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TAXONOMY AND DISTRIBUTION OF THE IDAHO GROUND SQUIRREL, *SPERMOPHILUS BRUNNEUS*

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ABSTRACT.—*Spermophilus brunneus* was found in isolated meadows surrounded by coniferous forests in Adams and Valley counties, Idaho, and also further south at lower elevations in the relatively xeric foothills north of the Payette River in Gem, Payette, and Washington counties. Marked differences in pelage coloration related to soil color exist between the disjunct northern and southern populations. Univariate and multivariate analyses of external, cranial, baculum, and pelage characters revealed significant sexual dimorphism in external and cranial characters and also that northern and southern *S. brunneus* are well-differentiated taxa. The bacula are about as distinct as those of *S. townsendii idahoensis* are from *S. washingtoni*, suggesting that the two *S. brunneus* may be approaching species-level differentiation. A change in soils, vegetation, and topography, but no apparent biogeographic barrier, separates the two taxa. Southern *S. brunneus* is described herein as a new subspecies.

The Idaho ground squirrel, *Spermophilus brunneus*, is endemic to west-central Idaho, but its exact range has not been reported and few details of its life history are known. The first specimens were collected by L. E. Wyman in 1913 and were described by A. H. Howell (1928) as *Citellus townsendii brunneus*, a subspecies of the Washington ground squirrel (presently, *S. washingtoni*—Howell, 1938). Howell (1938) raised the Idaho ground squirrel to species rank, *Citellus brunneus*, and this has not been challenged (Davis, 1939*b*; Hall and Kelson, 1959; Hall, 1981). *Spermophilus* is the generic name in current use (Hershkovitz, 1949), but *Cynomys* has priority if it is congeneric with *Spermophilus* (Dobson, 1985; Hafner, 1984).

Howell (1938) examined specimens from five localities and Davis (1939*b*) reported two additional sites. Later faunal works (Hall and Kelson, 1959; Larrison, 1967; Larrison and Johnson, 1981; Hall, 1981) have added no new localities.

Nadler et al. (1973) analyzed Giemsa-banded chromosomes of *S. brunneus*, and Nadler et al. (1974) studied blood transferrins by use of starch-gel electrophoresis; they speculated that *S. brunneus* was intermediate between, and possibly ancestral to, both the small-eared (*S. townsendii* and *S. washingtoni*) and large-eared (the remainder of subgenus *Spermophilus*) ground squirrels. Nadler et al. (1982) extended this phenetic analysis to other loci and to 21 Holarctic species of *Spermophilus*. They concluded that *S. brunneus* was most like the Eurasian *S. dauricus*, and that neither the morphologically similar *S. townsendii* nor *S. washingtoni* were sister groups to *S. brunneus*. Nadler et al. (1984) later concluded from a cladistic analysis of karyotypic evidence that *S. brunneus* was a sister group to the *S. townsendii* complex.

Because of its restricted and poorly known distribution, *S. brunneus* was listed as a species of concern by the U.S. Fish and Wildlife Service and by the Idaho Department of Fish and Game in 1978. This species was proposed as a candidate for threatened or endangered status by the U.S. Fish and Wildlife Service and a notice of review was published (Federal Register, 1985).

This study was undertaken to document the distribution of *S. brunneus*. However, field observations indicated a disjunct range with concordant differences in pelage coloration. These differences led to a reexamination of the taxonomy of *S. brunneus*.

METHODS

Approximately 650 man-hours were spent searching for sites with Idaho ground squirrels during February–July, 1979–1988. All localities known from published records (seven) or museum specimens (two additional localities) were visited. New localities were found by systematically searching the known range (Gem, Payette, Washington, Adams, and Valley counties). After finding several sites in this manner, other localities were found by studying aerial photographs and searching for habitat from a light aircraft, then visiting the areas so identified on foot or in a four-wheel drive vehicle. Searches also were made in areas outside the known range.

Specimens were prepared as conventional study skins and skulls, supplemented with postcranial skeletons in some cases. Bacula were prepared by clearing in 4% potassium hydroxide, staining with 0.002% alizarin red s, passing through increasing concentrations of glycerin, and storing in 100% glycerin (Lidicker, 1960).

Measurements of 115 specimens with fully erupted permanent dentition were used in the univariate analyses and measurements of those skulls without damage (92) were used in the multivariate analyses. Total length, length of tail, and length of hind foot were recorded from specimen label tags. In addition, 13 cranial and mandibular characters were measured with dial calipers to the nearest 0.1 mm. Skull characters (definitions provided by Cockrum, 1955) were as follows: greatest length of skull, zygomatic breadth, cranial breadth, postorbital breadth, length of nasals, greatest width of nasals, palatilar length, length of diastema, length of maxillary toothrow, condylo-alveolar length, and length of mandibular toothrow. Two additional measurements were palatal breadth between the alveoli of the third molars, and the distance between the alveolus of PM4 and the frontal bone at the anterior edge of the supraorbital notch (Robinson, 1973; Robinson and Hoffmann, 1975).

Bacula were measured to the nearest 0.1 mm by use of a dissecting microscope with a linear micrometer. Characters were total length, maximum width of disc, mid-shaft width, basal width, basal depth, number of spines on the right side of the disc, number of spines on the left side of the disc, number of posterior disc projections on the right side, number of posterior disc projections on the left side, and number of ventral or lateral projections of the shaft. Drawings of bacula were made by use of a reticle and graph paper.

Pelage characters were measured by carefully removing 10 blindly chosen hairs of each type (unbanded guard, banded guard, undercoat) from a 2-cm^2 area in the mid-dorsal region of randomly selected, nonmolting adults. Hair length was measured to the nearest 0.1 mm with a linear micrometer. Pelage and soil colors were described by use of Munsell soil color charts.

At 10 sites inhabited by each taxon, soil samples (200 g) were collected from the surface at three random locations, mixed in a paper bag, and sifted through a 2-mm mesh soil sieve to remove debris. A petri dish was filled with soil and reflectance values were obtained at 30-nm intervals from 415 to 685 nm by use of a Bausch & Lomb Spectronic 20 with reflectance apparatus.

The ground color of the squirrel's coat between spots was measured with the reflectance apparatus by placing a neutral gray mask with a 1-cm^2 opening mid-dorsally on the specimen. To avoid spots, the specimen was moved slightly until a low, stable reading was obtained. Three readings for each wavelength were averaged, and if any of the three readings differed by $>2\%$, the specimen was remeasured.

Specimens were assigned to five age classes based upon relative wear of the maxillary cheekteeth as follows: tooth wear class I (presumptive young of the year)—teeth not fully erupted, cusps unworn, no enamel lakes; II (presumptive yearlings)—permanent PM4 fully erupted, M3 unworn, small lakes may be present on cusps of other cheek teeth; III (presumptive adults)—lakes beginning to extend along protolophs and metalophs of M1 and M2, M3 with small lake; IV—teeth worn, lakes nearly continuous on protolophs and metalophs of most teeth; V—cusps worn nearly flat, lakes on protolophs and metalophs merge into one lake.

Univariate and multivariate analyses were performed by use of ONEWAY, NPAR, T-TEST, PLOT, MANOVA, and DSCRIMINANT modules of SPSS/PC+ (Norušis, 1986*a*, 1986*b*). Principal-components analysis was conducted by use of NTSYS-pc (Rohlf, 1988). Nested analysis of variance and the *G*-test were done with a hand calculator.

RESULTS

Specimens from the disjunct "southern" (lower elevation) portion of *S. brunneus*' range (Gem, Payette, and Washington counties; Fig. 1) had consistently paler colored, longer pelage than specimens from the "northern" (higher elevation) portion of the range (Adams and Valley counties). Because pelage color was consistent in both areas, the specimens were pooled for analysis into northern and southern groups.

Descriptive statistics indicated no significant skew or kurtosis for any character of either sex or geographic group. Box's M-tests were consistent with the hypothesis of multivariate normality. Results with $\log_{10}$-transformed and untransformed data were similar. Statistical results reported herein are for transformed data.

Univariate comparisons.—Samples were analyzed first for sexual dimorphism. For 15 of the 16 characters, males were larger than females ($\bar{X} = 2.44\%$ larger in northern *S. brunneus*, $\bar{X} = 2.57\%$ in southern *S. brunneus*). By use of one-way analysis of variance, 75% of the characters

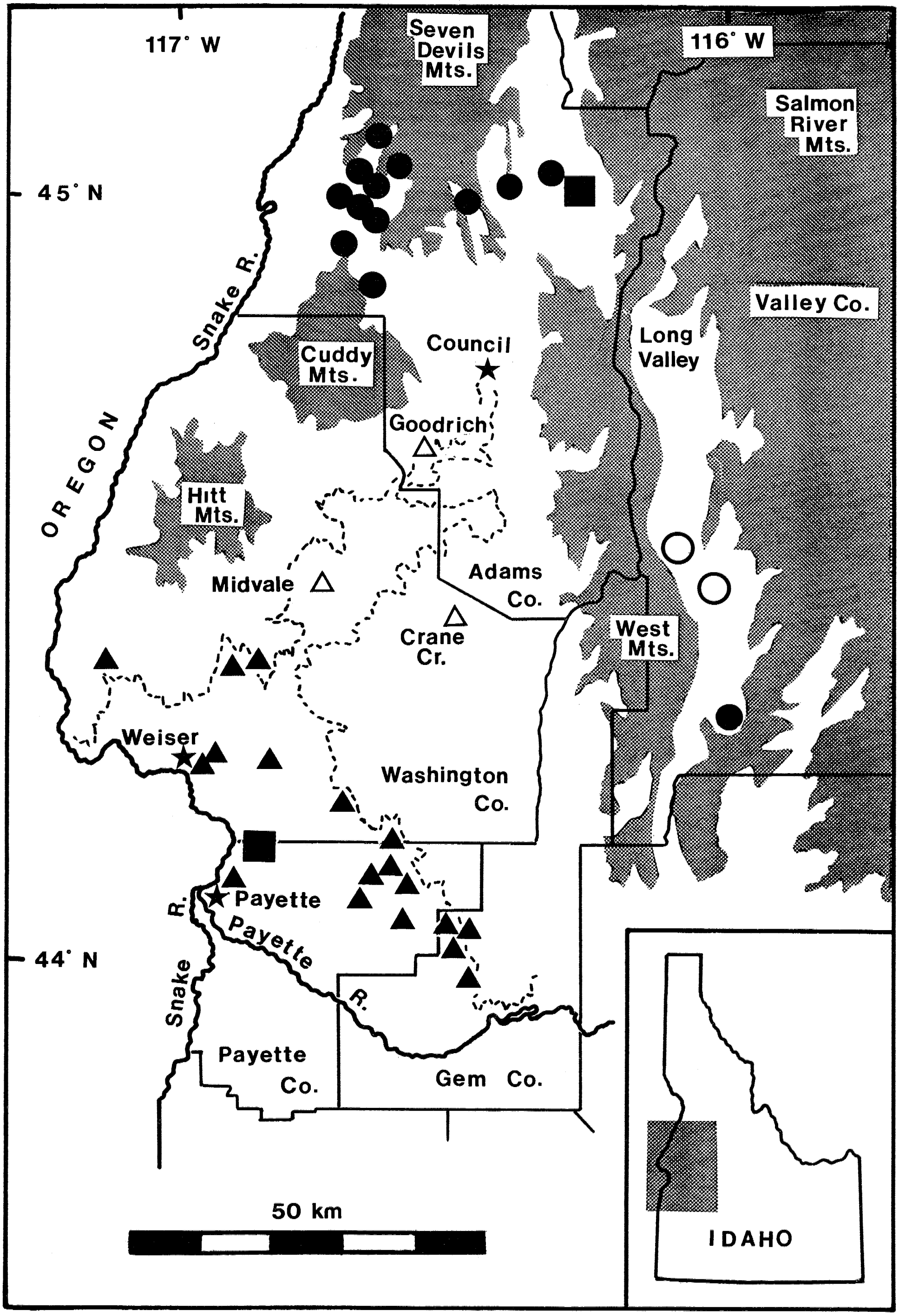

FIG. 1.—Distribution of *Spermophilus brunneus*. Symbols: solid, extant; open, extirpated; circles, northern *S. brunneus*; triangles, southern *S. brunneus*; squares, type localities. "Midvale Hill" runs diagonally to the southeast from the Hitt Mountains. Elevations above the 1,525-m contour interval are shaded; the 915-m contour interval is indicated by a dashed line. The Hitt, Cuddy, Seven Devils, and West mountains are predominantly basaltic, whereas the Salmon River Mountains are predominantly granitic.

TABLE 1.—*Means (±SE) for external and cranial characters (mm) and* F*-values (two sample analysis of variance) for univariate comparisons of sexual dimorphism and geographic differences in* Spermophilus brunneus.

	Northern populations					Southern populations					Geographic comparisons	
	♂		♀			♂		♀				
Character	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	Sexual dimorphism *F*-values	*n*	$\bar{X} \pm SE$	*n*	$\bar{X} \pm SE$	Sexual dimorphism *F*-values	*F*-values ♂	*F*-values ♀
Total length	15	233.7 ± 2.5	41	225.9 ± 1.9	5.12*	29	240.7 ± 1.7	24	233.4 ± 2.0	8.13**	5.90*	6.73*
Length of tail	15	54.0 ± 1.4	41	54.9 ± 0.9	0.28	29	55.1 ± 0.7	24	54.2 ± 1.1	0.56	0.69	0.23
Length of hind foot	15	35.0 ± 0.3	41	33.9 ± 0.2	8.97**	29	35.7 ± 0.3	24	34.8 ± 0.2	6.82*	2.74	7.28**
Greatest length of skull	15	39.0 ± 0.3	39	37.6 ± 0.2	20.75****	27	40.3 ± 0.2	19	39.2 ± 0.3	10.36**	12.45***	30.40****
Zygomatic breadth	15	25.2 ± 0.2	36	24.5 ± 0.1	7.74**	27	25.8 ± 0.2	20	25.1 ± 0.2	6.20*	3.94	8.30**
Least cranial breadth	15	17.5 ± 0.2	39	17.1 ± 0.1	6.16*	29	18.1 ± 0.1	20	17.7 ± 0.1	11.50**	17.87****	26.76****
Postorbital breadth	15	10.6 ± 0.1	40	11.0 ± 0.1	7.59**	29	10.4 ± 0.1	22	10.2 ± 0.1	1.50	2.77	48.91****
Greatest length of nasals	15	13.3 ± 0.2	40	12.9 ± 0.1	2.92	28	14.4 ± 0.1	22	14.0 ± 0.1	6.11*	21.13****	34.39****
Greatest width of nasals	15	5.8 ± 0.1	40	5.7 ± 0.0[a]	4.49*	29	6.0 ± 0.0[a]	22	5.9 ± 0.1	5.55*	5.85*	9.10**
Palatilar length	15	18.1 ± 0.1	40	17.4 ± 0.1	19.44****	28	18.9 ± 0.1	23	18.3 ± 0.1	11.63***	18.12****	48.28****
Length of diastema	15	9.0 ± 0.1	41	8.5 ± 0.1	18.55****	29	9.0 ± 0.1	22	8.5 ± 0.1	13.68***	0.38	0.07
Length of maxillary toothrow	15	8.1 ± 0.1	40	8.1 ± 0.0[a]	0.13	28	8.7 ± 0.0[a]	22	8.7 ± 0.1	0.16	77.17****	65.33****
Palatal breadth	15	4.6 ± 0.1	39	4.4 ± 0.1	4.27*	28	4.7 ± 0.0[a]	23	4.6 ± 0.1	2.58	4.58*	7.19**
Frontal height	15	10.3 ± 0.1	41	10.0 ± 0.1	15.22***	29	10.5 ± 0.1	21	10.3 ± 0.1	6.12*	2.50	17.64****
Condylo-alveolar length	15	23.1 ± 0.2	39	22.3 ± 0.1	11.74**	29	24.3 ± 0.1	22	23.5 ± 0.2	11.77**	26.14****	31.05****
Length of mandibular toothrow	15	7.7 ± 0.1	39	7.5 ± 0.1	3.01	29	8.2 ± 0.0[a]	22	8.0 ± 0.1	6.26*	60.03****	43.58****

[a] <0.1.
* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

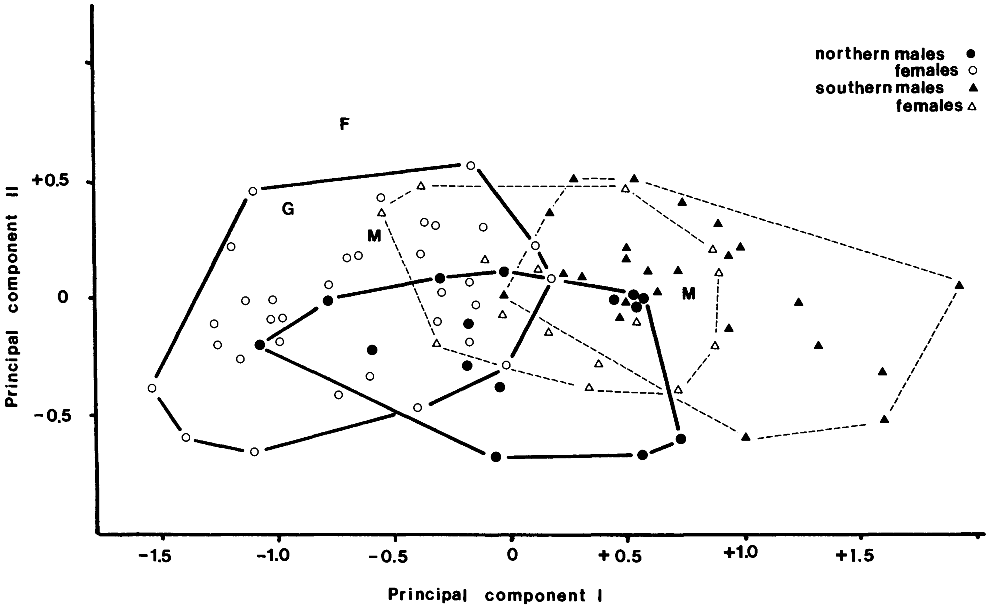

FIG. 2.—Plot of the first two principal components for external and cranial characters of 92 northern and southern male and female *Spermophilus brunneus*. Symbols refer to specimens indicating possible introgression: G, Goodrich female; M, Midvale males; F, Midvale female.

were significantly dimorphic in both subspecies (Table 1). The only character for which females were larger than males was the postorbital breadth in northern *S. brunneus,* which was significantly narrower in males than in females. Because of significant sexual dimorphism, males and females were not pooled in subsequent analyses.

Southern *S. brunneus* were significantly larger than the corresponding sex of northern *S. brunneus* in most measurements (Table 1). Females of the two groups differed significantly in more characters (14) than males (10).

Multivariate analyses.—A principal-components analysis was first used as an independent test of the validity of pooling the specimens into two groups based upon pelage differences and geographic distribution. The first three axes accounted for 73.9% of the variation. Axis I was interpreted as a size axis, whereas axes II and III were associated with length of tail and shape of the rostrum and palate. A projection of individual specimen scores onto the principal-components axes indicated four relatively distinct, but overlapping clusters showing within-group geographic homogeneity (Fig. 2). Consequently, the pooled geographic groups were accepted.

The principal-components ordination (Fig. 2) indicated relatively broader overlap between sexes in southern than in northern *S. brunneus*. When same sexes were compared, males of the two geographic groups were more separated than the females. As with the analysis of variance, differences between geographic groups were of greater magnitude than sexual dimorphism.

Multivariate analysis of variance was used to test the significance of sexual dimorphism and geographic differences in *S. brunneus*. Pillai's trace, Hottelling's trace, Wilk's criterion, and Roy's maximum root criteria were used to test the null hypotheses of no sexual dimorphism or geographic differences. Northern *S. brunneus* were significantly dimorphic ($P = 0.014$), but southern *S. brunneus* were not ($P = 0.277$). Same sex comparisons between the two geographic groups were highly significant ($P < 0.0001$) with all four test criteria.

Discriminant analysis was used to determine the characters contributing most to sexual and geographic differences in *S. brunneus*. The resulting two-group discriminant-analysis classification was correct in identifying the sexes of 83.3% of northern *S. brunneus* (Fig. 3a) and 82.5% of southern *S. brunneus* (Fig. 3b). Males were correctly classified into southern and northern

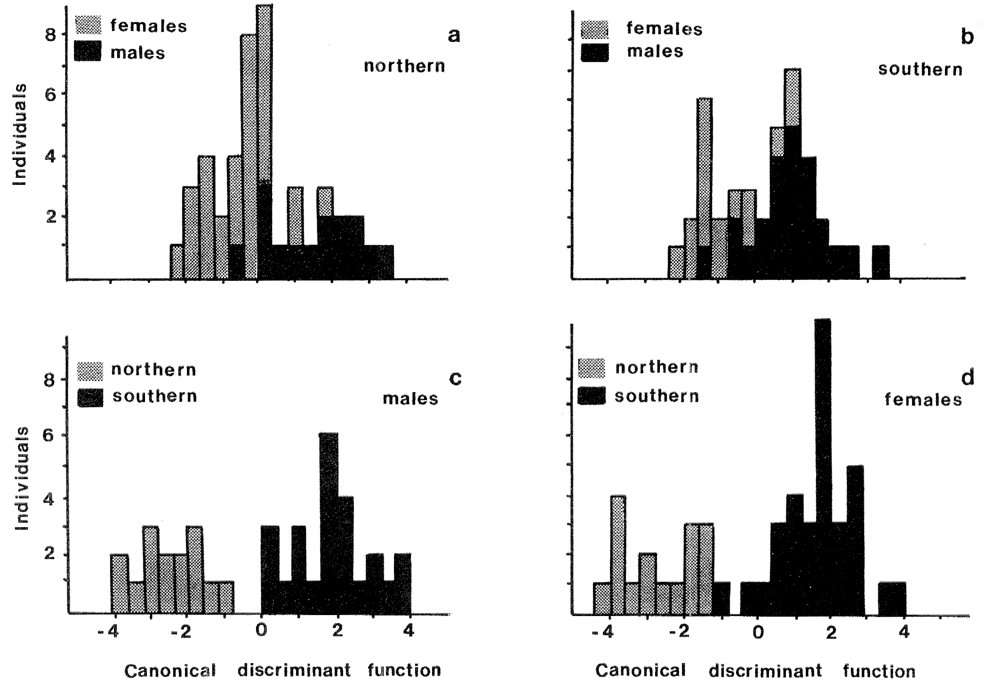

FIG. 3.—Histograms of discriminant scores for external and cranial characters: a, sexual dimorphism, northern *Spermophilus brunneus*; b, sexual dimorphism, southern *S. brunneus*; c, male northern *S. brunneus*-male southern *S. brunneus* comparisons; d, female northern *S. brunneus*-female southern *S. brunneus* comparisons.

groups in 100% of the cases (Fig. 3c) and 97% of the females were correctly classified by two-group discriminant analysis (Fig. 3d). Thus, the analysis showed about 17% error in discriminating between sexes within a geographic group, but virtually no error in same-sex comparisons of different geographic groups.

However, when all four groups were used in the analysis, the correctness of predicted group membership dropped considerably (northern males 73.3%, northern females 84.8%, southern males 75%, southern females 56.3%). Incorrectly classified specimens were placed with the opposite sex of the correct geographic group in all but three cases. This is shown further in a canonical plot of the four groups (Fig. 4).

Discriminant function axes I and II account for 84.8 and 12.0% of the total dispersion, respectively. Axis I was interpreted as a size axis related primarily to the length of the toothrow and adjacent structures, whereas axis II was related more to the extremities of the skull (greatest length, zygomatic width, nasals), and axis III was related to postorbital breadth. Eleven of 16 characters were used in the final classification. The best discriminating variables for separating northern from southern *S. brunneus* were (in descending order) length of the maxillary toothrow, palatilar length, condylo-alveolar length, length of the mandibular toothrow, length of nasals, and least cranial breadth.

Baculum comparisons.—Burt (1960), Meczynski (1971), Pocock (1923), and Wade and Gilbert (1940) studied bacula of several *Spermophilus* species, but the bacula of *S. brunneus*, the *S. townsendii* complex, and *S. washingtoni* remain undescribed. Differences in bacula frequently are indicative of reproductive isolation in mammals (Patterson and Thaeler, 1982), and the possibility that southern *S. brunneus* is reproductively isolated from northern *S. brunneus* must be entertained. Consequently, bacula of northern and southern *S. brunneus* were compared. Bacula of two geographically close and morphologically similar taxa, *S. townsendii idahoensis*

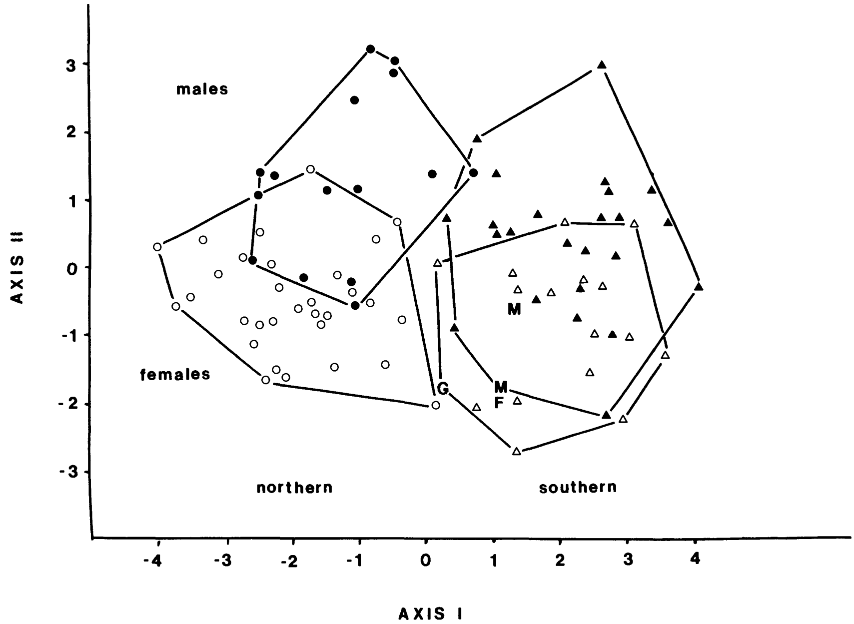

FIG. 4.—Canonical plots from discriminant-function analysis for 92 northern and southern *Spermophilus brunneus* based on 16 external and cranial characters. Symbols refer to specimens indicating possible introgression: G, Goodrich female; M, Midvale males; F, Midvale females.

and *S. washingtoni*, also were compared to *S. brunneus* to assess the magnitude of interspecific variation in the baculum among morphologically similar species of *Spermophilus*.

Like other members of subgenus *Spermophilus*, the baculum of southern *S. brunneus* had an expanded basal part, a corpus or shaft, and an asymmetrical, cupped disc or "spatula" with teeth or spines (Burt, 1960; Meczynski, 1971; Pocock, 1923; Wade and Gilbert, 1940). The stout shaft was twisted and arched slightly to the right (Fig. 5a). The disc was 1.3–1.6 mm wide with four to eight spines on each side (Table 2). The shape of the shaft tip was highly variable in all taxa examined.

In comparison, the baculum of northern *S. brunneus* was significantly shorter (Mann-Whitney *U*-tests, Table 2), the shaft was more delicate and arcuate than in southern *S. brunneus* (Fig. 5b), the disc was significantly narrower and had significantly fewer spines on each side, and there was a weak keel near the base of the shaft.

The baculum of *S. t. idahoensis* was shorter and narrower than the other two taxa with a narrower shaft and a well-developed keel always present below the base (Table 2). The number of spines was intermediate between northern and southern *S brunneus*. Seven of 11 specimens had projections on the shaft near the base of the disc (Fig. 5c).

Only two bacula of adult *S. washingtoni* were available for comparison. Both were shorter, more delicate, and more arcuate than those of *S. t. idahoensis* with a smaller disc with fewer spines and no keel below the base of the shaft (Fig. 5d).

The baculum is known to change with age in some mammals (Long and Frank, 1968). However, of 10 characters of the baculum, only mid-shaft width ($r = 0.584$, $P < 0.05$) and basal depth ($r = 0.502$, $P < 0.05$) were significantly correlated with tooth-wear class in southern *S. brunneus*. In northern *S. brunneus* none of the 10 characters was significantly correlated with tooth-wear class. In *S. t. idahoensis*, maximum width was negatively correlated ($r = -0.731$, $P < 0.05$) with tooth-wear class. Because only three of 30 correlations were significant, the size of the baculum probably is not correlated with age in these ground squirrels.

Individuals of tooth-wear classes I, and sometimes II, had bacula with shaft bases and peripheral

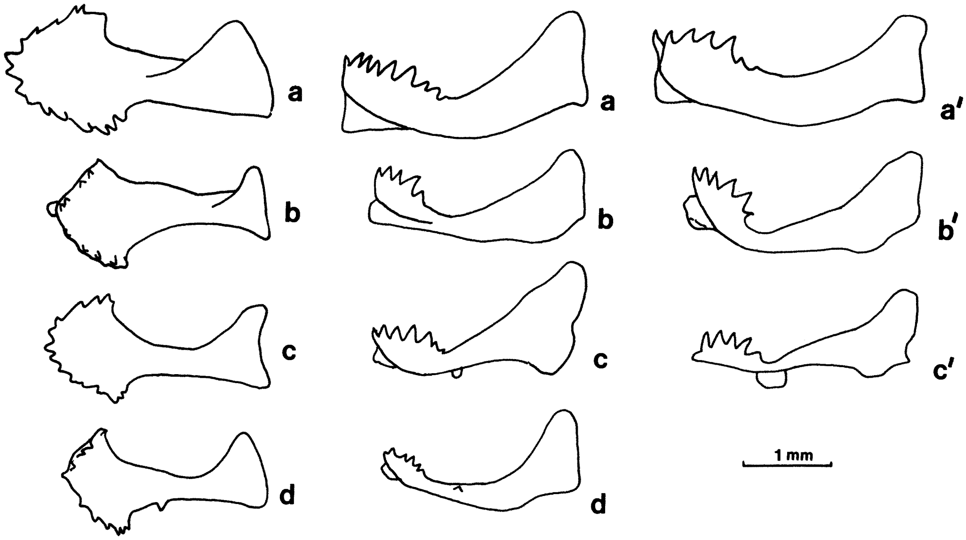

FIG. 5.—A representative example of bacula of ground squirrels (a–d, dorsal and lateral views) and a selected example to illustrate range of variation (a'–c', lateral views only): a, southern *Spermophilus brunneus*, CIMNH 231; a', CIMNH 239, b, northern *S. brunneus*, CIMNH 519; b', CIMNH 518; c, *S. townsendii idahoensis*, CIMNH 379; c', CIMNH 368; d, *S. washingtoni*, CIMNH 464.

portions of the discs with spines and projections still cartilaginous, but the entire structures were of adult size. Apparently, bacula reach adult proportions quickly, then ossify outward from the center of the disc and distal portion of the shaft. This observation may explain the paucity of significant correlations between age and size of the baculum.

The relationship between body size and size of the baculum was investigated by use of the length of the head and body as an index of overall body size (because of seasonal cycles of fat deposition, body mass could not be used). Within both groups of *S. brunneus* and in *S. t. idahoensis*, no significant correlations were found between the size of a ground squirrel's baculum and length of its head and body. However, in comparing taxa, mean length of the baculum increased with mean length of head and body in the two *S. brunneus* and *S. t. idahoensis*, but *S. washingtoni* had a relatively smaller baculum for its body size than the other three taxa (Table 2).

Long and Frank (1968) emphasized that bacula were more variable than cranial characters, and I found considerable intraspecific variation in the baculum also. Although some variation in baculum measurements may result from measuring small structures at an accuracy of only 0.1 mm, variation in such characters as numbers of spines is independent of this problem. However, despite the variation in bacula within taxa (Fig. 5), there were many significant differences among taxa in the 10 characters measured (Table 2).

A discriminant-function analysis based on characters of the baculum indicated that total length was the best discriminating variable, followed by maximum width of the disc, number of ventral or lateral processes, number of spines (right), basal width, number of posterior disc projections left, and number of spines (left). In the canonical plot of discriminant analysis (Fig. 6), axis I was interpreted as a measure of the width of the baculum, whereas axis II was a measure of the number of spines and projections. Axis III was negatively related to length of the baculum.

A prinipal-components analysis indicated a striking difference among bacula of *S. brunneus*. Although there is some overlap among *S. t. idahoensis*, *S. washingtoni*, and northern *S. brunneus*, bacula of southern *S. brunneus* form a cluster well separated in character space (Fig. 7).

Pelage.—*Spermophilus brunneus* has diffuse molt like other members of the subgenus *Spermophilus* (Hansen, 1954). Molt occurs in May and into early June in southern *S. brunneus* (12

TABLE 2.—*Means of lengths of head and body and baculum measurements (mm) of northern and southern* Spermophilus brunneus, S. townsendii idahoensis, *and* S. washingtoni. *Mann-Whitney* U_s*-values and significance levels for comparisons are shown.*

	Taxon				Comparison		
	S. brunneus						
Character	Southern	Northern	*S. townsendii*	*S. washingtoni*	Southern-Northern	Southern-*townsendii*	Northern-*townsendii*
n	18	8	11	2			
Length of head and body	184.4	182.0	183.2	186.0			
Total length	2.90	2.70	2.54	2.25	19.5**	10.5****	18.0*
Width of disk maximum	1.51	1.35	1.25	1.25	21.0**	0.0****	23.0
Width of mid-shaft	0.32	0.28	0.26	0.25	42.0*	42.0**	36.0
Basal width	1.06	0.96	0.85	0.90	26.5**	18.0***	16.5*
Basal depth	0.86	0.84	0.83	0.95	67.5	84.0	38.0
Number of spines (right)	5.72	4.12	5.45	4.50	12.5***	84.5	11.5**
Number of spines (left)	6.22	4.88	5.91	5.50	23.0**	85.0	22.5
Number of projections (right)	1.44	0.88	0.36	0.50	41.5*	22.0***	25.0
Number of projections (left)	1.56	0.38	0.64	0.50	27.0**	48.0*	30.5
Number of ventral projections	0.06	0.25	0.45	0.50	66.5	59.5*	32.0

* $P < 0.05$.
** $P < 0.01$.
*** $P < 0.001$.
**** $P < 0.0001$.

specimens collected 3 May–1 June were molting; 10 others had fresh pelts consistent with a molt during this period). In northern *S. brunneus*, molt was evident in eight specimens collected 2 June–2 July, and seven more collected in early June had just completed molt and must have molted during May. P. W. Sherman (pers. comm.) observed from the disappearance of dye on marked individuals of northern *S. brunneus* that molt occurs coincident with the time the young appear above ground (the end of lactation). For males it occurs a little later.

Mid-dorsal pelage in *S. brunneus* consists of undercoat; long, dark guard hairs; and shorter, dark guard hairs with one paler-colored band on the shield. The pattern of dorsal spots is a

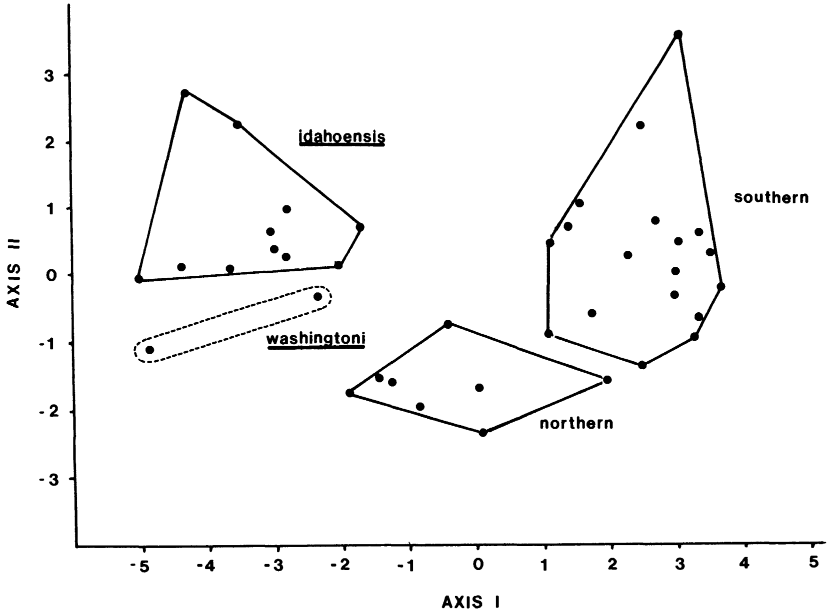

FIG. 6.—Canonical plot from discriminant-function analysis of 10 baculum characters for northern and southern *Spermophilus brunneus*, *S. townsendii idahoensis*, and *S. washingtoni*.

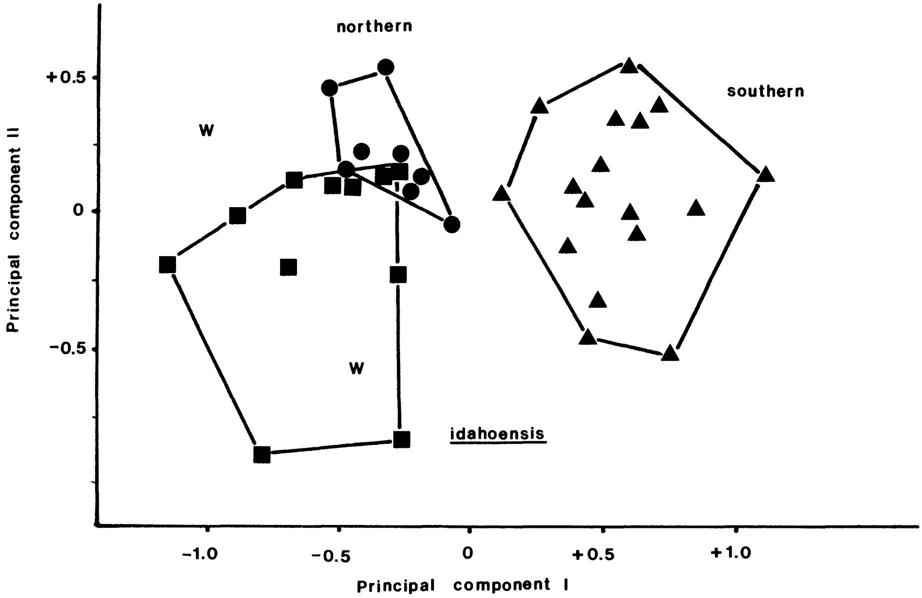

FIG. 7.—First two principal components of 10 baculum characters of northern and southern *Spermophilus brunneus* and *S. townsendii idahoensis*. The Ws indicate the positions in character space of the two bacula of *S. washingtoni*.

consequence of the juxtaposition of pale bands from adjacent guard hairs. The dorsal ground color is a consequence of the visual impact of the dark guard hairs, the nonjuxtaposed banded guard hairs, and the undercoat color. Bands are either yellowish-red (Munsell 5YR 5/8) or white, but the intensity of the pigment in the band varies from hair to hair. Undercoat is black basally turning to yellow-gray distally, or sometimes all black.

The visual impact of the ground color and spots is a dark, reddish-brown in northern *S. brunneus*. Southern *S. brunneus* appear grayish-brown (common) to brown (rare), depending upon the numbers of white as opposed to yellowish-red bands in the spots and the pigment intensity in the bands of the nonjuxtaposed guard hairs. The brown "phase" is distinct from the reddish-brown found in northern *S. brunneus*.

Most of the northern *S. brunneus* live on reddish soils, whereas most southern *S. brunneus* live on pale-gray soils. The selective value of pelage color to *S. brunneus* probably is related to camouflage. Raptors are predators of *S. brunneus* (Sherman, 1989) and common responses of *S. brunneus* to a raptor overhead are running to a burrow entrance and looking out or remaining motionless (P. W. Sherman, pers. comm.).

The correspondence between soil color and color of the dorsal pelage was explored by use of a reflectance apparatus. Both soil color and pelage coloration were consistently paler in samples from the range of southern *S. brunneus* than northern *S. brunneus* (Fig. 8). The differences between soil color in the two geographic areas were significant (*t*-tests) at all 10 wavelengths and the differences between northern and southern squirrels were significant (*t*-tests) at eight of 10 wavelengths.

Nonmolting, adult, southern *S. brunneus* had consistently longer pelage than northern *S. brunneus*. The mean (±*SD*) length of the unbanded, dark guard hairs was 13.62 ± 0.27 and 11.25 ± 0.68 mm, respectively ($n = 10$ for both). The mean length of banded guard hairs was 11.32 ± 0.34 and 9.60 ± 0.66 mm, and the mean length of the undercoat was 7.28 ± 0.38 and 6.41 ± 0.17 mm, respectively. These differences in lengths of hair were significant (nested analysis of variance: dark guard hairs, $P < 0.0001$; banded guard hairs, $P < 0.0001$; undercoat, $P < 0.0001$). Differences in length of hair between geographic groups accounted for 87.0, 65.2,

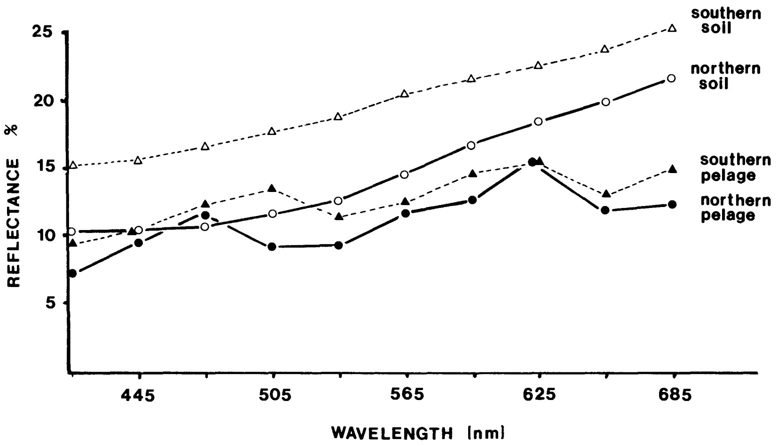

FIG. 8.—Mean percent reflectance of soils and mid-dorsal pelage for northern and southern *Spermophilus brunneus*. All soil differences and seven of 10 pelage differences were significant.

and 46.7% of the variation in dark guard hairs, banded guard hairs, and lengths of undercoat, respectively. There also were significant differences among squirrels ($P < 0.01$), but these differences accounted for a much lower proportion of the variation (7.9, 9.9, and 6.4%, respectively). Reasons for shorter pelts at higher elevations are not clear. Because the active season is 1–2 months later at higher elevations, both squirrels may be exposed to similar temperature regimes.

Life history.—Southern *S. brunneus* emerge in late January or early February and cease aboveground activity in late June or early July. Northern *S. brunneus* emerge in late March or early April and cease aboveground activity in late July or early August. Northern *S. brunneus* occur ca. 500–600 m higher in elevation where snow melt occurs 1–2 months later in spring and green vegetation desiccates there about 1 month later in summer. As with other *Spermophilus* (Michener, 1984; Smith and Johnson, 1985), adult males emerge first, followed by adult females, then yearlings. Entrance into seasonal torpor is in approximately the same order, with pups active ca. 1 month later than adult males.

Pigmented sites of implantation (placental scars) and embryos were counted on all females collected. There was no correlation between counts of placental scars and tooth-wear class in either geographic group. Counts of placental scars were significantly greater in southern *S. brunneus* (range, 5–10, $\bar{X} \pm SD = 7.5 \pm 1.74$, $n = 14$) than in northern *S. brunneus* (range, 2–9, $\bar{X} = 6.2 \pm 1.47$, $n = 26$) (t-test, $P < 0.05$). D. P. Struebel (pers. comm.) also counted placental scars on southern *S. brunneus*; his data were similar to mine (range, 4–10, $\bar{X} = 7.3 \pm 1.80$), although 35 of 38 squirrels were from one locality.

The same collecting techniques were used for both taxa (shooting), and collecting primarily was done 1 month postemergence and 1 month preimmergence in both areas. However, of squirrels with tooth wear greater than class I ($n = 115$), the ratio of males to females collected was ca. 1:2.6 in northern *S. brunneus* and ca. 1.5:1 in southern *S. brunneus*. These ratios are significantly different from an expected 1:1 ratio (G-test; $P < 0.01$). This may reflect behavioral differences between the sexes that affect vulnerability to shooting in the two geographic groups, although real sex ratio differences also may exist.

The mean tooth wear of the 115 specimens was class 2.8 for southern males, 2.8 for southern females, 3.7 for northern males, and 3.7 for northern females. These differences were significant (same sex comparisons, Mann-Whitney U-tests, $P < 0.01$). If tooth wear is a reliable index of age in Idaho ground squirrels, the mean life expectancy of southern *S. brunneus* is considerably shorter. Although southern *S. brunneus* has not been studied, there appear to be differences in behavior, longevity, and reproductive strategy between the two groups.

TABLE 3.—*Pearson product-moment correlation coefficients between tooth-wear class and 16 external and cranial characters in northern and southern populations of* Spermophilus brunneus. *Only specimens of classes II–V were used in the analysis.*

	Northern		Southern	
Character	Males	Females	Males	Females
n	9	23	19	13
Total length	0.020	0.099	0.180	0.232
Length of tail	−0.217	0.151	−0.074	−0.092
Length of hind foot	−0.201	0.166	0.075	−0.312
Greatest length of skull	0.196	0.541**	0.586**	0.232
Zygomatic breadth	0.312	0.516*	0.597**	0.293
Least cranial breadth	−0.261	0.171	0.292	0.048
Postorbital breadth	−0.714	−0.290	−0.510*	−0.496
Greatest length of nasals	0.270	0.012	0.491*	0.185
Greatest width of nasals	0.404	0.230	0.345	0.112
Palatilar length	0.135	0.448*	0.290	0.507
Diastema	0.270	0.551**	0.518	0.527
Length of maxillary toothrow	0.005	0.123	0.009	−0.549
Palatal breadth	−0.035	−0.508*	−0.432	−0.406
Frontal height	0.601	0.163	0.537*	−0.245
Condylo-articular length	0.409	0.447*	0.448	0.212
Length of mandibular toothrow	0.300	0.216	0.264	0.183

* $P < 0.05$.
** $P < 0.01$.

Age and cranial measurements.—Robinson and Hoffmann (1975) assumed there was no relationship between cranial measurements and age after the teeth were fully erupted. However, if growth were indeterminate, all comparisons should be made between similar age classes, as is the case in some other groups of rodents (*Peromyscus truei*—Hoffmeister, 1951).

Although tooth wear and dimensions of the baculum were not correlated, 13 of 64 correlations between tooth wear and the 16 external and cranial characters were significant. Some characters in at least one sex and geographic group continue to change in size throughout life (Table 3). Postorbital breadth decreased with age in males and was the one character showing reverse sexual dimorphism.

Ideally, same-age-class comparisons should have been made in this study; however, much larger samples of this rare species would be required. Nevertheless, the bias introduced is conservative, because southern *S. brunneus* is both younger and larger than northern *S. brunneus*. If greater numbers of older specimens were available to permit comparisons by age class, the morphometric differences between the two Idaho ground squirrels would be even greater than those reported herein.

DISTRIBUTION

Spermophilus brunneus is known from a five-country area in west-central Idaho ca. 125 km north to south and 90 km east to west. Most of this range coincides with the Weiser Embayment of the Miocene-age Columbia River basalt lavas (Fitzgerald, 1982), although the three Valley Co. sites are on soils derived from the Idaho batholith (Fig. 1, Salmon River Mountains and portions of the West Mountains).

Northern Spermophilus brunneus.—This squirrel has been collected at 17 sites (Fig. 1, Appendix I), but is now extirpated at three of them. It was seen at seven additional sites in Adams Co., all within 5 km of collecting localities. Populations are small (<200 individuals) and often isolated by several kilometers. These populations occur on a tableland between the Cuddy and Seven Devils mountains, in the valleys to the east (Lost Valley Reservoir, Price Valley, New Meadows), and in Long Valley further east and south. There are divides of 250 and 350 m elev. between these three areas. The main concentration of northern *S. brunneus* is in a large meadow complex near Bear (Adams Co.) measuring about 10 by 30 km, but the squirrels (21 sites combined) actually occupy <500 ha.

These localities generally are in drier meadows surrounded by Ponderosa pine (*Pinus ponderosa*) and Douglas-fir (*Pseudotsuga menziesii*) forests between 1,150 and 1,550 m elev. Mesic meadows in this area frequently are inhabited by Columbian ground squirrels (*S. columbianus*). Northern *S. brunneus* occurs in mesic meadows in the absence of *S. columbianus*.

The xeric meadows typically have a shallow (<1 m to bedrock), reddish-brown to yellowish-red (Munsell soil colors 5YR 3-4/4-6) skeletal-loam or clay-loam soil weathered from Miocene-age Columbia River basalt (Fitzgerald, 1982). Vegetation in these drier meadows often is dominated by stiff sage (*Artemisia rigida*) or mountain big sage (*A. tridentata vaseyana*), with *Lomatium* sp., *Sedum stenopetalum*, *Allium* sp., *Gilia aggregata*, *Brodiaea douglasii*, various bunchgrasses, and other forbs.

Southern Spermophilus brunneus.—This ground squirrel occurs at 670–975 m elev. in the low, rolling hills and valleys north of the Payette River in Gem, Payette, and Washington counties. Its range (Fig. 1) is bounded on the south by the Payette River, on the west by the Snake River, and on the northeast by lava flows with little soil development.

Spermophilus t. idahoensis occurs south of the Payette River. The habitat is similar on both sides of the river, but there is no evidence that *S. brunneus* has ever occurred south of the river (Davis, 1939*a*, 1939*b*; W. B. Davis, in litt.). However, L. E. Wyman (in litt.) noted that *S. townsendii* (modern nomenclature) occurred north of the Payette River in the bottomland on the east (Idaho) side of the Snake River between Payette and Weiser, and *S. brunneus* (modern nomenclature) occupied higher ground away from the river. This bottomland has since been converted to agricultural use and I have not been able to find *S. townsendii* north of the Payette River. However, *S. townsendii* apparently occupied the more mesic habitats and *S. brunneus* was confined to more xeric areas.

Southern *S. brunneus* is parapatric with *S. columbianus* in an area known locally as Midvale Hill. The microdistributions of the two species interdigitate, with *S. columbianus* occuping more mesic sites (higher elevations to the north or in the valley bottoms) and *S. brunneus* occupying more xeric sites. These ecological situations are analogous to those described by Durrant and Hansen (1954) and Turner (1972) for other *Spermophilus*.

Throughout the range of southern *S. brunneus*, soils generally are pale colored and were formed by granitic sands, silts, and clays from the Boise Mountains to the east and were deposited by Pliocene Lake Idaho and Pleistocene streams (Troeh et al., 1958). The region formerly was dominated by big sagebrush (*A. tridentata*), bitterbrush (*Purshia tridentata*), and bunch grass associations, but during the 1950s and 1960s the area was invaded by exotic annuals; subsequent range fires converted it to annual grassland dominated by medusa-head rye (*Taeniatherium asperum*) and cheatgrass (*Bromus tectorum*) with relict big sagebrush and bunch grasses.

Specimens of southern *S. brunneus* have been collected from 24 sites, and I have observed this taxon at several other nearby localities, all within 5 km of collecting localities. Southern *S. brunneus* is generally, but patchily, distributed throughout its restricted range. There are no potential barriers to gene flow among the sites in Gem, Payette, and Washington counties, in contrast to the isolated populations found in northern *S. brunneus*. The Weiser River could be crossed readily by ground squirrels (Davis, 1939*a*).

Southern *S. brunneus* formerly occurred in the large basin (the Midvale-Crane Creek-Goodrich areas) between the present distributions of northern and southern *S. brunneus* (Fig. 1). Unfortunately, these populations apparently are extirpated. Because of the possibility that these specimens might be intergrades, they were excluded from the initial discriminant analysis. A second discriminant analysis including all specimens was used to classify these geographically intermediate specimens. There were four specimens of tooth-wear class II available for multivariate analysis (3 Midvale, 1 Goodrich), and discriminant analysis classified all four with southern *S. brunneus*. Principal-components analysis can be useful in detecting hybrids (Wiley, 1981). In the principal-components ordination, the Goodrich specimen and two of the Midvale specimens occurred far outside of the appropriate envelope (Fig. 2), indicating that there may have been some introgression in the Midvale-Crane Creek-Goodrich basin (Fig. 1).

There are no obvious biogeographic barriers between Goodrich (850 m elev.) and the nearest northern *S. brunneus* site 19 km to the northwest and 250 m higher in elev., although there is a 5–8 km long "bottleneck" at the mouth of Hornet Creek near Council that might restrict gene flow. However, in this 19-km gap the topography changes abruptly from low, rolling hills to steep mountain slopes and the vegetation changes from sagebrush-bunchgrass associations to coniferous forest with scattered xeric meadows, some of which are inhabited by northern *S. brunneus*. All southern *S. brunneus* sites were at elevations <975 m, whereas all northern *S. brunneus* sites were at elevations >1,150 m.

TAXONOMY

The differences in external and cranial morphometrics, bacula, color of pelage, length of pelage, life histories, and biogeographic evidence indicate that northern and southern *S. brunneus* are taxonomically distinct. Because New Meadows, Adams Co. is the type locality for *S. brunneus*, southern *S. brunneus* is the undescribed taxon. There is a possibility that these two allopatric, sister taxa have reached species-level separation. Unfortunately, the significance of baculum variation in speciation events has not been studied in the genus *Spermophilus*. It seems prudent to describe southern *S. brunneus* as a subspecies rather than a species until more is known about it.

Spermophilus brunneus endemicus, new subspecies

Holotype.—USNM 565927. This is a female collected 30 March 1989 by E. Yensen, original number 932, preserved as a standard study skin and skull. The specimen was pregnant with six live (35 mm crown-rump length) and three dead (10 mm) embryos. Standard measurements (mm) were: total length, 243; length of tail, 61; length of hind foot, 36; length of ear 15; weight 194.9 g.

Type locality.—Idaho: Payette Co.; Sand Hollow, 1 km E (up canyon from) OX Ranch headquarters; T9N, R4W, Sec. 7, NE ¼; 5.6 km N, 5.0 km E Payette; elev. 750 m in rangeland dominated originally by big sagebrush and bunchgrasses and now invaded by cheatgrass and medusahead rye.

Distribution.—The range includes portions of Gem, Payette, and Washington counties, Idaho (Fig. 1).

Etymology.—The name *endemicus* is derived from the Greek "endemos" and refers to the restricted range of this taxon.

Diagnosis.—This subspecies differs from the nominate subspecies in its paler, reddish-gray rather than yellowish-red dorsal ground color, more numerous white rather than pale yellowish-red dorsal spots, significantly longer pelage, larger external and cranial measurements, and larger baculum with more spines.

Description.—A relatively small member of subgenus *Spermophilus*, the total length is 220–258 mm (males) and 216–255 mm (females), and the length of hind foot is 33–39 mm (males) and 32–37 mm (females). The tail is short, 49–61 mm (males) and 39–62 mm (females). The ear is moderate (12–19 mm from notch to tip of pinna). Measurements of the type (mm) are as follows: greatest length of skull, 40.5; zygomatic width, 25.2; least cranial breadth, 18.0; postorbital breadth, 9.9; greatest length of nasals, 13.4; greatest width of nasals, 5.7; palatilar length, 18.6; length of diastema, 8.4; length of maxillary toothrow, 9.0; palatal breadth between third molars, 4.6; frontal height, 10.0; condylo-alveolar length, 23.7; length of mandibular toothrow, 8.2.

The dorsal surface of the rostrum, posterior portion of hind legs, perianal area, and ventral base of tail are rufous (Munsell 5YR 5/8, yellowish-red), the dorsal ground color is dark-reddish gray (Munsell 5YR 4/2.5), and the dorsal spots are white to pale, yellowish-red. The pale reddish-brown (Munsell 5YR 6-6.5/3.5-4) lateral line is poorly defined. The eye ring, throat, and front legs are white. The venter is gray as a result of white-tipped, black hairs. The tail has yellowish-red hairs below and a mixture of all dark, single- and triple-banded shield guard hairs above, giving a variegated appearance. Spots may cover ≤50% of the mid-dorsal surface, as opposed to usually ≤30% in *S. b. brunneus*.

DISCUSSION

Because pelage differences between the two Idaho ground squirrels are so striking, it is surprising that *S. b. endemicus* was not recognized as a distinct taxon by Howell (1938) or Davis (1939*b*). However, Howell had a total sample of 14 *S. brunneus*. The only *S. b. endemicus* were a series from Weiser and Midvale in the Biological Survey Collection (USNM), collected late in the active season; the specimens were fat and discolored by grease. Davis examined 22 specimens from the Ralph Ellis Collection (KU). Six of the seven southern specimens were tooth-wear class I and the other was tooth-wear class II; he reasonably attributed the taxonomic differences to juvenile pelage (Davis, 1939*b*).

Given the differences in baculum between the two Idaho ground squirrels, reproductive isolation might be expected. However, the variability in characters of the baculum, especially the number of teeth, seems to argue against this. There are no comparable data on variation in bacula in other *Spermophilus*, although Meczynski (1971) noted variation in the presence of a lateral tooth on the shaft of the baculum of *S. citellus*. The teeth on the baculum may fit into vaginal rugae (Meczynski, 1974) during copulation, but there are no data on variation in vaginal rugae or how baculum shape acts as an isolating mechanism.

An alternative explanation for the differences in bacula is that they were clinal rather than the result of reproductive isolation between the two *S. brunneus*. Instead of reproductively isolating the two Idaho ground squirrels, the large baculum of *S. b. endemicus* may have been an isolating mechanism to prevent intergradation between it and the parapatric *S. t. idahoensis* to the south. As southern bacula diverged further, this may have restricted gene flow between northern and southern portions of the range of *S. brunneus*. Unfortunately, no bacula are available from the Goodrich or Midvale areas.

Postorbital breadth was the only character in which northern *S. brunneus* was significantly larger than southern *S. brunneus*. The character also showed females to be larger than males. Postorbital breadth is a character that varies inversely with age, especially in males in other sciurids (Hoffmann et al., 1979; Pizzimenti, 1975). Given the older age distribution and smaller size of northern *S. brunneus*, northern males would be expected to have narrower postorbital breadths than southern males. This was not the case, and indicates an additional difference between the two taxa.

Tooth wear as an index of age is subject to bias because the plant species growing in the ranges of the two subspecies are almost completely different. Dissimilar rates of wear could result from different diets. Also, the teeth presumably are not used during seasonal torpor, so that the amount of wear late one season should be similar to the amount of wear early in the next season, although in the second instance the animal is nearly 1 year older. Pending an investigation of tooth wear, no attempt was made to assign absolute ages to tooth-wear classes.

The greater number of placental scars in *S. b. endemicus* (7.5 as opposed to 6.2 in *S. b. brunneus*) implies a greater reproductive rate, whereas the mean tooth-wear class (2.8 and 3.7, respectively) implies a younger population (greater mortality). These compensating life-history traits are another indication that *S. b. endemicus* is under different selective pressures than *S. b. brunneus*.

The available evidence thus suggests that the two Idaho ground squirrels are well-differentiated subspecies that may be reaching species-level separation. The presence of the two taxa in a small geographic area is biogeographically interesting. Unfortunately, the limited ranges and small breeding populations also make them vulnerable to a variety of threats.

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APPENDIX I

Specimens Examined

A total of 188 specimens was examined. Many of these were juveniles or had damaged skulls. Numbers in parentheses indicate specimens used in statistical analyses. Collection acronyms are as follows: Boise State University (BSU); College of Idaho (CIMNH); Idaho Museum of Natural History (IDAHO); Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); University of Idaho (UIDA); University of Kansas (KU); National Museum of Natural History (USNM).

Spermophilus brunneus brunneus.—ADAMS CO.: Mill Creek, T18N, R3W, Sec. 25, 4,500 feet, 4 (1) BSU, 8 (6) CIMNH; 1 mile E Paradise Flat, T19N, R3W, Sec. 34, 3 (2) CIMNH; Lick Creek, T19N, R3W, S11, 2 (1) CIMNH; 4 miles S Bear, 2 UIDA; 3 miles S, 0.5 mile E Bear Post Office, 8 (1) KU; 2 miles S Bear, 1 CIMNH; Bear Cemetery, 11 (8) CIMNH; 1 mile N Bear Guard Station, 17 (10) KU, 1 (1) CIMNH; Cold Springs Creek, T20N, R2W, Sec. 22–23, 1 (1) BSU, 2 CIMNH; Summit Gulch, T19N, R3W, Sec. 9, 15 (9) CIMNH; Slaughter Gulch, 1 mile N Lost Valley Reservoir, T19N, R1W, Sec. 16, 3 CIMNH; Price Valley, T19N, R1W, Sec. 2, 2 (2) CIMNH; Little Mud Creek, T20N, R1E, Sec. 28, 6 (3) CIMNH; New Meadows, T19N, R1E, Sec. 11, 2 (2) USNM (including holotype), 3 (3) CIMNH.

VALLEY CO.: Van Wyck 1 (1) USNM; 2 miles S Cascade, 3 (3) USNM; Round Valley, 2 (2) USNM; 1 (1) CIMNH.

Spermophilus brunneus endemicus.—GEM CO.: 0.9 mile E Big Willow Creek, 1 (1) CIMNH; Sucker Creek, 11 miles N Emmett, 22 (13) CIMNH; Sucker Creek, 0.1 mile E Payette Co. line, 1 (1) CIMNH; 7 miles N Emmett, 2 (2) CIMNH.

PAYETTE CO.: Stone Quarry Gulch, T9N, R3W, Sec. 33, 1 BSU; Big Willow Creek, T8N, R2W, Sec. 4, 1 (1) BSU, 2 (2) CIMNH; Little Willow Creek, T9N, R3W, Sec. 13, 1 (1) BSU, 2 (1) IDAHO; Little Willow Creek, T9N, R3W, Sec. 15, 4 (1) IDAHO; 1 mile N Payette, 1 CIMNH; Dry Creek, T9N, R2W, Sec. 18, 4 (4) CIMNH; Sand Hollow, T9N, R4W, Sec. 8 (holotype) 1 (1) USNM, 1 (1) MVZ.

WASHINGTON CO.: Weiser, 6 (6) USNM; 1.7 miles N Weiser, 1 UIDA; 5.1 miles N Weiser, 1 BSU; Mann Creek at U.S. highway 95, 1 BSU; Mann Creek 2.5 miles N Weiser River Road, 8 (5) CIMNH; Weiser

Cove, T10N, R3W, Sec. 8, 6 (4) CIMNH; 14.5 road miles S Midvale, 1 UIDA; SW end Mann Creek Reservoir, T13N, R5W, 2 (1) IDAHO; Little Willow Creek, T10N, R3W, S36, 1 (1) IDAHO; Henley Basin, T12N, R7W, S2, 10 (7) CIMNH; Midvale, 3 (3), USNM; Crane Creek, 15 miles E Midvale, 5 (1), KU.

ADAMS CO.: Goodrich, 1 (1), USNM.