

# Characteristics and heritability analysis of head scales of the Hungarian meadow viper (*Vipera ursinii rakosiensis*, Méhely 1893)

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**Abstract.** The objective of our research was to determine the heritability of head scale numbers of *Vipera ursinii rakosiensis*. 430 specimens (177 males and 253 females) were included in the analysis, most of which were born and raised in the Hungarian Meadow Viper Conservation Centre between 2004 and 2008. Due to the controlled breeding conditions, the dams of the offspring were known, and the sires were known in 51% of the cases. Only the ancestors of the wild caught specimens were unknown, but these animals were included as parents in the analysis. Photographic identification was used to identify and characterise the specimens, the majority over consecutive years. We counted the following scales: loreal-, circumocular-, apical-, and crown (intercanthal- and intersupraocular-) shields, as well as presence-absence data of other characteristics which are detailed further in the article. The variance and covariance components were determined via the restricted maximum likelihood method. The repeatability animal model consisted of the year of birth and the sex of the snakes as fixed effects, the dam as permanent environmental, and the animal as random effects. Heritability values varied between 0.32 and 0.70. We also report scale numbers and statistics of differences between scale numbers of sexes.

**Keywords:** heritability, morphology, pholidosis, restricted maximum likelihood, *Vipera ursinii rakosiensis*.

## Introduction

Morphology is a well documented branch of herpetology. Many publications present evidence that environmental factors – especially temperature – affect the embryogenesis of snakes, through biasing survival chance, growth, skeletal structures or scale numbers (Fox, 1948; Vinegar, 1973, 1974; Osgood, 1978; Shine et al., 1997; Lourdais et al., 2004; O'Donnell and Arnold, 2005; Shine et al., 2005). Temperature effects on scale numbers was first proposed by Fox (1948) and was subsequently tested by Osgood (1978). These studies were later criticised by Arnold and Peterson (2002). They pointed out that amongst other concerns, littermates were treated independently, and thus

genetic relationships could not be taken into consideration.

Here we present a different approach. Our goal in this study was to estimate heritability values ( $h^2$ ) of head scales by applying a statistical method widely used in animal genetics: the animal model (Henderson, 1975; Lynch and Walsh, 1998; Kruuk, 2004). It is used to confirm the results of Arnold and Peterson (2002), which suggest that scalation is not environment-dependent, and to demonstrate a novel way to analyse genetical aspects of snake populations. With this analysis, we were able to estimate to what extent variation in a characteristic is genetically determined. Traits that display heritable variance have adaptive potential under natural selection, which is crucial to the survival of populations living in changing environments (King, 1997).

Quantitative genetic analyses of snake populations already exist in herpetological literature, yet to our knowledge, this is the first use of the animal model combined with a multigenerational approach. Dohm and Garland (1993) were the first to deal with heritability of head scales using the example of *Thamnophis sirtalis*

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*fitchi*. In this case, the authors also used a restricted maximum likelihood method (REML). Beatson (1976) estimated heritabilities and genetic correlation among different characteristics to predict evolutionary change in the disruptive coloration of *Nerodia* (former *Natrix*) *s. sipedon*. He “calculated the interclass correlation coefficient from analysis of variance on full-sib groups” to obtain estimates of heritability. King (1997) provided heritability values for morphological measurements as well as for some scale characteristics (ventral, subcaudal, labial and temporal scales) of the brown snake (*Soreria dekayi*), estimated from offspring-dam regression. Arnold (1988, unpublished) studied the inheritance, selection and microevolution of two traits of *Thamnophis elegans* (number of vertebrae in the body and tail) to compare two populations. In this case, statistical estimates of genetic variances and covariances were also achieved by regressions of offspring on dam’s value. In their papers, Arnold and Phillips (1999) and Phillips and Arnold (1999) presented another powerful tool in quantitative genetics: the comparison of additive genetic variance-covariance (G-) matrices based on common principal components (eigenvalues and eigenvectors) using the Flury hierarchy. Here the goal is similar to the abovementioned study; namely, to compare two populations of *Thamnophis elegans*. Genetic parameters were obtained in the manner of Arnold (1988, unpublished).

We analysed the head scales of the Hungarian meadow viper (*Vipera ursinii rakosiensis*, Méhely, 1893), a useful data set mainly because it is used to identify specimens in the Hungarian Meadow Viper Conservation Project, and are also used in taxonomic studies of viperids (Nilson and Andrén, 1988, 2001; Zinenko, Țurcanu and Strugariu, 2010). The meadow viper is one of the most endangered reptile species in Europe, and is thus strongly protected in Hungary (Edgar and Bird, 2006, unpublished; Újvári, Korsós and Péchy, 2000; Péchy, 2007). There is a LIFE-Nature Programme to preserve

this species in the Hungarian fauna which also includes a captive breeding programme. Vipers have been bred and raised in the Hungarian Meadow Viper Conservation Centre since 2004 in outdoor terraria. The breeding of the specimens in the centre is strictly controlled, and is thus amenable to heritability analysis (Halpern, 2007; Halpern, Major and Péchy, 2007; Halpern et al., 2010).

## Materials and methods

Most of the specimens we examined were bred and raised in the Hungarian Meadow Viper Conservation Centre between 2004 and 2008. 430 vipers (177 males and 253 females) were included in the analysis. Founders of the captive population were wild-caught and taken to the Conservation Centre; therefore, the parents of these vipers were not known (Halpern, Major and Péchy, 2007; Halpern et al., 2010). Due to the controlled breeding, the dams of the offspring were known, and the sires were known in 51% of the cases. In some terraria, several males were paired with one female to simulate the natural breeding process or wild-caught females were gravid when collected, thus 49% of the analysed specimens have unknown sires.

We present data from 3 generations (founding, F1 and F2) of Hungarian meadow vipers. The founding generation consisted of 12 specimens in the first year (2004) but other wild-caught vipers were included in the breeding programme in the later consecutive years. Altogether 34 specimens were introduced as parents to the breeding programme by 2008. In this analysis we used data from 15 wild-caught animals. The first generation of newborn meadow vipers was established in 2005 (with the exception of a handful of vipers which were born between 2001 and 2003 as the offspring of wild-caught captive specimens). This generation was included in the breeding programme in 2008. The F1 generation consisted of 252 specimens, and 163 vipers were born into the F2 generation through 2008. Average litter size was 9.84 newborns (stillborns included), litter size ranged from 1 to 27, and the percentage of stillborn vipers was 6.93%. Stillbirth ranged from 0 to 8/litter ( $n_{\text{specimens}} = 433$ ,  $n_{\text{litters}} = 44$ ).

We counted scales on photographs of the head, taken from three angles (above, left side, right side). Most of the specimens were photographed over consecutive years (fig. 1). We counted the following scales: loreal (LOR)-, circumocular (CIRCOC)-, apical (APIC)-, and crown (CROWN) shields. In cases of bilateral characteristics the sum of both sides was used in the analysis. LOR was further divided into anterior loreals (LORa), scales that directly touch the nasal shield and posterior loreals (LORp), scales that do not touch the nasal shield, but are between LORa and CIRCOC. CROWN consists of intercanthal (ICANTH) and intersupraocular (a.k.a. parafrontal) (ISOC) shields.



**Figure 1.** Example of head photography over consecutive years and lost scales (arrows) in *Vipera ursinii rakosiensis*.

Differences between sexes were tested using the Mann-Whitney test on the square root transformed dataset in SPSS 16.0.1 (SPSS Inc.) due to the non-normal distribution of our data. This statistic is a non-parametric, rank correlation-based test which has the condition of homogeneity of variances (Field, 2005; Reiczigel, Harnos and Solyosi, 2007); this assumption was tested using Levene’s test.

The animal model used in this study is a restricted maximum likelihood method (REML) which analyses data on the basis of a pedigree. The animal model is a mixed model with two components: fixed and random effects. “Fixed effects are unknown constants that affect the mean of a distribution. Random effects are used to describe factors with multiple levels sampled from a population of possible values, for which the analysis provides an estimate of the variance of the effects” (Kruuk, 2004). These models have the advantage of incorporating multigenerational information—not just parent-offspring relations— and are “not bound by assumptions of non-assortative mating, inbreeding or selection, and allow for unbalanced datasets” (Dohm and Garland, 1993; Kruuk, 2004). Another great benefit of using REML methods is that animals with unknown paternity can still be analysed. This is a remarkably powerful tool in the study of wild populations because “the effects of environmental heterogeneity can be quantified and controlled for through the appropriate model” (Kruuk, 2004).

To determine heritability values ( $h^2$ ), we applied the VCE-6 (Groeneveld, Kovač and Mielenz, 2008) software which uses the restricted maximum likelihood method to determine variance and covariance components. The variables were entered independently. The repeatability animal model consisted of the year of birth and sex of snakes as fixed effects, the dam as permanent environmental and the animal as random effects. Presence-absence data was also collected (see later), but could not be analysed with this method presumably due to the binary nature of the data.

The VCE-6 software determines the following variance components:

- Genetic variance ( $V_g$ ): Variance caused by alleles within the total phenotypical variance.

- Variance caused by maternal effect ( $V_{dam-pe}$ ): explains similarity between specimens of the same dam and difference between specimens of different dams.
- Error variance ( $V_e$ ): Maternal variance and all variance caused by interactions between genes.

From these results, the following parameters can be calculated:

- Phenotypical variance ( $V_{phe}$ ):

$$V_{phe} = V_g + V_{dam-pe} + V_e \quad (1)$$

- Heritability ( $h^2$ ): explains genetic originated difference between specimens.

$$h^2 = V_g/V_{phe} \quad (2)$$

- Proportion of variance explained by the maternal effect ( $Var_{dam-pe}$ ): explains similarity between specimens of the same litter, independently from genetic relationships. It can be interpreted as the permanent environmental (maternal) effect that influenced the specimens until the characteristic was measured.

$$Var_{dam-pe} = V_{dam-pe}/V_{phe} \quad (3)$$

- Residual proportion of variance ( $Var_{res}$ ): Proportion of variance not explained by effects in the model.

## Results

### Scale numbers

Levene’s test showed that ICANTH violates the assumption of homogeneity ( $F_{1,428} = 19.32$ ,  $p < 0.0001$ ), thus it was removed from further analysis regarding differences between sexes. APIC and CIRCOC of the vipers showed no difference between sexes; all other characteristics showed significant differences between the sexes with females exceeding males (table 1).

We present our counted scale numbers and scale numbers taken from Nilson and Andrén (2001), given as mean ± SE and range, and also the frequency of certain characteristics are mentioned (table 2). A powerful statistical comparison of the two datasets was not possible due to lack of data; however, in most cases, there seem to be only slight differences in scale counts taken by Nilson and Andrén (2001) and our own results (such as the case of CROWN of males, LORa of females, frequency of sec-

ond apical and divided frontal). We note here that in the case of the two former characteristics we were able to execute a two-sample *z*-test which showed significant differences between the two datasets in case of LORa of females and CROWN of males (two-sample *z*-test: *z* = -2.0003, *P*: <0.05; *z* = -1.6878, *P*: <0.05 respectively). A random sample of our data was used to match the sample size of Nilson and Andrén (2001). However, we must emphasise that this test is only reliable for non-normally distributed data if sample sizes are greater than 30 (Reiczigel, Harnos and Solymsi, 2007). This assumption is met by the female, but not male data. Otherwise the differences may be explained through the different sizes of the datasets, or slight differences in the method of counting scales.

Apart from the characteristics already listed in former sections, frequencies of the presence of certain characteristics were also observed as on one or both sides of head (table 3).

**Table 1.** Mann-Whitney *U* test statistics showing differences between sexes of *Vipera ursinii rakosiensis*. Abbreviations as in table 2.

Characteristic	Median		Mann-Whitney <i>U</i>	Significance ( <i>p</i> )	Effect size ( <i>r</i> )
	Males	Females			
APIC	1	1	21 701	0.40	-0.04
CIRCOC	17	17	22 047	0.78	-0.01
ISOC	6	6	19 440	<0.05	-0.11
LORa	5	6	18 269	<0.001	-0.16
LORp	0	1	15 351	<0.0001	-0.28
LOR	5	7	16 139	<0.0001	-0.24
CROWN	11	12	17 474	<0.0001	-0.19

**Table 2.** Comparison of scale counts and frequency of certain characteristics, given as mean ± SE and range. Abbreviations: APIC, apical; CIRCOC, circumocular; LORa, anterior loreal; LORp, posterior loreal; LOR, total sum of loreal; CROWN, crown; ISOC, intersupraocular; ICANTH, intercanthal scales.

	Nilson and Andrén (2001)		Üveges et al. (present study)	
	Males	Females	Males	Females
APIC	1.09 ± 0.04 1-2		1.15 ± 0.02 0-2	
CIRCOC	17.08 ± 0.25 15-20	17.02 ± 0.25 14-22	17.36 ± 0.06 14-21	17.33 ± 0.06 15-21
LORa	4.91 ± 0.33 2-8	5.52 ± 0.29 2-9	5.20 ± 0.07 2-8	4.80 ± 0.06 2-8
LORp	NaN	NaN	1.42 ± 0.07 0-7	0.76 ± 0.06 0-9
LOR	NaN	NaN	6.62 ± 0.11 2-14	5.56 ± 0.1 2-15
CROWN	11.30 ± 0.43 7-15	12.10 ± 0.46 8-20	12.65 ± 0.14 7-24	11.55 ± 0.14 6-20
ISOC	NaN	NaN	6.62 ± 0.12 2-16	6.05 ± 0.11 2-13
ICANTH	NaN	NaN	6.03 ± 0.05 3-12	5.50 ± 0.05 3-9
Frequency of second apical*	9.4%		15.6%	
Frequency of upper nasal split	91.8%		90.5%	
Preocular(s) in contact with nasal	69.4%		65.6%	
Divided frontal	1.6%		6.5%	
N	23	38	177	253
	62 (* = 64)		430	

*Heritability analysis*

Heritability of scale characteristics in meadow vipers ranged from moderate (0.15-0.50) to high (greater than 0.50) (Willis, 1991; table 4).

APIC ( $h^2 = 0.43$ ) and LORp ( $h^2 = 0.32$ ) were moderately heritable, with non-significant heritability values; all the other traits are considered to be highly heritable, and had statistically significant values. The greater the  $h^2$  value, the greater the genetic determination of the trait. Crown (CROWN) ( $h^2 = 0.70$ ), which consisted of intercanthals (ICANTH) ( $h^2 = 0.63$ ) and intersupraoculars (ISOC) ( $h^2 = 0.65$ ), had the highest heritability rating. This can be also interpreted as the variance in CROWN between the specimens is 70.11% genetic in origin. Con-

trary to this, LORp had the lowest heritability rating ( $h^2 = 0.32$ ).

$Var_{dam-pe}$  was also very low, showing that in general, maternal effects do not have high impact on the variance between specimens. APIC had the highest  $Var_{dam-pe}$  values, indicating a stronger maternal effect, although it still accounts only for 5.72% of the variance.

$Var_{res}$  was relatively high, in case of LORp particularly high ( $Var_{res} = 0.68$ ), indicating that factors outside the effects of the dam can account for much more of the variance; this effect was the lowest in case of the crown scales ( $Var_{res} = 0.25$ ).

**Discussion**

The scales counted at the Hungarian Meadow Viper Conservation Centre largely correspond to the scale numbers from Nilson and Andrén (2001), although there are some scale characteristics which have not been described before in *V. ursinii*, for instance, scale row between suboculars and supralabials. In case of LORa of females and CROWN of males an exact dataset of the original study would be necessary to find stronger support for differences.

To summarise the heritability analysis, most scales – except for APIC and LORp – are highly, significantly heritable ( $h^2$  range = 0.54-0.70). The crown scales had the highest heritability rating and the lowest residual variance rating, meaning they are less affected by environmental factors. Nonetheless, crown scales also had the third highest  $Var_{dam-pe}$  rating, which suggests a

**Table 3.** Frequency of presence of certain characters.

Character	%
Second column of posterior loreals	8.14
Canthal in contact with supraocular	93.95
Double first intersupraocular	34.65
Fragmented supraocular	0.47
Fusion of apical and canthal	0.23
Fusion of apical and intercanthal	0.47
Fusion of canthals	0.23
Fusion of intersupraocular and parietal	3.95
Loreal slipped down between supralabials	7.67
Multiple columns of intersupraoculars	24.65
Nasal in contact with lower praeocular	0.93
Nasal in contact with middle praeocular	39.77
Nasal in contact with upper praeocular	43.95
No apical	0.70
Partially divided apical	0.93
Posterior loreals	59.34
Presence of an interparietal scale	0.47
Scale between supralabials and suboculars	4.42
Scale row between suboculars and supralabials	0.70

**Table 4.** Variance components and heritability values  $\pm$  S.E. Significant  $h^2$  values are marked with an asterisk (\*). Abbreviations as in table 2.

Characteristic	$V_g$	$V_{dam-pe}$	$V_e$	$V_{phe}$	$h^2 \pm S.E.$	$Var_{dam-pe}$	$Var_{res}$
APIC	0.06	0.01	0.07	0.14	0.43 $\pm$ 0.17	0.06	0.51
CIRCO	0.69	0.01	0.59	1.28	0.54* $\pm$ 0.09	0.01	0.46
ISOC	3.53	0.21	1.71	5.44	0.65* $\pm$ 0.13	0.04	0.31
ICANTH	0.72	0.06	0.37	1.15	0.63* $\pm$ 0.13	0.06	0.32
LORa	1.10	0.06	0.75	1.91	0.58* $\pm$ 0.11	0.03	0.39
LORp	0.41	0.00	0.86	1.27	0.32 $\pm$ 0.14	0.00	0.68
CROWN	5.64	0.42	1.99	8.04	0.70* $\pm$ 0.12	0.05	0.25
LOR	0.80	0.07	0.60	1.46	0.55* $\pm$ 0.13	0.05	0.40

stronger influence of maternal effects relative to other traits, for example LOR, LORp, LORa, ISOC, and CIRCOC, although this value is still very small. In contrast, LORp had the lowest, non-significant heritability rating and  $\text{Var}_{\text{dam-pe}}$  with the highest residual variance proportion, indirectly suggesting an influence of environmental factors. Dohm and Garland (1993) found that for three out of four body traits and two out of four head scale counts, the majority of the phenotypic variation was of genetic origin in *Thamnophis sirtalis fitchi*. Exceptions in that study were ventrals, supralabials and postoculars. A different result can be seen in the study of Arnold and Phillips (1999), where subcaudals had high heritability values; ventrals, infralabials and supralabials moderate, and in agreement with the aforementioned study, postoculars had the lowest  $h^2$  values in *Thamnophis elegans*. Arnold and Peterson (2002) emphasise they were unable to detect effects of developmental temperature on scale count, and that phenotypic differences represent genetic differentiation. King (1997) found that tail and head length, ventral, subcaudal and temporal scales displayed high and significantly heritable variance in *Soreria dekayi*, while head width, jaw length, interocular distance and labial scales were not significantly heritable. Another interesting quantitative genetic study by Westphal et al. (2011) calculates heritability estimates of garter snake (*Thamnophis sirtalis*) colour patterns to show how postglacially expanding populations may display enhanced values of “heritable variation underlying ecologically relevant phenotypic traits” despite the fact that their genetic diversity at some loci is reduced. Apart from snakes, reptiles with temperature-dependent sex determination (TSD) such as *Chrysemys picta* (Rhen and Lang, 1998; McGaugh and Janzen, 2011), *Chelydra serpentina* (Janzen, 1992; Rhen and Lang, 1998), and *Alligator mississippiensis* (Rhen and Lang, 1998) provide an interesting opportunity for the study of “genetic variation to support an evolutionary response of TSD to sex-ratio selection”

which acts at nest site choice and the sex-determination threshold, i.e. the temperature at which a male producing genetic programme changes to produce females (McGaugh and Janzen, 2011).

Our results show that although different head scales of *V. ursinii rakosiensis* are not equally heritable, indirect evidence suggests that most of them are quite well-buffered against the effects of the environment, mostly in agreement with the findings of the aforementioned studies. This is also the case with regards to the role of maternal effects, since Beatson (1976) states that maternal effects should be minimal in case of ovoviviparous snakes.

Since 2004 the specimens in the Conservation Centre have been strictly monitored, and postnatal instability of head scales has not been found, seemingly contradicting the findings of Tomović et al. in the case of *Vipera ursinii macrops* (2008). When certain scales disappear due to trauma or shedding, after recovery, a wound epithelium or neogenic scale(s) can be seen on the damaged region, thus these cases should not be mistaken as postnatal instability (Maderson, Baranowitz and Roth, 1978) (fig. 1). Apart from this, Dohm and Garland (1993), King (1997) and Arnold and Phillips (1999) both emphasise that scales do not change during postnatal life.

Studies using the animal model are powerful tools to analyse genetic parameters of wild- and captive-bred populations. As already mentioned, heritable variation in characteristics is important in the survival or recovery of populations. The results published in this study are reassuring given that *Vipera ursinii rakosiensis* is a species of high conservation concern, because the data shows that this species has potential for adaptive variation concerning the studied characteristics, but a precisely designated dataset is needed to prove this hypothesis for characteristics with more adaptive value in a future study. Furthermore other traits such as body mass indices could be studied using this method over several generations in the Hungar-

ian Meadow Viper Conservation Centre, which could be a new tool for selecting breeding pairs, thus ensuring a greater likelihood of survival when reintroduced to the wild. Genetic research is also an important part of the Hungarian Meadow Viper Conservation Project and one of our future aims is to complete these results with the results of genetic paternity analyses.

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