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Spermophilus townsendii.

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Spermophilus townsendii Bachman, 1839

Townsend's Ground Squirrel

Spermophilus townsendii Bachman, 1839:61. Type locality "prairies near the Walla-walla [River]," Washington, or "On the Columbia River, about 300 miles above its mouth" (Townsend, 1839).

Spermophilus mollis Kennicott, 1863:157. Type locality "Camp Floyd . . . [near Fairfield, Utah Co.], Utah."

Citellus idahoensis Merriam, 1913:135. Type locality "Payette, at junction of Payette and Snake River [Payette Co.], Idaho."

Citellus leurodon Merriam, 1913:136. Type locality "Murphy, in hills of southwestern Idaho [Owyhee Co.] west of Snake River."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae, Tribe Marmotini, Genus *Spermophilus*, Subgenus *Spermophilus* (Black, 1963; Hall, 1981; Howell, 1938). Seven subspecies are recognized (Davis, 1939; Hall, 1981; Howell, 1938) as follows:

S. t. artemesiae (Merriam), 1913:137. Type locality "Birch Creek, [about 10 mi. S Nicholia, Clark Co.,] Idaho" (*pessimus* Merriam a synonym).

S. t. canus Merriam, 1898:70. Type locality "Antelope, Wasco Co., Oregon."

S. t. idahoensis (Merriam), 1913:135, see above.

S. t. mollis Kennicott, 1863:157, see above (*stephansi* Merriam, *leurodon* Merriam, and *washoensis* Merriam are synonyms).

S. t. nancyae Nadler, 1968*a*:153. Type locality "five miles north of Richland (Benton Co.), Washington."

S. t. townsendii Bachman, 1839:61, see above (*yakimensis* Merriam a synonym).

S. t. vigilis (Merriam), 1913:137. Type locality "Vale [Malheur Co.], eastern Oregon."

On the basis of chromosomal and biochemical variation, Nadler et al. (1982) considered the *townsendii*, *mollis*, and *vigilis* cytotypes as separate species or semispecies within the superspecies *S.* [*townsendii*] (sensu Amadon, 1966). A revision of the group is needed. Although this account treats the group as a single species, where published information on the various subspecies differs, separate consideration is given to each.

DIAGNOSIS. Townsend's ground squirrel (Fig. 1) is distinguishable from members of the subgenera *Callospermophilus* and *Ictidomys* by absence of conspicuous dorsal stripes or spots. It differs from members of the subgenera *Poliocitellus* and *Otospermophilus* by its smaller size (less than 300 mm total length) and relatively short tail (less than one-third length of head and body). Members of the subgenus *Xerospermophilus* have longer tails (more than one-third length of head and body), and relatively brachydont molars with parastyle ridge on M1 and M2 joining protocone without an abrupt change of direction. No members of subgenera *Ictidomys*, *Poliocitellus*, or *Xerospermophilus* are sympatric with *S. townsendii* (Hall, 1981; Howell, 1938).

Among Nearctic members of the subgenus *Spermophilus*, *S. townsendii* is distinguishable from *S. armatus*, *S. beldingi*, *S. columbianus*, *S. elegans*, *S. parryii*, and *S. richardsonii* by its smaller size (hind foot less than 39 mm), shorter ears, and relatively pale pelage. It differs from *S. brunneus* by its shorter ears, unspeckled dorsal pelage, larger auditory bullae, and longer, narrower rostrum. Morphologically it most closely resembles *S. washingtoni*, but can be distinguished from that species by its unspeckled dorsal pelage and smaller skull with a relatively broader braincase and interorbital region (Davis, 1939; Hall, 1981; Howell, 1938).

GENERAL CHARACTERISTICS. Ranges for external measurements (in mm) summarized from Howell (1938) are: total length, 167 to 271; length of tail, 32 to 72; length of hind foot 29 to 38. Males average slightly larger in linear dimensions (Davis, 1939). Adult body weight varies seasonally, primarily as a function of fat content. It is lowest at emergence from dormancy in late winter (82 to 205 g) and highest just before immergence into dormancy in early summer (202 to 325 g). Males are heavier than females, particularly late in the season (Rickart, 1982*a*, 1986*a*; Scheffer, 1941).

The general dorsal coloration is pale smoke gray, often washed with pinkish buff. In *S. t. mollis* and *S. t. idahoensis* there may be some dappling. Worn pelage is often brownish. Underparts are creamy white washed with pinkish buff (Howell, 1938). *S. t. mollis* from the Escalante Desert of southern Utah are considerably redder than those from northern populations (Hansen, 1954*a*). Alcorn (1940*b*) described a very pale colormorph from western Nevada.

The skull (Fig. 2) is relatively short and broad. The zygomata are heavy and widely expanded, and the braincase is broad. The rostrum is stout with nearly parallel sides. Supraorbital borders are slightly elevated, and the postorbital processes are long, slender, and decurved. The temporal ridges are lyrate, meeting posteriorly in old age to form a slight crest. Auditory bullae are moderately inflated, and the meatus is relatively long. The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Howell, 1938). The cheekteeth are hypsodont and P3 is of moderate size (Fig. 3). Cranial measurements (in mm) summarized from Howell (1938) are: greatest length of skull, 32.4 to 43.3; palatilar length, 15.3 to 21.2; zygomatic breadth, 21.0 to 26.8; cranial breadth, 15.6 to 19.0; interorbital breadth, 6.4 to 8.8; postorbital constriction, 8.9 to 11.0; length of nasals, 11.4 to 15.7; and length of maxillary toothrow, 7.0 to 9.0. Howell (1938) and Nadler (1968*a*) listed separate means and ranges for the different subspecies.

DISTRIBUTION. The seven recognized subspecies of *S. townsendii* are distributed through the Great Basin and Columbia Plateau, including most of Nevada, western Utah, extreme eastern California, southern Idaho, eastern Oregon, and south-central Washington (Fig. 4). Davis (1939) described intergradation between *S. t. idahoensis* and *S. t. artemesiae* in southern Idaho, and discussed the effectiveness of the Snake River as a dispersal barrier

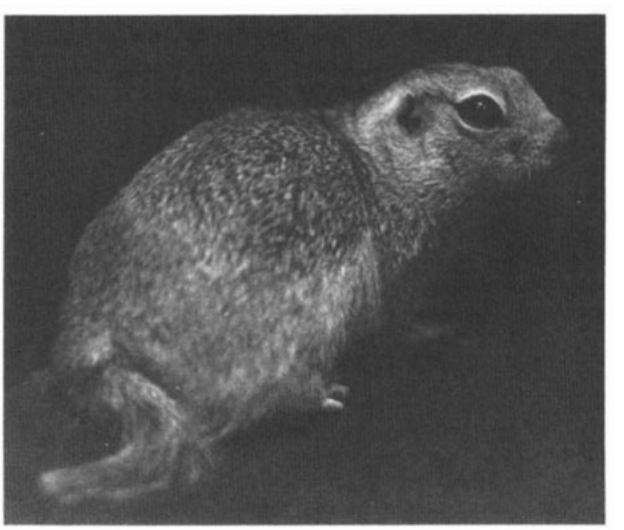

FIG. 1. Female *Spermophilus townsendii mollis* (16 months old) from Redmond, Sevier Co., Utah. Photograph by author.

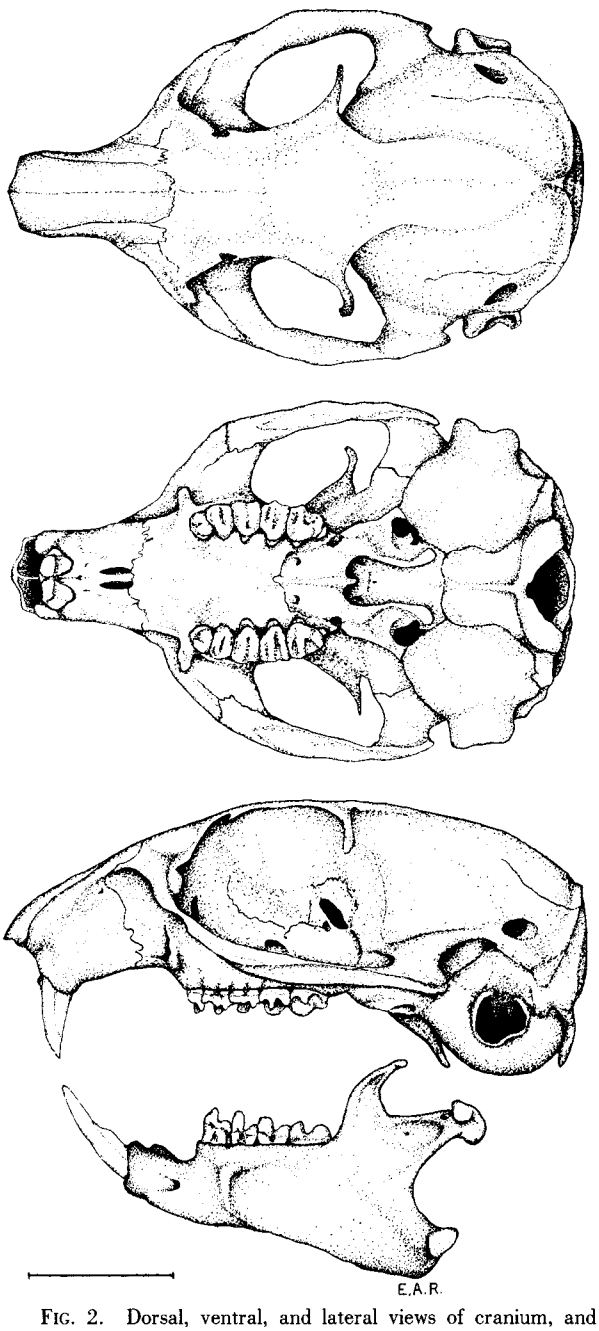

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Spermophilus townsendii mollis* (EAR 1069 male) from Delle, Tooele Co., Utah. Scale represents 10 mm. Drawings by author.

between *S. t. idahoensis* and *S. t. vigilis*. Davis (1939) also reported intergradation between *S. t. mollis* and both *S. t. artemisiae* and *S. t. vigilis*. North of the Columbia River in Washington the chromosomally distinct races *S. t. townsendii* and *S. t. nancyae* are separated by the Yakima River (Nadler, 1968*a*). Although mapped as parapatric by Hall (1981), there is a gap of more than 100 km between known ranges of *S. t. townsendii* and *S. t. canus* south of the Columbia River (Howell, 1938). *Spermophilus townsendii* is primarily an inhabitant of the Upper Sonoran life zone (Howell, 1938). In Nevada, specimens have been taken at elevations from 1,000 to 2,250 m (Hall, 1946).

FOSSIL RECORD. Fossils have been recovered from late Wisconsin–early Holocene localities in Idaho within the present range of *S. t. artemesiae*, in Nevada within the present range of *S. t. mollis*, and in Washington within the present range of *S. t. nancyae* (Kurtén and Anderson, 1980; Lyman and Livingston, 1983; Mead et al., 1982). Deavers and Greene (1978) reported *S. townsendii* from a late Holocene archaeological site in eastern Washington east of the Columbia River, approximately 100 km northeast of the nearest extant population. Lyman and Livingston (1983) considered this extralimital record as evidence of a more extensive distribution for *S. townsendii* in eastern Washington during a late Holocene interval that was more arid than at present. However, Deavers and Greene (1978) reported difficulty distinguishing *S. townsendii* from *S. washingtoni* (which presently occurs east of the Columbia), thus, the remains probably are of the latter species.

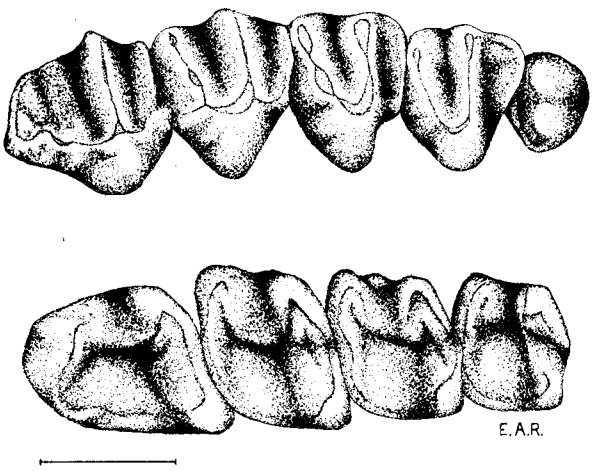

FIG. 3. Occlusal views of right upper (top) and left lower cheekteeth of *Spermophilus townsendii mollis* (EAR 1069). Scale represents 2 mm. Drawings by author.

The Pleistocene taxon *S. taylori* (Hay), known from a single specimen collected near San Diego in southern Texas, reportedly resembles *S. townsendii* (Hay, 1921).

FORM AND FUNCTION. According to Hansen (1954*a*, 1954*b*), adult *S. townsendii* molt once annually, during late April and May. The molt is "diffuse" without appearance of an external molt line.

Rickart (1982*a*, 1982*b*) used mandibular adhesion lines to determine age of *S. t. mollis*. Smith and Johnson (1985) used eyelens weight to differentiate yearling and adult *S. t. idahoensis*.

Mass of paired testes of *S. t. mollis* averaged 624 mg during the reproductive period immediately following emergence from dormancy, 86 mg 8 weeks after emergence, and 106 mg before immergence into dormancy (Rickart, 1982*b*).

At emergence from dormancy, adult male *S. t. mollis* have a body lipid content of about 10% of lean dry mass. Females emerge with relatively more fat than males (25 to 40% of lean dry mass) but much of this is lost during the breeding period. Males start to fatten about 6 weeks after emergence, whereas seasonal fattening of females is delayed another 2 to 3 weeks until after young are weaned. Just before dormancy, adult fat content reaches 150 to 250% of lean dry mass. Among juveniles, males gain mass more rapidly than females, but the latter fatten more rapidly. Fat stores of juveniles are about 200% of lean dry mass just before dormancy. Lean dry mass and water mass of adults also increases during the active season, but there is a significant depression in female water content during late lactation (Rickart, 1982*a*).

In captivity, dormant male *S. t. mollis* lost an average of 0.44 g/day at ambient temperatures between 5 and 18°C. Adult females, juvenile females, and juvenile males had substantially lower mean loss rates of 0.32, 0.31, and 0.34 g/day, respectively (Rickart, 1982*a*).

At ambient temperatures between 30 and 41°C, mean body temperatures of captive *S. t. mollis* ranged from 36.4 to 41.7°C. Resting body temperatures were consistently lower than those of *S. armatus*, *S. elegans*, *S. beldingi*, and *S. spilosoma* (Hudson and Deavers, 1973). Rectal temperatures of *S. t. townsendii* collected in midApril were between 38.3 and 38.9°C (Scheffer, 1941).

Mean metabolic rates for *S. t. mollis* at 30 and 41°C were 0.62 and 1.10 ml O_2 g^{-1} h^{-1}, respectively. Respiration increased linearly from about 50 breaths/min at 28°C to a maximum of about

250 breaths/min at 43°C. Animals dissipated 100% of metabolic heat by evaporative cooling at 42°C, and could withstand this temperature for 2 h without distress (Hudson and Deavers, 1973).

Hudson and Deavers (1976) reported seasonal variation in thyroid function of captive *S. t. mollis*, as measured by the release of ^{125}I. Mean biological half-life of ^{125}I was 51 days during the winter-spring period, and 2,398 days during the summer-fall period. Among eight ground squirrel species, *S. t. mollis* exhibited the slowest release rates. Thyroidectomy lowered metabolic rate 13 to 15%, but not below levels observed for intact animals with inactive thyroids.

Total serum thyroxine of free-living adult male *S. t. townsendii* averaged 109 ng/ml early in the active season, and 49 ng/ml late in the season. For juvenile males, average serum titers were 90 ng/ml at emergence from natal burrows and 27 ng/ml just before dormancy. For both age groups, midseason thyroxine titers of females were significantly lower than those of males. Low thyroid activity during the late active season may facilitate seasonal fattening (Rickart, 1982*b*, 1986*b*).

ONTOGENY AND REPRODUCTION. Male *S. t. mollis* mature as yearlings whereas most male *S. t. idahoensis* mature as 2-year-olds. Females of both subspecies breed as yearlings (Rickart, 1982*b*; Smith and Johnson, 1985). Breeding occurs in late January or early February for both *S. t. townsendii* (Svihla, 1939) and *S. t. idahoensis* (Smith and Johnson, 1985). Breeding of *S. t. mollis* occurs from midFebruary to early March, but is relatively synchronous within local populations (Alcorn, 1940*a*; Hansen, 1956*b*; Rickart, 1982*a*, 1982*b*).

During 5 years, pregnancy rates ranged from 49 to 92% for yearling *S. t. idahoensis* and from 97 to 100% for adults (Smith and Johnson, 1985). Among *S. t. mollis* sampled after the breeding period during 4 years, 95% of yearlings and all adults had bred (Rickart, 1982*b*). Alcorn (1940*a*) reported pregnancy rates in *S. t. mollis* of about 90% during normal years and about 50% during a period of population decline. During a year of severe drought, female *S. t. idahoensis* failed to attain breeding condition after emergence, resulting in a total suspension of reproduction (Smith and Johnson, 1985).

One litter per year is produced. Reported mean embryo or placental scar counts are: 8.3 for *S. t. townsendii* (Scheffer, 1941), from 7.2 to 9.1 for *S. t. idahoensis* (Smith and Johnson, 1985), and from 6.4 to 10.0 for *S. t. mollis* (Alcorn, 1940*a*; Rickart, 1982*b*). The reported maximum number of embryos is 16 (Alcorn, 1940*a*; Rickart, 1982*b*). Yearlings have smaller litters than older females. Smith and Johnson (1985) reported mean embryo and placental scar counts of 7.7 and 9.2 for yearling and older *S. t. idahoensis*. For *S. t. mollis*, means ranged from 5.9 to 9.0 for yearlings and from 7.0 to 10.8 for older cohorts (Rickart, 1982*b*). Svihla (1939) reported a mean size of 4.8 (range, 1 to 10) for 12 *S. t. townsendii* litters born in captivity. However, young from some of these litters may have been killed before being counted. Rickart (1986*a*) reported a mean size at birth of 8.6 (range, 6 to 12) for five *S. t. mollis* litters. Alcorn (1940*a*) found 15 and 17 newborn young in two excavated nests of *S. t. mollis*. Because these numbers are high relative to mean embryo and placental scar counts, the nests may have contained litters of more than one female. During 4 years, in utero embryo mortality for *S. t. mollis* ranged from 0 to 21.0% (Rickart, 1982*b*). Both Alcorn (1940*a*) and Svihla (1939) estimated the length of gestation at 24 days.

Means ($\pm SE$) and ranges of measurements (in mm) for 33 newborn *S. t. townsendii* were: total length, 52.6±0.4 (42 to 56); tail length, 6.3±0.1 (5 to 7); length of hind foot, 6.3±0.4 (5.5 to 7.1); and mass (in g), 3.7±0.7 (2.2 to 4.9; Svihla, 1939). Rickart (1986*a*) recorded a mean birth mass (in g) of 3.87±0.62 (2.75 to 5.15) for 21 *S. t. mollis*.

Newborn *S. t. townsendii* are unpigmented and hairless; the first dorsal pigment and hair develop within 24 h. By 8 days the pinnae and eyelids develop, and the front digits separate by 12 days. Lower incisors erupt by 12 days, and eyes open at 19 to 22 days (Svihla, 1939). Svihla (1939) reported that *S. t. townsendii* were weaned soon after eye opening. Young *S. t. mollis* were first seen taking solid food at 26 to 28 days, but they continued to suckle through 34 days (Rickart, 1986*a*).

Compared with other members of the genus, early postnatal growth of *S. t. mollis* is relatively slow. Captives achieved 50% of the average lean adult mass (about 70 g) in about 42 days, whereas most congeners reach 50% adult mass in less than 40 days. The mean growth constant (Levenson, 1979) from birth to 50 days was 0.066. After 60 days, mean masses of males were significantly greater than those of females (Rickart, 1986*a*).

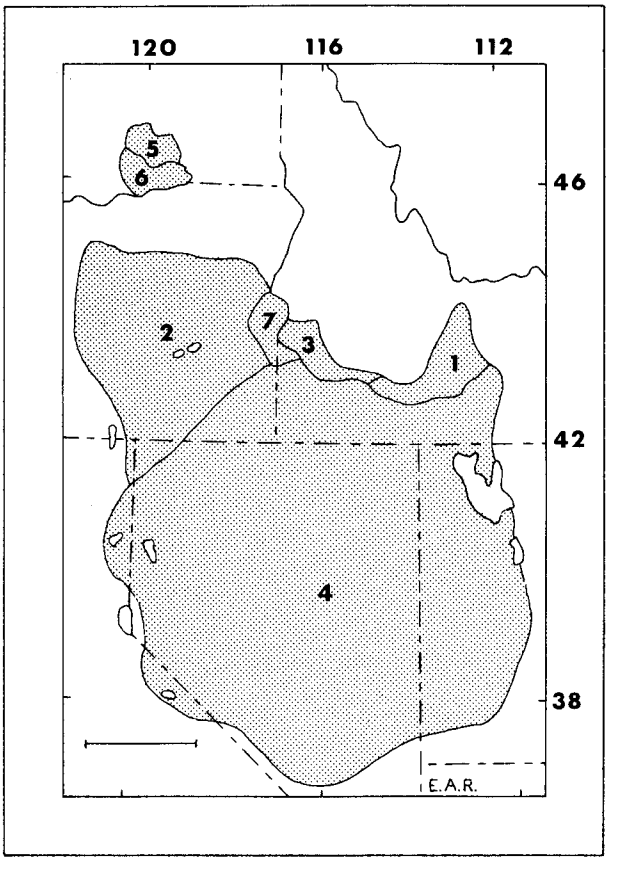

FIG. 4. Distribution of *Spermophilus townsendii* (after Hall, 1981). Subspecies are: 1, *S. t. artemesiae*; 2, *S. t. canus*; 3, *S. t. idahoensis*; 4, *S. t. mollis*; 5, *S. t. nancyae*; 6, *S. t. townsendii*; 7, *S. t. vigilis*. Scale represents 200 km.

ECOLOGY. With the exception of *S. t. vigilis* which is restricted to a limited area of relatively fertile river valley bottomland, Townsend's ground squirrels primarily occur in arid high desert habitats such as sagebrush (*Artemisia*), shadscale (*Atriplex*), or greasewood (*Sarcobatus*) communities (Davis, 1939; Hansen, 1954*a*; Howell, 1938; Smith and Johnson, 1985). They inhabit areas with well-drained soils such as ridge tops and hillsides, and often are particularly common along canal and railroad embankments, and on abandoned farmland (Davis, 1939). Although these squirrels occur in arid habitats, they are most abundant around desert springs and near irrigated fields (Hansen, 1954*a*). Where *S. townsendii* is locally sympatric with *S. armatus* or *S. beldingi*, habitat selection is influenced by competition. This restricts *S. townsendii* to the most arid situations (Durant and Hansen, 1954; Hall, 1946).

Estimated population densities of *S. t. idahoensis* (excluding juveniles) ranged from 3 to 32 individuals/ha (Smith and Johnson, 1985). Alcorn (1940*a*) reported densities of 296 and 331 individuals/ha (including juveniles) for *S. t. mollis*. These values were based on two samples obtained during a poisoning operation; they may overestimate true densities. Estimated proportions of immigrant, transient, and resident *S. t. idahoensis* (excluding juveniles) were: 32, 10, and 58% for males; and 18, 8, and 74% for females (Smith and Johnson, 1985). Smith and Johnson (1985) used the minimum convex polygon method to determine a mean ($\pm SE$) home range of 1,357±189.7 m^2 for 14 *S. t. idahoensis*. Alcorn (1940*a*) reported large numbers of juvenile *S. t. mollis* moving more than 400 m in 10 days.

Male : female sex ratios of 1.26:1, 0.75:1, and 0.74:1 were reported for juvenile, yearling, and adult *S. t. idahoensis*, respectively (Smith and Johnson, 1985). Rickart (1982*b*) reported ratios of 0.95:1, 0.81:1, and 0.72:1 for juvenile, yearling, and adult *S.*

t. mollis. Yearlings constituted 44% of animals other than juveniles in *S. t. idahoensis* populations (Smith and Johnson, 1985), whereas for two populations of *S. t. mollis* proportions of yearlings were 50 and 75% (Rickart, 1982*b*). Rickart (1982*b*) reported a longevity of 5 years for *S. t. mollis*.

Smith and Johnson (1985) estimated an overwinter survival rate of 28% for *S. t. idahoensis*. Females had higher survival rates than males among juveniles (30 and 15%) and adults (40 and 28%), but not among yearlings (39% for both sexes).

The diet consists primarily of green vegetation and seeds. Grasses and forbs are the most frequent food items, followed by shrub parts and animal matter (Alcorn, 1940*a*; Howell, 1938; Johnson,1977; Rogers and Gano, 1980; Smith and Johnson, 1985). The caloric value of dried stomach contents of *S. t. mollis* increases from 4 kcal/g in February and March to 4.5 kcal/g in May and June, coinciding with the appearance of seeds in the diet and the period of seasonal fattening (Rickart, 1982*a*).

Internal and external parasites of *S. t. mollis* listed by Jenkins and Grundman (1973) include: Protozoa, *Entamoeba citelli, Monocercomonoides pilleata*, and *Tritrichomonas muris*; Nematoda, *Citellina triradiata*, and *Physaloptera massino*; Acarina, *Dermacentor parumapertus, Haemolaelaps glasgowi*, and *Ixodes kingi*; and Siphonaptera, *Conorhinopsylla stanfordi, Diamanus montanus, Enderleinellus suturalis, Hoplopsylla anomalus, Monopsyllus wagneri, Neohaematopinus laeviusculus, Opisthocrostis labis, O. tuberculatus, Oropsylla idahoensis, Thrassis acamatus, T. bacchi, T. francisi francisi*, and *T. pandorae*. The parasite fauna of *S. t. mollis* is more similar to that of *Ammospermophilus leucurus* than to those of either *S. armatus* or *S. beldingi* (Jenkins and Grundman, 1973). Ectoparasites of *S. t. artemesiae* include: Acarina, *Dermacentor andersoni, Ixodes angustus, I. kingi, I. marmotae*, and *I. ochotonae*; and Siphonaptera, *Meringis parkeri, Monopsyllus eumolpi, M. wagneri, Opisthocrostis labis, O. tuberculatus, Rhadinopsylla sectilis, Thrassis francisi*, and *T. pandorae* (Allred, 1968*a*; 1968*b*). O'Farrell (1975) listed three species of fleas from *S. t. nancyae* (*Meringis shannoni, Opisthocrostis washingtonensis*, and *Thrassis petiolatus*). Whitaker and Wilson (1974) listed three additional mite species from *S. townsendii* (*Androlaelaps fahrenholzi, Hirstionyssus triacanthus*, and *Ornithonyssus bacoti*).

Sylvatic plague occurs in populations of *S. t. idahoensis* (Messick et al., 1983). Tularemia has been reported for *S. t. mollis* (Francis, 1922). Reports of extreme population fluctuations not associated with resource availability (Alcorn, 1940*a*; Grinnell and Dixon, 1918; Hansen, 1956*a*; Svihla, 1939) may indicate occurrence of epizootics.

Predators of Townsend's ground squirrels include: badgers, *Taxidea taxus*; coyotes, *Canis latrans*; long-tailed weasels, *Mustela frenata*; prairie falcons, *Falco mexicanus*; red-tailed hawks, *Buteo jamaicensis*; rough-legged hawks, *B. lagopus*; ferruginous hawks, *B. regalis*; Swainson's hawks, *B. swainsoni*; common ravens, *Corvus corax*; western rattlesnakes, *Crotalus viridis*; and gopher snakes, *Pituophis melanoleucus* (Alcorn, 1940*a*; Messick and Hornocker, 1981; Scheffer, 1941; Smith and Johnson, 1985).

Alcorn (1940*a*) discussed the use of *S. townsendii* as a food item by the Piute Indians, and suggested that its range may have been expanded through deliberate human introductions. In some areas, *S. townsendii* causes agricultural damage and has been the subject of control programs (Alcorn, 1940*a*; Howell, 1938).

Smith and Johnson (1985) used Pymatuning live traps baited with apple to capture *S. t. idahoensis*. Live traps of conventional design are ineffective for capturing *S. t. mollis*, but animals have been obtained by noosing and with steel traps with padded jaws concealed at burrow entrances (Rickart, 1982*a*). Captive *S. t. mollis* have been maintained on diets containing alfalfa, rabbit chow, rolled oats, meat, apple, bird seed, and fresh green vegetation (Alcorn, 1940*a*; Rickart, 1982*a*, 1986*a*).

BEHAVIOR. Townsend's ground squirrels emerge from dormancy during late winter (midJanuary to late February; Rickart, 1982*a*; Scheffer, 1941; Smith and Johnson, 1985). As in other ground squirrels, males emerge 2 to 3 weeks before females. For *S. t. idahoensis*, the emergence sequence is: adult males, adult females, yearling females, and nonreproductive yearling males (Smith and Johnson, 1985). In contrast, yearling *S. t. mollis* have scrotal testes and emerge simultaneously with older males (Rickart, 1982*a*, 1982*b*). Juveniles first emerge from natal burrows 6 to 8 weeks after adults (from late March to early May; Rickart, 1982*a*; Scheffer, 1941; Smith and Johnson, 1985). The timing of seasonal activity for *S. t. mollis* varies both geographically (Hansen, 1956*b*) and seasonally (Rickart, 1982*a*) as a function of local climate.

Animals enter dormancy in late spring and and early summer. For *S. t. mollis*, adult males immerge first, followed by adult females, juvenile females, and juvenile males (Rickart, 1982*a*). The period of dormancy usually encompasses 7.5 to 9 continuous months (Alcorn, 1940*a*; Rickart, 1982*a*; Scheffer, 1941). Poor food availability may either lengthen or shorten the active season or promote a separate period of activity in autumn (Alcorn, 1940*a*; Smith and Johnson, 1985).

Spermophilus townsendii is strictly diurnal, with most aboveground activity occurring during early morning. Animals tend to avoid the heat of midday, and are less active on windy days (Hansen, 1954*a*; Svihla, 1939).

Home burrows of adult *S. t. mollis* reach depths of up to 146 cm, and lengths of more than 17 m. They may contain one or more side tunnels, and several entrances. Home burrows of juveniles generally are shallower and lack both side passages and multiple entrances. Nests of grass or shredded bark are built in chambers from 17 to 25 cm in diameter. Burrow systems used for several years may contain more than one nest chamber. Short auxiliary burrows lacking nests are constructed near feeding areas. Twenty-five inhabited burrows excavated during March and April each contained only one adult (Alcorn, 1940*a*).

Townsend's ground squirrels commonly climb into bushes in search of food or to view surroundings. They are good swimmers and voluntarily cross water barriers of up to 7 m (Alcorn, 1940*a*; Davis, 1939).

Alcorn (1940*a*) observed several instances of infanticide and cannibalism in *S. t. mollis*. Victims generally were young animals that had not yet been weaned.

Vocalizations include both single-note and multi-note cells. Animals also emit faint, high-pitched calls while partly or completely underground. This last trait may serve to confuse ground predators (Davis, 1939; Howell, 1938). Davis (1939) reported differences in pitch and duration between alarm calls of *S. t. artemesiae* and *S. t. idahoensis*.

There are no studies dealing directly with social behavior of Townsend's ground squirrels. Armitage (1981) placed *S. townsendii* in his social class 2 that included species colonial in favorable habitats but with colony members living individually. Michener (1983) placed *S. townsendii* at grade 1 (asocial) or 2 (single-family female kin clusters). Although adults tend to be intolerant of one another in the wild, captives housed together coexist peacefully (Alcorn, 1940*a*).

GENETICS. There are three cytotypes characterized by differences in diploid and fundamental numbers: $2n = 46$, FN = 66 and 68 (the taxa *vigilis* and *canus*, respectively); $2n = 38$, FN = 66 (*mollis, idahoensis*, and *nancyae*); and $2n = 36$, FN = 68 (*townsendii*). No chromosomally intermediate individuals have been found between these groups. For all taxa, the X chromosome is a submetacentric, and the Y chromosome is a small acrocentric (Nadler, 1966, 1968*a*). My findings regarding chromosomes of *S. t. artemesiae* place this taxon in the $2n = 38$, FN = 66 group. Giemsa-band preparations for *S. t. mollis* and *S. t. vigilis* indicate that differentiation has resulted from Robertsonian rearrangements (Nadler et al., 1973, 1984). The diploid number of 46 seen in the *canus-vigilis* group is the highest for the genus, and has been considered as either primitive (Liapunova and Vorontsov, 1970; Nadler, 1966) or highly derived (Nadler et al., 1984).

On the basis of starch-gel electrophoresis, *S. townsendii* is biochemically distinct from other species in the subgenus *Spermophilus*. The primary distinguishing loci examined are transferrin, hemoglobin, albumin, and 6-phosphogluconate dehydrogenase. There is considerable polymorphism, particularly at the transferrin locus. Significant yearly differences in transferrin allelic frequencies have been noted for populations of the subspecies *townsendii, nancyae*, and *mollis*. A unique transferrin allele, Tf_{17}, is seen in *mollis* (Nadler, 1968*b*; Nadler et al., 1974, 1982).

REMARKS. The name *townsendii*, as applied to North American ground squirrels, has been subject to considerable confusion. The type locality of *S. townsendii* Bachman is not known precisely. For many years, the name was applied to the speckled

ground squirrel that occurs east of the Columbia River in southern Washington. Upon examining the pelage of Bachman's type, Howell (1938) reallocated the name to the unspeckled squirrel from the west side of the Columbia (previously known as *S. mollis yakimensis* Merriam) and named the speckled taxon *S. washingtoni*. Scheffer (1946) argued against this reallocation because it was not based on cranial comparisons. An additional source of confusion was Allen's (1877) naming of *S. richardsonii townsendi* (=*S. elegans elegans* Kennicott). Merriam (1891) subsequently recognized Allen's error, and applied Bachman's name to the squirrel he later designated *Citellus mollis artemesiae* (Merriam, 1913). Howell (1938) and Scheffer (1946) provide further details.

The generic name *Spermophilus* is derived from the Greek roots *sperma* (seed) and *philos* (loving). The specific epithet *townsendii* honors J. K. Townsend, collector of the holotype. Other vernacular names include: Piute ground squirrel (*S. t. mollis*), Malheur ground squirrel (*S. t. vigilis*), gray ground squirrel (*S. t. canus*), sagebrush or least Idaho ground squirrel (*S. t. artemesiae*), and Snake Valley or Payette ground squirrel (*S. t. idahoensis*; Davis, 1939; Howell, 1938).

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