



Morphologic Variation between Long-established and Pioneer Populations of the Meadow Vole (*Microtus pennsylvanicus*) in Illinois

Bradley J. Bergstrom

American Midland Naturalist, Vol. 112, No. 1 (Jul., 1984), 172-177.

Stable URL:

<http://links.jstor.org/sici?sici=0003-0031%28198407%29112%3A1%3C172%3AMVBLAP%3E2.0.CO%3B2-3>

American Midland Naturalist is currently published by The University of Notre Dame.

Your use of the JSTOR archive indicates your acceptance of JSTOR's Terms and Conditions of Use, available at <http://www.jstor.org/about/terms.html>. JSTOR's Terms and Conditions of Use provides, in part, that unless you have obtained prior permission, you may not download an entire issue of a journal or multiple copies of articles, and you may use content in the JSTOR archive only for your personal, non-commercial use.

Please contact the publisher regarding any further use of this work. Publisher contact information may be obtained at <http://www.jstor.org/journals/notredame.html>.

Each copy of any part of a JSTOR transmission must contain the same copyright notice that appears on the screen or printed page of such transmission.

JSTOR is an independent not-for-profit organization dedicated to creating and preserving a digital archive of scholarly journals. For more information regarding JSTOR, please contact support@jstor.org.

Morphologic Variation between Long-established and Pioneer Populations of the Meadow Vole (*Microtus pennsylvanicus*) in Illinois

BRADLEY J. BERGSTROM¹

Department of Ecology, Ethology and Evolution, University of Illinois, Urbana 61801

ABSTRACT: Variation in cranial dimensions was studied within and between two populations of *Microtus pennsylvanicus* in Illinois. One population has only colonized the Champaign County area in the last decade; the other has long inhabited the northern half of Illinois. Univariate statistics, as well as multivariate analysis of variance (MANOVA), principal component and discriminant function, were used to test for divergence in cranial morphology between the populations. These comparisons showed no significant differences in the population means or in the degree of variation, at least as compared to geographic variation between Illinois animals and specimens of an Ohio population of the same subspecies. Results are discussed with regard to population genetic theories concerning range expansions.

INTRODUCTION

The recent expansion of the range of the meadow vole *Microtus pennsylvanicus pennsylvanicus* (Ord) in central Illinois provided a situation for a comparative study of morphologic variation in natural populations. Prior to 1970, the species was absent from Champaign County but was common throughout the northern half of the state. *Microtus pennsylvanicus* occupies more mesic, densely vegetated habitats than does the prairie vole *M. ochrogaster*, which is widespread throughout Illinois (Hoffmeister and Mohr, 1972; Batzli *et al.*, 1977). Presently, *M. pennsylvanicus* is one of the most common mammals of roadside grassland habitats throughout the area, extending at least 50 km S of Champaign. Getz *et al.* (1978) hypothesized that the recently completed interstate highways were dispersal corridors in Illinois, providing the only unbroken stretches of dense grassy habitat across an extensive agricultural region. Getz *et al.* (1978) estimated the southward expansion of the range of *M. p. pennsylvanicus* at ca. 100 km in 6 years; Easterla and Damman (1977) reported similar findings in Missouri. In many areas of Champaign County where *M. ochrogaster* once occurred alone, *M. pennsylvanicus* has now displaced it (Getz *et al.*, 1978).

A basic question addressed was whether the pioneer populations of *Microtus pennsylvanicus* in central Illinois were derived from an isolated founding group or were the result of continuous use of interstate rights-of-way as dispersal corridors, as Getz *et al.* (1978) suggested. In the former case, the ancestral and pioneering populations might differ in mean or variance of some morphometric characters, as predicted by theory of genetic drift. Even if southward movement of voles were a continuous process, pioneer populations might be overrepresented by "disperser" genotypes, if demographic events in *Microtus* are indeed genetically selective (Keith and Tamarin, 1981). Morphologic characters have not usually been examined in tests of the Chitty hypothesis (Krebs, 1978), but there is no a priori reason why quantitative traits should be less likely to show responses to selection than the electrophoretic systems used in many microtine studies (*e.g.*, Keith and Tamarin, 1981). In fact, assuming differences between two populations for a given set of loci influencing a quantitative trait, electromorph differences are much more difficult to detect than the quantitative trait difference, provided that variation between the populations is in the same direction over all or most of the loci (Lewontin, 1984). Furthermore, phenotypic plasticity in the enzyme systems

¹ Present address: Museum of Natural History and Department of Systematics and Ecology, University of Kansas, Lawrence 66045.

traditionally used in microtine demographic studies may confound their interpretation (McGovern and Tracy, 1981).

Other studies comparing populations at the center and margin of a species' range have examined genetic drift as manifested by isozyme variability. Apparently, very low rates of gene flow were sufficient to mask founder effects; Dessauer *et al.* (1975) and Levin (1977) found no differences in the variability of isozymes between central and marginal populations nor for some island-mainland comparisons (Dessauer *et al.*, 1975). Schwaegerle and Schaal (1979) found a dramatic decrease in heterozygosity due to founder effect in some "island" populations, but these were likely the result of severe bottlenecks, perhaps involving single founders.

This study dealt with similar questions of genetic variability as related to demographic events, only using quantitative characters. Morphologic variation in *Microtus p. pennsylvanicus* was examined between long-established and pioneer populations in Illinois by use of both univariate and multivariate statistics. An outgroup sample was chosen from a long-established population in Ohio.

METHODS

Microtus p. pennsylvanicus were collected with snap traps set in lines in dense grassy habitat near county or interstate highways at various spots in Champaign, Vermilion and Cook counties in the autumn of 1978. This sample was augmented with specimens from research collections at the University of Illinois Museum of Natural History. Skulls from 105 voles were used in the analyses, 51 from long-established populations in northern Illinois (NIL) and 54 from pioneer populations in central Illinois (CIL). The sex ratio of the sample was 65% males from NIL and 52% males from CIL. NIL specimens were pooled from 16 counties in northern Illinois and three adjacent counties in northern Indiana, but the majority of NIL specimens were from Cook County. All CIL specimens were from Champaign and Vermilion counties, Illinois, and Warren Co., Indiana. An additional 37 males and 37 females from Wilkesville, Vinton Co., Ohio, were used as a reference sample for later comparison.

Intrapopulation variation was analyzed as follows: Variation between sexes was examined with a *t*-test for each character; variation due to age was factored out as much as possible before further analysis. Hoffmeister and Getz (1968) showed that growth of nearly all metric characters approached an asymptote at ca. 45 days in *Microtus o. ochrogaster*. A logarithmic curve is characteristic of determinate growth in mammals. To eliminate variation due to age, only individuals from the level part of the curve, *i.e.*, adults, were considered. The criteria for classification as adult included relative weighting of the following characters (adapted from Snyder, 1954): (1) prominence and coalescence of temporal ridges (0-4 points); (2) prominence of lambdoidal crest (1-3 points); (3) flatness of cranium (0-1 point); (4) degree of protrusion of paraoccipital process (0-1 point); (5) prominence of mastoid-exoccipital crest (0-1 point); (6) degree of wear on molars (0-1 point); (7) presence of lachrymal bone (0-1 point). Summing these produced 12 possible age classes. Only voles in age classes eight through 12 were considered adults.

Eleven cranial measurements were analyzed: greatest length of skull (GLS), length of incisive foramina (IF), length of diastema (LD), length of maxillary toothrow (LMT), interorbital breadth (IOB), zygomatic breadth (ZB), cranial breadth (CB), cranial height (CH), condylozygomatic length (CZL), length of nasals (LN), and horizontal inside diameter of auditory meatus (AM). The first three dimensions were measured with an ocular micrometer, and the remaining measurements were made with dial calipers to the nearest 0.1 mm.

Means, ranges, standard deviations and coefficients of variation (CV) were calculated for each population using a statistical package (OBSTAT) on the Cyber 175 computer at the University of Illinois. Multivariate analysis of variance (MANOVA) was used to test for differences between the population means. Further multivariate

analyses were done using principal component (PCNEWB) and discriminant function (DISANB) programs written by R. B. Selander.

RESULTS AND DISCUSSION

Intrapopulation variation.—Since no sexual dimorphism was found (t -test; $P > 0.05$) for any character in the three geographic samples examined, sexes were pooled. Of the skulls in age classes eight through 12 used in the analyses, the mean age classes were 10.0 for CIL, 9.83 for NIL, and 10.05 for Ohio. Thus neither sex nor age was a factor in the analyses.

The means of individual characters were not significantly different ($P > 0.05$) between the Illinois samples (Table 1). Coefficients of variation for the 11 measurements were comparable between the NIL and CIL voles; the small differences showed no consistent pattern. For both samples, length of incisive foramina, nasal length and diameter of auditory meatus were most variable. Length of incisive foramina and nasal length were also the most variable skull dimensions in *Microtus pennsylvanicus* in Pennsylvania (Snyder, 1954). Cranial breadth, cranial height, condylozygomatic length, greatest length of skull and zygomatic breadth are the least variable, also agreeing with Snyder (1954). Snyder found that interorbital breadth, cranial height and cranial breadth reach their full adult proportions at an early age. Given this, any sample including some subadults with adults would be less likely to show increased variation in these three measurements than in others. Statistics from the Ohio population were included in Table 1 for comparison—Ohio voles were significantly larger than Illinois voles for eight out of the 11 skull dimensions (Table 2).

Variation of individual characters among populations.—None of the F -ratios comparing the 11 cranial measurements between the Illinois populations was significant ($P > 0.05$), nor was the F -ratio for overall discrimination. Thus, skulls from NIL and CIL voles were random samples of the same population.

TABLE 1.—Mean, standard deviation and coefficient of variation for 11 cranial measurements of *Microtus pennsylvanicus* from northern Illinois (NIL), central Illinois (CIL) and Ohio. Abbreviations for measurements are explained in the text

Measurement	N	\bar{X} (mm) (sd)	CV	Measurement	N	\bar{X} (mm) (sd)	CV
GLS (NIL)	45	26.75(0.72)	2.68	ZB	49	14.57(0.51)	3.49
(CIL)	50	26.72(0.84)	3.14		52	14.46(0.47)	3.26
(Ohio)	74	27.23(0.84)	3.08		73	14.89(0.54)	3.64
IF	49	5.26(0.33)	6.30	CH	46	10.27(0.32)	3.08
	54	5.19(0.30)	5.87		53	10.32(0.28)	2.70
	74	5.53(0.29)	5.23		74	10.26(0.30)	2.90
LD	50	8.23(0.31)	3.74	CZL	45	20.32(0.50)	2.45
	54	8.16(0.36)	4.42		49	20.18(0.70)	3.46
	74	8.43(0.35)	4.13		74	20.56(0.57)	2.78
LMT	51	6.02(0.24)	4.06	LN	47	6.94(0.36)	5.19
	54	6.04(0.19)	3.17		53	6.89(0.41)	5.92
	74	6.06(0.20)	3.32		69	7.34(0.43)	5.87
IOB	51	3.63(0.13)	3.45	AM	48	2.54(0.15)	6.07
	53	3.66(0.15)	4.19		53	2.54(0.17)	6.50
	74	3.68(0.14)	3.70		74	2.72(0.13)	4.69
CB	48	10.69(0.36)	3.33				
	50	10.62(0.28)	2.67				
	74	10.91(0.28)	2.53				

The pooled Illinois samples were compared with an outgroup of 69 *Microtus p. pennsylvanicus* from a single locality in Ohio, roughly 650 km to the E. The latter was a long-established population just as was NIL. This comparison was made in order to establish whether significant morphologic variation could be found on any geographic scale within the subspecies, *i.e.*, to test the validity of examining cranial characters as manifestations of postulated genetic differentiation within *Microtus p. pennsylvanicus*. The degree to which clinal variation was expressed in cranial morphology was demonstrated by the Ohio vs. Illinois comparison. *F*-tests for length of maxillary toothrow, interorbital breadth and cranial height were not significant; all the others were highly significant, as was the overall *F*-ratio (Table 2). On this basis, the Illinois population was morphologically separable from the Ohio population. Diameter of auditory meatus, length of nasals and length of incisive foramina had the highest *F*-values and were most important in discriminating the groups.

Multivariate character variation between populations.—In the principal component analysis of *Microtus pennsylvanicus* from NIL and CIL, the first component accounted for ca. 44% of the variation and the second component for 14%, with a nearly complete overlap between the two samples. Voles from NIL showed less variation in both PC I

TABLE 2. — Comparison of 11 cranial measurements between Illinois and Ohio populations of *Microtus pennsylvanicus*

Measurement	<i>F</i> ¹	Measurement	<i>F</i>
GLS	15.73**	CB	22.57**
IF	41.59**	CH	1.34
LD	21.21**	CZL	11.49**
LMT	0.86	LN	47.51**
IOB	1.73	AM	53.85**
ZB	15.84**		

¹*F*-ratio for overall discrimination (11,142 df's) = 14.91**

***P* < 0.01; all other values, *P* > 0.05

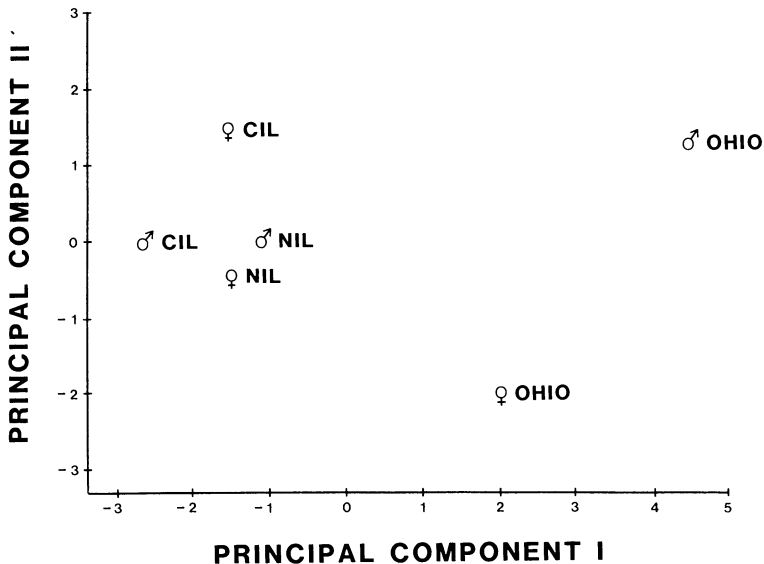


Fig. 1. — Plot of mean scores for the first two principal components of cranial measurements of *Microtus pennsylvanicus* from northern Illinois, central Illinois and Ohio

and PC II than did voles from CIL, but MANOVA indicated that the differences in variances were not significant.

In the principal component plot of population means for NIL, CIL and Ohio (Fig. 1), over 85% of the variation was accounted for by the first two principal components, with PC I accounting for 71%. Principal component scores in two-dimensional space seem to distinguish Ohio males and females nearly as much as voles from the two widely separated localities, but given the large first eigenvalue, vertical separation on this graph is relatively unimportant.

The first eigenvector for cranial height was notable in that it had the only strongly negative effect on PC I. Apparently, the larger individuals had somewhat flatter skulls. This agreed with other studies of morphogenesis in *Microtus* (e.g., Snyder, 1954). As far as the second eigenvector, interorbital breadth had a strong positive loading, and diameter of auditory meatus a strong negative loading.

Discriminant function analysis was used to analyze the effects of maximizing the separation between Illinois and Ohio voles. Centroids along the first canonical variate for the pooled Illinois sample and the Ohio sample were 2.43 and 2.81, respectively, reflecting the significantly larger skull size of the Ohio individuals. This comparison revealed that the two samples came from distinct populations, based on the small amount of overlap of discriminant function scores and the highly significant overall *F*-value from MANOVA. As these represented two spatially discrete and widely separated samples of a comparatively continuous distribution of the subspecies, their differences were attributed to clinal variation over this range.

Analyses of *Microtus p. pennsylvanicus* from Illinois yielded no evidence of morphologic distinction between long-established and pioneering populations. This would support the conclusion that a high degree of gene flow between the two populations was maintained by fairly rapid and continuous traversal of the interstate highway corridors over the period of range expansion. Since the "dispersers" were a random sample of the NIL populations, no indication of "genotype" differences—as predicted by the modified Chitty hypothesis of Krebs (1978)—was given by the polygenic quantitative traits examined.

With the unusually sudden and extensive range expansion, the possible movement into new niches, and the subsequent outcompeting of ecological equivalents, selection-mediated changes in the gene pool might have been expected, which would have distinguished these dispersers from their ancestral population. Such changes were not indicated by the morphologic characters examined. Further study is needed to document the timing and magnitude of actual dispersal events by long-term tracking of groups of voles along these dispersal corridors. This would provide some direct evidence for the speed of movement and amount of gene flow between populations.

Acknowledgments.—I thank D. F. Hoffmeister, V. E. Diersing and L. S. Ellis for their advice and guidance in this study; J. R. Sauer and an anonymous reviewer for comments on the manuscript; L. L. Getz and D. Tadzick for additional specimens from Champaign County, and R. B. Selander for advice on computer programs.

LITERATURE CITED

- BATZLI, G. O., L. L. GETZ AND S. S. HURLEY. 1977. Suppression of growth and reproduction of microtine rodents by social factors. *J. Mammal.*, **58**:583-591.
- DESSAUER, H. C., E. NEVO AND K. CHUANG. 1975. High genetic variability in an ecologically variable vertebrate, *Bufo viridis*. *Biochem. Genet.*, **13**:651-661.
- EASTERLA, D. A. AND D. L. DAMMAN. 1977. The masked shrew and meadow vole in Missouri. *NW No. State Univ. Stud.*, **37**:1-27.
- GETZ, L. L., F. R. COLE AND D. L. GATES. 1978. Interstate roadsides as dispersal routes for *Microtus pennsylvanicus*. *J. Mammal.*, **59**:208-212.
- HOFFMEISTER, D. F. AND L. L. GETZ. 1968. Growth and age classes in the prairie vole, *Microtus ochrogaster*. *Growth*, **32**:57-69.

- _____. AND C. O. MOHR. 1972. Fieldbook of Illinois mammals. Dover Publ., New York. 233 p.
- KEITH, T. P. AND R. H. TAMARIN. 1981. Genetic and demographic differences between dispersers and residents in cycling and noncycling vole populations. *J. Mammal.*, **62**:713-725.
- KREBS, C. J. 1978. A review of the Chitty hypothesis of population regulation. *Can. J. Zool.*, **56**:2463-2480.
- LEVIN, D. A. 1977. The organization of genetic variability in *Phlox drummondii*. *Evolution*, **31**:477-494.
- LEWONTIN, R. C. 1984. Detecting population differences in quantitative characters as opposed to gene frequencies. *Am. Nat.*, **123**:115-124.
- MCGOVERN, M. AND C. R. TRACY. 1981. Phenotypic variation in electromorphs previously considered to be genetic markers in *Microtus ochrogaster*. *Oecologia*, **51**:276-280.
- SCHWAEGERLE, K. E. AND B. A. SCHAAL. 1979. Genetic variability and founder effect in the pitcher plant *Sarracenia purpurea* L. *Evolution*, **33**:1120-1128.
- SNYDER, D. P. 1954. Skull variation in the meadow vole (*Microtus p. pennsylvanicus*) in Pennsylvania. *Ann. Carnegie Mus.*, **33**:201-234.

SUBMITTED 16 MAY 1983

ACCEPTED 8 MARCH 1984