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TAXONOMIC STATUS AND BIOGEOGRAPHY OF THE SOUTHERN BOG LEMMING, *SYNAPTOMYS COOPERI*, ON THE CENTRAL GREAT PLAINS

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We assessed geographic and nongeographic variation among populations of the southern bog lemming (*Synaptomys cooperi*) in Arkansas, Iowa, Illinois, Kansas, Missouri, Nebraska, and South Dakota based on morphological data. Univariate and multivariate analyses of 15 cranial characters revealed no consistent sexual dimorphism. Geographic variation in cranial morphology of adults varied clinally, with individuals increasing in size from north to south and east to west. The largest individuals overall were from southwestern Kansas (*S. c. paludis*) and southwestern Nebraska (*S. c. relictus*), and the smallest individuals were from populations in eastern Illinois (*S. c. gossii*). We found only minor steps in clinal variation of cranial morphology, which may be attributed to periodic or recent isolation. No individuals of *S. c. paludis* and *S. c. relictus* have been collected since 1946 and 1968, respectively, and these taxa may be extinct. Because of the paucity of specimens, taxonomic conclusions as to the intraspecific relationships of populations are speculative. We, therefore, recommend retention of the currently recognized subspecies *S. c. gossii*, *S. c. paludis*, and *S. c. relictus* until genetic characters can be analyzed.

Key words: *Synaptomys cooperi*, cranial morphometrics, taxonomy, biogeography, Great Plains

The southern bog lemming, *Synaptomys cooperi* (Rodentia: Muridae, Arvicolinae—Musser and Carleton, 1993), is endemic to North America. It is an eastern species (Armstrong et al., 1986) that has a spotty distribution and often unpredictable occurrence in the northeastern United States and southeastern Canada west to ca. 100°W on the Great Plains (Hall, 1981; Linzey, 1983; Musser and Carleton, 1993). Two of the nominal subspecies that occur in the Great Plains Physiographic Province, *S. c. paludis* and *S. c. relictus*, are believed to be biogeographic relicts left behind when the range of the species retreated northward and eastward sometime after the Pleistocene. These relict populations persisted where marshes and artesian springs provided suitable habitat (Hibbard and Rinker, 1942; Jones, 1958; Wetzel, 1955).

Hibbard and Rinker (1942) named *S. c. paludis* from Meade County State Park (=Meade State Lake) in southwestern Kansas. In comparison with eight adult *S. c. gossii* from eastern Kansas, many individuals had darker pelage and larger cranial and external measurements. Additionally, in 10 of the 19 skulls available for examination, two grooves, rather than the usual one, were present on the anterior surface of the upper incisors.

Jones (1954) caught one southern bog lemming (that he initially assigned to the subspecies *S. c. gossii*) at Rock Creek State Fish Hatchery in Dundy Co., southwestern Nebraska, in 1952. After three additional specimens were captured in 1956 at the same locality, Jones (1958) named the subspecies *S. c. relictus*. Most external and cranial characters of two specimens (an old

adult female and an adult female) were intermediate between *S. c. paludis* and *S. c. gossii.* He did not mention grooves on the upper incisors.

In their taxonomic revisions of *Synaptomys* in North America, both Howell (1927) and Wetzel (1955) showed that cranial size in *S. cooperi* varies clinally (as defined by Mayr and Ashlock, 1991) in the reverse of Bergmann's Rule, with dimensions increasing from north to south and from east to west throughout the species' range. Subsequent paleontological studies produced similar findings (Guilday et al., 1978; Semken, 1984). Wetzel (1955:18) observed that *S. c. paludis* was the largest subspecies in North America, being "distinctly larger (by two standard errors) than *S. c. gossii*" from eastern Kansas in characters other than "length of tail, length of maxillary toothrow, length of incisive foramen, and nasal width." Wetzel (1955:18), thus, agreed with Hibbard and Rinker (1942) that *S. c. paludis* was a valid subspecies, albeit only a "conservative or localized relic race" of the large prairie form, *S. c. gossii,* to the east. As Wetzel (1955:18) explained, "A gradation from Meade County to eastern Kansas would perhaps be observable could the geographical gap be spanned by series of specimens." Because *S. c. relictus* was described subsequent to the review by Wetzel (1955), it has never been evaluated taxonomically. In addition, populations of *S. c. gossii* in northcentral Kansas have been only recently discovered (Clark et al., 1986; Welker and Choate, 1994) and did not exist or were unknown to Jones (1954, 1958) and Wetzel (1955).

We used univariate and multivariate statistical techniques to investigate both geographic and nongeographic variation among populations of *S. cooperi* on the Great Plains based on cranial morphological data. Also, we examined skulls for the presence of grooves on the upper incisors and assessed differences among taxa in pelage coloration. We hypothesized that the elimination of marshy corridors across the short-

and mixed-grass prairie in western Kansas and Nebraska (Küchler, 1964) produced periodic barriers to gene flow among populations of *S. cooperi* on the Great Plains, thus enabling slight divergence of the isolated populations.

MATERIALS AND METHODS

We examined 911 specimens of *S. cooperi* from Arkansas, Illinois, Iowa, Kansas, Minnesota, Missouri, Nebraska, South Dakota, and Wisconsin (Appendix I). Because *S. cooperi,* like many other arvicoline rodents, possesses hypsodont dentition (Miller, 1896; Semkin, 1984), traditional methods used to estimate age of other murid rodents are inappropriate (Anderson, 1959; Carleton, 1985; Phillips, 1969). We assigned specimens to one of three age classes based on criteria similar to those described by Carleton (1985), Choate and Williams (1978), and Wetzel (1955), but we only used two age classes because of small samples for juveniles. Adults of *S. cooperi* can be distinguished easily from subadults by the fusion, or near fusion, of the interorbital ridges in the former and a wide separation in the latter (Wetzel, 1955). We assigned specimens that possessed many (but not all) features of adults to the subadult age class, thus ensuring that the adult age class was "pure."

We selected 15 mensural characters, as defined by DeBlase and Martin (1981), Howell (1927), Wetzel (1955), and Wilson (1994), because of their taxonomic utility and repeatability: width of upper incisors, width of nasal bone, length of nasal bone, length of rostrum (as described by Hooper, 1952), breadth of rostrum, length of incisive foramen, total length of toothrow, length of maxillary toothrow, zygomatic breadth, breadth of braincase, mastoidal breadth, interorbital breadth, condylobasilar length, greatest length of skull, and palatofrontal depth. We recorded measurements to the nearest 0.01 mm with digital calipers. We did not record external measurements from labels of study skins because these measurements often are unreliable.

We used the PC version (Release 6.03 Edition) of the Statistical Analysis System (SAS Institute, Inc., 1988*a,* 1988*b*) to analyze nongeographic and geographic variation within and among samples (localities). We calculated percentage contribution to the total variance by gender, age (adult, subadult), gender-by-age interaction, and

error categories from sums-of-squares estimates (VARCOMP procedure), as described by Leamy (1983) and Straney (1978), using all adults and subadults from all localities combined. We entered gender first and then age because gender is a fixed factor (Leamy, 1983). We used a one-way analysis of variance (ANOVA) to determine if each of the 15 morphometric characters differed significantly ($P \leq 0.05$) between subadult and adult age classes. We used an additional one-way ANOVA to ascertain whether the genders differed for each character within samples, with age being the main effect.

Phillips (1969) noted that rapid turnover in populations of arvicoline rodents leads to a disproportionate number of subadults in museum collections. This is evident for *S. cooperi*, particularly for specimens captured in Douglas Co., Kansas, in the late 1960s. Consequently, sample sizes for adults were small in several populations used in this study. We detected only minimal sexual dimorphism; thus, we pooled males, females, and individuals of unknown gender from geographically adjacent localities to maximize sample sizes for statistical analyses (Fig. 1). Pooled samples were: *Sample A*—ILLINOIS: McLean, Piatt, and Vermilion counties. *Sample B*—ILLINOIS: Alexander, Hardin, Pope, and Union counties. *Sample C*—ILLINOIS: Fulton, Hancock, Mason, McDonough, Morgan, and Pike counties. *Sample D*—MISSOURI: St. Charles and St. Louis counties. *Sample E*—ARKANSAS: Craighead, Greene, Lawrence, Poinsett, Randolph, St. Francis, and Woodruff counties; MISSOURI: Stoddard County. *Sample F*—MISSOURI: Audrain, Boone, Johnson, Pettis, Ralls, and Saline counties. *Sample G*—IOWA: Appanoose, Davis, and Henry counties; MISSOURI: Adair, Grundy, Knox, Macon, Mercer, Putnam, Schuyler, and Sullivan counties. *Sample H*—IOWA: Fremont, Mills, and Page counties; MISSOURI: Nodaway County. *Sample I*—KANSAS: Atchison, Brown, Jefferson, Leavenworth, Nemaha, Pottawatomie, and Washington counties; NEBRASKA: Gage and Richardson counties. *Sample J*—KANSAS: Anderson, Douglas, Osage, and Woodson counties. *Sample K*—KANSAS: Jewell, Lincoln, Osborne, Rooks, and Russell counties. *Sample L*—KANSAS: Meade County. *Sample M*—NEBRASKA: Dundy County. *Sample N*—NEBRASKA: Holt County; SOUTH DAKOTA: Gregory County. Based on range maps published by Hall (1981), *S. c. gossii* is represented by samples A through K and sample N, *S. c. paludis* by sample L, and *S. c. relictus* by sample M.

We used the UNIVARIATE procedure of SAS to compute descriptive statistics for adult individuals within each sample and a one-way ANOVA to test for morphological variation among sample (locality) means. Tukey's studentized range test (HSD), the tukey option of the General Linear Models Procedure (GLM) of SAS, identified maximally nonsignificant subsets for each morphometric variable within samples. The SAS procedure CANDISC performed canonical variates (CVA) analysis on the 15 cranial measurements. We calculated and constructed confidence ellipses (95%) around the population means (centroids) as described by Owen and Chmielewski (1985). We tested normality of data with the Shapiro-Wilk statistic (W). We relied primarily on multivariate tests because variables used in morphometric studies of variation within and among populations are inferred to be highly correlated (Willig and Owen, 1987; Willig et al., 1986).

RESULTS

Nongeographic variation.—When all subadult and adult individuals were included, variance partitioning indicated that, for 12 of the 15 cranial characters (except width of upper incisors, length of maxillary toothrow, and breadth of braincase), age effects accounted for most of the explained variation, averaging ca. 11%. Gender accounted for ca. 2% of the explained variation, whereas gender by age interaction contributed little (0.7%) to the total variation of any variable. Thus, within the explainable variation, age had more effect on the total variation than gender. The most important category was error (unexplainable variation), averaging 86%. The low values for age effect could be attributable to the fact that we kept the adult age class "pure" and did not measure many subadults. Nevertheless, a one-way ANOVA revealed that subadults contributed a statistically significant ($P < 0.05$) amount of intraclass size variation for each cranial character except length of maxillary toothrow ($P = 0.08$) and

breadth of braincase ($P = 0.38$). Therefore, we excluded subadults from subsequent statistical analyses.

We compared the extent of individual and secondary sexual variation in samples B, J, and L. A one-way ANOVA revealed that only two characters (greatest length of skull, sample L; width of nasal bone, sample B) showed a significant difference between genders. For both characters, males were larger than females. For sample B, the significant difference between genders could have resulted from relatively small samples. We found no significant difference between genders for any character in sample J; however, females averaged slightly larger than males in all characters except width of upper incisors, breadth of rostrum, total length of toothrow, mastoidal breadth, condylobasilar length, and greatest length of skull. Because only two of the 15 measurements revealed secondary sexual variation, we pooled genders to increase sample sizes for subsequent analyses. Wetzel (1955) and Robinson (1981), likewise, found little or no consistent secondary sexual variation in *S. cooperi*. However, Guilday (1951) documented sexual dimorphism in the pelvic girdles of *Microtus pennsylvanicus* and suggested that similar results seemed plausible for pelvic girdles of *Synaptomys*.

Geographic variation.—Descriptive statistics of adult *S. cooperi* from all samples are similar to values published by previous researchers (Hibbard and Rinker, 1942; Jones 1958; Wetzel 1955; Table 1). The ANOVA for geographic variation among samples of adult *S. cooperi* revealed a significant difference for each cranial character ($P < 0.01$ for all characters; Table 1). A Tukey multiple-range test revealed that all characters differed significantly among samples, but nonsignificant subsets overlapped broadly (Table 1).

Visual comparison of sample means for cranial characters suggested a pattern of geographic variation similar to that reported by Howell (1927) and Wetzel (1955); cranial size gradually increased in clinal fash-

ion from north to south and from east to west (Fig. 1; Table 2). Similar results were found by Anderson (1959), Choate and Williams (1978), and Snell and Cunnison (1983) for species of *Microtus*. In general, *S. cooperi* from western portions of the geographic area (Kansas, Nebraska, and South Dakota) exhibited consistently larger cranial dimensions than *S. cooperi* from eastern portions (Illinois; Table 2). Southern bog lemmings with the largest overall cranial dimensions were in sample L (*S. c. paludis*), which averaged larger than other samples in 11 of 15 cranial characters. Individuals in sample M (*S. c. relictus*) were largest in the remaining four cranial characters (width of nasal bone, length of incisive foramen, total length of toothrow, and length of maxillary toothrow). The smallest lemmings were from Illinois (samples A, B, and C). Southern bog lemmings of intermediate size were from the other samples.

A comparison of sample means for cranial characters in populations at about the same longitude revealed that cranial dimensions generally were larger in the south than in the north, although those differences often were not significant. For example, sample E averaged larger than sample C in all measurements, sample F averaged larger than G in every measurement except interorbital breadth and breadth of braincase, sample L averaged larger than sample M except in width of nasal bone, length of incisive foramen, total length of toothrow, and length of maxillary toothrow, and sample K averaged larger than sample N in all characters except breadth of rostrum, length of incisive foramen, zygomatic breadth, and mastoidal breadth (Fig. 1, Table 1). However, sample B averaged larger than sample A in only six (length of incisive foramen, interorbital breadth, breadth of braincase, mastoidal breadth, condylobasilar length, and greatest length of skull) cranial characters (Fig. 1, Table 1).

The first four canonical variates accounted for >80% (48.11, 15.92, 8.38, and 7.59%, respectively) of the total variation.

The influence of each variable on the total variation of the first two canonical vectors is listed in Table 2. Canonical vector 1 was primarily a size factor, with four negative and 11 positive character loadings. Length of maxillary toothrow, length of nasal bone, and breadth of rostrum had the greatest loadings. Canonical vector 2 was mainly a

TABLE 1.—*Mean (above) and standard deviation and sample size (in parentheses below) for cranial measurements (in mm) for samples of adult* Synaptomys cooperi. *All F-values indicate significance (P < 0.01). Means with the same superscript do not differ significantly (P > 0.05) as determined by Tukey studentized range test (HSD).*

Character and (F-value)	Samples					
Width of upper incisors	L[a]	M[a,b]	K[a,b]	F[a,b]	N[a,b]	J[b]
(F = 9.14)	4.55	4.34	4.18	4.17	4.16	4.16
	0.04 (12)	0.16 (2)	0.21 (2)	0.03 (9)	0.09 (3)	0.03 (28)
Width of nasal bone	M[a]	L[a]	K[a]	J[a]	N[a]	D[a]
(F = 5.32)	4.01	3.90	3.88	3.83	3.80	3.77
	0.12 (2)	0.03 (12)	0.01 (2)	0.03 (28)	0.14 (3)	0.03 (23)
Length of nasal bone	L[a]	K[a,b]	I[a,b,c]	M[a,b,c,d]	J[b,c,d]	H[b,c,d]
(F = 11.47)	8.81	8.57	8.11	8.10	8.05	7.98
	0.09 (11)	0.10 (2)	0.05 (19)	0.02 (2)	0.07 (28)	0.12 (8)
Length of rostrum	L[a]	K[a,b]	M[a,b,c]	N[a,b,c]	I[b,c]	J[b,c]
(F = 8.22)	10.37	10.19	9.89	9.74	9.73	9.70
	0.06 (11)	0.18 (2)	0.13 (2)	0.23 (3)	0.05 (19)	0.09 (28)
Breadth of rostrum	L[a]	N[a,b]	E[a,b]	J[a,b]	I[a,b]	K[b]
(F = 10.22)	6.61	6.29	6.22	6.21	6.18	6.18
	0.06 (12)	0.04 (3)	0.06 (12)	0.04 (28)	0.03 (19)	0.08 (2)
Length of incisive	M[a]	I[a]	N[a]	J[a]	F[a]	E[a]
foramen (F = 2.88)	5.59	5.57	5.53	5.50	5.48	5.47
	0.11 (2)	0.04 (19)	0.16 (3)	0.06 (28)	0.02 (11)	0.05 (11)
Total length of toothrow	M[a]	L[a,b]	K[a,b,c]	N[a,b,c]	I[a,b,c]	J[a,b,c]
(F = 14.99)	18.68	18.66	18.31	18.18	18.05	18.04
	0.13 (2)	0.09 (12)	0.13 (2)	0.07 (3)	0.10 (18)	0.11 (27)
Length of maxillary	M[a]	L[a,b]	K[a,b,c]	E[b,c]	N[b,c,d]	J[c,d,e]
toothrow (F = 16.73)	8.60	8.20	7.94	7.91	7.89	7.77
	0.09 (2)	0.06 (12)	0.06 (2)	0.05 (13)	0.02 (3)	0.04 (28)
Zygomatic breadth	L[a]	N[a,b]	M[a,b,c]	D[a,b,c]	I[a,b,c]	F[a,b,c]
(F = 8.47)	18.72	18.17	17.98	17.92	17.75	17.73
	0.12 (11)	0.22 (3)	0.13 (2)	0.08 (23)	0.10 (18)	0.22 (10)
Interorbital breadth	L[a]	E[a,b]	K[a,b]	J[a,b]	I[a,b]	G[a,b]
(F = 3.36)	3.54	3.49	3.45	3.44	3.41	3.40
	0.02 (9)	0.04 (12)	0.10 (2)	0.02 (27)	0.02 (19)	0.02 (18)
Breadth of braincase	L[a]	J[a,b]	M[a,b,c]	K[a,b,c]	N[a,b,c]	I[a,b,c]
(F = 5.54)	12.21	12.00	12.00	11.97	11.95	11.93
	0.09 (10)	0.04 (25)	0.13 (2)	0.22 (2)	0.09 (3)	0.08 (17)
Mastoidal breadth	L[a]	E[a,b]	N[a,b]	K[a,b]	M[a,b]	D[a,b]
(F = 3.95)	14.35	14.04	14.03	13.98	13.95	13.93
	0.15 (12)	0.06 (11)	0.16 (3)	0.02 (2)	0.20 (2)	0.06 (23)
Condylobasilar length	L[a]	K[a,b]	N[a,b,c]	I[a,b,c,d]	M[a,b,c,d,e]	J[a,b,c,d,e]
(F = 13.33)	28.10	27.67	27.19	27.10	27.09	27.03
	0.13 (12)	0.27 (2)	0.50 (3)	0.13 (18)	0.19 (2)	0.13 (25)
Greatest length of skull	L[a]	K[a,b]	N[a,b,c]	M[b,c,d]	I[b,c,d]	J[b,c,d]
(F = 15.29)	30.59	30.08	29.56	29.51	29.38	29.26
	0.14 (12)	0.41 (6)	0.44 (3)	0.25 (2)	0.15 (18)	0.19 (24)
Palatofrontal depth	L[a]	M[a,b]	K[a,b,c]	J[a,b,c]	N[a,b,c,d]	D[a,b,c,d]
(F = 11.77)	11.39	11.35	11.32	11.10	11.04	10.97
	0.06 (11)	0.09 (2)	0.16 (2)	0.10 (20)	0.09 (3)	0.04 (22)

shape factor, with five negative and 10 positive character loadings (greatest length of skull and total length of toothrow had the greatest loadings). All four MANOVA test criteria (Wilk's Lambda, Pillai's Trace, Hotelling-Lawly Trace, and Roy's Greatest Root) indicated significant ($P < 0.001$) morphological differences among samples. However, these differences were not reflected in the graphic depiction of the data (Fig. 2) as expressed in confidence ellipses plotted along the first two canonical vectors. Ellipses could not be drawn for samples H, K, M, and N because of small sample sizes

TABLE 1.—*Extended*

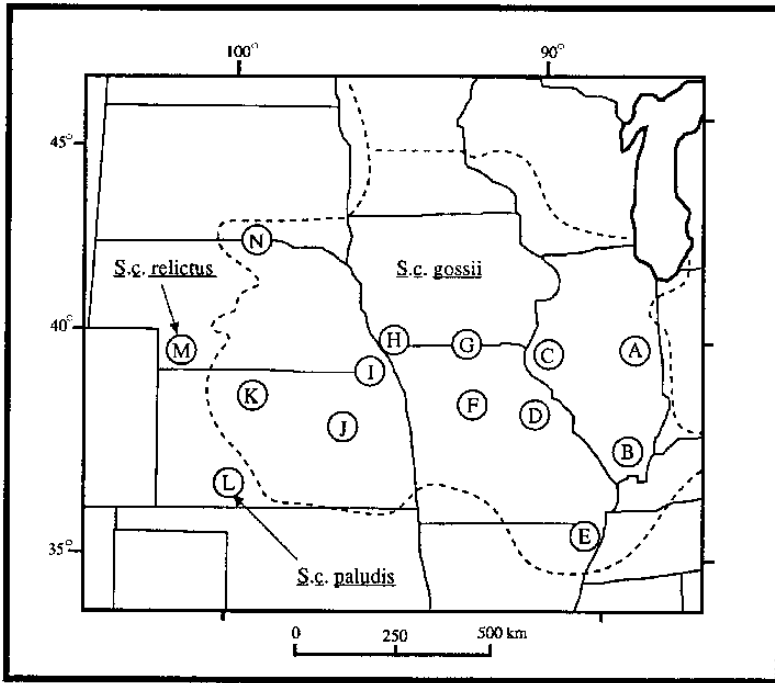| Samples							
E[b]	I[b]	D[b]	A[b]	H[b]	G[b]	B[b]	C[b]
4.11	4.09	4.09	4.01	4.00	3.99	3.97	3.89
0.05 (12)	0.04 (18)	0.04 (23)	0.04 (18)	0.05 (8)	0.04 (18)	0.02 (31)	0.08 (11)
A[a]	I[a]	F[a]	G[a,b]	H[a,b]	B[a,b]	E[a,b]	C[a,b]
3.72	3.70	3.70	3.63	3.61	3.57	3.56	3.55
0.04 (16)	0.03 (19)	0.06 (11)	0.05 (17)	0.04 (8)	0.03 (31)	0.06 (13)	0.06 (9)
N[b,c,d]	D[b,c,d]	E[b,c,d]	F[b,c,d]	A[b,c,d]	G[c,d]	B[d]	C[d]
7.97	7.96	7.91	7.83	7.81	7.77	7.68	7.52
0.12 (3)	0.07 (23)	0.05 (16)	0.09 (11)	0.06 (15)	0.07 (16)	0.05 (31)	0.06 (9)
D[b,c]	E[b,c]	F[b,c]	G[b,c]	A[b,c]	H[b,c]	B[b,c]	C[c]
9.68	9.64	9.55	9.49	9.47	9.40	9.35	9.18
0.07 (23)	0.08 (12)	0.10 (11)	0.07 (16)	0.08 (15)	0.13 (8)	0.05 (31)	0.06 (9)
F[b]	D[b]	G[b]	A[b]	M[b]	H[b]	B[b]	C[b]
6.17	6.16	6.06	5.99	5.96	5.95	5.95	5.85
0.07 (11)	0.03 (23)	0.04 (18)	0.04 (18)	0.13 (2)	0.06 (8)	0.03 (31)	0.07 (9)
L[a]	G[a]	D[a]	B[a]	K[a]	A[a,b]	C[a,b]	H[a,b]
5.43	5.41	5.37	5.37	5.35	5.28	5.18	5.15
0.06 (12)	0.07 (17)	0.04 (23)	0.04 (31)	0.06 (2)	0.06 (17)	0.07 (9)	0.08 (8)
E[a,b,c]	D[a,b,c]	F[a,b,c]	H[b,c,d]	G[b,c,d]	A[b,c,d]	C[b,c,d]	B[d]
18.02	17.91	17.78	17.51	17.51	17.46	17.42	17.18
0.07 (12)	0.06 (23)	0.17 (9)	0.17 (8)	0.08 (18)	0.09 (18)	0.14 (9)	0.06 (31)
I[c,d,e]	D[c,d,e]	H[c,d,e,f]	F[c,d,e,f,g]	C[c,d,e,f,g]	G[c,d,e,f,g]	A[c,d,e,f,g]	B[g]
7.76	7.75	7.74	7.65	7.57	7.55	7.48	7.32
0.06 (19)	0.06 (23)	0.08 (8)	0.06 (11)	0.04 (9)	0.04 (18)	0.02 (18)	0.03 (31)
K[a,b,c]	J[b,c]	E[b,c]	A[b,c]	G[b,c]	B[b,c]	C[c]	H[c]
17.73	17.67	17.65	17.39	17.34	17.27	16.91	16.91
0.34 (2)	0.15 (26)	0.10 (13)	0.11 (17)	0.09 (18)	0.08 (29)	0.21 (8)	0.16 (7)
C[a,b]	F[a,b]	D[a,b]	B[a,b]	A[a,b]	H[b]	N[b]	M[b]
3.40	3.37	3.36	3.34	3.28	3.27	3.26	3.23
0.08 (8)	0.04 (11)	0.03 (23)	0.02 (29)	0.03 (18)	0.04 (7)	0.06 (3)	0.16 (2)
D[a,b,c]	E[a,b,c]	C[a,b,c]	G[b,c]	B[b,c]	F[b,c]	H[b,c]	A[c]
11.87	11.84	11.73	11.71	11.70	11.67	11.61	11.59
0.07 (23)	0.12 (10)	0.13 (9)	0.06 (18)	0.04 (26)	0.07 (10)	0.15 (6)	0.04 (11)
J[a,b]	I[a,b]	F[a,b]	B[b]	A[b]	G[b]	C[b]	H[b]
13.91	13.90	13.84	13.66	13.66	13.61	13.52	13.38
0.09 (28)	0.08 (18)	0.13 (11)	0.07 (28)	0.09 (11)	0.09 (17)	0.18 (9)	0.13 (7)
D[b,c,d,e]	E[b,c,d,e]	F[b,c,d,e]	B[b,c,d,e]	G[b,c,d,e]	H[b,c,d,e]	C[e]	A[e]
26.71	26.65	26.57	26.02	26.01	25.99	25.65	25.62
0.11 (23)	0.10 (11)	0.22 (10)	0.11 (27)	0.13 (17)	0.34 (5)	0.21 (8)	0.14 (12)
E[b,c,d]	F[b,c,d]	D[b,c,d]	G[b,c,d]	B[b,c,d]	H[b,c,d]	C[d]	A[d]
29.14	29.07	29.05	28.32	28.30	28.23	27.89	27.87
0.14 (10)	0.26 (8)	0.11 (23)	0.16 (16)	0.11 (38)	0.38 (5)	0.24 (8)	0.09 (17)
I[b,c,d]	E[b,c,d]	F[b,c,d]	G[b,c,d]	A[b,c,d]	C[c,d]	B[d]	H[d]
10.90	10.85	10.75	10.73	10.60	10.51	10.44	10.25
0.06 (17)	0.09 (15)	0.03 (8)	0.06 (18)	0.05 (17)	0.17 (8)	0.04 (29)	0.05 (4)

FIG. 1.—Map showing geographic locations of pooled samples of *Synaptomys cooperi* used for statistical analyses. Letters correspond to samples identified in the Materials and Methods; specific locality information is in Appendix I. Map modified from Hall (1981).

(3, 2, 2, and 3, respectively); the centroids for these samples were plotted.

The first canonical vector separated sample L (*S. c. paludis*) from the remaining samples. However, the centroid for sample K was within the 95% confidence ellipsis of sample L. Canonical vector 2 revealed little information about geographic

TABLE 2.—*Percentage influence of each variable on the total variation of the first two canonical vectors plotted in Fig. 2.*

| Character	Canonical Coefficient	
	Vector 1 (48.11%)	Vector 2 (15.92%)
Width of upper incisors	0.063	0.041
Width of nasal bone	0.150	−0.348
Length of nasal bone	0.647	0.135
Length of rostrum	−0.126	0.143
Breadth of rostrum	0.603	0.304
Length of incisive foramen	0.018	0.111
Total length of toothrow	−0.565	−1.960
Length of maxillary toothrow	0.880	−0.486
Zygomatic breadth	−0.257	0.499
Interorbital breadth	0.106	0.010
Breadth of braincase	0.174	0.630
Mastoidal breadth	−0.476	−0.464
Condylobasilar length	0.163	0.011
Greatest length of skull	0.363	2.036
Palatofrontal depth	0.594	−0.405
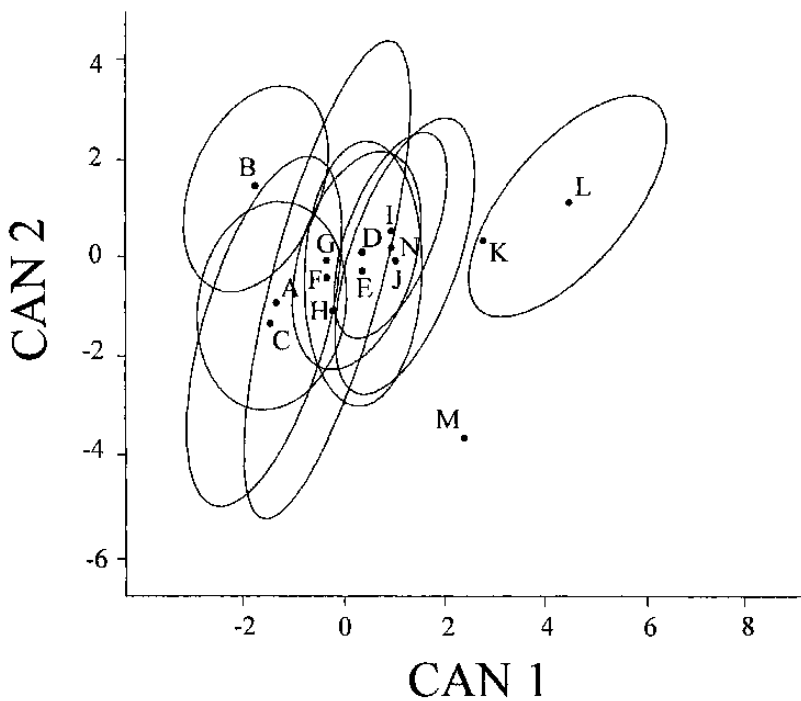
FIG. 2.—Plot of confidence ellipses using canonical variates of the first two canonical vectors for adult *Synaptomys cooperi* from pooled samples (Fig. 1). The centroid (mean value) for each group is indicated by a dot. Because of small samples, confidence ellipses for samples H, K, M, and N could not be calculated. See Fig. 1 and the Materials and Methods for identification of samples.

variation or subspecific relationships. The 95% confidence ellipses of samples A through J and N (*S. c. gossii*) overlapped appreciably, with sample B being somewhat distinct from the other samples. Clinal variation is apparent along canonical vector 1. The largest individuals (at the right in Fig. 2) represent populations from western Kansas and western Nebraska and the smallest individuals (at the left in Fig. 2) are from Illinois. Centroids positioned in the middle represent populations intermediate in size (Fig. 2).

Hibbard and Rinker (1942) observed that about one-half of all specimens of *S. c. paludis* available at that time possessed a faint, variably located, second groove on the anterior surface of the upper incisors. We found that the anterior surface of the upper incisors in several specimens of *S. c. gossii* was irregular, but only one specimen (MHP 30857, from St. Charles Co., Missouri) had

a recognizable, albeit faint, second groove. None of the specimens of *S. c. relictus* had a second groove.

Pelage coloration was as described by previous authors (Hibbard and Rinker, 1942; Jones, 1958). Coloration is darkest in *S. c. paludis*, palest in *S. c. gossii*, and intermediate (but more similar to *S. c. gossii*) in *S. c. relictus*.

DISCUSSION

The cranial morphometric differences that exist between nominal subspecies of *S. cooperi* on the central Great Plains suggest that little or no gene flow occurs between the relict populations in the west and the more eastern populations. Gene flow among populations of *S. cooperi* on the central Great Plains likely existed until mesic grasslands became more xeric during the past 5,000 years (Davis, 1987).

Hibbard and Rinker (1942:33–34) gave

an example of the kind of event that may have isolated the relict populations: "Until 1914 the Cimarron river [sic] was narrow, with grassy banks and extensive meadows on the flood plain, a permanent stream of clear, flowing water with some deep pools. . . . On May 1, 1914, there occurred one of the greatest floods along the Cimarron watershed that has ever been known . . . . the fast runoff of the water scoured the Cimarron river bed in places to a depth of thirty-five feet. As the flood cut the channel deeper, it filled it with sand. . . . The river channel changed from that of a narrow stream with a few feet of clear water to a broad sand bed with many sand bars. . . . The flood plain drained at once into the channel. Most of the river flow being underground, the meadows dried out and the grasses died, being replaced by sagebrush, sand plums, buffalo gourds, and small sand dunes."

The relict populations from the type localities of *S. c. paludis* (Meade Co., Kansas) and *S. c. relictus* (Dundy Co., Nebraska) may be extinct (Dalquest et al., 1990). The last specimens were trapped in 1946 and 1968, respectively, despite extensive trapping efforts in recent years (Wilson, 1994; P. W. Freeman, pers. comm.). Both subspecies are represented by specimens only from their type localities (Appendix I).

Synaptomys cooperi is uncommon, but not entirely absent, in central and western Kansas (Brillhart and Kaufman, 1992; Choate and Fleharty, 1975; Clark et al., 1986; Welker and Choate, 1994) and presumably in adjacent regions of Nebraska. Localized, extant populations of *S. cooperi* on the eastern Great Plains probably are restricted to mesic habitats that are ephemeral or dynamic in nature. In addition, southern bog lemmings may exhibit low vagility (Hibbard and Rinker, 1942); semi-arid short- and mixed-grass prairies may serve as a filter to their dispersal, although the filter almost certainly is less severe in northwestern Kansas and southwestern Nebraska than in southwestern Kansas.

The geographic distribution and local abundance of *S. cooperi* on the central Great Plains most likely has been in constant flux for the past 5,000 years as a result of periodic droughts (Tomanek and Hulett, 1970; Wooster, 1939). These short-term fluctuations in weather directly affect local plant communities, which in turn affect the abundance and distribution of small mammals (Choate and Fleharty, 1975), including *S. cooperi*. Southern bog lemmings may extend their geographic distribution via avenues of mesic vegetation along watercourses (and, more recently, in roadside ditches—Getz et al., 1978) in wet years, persist in suitable habitats during dry years, and again disperse in subsequent wet years. During periodic droughts, populations that become isolated (and thereby freed from the stabilizing effects of gene flow) could begin to diverge and acquire their own evolutionary tendencies. When mesic habitats are restored at the end of a drought, one would expect a swamping of any distinctive traits due to re-establishment of gene flow with adjacent populations. A similar explanation was given by Choate and Williams (1978) after they found little consistent geographical variation in populations of *M. ochrogaster* on the Great Plains. If *S. cooperi* extends and contracts its range as speculated above, interspecific competition between *S. cooperi* and species in the genus *Microtus* probably affects the abundance and distribution of bog lemmings (Beasley and Getz, 1986; Danielson and Gaines, 1987; Gaines et al., 1979; Gromov and Polyakov, 1977; Linzey, 1984; Rose and Spevak, 1978) on the Great Plains.

We hypothesize that narrow ribbons of mesic habitat along the Republican River and other watercourses in northern Kansas and southern Nebraska may serve as dispersal corridors for *S. cooperi*, resulting in periodic gene flow between the subspecies *S. c. gossii* and *S. c. relictus*. This would account for the absence of distinctive features in *S. c. relictus*. However, a similar

situation almost certainly does not exist for S. c. paludis in southwestern Kansas, where the effects of agriculture and drought have been more pronounced. Thus, cranial characters diverged much more, or for a longer period of time, in *S. c. paludis* than in *S. c. relictus.*

CONCLUSIONS

Philosophic concerns and merits relating to the use of trinomial nomenclature were discussed by Engstrom et al. (1994), Lidicker (1962), and Mayr and Ashlock (1991), among others. We agree with Engstrom et al. (1994:187) that "the real purpose of the trinomen is to describe formally patterns of geographic variation by calling attention to geographic discontinuities among distinctive, evolutionarily discrete subsets of populations." *S. c. paludis* and *S. c. relictus* differ from other populations of the species as described by their original authorities. *S. c. paludis* indeed may represent a distinctive, evolutionarily discrete population. *S. c. relictus,* however, may be the terminus of a geographic cline. We recommend that the current taxonomic arrangement be retained until information gathered from other techniques (possibly using traits associated with single heritable elements, such as mitochondrial DNA obtained from individuals comprising extant populations or skins of existing museum specimens) is available.

ACKNOWLEDGMENTS

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APPENDIX I

Specimens examined.—All specimens of *Synaptomys cooperi gossii* (*n* = 869), *S. c. paludis* (*n* = 36), and *S. c. relictus* (*n* = 6) that were examined for this study are listed. Specimens are deposited in the following collections (acronyms are those used by Yates et al., 1987): Collection of Recent Mammals, Arkansas State University (ASUMZ); American Museum of Natural History (AMNH); University of Arkansas at Little Rock Vertebrate Collections (UALRVC); Chicago Academy of Science (CAS); Carnegie Museum of Natural History (CM); Charles R. Conner Museum, Washington State University (CRCM); Cornell University Mammal Collection, (CU); Field Museum of Natural History (FMNH); Illinois Natural History Survey (INHS); Museum of Natural History, University of Iowa (IOWA); Illinois State Museum (ISM); Museum of Zoology, Iowa State University (ISUMZ); Indiana State University Vertebrate Collections (ISUVC); Joseph Moore Museum, Earlham College (JMM); University of Kansas Natural History Museum (KU); Natural History Museum of Los Angeles County (LACM); Sternberg Museum of Natural History, Fort Hays State University (MHP); Bell Museum of Natural History, University of Minnesota (MMNH); Michigan State University Museum (MSU); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); National Biological Survey/Museum of Southwestern Biology, University of New Mexico (NBS); North Carolina State University (NCS); Science Collections, Northeast Missouri State University (NEMSU); San Diego Natural History Museum (SDNHM); Southern Illinois University, Carbondale Mammal Collection (SIUCM); Tarleton State Collection, Tarleton State University (TSC); The Museum, Texas Tech University (TTU); University of Arkansas Mammal Collection, University of Arkansas, Fayetteville (UADZ); University of Alaska Museum (UAM); Florida State Museum, University of Florida (UF); University of Illinois Museum of Natural History (UIMNH); University of Michigan Museum of Zoology (UMMZ); University of Missouri Museum of Zoology (UNMZ); University of Nebraska State Museum (UNSM ZM); W. H. Over Museum, University of South Dakota (USD); United States National Museum of Natural History/United States Fish and Wildlife Service (USNM/FWS); University of Wisconsin Zoological Museum, University of Wisconsin, Madison (UWZ).

Synaptomys cooperi gossii (Coues).—ARKANSAS (*n* = 68). Craighead Co.: ASU campus at football stadium, 9 (ASUMZ); ASU campus at football field, 7 (ASUMZ); ASU campus, 1 (ASUMZ); cemetery by St. Benards Hospital, 12 (ASUMZ); Jonesboro, 1 (ASUMZ); no locality specified, 8 (ASUMZ). Cross Co.: no locality specified, 1 (ASUMZ). Greene Co.: ASU fish ponds, 1 (ASUMZ); ASU-Walcott catfish ponds, 2 (ASUMZ); Paragould, 2 (ASUMZ); no locality specified, 9 (ASUMZ). Lawrence Co.: 1 mile E Saffel, 1 (UADZ); 5 miles E Hoxie, 1 (UADZ); South Baptist campus, College City, 1 (UADZ); ca. 3.6 miles W Minturn near Clover Bend on Running Water Creek, 1 (ASUMZ); no locality specified, 1 (ASUMZ). Poinsett Co.: T11N, R3E, Sec. 1, 3 (ASUMZ); T12N, R3E, Sec. 36, 1 (ASUMZ); no locality specified, 2 (ASUMZ). Randolph Co.: Pocohontas, 1 (UADZ); no locality specified, 1 (UADZ). St. Francis Co.: 3 miles E Wheatly, 1 (UALRVC). Woodruff Co.: no locality specified, 1 (ASUMZ).

IOWA (*n* = 34). Appanoose Co.: 11 miles W Centerville, 2 (KU); 4 1/2 miles N, 1/2 mile E Unionville, 1 (KU). Boone Co.: no locality specified, 3 (ISUMZ). Davis Co.: 3 3/4 miles W Ash Grove, 1 (KU). Fremont Co.: 13 miles E Hamburg, 3 (KU); 4 miles E Hamburg, 1 (KU); 6 miles N, 4 1/2 miles W Hamburg, 3 (KU); 1/4 mile S, 2 miles W Tabor, 1 (IOWA). Harrison Co.: Logan, 1 (IOWA). Henry Co.: Hillsboro, 1 (USNM/FWS). Keokuk Co.: 1/2 mile S, 2 1/2 miles W Delta, 1 (KU). Mahaska Co.: 3 miles S, 9 miles W Oskaloosa, 2 (KU). Marion Co.: 1 mile N, 1 1/4 miles E Harvey, 1 (IOWA); Knoxville, 1 (USNM/FWS). Mills Co.: 3 miles S, 2 1/2 miles W Hillsdale, 1 (IOWA). Monroe Co.: 1 1/2 miles N Melrose, 1 (KU). Montgomery Co.: 4 miles S, 3/4 miles W Hawthorne, 1 (KU). Page Co.: 1 mile S, 3 miles E Northboro, 2 (KU); 7/10 mile S Coin, 1 (KU). Polk Co.: Middle Fork of Willow Creek, Fort Des Moines, 1 (MVZ).

Story Co.: Ames, 1 (ISUMZ). Van Buren Co.: no locality specified, 3 (1 ISUMZ, 2 UWZ). Wapello Co.: 4 1/4 miles E Chillicothe, 1 (KU).

ILLINOIS (*n* = 236). Alexander Co.: vicinity of Miller City, 1 (UIMNH). Champaign Co.: 1 1/2 miles S Champaign, 1 (UIMNH); Mahomet, 1 (UIMNH); 1 mile N, 3 miles E Urbana, 1 (UIMNH); Urbana, 1 (INHS). Clark Co.: ca. 5 miles W Indiana state line on I-70, 1 (ISUVC). Crawford Co.: Flat Rock, 3 (CAS). Fulton Co.: 1 mile W Canton, 3 (UIMNH); 1/2 mile W Canton, 1 (UIMNH); Canton, 1 (UIMNH); 1 mile N Norris, 1 (UIMNH); 1/2 mile N Norris, 3 (UIMNH). Hancock Co.: vicinity of Elvaston, 2 (UIMNH); Warsaw, 5 (UIMNH). Hardin Co.: Rosiclare, 7 (FMNH); vicinity of Eichron, 1 (UIMNH). Macoupin Co.: vicinity of Beaver Dam State Lake, 4 (UIMNH). Marion Co.: Odin, 1 (USNM/FWS). Mason Co.: 5 miles NE Havana, Illinois Natural History Survey Laboratory, 1 (UIMNH). McDonough Co.: vicinity of Fandon, 5 (UIMNH). McLean Co.: Bloomington, 3 (2 UIMNH, 1 UMMZ); 3 1/2 miles SE Bloomington, 1 (UIMNH); 5 miles SE Bloomington, 1 (UIMNH); 3 miles NW Le Roy, 1 (UIMNH); 2 miles N, 1/2 mile W Le Roy, 2 (UIMNH); near Le Roy, 1 (UIMNH). Morgan Co.: Meredosia, 1 (INHS). Peoria Co.: vicinity of Hanna City, 1 (UIMNH). Piatt Co.: Allerton, 2 (UIMNH); Allerton Park, 5 (2 AMNH, 3 UIMNH); Allerton Park, near Monticello, 2 (UIMNH); Monticello, Allerton Park, 1 (UF); 2 1/2 miles SW Monticello, 1 (UIMNH); Allerton Tract, 2 1/2 miles S, 5 miles W Monticello, 33 (1 TTU, 32 UIMNH); 2 1/2 miles S, 5 miles W Monticello, 11 (1 AMNH, 7 KU, 2 LACM, 1 TTU); 2 1/2 miles S, 5 miles W Monticello, Allerton Park, 1 (UF). Pike Co.: 3 1/2 miles S Pittsfield, 5 (UIMNH); vicinity of Pittsfield, 1 (UIMNH). Pope Co.: Dixon Springs, 25 (UIMNH); 4 miles SE Eddyville, 1 (UIMNH); vicinity of Eddyville, 18 (UIMNH); Glendale, 1 (UIMNH); vicinity of Glendale, 17 (UIMNH); Golconda, 1 (UIMNH); vicinity of Golconda, 3 (UIMNH); 1/2 mile E McCormick, 1 (UF). Richland Co.: Olney Bird Haven, 1 (FMNH). Saline Co.: 1/2 mile W Horseshoe, 1 (UIMNH). Sangamon Co.: Springfield, 1 (ISM); south end of Lake Springfield, Springfield, 1 (ISM); SE part of Lake Springfield, 1 (ISM); SW of Springfield, 1 (ISM); 3 miles S Springfield, 1 (ISM); 2 miles SE Springfield, 1 (ISM); 7 3/4 miles S Springfield, 4 miles E I-55, 2 (ISM); 8 miles S Springfield, 5 1/2 miles E I-55, 1 (ISM); 10 miles S Springfield, 4 1/2 miles E I-55, 1 (ISM); 11 1/4 miles S Springfield, 3 1/4 miles E I-55, 1 (ISM); no locality specified, 1 (ISM). Union Co.: 1 3/4 miles NE Aldridge, 1 (INHS); Aldridge-Pine Hills, 2 (UF); Aldridge-Pine Hills Swamp, 1 (SIUCM); 1/2 mile NE Codben, 1 (SIUCM). Vermilion Co.: Collison, 1 (UIMNH); Danville, 1 (FMNH); Kickapoo State Lake, 4 (FMNH); Muncie, 1 (INHS); Newton, 3 (UIMNH); Snider, 2 (UIMNH). Wayne Co.: 4 1/2 miles W Geff, 15 (1 CU, 13 MHP, 1 SDNHM); Geff, 2 (NCS); Sims, 1 (AMNH).

KANSAS (*n* = 317). Anderson Co.: 6 miles S Garnett, 5 (KU); no locality specified, 1 (KU). Atchison Co.: 1 1/2 miles S Muscotah, 4 (KU); 4 miles S Muscotah, 9 (3 KU, 6 UIMNH). Barber Co.: 3 miles N, 1 mile E Sharon, 6 (KU); Sharon, 1 (KU). Brown Co.: 1 mile S, 7 miles E Hiawatha, 3 (MHP); 1 mile N Horton, 1 (KU). Douglas Co.: 3/4 mile W NE corner Douglas County, 2 (KU); 7 miles NNE Lawrence, 6 (KU); 2 2/10 miles NNE Lawrence, 1 (KU); 2 1/2 miles N, 7/10 mile E Lawrence, 1 (UWZ); 2 1/2 miles N, 2 1/2 miles E courthouse (sandpits), Lawrence, 2 (KU); 2 miles N, 2 miles E Lawrence, 4 (2 ISM, 2 KU); 2 miles N, 2 miles E Lawrence (courthouse), 4 (KU); 2 miles N, 3/4 mile E Lawrence, 1 (MHP); 1 1/2 miles N, 1 1/5 miles E Lawrence, 3 (KU); 1 1/2 miles N, 1 1/5 miles E courthouse, Lawrence, 39 (KU); 1 1/2 miles N, 1 mile E Lawrence, 1 (KU); 1 1/2 miles N, 1 7/10 miles E courthouse, Lawrence, 1 (KU); sandpits, 1 1/2 miles N, 1 3/4 miles E courthouse, Lawrence, 49 (45 KU, 3 TTU, 1 UWZ); 1 1/4 miles N, 1 3/4 miles E courthouse, Lawrence, 3 (KU); 1 mile N, 4 miles W Lawrence, 1 (KU); 1 1/2 miles NW Lawrence, 1 (KU); ca. 10 miles W Lawrence, off Stull Road, 1 (KU); 7 1/2 miles SW Lawrence, 18 (15 KU, 3 MVZ); 7 miles SW Lawrence, 11 (10 KU, 1 NBS); 3 1/2 miles W Douglas County Courthouse, 1 (TTU); 2 1/2 miles W Lawrence, 2 (KU); 2 miles SW Lawrence, 3 (KU); 2 miles W Lawrence, 5 (KU); 1 3/4 miles W Lawrence, 1 (KU); 1 1/2 miles W Lawrence, 1 (KU); 1 mile SW Lawrence, 1 (KU); 1 mile W Lawrence, 9 (KU); 1 mile W Lawrence (cemetery), 9 (KU); 1/2 mile W Lawrence, 1 (KU); 150 yards SW Hungerford's House (sewer ditch), 1 (KU); 100 yards SW Hungerford's House, 1 (KU); 100 yards W Templin's House, 3 (KU); Lawrence, 4 (1 AMNH, 1 KU, 2 MVZ); west end of campus, Lawrence, 1

(KU); Lawrence, KU campus, 2 (1 KU, 1 USNM/FWS); Fish Lab area, Lawrence, 1 (MMNH); 1/2 mile SW Museum, Lawrence; 1 (KU); no locality specified, 10 (1 NBS, 1 CM, 1 FMNH, 1 ISUMZ, 6 KU). Jefferson Co.: 14 1/2 miles NE Lawrence, Nelson Environmental Study Area, 1 (KU); Nelson Environmental Study Area (T11S, R20E, Sec. 33), 4 (KU); Rockerfeller Tract, KU Natural History Reservation, 1 (KU). Jewell Co.: vicinity of Lovewell Reservoir (T15S, R7W, center N 1/2, Sec. 35), 1 (KU). Leavenworth Co.: Fort Leavenworth, 6 (USNM/FWS); Leavenworth, 1 (AMNH). Lincoln Co.: T12S, R10W, NW 1/4 Sec. 30, 3 (MHP). Lyon Co.: 0.8 mile S, 3.7 miles W Americus, 1 (UALRVC). Marion Co.: 1.5 miles N, 1.5 miles E Hillsboro (T19S, R2E, Sec. 23), French Creek Cove (9 MHP, 4 USD). Marshall Co.: 1 1/2 miles N, 1/2 mile W Oketo (T1S, R7E, NW 1/4 Sec. 11), 1 (MHP). Nemaha Co.: 3 1/2 miles S, 3/4 mile E Sabetha, 3 (KU); 4 miles S Sabetha, 2 (KU). Osage Co.: 3/4 mile S, 5 miles W Overbrook, 2 (KU); Osage County State Lake, 1 mile S, 4 miles W Overbrook, 1,127 feet, 1 (KU); 8 miles N, 9 miles E Osage City, 16 (2 CRCM, 11 MHP, 1 TTU, 2 UAM). Osborne Co.: 6 miles N, 2 1/4 miles W Alton (T6S, R15W, SW 1/4 Sec. 3), 4 (MHP). Pottawatomie Co.: 12 miles N, 8 1/2 miles W Westmoreland, 1 (MHP); 5 miles N Westmoreland, 4 (MHP). Republic Co.: Republic County State Lake, 1 (MHP). Riley Co.: vicinity of Ogden, 1 (TSC); Manhattan, 2 (AMNH). Rooks Co.: 8 miles N Woodston (T6S, R16W, N 1/2 Sec. 4), 1 (MHP); 6 miles N, 2 miles E Woodston (T6S, R16W, SE 1/4 Sec. 11), 1 (MHP); 5 miles N Woodston (T6S, R16W, SE 1/4 Sec. 16), 4 (MHP). Russell Co.: T12S, R12W, NW 1/4 Sec. 32, 1 (MHP). Stafford Co.: 7 miles S, 2 miles W Raymond, 1 (KU). Washington Co.: Washington County State Lake, 1 (KU). Woodson Co.: Neosho Falls, 2 (USNM/FWS); near type locality (Neosho Falls), 1 (KU).

MISSOURI (*n* = 169). Adair Co.: 1 mile N, 4 miles W Brashear, 1 (NEMSU); 1 mile N, 3.5 miles W Brashear, 1 (NEMSU); 1 mile N, 2.5 miles W Brashear, 1 (NEMSU); 8 miles N, 1 mile E Kirksville, 1 (NEMSU); 6 miles N Kirksville, 2 (1 NEMSU, 1 UIMNH); 5 miles N, 2 miles W Kirksville, 1 (NEMSU); 4.5 miles N, 3 miles W Kirksville, 1 (NEMSU); 1 mile S Kirksville, 1 (NEMSU); 1 mile S, 2 miles W Kirksville, 1 (NEMSU); 1.5 miles SE Kirksville, 1

(NEMSU); 2 miles S Kirksville, 2 (NEMSU); 3 miles S Kirksville, 2 (NEMSU); 5 miles S Kirksville, 1 (USNM/FWS); 6 1/2 miles S Kirksville, 2 (USNM/FWS); 7 miles SW Kirksville, 1 (MSU); 10 miles W Kirksville, 1 (NEMSU); 2 miles W Kirksville, Big Creek State Park, 1 (CM); Big Creek State Forest, 1 (NEMSU); 1 mile E Kirksville, 1 (NEMSU); 6 miles E Kirksville, 1 (NEMSU); 1.25 miles SE Millard, 1 (NEMSU); 2 miles SE Millard, 1 (NEMSU). Audrain Co.: 10 miles SE Mexico, 1 (NEMSU). Boone Co.: Ashland, 1 (UNMZ); Ashland area, 1 (UNMZ); Columbia, 7 (1 TTU, 6 UNMZ); 4 miles SE Columbia, 1 (UIMNH); 11 miles S Columbia, 1 (UIMNH); off AC Road S of Columbia, 1 (UNMZ); McBaine, 1 (UNMZ); orchard near McBaine, 1 (UNMZ); Midway Orchard, Midway, 1 (UNMZ); Tucker Prairie, 1 (UNMZ). Callaway Co.: Tucker Prairie, 1 (UNMZ). Clark Co.: 2 miles S, 3 miles W Alexandria, 1 (NEMSU). Grundy Co.: 6 1/2 miles S Mondena, 1 (MHP). Johnson Co.: Warrensburg, 1 (JMM); Warrensburg Science Building, 1 (ISM); Warrensburg, Pertle Springs, 1 (JMM); no locality specified, 2 (ISUMZ). Knox Co.: 5 miles W Hurdland, 2 (NEMSU); 7 miles S, 2 miles E Hurdland, 2 (NEMSU); 3 miles S, 3 miles W Novelty, 1 (NMSU). Lewis Co.: 2 miles S, 2 miles E Deer Ridge, 1 (CM); Meeman Biological Field Station, Memphis State University, 1 (MHP). Macon Co.: 5 miles E Macon, 1 (UNMZ). Mercer Co.: 1.5 miles S Goshen, 1 (CM). Nodaway Co.: 5 miles ENE Maryville, 1 (UF); no locality specified, 5 (2 NCS, 3 USNM/FWS). Pettis Co.: 4 miles NW Sedalia, 1 (KU); Sedalia, 1 (UNMZ). Putnam Co.: 4.5 miles N Livonia, 1 (NEMSU). Ralls Co.: 3 miles E Monroe City, 1 (CM). Ripley Co.: Pratt, 1 (UNMZ). Saline Co.: Marshall, 3 (UMMZ). Schuyler Co.: 1.8 miles N, 1 mile W Greentop, 1 (NEMSU). St. Charles Co.: Busch Wildlife Area, Weldon Springs, 1 (UNMZ); 2.8 miles NW Weldon Spring, 6 (MHP); 1.5 miles NW Weldon Spring, 2 (MHP); 0.8 mile W Weldon Spring, 2 (MHP); 0.7 mile SW Weldon Spring, 1 (MHP); 0.8 mile SW Weldon Spring, 12 (9 MHP, 3 TTU); 1.1 miles SW Weldon Spring, 1 (MHP); 1.2 miles SW Weldon Spring, 1 (MHP); 1.8 miles SW Weldon Spring, 19 (MHP); Weldon Spring Training Area, 5 (MHP); Weldon Spring Training Area, ADM 2, 1 (MHP); Weldon Spring Training Area, N of ADM 3, 1 (MHP); Weldon Spring Training Area, ADM 3, 4 (MHP); Weldon Spring Training Area,

Airport Field, Training Area 7, 2 (MHP); Weldon Spring Training Area, RAD 1, 2 (MHP); Weldon Spring Training Area, RAD 2, 3 (MHP); Weldon Spring Training Area, RAD 4, 1 (MHP); Weldon Spring Training Area, RAD 8, 1 (MHP); Weldon Spring Training Area, Training Area 1, 1 (MHP); Weldon Spring Training Area, Site 1, 1/2 mile NE rifle range, 2 (MHP); Weldon Spring Training Area, Site 3, 2 (MHP); Horseshoe Lake, 15 (1 KU, 14 USNM/FWS); 2 miles NW O'Fallon, 1 (NEMSU). St. Louis Co.: near Blackjack, 1 (NEMSU). Stoddard Co.: Gaylord Memorial Laboratory, 1 (UNMZ); Mingo National Wildlife Refuge, 2 (1 CM, 1 MHP); 1.5 miles N Puxico, 1 (NEMSU); Puxico, 1 (UNMZ). Sullivan Co.: 2 miles S, 3 miles W Milan, 2 (NEMSU). Vernon Co.: 1 mile S, 1 mile E Nevada, 2 (MHP).

NEBRASKA (*n* = 35). Brown Co.: Fairfield Creek, 1 (UNSM ZM); Butler Co.: 4 miles N, 1/2 mile E Octavia, 1 (KU). Cass Co.: 1 mile E Louisville, 2 (KU); 1 mile N, 2 miles W Weeping Water, 1 (KU); 3/10 mile S, 2 miles W Weeping Water, 3 (KU); Custer Co.: 1 mile NW Callaway, 1 (UNSM ZM). Gage Co.: 1/4 mile W Homestead National Monument, 4 (KU). Holt Co.: 6 miles N Midway, 2 (KU). Lancaster Co.: Lincoln, 5 (3 UNSM ZM, 2 USNM/FWS); Stevens Creek, near Lincoln, 1 (UNSM ZM). Lincoln Co.: 4.5 miles S, 1.5 miles W Brady, 1 (UNSM ZM). Richardson Co.: 3 1/2 miles S, 1 mile W Dawson, 6 (KU); 5 miles N, 2 miles W Humboldt, 1 (KU); Indian Cave State Park, 3 (UNSM ZM). Saline Co.: 1 mile S, 3 miles E Crete, 1 (KU); 3 miles S, 2 miles E Crete, 1 (KU). Seward Co.: 1 mile N Pleasant Dale, 1 (KU).

SOUTH DAKOTA (*n* = 7). Gregory Co.: 1 mile N Fort Randall Dam, 1 (UIMNH); 1/2 mile W Fort Randall Dam, 6 (UIMNH).

WISCONSIN (*n* = 3). Crawford Co.: Lynxville, 3 (USNM/FWS).

Synaptomys cooperi paludis Hibbard and Rinker.—KANSAS (*n* = 36). Meade Co.: 14 miles SW Meade, Meade County State Park (=Meade State Lake), 36 (1 AMNH, 31 KU, 4 UMMZ). Additional specimens not examined: 2 (TCWC, Texas Cooperative Wildlife Collection, Texas A&M University).

Synaptomys cooperi relictus Jones.—NEBRASKA (*n* = 6). Dundy Co.: 5 miles N, 2 miles W Parks, Rock Creek Fish Hatchery, 6 (4 KU, 2 MHP).