

Tamias umbrinus (Rodentia: Sciuridae)

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Abstract: *Tamias umbrinus* Allen, 1890, a medium-sized chipmunk commonly called the Uinta chipmunk, is 1 of about 25 species of extant chipmunks. It is distributed in the western United States from southern Montana south to Arizona and from Colorado west to eastern California. *T. umbrinus* prefers montane and subalpine coniferous forest at elevations between 1,417 and 3,660 m. The species is listed as “Least Concern” by the International Union for Conservation of Nature and Natural Resources; although the distribution is fragmented, the species is common locally and the distribution includes protected areas.

Key words: chipmunk, North America, sciurid, Uinta chipmunk, United States

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Tamias umbrinus Allen, 1890 Uinta Chipmunk

Tamias umbrinus Allen, 1890:58, 96. Type locality “Uintah Mountains, south of Fort Bridger [Sweetwater County, Wyoming],” Summit County, Utah; restricted by A. H. Howell (1929:94) to “Blacks Fork, Uinta Mountains, Utah (altitude about 9,500 feet).”

Eutamias umbrinus: Miller and Rehn, 1901:45. Name combination.

[*Tamias* (*Eutamias*)] *umbrinus*: Elliot, 1901:75. Name combination.

Eutamias quadrivittatus umbrinus: Hayward, 1945:53, 62. Name combination.

Eutamias umbrinus umbrinus: White, 1953b:571. Name combination.

Eutamias speciosus inyoensis Merriam, 1897:194, 202, 208. Type locality “from White Mts., Inyo Co.,” California; restricted by Grinnell (1933:129) to “White Mountains (southern end, at about 9000 feet altitude, near head of Black Canyon of U.S.G.S. Bishop Quadrangle, edition of May, 1913).”

[*Tamias* (*Eutamias*) *callipeplus*] *inyoensis*: Elliot, 1901:73. Name combination. Incorrectly typeset on page with *inyoensis* rather than with *speciosus* (Elliot 1905).

[*Eutamias callipeplus*] *inyoensis*: Trouessart, 1904:332. Name combination.

Eutamias adsitus Allen, 1905:118. Type from “Briggs Meadow, Beaver Range Mountains, [Beaver County], Utah (alt. 10,000 ft.).”

Tamias [(*Eutamias*)] *speciosus inyoensis*: Elliot, 1905:89. Name combination.

Tamias [(*Eutamias*)] *adsitus*: Elliot, 1905:95. Name combination.

Eutamias quadrivittatus inyoensis: Howell, 1929:84. Name combination.

Eutamias quadrivittatus nevadensis Burt, 1931:299. Type locality “Hidden Forest, Sheep Mountains, Clark County, Nevada; altitude 8500 feet.”

Eutamias quadrivittatus adsitus: Hardy, 1945:87. Name combination.

Eutamias umbrinus adsitus: White, 1953b:572. Name combination.



Fig. 1.—An adult *Tamias umbrinus* from Bryce Point, Bryce Canyon National Park, Garfield County, Utah, elevation approximately 2,400 m. Used with the permission of the photographer D. Welling.

Eutamias umbrinus sedulus White, 1953b:573. Type locality “from Mount Ellen, Henry Mountains, Garfield County, Utah.”

Eutamias umbrinus inyoensis: White, 1953b:573. Name combination.

Eutamias umbrinus nevadensis: White, 1953b:574. Name combination.

Eutamias umbrinus fremonti White, 1953b:575. Type locality “from 31 mi. N Pinedale, 8,025 ft., Sublette County, Wyoming.”

Eutamias umbrinus montanus White, 1953b:576, fig. 6. Type locality “from 1/2 mi. E and 3 mi. S Ward, 9,400 ft., Boulder County, Colorado.”

CONTEXT AND CONTENT. Order Rodentia, suborder Sciuromorpha, family Sciuridae, subfamily Xerinae, tribe Marmotini, genus *Tamias*, subgenus *Neotamias*. Seven subspecies are recognized (Thorington and Hoffmann 2005):

T. u. adsitus (Allen, 1905:118). See above.

T. u. fremonti (White, 1953b:575). See above.

T. u. inyoensis (Merriam, 1897:194, 202, 208). See above.

T. u. montanus (White, 1953b:576, fig. 6). See above.

T. u. nevadensis (Burt, 1931:299). See above.

T. u. sedulus (White, 1953b:573). See above.

T. u. umbrinus Allen, 1890:96. See above.

NOMENCLATURE NOTES. The type locality of *Tamias umbrinus adsitus* frequently has been given as “Briggs (= Britt’s or Britts) Meadow” (e.g., Durrant 1952; Hall 1981; Howell 1929). The localities appear to refer to different locations at different elevations (Van Cott 1990) and suggest that further clarification is needed. Type specimens for taxa given above are present in the collections at the American Museum of Natural History (*T. u. adsitus* AMNH 28728), United States National Museum of Natural History (*T. u. inyoensis* USNM 29387, *T. u. sedulus* USNM 158181, and *T. u. umbrinus* USNM 186463), University of California, Los Angeles, Dickey Collection (*T. u. nevadensis* UCLA 15884), and University of Kansas, Museum of Natural History (*T. u. fremonti* KU 41790 and *T. u. montanus* KU 20105). Goodwin (1953) and Lawrence (1993) commented on *T. u. adsitus* AMNH 147870, which has the same locality, date, and collector as AMNH 28728, and the word type and a reference to Allen’s (1905) publication; the museum label number, however, of AMNH 147870 is “391 [452],” whereas that of AMNH 28728 is “452.”

Recognition of the subgenus *Neotamias* as a genus is supported by molecular and ectoparasite data (Jameson 1999; Piaggio and Spicer 2001). Specific distinctness of *T. umbrinus* from *T. quadrivittatus* is based on bacular morphology, baubellar morphology, cranial morphology, and pelage coloration (Bergstrom and Hoffmann 1991; Long and Cronkite 1970; White 1953b) and molecular data

(Piaggio and Spicer 2000). Molecular data (Piaggio and Spicer 2000, 2001), as well as morphology of the baubellum and baculum, and cranial and external morphometrics (Nadler et al. 1985; Sutton 1982), but not genic data (Nadler et al. 1985), support the recognition of *T. palmeri* as a subspecies of *T. umbrinus*.

DIAGNOSIS

Tamias umbrinus is distinguished from other species of chipmunk that occur in its general distributional range by a combination of characters including size, pelage coloration, and morphology of the baculum (Fig. 1). Compared with other species, except *T. palmeri* (Palmer’s chipmunk), the baculum of *T. umbrinus* is distinguishable by the following characters in combination: width of base greater than one-third the length of shaft; distal one-half of the shaft laterally compressed; and keel one-fourth of the length of the tip (White 1953a). *T. umbrinus* may be distinguished from *T. quadrivittatus* (Colorado chipmunk) by external, cranial, bacular, and baubellar characters. General coloration of *T. umbrinus* is brownish (paler, reddish yellowish or reddish brown in *T. quadrivittatus*) and the dorsal stripes less distinct and do not extend to the base of the tail (Allen 1890; Bergstrom 1999; Fitzgerald et al. 1994; White 1953b). The skull of *T. umbrinus* is longer and narrower (relatively shorter and absolutely broader in *T. quadrivittatus*—Armstrong 1972; Fitzgerald et al. 1994; White 1953b); the ratio of zygomatic breadth to the greatest length of skull is 0.5360 in *T. umbrinus* compared with 0.5465 in *T. quadrivittatus* and the zygomatic arch is lighter and more slender (Armstrong 1972). The diameter of the jugal is a diagnostic character that distinguishes *T. umbrinus* from *T. quadrivittatus* (Armstrong 1972; Bergstrom and Hoffmann 1991; Fitzgerald et al. 1994; White 1953b); in lateral aspect the jugal is narrower, with mean width of 1.49 compared with 1.96 in *T. quadrivittatus quadrivittatus* and 1.84 in *T. quadrivittatus hopiensis* (Armstrong 1972). The baculum of *T. umbrinus* is shorter, more robust, has a pronounced keel, and is more rectangular (angle of baculum tip to shaft $100^\circ \pm 8.8^\circ$) than in *T. quadrivittatus* (Bergstrom and Hoffmann 1991) and the base is wider (White 1953b); characters of the baculum are distinct even in zones of contact (Long and Cronkite 1970). *T. umbrinus* can be distinguished from *T. dorsalis* (cliff chipmunk) by the generally more distinct dorsal stripes (stripes faint in *T. dorsalis*), more brightly colored pelage (paler and grayer in *T. dorsalis*), larger skull, and expanded bacular base (base not noticeably expanded in *T. dorsalis* (White 1953c). Compared with *T. minimus* (least chipmunk), *T. umbrinus* is larger, less brightly colored, with the general coloration more brownish (dorsum is lighter, reddish yellowish in *T. minimus*—Armstrong 2008; Fitzgerald et al. 1994; White 1953c), and has a bushier tail (Armstrong 2008). In *T. umbrinus*, the base of the baculum

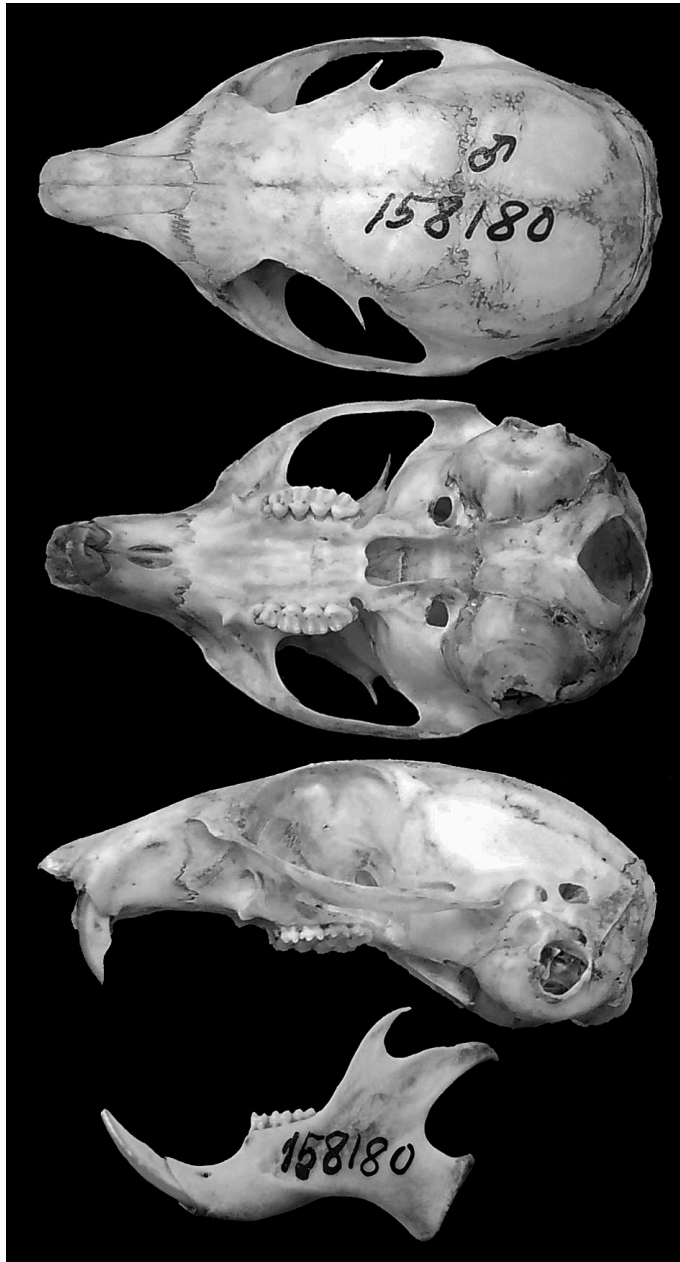


Fig. 2.—Dorsal, ventral, and lateral views of skull and lateral view of mandible of an adult male *Tamias umbrinus* (USNM [United States National Museum of Natural History] 158180) from Mt. Ellen, Henry Mountains, Garfield County, Utah. Occipitonasal length is 33.48 mm. Photograph by M. A. Mares.

is widened, but about the width of the least diameter of the shaft in *T. minimus* (White 1953c). *T. umbrinus* is larger than *T. amoenus* (yellow-pine chipmunk) and the venter is whitish rather than yellowish or buff (White 1953c). Compared with *T. panamintinus* (Panamint chipmunk), *T. umbrinus* is larger, the facial and dorsal stripes are more distinct, and the coloration is brownish (reddish gray in *T. panamintinus*—Blake 1999).

GENERAL CHARACTERS

Tamias umbrinus is a medium-sized chipmunk (White 1953a) and, like other members of the genus, has internal cheek pouches (Howell 1929). Ears are long and pointed (Howell 1929; White 1953a, 1953b 1953c) and the tail is dorsoventrally flattened (Howell 1929). Dorsal color in summer is dark brownish, reddish ochraceous or chestnut brown, or yellowish brown–gray. *T. umbrinus* has 3 dark dorsal stripes. The median dark dorsal stripe is black mixed with yellowish brown or rusty brown; the 2 lateral stripes, parallel to the median dark stripe, are blackish mixed with dull rusty brown. Lateral stripes generally are shorter and narrower than the median stripe, and often are indistinct or obsolete. Four light-colored dorsal stripes are present; the 2 median stripes are light gray and the 2 outer stripes are whiter and broader. *T. umbrinus* exhibits seasonal variation in pelage coloration. Winter pelage similar to that of summer but duller (Durrant 1952), grayish with the dark stripes more obscure (Long and Cronkite 1970). The nape and top of the head are grayish. The head is bordered on each side by a dark brownish stripe; the ocular stripe is narrow and dark brownish; and the malar stripe is narrow and dull, dusky brown, and often indistinct. The light-colored facial stripes are light gray or grayish white. The ears are black externally and bordered with grayish white hairs; medium-sized postauricular patches are grayish white. The flanks are grayish to dull yellowish brown and the venter is grayish white. Dorsally, the color of the tail is a mixture of orange and black; ventrally, the coloration is orange rufous centrally and bordered by black and a fringe of yellow or yellowish buff (Allen 1890; Elliot 1901; Fitzgerald et al. 1994; Howell 1929; Long and Cronkite 1970).

Cranial and dental characters are typical for the genus and subgenus (Fig. 2; Howell 1929; Moore 1959; White 1953a). The infraorbital foramen is ovoid in shape and narrow. The postorbital processes are slender and their bases are narrow. The zygomatic plate is broad and the interorbital constriction is pronounced. The lambdoidal crests are not strongly developed and the temporal ridges do not meet to form a sagittal crest. Supraorbital notches are in line with, or posterior to, the posterior notch of the zygomatic plate. The auditory bullae are relatively large and each has 2 transbullar septa. Upper incisors are opisthodont and the microscopic longitudinal striations are present in the enamel faces. The upper molar tooththrows are nearly parallel. The palate is short, the posterior border terminating beyond M3. Two upper premolars are present, the anteriormost being peglike; a small cusp is present on the lower molars.

External measurements (mean and range, mm) for males ($n = 6$, unless noted otherwise) and females ($n = 6$, unless noted otherwise) of *T. u. adsitus* (Durrant 1952; White 1953b), respectively, were: total length, 214.0 (203.0–225.0), 228.0 (215.0–233.0); length of tail, 89.6 (73.0–95.0), 96.5

(95.0–98.0); length of hind foot ($n = 2, n = 3$), 33.0, 33.0, 30.7 (30.0–32.0); length of ear ($n = 1, n = 3$), 11.0, 11.7 (11.0–12.0). External measurements (mean and range, mm) for males ($n = 8$) and females ($n = 6$) of *T. u. fremonti* (White 1953b), respectively, were: total length, 223.0 (216.0–243.0), 229.0 (223.0–239.0); length of tail, 99.0 (95.0–111.0), 101.0 (92.0–110.0). External measurements (mean and range, mm) for males ($n = 12$, unless noted otherwise) and females ($n = 5$, unless noted otherwise) of *T. u. inyoensis* (Durrant 1952; White 1953b), respectively, were: total length, 208.0 (196.0–220.0), 215.0 (204.0–226.0); length of tail, 89.5 (85.0–100.0), 92.8 (86.0–102.0); length of hind foot ($n = 3, n = 4$), 32.33 (31.0–34.0), 33.0 (31.0–34.0); length of ear ($n = 3, n = 4$), 18.0 (17.0–19.0), 17.0 (14.0–19.0). External measurements (mean and range, mm; body mass, g) for males ($n = 14$) and females ($n = 3$, unless noted otherwise) of *T. u. montanus* (Armstrong 1972), respectively, were: total length, 228.5 (215.0–235.0), 226.3 (220.0–231.0); length of tail, 101.6 (93.0–110.0), 93.0 (88.0–96.0); length of hind foot, 33.8 (33.0–34.0), 34.67 (34.0–35.0); length of ear ($n = 14, n = 2$), 18.0 (16.0–19.0), 18.0, 19.0; and body mass (1 male and 2 females), 66.2, 65.8, 68.7, respectively. Additional data (means, standard deviations, and coefficients of variation for males and females combined) for *T. u. montanus* are given in Bergstrom and Hoffmann (1991). External measurements (mm) of the holotype of *T. u. nevadensis* were (Burt 1931): total length, 205; length of tail, 89; length of hind foot, 32; length of ear, 13. External measurements (mean and range, mm) for males ($n = 5$) and females ($n = 2$) of *T. u. sedulus* (White 1953b), respectively, were: total length, 218.0 (213.0–224.0), 227.0 (224.0–231.0); length of tail, 93.0 (89.0–97.0), 98.0 (96.0–100.0). Means and ranges of external measurements (mm) for males ($n = 11$, unless noted otherwise) and females ($n = 4$, unless noted otherwise) of *T. u. umbrinus* (Durrant 1952; White 1953b), respectively, were: total length, 218.0 (215.0–228.0), 224.0 (204.0–234.0); length of tail, 96.2 (81.0–112.0), 96.4 (90.0–100.0); length of hind foot ($n = 6, n = 2$), 34.0 (32.0–35.0), 34.0, 35.0; length of ear ($n = 6, n = 2$), 17.0 (5–19), 18.0, 18.0.

Cranial measurements (mean and range, mm) for males ($n = 6$) and females ($n = 6$) of *T. u. adsitus* (White 1953b), respectively, were: greatest length of skull, 34.8 (34.3–35.4), 35.1 (33.9–36.2); zygomatic breadth, 18.9 (18.5–19.6), 19.5 (18.9–20.0); cranial breadth, 15.5 (15.3–16.1), 16.0 (15.9–16.3); length of nasals, 10.8 (10.4–11.3), 11.0 (10.6–11.8); length of mandibular tooththrow, 5.16 (4.64–5.34), 5.11 (5.00–5.33). Cranial measurements (mean and range, mm) for males ($n = 8$) and females ($n = 6$) of *T. u. fremonti* (White 1953b), respectively, were: greatest length of skull, 35.6 (35.2–36.5), 35.3 (34.5–36.0); zygomatic breadth, 19.3 (18.9–19.7), 19.6 (19.3–20.0); cranial breadth, 15.9 (15.8–16.1), 15.9 (15.7–16.5); length of nasals, 11.4 (11.1–11.8), 11.3 (10.9–12.0); length of mandibular tooththrow, 5.34 (5.22–5.57), 5.40 (5.35–5.44). Cranial measurements (mean and

range, mm) for males ($n = 8$) and females ($n = 12$) of *T. u. inyoensis* (Johnson 1943), respectively, were: greatest length of skull, 35.2 (34.0–36.0), 35.6 (35.1–36.1); condylobasal length, 31.7 (31.0–32.3), 32.0 (31.3–32.6); zygomatic breadth, 19.3 (18.7–19.8), 19.6 (18.6–20.1); interorbital constriction, 8.0 (7.6–8.4), 7.8 (7.4–8.2); length of nasals, 11.0 (9.9–11.4), 11.1 (10.7–11.7); length of mandibular tooththrow, 5.5 (5.3–5.6), 5.4 (5.3–5.6). Cranial measurements (mean and range, mm) for males ($n = 14$) and females ($n = 3$, unless noted otherwise) of *T. u. montanus* (Armstrong 1972), respectively, were: greatest length of skull ($n = 14, n = 2$), 35.67 (35.0–36.6), 36.3, 36.5; condylobasal length, 32.73 (31.2–33.8), 33.3 (33.2–33.5); zygomatic breadth, 19.05 (18.6–19.3), 19.37 (19.2–19.5); interorbital constriction, 7.68 (7.3–8.4), 7.43 (7.2–7.6); length of nasals ($n = 14, n = 2$), 11.03 (10.7–11.6), 11.1, 11.7; length of mandibular tooththrow, 5.66 (5.5–5.9), 5.77 (5.7–5.8). Cranial measurements (mm) of the holotype of *T. u. nevadensis* were (Burt 1931): greatest length of skull, 34.8; zygomatic breadth, 19.3; cranial breadth, 16.2; length of nasals, 11.0. Cranial measurements (mean and range, mm) for males ($n = 5$) and females ($n = 2$) of *T. u. sedulus* (White 1953b), respectively, were: greatest length of skull, 34.7 (33.5–35.5), 34.9, 34.9; zygomatic breadth, 18.7 (18.4–19.1), 19.3, 19.5; cranial breadth, 15.6 (15.4–15.9), 16.1, 16.1; length of nasals, 10.7 (10.1–11.2), 11.1, 11.3; length of mandibular tooththrow, 5.21 (5.09–5.28), 5.24, 5.42. Cranial measurements (mean and range, mm) for males ($n = 11$) and females ($n = 4$) of *T. u. umbrinus* (White 1953b), respectively, were: greatest length of skull, 34.7 (34.3–35.2), 35.1 (34.9–35.4); zygomatic breadth, 18.9 (18.3–19.4), 19.2 (18.6–20.0); cranial breadth, 15.7 (15.6–16.0), 15.9 (15.7–16.2); length of nasals, 10.9 (10.3–11.7), 11.0 (10.3–11.8); length of mandibular tooththrow, 5.13 (4.79–5.42), 5.17 (5.11–5.22). Differences in size between males and females are insignificant (Bergstrom and Hoffmann 1991; Hoffmeister 1986; Long and Cronkite 1970; White 1953b).

DISTRIBUTION

Tamias umbrinus occurs from eastern California and northern Arizona to northern Colorado, southeastern and northwestern Wyoming, and extreme southwestern Montana (Fig. 3). The fragmented distribution consists of 6 or 7 disjunct populations that may reflect the expansion and contraction of the forest during glacial and interglacial periods (Bergstrom 1999; Fitzgerald et al. 1994). *T. umbrinus* has been recorded from elevations between 1,417 and 3,660 m (4,650–12,008 feet). Geographic variation in minimum capture elevations is exhibited by *T. umbrinus* in the Great Basin of Nevada; relatively high minima are shown at low latitudes and relatively low minima are shown at higher latitudes (Skaggs and Boecklen 1996).

Tamias umbrinus adsitus is restricted to the southern Wasatch Range of south-central and southwestern Utah and

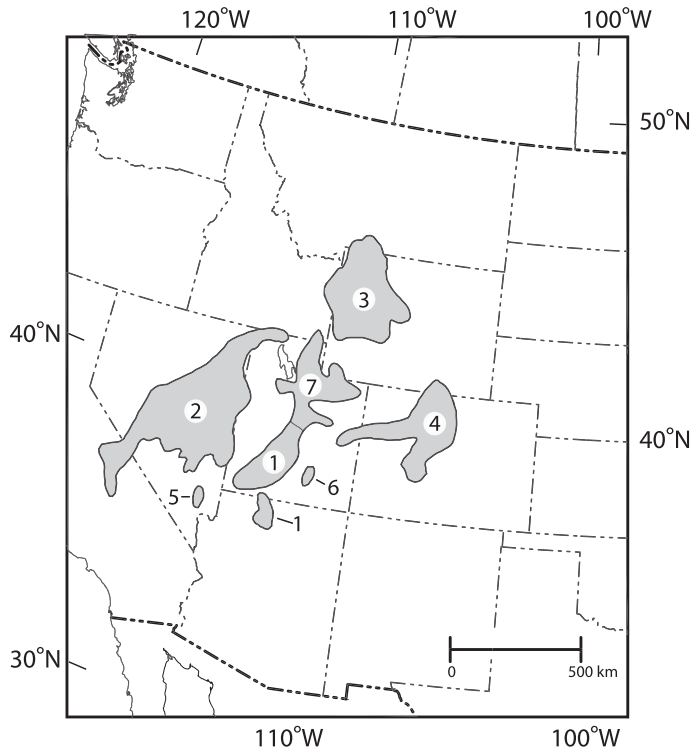


Fig. 3.—Geographic distribution of *Tamias umbrinus*. Subspecies are: 1, *T. u. adsitus*; 2, *T. u. inyoensis*; 3, *T. u. fremonti*; 4, *T. u. montanus*; 5, *T. u. nevadensis*; 6, *T. u. sedulus*; 7, *T. u. umbrinus*. Map redrawn from Hall (1981).

the Kaibab Plateau of north-central Arizona (Allen 1905; Bergstrom 1999; Durrant 1952; Hoffmeister 1986; White 1953b). *T. u. fremonti* is distributed in northwestern and north-central Wyoming, eastern Idaho, and the Absaroka Range of southwestern Montana (Bergstrom 1999; White 1953b, 1953c, 1953d). *T. u. inyoensis* occurs in the White and Inyo mountains of the southern Sierra Nevada of eastern California, central and east-central Nevada, and extreme western (Deep Creek Mountains) and northwestern (Raft River Mountains) Utah (Bergstrom 1999; Durrant 1952; Elliot 1901, 1905; Grinnell 1913; Hall 1995; White 1953b). The distribution of *T. u. montanus* extends from the Snowy Range of south-central Wyoming, south to the Rocky Mountains of north-central Colorado, and west along the White River and Road plateaus to eastern Utah (Armstrong 1972; Bergstrom 1999; Long and Cronkite 1970; White 1953b). *T. u. nevadensis* is restricted to the Sheep Mountains of southern Nevada (Bergstrom 1999; Burt 1931; Hall 1995). *T. u. sedulus* is known only from Mt. Ellen in the Henry Mountains of Utah (Bergstrom 1999; White 1953b). *T. u. umbrinus* occurs from extreme southeastern Idaho and southwestern Wyoming, into the Wasatch and Uinta ranges of northern and central Utah (Bergstrom 1999; Durrant 1952; Elliot 1901, 1905; White 1953b, 1953c, 1953d). No fossils of *T. umbrinus* are known.

FORM AND FUNCTION

Form.—Number of mammae is 8 arranged in 4 pairs—1 pectoral, 2 abdominal, and 1 inguinal (Howell 1929; Moore 1961). Dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22. P3 is present and shows wear in old adults; the anterior root of P4 projects labially of the masseteric knob (White 1953a).

The structure of the malleus was described by White (1953a). The malleus is composed of a head, neck, and manubrium; the head is not elongated; the tip of the manubrium is spatulate; a muscular process is located midway between the head and the manubrium; the articular facet begins on the neck and extends halfway around the head; a lamina (about one-half the length of the head, neck, and manubrium) extends from the anterior edge of the head and neck, and gradually tapers to where it joins the tympanic bulla.

The hyoid apparatus consists of an arched basihyal, 2 thyrohyals, 2 ceratohyals, and 2 stylohyals (White 1953a); the lateral edge of the stylohyal is attached loosely to the tympanic bulla and the posterior end is attached firmly to the bulla slightly ventral and posterior of the auditory meatus; the hypohyal and ceratohyal are fused in adults. The musculature of the hyoid apparatus is similar to that described by Bryant (1945) for the Nearctic Sciuridae (White 1953a), although the conjoining tendon of the anterior and posterior pairs of digastric muscles is ribbonlike and appears flattened in cross section.

The baubellum of *Tamias umbrinus* is U-shaped and positioned with the proximal end of the base directed caudally, the shaft parallel to the body and directed posteriorly, and the distal tip pointed ventrally (right) about 30° (Sutton 1982). The base is long and straight; the proximal end has a deep notch between 2 knobs. The shaft is straight and flattened laterally; a tubercle (heel) usually is present at the angle formed by the tip and shaft. The angle between the base and the shaft is about 80°. The length of the tip is slightly greater than the length of the shaft; a keel is present on the ventral surface; the side of the tip opposite the keel is slightly concave; and lateral flanges are present. Means and ranges of measurements (mm, except angle in degrees) of the baubellum are: length of the base, 0.866 (0.78–0.91); length of the shaft, 0.552 (0.46–0.72); depth of the shaft, 0.357 (0.29–0.42); length of the tip, 0.606 (0.59–0.65); keel, 0.281 (0.26–0.33); and angle of the tip–shaft, 146.33° (128–157°). The baubellum also was described by Layne (length, 1.3 mm—1954).

Variation (individual and age) in bacular morphology in *T. umbrinus* is small, although in some individuals, the baculum may be small and S-shaped (White 1953d). The baculum is relatively short, thick, wide at the base (base width > 2 × base height), and distinctly bent at midlength; the length of the tip is 36–50% of the length of the shaft and angled dorsally 90–100°; the keel on the dorsal surface of the tip is low (about 25% of the length of the tip); and the distal

one-half of the shaft is compressed laterally (Burt 1960; White 1953d). Measurements (mm) were (White 1953d): length, 3.1, 3.3 (2.51–3.03; Burt 1960); length of tip, 1.0, 1.2; width of tip, 0.3, 0.5; height of base, 0.3, 0.4; width of base, 0.7, 0.9. Bacular length is correlated positively with length of head and body, but the relationship is not statistically significant (Patterson 1983).

Function.—*Tamias umbrinus* undergoes 2 molts annually (Howell 1929; Johnson 1943; Merriam 1897; White 1953c). The molt from the winter to the summer pelage occurs between May and August (Howell 1929; Johnson 1943; Merriam 1897). Timing of molt is related to sex of the individual, geographic location, and reproductive condition. Males usually molt in spring before females molt; pregnant and lactating females retain the winter pelage through the summer and molt into the summer pelage in late summer or early autumn later after weaning (Allen 1890; Burt 1934; Johnson 1943; Long and Cronkite 1970). The molt begins on the nose or head and advances to the posterior, sometimes in a regular progression, but more commonly in irregular patches; a distinct molt line generally is present (Burt 1934; Howell 1929; Johnson 1943; Merriam 1897). Summer pelage is short, coarse, and bright in coloration and is maintained for about 3 months (Howell 1929; Johnson 1943; Merriam 1897).

The molt from the summer to the winter pelage occurs from September to November (Howell 1929; Johnson 1943; Merriam 1897). New fur appears 1st on the rump and advances toward the head uniformly; however, a distinct molt line generally is not apparent. Winter pelage is soft, silky, and duller in coloration than the summer or postbreeding pelage, and guard hairs are longer. The winter pelage is maintained through the winter until the spring–summer molt—about 9 months. The winter pelage at the termination of the breeding season is worn, shabby, and the hairs often so short that the distinct dorsal stripes are obsolete.

In young *T. umbrinus* the pelage is thin, silky, and dull colored, and the tail is narrower and more thinly haired compared to adults; the pelage thickens, the color brightens, and the tail becomes fuller and more bushy with age, and adult coloration is attained by September (Allen 1890).

ONTOGENY AND REPRODUCTION

Breeding occurs after arousal in spring and the gestation period is about 30 days (Armstrong 2008; Clark and Stromberg 1987; Fitzgerald et al. 1994). Females are pregnant in May in Colorado (Bergstrom and Hoffmann 1991) and in June in Arizona (Hoffmeister 1986). In northern Colorado, parturition occurs from late May until early June (Bergstrom 1986); in Arizona, young are born in late June and early July (Hoffmeister 1986). *Tamias*

umbrinus has 1 litter per year and litter size ranges from 3 to 5 (Fitzgerald et al. 1994); females with 5 embryos and 4 uterine scars (Arizona—Hoffmeister 1986) and 7 placental scars (Wyoming—Negus and Findley 1959) have been reported. Lactating females are reported in July in Wyoming (Negus and Findley 1959), July and September in Nevada (Burt 1934), and in mid- and late June and late August in Arizona (Hoffmeister 1986). In Colorado, weaned young 1st appear above ground when they are about 25 days old and from mid-June to early August (Bergstrom 1986); in Arizona, young of the year are present above ground in mid-July and are about two-thirds the size of adults (Hoffmeister 1986); and young individuals were observed in mid-September in Nevada (Burt 1934). Postweaning estrus has been reported for females ($n = 3$) in northern Colorado in early July; a male that sired 1 of the 1st litters also became reproductively active (scrotal) at this time (Bergstrom 1986). In the Front Range of Colorado, the last records of breeding (scrotal) males and the 1st appearances of young above ground occurred later in the summer at higher elevations than at lower elevations (Bergstrom 1986).

ECOLOGY

Population characteristics.—Population densities of *Tamias umbrinus* may be affected by natural perturbations, such as timing, duration, and intensity of winter snowpack (Andersen et al. 1980; Bergstrom and Hoffmann 1991); and diseases, such as bubonic plague, or poor mast crop (Bergstrom and Hoffmann 1991). Density (individuals/ha) of *T. umbrinus* in Utah is highest in early summer (1.5–17.0) and decreases through mid- (2.7–8.9) and late summer (0.7–9.5—Andersen et al. 1980). Populations in the Front Range of Colorado declined over several years from a minimum number known alive of 40 to 20; 1 population went locally extinct (Bergstrom and Hoffmann 1991). Survivorship of *T. umbrinus* over winter is 27.5% (*T. umbrinus*, *T. minimus*, and *T. quadrivittatus* combined) and survival for more than 2 years is uncommon or rare (Bergstrom and Hoffmann 1991).

Space use.—The preferred habitat of *Tamias umbrinus* throughout its range is montane coniferous forest. In Arizona, *T. umbrinus* inhabits habitats of ponderosa pine (*Pinus ponderosa*), white fir (*Abies concolor*), subalpine fir (*Abies lasiocarpa*), blue spruce (*Picea pungens*), and quaking aspen (*Populus tremuloides*), but also is found in piñon (*Pinus*), juniper (*Juniperus*), and scrub oak (*Quercus*) habitat (Hoffmeister 1986). Preferred habitats averaged 243 trees/ha, with an average distance between trees of 6.4 m, 34% shrub cover (especially conifer seedlings), and 11% deadfall cover or dead, woody vegetation (Hoffmeister 1986). In Colorado, *T. u. montanus* inhabits montane forest, montane subalpine meadow, and subalpine forest (Armstrong 1972), as well as ponderosa pine–coast Douglas fir (*Pseudotsuga menziesii*)

habitat (Bergstrom 1988) and piñon–juniper woodlands and montane shrublands (Fitzgerald et al. 1994). Although *T. umbrinus* is more common in forest-edge associations (Armstrong 2008; Fitzgerald et al. 1994), it occasionally is found in subalpine forest (Fitzgerald et al. 1994), or along cottonwood–willow river bottoms (Long and Cronkite 1970). The habitat preference of *T. umbrinus* is related to shallow soil, exposed rock, rock interstices, steep slopes, log litter, and pine trees (Cary et al. 1980) and reflects its being found on rocky areas and frequently on talus slopes (Fitzgerald et al. 1994). In Wyoming, the northern limit of the distribution, *T. u. montanus* occurs in the closed tree canopy and open understory of lodgepole pine (*Pinus contorta*) to Douglas fir habitat associations and in rocky areas of ponderosa pine to subalpine pine (Clark and Stromberg 1987). In southeastern Nevada, the distribution of *T. u. nevadensis* is isolated from other mountain ranges by desert habitat; in this restricted range, it occurs commonly in Rocky Mountain ponderosa pine (*Pinus ponderosa scopulorum*), white fir (*Abies concolor*), and Great Basin bristlecone pine (*Pinus longaeva*) habitat associations (Burt 1931, 1934). In Wyoming, *T. u. fremonti* lives in spruce–fir forest, most frequently on borders of clearings and meadows in woods, but it also occurs on cliffs above timberline (Negus and Findley 1959). In California, *T. u. inyoensis* occurs in open forests of stunted limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) on exposed and well-drained ridges and slopes near timberline (Johnson 1943) in the transition and boreal zones (Grinnell 1913). In Nevada, this subspecies exhibits a preference for open, rocky habitat (Brown 1971). In Utah, *T. umbrinus* is found in ponderosa pine forest up through the subalpine zone (Bradley et al. 1992). Numbers of individuals of *T. umbrinus* per hectare were highest in the conifer climax upper montane forest (23.3% of small mammals) and the subclimax spruce–fir upper montane forest (4.9% of small mammals); *T. umbrinus* was absent or rare in the lower montane forest habitats (Hayward 1945).

A seasonal shift in habitat use has been reported for *T. umbrinus* in Colorado (Telleen 1978). In summer, *T. umbrinus* was associated with lodgepole pine (33%), limber pine (13%), and Douglas fir (12%) habitats. In late summer and early autumn, however, individuals also were captured in ponderosa pine (12% of captures).

Ranges of home-range size for *T. umbrinus* in Colorado estimated from radiotelemetry and trapping, respectively, are (Bergstrom 1988): minimum-convex polygon (ha), 1.95–5.34, 0.30–0.92; home range length (m), 179–457, 201–341. Mean sampling area estimates vary based on the size of the trapping grid (Andersen et al. 1980) from 0.44 ha for small grids (7-m spacing) and to 2.41 ha for large grids (15-m spacing). Central-place foragers such as *T. umbrinus* generally have circular home ranges; however, the home range shape in *T. umbrinus* is noncircular, with the major

axis aligned approximately perpendicular to the major slope and may reflect the topography and patchy distribution of resources in the habitat (Bergstrom 1988).

Tamias umbrinus constructs nests in hollow logs and rock crevices (Bradley et al. 1992), as well as in burrows dug under logs, rocks, and shrubs (Fitzgerald et al. 1994), and the exposed roots of conifers and perhaps in natural tree cavities (Bergstrom 1986; Hoffmeister 1971, 1986). In the Front Range of Colorado, individuals of *T. umbrinus* resting or grooming were observed mostly in trees (Bergstrom 1986). Individuals were observed nesting overnight in a converted American robin (*Turdus migratorius*) nest located 1.5 m above ground in a common juniper (*Juniperus communis*) and nesting in a large stick nest located 4 m above ground in the crotch of a Douglas fir (Bergstrom 1986). A female used a cavity 16 m high in a mature ponderosa pine to raise a litter (Bergstrom 1986).

Diet.—*Tamias umbrinus* feeds primarily on seeds and fruits (Armstrong 2008; Bergstrom 1986; Brown 1971; Fitzgerald et al. 1994; Hayward 1945; Hoffmeister 1986) and is dependent on conifer mast crops (Bergstrom and Hoffmann 1991). The diet includes ponderosa pine (*Pinus ponderosa*), Douglas fir (*Pseudotsuga menziesii*), Utah juniper (*Juniperus osteosperma*), Rocky Mountain juniper (*Juniperus scopulorum*), Engelmann spruce (*Picea engelmannii*), piñon (*Pinus monophyla*), mountain mahogany (*Cercocarpus montanus*), prickly pears (*Opuntia*), wild roses (*Rosa*), raspberries (*Rubus*), chokecherry (*Prunus virginiana*), red gooseberries (*Ribes*), fruit of *Vaccinium*, and forbs and grasses. New terminal growth of conifers is eaten, and the diet is supplemented with fungi, insects, and other animal matter including carrion (Armstrong 2008; Brown 1971; Fitzgerald et al. 1994; Hoffmeister 1986), as well as pollen of the ponderosa pine (*P. ponderosa*) and Douglas fir (*P. menziesii*)—Bergstrom 1986). Hypogeous fungi were 1 of the most frequent dietary items of *T. umbrinus* in the Front Range, more than for either of its 2 congeners, and comprised a higher frequency of the feces of *T. umbrinus* from microhistological analysis than any other type of food item, including seeds, vegetation, and arthropods (Bergstrom 1986).

Diseases and parasites.—Ectoparasites of *Tamias umbrinus* include ticks (Ixodida: *Dermacentor andersoni*—Cary et al. 1980); mites (Trombidiformes: *Euschoengastia pomerantzi*, *E. sciuricola*, *Trombicula kardosi*, and *Walchia americana*—Allred and Beck 1966; Loomis 1954; Webb 2000); and fleas (Siphonaptera: *Catallagia decepiens* and *Monopsyllus ciliatus kincaidi*—Tipton 1950). At elevations above 2,200 m in the Front Range of northern Colorado, *T. umbrinus* is rarely infested with bot fly larvae (Diptera: *Cuterebra fontinella*—Bergstrom 1992). At elevations below 2,200 m (the lower limits of the distribution in the region), incidence over 4 years averaged 34% and the average number of larvae/host was 1.72 (maximum = 5). Bot warbles were found in inguinal (54%), anteroventral

(including throat; 18%), and dorsolateral (28%) positions on *T. umbrinus*. Bot parasitism may have an important role in elevational parapatry of *T. umbrinus* and *T. quadrivittatus*.

In Colorado, *T. umbrinus* is culture positive (20%) for the spirochete *Borrelia bissettii*, but is not positive for the agent of human granulocytic ehrlichiosis, a zoonotic tick-borne infectious disease (DeNatale et al. 2002). The etiological agent of Colorado tick fever (a small RNA virus of the genus *Orbivirus*; family Reoviridae) has an isolation rate of 12.1% (12.1 isolations/100 captures) in *T. umbrinus* (Cary et al. 1980). For the wood tick (*Dermacentor andersoni*), the infestation (ticks/animal) and minimum infection rates, respectively, are: larvae, 2.3, 1.16; nymphs, 0.29, 29.41. Although the values are among the highest of the 5 mammal species examined, *T. umbrinus* is not considered a principal host for immature ticks or the Colorado tick fever virus because of its low abundance.

The Colorado tick fever virus was isolated from blood of *T. umbrinus* (Bowen et al. 1981b; McLean et al. 1981); 2.3% were viremic and 12.0% were antibody positive (Bowen et al. 1981b). In the laboratory, all individuals (100%) of *T. umbrinus* inoculated with the E 1455 strain of Colorado tick fever virus became viremic; the mean duration of viremia was 11.5 days (5–20 days) and the virus was isolated from 1 individual 23 days after inoculation (Bowen et al. 1981a). Detectable neutralizing antibodies were found in 88% of adult viremic individuals after inoculation; however, 43% of antibody-positive individuals did not show detectable antibodies 5 months after inoculation. The rate of infection of *T. umbrinus* is lower at higher elevations due to the lower virus transmission rate at higher elevations; at lower elevations, the percentage of viremic individuals is similar to that of *T. minimus*, which was found to be the most important small mammal host in the region.

Interspecific interactions.—*Tamias umbrinus* is associated with many species of small mammals throughout its range. In Colorado, this species occurs with *Peromyscus maniculatus* (North American deermouse), *Spermophilus lateralis* (golden-mantled ground squirrel), *S. richardsonii* (Richardson's ground squirrel), and *T. minimus* (Bowen et al. 1981b; Cary et al. 1980; McLean et al. 1981). In montane forest in Utah, small mammal associates are *T. minimus*, North American deermouse, *Myodes gapperi* (southern red-backed vole), *Microtus longicaudus* (long-tailed vole), *Sorex vagrans monticola* (vagrant shrew), and *Zapus princeps* (western jumping mouse), but only include *Phenacomys intermedius* (western heather vole), southern red-backed vole, long-tailed vole, and *T. minimus* in the krumholz ecotone adjacent to the alpine meadow (Hayward 1945). *T. umbrinus* occurs with *Thomomys talpoides* (northern pocket gopher), North American deermouse, *T. minimus*, *Glaucomys sabrinus* (northern flying squirrel), southern red-backed vole, *Erethizon dorsatum* (North American porcupine), *Lepus americanus* (snowshoe hare), and *Tamiasciurus hudsonicus* (red squirrel) in both fir and spruce forest in Utah; with all but snowshoe

hare and red squirrel in aspen forest; and only with northern pocket gopher, North American deermouse, North American porcupine, and *T. minimus* in meadow. The golden-mantled ground squirrel, *Neotoma lepida* (desert woodrat), and western jumping mouse also are present in the community, but are rare or uncommon (Andersen et al. 1980). Other small mammals associated with *T. umbrinus* include *Sciurus aberti* (Abert's squirrel), red squirrel, *N. cinerea* (bushy-tailed woodrat), and *Arborimus longicaudus* (red tree vole—Bergstrom 1999). In Colorado, whereas Abert's squirrel and the red squirrel preferred ponderosa pine and lodgepole pine, respectively, *T. umbrinus* exhibited a distinct preference for Douglas fir over other tree species (Bergstrom 1986).

In parts of its distribution, *T. umbrinus* is sympatric with *T. minimus*, *T. amoenus*, and *T. dorsalis*, and parapatric with *T. quadrivittatus* and *T. panamintinus* (Bergstrom 1988, 1992, 1999; Bergstrom and Hoffmann 1991; Fitzgerald et al. 1994). Among species of chipmunk that are sympatric, ecological separation generally is observed. *T. umbrinus* inhabits a narrower elevational range and is more common in closed, canopied habitats than is *T. minimus*, which has a broad elevational range and forages in open habitats (Armstrong 2008; Bergstrom 1988, 1999; Perault et al. 1997; Telleen 1978). *T. umbrinus* and *T. dorsalis* may exclude each other from habitats at some elevations (Brown 1971). When both are present, *T. umbrinus* is limited to higher-elevation forests and *T. dorsalis* to lower-elevation piñon-juniper habitats. The distributions also are correlated with the density and size of trees; in areas where piñons and junipers are dense and the branches interlocking, *T. dorsalis* is replaced by *T. umbrinus* (Brown 1971). In areas where only 1 species is present, it occupies the entire range of habitats.

In Colorado, the 2,130-m elevation contour is a predictor of the parapatric distribution of *T. umbrinus* and *T. quadrivittatus* (Bergstrom 1988, 1992, 1999; Long and Cronkite 1970; White 1953b). When both species are present, *T. umbrinus* occurs primarily in pine, Douglas fir, and spruce-fir forests above 2,130 m and *T. quadrivittatus* occurs primarily in either ponderosa pine-juniper woodland or montane scrub or piñon-juniper below 2,130 m. However, in areas where only 1 species occurs, the elevation range is broader (Armstrong 1972). Aggressive exclusion of *T. quadrivittatus* by *T. umbrinus* may prevent *T. quadrivittatus* from occupying upper-elevation habitats and parasitism by bot flies may limit *T. umbrinus* from inhabiting habitats at lower elevation (Bergstrom 1992).

Tamias umbrinus may be one of the principal contributors to total biomass, annual consumption, respiration, and production in a community (Andersen et al. 1980). Total biomass and percent contribution to total biomass vary between years and among communities. *T. umbrinus* contributed 24% of the biomass in spruce forest and 20% in fir forest, but only 16% in aspen forest and 8% in meadow.

Information on predators of *T. umbrinus* is very limited; the northern goshawk (*Accipiter gentilis*) is known to prey on individuals (Hoffmeister 1986). To escape from predators, *T. umbrinus* will take cover among talus boulders (Long and Cronkite 1970) and climb trees (Hoffmeister 1986; Long and Cronkite 1970), often flattening its body on the upper surfaces of branches (Long and Cronkite 1970). Adult dark-eyed juncos (*Junco hyemalis*) will chase chipmunks from the vicinity of a nest (Smith and Andersen 1982).

Miscellaneous.—*Tamias umbrinus* habituates quickly to observers (Brown 1971). Individuals have been captured with Sherman live traps (H. B. Sherman Traps, Inc., Tallahassee, Florida) baited with scratch grain and sunflower seeds (Bergstrom 1988, 1992), oatmeal, scratch grain, and sunflower seeds (Bergstrom and Hoffmann 1991), and peanut butter and oatmeal (Andersen et al. 1980), or with National live traps (National Live Trap Corp., Tomahawk, Wisconsin) baited with oatmeal (Bowen et al. 1981a, 1981b). *T. umbrinus* can be observed at artificial feeding stations baited with crushed peanuts (Brown 1971). Methods of marking of *T. umbrinus* include ear tagging with colored plastic discs (Brown 1971), ear tagging and marking with Nyanzol B dye (Bergstrom 1992), toe clipping (Andersen et al. 1980; Brand 1976), and ear tagging and fitting with tuned-loop-collar radiotransmitters (Bergstrom 1988).

Tamias umbrinus has been maintained in the laboratory in stainless steel cages (9 by 10 by 18 inches; 1 individual/cage); water was freely available and the diet of mouse chow was supplemented 2 times per week with apples or carrots (Bowen et al. 1981a).

BEHAVIOR

Grouping behavior.—*Tamias umbrinus* is aggressive toward other members of its species and individuals of other species of chipmunks (Bergstrom 1992; Brown 1971). At artificial feeding stations, *T. umbrinus* establishes dominance hierarchies where higher-ranking individuals chase away and defend the area against subordinate chipmunks (Brown 1971). *T. umbrinus*, however, frequently approaches a feeding station in pairs of varying combinations of ages, sexes, and individuals (Brown 1971).

Communication.—The vocal repertoire of *Tamias umbrinus* includes chips, chipping, trills, squeals (Bergstrom and Hoffmann 1991; Brand 1976), and chucks (Brand 1976). The chip (sharp, loud sound covering a wide frequency range in a short interval) is the most common vocalization and more frequently given in bursts rather than series (Brand 1976). In a sonogram, a chip appears as a sharp (peaked) tone in the form of chevrons with several harmonics; a short, low-frequency pulse often follows the chevron; dominant frequencies vary from 4.5 to 15 kHz (Bergstrom and Hoffmann 1991). Mean (and range) measurements of chips (Brand 1976) were: number of chips/min, 55 (26–150);

number of chips/burst, 2.4 (1.0–4.72); number of bursts/min, 40 (6–150); length (in s) of chip syllable, 0.065 (0.02–0.10); and interval length (in s) between chips within bursts, 0.175 (0.035–0.36). Chips with a mean syllable length of 54.8 ms, mean pulse frequency of 194 chips/min, and bout duration ranging a few seconds to 15 min were reported by Bergstrom and Hoffmann (1991). Chucks are low-pitched calls with lowest frequencies at the beginning and the end (Brand 1976). Chipping is a rapid, irregular series of syllables of chips and chucks of short duration (several seconds—Brand 1976); the number and spacing of pulses, frequency, and tonal quality is highly variable (Bergstrom and Hoffmann 1991). Trills consist of an initial chip followed by a rapid, evenly spaced series of similar syllables (Brand 1976); these lower-frequency pulses are spaced about 30 ms apart and alternate in tonal quality between clear and raspy (Bergstrom and Hoffmann 1991). Vocalizations recorded for other species of *Tamias* include chatters, growls, squeals, and whistles (Brand 1976). Squeals are complex and consist of pulses ranging from 290 to 375 ms, with several intense bands (the lowest frequency band at 4 kHz) and several harmonics (Bergstrom and Hoffmann 1991).

Tamias umbrinus commonly chips from rock outcrops (Bergstrom and Hoffmann 1991; Long and Cronkite 1970) and the branches of fir trees (Long and Cronkite 1970); chips seldom are given in response to the presence of a predator (Bergstrom and Hoffmann 1991). During long bouts of chipping, regularly spaced chips are given in synchrony with tail flicks—generally a slow, side-to-side “sway” movement of the tail (Bergstrom and Hoffmann 1991). Chipping is emitted during flight as in a flight response to the observation of a predator (Bergstrom and Hoffmann 1991; Brand 1976). Chips and trills often are given by individuals in traps when approached by observers; 55% of individuals in traps vocalized (Bergstrom and Hoffmann 1991). When handled, 16% of individuals emitted squeals, which are similar to the vocalization of juveniles when distressed (Bergstrom and Hoffmann 1991). Chucks have been observed primarily at artificial feeding stations (Brand 1976). *T. umbrinus* frequently enters a “trance” lasting about 1 min when held by the nape during handling (Bergstrom and Hoffmann 1991). Infestation with bot larvae decreases calling frequency and intensity (Bergstrom 1992) and vocalizations are absent in early summer before the young of the year emerge (Long and Cronkite 1970).

Miscellaneous behavior.—*Tamias umbrinus* is active during the winter in Utah, except during periods of severe weather (Hayward 1945). In Arizona, where the range includes areas that receive heavy snowfall, it is probably inactive during winter (Hoffmeister 1986). Individuals enter winter dens by early November in Colorado; although they are inactive during most of the winter, they may arouse periodically to feed on stored food (Fitzgerald et al. 1994). *T. umbrinus* is most active from sunrise to about 0930 h with activity decreasing in the afternoon (Brown 1971).

Tamias umbrinus is highly arboreal and climbs trees and shrubs to forage (Brown 1971; Fitzgerald et al. 1994; Hayward 1945; Hoffmeister 1986; Long and Cronkite 1970). Based on data from a radiotelemetry study in Colorado (Bergstrom 1986), *T. umbrinus* was more arboreal than *T. minimus* or *T. quadrivittatus*. Of 909 (radiotelemetry and incidental) observations of *T. umbrinus*, 23.9% were in trees and 20.6–41.5% of daytime telemetry fixes located individuals ($n = 5$) in trees (Bergstrom 1986). *T. umbrinus* will approach artificial feeding stations from clumps of trees, and when disturbed, generally will climb the nearest tree and “freeze” (Brown 1971). Seeds are carried in the internal cheek pouches and stored in burrows; chipmunks also have been observed carrying entire cones down from Engelmann spruce trees in their mouth (Hayward 1945).

Interspecific encounters between individuals of *T. umbrinus* and *T. quadrivittatus*, and *T. umbrinus* and *T. dorsalis* were observed by Bergstrom (1992) and Brown (1971), respectively. Aggressive interactions with *T. quadrivittatus* were won by owners of the territory or, if territorial status was coequal or undetermined, by *T. umbrinus* (Bergstrom 1992). When *T. umbrinus* and *T. dorsalis* inhabit the same area, they are limited by competitive exclusion (competition for resources such as food patches—Brown 1971). Although *T. dorsalis* is more aggressive than *T. umbrinus*, winning 80% of interspecific interactions, *T. umbrinus* is more arboreal and able to escape up trees. *T. umbrinus* also frequently approaches artificial feeding stations in pairs (combinations of ages, sexes, and individuals). Despite the presence of more-aggressive *T. dorsalis*, the number of individuals of *T. umbrinus* visiting feeding stations may increase, until *T. dorsalis* abandons the station due to aggressive neglect (Brown 1971).

GENETICS

Cytogenetics.—Six subspecies of *Tamias umbrinus* examined cytogenetically (excluding *T. u. nevadensis*) have a modal diploid number ($2n$) of 38 and type B karyotype (Nadler and Block 1962; Sutton and Nadler 1969). Autosomal chromosomes include (Nadler and Block 1962; Sutton and Nadler 1969): 4 pairs of large metacentrics with median centromeres (group I); 6 pairs of large submetacentrics with submedian centromeres (group II); 4 pairs of large acrocentrics with terminal or subterminal centromeres (group III); 1 pair of small metacentrics with median centromeres (group IV); and 3 pairs small acrocentrics with terminal or subterminal centromeres (group V). The X chromosomes are large submetacentrics and the Y is a small acrocentric (Nadler and Block 1962; Sutton and Nadler 1969). The Giemsa-band pattern for the chromosomes is described by Nadler et al. (1977); the group IV chromosomes lack bands.

Molecular genetics.—The hemoglobin of *Tamias umbrinus* is polymorphic with 3 phenotypes (HbI, HbII, and

HbIII) and indicates 3 active structural loci (Jensen et al. 1976). Polymorphism is present in gamma-, beta-, and alpha-albumin serum protein fractions; the latter consists of distinct multiple fractions that are fast migrating (Seaman 1975; Seaman and Nash 1977).

Average heterozygosity is 0.0222–0.0851 among 4 subspecies (Levenson et al. 1985). Of 20 proteins, red cell aldolase (Ald), esterase (Est), liver glutamate oxalate transaminase (Got-1 and Got-2), alpha-glycerophosphate dehydrogenase (α Gpd), hemoglobin (Hgb), kidney isocitric dehydrogenase (Icd-1 and Icd-2), red cell lactate dehydrogenase (Ldh-1 and Ldh-2), liver malate dehydrogenase (Mdh-L), and red cell malate dehydrogenase (Mdh-R) were monomorphic; serum albumin (Alb-1 and Alb-2), serum leucine aminopeptidase (Lap), and serum transferrin (Tf) each had a rare allozyme (frequency < 0.50); glucose-6-phosphate dehydrogenase (G6pd), 6-phosphogluconate dehydrogenase (6Pgd), and red cell phosphoglucomutase (Pgm-1 and Pgm-2) were polymorphic.

Phylogenetic analysis of genic data found *T. umbrinus* as a sister taxon to *T. amoenus*; this clade was sister to *T. cinereicollis* (gray-collared chipmunk) + cf. *T. canipes* (gray-footed chipmunk—Levenson et al. 1985; Nadler et al. 1985). Analysis of the mitochondrial DNA cytochrome oxidase subunit II and cytochrome-*b* genes found *T. umbrinus* in the *T. quadrivittatus* species group clade of *T. bulleri* (Buller's chipmunk), *T. canipes*, *T. cinereicollis*, *T. dorsalis*, *T. durangae* (Durango chipmunk), *T. palmeri*, *T. quadrivittatus*, and *T. rufus* (Hopi chipmunk—Piaggio and Spicer 2000, 2001). The paraphyletic relationship of *T. umbrinus*, *T. cinereicollis*, *T. dorsalis*, and *T. palmeri* indicated close genetic similarity in contrast to their morphological distinctness (Piaggio and Spicer 2000, 2001) and suggested recent speciation and an ongoing sorting event. Similar results using the mitochondrial DNA control region gene provided resolution of intracladal relationships (Banbury and Spicer 2007).

The recognition of *T. palmeri* as a subspecies of *umbrinus* was suggested by examination of morphological (Sutton 1982) and molecular (Piaggio and Spicer 2000, 2001) data, but is not supported by genic data (Levenson et al. 1985; Nadler et al. 1985).

Population genetics.—Average heterozygosity of populations of *Tamias umbrinus umbrinus* from 11 sites from the Uinta Mountains in northeastern Utah is 0.088; the average proportion of polymorphic loci is 0.17 and the average number of alleles per locus is 1.4 (Perault et al. 1997). Of 20 proteins, esterase (Est-1 and Est-2), serum leucine aminopeptidase (Lap-2), mannosephosphate (Mpi), and peptidase (Pep-1 and Pep-2) were polymorphic; isocitric dehydrogenase (Idh-1), red cell lactate dehydrogenase (Ldh-2), and malate (Me-2) had fixed alleles. Gene flow was inversely correlated with spatial scale and related to habitat availability and use. Although *T. umbrinus montanus* from the Front Range of Colorado differed from *T. quadrivittatus*

quadrivittatus only at the esterase protein locus, whereas it converged allozymically at 4 other loci found to be diagnostic between the species elsewhere (Levenson et al. 1985), no evidence for hybridization (presence of heterozygotes) was detected (Bergstrom and Hoffmann 1991).

CONSERVATION

Tamias umbrinus is listed as a species of “Least Concern,” although the distribution is fragmented, the species is common locally, the range includes protected areas, and no specific major threats are known (Linzey and Hammerson 2008). In Utah, *T. umbrinus* may be affected by hot surface fires that consume preferred ground debris (Bradley et al. 1992). *T. umbrinus* is not predicted to go extinct locally from mountain ranges in the Great Basin due to the effects of global warming and it is predicted to survive on all mountains where it presently occurs (McDonald and Brown 1992). Two subspecies are of conservation concern (Hafner et al. 1998). *T. u. nevadensis* is considered “Critically Endangered” and possibly extinct. This subspecies, known only from the Sheep Mountains of Nevada at localities above 2,500 m, has not been observed or detected since before 1960. *T. dorsalis*, which was reported as occurring at lower elevations in 1931 when *T. u. nevadensis* was described, currently is found at all elevations in the Sheep Mountains. Because the Sheep Mountains have been protected since the 1930s, the possible local extinction of *T. u. nevadensis* may be due to climate change and not human impact. *T. u. sedulous* is considered “Data Deficient” (Hafner et al. 1998). The distribution and population status of this subspecies, which has been reported only from Mt. Ellen and the Henry Mountains of Utah, are unknown and this range includes no protected areas.

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