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#### BIOGEOGRAPHIC INTERPRETATION OF VARIATION WITHIN AND AMONG POPULATIONS OF THE PRAIRIE VOLE, *MICROTUS OCHROGASTER*

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The prairie vole, *Microtus ochrogaster*, is one of few species of mammals (see Hoffmann and Jones, 1970:363-367) autochthonous to the Great Plains Physiographic Province of North America. The present distribution of the species includes much of the central and northern Great Plains and extends eastward into that portion of the Central Lowland Physiographic Province in which the potential natural vegetation (Küchler, 1964) is a mosaic of bluestem prairie and oak-hickory forest. The latter region possibly became inhabited by the species during the Xerothermic [Sub-Boreal] Interval (approximately 5000 to 2500 years BP), when the Prairie Peninsula displaced the forests south of the Great Lakes (Smith, 1957; Jones, 1964:27-28; Bryson *et al.*, 1970). Earlier shifts in distributional patterns of *Microtus* had been associated with long-term glacial episodes during the late Pleistocene (Hoffmann and Jones, 1970:366), whereas more recent distributional shifts have resulted at least in part from short-term climatic fluctuations.

Within the range of *Microtus ochrogaster*, a total of six nominal subspecies [*M. o. haydenii* (Baird), *M. o. ludovicianus* V. Bailey, *M. o. minor* (Merriam), *M. o. ochrogaster* (Wagner), *M. o. ohioensis* Bole and Moulthrop, and *M. o. taylori* Hibbard and Rinker] currently are recognized (Hall and Kelson, 1959:748-749; Lowery, 1974:264). In practically every instance, the principal characteristics by which these subspecies were differentiated pertained to size and

color: *haydenii* was said to be larger and paler than *ochrogaster* (Baird, 1858:543-544); *ludovicianus* was characterized as having larger molars and more rounded auditory bullae than other subspecies (Bailey, 1900:74-75; Lowery, 1974:261); *minor* was said to be smaller than *ochrogaster* (Merriam, 1888:599-600); *ohioensis* was described as paler ventrally and darker dorsally than *ochrogaster* (Bole and Moulthrop, 1942:156); *taylori* was characterized as larger than *ochrogaster* and darker than *haydenii* (Hibbard and Rinker, 1943:259-261). However, precursory examination of specimens housed in museum collections revealed that some of the criteria employed to distinguish these subspecies might vary as much or more within a population as among different populations. Accordingly, the objectives of this study were to assess the extent of variation in both size and color within and among populations of *Microtus ochrogaster* and to relate that variation to the historical biogeography of the species. The region encompassed by the study includes all of the range of *M. o. taylori*, most of the range of *M. o. haydenii*, and part of the range of *M. o. ochrogaster*.

#### METHODS AND MATERIALS

Examination of series collected in close geographic proximity and in every month of the year revealed that specimens of *Microtus ochrogaster* can be assigned readily to one of four categories of maturity:

*Old adults.*—Braincase flattened and skull angular; interorbital ridges fused or nearly fused; postorbital shelves prominent; cranial sutures fused; adult pelage.

*Adults.*—Braincase slightly rounded and skull not especially angular; interorbital ridges not fused; postorbital shelves prominent; cranial sutures fused; adult pelage.

*Subadults.*—Braincase and skull distinctly rounded; interorbital ridges lacking or faint; postorbital shelves not prominent; most cranial sutures fused; adult pelage.

*Young.*—Braincase and skull distinctly rounded; interorbital ridges lacking; postorbital shelves absent; most cranial sutures not fused; juvenal pelage or molting to adult pelage.

Use of these categories enabled satisfactory recognition of relative maturity and circumvented most of the problems that have been associated in the past with determination of age in microtine rodents (for example, see Anderson, 1959:433). Population turnover in the species is very rapid (Fleharty, 1972) so that the individuals of

a population tend to form a continuum with regard to age-related characteristics and give the appearance of continuing to grow and mature throughout life (see Phillips, 1969:459-460); few individuals survive to become adults (as defined above), and even fewer survive to become old adults. Based on preliminary analyses, adults and old adults were judged to be the only categories that would provide consistent and reliable estimates of size and were the ones employed in our subsequent morphometric analyses.

Mensural characters were selected for their utility and repeatability. External measurements (and weights, when available) used were those recorded on specimen labels, and probably were taken in slightly different ways by different preparators. Dial calipers were used to take the following seven cranial measurements: *greatest length of skull*, distance from anteriormost point on incisors to posteriormost point on either the occipital condyles or parietal bone (whichever extended farther posteriorly); *zygomatic breadth*, greatest distance across zygomatic arches; *mastoidal breadth*, greatest distance across mastoids; *interorbital constriction*, least breadth of interorbital region; *prelambdaid breadth*, least breadth of skull posterior to zygomata, anterior to mastoids, and ventral to squamosals; *rostral length*, distance in straight line from shallow notch lateral to lacrimal bone (on superior orbital border of zygomatic arch), anteromedially to tip of nasal on same side of skull (see Hooper, 1952:11); *total length of toothrow*, distance from anterior base of one or the other incisor to posteriormost crown surface of corresponding third upper molar.

Quantitative assessments of color were obtained with a Bausch and Lomb Spectrophotometer 20 with a color reflectance attachment. In this manner, the reflected rather than absorbed light was measured. Magnesium carbonate was employed as a pure-white color standard, and Illuminant C (Hardy, 1936:4) served as a light source. A reflectance factor was determined for each of ten wavelengths (415, 445, 475, 505, 535, 565, 595, 625, 655, and 685 nanometers) at approximately the mid-dorsum of each specimen selected for study; only nonmolting individuals in fresh adult pelage were examined. Reflectance factors then were converted, by means of a computer program, to the tristimulus values X, Y, and Z. The computer program then used these values to compute the trichromatic coefficients  $x$ ,  $y$ , and  $z$ , which are standard chromaticity (color quality) references (Hardy, 1936:9). Thereafter, variation in color was compared, both within and among populations, by means of statistical analyses of the following: reflectance factors at each wave-

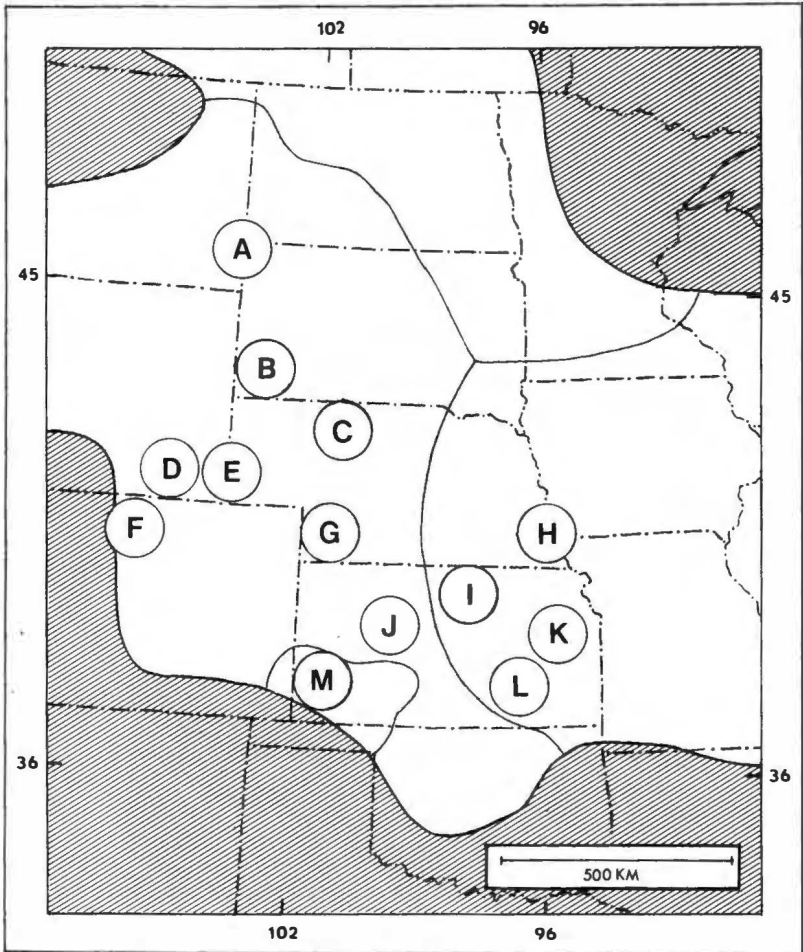


FIG. 1.—Map of the central plains region showing the locations of samples and their relationship to taxonomic boundaries (described in text).

length; tristimulus values for all wavelengths combined; trichromatic coefficients.

A total of 1641 specimens of *M. ochrogaster* from the central plains region was examined. An annotated list of specimens examined is on file in the Museum of the High Plains, Fort Hays State University, and copies will be provided by the senior author upon request.

After size and color measurements were obtained, the specimens were assigned to 13 samples (Fig. 1) for analysis of morphometric

variation within populations. These samples were selected as representative of most geographic regions within the study area. Geographic areas represented in each sample were kept as small as possible; however, in many instances it was necessary to include specimens from more than one county so that adequate numbers of individuals would be available. Samples were composed of the following counties: *Sample A*, Montana: Big Horn, Dawson, Powder River, and Richland counties; South Dakota: Harding County; *Sample B*, South Dakota: Custer and Fall River counties; *Sample C*, Nebraska: Cherry County; *Sample D*, Wyoming: Albany County; *Sample E*, Nebraska: Kimball and Scotts Bluff counties; Wyoming: Laramie and Platte counties; *Sample F*, Colorado: Larimer County; *Sample G*, Nebraska: Dundy County; *Sample H*, Iowa: Fremont, Mills, Montgomery, and Page counties; Nebraska: Cass, Nemaha, Otoe, Pawnee, Richardson, Sarpy, Saunders, and Washington counties; *Sample I*, Kansas: Jewell and Republic counties; *Sample J*, Kansas: Ellis County; *Sample K*, Kansas: Atchison and Douglas counties; *Sample L*, Kansas: Greenwood County; *Sample M*, Kansas: Ford, Hamilton, Kearney, and Meade counties.

The 13 samples selected for statistical analyses consisted of specimens from the geographic ranges of the three subspecies of *Microtus ochrogaster* that occur in the study area. Based on ranges defined by Hall and Kelson (1959), *M. o. haydenii* is represented by samples A, B, C, D, E, F, G, J; *M. o. ochrogaster* by samples H, I, K, L; and *M. o. taylori* by sample M (Fig. 1).

For the purposes of this study all variation within a population was assumed to be due to secondary sexual differences, age, or simply individual variation produced by either genetic or environmental effects. The extent of mensural variation with age was determined by comparing old adults of each sex with adults of the same sex. Secondary sexual variation was assessed by comparing samples of old adult males with old adult females. Age and secondary sexual variation were examined in three different geographic regions to determine the consistency of any such variation. Individual variation was estimated by means of coefficients of variation for samples comprised of old adults of the same sex.

Variation within and among populations was studied by employing a computer program (UNIVAR, see Power, 1970) that calculated standard statistics (mean, standard deviation, standard error of the mean, coefficient of variation,  $g_1$ , and  $g_2$ ) and conducted single classification analysis of variance to test ( $F$ -test) for significant differences among means of samples for each mensural character. Whenever

significant differences were found, Gabriel's (1964) Sums of Squares Simultaneous Testing Procedure (SS-STP) was used to determine nonsignificant subsets of sample means and thereby to facilitate interpretation of trends in variation of individual characters. Additionally, multivariate data were analyzed by means of several sub-routines of NT-SYS (see Schnell, 1970).

## RESULTS

### *Variation Within Populations*

Analysis of variance was used to determine if the means of the three external and seven cranial measurements used in this study differed significantly between adults and old adults. The results of the analysis, which was performed on samples F, H, and J to assess consistency over a wide geographic range, are given in Table 1. For all characters, except interorbital constriction, there was an increase in size from adults to old adults, as might be expected. However, interorbital constriction decreased with age in samples F and H, and remained the same in sample J. Constriction of the interorbital region of the skull apparently is related to the development of interorbital ridges and is characteristic of growth and development of the cranium in *M. ochrogaster*. The observed inconsistency of variation due to age at the three widely separated localities suggests that growth and development of individuals may vary either ecophenotypically or genetically in different regions.

Analysis of variance also was used to determine if the means of the three external and seven cranial measurements of old adults differed significantly between the sexes. As above, this determination was performed for samples F, H, and J (Table 1). With the exception of total length at locality J, there were no significant differences between males and females for any character examined. The difference for total length at locality J was at only the 0.05 level of confidence and conceivably could be the result of small sample size or measurement error. Because there were essentially no differences between them, data for both sexes were combined for geographic analyses. No geographic trends in secondary sexual variation were evident. In sample F, means for males were slightly larger than those for females (except length of tail and rostral length). In sample H, means for females were slightly larger than those for males (except interorbital constriction and rostral length). In sample J, means for males exceeded those for females for total length, length of hind foot, zygomatic breadth, and rostral length; means for mastoidal

breadth, interorbital constriction, and prelamdboidal breadth were the same in both sexes; means for females were greater for the remaining characters.

Coefficients of variation (CV) for the three external measurements in a series of old adults in sample J ranged from 4.49 (length of hind foot in females) to 14.71 (length of tail in males). Because of the high coefficient of variation in length of tail, this character was dropped from multivariate analyses. The range of CV for the seven cranial measurements was from 2.54 (greatest length of skull in males) to 5.75 (interorbital constriction in females). Males had higher coefficients of variation for length of tail, length of hind foot, zygomatic breadth, mastoidal breadth, and prelamdboidal breadth, whereas females exhibited greater variation in total length, greatest length of skull, interorbital constriction, rostral length, and length of maxillary tooththrow.

#### *Variation Among Populations*

Analysis of variance was used to determine if the means of the three external and seven cranial measurements in old adults differed significantly among the various geographic samples. Univariate analysis was conducted on 11 samples having adequate numbers of individuals. Samples L and K, consisting of one and two individuals, respectively, were added for multivariate analyses. Standard statistics for external and cranial measurements of the samples used are given in Table 2. Table 3 contains results obtained by the application of a Sums of Squares Simultaneous Testing Procedure to selected cranial measurements. Standard statistics for selected wavelengths of X and Y reflectance values are on file in the Museum of the High Plains, Fort Hays State University, and will be provided by the senior author upon request.

#### Univariate Analysis

All external measurements exhibited geographic variation. The SS-STP revealed three nonsignificant subsets for total length and length of hind foot and four nonsignificant subsets for length of tail. In most instances, the subsets overlapped broadly. For external measurements, there was no apparent consistency of samples making up any subsets for different characters. The only notable subset was one consisting only of sample M for length of hind foot; examination of measurements recorded by the original preparators for these individual specimens suggested that this variation is the result





TABLE 1.—Continued.

N	Hind foot length.										Significance Level	
	27	20	63	10	33	29	5	15	5	5		21
Mean	21.3	21.4	20.0	20.2	19.4	19.9	21.7	21.3	19.8	20.6	19.9	19.7
Minimum	19.0	20.0	17.0	18.0	16.0	18.0	20.5	20.0	18.0	20.0	18.0	18.0
Maximum	22.5	23.0	25.0	21.0	25.0	22.0	23.0	22.5	21.0	21.0	22.0	21.0
2 se	0.31	0.39	0.31	0.65	0.66	0.38	0.87	0.43	1.17	0.49	0.48	0.63
F-Value/	1.609/NS										1.600/NS	0.126/NS
Significance Level	0.342/NS										0.785/NS	
N	Greatest length of skull										Significance Level	
	24	20	59	9	24	25	5	15	4	5		17
Mean	28.4	28.9	27.5	28.6	27.6	29.0	29.3	28.7	28.1	29.0	29.0	29.1
Minimum	26.9	26.4	25.5	27.5	26.5	27.8	28.3	26.4	27.5	28.3	27.8	27.8
Maximum	30.3	30.7	29.2	29.9	29.0	30.7	30.7	29.7	28.8	29.9	30.6	30.7
2 se	0.33	0.40	0.21	0.45	0.25	0.34	0.87	0.44	0.53	0.53	0.36	0.76
F-Value/	13.760/***										4.581/NS	0.165/NS
Significance Level	3.445/NS										1.510/NS	
N	Zygomatic breadth										Significance Level	
	25	19	59	10	33	27	5	14	5	5		19
Mean	16.1	16.2	15.5	16.3	15.6	16.4	16.5	16.1	16.3	16.4	16.5	16.3
Minimum	15.0	15.3	14.1	15.5	14.6	15.4	16.0	15.3	15.5	15.6	15.4	15.4
Maximum	16.9	17.3	18.5	17.1	16.9	17.5	17.3	16.8	16.6	17.1	17.5	17.2
2 se	0.18	0.23	0.19	0.31	0.18	0.26	0.47	0.25	0.42	0.50	0.31	0.47
F-Value/	11.364/**										0.232/NS	0.193/NS
Significance Level	28.606/***										1.735/NS	

TABLE 1.—Continued.

N	Mastoidal breadth									
	24	19	57	9	25	25	5	14	4	7
Mean	12.7	12.9	12.4	12.8	12.3	12.8	13.0	12.8	12.6	12.8
Minimum	12.0	12.1	11.4	12.1	11.2	12.1	12.4	12.1	12.5	12.1
Maximum	13.4	13.7	13.2	13.2	13.0	13.8	13.7	13.5	12.8	13.5
2 SE	0.16	0.21	0.10	0.25	0.14	0.20	0.46	0.23	0.14	0.41
F-Value/ Significance Level	1.228/NS		8.250/**		15.336/***		0.808/NS		1.513/NS	0.007/NS
N	Interorbital constriction									
	26	20	63	10	33	27	5	15	5	8
Mean	3.9	3.7	4.2	4.1	4.1	4.1	3.8	3.7	4.1	4.1
Minimum	3.5	3.5	3.8	3.7	3.6	3.7	3.5	3.6	3.9	3.7
Maximum	4.3	4.1	4.5	4.3	4.4	4.4	4.1	4.0	4.3	4.3
2 SE	0.07	0.07	0.04	0.11	0.07	0.07	0.23	0.06	0.16 <sub>1</sub>	0.15
F-Value/ Significance Level	17.240/***		3.930/NS		0.109/NS		1.399/NS		1.158/NS	0.023/NS
N	Prelambdoidal breadth									
	24	20	58	9	28	24	5	15	5	7
Mean	10.9	10.9	10.8	11.0	10.9	11.0	11.1	10.9	10.9	11.0
Minimum	10.3	10.4	10.1	10.6	10.1	10.4	10.6	10.4	10.6	10.4
Maximum	11.8	12.0	11.8	11.6	11.5	11.9	12.0	11.5	11.3	11.5
2 SE	0.15	0.17	0.10	0.25	0.12	0.17	0.50	0.14	0.27	0.47
F-Value/ Significance Level	0.086/NS		2.362/NS		1.495/NS		2.025/NS		0.685/NS	0.046/NS

TABLE 1.—Continued.

N	Rostral length									
	27	19	58	10	32	24	4	15	5	8
Mean	8.8	9.0	8.4	8.9	8.7	9.1	8.9	9.1	9.0	9.0
Minimum	8.1	8.3	7.4	8.4	8.2	8.4	8.3	8.7	8.5	8.4
Maximum	9.5	9.6	9.7	9.3	9.8	9.7	9.2	9.6	9.3	9.7
2 SE	0.15	0.13	0.13	0.22	0.13	0.15	0.41	0.13	0.34	0.27
F-Value/ Significance Level	5.537/*		7.285/**		16.166/***		1.290/NS		0.830/NS	1.421/NS
N	Length of maxillary toothrow									
	26	20	55	9	32	28	5	15	5	8
Mean	16.6	17.0	16.4	16.9	16.2	17.0	17.4	16.8	16.6	17.1
Minimum	15.7	15.6	15.5	15.6	15.5	15.9	16.9	15.6	15.6	15.9
Maximum	17.8	18.1	17.8	17.7	17.4	17.9	18.1	17.5	17.2	17.9
2 SE	0.19	0.29	0.15	0.44	0.17	0.20	0.57	0.31	0.59	0.31
F-Value/ Significance Level	4.965/*		6.181/*		40.982/***		3.444/NS		4.700/NS	0.038/NS

TABLE 2.—Geographic variation in external and cranial dimensions among 13 samples of *Microtus ochrogaster*.

Statistics	Sample A	Sample B	Sample C	Sample D	Sample E	Sample F	Sample G	Sample H	Sample I	Sample J	Sample K	Sample L	Sample M
N	11	10	18	21	13	20	11	10	17	29	2	1	7
Mean	159.0	163.1	164.6	162.4	159.8	171.7	162.3	163.0	156.8	154.5	167.0	153.0	164.4
Minimum	141.0	148.0	137.0	148.0	146.0	162.0	155.0	142.0	136.0	136.0	164.0		153.0
Maximum	171.0	176.0	186.0	178.0	170.0	188.0	171.0	174.0	175.0	170.0	170.0		180.0
2 SE	5.85	6.36	5.68	2.61	4.56	3.29	2.67	6.05	5.27	3.50			7.96
Total length ( $F=5.173$ ) <sup>*</sup>													
N	11	10	16	21	13	20	11	10	17	29	2	1	7
Mean	38.5	38.3	37.3	40.6	38.9	44.6	36.4	38.3	35.3	35.3	36.0	37.0	34.3
Minimum	30.0	32.0	30.0	33.0	31.0	39.0	26.0	32.8	30.0	25.0	35.0		22.0
Maximum	45.0	42.0	46.0	48.0	47.0	53.0	45.0	43.0	43.0	46.0	37.0		42.0
2 SE	2.52	2.15	2.29	1.52	2.36	1.70	3.05	1.77	2.11	1.88			5.03
Tail length ( $F=7.772$ ) <sup>**</sup>													
N	12	10	18	22	13	20	11	10	17	29	2	1	6
Mean	20.6	20.6	20.9	20.7	20.2	21.4	20.9	20.2	19.9	19.9	21.0	20.0	25.7
Minimum	19.0	19.0	18.0	19.0	19.0	20.0	20.0	18.0	18.0	18.0	21.0		20.0
Maximum	21.0	22.0	23.0	22.0	21.5	23.0	22.0	21.0	21.0	22.0	21.0		36.0
2 SE	0.39	0.61	0.64	0.30	0.53	0.39	0.42	0.65	0.47	0.38			6.23
Hind foot length ( $F=7.146$ ) <sup>**</sup>													

TABLE 2.—Continued.

Greatest length of skull ( $F=1.655$ )*												
	10	10	16	19	9	20	9	9	17	25	2	6
N	10	10	16	19	9	20	9	9	17	25	2	6
Mean	28.0	28.6	28.9	28.6	28.6	28.9	29.1	28.6	28.4	29.0	28.5	28.9
Minimum	26.0	27.2	27.6	26.9	27.5	26.4	28.4	27.5	27.3	27.8	28.0	27.5
Maximum	30.0	30.4	30.8	29.9	29.8	30.7	29.5	29.9	29.7	30.7	29.1	30.4
2 SE	0.91	0.54	0.44	0.34	0.54	0.40	0.22	0.45	0.33	0.34		0.89
Zygomatic breadth ( $F=1.480$ )*												
N	10	8	15	20	10	19	10	10	16	27	1	7
Mean	15.9	16.5	16.4	16.3	16.1	16.2	16.4	16.3	16.0	16.4	16.2	16.5
Minimum	14.5	15.8	15.5	15.8	15.2	15.3	15.4	15.5	15.3	15.4		16.2
Maximum	17.0	16.9	17.5	17.1	16.7	17.3	17.3	17.1	16.7	17.5		17.0
2 SE	0.51	0.31	0.28	0.19	0.31	0.23	0.39	0.31	0.25	0.26		2.13
Mastoidal breadth ( $F=2.011$ )*												
N	10	10	16	19	9	19	9	9	16	25	2	7
Mean	12.4	12.6	12.7	12.5	12.3	12.9	12.6	12.8	12.7	12.8	12.1	12.6
Minimum	11.8	12.2	12.1	12.0	11.7	12.1	12.1	12.1	12.0	12.1	11.5	12.2
Maximum	13.5	12.9	13.8	13.2	12.8	13.7	13.0	13.2	13.2	13.8	12.7	13.1
2 SE	0.37	0.14	0.23	0.13	0.23	0.21	0.22	0.25	0.15	0.20		0.24
Interorbital constriction ( $F=8.529$ )**												
N	12	10	16	21	12	20	11	10	17	27	1	7
Mean	3.7	3.7	3.8	3.8	3.7	3.7	3.8	4.1	3.9	4.1	3.7	3.5
Minimum	3.3	3.4	3.4	3.3	3.5	3.5	3.6	3.7	3.5	3.7		3.2
Maximum	4.1	3.8	4.3	4.0	4.1	4.1	4.1	4.3	4.4	4.4		3.9
2 SE	0.12	0.09	0.12	0.09	0.12	0.07	0.08	0.11	0.14	0.07		0.23

TABLE 2.—Continued.

Prelambdoidal breadth ( $F=1.059$ ) NS												
N	10	10	15	18	9	20	9	9	15	24	1	7
Mean	10.8	10.9	10.9	11.0	10.7	10.9	10.8	11.0	11.1	11.0	11.0	11.0
Minimum	9.9	10.5	10.4	10.2	10.2	10.4	10.3	10.6	10.3	10.4		10.4
Maximum	11.8	11.1	11.8	11.5	11.1	12.0	11.5	11.6	11.8	11.9		11.4
2 SE	0.33	0.12	0.20	0.16	0.19	0.17	0.26	0.25	0.21	0.17		0.28
Rostral length ( $F=0.851$ ) NS												
N	8	9	15	21	11	19	11	10	15	24	2	6
Mean	8.7	9.1	8.9	9.0	8.9	9.0	9.1	8.9	9.0	9.1	8.9	8.9
Minimum	8.0	8.2	8.0	8.1	8.0	8.3	8.5	8.4	8.3	8.4	8.8	8.4
Maximum	9.6	10.1	10.0	10.0	9.7	9.6	9.4	9.3	9.6	9.7	9.1	9.6
2 SE	0.42	0.38	0.30	0.20	0.27	0.13	0.15	0.22	0.21	0.15		0.37
Length of maxillary toothrow ( $F=1.113$ ) NS												
N	12	10	15	21	13	20	11	9	16	28	2	7
Mean	16.7	17.0	17.2	17.0	16.9	17.0	17.3	16.9	16.7	17.0	17.3	17.3
Minimum	15.3	16.2	16.1	16.2	15.6	15.6	16.5	15.6	15.8	15.9	17.1	16.2
Maximum	18.0	18.1	18.4	17.8	17.6	18.1	18.1	17.7	17.7	17.9	17.5	17.6
2 SE	0.52	0.33	0.31	0.21	0.28	0.29	0.26	0.44	0.26	0.24		0.41

TABLE 3.—Results of SS-STP analyses for geographic variation of three cranial measurements in *Microtus ochrogaster*. Vertical lines to the right of each array of means connect maximally nonsignificant subsets at the 0.05 level. See text for key to sample numbers.

Greatest length of skull	Zygomatic breadth	Mastoidal breadth
G 29.10	M 16.54	F 12.88
J 29.04	B 16.49	J 12.78
M 28.95	J 16.43	H 12.77
C 28.94	G 16.42	I 12.69
F 28.86	C 16.39	C 12.66
B 28.64	H 16.34	M 12.64
D 28.61	D 16.34	G 12.59
E 28.60	F 16.24	B 12.57
H 28.60	E 16.09	D 12.54
I 28.44	I 16.02	A 12.43
A 28.03	A 15.94	E 12.34

of erroneous measurement of this character. Further examination revealed that means for samples I and J were consistently smaller than those in most other samples, and that the means for sample F were consistently larger than those in most other samples.

Only four of the seven cranial measurements exhibited geographic variation. Results of analysis of greatest length of skull, zygomatic breadth, and mastoidal breadth by SS-STP are given in Table 3; means for the fourth, interorbital constriction, were arranged in four broadly overlapping nonsignificant subsets. Analyses of pre-lambdoidal breadth, rostral length, and length of maxillary tooth-row revealed no significant differences between individual samples or groups of samples.

Examination of all size relationships of cranial characters suggests a gradation of slightly smaller to slightly larger means arranged from north to south. Sample A, for example, was consistently smaller than most other samples, whereas sample J averaged larger than most other samples. Size relationships based on external characters, however, are inconsistent with those based on cranial characters and suggest a gradation from slightly smaller to slightly larger means arranged from east to west. Samples I and J, for example, were smaller than other samples, whereas sample F was larger than other samples.

The SS-STP revealed no obvious relationships among samples based on reflectance analyses. Comparisons that exhibited significant differences (at least at the 0.05 level) were characterized by

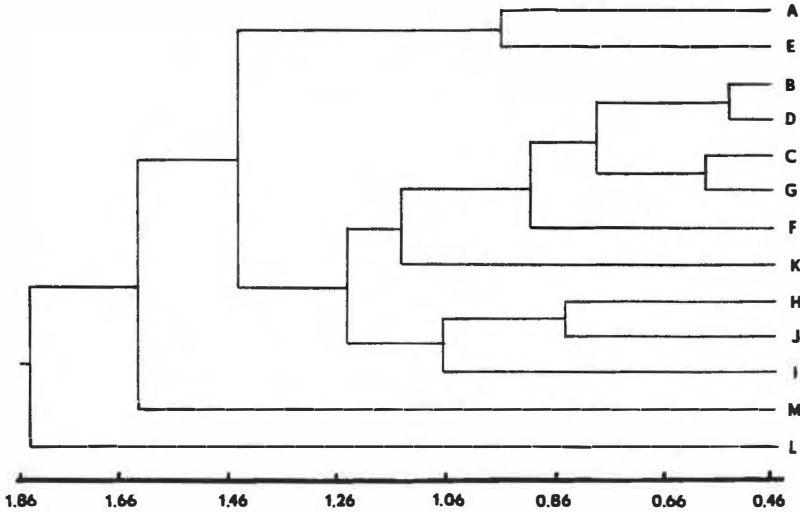


FIG. 2.—Distance phenogram resulting from cluster analysis of 13 samples of *Microtus ochrogaster*.

having two or three broadly overlapping, nonsignificant subsets. For X-reflectance, wavelengths 415, 655, and 685 differed significantly among samples, and Y-reflectance wavelengths 475, 505, 625, 655, and 685 differed significantly among samples. The only significant differences among samples with Z-reflectance were at wavelengths 415 and 505. No clinal patterns of geographic variation were detectable.

#### Multivariate Analysis

Means of external (excluding length of tail) and cranial measurements for all samples were included in an NT-SYS multivariate analysis. Phenetic relationships of samples were expressed by phenograms, which were computed by cluster analysis from correlation and distance matrices. The distance phenogram, resulting from analysis of 13 geographic samples, is shown in Fig. 2. Samples represented in the phenogram are divided into four major groups. Two of the groups (L and M) consist of single samples; another group includes samples A and E; the fourth group includes samples B, C, D, F, G, H, I, J, and K. Consideration of the geographic origin of these samples (Fig. 1) does not reveal a readily discernible pattern of geographic variation. The coefficient of cophenetic correlation for the distance phenogram is 0.798.



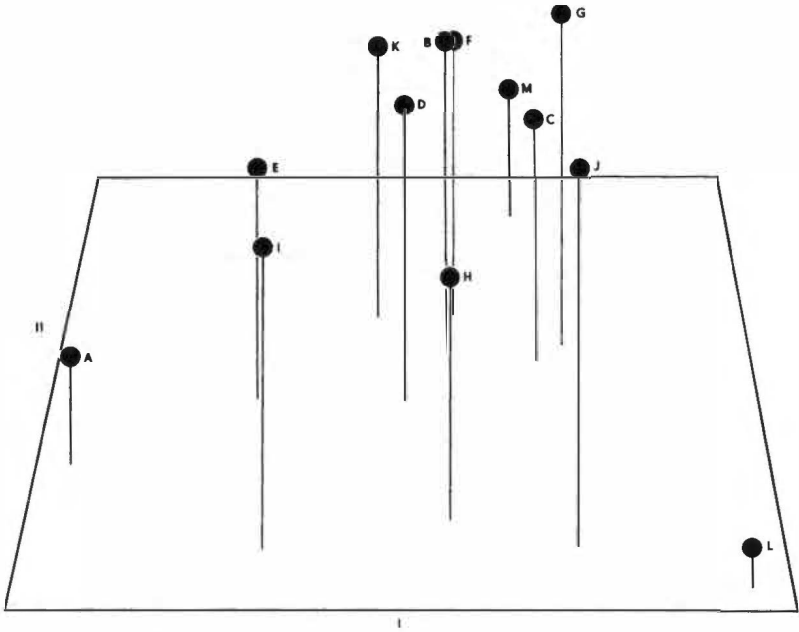


FIG. 3.—Three-dimensional projection of the first three principal components showing the phenetic position of 13 samples of *Microtus ochrogaster*.

Computation from the matrix of correlation was used to derive the first three principal components. Because the first principal component (which usually accounts for variation based on differences in size) accounted for only 31.1 per cent of the variation, it is assumed that size is not a dominant source of variation. The next two principal components accounted for 26.7 and 13.9 per cent, respectively, of the variation. The amount of total variation attributed to the first three principal components is 71.7 per cent. A three-dimensional plot of the first three principal components is shown in Fig. 3. Examination of the first two dimensions reveals no organization of samples that can be attributed to geographic or subspecific relationships. For these dimensions, samples A, L, and M form three outer points of the cluster. Samples H, I, and J group loosely together outside of the main body of the cluster. Incorporation of the third dimension resulted in a better clustering of the samples, but still gives no indication of geographic or taxonomic relationships. Examination of the first and third axes depict A and L as the terminal points of an elliptical cluster pattern. An elliptical pattern, in this case with samples L and M forming the terminal

points, also can be seen when the second and third axes are examined. Again, there are no strong indications of geographic or taxonomic relationships, although the second and third axes do suggest a weak clustering of samples H, I, and J, and samples B, C, D, E, F, and G.

#### DISCUSSION

The central plains, from which populations of *Microtus ochrogaster* were sampled for this study (Fig. 1), includes at least part of all the major floral regions of the Great Plains except the Llano Estacado (which is not inhabited by *M. ochrogaster*). No attempt was made in this study to sample populations inhabiting the Prairie Peninsula, because the systematic relationships of those populations have been studied by William D. Severinghaus at the University of Illinois and presumably will be reported on elsewhere.

Within the central plains, the principal floral divisions are a zone of True Prairie (tall-grass prairie) in the east, the Mixed Prairie (mixed-grass prairie) on much of the central Great Plains, and the High Plains (short-grass prairie) in the west. The Mixed Prairie, although consisting largely of a zone of transition between the other, more distinctive vegetative zones, is perhaps the most important of the three in terms of biogeography because of the vegetative changes that occur within this zone as a result of climatic fluctuations. The biogeography of *M. ochrogaster* is a case in point.

The distribution and relative abundance of *M. ochrogaster* suggests a center of origin on the True Prairie. The occurrence of the species to the east of the True Prairie doubtlessly represents an expansion of range after the development of the Prairie Peninsula nearly 5000 years ago, and geographic variation in those populations of *M. ochrogaster* likely reflects responses to subsequent directional selection resulting from the different humidity, vegetation, and background coloration that exist in that region. The occurrence of the species to the west of the True Prairie represents the effects of dispersal into habitats not unlike those of the more easterly tall-grass prairie. On the Mixed Prairie, these habitats are constantly expanding or contracting, depending on the climate, but frequently are widespread in low-lying areas (see Albertson, 1937). Farther to the west, on the High Plains, tall-grass habitats are restricted to riparian lowlands or marshy areas and, accordingly, the distribution of *M. ochrogaster* usually exhibits a dendritic pattern in response to the availability of suitable cover (see Jones, 1964:222, for

western Nebraska; Andersen and Jones, 1971:381, for northwestern South Dakota; Armstrong, 1972:243-244, for northeastern Colorado; Genoways and Jones, 1972:25, for southwestern North Dakota). This dependence on the availability of suitable grassy cover and a layer of mulch in which to burrow doubtlessly is related in part to the fact that the species is active during daylight (Carley *et al.*, 1970) and therefore is especially susceptible to diurnal predators. For a more detailed account of the importance of vegetative cover to *Microtus* populations, see Birney *et al.* (1976).

The close association, on both the High Plains and the Mixed Prairie, of the distribution of *M. ochrogaster* with the distribution of mesic habitats comprised of relatively tall grasses means that the distribution of *M. ochrogaster* is necessarily irregular, like that of its habitat. In other words, the prairie vole would be expected to expand its range during or following wet periods as the vegetation responded to increased soil moisture and to contract its distribution during dry periods as the tall grasses were replaced by species adapted to more arid conditions. Examples of this are found on both the High Plains and the Mixed Prairie.

On the High Plains, Armstrong (1972:244) mentioned a specimen of *M. ochrogaster* obtained in 1892 in the valley of the Arkansas River at Cañon City. This locality is more than 300 kilometers west of the nearest known extant population in the Arkansas River Valley in southwestern Kansas. Another extant population of prairie voles is located nearer Cañon City in northeastern Colorado, but much of the intervening region is dominated by inhospitable (for *M. ochrogaster*) short-grass prairie that affords little cover if grazed and that doubtfully has supported populations of prairie voles during Recent time. Accordingly, the specimen from Cañon City probably represents a former population that occurred in a narrow ribbon of mesic grassland extending along the Arkansas River from the Mixed Prairie in Kansas to the foothills of the Rocky Mountains in Colorado. In this regard, another mesic-adapted species, *Synaptomys cooperi*, is known to have left relict populations in southwestern and central Kansas (Cockrum, 1952:193-194) and in southwestern Nebraska (Jones, 1958; Jones, 1964:222) as its range contracted far to the east. Furthermore, Baker (1889:56-57) reported what he described as "*Jaculus hudsonius*" [= *Zapus hudsonius*, another mesic-adapted species] from near WaKeeney in northwestern Kansas (Choate and Fleharty, 1975:62); the range of this species in Kansas presently occurs far to the east in the more mesic True Prairie. Finally, *Peromyscus leucopus*, which presently

occurs in the sparse riparian woodlands of western Kansas, was said to have occurred at Fort Hays on the floodplain of Big Creek (a tributary of the Smoky Hill River) in northwestern Kansas (Allen, 1874:49) but apparently later withdrew to the east for a considerable period of time before again dispersing into the region (Fryden-dall, 1961; Choate and Fleharty, 1975:35). We suspect that all four of these pronounced contractions of geographic distribution were influenced by droughts.

On the Mixed Prairie, the effects of the great drought of the middle 1930s on the distribution and abundance of *M. ochrogaster* are relatively well documented. Wooster (1939; see also Tomanek and Hulett, 1970:210) estimated that Ellis County, Kansas, was inhabited by an average of three prairie voles per acre in 1933, at the beginning of the drought. However, during the drought years of 1933 to 1939 the species "completely disappeared" from the region (Wooster, 1939; see Choate and Fleharty, 1975:46) as the dominant vegetation changed (Tomanek and Hulett, 1970:205) from a dense cover (more than 85 per cent of the ground covered by vegetation) of tall and mid-height grasses to a sparse cover (more than 80 per cent of the ground devoid of vegetation) of short blue grama (*Bouteloua gracilis*) and buffalo grass (*Buchloë dactyloides*). The effects of the drought on vegetation persisted for nearly a decade, and it can be assumed that the effects on mammals did likewise (for a review of literature, see Tomanek and Hulett, 1970; Choate and Fleharty, 1975).

If the distribution of *M. ochrogaster* was severely restricted by the drought of the middle 1930s, then it is reasonable to assume that any patterns of geographic variation previously established on the western and central plains were obliterated. Additionally, although relict populations that endured the drought in isolated mesic areas would have been freed from the stabilizing effects of gene flow, any genetic divergence that occurred in these isolated enclaves would have been swamped after the drought ended.

Data presented herein generally support these assumptions. Although color of pelage previously has been regarded as a diagnostic subspecific characteristic in *M. ochrogaster*, our results indicate that color varies appreciably both within and among demes of the populations that comprise those subspecies. We do not deny that the pelage of prairie voles usually contains less red pigment (and therefore appears grayer) in the more arid regions of the range of the species, nor do we deny that most samples representing the western or northern extremes of *M. o. haydenii* readily can be distinguished

on the basis of pelage coloration from most samples representing *M. o. ochrogaster*. However, the geographic pattern of variation between these extremes not only is gradual but also is erratic, with adjacent populations sometimes resembling distant populations more than their neighbors. Likewise, color of the holotype and paratypes of *M. o. taylori* differs from that of samples with which comparison was made by Hibbard and Rinker (1943). These authorities noted (p. 260) that "the color... [*ochrogaster* from Indiana] is darker [than that of *taylori*], possessing a definite grizzled appearance on rump, back and head due to light tipped hairs in contrast to the black tipped guard hairs. The type of *M. o. taylori* lacks the grizzled appearance." Hibbard and Rinker also stated (p. 60) that "*M. o. taylori* can be separated at once from *haydenii* [from Nebraska] which possesses a decidedly lighter grayish color and a silvery belly." However, those differences are less pronounced in specimens recently collected a short distance from the type locality and in other specimens that have been referred to *taylori*. The original population of *taylori* has been extirpated, and the gene pools of nearby populations subsequently assigned to *taylori* (which was discovered and described soon after the drought of the 1930s) presumably were swamped as genes from *ochrogaster* or relict populations of *haydenii* flowed into those populations after complete recovery from the drought.

Size (both external and cranial), like color, exhibits no pronounced pattern of geographic variation among populations of *M. ochrogaster* inhabiting the central plains region. Moreover, although zones of apparent secondary intergradation are prevalent, no clear-cut steps in the mosaic of morphometric clines were found in this study. Statements in the literature to the effect that "good" specimens of *M. o. haydenii* average larger than those of *M. o. ochrogaster* are absolutely correct if most populations in the central plains region that are now referred to one or the other subspecies are relegated to the status of intergrades.

#### CONCLUSIONS

The use of subspecies to depict geographic variation is a relatively static concept that provides for geographic or temporal replacement of one subspecies by another but cannot readily accommodate the genetic and phenetic changes that occur within populations of subspecies with the passage of time. In most instances, especially those in which subspecies are geographically isolated, this shortcoming is of no great consequence; however, in instances where the

distributions of the populations comprising a subspecies are continually changing and gene flow between them is at one time appreciable and at another time negligible, the use of subspecies implies much greater understanding of systematic relationships than the concept can provide. In such instances, it is often better to describe the observed patterns of variation with words than with names.

*Microtus ochrogaster* probably originated on the True Prairie and subsequently dispersed both eastward and westward into habitats resembling those on the True Prairie. It is a geographically variable species having relatively narrow ecological requirements and a continuously changing geographic distribution, at least within the central plains region. We have no reason to doubt that clearly defined subspecies exist within the species; however, recognition of subspecies in the central plains region simply is not tenable (given the characters assessed in this study) because established patterns of geographic variation periodically are disrupted by the effects of droughts. Accordingly, we have opted to regard the name *Microtus ochrogaster taylori* Hibbard and Rinker as a subjective junior synonym of *M. o. haydenii* (Baird), and to restrict the name *M. o. ochrogaster* (Wagner) to populations inhabiting regions to the east of the central plains at least as far as the type locality. Therefore, all populations sampled for this study now pertain to the subspecies *M. o. haydenii* (Baird).

#### ADDENDUM

After this paper went to press, Severinghaus (Proc. Biol. Soc. Washington, 90:49-54, 1977) described as a new subspecies (*M. o. similis*) the populations of *M. ochrogaster* inhabiting central and southern Montana, central and northwestern Wyoming, southwestern South Dakota, and northwestern Nebraska. This would include the populations herein referred to as sample A and at least part of sample B, which Severinghaus (pp. 49-50) described as being "smaller . . . in all external and cranial measurements, especially preambdoidal breadth and incisive foramina" than are populations of *M. o. haydenii*. As noted herein, specimens in sample A indeed were smaller than those in most other samples, and specimens in sample B fell nearer the low than the high end of the range of variation for three of the four cranial measurements that exhibited significant geographic variation. These data lend support to the distinctness of *M. o. similis*, and both the univariate and multi-

variate data presented herein suggest that sample A should be referred to that subspecies and that sample B includes representatives of both subspecies and of intergrades between them.

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