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MICROGEOGRAPHIC VARIATION IN THE MEXICAN VOLE, *MICROTUS MEXICANUS*

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ABSTRACT

Altitudinal variation was assessed in 115 (62 male; 53 female) Mexican voles *(Microtus mexicanus)* from six localities in Jalisco, Mexico. Univariate and multivariate statistical techniques were employed in the data analyses. A total of 49 skeletal measurements were investigated, and of these, 17 showed significant interlocality variation. Rostral breadth, depth of braincase, rostral height, width of third molar and nasal length were found to be the most variable characters. Component I (a size factor) accounted for 36% of the total phenetic variation; components II and III accounted for 30% and 19%, respectively. Larger individuals were found to occur at lower altitudes; smaller individuals occurred at higher altitudes. Size variation was expressed in reverse to Bergmann's Ecogeographical Rule.

INTRODUCTION

Large scale geographic variation studies, those spanning several states or complete countries have increased in recent years. These studies have played major roles in debates concerning the nature of species and speciation, as well as reflecting evolutionary processes. On the other hand, spatial variation over more local areas, or microgeographic variation, has received little attention. Dubach (1975) and Price and Kennedy (1981) demonstrated genic variation in a small geographic area to exhibit levels as great as those previously reported for larger geographic areas in the deer mouse, *Peromyscus maniculatus.* Possibly, the levels of genic or morphologic variability selected to represent regions for large scale studies, may in reality reflect only the site chosen within a local area. An understanding of microgeographic variation appears to be critical in order to completely understand adaptive strategies at the macrogeographic level.

The adaptive significance of spatial variation in body size has been discussed by Bergmann (1847), Rosenzweig (1968), McNab (1971), and others. The classical interpretation of body size is reflected in Bergmann's Ecogeographic Rule. In relation to endotherms, small forms of individuals of the same species are located in southern parts of the range and large forms in northern parts of the range. The validity of Bergmann's Rule remains a central issue in discussion of modern systematics and evolutionary theory.

The Mexican vole, *Microtus mexicanus,* appears to provide an excellent model for studying the patterns of microgeographic size variation and for exploring the occurrence of Bergmann's Rule on a microgeographic scale. This boreal rodent ranges from southernmost Utah and Colorado south to Oaxaca de Juarez and occurs at higher elevations. The isolated nature of mountains in the Southwest provides for a series of small isolated populations along mountain tops

Table 1. Collection sites of *Microtus mexicanus* from Jalisco, Mexico.

Locality No.	Collection site/altitude	N Male	N Female
1	24.3 mi. W Atenquique, ca. 2770 m	6	6
2	26 mi. W Atenquique, north slope Volcan de Fuego, ca. 2835 m	26	30
3	27.3 mi. W Atenquique, Volcan de Fuego, ca. 2835 m	4	6
4	25.1 mi. W Atenquique, ca. 2850 m	6	5
5	26 mi. W Atenquique, north slope Volcan de Fuego, ca. 2896 m	13	3
6	26 mi. W Atenquique, north slope Volcan de Fuego, ca. 2990 m	5	3
	Total	62	53

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Table 2. *Microtus mexicanus* Interlocality variation in 17 skeletal characters

Character	d.f.	F-ratio[1]
Greatest skull length	5,96	2.214
Incisive foramen length	5,107	3.964
Diastema	5,108	3.883
Width of third molar	5,109	5.982
Mastoidal breadth	5,103	2.229
Pre-lambdoidal breadth	5,103	2.602
Interorbital constriction	5,106	2.169
Rostral breadth	5,109	10.367
Nasal length	5,101	5.626
Rostral height	5,105	6.218
Depth of braincase	5,104	6.662
Foramen magnum height	5,105	3.167
Tibia length	5,42	2.225
Tibia proximal width	5,99	2.568
Pelvis length	5,93	2.506
Obturator foramen length	5,104	2.153
Width of fused vertebrae	5,90	2.612

[1] Single classification analysis of variance; $p \leq .05$ for F-ratio exceeding 2.17.

Table 3. Character loadings on the first three principal components of interlocality phenetic variation in *Microtus mexicanus*.

Character	Principal Components I	II	III
Greatest skull length	.691	-.640	.032
Incisive foramen length	-.338	-.899	-.096
Diastema	-.617	-.654	.427
Width of third molar	.524	-.547	.482
Mastoidal breadth	-.746	-.417	-.283
Pre-lamboidal breadth	.619	-.383	-.587
Interorbital constriction	.540	-.459	-.697
Rostral breadth	.467	.066	-.824
Nasal length	.839	-.330	.276
Rostral height	.606	-.253	-.261
Depth of braincase	-.279	-.758	.200
Foramen magnum height	-.799	-.532	.082
Tibia length	-.474	-.798	-.167
Tibia proximal width	.569	.343	.640
Pelvis length	.487	-.244	.790
Obturator foramen length	.340	-.837	.057
Width of fused vertebrae	.838	-.254	.085

throughout its range. Gene flow across mountain tops is not likely; therefore, disjunct populations (suggesting population fragmentation) may exist.

M. mexicanus has been studied over a larger geographic area in New Mexico, Arizona, Utah and Colorado (Findley and Jones, 1962), and in Utah and New Mexico (Wilhelm, 1982). These studies involved distribution patterns, geographic variation and evolutionary relationships. Also, *M. mexicanus* has been studied karyotypically by Lee and Elder (1977).

The purpose of the present investigation was to evaluate microgeographic size variation in *M. mexicanus* using univariate and multivariate statistical techniques. This study was designed to concentrate on morphologic variability over a small geographic area, as well as provide additional insight into the validity of Bergmann's Ecogeographical Rule at the microgeographic level.

METHODS AND MATERIALS

From 31 December 1978 through 4 January 1979, 126 *M. mexicanus* were live-trapped from six localities on a volcanic mountain site in Jalisco, Mexico. Elevations of trap sites ranged from 2770 m to 2990 m above mean sea level. Specific location and corresponding sample sizes for each trap site are presented in Table 1. Specimens were prepared as standard museum study skins and skeletons and are housed in the Memphis State University Museum of Zoology. Specimens were aged according to the criteria of Choate and Williams (1978) and assigned to four age classes: old adult, adult, sub-adult and juvenile. Following their recommendations, sub-adults and juveniles were not included in the statistical analysis. The resulting sample size was 115 animals, consisting of 62 males and 53 females.

Twenty-three cranial and twenty-five post-cranial measurements were taken to the nearest 0.1 mm with the aid of dial calipers. Skeletal measurements followed Servinghaus (1976), Best (1978), Coate and Williams (1978), Kennedy and Schnell (1978) and Wilhelm (1982) with the following exceptions: ***atlas width***, greatest distance across the atlas; ***diagonal through the orbit***, greatest distance across the orbit on a diagonal; ***foramen magnum width***, greatest distance across the foramen magnum; ***foramen magnum height***, greatest height of foramen magnum; ***ilium length***, distance from the anterior tip of the ilium to the nearest edge of the acetabulum.

Univariate procedures were used initially to test the character set for sexual dimorphism followed by determination of interlocality variability. A single classification of analysis of variation for character means (ANOVA) and sum-of-squares simultaneous test procedures (SS-STP) were carried out by a modified univar program developed by Powers (1969). Trends in variation of individual characters and identification of maximally non-significant subsets were obtained from the SS-STP procedures. Characters exhibiting sexual dimorphism, when tested with a critical F-ratio of 3.92 at the 0.05 significance level, were removed from the data set; and sexes were combined in the remaining statistical analysis. Interlocality variation at the 0.05 significance level was indicated by an F-ratio exceeding 2.17.

Multivariate analyses were performed using the NT-SYS programs of Rohlf et al. (1978), which computed matrices of Pearson's product-moment correlations and derived phenetic distance coefficients from standardized character values. Clusters of characters were obtained with the unweighted pair-group method using arithmetic averages (UPGMA). Correlations among characters were summarized using dendrograms generated from the correlation matrices. Principal components were calculated from a correlation matrix among characters, and projections of localities were plotted onto the first three components. A shortest minimally connected network (computed from the original matrix of distances between localities) was superimposed upon the resulting three-dimensional plot and was used to connect most similar localities. The relationship between size and elevations was assessed using Kendall's correlation routine of SPSS (Nie et al., 1975).

RESULTS

Of the 49 original measurements examined, four showed significant sexual dimorphism: obturator foramen width (F-ratio: 7.419); pelvis depth (F-ratio: 7.448); pubis length (F-ratio: 7.950); and pubis width (F-ratio: 33.442). Seventeen of the remaining 45 measurements were found to have significant interlocality variation ($P < 0.05$). These characters are presented in Table 2. The remaining characters exhibited no significant variation; these characters were removed from subsequent analysis, following Sneath and Sokal (1973). Relative to the degree of interlocality variation, rostral breadth showed the greatest interlocality variation followed by depth of braincase, rostral height, width of third molar and nasal length. Whereas, obturator foramen length, interorbital constriction, greatest skull length, tibia length and mastoidal breadth had the lowest F-values.

A dendrogram summarizing variation among characters is presented in Fig. 1. There were two major clusters each containing two sub-clusters.

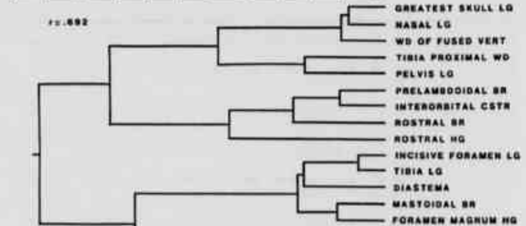

Figure 1. Dendrogram summarizing variation between characters for *Microtus mexicanus* from Jalisco, Mexico.

The sub-clusters were composed of greatest skull length through pelvis length; pre-lambdoidal breadth through rostral height; incisive foramen length through foramen magnum height; and width of third molar through depth of braincase. Incisive foramen length and tibia length were the most highly correlated characters. Additionally, greatest skull length and nasal length were highly correlated. Overall, the correlations appeared relatively low, indicating little redundency in information. Rostral height, depth of braincase, pelvis length and foramen magnum height were characters which contained independent information.

Principal components extracted to summarize character variation among localities indicated that 85% of the total phenetic variation was accounted for by the first three principal components. Therefore, reduction of the 17 character matrix to three dimensions resulted in little distortion. Character loadings indicating the correlation of characters with the first three principal components are presented in Table 3. Projections of the six localities onto the first three components are presented in Fig. 2.

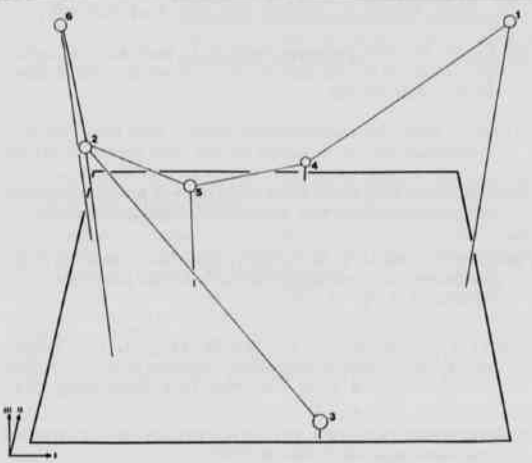

Figure 2. Three-dimensional projection of 6 localities onto the first three principal components of variation in the matrix of correlations of 17 morphological characters of *Microtus mexicanus* from Jalisco, Mexico. Numbers correspond to those given in Table 1. Shortest minimally connected network values between localities; 1-4 = 1.488; 4-5 = 1.290; 5-2 = 1.076; 2-6 = 0.932; 2-3 = 1.218.

Principal component I accounted for the majority of the total interlocality variation. This factor is taken to represent body size in the classic meaning of ecogeographical variation analysis (Niles, 1973). Nasal length, width of fused vertebrae, foramen magnum height and mastoidal breadth loaded high for this component. Variation along this axis showed a decrease in size of animals from left to right in Fig. 2 (animals from locality 1 were the largest; those from locality 6 were the smallest). This decrease, in general, corresponded with an increase in elevation. Therefore, animals obtained from locality 1 (2770 m) were relatively larger than those obtained from locality 6 (2990 m). Individuals obtained from those localities positioned in the middle of Fig. 2 were intermediate in size. The only exception to the generalization were the animals in locality 2. These were small animals but at a low elevation. Furthermore, a Kendall's correlation on principal components I and elevation showed that there was a statistical relationship between size and elevation, indicating elevation should be considered in examining the species over large geographic areas.

Component II had highest correlations (negative) for incisive foramen length, obturator foramen length, tibia length, depth of braincase, greatest skull length and diastema length. Component II explained 30% of the phenetic variability. Animals from localities that were situated near the front of Fig. 2 had long, deep skulls and relatively longer tibiae. Those from localities situated toward the back had short shallow skulls and short tibiae.

The third component had its highest correlations with rostral breadth, interorbital constriction, pelvis length and tibia proximal width. It accounted for 19.3% of the variability. Localities with individuals which tended to be relatively large for those highly-correlated characters are shown as being highest above the base of Fig. 2 (having tall "sticks").

DISCUSSION

Wilhelm (1982), using cranial and external measurements, found depth of skull and interorbital breadth to be sexually dimorphic. In this study, using both cranial and postcranial measurements, we found obturator foramen width, pelvis depth, pubis length and pubis width to be the only characters to be sexually dimorphic. Sexually dimorphic characters in our study corresponded well with those reported for other Microtines: *M. californicus* (Dunmire, 1955), *Clethrionomys glareus* and *M. agrestis* (Brown and Trigg, 1969) and *M. ochrogaster* (Servinghaus, 1976). The sexually dimorphic characters found in this study were those associated with the pelvic girdle; these characters would be expected to be dimorphic, considering demands placed on females during the delivery of young.

The univariate analysis indicated that there was significant morphologic interlocality variation in single characters for *M. mexicanus* within the study area. Although no overall continuous altitudinal gradients were found in the characters examined, there were some apparent trends in regard to principal component I. A decrease in the character means was found to generally correspond to an increase in elevation.

The present study indicated that specimens from about the same elevation (localities 3 and 4) which were only a few kilometers apart may be approximately the same size. However, localities 2 and 3 (occurring at about the same elevation and also only a few kilometers apart) appeared dissimilar in size. The amount of overall difference in size between individuals from localities 2 and 3 or 1 and 6, while shown at separate ends of the principal component I axis (Fig. 2), was only a few millimeters. The degree of morphologic variation at the local level may not be great enough to distort overall broad patterns. However, this study suggested that microgeographic variation should be given attention when studying variability at the macro level.

In regard to Bergmann's Rule, James (1970) reformulated the rule to predict that larger size should be found in cooler, drier locales which would correspond to areas of high elevation or latitude. In this study, overall size (which was represented by principal component I) exhibited the reverse of Bergmann's Rule. With the exception of locality 2, larger animals were found at lower elevations, and the smaller animals were found at the higher elevations. The exception probably reflected the very close proximity of localities 2, 5 and 6. There appeared to be some type of selective pressure influencing body size other than the combined effects of temperature and humidity which produced the situation described by Bergmann's Rule. Otto (1978) found significant differences in skeletal variation of male bank voles *C. glareus* along an altitudinal gradient. He described a situation wherein smaller animals were found at intermediate elevations. He attributed this distribution pattern to density factors which might put a selective premium on larger size.

Brown (1975) implied that important resources of habitat were competed for and partitioned among species on the basis of size. However, the occurrence of no other microtine species in the study area indicated that this is probably not in effect here. Another approach to account for the pattern of distribution exhibited by principal component I might be to relate a change in amount of available habitat or food over the range of elevations. Rosenzweig (1968) discussed body size in relation to primary productivity. He suggested that one way for natural selection to adjust consumers to various energy flow rates might be to modify body size in accordance with productivity. Relatively meager food supplies tended to set upper limits to body size. Habitat changes significantly across the range of elevations in this microgeographic area. This could correlate with a change in primary productivity and perhaps influence overall body size.

Principal components II and III are considered to represent shape rather than size (Niles, 1973). Principal component II indicated a pattern wherein animals from extreme elevations (localities 1 and 6) grouped as an intermediate form and animals from the intermediate elevations (localities 2, 3 and 4) grouped as relatively large or small forms. In this situation there are also selective pressures, perhaps the same as those suggested for principal component I, influencing the distribution pattern. Principal component III showed no recognizable trends.

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