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Tamias senex.

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Tamias senex J. A. Allen, 1890

Shadow Chipmunk

Tamias senex Allen, 1890:83. Type locality "from summit of Donner Pass, Placer Co., Calif."
Eutamias senex: Merriam, 1897:194, 196.
Tamias townsendii senex: Elliot, 1901:71.
Eutamias senex: Sutton and Nadler, 1974:211.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciurognathi, Family Sciuridae, Subfamily Sciurinae, Subgenus Neotamias (Wilson and Reeder, 1993). *Tamias senex* is monotypic (Hall, 1981).

Tamias senex resembles other members of the *townsendii* species group (*T. townsendii, T. ochrogenys,* and *T. siskiyou*) but differs from them in characters of the ossa genitalia (Kain, 1985; Sutton, 1987) and in chip vocalizations (Gannon and Lawlor, 1989). Based on characters of the ossa genitalia, Sutton and Nadler (1974) proposed elevation of *T. senex* to species rank. Hall (1981), Jones et al. (1992), and Wilson and Reeder (1993) accepted this arrangement. Others, however, argued that *T. senex* should be retained as a subspecies of *T. townsendii* (Levenson and Hoffmann, 1984; Nadler et al., 1985). Disagreement also exists regarding the usage of *Eutamias* for western chipmunks and *Tamias* for the eastern chipmunk (Gannon and Lawlor, 1989; Patterson and Heaney, 1987).

DIAGNOSIS. *Tamias senex* (Fig. 1) is distinguished from other *Tamias* by its large size (mass greater than 60 g); the grayish wash over generally ochraceous upper parts, particularly the top of the head, rump and thighs; and the sharply defined and conspicuous eye stripes and postauricular patches (Hall, 1981; Howell, 1929; Johnson, 1943). The size, shape, and depth of the baculum and depth of the baubellum of *T. senex* (Fig. 2) are distinctive (Hall, 1981; Sutton, 1992; Sutton and Nadler, 1974). The chip vocalization of *T. senex* has a rapid, intense series usually consisting of 3–5 syllables in a call with maximum frequency 12.98 kHz, minimum frequency 4.56 kHz, 0.39 s between syllables, and mean call duration 0.81 s (Gannon and Lawlor, 1989). Compared with the calls of other species, those of *T. senex* are of medium frequency, with the call frequency peak usually not extending beyond 13 kHz.

Tamias senex may be distinguished from other members of the *townsendii* species group as follows. Pelage coloration varies from an overall dark pelage and obscure dorsal stripes where it is found along the coastal portion of its range, to grayish-ochraceous general coloration with conspicuous dorsal stripes and white dorsum inland in the Sierra Nevada Mountain portion (Johnson, 1943). Coastal populations of *T. senex* are large and dark and resemble *T. ochrogenys, T. siskiyou,* and *T. townsendii* (Sutton, 1987). Although coastal *T. senex* is dark, resembling *T. townsendii,* inland populations are paler, have an ochraceous wash with gray on rump and shoulders and not the cinnamon buff to tawny gray wash found in some populations of *T. townsendii.* Across the entire range, bacula shaft at the base is thicker and longer (0.5–1.5 mm longer), and keel depth is 0.4 mm (compared with 0.2 mm in *T. townsendii;* Sutton, 1993). Compared with *T. siskiyou,* inland populations of *T. senex* are paler; across their entire range, *T. senex* is larger (mean 148.0 mm versus mean of 145.4 mm, respectively), and has a larger skull (mean 39.4 mm versus 38.7 mm, respectively; Sutton, 1987). *T. siskiyou* is the only chipmunk related to *T. senex* in which the tip length of the baculum is greater than its shaft length. Compared with *T. ochrogenys, T. senex* is paler in inland populations where its dorsal pelage is ochraceous washed with gray, rather than dark tawny olive, and it has a smaller skull (mean of 38.7 for *T. senex* versus 40.1 mm in *T. ochrogenys;* Howell, 1929). The body length is less (mean 141.6 mm versus mean of 149.1 mm; Howell, 1929) and the shaft of the baculum is longer (mean 3.09 versus mean of 2.47 mm, respectively) and more slender (Kain, 1985). Except for differences in the bacula and call, coastal *T. senex* and *T. ochrogenys,* cannot be distinguished from *T. ochrogenys* in the field (Jameson and Peeters, 1988; Johnson, 1943). Especially for inland populations, *T. senex* is the palest and grayest member of the *townsendii* species group, although it is the darkest chipmunk in Nevada (Hall, 1946; Howell, 1929).

Aside from other members of the *townsendii* species group,

FIG. 1. Photo of *Tamias senex.* (Photo by D. A. Sutton)

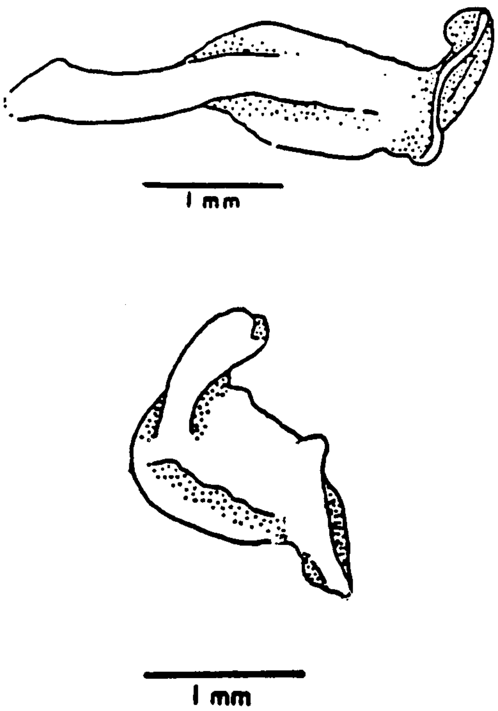

FIG. 2. Right lateral view of baculum (top) and left lateral view of baubellum (bottom) of *Tamias senex* (Sutton and Nadler, 1974:208, 210).

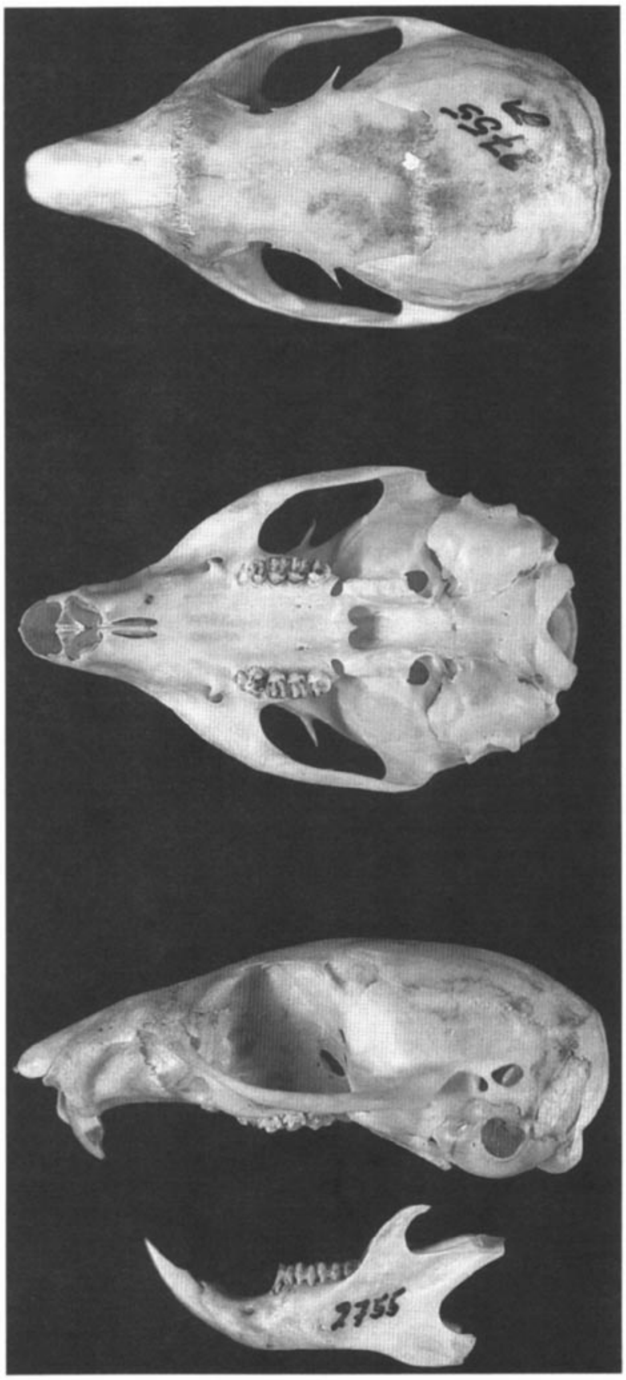

FIG. 3. Lateral (including lateral view of mandible), ventral, and dorsal views of cranium of *Tamias senex* (Humboldt State University, 2755, male, from ca. Carlotta, Humboldt Co., California). Greatest length of cranium is 38.9 mm. (Photo by R. B. Forbes)

Tamias senex may be distinguished from other chipmunks within its geographic range as follows. Compared with *T. alpinus*, *T. amoenus*, *T. minimus*, *T. speciosus*, and *T. umbrinus*, *T. senex* is larger, duller in color, and has a larger skull (average greatest length of skull exceeding 36.5 mm; less in the others). Compared with *T. speciosus*, the tail edging of *T. senex* is faintly, rather than distinctly, buffy, and the incisors of *T. senex* are short and incurved rather than short and straight. Compared with *T. merriami*, *T. senex* has a less bushy tail, more distinct lateral dorsal stripes, and a shorter, thicker baculum (Jameson and Peeters, 1988). Compared with *T. quadrimaculatus*, *T. senex* specimens from the Sierra-Nevada Mountains of California are more grayish and have shorter ears (less than 18.8 mm from the notch), more pointed ears, and no conspicuous black area below the ear (Jameson and Peeters, 1988; Johnson, 1943). Compared with *T. sonomae*, the tail of *T. senex* is less bushy; the back of the ears of *T. senex* is distinctly bicolored in summer; the upper incisors of *T. senex* are incurved and scarcely notched posteriorly rather than strongly incurved and deeply notched; and the tips of the nasal bones of *T. senex* are not separated by a notch whereas they are in *T. sonomae* (Ingles, 1965; Johnson, 1943).

GENERAL CHARACTERS. Pelage coloration varies from an overall dark pelage and obscure dorsal stripes along the coastal portion of the range of *T. senex*, to grayish-ochraceous general coloration with conspicuous dorsal stripes and white dorsum inland in the Sierra-Nevada Mountains of California (Johnson, 1943). Although coastal *T. senex* is dark, resembling *T. townsendii*, inland populations are paler, have an ochraceous wash with gray on rump and shoulders and not a cinnamon buff to tawny gray wash that is found in some populations of *T. townsendii*. Individuals in coastal populations of *T. senex* are large and dark colored and resemble *T. ochrogenys*, *T. siskiyou*, and *T. townsendii* (Sutton, 1987).

Tamias senex is a large chipmunk characterized by the grayish pelage, especially on the top of the head and on the rump and thighs, more noticeable in winter pelage (Merriam, 1897). Except for the dark median dorsal stripe, the markings on the body are relatively indistinct. The tail is comparatively short, narrow, pale fulvous underneath and at the base of hairs on the upper side, and has an indistinctly buffy edging. The fully furred ears have a conspicuous white third posteriorly in all pelages making postauricular spots sharply defined and obvious (Johnson, 1943).

Inland populations of *T. senex* show comparatively little geographic variation in color (Grinnell and Storer, 1924; Hall, 1946; Howell, 1929; Merriam, 1897). The pelage of *T. senex* varies seasonally in length, quality, and color. In both winter and summer pelages, the underparts are white, the top of the head and rump are grizzled grayish, and the median dark dorsal stripe is black. Fresh winter pelage is long, full, and soft, and the general color of the upper parts is gray. The top of the head is mixed pinkish cinnamon and fuscous, tinged with grayish white and bordered on each side with a stripe of fuscous. The sides of the nose are cinnamon. The dark facial stripes are sayal brown, shaded with fuscous, with a blackish patch behind the eye. The antorbital part of the middle facial stripe is only slightly marked. The light facial stripes are grayish white, tinged with buff. The sides of the face are never suffused with yellowish. The ears are fuscous or fuscous black bordered posteriorly with grayish white. The postauricular patches are sharply defined and conspicuous. The shoulders usually are washed with smoke gray. The dark dorsal stripes are fuscous black, more or less mixed with mikado brown. The lateral pair of light stripes is grayish white and the inner pair grizzled grayish, at times clouded with cinnamon. The sides are clay color. The rump and thighs are dark smoke gray or mouse gray. The hind feed are clay color or pale ochraceous tawny; the toes are cinnamon buff as are the front feet. Above, the tail is fuscous black overlaid with pale smoke gray. Below, the tail is sayal brown or pale ochraceous tawny, bordered with fuscous black and edged with pale smoke gray (Johnson, 1943).

External measurements (mm) are: total length, 229–261; length of tail, 90–112; and length of hind foot, 34–38 (Hall, 1946; Hall, 1981). Tail lengths (mean, in mm) of 30 male and 52 female *T. senex* were 103.57 and 107.59, respectively (Sutton and Nadler, 1974). Mean body masses (g, range in parentheses) of 10 adult male and 10 adult female *T. senex* from Yosemite National Park were 82.8 (66.8–99.3) and 95.9 (73.0–108.5), respectively (Hall, 1946). *T. senex* had a mean dimorphism ratio of 1.033 with females slightly larger than males (mean head and body lengths 144.12 mm and 139.54 mm, respectively—Levenson, 1990). Other measurements (means in mm, except for angle of bacular shaft to tip; range and sample size in parentheses) of adult males are (Sutton, 1987): length of head and body, 148.0 (123–164; 26); length of hind foot, 36.04 (31–40; 25); greatest length of skull, 39.38 (37.5–41.1; 20); condylobasal length, 34.60 (31.9–36.1; 21); zygomatic width, 21.82 (20.2–22.8; 21); least cranial width posterior to the zygomatic arches, 17.38 (16.5–18.1; 23); interorbital width, 8.536 (8.0–9.7; 23); length of nasal bones, 12.62 (11.1–13.5; 19); length of mandibular tooth row, 6.367 (5.6–6.8; 23); length of the mandible, 20.79 (19.6–21.65; 15); length of bacular shaft, 3.087 (2.8–3.32; 22); length of bacular tip, 1.383 (1.26–1.71; 22); height of bacular keel, 0.462 (0.380–0.560; 22); and angle of bacular tip to shaft (degrees), 108.9 (100–121; 22). Other measurements (mean) from bacula of 30 males, are (Sutton and Nadler, 1974): width at base, 1.1400 mm; dorsoventral shaft width two-thirds of the distance from base to angle, 0.7364 mm; ratio of length of bacular tip to length of shaft, 0.4808; and ratio of height of keel to height of tip, 0.3106. Measurements (means in mm, except for angle of baubellar shaft to tip; range and sample size in parentheses) for samples of adult females are (Sutton, 1987): length of head and body, 149.0 (116–173; 45); length of hind foot, 36.73 (40.33; 45); greatest length of skull, 39.47 (37.2–41.05; 30); condylobasal length, 34.73 (32.0–36.5; 32); zygomatic width, 21.66 (19.85–22.9; 34); least cranial width posterior to zygomatic arches, 17.39 (16.6–18.0; 33); interorbital breadth, 8.465 (8.0–8.9; 35); length of mandibular tooth row, 6.391 (6.0–6.9; 39); mandibular length, 20.78 (19.1–22.08; 25); length of baubellar shaft, 1.211 (0.95–1.75; 33); length of baubellar tip, 0.885 (0.7–1.1; 33); height of baubellar keel, 0.415 (0.35–0.55; 33); and angle of baubellar tip to shaft (degrees), 131.4 (110–150; 32).

DISTRIBUTION. Generally, *Tamias senex* occupies a geographic range (Fig. 4) from the northwest coast of California east to the border of California and Nevada (the Warner Range; Hall 1981). From its southernmost records near Yosemite in the southeastern portion of the Sierra-Nevada Mountains of California (headwaters of the Merced River in Yosemite National Park), *T. senex* extends northward to more than half way through the central portion of Oregon (Hall, 1981).

In northern California, the range of *T. senex* is limited to the area between the southern bank of the Klamath River and the northern bank of the Eel River, Humboldt Co. (Gannon and Lawlor, 1989; Kain, 1985; Sutton, 1987). In the central portions of the Sierra-Nevada Mountains of California, *T. senex* is confined to higher elevations (above 1500 m) and does not approach the base level of either the eastern or western slopes of the mountains (Merriam, 1897). No fossils of *T. senex* are known.

FORM AND FUNCTION. The malleus of *T. senex* (from Lake Tahoe, California) was used by White (1953) in distinguishing *Tamias* from *Eutamias*. The head of the malleus of *T. senex* is less elongated than is that of *T. striatus*. In *T. senex*, the plane formed by the lamina makes an angle of 90° (60° in *T. striatus*) with the plane formed by the manubrium. Mallei of *T. senex* more closely resemble those of *Eutamias sibiricus* than those of *T. striatus* (White, 1953).

Both male and female genital bones are diagnostic for *T. senex* (Kain, 1985; Sutton and Nadler, 1974). The third upper premolar is present in *T. senex* as in all western chipmunks, but absent in the eastern chipmunk, *T. striatus* (Hall, 1981; White, 1953).

Relative brain size in *T. senex* is significantly greater than in *T. amoenus* and *T. minimus*, but slightly less than that in *T. townsendii* (Budeau and Verts, 1986). Larger brain size in *T. senex* may be related to the more complex habitat in which this species occurs compared with habitats in which *T. amoenus* and *T. minimus* occur sympatrically with *T. senex* (Budeau and Verts, 1986).

ONTOGENY AND REPRODUCTION. Near Quincy, Plumas Co., California, *T. senex* has one short annual summer breeding season. Young animals reproduce during the breeding season following their birth. Males are considered to be in breeding condition when the cauda epididymis, after being cut, exudes seminal fluid teeming with spermatozoa. The reproductive organs enlarge tremendously from their quiescent state. Length of testis doubles, cauda epididymis and prostate triple in width, and lengths of the seminal vesicles and diameter of bulbo-urethral gland increase five-fold. Enlargement and post-breeding retrogression of testes are gradual, but sizes of the seminal vesicles and bulbo-urethral glands change abruptly. Mean dimensions (in mm) for 27 fertile male *T. senex* are: testicular length, 17; length of seminal vesicles, 10; diameter of bulbo-urethral glands, 9; diameter of prostate gland, 6; and maximum thickness of cauda epididymis, 4 (Tevis, 1955).

At the onset of estrus in the female, the genital eminence becomes turgid, the vulva perforate, and the uterine horns inflated and twisted. Nipples enlarge during estrus and pregnancy, reach maximum size at lactation, and decrease in size following lactation (Tevis, 1955).

Mating activity in *Tamias senex* begins about one month after emergence from hibernation in the spring and continues for about four weeks. Mating season begins earlier in populations in the Great Basin than in those in the Sierra Nevada or on the Volcanic Plateau. Embryo counts for six females were 5 in four individuals, 4 in one individual, and 3 in another individual (average 4.5). Uterine scars were not reliable indicators of litter size. Young animals were well developed before being weaned and beginning to forage for themselves. The earliest date of weaning was 15 June but it was not until early July at Lake Almanor (Plumas Co., California) that the "highway around the lake was spotted with crushed (*T. senex*) bodies" (Tevis, 1955:75).

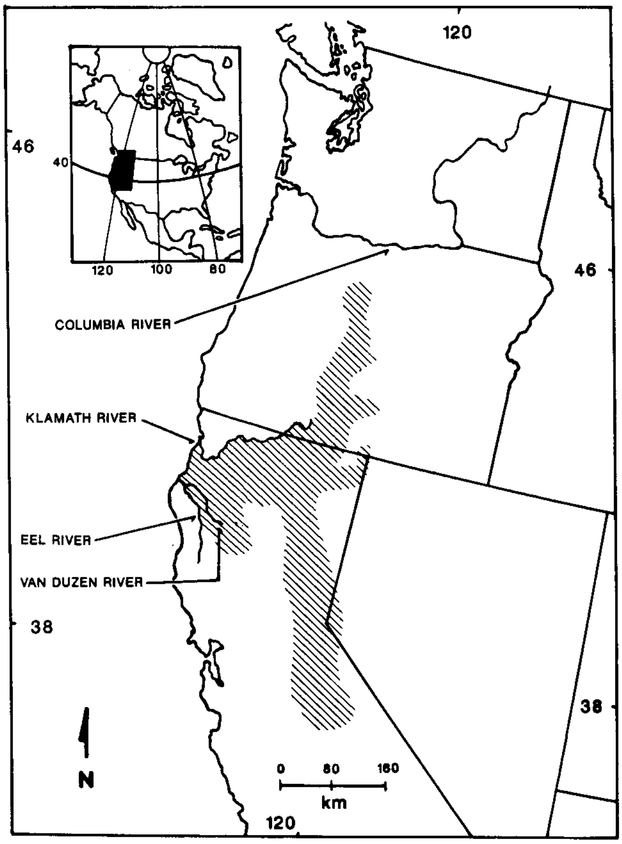

FIG. 4. Distribution of *Tamias senex* as suggested by Sutton and Nadler (1974), Kain (1985), Sutton (1987), and Gannon and Lawlor (1989). (Drawn by J. Sherrod and W. L. Gannon)

Tamias senex has two molts annually. A post-breeding molt in early to mid-summer results in replacement of worn winter pelage by a relatively short, hispid, bright ochraceous pelage. This molt begins on the head and proceeds posteriorly in an irregular, patchy manner. A second molt, occurring in late summer or autumn before the onset of hibernation, results in replacement of the bright summer pelage by a longer, fuller, softer, more grayish pelage. This molt begins on the rump and proceeds anteriorly in a regular pattern. It is possible to recognize three pelages in *T. senex* and other chipmunks of the Sierra Nevada and Cascade mountains—the short, hispid, reddish, fresh post-breeding pelage, which lasts only for a few months; the longer, softer, grayish, fresh winter pelage; and the thin, faded, worn winter pelage which remains until breeding has been completed (Howell, 1929; Merriam, 1897; Tevis, 1955).

ECOLOGY. *Tamias senex* inhabits relatively dense, moist brushy areas from sea level in northwestern California to ca. 2,900 m in Yosemite National Park. Although it occurs in coniferous areas near Lake Tahoe, *T. senex* avoids the arid forests of the Great Basin (Tevis, 1955). Near South Fork Mountain, Trinity County, California, *T. senex* was found in red fir (*Abies magnifica*) and white fir (*A. concolor*) forests in which the dominant shrub was *Ceanothus thyrsiflorus* (Miller, 1944). In the northern Sierra Nevada, *T. senex* was abundant from 1,220 to 1,830 m in various habitats that included: *Pinus ponderosa*, *P. jeffreyi*, *P. lambertiana*, *Abies concolor*, *Pseudotsuga menziesii*, *Libocedrus decurrens*, *Quercus kelloggii*, *Purshia tridentata*, *Cercocarpus ledifolius*, *Ceanothus thyrsiflorus*, *C. integerrimus*, *C. prostratus*, *Garrya fremontii*, *Arctostaphylos uva-ursi*, *A. patula*, *A. viscida*, and *Artemisia tridentata* (Tevis, 1952).

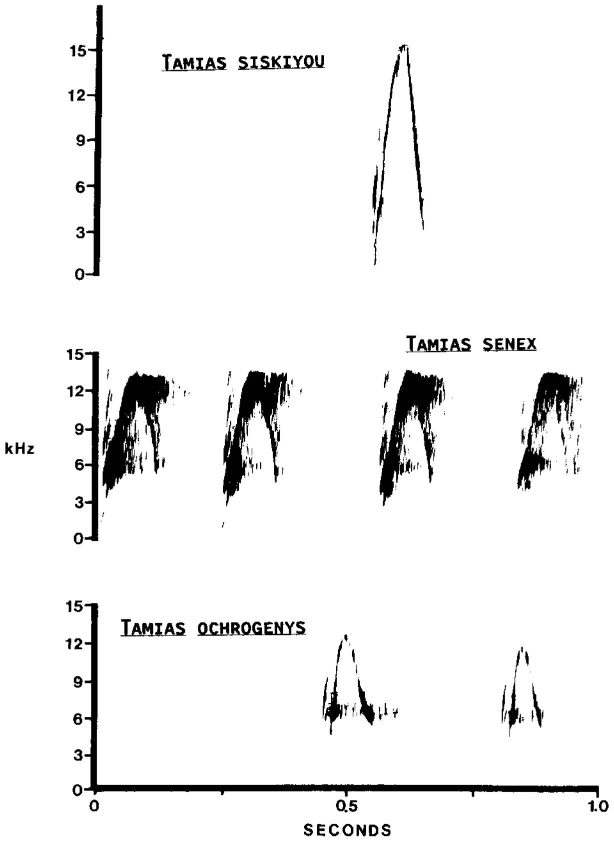

FIG. 5. Sound spectrographs of the chip vocalization from *Tamias siskiyou* (top), *T. senex* (middle), and *T. ochrogenys* (bottom). X- and Y-axes are time (s) and call frequency (kHz), respectively (from Gannon and Lawlor, 1989).

Tamias senex occupies habitats in the Canadian and upper Transition life zones ranging in elevation from near sea level between the Eel and Klamath rivers in northwestern California to near 2,900 m in Yosemite National Park. *T. senex* is contiguously allopatric with other members of the *townsendii* species group. *T. senex* is zonally and ecologically separated from its sympatric congeners *T. alpinus*, *T. amoenus*, *T. merriami*, *T. minimus*, *T. quadrimaculatus*, *T. sonomae*, *T. speciosus*, and *T. umbrinus* (Chappell, 1978; Heller, 1971; Ingles, 1965; Johnson, 1943; Merriam, 1897; Sharples, 1983). For example, in the Sierra Nevada *T. senex* occurs at higher elevations than does *T. merriami* and at lower elevations than does *T. alpinus*. *T. senex* shares parts of the Canadian and upper Transition life zones with, but is behaviorally and ecologically separated from, the other six congeners mentioned (Ingles, 1965; Jameson and Peeters, 1988; Merriam, 1897). Such contiguously allopatric, parapatric, or slightly sympatric species coexist only in narrow zones or border each other corresponding with major life zones, which in turn correspond to differences in elevation and slope aspect (Chappell, 1978; Heller, 1971; Sharples, 1983). These ecological distributions may be maintained by competitive exclusion (Brown, 1971; Heller, 1971; Meredith, 1977). Habitat and resource partitioning may have allowed chipmunks to undergo the considerable adaptive radiation and speciation that have occurred in this subgenus. For instance, of the four overlapping species of *Tamias* from the same elevation in the Sierra Nevada Mountains of California, Sharples (1983) found that *T. senex* was the only species of chipmunk that preferred closed old-growth canopy. Its congeners exhibited preferences for different habitats; *T. speciosus* was associated with scattered trees, *T. amoenus* preferred brushy plots, and *T. quadrimaculatus* preferred transition or disturbed habitats. Although *T. senex* prefers intact forests and avoids the bare ground that follows logging, numbers of *T. senex* were found to increase with the increase in herbaceous growth following logging of coniferous forests near Salyer, Trinity County, California (Tevis, 1956). The principal flower consumed by *T. senex* was that of *Arctostaphylos* spp., but to a lesser extent the staminate cones of *Abies concolor* and the heads of bull thistle (*Cirsium lanceolatum*) were also eaten (Tevis, 1956).

Analysis of stomachs of 78 *T. senex* taken in Plumas National Forest, California in autumn, revealed that, by volume, these animals had consumed hypogeous fungi (81%), seeds (13%), insects (4%), and unidentified material (2%; Tevis, 1952). In Jeffrey pine-chaparral and virgin conifer forest, *T. senex* consumed mostly fungi (54% and 99%, respectively) followed by seeds (29% in pine-chaparral only), insects (9% in pine-chaparral only), and unidentified material (8% and 1% for each habitat; Tevis, 1952). Stomach contents from 48 *T. senex* collected near Quincy, Plumas Co., California revealed that in spring these chipmunks consumed, by volume, 62% fungi, 30% flowers, and 8% seed. In summer, stomachs contained 66% fungi, 21% arthropods, and 13% seed and fruit. In contrast to the foods taken in the Sierra Nevada, the percentage volumes of food items taken by *T. senex* at this coastal coniferous site were: hypogeous fungi 41%, insects 23%, herb and brush seed 32%, unidentified material 4% (Tevis, 1956). In fall, the percent by stomach volume of fungi rose to 89%; only 11% was seed and arthropods (Tevis, 1953). One *T. senex* captured beneath incense cedar (*Thuja plicata*) with ripe cones scattered about had its cheek pouches filled with fungi, not seeds (Tevis, 1953). *Tamias senex* was the only chipmunk noted that collected the seeds that it ate which suggests that it may be more detrimental to forest regeneration programs than are other sciurids (Tevis, 1955). Although consumption of fungi may have been due to an unusually poor seed crop production in 1950, *T. senex* became fat and heavy in preparation for winter torpor despite a diet consisting almost entirely of fungi (Trevis, 1952). In contrast to other chipmunks, *T. senex* consumed hypogeous fungi to the exclusion of the other species (Tevis, 1953). Areas where *T. senex* foraged were revealed by the numerous pits left by truffle-digging chipmunks (Tevis, 1952). The large amount of fungi consumed by *T. senex* is related to its large size. It is more efficient for a large chipmunk that is an effective digger to ingest large amounts of abundant food rather than to search widely for patchy, low volume foods; smaller chipmunks forage more effectively by searching out smaller items (Tevis, 1953).

The last *T. senex* seen for the season near Quincy, Plumas Co., California, was observed on 29 November (Tevis, 1955). Hibernation was assumed to begin by about that date. Average date of entry into hibernation may be adjusted to average environmental conditions and not be subject to the vagaries of different years. Emergence of *T. senex* from hibernation was first noted on 19 March; individuals continued to emerge through mid-April. Before hibernation, fat is deposited subcutaneously, becoming especially thick in the inguinal area, coelom (clinging to mesenteries), gonads, and around the kidneys. The average gain in weight for an adult is about 20%. Upon emergence, fat deposits are small, dirty-white, dull, and cheese-like in appearance, in contrast to the glistening, pure white fat deposits found in animals before they hibernate (Tevis, 1955).

Near Quincy, Plumas Co., California, 65% (23 of 37 chipmunks examined) of the *T. senex* had the following flea species (numbers of fleas in parentheses): *Diamanus montanus* (1), *Oropsylla idahoensis* (1), *Monopsyllus eumolpi* (17), *M. ciliatus* (48; Tevis, 1955). Of the fleas collected from *T. senex* hosts, *M. eumolpi* was most common from hosts collected in relatively open, arid forests; *M. ciliatus* was most common from hosts collected in moist, closed forests (Hubbard, 1947).

BEHAVIOR. Specific differences in call notes were first reported by Miller (1944) who noted that *T. senex* (reported by him as *E. t. siskiyou* in Trinity County, California) emitted a call that was easily distinguishable from that of *T. sonomae*. The call of *T. senex* was described as an "excitable bark" composed of 3–5 notes in a series. This pattern was verified at South Fork Mountain, Trinity Co. and Carlotta, Humboldt Co., California (Miller, 1944). Interspecific and interpopulational differences between *T. senex*, *T. ochrogenys*, and *T. siskiyou* have been described for the chip vocalization (Fig. 5; Gannon and Lawlor, 1989). *T. senex* has a rapid, intense series usually consisting of 3–5 syllables in a call. Compared with the other species, these calls are of medium frequency, with the most intense part (upper part of middle spectrograph, Fig. 5) usually not extending beyond 13 kHz. The temporal call pattern usually is a rapid series of syllables per calling bout. The chip call of *T. siskiyou* is distinguished by a single intense syllable that extends from 3 to more than 16 kHz (beyond the upper limit of the spectrograph). The chip call of *T. ochrogenys* is distinguished by a two-syllable chip of low frequency as well as other characters relative to the other species (Gannon et al. 1993). Recordings of *T. senex* from Lake Almanor, California, averaged 0.4 s between chips. Chips given in bursts averaged 3.2 s between bursts, and 0.165 s between chips within bursts. *T. senex* chipped while sitting still either on the ground ($N = 6$) or more commonly, on some elevated object ($N = 230$), and never when fleeing. They called in response to dogs, coyotes, hawks, or humans, or after being released from a live trap; this seemed to function as an alarm call. Upon the approach of a predator (including humans), *T. senex* stopped calling and remained motionless; calling resumed after the predator moved on. When some chipmunks began chipping, others fled into brush or up trees, then sat in an alert posture. Eventually, these individuals returned to their pre-calling location and resumed their previous activity, usually feeding. The same response was observed when other species gave a chip call. Often, when one chipmunk began to call, others joined the chorus for 15 min or more. Eight captive *T. senex*, however, never called during 95 h of observation. Unlike other chipmunk species, *T. senex* does not produce a whistle vocalization (Brand, 1976).

Before the onset of hibernation, *T. senex* became quiet, secretive, and relatively inactive. The first individuals to emerge in mid-March were quiet and secretive as well, but as the active population grew to a critical number they became noisy and aggressive, giving the impression of a population explosion when in fact the active population had been growing steadily for a month (Tevis, 1955).

In the Sierra Nevada Mountains, California, a nest of *T. senex* was found with a brood of young high in a tree near the time when these chipmunks were beginning to enter hibernation. Young were seen in nests in two white fir trees the tops of which had broken off 12 and 27 m above the ground, respectively. Chipmunks in these nests were active around 0700 and 1900 hours during observations in two different years. *T. senex* was also seen nesting in woodpecker holes and in stumps. In captivity, *T. senex* preferred the higher nestboxes, seldom using those at floor-level (Brand, 1970).

Tamias senex probably performs more complex activities in its coniferous arboreal habitat than do less arboreal species such as *T. minimus*. Complex motor skills are correlated with a larger relative brain size (Budeau and Verts, 1986). While *Tamias senex* is more terrestrial than some of its sympatric congeners (Grinnell and Storer, 1924; Hall, 1946), it is one of the most arboreal species of chipmunks in the Sierra Nevada. It easily runs up and down trees and jumps between trees and branches that are more than 1 m apart; it also stores seeds occasionally in the crotches of tree trunks. A maximum movement of 400 m was observed for *T. senex* (Gashwiler, 1959). *T. senex* may change its use of space depending upon available food resources. Two other chipmunk species (*T. amoenus* and *T. quadrimaculatus*) joined *T. senex* at one time beneath two large sugar pine trees (*Pinus lambertiana*) that were in seed (Brand, 1970). Home range was estimated for *T. senex* as ranging from 0.4 to 3.31 ha with the longest axis of the home range ranging from 60 to 230 m.

GENETICS. *T. senex* has the B karyotype, which is also characteristic of *T. siskiyou*, *T. ochrogenys*, and *T. townsendii* (Sutton, 1987).

REMARKS. Vernacular names for *Tamias senex* include Allen's chipmunk, California chipmunk (Hall, 1981), Shadow chipmunk (Jameson and Peeters, 1988), Large Mountain chipmunk (Howell, 1929), Gray chipmunk, and Was-La of the Klamath (Bailey, 1936; Grinnell, 1933; Johnson, 1943). Shadow chipmunk was used most recently by Jameson and Peeters (1988) because the name referred to the dark coloration and preference for heavily shaded areas of the forest. The generic name *Tamias* is derived from the Greek word *tamias*, meaning steward. The specific name *senex* is Latin meaning dim or shadowy (Jaeger, 1955). The type specimen of the *Tamias senex*, collected by Lyman Belding (No. 1133, Merriam Collection) from the summit of Donner Pass, Placer County, California, 1 July 1885, is now housed in the United States National Museum, No. 186461.

There is disagreement over the generic status of *Eutamias* versus *Tamias*, and more discussion and evidence are warranted. Continuing investigation of the taxonomic relationships of the western chipmunks has been of interest. White's (1953) thorough verification of the relative affinity of Asiatic *Eutamias* with North American *Neotamias* (*sensu* western chipmunks) was based on 10 taxonomic characters that verified Merriam's (1897:189–190) initial elevation of the western chipmunks to the genus *Eutamias* from Trouessart's (1880:86–87) initial proposal. Recent authorities have not used the genus name *Eutamias* (e.g., Nadler et al., 1985; Wilson and Reeder, 1993), however it is still used by some (e.g., Gannon and Lawlor, 1989; Patterson and Heaney, 1987). Sutton and Nadler (1974), Kain (1985), and Williams (1980) separated *T. senex* from *T. siskiyou* and *T. ochrogenys* by statistical differences of the greater overall shape and depth of the shaft of the baculum as well as the great depth of the baubellum. Levenson and Hoffmann (1984) concluded that evidence was at best equivocal and that *T. senex*, and other Townsend's chipmunks, were not sufficiently distinct from each other to warrant species designation. However, analysis of 14 characters measured from 296 specimens revealed that riverine boundaries reliably separated four species (including *T. senex*) in the *townsendii* species group and that there was no intergradation between them (Sutton, 1987).

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