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CRANIAL VARIATION IN THE BOBCAT (FELIS RUFUS) FROM TEXAS AND SURROUNDING STATES

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The bobcat (*Felis rufus*) is distributed from southern Canada across the continental United States into southern Mexico. It occurs throughout Texas and is adapted to a wide variety of habitats, ranging from timbered swamps to broken forests, rocky or brushy arid lands to mountain ranges, and broken farmland.

Considerable geographic variation exists in external and cranial features of the bobcat as evidenced by the recognition of 11 subspecies (Hall, 1981). However, in the 200 years the bobcat has been known to science, there has been no comprehensive assessment of geographic variation in the species, although several partial reviews have treated variation in selected portions of the range. Grinnell and Dixon (1924) and Peterson and Downing (1952) studied geographic variation and delineated subspecies in California and in the northeastern United States and adjacent Canada, respectively. Samson (1979) made morphometric comparisons of each of the subspecies listed by Hall and Kelson (1959), but he made no assessment of geographic variation. Van Zyll de Jong (1974) studied variation in a race of a closely related species, the lynx (*Felis lynx subsolana*), in Newfoundland.

The present study is limited to bobcats from Texas and the surrounding states of New Mexico, Oklahoma, Arkansas, and Louisiana. Four of the 11 currently recognized subspecies occur in this area: *F. r. texensis, F. r. baileyi, F. r. rufus,* and *F. r. floridanus* (Hall, 1981); the first two of these are known from

Texas. The purpose of this study is to describe patterns of nongeographic and geographic variation in cranial characteristics of bobcats from this region.

MATERIALS AND METHODS

Measurements and Samples

A total of 956 specimens (595 males and 361 females) was examined. Animals were obtained from two different sources. The Texas Parks and Wildlife Department provided 506 skulls that were obtained from trappers required to register their pelts during the 1978-79 trapping season; these specimens are deposited in the Texas Cooperative Wildlife Collections at Texas A&M University. The remaining 450 specimens were from the following museum collections: American Museum of Natural History, New York City; Zoology Department, University of Arkansas, Fayetteville; Museum of Natural and Cultural History, Oklahoma State University, Stillwater; Stovall Museum of Science and History, University of Oklahoma, Norman; Museum of Southwestern Biology, University of New Mexico, Albuquerque; Museum of Zoology, Louisiana State University, Baton Rouge; Midwestern University, Wichita Falls, Texas; Texas Cooperative Wildlife Collection, Texas A&M University, College Station; National Museum of Natural History, Washington, D.C.; The Museum, Texas Tech University, Lubbock.

Twenty-six cranial measurements were recorded from each specimen with dial calipers to the nearest .05 mm as follows: GSL, greatest skull length (greatest length of skull including incisors); ZB, zygomatic breadth (greatest width across the zygomata measured parallel to the long axis of the skull); SB, squamosal breadth (greatest width across squamosal immediately posterior to zygomatic arch and parallel with long axis of skull); POC, postorbital constriction (narrowest width of skull immediately posterior to the postorbital process measured at right angles to the long axis of the skull); LN, length of nasals (greatest distance from the anteriormost projection of nasal bones to the posteriormost projection along their medial suture); IC, interorbital constriction (the least width between the orbits); DUC, diameter of upper canine (diameter from anteriormost point to posteriormost point of tooth measured at the alveolus); PM, length of upper fourth premolar (greatest distance from anteriormost point to posteriormost point of P4 measured at alveolus); WR, width of rostrum (greatest width across rostrum immediately anterior to zygomatic plate); PMT, premolar-molar toothrow length (least distance from anterior lip of alveolus of P3 to the posterior lip of M2); WMT, width across maxillary toothrow (measured at junction between P3 and M1); MT, maxillary toothrow length (measured from anteriormost edge of canine to posteriormost point of M2); PL, palatilar length (measured from a point immediately posterior to the incisors to the posterior edge of the palatine bone at its medial suture); CH, cranial height (least distance from dorsalmost portion of skull to ventralmost portion of palatine); MB, mastoid breadth (greatest width of skull across the mastoid region); BL, basilar length (greatest distance from anterior surface of the premaxillae protruding from between the incisors to the anteriormost lip of the foramen magnum); CBL, condylobasal length (greatest distance from anterior surface of premaxillae to posteriormost portion of the occipital condyles); LM, length of mandible (measured from posteriormost portion of condyloid process to anteriormost portion of incisors); CRH, coronoid height (measured from the dorsalmost portion of the coronoid process to the ventralmost portion of the angular process); DM, length of anterior mandibular toothrow (measured from anterior surface of I3 to anterior alveolus of M1); PPL, postpalatal length (measured from anteriormost edge of foramen magnum to the postpalatal notch); NFL, nasal-frontal length (measured from anterior portion of nasal bone at its medial suture to the right orbital constriction immediately posterior to the postorbital process); GLB, greatest length of auditory bullae (measured from posteriormost point of paroccipital process to the anteriormost portion of the auditory bullae); WAB, width of the auditory bullae (measured across bullae from posterior edge of the external auditory meatus at a right angle to the long axis of the skull); DFM, diameter of foramen magnum (greatest distance from the interlip of the anteriormost portion of the foramen magnum to the lip of the posteriormost portion of the foramen magnum); HOB, height of occipital bone (measured from posteriormost lip of foramen magnum to dorsalmost point of lamboidal ridge).

Specimens were examined from approximately 334 localities. These were grouped into 67 samples for purposes of statistical analysis (see Table 1). All major regions of Texas were represented by samples with the exception of the western half of the High Plains and the extreme northeastern corner of the state

TABLE 1.—*Designations, locations, and number of individuals for samples of male (M) and female (F) bobcats used in the univariate and multivariate analysis of geographic variation.*

Sample no.	County or parish	Sample size
	Texas (Males)	
1	Cherokee, Hardin, Liberty, Montgomery, Polk, San Jacinto, Walker	13
2	Grayson, Hopkins, Lamar	6
3	Burleson, Grimes, Leon, Madison, Robertson	22
4	Brazoria, Harris, Jackson, Matagorda	14
5	Bastrop, Colorado, Fayette	6
6	Falls, McLennan, Milam, Williamson	13
7	Archer, Clay, Cooke, Montague, Wise, Young	11
8	Bosque, Eastland, Erath, Palo Pinto, Stephens	7
9	Brown, Burnet, Mills	5
10	Atascosa, Bexar, Goliad, Karnes	6
11	Aransas, Calhoun, Kleberg, Nueces, Refugio	12
12	Brooks, Cameron, Kenedy	10
13	Bee, Duval, Jim Wells, Live Oak, McMullen	17
14	LaSalle, Webb	13
15	Frio, Maverick, Medina, Uvalde	22
16	Edwards, Gillespie, Kerr, Kimble, Llano, Mason Menard, Schleicher, Sutton	15
17	Coleman, Nolan, Tom Green	6
18	Baylor, Cottle, Haskell, King, Knox, Wichita Wilbarger	12
19	Armstrong, Briscoe, Childress, Collingsworth	12
20	Hartley, Hemphill, Hutchinson, Moore, Ochiltree, Randall, Roberts, Wheeler	14
21	Bordon, Crosby, Dickens, Garza, Howard, Mitchell, Scurry	18
22	Glasscock, Reagan, Upton	12
23	Crockett, Val Verde	10
24	Brewster, Pecos, Terrell	13
25	Culberson, Hudspeth, Jeff Davis, Reeves	7
	Texas (Females)	
26	Anderson	9
27	Chambers, Galveston, Jefferson	4
28	Victoria, Wharton	10
29	Refugio, Nueces, Kleberg	10
30	Starr, Cameron	5
31	Webb, LaSalle, Duval	12
32	McMullen, Live Oak, Duval, Jim Wells	13
33	Caldwell, LaVaca	8
34	Brazos, Washington, Robertson, Madison	11
35	Coryell	10
36	Blanco, McCulloch, San Saba	10
37	Sterling	12

TABLE 1.—*Continued.*

38	Crane, Presidio, Ward	14
39	Kent	9
40	Callahan, Taylor	8
41	Jack, Parker	10
42	Hardeman	7
43	Motley	5
44	Armstrong, Collingsworth	8
45	Gray, Potter	11
46	Zavala	12
	Louisiana	
47	Natchitoches	2M, 4F
48	Vermilion, West Baton Rouge, Iberville	6M
49	East Baton Rouge, Livingston, St. Helena, Tangipahoa	2M, 3F
50	Catahoula, Concordia, Madison, Tensas	6M, 7F
	Arkansas	
51	Arkansas, Ashley, Cross, Drew, Jackson, Lawrence, Lee, Phillips, Randolph	8M, 13F
52	Bradley, Calhoun, Hemstead, Sevier	22M, 5F
53	Clark, Conway, Franklin, Garland, Hot Springs, Howard, Johnson, Montgomery, Nevada, Perry Polk, Pope, Pulaski, Scott, Sebastian, Yell	31M, 15F
54	Boone, Carroll, Izard, Madison, Newton, Stone, Van Buren, Washington	36M, 16F
	Oklahoma	
20	Cimarron, Beaver	1M, 1F
55	Atoka, Latimer, Le Flore	8M, 5F
56	Bryan, Cleveland, Creek, Hughes, Lincoln, Logan, Lore, McClain, Oklahoma, Osage, Pawnee, Pottawatomie, Pontotoc, Stephens, Washington	15M, 10F
57	Comanche, Kiowa, Tillman	4M, 1F
58	Caddo, Canadian, Dewey, Garfield, Major Roger Mills	4M, 3F
	New Mexico	
59	Chavez, Dona Ana, Eddy, Lea, Lincoln, Otero	31M, 27F
60	Catron, Grant, Hidalgo, Sierra, Socorro	43M, 18F
61	Bernalillo, Colfax, Mora, Arriba, San Juan, Sandoval, Santa Fe, Taos, Valencia	30M, 16F
62	DeBaca, Guadalupe, Harding, Quay, San Miguel, Union	15M, 10F
	Arizona	
63	Graham, Pima, Yuma	9M, 1F
64	Coconino, Mohave, Yavapai	7M, 3F

TABLE 1.—*Continued.*

	Florida	
65	Dade, Pinellas, Putman	3M
	Georgia	
66	Marion, Talbot	7M
67	Thomas	3M

(Fig. 1). Slightly different sample groupings (1-25 for males; 26-46 for females) had to be formed for the two sexes in Texas because specimens came from such a variety of localities. Sample groupings (and their attendant numerical designations) are the same for both sexes in Louisiana, Arkansas, Oklahoma, and New Mexico. In addition to the material from the study area, two reference samples of *F. r. baileyi* from Arizona (63, 64) and three samples of *F. r. floridanus* from Florida (65) and Georgia (66, 67) also were included.

Aging Technique

Each specimen was assigned to one of five age categories using the technique of Grinnell and Dixon (1924). In addition, one upper canine from each specimen collected by the Texas Parks and Wildlife Department was extracted and aged using the modified technique of Linhart and Knowlton (1967). Using this method, Blankenship (1979) was able to provide the estimated age in months for each Texas specimen. This information was combined with the aging technique described by Grinnell and Dixon (1924) to form the five age categories described in Table 2.

Statistical Analysis

Individual, age, and sexual variations were assessed in two samples of *F. r. texensis* from Texas, one of 64 individuals from Robertson-Madison counties (sample 3 of males and 34 of females) and another of 57 individuals from Webb-Duval counties (sample 14 of males and 31 of females), using the Statistical Analysis System (SAS) designed and implemented by Barr *et al.* (Helwig, 1976). Means were calculated for each character in the two samples. Analysis of variance (ANOVA) and Duncan's Multiple Range Mean Test (DUNCAN) were employed to evaluate significant differences among age classes with sexes

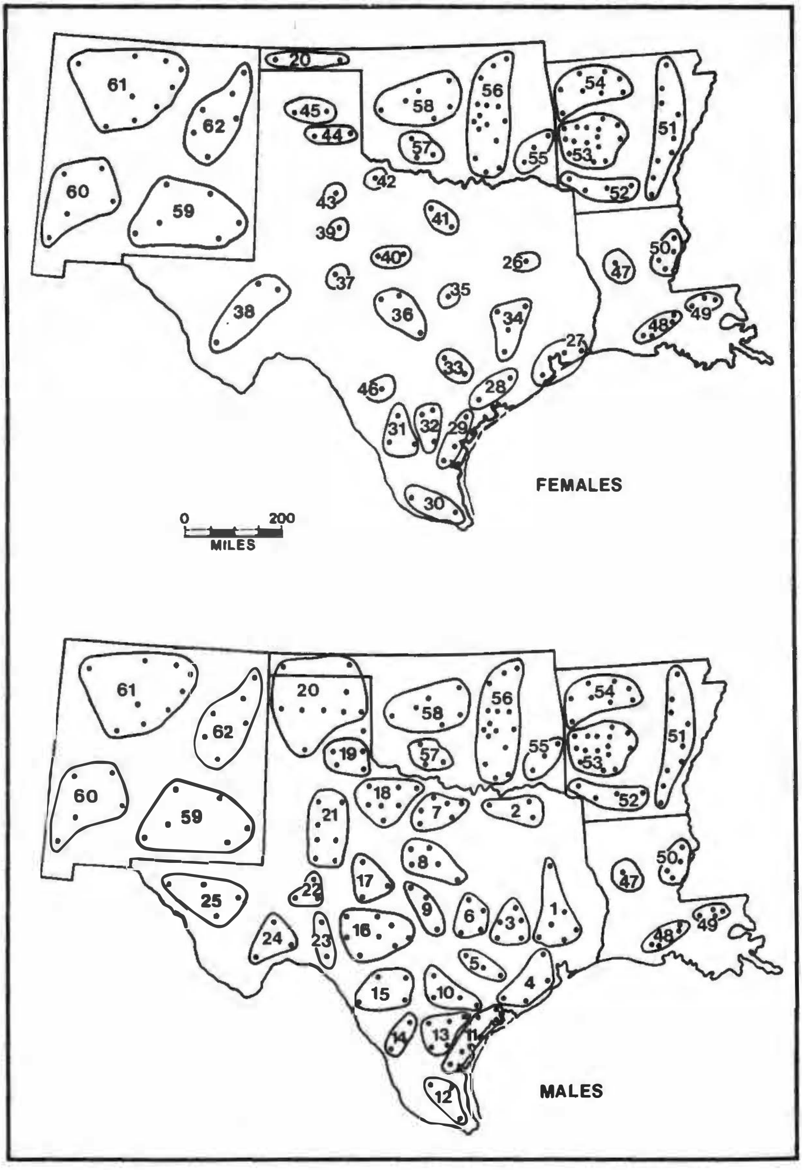

FIG. 1.—Geographic localities for female (top) and male (bottom) *Felis rufus* from Texas, New Mexico, Oklahoma, Arkansas, and Louisiana. Grouped samples used in the statistical analysis are outlined and numbered. See Table 1 for designation and site of each sample.

TABLE 2.—*The five age classes, as defined by morphological characteristics and tooth ring counts, used in the study of nongeographic variation.*

Age class	Age in months[1]	Cranial and dental characters
IA	0-9	basioccipital suture open; palatal sutures not tightly fused; temporal ridges undetectable; molar teeth just breaking gum line
IB	9-24	basioccipital suture fused but highly visible; palatal sutures fused tightly but visible; temporal ridges visible but not pronounced; muscle attachments on frontals not detectable
II	24-31	basioccipital suture tightly fused but still visible; temporal ridges well defined but not pronounced; muscle attachments on frontals detectable
III	31-36	basioccipital suture no longer visible; temporal ridges sharp; muscle attachments on frontals well developed
IV	36-48	temporal ridges pronounced; muscle attachments on frontals highly developed with distinct valley between frontals
V	48+	all ridges and muscle attachments highly pronounced with a massive coarse bone structure

[1]Derived from tooth ring counts by Blankenship (1979).

separated. A *t*-test was used to test for significant differences between sexes of the same age class in both samples. Coefficients of variation (CV) were calculated to determine the extent of variability for each character.

Geographic variation was analyzed using a variety of univariate statistics (mean, range, standard deviation, standard error, and coefficient of variation) calculated for each character in every sample. Statistical analysis employed ANOVA and DUNCAN test for all samples treating males and females separately.

To assess clinal patterns of variation, north-south and east-west transects were constructed among selected samples, and modified Dice-Leraas diagrams (Dice and Leraas, 1936) were drawn for four variables in males (greatest length of skull, squamosal breadth, cranial height, and length of the upper fourth premolar). A single north-south transect was established as follows: *Transect A*, from Oklahoma Panhandle to southern tip of Texas (samples 20, 19, 18, 17, 16, 10, 13, 12). Four west-to-east transects were established as follows: *Transect B*, from western Texas to eastern Arkansas (samples 25, 21, 18, 7, 2, 55, 53, 51); *Transect C*, from northwestern Arizona to southern Texas (reference sample 64; samples 60, 59, 25, 24, 23, 15, 13, 11);

Transect D, from northwestern Arizona to south-central Florida (reference sample 63; samples 60, 59, 21, 18, 7, 2, 52, 51; and reference sample 66); and *Transect E,* from northwestern Arizona to eastern Arkansas (reference sample 64; samples 61, 62, 20, 58, 56, 53, 51).

Several multivariate statistical techniques, using the Numerical Taxonomy Program (NT-SYS) of Rohlf and Kishpaugh (1972), were employed to cluster samples according to phenetic affinity. Cluster analysis was performed on standardized character means using average taxonomic distance as a measure of similarity and the UPGMA cluster option. The first three principal components were extracted from a matrix of correlation among characters, and projections of the samples onto the first two components were made.

RESULTS

Nongeographic Variation

The pattern of individual, age, and secondary sexual variation was almost identical in the two samples of *F. r. texensis*; therefore, only the data for the Robertson-Madison County sample are presented and discussed. No individuals of age class IA were included in this sample; therefore, all reference to age class I is to individuals in category IB (see Table 2).

Age variation.—ANOVA and DUNCAN test revealed that significant differences exist in most measurements among age classes of males. Generally, subadults (age class I) were significantly smaller than were older adults (age classes II, III, IV, V) in most measurements. Age class I in males completely separated from the other age classes in 18 of 26 characters (Table 3). In breadth of squamosal, males of age class I were significantly different ($F = 3.55$; $p \leq .05$) from age class V but not age classes II, III, and IV. In length of the maxillary toothrow, age class I males differed significantly ($F = 8.93$; $p \leq .0001$) from age classes III, IV, and V but not age class II. In mastoid breadth of males, age classes I and II separated distinctly ($F = 4.38$; $p \leq .002$) from age classes III, IV, and V. There were no significant differences among age classes in four characters of males (postorbital constriction, length of upper fourth premolar, premolar-molar toothrow length, and diameter of foramen magnum).

There was little significant age variation among females. Except for width of rostrum and length of mandible, none of the

TABLE 3.—*Variation with age in cranial measurements of* Felis rufus *from Robertson and Madison counties, Texas. Age classes are defined in Table 2. Statistics given are number, mean, two standard errors of mean, range, coefficient of variation,* F, *and* F_t. *Symbols alongside age classes indicate nonsignificant subsets according to DUNCAN test.*

Sex and age classes	N	Mean ± 2 SE	Range	CV	F/F_t	DUNCAN results
Greatest Length of Skull						
Male						
IV	8	129.94 ± 3.98	118.45-137.60	4.30		
V	5	128.71 ± 5.80	119.50-135.05	5.04	12.18	
III	5	128.48 ± 4.04	122.95-133.50	3.52	0.0001	
II	2	125.05 ± 11.80	119.15-130.95	6.67		
I	7	109.10 ± 5.98	99.20-123.60	7.30		
Female						
II	3	122.75 ± 6.20	119.40-128.95	4.38	0.63	
V	2	121.80 ± 17.30	113.15-130.45	10.04	ns	
III	2	121.00 ± 3.60	119.20-122.80	2.10		
I	5	117.42 ± 3.40	112.60-123.25	3.23		
Zygomatic Breadth						
Male						
IV	9	89.92 ± 2.54	82.45-95.50	4.25	26.10	
III	6	88.80 ± 2.32	84.15-91.80	3.20	0.0001	
V	5	88.21 ± 3.26	82.45-91.90	4.13		
I	12	75.51 ± 2.98	66.95-86.10	6.83		
Female						
V	2	83.55 ± 5.50	80.80-86.30	4.66	1.76	
III	3	83.17 ± 2.94	81.70-86.10	3.06	ns	
II	4	82.64 ± 4.68	76.80-88.15	5.65		
I	7	78.29 ± 3.26	72.10-82.50	5.45		
Squamosal Breadth						
Male						
V	4	54.54 ± 0.58	53.50-55.25	1.18	4.65	
II	2	54.00 ± 3.20	52.40-55.60	4.19	0.0057	
III	6	53.88 ± 0.96	51.90-55.20	2.18		
IV	9	53.47 ± 1.12	50.20-55.20	3.13		
I	9	52.50 ± 1.04	49.50-54.05	3.02		
Female						
V	2	52.98 ± 1.46	52.25-53.70	1.94	0.44	
II	3	52.77 ± 1.74	52.45-54.40	2.84	ns	
III	1	52.50				
I	5	51.74 ± 1.48	49.65-53.70	3.20		

TABLE 3.—*Continued.*

		Postorbital Constriction			
Male					
III	6	37.86 ± 2.12	35.65-42.95	6.87	0.69
I	10	37.38 ± 1.36	32.80-39.70	5.72	ns
V	5	36.98 ± 2.22	34.20-39.50	6.72	
II	2	36.78 ± 0.06	36.75-36.80	1.09	
IV	9	36.02 ± 1.52	31.90-38.40	6.35	
Female					
II	3	37.98 ± 1.34	37.10-39.30	3.06	1.91
V	2	37.03 ± 2.86	35.60-38.45	5.44	ns
I	5	35.46 ± 1.60	33.70-38.20	5.06	
III	1	34.55			
		Length of Nasals			
Male					
II	3	27.52 ± 1.52	26.00-28.35	4.78	6.83
V	6	27.06 ± 1.94	24.50-31.20	8.74	0.0003
IV	13	26.87 ± 1.16	23.90-31.45	7.72	
III	8	25.89 ± 1.50	23.25-28.85	8.15	
I	13	23.55 ± 0.78	22.20-27.50	5.98	
Female					
III	3	25.48 ± 1.44	24.25-26.75	4.91	0.19
V	3	25.47 ± 2.52	23.25-27.60	8.55	ns
I	6	25.01 ± 1.08	23.35-28.15	6.43	
II	5	24.54 ± 2.54	21.40-27.60	11.60	
		Diameter Upper Canine			
Male					
IV	13	7.67 ± 0.34	6.75-8.70	7.87	6.53
V	6	7.66 ± 0.74	6.40-8.70	11.84	0.0005
II	3	7.20 ± 0.98	6.35-8.05	11.80	
III	8	7.04 ± 0.24	6.40-7.60	4.90	
I	10	6.35 ± 0.46	5.00-7.85	11.45	
Female					
V	3	7.10 ± 0.80	6.40-7.80	9.86	1.56
II	5	7.03 ± 0.24	6.70-7.45	3.92	ns
III	3	7.02 ± 0.68	6.65-7.70	8.44	
I	9	6.56 ± 0.34	5.60-7.30	7.83	
		Interorbital Constriction			
Male					
V	6	24.51 ± 0.86	23.30-26.00	4.29	19.41
IV	11	23.90 ± 0.97	21.65-26.35	6.52	0.0001
III	8	23.25 ± 1.20	21.20-25.10	7.25	
II	3	22.38 ± 1.26	21.15-23.25	4.90	
I	13	19.14 ± 1.00	16.40-23.35	9.39	

TABLE 3.—*Continued.*

Female					
V	2	23.55 ± 2.30	22.40-24.70	6.91	3.02
II	4	22.69 ± 1.70	21.05-24.65	7.50	ns
III	3	22.10 ± 1.84	20.50-23.70	7.24	
I	9	19.91 ± 1.50	15.70-22.85	11.35	

Length of Upper Fourth Premolar

Male					
V	6	14.28 ± 1.04	12.35-15.55	8.88	1.26
IV	13	14.04 ± 0.32	13.30-14.80	4.11	ns
II	3	13.97 ± 1.10	13.00-14.90	6.80	
III	8	13.96 ± 0.48	12.95-15.15	4.85	
I	12	13.45 ± 0.54	10.90-14.60	6.87	
Female					
III	3	14.02 ± 0.70	13.40-14.60	4.29	2.59
II	5	13.94 ± 0.66	13.10-14.75	5.26	ns
V	3	13.25 ± 0.76	12.50-13.65	4.91	
I	8	13.16 ± 0.36	12.30-13.90	3.95	

Width of Rostrum

Male					
IV	13	33.07 ± 1.12	29.70-36.55	6.08	8.85
V	5	33.01 ± 1.70	30.95-35.55	5.75	0.0001
III	8	32.56 ± 1.24	28.60-33.85	5.40	
II	3	31.88 ± 3.00	29.40-34.60	8.18	
I	14	29.29 ± 0.82	26.60-32.05	5.23	
Female					
V	3	32.03 ± 1.44	30.70-33.20	3.93	6.49
II	5	31.84 ± 1.20	30.15-33.50	4.28	0.0044
III	3	31.23 ± 1.22	30.10-32.20	3.39	
I	9	29.56 ± 0.62	28.25-30.75	3.22	

Premolar-Molar Toothrow Length

Male					
V	6	25.33 ± 1.92	21.75-28.50	9.24	1.72
IV	13	25.11 ± 0.54	23.85-26.50	3.84	ns
III	8	24.84 ± 0.80	22.50-26.20	4.60	
II	3	24.62 ± 1.42	23.25-25.60	4.99	
I	14	23.89 ± 0.78	21.35-27.30	6.14	
Female					
II	5	24.79 ± 1.20	23.35-26.45	5.40	0.64
III	3	24.32 ± 0.02	24.30-24.35	0.12	ns
I	9	24.16 ± 0.45	23.00-25.80	3.50	
V	3	23.90 ± 1.32	22.65-24.90	4.79	

TABLE 3.—*Continued.*

Width Across Maxillary Toothrow					
Male					
IV	13	38.30 ± 1.00	34.40-42.40	4.73	4.45
V	6	37.97 ± 1.60	35.40-40.45	5.14	0.0048
III	7	37.80 ± 1.10	34.85-39.35	3.91	
II	3	37.32 ± 2.20	35.30-39.10	5.12	
I	14	35.26 ± 1.32	30.00-38.74	7.01	
Female					
II	5	37.32 ± 1.48	35.70-39.95	4.44	1.65
V	3	37.15 ± 1.96	35.20-38.20	4.55	ns
III	3	36.62 ± 1.44	35.25-37.70	4.31	
I	9	35.79 ± 0.74	34.55-38.50	3.09	
Length of Maxillary Toothrow					
Male					
IV	13	39.18 ± 0.88	36.50-41.00	4.08	5.66
V	6	38.82 ± 2.66	34.25-43.65	8.42	0.0011
III	8	38.13 ± 1.14	35.40-39.80	4.25	
II	3	38.12 ± 3.06	35.20-40.40	6.97	
I	14	35.75 ± 0.94	31.95-38.10	4.88	
Female					
II	5	37.52 ± 2.06	35.40-41.00	6.16	0.40
V	3	36.92 ± 2.06	35.05-38.60	4.83	ns
III	3	36.83 ± 1.06	36.30-37.90	2.50	
I	9	36.52 ± 0.90	34.15-38.60	3.67	
Palatilar Length					
Male					
IV	13	49.82 ± 1.40	45.40-52.65	5.04	11.71
V	6	48.61 ± 3.18	44.00-53.80	8.01	0.0001
III	7	48.28 ± 2.30	43.90-51.75	6.32	
II	3	47.27 ± 2.90	45.65-50.15	5.30	
I	13	42.54 ± 1.50	37.70-45.50	6.35	
Female					
V	3	46.87 ± 2.33	44.55-48.70	4.52	1.06
III	3	46.35 ± 0.76	45.95-47.10	1.40	ns
II	5	46.34 ± 2.76	42.25-50.90	6.67	
I	9	44.52 ± 1.70	40.75-49.00	5.69	
Cranial Height					
Male					
IV	12	45.45 ± 1.70	41.00-50.70	6.45	11.96
III	5	45.50 ± 2.26	41.60-47.80	5.55	0.0001
V	6	45.09 ± 1.94	42.25-48.00	5.27	
II	3	42.78 ± 1.84	41.15-44.35	3.74	
I	12	39.20 ± 1.26	35.90-42.95	5.57	

TABLE 3.—*Continued.*

Female					
V	2	45.03 ± 6.14	41.95-48.10	9.66	1.68
III	3	42.50 ± 2.66	40.45-45.00	5.43	ns
II	4	42.34 ± 3.60	40.40-46.40	6.45	
I	8	40.43 ± 1.84	35.56-42.70	6.43	
Mastoid Breadth					
Male					
IV	9	56.48 ± 1.18	53.70-58.90	3.16	13.24
III	6	55.73 ± 1.30	54.00-58.45	2.98	0.0001
V	5	55.14 ± 1.50	52.60-56.75	3.03	
II	1	50.70			
I	8	50.48 ± 1.58	47.75-53.90	4.42	
Female					
II	3	52.97 ± 3.60	50.10-55.30	5.90	0.37
III	1	52.45			ns
V	1	49.85			
I	5	48.82 ± 5.98	37.40-55.00	13.67	
Basilar Length					
Male					
IV	9	108.11 ± 1.92	103.80-113.05	2.67	13.93
V	5	106.38 ± 5.20	96.95-112.60	5.45	0.0001
III	5	106.22 ± 3.66	100.45-110.85	3.85	
II	2	102.58 ± 8.20	98.65-106.50	5.41	
I	6	90.70 ± 5.08	81.70-99.60	6.87	
Female					
III	2	102.00 ± 2.40	100.80-103.20	1.66	0.83
II	3	101.20 ± 5.52	97.50-106.60	4.72	ns
V	2	100.50 ± 12.80	94.10-106.90	9.01	
I	4	95.40 ± 6.30	87.45-102.80	6.60	
Condylobasal Length					
Male					
IV	8	118.45 ± 2.52	112.55-124.30	3.02	12.69
V	5	117.63 ± 5.10	108.70-123.75	4.85	0.0001
III	5	117.32 ± 3.90	110.45-120.90	3.73	
II	2	113.00 ± 8.20	108.90-117.10	5.13	
Female					
II	2	114.20 ± 8.80	109.80-118.60	5.45	1.12
III	2	111.83 ± 1.36	111.15-112.50	0.85	ns
V	2	111.38 ± 12.66	105.05-117.70	8.03	
I	4	105.21 ± 6.38	97.10-112.60	6.05	

TABLE 3.—*Continued.*

Length of Mandible					
Male					
IV	11	76.55 ± 2.34	69.35-81.00	5.08	11.32
V	6	75.27 ± 3.60	68.95-79.85	5.86	0.0001
III	7	74.16 ± 3.04	68.65-78.25	5.43	
II	3	73.00 ± 4.76	70.55-77.75	5.63	
I	13	65.68 ± 2.66	56.80-73.75	7.28	
Female					
V	2	74.58 ± 1.06	74.05-75.10	1.00	3.06
III	3	71.33 ± 1.56	69.80-72.35	1.89	0.0629
II	5	51.33 ± 3.10	66.85-75.70	4.85	
I	8	68.13 ± 2.30	62.15-71.35	4.77	
Height of Coronoid					
Male					
IV	12	38.57 ± 1.80	33.25-42.55	8.07	8.31
V	5	37.17 ± 4.26	32.30-44.85	12.82	0.0001
III	6	36.23 ± 1.98	33.10-39.15	6.68	
II	3	35.92 ± 2.72	33.35-38.00	6.58	
I	13	31.63 ± 1.56	26.90-37.15	8.90	
Female					
V	2	36.30 ± 1.70	35.45-37.15	3.31	2.42
III	3	35.73 ± 2.00	34.40-37.70	4.87	ns
II	5	33.96 ± 2.46	30.75-38.20	8.12	
I	8	32.47 ± 1.58	28.60-35.00	6.91	
Length of Anterior Mandibular Toothrow					
Male					
IV	11	17.06 ± 0.66	15.10-18.55	6.34	10.32
V	6	16.35 ± 0.70	15.20-17.30	5.23	0.0001
II	3	16.05 ± 1.62	14.90-17.60	8.68	
III	7	16.01 ± 0.58	15.00-17.45	4.72	
I	13	14.58 ± 0.50	12.75-16.55	6.29	
Female					
V	3	16.18 ± 0.60	15.60-16.55	3.16	2.79
II	5	16.00 ± 1.12	14.60-17.95	7.84	ns
III	3	15.67 ± 0.44	15.40-16.10	2.42	
I	8	14.83 ± 0.56	13.70-15.90	5.30	
Postpalatal Length					
Male					
IV	9	57.59 ± 1.06	55.50-61.25	2.75	15.96
V	5	57.11 ± 2.02	53.20-58.95	3.94	0.0001
III	5	57.06 ± 2.20	54.20-61.00	4.31	
II	2	54.78 ± 3.96	52.80-56.75	5.10	
I	7	49.81 ± 1.76	47.70-54.25	4.68	

TABLE 3.—*Continued.*

Female					
III	2	55.43 ± 3.66	53.60-57.25	4.66	0.76
V	2	54.08 ± 7.96	50.10-58.05	10.40	ns
II	3	54.00 ± 1.92	52.80-55.90	3.08	
I	4	51.46 ± 3.34	46.90-54.60	6.48	
Nasal-Frontal Length					
Male					
V	6	54.61 ± 2.78	53.30-61.95	5.90	10.72
III	8	56.82 ± 2.00	53.55-60.50	5.00	0.0001
IV	13	56.61 ± 1.76	51.05-61.15	5.63	
II	2	55.77 ± 4.66	53.05-60.40	7.23	
I	11	49.76 ± 1.62	45.70-54.15	5.37	
Female					
II	5	54.97 ± 1.36	53.40-57.45	2.78	1.87
V	2	53.15 ± 7.70	49.30-57.00	10.24	ns
III	3	53.02 ± 2.40	51.05-55.20	3.93	
I	9	51.46 ± 1.82	47.45-56.05	5.30	
Greatest Length of Bullae					
Male					
IV	10	32.06 ± 1.08	29.50-34.40	5.33	14.32
V	5	31.21 ± 0.86	30.00-32.40	3.08	0.0001
III	8	31.11 ± 1.14	28.80-32.80	5.20	
II	3	30.63 ± 2.02	29.15-32.55	5.68	
I	10	27.14 ± 0.98	24.70-29.55	5.73	
Female					
II	3	30.37 ± 1.86	28.70-31.90	5.28	0.72
V	2	29.72 ± 5.56	26.95-32.50	13.20	ns
III	2	29.10 ± 0.50	28.85-29.35	1.22	
I	6	28.39 ± 1.42	25.45-30.30	6.12	
Width of Bullae					
Male					
IV	10	15.78 ± 0.52	14.65-16.90	5.11	9.60
III	8	15.43 ± 0.44	14.55-16.10	3.96	0.0001
V	5	15.22 ± 0.60	14.60-16.30	4.46	
II	3	15.13 ± 0.54	14.60-15.45	3.07	
I	12	14.10 ± 0.36	13.15-15.15	4.46	
Female					
III	2	14.85 ± 0.50	14.60-15.10	2.38	0.15
I	6	14.60 ± 0.94	12.90-15.70	7.90	ns
V	2	14.58 ± 2.24	13.45-15.70	10.92	
II	4	14.28 ± 0.76	13.60-15.30	5.26	

TABLE 3.—*Continued.*

		Diameter Foramen Magnum			
Male					
V	5	13.69 ± 0.54	13.25-14.75	4.44	0.87
IV	9	13.52 ± 0.46	12.55-14.55	4.98	ns
III	6	13.40 ± 0.68	12.65-15.00	6.24	
I	7	13.39 ± 0.84	11.75-14.80	8.44	
II	2	12.38 ± 1.96	11.40-13.35	11.14	
Female					
V	2	13.98 ± 0.06	13.95-14.00	0.25	3.20
II	3	13.80 ± 0.26	13.60-14.00	1.45	ns
III	2	12.48 ± 1.96	11.50-13.45	11.05	
I	4	12.31 ± 0.92	11.50-13.30	7.51	
		Height of Occipital			
Male					
IV	8	21.83 ± 0.88	20.00-24.00	5.70	8.90
III	6	21.27 ± 0.52	20.45-22.20	2.95	0.0002
V	5	21.24 ± 0.74	20.15-22.40	3.93	
II	2	20.73 ± 2.86	19.30-22.15	9.72	
I	7	18.65 ± 0.90	17.20-20.40	6.44	
Female					
III	2	20.13 ± 1.56	19.35-20.90	5.45	0.35
V	2	19.95 ± 1.70	19.10-20.80	6.03	ns
II	3	19.72 ± 2.38	17.75-21.85	10.42	
I	3	18.87 ± 1.44	17.45-19.75	6.57	

measurements showed a significant F-value in the ANOVA. Age class I females differed significantly from the other age classes in only a single measurement (width of rostrum). In length of mandible, age class I differed significantly from age class V but not age classes II and III.

Secondary sexual variation.—Males averaged larger than females in all cranial measurements except diameter of the foramen magnum. The average percent of difference was 5.75, ranging from a low of 1.6 percent for postorbital constriction to a high of 10.34 percent for height of occipital bone. Males and females differed significantly ($p \leq .05$) in 17 of 26 cranial measurements (Table 4). Measurements reflecting length, width, and depth of skull were significantly different except for squamosal breadth and cranial height. Postorbital and interorbital constriction, as well as measurements of dentition (premolar-molar toothrow length, length of upper fourth premolar, diameter of the upper canine, and length of the diastema), did not differ significantly between sexes. Because of

TABLE 4.—*Secondary sexual variation in 23 cranial and three mandibular characters of adult* Felis rufus *from Robertson and Madison counties, Texas. Statistics given are number, mean ± two standard errors, range, and* t*-value. See text for character abbreviations.*

Character (*N*)	Males	Females	*t*-value
GSL (24;22)	128.43 ± 5.34 (119.70-138.45)	122.88 ± 5.13 (115.20-135.80)	3.59**.
ZB (24;14)	86.86 ± 3.62 (78.15-92.05)	84.19 ± 3.99 (79.05-92.40)	2.12*.
SB (17;13)	53.19 ± 1.44 (50.60-56.05)	52.42 ± 2.25 (49.00-57.40)	1.14
POC (24;19)	36.97 ± 2.18 (31.75-40.20)	37.26 ± 1.92 (33.95-40.75)	−0.45.
LN (32;25)	25.88 ± 1.73 (22.10-29.80)	25.07 ± 1.68 (21.20-27.40)	1.79
IC (31;21)	23.20 ± 1.79 (18.55-27.55)	22.76 ± 1.67 (20.20-26.20)	0.90
DUC (31;24)	7.25 ± 0.59 (6.30-8.60)	6.62 ± 0.48 (5.75-7.75)	4.23**
PM (32;24)	13.59 ± 0.75 (12.20-15.25)	13.37 ± 0.83 (11.30-14.55)	1.04
WR (30;23)	32.64 ± 1.66 (29.80-35.85)	31.19 ± 1.78 (28.05-34.15)	3.05**
PMT (32;24)	24.53 ± 1.15 (22.20-27.35)	24.39 ± 1.10 (21.55-25.95)	0.46
WMT (30;22)	37.89 ± 1.36 (35.00-40.50)	36.08 ± 2.56 (27.80-39.70)	3.02**
MT (31;24)	38.20 ± 1.65 (35.20-41.70)	36.95 ± 1.76 (33.80-40.30)	2.71**
PL (31;22)	47.73 ± 2.28 (43.50-52.80)	46.55 ± 1.99 (43.35-51.75)	1.95**
CH (29;20)	44.27 ± 1.90 (41.35-47.95)	43.49 ± 1.58 (40.00-45.90)	1.49
MB (24;17)	55.18 ± 2.66 (51.75-61.05)	53.63 ± 2.51 (50.10-58.35)	1.88
BL (21;16)	105.06 ± 4.20 (97.25-113.65)	100.31 ± 4.36 (93.00-111.35)	3.36**
CBL (23;17)	115.57 ± 5.06 (102.50-124.55)	110.84 ± 4.64 (103.60-123.45)	3.03**
LM (29;24)	74.72 ± 3.35 (66.95-80.20)	71.38 ± 4.19 (58.05-80.20)	3.22**
CRH (28;24)	36.50 ± 2.41 (32.20-41.55)	34.88 ± 2.21 (30.80-40.05)	2.51*
DM (31;24)	16.49 ± 1.11 (14.25-19.00)	15.43 ± 0.91 (13.65-17.25)	3.80**
PPL (19;15)	57.65 ± 2.81 (53.70-65.10)	54.54 ± 2.33 (51.50-59.75)	3.44**
NFL (30;22)	57.12 ± 2.85 (50.50-62.40)	55.40 ± 2.47 (51.35-59.75)	2.27*
GLB (28;21)	31.44 ± 1.76 (27.40-34.90)	30.10 ± 1.29 (27.85-32.35)	2.94**
WAB (29;22)	15.22 ± 0.91 (13.15-17.60)	14.70 ± 0.77 (13.30-16.15)	2.17*
DFM (23;19)	13.54 ± 0.91 (11.90-15.70)	13.53 ± 0.89 (12.55-15.55)	0.01
HOB (24;22)	21.56 ± 1.38 (19.25-24.40)	20.30 ± 1.04 (18.80-22.90)	3.48**

*Significant at .05-.01.
**Significant at .01-.001.

the extent of sexual variation, the sexes were separated for analysis of geographic variation.

Individual variation.—The average CV for 26 measurements in the Robertson-Madison county sample (see Table 3) was 5.57, and CV's of females (5.52) averaged slightly smaller than those for males (5.69). Average CV's for males of the age classes were: I, 6.42; II, 6.12; III, 4.85; IV, 5.09; and V, 5.99; for females, these same values were 5.97, 5.49, 3.81, ——, and 6.42, respectively. Thus, younger males (age classes I and II) were slightly more variable than were older males (age classes IV and V), whereas the opposite was true in females. Age class III exhibited the lowest CV in both sexes.

The measurements with the lowest CV's for males were squamosal breadth, mastoid breadth, postpalatal length, condylobasal length, and width across the auditory bullae; for females, the measurements with the lowest CV's were squamosal breadth, width across the auditory bullae, mastoid breadth, width across the maxillary toothrow, and length of mandible. The most variable (highest CV's) measurements for males were diameter of upper canine, coronoid height, length of nasals, diameter of foramen magnum, and postorbital constriction; for females, the most variable measurements were postpalatal length, interorbital constriction, length of nasals, diameter of upper canine, and height of occipital bone.

Geographic Variation

Because of small sample sizes and the greater variation in size characters of females, emphasis on the analysis of geographic variation was given to males, although some information for females is presented for comparison.

Univariate Analysis

Patterns of univariate variation along the north-to-south and west-to-east transects for males, as depicted by Dice-Leraas diagrams, are illustrated in Figs. 2-6. The overall pattern of univariate variation along these transects is erratic for most characters, with alternating sections of increasing and decreasing size. Smooth clines are rare in most measurements, and clinal changes from north to south and from west to east are evident only in localized parts of the range.

Transect A.—The four measurements do not follow a concordant pattern along this transect, although the deviations among them are relatively minor (Fig. 2). Proceeding from north to south, there is a slight size decrease in squamosal breadth and length of upper fourth premolar, whereas a slight increase in size is evident in cranial height and skull length. Individuals from sample 17 (central Texas) are significantly larger than those from adjacent samples in skull length and length of the upper fourth premolar, but this trend is not apparent in the other two measurements. Thus, variation along this transect is erratic with few concordant breaks or character shifts.

Transect B.—The smallest individuals are found in the eastern samples of this transect, with size gradually increasing in samples

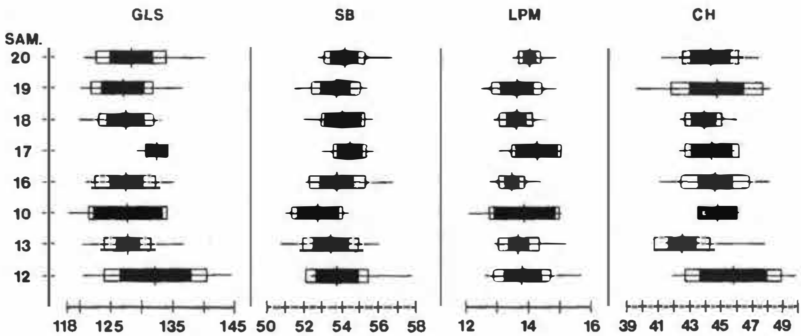

FIG. 2.—Geographic variation, expressed by Dice-Leraas diagrams of selected characters, among samples of *Felis rufus* along transect A in the study area. Sample designation (Sam.) appears along the left margin. See Fig. 1 and Table 1 for location of samples. The horizontal line represents the range; vertical line, the mean; open rectangle, one standard deviation; and closed rectangle, two standard errors of the mean.

progressing toward the southwest (Fig. 3). The magnitude of variation is much less in length of the upper fourth premolar than in the other measurements. In most geographic regions, character transitions follow a pattern of smooth, gradual change with few significant breaks. Exceptions include sample 25 (northern Trans-Pecos Texas), which has a significantly larger skull length than the adjacent sample (21) from the High Plains; sample 7 (north-central Texas), which has a significantly smaller squamosal breadth than the two adjacent samples in central Texas (18, 2); and sample 21 (High Plains of Texas), which has a significantly greater cranial height than the adjacent sample (18).

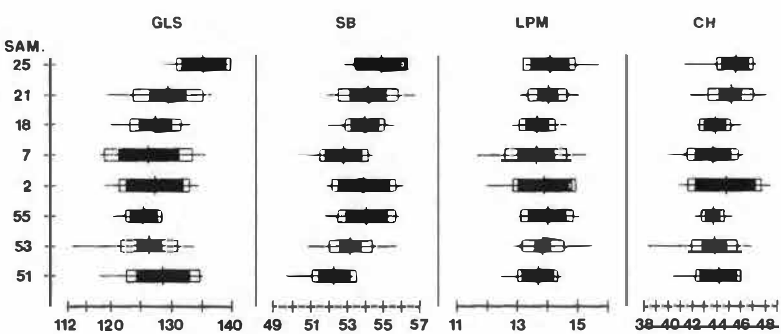

FIG. 3.—Geographic variation of *Felis rufus*, expressed by Dice-Leraas diagrams of selected characters, along transect B in the study area. See Fig. 1 and Table 1 for location of samples and Fig. 2 for an explanation of the diagrams.

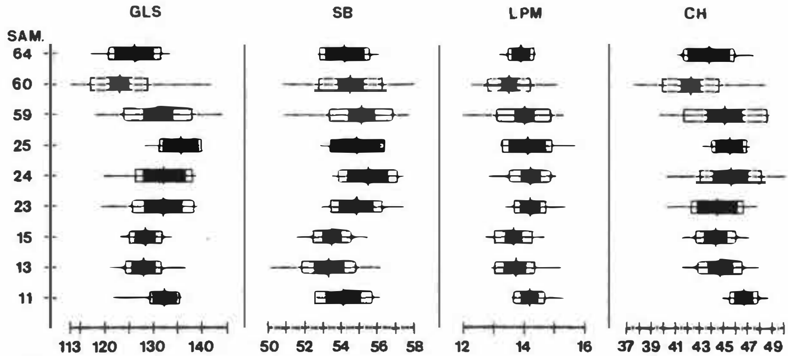

FIG. 4.—Geographic variation of *Felis rufus*, expressed by Dice-Leraas diagrams of selected characters, along transect C in the study area. See Fig. 1 and Table 1 for location of samples and Fig. 2 for an explanation of the diagrams.

Transect C.—The pattern of variation along this transect is more erratic than that observed for the other transects (Fig. 4). Samples 64 and 60 (Arizona and southwestern New Mexico) have significantly smaller skull lengths than other samples in the transect. Sample 25 (northern Trans-Pecos Texas) averages larger in skull length than the two adjacent samples (59 from southeastern New Mexico and 24 from the Big Bend region of Texas), whereas samples 13 and 15 (southern Texas) average smaller in this measurement than adjacent samples (11 from the Texas Coast and 23 from the Stockton Plateau). Length of the upper fourth premolar shows an almost identical pattern of variation except that individuals in sample 64 (Arizona) are significantly larger than those of sample 60 (southwestern New Mexico). The same general pattern is also evident in cranial height; samples 64 and 60 are significantly smaller than other samples in the transect, and sample 11 averages larger than sample 13.

Transect D.—Three of the four measurements (skull length, length of upper fourth premolar, and cranial height) exhibit a similar pattern of variation along this transect (Fig. 5). These measurements in the western samples (sample 63 from southeastern Arizona and sample 60 from southwestern New Mexico) are small and a significant size increase occurs between samples 60 (southwestern New Mexico) and 59 (southeastern New Mexico). Beginning with sample 59 and continuing east through Texas and Arkansas, size gradually declines. The reference sample of *floridanus* (66) is significantly smaller in skull length and length of upper fourth premolar than samples from Arkansas.

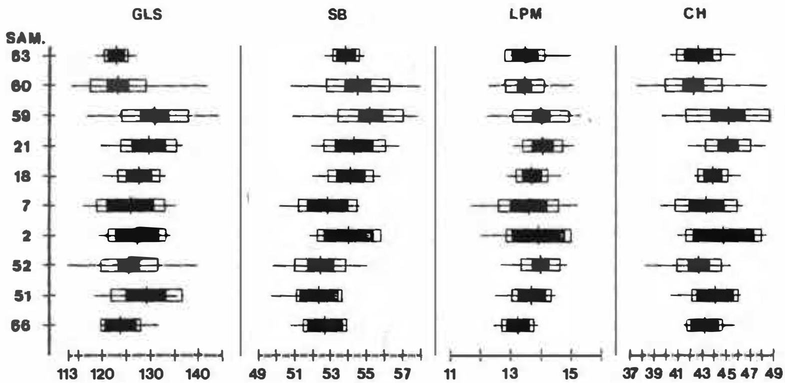

FIG. 5.—Geographic variation of *Felis rufus*, expressed by Dice-Leraas diagrams of selected characters, along transect D in the study area. See Fig. 1 and Table 1 for location of samples and Fig. 2 for an explanation of the diagrams.

Squamosal breadth gradually increases over the first three samples (63, 60, 59) and then, with the exception of sample 2, decreases in size through the remainder of the transect.

Transect E.—There was no consistent pattern of variation in the four measurements along this west-to-east transect across the northern portion of the study area (Fig. 6). Little significant variation was evident in skull length and cranial height, and the pattern for length of the upper fourth premolar was highly erratic. The only measurement to show a definite pattern was squamosal breadth, which exhibited a classic pattern of clinal change beginning with smaller size in eastern samples and gradually increasing in size toward the west.

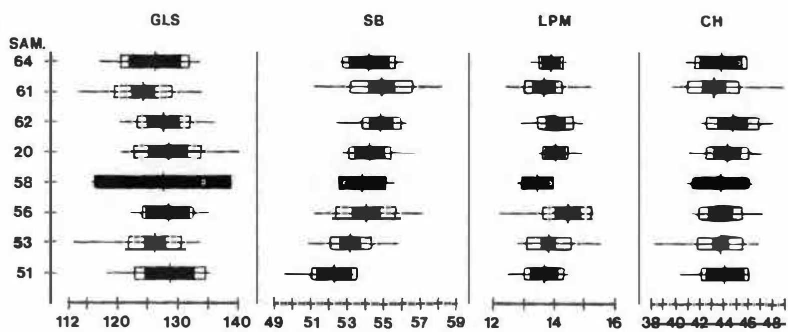

FIG. 6.—Geographic variation of *Felis rufus*, expressed by Dice-Leraas diagrams of selected characters, along transect E in the study area. See Fig. 1 and Table 1 for location of samples and Fig. 2 for an explanation of the diagrams.

Males.—The number of maximally nonsignificant subsets generated for the 26 characters in the DUNCAN analysis of males varied from two (diameter of the foramen magnum) to 10 (mastoid breadth) with all but four of the measurements (diameter of the foramen magnum, length of nasals, length of upper fourth premolar, and greatest length of auditory bullae) requiring at least six nonsignificant subsets to cover the range of variation. Considerable overlap was evident among the arrays of subsets for each character, and there were no instances where one array was completely segregated from the others. In overall size, the smallest male bobcats were from southern Louisiana (47-49) and west of the Continental Divide in New Mexico (60, 61) and Arizona (63, 64). The largest individuals were from southeastern New Mexico (59) and western (17, 22-25) and southern (11, 12) Texas.

Females.—A similar but slightly different pattern was evident in the DUNCAN analysis of females. The arrays of maximally nonsignificant subsets ranged from two (diameter of the foramen magnum) to 12 (mastoid breadth) with all but three characters (length of nasals, width of rostrum, and diameter of the foramen magnum) having six or more arrays of subsets, all of which overlapped substantially. The smallest females were from Arizona (63), southeastern Oklahoma (55), Arkansas (51-54) and eastern Louisiana (49). The largest bobcats in most measurements were from central Oklahoma (57, 58), western Texas (38, 40, 42, 58), and southeastern New Mexico (59).

Multivariate Analysis

Cluster analysis.—A distance phenogram was generated using all samples of males and females separately, and the results were substantially different. The phenogram for males (Fig. 7) separates into two groups (A and B), with the exception of sample 47 (comprised of only two individuals from Natchitoches Parish, Louisiana), which segregates by itself. Group A includes reference samples of *F. r. floridanus* (65, 66) and *F. r. baileyi* (63), two samples (60, 61) from west of the Continental Divide in New Mexico, and a sample (49) from east of the Mississippi River in Louisiana. These bobcats are the smallest in overall size. Group B contains the remaining samples from the study area plus single samples of the *floridanus* (67) and *baileyi* (64) reference samples. This group can be further divided into subgroups I and II. Subgroup I, which includes bobcats of large overall size, is made

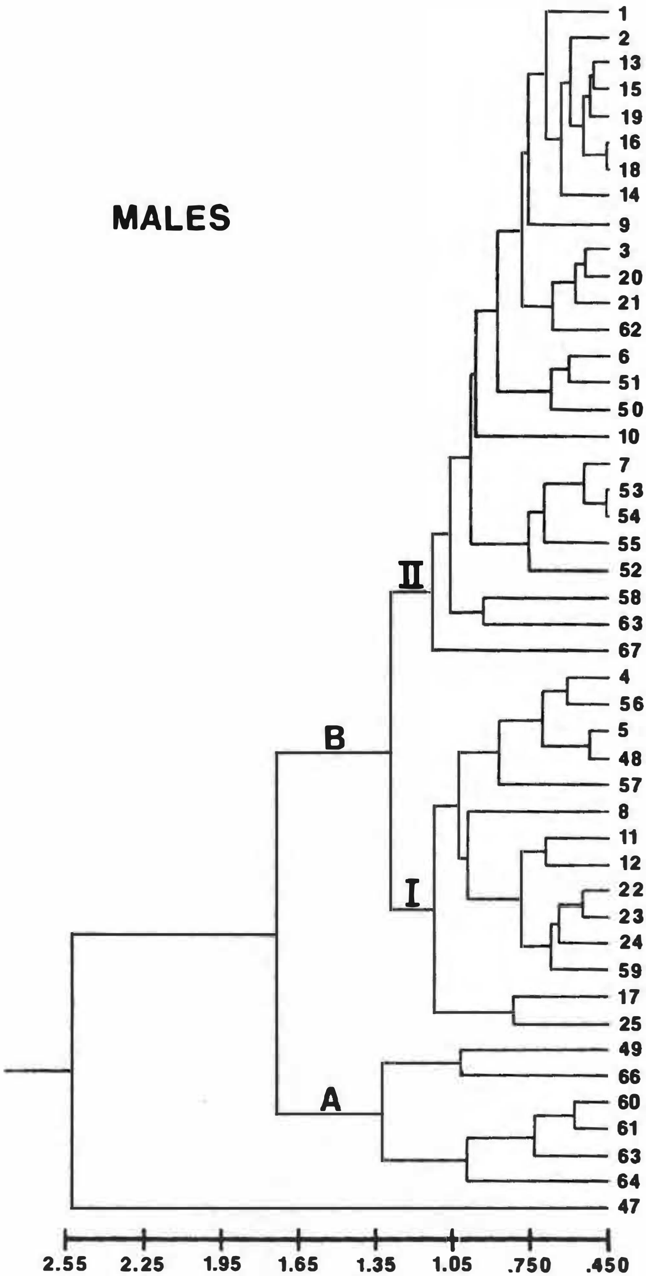

FIG. 7.—Distance phenogram of the cluster analysis for samples of male *Felis rufus*. The cophenetic correlation coefficient for the phenogram is 0.772.

up of samples from the coastal bend of Texas (4, 5, 11, 12), western Texas (22-25), southeastern New Mexico (59), and central Oklahoma (56, 57). Subgroup II, which includes bobcats of intermediate size, consists of samples from central Texas (18-21, 1-3, 6, 7, 9, 10, 13-16), southeastern Oklahoma (55), and Arkansas (51-54).

The phenogram for females (Fig. 8) also separates into two major groups. Group A, which comprises those females of relatively small size, includes reference samples of *F. r. baileyi* from Arizona (63, 64) plus samples from western Arkansas, southeastern Oklahoma, and the lower Mississippi River Valley in Louisiana. Group B, which includes the remaining samples, is further divided into two subgroups. Subgroup I includes female bobcats of intermediate size from western New Mexico, a single sample (51) from eastern Arkansas, and a series of samples stretching from central Oklahoma southward into central and southern Texas. Subgroup II, which includes females of relatively large size, is comprised primarily of samples from western and southern Texas.

Principal components analysis.—The first three principal components were computed from the matrix of correlation among the 26 characters. For males, the first principal component expresses 60.72 percent of the phenetic variation; the second, 11.11; and the third, 5.05; for females, these values are 69.59, 10.82, and 3.80, respectively.

Loadings (Table 5), which indicate the correlations of characters with the first three principal components, indicate that component I is essentially a general size factor with high positive correlations for all characters except postorbital constriction and diameter of the foramen magnum. The six characters with the largest loadings in both sexes are skull length measurements. For males, these are basilar length, condylobasal length, length of mandible, greatest length of skull, palatilar length, and premolar-molar toothrow length; for females, they are length of mandible, greatest length of skull, basilar length, condylobasal length, maxillary toothrow length, and palatilar length. With respect to positioning of samples along component I, samples containing specimens that were smallest in these measurements are located on the far left; from that point, samples are arranged in ascending order relative to size, with those containing the largest individuals on the far right of the plot (Fig. 9). For males, the smallest bobcats are from Arizona, western New Mexico, and

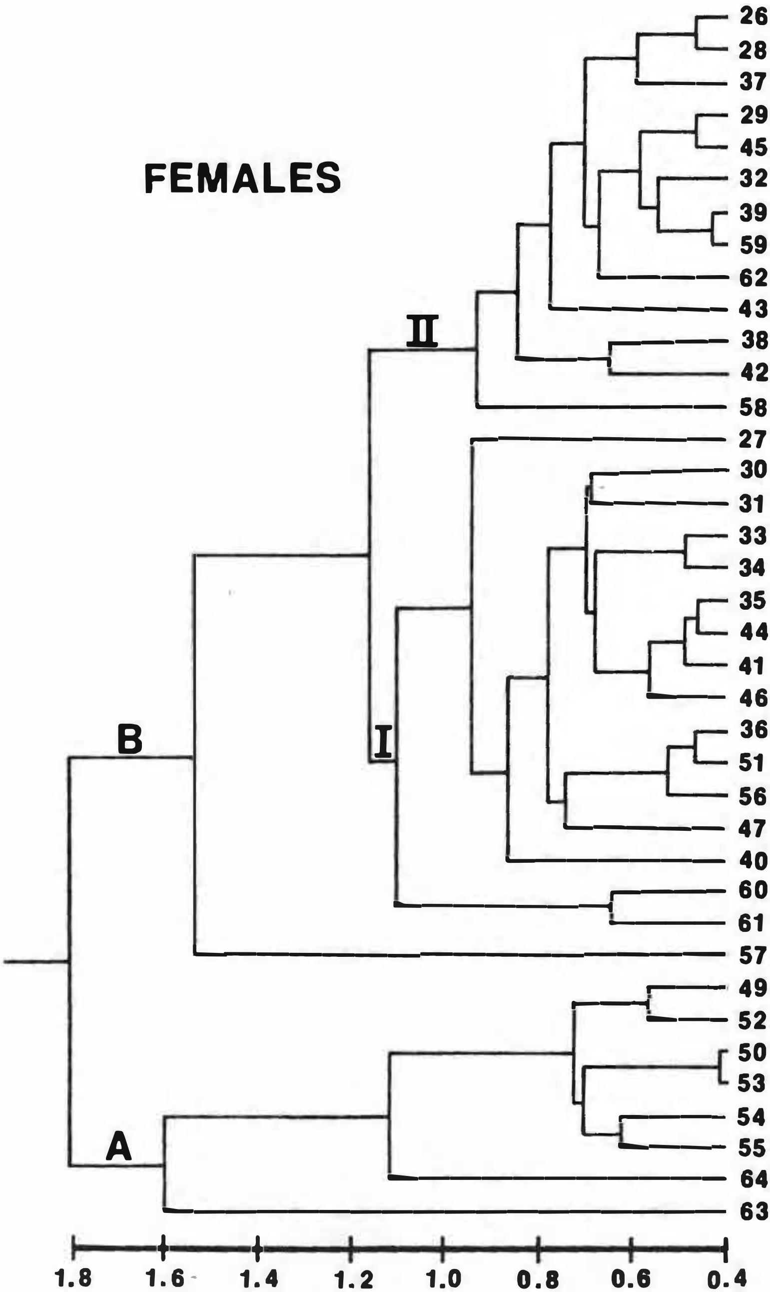

FIG. 8.—Distance phenogram of the cluster analysis for samples of female *Felis rufus*. The cophenetic correlation coefficient for the phenogram is 0.709.

TABLE 5.—*Character loadings on the first three principal components of interlocality phenetic variation in males (M) and females (F) of* Felis rufus. *See text for character abbreviations.*

	Principal components					
	I		II		III	
Character	M	F	M	F	M	F
GSL	.939	.961	−.011	−.013	.019	.110
ZB	.785	.867	.314	−.358	.162	−.016
SB	.466	.568	.722	−.791	−.202	.064
POC	−.071	−.274	.764	−.868	.173	−.023
LN	.819	.642	−.289	.201	−.483	−.075
IC	.776	.611	.570	−.445	.326	−.103
DUC	.747	.737	−.454	.466	−.074	−.274
PM	.753	.712	.009	.324	−.372	−.019
WR	.851	.840	−.320	.335	.028	−.214
PMT	.814	.864	.076	.240	−.147	.020
WMT	.904	.842	−.191	.034	.018	−.258
MT	.948	.834	−.145	.111	−.092	−.035
PL	.951	.893	−.334	−.032	−.032	−.016
CH	.832	.812	−.023	.003	.080	−.223
MB	.880	.838	.423	−.359	−.053	.123
BL	.958	.952	−.007	−.044	−.028	.074
CBL	.948	.950	−.014	−.046	−.067	.090
LM	.978	.942	−.162	.012	.122	−.028
CRH	.915	.844	−.023	.043	.176	−.112
DM	.841	.717	−.258	.005	.025	−.067
PPL	.926	.843	.159	.013	.032	.120
NFL	.932	.868	.042	−.129	.221	.116
GLB	.901	.838	.087	.006	−.229	.055
WAB	.668	.542	.589	−.461	−.120	.148
DFM	−.326	−.349	.372	−.438	−.678	−.763
HOB	.919	.779	−.048	.073	.254	.184

the southeastern United States (Georgia, Florida, Louisiana, and Arkansas); bobcats of medium to large size occupy a geographic area including eastern New Mexico, Texas, and most of Oklahoma. The same general geographic trend is evident for females with the smallest bobcats being from the western (Arizona and New Mexico) and eastern (Arkansas and Louisiana) parts of the study area and bobcats of medium and large size occurring in the intervening areas.

Component II for males has high positive loadings for characters affecting shape of braincase and width of skull, including postorbital constriction, squamosal breadth, width of the auditory bullae, interorbital constriction, and mastoid breadth, and a high negative loading for diameter of the upper

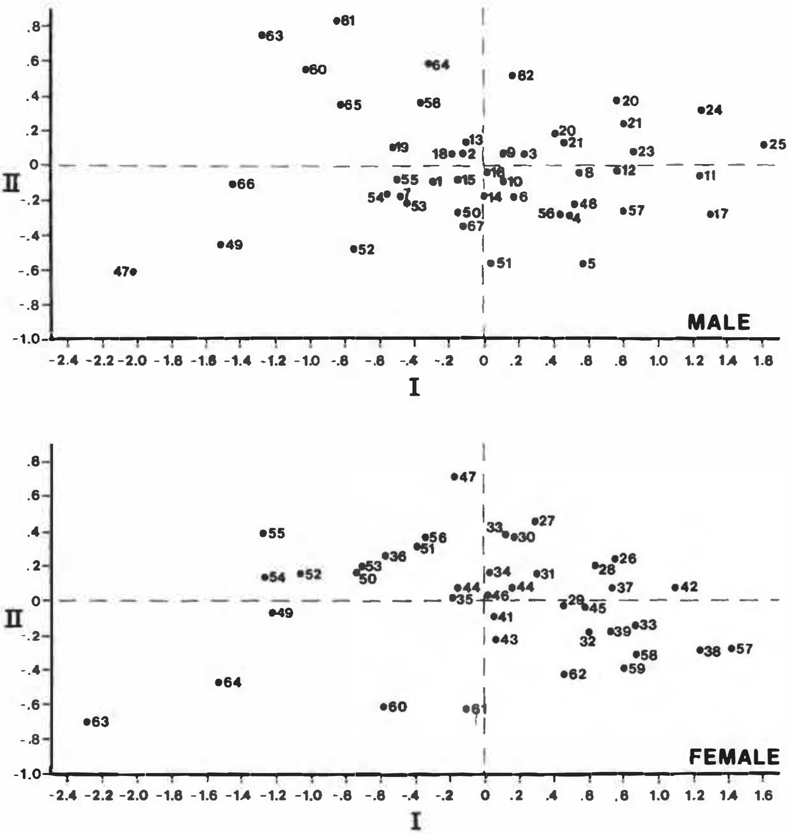

FIG. 9.—Two-dimensional projections of the samples of male and female *Felis rufus* onto the first two principal components.

canines (Fig. 10). The loadings for females on this component are a mirror image of those in males with high negative loadings for the same characters affecting braincase shape and skull width, and a high positive loading for diameter of the upper canines. With respect to positioning of samples along component II, the pattern is similar for both males and females. Most samples of males with positive values and those of females with negative values are from the shrub-grassland habitats in the western half of the study area (west of longitude 99° W). These bobcats are characterized by skulls with a wide squamosal breadth, postorbital constriction, interorbital constriction, mastoid breadth, and auditory bullae, and a narrow diameter of the upper canines. Most samples of males with negative loadings and those

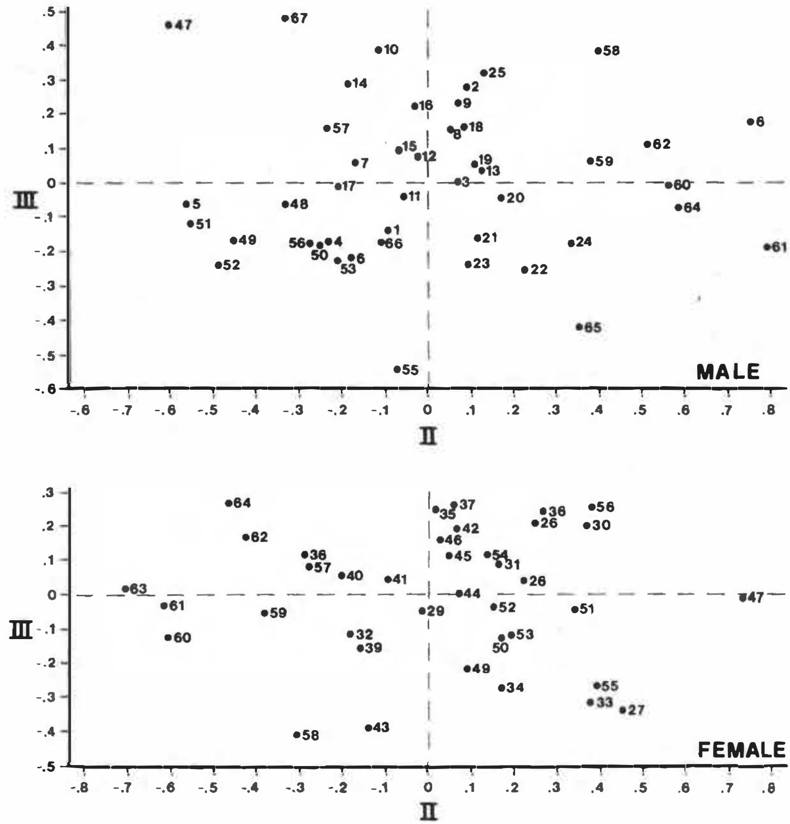

FIG. 10.—Two-dimensional projections of the samples of male and female *Felis rufus* onto the second and third principal components.

of females with positive loadings are from the broadleaf and needleleaf eastern forests and the grassland-forest habitats in the eastern half of the study area (east of longitude 99° W). The skulls of these bobcats have a narrow squamosal breadth, postorbital constriction, mastoid breadth, and auditory bullae, and a large diameter of the upper canines.

Component III in males has high negative loadings for nasal length, length of upper fourth premolar, and diameter of the foramen magnum. Interorbital constriction and height of the occipital bone are the only characters with a high positive loading. Characters with high negative loadings on this component in females include diameter of the foramen magnum, diameter of the upper canine, interdentary breadth, cranial height, and rostral width. The only character with a high positive loading is height of the occipital bone. Most samples of males with negative values for component III (narrow interorbital constriction, large diameter of foramen magnum, and short height of the occipital bone) are distributed in the eastern half of the study area, whereas those with positive values (character trends opposite those above) are from the western half of the region. Samples of females with negative values for component III have a slightly larger diameter of upper canines, wider rostrum, greater cranial height, and greater diameter of the foramen magnum than samples with positive values for this component. However, there is no obvious geographic trend with respect to the positioning of samples of females along component III.

Discussion

Nongeographic Variation

The greatest nongeographic variation is with age and involves proportions as well as general size. Analysis of age variation in male bobcats suggests that adult size is reached at about 24 months of age at which time the temporal ridges and muscle attachments on the frontals become well defined. Male bobcats do not increase appreciably in size from 24 to 48 months of age, but the temporal ridges and muscle attachments become more pronounced. Females seem to attain adult size much earlier than males. In most cranial measurements of females, there was no significant difference between age classes I and II; however, age class I females lacked temporal ridges and frontal muscle attachments. These results are consistent with those of Grinnell and Dixon (1924) who noted that bobcat teeth are not subject to much wear or breakage and that comparative age is best determined by degree of development of the attachments for muscles and by the stage reached in the effacement of sutures than by degree of wear shown by the teeth.

With respect to sex, the skulls of males are significantly larger, longer, and more sharply ridged than those of females of the same age. These results agree with those of Grinnell and Dixon (1924) who found that male bobcats in California were roughly one-fourth larger than females. Samson (1979) reported that nine measurements useful in distinguishing the 11 subspecies of *F. rufus* showed no clear sexual dimorphism and he combined sexes for purposes of making phenetic comparisons among the subspecies. To the contrary, our data, together with the conclusions of Grinnell and Dixon (1924), strongly suggest the sexes should be treated separately in studies of geographic variation. Combining sexes for purposes of geographic comparisons could produce erroneous results.

With respect to individual variation in cranial characters, bobcats from the south-central United States seem to be slightly more variable than those from other geographic regions. Long (1968) reported that *F. rufus* from Wyoming had CV's ranging from 3.45 (greatest skull length) to 5.96 (interorbital breadth). The Robertson-Madison County sample showed a much wider range of values, with 16 of the 26 measurements having CV's larger than the upper limit reported by Long (1968).

Geographic Variation

The trend of geographic variation in cranial characteristics of bobcats from the study area, considering both univariate and multivariate analyses, may be summarized as follows: 1) bobcats from the eastern deciduous forests of Louisiana and Arkansas have small rounded skulls; 2) progressing westward into Oklahoma and Texas skulls increase in size so that bobcats from this region are medium to large in cranial measurements; and 3) continuing westward across the Continental Divide skulls decrease in size and the smallest bobcats occur in this portion of the study area.

The region of greatest phenetic divergence is across the Continental Divide in New Mexico. Specimens from west of the Divide are significantly smaller in most measurements than those from east of the Divide. There is a lack of distinct separation among populations in most other geographic areas and intergradation appears to be evenly progressive instead of step-like. A broad zone of intergradation exists between bobcats of intermediate and large size, which occur in Oklahoma and central Texas, and the smaller bobcats found in Arkansas and Louisiana. Unlike the specimens from New Mexico, which display a step-like break associated with a physiographic barrier (Continental Divide), the individuals from the eastern portion of the study area seem to respond to major vegetative types, with large- to medium-sized bobcats having evolved in the more open habitats and smaller bobcats in the forested situations. The zone of intergradation between these two size groups corresponds to the broad ecotone created by the transition from the broadleaf and pine forests of the eastern United States and the prairie habitats of central Texas and Oklahoma.

The variational pattern described is understandable in light of the continuous and broad distribution of bobcats. The degree and magnitude of geographic variation probably results from selective pressures exerted by the ecological conditions characteristic of the most distinctive habitats that bobcats occupy. However, the complex array of environmental pressures that have produced the observed variational patterns cannot be individually dissected given the information base presently available.

Subspecies

We find little justification for recognizing more than one subspecies of the bobcat in Texas. Although regional trends are evident in the size and shape of bobcat skulls over the state, there are no geographic regions where populations are significantly distinctive and strongly demarked from populations in nearby areas by sharp phenetic breaks indicative of reduced gene flow. Therefore, we refer all populations from Texas examined in this study to the taxon *F. r. texensis* (Merriam).

The western boundary of *F. r. texensis* corresponds with the location of the Continental Divide in New Mexico. The most distinctive bobcats we examined are those from west of the Continental Divide in New Mexico and Arizona, and to this group the trinomial *F. r. baileyi* (Merriam) applies. None of the Texas bobcats we studied can be appropriately assigned to the latter, although Hall (1981:1053) previously mapped the Panhandle and Trans-Pecos portions of the state as occurring within its range. Specimens from eastern New Mexico (samples 59 and 62) are indistinguishable to us from those of *F. r. texensis* in western Texas.

Our reference samples of *F. r. floridanus* from Florida and Georgia are well differentiated by their smaller size from Texas samples of *F. r. texensis.* Lowery (1974:470) and Hall (1981:1053) referred specimens from eastern Louisiana and Arkansas to *F. r. floridanus.* Our analysis, however, suggests that specimens from these states represent intergrades between *F. r. texensis* and *F. r. floridanus.* Because their overall cranial characteristics resemble the former subspecies more than the latter, we have tentatively referred them to the subspecies *F. r. texensis.* Bobcats from east of the Mississippi River in Louisiana (sample 49) are especially like *F. r. floridanus,* suggesting this river may form an appropriate boundary for this subspecies.

The taxonomic assignment of material from Oklahoma and Arkansas to *F. r. texensis* must be considered tentative because we did not examine specimens of the subspecies *F. r. rufus*, to which Hall (1981:1053) referred specimens from eastern Oklahoma and western Arkansas. Our analysis reveals that samples from central Oklahoma (56-58) are virtually indistinguishable from samples of *F. r. texensis* from Texas and that specimens from southeastern Oklahoma (55) and western Arkansas (52-54) are phenetically close to Louisiana samples of the same subspecies.

Early authors (Baird, 1858; Merriam, 1890) stressed the importance of coloration in recognizing subspecies and varieties of the bobcat. Although we did not analyze pelage coloration quantitatively, general color descriptions and comments were noted, particularly among specimens housed in the United States Museum of Natural History. Considerable color variation was evident in pelts from the same locality, and this seemed to correlate with age, season of year, and degree of pelage wear. Pelage color often differed substantially among specimens from nearby localities, whereas other individuals from widely removed localities were identical in color. For these reasons, pelage coloration was considered unsuitable as a taxonomic character for bobcats. Grinnell and Dixon (1924) and Peterson and Downing (1952) reached similar conclusions for the geographic areas in which they studied bobcats.

Samson (1979) used cranial measurements to make a morphometric comparison of the 11 recognized subspecies of *F. rufus* as listed by Hall and Kelson (1959). However, Samson used a statistical approach (stepwise discriminant analysis) in analyzing his data that requires an *a priori* assignment of specimens to groups (in Samson's case, subspecies). This technique maximizes the detection of morphological separation among groups, and it is not surprising that the subspecies of *F. rufus* could be discriminated from one another using this approach. More conservative multivariate techniques (cluster analysis and principal components analysis), requiring no *a priori* assumptions regarding the data, were used in this study to provide a representation of the distances among samples. Use of these more appropriate and conservative techniques did not produce results consistent with the existing taxonomic arrangement for bobcats in the study area. Therefore, we doubt the validity of Samson's conclusions concerning bobcat subspecies and suspect that there are far fewer valid intraspecific taxa than are currently recognized.

Management and Legal Implications

In 1979, Defenders of Wildlife filed suit in U.S. District Court to prohibit the export of pelts from certain states (including all those in the study area) on the grounds that available data were not adequate to define population trends in certain subspecies and geographic areas (Defenders of Wildlife, Inc., *vs* Endangered Species Scientific Authority *et al.*, Civil Action no. 79-3060, U.S. District Court for the District of Columbia, 12 December 1979). The court dismissed the plaintiff's claims as to Arkansas, Louisiana, and Oklahoma, but enjoined export of bobcat pelts from New Mexico and the High Plains of Texas on the grounds that this geographic area roughly corresponds to the range of *Felis rufus baileyi* and that export from that area would threaten the survival of *baileyi* as a subspecies (Memorandum Opinion, p. 7 in the transcript on the hearing in District Court). Our analysis reveals that bobcats in Texas belong to a single subspecies, *F. r. texensis*, and that the threatened subspecies, *F. r. baileyi*, is restricted to the region west of the Continental Divide in New Mexico and Arizona. Therefore, there seems to be little justification for prohibiting the export of bobcat pelts collected in Texas unless it can be demonstrated that the survival of *F. r. texensis* would be threatened by such activity.

Synopsis

Felis rufus texensis (J. A. Allen)

1829. *Felis maculata* Horsfield and Vigors, Zool. Jour., 4:381, pl. 13, type from Mexico. Not *Felis (Lynx) vulgaris maculatus* Kerr, 1792.

1895. *Lynx texensis* J. A. Allen, Bull Amer. Mus. Nat. Hist., 7:188, based on the description of a bobcat by Audubon and Bachman, The viviparous quadrupeds of North America, 2:293, 1851.

1897. *Lynx rufus texensis* Mearns, Preliminary diagnoses of new mammals of the genera *Lynx, Urocyon, Spilogale*, and *Mephitis*, from the Mexican boundary line, p. 2, 12 January 1897 (preprint of Proc. U.S. Nat. Mus., 20:458, 24 December 1897).

Holotype.—None designated; two syntypes, one of which is figured (Plate XCII), were described by Audubon and Bachman (see synonomy above); they are from the vicinity of Castroville, headwaters of Medina River, Medina Co., Texas.

Distribution.—New Mexico east of the Continental Divide; throughout Texas, Oklahoma, Arkansas, and Louisiana west of the Mississippi River.

Diagnosis.—A medium-sized, reddish brown or grayish subspecies of *F. rufus* characterized by a large deep skull with a relatively narrow braincase, medium-sized auditory bullae, and relatively large canine teeth.

Comparisons.—For a comparison with *F. r. baileyi*, see account of that subspecies. From *F. r. floridanus*, the subspecies *texensis* differs in being larger in overall size, with a more rounded and higher skull (as reflected in the measurements depth of cranium and height of occipital bone).

Measurements.—The following are mean values (in mm) of 23 cranial and three mandibular measurements for seven males (sample 8) and 11 females (sample 35) of this subspecies from central Texas (mean values for females are in parentheses and follow those of males): greatest length of skull, 129.59 (121.40); zygomatic breadth, 92.31 (83.76); squamosal breadth, 54.63 (52.52); postorbital constriction, 35.48 (36.84); length of nasals, 26.36 (24.23); interorbital constriction, 23.43 (21.43); diameter of upper canine, 7.69 (6.46); length of upper fourth premolar, 14.10 (12.95); width of rostrum, 33.35 (30.55); premolar-molar toothrow length, 25.27 (23.63); width across maxillary toothrow, 38.78 (35.78); maxillary toothrow length, 37.45 (36.50); palatilar length, 48.90 (46.05); cranial height, 44.54 (42.24); mastoid breadth, 56.28 (52.21); basilar length, 108.53 (98.98); condylobasal length, 118.69 (111.42); post-palatal length, 60.38 (54.35); nasal-frontal length, 57.78 (53.66); greatest length of auditory bullae, 31.65 (28.92); width of auditory bullae, 15.22 (14.90); diameter of foramen magnum, 13.30 (13.22); height of occipital bone, 21.75 (19.49); mandibular length, 76.36 (70.34); coronoid height, 38.75 (34.19); mandibular diastema, 16.64 (15.29).

Samples.—Comprised of specimens in our study from the following samples (Table 2 and Fig. 1): *New Mexico*: 59, 62; *Oklahoma*: 55-58; *Arkansas*: 51-54; *Louisiana*: 47, 48, 50; *Texas* (males): 1-25; (females): 26-46. Included, in addition, are the following specimens deposited at The Museum, Texas Tech University: *Texas*: Armstrong Co.: 29 mi SE Claude, 1; Brewster Co.: Arnette Ranch, 20 mi S Marathon, 8; Crosby Co.: near Crosbyton, 2; Dickens Co.: 6 mi N, 16 mi E Dickens, 1; Foard Co.: no specific locality; Garza Co.: 10 mi N Post, 1; 4 mi N Post, 1; Hardeman Co.: near Lazare, 1; Haskell Co.: 25 mi SE Haskell, 1; Jeff Davis Co.: 13 mi NW Marfa, 1; 9.5 km E, 9 km N Ft. Davis, 1; Lubbock Co.: no specific locality, 1; 4.8 mi NW Lubbock, Hwy 82, 1; McCulloch Co.: 12.6 mi S Winchell, 1; Motley Co.: 1 mi E Matador, 1; Pecos Co.: 16.4 mi N Sheffield, 2; Stephens Co.: 13 mi NW Breckenridge, 1.

Felis rufus baileyi (Merriam)

1890. *Lynx baileyi* Merriam, N. Amer. Fauna, 3:79.
1901. *[Lynx rufus] baileyi*, Elliot, Field Columbia Mus. Publ. 45, Zool. Ser., 2:297.
1905. *Felis rufa baileyi*, Elliot, Field Columbia Mus. Publ. 105, Zool. Ser., 6:372.
1978. *Felis rufus baileyi*, Anderson, Bull. Amer. Mus. Nat. Hist., 148:388.

Holotype.—U.S. National Museum, Biological Survey Collection, no. 5214/5909; from Moccasin Spring, north of Colorado River, Coconino Co., Arizona. Type examined.

Distribution.—Arizona and New Mexico west of the Continental Divide in the study area; also known from southern Utah and Nevada as well as the southeastern arid region of California (Hall, 1981:1053).

Diagnosis.—A pale-colored (yellowish gray in winter and pale yellowish in summer) subspecies of *F. rufus* characterized by a short, narrow, and shallow skull with a large braincase, well rounded auditory bullae, and relatively small canines.

Comparisons.—Compared to *F. r. texensis*, the subspecies *baileyi* averages smaller in skull length and width (as reflected by greatest length of skull, zygomatic breadth, and mastoid breadth), but is larger in width of the braincase (as reflected by squamosal breadth and postorbital constriction) and width of the auditory bullae.

Felis rufus baileyi is similar in overall size to *F. r. floridanus*, but its skull is slightly shorter, flatter, and more angular with wider measurements in the braincase region (as reflected by squamosal breadth and mastoid breadth), narrower rostral measurements (as reflected by width of rostrum, width across maxillary toothrow, and zygomatic breadth), and a shorter cranial height and height of the occipital bone.

Measurements.—The following are mean values (in mm) of 23 cranial and three mandibular measurements for 43 males and 18 females of this subspecies from sample 60 in southwestern New Mexico (mean values for females are in parentheses and follow those of males): greatest length of skull, 123.55 (117.80);

zygomatic breadth, 86.92 (84.26); squamosal breadth, 54.50 (54.12); postorbital constriction, 38.70 (38.86); length of nasals, 25.29 (23.44); interorbital constriction, 23.56 (22.69); diameter of upper canine, 6.98 (6.58); length of upper fourth premolar, 13.53 (13.23); width of rostrum, 30.88 (29.61); premolar-molar toothrow length, 24.31 (23.70); width across maxillary toothrow, 36.68 (35.26); maxillary toothrow length, 37.73 (36.20); palatilar length, 46.78 (44.88); cranial height, 42.38 (41.03); mastoid breadth, 54.08 (52.79); basilar length, 101.51 (96.68); condylobasal length, 112.32 (107.24); post-palatal length, 55.42 (52.13); nasal-frontal length, 56.42 (53.55); greatest length of auditory bullae, 30.13 (29.16); width of auditory bullae, 15.34 (15.25); diameter of foramen magnum, 13.92 (14.35); height of occipital bone, 19.63 (17.99); mandibular length, 73.02 (69.77); coronoid height, 35.94 (33.28); mandibular diastema, 16.31 (15.81).

Samples.—Comprised of specimens in our study from the following samples (Table 1): *New Mexico*: 60, 61; *Arizona*: 63, 64.

Felis rufus floridanus (Rafinesque)

1817. *Lynx floridanus* Rafinesque, Amer. Monthly Mag., 2(1):46.
1858. *Lynx rufus* var. *floridanus*, Baird, Mammals in Repts. Expl. Surv. . . , 8(1):91.

Holotype.—Philadelphia Acad. Sci., no. 12763; from Biscayne Bay, 6 mi. S Miami, Dade Co., Florida. Type not examined.

Distribution.—Confined to the southeastern United States, east of the region of concern for this study.

Diagnosis.—A small, dark subspecies of *F. rufus* characterized by a short, narrow, relatively deep skull with a small braincase, narrow auditory bullae, and relatively large canine teeth.

Comparisons.—For comparison with *F. r. baileyi* and *F. r. texensis*, see accounts of those subspecies.

Measurements.—The following are mean values (in mm) for 23 cranial and three mandibular measurements of 7 male *F. r. floridanus* (sample 66) from Georgia: greatest length of skull, 123.76; zygomatic breadth, 85.46; squamosal breadth, 52.56; postorbital constriction, 37.05; length of nasals, 26.56; interorbital constriction, 21.62; diameter upper canine, 7.01; length of upper fourth premolar, 13.21; width of rostrum, 31.29; premolar-molar toothrow length, 23.74; width across maxillary toothrow, 36.38; maxillary toothrow length, 37.13; palatilar length, 46.89; cranial height, 43.26; mastoid breadth, 52.98; basilar length, 101.26; condylobasal length, 111.67; post-palatal length, 54.74; nasal-frontal length, 54.94; greatest length of auditory bullae, 30.52; width of auditory bullae, 14.86; diameter of foramen magnum, 13.91; height of occipital bone, 19.66; mandibular length, 72.41; coronoid height, 35.64; mandibular diastema, 16.57.

Samples.—Comprised of specimens in our study from the following samples (Table 1): ***Florida***: 65; *Georgia*: 66, 67; ***Louisiana***: 49.

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