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Phenetic variation in the European souslik, *Spermophilus citellus* (Mammalia: Rodentia)

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Abstract. To describe the geographic variability in *Spermophilus citellus* (Linnaeus, 1766), thirteen cranial measurements from 229 male and 278 female animals were taken from 16 geographic samples and subjected to both univariate and multivariate analyses. One-way analysis of variance demonstrated highly significant inter-locality heterogeneity in all skull dimensions for both sexes. Similarly, the first Principal Component explained more than half of the variance within the original data set, and was considered to represent a size vector, showing a mosaic-like pattern of geographic variation. In stepwise multiple regression analyses, four climatic variables explained 83 % of the size variation observed in males, and 72 % in females; thus climate is a good predictor of general size. Ordination and clustering of size-free data showed that three peripheral populations from Poland, Slovakia, and Macedonia show phenetic (and apparently phyletic) distinctness. Although nine subspecies of the European souslik have been recognised, this is not consistent with the interlocality variation observed, and actually obscures much of the pattern of geographic variation. Skull characters, ratios and colouration were found to be of low diagnostic value, thus no formal division of the European souslik into subspecies is proposed here.

Key words. Mammalia, Rodentia, *Spermophilus citellus*, phenetics, geographic variation.

Introduction

Among the 13 Palaearctic sousliks recognised by Gromov et al. (1965), the European souslik, *Spermophilus citellus*, inhabits the westernmost part of the genus' distributional area. In the 20th century it populated the area from Bohemia in the west to the Black Sea coast in the east, and from eastern Germany and southern Poland in the north as far south as Thessaloniki and Thrace. Its preferred habitats are steppes and wooded steppes, rising from the maritime coast to an altitude of 2500 m (Gromov et al. 1965, Ružić 1978). The species' distribution is disjunct and composed of two large populations: a Pannonian and a Balkan one (Ružić 1978), separated by the Carpathians and by the Djerdap Canyon of the Danube. Small population isolates also occur in Germany, Poland, Moldavia, Macedonia, Serbia and northern Greece around the entire periphery of the species' present range. Some of these isolated populations, notably those in Germany and Poland, became extinct within the last few decades (Meczynski 1985, Stubbe & Stubbe 1994).

Although Linnaeus (1766) was familiar with the European souslik, authors as recent as Miller (1912) still considered the species to be monotypic. Eight subspecies have been described since 1929, most coming from the southern border of the species' range. A brief synopsis of the souslik's current taxonomic status is presented below.

Spermophilus citellus (Linnaeus, 1766)

1766. *Mus citellus* Linnaeus, Systema Naturae, 12 ed. I: 80.

Holotype. — Not extant. Linnaeus probably never saw the animal, relying instead on Gesner, Aldrovandi and Ray (Linnaeus 1766). An adult male housed in the Zoological Institute of the Bulgarian Academy of Sciences (No. 51/67, obtained on 4 May 1951 by K. Bauer at Neusiedl, Austria) was designated as a lectotype by Markov (1957). This is contrary to the 1985 International Code of Zoological Nomenclature and is hence invalid.

Linnaeus (1766) listed *Mus citellus* from Austria, Bohemia and Poland, with Austria being accepted as the type locality by Miller (1912). Martino & Martino (1940) considered a specimen from Wagram, Austria, as being topotypic with the nominate form, with Bauer (1960) accepting Wagram as a restricted type locality. The unsuitability of Neusiedl as a restricted type locality, as suggested by Markov (1957), was also discussed by Bauer (1960). A detailed description of Austrian sousliks is provided by Bauer (1960).

Spermophilus citellus gradojevici (Martino & Martino, 1929)

1929. *Citellus citellus gradojevici* Martino and Martino, J. Mammal. 10: 76.

Holotype. — Adult male (skin and skull), Zoological Institute, St. Petersburg 33844; from Gevgelija, Macedonia; obtained on 30 May 1928 by M. Gradojević.

Spermophilus citellus istricus (Calinescu, 1934)

1934. *Citellus citellus istricus* Calinescu, Z. Säugetierk. 9: 106.

Holotype. — None designated. Type locality: Muntenien, Romania.

Spermophilus citellus karamani (Martino & Martino, 1940)

1940. *Citellus citellus karamani* Martino & Martino, Ann. Mag. nat. Hist. Ser. 11 (5): 467. Holotype. — Adult male (skin and skull), British Museum (Nat. Hist.) 1938.12.27.1, from meadows above Patiška (= Patiška reka or river), altitude 2000 m, on Mt. Karadžica, 30 km south of Skopje, Macedonia; obtained on 1 August 1938 by V. Martino.

Ondrias (1966) included the Bulgarian sousliks (*S. c. martinoid* and *S. c. balcanicus*) in *S. c. karamani*, but this is not widely accepted (cf. Ružić 1978).

Spermophilus citellus laskarevi (Martino & Martino, 1940)

1940. *Citellus citellus laskarevi* Martino & Martino, Ann. Mag. nat. Hist. Ser. 11 (5): 468. Holotype. — Adult female (skin and damaged skull), British Museum (Nat. Hist.) 1938.12.27.2, from Dolovo in south-eastern Banat, Yugoslavia; obtained on 15 May 1938 by B. Petrov.

Spermophilus citellus martinoid (Peshev, 1955)

1955. *Citellus citellus martinoid* Peshev, Izvestija na Zoologičeskija Institut Sofija 4—5: 290. Holotype. — Female, Chair of Zoology, University of Sofia 170, from the peak Kolarov of Mt. Rila, Bulgaria; obtained on 14 August 1952 by Z. Peshev.

Ondrias (1966) synonymised this form with *S. c. karamani*.

Spermophilus citellus balcanicus (Markov, 1957)

1957. *Citellus citellus balcanicus* Markov, Izvestija na Zoologičeskija Institut Sofija 6: 465. Holotype. — Adult male, Zoological Institute of the Bulgarian Academy of Sciences, Sofia, 10/54, from the vicinity of Lokorsko, near Sofia (Bulgaria); obtained on 15 May 1954.

Ondrias (1966) synonymised *S. c. balcanicus* with *S. c. karamani*, Ružić (1978) with *S. c. martinoid*.

Spermophilus citellus thracius (Mursaloglu, 1964)

1964. *Citellus citellus thracius* Mursaloglu, Communis Fac. Sci. Univ. Ankara 9: 260. Holotype. — Adult female (skin and skull), Department of Zoology, University of Ankara 218, from the south-eastern slope of Murattepe near Yenibedir, Lüleburgaz, European Turkey; obtained on 6 May 1963.

Spermophilus citellus macedonicus (Fraguedakis-Tsolis, 1977)

1977. *Citellus citellus macedonicus* Fragedakis-Tsolis, Mammalia 41: 65. — 1985. *Citellus citellus macedonicus* Fragedakis-Tsolis & Ondrias, Säugetierk. Mitt. 32: 196.

Holotype. — Adult female, Zoological Museum, University of Patras 10051, from Pontokomi near Kozani (Greece); obtained on 15 September 1965 by J. C. Ondrias.

This subspecies was proposed by Fragedakis-Tsolis (1977) on the basis of immunochemical data derived from a comparative study of *S. c. gradojevici* and *S. c. thracius*. Fragedakis-Tsolis & Ondrias (1985) provide a detailed description of morphological characters, designate a holotype and a type locality, and compare the taxon with *S. c. thracius* and *S. c. gradojevici*.

Subspecies have been diagnosed primarily on the basis of size and colour, and also by peculiarities of proportion and shape. Bauer (1960) noted that size varies in a mosaic-like pattern, and emphasised the need for comprehensive taxonomic review. Peshev (1968) expressed doubts as to whether all the races described were valid, whilst Grulich (1960) denied the existence of any clearly-defined subspecific taxa within the European souslik. Ružić (1978) briefly reviewed all the described forms except *S. c. macedonicus*, but diagnostic characters are vague where given at all and include size, relative tail length, and colour. Not surprisingly, Corbet (1978) was skeptical of the validity of the various forms which were “based on slight differences of proportions with no proof of discontinuity.”

Subspecific division of *S. citellus* comes from the time of the conventional subspecies, when taxonomists were attempting to answer the question, “Is the population different?”, rather than trying to understand patterns within the observed variation and to estimate the relative similarity of different populations (Thorpe 1987). Frequently subspecies were erected from single populations while their diagnoses were based on a small number of characters. These characters were investigated by univariate statistics, an approach now considered inadequate in the evaluation of overall group differences (Willig et al. 1986).

Given the lack of a comprehensive taxonomic review, it remains unclear whether the nine or so subspecies represent discrete portions of species, or just subtle local variants which differ from other populations only in the statistical sense. My aim has been to analyse the pattern of geographic variation in phenotypic characters in 16 geographic samples of *Spermophilus citellus*.

Material and methods

I examined over nine hundred European sousliks (mainly skins and skulls) housed in the following collections (acronyms in brackets): British Museum (Natural History), London (BMNH); Department of Zoology, Charles University, Prague (PFUK); Hungarian Natural History Museum, Budapest (MNM); Institute of Landscape Ecology, Academy of Sciences of the Czech Republic, Brno (ILE); Mammal Research Institute, Białowieża (MRI); Institute of Zoology, Bulgarian Academy of Sciences, Sofia (ZIBAN); National Museum, Prague (NM); Naturhistorisches Museum Wien, Vienna (NMW); Slovene Museum of Natural History, Ljubljana (PMS); Department of Biology, University of Trakya, Edirne (TUBD); Zoologische

Staatssammlung München, Munich (ZSM). Only adult specimens, those having attained at least their second calendar year, were selected for analysis. Age was estimated on the basis of tooth wear (Ružić 1966) and the date of collection. Significant sexual dimorphism exists in the European souslik, with males being bigger (Ružić 1978), so the sexes were treated separately. Unsexed specimens and those with damaged skulls were excluded from craniometric analysis. Eventually, 507 complete skulls, 229 male, 278 female, were ascribed to 16 geographic samples. In several cases they were pooled where localities were physiographically and climatically continuous and also expected to include the interbreeding populations. However, no sample areas transgressed a previously designated taxonomic boundary.

The geographic samples are listed below, as are their designation numbers (Fig. 2); sample sizes are in brackets. Specimen genders are designated by M (males) and F (females): Sample 1 — Poland, Nakło (MRI 15 M, 15 F). Sample 2 — Slovakia, Jablonov and Turnou (ILE 3 M, 10 F). Sample 3 — Hungary, Hortobagy, Mata (MNM 42 M, 33 F), Hajdubagos (ILE 1 M; NMW 2 M). Sample 4 — Southern Moravia and adjacent Austria: Znojmo (BMNH 1 M, 3 F; ILE 2 F), Brno (ILE 6 M, 5 F), Pohorelice (ILE 4 M, 5 F), Neudegg (NMW 1 F), Matzen (NMW 1 M), Gross Engersdorf (NMW 1 F), between Oberweiden and Baumgarten (NMW 1 M). Sample 5 — Austria, Neusiedlersee: Ilmitz (NMW 2 M, 9 F), Kalvarienberg (NMW 8 M, 4 F), Parndorf (NMW 6 M, 19 F), Apetlon (NMW 3 M, 3 F), Eichenwald (NMW 1 F), Lehmstätten (NMW 1 M, 3 F). Sample 6 — Hungary, Lake Balaton: Kisbalaton (ILE 3 M, 7 F), Tihany (MNM 1 M). Sample 7 — Hungary, Bugac: Bugacpuszta (MNM 5 M, 5 F), Moricgati (MNM 2 M, 1 F). Sample 8 — Serbia, Srem: Indjija (PMS 7 M, 8 F), Fruška gora (PMS 3 M, 3 F; BMNH 1 M), Čortanovci (BMNH 1 M, 9 F), Sremski Karlovci (PMS 1 M). Sample 9 — Serbia, Deliblatska peščara: Dolovo (BMNH 6 M, 2 F), Banatska Palanka, Devojačko brdo (PMS 5 M, 9 F), Samoš (PMS 1 M, 4 F), Šušara (PMS 3 F). Sample 10 — Zrenjanin, Orlovat (PMS 4 M, 14 F). Sample 11 — Jakupica and Karadjica Mts.: Patiška reka (BMNH 3 M, 6 F), Gorno Begovo (PMS 8 M, 16 F; ZSM 1 M, 2 F), Solunsko pole (PMS 3 M). Sample 12 — lowlands along the Vardar (Axios) River in Macedonia and Greece: Lake Dojran, Ačikot (PMS 6 M, 9 F), Gevgelija (BMNH 1 F, PMS 1 M), Star Dojran (NM 2 M, 1 F), Bogorodica (PMS 2 F), Rabrovo (PMS 1 F), Grčište (PMS 1 F), Matgara (BMNH 3 M, 3 F), Samli (BMNH 1 M, 1 F). Sample 13 — Bulgaria, Kazanlak, Krn (ZIBAN 41 M, 40 F). Sample 14 — Bulgaria, Sliven (ILE 4 M, 5 F). Sample 15 — Romania, Dobrogea: Murigheol (PFUK 5 M, 4 F), Malcoci (BMNH 4 M, 2 F). Sample 16 — Turkey, Thrace: Istanbul (MNM 1 M), Uskumruköy, Kilyos (TUBD 2 M), Tèrkos (TUBD 1 M), Firüzköy (TUBD 1 M, 1 F), Selimpasa, Silivri (TUBD 2 M, 3 F), Inecik (TUBD 1 F), Orhaniye Köyü (TUBD 4 M, 1 F), Harmang Köyü, Uzunkohprü (TUBD 1 M).

Thirteen linear measurements were taken from each skull using a vernier calliper accurate to the nearest 0.1 mm: CbL — condylobasal length, DiL — diastema length, MxT — maxillary tooth-row length, NaL — nasal length, OrD — diameter of orbit, ZgB — zygomatic breadth, BcB — braincase breadth, IoC — interorbital constriction, PoC — postorbital constriction, NaB — nasal breadth, IfB — breadth across infraorbital foramen, RoH — rostral height on the anterior alveolar margin of the upper premolar, MdH — mandibular coronoid height.

Reflective colour was measured in an area with a diameter of 8 mm located in the middle of the back using a Minolta Croma Meter CR-200 tristimulus colors analyser. As the colour of voucher specimens can be altered by prolonged exposure to light, all the animals used for this analysis had been collected within the last 15 years and since stored in dark specimen cabinets. The Commission Internationale de l'Eclairage (CIE) Yxy color system was used to describe individual colours. The lightness factor (Y) is expressed as a percentage based on perfect 100 % reflectance, whilst x and y are the chromaticity coordinates of the CIE x, y Chromaticity Diagram.

Fourteen log-transformed variables were used to represent climatic factors. Mean monthly temperatures and precipitation during the growing season of April–September were recorded for each sample. The standard deviations of the means of the average monthly temperatures and precipitation levels were used as indices of seasonality for both factors. Climatic data were taken from Steinhauser (1970) and the Climatic Atlas of the Socialist Federative Republic of Yugoslavia (undated).

Variations in mensural characters amongst the geographic samples were analysed using a one-way variance analysis. Phenetic affinities among geographic samples were assessed by a Principal Components Analysis (PCA) of the correlation matrix, and by Discriminant Function Analysis (DFA). Size effects were removed by Burnaby's method for size adjustment. The resulting adjusted data matrix was used for both PCA and UPGMA clustering using the Average taxonomic distance (ATD) matrix. Stepwise multiple regression was used to establish functional relationships between phenetic and climatic variables.

Results

Morphometric variability

One-way analysis of variance demonstrated a highly significant interlocality heterogeneity ($p < 0.0001$) amongst all the skull dimensions introduced into the analysis. The characters most affected by geographic variability were ZgB, BcB, CbL, and RoH (both sexes), but with females being more variable in all dimensions.

Z-standardised data were subjected to PCA. Character loadings on the first Morphological Principal Component (MPC1) were significantly positively correlated with all the cranial characters, suggesting that positive intercorrelations exist between different skull characters. Since the first Principal Component explains the maximum possible variation within the data, as all the characters utilised in the study are highly size dependent, MPC1 is explicable as a size vector. This represents a widespread phenomenon, observed repeatedly in morphometric data sets (Lemen 1983). The first component explained 57.8 % of the total variance in males, and 63.6 % in females. Over one half of the variance in the original data set was therefore due to size. A very good fit exists between MPC1 scores for both males and females from the 16 samples ($r = 0.959$, $p < 0.0001$), showing that larger male size is associated with a larger female size (and vice versa) (Fig. 1).

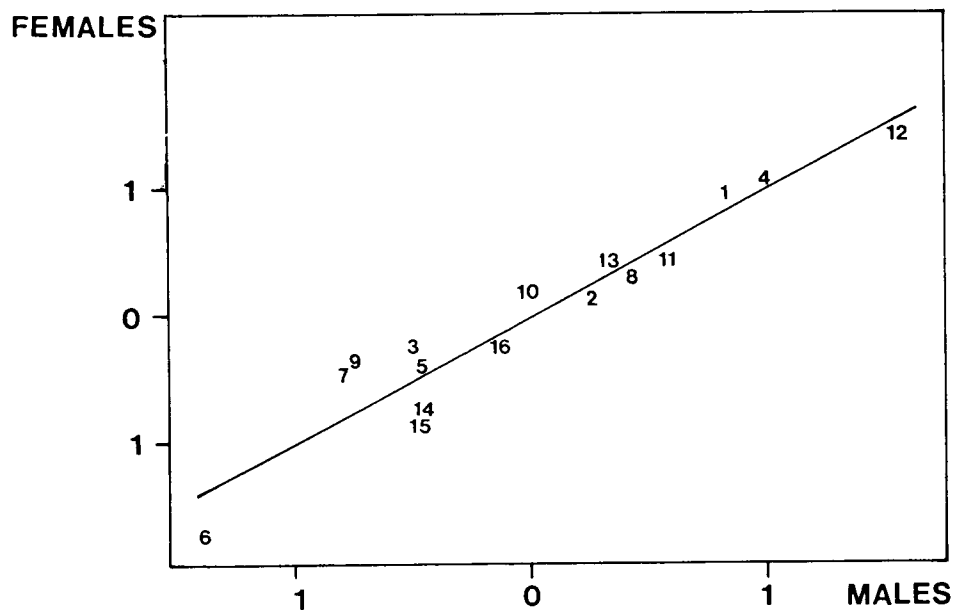


Fig. 1: Sexual dimorphism of size in *Spermophilus citellus*, based on mean values of Morphological Principal Component 1 scores. See Fig. 2 for identifying numbers of samples.

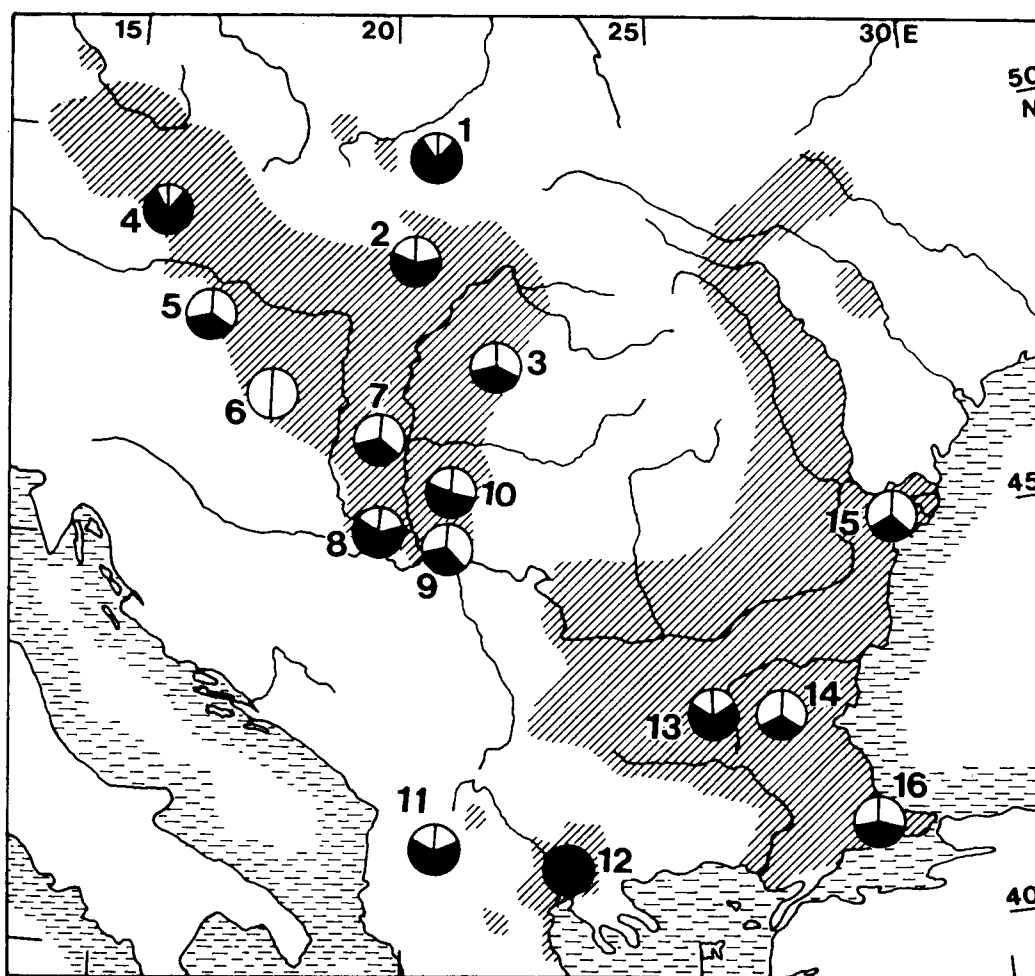


Fig. 2: Geographic variation in Morphological Principal Component 1 of 16 *Spermophilus citellus* localities. The value is proportional to the black area in the pie diagrams, the higher the score, the darker the circle. Open circles represent the smallest sousliks, filled circles represent the largest. Male scores are on the right and female scores are on the left half of individual circles. See text for sampling sites and locality identities. The approximate range of the species (shaded) follows Ružić (1978).

To place size variations into a geographic context, the MPC1 scores were projected onto a map of the distributional range using pie diagrams (Fig. 2). Despite this, no simple pattern was apparent from the geographical distribution of variation. Large populations are found on both the northern and the southern border, whilst both large and small populations occur close to one another. MPC1 scores do not correlate with longitude ($r = -0.075$ in males, $r = -0.173$ in females; n. s.), nor with latitude ($r = -0.132$ in males, $r = -0.041$ in females; n. s.).

The morphological Principal Component 2 (MPC2) was significantly, positively correlated with MxT and IoC in both sexes, and explained a further 14.1 % of the variance observed in both sexes. As principal components are not intercorrelated, size would be expected to exert a very low influence upon these two characters. A low correlation of the interorbital constriction (IoC) with other skull dimensions is

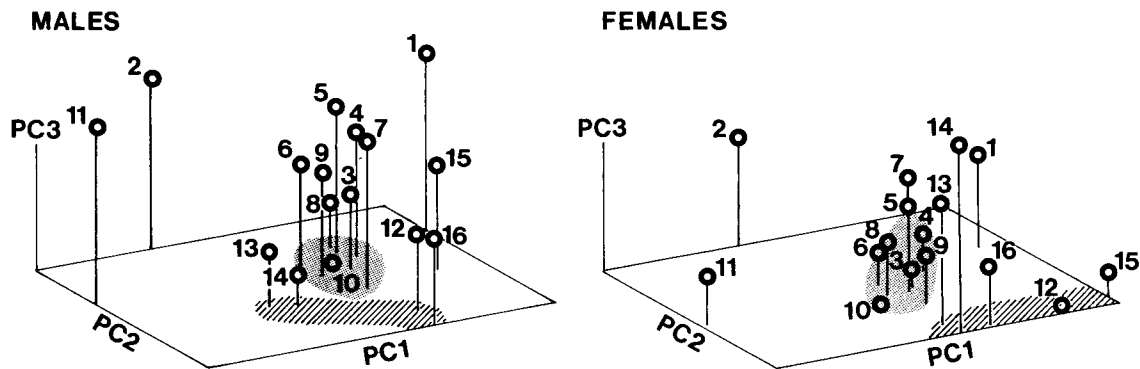


Fig. 3: Projection of 16 *Spermophilus citellus* sample centroids onto the first three principal components of size adjusted cranial data, males and females separate. Pannonian samples are indicated by dotted areas and Balkan ones by hatched areas. See Fig. 2 for identifying numbers of samples.

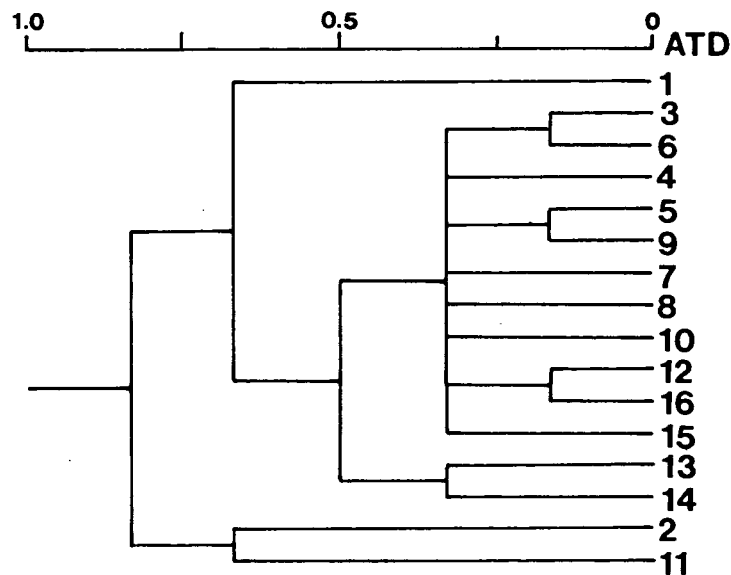


Fig. 4: Consensus tree summarising ATD matrices for 16 samples of male and female *Spermophilus citellus*. For sample designation, see Fig. 2. ATD — Average taxonomic distance, based on 13 size adjusted cranial variables.

not uncommon in mammals (e. g. Pankakoski & Nurmi 1986). Again, no correlation exists between MPC2 and longitude ($r = -0.237$ in males, $r = -0.359$ in females; n. s.), nor with latitude ($r = 0.004$ in males, $r = 0.102$ in females; n. s.).

The projection of the 16 sample group centroids onto the first three principal components (not shown) was not consistent with either their geographic derivation, or subspecific designation as proposed by Ružić (1978). I then eliminated size effects by Burnaby's Method (Rohlf 1989). The resultant adjusted data matrix supposedly not influenced by size variation was subjected to PCA. The group centroids obtained were projected onto the first three principal components; this explained 67 % of the variance of the original male data (35.1, 18.3 and 13.5 % respectively) and 70.1 % of

the female data (31.8, 19.9 and 18.3 % respectively). Results were similar for both sexes (Fig. 3). Sousliks from the Pannonian Plain (samples 3 to 10) and the Balkans (samples 12 to 14, and 16) formed two distinct clusters. Sample 11 was the most distinct, followed by samples 2 and 1. These results suggest that the most phenetically unique populations are also the marginal ones. Two of these (samples 1 and 11) also represent geographical isolates. Sample 15 is anomalous; its females being allocated to the Balkan cluster, but males being entirely independent.

The adjusted data matrix was also used to compute an Average Taxonomic Distance (ATD) matrix. Since the matrices for the two sexes did not differ significantly ($r = 0.79$, Mantel t -test = 4.33, $p = 1.00$), a consensus tree was produced (Fig. 4). The results mainly accord with those obtained by ordination (Fig. 3); however, four of the Balkan samples (12–14, 16) failed to fall within a single cluster. The three marginal populations (samples 1, 2, 11) also had independent positions in this analysis.

The Mantel test showed a very poor fit between ATD and geographic distance matrices ($r = 0.356$, $p = 0.996$ in males, $r = 0.416$, $p = 0.999$ in females), suggesting a weak increase in phenetic distinctness with increasing geographic distance. This test was repeated on Pannonian sousliks (samples 3 to 10), which inhabit a relatively homogeneous area. Again, no correlation was found between phenetic and geographic distances ($r = 0.124$, $p = 0.732$ in males, $r = -0.022$, $p = 0.458$ in females).

Clustering (Fig. 4) acted as a classificatory factor in Discriminant Function Analysis (DFA). Six samples were recognised, three of which have been pooled. The designations and definitions of the pooled samples are as follows: pooled sample A (Pannonian Plain, samples 3 to 10), pooled sample B (southern Balkans: samples 12, 16), and pooled sample C (central Balkans: samples 13, 14). Since the phenetic relationships of sample 15 were unclear, this sample was omitted from the DFA.

Table 1: Classification by discriminant analysis of six samples of male and female *Spermophilus citellus*. Rows are actual groups and columns are predicted groups. See text for identifying symbols.

	1	A	B	C	2	11	Total
MALES							
Sample 1	15						15
Sample A	8	95	3	4	3		113
Sample B		2	22	1	1		25
Sample C		4	2	30	1	2	39
Sample 2					3		3
Sample 11						15	15
FEMALES							
Sample 1	14						14
Sample A	9	115	1	9	3	3	140
Sample B		2	21	1			24
Sample C	1	4	3	28		1	37
Sample 2	1				9		10
Sample 11				1	1	22	24

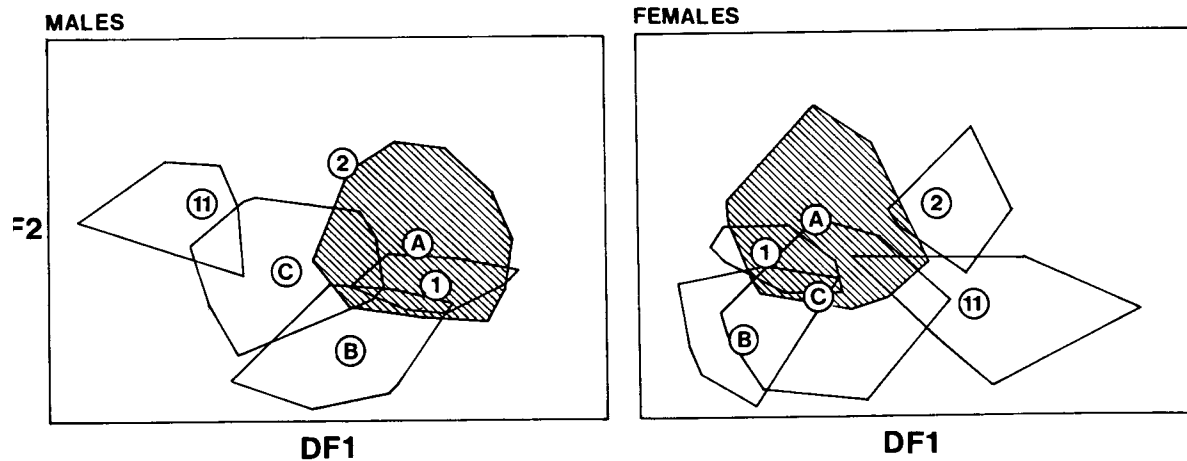


Fig. 5: Projection of six samples of *Spermophilus citellus* onto the first two discriminant variates, males and females separate. Polygons enclose scores for all individuals within a locality group, and symbols are placed on group centroids. Male sample 2 with only three specimens is given as a group centroid. Polygon of pooled Pannonian samples is striped. See text for identifying symbols.

Discriminant analysis was performed upon the raw data, and separately for each sex. The first two discriminant functions (DF) explained 75.1 % of the variance in the original data set in males (50.9 and 24.2 % respectively), and 75.5 % in females (42.0 and 33.5 % respectively). 83.9 % of the male specimens were allocated into their actual group, and 85.7 % of the females (Table 1). Despite the relatively high proportion of appropriately classified specimens, overlap between the samples was high. Polish sousliks (sample 1) entirely overlapped with the pooled Pannonian sample for both sexes (Fig. 5). Sample 2 also suggested a closer affinity with Pannonian rather than Balkan sousliks, what does accord with its geographic position. Two pooled Balkan samples (B and C) were closer to the pooled Pannonian sousliks than those from the Jakupica/Karadjica Mts. (sample 11). At least females from pooled sample C had a greater affinity with sousliks from Pannonia than those within pooled sample B. Phenetic relations such as these could also be expected from the geographic derivations of these samples.

Although it has been suggested that ratios are best avoided in statistical treatments (Sokal & Rohlf 1981), they remain appropriate as diagnostic characters in subspecies of the European souslik. Ružić (1978) distinguished south Pannonian sousliks from those from the central Balkans by their relatively shorter tails. I tested this on six geographic samples: three from the southern margin of the Pannonian Plain (samples 8 to 10), and two from Macedonia (samples 11 and 12). Also included were sousliks from Lake Vlasina in eastern Serbia. In this case only skins were available in statistically valid numbers, hence their exclusion from craniometric analyses. Samples 9 and "Vlasina" presumably correspond respectively to the "S-Pannonian" and "Central Balkan" samples of Ružić (1978: 131). Only specimens in which the head and body and tail lengths could be measured in a uniform manner were considered, thus eliminating errors through technical inconsistencies. Relative tail length

was expressed as a quotient of tail length with head and body length multiplied by 100. This ratio was not affected by sex (in sample 11, F-ratio = 0.01, n. s.), allowing the sexes to be pooled. Heterogeneity among samples was highly significant (F-ratio = 11.18, $p < 0.0001$) and three homogeneous sets could be established (Table 2). Each of the three Pannonian samples fitted with one of the homogeneous groups, suggesting significant heterogeneity in relative tail length, even between sousliks from restricted areas. Sousliks from Lake Vlasina (i. e. from the central Balkans) formed a homogeneous group with Pannonian sample 8. It therefore seems unlikely that relative tail length is of genuine taxonomic significance.

Twelve skull characters were transformed into ratios using CbL as the denominator, and then subjected to one way analysis of variance. All the ratios demonstrated highly significant interlocality heterogeneities ($p < 0.0001$) for both sexes. Sample 3 was used to test the influence of sex on the ratios. Ratios using MxT, IfB, and PoC showed significant heterogeneity between males and females ($p < 0.005$) and were excluded from further analyses. Sexes were pooled in the remainder, and mean values regressed against longitude and latitude to detect eventual trends in geographic variation. Six ratios of nine significantly correlated with at least one geographic variable (Table 3). Mean relative values for nasal length, postorbital breadth and nasal breadth decreased towards the east. Relative nasal length was larger in northern populations, and the same was true of the relative orbital diameter. The opposite trend, namely a decrease towards the north, is evident in the relative zygomatic breadth and breadth of the braincase. Because of the gradual change with increasing geographic distance, this was described as clinal variation within these characters.

Table 2: Mean relative tail lengths for six geographic samples of *Spermophilus citellus*. Homogeneous sets are connected by a vertical line. See Fig. 2 for identifying numbers.

Sample	N	Relative tail length	Homogeneous set
9	8	24.9	X
11	23	26.6	XX
10	18	26.7	X
12	17	26.9	X
Vlasina	15	29.4	X
8	18	29.7	X

Table 3: Regression onto two geographic variables of skull measurements transformed to ratios with the condylobasal length as denominator. Only correlation coefficients differing significantly from zero are shown. * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

Ratio with	Longitude	Latitude
NaL	—0.593*	0.799***
OrD		0.544*
ZgB		—0.722**
BcB		—0.663**
IoC	—0.623**	
NaB	—0.523*	

The division of clines into taxonomic categories is necessarily arbitrary (Thorpe 1987). By comparing these results with the diagnoses of the various subspecies of the European souslik, it is clear that this also occurs in the present case: for example, the diagnoses of the three 'southern' taxa (*S. c. gradojevici*, *S. c. isticus* and *S. c. karamani*) include relatively broader skulls across the zygomatic arches.

Association of the skull and climatic variables

Morphological Principal Component 1 correlated significantly only with temperature seasonality ($r = 0.63$, $p < 0.01$ in males; $r = 0.55$, $p < 0.05$ in females). In a stepwise multiple regression, four climatic variables explained 83 % of the variation in MPC1 in males ($R^2 = 0.83$), and 72 % in females ($R^2 = 0.72$; Table 4). Climate is thus quite a good predictor of size in the European souslik. The first variable introduced into the model was the standard deviation of the mean average monthly temperature, which explained 40 % of the variation in MPC1 in males, and 30 % in females. There is, however, no significant correlation of MPC1 with any individual monthly mean temperature in either sex. Three further climate parameters used in the model were monthly precipitation in May, June and September. MPC1 correlated positively with May and June precipitation, but negatively with those in September for both sexes. Warm, wet summers, associated with wet springs and dry autumn therefore favour larger body sizes in European sousliks.

Table 4: Results of stepwise multiple-regression analyses of Morphological Principal Component 1 as a size factor and 14 climatic variables for 16 geographic samples of male and female *Spermophilus citellus*. The standardised regression coefficients reflect their explanatory power when all variables were entered. The coefficients of multiple determinations (R^2 and adjusted R^2) with all variables entered were in parentheses, opposite the heading for each set of independent variables. SD Temp — standard deviation of the mean for average monthly temperature; P — precipitation level; * F-to-enter >1 , ** F-to-enter >5 .

Climatic variable	Males		Females	
	Step entered	Standardised regression coeff.	Step entered	Standardised regression coeff.
	$(R^2=0.83; \text{adjusted } R^2=0.77)$		$(R^2=0.79; \text{adjusted } R^2=0.72)$	
SD Temp	1**	0.83	1**	0.83
P May	2**	0.50	2**	0.56
P Sept	3*	−0.42	3*	−0.45
P June	4**	0.35	4**	0.37

Colour

Significant heterogeneity among samples is evident for all three quantities within the CIE Yxy colour system. Lightness factor Y showed a lower amount of interlocality variation (F-ratio = 4.42, $p < 0.005$) than chromaticity coordinates x (F-ratio = 32.34, $p < 0.0001$) and y (F-ratio = 23.02, $p < 0.0001$). Colour differs significantly between the five geographic samples. On the basis of the lightness factor, the palest sousliks were those in sample 12, and the darkest were in sample 9 (Table 6). Since sousliks from Macedonia (samples 11 and 12) and the Pannonian Plain (sample 8)

Table 5: Mean lightness factor (Y) for pelage colour in five geographic samples of *Spermophilus citellus*. Homogeneous sets are connected by a vertical line. See Fig. 2 for identifying numbers.

Sample	N	Lightness (Y)	Homogeneous set
9	23	7.75	X
10	18	8.12	XX
11	8	9.33	XX
8	20	9.52	X
12	20	9.65	X

were included in the same homogeneous set, successful separation of geographic samples on the base of lightness alone does not seem likely.

Regression of the lightness factor on climatic variables resulted in no statistically significant correlations. A good fit between lightness and mean July temperature ($r = -0.83$, not statistically significant) does, however, suggest that paler sousliks occur in regions with high July temperatures.

The multiple range test of chromaticity coordinates x and y resulted in three homogeneous sets: 8 and 10, 9 and 11, and 12. Projection of these two coordinates onto the CIE chromaticity diagram is shown in Figure 6. Although three significantly different sets can be distinguished, the overlap between samples was considerable. The most distinct sample is number 12, which is topotypical with *S. c. gradojevici*, a subspecies that has usually been recognised by its colour (e. g. Ružić 1978).

The colour of most terrestrial mammals closely resembles the colour of the soil upon which they live (Vaughan 1986). These types of adaptations also occur in nocturnal mammals, e. g. heteromyids living on different substrata (Best 1993), and even between and within the species of subterranean mole rats, *Spalax ehrenbergi* (Heth et al. 1988). Correlation of pelage colour with the background is even more likely in diurnal terrestrial squirrels. Pizzimenti (1976) demonstrated a significant correlation between pelage brightness and soil brightness in prairie dogs, although he failed to find any relationship between pelage brightness and the chromosome number. Although our samples were insufficient to statistically demonstrate that a significant correlation existed between lightness and environmental variables, pale sousliks seemed to be associated with hot summers, when the vegetation was likely to dry to a yellowish colour.

Discussion

Mammalian taxonomy is traditionally based on characters of the skin and the skull, but geographical variation is influenced by ecology and historical processes (Thorpe 1987). Since the phenotype is not independent of selection effects, ecological causation may seriously distort phylogenetic information incorporated into it. Should this occur, the phenotype would be of very low phyletic value. Furthermore, cranial morphology is frequently regarded as being unsuitable for taxonomic purposes in Sciuridae, and particularly so in tree squirrels and chipmunks. However, greater phyletic information is embodied in skull characters in ground squirrels (Patterson 1983).

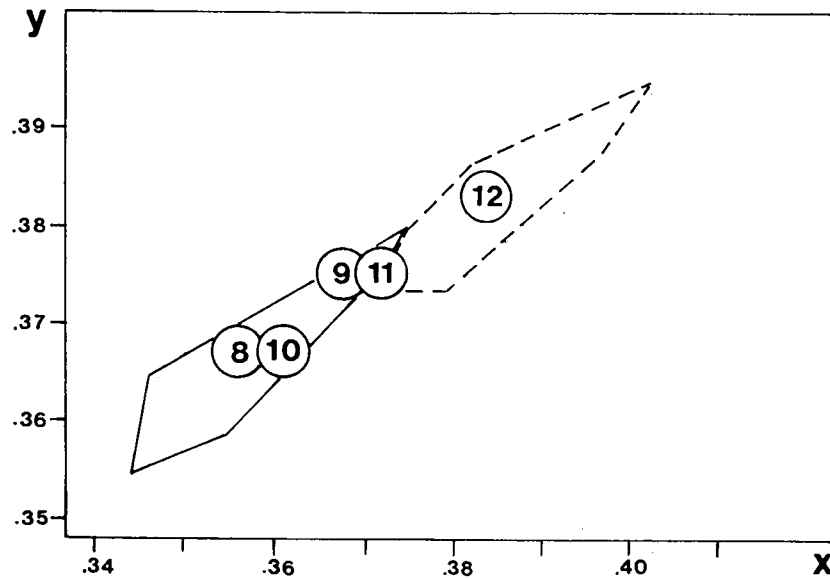


Fig. 6: Projection of five *Spermophilus citellus* group centroids onto the CIE x, y (1931) chromaticity diagram (insert). Individuals of the most distinct samples (8 and 12) are enclosed by polygons. For sample designation see Fig. 2.

Cranial size in the European souslik is significantly correlated with climatic variables, what suggests that it is of adaptive significance. Smith & Patton (1988) demonstrate that body size had a strong non-genetic, or environmental, basis in pocket gophers, *Thomomys bottae*. They were further able to identify evolutionary units from the cranial shape, which they considered “to represent underlying genetic influences and to identify more closely historical (phyletic) evolutionary units”. In their view, “these evolutionary units should form the basis for the infraspecific taxonomy of pocket gophers, and other animals as well.” In the case of the European souslik, size-free data identified geographically homogeneous sets which represent possible evolutionary segments of the species’ range.

The pattern of geographic variability in the European souslik suggests that a very limited divergence has occurred between adjacent populations inhabiting the Pannonian Plain. Divergence increases amongst the Balkan samples, with the most distinct samples being three populations from the periphery of the species’ current geographic range. Different geographical trends in the extent of interlocality divergence are not exceptional and have already been demonstrated in both human and animal populations (see Thorpe 1987).

Relative homogeneity among Pannonian sousliks had already been suggested by analysis of the frequency of nonmetric cranial traits in three south-Pannonian samples (identical to samples 8 to 10 of this study; Kryštufek 1990). Low inter-population divergence is probably due to the comparatively recent colonization of the area by the European souslik, steppe vegetation having appeared relatively late in the Pannonian Basin (Godicl 1980). Grulich (1960) concluded that the range expansion of the European souslik in this area largely followed human activities in the last few centuries. From the palaeozoological evidence available, this species first ap-

peared in Central Europe approximately 3000 years before the present (BP), but its extensive spread occurred no longer than 1000 years ago (Horaček & Ložek 1988).

On the other hand, the European souslik has been present in the Balkan Peninsula since the Middle Pleistocene (Dimitrijević 1991, Mayhew 1978, Marković & Pavlović 1991, Popov 1984, 1989) and it is therefore likely that it is the center of origin of the European sousliks. The divergence seen among Balkan sousliks is of approximately the same magnitude as their differentiation from Pannonian ones, and the two population groups are very close phenetically. Assuming that around 3000 years ago Central Europe was inhabited by sousliks from the Balkans, one might expect that the divergence in the majority of Balkan samples is of approximately the same age. The only exception is the phenetically well-differentiated sample (number 11) from the high altitudes of the Jakupica/Karadjica Mts. in central Macedonia. During the Late Pleistocene the European souslik lived to the west of its present distributional area (Dimitrijević 1991). It is likely that sample 11 is a relict of that period, expanding forests having restricted it to a few high mountain pastures where it diverged allopatrically.

The two northern populations (1 and 2), which are also well differentiated, are more enigmatic. One possible explanation is that Central Europe was colonised by sousliks several times. In this case, supposedly older peripheral populations could have diverged in allopatry following regressions in the species' distributional area. As yet there is no palaeontological evidence to support this view. Records of *Spermophilus* from the Central European Middle and Upper Pleistocene are mainly ascribed to *S. citelloides* (Janossy 1986, Nadachowski 1989), and its relationship with *S. citellus* is a source of debate. According to Gromov et al. (1965), it is more closely related to *S. suslicus*, but Nadachowski (1989) considers it to be the immediate ancestor of the European souslik.

Is it reasonable to recognise formal subspecies in the European souslik? Although the subspecies concept has been seriously criticised, with some workers even suggesting that the use of subspecies should be avoided entirely (e.g. Wilson & Brown 1953, Burt 1954), Fjeldså (1985) considered it to be a useful sorting device with considerable heuristic value. Lidicker's (1962) definition of a subspecies provides a good theoretical basis for an approach to this topic. From a practical point of view, it is difficult to decide what should be chosen as the minimum level of differentiation between two subspecies. Grulich (1960) used univariate statistics to demonstrate that differences among populations of *S. citellus* are far beyond the "75 % level". Corbet (1978) advocated "objective boundaries" between different subspecies whose members should be "recognisably different": namely, the diagnostic characters should have true discriminative value, thus allowing the allocation of individual specimens (or their majority) from an unknown sample into the correct subspecific category. As long as only two subspecies (*S. c. gradojevici* and *S. c. karamani*) were analysed, it was possible to allocate each specimen to an adequate taxon (Kryštufek 1993). With the increasing number of populations, as in the case of this study, the discriminatory value of sets of cranial characters decreased rapidly, and characters overlapped significantly among samples. In this context, I agree with Corbet (1978) that subspecies in *S. citellus* "are based on slight differences ... with no proof of

discontinuity", as long as conventional taxonomic characters such as the skin and skull are used. On the other hand, multivariate analyses of averaged skull characters demonstrated the existence of geographically homogeneous sets. These sets, which probably represent different phyletic lines, could not be diagnosed with sufficient accuracy on the base of the material available, so trinomials would be of very little help. In spite of this, the subspecies of the European souslik currently recognised are not congruent with the interlocality variability observed in the species, and thus act to obscure much of the pattern of geographic variation present.

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Zusammenfassung

Zur Beschreibung der geografischen Variation des Ziesels *Spermophilus citellus* (Linnaeus, 1766) wurden 13 Schädelmaße von 229 Männchen und 278 Weibchen aus 16 geografischen Stichproben genommen und univariaten und multivariaten Analysen unterworfen. Die Varianzanalyse ergab für beide Geschlechter und alle Maße eine hochsignifikante Heterogenität zwischen den Stichproben. Die erste Hauptachse, die mehr als die Hälfte der Varianz innerhalb des Datenmaterials erklärte, wurde als Größenvektor eines mosaikartigen geografischen Variationsmusters interpretiert. In einer schrittweisen multiplen Regressionsanalyse konnten vier klimatische Variablen 83 % der Größenvariation der Männchen und 72 % der Weibchen erklären; das Klima läßt daher gute Voraussagen über die Größe zu. Die weitere Analyse größenbereinigter Daten ergab deutliche phenetische (und offenbar auch phyletische) Unterschiede für drei periphere Populationen aus Polen, Slowakien und Mazedonien. Die gegenwärtige Unterscheidung von 9 Unterarten für den Europäischen Ziesel ist nicht konsistent mit der beobachteten Variation zwischen den Stichproben und scheint eher die reale geografische Variation zu verschleiern. Der diagnostische Wert von Schädelmerkmalen, Indices und Färbung erwies sich als gering; gegenwärtig wird daher keine formale Unterteilung in Unterarten vorgenommen.

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