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INTERRELATIONS BETWEEN DIFFERENT FORMS OF GROUP VARIABILITY OF QUANTITATIVE TRAITS IN *MICROTUS SOCIALIS* (CRICETIDAE, MAMMALIA) IN THE PEAK PHASE OF POPULATION ABUNDANCE

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Interrelations Between Different Forms of Group Variability of Quantitative Traits in *Microtus socialis* (Cricetidae, Mammalia) in the Peak Phase of Population Abundance. Peskov V. N., Sinyavskaya I. A., Emelyanov I. G. — The amount of input and the interrelation of various forms of group variability of quantitative traits in general morphological disparity of *M. socialis* in the peak phase of the population abundance was studied. It was found that the variability of 4 exterior and 11 interior traits are determined primarily by the age of the animals, whereas the influence of sex and the season is very low. With ageing, the intensity of sexual differences and seasonal variability increase. The correlated variability of morphological traits was almost the same (Rs = 0.820–0.98) in males and females during different seasons.

Key words: *Microtus socialis*, group variability, age variability, sexual differences, seasonal variation

Соотношение разных форм групповой изменчивости количественных признаков у *Microtus socialis* (Cricetidae, Mammalia) в фазе пика численности популяции. Песков В. Н., Синявская И. А., Емельянов И. Г. — Проведено исследование величины вкладов и соотношения разных форм групповой изменчивости количественных признаков в общем морфологическом разнообразии *M. socialis* в фазе пика численности популяции. Показано, что изменчивость 4 экстерьерных и 11 интерьерных признаков определяется, прежде всего, возрастом животных и в меньшей степени полом и сезоном. С возрастом полевок выраженность половых различий и сезонной изменчивости увеличивается. Коррелированная изменчивость признаков практически одинакова (Rs = 0,820–0,98) у самцов и самок разных сезонов.

Ключевые слова: *Microtus socialis*, групповая изменчивость, возрастная изменчивость, половые различия, сезонная изменчивость.

Introduction

Currently, much attention is given to the study of different forms of group variability in mammals (Markowski, Ostbye, 1992; Stamps, 1993; Zuercher et al., 1999; Schulte-Hostedde, Millar, 2000; Lammers et al., 2001; Badyaev, 2002; Isaac, 2005; Abramov, 2010; Lisovskiy, Obolenskaya, 2011). However, so far there are only a few papers on the analysis of their interrelation (Pavlinov et al., 1993; Pavlinov et al. 2008; Nanova, Pavlinov 2009; Pavlinov, Nanova, 2009; Abramov, 2010; Pozdnyakov, 2010; Vasilyev et al., 2010).

Social vole (*Microtus socialis* Pallas, 1773) is a cyclomorphic rodent species, therefore, as most other species of this group of mammals it is characterized by such forms of group variability as age, sex, seasonal, annual, cyclical and others (Schwarz, 1980). The described forms of morphological disparity of voles are the components of common population morphospace, and the interrelationship between different forms makes the morphospace structure (Pie, Weitz, 1997; Roy, Foote, 2005; Pavlinov, 2008; Pozdnyakov, 2010). For this reason, the study of the input of different forms of group variability into the total morphodisparity and the analysis of the interrelation of these forms in different species are necessary to understand the causes, which determine the amount and structure of morphological disparity in natural populations of animals.

Table 1. The amount of studied material
Таблица 1. Объем исследованного материала

Seasonal samples	n	Males (n = 303)			Females (n = 341)		
		Juvenis	Subadultus	Adultus	Juvenis	Subadultus	Adultus
Winter	140	31	9	28	20	23	29
Spring	181	93	9	9	39	16	15
Summer	143	14	16	15	57	32	9
Autumn	180	48	16	15	46	44	11

The aim of the present study is to analyze the interrelation between the basic forms of group variability of morphological traits (sexual differences, age and seasonal variation) in order to assess the input of these forms of variability into the overall morphological disparity implemented in *M. socialis* population in the phase of peak abundance.

Material and methods

The study is based on the data on *Microtus socialis* morphology, which were collected in different seasons of 1973 by the expedition of the Department of Population Ecology of I. Schmalhausen Institute of Zoology NAS of Ukraine on the territory of the virgin steppe reserve "Askania-Nova". During this period, the population was in the peak phase and characterized by the highest number and density. See brief characteristics and number of samples in table 1. Totally were studied 644 specimens of *M. socialis* of different age.

The relative age of voles was estimated according to the degree of skull sculpturing (Bashenina, 1953; Larina, Lapshov, 1974; Emelyanov, Zolotukhina, 1975) and the data on vole body length and mass, with attraction as an additional targets length and body mass of voles. As a result of the performed analysis, the animals were divided into three age groups: juveniles, subadults and adults.

There were analyzed 4 standard exterior characters (body length — L, tail length — Ca, foot length — Pl, ear length — Au) and 9 interior characters (body weight — W, spleen — Lie, adrenal glands — Adr, kidneys — Ren, intestines — Int, liver — Hep, heart — Cor, lungs — Pul and thymus — Th). The masses of the kidneys and adrenal glands were considered separately from the left and from the right sides as the individual indices.

Intergroup variability was analyzed by the two and three-way Analysis of Variance (Factorial Anova, see Statistica, 2001). The forms of variability (sexual, age, seasonal) were considered by this methods as independent variables (factors), and morphological traits as dependent variables (factors). For each form of variability was assessed numerically (in %) the portion of factorial dispersion (s) in the entire morphological disparity (S) for each characteristic. The obtained data on interrelations between the portions of characteristic dispersion, connected with different forms of group variability, were analyzed and presented graphically. As a criterion of reliability of factors influence have used the criterion of Wilks-Lambda (Wilks' Lambda)

For the statistical analysis of the data were used the following standard methods of univariate and multivariate statistics: LSD-test (significant differences considered when $P < 0.05$), Spearmen's rank correlation coefficient (Rs), multivariate method — Analysis of Principal Components, (Plokhinskiy, 1971; Kim et al., 1989; Statistica, 2001). All calculations were performed with the statistical package Statistica for Windows, version 6.0.

Results and discussion

According to the results of the factor analysis of the seasonal samples of *M. socialis,* it was found that the variability of 15 measurable morphological traits was described at 60–80 % of the first principal component (PC_1). Assuming that all traits, except for the weight of the thymus have significant factor loadings on this component with a positive sign, and its values calculated for each individual increase from juvenile to adult voles, it is possible to state that the PC_1 characterizes the age correlated variability of the analyzed traits. The negative sign of the thymus loading factor is determined by the fact that the weight of thymus decreases with age due to the slowdown or interruptions of grow processes (Schwartz et al, 1968; Olenev, 1967).

Comparison of factor loadings of traits in PC_1 in 8 seasonal samples of males and females shows, that trends of age variability traits in these samples are quite similar (Rs = 0.82–0.98). Similar results were obtained when comparing the trends of the age variability of cranial traits in closely related species of grey voles, wood mice, (Peskov et al., 1996; Dzeverin, Lashkova, 2005), reindeer of different populations (Abramov, 2010) and morphometric traits in sand and green lizards (Malyuk, 2010). All these data show high stability of morphogenetic processes in the ontogeny of vertebrates.

The results of analysis of variance prove that the age of voles affects statistically significantly the variability of all of the analyzed traits (Wilks-Lamba = 0.136 P < 0.05) (see table 2). The maximum impact of age was observed for weight and body length, kidney, heart and lungs mass (54.78–61.02 %), a little less for the mass of the adrenal glands, liver, intestine, thymus and tail length (36.36–49.61 %), and minimal for the length of the foot (19.48 %) and spleen mass (13.94 %).

The influence of sex and season, as well as the combined effect of all three factors on the variability of measurable traits in combined samples of *M. socialis* is negligible (table 3). For this reason sexual differences and seasonal variability of the traits were analyzed separately for each age group of voles.

Sexual differences in a group of juvenile voles was observed only in the adrenal glands, the average mass was significantly (P < 0.01) greater in females compared with males. The

Table 2. Factor loadings of morphological characters on the first principal component in the seasonal samples of male and female social vole

Таблица 2. Факторные нагрузки морфологических признаков на первую главную компоненту в сезонных выборках самцов и самок общественной полёвки

N	Characters	Winter		Spring		Summer		Autumn	
		F	M	F	M	F	M	F	M
1	L	0.94	0.97	0.98	0.94	0.98	0.95	0.97	0.97
2	Ca	0.78	0.80	0.87	0.74	0.91	0.75	0.74	0.70
3	Pl	0.55	0.78	0.59	0.66	0.73	0.73	0.45	0.81
4	Au	0.82	0.86	0.83	0.52	0.90	0.70	0.81	0.76
5	W	0.96	0.98	0.99	0.98	0.99	0.97	0.97	0.98
6	Lie	0.48	0.53	0.56	0.68	0.67	0.08	0.35	0.34
7	s. Adr	0.84	0.92	0.94	0.86	0.95	0.78	0.25	0.87
8	d. Adr	0.86	0.88	0.95	0.81	0.94	0.71	0.89	0.87
9	s. Ren	0.84	0.96	0.95	0.96	0.97	0.78	0.95	0.97
10	d. Ren	0.84	0.96	0.94	0.96	0.96	0.94	0.95	0.97
11	Int	0.80	0.91	0.93	0.88	0.92	−0.72	0.82	0.82
12	Hep	0.84	0.95	0.98	0.97	0.96	0.91	0.95	0.97
13	Th	−0.67	−0.72	−0.68	−0.05	−0.44	−0.70	−0.71	0.32
14	Cor	0.89	0.98	0.98	0.96	0.98	0.94	0.97	0.95
15	Pul	0.92	0.94	0.93	0.93	0.96	0.84	0.88	0.83
% of total variance		66.20	78.24	78.20	64.20	80.10	60.00	65.70	69.70

Table 3. The portion of variance of different forms of variability in morphological characters of social voles

Таблица 3. Доли дисперсии разных форм изменчивости морфологических признаков общественной полёвки

Characters	Portion of variance, %						
	sex	season	age	sex* season	sex* age	season*age	sex*season*age
L	0.04	**0.36**	**59.68**	0.22	0.16	0.16	0.32
Ca	**1.74**	**2.19**	**42.38**	0.38	**1.14**	0.56	0.37
Pl	**4.00**	**1.18**	**19.48**	0.09	**0.83**	0.68	**1.80**
Au	0.00	**0.79**	**38.14**	0.09	0.41	0.50	**1.02**
W	**0.16**	**1.53**	**61.02**	0.09	0.09	**1.17**	**0.42**
Lie	**0.49**	**3.95**	**13.94**	1.29	0.01	0.63	2.19
s. Adr	**4.93**	**0.67**	**47.57**	0.22	**1.46**	0.36	0.05
d. Adr	**4.22**	**0.80**	**47.25**	0.11	**1.41**	0.26	0.11
s. Ren	0.04	**0.78**	**57.60**	**0.49**	0.04	**0.76**	**0.86**
d. Ren	0.03	**0.96**	**57.45**	**0.58**	0.03	**0.80**	**0.83**
Int	**1.54**	**2.79**	**40.98**	0.07	**1.11**	**2.12**	0.52
Hep	**2.27**	**5.24**	**49.61**	0.03	**1.50**	**2.13**	0.17
Th	0.03	**0.64**	**36.36**	0.23	0.03	**1.56**	**1.09**
Cor	0.10	**2.60**	**54.78**	0.13	0.04	**0.93**	0.36
Pul	0.13	**0.73**	**55.21**	0.08	0.10	**0.66**	0.22

Note. Designation forms of variability and traits given in the text. Statistically significant relationships are marked in bold.

Table 4. The portion of variance of different forms of variability in morphological characters of social voles
Таблица 4. Доли дисперсии разных форм изменчивости морфологических признаков общественной полёвки

Characters	Portion of variance, %								
	Juvenis			Subadultus			Adultus		
	sex	season	sex* season	sex	season	sex* season	sex	season	sex* season
L	0.30	1.07	**3.79**	**3.17**	**7.66**	3.38	2.59	**11.37**	2.47
Ca	0.00	**3.41**	1.06	**5.25**	3.79	1.92	**14.11**	**16.69**	2.21
Pl	0.87	1.70	**3.37**	**11.53**	2.09	**0.58**	**16.12**	**9.12**	2.25
Au	0.91	**2.16**	**2.87**	0.01	3.73	0.81	2.18	5.18	4.29
W	0.27	0.77	**3.91**	0.12	**18.82**	**0.82**	**4.35**	**26.30**	3.06
Lie	0.38	**6.60**	0.15	1.08	2.84	4.37	0.77	**12.99**	**10.90**
s. Adr	**2.52**	0.43	**2.37**	**24.57**	3.01	0.43	**24.55**	4.57	0.89
d. Adr	**1.56**	0.78	**2.58**	**20.93**	3.61	0.36	**19.47**	**3.49**	0.23
s. Ren	0.00	1.347	1.68	0.72	**6.69**	**8.14**	0.00	**9.09**	4.83
d. Ren	0.04	1.52	1.88	0.69	**7.43**	**8.75**	0.00	**12.91**	4.69
Int	0.00	1.53	**4.37**	**10.56**	**16.77**	0.60	**4.59**	**17.68**	0.96
Hep	0.00	**5.19**	1.77	**9.20**	**34.81**	0.36	**18.94**	**21.47**	0.34
Th	0.04	0.72	1.04	0.43	**12.42**	**4.18**	0.05	**12.84**	**15.06**
Cor	0.05	1.15	**3.35**	1.53	**18.69**	1.04	0.56	**37.22**	2.92
Pul	0.00	**2.39**	1.29	0.34	3.07	1.71	1.52	**7.57**	0.61

adrenal glands are known to be an indicator of stress in animals (Schwartz et al, 1968; Ivanter et al, 1985). In this case, a higher level of stress in females, in our opinion, can be explained by the fact that they grow, become sexually mature and come into breeding faster than males. It should be noted that these differences increase significantly with age (table 4).

In the group of subadult voles there are significant sexual differences in the length of body, tail and feet, as well as in the weight of the adrenal glands, intestines and liver (Wilks-Lamba = 0.371, $P < 0.05$). The length of the body and tail, and the weight of the adrenal glands, intestine and liver were significantly greater in females, which is explained not only by their faster growth and development compared with males ($P < 0.05$ — 0.001), but also by the increased levels of metabolic processes connected with bearing and nursing offspring. The length of a foot on average is bigger in males, which is typical for many species of voles (Bashenina, 1977; Meyer et al, 1996).

Adult males and females do not differ in body length, while the average body weight was significantly greater in males of winter and spring samples ($P < 0.01$). Sexual differences on other traits were similar to those in subadult voles (table 4).

Seasonal variation on murine rodents is determined by differences in the animals' growth rate and duration of different seasons, sex and age structure of population, weather and feeding conditions (Schwartz et al, 1968; Schwartz, 1980; Ivanter et al, 1985).

Seasonal variability in young voles is proven for the length of the tail and ear, weight of spleen, liver and lungs (Wilks-Lamba = 0.513 $P < 0.05$). With age in voles increase not only the number of traits, for which reliable seasonal differences are set, but also the level of the season impact on the variability of these traits (table 4). In the subadult voles seasonal variation is determined for body and weight; weight of kidney, intestine, liver, thymus and heart; in adults — for the length of the body, tail and feet; weight of body, spleen, kidney, intestine, liver, thymus, heart and lungs (subadults Wilks-Lamba = 0.127 $P < 0.05$; adults Wilks-Lamba = 0.078 $P < 0.05$). This fact suggests that the expression of seasonal variability in social voles with age increases significantly. This could be explained by the fact that with age in post-embryonic development of the voles, the grow processes cease to dominate, while the influence of such parameters as seasonal variation in climate, food resources, intensity of reproduction, sex and age structure of populations increases noticeably.

Graphical analysis of the interrelation between the portions of season and sex impact demonstrates that in juvenile voles the sex influence is most clearly seen in the variability of spleen and liver weight, the season influence is evident in the variability of adrenal glands. In the subadult voles, variability in the length of tail and feet and the adrenal glands weight is determined by the sex influence. Season determines the variability of weight of body, kidney, thymus and heart. The combined effects of sex and season is determined for the weight of kidneys, thymus, and to a lesser extent for the length of the foot and body weight (fig. 1). In adult voles, only a variation of the adrenal glands weight is determined by the sex influence; while variability of body length, weight of spleen, kidneys,

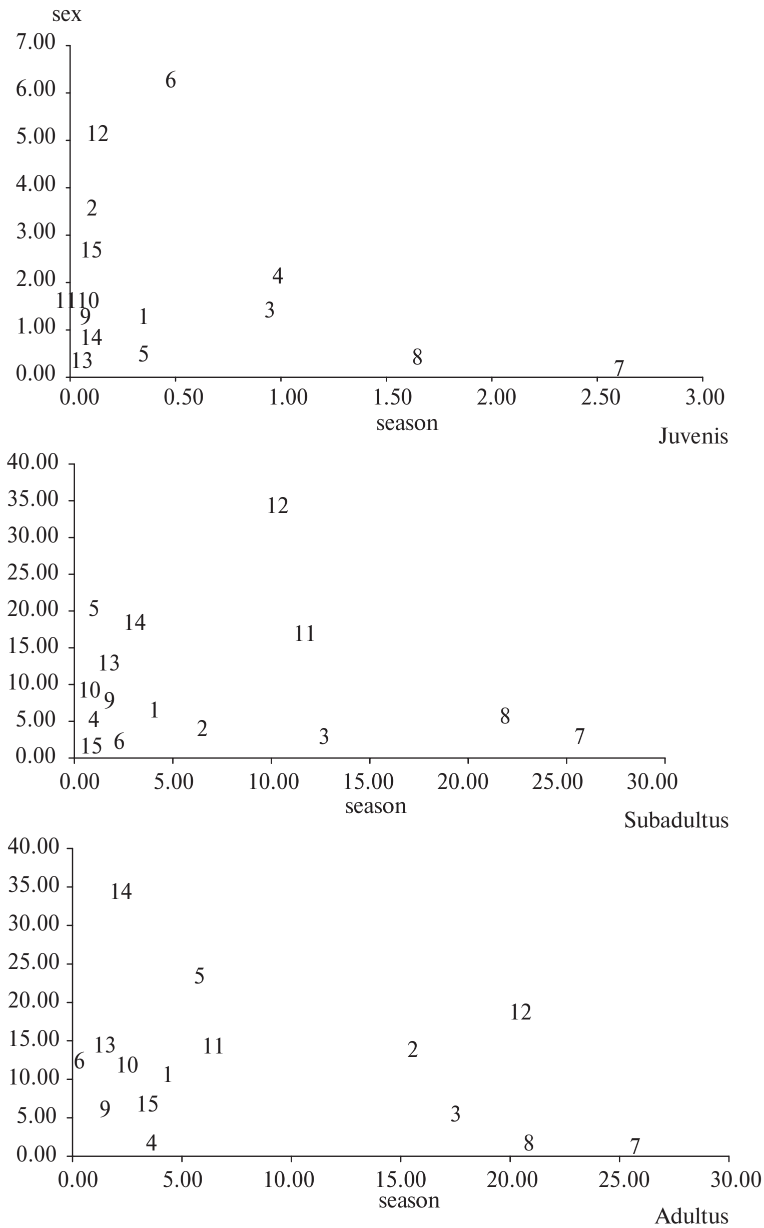

Fig. 1. The relation between the portions of variance (%) of different forms of variability in morphological characteristics of age groups of social voles. Designation of form and variability of the features is given in the text.

Рис. 1 Соотношение между долями дисперсии (%) разных форм групповой изменчивости в популяции общественной полёвки. Обозначение форм изменчивости и соответствующих признаков приведены в тексте.

thymus, heart and lungs are more affected by season. The combined effect of season and sex on the variability of the analyzed traits is practically not observed.

Summarizing all the above, it is necessary to note that the variability of quantitative morphological traits in the post-embryonic development of social voles is determined primarily by age of the animals and very slightly by sex, season, and the combined influence of these factors. It is most vividly expressed in juvenile voles. Sexual differences and seasonal differences in quantitative morphological traits are formed mainly in adult voles, when the organism almost ceases to grow, and the grow processes no longer dominate in morphogenesis. Correlative variability in late ontogeny is almost identical in a different seasonal samples of males and females, indicating stability of morphogenetic processes in vertebrate animals.

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