

An Evaluation of Geographic Variation Within an Isolated Population of Big-eared Bats (*Corynorhinus townsendii*) in Oklahoma, Kansas and Texas

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The distribution of big-eared bats (*Corynorhinus townsendii*) in western Oklahoma and neighboring areas of Kansas and Texas has been presented as a continuous range. However, a plot of the localities of collection indicated that these bats actually may occur in demes isolated by cave-producing geological structure or biogeographic provinces. A morphometric analysis of 18 cranial measurements in 246 specimens from five physiographic areas supported the hypothesis that the apparent isolation of groups correlates with morphological differences among samples. © 2004 Oklahoma Academy of Science

INTRODUCTION

Corynorhinus (= *Plecotus*) *townsendii* has the largest geographic range of the genus, and five subspecies are recognized (Handley 1959). *Corynorhinus townsendii pallescens* is found throughout much of western North America, but an isolated population inhabits the region including gypsum caves in western Oklahoma, south-central Kansas, and north-central Texas (Handley 1959, Barbour and Davis 1969, Caire et al 1989). Specimens from this region represent an intergraded subspecies identified by Handley (1959) as *C. t. pallescens*.

Although very mobile, big-eared bats are quite philopatric. In California, most banded specimens of *C. townsendii* were recovered within 2.4 km of the original banding site (Pearson et al 1952). Radio-tagged *C. t. ingens* in Arkansas remained within the area of the roost (<1 km²), with the exception of a female which flew 2 km (Wilhide et al 1998). In Kansas and Oklahoma, the average distance moved between maternity roosts and hibernacula by *C. townsendii* was 11.6 km, the longest movement recorded was just over 39 km, and 85.5% of bats that moved traveled <1.6 km (Humphrey and Kunz 1976).

The gypsum hills regions in Oklahoma, Kansas, and Texas are isolated geological pockets located farther apart than these bats

are known to fly, thus it might be reasonable to presume that the population presented in literature actually represents several smaller populations. If gene flow is inhibited by isolation, variation in morphology might be anticipated. The purpose of this study was to examine geographic variation in crania among putative demes within the Kansas-Oklahoma-Texas portion of the species range.

METHODS AND MATERIALS

Two hundred forty-six specimens were borrowed from museums (see appendix). A plot of the distribution of collection localities of specimens (Fig. 1) indicated apparently isolated groups, which corresponded well with geological formations (Bailey 1980). Specimens from Kiowa (1), Comanche (7), and Barber (13) Counties of Kansas, and Woods (21), Woodward (25), Major (10), and Blaine (6) Counties of Oklahoma were from the area of the Cimarron Gypsum Hills (LOCA1). Nine specimens from Washita County, Oklahoma, all came from the Weatherford Gypsum Hills region (LOCA2), and the Wichita Mountains (LOCA3) produced the specimens from Comanche (8), and Kiowa (11) Counties. Specimens from southwestern Oklahoma in Harmon (24), and Greer (11) Counties came from the Mangum Gypsum Hills (LOCA4). Most

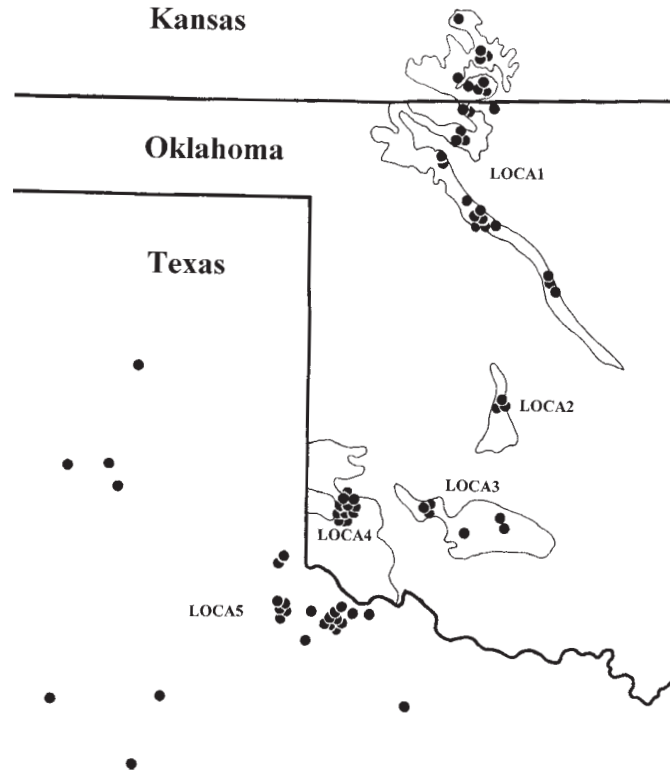


Figure 1. Distribution of specimens of *Corynorhinus townsendii* in Kansas, Oklahoma, and Texas. Specimens from Kansas are within the region of gypsum caves (Humphrey and Kunz 1976), and geographically isolated regions in Oklahoma are outlined based on the geomorphic provinces map of Johnson et al (1972). Bailey's (1980) biogeographical provinces separate Texas specimens at the Red River.

Texas specimens (LOCA5) were collected in Childress and Hardeman Counties (24 and 61, respectively), but the sample also included specimens from Armstrong (4), Baylor (1), Crosby (3), Foard (1), Garza (3), Hockley (1), and Randall (2) Counties. The first two of these counties border the Mangum Gypsum Hills region of Oklahoma, but the Texas specimens were treated separately because that area is relegated to a different biogeographic province. All of the Oklahoma and Kansas samples came from the Bluestem (*Andropogon* sp.) — Grama (*Bouteloua* sp.) section of the Tallgrass Prairie province, but the Texas counties bordering Oklahoma are from the Mesquite (*Prosopis* sp.) — Buffalo Grass (*Buchloë* sp.) section of the Prairie Brushland province (Bailey 1980). Counties from the Texas panhandle outside this region were in the Great

Plains Shortgrass Prairie province (Grama-Buffalo Grass), but were included in the rest of the Texas sample for evaluation because they could not be reasonably grouped because the various localities of collection were quite far apart.

Eighteen cranial measurements were taken by using a Lasico digitizer and were recorded to the nearest 0.1 mm. Cranial measurements were total length (X1), zygomatic breadth (X2), cranial breadth (X3), mastoid breadth (X4), postorbital constriction (X5), length of maxillary tooth row (X6), palatal length (X7), basicranial length (X8), length of the auditory bulla (X9), intercanine width (X10), palatal breadth across the third molars (X11), interpterygoid width (X12), cranial depth (X13), length of the dentary (X14), moment arm of the temporal (X15), moment arm of the masseter (x16), coronoid

to angle distance (x17), and mandibular fossa to condyle distance (x18). Measurements were illustrated by Tumilson (1991). Data were collected on adult specimens only, adults being recognized by fused epiphyses in wing bones. Sex was recorded from specimen labels.

Means for each measurement within locality samples were calculated for comparison. Because sexual dimorphism also is known to occur in this genus (Handley 1959), a two-way analysis of variance (ANOVA) was performed to examine variation due to sex and location. This test demonstrated that both geographic and sexual dimorphism existed (Table 1); so all the measurements were zwittered to remove the effect of sex (Schnell et al 1985). One-half of the difference between means for each sex was added to the smaller mean and sub-

tracted from the larger mean for each character within each locality. A second ANOVA demonstrated that zwittering the data provided a sexless data set, permitting a less complicated evaluation of geographic variation.

Sex-adjusted data were transformed to base 10 logarithms. This procedure helps linearize the size component of the data (Owen 1988), legitimizes linear statistics (Humphries et al 1981), and functions much as standardization of characters (Schnell 1970). Principal component analysis was performed and scores for individuals were plotted on the plane of the first two vectors to explore the data for geographic groupings. Centroids for samples were calculated from the scores of individuals on the first two principal-components axes and plotted also.

Table 1. Means by sex (M, F - sample sizes in parentheses) for each of five locality samples of *Corynorhinus townsendii* from Kansas, Oklahoma, and Texas.

Character	LOCA1		LOCA2		LOCA3		LOCA4		LOCA5	
	M (30)	F (52)	M (5)	F (4)	M (8)	F (12)	M (17)	F (18)	M (49)	F (51)
X1 (0.0001) ¹	16.13	16.19	16.10	16.20	16.15	16.21	16.01*	16.22	15.99*	16.15
X2 (>0.05)	9.09	9.18	9.16	9.20	9.09	9.12	8.98*	9.14	8.93*	9.08
X3 (>0.05)	7.74	7.71	7.76	7.68	7.71	7.77	7.73	7.78	7.70*	7.77
X4 (0.0050)	9.21	9.29	9.40	9.25	9.25	9.33	9.21*	9.36	9.13*	9.27
X5 (0.0400)	3.74	3.74	3.78	3.75	3.69	3.73	3.76	3.78	3.69*	3.73
X6 (0.0001)	5.19*	5.25	5.24	5.18	5.16	5.23	5.18	5.21	5.07	5.10
X7 (0.0001)	5.46	5.52	5.50	5.48	5.48	5.49	5.44	5.49	5.36	5.42
X8 (0.0001)	13.12	13.21	13.20	13.18	13.06	13.20	13.05	13.21	12.83*	12.99
X9 (>0.05)	4.16	4.16	4.18	4.13	4.16	4.19	4.12*	4.21	4.14	4.16
X10 (0.0001)	2.34*	2.38	2.30	2.35	2.30	2.34	2.29	2.35	2.24	2.28
X11 (0.0001)	6.05*	6.13	6.08	6.08	6.00	6.00	5.99	6.09	5.90*	6.01
X12 (0.0001)	2.51	2.51	2.58	2.58	2.50	2.51	2.44	2.51	2.37	2.40
X13 (0.0001)	5.93	5.86	5.94	5.88	5.89	5.94	5.88	5.88	5.68	5.75
X14 (0.0001)	10.14*	10.27	10.06	10.13	10.00	10.17	9.93*	10.18	9.91*	10.06
X15 (0.0002)	2.79	2.83	2.82	2.90	2.83	2.88	2.80	2.89	2.75	2.79
X16 (0.0009)	2.34	2.36	2.30	2.33	2.37	2.28	2.35	2.39	2.28	2.29
X17 (0.0001)	4.10*	4.17	4.08	4.20	4.09	4.07	4.02*	4.21	3.98*	4.06
X18 (0.0420)	3.27	3.33	3.24	3.28	3.26	3.38	3.31	3.39	3.23*	3.33

¹ P levels for geographically variable measurements are given in () by the respective character. * indicates significant difference ($P < 0.05$) between sexes. LOCA1 = Cimmaron Gypsum Hills, LOCA2 = Weatherford Gypsum Hills, LOCA3 = Wichita Mountains, LOCA4 = Mangum Gypsum Hills, and LOCA5 = Texas specimens. Measurement variables (X1-X18) defined in text.

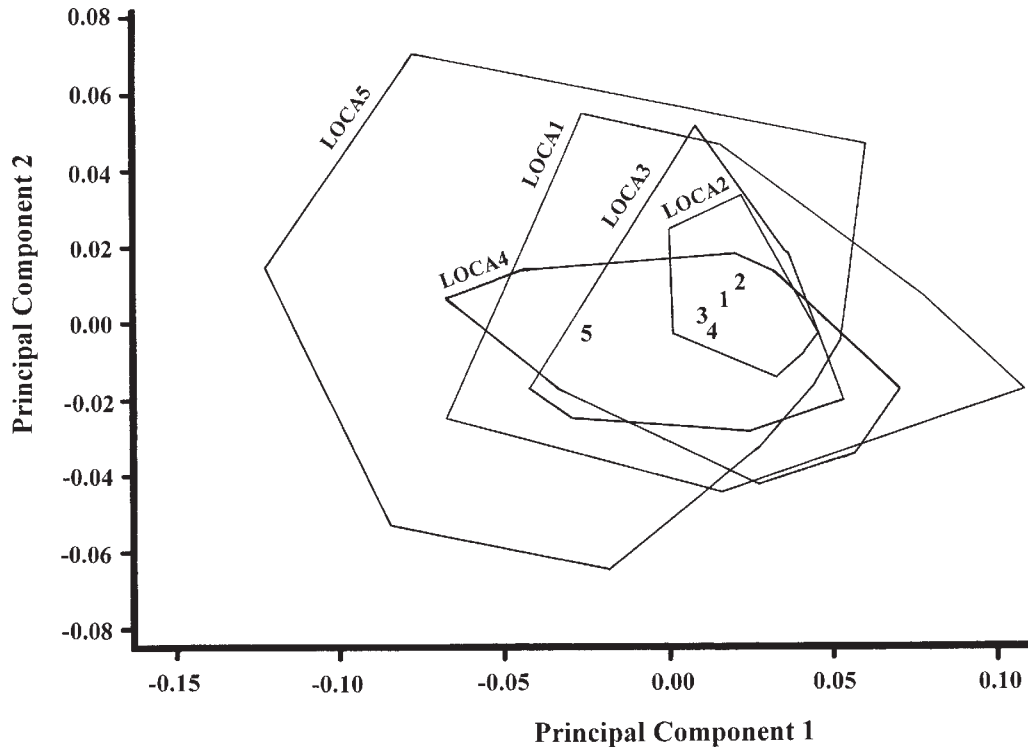


Figure 2. Plot of Principal-Components I and II generated from the variance-covariance matrix of 18 cranial characters for five samples of *Corynorhinus townsendii*. Numbers represent centroids for specimens from each locality. Polygons represent the total scatter of individuals within the groups.

Multivariate Analysis of Variance (MANOVA) was used to examine differences related to localities. Significance of Mahalanobis distances between group centroids was tested with *F*-statistics. The DISCRIM Procedure of the Statistical Analysis System (SAS Institute 1988) was used to determine the posterior probability of membership in each locality sample.

RESULTS

Five of the 18 cranial characters were sexually dimorphic in LOCA1 ($P < 0.05$). No significant sexual dimorphism was apparent at LOCA2 or LOCA3; however, six of 18 characters were sexually dimorphic for LOCA4, and 10 of 18 characters were dimorphic at LOCA5. Males typically were smaller for most measurements, except within LOCA2 (Weatherford Gypsum Hills), in which males averaged slightly but insignificantly

larger on eight of the 18 characters (Table 1).

The localities of collection of samples of *Corynorhinus* from within geological formations in Kansas, Oklahoma, and Texas were isolated from each other by 40-80 km. Principal-components analysis indicated coherent regional grouping (Fig. 2). The generally uniform character loadings indicated that the first principal component, which provided the best separation of groups, is a general size vector. The first axis sorted the usually smaller Texas specimens from typically larger specimens collected in Oklahoma and Kansas. Individuals from central locations (LOCA2-LOCA4) had intermediate scores on the first principal component, indicating minor clinal variation from north to south.

The second principal component represented a contrast between size of the skull and the length of mandibular processes

(X15-X18) involved with mastication. The skulls of specimens from Texas were relatively small, but the processes remained about the same size as those of other samples (i.e., these variables were relatively large in the Texas specimens).

MANOVA using Wilk's Lambda statistic demonstrated that differences existed related to locality ($P < 0.0001$). Posterior probability of membership in each location determined by the DISCRIM procedure indicated that 75 of 79 (94.9%) specimens from LOCA1 were statistically identifiable as originating from that sample. Statistical identifications of all specimens from LOCA2 and LOCA3 correctly matched their known origin. Thirty of 31 specimens (96.8%) were consistent within LOCA4, and 91 of 98 (92.9%) specimens from LOCA5 were statistically identified with that locality.

The most common statistical misidentifications were between LOCA1 and LOCA5, reflecting the greater variance in size within those samples. Furthermore, LOCA1 and LOCA5 were the largest samples (83 and 100, respectively), which partly accounts for the greater variation seen in these groups due to a greater probability that more extreme specimens would be included in the sample. The Texas sample covered a large land area extending into the panhandle region, but specimens from counties other than Hardeman and Childress still were statistically identified as belonging to LOCA5. The most common misidentifications were of specimens from counties bordering Oklahoma. Mahalanobis distances indicated statistical differences only between LOCA1 and LOCA4 ($P < 0.0002$) in the Oklahoma and Kansas samples, but all locations differed from LOCA5 in Texas ($P < 0.0001$).

DISCUSSION

MANOVA detected significant size differences among sample groups. Clinal variation is evident, with larger specimens to the north and smaller specimens to the south,

particularly in the Texas sample. Even groups located close together (Mangum Gypsum Hills and Texas) exhibited significant variation, indicating that isolation has allowed these groups to evolve independently.

Corynorhinus townsendii has an affinity for gypsum caves in which they roost, hibernate, and reproduce (Hibbard 1934, Hollander et al 1987, Humphrey and Kunz 1976, Kunz and Martin 1982, Twente 1955). As a Pleistocene relict population, the isolated pockets have had only about 10,000 y to possibly diverge since the Recent interglacial period (Humphrey and Kunz 1976). With greater isolation and a longer period since the Wisconsin glacial (Humphrey and Kunz 1976), *C. townsendii* has diverged into subspecies (Handley 1959) in the southern Appalachians (*C. t. virginianus*) and in the Ozarks (*C. t. ingens*). The differences found herein are within a smaller geographic distribution, with more opportunity for gene flow and likely with milder selective forces.

Specimens from LOCA2 were different from the other subpopulations in that males were larger than the females for several measurements. The LOCA3 sample originated in a granite region rather than in gypsum caves. Based on cranial morphology, these samples were statistically from the same population although the discriminant function properly associated specimens with their locality of origin. However, specimens from Texas were significantly different from those across the Red River in bordering Oklahoma counties, as well as from all other samples, indicating that the different ecoregions supported isolated populations that may be subject to different selective forces or that may exhibit genetic drift due to restricted gene flow between populations. In either scenario, the separation apparently has been adequate to promote some morphological differentiation.

The elongated north-south distribution of *Corynorhinus townsendii* has been illustrated to represent a continuous population (Handley 1959, Barbour and Davis 1969,

Caire et al 1989). However, a plot of collection localities indicated potentially isolated populations within this distribution. Results of this study indicate that morphometric variation does exist within this geographic range. However, the geographic isolation of the Kansas-Oklahoma subpopulations in the gypsum hills regions has not been adequate to produce significant morphological variation in the crania. Yet, the difference in biogeographical provinces distinguishing the Kansas-Oklahoma samples from the Texas sample apparently relates to changes in *C. townsendii* from Texas. Hypothetically, the Texas specimens with smaller skulls but relatively large processes used in mastication may be effected by differences in the insect prey base that reflect the different habitat. Consequently, variation in morphology is apparent within geographically isolated samples of a subspecies (i.e., a geographical variant).

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APPENDIX

Specimens Examined: Museum acronyms follow Yates et al (1987), numbers represent sample size from each county.

KANSAS: Barber Co.; 5 (KU), 6 (MHP), 2 (FSM). Comanche Co.; 7 (KU). Kiowa Co.; 1 (MHP). OKLAHOMA: Blaine Co.; 1 (OSU), 5 (KU). Comanche Co.; 2 (OSU), 3 (MWSU), 3 (USNM). Greer Co.; 5 (OSU), 2 (ASUMZ), 1 (OU), 3 (KU). Harmon Co.; 10 (OSU), 7 (OU), 3 (ASUMZ), 4 (UCONN). Kiowa Co.; 8 (OSU), 3 (KU). Major Co.; 2

(OSU), 1 (FSM), 7 (OU). Washita Co.; 8 (OSU), 1 (KU). Woods Co.; 9 (OSU), 1 (UMNH), 9 (MHP), 1 (MSUMZ), 1 (UCM). Woodward Co.; 1 (JMM), 22 (OSU), 2 (UCM). TEXAS: Armstrong Co.; 4 (TCWC). Baylor Co.; 1 (MWSU). Childress Co.; 19 (MWSU), 3 (TTU), 2 (MMNH). Crosby Co.; 2 (TTU), 1 (ASUMZ). Foard Co.; 1 (MWSU). Garza Co.; 3 (TTU). Hardeman Co.; 53 (MWSU), 2 (MMNH), 6 (TTU). Hockley Co.; 1 (TTU). Randall Co.; 1 (MWSU), 1 (TCWC).

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