119	1.332	0.8386
	M	-0.5251	-0.9043	-0.146	1.093	0.8009	1.385	0.7645
HW	F	-0.435	-0.6261	-0.2438	1.186	1.039	1.333	0.9298
	M	-0.6383	-1.093	-0.1834	1.34	0.9905	1.69	0.7399
INS	F	-0.6884	-0.882	-0.4948	1.045	0.8968	1.194	0.9073
	M	-0.8702	-1.188	-0.5701	1.208	0.9707	1.446	0.8522
INO	F	-0.3543	-0.5239	-0.1847	0.9465	0.8165	1.077	0.9132
	M	-0.6601	-1.033	-0.2875	1.195	0.9087	1.481	0.7806
PLL	F	-0.1173	-0.291	-0.05639	0.9219	0.7887	1.055	0.904
	M	-0.3432	-0.699	0.01254	1.105	0.8316	1.379	0.7661

Figure 2 (next page) – Relationships between log-transformed SVL and log-transformed tail length (TL), head length (HL), head width (HW) and head height (HH) in *Vipera berus* and *V. renardi*; males (black triangles, dashed line) and females (open circles, solid line).



V. berus *V. renardii*

TABLE 4

Intercepts, slopes and 95% confidence intervals of RMA-regression of head and tail measurements regressed on SVL or HL of male and female *Vipera renardi*. Abbreviations: HH = head height; HL = head length; HW = head width; INS = internarial distance; INO = interorbital distance; PLL = pileus length; TL = tail length.

		Intercept	95% confidence intervals		Slope	95% confidence intervals		r^2
Baseline: SVL								
HH	F	-1.021	-1.394	-0.6483	0.7375	0.5903	0.8847	0.8581
	M	-0.9292	-1.462	-0.396	0.6952	0.4862	0.9401	0.655
HL	F	-0.3532	-0.6262	-0.0802	0.6407	0.533	0.7485	0.8994
	M	-0.3576	-0.6039	-0.1113	0.6463	0.5494	0.7431	0.9084
HW	F	-0.8937	-1.36	-0.6075	0.8189	0.6704	0.9674	0.883
	M	-0.6863	-1.297	-0.07594	0.6961	0.4561	0.9362	0.5152
INS	F	-0.9152	-1.173	-0.6575	0.6025	0.5008	0.7041	0.8986
	M	-0.8154	-1.191	-0.4398	0.5728	0.4251	0.7205	0.7288
INO	F	-0.4904	-0.7461	-0.2346	0.5344	0.4334	0.6353	0.873
	M	-1.17	-1.713	-0.6272	0.803	0.5895	1.016	0.7117
TL	F	-0.8536	-1.153	-0.554	0.9487	0.8305	1.067	0.9447
	M	-0.845	-1.32	-0.37	0.9956	0.8083	1.183	0.8649
PLL	F	-0.6194	-1.044	-0.1948	0.6615	0.4939	0.829	0.7715
	M	-0.5376	-0.9382	-0.137	0.6351	0.4775	0.7926	0.7491
Baseline: HL								
HH	F	-0.6149	-0.8431	-0.3867	1.151	0.9715	1.331	0.9134
	M	-0.4859	-0.7753	-0.1965	1.031	0.8071	1.256	0.8194
HW	F	-0.5323	-0.8357	-0.2289	1.278	1.039	1.517	0.8758
	M	-0.301	-0.7373	0.1352	1.077	0.738	1.416	0.5956
INS	F	-0.5831	-0.7209	-0.4453	0.9402	0.8318	1.049	0.9527
	M	-0.4984	-0.7436	-0.2532	0.8864	0.6958	1.077	0.8114
INO	F	-0.1958	-0.3394	-0.05218	0.834	0.721	0.947	0.9347
	M	-0.7258	-1.191	-0.2607	1.243	0.881	1.604	0.6546
PLL	F	-0.2548	-0.583	0.07343	1.032	0.7741	1.29	0.7773
	M	-0.1862	-0.409	0.1191	0.9827	0.7453	1.22	0.8732

to be rarely used in sexual interaction (SHINE 1991), a growing number of studies reported relative size and shape differences between males and females (e.g., ANDJELKOVIĆ 2016; TAMAGANINI *et al*. 2018). There are several possible explanations for this pattern of dimorphism. It is possible that the bigger HH in males may be a side effect of hormone activity and not an adaptive, sexually selected characteristic (see also CAMILLERI & SHINE 1990; MURTA-FONSECA *et al*. 2019). It may also reflect a possible sexual role of head dimorphism.

The head houses the central nervous system and sensory organs. Chemosensory cues play an important role in mate searching and recognition (e.g., ANDRÉN 1982; see the next paragraph). Moreover, visual cues are involved in reproductive behaviour, at least in some snake species (SHINE 2005), and in several there is dimorphism in relative eye size, being male-biased in viperids (FAIMAN *et al*. 2018). Thus, the differences in sensory structures may be reflected in the skull bones supporting these structures (and thus affecting the head shape). Sexual dimorphism in the skull bones supporting the eyes and nasal region (housing chemosensory structures) exists in at least some snake species (ANDJELKOVIĆ *et al*. 2016; BORCZYK *et al*. 2021; BORCZYK 2023).

Variation in internarial distance has rarely been studied in the context of male-female differences in snakes. Recent studies of head-shape dimorphism have completely ignored this distance (e.g., HENAO-DUQUE & CEBALLOS 2013; LÓPEZ *et al*. 2013; TAMAGNINI *et al*. 2018). However, ANDJELKOVIĆ *et al*. (2016) reported sexual differences in the nasal bones in the genus *Natrix*, and BORCZYK *et al*. (2021) and BORCZYK (2023) reported some dimorphism in this region in *Aipysurus eydouxii* and *Laticauda colubrina*, respectively. Our findings show that males of *V. berus* and *V. renardi* have a relatively wider inter-nostril distance. Taking into account the observations of ANDJELKOVIĆ *et al*. (2016), BORCZYK *et al*. (2021) and BORCZYK (2023), we assume that this characteristic may also be dimorphic in other species and suggest that such variation may be linked to the chemosensory system in snakes. Males rely strongly on olfactory cues (ANDRÉN 1982), so the olfactory bulbs, and also the vomeronasal organ, which is involved in pheromone detection, may be better developed, thus making mate searching more effective. This hypothesis is indirectly supported by the sexual dimorphism of the tongue fork, as reported by SMITH *et al*. (2008) in the viperid *Agkistrodon contortrix*. In this case, the tongue in males is longer and more deeply bifurcated than the female one, which clearly improves their mate-searching efficiency. Such dimorphism may be paralleled by skull structures involved in chemosensory perception. We encourage further studies on sexual dimorphism in viperids and other snakes, which should include this variable.

Female *Vipera* snakes are generally larger than males (MADSEN 1988; FORSMAN 1991b; NILSON & ANDREN 2001; TOMOVIĆ *et al.* 2002; STRUGARIU & ZAMFIRESCU 2011), but in some populations there is either no size dimorphism (e.g., STRUGARIU *et al*. 2011) or dimorphism is male-biased (TOMOVIĆ *et al*. 2009; GENTILLI *et al*. 2006). We detected no SSD in *V. renardi* and *V. berus* in our samples. First of all, the magnitude of dimorphism can vary in relation to locally available food resources, sometimes reducing the differences between males and females (FORSMAN 1991b). Secondly, the operational sex ratio in the adder fluctuates (MADSEN & SHINE 1993), which means that the range of size differences among males and females may also fluctuate as an outcome of differential competition among males. More specifically, in years when females are underrepresented, competition among males is more intense, which favours a larger male size and thus reduces sex-specific differences in body size (MADSEN & SHINE 1993).

The patterns in tail length are quite uniform among snakes, with males of most species having proportionally longer tails (e.g., KING 1989; SHINE 1993; KING *et al*. 1999; SHINE *et al*. 1999; BORCZYK 2015). This aspect has frequently been explained by the presence of copulatory organs (the "morphological constraint" hypothesis), its role in mating behaviour (KING 1989; SHINE *et al*. 1999) or as a result of different roles in reproduction and energy allocation, i.e., females investing more in body elongation and thus in litter size and number (BONNET *et al*. 1998). These hypotheses are not mutually exclusive, however; in the case of viperids, we would not advocate for the selective factor related to mating behaviour, as male-male interactions in this group do not involve tail-wrestling. Nevertheless, tail length may play a role in copulation, during which a male may use his tail to stabilize his position.

Allometry

In both species, the head dimensions scaled with negative allometry with respect to SVL. In other words, larger snakes have relatively smaller heads, a general trend observed in snakes and other vertebrates (e.g., López *et al*. 2013; Borczyk 2015). However, when scaling head dimensions to HL, head width and head height scaled with positive allometry. In contrast, Tamagnini *et al*. (2018) reported a lack of such allometries in the adder head. The increase in head height and width relative to head length may result from several, not mutually exclusive, factors. Firstly, the head width is the sum of the skull width and the length of the lateral projection of the quadrate bones (plus soft tissues and skin layers). The quadrate length strongly contributes to the gape size in viperids (Hampton & Moon 2013), and in many other species it shows positive allometry with respect to skull length (Borczyk 2023); moreover, its elongation may enhance snake feeding performance. Furthermore, in many snake species there is a shift in the preferred prey during ontogeny (from small cylindrical, usually reptilian, prey to bulky mammalian and avian prey), which may be reflected by a complete 'switch' to a new category of prey or else by the inclusion of a new prey type in addition to the previous one after some threshold size has been attained (Arnold 1993; Vincent *et al.* 2007; López *et al*. 2013). Thus, there may be selective pressure underlying the positive allometry of snake head width related to feeding performance. Secondly, as shown by Valkonen *et al*. (2011), the triangular head shape, typical for vipers, can act as a warning signal to predators and is an important factor in reducing predator attacks. Thus, the relative increase in head width in relation to head length (i.e., the head becomes more nearly triangular) may be an antipredatory tactic, and the strength of such a signal may increase with snake size (Niskansen & Mappes 2005). Although feeding performance and aposematic signals are unrelated to each other, both may exert selective pressure acting in the same direction. Finally, apart from feeding performance and aposematic signals, a larger (wider and higher) head provides more space for the venom glands and jaw musculature, which may be yet another selective force mediating head shape ontogeny. However, although jaw adductors scale with positive allometry in relation to snake mass (Vincent *et al*. 2007), the pattern of gland growth remains understudied.

Conclusions

Both *V. renardi* and *V. berus* exhibit a distinct sexual dimorphism in head size and tail length. Although the patterns of sexual dimorphism in the two species are similar, the growth patterns of these characteristics reveal both inter- and intraspecific differences. There are intersexual male-biased differences in the snake head characteristics possibly related to perception (chemosensory and visual). Nevertheless, further studies on sexual dimorphism in viperids and other snakes including this variable are needed.

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