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GEOGRAPHIC VARIATION IN PELAGE COLOR
OF PIÑON MICE (*PEROMYSCUS TRUEI*)
IN THE NORTHERN GREAT BASIN AND ENVIRONS

Leslie N. Carraway¹ and B.J. Verts¹

ABSTRACT.—Cluster analyses of values for hue, value, and chroma (based on Munsell soil-color charts) obtained at 6 points on pelages of 202 adult piñon mice (*Peromyscus truei*) from the northern Great Basin and environs produced dendrograms with specimens grouped into 5 clusters. In most instances distribution of specimens forming clusters reflected those published for nominal races. In instances in which previous distributions of nominal races were not supported and for specimens previously unclassified, geographic distribution of groups of color morphs was logical and suggested avenues for additional research on geographic variation in the species.

Key words: *Peromyscus truei*, piñon mice, pelage color, geographic variation, northern Great Basin.

Piñon mice (*Peromyscus truei*) occur from southwestern and central Oregon, southwestern Idaho, southwestern Wyoming (likely extirpated), eastern Colorado, extreme western Oklahoma, and western Texas, south to central Baja California, Mexico, central Arizona, and southern New Mexico (Gafur et al. 1980, Hoffmeister 1981, Modi and Lee 1984, Clark and Stromberg 1987, Caire et al. 1989, Carraway et al. 1993, Davis and Schmidly 1994, Ramírez-Pulido et al. 1996). Also, a disjunct population occurs near the southern tip of Baja California Sur (Hall 1981). In the northern Great Basin, the species usually is associated with rocky habitats vegetated by old-growth piñon pine (*Pinus edulis*) or junipers (*Juniperus*; Hall 1946, Hoffmeister 1951, Carraway et al. 1993), but those in southwestern Oregon and northwestern California are associated with oak (*Quercus kelloggii* and *Q. garryana*) or redwood (*Sequoia sempervirens*) and Douglas-fir (*Pseudotsuga menziesii*; Hoffmeister 1951, Fisher 1976).

Dorsal pelage of *P. truei* usually is some shade of grayish brown, but color varies considerably geographically (Hall 1981). Five nominal subspecies occur in the northern Great Basin and adjacent areas: *P. t. gilberti*, *P. t. nevadensis*, *P. t. preblei*, *P. t. sequoiensis*, and *P. t. truei*. Pelage color originally was involved in differentiating among these races (Shufeldt

1885, Allen 1893, Bailey 1936, Hall and Hoffmeister 1940, Hoffmeister 1941) and was used extensively as a diagnostic character in the most recent taxonomic treatment of the species (Hoffmeister 1951). The latter author described dorsal pelage color for the 5 races in the northern Great Basin and environs based on Ridgway's (1912) classification as "Sepia," "Buffy Brown," "Mummy Brown," "Brussels Brown," and "Tawny-Olive to Saccardo's Umber," respectively. Nevertheless, no quantitative analysis of pelage color as a character for distinguishing these races has been conducted.

In 1992 we collected specimens of *P. truei* in southeastern Oregon about 225 km from the nearest previously published record in the state. Subsequently, we collected other specimens and located other records from regions in Oregon and Idaho north and east of the known range of the species (Carraway et al. 1993). Because of the proximity of several nominal races to these collection sites (Hoffmeister 1951), we chose not to assign the newly acquired specimens to a subspecies at that time. To assign newly acquired specimens to appropriate subspecies and to delineate more precisely ranges of nominal subspecies of *P. truei* in the northern Great Basin and environs, we analyzed pelage color of 202 museum specimens collected in Oregon, Idaho, Nevada, northern California, and western Utah.

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METHODS

For analyses we used 105 complete (skin and skull) museum specimens of *Peromyscus truei* collected at 43 sites in April–August (summer) and 97 collected at 35 sites in September–March (winter). These groups include specimens selected from within ranges of the 5 recognized subspecies of *P. truei* in the northern Great Basin and environs and specimens unclassified to subspecies from Oregon and Idaho. All specimens are adults in full, clean pelage free of visible grease and exhibiting no molting. Adults were identified by molars being fully erupted and exhibiting wear, and all skull sutures being completely fused. Collection locality (Appendix 1), date of collection, and pelage color were recorded for each specimen.

Pelage color was measured on specimens by comparing color at each of 7 points (Fig. 1) with those of Munsell soil-color chips; hue, value, and chroma were recorded for each color (Munsell Color 1975). We used this color-comparison technique in preference to more precise electronic methods because necessary equipment was easily transported to various systematics collections, cost less, and had the potential of being used in the field. The 3 hues found in *P. truei* (5YR, 7.5YR, 10YR) were coded 1, 2, and 3, respectively, but actual numbers for color value and chroma read from color chips were used in analyses (Appendix 2). For example, for a specimen with a measured color of 10YR3/2 at a point, the data for that point appeared as 3 3 2. Because values for midventer color (Fig. 1) were the same for all specimens (10YR8/1), this character was not used in statistical analyses; thus, each specimen was represented by 18 numerals.

Separate data matrices were formed for specimens collected in summer and winter. We analyzed each data matrix by use of a dissimilarity association matrix from Euclidean distance with unweighted pair-group method using arithmetic averages (UPGMA) method within Hierarchical Cluster Analysis in BioStat II (Pimentel 1994). Clusters were designated A, B, C, D, and E, and collection localities for specimens within each cluster were superimposed on a map of Hoffmeister's (1951) distributions of nominal subspecies occurring in the northern Great Basin and adjacent regions.

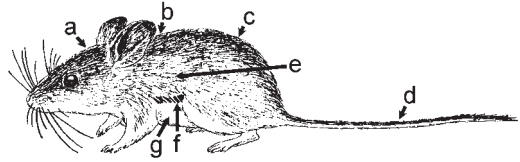


Fig. 1. Sketch of a *Peromyscus truei* illustrating points of reference for determining pelage color: a, pate; b, anterior dorsum; c, posterior dorsum; d, dorsal tail stripe; e, side above lateral stripe; f, lateral stripe; and g, midventer.

RESULTS

All characters, other than midventer color, exhibited some variation among both summer- and winter-caught specimens (Table 1). Most variation was in value and chroma, as the most common hue recorded was yellowish brown (10YR). Despite this variation, at sites at which multiple specimens were available, all individuals grouped in the same cluster.

Analyses of data matrices for *P. truei* collected in summer resulted in 5 distinct clusters, whereas those collected in winter resulted in only 4 clusters (Figs. 2a, 2b). Cophenetic correlation coefficients (r_{cs}) for these dendrograms were 0.967 and 0.963, respectively, indicating a high level of agreement between similarity values implied by dendrograms and those of original similarity matrices.

Specimens forming cluster A were from western Josephine County, Oregon, and coastal California; those in cluster B were from Shasta Valley, Siskiyou County, California; those in cluster C were from eastern Nevada, western Utah, southern Idaho, and Crook, Deschutes, Jefferson, and Harney counties, Oregon; those in cluster D were from Nevada; and those in cluster E were from Jackson, eastern Josephine, Klamath, and Lake counties, Oregon (Fig. 3). Because geographic distributions of clusters A, C, D, and E for winter-caught specimens were in accord with those of summer-caught specimens, seasonal groups were combined for plotting (Fig. 3). No winter-caught specimens from Siskiyou County, California, with requirements for inclusion were available for study, accounting for absence of a cluster B produced by that analysis (Fig. 2b).

We also reanalyzed our matrices, eliminating data for 1 point on the pelage at a time to ascertain whether relationships among clusters

TABLE 1. Munsell color determinations of pelage color of *Peromyscus truei* from the northern Great Basin and adjacent areas at 6 points of reference. Vertical listings of colors indicate variation possible within a cluster (geographic region); thus, horizontal listings do not indicate colors for any particular individual.

Cluster	Season	Pate	Anterior dorsum	Posterior dorsum	Dorsal tail	Lateral side	Lateral stripe
A	Summer	10YR2/1	10YR2/1	10YR2/1	7.5YR3/2	7.5YR7/6	7.5YR7/6
	Winter	10YR2/1	10YR2/1	10YR2/1	7.5YR3/2	7.5YR7/6	7.5YR6/6
B	Summer	10YR7/4	10YR7/4	10YR7/4	10YR3/2	10YR6/6	10YR6/8
C	Summer	10YR8/3	10YR8/3	7.5YR6/6	5YR3/4	10YR7/4	10YR7/4
		10YR8/6		10YR8/6	7.5YR3/4	10YR7/6	10YR7/6
	Winter	10YR8/6	10YR7/3	10YR7/6	5YR3/4	10YR8/4	10YR7/6
			10YR8/3	10YR8/6	7.5YR3/4	10YR8/6	10YR8/6
D	Summer	7.5YR7/6	7.5YR7/6	7.5YR7/6	10YR2/1	7.5YR7/6	7.5YR7/8
		10YR8/3	10YR8/3	7.5YR8/4	10YR3/2	7.5YR8/6	7.5YR7/6
	Winter	10YR7/4	10YR8/3	7.5YR7/6	10YR2/1	7.5YR7/6	7.5YR6/6
			10YR8/4	10YR8/4	7.5YR8/4	10YR3/1	10YR7/3
E	Summer	10YR7/4	10YR7/4	7.5YR6/6	7.5YR2/0	10YR6/8	10YR6/8
			10YR8/4	10YR8/4	10YR8/4	10YR3/2	10YR7/8
	Winter	10YR7/4	10YR8/3	7.5YR7/6	10YR2/1	7.5YR7/6	7.5YR6/6
			10YR8/4	10YR8/4	7.5YR8/4	10YR3/1	10YR7/3
	Summer	10YR7/4	10YR7/4	7.5YR6/6	7.5YR2/0	10YR6/8	10YR6/8
			10YR8/6	10YR8/6	10YR8/6	10YR3/2	10YR7/8
	Winter	10YR7/4	10YR7/4	7.5YR6/6	10YR2/1	7.5YR7/6	7.5YR7/6
			10YR8/6	10YR8/6	10YR8/6	10YR3/1	7.5YR7/8
	Summer	10YR7/4	10YR7/4	7.5YR6/6	7.5YR2/0	10YR6/8	10YR6/8
			10YR8/6	10YR8/6	10YR8/6	10YR3/2	10YR7/8
	Winter	10YR7/4	10YR7/4	7.5YR6/6	10YR2/1	7.5YR7/6	7.5YR7/6
			10YR8/6	10YR8/6	10YR8/6	10YR3/2	10YR6/8

were affected. Results were not altered greatly by sequentially eliminating data points (Fig. 2). Such suggests that the set of variables was correlated over the body.

DISCUSSION

Distribution of specimens in cluster A conforms most closely with that depicted for *P. t. sequoiensis* at the northern extent of its range (Fig. 3). The greater Euclidean distance separating cluster A from other clusters, combined with the larger body size, shorter tail, and shorter ears reported for specimens from the region (Hoffmeister 1951), suggests that morphometric and genetic analyses might indicate that *sequoiensis* is specifically different from the remaining *P. truei*. Whether *sequoiensis* and *gilberti* are sympatric or remain parapatric in that region is unknown.

Based on analyses of matrices containing all 6 characters, distribution of all specimens forming cluster D (Fig. 3) conforms with that depicted for *P. t. truei* (Hoffmeister 1951, Hall 1981). However, southwestern Utah contains localities from which specimens group into cluster C (Fig. 3). Such suggests that the zone of intergradation between clusters C and D is

slightly farther west and south than depicted for *truei* and *nevadensis* by Hoffmeister (1951).

Specimens forming cluster E were all collected at localities in Oregon: 3 in Josephine County, 3 in Jackson County, 1 in Klamath County, and 3 in Lake County. Those from Josephine County suggest that the range of *P. t. gilberti* extends farther west than previously believed and those from Klamath and Lake counties extend the range farther north and eastward (Fig. 3). Hoffmeister (1951) and Hall (1981) indicated that the range of *P. t. truei* extended from Nevada into south central Oregon, encompassing localities at which the Lake County specimens were collected. However, as specimens from that region were not available to them, the depicted ranges for these 2 races must have been based on conjecture. Winter-caught specimens forming cluster E separated into 2 clusters when matrices were analysed after removal of color of pate, anterior dorsum, or posterior dorsum (Figs. 2f, 2j, 2n). We consider the separation spurious because both clusters so formed included individuals from more than 1 of the geographic groups of specimens forming cluster E (Fig. 3). Several other species of small mammals and races thereof associated primarily with

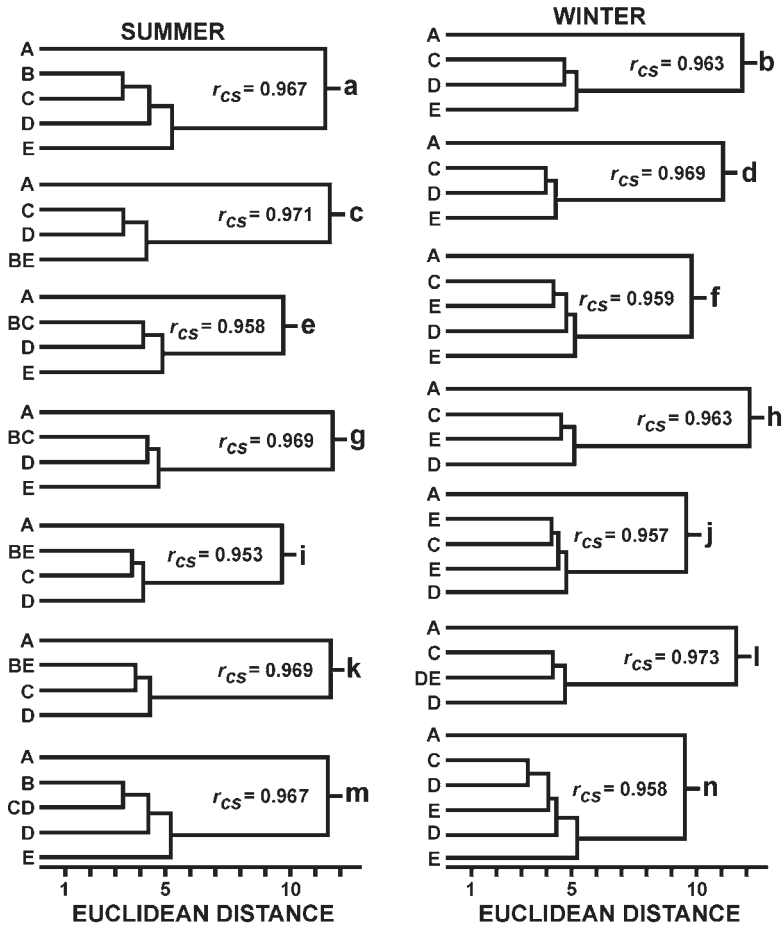


Fig. 2. Dendrograms with accompanying cophenetic correlation coefficients (r_{CS}) produced from data matrices formed for specimens of *Peromyscus truei* collected in summer and winter with: a–b, all characters included; c–d, with dorsal tail color removed; e–f, with anterior dorsum color removed; g–h, with lateral stripe color removed; i–j, with posterior dorsum color removed; k–l, with lateral side color removed; and m–n, with pate color removed.

habitats in either eastern or western Oregon have ranges that extend through a gap in the Cascade Range near the southern border of that state (Verts and Carraway 1998). Thus, classification of specimens of *P. truei* from Klamath and Lake counties as *gilberti* is not surprising.

Summer-caught specimens forming cluster B grouped with those in cluster E in analyses in which 1 of 3 color characters (dorsal tail, posterior dorsum, or lateral side) was excluded (Figs. 2c, 2i, 2k). However, when 1 of the other 3 characters (pate, anterior dorsum, or lateral stripe) was excluded and when all 6 characters were included, dendrograms indicated that cluster E was distinct from cluster B and, that

other than cluster A, was the most divergent group from the remaining clusters (Figs. 2e, 2g, 2m). Also, specimens in cluster B grouped with those in cluster C when colors of either the anterior dorsum or the lateral stripe were excluded (Figs. 2e, 2g). One locality in Siskiyou County, California, from which specimens forming cluster B were taken, was within the range of *P. t. gilberti* depicted by Hoffmeister (1951); 3 other localities were only slightly to the east of the depicted range (Fig. 3). From geographic proximity involved (Fig. 3) and from combining of specimens in 3 dendrograms (Figs. 2c, 2i, 2k), specimens in cluster B seem to be consubspecific with those in cluster E. However, the Euclidean-distance

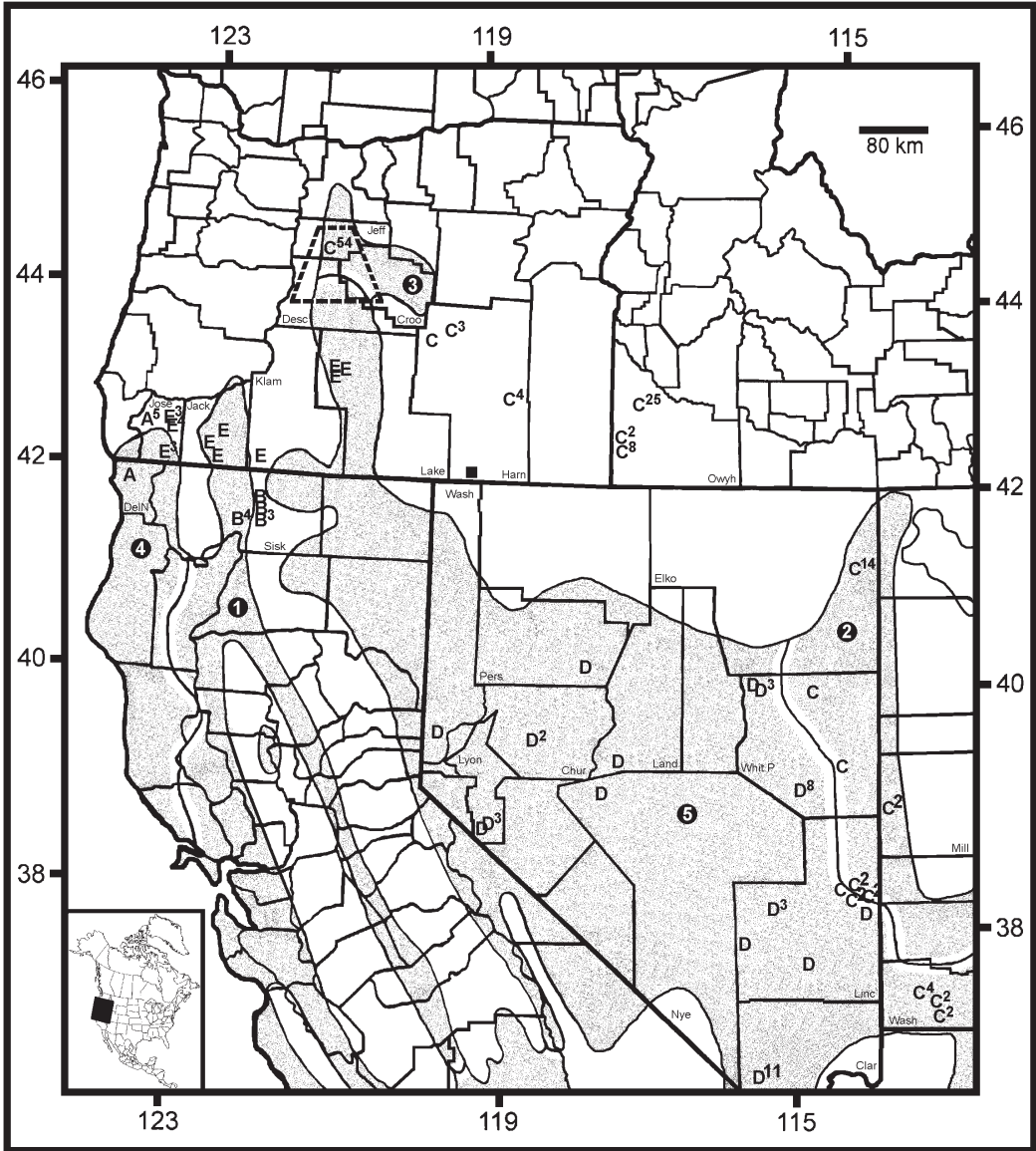


Fig. 3. Distribution of localities of specimens of *Peromyscus truei* forming the 5 clusters overlain on a distribution map of subspecies (stippled areas) following Hoffmeister (1951): 1, *P. t. gilberti*; 2, *P. t. nevadensis*; 3, *P. t. preblei*; 4, *P. t. sequoiensis*; and 5, *P. t. truei*. Superscript numerals following cluster-letters indicate number of specimens from that locality; absence of numeral indicates only 1 specimen. Dashed-line trapezoid in central Oregon contains 23 localities. Solid square in Harney Co., Oregon, is locality at which KU 157813 was collected. Names of counties referred to in text are abbreviated.

relationship between clusters B and E in 4 dendrograms (Figs. 2a, 2e, 2g, 2m) and the fact that all individuals forming cluster B were from a restricted area (Shasta Valley) suggest that these groups are taxonomically distinct. Color analysis combined with morphometric and genetic analyses of additional specimens,

including some caught in winter, from central Siskiyou County, California, might aid significantly in clarifying the relationship of this somewhat tenuous colormorph.

Except for 2 groups of localities in southwestern Utah and extreme eastern Nevada near the periphery of the depicted range of *P. t.*

truei, the distribution of specimens forming cluster C includes regions depicted by Hoffmeister (1951) and Hall (1981) as occupied by *P. t. preblei* and *P. t. nevadensis* (Fig. 3). In addition, cluster C also includes specimens from eastern Oregon (other than those from Lake County) and southwestern Idaho collected north and east of the previously described geographic range of the species (Fig. 3). Distributions of *P. t. preblei* and *P. t. nevadensis* (Hoffmeister 1951, Hall 1981), combined with localities of more recently collected specimens in cluster C, form a band in a more-or-less continuous arc from central Oregon, through southwestern Idaho, and along the Nevada–Utah state boundary (Fig. 3). Despite this logical grouping of 2 nominal subspecies, we are reluctant to synonymize these races in the absence of morphometric and genetic analyses.

Absence of available specimens from much of southeastern Oregon and the northern portion of Nevada (Fig. 3; Hoffmeister 1951, Hall 1981) may not represent the true distribution of the species. In August 1998 we collected a specimen (KU 157813) near the center of this broad region at Juniper Spring (T40S, R31E, SE1/4 SE1/4 Sec. 12), Harney County, Oregon (Fig. 3). Unfortunately, it was a juvenile and so could not be included in the present analyses. However, its occurrence in a region heretofore considered not occupied by the species, combined with the extremely restricted habitat occupied by the species (Carraway et al. 1993), suggests that additional effort to acquire specimens from the region might be productive. Scattered stands of either *Pinus edulis* or *Juniperus*, the appropriate vegetative habitats, occur over much of the region (Johnson 1995). Specimens from this region might provide additional insight into the relationship between those presently classified as *P. t. preblei* and *P. t. nevadensis*.

Overall, distributions of nominal races of *P. truei* in the northern Great Basin and environs based on our analyses of pelage color tend to support conclusions of previous researchers. In instances in which previous conclusions were not supported and for specimens from areas outside the previously known range of the species, distributions based on our color analyses are logical and suggest avenues for additional research on geographic variation in the species.

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- 1323–1324, 1326; CIMNH 639, 790–798, 801); T9S, R5W, Sec. 17 (BSU 1293–1294). NEVADA, **Churchill Co.:** 16 mi E Stillwater (USNM 93403–93404). **Clark Co.:** Charleston Mts. (KU 75703; USNM 26888/34304, 205558); Charleston Peak (USNM 26253/33659, 26268/33674, 26891/34307, 26894/34310, 26895/34311, 26899/34315, 26922/34338, 208980). **Elko Co.:** 0.5 mi W Debbs Cr., Pilot Peak (MVZ 68468–68473, 68475–68479*, 68480–68482). **Lander Co.:** Reese River, lat. 39 (USNM 93408). **Lincoln Co.:** 0.25 mi W UT–NV boundary+ (MVZ 59565); 3.5 mi N Eagle Valley (MVZ 48770); SW base Groom Baldy, T5S, R55/56E (MVZ 48753); E slope Irish Mts. (MVZ 48755, 48760, 48763); Meadow Valley (MVZ 48765); Panaca (USNM 28409/40513); 11 mi E Panaca (MVZ 48767, 48769); 2 mi S Pioche (MVZ 59562–59563); 2 mi SE Pioche (MVZ 59561, 59564). **Lyon Co.:** 2 mi SW Pine Grove (MVZ 64408, 64412, 64428); 3.5 mi SW Pine Grove (MVZ 64410). **Nye Co.:** Grapevine Mts. (USNM 28696/40800). **Pershing Co.:** S slope Granite Peak (MVZ 74174). **Washoe Co.:** 3 mi E Reno (MVZ 71072). **White Pine Co.:** Cheery Creek (MVZ 46226); Cleve Creek, T16N, R65E, NE1/4 (MVZ 46224); 8 mi N Lund (MVZ 53152–53159); Overland Pass, E slope Ruby Mts. (KU 47146); W side Ruby Lake (KU 47143–47145). OREGON, **Crook Co.:** at mouth Bear Creek (MVZ 87730–87732); mouth Bear Creek on Crooked River (MVZ 87727–87728); 13.5 mi S, 2.5 mi W Prineville (OSUFW 1635); 12 mi S, 2.5 mi E Prineville (UW 20029–20031). **Deschutes Co.:** 14 mi S, 10 mi E Bend (OSUFW 2753); Crooked River, 20 mi SE Prineville (USNM 78660*); 2 mi N, 4 mi E Redmond (OSUFW 2778); 3 mi N, 1 mi W Redmond (OSUFW 2232); 2 mi S, 1 mi E Redmond (OSUFW 2652); 3 mi N, 3 mi E Sisters (OSUFW 1508); 3 mi N, 4 mi E Sisters (OSUFW 2207); 9 mi N, 6.5 mi E Sisters (OSUFW 2651); 10 mi N, 4 mi W Sisters (OSUFW 2231); 2 mi S, 5 mi E Sisters (OSUFW 2887); 0.25 mi N, 4 mi W Terrebonne (OSUFW 5508); 1 mi N, 1 mi W Terrebonne (OSUFW 3084); 1 mi N, 3 mi W Terrebonne (OSUFW 3035); 1 mi S, 3 mi W Terrebonne (OSUFW 2989); 2 mi S, 8 mi W Terrebonne (OSUFW 2187); 3 mi W Terrebonne (OSUFW 2888, 2911, 3016, 3072, 3248, 3477, 3523, 4185–4192, 5154, 7070, 7896, 7971, 7982, 8095); 4 mi W Terrebonne (OSUFW 3432, 3862–3864, 5451). **Harney Co.:** 9 mi NE Riley (BSU 1304–1306); T24S, R25E, N1/2 Sec. 3 (KU 145222); T30/31S, R35E, Sec. 35/2 (KU 145215–145217, 145218). **Jackson Co.:** Brownsboro (USNM 262546); 7 mi S, 15 mi W Medford (OSUFW 3479); T38S, R2E, Sec. 22 (PSU 2717). **Jefferson Co.:** 10 mi S Madras (PSU 1256); 10 mi W Metolius (OSUFW 5144–5145, 5197). **Josephine Co.:** 13 mi SW Galice (USNM 203581–203584, 203587); Grants Pass (USNM 17276/24205, 32135/43947, 32137/43949, 203653); 2 mi N, 1 mi W Grants Pass (OSUFW 2478, 2487, PSU 2468); T39S, R7W, Sec. 34 (PSU 2716, 2718–2719). **Klamath Co.:** 0.7 mi N, 0.7 mi E Keno (PSU 2721). **Lake Co.:** Oatman Flat, 8 mi NW Silver Lake (PSU 1888); Oatman Flat, 7 mi N Silver Lake (PSU 882); Oatman Flat, 7 mi N, 1 mi W Silver Lake (PSU 680). UTAH, **Millard Co.:** Wah Wah Mts. (USNM 356962–356963). **Washington Co.:** 11 mi N St. George (USNM 327174, 327181); Mt. Meadows (USNM 167535–167537, 167542); Pine Valley (USNM 166769, 166776).

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APPENDIX 1. Specimens of *Peromyscus truei* examined. Type specimens indicated by an asterisk [*]. Localities followed by a plus [+] were not plotted on Figure 3. Museum acronyms follow Hafner et al. (1997).

U.S.A.—CALIFORNIA, **Del Norte Co.:** Gasquet (USNM 91540). **Siskiyou Co.:** 1.5 mi SW Edgewood (MVZ 69422, 69424–69426); 10 mi E Montague (MVZ 69413); 11 mi NE Weed (MVZ 69414–69416); Mayten (MVZ 13333). IDAHO, **Owyhee Co.:** T10S, R5W, Sec. 22/27 (BSU 1352–1359); T4S, R3W, Sec. 26, 1500 m (BSU 1285–1286, 1288–1290, 1292, 1315–1317, 1319–1320,

APPENDIX 2. Hue, value, and chroma with Munsell Color (1975) names for colors found in *Peromyscus truei* in the northern Great Basin and environs.

10YR2/1	Black	7.5YR3/2	Dark brown
10YR6/6	Brownish yellow	7.5YR3/4	Dark brown
10YR6/8	Brownish yellow	7.5YR6/6	Reddish yellow
10YR7/3	Very pale brown	7.5YR7/6	Reddish yellow
10YR7/4	Very pale brown	7.5YR7/8	Reddish yellow
10YR7/6	Yellow	7.5YR8/4	Pink
10YR7/8	Yellow	7.5YR8/6	Reddish yellow
10YR8/1	White	7.5YR2/0	Black
10YR8/3	Very pale brown		
10YR8/4	Very pale brown	5YR3/4	Dark reddish brown
10YR8/6	Yellow		
