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Sexual dimorphism of craniological characters in the European badger, *Meles meles*, (Carnivora, Mustelidae) from the Western Carpathians

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Abstract. In the Carpathian population of the European badger, existing studies show a considerable discrepancy in the level of sexual dimorphism. The main goal of the study was to assess the sexual size dimorphism of the Carpathian *Meles meles* population in the light of the main hypotheses explaining this phenomenon. We measured 22 craniometric characteristics on sexed skulls of adult specimens from the Western Carpathians and assessed the morphological differences between males and females. A multi-model approach combined with predictive modelling was used to identify craniological parameters that discriminate badger sexes. The sexual size dimorphism was manifested mainly in differences of the feeding apparatus. The inner (IMW) and outer width of mandible (OMW) showed the highest power to discriminate between males and females (classification accuracy > 80 %). The IMW and OMW of 30 and 69 mm, respectively, may be used as rough threshold values for determination of the badger sex in the Western Carpathians. Our results seem to be in accordance with the hypothesis of sexual selection. We suppose that more even distribution of small families or individuals in the mainland Europe implicates higher level of mating competition which leads to favouring bigger and stronger males. We suppose also some role of a predatory selection by large carnivores and competition with other burrowing species leading to a potentially higher survival chance of bigger individuals in the Carpathians.

Key words: morphometry, predictive modelling, mandible, hypotheses, Slovakia

Introduction

Formerly, only one badger species was assumed to occupy almost the whole Palearctic (Lynch et al. 1997). Subsequent analyses based on the mitochondrial DNA distinguished four phylogeographic groups in the *Meles* genus (Marmi et al. 2006), leading to the recognition of four species: the European badger *Meles meles* (Linnaeus, 1758), the Asian badger *M. leucurus* (Hodgson, 1847), the Japanese badger *M. anakuma* Temminck, 1844, and *M. canescens* Blanford, 1875 from Southwest Asia and the mountains of Middle Asia (Abramov & Puzachenko 2013, Sato 2016). Recent studies recognise three subspecies of the European badger (Abramov & Puzachenko 2013): the Scandinavian *M. m. meles* (Linnaeus), the Norwegian

M. m. milleri Baryshnikov et al. 2003, and the European *M. m. taxus* (Boddaert, 1785).

Within the badger species, there is little sexual size dimorphism (SSD). Several studies did not find clear differences in quantitative craniological parameters between sexes of the European badger (e.g. Wiig 1986, Hell & Paule 1989). Sharp SSD in craniometric characteristics has been seldom reported (Lüps & Roper 1988, Lee & Mill 2004, Florijančić et al. 2011). A meta-analysis performed by Lynch et al. (1997) showed the highest level of SSD in the population from Slovakia (the Carpathians), and the lowest one in the populations from Ireland and Great Britain. Abramov & Puzachenko (2005) argue that the degree of SSD in the European badger varies geographically

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and SSD provides an opportunity for more or less rapid modifications in response to changes in environmental factors, such as population density, seasonality, climate change, diet etc.

Carnivores are known to exhibit SSD while several hypotheses have been proposed to explain this phenomenon. These hypotheses fall into two main categories (Johnson & Macdonald 2001, Stevens & Kennedy 2005): sexual selection (Erlinge 1979, Moors 1980) and resource partitioning (Brown & Lasiewski 1972). The first of them is based on a presumption that bigger males have greater chance to be successful in mating whereas smaller females save energy for feeding cubs. The second hypothesis predicts that different size of sexes, leading to partial dietary separation, reduces intraspecific competition for food.

In a heavily modified European landscapes, the Carpathians have a specific position owing to their high biodiversity, well-preserved natural or semi-natural forest networks, as well as continuous presence of all carnivores (Zingstra et al. 2009). Thus, these mountains offer an exceptional opportunity to study natural relationships in animal populations (Lešo & Kropil 2007). The main goal of the study was to assess SSD of the Carpathian *M. meles* population in the light of the main hypotheses. The only complex craniometrical data analysis of the badger skulls from the Carpathians was published by Hell & Paule (1989). They found a very slight sexual dimorphism in the size and shape of the skulls, which contrasts with the meta-analysis performed by Lynch et al. (1997). Thus, different interpretation of the results in

the context of two main hypotheses may arise. In order to solve this discrepancy, we collected sexed skulls of the European badger from the Western Carpathians and aimed 1) to assess a morphological difference between males and females and 2) to identify the best craniological parameters that discriminate between the badger sexes. In contrast to previous studies, we went beyond the significance tests of null model hypotheses and validated the predictive accuracy of discrimination models on out-of-sample data, which allows evaluating practical usefulness of craniometric measures for differentiation between sexes. Moreover, we estimated threshold values for various morphological characteristics that may be used for determination of the badger sexes.

Material and Methods

Cranial morphometry

The study is based on 90 skulls of adult individuals of the European badger (50 females and 40 males). The skulls were measured on annual hunting displays in 10 districts during the period 2014-2016. The districts were evenly distributed across the area of Slovakia belonging to the Western Carpathians. All the badger skulls of adult individuals hunted within each district were measured. Since skull growth in badgers is complete by the third year of life (Lynch et al. 1997), the individuals younger than 2.5 years were excluded from the analysis to minimize the variability caused by age differences (Lee & Mill 2004). The age of each individual was estimated using the morphological features of skull structure, especially the development

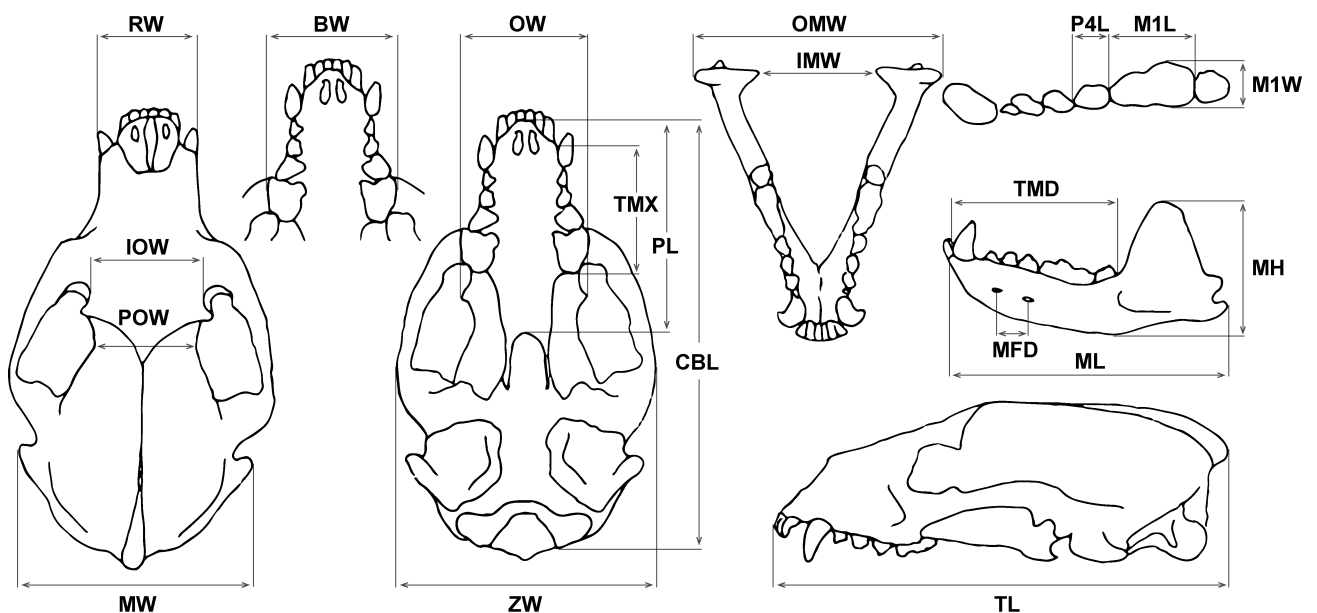


Fig. 1. The scheme of the cranial measurements. For codes of craniometric measures see Table 1.

Table 1. Summary characteristics of 22 craniometric measures of the European badger. Mean values \pm standard errors and ranges [min-max] are displayed separately for the female and male skulls.

Craniometric characteristics	Unit	Code	Female (n = 50)	Male (n = 40)
Condylbasal length	mm	CBL	128 \pm 0.46 [122-135]	130 \pm 0.58 [124-139]
Total length	mm	TL	129 \pm 0.57 [122-139]	131 \pm 0.71 [125-139]
Length of teeth row in maxilla	mm	TMX	44 \pm 0.45 [41-56]	45 \pm 0.65 [37-58]
Palatal length	mm	PL	72 \pm 0.51 [63-79]	73 \pm 0.47 [64-78]
Zygomatic width	mm	ZW	76 \pm 0.49 [68-84]	78 \pm 0.72 [72-89]
Orbital width	mm	OW	36 \pm 0.19 [34-38]	37 \pm 0.16 [34-38]
Interorbital width	mm	IOW	32 \pm 0.41 [27-39]	33 \pm 0.45 [28-42]
Postorbital width	mm	POW	24 \pm 0.27 [21-29]	25 \pm 0.36 [19-33]
Mastoid width	mm	MW	61 \pm 0.58 [42-70]	63 \pm 0.32 [58-67]
Bimolar width	mm	BW	43 \pm 0.32 [39-49]	43 \pm 0.31 [39-49]
Width of rostrum	mm	RW	32 \pm 0.33 [29-39]	32 \pm 0.23 [29-39]
Neurocranial capacity	cm ³	NC	52.6 \pm 0.57 [43.0-64.0]	53.3 \pm 0.53 [43.0-62.0]
Length of teeth row in mandible	mm	TMD	50 \pm 0.54 [41-59]	51 \pm 0.36 [46-54]
Maximal height of mandible	mm	MH	37 \pm 0.29 [31-41]	37 \pm 0.24 [35-41]
Length of mandible	mm	ML	90 \pm 0.49 [85-99]	91 \pm 0.45 [85-99]
Inner width of mandible	mm	IMW	28 \pm 0.30 [26-38]	32 \pm 0.55 [27-39]
Outer width of mandible	mm	OMW	67 \pm 0.42 [62-76]	71 \pm 0.47 [64-79]
Distance between mental foramens	mm	MFD	5 \pm 0.12 [4-7]	5 \pm 0.12 [4-6]
Length of upper P4	mm	P4L	7.8 \pm 0.08 [7.0-9.0]	7.8 \pm 0.09 [6.5-9.0]
Length of upper M1	mm	M1L	16.1 \pm 0.18 [13.5-19.8]	15.9 \pm 0.14 [13.3-17.4]
Width of upper M1	mm	M1W	12.0 \pm 0.20 [11.0-19.0]	11.9 \pm 0.07 [11.1-13.0]
Ratio of cranium length to width		C/W	1.7 \pm 0.01 [1.5-1.8]	1.7 \pm 0.02 [1.5-1.9]

of a sagittal crest, complete adult dentition and sutures ossification. Skulls with complete adult dentition, distinct sagittal crest and ossified nasal sutures were considered to be adult (following polecats age estimation by Ansorge & Suchentrunk 2001). Since all badgers were hunted in autumn (legal hunting season), the age estimation was restricted to distinguishing 1.5 years old individuals from the older ones. The skulls with ambiguous characteristics for reliable age estimation were avoided. Only the skulls of known origin (locality and date of killing) and sex were included in the analysis.

For craniometric measurements, a calliper accurate to 0.1 mm was used. Neurocranial capacity was measured by filling the neurocranial space with small lead shots and subsequently measuring their volume in graduated cylinder. Altogether, 22 parameters were measured on each skull (Fig. 1) or derived from measurement as a length/width ratio. Summary characteristics of craniometric parameters are given in the Table 1.

Data analysis

We assessed sexual dimorphism of the European badger using a multi-model approach in combination with predictive modelling. The craniological data were fitted by several models of different complexity in order to prevent discarding any important information and to ensure robustness of the results.

As a first step, we evaluated sexual dimorphism using all craniological measures simultaneously. We performed the partial least squares discriminant analysis (PLS-DA) which is capable to effectively handle many highly correlated predictors in a single model (Barker & Rayens 2003). Prior to the analysis, craniometric characteristics were standardized equalizing the weight of the dimensionally heterogeneous variables. The optimal number of components maximizing the classification success of the model was selected using the ten-fold cross-validation (see below for further details). The amount of variance explained by PLS-DA components was assessed by the randomization test in which the observed variance was compared with

Table 2. Results of the simple logistic GLMs testing for the craniometric differences between females and males of the European badger. Cross-validated classification accuracy and its 95 % confidence intervals (in square brackets) are given along with the test criteria (χ^2) and probabilities (p) from the likelihood-ratio tests. In addition, threshold values [95%CI] and classification to sex above these thresholds are also displayed. Note that we did not calculate thresholds for models with inflection points out of range of the data (N/A). Threshold units are listed in the Table 1.

Craniometric characteristics	Accuracy (%)	χ^2	p	Threshold	Sex
Condylbasal length	58 [47-66]	4.77	0.0289	130 [127-135]	male
Total length	63 [52-73]	5.22	0.0223	132 [128-137]	male
Length of teeth row in maxilla	56 [49-62]	1.20	0.2731	47 [40-55]	male
Palatal length	56 [48-63]	2.51	0.1133	74 [69-78]	male
Zygomatic width	67 [55-78]	6.86	0.0088	78 [75-83]	male
Orbital width	69 [64-73]	16.95	< 0.0001	37 [36-37]	male
Interorbital width	55 [45-64]	4.05	0.0441	34 [31-39]	male
Postorbital width	58 [52-64]	2.54	0.1109	25 [22-31]	male
Mastoid width	57 [49-65]	5.07	0.0243	63 [61-67]	male
Bimolar width	53 [47-58]	0.98	0.3213	44 [41-48]	male
Width of rostrum	51 [48-52]	0.12	0.7321	37 [31-39]	male
Neurocranial capacity	53 [48-60]	0.76	0.3840	56.1 [48.3-63.0]	male
Length of teeth row in mandible	45 [36-52]	0.93	0.3336	53 [46-59]	male
Maximal height of mandible	55 [40-67]	1.96	0.1620	38 [35-41]	male
Length of mandible	50 [41-63]	2.47	0.1159	92 [88-97]	male
Inner width of mandible	83 [71-91]	43.03	< 0.0001	30 [29-31]	male
Outer width of mandible	81 [70-88]	37.95	< 0.0001	69 [68-71]	male
Distance between mental foramens	63 [53-70]	4.47	0.0346	5 [4-6]	female
Length of upper P ⁴	47 [35-53]	0.03	0.8525	N/A	N/A
Length of upper M ¹	49 [43-53]	0.65	0.4206	15.0 [13.3-15.7]	female
Width of upper M ¹	52 [46-55]	0.29	0.5881	N/A	N/A

its distribution under the null model (no craniometric differences between female and male skulls) obtained from 10000 simulated datasets with randomly reshuffled sexes among individuals (Manly 1997). The importance of each craniometric measure for discrimination of the badger sexes was calculated as a sum of the absolute model coefficients weighed proportionally to the reduction in the sums of squares by each PLS-DA component (Kuhn & Johnson 2013).

Subsequently, we fitted the generalized linear model (GLM) with binomial errors and logit link function (McCullagh & Nelder 1989) to discriminate sex of the European badger using as few craniometric variables as possible. To avoid a collinearity problem, we screened correlation matrix of 22 craniometric characteristics (Table 3) while focusing on strongly correlated pairs (absolute Pearson's $r > 0.7$) and removing that variable from each pair which showed the largest mean absolute correlation. Altogether, two variables were excluded from the analysis due to collinearity; condylbasal length and zygomatic

width. The remaining craniometric characteristics did not show considerable multicollinearity when included in the full model with all variables (variance inflation factor < 10, cf. Quinn & Keogh 2002). The minimum adequate GLM was built via sequential deletion of the non-significant terms from the full model using likelihood-ratio tests ($\alpha = 0.05$).

To ensure that we did not overlook any important sex discriminator, we fit a series of simple logistic GLMs relating sex of European badger to individual craniometric characteristics. Again, significance of the models was assessed using likelihood-ratio tests. In addition, we calculated the threshold value for each craniometric characteristic as an inflection point of the logistic curve ($p = 0.5$) above which the model predicts a higher probability of being of opposite sex than below the threshold. Ninety-five percent confidence intervals were calculated for each threshold using a non-parametric bootstrap procedure (10000 replicates) and percentile method (Efron & Tibshirani 1986).

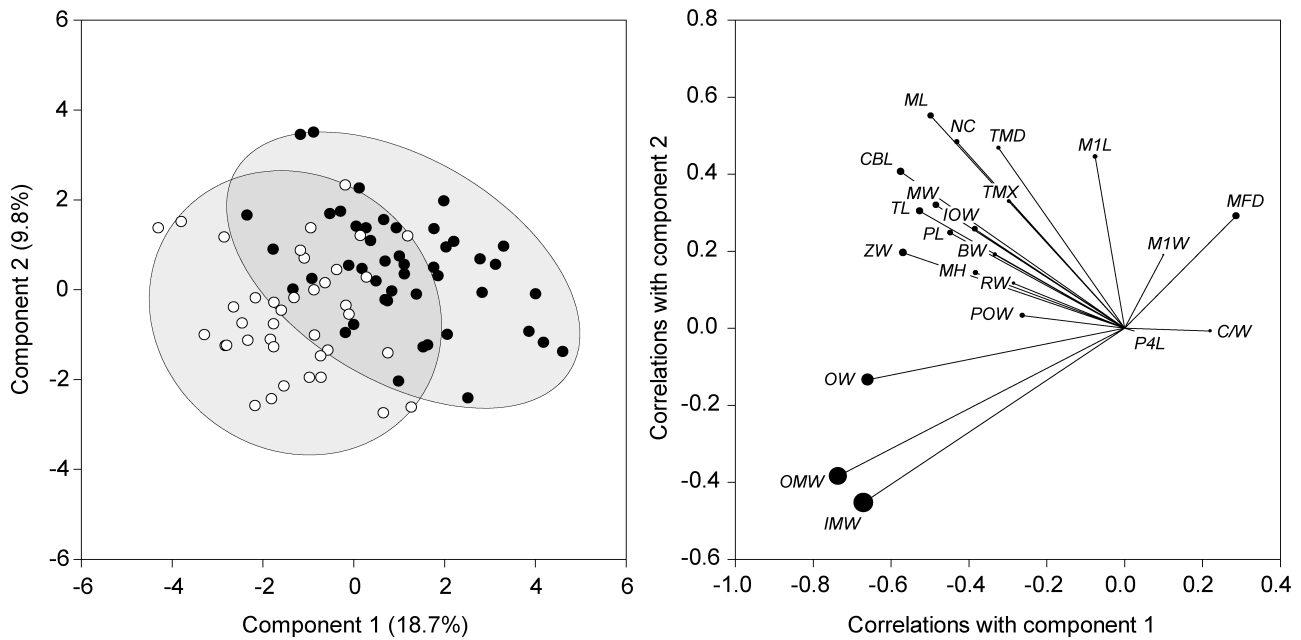


Fig. 2. The PLS-DA plot. The plot shows the morphological differentiation between males (white circles) and females (black circles) of the European badger based on 22 craniometric characteristics (left). Correlations of the measured characteristics with discriminant components (Pearson's r) and the importance of each variable for discrimination are displayed as vectors and circles of the size proportional to the variable importance, respectively (right). Ninety-five percent prediction ellipses (depicted in gray) and proportion of variance explained by each component (in parentheses) are displayed to facilitate the interpretation of the results. For codes of craniometric measures see Table 1.

Finally, we went beyond potentially misleading significance tests (cf. Johnson 1999) and evaluated predictive performance of each model on out-of-sample data (Shmueli 2010) using 10-fold cross-validation which ensures the unbiased estimate of classification success (Kuhn & Johnson 2013). This approach allowed us to assess practical relevance of the results and ability of the models to generalize to out-of-sample situations, such as sex determination of new badger skulls. Proportion of specimens correctly classified to sex (classification accuracy) was used as a measure of predictive performance. Mean classification accuracy averaged across validation folds was reported along with bootstrap 95 % confidence intervals (10000 replicates). All analyses were conducted in R version 3.2.3 (R Core Team 2015) using the packages *caret* (Kuhn 2016) and *ppls* (Mevik et al. 2015).

Results

Combination of all craniometric measures in the PLS-DA model with two components showed significant differences in morphology of male and female skulls of the European badger (expl. variance = 28.5 %, $p = 0.0068$). The model correctly classified the sex of 81 % of the badger skulls (95 % confidence interval (CI) of classification accuracy: 70-89 %). The inner width of mandible (IMW), outer width of mandible (OMW) and orbital width (OW) played the most important role in discrimination between sexes (Fig. 2).

Cross-validated predictive performance of the minimum adequate GLM slightly outperformed PLS-DA (classification accuracy [95%CI]: 83 [72-92] %). The minimum adequate GLM ($\chi^2_{(4)} = 55.3$, $p < 0.0001$) involved the four craniometric variables: interorbital width (IOW), width of rostrum (RW), inner width of mandible (IMW), and outer width of mandible (OMW). Probability of being classified as a female can be calculated from the following logistic equation:

$$\frac{1}{1 + e^{-(33.83 - 2.34IOW + 4.18RW - 4.57IMW - 3.75OMW)}}$$

Finally, a series of simple logistic GLMs revealed nine significant craniometric characteristics that can be used for determination of the European badger sexes (Table 2). In general, simple logistic GLMs showed a significantly lower classification accuracy than more complex models. Notable exceptions are two GLMs involving the inner (IMW) and outer (OMW) width of mandible with classification accuracy comparable to minimum adequate GLM and PLS-DA.

Discussion

Craniological parameters discriminating between the badger sexes

We have shown that males and females of the Carpathian badger population significantly differ in several morphometric parameters of their skulls. Our

Table 3. Correlation matrix of craniometric characteristics of the European badger. Pearson's correlation coefficients and *p*-values are displayed above and below the diagonal, respectively. For codes of craniometric measures see Table 1.

	CBL	TL	TMX	PL	ZW	OW	IOW	POW	MW	BW	RW	NC	TMD	MH	ML	IMW	OMW	MFD	P4L	MIL	MIW	C/W
CBL	-	0.86	0.42	0.36	0.30	0.34	0.29	0.19	0.29	0.14	0.02	0.35	0.37	0.10	0.47	0.12	0.21	-0.03	0.04	0.07	0.09	0.23
TL	<0.001	-	0.33	0.34	0.24	0.27	0.20	0.12	0.21	0.19	-0.02	0.27	0.30	-0.01	0.37	0.18	0.25	0.01	0.02	0.11	0.01	0.37
TMX	<0.001	0.002	-	0.19	-0.01	0.23	0.12	0.09	0.33	0.01	0.06	0.21	0.33	0.01	0.28	0.00	0.05	-0.07	0.00	0.11	-0.07	0.21
PL	0.001	0.001	0.076	-	0.34	0.23	0.13	0.10	0.24	0.12	0.17	0.07	0.20	0.05	0.29	0.14	0.27	-0.01	0.02	0.10	0.10	-0.12
ZW	0.006	0.026	0.946	0.001	-	0.42	0.37	0.07	0.26	0.11	0.08	0.27	0.07	0.26	0.35	0.13	0.27	-0.10	-0.03	0.12	0.07	-0.81
OW	0.002	0.012	0.032	0.035	<0.001	-	0.23	0.02	0.27	0.13	0.19	0.12	0.01	0.12	0.18	0.32	0.48	-0.13	-0.04	0.06	-0.12	-0.23
IOW	0.006	0.071	0.271	0.239	0.001	0.035	-	0.09	0.29	0.13	0.05	0.30	0.20	0.17	0.22	0.09	0.09	0.14	-0.06	0.17	0.05	-0.24
POW	0.076	0.287	0.412	0.346	0.521	0.868	0.429	-	0.23	-0.13	-0.07	0.45	0.10	0.06	0.10	0.20	0.08	0.07	0.07	-0.03	-0.08	0.01
MW	0.007	0.049	0.002	0.025	0.017	0.013	0.007	0.033	-	0.20	0.13	0.49	0.25	0.14	0.34	0.18	0.10	-0.06	-0.20	0.00	-0.01	-0.12
BW	0.218	0.081	0.928	0.262	0.336	0.227	0.248	0.227	0.066	-	0.20	0.09	0.26	0.19	0.17	0.26	0.22	-0.14	0.08	0.24	-0.13	0.03
RW	0.888	0.860	0.616	0.129	0.461	0.084	0.635	0.502	0.229	0.064	-	0.23	-0.08	0.12	0.12	0.31	0.24	-0.07	-0.09	0.01	-0.17	-0.08
NC	0.001	0.012	0.059	0.533	0.011	0.264	0.005	<0.001	<0.001	0.417	0.038	-	0.22	0.30	0.45	0.15	0.10	0.04	-0.15	0.10	0.02	-0.10
TMD	0.001	0.006	0.002	0.067	0.535	0.950	0.072	0.347	0.020	0.018	0.472	0.046	-	0.16	0.64	0.05	0.14	-0.02	0.13	0.29	0.11	0.13
MH	0.353	0.923	0.960	0.664	0.016	0.267	0.115	0.573	0.206	0.078	0.286	0.005	0.138	-	0.28	0.28	0.26	-0.09	-0.05	0.14	0.00	-0.24
ML	<0.001	<0.001	0.009	0.008	0.001	0.098	0.047	0.341	0.002	0.110	0.288	<0.001	<0.001	0.008	-	0.14	0.18	-0.04	0.10	0.22	0.28	-0.10
IMW	0.280	0.093	0.989	0.198	0.220	0.003	0.402	0.073	0.103	0.016	0.004	0.163	0.623	0.010	0.189	-	0.59	-0.21	0.06	-0.05	-0.14	-0.01
OMW	0.054	0.020	0.634	0.011	0.012	<0.001	0.412	0.460	0.350	0.043	0.026	0.365	0.193	0.017	0.103	<0.001	-	-0.26	-0.05	0.06	-0.23	-0.10
MFD	0.753	0.956	0.549	0.923	0.370	0.236	0.209	0.544	0.590	0.193	0.522	0.750	0.848	0.405	0.713	0.051	0.015	-	-0.07	0.17	-0.03	0.10
P4L	0.691	0.867	0.985	0.873	0.788	0.697	0.561	0.505	0.068	0.495	0.410	0.163	0.253	0.639	0.369	0.577	0.666	0.545	-	0.10	0.04	0.05
MIL	0.542	0.311	0.320	0.379	0.287	0.596	0.110	0.816	0.967	0.030	0.943	0.379	0.008	0.208	0.041	0.638	0.606	0.123	0.352	-	-0.05	-0.05
MIW	0.438	0.961	0.507	0.339	0.510	0.275	0.638	0.474	0.947	0.243	0.116	0.888	0.328	0.994	0.009	0.186	0.036	0.764	0.737	0.660	-	-0.08
C/W	0.037	0.001	0.058	0.258	<0.001	0.031	0.026	0.954	0.287	0.802	0.472	0.346	0.239	0.026	0.345	0.958	0.384	0.347	0.657	0.683	0.466	-

results support the previous conclusions that, in the European mainland, the European badger displays a certain degree of sexual dimorphism (Wiig 1986, Lüks & Roper 1988, Lynch et al. 1997, Florijančić et al. 2011).

In the Western Carpathians, Hell & Paule (1989) found only slight differences in quantitative skull parameters. However, they based the analysis on 47 skulls (33 males, 14 females) and the small sample size might be one of the reasons for a weak differentiation between sexes. They found wider skulls, thicker mandibles and greater neurocranial capacity in males. The authors concluded that sexual differences between male and female skulls were based on their size, not on their shape. On the contrary, the multi-model approach adopted here revealed some significant differences in morphology of male and female skulls, which supports the findings of Lynch et al. (1997). In particular, measures of mandible width emerged as the best discriminators of the badger sexes with high classification accuracy. The badger skulls investigated here were generally smaller than those analyzed by Hell & Paule (1989). For example, the observed mean total lengths of male and female skulls were 131 and 129 mm, which contrasted with 137 and 131 mm presented by the mentioned authors. However, condylobasal length was very similar (females: 128 vs. 125 mm, males: 130 vs. 130 mm). Also the skull width was comparable between the data sets. The difference in skull sizes between our data and those of Hell & Paule (1989) lies probably in the source of skull material. We examined a random sample of skulls from all hunted animals while Hell & Paule (1989) measured mostly skulls presented at the national hunting exhibition (majority of those skulls were of medal category) which likely introduced a bias towards above-average skull sizes since medal specimens are usually the oldest with well-developed sagittal crest, which contributes notably to the total skull length.

Various measures were evaluated to distinguish between the sexes in the badger. Lee & Mill (2004) analysed British badgers and found sexual dimorphism primarily manifested in the height of the sagittal crest opposed to the width of the zygomatic arch. Florijančić et al. (2011) quoted sharp differences between sexes in several craniometric characteristics of the badgers from Croatia, although their analysis was restricted to 19 skulls only. Apart from some special parameters, they confirmed significantly higher values of the average skull length and breadth in males. This finding was not confirmed in other populations, including our results. It seems that the size of skull only is not a good

tool to detect sexual dimorphism. Size is rather plastic and thus responds more directly to the environment (Cardini & Elton 2017).

In our study, sexual size dimorphism was manifested mainly in differences of the feeding apparatus. Specifically, females showed significantly lower inner (IMW) and outer width of mandible (OMW) than males. Dimorphism in the feeding apparatus was observed in other studies as well. For example, Lüks & Roper (1988) recorded a significant sex difference in the condylobasal length and size of the canines in the Swiss population of the European badger. Johnson & Macdonald (2001) demonstrated significant sexual dimorphism in the zygomatic arch width, both canine cross-section length and canine cross-section width. In general, canine dimensions seem to be the most widely used parameters distinguishing the European badger sexes (e.g. Lüks & Roper 1988, Johnson & Macdonald 2001, Abramov & Puzachenko 2005). The differences in feeding apparatus are usually attributed to some level of selection for niche separation between the sexes (Dayan & Simberloff 1996, Johnson & Macdonald 2001). Other researchers, however, pointed to the absence of actual resource partitioning in badgers and assumed that this sexual dimorphism may rather be related to interspecific or intergroup aggression (Lynch et al. 1997, McDonald 2002). Also Abramov & Puzachenko (2005) concluded that it is highly improbable that dietary differences alone can explain sexual dimorphism in the European badger.

Main hypotheses explaining the phenomenon of sexual dimorphism

In general, there are two principal hypotheses for sexual dimorphism in carnivores: sexual selection and resource partitioning (Johnson & Macdonald 2001). The sexual selection hypothesis predicts that SSD results from mate competition among males (bigger males have higher success in mating), and bioenergetic constraints of reproduction among females (smaller females have lower food requirements; Erlinge 1979, Moors 1980). Some authors mentioned also better passability of burrows for smaller females when pursue prey or during pregnancy (Gliwicz 1988). The European badger belongs to the most social mustelid species which are known to have a relatively low level of SSD (Johnson et al. 2000, Johnson & Macdonald 2001). The lower importance of male mate competition may be one of the reasons on low level of SSD. The European badger population from the British Islands has a relatively low sexual dimorphism in body mass, probably due to its

more patchy distribution (social groups) and social behaviour based on hierarchical structure (Johnson et al. 2000). However, no correlation was revealed between the SSD level and sociality or diet in different populations of two badger species (Abramov & Puzachenko 2005). On the other hand, Lynch et al. (1996) found that the European otter *Lutra lutra* in the Shetlands, where it is particularly social, had a lower cranial and dental sexual dimorphism than within populations of conspecifics elsewhere. Our results seem to be in accordance with this finding. Population distribution of the badger in the continental Europe is more even. The species occurs in smaller families or individually which probably results in higher level of mate competition among males comparing to British Islands where badgers occur in big societies with hierarchical structure leading to exceptionally high density (Griffiths & Thomas 1997, Lara-Romero et al. 2012, Chiatante et al. 2017). Thus, male competition for females should play more important role in the Western Carpathians which may lead to higher level of SSD. However, differences in the level of intraspecific competition between even distributed populations and those from large societies might not be so clear. Macdonald (1983) formulated a resource dispersion hypothesis which predicts that food resource patches within a territory may be rich enough to sustain nutrition requirements of large groups of badgers. In such groups, the feeding competition might be relatively low. In contrast, Johnson & Macdonald (2001) confirmed significant SSD also in socialized populations which leads to the suggestion that feeding competition may not necessarily be low even in large social groups.

The resource partitioning hypothesis predicts that SSD reduces intraspecific competition for food (Brown & Lasiewski 1972). SSD as a result of intersexual selection displays in different food exploitation by males and females enabling both sexes to exploit different food sources in the same area (Erlinge 1979, Magnusdottir et al. 2012). Thus, sexual dimorphism might contribute to a certain degree of dietary separation between sexes (Abramov & Tumanov 2003). Van Valen (1965) formulated the niche variation hypothesis, which can be considered as some development of the resource partitioning hypothesis. The hypothesis predicts greater morphological variability in populations occupying wide ecological niches than in those occupying narrow ones. Meiri et al. (2005) did not support this hypothesis, since they found no consistent difference in the degree of sexual size dimorphism between insular and mainland carnivores for either

skull length or canine diameter. They hypothesized that gene flow was the main source of the greater variability in mainland populations. Otherwise, recently Law & Mehta (2018) highlighted niche divergence as an important mechanism that maintains the evolution of sexual dimorphism in musteloids, displaying in cranial size and bite force dimorphism rather than in cranial shape. Korablev et al. (2013) interpreted differences in the degree of SSD in four Mustelidae species in accordance with the niche variation hypothesis. Results of Zalewski (2007) suggest that food-niche partitioning between male and female pine martens changes across different habitat and food conditions, and is not related to sexual size dimorphism, but rather to behavioural differences between sexes. Rozhnov & Abramov (2006) found a low level of SSD in marbled polecat occupying narrow trophic niche. The food niche of badgers was found to be the broadest at 45-55° N and became narrower at both lower and higher latitudes (Goszczyński et al. 2000), which might lead to higher level of its morphological variability in temperate zone sensu Van Valen (1965). Several studies dealing with the badgers' diet in Central Europe have been published (Goszczyński et al. 2000, Lanszki 2004, Lanszki & Heltai 2011) but none of them was focused on differences between sexes. Some authors have found differences in the diet of males and females (Madsen et al. 2002), but no results are known from the Carpathians. The available data on the European badger foraging ecology does not allow us to consider the relatively higher (comparing to island populations) distinctions in cranial parameters between males and females to be attributed to differences in foraging preferences.

Genetic models suggest that all of the above hypotheses are plausible and each of the mechanisms operates in natural populations (Hedrick & Temeles 1989). Difficulty of understanding the differences in morphological characters found in this species probably lies also in the variability of its ecological adaptations, behaviour and social systems across the area (Kruuk 1989). Contrary to Western Europe and British Islands, the carnivore guild in the Carpathians has multispecies composition. The specificity of the Carpathians is an optimally saturated population density of large carnivores (Chapron et al. 2014, Lešová 2015). Contrary to the Western Europe, the large carnivores have been occupying the area of the Carpathians continuously. The phenomenon of the Carpathians was proved also in wolf. Sexual dimorphism in wolf was much more pronounced among individuals from the Carpathian mountains

than from lowland forests of the Białowieża Primeval Forest (Okarma & Buchalczyk 1993). We suppose also some role of predatory selection leading to a potentially higher survival chance of bigger individuals (e.g. when attacked by lynx or wolf; Palomares & Caro 1999) in affecting morphological characters of the European badger in the Carpathians. However, this effect has not been tested and the role of predation in the SSD accentuating seems to be questionable, since predatory pressure would affect also females. The effect of predation may affect also indirectly by means of modifying badgers' diet (Sidorovich et al. 2011). Moreover, the badger is a species that compete with other burrowing species such as the red fox and the raccoon dog. Especially the red fox is an important competitor to the European badger (Macdonald et al. 2004). The stronger feeding apparatus, mainly in male, of the badger might reflect one of the responses to the competitive pressure. This relationship was confirmed in fox species. Szuma (2008) found that red foxes from regions of sympatric co-occurrence with other closely-related *Vulpes* species were more sexually dimorphic in terms of tooth size than red foxes from allopatric regions. Irrespective of the underlining hypotheses, we suggest IMW and OMW may be used as easily measurable and reliable (> 80 % correctly classified

out-of-sample skulls) craniological parameters for a quick sex determination. The threshold values of several craniometric characters reported in this study (Table 2) might be used as simple decision rules for determination of the European badger sex, especially in the case of the limited availability of craniometrical measures (e.g. determination of skull fragments etc.). Still, the reliability of these thresholds outside the Western Carpathians need to be verified or adjusted regionally, since badgers' morphological parameters may vary considerably even in a relatively small area (Pertoldi et al. 2003, Abramov & Puzachenko 2005). Although molecular genetics has become the most reliable method for taxonomic studies, craniometry remains an important tool for practical determination of sexes or geographical forms of mammal species as well as in ecological research and conservation biology (Pertoldi et al. 2003, Sládek & Bútorá 2005).

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