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Sorex trowbridgii.

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Sorex trowbridgii Baird, 1857

Trowbridge's Shrew

Sorex trowbridgii Baird, 1857:13. Type locality "Astoria [Clatsop Co.], Oregon."

S. montereyensis Merriam, 1895:79. Type locality "Monterey [Monterey Co.], California."

CONTEXT AND CONTENT. Order Insectivora, Family Soricidae, Subfamily Soricinae, Tribe Soricini, Genus *Sorex*, Subgenus *Sorex* (Repenning, 1967; Junge and Hoffmann, 1979). Five subspecies are recognized (Hall, 1981):

S. t. destructioni Scheffer and Dalquest, 1942:334. Type locality "Destruction Island, Jefferson Co., Washington."

S. t. humboldtensis Jackson, 1922:264. Type locality "Carson's Camp, Mad River, Humboldt Bay, Humboldt County, California."

S. t. mariposae Grinnell, 1913:189. Type locality "Yosemite Valley at 4000 feet altitude, Mariposa County, California."

S. t. montereyensis Merriam, 1895:79, see above.

S. t. trowbridgii Baird, 1857:13, see above.

DIAGNOSIS. Externally, *S. trowbridgii* may be distinguished from other species in the genus by its sharply bicolored tail and the dark venter that is almost concolor with the dorsum (Jackson, 1928). As with other members of the subgenus *Sorex*, the ridge extending from the apex of the unicuspid toward the interior edge of the cingulum is only slightly pigmented and almost never pigmented to the cingulum, separated from the cingulum by an anter-posterior groove, never ending in a distinct cusplet. The third unicuspid is smaller than the fourth; it is the only member of the subgenus with this character (Jackson, 1928; Junge and Hoffmann, 1979). Trowbridge's shrews usually possess a post-mandibular foramen; the orbit is placed relatively far back at the level of the metastyle of M2; the lacrimal foramen is at the interface of M1 and M2; and the border of the infraorbital foramen is on a line between the mesostyle and metastyle of M1 (Carraway, 1987; Junge and Hoffmann, 1979; van Zyll de Jong, 1983).

GENERAL CHARACTERS. *Sorex trowbridgii* is a medium-sized, long-tailed shrew (Fig. 1; Jackson, 1928). The species has a dark gray pelage slightly more brownish in summer than in winter. Whiskers are numerous and moderately long. The ears are almost hidden by the pelage. The tail is hairy in young animals, becoming naked as individuals age. The feet are pentadactylous, as in all *Sorex*, and vary in color "from whitish to very light tan" (Maser et al., 1981:61). There are five unicuspidate teeth in the upper jaw, one incisor with two cusps, and four molariform teeth; the lower jaw possesses one incisor, two unicuspidate teeth, and three molariform teeth (Fig. 2). The teeth are pigmented a dark reddish-brown. The skull is medium-sized for *Sorex* and moderately depressed (Baird, 1857; Jackson, 1928; Maser et al., 1981; Repenning, 1967; van Zyll de Jong, 1983).

Means (in mm) and ranges (in parentheses) of five samples representing Canadian *S. t. trowbridgii* (van Zyll de Jong, 1983), American *S. t. trowbridgii*, *S. t. humboldtensis*, *S. t. montereyensis*, and *S. t. mariposae* (Jackson, 1928) are as follows: total length, 113.0 (104 to 124), 119.2 (113 to 130), 131.2 (129 to 133), 122.5 (114 to 131), 118.5 (116 to 121); length of tail, 54.3 (50 to 59), 55.6 (52 to 59), 60.8 (60 to 62), 52.2 (48 to 56), 50.5 (50 to 51); length of hind foot, 13.1 (12.1 to 14.5), 13.5 (13 to 14), 14.5 (14 to 15), 14.4 (13.5 to 15), 14.2 (14 to 15); condylobasal length, 17.2 (16.8 to 17.5), 17.4 (17.1 to 17.6), 18.1 (17.8 to 18.3), 18.2 (18.0 to 18.4), 18.6 (18.4 to 18.8); cranial breadth, 8.6 (8.3 to 8.9), 8.7 (8.3 to 8.9), 9.0 (8.9 to 9.1), 9.0 (8.7 to 9.2), 9.3 (9.2 to 9.4); interorbital width, 3.8 (3.7 to 3.9), 3.8 (3.6 to 3.9), 4.0 (3.9 to 4.1), 4.2 (4.0 to 4.3), 4.2 (4.1 to 4.3); maxillary width, 4.9 (4.9 to 5.1), 4.9 (4.8 to 5.0), 5.3 (5.3 to 5.4), 5.6 (5.4 to 5.7), 5.6 (5.5 to 5.7).

DISTRIBUTION. *Sorex trowbridgii* occurs from coastal southwestern British Columbia south of Burrard Inlet, through western Washington and Oregon to northwestern California; from there, south through the coast ranges to Santa Barbara County, California, and east to the Warner Mountains of northeastern California and south through the Sierra Nevada to Kern County, California (Fig. 3; Cowan and Guiguet, 1960; Dalquest, 1948; Hall, 1981; Verner and Boss, 1980).

FOSSIL RECORD. *Sorex trowbridgii* is known only from one site, an asphalt trap at Carpinteria, California, dated from the Wisconsinan (late Rancholabrean); this site is at the extreme southern edge of the species' present distribution (Kurtén and Anderson, 1980; Lundelius et al., 1983). The lack of fossils may be because there are few late Cenozoic deposits from the Pacific Coast north of San Francisco Bay (Lundelius et al., 1983). George (1988) speculated that the lineage is considerably older than late Pleistocene, possibly diverging from its ancestral stock in the early Pliocene.

FORM AND FUNCTION. There are two molts each year. Autumn molt occurs from September to early November, but a few specimens have been found molting to winter pelage as early as late July and August (Jackson, 1928; Jameson, 1955). In spring, a few animals molt to a brown summer coat; this occurs from late April to June, but takes place as late as July and August in the Sierra Nevada. The winter coat is thicker, longer, and paler in color than the summer coat (Jackson, 1928). Before their first molt, juveniles are more brownish than adults (van Zyll de Jong, 1983).

Like all *Sorex*, the separate cranial bones anastomose into one "compact whole" while the shrews are still juvenile, making comparison of individual bones of the skull impossible (Jackson, 1928: 1). Food consumption is high (0.91 g food g body mass^{-1} day^{-1} for breeding individuals; 1.43 g food g body mass^{-1} day^{-1} for nonbreeding individuals), presumably to maintain a high metabolic rate (Rust, 1978; Terry, 1978).

ONTOGENY AND REPRODUCTION. Pregnant female Trowbridge's shrews have been found from March to May in Washington, carrying three to four embryos (Dalquest, 1941; Scheffer and Dalquest, 1942). An average of 3.89 embryos was found in a sample of 463 Oregon females (Gashwiler, 1976). In the Sierra Nevada, *S. trowbridgii* breeds from February until early June, and the mean number of embryos carried is five (varying from three to six, with one occurrence of one; Jackson, 1928; Jameson, 1955).

FIG. 1. Photograph of *Sorex t. trowbridgii* from Washington. Photograph courtesy of V. B. Scheffer.

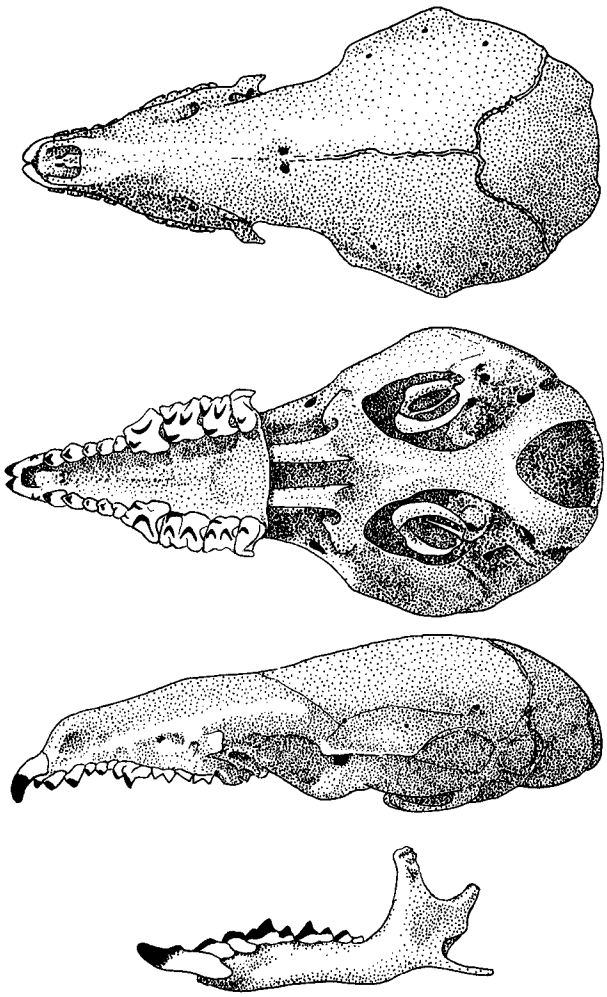

FIG. 2. Dorsal, ventral, and lateral views of skull of *Sorex trowbridgii humboldtensis* (Natural History Museum of Los Angeles County 37016, male, 2 mi S, 3.5 mi E Orick, Humboldt Co., California). Greatest length of cranium is 18.1 mm. Illustration by M. Butler.

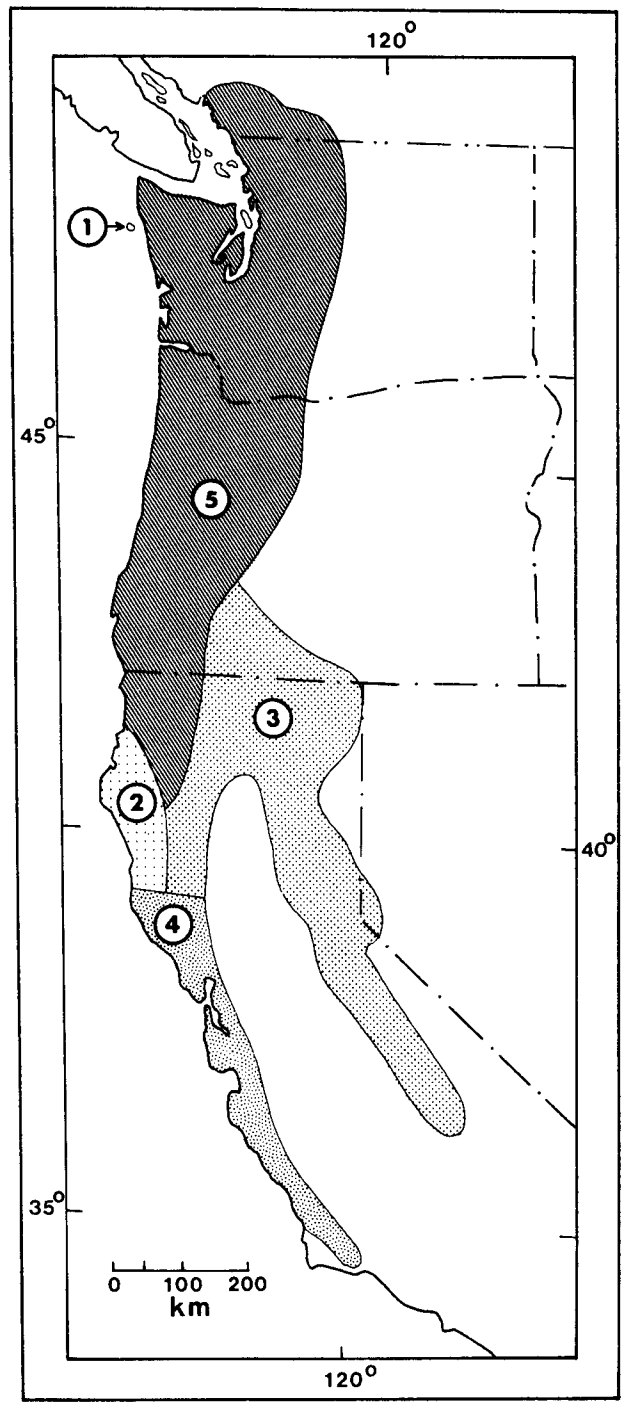

FIG. 3. Geographic distribution of *Sorex trowbridgii* (Hall, 1981). Subspecies are: 1, *S. t. destructioni*; 2, *S. t. humboldtensis*; 3, *S. t. mariposae*; 4, *S. t. montereyensis*; 5, *S. t. trowbridgii*. Illustration by M. Butler.

Twelve percent of gravid females in the Sierra Nevada were lactating, suggesting that post-partum pregnancies are probably frequent (Jameson, 1955).

Onset of sexual maturity in the Sierra Nevada is accompanied by increased mass and testis size in males and increased mass and width of the uterine horns in females. This may be affected by local conditions and variability in climate from year to year, with populations in warmer sites and during warmer years attaining maturity at earlier dates (Jameson, 1955). Females appear to mature about 2 weeks later than males. After the conclusion of the breeding season, the reproductive structures shrink and become non-functional. Mass of breeding individuals averages 5 g, whereas mass of non-breeding individuals averages 3.8 g (van Zyll de Jong, 1983).

ECOLOGY. Predators of *S. trowbridgii* include barred owl (*Strix varia*—Leder and Walters, 1980), Pacific giant salamander (*Dicamptodon ensatus*—Maser et al., 1981). Domestic cats will kill Trowbridge's shrews, but usually refuse to eat them (Maser et al., 1981).

Ticks found on *S. trowbridgii* include *Ixodes angustus* and *I. soricis* (Bishopp and Trembley, 1945; Easton and Goulding, 1974). Mites include the laelapid species *Hirstionyssus obsoletus*, *H. utahensis* (Herrin, 1970), *Haemogamasus keegani* (Whitaker and Wilson, 1974), *H. occidentalis*, *H. reidi*, *Androlaelaps fahrenholzi*, *A. casalis*, *Eulaelaps stabularis*, *Eubrachylaelaps debilis*, and *Alphalaelaps aplodontiae*, the myobiid *Protomyobia brevisetosa*, glycyphagid species *Orycteroxenus soricis* and *Glycyphagus hypudaei*, the cheyletid *Eucheyletia bishoppi*, pygmephorid species *Pygmephorus horridus*, *P. designatus*, *P.* sp., and *Bakerdania* sp., plus *Euryparasitus* sp., *Cyrtolaelaps* sp., *Pseudoparasitus* sp., *Proctolaelaps* sp., an unidentified anoetid (Whitaker et al., 1980), and the tarsonemid *Pygmephorus plurispinosus* (Mahunka, 1975). The chigger, *Comatacarus americanus*, attaches in or around the ear canal of shrews, not in the pinna (Easton, 1975). The only coleopteran recorded from *S. trowbridgii* is *Leptinus testaceus* (Gould and Beal, 1952; Maser and Hooven, 1971). Fleas include *Nearctopsylla princei* and *Corypsylla kohlsi* (Lewis, 1974). Hertel and Duszynski (1987) found 10 to 48 (21%) individuals infected with coccidia; coccidian species included *Eimeria palustris*, *E. vagrantis*, and *Isospora palustris*.

Jameson (1955:340) characterized the habitat of *S. trowbridgii* throughout its range as "mature forest type with an abundant

ground litter." Dalquest (1948) stated that Trowbridge's shrews are most common over dry ground beneath fir forest, are abundant in ravines and swampy woods when other shrews are absent, but avoid open meadows and marshes. Habitat of *S. t. destructioni* on Destruction Island, off the Pacific coast of Washington, is characterized by grass and tall brush, with highest abundances of shrews in "deep, rank, grass at the border of salmon-berry thickets" (Scheffer and Dalquest, 1942:333). Jackson (1928:4) stated that *S. trowbridgii* could be found in the "regulation" damp, mossy, shrew habitat, but that it "displays a marked preference for the drier woods." This preference might be explained by Dalquest's (1941) work in western Washington demonstrating that the removal of *S. vagrans* from a wet ravine bottom resulted in the invasion of *S. trowbridgii* from surrounding dry slopes of Douglas fir (*Pseudotsuga menziesii*). Removal of populations of *Peromyscus maniculatus* resulted in greatly inflated numbers of both species of *Sorex* (Dalquest, 1941). Whitaker and Maser (1976) suggested that in densely forested areas of western Oregon where *S. trowbridgii* is found sympatric with other species of *Sorex*, *S. trowbridgii* is found in the greatest numbers because it possesses the least specialized diet.

The habitat of *S. trowbridgii* has been quantified as having a relatively thick organic layer, low water table, and large amounts of ground cover or canopy. The species is more a burrower in organic layers of soils than is the sympatric *S. monticolus*, which is found more often in surface debris. These two species probably are separated by micro-habitat rather than by competition; this is supported by the fact that the species are similarly distributed in all areas where they are found, sympatrically or not. In contrast, the burrowing capabilities of *S. trowbridgii* probably give it an advantage over the non-burrowing *S. vagrans*, which is displaced in drier, more friable soils (Terry, 1981).

In the Oregon Cascade Mountains, significantly more *S. trowbridgii* were caught in riparian fringe habitat (15 to 25 m from streams) than at stream-side (within 1 m of streams; Chi-square contingency test, $P < 0.05$). More Trowbridge's shrews were captured in mature forest than in old-growth or young forest, however, small samples precluded significance testing (Anthony et al., 1987).

In the central and southern Sierra Nevada, *S. trowbridgii* is limited to the western slope (Verner and Boss, 1980). There, the species is found from 1,230 m elevation in the upper ponderosa pine (*Pinus ponderosa*) forest, through the mixed conifer zone where it was most abundant, up to 2,300 m on dry slopes among *Ceanothus* clumps in red fir (*Abies magnifica*) forest (Williams, 1984, in press). At the southwestern limits of its range, Grinnell (1933:80) stated that *S. trowbridgii* inhabits dryish hillsides beneath chaparral, as well as moist forest-shaded cañon bottoms."

In Oregon, population densities of *S. trowbridgii* are greatest in uncut, mature forest, less in clear-cut forest, and the least in stands that are clear-cut and slash-burned (Gashwiler, 1970; Hooven and Black, 1976; Moore, 1942). Gashwiler (1970) noted that 6 years passed before population densities on a clear-cut area approached densities in virgin forest. In contrast, Gunther et al. (1983) found the highest abundances of Trowbridge's shrews on clear-cut plots in the Cascade Mountains of north-central Washington. They attributed this difference to a higher percentage of ground cover in Washington clear-cuts, providing a more favorable microhabitat, higher invertebrate populations than in uncut forest, and better protection from predators. Current timber-management activities of clear-cutting forest should benefit *S. trowbridgii* by maintaining areas with good ground cover (Silovsky and Pinto, 1974). Shrew densities do decline, however, after forest wildfires (Black and Hooven, 1974; Hooven, 1969).

At upper elevations on the west slope of the Sierra Nevada, insectivores associated with *S. trowbridgii* are *S. monticolus* and *S. palustris*, and at lower elevations, *S. ornatus* and *S. palustris* (Williams, in press). Species found with *S. trowbridgii* in the Trinity region of northern California include *S. vagrans, Scapanus latimanus, Aplodontia rufa, Eutamias senex, Spermophilus beecheyi, S. lateralis, Tamiasciurus douglasii, Glaucomys sabrinus, Thomomys monticolus, Peromyscus maniculatus, Neotoma cinerea, N. fuscipes, Microtus longicaudus, Clethrionomys californicus, Zapus trinotatus, Martes americana, Mustela erminea, M. frenata, M. vison, Procyon lotor, Ursus americanus,* and *Odocoileus hemionus* (Grinnell, 1916; Kellogg, 1916). In the Cascade Mountains of western Oregon, *S. trowbridgii* is found in association with *S. bendirii, S. vagrans* [this probably includes *S. monticolus*], *Neurotrichus gibbsii, Scapanus orarius, Ochotona princeps, Lepus americanus, Aplodontia rufa, Spermophilus beecheyi, Eutamias townsendii, Tamiasciurus douglasii, Glaucomys sabrinus, Peromyscus maniculatus, Neotoma cinerea, Clethrionomys californicus, Arborimus albipes, Microtus oregoni, M. richardsoni, Zapus trinotatus, Erethizon dorsatus, Mustela erminea, M. frenata,* and *Spilogale putorius* (Hooven and Black, 1976). Sign of *Thomomys mazama, Canis latrans, Procyon lotor, Lynx rufus, Ursus americanus, Cervus canadensis,* and *Odocoileus hemionus* also has been found in the area where Trowbridge's shrews are caught. In the Coast Range of Oregon, *S. trowbridgii* has been found in association with *S. pacificus, Eutamias townsendii, Peromyscus maniculatus, Microtus oregoni, M. longicaudus, Arborimus albipes, Mustela erminea,* and *Sylvilagus bachmani* (Maser and Hooven, 1969), plus *S. vagrans, Tamiasciurus douglasii, Glaucomys sabrinus, Neotoma cinerea, Clethrionomys californicus, Mustela erminea,* and *Lepus americanus* (Gashwiler, 1959). In Washington, mammals associated with *S. trowbridgii* are *S. vagrans, S. monticolus,* and *Neurotrichus gibbsii* (Terry, 1981), plus *Scapanus orarius, Aplodontia rufa, Eutamias townsendii, Peromyscus maniculatus, Microtus oregoni,* and *Zapus trinotatus* (Dalquest, 1941).

In studies to determine the effects of herbicides (2,4-D, atrazine, dalapon, silvex) on small mammal populations, *S. trowbridgii* is found in significantly greater numbers on herbicide-treated plots than on untreated plots (Black and Hooven, 1974; Borrecco et al., 1979). This is interpreted as a response to the decrease of herbaceous cover and the corresponding increase in tree cover on the treated plots.

Eighteen months is probably the maximum life span of *S. trowbridgii*, as most adults that survive a winter disappear rapidly in the following May, June, and July; over-wintering adults have disappeared by the subsequent November (Jameson, 1955). Because of high spring and summer recruitment, populations in the autumn tend to be double the size of spring populations (Gashwiler, 1970).

Terry (1978:43) stated that Trowbridge's shrews were "generalists with regard to food." An examination of 80 stomachs of *S. trowbridgii* from the Sierra Nevada indicated that the diet was primarily small arthropods, including Neuroptera, Coleoptera, Diptera, Lepidoptera, Hemiptera, and Hymenoptera, plus Arachnida, Chilopoda, Annelida, and *Planaria* (Jameson, 1955). In Oregon, results of a study of 158 stomachs of wild-caught shrews found 47 types of food; the most common foods were Chilopoda (15.4%), Arachnida (11.6%), internal organs of Coleoptera (10.5%), and Mollusca (9.4%; Whitaker and Maser, 1976).

Trowbridge's shrews often eat Douglas fir seed and other plants as well (Moore, 1942). In seed selection experiments, *S. trowbridgii* is restricted to smaller food items (seeds <35 mg), seemingly because of the inability to penetrate heavy seed coats and capsules, and thick exoskeletons in the case of insects. Seeds of *Pseudotsuga menziesii, Pinus monticola,* and *Picea sitchensis* are selected over those of *Abies procera* and *A. amabilis*; the only seed consistently rejected is that of *Digitalis purpurea* (Terry, 1978). Of two stomachs examined for spores, 10% of the volume of one stomach was hypogeous Endogonaceae only, with no basidomycetes or ascomycetes (Maser et al., 1978).

Trapping for *S. trowbridgii* is most effective when using pitfall traps (Williams and Braun, 1983). In the Oregon Cascade mountains, significantly more shrews are caught with Museum Special snap traps than with Victor rat traps (Chi-square, $P < 0.001$; Anthony et al., 1987). When compared, significantly more of the "newer" model of Museum Special snap traps catch Trowbridge's shrews than the "older" model (G-test, $P < 0.001$; West, 1985). In Oregon, *S. trowbridgii* is usually the most common shrew, and often the most common mammal collected in coniferous forest (Bailey, 1936; Maser et al., 1981).

BEHAVIOR. Hoarding behavior, wherein Trowbridge's shrews carry seeds away from the source and bury them, has been noted in captivity (Terry, 1978). To identify whether a Douglas fir seed contains a kernel, it is necessary for *S. trowbridgii* to sample each seed individually, whereas mice evidently can determine this by simply picking up the seed (Moore, 1942).

Sorex trowbridgii is active for 39% of a 24-h period, in "short bursts at regularly spaced intervals followed by periods of quiescence"; the short-term cycles have an average periodicity of approximately 1 h (Rust, 1978). Although Whitaker and Maser (1976) stated that *S. trowbridgii* is nocturnal, both Rust (1978) and Terry (1978) found that in captivity, the species was active at all times of the day and night (although more active in hours of darkness),

with no long rest periods. Old adults tend to be more active in the spring than in the winter, and young adults tend to be more active in the autumn than in the late summer; these levels of activity correspond to breeding seasons (Rust, 1978). Breeding individuals are more active than non-breeding individuals, but their food consumption is significantly less (Student's t-test, $P < 0.001$; Rust, 1978).

Dalquest (1948) and Maser et al. (1981) found *S. trowbridgii* to be the most difficult shrew to maintain in captivity. Terry (1978) was successful with a diet of canned dogfood, insect larvae, conifer seeds, and mushrooms.

GENETICS. *Sorex trowbridgii* from Oregon and California had diploid numbers of 34 chromosomes with 2 metacentric, 4 submetacentric, and 26 acrocentric autosomes (Brown, 1974). In an examination of allozymic variability among 10 individuals of Trowbridge's shrews from Oregon and Washington, 3 of 26 presumptive loci were polymorphic, and average individual heterozygosity was 0.02 (George, 1988).

REMARKS. The genus name *Sorex* is a Latin word meaning "shrew-mouse." The species name *trowbridgii* is a patronymic honoring Lt. W. P. Trowbridge, the collector of the type specimen. Subgeneric classification of *S. trowbridgii* has been equivocal; Findley (1955) and Junge and Hoffmann (1979) assigned *S. trowbridgii* to the subgenus *Sorex* on the basis of the post-mandibular foramen, whereas van Zyll de Jong (1983) pointed out that the structure of the unicuspids, the reduced size of the third unicuspid, and the presence of 13 pairs of ribs link it to the subgenus *Otisorex*. Based on allozymic characters and the retention of a number of ancestral morphologic characters, George (1988) suggested that *S. trowbridgii* should be classified in a third, as yet unnamed subgenus along with *S. merriami* and *S. arizonae*. Subspecific designations are based on variations in relative size of the tail, palate, and molariform teeth, as well as differences in coloration (Jackson, 1928).

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