Russian J. Theriol. 8(1): 17–28

Spatial variation of sexual dimorphism in the Siberian weasel *Mustela sibirica* (Mustelidae, Carnivora)

Alexei V. Abramov & Andrey Yu. Puzachenko

ABSTRACT. Spatial variation in sexual size dimorphism was assessed for the Siberian weasel (*Mustela sibirica*) across localities in Western, Central and Eastern Siberia. Twenty-three cranial measurements from 192 adult specimens were studied using univariate morphometric and non-metric multidimensional scaling techniques. Males found to be larger than females for all characters. Significant spatial variation in degree of SSD was found. The larger degree of sexual dimorphism was found in *M. sibirica* from Far East and smaller degree of SSD in samples from Western and Central Siberia. Results were interpreted to support the resource partitioning hypothesis.

KEY WORDS: geographic variation, *Mustela sibirica*, sexual size dimorphism, skull.

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Географическая изменчивость полового диморфизма колонка *Mustela sibirica* (Mustelidae, Carnivora)

А.В. Абрамов, А.Ю. Пузаченко

РЕЗЮМЕ. Исследована географическая изменчивость размерного полового диморфизма в популяциях колонка *Mustela sibirica* из Западной, Центральной и Восточной Сибири. Двадцать три краниометрических признака проанализированы у 192 взрослых экземпляров при помощи методов многомерного шкалирования. По всем промерам самцы были крупнее самок. Обнаружена значимая географическая изменчивость в степени проявления размерного полового диморфизма. Большая степень диморфизма обнаружена у *M. sibirica* с Дальнего Востока, меньшая – у популяций колонков из Западной и Центральной Сибири. Полученные данные свидетельствуют в пользу гипотезы разделения пищевых ресурсов.

КЛЮЧЕВЫЕ СЛОВА: географическая изменчивость, *Mustela sibirica*, размерный половой диморфизм, череп.

Introduction

Sexual size dimorphism (SSD) is a typical phenomenon of the mustelids (Carnivora, Mustelidae). The main hypotheses attempting to explain the pronounced sexual dimorphism in Mustelidae, with males being larger than females, include resource partition, sexual selection and bioenergetics (see Holmes & Powell, 1994; King & Powell, 2007). Under resource partition hypothesis the size dimorphism allows the sexes to consume the different prey and thus reduces dietary overlap and feeding competition between males and females of the same species (Brown & Lasiewski, 1972; Dayan *et al*., 1989; Dayan & Simberloff, 1994; Gittleman & Van Valkenburgh, 1997). The other hypothesis explains sexual dimorphism by different sex-specific pressures taking into account the mustelid polygynous mating system. Under sexual selection larger males are favoured in competition to achieve the highest reproductive success by mating with the highest possible number of breeding females (Ralls, 1977; Erlinge, 1979; Powell, 1979; Moors, 1980). The third hypothesis considers the sexual dimorphism as the result of selective pressure influencing on male and female body size independently. Males have a minimal parental investment, whereas small-sized females are more energetically efficient for reproduction. They need less energy for own maintenance and can channel more energy into reproduction (Powell, 1979; Moors, 1980; Erlinge, 1981). SSD in cranial characters have been studied in several species of *Mustela* and other small mustelids, but the geographic variation in degree of SSD was assessed just for few species (Ralls & Harvey, 1985; Zyll de Jong, 1992; Reig, 1997; Abramov & Baryshnikov, 2000; Stevens & Kennedy, 2005).

Significant spatial variation in degree of SSD was found in all small mustelids. In large subspecies of *Mustela nivalis* Linnaeus, 1766 the sexual difference in size is much more pronounced than in small ones (Reichstein, 1957). According to Beaucournu & Grulich (1968), SSD in the skull of *M. nivalis* becomes more pronounced from north to south across Europe, i.e.,

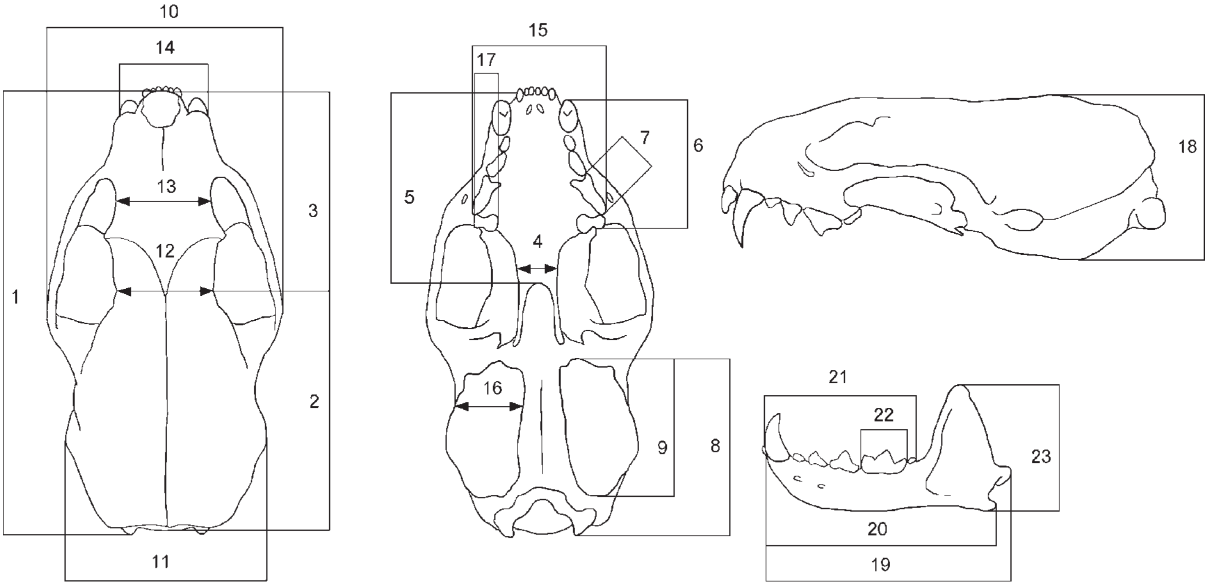

Figure 1. Measurements taken of *Mustela sibirica* skulls: 1 — condylobasal length (CbL), 2 — neurocranium length (NcL), 3 — viscerocranium length (VcL), 4 — minimal palatal width (MpW), 5 — palatal length (PL), 6 — maxillary tooth-row length (MxtL), 7 — upper carnassial tooth Pm^4 length (PM^4L), 8 — length of the auditory bulla (AbL), 9 — greatest length between oral border of the auditory bulla and aboral border of the occipital condyles (BcL), 10 — zygomatic width (ZyW), 11 — mastiod width of skull (MW), 12 — postorbital width (PoW), 13 — interorbital width (IW), 14 — width of rostrum (RW), 15 — greatest palatal width (GpW), 16 — width of the auditory bulla (AbW), 17 — width of upper molar M^1 (M^1W), 18 — cranial height (CH), 19 — total length of the mandible (ML), 20 — length between the angular process and infradentale (AL), 21 — mandibular tooth-row length (MatL), 22 — length of lower carnassial tooth M_1 (M_1L), 23 — height of mandible in the vertical ramus (MaH).

proportionately to the increase in general size of the animals. Similar results for samples across the distribution range of *M. nivalis* were obtained by Zyll de Jong (1992) and Abramov & Baryshnikov (2000). Stevens & Kennedy (2005) examined the SSD in skull of American mink *Neovison vison* (Schreiber, 1977) from 35 localities in North America and found significant spatial variation in degree of dimorphism. However spatial patterns of sexual dimorphism in American mink did not closely follow geographic patterns of body size. The largest degree of SSD was found among middle-sized minks from Pennsylvania and the smallest minks from Florida, whereas smallest degrees of SSD were found in largest Alaskan minks and smallest minks from Quebec. For three species of North American weasels (*M. nivalis*, *M. erminea* Linnaeus, 1758 and *M. frenata* Lichtenstein, 1831), no correlation has been revealed between the degree of SSD and geographical origin (Ralls & Harvey, 1985).

Similar other small mustelids Siberian weasel *Mustela sibirica* Pallas, 1773 exhibits a pronounced sexual dimorphism in body size and body weight (Shubin & Shubin, 1975, Sheng Helin, 1987). However SSD in the skull of *M. sibirica* never has been discussed in earlier works. The Siberian weasel is widely distributed throughout Asia from the Ural Mountains to the Far East and Korea; eastern Pakistan east to northern Myanmar, northern Thailand, China and Taiwan. The most part of distribution area from Urals to Eastern Siberia inhabited by middle-sized form *M. s. sibirica*, in Far East distributed large subspecies *M. s. manchurica* (Abramov, 2000). We investigated sexual dimorphism in cranial measurements of *M. sibirica* from different parts of wide distribution area in Siberia.

Material and methods

The study was based on 192 skulls of adult *M. sibirica* from Siberia. The specimens are kept in the collections of the Zoological Institute, Russian Academy of Sciences (Saint-Petersburg) and the Institute of Animal Systematics and Ecology, Russian Academy of Sciences (Novosibirsk). The skulls were grouped in three geographic samples. The animals of first, «Baraba», sample (30 males, 35 females) were collected in the Baraba steppe in Novosibirsk Province (Western Siberia). Other, «Turukhansk», sample (32 males, 32 females) was collected in valley of Podkamennaya Tunguska River in Krasnoyarsk Province (Central Siberia). Third, «Far Eastern», sample (32 males, 31 females) was collected in the Sikhote-Alin Nature Reserve in Russian Far East (Eastern Siberia). Trying to isolate the effect of heterogeneity of collection samples we use for analysis only homogeneous samples consisted of specimens collected in one place during the short period. Twenty three were taken on each skull using sliding callipers to the nearest 0.1 mm. The scheme of measurements used is shown in Fig. 1.

For the assessment of sexual dimorphism the standard methods of and multivariate analyses were used, preference was given to non-parametric methods. The methods and mathematical approach of SSD analysis were expanded in Puzachenko (2001, 2006), Abramov & Puzachenko (2005), and Zagrebelny & Puzachenko (2006).

As a measure of SSD by single variable we chose both absolute mean difference between sexes (DS) and the index of male size to female size because they are intuitively simple and easily interpretable. SSD indices were calculated as $S = (\text{mean}_{\text{male}} - \text{mean}_{\text{female}} / \text{mean}_{\text{male}} + \text{mean}_{\text{female}}) \times 100$.

Variables (see Fig. 1 caption) were standardized to exclude influence of the «scale» of the different measurements on the results. Transformation was done according to the following equation: $\hat{x}_i = (x_i - x_{min}) / (x_{max} - x_{min})$, where $\hat{x}_i$ is standardized measurement, x_i, x_{min}, x_{max} are observed, minimum and maximum value of *i-th* variable, respectively, for the individual sample and subsamples (joint males and females sample, subspecies subsamples, local populations, etc.) The new scale begins from 0 to 1.0. This transformation is sensitive to outliers, but better preserves the individual variable' variances than standardized by the sample mean and standard deviation. During the preliminary data investigation we excluded any clear outliers (extremes) from the data set. The data values from joint males and females sample greater-than (less-than) of non-outliers range (median plus 90-th percentile; median minus 10-th percentile) were considered as outliers and eliminated from the sample.

The square dissimilarity matrix contained the Euclidean distances and matrix of Kendall's tau-b rank-order coefficients among all the pairs of specimens were calculated based the all variables. The elements of rank Kendall's matrix (r_{ij}) were transformed in dissimilarity according to equation: $D_{ij} = \sqrt{1 - r_{ij}}$. Euclidean metric, as simple geometric distance in the multidimensional space, describes the variability of the skull sizes. Kendall's coefficient is the difference between the probabilities that the observed data are in the same order for the two specimens vs. the probability that they are in a different order. For any individual, the characters (measurements) may be ranked by their values (e.g., $V_1 > V_3 > V_5 > \ldots V_k$). If any two specimens have equal sequences of variables it impels high similarity of their «proportions» or shape. Thus, rank Kendall's coefficient between any pairs of specimens can be interpreted as an integrated metric that describes the variation of skull «shape».

Matrix of Euclidean distances and matrix of Kendall's coefficients were used in the non-metric multidimensional scaling (MDS) procedure which visualizes proximity relations of objects by distances between points in a low dimensional Euclidean space (Shepard, 1962; Davison & Jones, 1983). Initial configuration was calculated according to the classical metric algorithm (Torgerson, 1952). Metric solution was used as a starting configuration for the non-metric algorithm (Kruskal, 1964). MDS allows us to take into account a nonlinear part of variability unlike the different methods of factor analysis (James & McCulloch, 1990). Thus, MDS is nonparametric analog of well-know PCA and the other alike parametric techniques. MDS is one of the most unprejudiced and robust statistical methods in case we have no assumptions about type of multivariate sample distribution and about clear linear relationships between variables. In this sense MDS has methodological preference over standard pribcipal component analysis (PCA) and over the other parametric linear methods of multivariate exploratory data analysis (for details see, James and McCulloch 1990). MDS allows to use any kind of distance or similarity matrix (e.g., Euclidian, nonparametric correlations, simple Pearson correlation, etc.) opposed to traditional PCA and factor analysis which are based on correlation/covariation matrixes. Therefore, MDS is more flexible method then the standard ordination techniques. In the most case, as practice shown, MDS results are close to PCA results. But in the cases when non-linear component of variation is significant the MDS axes better reproduce observed variables then the PC (see Fig. 2 A, B). MDS produces underlying non-correlated dimensions (MDS-axes) which are carrying main information about variation of the specimens (analogue of the factor scores in PCA). The «best-minimum» dimension (number of MDS axes) in MDS model was estimated based on «stress formula 1»[1] (Kruskal Stress) according to Puzachenko (2001). It is assumed that if the distribution of the dissimilarities in the input matrix is close to random (normal distribution), the value of the Kruskal Stress ($Stress_{\text{mod}}$) must be maximal, and the stress monotonic decreases according to increasing of the number of dimensions. For the values of stress received from observations it is possible to write down the linear regression model: $Stress_i = \mathrm{B} \cdot Stress_{i,\,\text{mod}} - \mathrm{A} + e_i$, where $Stress_i$ – observed Kruskal Stress for *i-th* dimension (*i* from 1 to 15, in our case), *A* and *B* are constants, e_i — residual. Required value of *i* corresponds to dimension («best-minimum» dimension) of MDS model which have maximum negative residual e_i. According to the initial assumption, in the last case locations of the individuals in multidimensional space are mainly deviate from stochastic distribution. In this study the «best-minimum» dimension will be marked as d_E, for MDS model based on Euclidean distances matrix, and as d_K — for model based on Kendall's rank correlation matrix. The MDS-axes for a model based on Euclidean distances matrix are marked as E1, E2… and MDS-axes based on Kendall's rank correlation matrix are marked as K1, K2…In the first case, the «best-minimum» dimension for MDS models will be marked as d_E, and in the second one as d_K.

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[1] The smaller $Stress_{\text{mod}}$ value, the better is the fit of the reproduced distance matrix to the observed distance matrix. Kruskal Stress is the standard deviation of the reproduced distances from the observed ones.

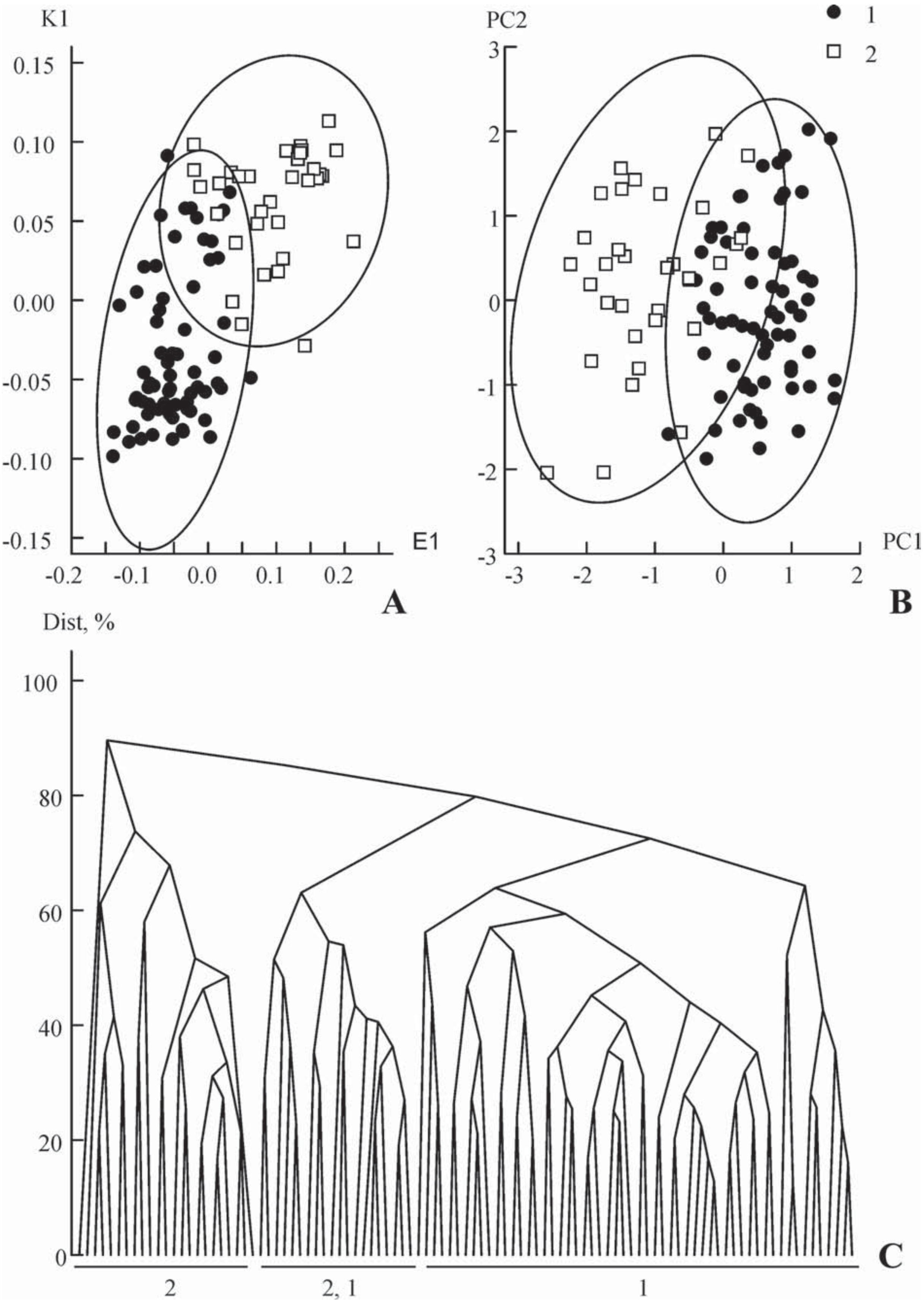
K1
0.15
0.10
0.05
0.00
-0.05
-0.10
-0.15
E1
-0.2
-0.1
0.0
0.1
0.2
A
PC2
● 1
□ 2
3
2
1
0
-1
-2
-3
PC1
-3
-2
-1
0
1
2
B
Dist, %
100
80
60
40
20
0
C
2
2, 1
1

Table 1. A variance component for each random effect for «sex» and «geographic location» factors in the MDS axes (%) for joint sample of males and females.

Source	MDS axes									
(factors)	E1	E2	E3	E4	E5	E6	K1	K2	K3	K4
(1) «Sex»	91.6	0.0	0.0	0.0	0.0	0.0	59.3	4.5	7.9	10.0
(2) «Geographic location»	0.0	21.0	37.8	2.9	5.3	8.9	0.0	40.5	0.0	18.8
1*2	5.9	15.9	0.0	2.9	12.3	0.0	13.7	1.4	3.95	0.0
Error	2.6	63.0	62.2	94.2	82.5	91.1	26.9	53.5	88.2	71.2

We used both the Spearman rank order correlation coefficients as a nonparametric analogue of factor loadings in principal components analysis and the coefficients of determination between the MDS axes and measurements as value of explained variance, in order to interpret their biological content. We have considered that important things are modules of Spearman coefficients that are equal or higher than 0.5, which correspond to Pearson correlation which is approximately about or higher than 0.6. The measurements with low value of explained variance ($r^2 < 0.5$) had more «disordered or stochastic variability» unlike other measurements.

We estimated effects of «sex» and «geographical» factors in MDS axes variation used variance components analysis (Straney, 1978; Searle *et al*., 1992). Geographical factor was treated as categorical and associated with three studied localities.

Based on the MDS axes, a hierarchic classification (Unweighted Pair Group Method using Arithmetic Mean — UPGMA, Euclidian distance) was produce. We also used different methods of clustering: non-hierarchic dichotomy clustering, k-means and fuzzy clustering (Kaufman & Rousseeuw, 1990). The dichotomy clustering was calculated using Fracdim ver. 1.9 (this software created by Yu.G. Puzachenko and G.M. Aleshchenko, 2004[2]). When the results of different classifications were close in general we used the following formal selection criterion: we choose the best classification based on a level of the morphological differentiation between clusters based on *F*-criteria in one-way ANOVA. The best classification must have maximal value of *F* in this test.

Results

Six (d_E) and four (d_K) «best-minimum» dimensions contributed significantly to variation of the skull measurements and proportions in MDS models for joint sample of males and females. Average coefficient of determination for the multiple regression models among all 23 measurements is 0.96 (0.90–0.99). The variance components in MDS axes for each random effect for dependent variables («sex» and «geographical location») is shown in Tab. 1. The first MDS axes (E1 and K1) describe sex dimorphism in sizes and proportions of skull. Spearman correlation coefficients between measurements and axis E1 vary from 0.63 to 0.97 and for axis K1 — from 0.43 to 0.86. The variance of the E2, E3 and K2 reflects the effect of «geographical location». Spearman rank correlations between these axes and measurements are less than 0.5.

Approximately 80–90% of variance of each measurement is caused by «sex» factor with the only exception of postorbital width, in which sexual dimorphism defines just 50% of variance. Thus the SSD is a major factor of skull variability in the Siberian weasel.

The structure of skull variability in males and females of the Siberian weasel is different and can be described by eight and seven MDS axes respectively. Average coefficient of determination for male cranial measurements is 0.76 (0.56–0.98) and for female — 0.70 (0.46–0.90).

The first MDS axis E1 explains the variation of 16 (males) and 18 (females) measurements. In males, the axis E2 mainly reflects the variation of the neurocranium length, and in females — the length of upper carnassial tooth PM^4, width of upper molar M^1, and length of lower carnassial tooth M_1. The axis E3 mainly reflects the variation of greatest length between oral border of the auditory bulla and aboral border of the occipital condyles in males. In females, the axis E3 correlates with neurocranium length, postorbital width and cranial height. The axis E4 is presented for male sample only, and it has no high correlations with anyone of the measurements.

A high correlation of the characters with the MDS axes K1–K4 related to allometric variation. In males, significant allometric variation is recorded for condylobasal length, viscerocranium length, palatal length, mastiod width of skull, zygomatic width, interorbital width,

Figure 2. Morphometric separation of male sample: A — MDS analysis, first MDS axes (E1, K1), B — principal components analysis (PC1, PC2), C — UPGMA tree based on the all MDS axes (E1–E4, K1–K4). Morphological clusters are marked: 1 — «small» specimens, 2 — «large» specimens. Take the note of the better clusters differentiation in the MDS axes dimension than in the PCA dimension.

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[2] For order Fracdim software (Russian version only), please, apply for information to A.Yu. Puzachenko, puzak1@rambler.ru

Table 2. Variance components in the MDS axes for random effect of «geographic location» factor (%) for males and females models separately.

Source (factor)	MDS axes							
	E1	E2	E3	E4	K1	K2	K3	K4
	Males							
Effect	68.5	17.9	0.0	1.2	60.2	9.5	0.0	14.8
Error	31.5	82.1	100.0	98.8	39.8	90.5	100.0	85.2
	Females							
Effect	37.7	32.8	12.3	-	36.7	18.3	2.8	1.1
Error	62.3	67.2	87.7	-	63.3	81.7	97.2	98.9

Table 3. Distribution (%) of the morphological clusters (1, 2) by the three geographical samples of *Mustela sibirica*.

Sample	Cluster	
	1	2
Males		
«Turukhansk»	96.9	3.1
«Baraba»	94.3	5.7
«Far Eastern»	6.3	93.8
Females		
«Turukhansk»	62.5	37.5
«Baraba»	80.0	20.0
«Far Eastern»	16.1	83.9

total length of the mandible, length between the angular process and infradentale and height of mandible in the vertical ramus. In females, the axis K1 correlates with the dental characters (MxtL, PM^{4}L, M^{1}W, MatL, and M$_1$L). In males the axis K2 reflects the allometric variation of the length of the auditory bulla, length between auditory bulla and occipital condyles (BcL), and in the females – condylobasal length and viscerocranium length moreover. The axis K3 correlates with length of lower carnassial tooth M$_1$ in males and with minimal palatal width and length of mandible (AbL) in females. The axis K4 correlates with postorbital width only for male sample.

Four or three (d$_E$) and four (d$_K$) «best-minimum» dimensions contributed to variation of the skull measurements and proportions in MDS models for separate samples of males and females. The part of MDS axes variance, which reproduced the effect of «geographical location» factor, is given in Tab. 2. Main effect of this factor have been revealed E1 (68%), K1 (60%) axes in males, and E1 (38%), E2 (33%), and K1 (37%) axes in females. According to these data, the geographical variability of skull in males is expressed more strongly in comparison with females.

The analysis of the MDS models for different subsamples (subspecies, populations, and sexes within local population) has allowed to recognize two sets of measurements which are responsible for high (>2–3 MDS axes) dimension of these models. The first group includes measurements which variability is rather insignificant and independent from the basic set of characters: NcL, PM^{4}L, CH, M$_1$L. The second group includes measurements with high and considerably independent variability such as PoW, AbL, AbW, BcL and ZyW.

High dimension of MDS model mainly based on two measurements — neurocranium length and postorbital width. The length of neurocranium is very stable character of the Siberian weasel skull (see Tab. 4). The postorbital width is very variable especially among populations.

Males and females separately were divided into two morphologically distinct clusters by dichotomy clustering (Figs. 2, 3, 4). Dichotomy clustering produced more differentiated (according to *F* test) groups then all other classification procedures. Clusters inferred from the UPGMA analysis are close to those based on dichotomy clustering. The members of the cluster 1 are smaller than in the cluster 2 for all measurements except of postorbital width in females. Differences among the clusters are better expressed in males than in females (Fig. 4). The geographical pattern has been discovered in locality ratio of the two morphological clusters (Tab. 3). Small males from the cluster 1 are predominated in the samples from Western and Central Siberia. In the Far-Eastern sample large males from a cluster 2 are dominated absolutely. In females, vice versa, large individuals have been more often discovered in the «Baraba» and «Turukhansk» samples. Thus the patterns of geographical variation are differing for males and females.

The relative morphological differences and sexual dimorphism estimations of the studied populations of the Siberian weasel are presented in Tab. 4. For this analysis the «Baraba» and «Turukhansk» samples were merged, as they are very similar on the related proportions of the cluster 1 and cluster 2 (Pearson Chi-square =0.72, $p = 0.39$). SSD within the samples is statistically significant ($p < 0.0001$ in Kruskal-Wallis tests) for all measurements. The mean SSD level (S) in the joint sample («Baraba» + «Turukhansk») is 6.2±0.9% (3.9–9.1), whereas in the Far Eastern sample it is 9.3±0.9% (4.8–13.5). The difference between these values is statistically significant ($p < 0.001$). Thus, sexual dimorphism in Far-Eastern population is higher than in the Siberian populations. The patterns of SSD indices in all samples are very similar ($r = 0.94$, $p < 0.0001$; Fig. 5).

Table 4. Mean (in mm) and standard error of the measurements, absolute mean difference between sexes (DS) and SSD indices (S) in the Siberian weasel *Mustela sibirica*; pS — difference between S and its statistical significance according to *t*-criteria (*df*=1): * — <0.05, ** — <0.01; ΔM, ΔF — difference among males and females from the different samples; pΔM, pΔF, p_{smpl} — significance of differences between males, females and between population's means (males and females) according to Kruskal-Wallis tests: "-" n.s. (=0.05), * — <0.05, ** — <0.01, *** — <0.0001.

	«Baraba» and «Turukhansk» sample				«Far Eastern» sample									
Character	M, n=67	F, n=62	ΔS, mm	S, %	M, n=32	F, n=31	ΔS, mm	S, %	pS	ΔM, mm	ΔF, mm	pΔM	pΔF	p_{smpl}
CbL	61.4±0.12	55.0±0.13	6.4±0.28	5.5±0.11	64.3±0.24	54.2±0.17	10.1±0.29	8.5±0.11	-3.0*	2.94±0.12	-0.79±0.08	***	**	-
NcL	37.0±0.15	33.8±0.12	3.2±0.25	4.5±0.08	37.2±0.17	33.9±0.16	3.4±0.23	4.8±0.08	-0.3	0.27±0.02	0.08±0.04	-	-	-
VcL	29.3±0.14	25.2±0.13	4.1±0.21	7.5±0.05	31.7±0.22	24.3±0.14	7.4±0.26	13.3±0.06	-5.8**	2.44±0.08	-0.90±0.02	***	***	-
MpW	6.3±0.03	5.5±0.03	0.8±0.07	6.5±0.24	6.8±0.06	5.6±0.03	1.2±0.07	9.8±0.24	-3.3	0.46±0.03	0.02±0.02	***	-	-
PL	27.1±0.08	24.0±0.07	3.1±0.14	6.1±0.09	28.5±0.16	23.6±0.1	4.9±0.19	9.4±0.09	-3.3*	1.39±0.09	-0.39±0.02	***	**	-
MxtL	17.9±0.05	16.1±0.04	1.8±0.08	5.4±0.06	18.1±0.07	15.5±0.07	2.6±0.1	7.6±0.07	-2.2*	0.22±0.02	-0.51±0.001	**	***	-
PM^{4}L	6.6±0.02	6.0±0.02	0.7±0.05	5.2±0.23	6.7±0.04	5.7±0.03	1.0±0.05	8.1±0.23	-2.9	0.05±0.02	-0.30±0.02	-	***	-
AbL	23.8±0.06	21.5±0.07	2.3±0.17	5.0±0.21	24.6±0.12	21.3±0.1	3.3±0.16	7.2±0.20	-2.2	0.79±0.06	-0.24±0.05	***	*	-
BcL	18.3±0.05	16.8±0.07	1.5±0.16	4.3±0.29	18.8±0.09	16.5±0.08	2.2±0.12	6.3±0.29	-2.0	0.45±0.04	-0.26±0.08	**	*	-
ZyW	32.2±0.15	27.7±0.10	4.6±0.31	7.7±0.21	33.9±0.18	27.1±0.11	6.8±0.22	11.1±0.21	-3.4*	1.61±0.04	-0.57±0.15	***	**	-
MW	27.4±0.08	24.2±0.08	3.2±0.19	6.1±0.17	29.4±0.15	23.8±0.12	5.7±0.19	10.7±0.17	-4.6*	2.05±0.07	-0.47±0.05	***	**	-
PoW	11.5±0.07	10.7±0.08	0.9±0.12	3.9±0.12	12.3±0.13	11.1±0.07	1.2±0.15	5.2±0.11	-1.3	0.74±0.06	0.39±0.02	***	**	***
IW	12.0±0.06	10.5±0.05	1.4±0.11	6.4±0.16	12.7±0.10	10.3±0.07	2.5±0.13	10.6±0.16	-4.3*	0.76±0.04	-0.25±0.02	***	**	-
RW	12.7±0.08	10.7±0.08	2.0±0.08	8.4±0.11	13.9±0.09	10.6±0.06	3.3±0.11	13.5±0.11	-5.1*	1.27±0.02	-0.08±0.02	***	-	*
GpW	19.1±0.06	16.9±0.05	2.2±0.14	6.1±0.16	19.9±0.10	16.7±0.08	3.2±0.12	8.8±0.16	-2.7*	0.76±0.03	-0.26±0.04	***	**	-
AbW	9.2±0.04	8.0±0.04	1.2±0.1	6.8±0.28	9.4±0.08	7.7±0.05	1.7±0.09	10.2±0.28	-3.3	0.25±0.03	-0.32±0.04	-	***	-
M^{1}W	4.9±0.02	4.3±0.02	0.6±0.04	6.9±0.17	5.0±0.03	4.1±0.03	0.9±0.04	9.9±0.17	-3.0*	0.06±0.01	-0.20±0.01	-	***	-
CH	22.7±0.08	20.3±0.09	2.4±0.2	5.6±0.24	22.8±0.17	19.7±0.11	3.1±0.2	7.4±0.25	-1.8	0.09±0.09	-0.63±0.08	-	***	-
ML	34.9±0.08	30.2±0.09	4.7±0.2	7.2±0.17	36.8±0.19	29.7±0.12	7.1±0.22	10.7±0.17	-3.5*	1.92±0.11	-0.48±0.07	***	**	-
AL	33.1±0.08	28.8±0.10	4.3±0.24	6.9±0.24	34.8±0.15	28.2±0.1	6.6±0.18	10.4±0.23	-3.5	1.64±0.08	-0.63±0.12	***	***	-
MatL	21.2±0.06	18.8±0.06	2.4±0.11	5.9±0.05	21.9±0.10	18.4±0.08	3.5±0.12	8.7±0.06	-2.7*	0.74±0.03	-0.39±0.01	***	**	-
M$_1$L	7.3±0.02	6.5±0.03	0.8±0.06	6.1±0.24	7.4±0.04	6.3±0.03	1.1±0.05	8.4±0.24	-2.3	0.09±0.02	-0.22±0.03	-	***	-
MaH	17.1±0.07	14.3±0.06	2.9±0.18	9.1±0.31	18.3±0.11	14.1±0.09	4.2±0.14	12.9±0.3	-3.8	1.21±0.04	-0.14±0.08	***	-	-
mean of S, %				6.2±0.9				9.3±0.9						

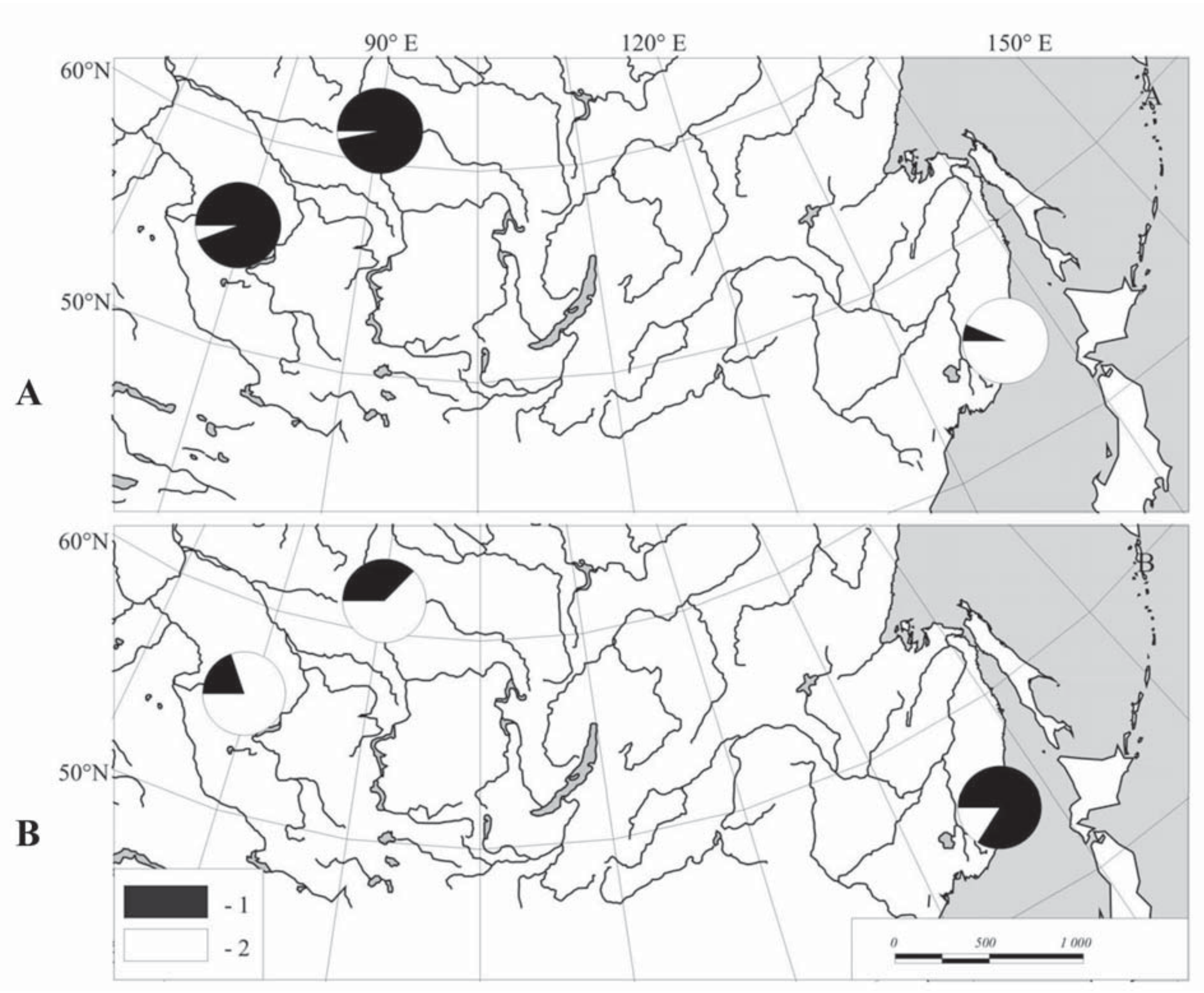

Figure 3. The ratio of two morphological clusters (1, 2) in the three geographical samples of the Siberian weasel: A — males, B — females.

The most essential distinctions between Siberian and Far East populations are found in viscerocranium length, condylobasal length, length between the angular process and infradentale, palatal length, and zygomatic width (Tab. 4). Males from all three populations have statistically non-significant differences on upper carnassials tooth PM^4 length, width of upper molar M^1, length of lower carnassial tooth M$_1$ and cranial height. The list of such measurements in females includes neurocranium length, minimal palatal width and height of mandible in the vertical ramus. For some characters the population differences are statistically significant only for males or only for females. Females from the Far East are smaller than females from Siberian populations in all measurements except NcL and MpW.

Discussion

The examined MDS models well fit the cranial variation in the Siberian weasel. The analysis of the effects of sex and geographical location found that SSD is a main component of a cranial variation. Main part (80-90%) of variance of each measurement is caused by this factor with the only exception of postorbital width. The sexes of Siberian weasel show clear male-biased skull dimorphism.

The differences between sexes are mainly described by a general size factor, as in the majority of the carnivores. Our results indicate that both size and shape are important components of morphological differentiation of males and females in *Mustela sibirica*. Nevertheless the sexual dimorphism is most clearly expressed on size than on shape. The «shape» variation is mainly allometric (proportions are connected with the general skull size).

The structure of skull variability in males and females of the Siberian weasel is different and can be described by different sets of MDS axes. The number of axes in MDS models depends on the number of independent components of skull variability. In our case it depends on the several «hard-coded» measurements, such as neurocranium length and cranial height

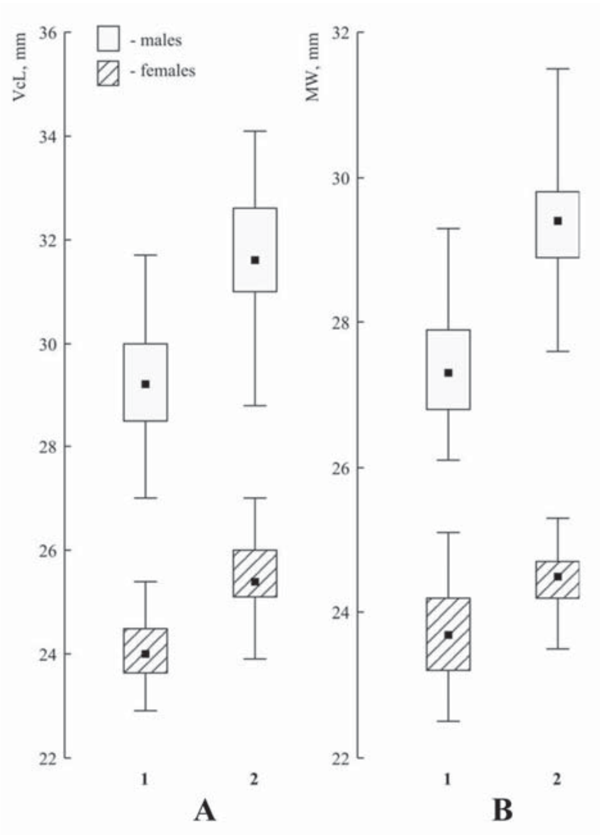

Figure 4. Examples of differentiations between two morphological clusters (1, and 2 in males and females of the Siberian weasel: A — viscerocranium length (VcL), B — mastoid width of skull (MW); ¦ — median, box — 25%, 75% percentiles, whiskers — min-max.

or high variable characters as postorbital width. Explanation for the differences in MDS axes should be sought in natural selection acting differentially on males and females, thus modifying intersexual differences in morphology. The significant differences between males and females skulls are functionally related to rostral part of skull and dental characters whereas the «hard-coded» measurements (neurocranium length and cranial height) do not vary significantly between sexes.

The spatial variation of sexual dimorphism in the Siberian weasel conforms to the data known for other *Mustela* species (Shubin & Shubin, 1975; Zyll De Jong, 1992; Abramov & Baryshnikov, 2000; Abramov & Tumanov, 2003), in which sexual dimorphism is more pronounced in large forms than in smaller ones. The large Far Eastern subspecies *M. s. manchurica* displays a greater degree of sexual dimorphism than the smaller nominative form *M. s. sibirica* distributed in Western and Central Siberia (see also Abramov, 2000). Similarly, Sheng Helin (1987) found that larger *M. sibirica* from plain areas of Yangtze and Huai rivers have a higher SSD than the smaller Siberian weasels from the Lesser Hinganling and Changbai mountains.

The significant difference in sexual selection (as competition between males for mates or maintenance cost and food requirements for females during reproduction) among different populations of the species can hardly be conceived. Indirectly the role of sexual selection can be investigated in the analysis of variables indicating female fecundity and variables indicating investment in individual offspring (see Lindenfors *et al.*, 2007). Therefore the Far Eastern *M. sibirica* should differs from Siberian populations in these parameters. Nevertheless available data on female fecundity (age at first birth, gestation length, litter size, interbirth interval, birth rate, maximum longevity) and investment in individual offspring (neonatal mass, weaning age) do not differ in Siberian and Far Eastern populations of this species (Stroganov, 1962; Heptner *et al.*, 1967; Yudin, 1984).

Powell & King (1997) showed that SSD in *Mustela erminea* differs among cohorts: cohorts born during a year of food abundance develop greater SSD than cohorts born in years of food shortage because males grow bigger when food is abundant while females do not (or do less so). This result supports the sexual selection hypothesis. It is difficult to completely test such hypothesis in Siberian weasel because we do not know the abundance of food during the years of growth for the weasels in studied samples. However, all specimens of «Baraba» sample were collected during winter 1960–1961. In 1959–1962 in Baraba steppe was mass reproduction and high population density of water vole *Arvicola amphibius* (Linnaeus, 1758), which is main prey of Siberian weasel there (Ternovsky & Danilov, 1965). Therefore *M. sibirica* from Baraba should have high level of SSD. Nevertheless it is not observed in our data.

Among main possible explanations of geographic variation of SSD might be the resource partition hypothesis (see Holmes & Powell, 1994). Cranial characters associated with feeding habits should have larger degree if males and females were partitioning food resources. The difference in SSD indices among Far Eastern and Siberian samples is more expressed in viscerocranium length and width of rostrum, and also in mastiod width and interorbital width. The latter cranial features correspond to larger size jaw musculature and more powerful neck muscles (Radinsky, 1981), associated with biting. The relatively large rostrum providing a support for the larger canines, seems to be a good indicator of a trophic selection (Dayan *et al.*, 1989; Dayan & Simberloff, 1994; Gittleman & Van Valkenburgh, 1997). Sex-related prey differences were found among the stoats, the polecats, the pine marten and the American mink (see Dayan & Simberloff, 1994 and references therein).

Belyk (1967) analyzed of stomach contents from 265 of Siberian weasel collected in Central Siberia (Yakutia). She did not found significant differences in the diet between males and females. According to Belyk (1967), small rodents are the main prey of Siberian

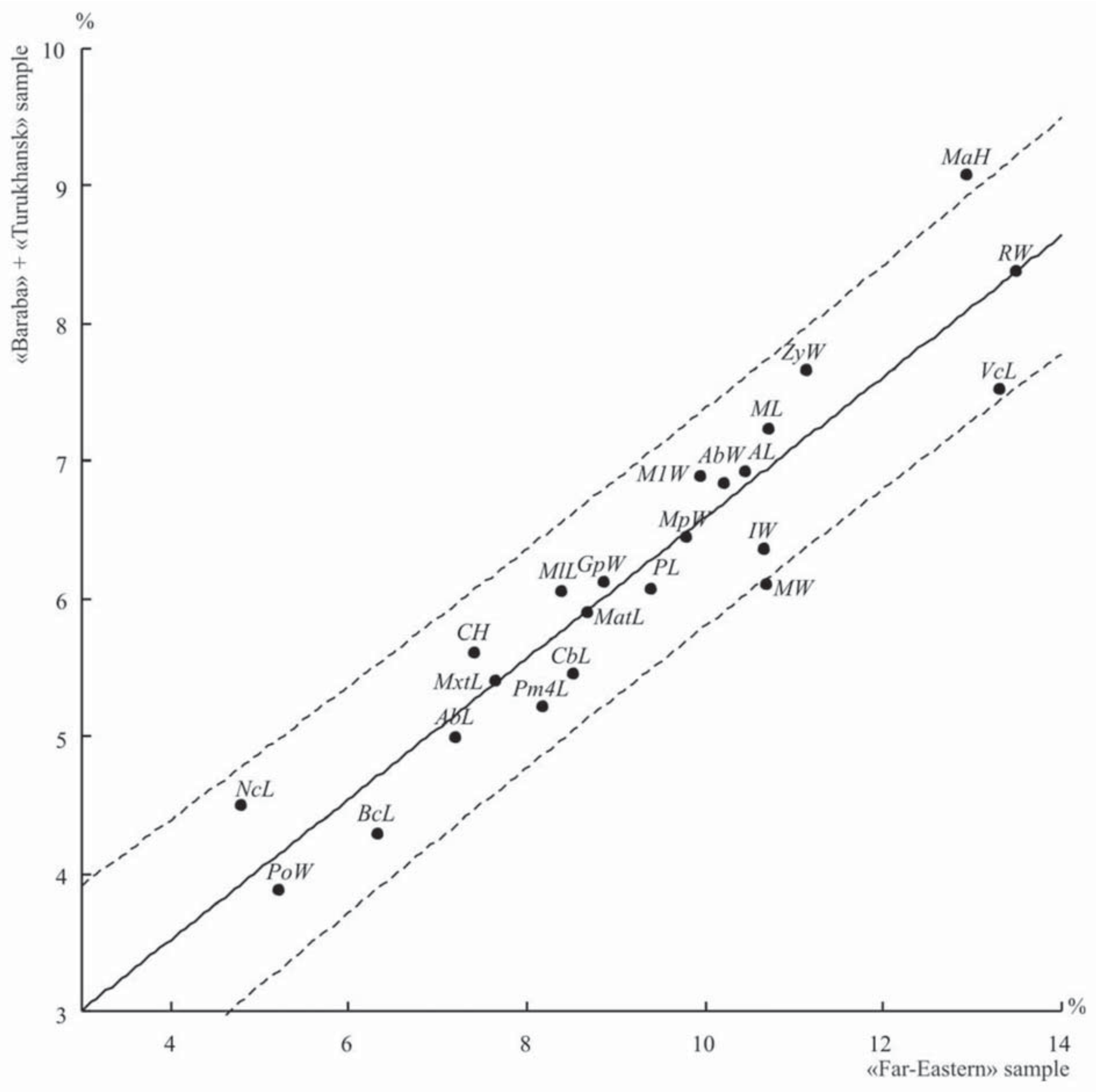

Figure 5. Regression with 90% prediction bands between SSD indices (S, %) in the joint «Baraba»+«Turukhansk» sample and «Far Eastern» sample of the Siberian weasel. Abbreviations of measurements in Figure 1.

weasel in Central Siberia and most abundant prey is water vole *Arvicola amphibius*. Long-term study of Siberian weasel ecology in Baraba steppe (West Siberia) found that a main prey was also *A. amphibius* (Ternovsky & Danilov, 1965). Thus the smaller level of SSD in Western and Central Siberian populations can be explained by similarity in feeding habits and relative stenophagy. On the contrary *M. sibirica* in Russian Far East is known having wide range of prey including small rodents (mice and voles), squirrels, pikas and birds (Heptner *et al*., 1967; Voilochnikov, 1977; Yudin, 1984). Higher level of SSD in Far Eastern weasels may allow to females and males to explore a wide range of available prey.

No studies have argued that either one or another hypothesis is the main reason for the sexual size dimorphism. This complex phenomenon is difficult to test because of interacting variables. Factors affecting to spatial variation of SSD may be multifarious like resource partitioning, habitat differences and temporal variation in accessible resources, genetic differences among populations, as well as history of speciation events and the formation of intraspecific distribution ranges (Abramov & Puzachenko, 2005; Stevens & Kennedy, 2005). Additional investigations of the intraspecific variation in size among sexes in different species could provide valuable information for understanding of SSD phenomenon.

ACKNOWLEDGMENTS. We thank to Elena I. Zholnerovskaya for access to the collection of the Institute of Animal Systematic and Ecology (Novosibirsk) used in this work. We are obliged to Dmitry V. Logunov for improving the English of the final draft. We thank to P. David Polly and Roger A. Powell for the constructive comments on the earlier draft of this manuscript. The study was supported in part by the Russian Foundation for Basic Research (grants Nos. 06-04-49575, 07-04-91202, 09-04-01303 and 09-04-00073) and the Program of Russian Academy of Sciences «Biodiversity».

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