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Spermophilus brunneus.

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Spermophilus brunneus (A. H. Howell, 1928)

Idaho Ground Squirrel

Citellus townsendii brunneus A. H. Howell, 1928:211. Type locality "New Meadows, Adams County, Idaho."
Citellus brunneus A. H. Howell, 1938:72.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognatha, Family Sciuridae, Subfamily Sciurinae, Tribe Marmotini, Genus *Spermophilus*, Subgenus *Spermophilus* (Hoffmann et al. 1993). Davis (1939) divided the Nearctic members of subgenus *Spermophilus* into "large-eared" and "small-eared" species groups, with *S. brunneus* in the large-eared group. Currently, two subspecies of *S. brunneus* are recognized:

S. b. brunneus (Howell), 1928:211, see above.
S. b. endemicus Yensen, 1991:596. Type locality "Sand Hollow, 1 km E (up canyon from) OX Ranch headquarters; T9N, R4W, Sec. 7, NE 1/4; 5.6 km N, 5.0 km E Payette, elev. 750 m, Payette Co., Idaho."

Howell (1928) originally described *S. brunneus* as a subspecies of *S. townsendii*. In 1938, Howell described *S. washingtoni* and elevated *S. brunneus* to species status. He made it clear that he had thought *S. brunneus* was a subspecies of what is now *S. washingtoni*, not a member of the *S. townsendii* complex (Howell, 1938; Scheffer, 1946). The two allopatric subspecies of *S. brunneus* are significantly different in bacular morphology, cranial morphometrics, pelage color and texture, annual cycles (Yensen, 1991), and allozyme frequencies (Gill and Yensen, 1992), suggesting that they are actually distinct species.

DIAGNOSIS. Compared to congeners, *Spermophilus brunneus* (Fig. 1) is recognized by a combination of small size (head and body <200 mm, hind foot <40 mm); medium-sized pinnae (13–18 mm), short tail (39–65 mm); brownish dorsal coloration with light spots; rufous legs, nose, and ventral tail surface; and sharply contrasting off-white eye ring (Davis, 1939; Howell, 1938; Yensen, 1991).

Compared to the similar-sized *S. townsendii* (sensu latu), *S. brunneus* has much larger pinnae (13–18 vs. 6–9 mm), browner dorsal coloration, a spotted rather than flecked dorsum, less distinct lateral line, smaller auditory bullae, and a shorter, wider rostrum. Compared to *S. washingtoni*, *S. brunneus* has larger pinnae (13–18 vs. 10–13 mm), darker brown dorsal coloration, less distinct dorsal spots, less contrasting lateral line, and larger and more intensely pigmented rufous patches above the nose and on the thighs. *S. brunneus* is distinguished from *S. columbianus* by its much smaller size (total length <258 mm vs. >320 mm), lack of rufous color on the throat, and less bushy, shorter tail (<65 mm vs. >80 mm). *S. beldingi*, *S. elegans*, and *S. armatus* are all larger (head plus body length >200 mm), more gray-colored than *S. brunneus*, and are unspotted (Davis, 1939; Howell, 1938; Hall, 1981; Yensen, 1991). Keys to species of *Spermophilus* are presented in Hall (1981), Howell (1938), and Rickart and Yensen (1991).

GENERAL CHARACTERS. *Spermophilus brunneus* is a small, brownish, dorsally-spotted ground squirrel with a short tail and medium-sized pinnae. Adult measurements (n = 109; in mm; for means and standard errors see Yensen, 1991): total length, 209–258; length of tail, 39–65; length of hind foot, 32–39; length of ear, 13–18; greatest length of skull, 36.1–42.5; zygomatic breadth, 23.1–27.7; length of palate, 16.3–20.1; cranial breadth, 16.2–18.9; interorbital breadth, 7.5–9.2 (Howell, 1938); postorbital constriction, 9.2–11.8; length of nasals, 11.6–16.5; maxillary tooth row, 7.4–9.1. The skull (Fig. 2) has a relatively short rostrum and broad braincase. The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. The upper toothrows are slightly convergent posteriorly.

In *S. b. brunneus*, the dorsal pelage appears dark reddish-gray as the result of a mixture of black unbanded and yellowish-red banded guard hairs. Juxtaposition of bands creates the small, rectangular, whitish-buff spots. The eye ring is buffy-white (Yensen, 1991). In *S. b. endemicus*, the dorsal coloration is grayish-brown as a result of less intense pigment in the banded guard hairs (Yensen, 1991). The legs and base of tail are russet and the underparts are grayish-white (Howell, 1938). The eye ring is creamy-white.

Differences in dorsal coloration between *S. b. brunneus* and *S. b. endemicus* correspond to differences in soil color between their geographic ranges (Yensen, 1991). Unbanded dark guard hairs, banded guard hairs, and undercoat are all significantly longer

FIG. 1. Idaho ground squirrel (*Spermophilus brunneus brunneus*) from Adams County, Idaho. Photograph by George D. Lepp.

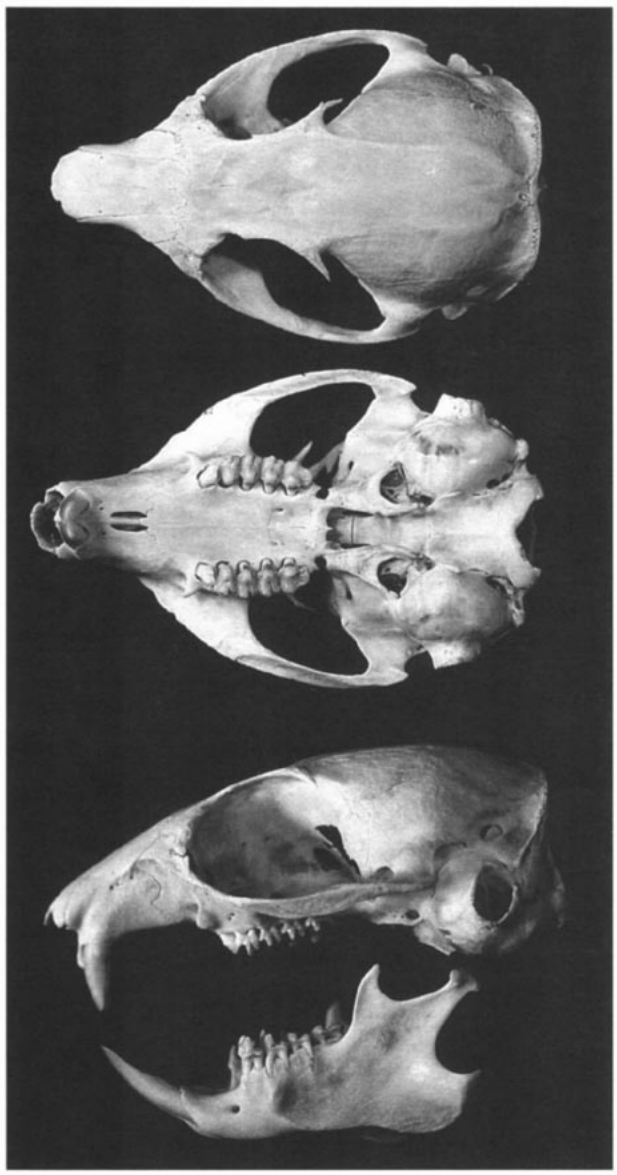

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of the holotype of *Spermophilus brunneus endemicus* from Payette County, Idaho (female, National Museum of Natural History 565927). Greatest length of cranium is 40.5 mm.

in *S. b. endemicus* than in *S. b. brunneus* (Yensen, 1991). Molt is diffuse, as in most other members of subgenus *Spermophilus* (Hansen, 1954); one molt occurs in late May and June in both subspecies (Yensen, 1991). There is no "molt line."

DISTRIBUTION. *Spermophilus b. brunneus* is endemic to west-central Idaho (Fig. 3) where it is known from 30 sites in Adams and Valley counties (as of 1997). These localities are in xeric montane meadows at 1150–1550 m elevation, and most are surrounded by coniferous forests. Twenty-one of the sites are in an area of 30 by 10 km (Yensen, 1991). *S. b. endemicus* occurs in an area of 70 by 30 km in the low, rolling hills north of the Payette River at 670–975 m elevation in Gem, Payette, and Washington counties. The subspecies formerly occurred further north in a large basin in Washington County. The northernmost site where *S. b. endemicus* has been collected is 19 km S of the southernmost *S. b. brunneus* site. However, as of 1991, the two populations were separated by 48 km (Yensen, 1991:fig. 1). No fossils assignable to *S. brunneus* are known.

FORM AND FUNCTION. *Spermophilus brunneus* is sexually dimorphic, with males averaging 2.4–2.6% larger than females in external and cranial measurements. *S. b. endemicus* averages 3.3% larger in external and cranial measurements than *S. b. brunneus* (Yensen, 1991).

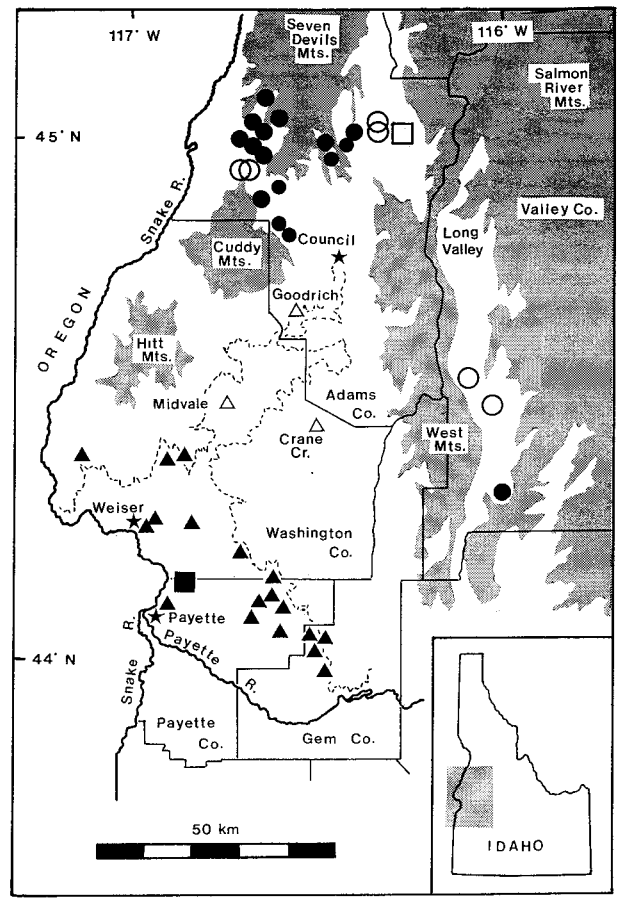

FIG. 3. Distribution of *Spermophilus brunneus*. Shaded areas represent elevations above 1525 m (5000 ft); relevant portions of the 915 m (3000 ft) contour interval are indicated by the dashed line. Symbols: circles = *S. b. brunneus* populations, triangles = *S. b. endemicus* collecting sites, squares = type localities. Open symbols represent sites where *S. brunneus* is extirpated (modified from Yensen, 1991).

There are five pairs of mammae: one pair in the axillary region, one pair just below the diaphragm, one pair in the abdominal region, and two pairs in the inguinal area, as in other members of subgenus *Spermophilus* (Moore, 1961). Bacula (Fig. 4) have an expanded spatulate distal portion bearing spines (Yensen, 1991), similar to other members of subgenus *Spermophilus* (Burt, 1960). There are species-specific differences in baculum proportions and number of spines among *S. brunneus*, *S. washingtoni*, and *S. town-*

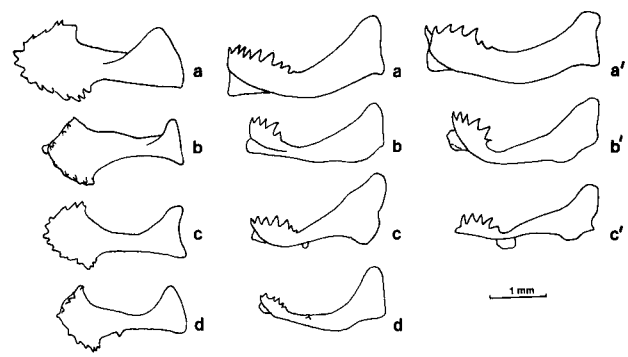

FIG. 4. Bacula (dorsal and lateral views) of (a) *S. b. endemicus* and (b) *S. b. brunneus*, with (c) *S. townsendii idahoensis* and (d) *S. washingtoni* shown for comparison; a'–c' are most divergent bacula examined for each taxon (Yensen, 1991).

sendii. The bacula of *S. b. brunneus* and *S. b. endemicus* also differ significantly from each other in proportions and in spine number (Yensen, 1991).

ONTOGENY AND REPRODUCTION. There is one litter per year in each subspecies. Litters emerge in late March–early April in *S. b. endemicus* and late May–early June in *S. b. brunneus*. Litter sizes in *S. b. endemicus* are significantly larger (*t*-test, $P < 0.05$; number of placental scars = 5–10; $\bar{X} \pm 1\ SD = 7.5 \pm 1.7$; $n = 14$) than in *S. b. brunneus* (2–9; $\bar{X} \pm 1\ SD = 6.2 \pm 1.5$; $n = 26$—Yensen, 1991). There are 5.2 (± 1.4) weaned young/litter in *S. b. brunneus* ($n = 59$) (Sherman, 1989).

ECOLOGY. Individual *S. brunneus* are active above ground for less than four months per year, but each population is active ca. 4.5–5 months (Yensen, 1991). *S. b. endemicus*, which lives at lower elevations, emerges from seasonal torpor in late January or early February, sometimes while snow is still on the ground. The animals cease above ground activity in late June or early July, presumably in response to drying of grasses and forbs which occurs at the onset of summer drought in southwestern Idaho (Yensen, 1991).

Spermophilus b. brunneus, which lives at higher elevations, emerges in late March or early April (about the time of snowmelt) and ceases above ground activity in late July or early August (coincident with summer drought). They then remain underground until the following spring. Adult males emerge first, followed by adult females and yearlings; the lightest yearling females sometimes emerge before adults, apparently in search of food. Immergence is in the same sequence, with young of the year immerging last (Yensen, 1991). In *S. b. brunneus*, the sex ratio of adults and yearlings is biased slightly in favor of females (Yensen, 1991).

The distribution of *S. b. brunneus* is determined by the availability of suitable habitat. In one relatively dense population, the distance between nest burrows of newly-emerged females averaged >100 m (Sherman, 1989). Density of nest burrows of females was only 2–14/ha.

At two meadows in Adams Co., Idaho, *S. b. brunneus* consumed 40–50 species of plants, but only 5–7 species comprised >5% of their diet (Dyni and Yensen, 1996). Grasses (*Poa bulbosa*, *Stipa* seeds, *Bromus commutatus*), dicot leaves (*Microseris nigrescens*, *Lupinus*, *Medicago sativa*), flowers, roots and bulbs, and later in the season, seeds (*Madia*, Asteraceae, *Cryptantha*, Scrophulariaceae) were especially important in the diet. Some insects (4.3–5.1% by volume), but only trace amounts of fungi, were consumed. The diet was similar to that of Columbian ground squirrels (*S. columbianus*). Food habits of *S. b. endemicus* have not been studied.

Spermophlius b. brunneus constructs three types of burrows: nest burrows in which they rear their young, auxiliary burrows which do not contain nests, and hibernation burrows (Yensen et al., 1991). Burrow openings are placed under rocks, shrubs, or fallen timber when these are available, but burrow entrances also occur in the open (Davis, 1939; Yensen et al., 1991). Nest burrows are 50–121 cm deep, have 3–11 openings, 2–13 branching tunnels, 1–7 chambers, and the nests usually are built near the deepest part of the burrow system. Nest burrows are located in well-drained soils >1 m deep. Auxiliary burrows are shallower (<50 cm deep) and constructed at distances of up to 100 m from nest burrows, often in areas with shallow soils (<50 cm deep). Auxiliary burrows may consist of an unbranched tunnel that descends steeply to a single chamber, or the tunnels may meander near the surface like those of pocket gophers (*Thomomys*). Special burrows are used for hibernation. These consist of a single tunnel (branched or unbranched) that descends steeply to a single chamber with a nest (Yensen et al., 1991).

In digging burrows, soil is brought from below and scattered, rather than leaving a pile of soil just outside the opening. Openings of nest burrows are generally small and inconspicuous early in the season and become enlarged later. For all burrow types, openings averaged 6.3 cm (4–15) wide and 5.4 cm (4–17) tall. Nest burrows may be reused for many years, and at some localities they may occur on a built-up mound of soil 50 cm tall and 2–3 m in diameter (Yensen et al., 1991).

Predators of *S. b. brunneus* include prairie falcons (*Falco mexicanus*), Cooper's hawks (*Accipiter cooperi*), goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), northern harriers (*Circus cyaneus*), badgers (*Taxidea taxus*), and, occasionally, long-tailed weasels (*Mustela frenata*—Sherman, 1989). Hawks prey most heavily on males during the mating period soon after spring emergence. Badgers prey on nursing young, especially just before their first emergence above ground, and also dig out many burrows just after seasonal immergence. Both *S. b. brunneus* and *S. b. endemicus* have only one type of alarm call (a high-pitched ventriloquial whistle) for both terrestrial and aerial predators, unlike some other ground squirrels (e.g., *S. beldingi*), which have acoustically different calls for these different predator types (Sherman, 1985). Alarm calls are given most frequently by females when their young first emerge from the natal burrow.

Ectoparasites of *S. b. brunneus* include ticks (Acarina: *Ixodes sculptus*), fleas (Siphonaptera: *Neopsylla inopina*, *Oropsylla tuberculata tuberculata*, *Oropsylla idahoensis*, *Thrassis pandorae pandorae*, *Foxella ignota*, and *Catellagia*), and nematode eyeworms (*Rhabditis orbitalis*). *S. b. endemicus* has mites (Acarina: *Androlaelaps fahrenholzi*), lice (Anopleura: *Neohaematopinus laeviusculus*), and fleas (*Rhadinopsylla*, *Oropsylla tuberculata tuberculata*, *Thrassis francisi barnesi*, *T. f. francisi*, and *T. f. rockwoodi*—Baird and Saunders, 1991; Yensen et al., 1996). *S. brunneus* is host to fewer ectoparasite species than other congeneric ground squirrels. Moreover, *S. b. brunneus* has fewer ectoparasite species and fewer parasites per individual host than *S. b. endemicus*. Both findings suggest that parasite loads are reduced in small, isolated host populations. No evidence of plague or other diseases has been observed in *S. b. brunneus* (Yensen et al., 1996).

An analysis of 25 habitat variables associated with the presence of *S. b. brunneus* or *S. columbianus* at ten study sites indicated that *S. brunneus* could inhabit nearly the same range of sites as *S. columbianus* (Yensen and Sherman, unpubl.). However, *S. b. brunneus* could also utilize more xeric microhabitats with shallower soils than *S. columbianus*. This implies that *S. b. brunneus* was excluded from mesic sites by competition with *S. columbianus*, as originally suggested by Davis (1939).

The original vegetation in the present range of *S. b. endemicus* was big sagebrush (*Artemisia tridentata*) and bitterbrush (*Purshia tridentata*), along with several species of native bunchgrasses and forbs (Yensen, 1991). However, the area was invaded by cheatgrass (*Bromus tectorum*) and medusahead (*Taeniatherium asperum*) in the 1950s and 1960s. These exotic grasses are highly flammable when dry, and their presence greatly increased the severity and frequency of wildfires, interrupting natural succession and converting the area to a grassland dominated by exotic annuals (Whisenant, 1990). Similar vegetation changes have had detrimental effects on *S. townsendii* (Yensen et al., 1992).

The original forests in the range of *S. b. brunneus* were open stands of conifers with an herbaceous understory. As a result of logging and fire suppression in post-settlement times, these open forests have been replaced by dense stands of young trees without an herbaceous understory (Crane and Fischer, 1986; Steele et al., 1986). This has eliminated much suitable habitat, and has fragmented and isolated the few surviving populations of *S. b. brunneus*.

BEHAVIOR. In one well-studied population of about 100 *S. b. brunneus*, the mating season lasted 13 days in 1987 and 12 days in 1988 (Sherman, 1989). Females were sexually attractive to males for 3–5 hours on the first or second afternoon after they emerged from hibernation. During that time, most females mated with just one male. Copulations occurred below ground and vaginal plugs were formed. Newly emerged females remained near their hibernacula, where they were located and courted by males that were >2 yr old (and by a few large 1-yr-old males) who themselves had emerged 1–2 weeks previously. Receptive females were widely scattered (119 ± 36 m, $n = 24$; Sherman, 1989), and males searched for them and guarded them once they were found until mating occurred. When female density was especially low, or when there were few receptive females on a given day, males also guarded females after copulating. Heavier males displaced lighter males, and paternity exclusion by electrophoretic analysis showed that 66–100% of young were sired by the male that guarded last and longest. The distance between burrows makes mate-guarding an evolutionarily stable strategy because searching for mates was time consuming, dangerous due to hawk predation, and the probability of obtaining sexual access was low for all except the largest and most active males (Sherman, 1989).

After females are fertilized, they construct nest burrows and nests; females defend only a small area around their nest burrow entrance (Sherman, 1989). The time from the day a female mates until her young first emerge is 50–52 days. Young begin to disperse within 2–3 days after they emerge from their natal burrows (Sherman, 1989). Infanticide has not been reported. Males do not live near their mates or behave paternally, and females do not cooperate with close kin to defend burrows or rear young as in some other ground squirrel species (Michener, 1983; Sherman, 1981).

GENETICS. *Spermophilus b. brunneus* has a diploid number of 38 chromosomes, with 14 metacentric, 16 submetacentric, and 6 subacrocentric autosomes, a submetacentric X, and an acrocentric Y. This karyotype is similar to that of *S. townsendii mollis* (Nadler et al., 1973). Electrophoretic data initially suggested that *S. brunneus* was intermediate between, and possibly the common ancestor of, the small-eared and big-eared species groups (sensu Davis, 1939) of the subgenus *Spermophilus* (Nadler et al., 1973, 1974*a*, 1974*b*, 1982), and that *S. brunneus* was closest to the Asian *S. dauricus* (Nadler et al., 1982). Subsequently, Nadler et al., (1984) concluded that *S. brunneus* was a sister taxon to *S. townsendii*.

In an electrophoretic comparison of allozymes, 13 and 12 of 31 loci examined were polymorphic in *S. b. brunneus* and *S. b. endemicus*, respectively. Mean proportion of loci heterozygous per individual (*H*) was 0.123 and 0.108 for *S. b. brunneus* and *S. b. endemicus*, respectively (Gill and Yensen, 1992). These values are slightly higher than those in some other ground squirrels (e.g., *S. tridecemlineatus*, *S. mexicanus*, *S. spilosoma*—Cothran et al., 1977). Genetic distance between the two nominal subspecies was compatible with differentiation at either the subspecific or the specific level (Jacard's coefficient = 0.893; Gill and Yensen, 1992).

A second starch-gel electrophoresis survey of 55 loci (T. A. Gavin, P. W. Sherman, E. Yensen, B. May, unpublished data) confirmed that there is a difference at least at the subspecific level between *S. b. brunneus* and *S. b. endemicus*, and that both were separated from *S. mollis idahoensis* by four fixed alleles. *S. brunneus* was more distantly related to *S. columbianus* and *S. washingtoni*. Analysis of 12 populations of *S. b. brunneus* indicated that seven of 55 loci were polymorphic. Among these populations, the proportion of polymorphic loci ranged from 11.5 to 19.2%, and *H* values ranged from 0.041 to 0.080. The F_{st} was 0.317, which confirms that there is genetic subdivision among populations, despite their close geographic proximity, apparently due to habitat fragmentation. Similar F_{st} values have been obtained for other species of ground squirrels, but these were sampled over a much broader geographic range (Barrowclough, 1983; Cothran et al., 1977).

To study the population structure of *S. b. brunneus*, May et al. (1997) identified 13 microsatellite loci. Primer sequences for these loci are available in GenBank. Initial tests of these primers on other species of *Spermophilus* produced bright, resolved, polymorphic amplicons, suggesting that they will be useful in studies of kinship and population structure in other sciurids.

CONSERVATION STATUS. The Idaho ground squirrel was proposed as a candidate species for "threatened or endangered" status by the U.S. Fish and Wildlife Service, and a notice of review was published in the Federal Register (vol. 50, No. 181:37958–37967) on 18 September 1985. *S. b. brunneus* was proposed for endangered status (Category 1) and *S. b. endemicus* for threatened status (Category 2). In 1994, *S. b. brunneus* became part of a pilot program by the U.S. Fish and Wildlife Service which involves managing recovery through interagency Conservation Agreements in lieu of listing under the Endangered Species Act, and a Conservation Agreement was signed in 1996 between the Payette National Forest and the U.S. Fish and Wildlife Service. In 1995, Category 2 species including *S. b. endemicus* were dropped by the U.S. Fish and Wildlife Service from further consideration for listing under the Endangered Species Act, but *S. b. brunneus* remained a Category 1 species. The International Union for Conservation of Nature (IUCN) has designated *S. b. brunneus* as "Critically Endangered" and *S. b. endemicus* as "Vulnerable" (Yensen, in press).

REMARKS. Davis (1939), Howell (1928, 1938), and Nadler et al. (1973) used the common name "Idaho spotted ground squirrel," but this usage has not been followed elsewhere (e.g., Hall, 1981; Jones et al., 1986). "Northern Idaho ground squirrel" has been used for *S. b. brunneus* and "southern Idaho ground squirrel" for *S. b. endemicus*.

As of 1997, *S. b. brunneus* survived at 21 of 30 known sites. Live-trapping indicated that the total population was 1000–1200 individuals in 1993, but it fell to 600–800 in 1994 (T. A. Gavin, P. W. Sherman, and E. Yensen, original data). Only one known population exceeded 100 individuals in 1993–1996. Fire suppression has resulted in continuing invasion of suitable meadows by conifers and elimination of suitable food plants. Competition with Columbian ground squirrels limits the range of available sites still further. Together, these influences have left only small, remnant demes which differ from each other genetically.

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LITERATURE CITED

BAIRD, C. R., AND R. C. SAUNDERS. 1992. An annotated checklist of the fleas of Idaho (Siphonaptera). University of Idaho, College of Agriculture, Research Bulletin No. 148:1–34.

BARROWCLOUGH, G. F. 1983. Biochemical studies of microevolutionary processes. Pp. 223–261, *in* Perspectives in ornithology (A. H. Brush and G. A. Clark, Jr., eds.). Cambridge University Press, Cambridge, U.K., 560 pp.

BURT, W. H. 1960. Bacula of North American mammals. Miscellaneous Publications of the Museum of Zoology, University of Michigan, 113:1–75.

COTHRAN, E. G., E. G. ZIMMERMAN, AND C. F. NADLER. 1977. Genic differentiation and evolution in the ground squirrel subgenus *Ictidomys* (genus *Spermophilus*). Journal of Mammalogy, 58:610–622.

CRANE, M. F., AND W. C. FISCHER. 1986. Fire ecology of the forest habitat types of central Idaho. U.S.D.A. Forest Service, Intermountain Research Station, General Technical Report INT-218:1–86.

DAVIS, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho, 400 pp.

DYNI, E. J., AND E. YENSEN. 1996. Dietary similarity of sympatric Idaho and Columbian ground squirrels (*Spermophilus brunneus* and *S. columbianus*). Northwest Science, 70:99–108.

GILL, A. E., AND E. YENSEN. 1992. Biochemical differentiation in the Idaho ground squirrel, *Spermophilus brunneus* (Rodentia: Sciuridae). Great Basin Naturalist, 52:155–159.

HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley & Sons, New York, 1:1–600 + *90*.

HANSEN, R. M. 1954. Molt patterns in ground squirrels. Proceedings of the Utah Academy of Science, Arts, and Letters, 31: 57–60.

HOFFMANN, R. S., C. G. ANDERSON, R. W. THORINGTON, JR., AND L. R. HEANEY. 1993. Family Sciuridae. Pp. 419–465, *in* Mammal species of the world: a taxonomic and geographic reference. Second ed. (D. E. Wilson and D. M. Reeder, eds.). Smithsonian Institition Press, Washington, D.C., 1206 pp.

HOWELL, A. H. 1928. Descriptions of six new North American ground squirrels. Proceedings of the Biological Society of Washington, 41:211–214.

———. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. North American Fauna, 56:1–256.

JONES, J. K., JR., D. C. CARTER, H. H. GENOWAYS, R. S. HOFFMAN, D. W. RICE, AND C. JONES. 1986. Revised checklist of North American mammals north of Mexico, 1986. Occasional Papers, The Museum, Texas Tech University, No. 107:1–22.

MAY, B., T. A. GAVIN, P. W. SHERMAN, AND T. M. KORVES. 1997. Characterization of microsatellite loci in the northern Idaho ground squirrel, Spermophilus brunneus brunneus. Molecular Ecology, 6:399–400.

MICHENER, G. R. 1983. Kin identification, matriacrchies, and the evolution of sociality in ground-swelling sciurids. Pp. 528–572, *in*: Recent advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Special Publication The American Society of Mammalogists, 7:1–753.

MOORE, J. C. 1961. Geographic variation in some reproductive

characteristics of diurnal squirrels. Bulletin of the American Museum of Natural History, 122:1–32.

NADLER, C. F., R. S. HOFFMANN, R. I. SUKERNIK, AND N. N. VORONTSOV. 1974*a*. A comparison of a biochemical and morphological evolution in Holarctic ground squirrels (*Spermophilus*). First International Theriological Congress, 2:3–4.

NADLER, C. F., L. W. TURNER, R. S. HOFFMANN, AND L. DEUTSCH. 1973. Chromosomes and Giemsa-bands of the Idaho spotted ground squirrel, *Spermophilus brunneus* (Howell). Experientia, 29:893–894.

NADLER, C. F., R. S. HOFFMAN, N. N. VORONTSOV, J. W. KOEPPL, L. DEUTSCH, AND R. I. SUKERNIK. 1982. Evolution in ground squirrels II. Biochemical comparisons in Holarctic populations of *Spermophilus*. Zeitschrift für Säugetierkunde, 47:198–215.

NADLER, C. F., E. A. LYAPUNOVA, R. S. HOFFMANN, N. N. VORONTSOV, L. L. SHAITAROVA, AND Y. M. BORISOV. 1984. Chromosomal evolution in Holarctic ground squirrels (*Spermophilus*) II. Giemsa-band homologies of chromosomes and the tempo of evolution. Zeitschrift für Säugetierkunde, 49:78–90.

NADLER, C. F., R. I. SUKERNIK, R. S. HOFFMANN, N. N. VORONTSOV, C. F. NADLER, JR., AND I. I. FORMICHOVA. 1974*b*. Evolution in ground squirrels: I. Transferrins in Holarctic populations of *Spermophilus*. Comparative Biochemistry and Physiology, 47A:663–681.

RICKART, E. A., AND E. YENSEN. 1991. *Spermophilus washingtoni*. Mammalian Species, 371:1–5.

SCHEFFER, T. H. 1946. Re-allocation of the Townsend ground squirrel. Journal of Mammalogy, 27:395–396.

SHERMAN, P. W. 1981. Kinship, demography, and Belding's ground squirrel nepotism. Behavioral Ecology and Sociobiology, 8:251–259.

———. 1985. Alarm calls of Belding's ground squirrels to aerial predators: nepotism or self-preservation? Behavioral Ecology and Sociobiology, 17:313–323.

———. 1989. Mate guarding as paternity insurance in Idaho ground squirrels. Nature, 338:418–420.

STEELE, R., S. F. ARNO, AND K. GEIER-HAYES. 1986. Wildfire patterns change in Idaho's ponderosa pine–Douglas-fir forest. Western Journal of Applied Forestry, 1:16–18.

WHISENANT, S. G. 1990. Changing fire frequencies on Idaho's Snake River Plains: ecological and management implications. Pp. 4–10, *in* Proceedings—symposium on cheatgrass invasion, shrub die-off, and other aspects of shrub biology and management. (E. D. McArthur, E. M. Romney, S. D. Smith, and P. T. Tueller, compilers). U.S.D.A. Forest Service, Intermountain Research Station General Technical Report INT-276:1–351.

YENSEN, E. 1991. Taxonomy and distribution of the Idaho ground squirrel, *Spermophilus brunneus*. Journal of Mammalogy, 72: 583–600.

———. In press. *Spermophilus brunneus*. *In* North American rodents: action plans for species of conservation concern. (D. J. Hafner, E. Yensen, G. L. Kirkland, eds.). International Union for Conservation of Nature, Gland, Switzerland.

YENSEN, E., C. R. BAIRD, AND P. W. SHERMAN. 1996. Larger ectoparasites of the Idaho ground squirrel (*Spermophilus brunneus*). Great Basin Naturalist, 56:237–246.

YENSEN, E., M. P. LUSCHER, AND S. BOYDEN. 1991. Structure of burrows used by the Idaho ground squirrel, *Spermophilus brunneus*. Northwest Science, 65:93–100.

YENSEN E., D. L. QUINNEY, K. JOHNSON, K. TIMMERMAN, AND K. STEENHOF. 1992. Fire, vegetation changes, and population fluctuations of Townsend's ground squirrels. American Midland Naturalist, 128:299–312.

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