

A review of sexual dimorphism of eye size in Colubroidea snakes

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Abstract

Eye size is interesting in snakes because in most species body length differs between the sexes, while the eye's performance depends on its absolute size. So, does the smaller sex see less well? We hypothesized that eye sexual mensural dimorphism (SMD) would be smaller than Body SMD. We found among 26 snake populations that body length SMD was female biased in 47.6% and male biased in 38.1% of samples. Often the larger sex's head was further enlarged but the SMD of absolute eye size was mitigated or annulled by the smaller sex's eye being enlarged within the head, and the head enlarged relative to the body. Overall generally the SMD of eye size was smaller than body SMD. This accords with a hypothesis that eye size affects the evolution of head size and its SMD, both reflecting and emphasizing that absolute eye size is functionally important. Although Colubridae exceed Viperidae in length, Viperidae have larger eyes in absolute terms. In Colubridae the females have larger eyes and in Viperidae the males have larger eyes. Additionally we examine to what extent SMD in different characters is correlated, and briefly review other aspects of SMD, including some aspects of RENSCH's rule.

Key words

Colubridae, Head size, Prey size, RENSCH's rule, Reproductive success, Reptiles, Resource partitioning, Sexual size dimorphism, Sight, Viperidae.

Introduction

Sexual size dimorphism (SSD) is widespread in animals (REISS, 1989; FAIRBAIRN, 1997) and the ophidian body length is easily measured (KOPSTEIN, 1941; FITCH, 1981; MADSEN, 1983; GREGORY, 2004; COX, BUTLER & JOHN-ALDER, 2007). In Colubroidea (LEE & SCANLON, 2002;

FIGUEROA *et al.*, 2016) mostly the females are larger than the males (GREENE, 1997). In Fitch's (1981) review, females were larger in 63.5% of 278 taxa; their length ranged from < 80% to > 130% of male length (female-to-male ratio, FMR).

Dedicated to Dr. FRANCK JOSEPH DOUIEB, Enaim Medical Center, Jerusalem, who deftly resurrected one of our eyes.

Beyond SSD, snake sexual mensural dimorphism (SMD) occurs in tail length (KLAUBER, 1943; WERNER *et al.*, 1999) and head size (SHINE *et al.*, 1996a; WERNER *et al.*, 1999; Shine & Wall, 2007). Tail length and other sexual dimorphism in snakes remain outside our scope.

Eye size has usually been ignored, despite the interest in eye anatomy with regards to the evolution of the snakes (CAPRETTE *et al.*, 2004) and despite the precedent of eye-size SMD in urodeles (MÖLLER, 1950). But the dependence of the eye's performance (resolution and sensitivity) on its absolute size (WALLS, 1942; HOWLAND, MEROLA & BASARAB, 2004; NUMMELA *et al.*, 2013) raises a question: does the smaller sex see less well? Hypothetically, the smaller sex might (1) maintain isometry and have smaller eyes and poorer eyesight; or (2) its eyes could have the same absolute size as in the larger sex, being larger in percents of rostrum-anus length (PERCRA – Werner, 1971). For this, its head could either (2a) be relatively larger, retaining isometric architecture, or (2b) the eyes could be allometrically larger within the head.

These hypotheses were tested by WERNER & SEIFAN (2006) in gekkonoid lizards (HAN, ZHOU & BAUER 2004) whose eyelids, too, comprise a transparent spectacle (BELLAIRS, 1948; HILLER, REHOREK & WERNER, 2007), facilitating eye measurement. In four of those species with the male larger, its absolute eye size, too, exceeded the female's (hypothesis 1). In three of these, relative eye size (PERCRA) was equal in the two sexes (still fitting hypothesis 1). However, in *Gekko gecko* the females' eyes were larger in PERCRA (hypothesis 2); and so was also their eye size relative to head length (HdL) (hypothesis 2b). This was the only species in which eye size relative to HdL showed SMD.

Similarly, in three of the gecko species with males the smaller sex, their absolute eye size, too, appeared smaller than the females' (hypothesis 1). In two of these, eye size in PERCRA lacked sexual dimorphism (again fitting hypothesis 1). Only in *Stenodactylus doriae* did the males' eyes seem larger in PERCRA than the females'; but eye size relative to HdL was equal in the two sexes (hypothesis 2a).

For snakes the data are heterogeneous. There is no eye-size sexual dimorphism in seven viperid species (DULLEMEIJER, 1969) nor in the colubrid *Thelotornis capensis* (SHINE *et al.*, 1996b). Among 33 Malaysian species, eye-size sexual dimorphism occurs only in *Dendrelaphis pictus* in which the male, the smaller sex with smaller head, has larger eyes in absolute terms (MERTENS, 1937; KOPSTEIN, 1941); compatible with hypothesis 2b and "overshooting". Similar is the case of *Bothrops moojeni* (LELOUP, 1975). Yet in *Crotaphopeltis hotamboeia* the smaller male maintains head isometry and has absolutely smaller eyes (hypothesis 1; KEOGH, BRANCH & SHINE, 2000). Extraordinarily, in *Mehelya* sp. (Colubridae), the female is the larger sex, its head further enlarged, within it the eyes enlarged, significantly surpassing the male's in absolute size (SHINE *et al.*, 1996a). This deviant situation may still accord with the above hypotheses. *Mehelya* are nocturnal (SHINE *et al.*, 1996a) but the small-eyed males

Table 0. Abbreviations.

Abbreviation	Definition
CD	Coefficient of difference (MAYR, 1969; see Materials and Methods)
F	Female
FMR	Female-to-Male Ratio; measure in females as percent of measure in males (FITCH, 1981)
HdL	Head length
M	Male
PERCRA	Percents of rostrum–anus length (WERNER, 1971)
RA	Rostrum–anus length (WERNER, 1971)
SMD	Sexual mensural dimorphism
SSD	Sexual size dimorphism.

might forage at relatively illuminated times. Recently LIU *et al.* (2012) surveyed eye size in colubrids, ignoring sexual dimorphism.

Thus eye-size, despite its function, is insufficiently known in snakes, and under-represented in books on snake life (GREENE, 1997; LILLYWHITE, 2014). Therefore we wished to explore how ophidian evolution maintains optimal eye size while developing major sexual size dimorphism (SHINE & WALL, 2007). We hypothesized that among snake species, the SMD of eye size would be smaller than the SSD. Following preliminary observations on five species (FAIMAN *et al.*, 2005) we examined additional species (RAZZETTI, FAIMAN & WERNER, 2007) and literature data. We tested sexual dimorphism of absolute and relative eye size, and of related body proportions. Finally, we explored the relations among these variables, searching for functional and evolutionary trends.

Material and Methods

The abbreviations used throughout the study are also listed in Table 0.

Our data-base comprised 23 taxa (species or subspecies). Two were further subdivided geographically because their morphometry seemed to vary geographically (WERNER, 2016, fig.10; unpublished) as may happen even within a subspecies (KLAUBER, 1956) and geographical variation in sexual dimorphism occurs in snakes (THORPE, 1989; BABOCSAY, 2001; COX *et al.*, 2007). Hence Table 1 lists 26 samples of Colubridae and Viperidae. Sample sizes range 2–70 per sex. Nine samples represent data used by RAZZETTI *et al.* (2007) from specimens in the museums listed in the Acknowledgements; the others are from the literature quoted in Table 1.

The mensural characters considered were: Sex, male (M) or female (F) (we excluded juveniles, which could not be easily sexed); rostrum-anus length (RA – WERNER, 1971); head length (HdL), taken axially to behind the angle of the jaw, in our samples using GOREN and WERNER (1993) calipers (the method varies among sources but

Table 1. List of taxa with sample sizes by sex (M, F) and source references.*

Family and Species	Old names in the source reference	Ref.	Locality	M	F
Colubridae					
<i>Coronella austriaca</i> LAURENTI, 1768	<i>Coronella austriaca</i> LAURENTI, 1768	7	Central Europe	9	3
<i>Eirenis coronella</i> (SCHLEGEL, 1837)	<i>Eirenis c. coronella</i> (SCHLEGEL, 1837)	8	Israel, Jordan, Syria, Iraq	29	34
<i>Eirenis c. fennelli</i> ARNOLD, 1982	<i>Eirenis c. fennelli</i> ARNOLD, 1982	8	Arabia	3	3
<i>Eirenis c. ibrahimi</i> SIVAN & WERNER, 2003	<i>Eirenis c. ibrahimi</i> SIVAN & WERNER, 2003	8	Sinai	4	3
<i>Eirenis coronelloides</i> (JAN, 1862)	<i>Eirenis coronelloides</i> (JAN, 1862)	8	Iraq, Turkey, Syria, Jordan	16	10
<i>Hemorrhais nummifer</i> (REUSS, 1834)	<i>Coluber nummifer</i> REUSS, 1834	4	Central & N Israel	16	15
<i>Hierophis viridiflavus</i> (LACÉPÈDE, 1789)	<i>Hierophis viridiflavus</i> (LACÉPÈDE, 1789)	7	Central Europe	17	2
<i>Natrix natrix</i> (LINNAEUS, 1758)	<i>Natrix natrix</i> (LINNAEUS, 1758)	7	Europe	10	13
<i>Natrix tessellata</i> (LAURENTI, 1768)	<i>Natrix tessellata</i> (LAURENTI, 1768)	7	Europe	2	4
<i>Natrix tessellata</i> (LAURENTI, 1768)	<i>Natrix tessellata</i> (LAURENTI, 1768)	7	Levant	47	29
<i>Platyceps tessellatus</i> (WERNER, 1909)	<i>Platyceps saharicus</i> SCHÄTTI & MCCARTHY, 2004	7	Egypt	6	2
<i>Platyceps tessellatus</i> (WERNER, 1909)	<i>Platyceps saharicus</i> Schätti & McCarthy, 2004	7	Sinai	16	5
<i>Platyceps tessellatus</i> (Werner, 1909)	<i>Platyceps saharicus</i> SCHÄTTI & MCCARTHY, 2004	7	Negev, Israel	8	4
<i>Psammophis schokari</i> (FORSKAL, 1775)	<i>Psammophis schokari</i> (FORSKAL, 1775)	5	Israel	40	36
Viperidae					
<i>Cerastes c. cerastes</i> (LINNAEUS, 1758)	<i>Cerastes c. cerastes</i> (LINNAEUS, 1758)	10	N. Africa, Sinai	70	56
<i>Cerastes c. hoofeni</i> WERNER & SIVAN, 1999	<i>Cerastes c. hoofeni</i> WERNER & SIVAN, 1999	10	Yemen	2	3
<i>Cerastes g. gasperettii</i> LEVITON & ANDERSON, 1967	<i>Cerastes g. gasperettii</i> LEVITON & ANDERSON, 1967	10	Arabia, Iraq	22	28
<i>Cerastes gasperetti mendelsohnii</i> WERNER & SIVAN, 1999	<i>Cerastes g. mendelsohnii</i> WERNER & SIVAN, 1999	9	Arava	30	57
<i>Crotalus cerastes</i> HALLOWELL, 1854	<i>Crotalus cerastes</i> HALLOWELL, 1854	4,6	California, Mexico	11	7
<i>Echis borkini</i> CHERLIN, 1990	<i>Echis varia borkini</i> CHERLIN, 1990	3	Saudi Arabia, Yemen, Aden	28	18
<i>Echis carinatus sochureki</i> STEMMLER, 1969	<i>Echis carinatus sochureki</i> STEMMLER, 1969	3	Oman, Dubai, UAE	22	21
<i>Echis coloratus coloratus</i> GÜNTHER, 1878	<i>Echis coloratus. coloratus</i> GÜNTHER, 1878	1	Egypt, Arava, Saudi Arabia, Jordan, Negev, Sinai	42	31
<i>Echis c. terraesanctae</i> BABOCSAY, 2003	<i>Echis c. terraesanctae</i> BABOCSAY, 2003	1	Jordan Valley, Negev, Judean desert	37	34
<i>Echis khosatzkii</i> CHERLIN, 1990	<i>Echis khosatzkii</i> CHERLIN, 1990	3	Oman.	6	3
<i>Echis omanensis</i> BABOCSAY, 2004	<i>Echis omanensis</i> BABOCSAY, 2004	2	Oman, UAE (Arabia)	18	15
<i>Vipera aspis</i> (LINNAEUS, 1758)	<i>Vipera aspis</i> (LINNAEUS, 1758)	7	Italy, Switzerland	15	10

* References: 1) BABOCSAY, 2003 and unpublished; 2) BABOCSAY, 2006; 3) BABOCSAY, unpublished; 4) HUIJ Collection; 5) KARK *et al.*, 1997; 6) MCZ Collection; 7) RAZZETTI *et al.*, 2007; 8) SIVAN & WERNER, 2003; 9) WERNER *et al.*, 1994; 10) WERNER *et al.*, 1999.

not within samples); and spectacle diameter, which here properly represents the size of the eyeball (WALLS, 1942; WERNER, 1969). The eye may show directional asymmetry (WERNER, ROTHENSTEIN & SIVAN, 1991; WERNER & SEIFAN, 2006), which may differ between the sexes (RAZZETTI *et al.*, 2007), but herein we use the means of the two sides.

We presented for each individual the HdL also in PERCRA, mean eye size in mm, and relative eye size in PERCRA and in percents of HdL. This enables comparison of single specimens to our data. For all characters we computed the female-to-male ratio (FMR – mean female value as percent of mean male value), matching Fitch’s (1981) data. Each FMR value is considered significant if the female and male means from which it originated, differed significantly by T-test ($P < 0.05$,

without BONFERRONI-type corrections for multiple tests). Ontogenetic allometry is addressed in the Discussion.

We quantified the difference between samples by the simple coefficient of difference (CD). For the difference between samples *a* and *b* (*b* having the larger mean, (M), $CD = (Mb - Ma) / (SDa + SDb)$, where SD is the standard deviation. In classical taxonomy $CD \geq 1.28$ characterizes subspecific differences or above (MAYR, 1969). Characters were compared between the sexes using the Two-Sample T-test or, for non-normally distributed samples, the Mann-Whitney U-test. We adopted the significance threshold of $\alpha = 5\%$. Linear regression was tested between normally distributed variables to determine the form and strength of their relationship. The interaction between regressions was addressed by ANCOVA after

Table 2A. Characters of snake samples, including mean ± SD, min-max, for males (M) and females (F) separately: body length (RA), relative head length (PERCRA) and FMRs. Boldface, significant at P≤0.05.

Taxon	RA (mm)						Head length PERCRA		
	M	F	FMR	FMR max	P	Mean M&F	M	F	FMR
Colubridae									
<i>Coronella austriaca</i>	378±61.3 272–465	394±60.9 328–448	104.2	96.3	0.603	381	4.1	3.7	90.2
<i>Eirenis coronella coronella</i>	176±33.1 93–230	194±48.8 105–269	110.2	117	0.955	185	5.6	4.8	85.7
<i>Eirenis c. fennelli</i>	223.3±35 197–263	186±53.4 141–245	83.3	93.2	0.261	204.7	n/a	5.1	n/a
<i>Eirenis c. ibrahimi</i>	202±42.1 142–238	254±17.7 242–274	125.7	115.1	0.952	228	5.1	4.2	82.4
<i>Eirenis coronelloides</i>	177±24.5 96–211	153±39.6 97–210	86.4	99.5	0.05	165	n/a	4.7	n/a
<i>Hemorrhois nummifer</i>	762±113 545–1000	747±126.5 620.5–907	98	90.7	0.366	754.5	4.2	4.1	97.6
<i>Hierophis viridiflavus</i>	779±120 530–953	754±26.2 736–773	96.8	81.1	0.253	766.5	3.7	3.5	94.6
<i>Natrix natrix</i>	543±156 366–859	735±188 478–1059	135.4	123.3	0.007	639	4.3	4.2	97.7
<i>Natrix tessellata</i> (Europe)	425±80.6 368–482	614±52.8 540–654	144.5	135.7	0.036	519.5	4.3	4.5	104.7
<i>Natrix tessellata</i> (Levant)	560±84.1 368–741	578±124 346–792	103.2	106.9	0.753	569	4.3	4.5	104.7
<i>Platyceps tessellatus</i> (Egypt)	575.3±64 467–657	557±90.5 493–621	96.8	94.5	0.609	566	3.5	3.4	97.1
<i>Platyceps tessellatus</i> (Sinai)	862±113 656–962	709±209 542–937	82.3	97.4	0.88	785.5	2.5	2.6	104
<i>Platyceps tessellatus</i> (Negev)	687±196 483–977	686±129 572–846	99.9	86.6	0.504	686.5	2.9	2.8	96.6
<i>Platyceps tessellatus</i> (pooled)	758.1±176.9 467–977	673±163 493–937	88.8	95.9	N/S	715.5	2.9	2.8	96.6
<i>Psammophis schokari</i>	500±118 291–703	481±108 304–685	96.2	97.4	0.767	490.5	4.1	4.1	100
Viperidae									
<i>Cerastes cerastes cerastes</i>	443±95.7 234–798	452±109 235–709	102	88.8	0.314	447.5	5.8	5.6	96.6
<i>Cerastes cerastes hoofeni</i>	429±27.6 410–449	365.3±44 318–405	85.2	90.2	0.07	397	5.6	6.4	114.3
<i>Cerastes gasperetti gasperetti</i>	425±95.6 281–640	424±132 239–785	99.8	122.7	0.512	424.5	6	5.6	93.3
<i>Cerastes g. mendelsohni</i>	502±94.3 310–677	552±125 237–734	110	108.4	0.02	527	5.5	5.2	94.5
<i>Crotalus cerastes</i>	468±40.1 407–565	476±123 320–676	101.7	119.6	0.43	472	5.1	5.5	107.8
<i>Echis borkini</i>	331±1047 157–509	407±123 156–599	123	117.7	0.019	369	6.2	5.9	95.2
<i>Echis carinatus sochureki</i>	305±63.6 210–332	332±77 178–461	108.9	138.9	0.108	318.5	5.9	5.8	98.3
<i>Echis coloratus coloratus</i>	464±123 198–692	433±113 208–631	93.3	91.2	0.866	448.5	5.1	5.2	102
<i>Echis c. terraesanctae</i>	415±120 215–593	400±116 217–576	96.4	97.1	0.703	407.5	5.1	5.4	105.9
<i>Echis khosatzkii</i>	320±111 207–450	406±206 168–533	126.9	118.4	0.306	363	5.7	6.2	108.8
<i>Echis omanensis</i>	440±125 219–606	438±140 213–603	99.5	99.5	0.516	439	5.5	5.7	103.6
<i>Vipera aspis</i>	435±79 247–532	506±54.2 391–589	116.3	110.7	0.007	470.5	5.1	4.9	96.1

confirming homogeneity of the regression assumption. Intraspecific variation in characters was analyzed for difference by ANOVA and the *post hoc* Least Significant Difference (LSD) test was used to determine which groups differed from which (DYTHAM, 2003).

Results

Intraspecific observations: body size. The biometrical data in Tables 2A,B represent 23 taxa (26 samples) as statistical reduction, per taxon, sex, and character. Sample sizes are in Table 1. The justification for segregating the wide-ranged *Natrix tessellata* and *Platyceps tessellatus* into geographical samples is apparent from the data in Table 2B. In *P. tessellatus* the geographical variation is not clinal; in the Sinai sample the measures are larger than in both the more western sample (Egypt) and the more eastern sample (Negev), while the latter two relatively resemble each other (RAZZETTI *et al.*, 2007).

Excluding five small samples (N<10), few samples failed to show any significant FMR (Table 3, Fig. 1A). For RA, FMR>100 in 10/21 samples (significant in 4/10 samples), FMR<100 in 9/21 samples (significant in 3/9 samples) and FMR≈100 in 3/21 samples. The number of samples with significantly FMR≠100 greatly exceeds that statistically expected. The generalization that RA lengths of snake species have FMR≠100 applies to our material. For the hard-to-define character RA (SEIFAN *et al.*, 2009) Table 3 presents in addition to the FMR derived from means also the FMR derived from the longest male and female of each sample (though sample sizes vary greatly; Table 1). Within the Colubridae these two FMR values are correlated across species (r=0.681, P=0.021; Table 5).

Intraspecific observations: eye size and head size. Absolute eye size (Table 2B) was greater in the larger sex (Table 2A), based on the largest male and female, in 19/26 samples, regardless which sex was larger, and re-

Table 2B. Characters of snake samples, including mean ± SD, min-max, for males (M) and females (F) separately: Eye diameter (relative and absolute) and FMRs. Boldface, significant at P≤0.05.

Taxon	Eye diameter % RA				Eye diameter% Head length					Eye diameter (mm)				
	M	F	FMR	Av. M&F	M	F	FMR	FMR max	P	M	F	FMR	FMR max	P
Colubridae														
<i>Coronella austriaca</i>	0.61	0.56	91.8	0.58	15.6±2.3 13–19.8	15±1.8 14–17.1	96.2	86.4	0.34	2.3±0.3 1.8–2.6	2.2±0.3 1.8–2.4	95.7	92.3	0.37
<i>Eirenis c. coronella</i>	1.65	1.39	84.5	1.52	15.4±1.5 12.6–18.4	15.5±1.7 12.1–20.5	101	111	0.60	2.9±0.6 1.5–3.9	2.7±0.5 1.3–3.7	93.1	94.9	0.08
<i>E. c. fennelli</i>	0.90	1.24	138	1.07	n/a	15.1±0.6 14.4–15.5	n/a	n/a	n/a	2±0.5 1.6–2.6	2.3±0.5 1.7–2.6	115	100	0.66
<i>E. c. ibrahimi</i>	1.39	1.22	88	1.30	14.2±1.6 12.9–16.6	14.6±0.7 13.9–15.3	103	92.2	0.66	2.8±0.2 2.5–3.1	3.1±0.3 2.9–3.4	111	110	0.82
<i>E. coronelloides</i>	1.44	1.65	115	1.54	16.1±1.6 13.3–19	15.9±1.1 14.2–17.2	98.8	90.5	0.35	2.54±1.2 1.3–3.8	2.53±0.4 1.8–3.3	99.6	86.8	0.49
<i>Hemorrhoids nummifer</i>	0.63	0.62	97.8	0.62	15±1.3 12.1–16.7	15.5±1.4 12.9–18	103	108	0.84	4.8±0.6 3.9–6	4.6±0.5 3.8–5.3	95.8	88.3	0.16
<i>Hierophis viridiflavus</i>	0.59	0.60	101	0.59	16.2±1.2 13.7–18.6	17.1±0.7 16.6–17.6	106	94.6	0.88	4.6±0.6 3.6–5.5	4.5±0.2 4.4–4.7	97.8	85.5	0.38
<i>Natrix natrix</i>	0.66	0.57	86.2	0.62	16.1±1.8 12.9–18.7	13.8±1.8 10.6–17	85.7	90.9	0.00	3.6±0.8 2.8–5.6	4.2±0.6 3.6–5.4	117	96.4	0.97
<i>N. tessellata</i> (Europe)	0.68	0.62	90.7	0.65	15.9±0.2 15.8–16.1	13.8±0.8 12.7–14.5	86.8	90.1	0.03	2.9±0.2 2.7–3	3.8±0.3 3.3–4.1	131	137	0.99
<i>N. tessellata</i> (Levant)	0.63	0.62	99.7	0.62	14.5±1 12.3–16.7	13.7±1.1 11.7–16.2	94.5	97	0.21	3.5±0.5 2.3–4.5	3.6±0.5 2.4–4.7	103	104	0.8
<i>P. tessellatus</i> Egypt)	0.50	0.48	96.2	0.49	14.2±0.6 13.6–15.3	14.1±0.5 13.8–14.5	99.3	94.8	0.36	2.9±0.3 2.4–3.1	2.7±0.3 2.5–3	93.1	96.8	0.24
<i>P. tessellatus</i> (Sinai)	0.39	0.44	111	0.42	15.2±1.3 13.5–17.1	16.7±0.2 16.6–17	110	99.4	0.99	3.4±0.4 2.6–3.8	3.1±0.7 2.5–3.8	91.2	100	0.20
<i>P. tessellatus</i> (Negev)	0.47	0.44	93.9	0.45	15.3±0.4 14.7–15.8	15.9±1.5 13.9–17.5	104	111	0.70	3.2±0.8 2.3–4.1	3±0.3 2.7–3.5	93.8	85.4	0.82
<i>P. tessellatus</i> (pooled)	0.42	0.45	106	0.43	15.0±1.1 13.5–17.1	15.9±1.3 13.8–17.5	106	102	0.98	3.2±0.5 2.3–4.1	3±0.5 2.5–3.8	93.8	92.7	0.13
<i>Psammophis schokari</i>	0.82	0.81	98.9	0.82	20.5±2.1 18.1–30.6	20.3±1.5 17.2–23.6	99	77.1	0.32	4.1±0.7 2.9–5.9	3.9±0.6 3–5.1	95.1	86.4	0.09
Viperidae														
<i>Cerastes c. cerastes</i>	0.99	0.91	91.3	0.95	17.3±1.7 12.5–21.5	16.9±1.9 13.1–21.7	97.7	101	0.11	4.4±0.6 2.6–5.8	4.1±0.6 2.6–5.3	93.2	91.4	0.00
<i>C. c. hoo-fieni</i>	0.93	1.07	115	1.00	16.4±1 15.7–17.1	17±0.5 16.5–17.4	104	102	0.78	4±0.4 3.7–4.2	3.9±0.4 3.5–4.3	97.5	102	0.41
<i>C. g. gasporetii</i>	0.99	0.94	95.5	0.97	16.9±1.7 12.1–19.5	17.7±2.2 13.2–22.5	105	115	0.92	4.2±0.6 3.3–5.2	4±0.7 2.9–5.8	95.2	112	0.14
<i>C. g. mendelsohni</i>	0.90	0.85	95	0.87	16.7±1.6 12.8–20.8	16.9±1.7 12.3–21.7	101	104	0.70	4.5±0.6 3.2–5.7	4.7±0.7 3–6.2	104	109	0.92
<i>Crotalus cerastes</i>	0.83	0.76	90.8	0.79	16.1±1.4 13.2–18.4	14.4±1.3 12.3–15.7	89.4	85.3	0.01	3.9±0.4 3.2–4.7	3.6±0.5 3–4.3	92.3	91.5	0.1
<i>Echis bor-kini</i>	1.18	0.93	79.2	1.06	24.5±2.5 17.9–27.5	18.8±2.1 16.2–23	76.7	83.6	0.00	3.9±0.7 2.4–5.1	3.8±0.8 2.6–5.1	97.4	100	0.33
<i>E. carinatus sochureki</i>	1.21	1.20	99.3	1.21	21.4±12 18.6–25.5	21.2±1.6 18.7–23.4	99.1	91.8	0.32	3.7±0.4 3.2–4.4	4±0.5 2.8–4.5	108	113	0.98
<i>E. coloratus coloratus</i>	0.78	0.76	98.2	0.77	15.9±2.2 13–20.5	16.2±2.6 10.7–21.7	102	106	0.70	3.6±0.5 2.3–4.4	3.3±0.4 2.3–4.1	91.7	93.2	0.00
<i>E. c. erraes-sanctae</i>	0.87	0.90	104	0.88	17.2±2 14.5–21.3	17.4±2.2 14–22.4	101	105	0.65	3.6±0.6 2.3–4.6	3.6±0.7 2.4–4.8	100	104	1.00
<i>E. khosatzkii</i>	1.06	0.86	81.1	0.96	19.6±2 16.9–21.7	18.5±5.4 14.7–22.3	94.4	103	0.39	3.4±0.6 2.8–4.3	3.5±1.3 2.5–4.4	103	102	0.54
<i>E. omanensis</i>	0.86	0.87	101	0.87	17±1.9 14.2–19.8	17.4±3 14.1–23.7	102	120	0.67	3.8±0.9 2.6–5	3.8±0.8 2.6–4.9	100	98	1.00
<i>Vipera aspis</i>	0.69	0.63	91.7	0.66	13.8±1.5 12.4–17.4	13.4±1.5 11.3–16.5	97.1	94.8	0.26	3±0.5 1.9–3.7	3.2±0.4 2.5–3.9	107	105	0.86

Table 3. FMR values for the available characters and taxa. Italics, $N < 10$. Boldface, $P \leq 0.05$.

Taxon	RA from mean (mm)	RA from largest (mm)	Head length PERCRA	Eye diameter PERCRA	Eye diameter% Head length	Eye diameter (mm)
Colubridae						
<i>Coronella austriaca</i>	104.2	96.3	90.2	91.8	96.4	95.7
<i>Eirenis coronella coronella</i>	110.2	117.0	85.7	84.5	100.7	93.1
<i>Eirenis c. fennelli</i>	83.3	n/a	n/a	n/a	n/a	115.0
<i>Eirenis c. ibrahimi</i>	125.7	n/a	82.4	n/a	n/a	110.7
<i>Eirenis coronelloides</i>	86.4	99.5	n/a	115.2	99.1	99.6
<i>Hemorrhois nummifer</i>	98.0	90.7	97.6	97.8	103.1	95.8
<i>Hierophis viridiflavus</i>	96.8	81.1	94.6	101.1	105.6	97.8
<i>Natrix natrix</i>	135.4	123.3	97.7	86.2	85.9	116.7
<i>Natrix tessellata</i> (Europe)	144.5	n/a	104.7	n/a	86.8	131.0
<i>Natrix tessellata</i> (Levant)	103.2	106.9	104.7	99.7	92.0	102.9
<i>Platyceps tessellatus</i> (Egypt)	96.8	94.5	97.1	96.2	99.3	93.1
<i>Platyceps tessellatus</i> (Sinai)	82.3	97.4	104.0	110.9	109.9	91.2
<i>Platyceps tessellatus</i> (Negev)	99.9	86.6	96.6	93.9	103.9	93.8
<i>Platyceps tessellatus</i> (all)	88.8	95.9	96.6	105.6	105.9	93.8
<i>Psammophis schokari</i>	96.2	97.4	100.0	98.9	99.0	95.1
Viperidae						
<i>Cerastes cerastes cerastes</i>	102.0	88.9	96.6	91.3	97.9	93.2
<i>Cerastes cerastes hoofi</i>	85.2	n/a	114.3	n/a	103.9	97.5
<i>Cerastes g. gasperettii</i>	99.8	122.7	93.3	95.5	104.6	95.2
<i>Cerastes g. mendelsohni</i>	110.0	108.4	94.5	95.0	101.1	104.4
<i>Crotalus cerastes</i>	101.7	119.7	107.8	90.8	90.6	92.3
<i>Echis borkini</i>	123.0	117.7	95.2	79.2	92.1	97.4
<i>Echis carinatus sochureki</i>	108.9	138.9	98.3	99.3	99.0	108.1
<i>Echis coloratus coloratus</i>	93.3	91.2	102.0	98.2	101.9	91.7
<i>Echis c. terraesanctae</i>	96.4	97.1	105.9	103.8	101.7	100.0
<i>Echis khosatzkii</i>	126.9	n/a	108.8	n/a	94.3	102.9
<i>Echis omanensis</i>	99.5	99.5	103.6	100.5	102.4	100.0
<i>Vipera aspis</i>	116.3	110.7	96.1	91.7	96.7	106.7

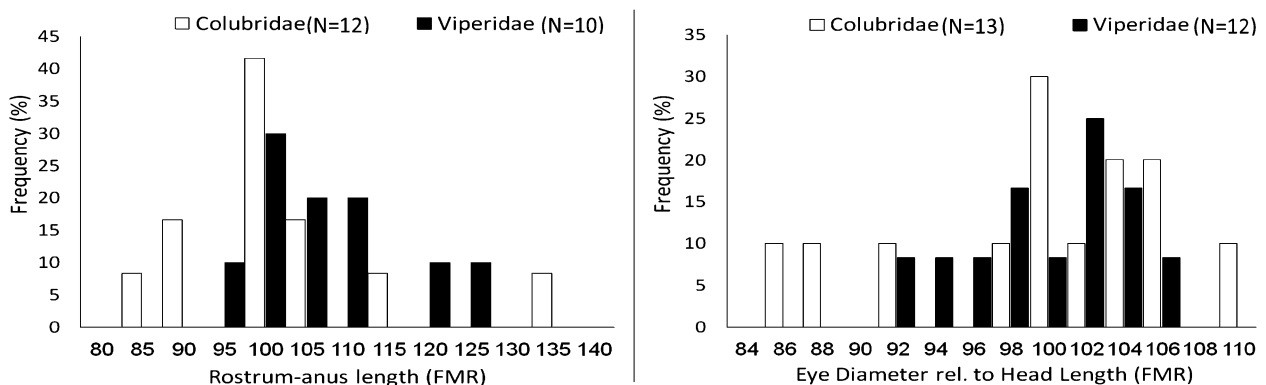


Fig. 1. Distribution of FMR values of mensural characters among snake taxa ($N = 26$ samples). White, Colubridae; black, Viperidae. **A** (left), The FMR of RA; **B** (right), The FMR of eye diameter relative to head length. Note that the ranges of FMR values are wider in A than in B.

ardless of family (Fig. 2). However, its FMR was rarely significant (Table 3). This remained true in 18/26 samples when based on the sex means. Among the species with eye larger in the larger sex, the FMR of eye size was often more moderate (closer to 100) than that for RA: using FMRs based on sample maxima, this occurred in

10/19 samples but with FMRs based on sample averages, it occurred in 15/18 samples.

Among the species deviating from this pattern, there occurred different patterns. In 5/26 samples the male had absolutely larger eyes although the female was the larger sex; e.g., *Echis borkini*. In three of the remaining samples

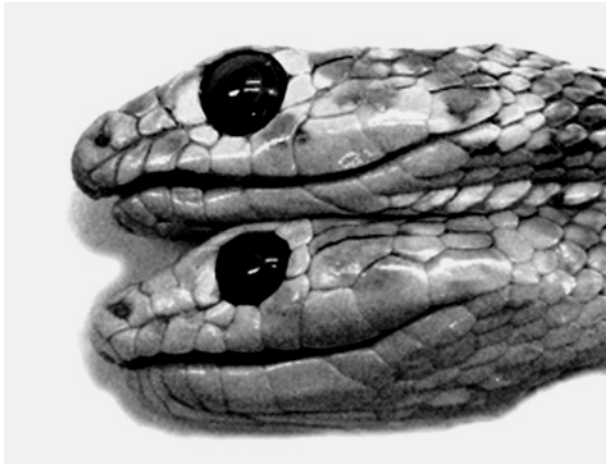


Fig. 2. Sexual difference in eye size: Preserved adult *Platyceps tessellatus* from Sinai. Top, female (HUJ-R 8326), total length 121 cm. Bottom, male (HUJ-R 8487), total length 116 cm. In this population the males are longer (FMR=82), the females have relatively (PERCRA) larger heads (FMR=102) with the eye much enlarged relative to the head (FMR=110), so that average absolute eye size is almost equated (FMR=92) but in these individuals the longer female's eye diameter (3.8 mm) surpasses the male's (3.3 mm). (Photo: ROY FAIMAN.)

eye size was identical in the two sexes although RA differed between them, e.g., *E. coloratus terraesanctae*. In contrast, *Eirenis coronella fennelli* females had the larger eyes despite being the smaller sex (Table 2A,B) but sample size was only 3+3 (Table 1).

Among the five samples in which the eye was bigger in the male, although the smaller sex, this apparently accrued differently in different species. The FMRs were statistically insignificant but in *Eirenis c. coronella* they derived from 29 males and 34 females; RA FMR=110.2 (or from the maxima, 117), and Eye (mm) FMR=93.1. This “over-correction” of eye size was achieved through HdL PERCRA being greater in males, FMR=85.7. Eye size relative to HdL was isometric, FMR=100.7 (hypothesis 2a). In *Coronella austriaca*, *Cerastes c. cerastes* and *Echis borkini* with RA FMR=104.2, 102 and 123 respectively, and absolute eye size FMR=95.7, 92.3 and 97.4 respectively, the “over-correction” was achieved in two steps. Relative head size seemed only moderately increased in the smaller sex, being FMR=90.2, 96.6 and 95.2 respectively, but FMR for eye size relative to HdL was 96.4, 89.4 and 92.1 (hypotheses 2a+2b). Finally, in *Crotalus cerastes*, while females were larger than males (see also KLAUBER, 1944), mean FMR=101.7 (between largest specimens FMR=119.7), absolute eye size had FMR=92.3 (Fig. 3). This was achieved despite the male's head being relatively smaller, FMR=107.8, through the male's eye being greatly enlarged relative to the head, FMR=90.6 (hypothesis 2b).

In sex-specific terms, absolute eye size (Tables 2, 3) was greater in the males (FMR≤99) in 15/26 samples (significant in 2/15 cases), greater in the females (FMR≥101) in 8/26 samples (but not significantly), and

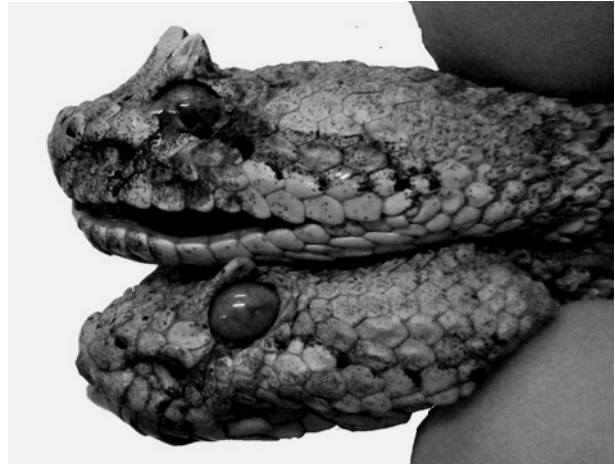


Fig. 3. Sexual difference in relative eye size: Preserved adult *Crotalus cerastes* from California showing SMD in eye size relative to HdL and in absolute terms. Top, female (CAS 19821), total length 54.7 cm, HdL 25.9 mm, left eye diameter 3.85 mm. Bottom, male (HUJ-R 3359), total length 55.7 cm, HdL 25.2 mm, left eye diameter 4.1 mm. (Photo: NURIT WERNER.)

equal in the two sexes ($99 < \text{FMR} < 101$) in 3/26 samples.

Eye diameter as percent of head length (%HdL; Tables 2, 3) was greater in the males (FMR≤99) in 10/24 samples with relevant data (significantly in 3/10 cases), in the females (FMR≥101) in 10/24 samples (significantly in 2/10 cases), and equal in the two sexes ($99 < \text{FMR} < 101$) in 4/24 cases (Fig. 1B).

In all four samples where the FMR of eye diameter-%HdL (Table 3) was significant (Fig. 3), the eye was larger, relative to HdL, in the smaller sex (sometimes the SSD of RA was clearer between maxima than between means). In two of these cases the FMR of relative HdL resembled the (insignificant) FMR of RA (*Natrix tessellata* from the Levant and *Crotalus cerastes*, discussed below). If despite the insignificance such cases do occur, relative head size seems to increase the head-size difference between the sexes. But in the smaller sex, with smaller head, the eye was allometrically enlarged within the head. Therefore, in *N. tessellata* the FMR of eye size (in mm) resembled that of RA (hypothesis 2b).

In the two other samples with significant FMR of mean Eye%HdL, *Natrix natrix* and *Platyceps tessellatus* from Sinai (Fig. 4), the smaller sex had a relatively larger head and within the head relatively larger eyes, so that the FMR of absolute eye size was greatly moderated compared to the FMR of RA, the difference approximately halved (hypotheses 2a plus 2b).

The ontogenetic allometry of eye size sexual dimorphism is exemplified in Fig. 5, *Natrix tessellata* representing the majority trend (eye larger in the larger sex), with intraspecific variation. Figure 5A shows the increase in HdL as a function of RA, Figure 5B shows the increase of actual eye size as a function of HdL, and Figure 5C shows the decrease of relative eye size with increasing HdL (see also Table 3). In each, the regression lines of

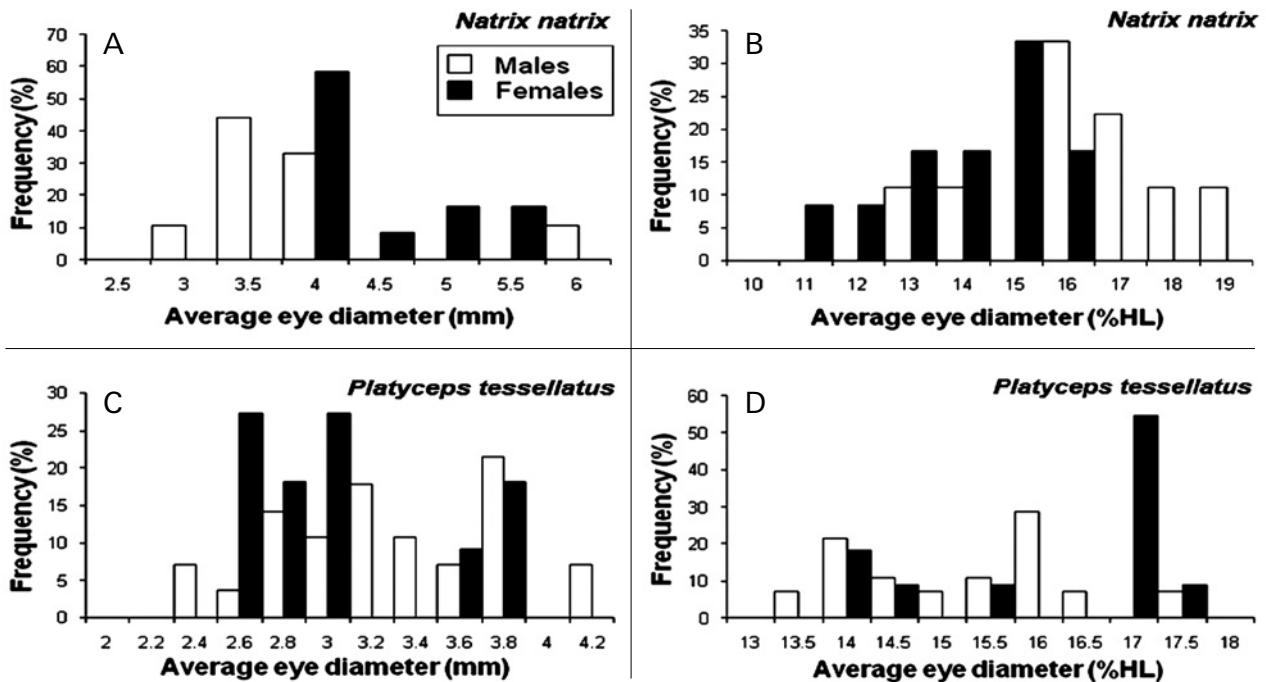


Fig. 4. Sexual dimorphism of eye size, compared in *Natrix natrix* and *Platyceps tessellatus* (pooled regions). In both species the dimorphism seen in absolute eye size, is reversed in terms of eye size relative to head size. **A** and **C**: Frequency distribution of absolute eye size, in *N. natrix* (**A**) greater in females, in *P. tessellatus* (**C**) slightly greater in males. **B** and **D**: frequency distribution of eye diameter relatively to HdL, in *N. natrix* (**B**) greater in males, in *P. tessellatus* (**D**) greater in females.

males and females differ in intercept; the difference between their slopes approaches significance only for absolute Eye%HdL (Fig. 5B).

Interspecific observations: differences between families. Before exploring interspecific relations among characters, we heeded that morphology varies among snake families (RIEPEL, 1988; LEE & SCANLON, 2002) and asked whether interspecific analysis of characters should be applied to the pooled material or separately by family. For each sex, we compared each character between Colubridae and Viperidae (T-test and CD), as shown in Table 4. The number of taxa per character was 12–14 in Colubridae and 12 in Viperidae. As a group, Colubridae had greater RA length than Viperidae (significantly in both sexes). In each family, female RA exceeded male RA. The FMR was similar in the two families (resp. FMR=104.5 and 105.3, the difference was not significant). In contrast, absolute eye diameter (mm) was greater in the Viperidae as a group than in the Colubridae (significantly in both sexes). This resulted from two allometric differences: Both HdL PERCRA, and eye%HdL, were greater in the Viperidae. The latter differences were not statistically significant but the picture appeared coherent.

Interspecific observations: the dependence of FMR on species size. We explored the effect of body size on the FMR of the eye, by comparing the FMRs of different measures of eye size, to those of body size. In view of the differences between Colubridae and Viperidae (Table 4),

we computed the interspecific correlations among FMR values for the pooled taxa (Colubridae and Viperidae, Table 5A) but also separately among Colubridae (Table 5B) and among Viperidae (Table 5C). Initially the correlations were calculated based in turn on three RA sets, mean male RA, mean female RA, and their average. This detail was inconsequential and we present only the results using male sizes.

The pooled families (Table 5A) showed highly significant correlations of the FMR of absolute eye diameter (mm) with those of RA (based on means) and of relative eye diameter (PERCRA). Further details differed between the families.

In the Colubridae (Table 5B), the FMRs of RA based on means and based on maxima were correlated. The FMR of eye size (mm) correlated with both RA FMRs but the FMRs of relative eye size (as PERCRA and as%HdL) negatively correlated with both. Eye diameter PERCRA was correlated with HdL PERCRA. But absolute eye size (mm) and Eye size (%HdL) were correlated negatively.

In contrast, among the Viperidae (Table 5C) the only significant correlations were that the two FMRs of relative eye size (PERCRA, and as%HdL) were correlated and each was negatively correlated with that of RA (from means).

Interspecific observations: correlations among FMRs of characters. Is sexual dimorphism expressed similarly in different morphological characters, as it would under isometry? Inter-specifically, the FMR of absolute eye size was significantly correlated with that of body length (RA)

Table 4. Comparing characters between the families Colubridae and Viperidae. Numbers of taxa are after excluding samples of N<10. CD=coefficient of difference. P value was obtained by independent sample T-test in SPSS v.17. Boldface, significant at P≤0.05.

Character	Family	Males					Females				
		N	Mean	Std. Deviat.	CD	P	N	Mean	Std. Deviat.	CD	P
RA (mm)	Colubridae	14	489.21	234.9	0.25	0	14	503	226.3	0.25	1E-04
	Viperidae	12	414.75	62.56			12	432.6	59.63		
FMR of RA	Colubridae	14	104.49	18.73	-0.02	0.29					
	Viperidae	12	105.25	12.25							
Head length PERCRA	Colubridae	12	4.05	0.84	-1.22	0.12	14	4.01	0.74	-1.4	0.075
	Viperidae	12	5.55	0.38			12	5.61	0.43		
Eye diameter (mm)	Colubridae	14	3.25	0.82	0.47	0.05	14	3.3	0.8	-0.4	0.005
	Viperidae	12	3.83	0.42			12	3.79	0.4		
Eye diameter PERCRA	Colubridae	14	0.81	0.39	-0.24	0.02	14	0.8	0.4	-0.2	0.002
	Viperidae	12	0.94	0.15			12	0.89	0.15		
Eye diameter (% Head length)	Colubridae	13	15.71	1.6	-0.45	0.1	14	15.5	1.74	-0.4	0.775
	Viperidae	12	17.73	2.84			12	17.15	2		

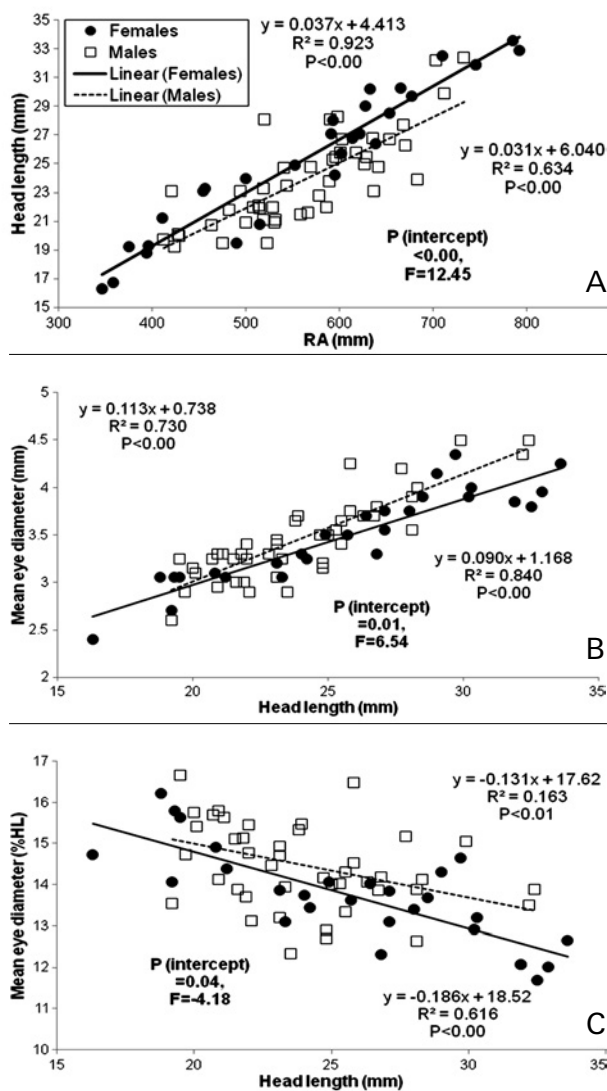


Fig. 5. The ontogeny of sexual dimorphism in eye size, exemplified in *Natrix tessellata*. **A:** HdL as a function of RA. The slopes did not significantly differ between the sexes ($P_{slopes} = 0.19$, $F = 1.76$), so the lines may be pooled as $y = 0.035x + 4.927$. Note that the head allometrically grows less than the body. **B:** Mean absolute eye size as function of HdL. The slopes did not significantly differ between the sexes ($P_{slopes} = 0.08$, $F = 3.14$), so the lines may be pooled as $y = 0.1x + 0.976$. Note that the eye allometrically grows less than the head. **C:** Mean eye size relative to HdL, as a function of HdL. The slopes did not significantly differ between the sexes ($P_{slopes} = 0.33$, $F = 0.98$), so the lines may be pooled as $y = -0.16x + 18.093$. Note how relative eye size allometrically diminishes.

(Fig. 6): $Y = 0.5X + 47.27$, $P = 0.0001$ ($N = 26$), much more so among the Colubridae: $Y = 0.4371X + 56.568$, $P = 0.006$ ($N = 14$) than among the Viperidae: $Y = 0.22X + 75.83$, $P = 0.106$ ($N = 12$). However, while throughout RA $FMR \leq 100$ (i.e., male-biased sexual dimorphism) the sample averages belonging to either family were scattered on both sides of the equality line, throughout RA $FMR \geq 100$ (i.e., female biased sexual dimorphism) the sample averages were below the equality line. Overall, eye size FMR was smaller (closer to 100) than RA FMR.

Discussion

Aspects of sexual dimorphism in snakes. In snakes SMD has been investigated mainly in total length, RA length, tail length and head length; sometimes proportions within the head; but only exceptionally spectacle diameter, as reviewed in the Introduction.

All these and diergic characters (fecundity, diet) interact. Our discussion of sexual dimorphism focuses on eye size. In our material most taxa showed some SMD, confirming earlier conclusions that in snakes usually females are longer than males (FITCH, 1981; COX *et al.*, 2007). The values of SSD and other SMD vary geographically and temporally (MADSEN & SHINE, 1993a), increasing the variation in our data.

For an individual specimen ‘length’ is the easiest character to measure. However, for a population (or sex) it is the most difficult character to define, due i.a. to ontogeny (FITCH, 1981, SEIFAN *et al.*, 2009).

Table 5. Correlations among FMR values of characters. **A:** Across all species; **B:** Across Colubridae; **C:** Across Viperidae. Sample sizes as in Table 4. Boldface, significant at $P \leq 0.05$.

A – Colubridae and Viperidae		RA mean (mm)	RA max (mm)	Head length PERCRA	Eye diameter (mm)	Eye diameter PERCRA	Eye diameter (% Head length)
RA mean (mm)	R	1					
	P						
RA max (mm)	R	-0.143	1				
	P	0.538					
Head length PERCRA	R	0.067	0.101	1			
	P	0.755	0.664				
Eye diameter (mm)	R	0.52	-0.312	-0.066	1		
	P	0.006	0.169	0.759			
Eye diameter PERCRA	R	0.218	-0.364	-0.062	0.635	1	
	P	0.343	0.105	0.789	0.002		
Eye diameter (% Head length)	R	-0.068	-0.377	-0.096	-0.068	0.003	1
	P	0.753	0.092	0.655	0.752	0.99	

B – Colubridae		RA mean (mm)	RA max (mm)	Head length PERCRA	Eye diameter (mm)	Eye diameter PERCRA	Eye diameter (% Head length)
RA mean (mm)	R	1					
	P						
RA max (mm)	R	0.681	1				
	P	0.021					
Head length PERCRA	R	-0.131	-0.118	1			
	P	0.684	0.745				
Eye diameter (mm)	R	0.697	0.591	0.172	1		
	P	0.006	0.05	0.593			
Eye diameter PERCRA	R	-0.816	-0.441	0.717	-0.258	1	
	P	0.002	0.175	0.02	0.445		
Eye diameter (% Head length)	R	-0.838	-0.696	-0.208	-0.826	0.458	1
	P	0.001	0.017	0.54	0.001	0.156	

C – Viperidae		RA mean (mm)	RA max (mm)	Head length PERCRA	Eye diameter (mm)	Eye diameter PERCRA	Eye diameter (% Head length)
RA mean (mm)	R	1					
	P						
RA max (mm)	R	0.46	1				
	P	0.181					
Head length PERCRA	R	-0.367	-0.238	1			
	P	0.24	0.507				
Eye diameter (mm)	R	0.489	0.437	-0.167	1		
	P	0.107	0.207	0.604			
Eye diameter PERCRA	R	-0.738	-0.195	0.419	0.208	1	
	P	0.015	0.589	0.228	0.564		
Eye diameter (% Head length)	R	-0.665	-0.265	-0.011	0.02	0.742	1
	P	0.018	0.459	0.974	0.952	0.014	

The ontogeny of size and sexual size difference – who is adult? Reptiles continue growing after sexual maturity (ANDREWS, 1982; SHINE & CHARNOV, 1992). They grow allometrically, changing proportions among body parts. Therefore discussion of SSD and SMD requires defining which individuals are included. This definition depends on the context. For an ecological question whether in a species with the males having larger heads, the sexes eat different prey sizes, we should use all sexed or sexually mature individuals. But if we investigate the sexual dimorphism of species to characterize their morphology, we better use full-sized individuals that have realized their growth curves (SEIFAN *et al.*, 2009).

When dealing with proportions among body parts this dilemma can be bypassed by using their allometric growth equations. This option is unavailable for body size. Its assessment has therefore been addressed in several investigations. One proposal to estimate maximum size uses the largest individuals in large samples (STAMPS & ANDREWS, 1992; STAMPS, 1993; STAMPS, KRISHNAN & ANDREWS, 1994).

A new difficulty in defining the representative size of a taxon accentuates the need for adequate samples. The length of young squamates is phenotypic, mitigating the interest in body size and sexual dimorphism. Individual snakes may grow faster and become larger in response

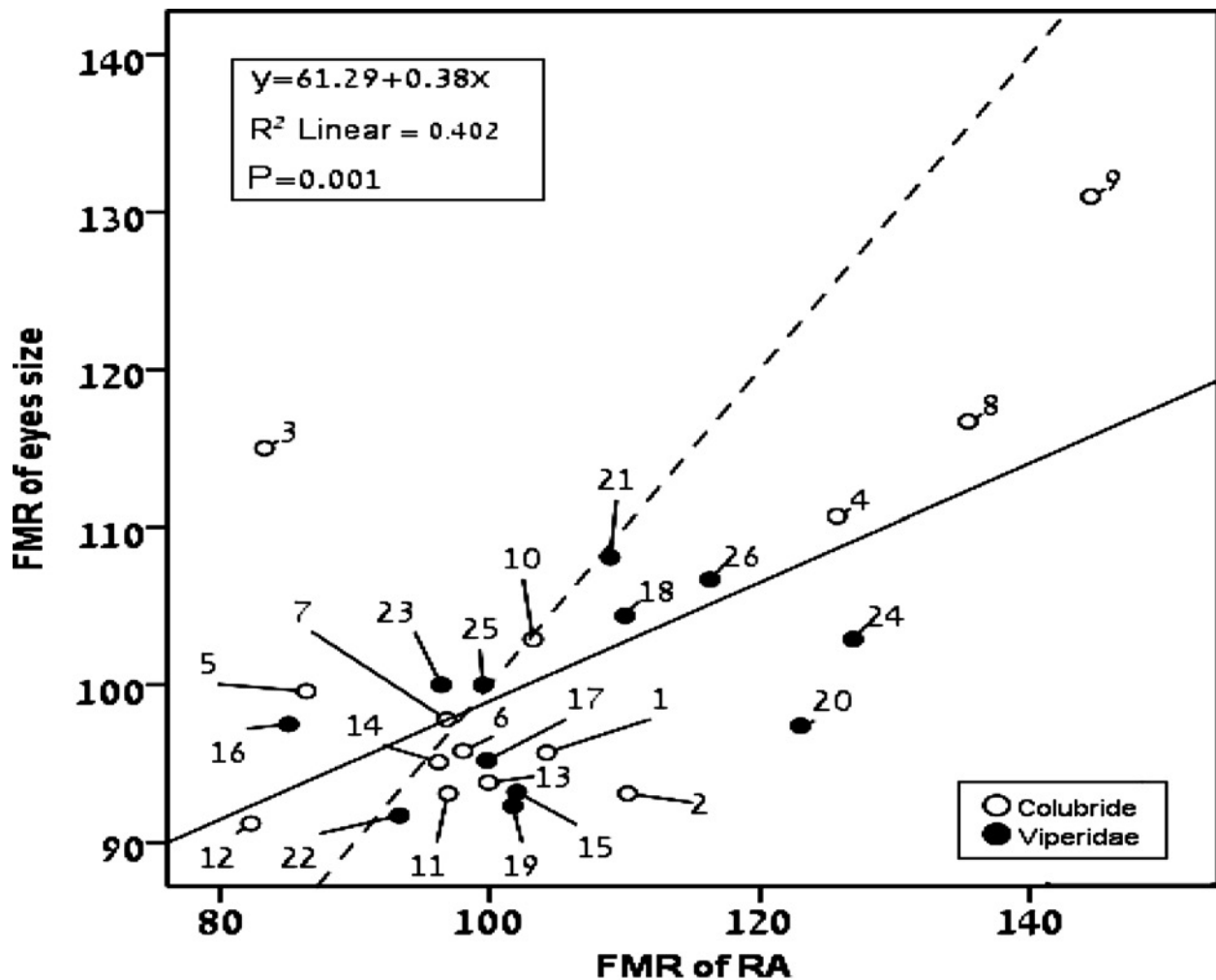


Fig. 6. The inter-specific correlation of FMR of eye size with the FMR of body size (RA). Dashed line, line of equation. Open symbols, maxima of samples of Colubridae. Solid symbols, maxima of samples of Viperidae. Species identification – Colubridae: 1) *Coronella austriaca*; 2) *Eirenis Coronella coronella*; 3) *Eirenis c. fennelli*; 4) *Eirenis c. ibrahimi*; 5) *Eirenis coronelloides*; 6) *Hemorrhphis nummifer*; 7) *Hierophis viridiflavus*; 8) *Natrix natrix*; 9) *Natrix tessellata* (Europe); 10) *Natrix tessellata* (Levant); 11) *Platyceps tessellatus* (Egypt); 12) *Platyceps tessellatus* (Sinai); 13) *Platyceps tessellatus* (Negev); 14) *Psammophis schokari*. Viperidae: 15) *Cerastes cerastes cerastes*; 16) *Cerastes c. hoofeni*; 17) *Cerastes gasperettii gasperettii*; 18) *Cerastes g. mendelsohni*; 19) *Crotalus cerastes*; 20) *Echis borkini*; 21) *Echis carinatus sochureki*; 22) *Echis coloratus coloratus*; 23) *Echis c. terraesanctae*; 24) *Echis khosatzkii*; 25) *Echis omanensis*; 26) *Vipera aspis*.

to ample food, e.g., *Vipera berus* (FORSMAN, 1991) and *Nerodia sipedon* (QUERAL-REGIL & KING, 1998). Second, body length at hatching may be affected by incubation temperature, e.g., *Pantherophis obsoletus* (BLOUIN-DEMERES, WEATHERHEAD & ROW, 2004), although no temperature effects occurred in *Thamnophis sirtalis* (ARNOLD & PETERSON, 1989). Little is known of the later ontogeny. In *Vipera berus*: juvenile females grow faster than juvenile males, reach maturity at older age and are larger (MADSEN & SHINE, 1994). Moreover, in *Thamnophis sirtalis*, a male-biased SSD in RA at birth reversed later, females becoming the longer adults (KRAUSE & BURGHARDT, 2007).

At another level, SHINE & CHARNOV (1992) suggested to derive the maximum RA from size at maturity by a relatively constant proportion between these two variables. However, of 17 species they reported, in two maximum

size was $\geq 200\%$ of the size at sexual maturity, but in two others, $\leq 116\%$. Moreover, maxima derive from ranges, ranges depend on sample size, but sample sizes were not given.

Herein our pragmatic solution for defining the body length of samples comprised three measures. (1) Using only specimens of known sex; (2) assessing the body size of a taxon (or sample) both from the average and from the largest individuals, and (3) viewing the size of body parts in terms of proportions. We lack calculations of asymptotic sizes (STAMPS & ANDREWS, 1992) but consider that what functions in the animals' life, and sustains selective pressure, is the actual body-part size prevalent in the population.

Which sex is larger, and why? Herein (Table 3) SSD was significant in 7/26 samples: 4/7 samples (57%) were

female-biased with significant RA FMR = 109–135, and 3/7 (43%) samples were male-biased with significant RA FMR = 82–96. If we consider also the FMR values that were not in themselves significant (but in all samples $N \geq 10$), then 10/21 samples (48%) were female-biased with RA FMR = 101–135; 8/21 (38%) samples were male-biased with RA FMR = 82–98; and 3/21 (14%) were neutral, $99 < \text{FMR} < 101$. This accords with previous knowledge. COX *et al.* (2007) have summarized that in snakes, unlike lizards, in most species SSD is female-biased. Females may exceed males by an order of magnitude. Males may exceed females by up to 50%. (FITCH, 1981; SHINE, 1994; GREER, 1997; COX *et al.*, 2007).

In the evolution of SSD proximate and ultimate factors interact simultaneously (DUVALL & BEAUPRE, 1998). We pragmatically investigate one factor at a time. The proximate causes for SSD may be genotypic and may operate through any of four mechanisms and their combinations. (1) Early differentiation during embryonic development. In some squamate species, SSD occurs already in hatchlings, remaining isometric during ontogeny. To the species with FMR not changing with RA listed by FITCH (1981) we add besides *Natrix tessellata* (herein) also *Natrix natrix* (GREGORY, 2004) and the lizard *Acanthodactylus boskianus* (SEIFAN *et al.*, 2009). Among four natricine species the differences in body persist, increase, or decrease (KING *et al.*, 1999). (2) Faster growth of one sex (length, relative head length, relative tail length, existing from birth, may occur during ontogeny MADSEN, 1988; FORSMAN, 1991; GREER, 1997). (3) Extended growth period of one sex (SHINE, 1994). In *Natrix natrix* females this mechanism operates together with mechanism 2, faster growth (MADSEN, 1983). (4) Longer life-span of one sex (MINAKAMI, 1979).

Additionally, proximate causes for SSD may also be phenotypical, through environmental effects differing between the sexes (KRAUSE, BURGHARDT & GILLINGHAM, 2003; TAYLOR & DENARDO, 2005). The sexually differing growth rate and ensuing SSD in *Vipera berus* was ascribed to different responses to prey abundance (FORSMAN, 1991). The differing growth rate and consequent SSD in wild populations failed to recur in the laboratory, in *Natrix natrix* (MADSEN & SHINE, 1993b) and *Crotalus atrox* (JOHN-ALDER, COX & TAYLOR, 2007).

The ultimate causes for SSD differ between the sexes. Female-biased SSD is usually ascribed to reproductive capacity. Intraspecifically or interspecifically larger squamate females carry heavier relative clutch masses, usually comprising more numerous eggs (FITCH, 1985). This is common among lizards (FRANKENBERG & WERNER, 1992; COX, SKELLY & JOHN-ALDER, 2003). Among snakes, inter-specifically, RENSCH (1959) noted that for five species whose adult length cumulatively ranged 33–150 cm, clutch sizes cumulatively ranged 5–35 eggs; but in four species with a cumulative adult length of 3–10 m, the clutches cumulatively ranged 30–100 eggs. This principle indeed holds both intraspecifically (CLARK, 1970; SHINE, 1989a) and interspecifically (SHINE, 1989a).

Rarely, the eggs laid by intraspecifically relatively larger females are larger, rather than more numerous, e.g., *Acanthodactylus schreiberi* (Lacertidae; FRANKENBERG & WERNER, 1992), *Spalerosophis diadema* (Colubridae; FORD & SEIGEL, 2010). Additionally, viviparity is associated with greater SSD (SHINE, 1994). Some male snakes select and court the larger females (SHETTY & SHINE, 2002).

Males of many snake species have relatively longer heads, paralleling the situation in lacertid lizards. The male lizard's relatively longer head may reflect the female's trunk becoming allometrically elongated for reproduction (BRAÑA, 1996; KRATOCHVÍL *et al.*, 2003). This may apply also to snakes, at least as a contributing factor. Furthermore, a male's enlarged head may serve in combat (LOWE, 1948; SHINE *et al.*, 1981).

However, some largest females benefit more from non-reproductive-ecological advantages. In these, maximum fertility may occur in intermediate-sized females (BONNET *et al.*, 2000).

Male-biased SSD in snakes presumably relates to male-male combating (ANDRÉN, 1986), affecting reproductive success (MADSEN *et al.*, 1993; CAPULA & LUISELLI, 1997). The generalization that combating males are relatively large (BOGERT & ROTH, 1966) preceded the linking of combating to male-biased SSD. But there is a strong interspecific correlation of the male being the larger, with occurrence of male combats (SHINE *et al.*, 1981). Among 374 snake species, male-male combats occur in 124 species. In most of these the males grow larger than females relative to related non-combating species (SHINE, 1978, 1994). Furthermore, at least in *Thamnophis sirtalis parietalis* the larger males are more successful in forcibly inseminating females (SHINE & MASON, 2005).

However, because fecundity selection for enlarging the female and sexual selection for enlarging the male are competing, exceptions are possible. In *Vipera berus* the females are the larger sex despite the males' combating, suggesting stronger selection of female size for fecundity (MADSEN, 1988). Similarly in *Natrix* spp. mating aggregations (BORCZYK, 2007) longer males prevail (MADSEN & SHINE, 1993c) even without combat (STEMMLER-MORATH, 1935; CAPULA & LUISELLI, 1997).

Ophidian SMD includes differences in head and gape sizes, and sometimes these are allometrically further increased in the larger sex. Snakes being gape-limited predators, and prey size tending to correlate with gape size (WERNER, 1994; PIZZATTO, MARQUES & FACURE, 2009), head enlargement may lead to food-resource partitioning between the sexes (CAMILLERI & SHINE, 1990; FORSMAN & SHINE, 1997; SHINE & WALL, 2007), presumably enabling a denser population, as discovered in lizards (SCHOENER, 1967). This is not always the case and in some lizards (BRAÑA, 1996; STAMPS, LOSOS & ANDREWS, 1997) and in *Naja melanoleuca*, despite differing relative head size, the sexes ate similar food. This dimorphism may have had other causes (LUISELLI *et al.*, 2002). Yet such dimorphism might have evolved in relation to diet without the relation being always manifested. SHINE AND

WALL (2005) reviewed SSD and ecological sexual dimorphism in 52 snake species. Among those with larger female, prey size differed between the sexes in 20/35 species but among those with larger male, prey size differed only in 2/13 species. Females ate larger prey also in the 1/4 species lacking SSD. Hence females appear to prefer large prey independently of their gape size.

Sexual dimorphism in head size, head structure, or both, even without SSD but due to allometry, enables feeding diergism, e.g., in *Agkistrodon piscivorus* (VINCENT, HERREL & IRSCHICK, 2004). Only rarely does allometric head enlargement in the smaller sex annul the morphological basis for dietary differentiation (SHINE, 1989b).

The correlation of prey size and gape size is reciprocal, and available prey may phenotypically affect head size (QUERAL-REGIL & KING, 1998; Krause, BURGHARDT & GILLINGHAM, 2003; SCHUETT *et al.*, 2005). Furthermore, other experimenters have questioned the concept that the correlation of prey size with gape size is due to active selection of larger prey by larger snakes (DOWNES, 2002).

Are larger species more size-dimorphic? Do larger species show greater SSD (REISS, 1986; SHINE, 1994)? Within groups the correlation often occurs: In Australian Typhlopidae (as viewed before the revision of HEDGES *et al.*, 2014) the females are larger and FMR correlates with RA (SHINE AND WEBB, 1990). Elapidae are male-biased and the larger species show greater SSD (SHINE, 1989a; GREER, 1997).

According to prevailing hypotheses, (1) males gain social, hence reproductive, advantages from (1a) being large (SHINE, 1978; ABOUHEIF & FAIRBAIRN, 1997), as the larger male wins combats (GREENE & MASON, 2000), or merely (1b) having a heavy head (SHINE *et al.*, 1981). Sometimes the species secondarily benefits through (2) dividing food resources between the sexes (SHINE & WALL, 2005).

Females gain a reproductive advantage from (3a) being long, or (3b) merely having a long abdomen (SHINE, 1992). When the species is relatively small, this factor becomes dominant; females are larger than males. The smaller the species, the greater this SSD. In larger species the male is the larger sex, and the larger the species, the greater the SSD. These relations are depicted in FAIRBAIRN & PREZIOSI (1994) and ABOUHEIF & FAIRBAIRN (1997).

These SSD trends have been called RENSCH'S Rule (ABOUHEIF & FAIRBAIRN, 1997; FAIRBAIRN 1997) although RENSCH (1950, 1959) never explicitly formulated it (SEIFAN *et al.*, 2009). For reptiles the rule that among related species the direction and extent of SSD depend on species size was apparently first formulated by FITCH (1981) when reviewing SSD across Reptilia. His text ended with "Fig. 9. Average adult size in lizards and snakes correlated with SSD showing that in both groups SSD (especially with male superiority) tends to be greater in species of large body size and less in small species". The FMR axis ranged 70–155.

Data supporting RENSCH'S rule have been reported from assorted squamate groups. Among Elapidae, generally in smaller species the female was the larger sex but in larger species the male was larger (SHINE, 1991a). Five Israeli *Eirenis* (Colubrinae) species conspicuously displayed RENSCH'S rule (WERNER & VENTURA, 2010, 2011) and a sixth Iranian species (SADEGHI, RASTEGAR-POUYANI & YOUSEFKHANI, 2014) fit into the same regression of FMR over RA. Most reptile lineages with frequent male combat and male-biased SSD followed RENSCH'S rule (Cox *et al.*, 2007). Recently the validity of RENSCH'S rule was discussed for turtles and demonstrated in the *Testudo graeca* complex (WERNER *et al.*, 2015). Some snake and turtle lineages indicated an opposite pattern but significantly so only in natricine snakes. The ultimate explanations for both the general trend and its exceptions remain unclear (Cox *et al.*, 2007; WERNER *et al.*, 2015).

Head size and eye size. Environmental effects on head size and shape during embryogenesis have been reported only from a lizard (ULLER & OLSSON, 2003) and are unknown in snakes. However, postnatal food availability may affect head size and shape in snakes (QUERAL-REGIL & KING, 1998; KRAUSE *et al.*, 2003).

Among 114 snake species, in 47% of the species relative HdL showed significant SMD. In most species the female was the larger sex and additionally had a relatively larger head, enabling diet divergence; often the difference was present from birth, e.g., in *Natrix natrix* (SHINE, 1991b; GREER, 1997; GREGORY, 2004). At least in *Dendrelaphis punctulata* (Colubridae) in which female RA ≤ 200 cm while male RA only ≤ 110 cm, and the female has a relatively larger head, the female's jaw bones are further enlarged relative to head size (CAMILLERI & SHINE, 1990). Strong female-biased SSD augmented by head enlargement has dietary consequences in *Acrochordus arafurae* (SHINE, 1986). Also when the larger sex is the male can its head be further enlarged, e.g. in *Hierophis viridiflavus* (FORNASIERO *et al.*, 2007). In *Agkistrodon piscivorus* the male's gape is enlarged through elongation of the quadrate bones, without significant head enlargement (VINCENT *et al.*, 2004).

The frequent further enlargement of the feeding apparatus in the larger sex fits the hypothesis that SSD arises for ecological reasons, viz. prey partitioning (SHINE, 1989b). Though head size and prey size often agree (WERNER, 1994; VINCENT & HERREL, 2007), this hypothesis seems countered by the smaller sex often having a relatively enlarged head, mitigating head SMD and reducing the basis for dietary differentiation. This occurs in both colubrids and viperids (VITT, 1980; VITT & VANGILDER, 1983; here in Table 3): For example, *Natrix natrix* RA FMR = 135.4 but HdL PERCRA FMR = 99.4; and *Echis c. terraesantae* RA FMR = 96.4 but HdL PERCRA FMR = 105.3; and 12 other taxa in which RA is greater in one sex and HdL PERCRA in the other. Conceivably sometimes the advantage of broadening the range of prey sizes available to the smaller sex, exceeds the advantage of reducing the food competition between the sexes.

Almost all head SMD reports mentioned have considered prey ingestion, but not the eye that often detects the prey. Regnum-wide, eye size sexual dimorphism is not rare. Among 16 butterfly species, the eye was generally larger in the males (RUTOWSKI, 2000). In chickens (*Gallus gallus domesticus* LINNAEUS, 1758) male eyes average larger than female eyes (ZHU *et al.*, 1995). The situation in geckos was summarized in the Introduction. But for snakes, beyond the cases reviewed in the Introduction, we found few data of apparent, statistically insignificant, sexual dimorphism of eye size (TOMOVIC *et al.*, 2002; COTTONE & BAUER, 2009a,b,c).

Herein few species showed isometric eye size, the eyes having similar relative size in the sexes, the larger sex having larger eyes. In these the FMR of absolute eye size was nevertheless more moderate than that of RA (Table 3). In the remaining taxa usually either the sexes had similar RA, or absolute eye size was similar despite SSD. This overall situation is interpreted as reflecting an ecological advantage for the smaller sex to share the eye size and eyesight of the larger sex. But in four taxa the eyes were larger (in mm) in the smaller sex – all males – than in the females. Of these, *Coronella austriaca* and *Eirenis c. coronella* were diurnal, and *Crotalus cerastes* (Fig. 3) and *Echis borkini* were nocturnal. Though statistically insignificant, this masculine connection may reflect additional tasks for the male's eyes, e.g., finding females.

The corrective equating of eye size between the sexes, sometimes overshooting to exaggerated eye size in the smaller male, is achieved in different ways. Each hypothetical allometric route foreseen in the Introduction was realized in some taxon: enlarging the eye within the head, enlarging the head relative to the body, or both. The details can vary within a genus, e.g., *Psammophis* (COTTONE & BAUER, 2009a,b,c; and herein).

One wonders about eye-size in the species whose head size has already been reported elsewhere. Three such species are included here. Our *Hierophis viridiflavus* data agree with the literature: the male is larger with a relatively yet larger head. From our data (although statistically insignificant) eye size relative to the head appears to be larger in the female, so the sexual dimorphism in absolute eye size is more moderate than the SSD. Our *Natrix natrix* data agree with the literature that the female is larger; in our sample the female's head is not further enlarged; Eye%HdL is significantly greater in the male, and hence the sexual dimorphism in absolute eye size is more moderate than the SSD. Our *Crotalus cerastes* data agree with the literature (KLAUBER, 1956): the female is a little larger than the male, and has the head somewhat proportionately enlarged. In our data Eye%HdL is significantly greater in the male, and in absolute terms his eye is larger than the female's. These observations fit a hypothesis that eye size affects the microevolution of head size.

There is no SMD of head size in the pythons, that have strong female-biased SSD but across species, FMR (of RA) is not correlated with RA (GREER, 1997). Conceivably many are large enough for the size of the eye not to be critical.

Indeed, it seems useful to investigate such questions separately in different evolutionary units. We found profound inter-family differences (Tables 4, 5). Colubridae average longer than Viperidae but absolute eye size is greater in the Viperidae. In both families females are larger than males. HdL PERCRA appears greater in the Viperidae. In both families it is similar in the sexes (near isometry), so that absolute HdL is a little greater in the females. Eye size is greater in the Viperidae also in relative terms, in PERCRA and in %HdL. Its SMD differs between the families: In Colubridae, eye diameter (%HdL) is slightly greater in the males, eye diameter PERCRA is about the same in the sexes, and absolute eye size is a little greater in females. Among Viperidae, eye diameter (%Head length), eye diameter PERCRA and absolute eye size are greater in the males. It remains unclear whether the mostly nocturnal viperids having larger eyes reflects the families' heritages or ecological adaptations (CAPRETTE *et al.*, 2004).

In computing these inter-family differences we have not screened the data for "phylogenetic contrasts", namely whether the number of events of a shift from diurnal to nocturnal life had been smaller than the number of nocturnal species. In the context of behavioural ecology, the relevant variable seems to be, how many extant discrete taxa thrive with a given combination of characters. Moreover, at least in gekkonoid lizards, eye morphology and the correlated diel activity cycle are highly plastic as seen among assorted diurnal genera (RÖLL, 2001) and in the genus *Ptyodactylus* (WERNER & SEIFAN, 2006).

We are not contesting the prevalent hypotheses about the selective forces driving SSD and SMD in snakes. We merely hold that head SMD is sometimes modulated also by the requirements of eyesight. Moreover, it remains to be seen to what extent eye size in snakes may be correlated (positively or negatively) with the sizes of the other major sensory organs (NUMMELA *et al.*, 2013).

Conclusions

1. Most snakes are sexually size-dimorphic. Of 26 samples (species, subspecies, geographical populations), 12 (46.2%) showed significant SMD in at least one of 3–6 mensural or computed characters.
2. Snake SMD may show intraspecific geographical variation of unpredictable pattern; its study should take such variation into consideration.
3. Of the mensural characters, RA was significantly greater in females in 10/21 samples of sufficient size (significantly in 4/10), in males in 8/21 samples (significantly in 3/8), and equal in three samples.
4. Relative HdL tended to be male-biased in taxa with female-biased RA and female-biased in taxa with male-biased RA.
5. The relatively longer HdL in males may result in part from the elongation of the females' abdomen as a reproductive adaptation.

6. Species varied in the SMD of absolute eye size; generally this was mitigated compared to SSD of RA, due to allometric relationships among eye size, head size, and RA. Sometimes the eye was even larger in the smaller sex. These observations fit our hypothesis: eyesight may affect the evolution of head size.
7. The FMR of few characters correlated with the FMR of RA, and sometimes differently in Colubridae and Viperidae, at least as sampled in the Levant.
8. Before generalizing, it may be useful to study such issues separately in different evolutionary units. Herein, Colubridae exceeded Viperidae in RA but Viperidae had larger eyes. In Colubridae the females tended to have slightly larger eyes and in Viperidae the males tended to have slightly larger eyes.

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