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Tamias speciosus.

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Tamias speciosus Merriam, 1890

Lodgepole Chipmunk

Tamias speciosus Merriam, in J. A. Allen, 1890:86. Type locality Head of Whitewater Creek, 7,500 feet (Miller, 1924:205), "San Bernardino Mts. [San Bernardino Co.—Miller and Rehn, 1901:45], Cal."

Tamias frater J. A. Allen, 1890:88. Type locality "Donner [Sierra Nevada Mountains, Placer Co.], Cal."

Tamias callipeplus Merriam, 1893:136. Type locality "summit of Mount Piños [8,800 feet—Miller and Kellogg, 1955:231], Ventura County, California."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993); *T. speciosus* is in the subgenus *Neotamias* (Levenson et al., 1985). Four subspecies are recognized (Hall, 1981):

T. s. callipeplus Merriam, 1893:136, see above.

T. s. frater J. A. Allen, 1890:88, see above.

T. s. sequoiensis (A. H. Howell, 1922:180). Type locality "Mineral King, east fork of Kaweah River [Tulare Co.—Miller, 1924: 205], California (altitude 7,300 feet)."

T. s. speciosus Merriam, in J. A. Allen, 1890:86, see above.

DIAGNOSIS. *Tamias speciosus* (Fig. 1) is sympatric or parapatric with *T. alpinus*, *T. amoenus*, *T. merriami*, *T. minimus*, *T. obscurus*, *T. quadrimaculatus*, *T. senex* (Callahan, 1976), and *T. umbrinus* (Hall, 1946). *T. speciosus* is distinguished from other California *Tamias*, except *T. amoenus*, *T. panamintinus*, and *T. umbrinus*, by larger size (Johnson, 1943).

Compared with *T. amoenus*, *T. speciosus* is larger, has longer and narrower ears, and has more sharply contrasting pale and dark stripes. In *T. speciosus*, the medial pair of pale dorsal stripes is narrower and the lateral pair of pale stripes, although not always broader, is more conspicuous. The pale facial stripes are less washed with ochraceous and the dark facial stripes usually are blacker. The skull of *T. speciosus* (Fig. 2) is more massive, with a less pointed rostrum and larger incisive foramina (Johnson, 1943).

Compared with *T. panamintinus*, *T. speciosus* is larger, and has more pointed ears, more black in the dark facial and dorsal stripes, more ochraceous wash over the pale stripes and underparts, and a broader subterminal black band across the underside of the tail. The skull of *T. speciosus* is relatively narrower, but has a broader and less-pointed rostrum. The roof of the braincase is less flattened, and the upper rows of cheekteeth are more divergent anteriorly (Johnson, 1943).

Compared with *T. umbrinus*, *T. speciosus* is smaller, and has longer ears and a slightly shorter tail. *T. speciosus* is darker, the crown of the head and the shoulders are brown rather than gray, the dark facial stripes are darker, the submalar stripe has a black center below the eye, and the ocular stripe is black. The medial pair of pale dorsal stripes is not as gray, the lateral pair is not as white, and both pairs are heavily washed with ochraceous. The subterminal black area on the underside of the tail is less restricted than in *T. umbrinus*, being ca. 20 mm. The skull of *T. speciosus* is shorter and broader. The upper incisors are shorter and more recurved, and their outer borders form an arc of a circle having a radius of ca. 5.0 mm, compared with 5.7 mm in *T. umbrinus* (Johnson, 1943).

The baculum (os penis; Fig. 4) of *T. speciosus* has a wider base and thicker shaft than do those of *T. alpinus*, *T. amoenus*, and *T. minimus*. Compared with *T. merriami*, the baculum of *T. speciosus* is not incised dorsally, the base is wider, the shaft is thicker, and the tip is proportionately longer. Compared with *T. panamintinus*, the baculum of *T. speciosus* has a base of keel that is proportionately shorter, and the angle formed by the tip and shaft is less. Compared with *T. quadrimaculatus*, the baculum of *T. speciosus* has a shorter shaft, wider base, and lesser angle formed by tip and shaft. From *T. umbrinus*, the baculum of *T. speciosus* is distinguished by a higher keel, the angle formed by the tip and shaft is less, the distal 66% (not 50%) of the shaft is laterally compressed, and the base is wider (White, 1953).

GENERAL CHARACTERS. Body size of *T. speciosus* is medium for the genus. The color usually is bright, with contrasting pale and dark elements. The crown of the head is brown and grizzled with gray. The sides vary from ochraceous tawny to sayal brown in summer pelage, and the dark facial stripes are black and bordered with brown. The submalar stripe is black centrally below the eye. The dorsal stripes contrast sharply, and the median stripe is black, usually fading to brown over the shoulder region. The medial pale stripes are washed with ochraceous, and the lateral pale stripes are broad, white, and conspicuous. The subterminal black area on the underside of the tail is 13–20 mm long (color nomenclature follows Ridgway, 1912—Johnson, 1943). The color pattern is consistent within populations (Westermeier, 1974).

The skull (Fig. 2) is moderately broad; zygomatic breadth averages 61% of condylobasal length. The dorsal outline is arched, and the zygomatic arches are moderately appressed to the skull; the outer borders of the temporal parts are bowed and slope inward anteriorly. The rostrum is short, broad at the base, and narrows anteriorly. The interorbital region is broad; interorbital breadth averages ca. 25% of condylobasal length. The upper incisors are short and recurved; curvature of the outer border of each incisor forms an arc of a circle with a radius of ca. 5 mm. The inner margins of the upper rows of cheekteeth diverge anteriorly (Johnson, 1943). Except for breadth of zygomatic plate, most cranial characters have low coefficients of variation. Generally, condylobasal length, zygomatic breadth, breadth of braincase, and depth of skull have lower coefficients of variation than do measurements of smaller structures

FIG. 1. A young *Tamias speciosus* climbing a lodgepole pine (*Pinus contorta*) near Saddlebag Lake, ca. 3,030 m, Mono Co., California. Photograph courtesy of H. E. Broadbooks.

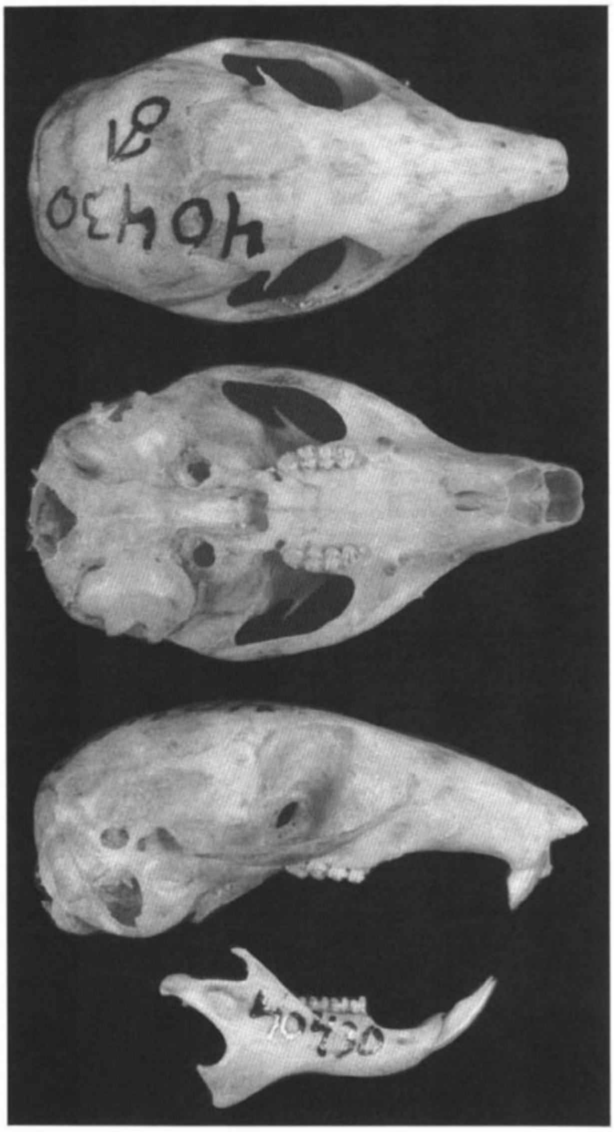

FIG. 2. Dorsal, ventral, and lateral views of cranium, and lateral view of mandible of *Tamias speciosus* from Heart Bar Campground, San Bernardino National Forest, San Bernardino Co., California (male, University of New Mexico Museum of Southwestern Biology 40430). Greatest length of cranium is 35.7 mm. Photographs by T. H. Henry.

such as postorbital breadth, length of frontal bones, and rostral breadth (Westermeier, 1974).

Sexual dimorphism in length of head and body was the greatest observed in 21 species of *Tamias* (Levenson, 1990). Males are larger than females in condylobasal length and length of frontal bones; females have greater zygomatic breadth (Westermeier, 1974) and larger average length of head and body (Levenson, 1990), but most characters exhibit no sexual dimorphism (Westermeier, 1974).

Average and range of measurements (in mm; sexes combined) for *T. s. callipeplus*, *T. s. frater*, *T. s. sequoiensis*, and *T. s. speciosus*, respectively, are: total length, 213 (203–231), 217 (204–231), 225 (214–241), 211 (202–220); length of tail, 91 (84–100), 91 (86–100), 98 (92–114), 86 (80–91); length of hind foot, 34 (33–35), 35 (33–36), 35 (33–36), 33 (32–35); length of ear, 15.4 (14.5–16.0), 14.2 (13.0–17.0), 16.2 (15.0–18.0), 15.7 (15.0–17.5); greatest length of skull, 35.4 (34.6–36.0), 35.3 (34.5–36.2), 36.0 (35.3–36.8), 35.5 (34.6–36.7); zygomatic breadth, 19.0 (18.6–19.4), 19.4 (18.7–20.0), 19.4 (18.7–19.8), 19.3 (19.0–20.0); cranial breadth, 14.7 (14.4–15.0), 14.9 (14.6–15.2), 15.0 (14.4–16.6), 15.0 (14.3–15.4); interorbital breadth, 8.4 (8.2–8.9), 8.0 (7.3–8.5), 8.2 (7.9–8.7), 7.8 (7.5–8.0); length of nasals, 11.9 (11.6–12.3), 11.4 (10.7–12.2), 11.7 (10.7–12.5), 11.5 (10.4–12.3—Howell, 1929). Average mass is 52–72 g (Chappell et al., 1978; Hall, 1946; Heller and Poulson, 1972; Howell, 1929).

Coefficients of variation for bacular characteristics are greater than those for cranial characters. Significant geographic variation occurs in length, width, and angles of the baculum. There is a decrease in total length and height of tip of the baculum from north to south with a sharp break between populations at Huntington Lake and the southern Sierra Nevada (Westermeier, 1974).

The occurrence of populations on isolated summits of mountains in southern California suggests relative antiquity of the species. These populations appear to occupy remnants of a formerly continuous range that extended from the Sierra Nevada through the Tehachapi region to Mount Piños and then southeastward at least to the San Jacinto Mountains. It seems that isolation has had little influence on most characters of *T. speciosus*. *T. s. frater* is distinguished from *T. s. callipeplus*, *T. s. sequoiensis*, and *T. s. speciosus* by its more reddish sides, narrower lateral pale dorsal stripes, broader skull, and geographic occurrence in the northern and central Sierra Nevada. *T. s. sequoiensis* and *T. s. speciosus* differ from *T. s. callipeplus*, which occurs only in the vicinity of Mount Piños, in possessing a black subterminal area on the underside of the tail that is >15 mm long, compared with <15 mm for *T. s. callipeplus*. *T. s. sequoiensis* has a paler underside of tail and occurs in the southern Sierra Nevada compared with *T. s. speciosus*, which has a darker underside of tail and occurs in the Piute, San Gabriel, San Bernardino, San Jacinto (Johnson, 1943), and San Josito mountains (Howell, 1929). The population in the Piute Mountains is intermediate in characters between *T. s. speciosus* and *T. s. sequoiensis*, and although it is separated from southern populations of *T. s. speciosus* by the Mojave Desert, it apparently is nearer to *T. s. speciosus* than to *T. s. sequoiensis* of the High Sierra, with which its range must be nearly continuous (Howell, 1929).

DISTRIBUTION. *Tamias speciosus* occurs at 1,500–3,300 m elev. in transition, Canadian, and Hudsonian life zones of California and near Lake Tahoe, Nevada (Fig. 3). *T. s. callipeplus* occurs only on Mount Piños, California, *T. s. frater* is in Nevada near Lake Tahoe and on upper slopes of the northern Sierra Nevada, California, *T. s. sequoiensis* is on upper slopes of the southern Sierra Nevada, California, and *T. s. speciosus* has a discontinuous range on upper slopes of the San Josito, San Jacinto, San Bernardino, San Gabriel, and Piute mountains, California (Grinnell and Storer, 1924; Hall, 1981; Howell, 1929; D. F. Williams, in litt.).

D. A. Sutton (in litt.) has questioned the occurrence of *T. speciosus* in Nevada Co., California, as reported by Sharples (1983). Based upon his own field data from Nevada Co. and identification of specimens he obtained using measurements, color, and characteristics of genital bones, D. A. Sutton did not find *T. speciosus*. Howell (1929) listed 31 specimens of *T. speciosus* from near Lake Almanor, Plumas Co., and Johnson (1943) listed 73 specimens of *T. speciosus* from Plumas, Shasta, and Lassen counties, but field investigations revealed only *T. amoenus* in these localities (D. A. Sutton, in litt.). Thus, the northern boundary of the range of *T. speciosus* actually may be somewhere between Tuolumne Co. and perhaps Nevada Co., if the Sharples (1983) identifications ultimately are confirmed (D. A. Sutton, in litt.).

FOSSIL RECORD. The genus *Tamias* evolved by the early Miocene (Black, 1972). No fossils of *T. speciosus* are known.

FORM AND FUNCTION. As in all members of the subgenus *Neotamias*, the dental formula of *T. speciosus* is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Howell, 1929). No cranial or dental abnormalities were present in 582 adults (Westermeier, 1974). Sebaceous glands, but no sudoriferous or mucous glands, are present at the oral lips and angle (Quay, 1965).

The lodgepole chipmunk has internal cheekpouches. These are thin membrane-like sacs, one on each side of the face, between the oral cavity and outer skin, and opening inside the mouth. Seeds and nuts are passed between the mouth and cheekpouches by action of the cheek muscles and tongue, without aid from the forepaws (Grinnell and Storer, 1924).

The hind foot can be turned backward so that it will support nearly the entire weight on the side of a tree (Grinnell et al., 1930). The forefeet are relatively longer and narrower, and the claws are relatively smaller than those in many sciurid genera. The musculature is similar to other sciurids, except for variability in size, shape, and attachment. *T. speciosus* has limbs that are long and slender, and tendons of the long extensors and flexors are relatively longer than in other sciurid genera (Bryant, 1945).

The eye is surrounded by a pale ring that is interrupted at the angles, and the anterior margin of the auricula of the ear is folded over more than it is in some species of *Spermophilus* (Bryant, 1945). Other physical characters are: total surface area, 121 cm^2; thickness of pelage, 0.39 cm; length of pelage, 0.99 cm (Heller and Gates, 1971); maximum length of dorsal guard hairs, 12 mm; width of dorsal guard hairs, ≤ 35 μm (Mayer, 1952).

Molt varies depending upon age, sex, and reproductive condition. There are two molts each year; one to bright summer pelage and another to dull winter pelage (Tevis, 1955). Summer pelage (spring molt occurs in May–June) is thinner and brighter than winter pelage (autumn molt occurs in late September), which is thicker and somewhat duller. Generally, spring molt occurs earlier in males and non-pregnant females than in pregnant females, where it occurs after parturition (Westermeier, 1974). Some males have bright summer pelage for 2–3 months, whereas many females no sooner attain summer pelage, than it is replaced with dull winter pelage (Tevis, 1955). Spring molt proceeds from head to rump and autumn molt proceeds from the rump forward. Juveniles born in early summer usually do not develop adult pelage until middle or late September (Westermeier, 1974), when adult males and females molt. Autumn molt is completed before hibernation (Tevis, 1955).

Body temperature is lower during sleep (range, 36.3–39.5°C; average, 38.2°C) than when active (range, 39.3–41.0°C). The <2°C range in body temperature during activity suggests a narrow range in temperature tolerance and a short activity time (Chappell et al., 1978). At an ambient temperature of 40°C, *T. speciosus* exhibits hyperthermia (Heller and Poulson, 1972); it will not survive a prolonged body temperature >40.4°C (Chappell et al., 1978).

The proportion of body heat dissipated by water loss is 30.4% at an ambient temperature of 25°C and 41.1% at 35°C. Rate of rise in heat content of the body at an ambient temperature of 40°C is 2.9 calories g^{-1} h^{-1}; the total is 208.8 calories/h (Heller and Poulson, 1972). Thermoregulatory characteristics of the central nervous system at ambient temperatures of 10, 20, and 30°C, respectively, are: metabolic heat production, −4.9, −5.0, and −5.0 watts kg^{-1} $°C^{-1}$; threshold temperature, 41.4, 40.3, and 37.6°C; minimal metabolic rate, 8.4, 8.7, and 9.1 watts/kg. Energy exchange parameters for *T. speciosus* are: mass-specific minimal metabolic rate, 0.12 calories g^{-1} min^{-1}; mass-specific evaporative water loss at 35°C, 0.046 calories g^{-1} min^{-1}; minimal metabolic rate, 8.64 calories/min; resting evaporative water loss, 3.30 calories/min; absorptivity of solar energy, 73%; emissivity of thermal energy, 99%; area for radiant energy exchange, 130 cm^2. Rates of energy storage (in calories/min) are: rate of metabolic heat production (3 times minimal metabolic rate), 25.8; rate of evaporative heat loss (3 times minimal evaporative water loss), 9.9; rate of radiation absorption, 130; emitted radiation, 101.4; rate of energy storage, 44.5. Time available for activity before maximum body temperature is exceeded: rate of energy storage, 44.5 calories/min; heat capacity, 0.82 calories $°C^{-1}$ g^{-1}; rate of rise of body temperature, 0.76°C/min; body temperature scope, 2.0°C; time available for activity, 2.64 min (Chappell et al., 1978). Average values of insulation at an ambient temperature of 30°C are: net heat production, 0.046 calories min^{-1} cm^{-2}; body temperature minus surface temperature, 3.8°C; quality of insulation of fat and pelage, 82.61 cm^2 $°C^{-1}$ min^{-1} $calorie^{-1}$ (Heller and Gates, 1971).

Metabolic rates for *T. speciosus* are: basal metabolic rate, 1.48 ml oxygen g^{-1} h^{-1}; metabolic rate below thermoneutrality (in ml oxygen g^{-1} h^{-1}), −0.086 (ambient temperature in °C) + 3.805; surface-area specific metabolic rate below the thermoneutral zone (in calories cm^{-2} min^{-1}), −0.0047 (ambient temperature in °C) + 0.188. The slope of the regression of mass-specific metabolic rate on ambient temperature below thermoneutrality is lower for *T. speciosus* than for *T. alpinus*, *T. amoenus*, and *T. minimus*. This is expected because of the larger body of *T. speciosus*. The ambient temperature at which *T. speciosus* can tolerate its maximum absorption of radiation in still air is ca. 12°C lower than the ambient temperature at which *T. alpinus*, *T. amoenus*, and *T. minimus* can tolerate the same absorbed radiation. This difference is reduced to ca. 5°C at a wind velocity of ca. 100 cm/s and practically disappears at a wind velocity of 1,000 cm/s. Winds of this velocity rarely occur close to the ground surface (Heller and Gates, 1971).

Tamias speciosus is less tolerant of exposure to severe heat loads than are *T. amoenus* and *T. minimus* (Chappell et al., 1978). Despite its limited heat-storage capabilities, *T. speciosus* may not be prevented by physiologic limitations from brief occupation of open, arid habitats, but its foraging efficiency would be impaired, especially during summer months. *T. speciosus* may be unable to overwinter and reproduce in sagebrush (*Artemisia*) areas, even in the absence of competition from a more efficient, heat-tolerant animal such as *T. minimus*. It is unlikely that the sagebrush zone is included within the fundamental niche of *T. speciosus*. In woodlands, trees provide patches of shade and cool, and elevated perches—refuges that tip the competitive balance in favor of this larger, less heat-tolerant species (Chappell, 1978).

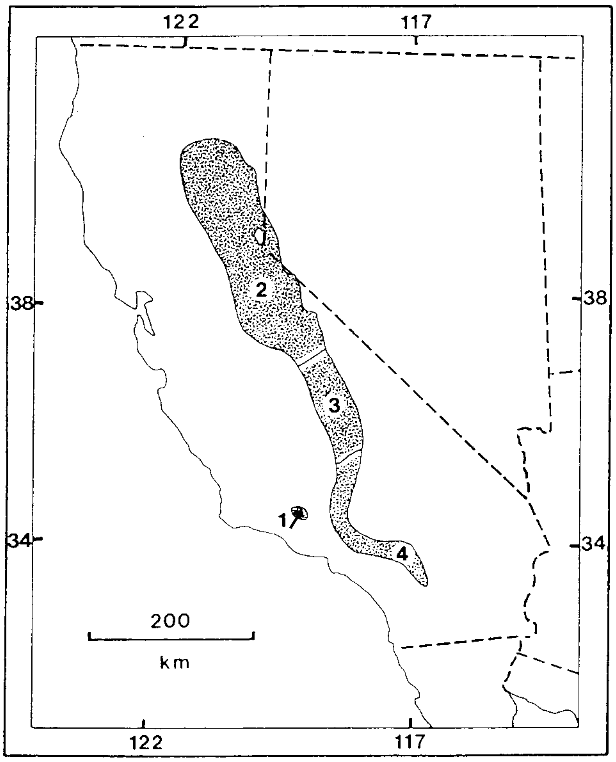

FIG. 3. Distribution of *Tamias speciosus* in California (Hall, 1981): 1, *T. s. callipeplus*; 2, *T. s. frater*; 3, *T. s. sequioensis*; 4, *T. s. speciosus.*

Internally heated, pelt-covered metal casts of *T. speciosus* were used to measure the coefficient of convection and effective surface area for emission and absorption of thermal radiation. The coefficient of convection for *T. speciosus* is 0.0037 watts cm^{-2} $°C^{-1}$ × 10^3, compared with 0.0049, 0.0053, and 0.0044 for *T. alpinus*, *T. amoenus*, and *T. minimus*, respectively. This is expected because of the larger size of *T. speciosus* (Heller, 1972). Investigations of thermal adaptations that apply Newton's law to express heat loss from *T. speciosus* must consider more than Newton's proportionality constant; they also must separate effects of body size and wind speed on conductance of the animal (Tracy, 1972).

Relative thickness of the medulla of the kidney of *T. speciosus* is less than that of *T. alpinus*, *T. amoenus*, and *T. minimus*. There is no difference between mass-specific rates of evaporative water loss of *T. speciosus*, *T. alpinus*, and *T. amoenus* at 25°C, but *T. minimus* shows a higher value than any of these species. When stressed, *T. speciosus* can decrease its water requirement by an average of 50%. In the laboratory, water relationships include: ad lib. consumption of water, 15.9% of body mass; minimum consumption of water, 7.9% of body mass; water content of feces, 47.0% of wet weight. *T. speciosus* produces a more concentrated urine when deprived of water. Average evaporative water loss at ambient temperatures of 25, 35, and 40°C, respectively, are 2.8, 5.1, and 18.0 ml × 10^3 g^{-1} h^{-1}. On a diet of sunflower seeds, water gains and losses (in ml g^{-1} h^{-1} × 4) were: loss of water in feces, 0.0005; loss of water in urine, 0.0016; evaporative loss of water, 0.0204; total loss of water, 0.0225; water gained by oxidation, 0.0031; gain of preformed water, 0.0006; total gain of water,

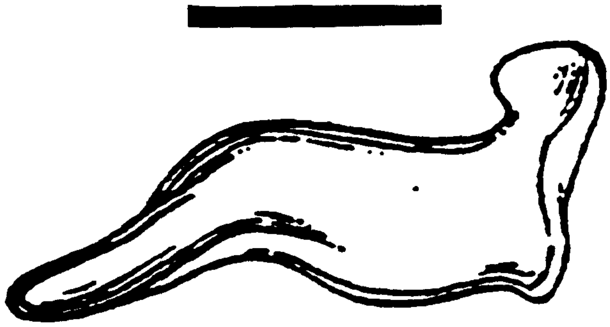

FIG. 4. Lateral view of the right side of the baculum (bar is 1 mm in length) of *Tamias speciosus sequoiensis* from Mount Whitney, Tulare Co., California (White, 1953).

0.0037; free water requirement (total loss minus total gain), 0.0188 ml g^{-1} h^{-1} × 4 (Heller and Poulson, 1972).

In the laboratory, *T. speciosus* enters hibernation in late October and emerges in mid-April. At an ambient temperature of 4–6°C, *T. speciosus* arouses every 1–2 days near the beginning and end of hibernation, but in mid-winter it is dormant for periods of 5–6 days. At the beginning of hibernation, it remains active from 1 to several days during periodic arousals, but in mid-winter it is active for only 1 to several h between periods of dormancy. At an ambient temperature of 4°C, rectal temperatures are 4.8–5.2°C when torpid, and breathing is slow (138 breaths/h—Jameson, 1964).

Throughout summer, lipid indices are ca. 12, and there is no marked increase in body fat until November (Jameson and Mead, 1964). Hibernation fat develops subcutaneously, being especially thick in the inguinal region and coelom, where large amounts cling to mesenteries of gonads and extend craniad on either side of the spine to cover the kidneys. Average gain in body mass is ca. 20%. Because of the speed at which deposits develop and subsequent rapid disappearance of animals into hibernation, the period when a fat chipmunk is active is short. On emerging from hibernation >50% of the animals have a remnant of fat, which appears dirty-white, dull, and cheese-like in contrast to the white and glistening appearance of fresh deposits (Tevis, 1955). *T. speciosus* emerges from winter dormancy with the same body mass as the previous November, and there is a small and steady increase in mass from April to June. The lipid index decreases in June and July when young first emerge from the nest. Lipid indices for *T. speciosus* are less than those for the golden-mantled ground squirrel (*Spermophilus lateralis*). *T. speciosus* accumulates proportionately less fat in autumn than does the golden-mantled ground squirrel. It is possible that *T. speciosus* continues to accumulate fat, but heavy snowfall makes this unlikely (Jameson and Mead, 1964). When held without food at 3–4°C for 9 days, *T. speciosus* lost 43 g, starting at a mass of 94.1 g, for an average loss of 4.8 g/day (Cade, 1963).

Succinic dehydrogenase activity of the choroid plexi and associated ependyma of the lateral, third, and fourth ventricles are 143.1, 108.0, and 172.2 μmoles of tetrazolium reduced/μg of dry tissue, respectively. In a solution of sodium phosphate buffer, sodium cyanide, sodium succinate, aluminum trichloride, calcium dichloride, and 2,3,5-triphenyl-2H-tetrazolium chloride, mixed and adjusted to pH 8.25, 100.1 μmoles of tetrazolium were reduced/μg of dry tissue from the epiphysis cerebri (pineal body) of *T. speciosus* (Quay, 1960).

The baculum (Fig. 4) is the most distinctive of the genus. It has a short thick shaft with a distinct bend, and a flattened, bifid base that is more than twice as wide as high. The tip is about at right angles to the shaft (Burt, 1960). The keel is of medium height and 33% of length of tip. The tip is 47–55% of length of shaft (White, 1953). Measurements (in mm) of three bacula are: length of shaft, 2.6, 2.7, 2.8; length of tip, 1.3, 1.3, 1.2; width of tip, 0.4, 0.5, 0.5; height of base, 0.4, 0.4, 0.3; width of base, 0.9, 0.9, 0.9 (Burt, 1960). Approximate size (in mm) of reproductive organs of reproductively active males are: length of testis, 15; length of seminal vesicle, 9; maximum diameter of bulbourethral gland, 8; maximum diameter of prostate gland, 5; maximum thickness of cauda-epididymis, 3 (Tevis, 1955).

Except for the tip, form of the baubellum (os clitoris; Fig. 3) in *T. speciosus* differs from that of any other species. The base is a thin, comma-like projection with two divergent knobs on the proximal end, set at a right angle to the short, bulbous shaft. The heel is prominent and the keel is large, extending ca. 66% of the length of tip. Flanges are narrow and define a depression that extends, with a break at the flange, well onto the distal end of the shaft. The side of the tip opposite the keel is concave. The shaft and tip are bend together ca. 25° to the right. Average and range of measurements (in mm) of baubella of *T. speciosus* are: length of base, 0.70 (0.55–0.94); length of shaft, 1.05 (0.78–1.40); depth of shaft, 0.59 (0.46–0.72); length of tip, 0.85 (0.75–1.20); length of keel, 0.36 (0.29–0.46); tip-shaft angle, 119° (98–130°—Sutton, 1982).

ONTOGENY AND REPRODUCTION. Several California chipmunks, including *T. alpinus*, *T. speciosus*, *T. quadrimaculatus*, and *T. merriami* (in order from high to low elevations), show a trend toward breeding later at higher elevations (Hirshfeld, 1975). Indicators of reproductive activity in males are the black scrotum and pendulous position of testes. The terms scrotal and abdominal, often used to describe the position of testes, are uninformative because the small testes of non-breeding males usually are in the scrotum as are large ones. At the end of the breeding season, testes of adults are flaccid, bluish in color, and have undulating blood vessels. Testes of subadults are firm, pinkish or whitish, with straight vessels, and are smaller than those of adults (Tevis, 1955).

Uterine horns of adults are long and thick; those of subadults are short, thin, delicate, and threadlike (Tevis, 1955). There are four pair of mammae; one pectoral, two abdominal, and one inguinal (Bryant, 1945). Mammae are small or absent in subadults, and usually are not apparent until sexual maturity. In adults, mammae grow during estrous and pregnancy and reach maximum size at lactation. There is much individual variation; some lactating females have smaller mammae than pregnant individuals. After lactation, mammae decrease in size. They become covered with scab-skin that eventually sloughs off, although sometimes not until pregnancy of the following year (Tevis, 1955).

The lodgepole chipmunk has one annual breeding season that lasts ca. 4 weeks. This occurs ca. 1 month after emerging from hibernation (Tevis, 1955). At this time, the habitat is well covered with snow, but daily temperatures are relatively warm, and spots of bare ground are beginning to appear. The breeding season occurs in May and June (Grinnell and Storer, 1924; Stephens, 1906). One litter is produced each year (Tevis, 1955). Young are born in spring and early summer (Jameson and Peeters, 1988; Tevis, 1955). The number of young ranges from three to six and averages about four. Pregnancies observed were: 16 June, six small embryos; 16 June, three embryos; 18 June, three large embryos; 27 June, four embryos; 28 June, three large embryos; 1 July, six large embryos (Grinnell and Storer, 1924). Resorption of embryos is rare (Tevis, 1955).

In Plumas Co., California, young were foraging independently beginning ca. 15 June (Tevis, 1955). In the San Jacinto Mountains, young were not seen before 20 July, but after 23 July juveniles were plentiful (Grinnell and Swarth, 1913), and many young were abroad by 31 July (Grinnell and Storer, 1924). In the San Bernardino Mountains, small juveniles were ignored by their parents (Grinnell, 1908).

Pelage of young *T. speciosus* (Fig. 1) is similar to that of adults in breeding pelage, but colors of young are brighter and markings are stronger (Allen, 1890). Young chipmunks molt after they begin to forage independently. The sparse, dull coat of immaturity is replaced by pelage indistinguishable from that of adults; young soon undergo a second molt to drab winter pelage. Young reproduce in the spring following their birth (Tevis, 1955).

ECOLOGY. *Tamias speciosus* is not dependent upon lodgepole pine (*Pinus contorta*) for survival (Tevis, 1955), but it inhabits forests of lodgepole pine, Jeffrey pine (*Pinus jeffreyi*), and red fir (*Abies magnifica*—Johnson, 1943). Its habitat has ca. 40% cover of vegetation, with many large boulders and some open ground (Heller, 1971). Present boundaries of the range of *T. speciosus* correspond to distribution of suitable habitat, except in the north where the canyon of the Pit River seems to have stopped northward dispersal along the Cascades (Johnson, 1943).

In the San Gabriel Mountains, the lodgepole chipmunk is associated with lodgepole pine, chinquapin (*Castanopsis sempervirens*), manzanita (*Arctostaphylos patula*), and whitethorn (*Ceanothus cordulatus*), but it usually shuns pure stands of conifers, except as temporary foraging areas (Vaughan, 1954). It occurs in lodgepole pine forests in the San Bernardino Mountains (Grinnell,

1908) and on chinquapin slopes in the San Jacinto Mountains (Grinnell and Swarth, 1913). In Fresno Co., California, *T. speciosus* occurs in mixed-conifer and red fir forests of the western Sierra Nevada. Vegetation here includes white fir, red fir, Jeffrey pine, sugar pine (*Pinus lambertiana*), lodgepole pine, incense cedar (*Libocedrus decurrens*), and California black oak (*Quercus kelloggii*—Williams and Braun, 1983); it is common around corrals, barns, and brushpiles (Swarth, 1919). In Yosemite National Park, *T. speciosus* is the only chipmunk in forests consisting entirely of lodgepole pine (Brand, 1970). Near Mount Whitney, it is one of the most abundant mammals in meadows, but at >3,000 m elev. it becomes rare, it seldom is seen near timberline, and few occur <2,400 m elev. (Elliot, 1904). In Plumas Co., *T. speciosus* occurs in forests of ponderosa pine (*Pinus ponderosa*), Jeffrey pine, sugar pine, Douglas fir (*Pseudotsuga menziesii*), white fir, and incense cedar. This area has been subjected to every degree of logging. Shrubs include manzanita, whitethorn (Tevis, 1953*b*), bitter cherry (*Prunus emarginata*), and squaw carpet (*Ceanothus prostratus*—Tevis, 1953*a*). In Nevada Co., California, *T. speciosus* occurs on the eastern slope of the Sierra Nevada in association with Jeffrey pine, ponderosa pine, and white fir. Shrub understory consists of sticky laurel (*Ceanothus velutinus*), manzanita, currant (*Ribes cereum*), antelope-brush (*Purshia tridentata*), and big sagebrush (*Artemisia tridentata*—Sharples, 1983). In Mono Co., California, almost 100% of *T. speciosus* were captured in wooded areas (riparian lodgepole pine forests); only five of 130 were in sagebrush (Chappell, 1978).

Food seldom is limiting for *T. speciosus* (Heller, 1971). It is omnivorous (Sumner and Dixon, 1953), and eats seeds of grasses, forbs, and trees (Jameson and Peeters, 1988), fruits and berries, insects, picnic scraps (Sumner and Dixon, 1953), and flesh (Grinnell, 1908; Tevis, 1953*b*). The annual dietary volume of fungi is 32% (Fogel and Trappe, 1978; Tevis, 1953*b*). *T. speciosus* eats seeds of white fir, red fir (Sumner and Dixon, 1953), sugar pine (Brand, 1970), Jeffrey pine (Smith, 1943), bindweed (*Convolvulus*), geranium (*Geranium*), phacelia (*Phacelia*), borage (Boraginaceae), sedge (*Carex*—Grinnell and Storer, 1924), antelope-brush, sagebrush, snowberry (*Symphoricarpos*), mountain mahogany (*Cercocarpus*), and gooseberry (*Ribes*—Chappell, 1978). In Plumas Co., diet in spring, summer, and autumn predominately is seeds, fungi, and arthropods. In spring, leaves and flowers also are consumed. Additional foods are flowers in autumn, fruit in summer, and flesh in summer. *T. speciosus* will eat pollen of white fir, strawberries (*Fragaria californica*), and Sierra gooseberries (*Ribes roezli*). Feces of lodgepole chipmunks that ate staminate cones of white fir (*Abies concolor*) were golden in color (Tevis, 1953*b*).

Among insects, *T. speciosus* favors caterpillars (Jameson and Peeters, 1988). In Plumas Co., it consumed pupae of California tortoise-shell butterflies (*Nymphalis californica*). It did not select hairy caterpillars, but instead searched in trees and bushes for chrysalids (Tevis, 1953*a*). *T. speciosus* eats aphids associated with white fir (Baysinger, 1940); 64% of the total volume of stomachs contained aphids (*Chermes pinicorticis*) that had infested young needles of white fir. These insects were swallowed whole, and often bits of needles were included. Giant carpenter ants (*Camponotus levigatus*) also are consumed (Tevis, 1953*b*).

The lodgepole chipmunk climbs in shrubs to gather seeds or fruits. Some food (e.g., pine seeds, fungi, and picnic scraps) is sought on the ground (Grinnell and Storer, 1924). When cheekpouches are full, the food is buried in the soft, dry earth. Because these seeds are planted at about the right depth for germination, those not eaten may develop into seedlings (Sumner and Dixon, 1953).

In the San Bernardino Mountains, the call of a lodgepole chipmunk was heard, accompanied by calling and bill-snapping of two western wood pewees (*Contopus sordidulus*). The chipmunk had robbed their nest, leaving only parts of egg shells. The nest was 3 m aboveground and on a branch 1.8 m from the tree trunk (Grinnell, 1908).

In captivity, *T. speciosus* will consume commercial rat chow, fruit, vegetables, birdseed, hard-boiled eggs, and water (Chappell et al., 1978). It shows a strong selection for sunflower seeds, apple, and peanut butter–oatmeal mixture; sunflower seeds were the only food stored. These stored seeds always were shelled and placed in the bottom of the cotton lining of the nest (Cade, 1963).

Tamias speciosus hibernates in nests that it builds in stumps, logs, and cracks and crevices of rock piles (Sumner and Dixon, 1953). One autumn nest was constructed in the cavity of an erect dead tree in the San Bernardino Mountains (Jaeger, 1929). Young may be born in an underground den or high up in a woodpecker hole. Fallen tree trunks in open places, at the edge of mountain meadows, are common den sites. *T. speciosus* usually digs its burrows under or near such sheltering objects (Sumner and Dixon, 1953).

Populations fluctuate seasonally (Grinnell, 1908) and annually (Chappell, 1978). The spring population of *T. speciosus* may be ca. 1/ha (Grinnell and Storer, 1924). By July, young-of-the-year may double the population present earlier in the season (Grinnell, 1908). In Mono Co., densities of 0.11/ha were followed by a 9-fold increase over the previous year to 1.06/ha. These increased populations probably were due to the wet summer and mild winter, conditions leading to high reproductive success and low overwinter mortality (Chappell, 1978).

Average size of home range is 1.49 ha for adult males, 1.28 ha for breeding females, and 1.60 ha for young females (Chappell, 1978). In Yosemite National Park, average size of home range was 2.6 ha and the longest axis of a home range was 252 m (Brand, 1970). In Mono Co., <25% of individuals had stable home ranges; the rest probably were transients from nearby riparian forests (Chappell, 1978).

Tamias speciosus is zonally separated from its sympatric congeners. *T. alpinus* occurs at higher elevations in the alpine zone; *T. amoenus* and *T. minimus* occur at lower elevations in pinyon pine–sagebrush (*Pinus–Artemisia*) and the sagebrush zone, respectively (Blankenship, 1985). Behavioral experiments, in which interspecific pairs were allowed to interact, revealed interspecific aggression and interspecific dominance relationships between all pairs having zones of contact in nature. Upper and lower limits of *T. speciosus* may be explained by aggressive dominance of *T. alpinus* and *T. amoenus*, respectively (Heller, 1969). Although niches of *T. alpinus* and *T. amoenus* include habitat of *T. speciosus*, presence of *T. speciosus* may reduce their success in this habitat by repeatedly eliciting their aggression and by not being excluded by them (Heller, 1971). *T. speciosus* aggressively excludes *T. amoenus* and *T. minimus* from its mesic habitat. Although considerable overlap exists in diet, *T. speciosus* eats significantly more antelope-brush than *T. minimus* (Chappell, 1978).

In Placer Co., *T. speciosus* occurs sympatrically with *T. senex* and *T. amoenus* (Allen, 1890). In Nevada Co., *T. speciosus* is found only in open-canopy forests, a habitat also occupied by *T. amoenus*. In the same area, *T. senex* was the most common chipmunk in closed-canopy forests (Sharples, 1983). Where *T. speciosus* and *T. umbrinus* meet, *T. speciosus* occurs in or near dense stands of lodgepole pine and the damper and more sheltered basins, whereas *T. umbrinus* occurs in the vicinity of open forest of stunted limber pine (*Pinus flexilis*) and whitebark pine (*Pinus albicaulis*) on exposed and well-drained ridges and on slopes near timberline (Hall, 1946). *T. speciosus* is sympatric with *T. merriami* and *T. obscurus* in the San Bernardino and San Jacinto mountains (Blankenship, 1985). In the San Bernardino Mountains, *T. speciosus* occurs with *T. merriami* at 1,500–2,700 m elev., but at elevations >2,700 m only *T. speciosus* is present (Allen, 1890).

Tamias speciosus also is sympatric with *Sorex monticolus*, *S. palustris*, *S. trowbridgii*, *Scapanus latimanus*, *Thomomys bottae*, *T. monticola*, *Peromyscus boylii*, *P. maniculatus*, *Reithrodontomys megalotis*, *Microtus longicaudus*, *Zapus princeps*, and *Mustela erminea* (Williams and Braun, 1983). Predators include the coyote (*Canis latrans*—Sumner and Dixon, 1953), Cooper's hawk (*Accipiter cooperi*), and red-tailed hawk (*Buteo jamaicensis*—Swarth, 1919).

Plague (*Yersinia pestis*) has been detected in *T. speciosus* (Nelson, 1980). Ectoparasites include the fleas *Trichopsylla ciliata* (da Costa Lima and Hathaway, 1946), *Diamanus montanus*, *Oropsylla idahoensis*, *Monopsyllus eumolpi*, *M. ciliatus*, *Catallagia sculleni* (Tevis, 1955), *Ceratophyllus ciliatus* (Traub et al., 1983), and *Callistopsyllus terinus* (Tipton et al., 1979), the lice *Neohaematopinus pacificus* and *Hoplopleura arboricola* (Ferris, 1916), and the ticks *Ixodes hearlei*, *I. texanus* (Cooley and Kohls, 1945), *I. angustus*, *Dermacentor andersoni*, and *D. occidentalis* (Furman and Loomis, 1984).

Drift fences, pitfall traps, and live traps are effective in capturing lodgepole chipmunks; peanut butter is an attractive bait (Williams and Braun, 1983). *T. speciosus* has been exhibited in zoos (Dolan and Moran, 1969).

Tamias s. callipeplus occurs on Mount Abel and Mount Frazier in an area with a high level of recreational activities, including extensive vacation-home developments. This may lead to a population reduction, but widespread occurrence of this subspecies on public lands and its selection of open forests suggest that it is not threatened (D. F. Williams, in litt.). Automobiles are a significant cause of death for young-of-the-year (Tevis, 1955).

BEHAVIOR. The lodgepole chipmunk is secretive (Howell, 1924) and diurnal, often emerging when the sun is well up and retiring before sundown (Cade, 1963). In Mono Co., it was not active after 1400 h (Chappell, 1978).

Tamias speciosus is active through most of the year (Cade, 1963; Grinnell and Storer, 1924; Vaughan, 1954). In the San Bernardino and San Gabriel mountains, it is active every month (Cade, 1963). Its circannian rhythm is related to body size, availability of food, and rigor of winter environment. This rhythm also allows onset of hibernation to be flexible (Heller and Poulson, 1970). The lodgepole chipmunk is active until the first storm of the season, which may bring warm rain and is followed by days of sunshine. After early storms, it may become relatively inactive as hibernation approaches (Tevis, 1955). Light snows of early winter do not drive all individuals into hibernation, although most enter hibernation with the first heavy snow of the season (Grinnell and Storer, 1924). During times of deep and prolonged snow cover, *T. speciosus* may be inactive for several days. However, it is likely to be active on bright sunny days even in December and January (Cade, 1963).

When the lodgepole chipmunk emerges from hibernation in March or early April (Sumner and Dixon, 1953; Tevis, 1953*b*), it may appear first on warm southern and west-facing rocky areas. Although snow was ca. 1 m deep on 14 April, some granite domes and warm exposures were free of snow. In such warm spots, several lodgepole chipmunks had emerged and were running among manzanita bushes and over the snow (Sumner and Dixon, 1953).

Tamias speciosus is active on snow banks, between logs, and on tree trunks. It runs on the ground, over fallen logs, and at times it climbs shrubs to harvest seeds or fruit. Two chipmunks may engage in play-like pursuit of one another that may last for minutes and carry the two over and beneath logs, through brush, across open places in the forest, and up, around, and down trunks of one or more trees. This behavior occurs at various seasons and young often engage in it, indicating that it is not related to mating (Grinnell and Storer, 1924).

Tamias speciosus is noted for its climbing ability (Grinnell et al., 1930), and it is a better climber than most congeners, often running up smaller trees and sitting on a knot or limb and chipping at intruders (Stephens, 1906). It is the only species of chipmunk in Yosemite that habitually takes refuge well up in trees (Grinnell and Storer, 1924). *T. speciosus* may rapidly ascend a tree on the opposite side from the intruder, now and then peeping around (Grinnell, 1908; Howell, 1924). Often it climbs as high as 9–12 m, takes refuge on top of a branch, and sits motionless (Grinnell, 1908). Its plume-like tail often hangs to one side of a branch, waving back and forth. Even when not frightened, it moves about actively in trees. The lodgepole chipmunk can climb perpendicular trunks, even of such smooth-barked trees as young lodgepole pines and firs. It is able to run down smooth-barked trees head first with ease. It may leap short distances from one branch to another, and it may drop 3.0–4.5 m to the ground (Grinnell and Storer, 1924). *T. speciosus* also may use uppermost stems of chaparral plants (*Adenostoma*, *Arctostaphylos*, *Quercus*) as vantage points, and when disturbed, it runs over thorny surfaces of brush taking refuge in tangled growth (Vaughan, 1954).

In Nevada Co., typical behavior of *T. speciosus* released from traps was to climb the nearest tree and remain motionless on a limb. In contrast, *T. amoenus* often skirted around tree trunks and disappeared into brush or down holes among roots of trees and shrubs. *T. speciosus* used the vertical aspect of vegetation for escape routes more often than *T. amoenus* (Sharples, 1983).

Tree-climbing by *T. speciosus* provides an effective escape from ground squirrels (*Spermophilus*), but not from other chipmunks. Even though *T. speciosus* is quite arboreal, an escaping individual seldom climbs a tree when pursued by another chipmunk, because the pursuer may follow it up the tree. In Yosemite National Park, *S. lateralis* often chases *T. speciosus*. When chased by *S. lateralis*, a lodgepole chipmunk may run up a tree and stop; *S. lateralis* was never observed to follow (Brand, 1970).

Tamias speciosus tends to call from trees; the tail usually is flipped upward during vocalizations (Brand, 1970). Calls include a high "whisk," shrill "tsew," rapid "pst-pst-pst-a-kū" (Storer and Usinger, 1963), chip, chippering, chuck, chattering (in courtship), and whistle. There is geographic variation in temporal arrangements of chips in chipping sequences. Vocalization rates at Lake Almanor, Plumas Co., and Yosemite, Mariposa Co., California, respectively, are: chips/min, 83 (range, 24–160), 47 (22–88); chips/burst, 1, 1; bursts/min, 83 (24–160), 47 (22–88); length of syllable (in s), 0.030 (0.015–0.045), 0.035 (0.025–0.050). Frequency rates (in kHz) are: bottom of upsweep, 1.5 (1.0–2.0), 1.5 (1.0–1.5); top of upsweep, 11.5 (9.5–14.0), 13.0 (11.0–14.5); bottom of downsweep, 7.0 (2.0–10.0), 8.0 (5.0–10.0—Brand, 1976). Syllables of vocalizations resemble those of *T. minimus*, except *T. speciosus* reaches higher frequencies, and downsweeps are shorter and less frequent (Brand, 1970).

Tamias speciosus readily drinks and eats in captivity; taking 1–2 ml of water daily. Water is sucked, not lapped, into the mouth; but sometimes it puts its tongue into the water before drinking (Grinnell and Storer, 1924).

In summer and autumn, the lodgepole chipmunk devotes much activity to gathering and storing food (Grinnell and Storer, 1924). On 19–24 August, *T. speciosus* was observed gathering seeds of lupine and fruits of gooseberry and *Ceanothus*. These foods were carried into and beneath old logs and into rock piles (Grinnell, 1908). Lodgepole chipmunks also will cache seeds in forks and foliage of trees (Brand, 1974). *T. speciosus* buries one or more seeds and nuts in a place. It uses the forepaws to excavate a small hole and to transfer contents of cheekpouches to the hole; then the hole is filled, the surface is smoothed, and patted down. The method used to relocate buried seeds is unknown, but the sense of smell probably is important. It uses its forefeet to hold food, usually employing both feet, but sometimes only one. If hungry, *T. speciosus* may stuff food into the cheekpouches without using its paws. After the cheekpouches are filled, it slips out one grain at a time and nibbles the kernel while holding it in the paws (Grinnell and Storer, 1924).

Tamias speciosus, *T. amoenus*, *T. quadrimaculatus*, and *T. senex* live in the same area of Yosemite National Park. They forage on the same food sources at the same time without exhibiting much aggression (Brand, 1970). Field observations reveal that *T. speciosus* is dominant to *T. amoenus* and *T. minimus* (Chappell, 1978). However, *T. speciosus* may be excluded from more arid habitats of *T. alpinus* and *T. amoenus* by their aggressive dominance (Heller, 1971). Thus, physiologic limitations on *T. speciosus* probably are not primary in restricting its local distribution (Heller and Poulson, 1972). In laboratory encounters, *T. speciosus* usually was subordinate to *T. amoenus* and *T. alpinus*, in contrast to field observations. Possibly, the laboratory environment inhibits aggressiveness of *T. speciosus* (Heller, 1971).

In Mono Co., activities of *T. speciosus* in woodlands, ecotonal areas, and sagebrush habitats predominantly were related to travel, feeding, grooming, resting, or alert posture. *T. speciosus* is able to defend sources of food and maintain exclusive dominance over *T. amoenus* and *T. minimus* (Chappell, 1978). In field studies, *T. speciosus* usually remained around the edge of the feeding area and did not appear to be as bold as other species of chipmunks (Brand, 1970).

Under constant conditions, *T. alpinus* and *T. speciosus* show an endogenous rhythm. When exposed to low ambient temperature or dehydration, they respond with longer periods of inactivity and with higher incidence of torpor than do *T. amoenus* or *T. minimus* (Heller and Poulson, 1970). Under conditions of heat stress, *T. speciosus* never sprawled, always remained awake, and exhibited no tendency to become hypothermic (Chappell et al., 1978).

Exposure to silhouettes of aerial predators and discs elicited equally strong responses from *T. speciosus*. At the appearance of the model overhead, each chipmunk typically ran into its nest box and stayed inside for several seconds to several hours. They often crouched or assumed the upright, alert posture outside the nest box. Fleeing into the box, time spent there, and frequency and duration of crouching or alert posture varied (Müller-Schwarze and Müller-Schwarze, 1971).

GENETICS. *Tamias speciosus* has karyotype B of *Tamias* (Fig. 5; Nadler, 1964). The modal diploid number of chromosomes is 38 (Nadler and Block, 1962); including four pair of large metacentric, six pair of large submetacentric, four pair of large acrocentric, one pair of small metacentric, and three pair of small acrocentric chromosomes. The X chromosome is submetacentric and the Y is acrocentric (Sutton and Nadler, 1969). The diploid number may vary from 36 to 39 (Nadler, 1964).

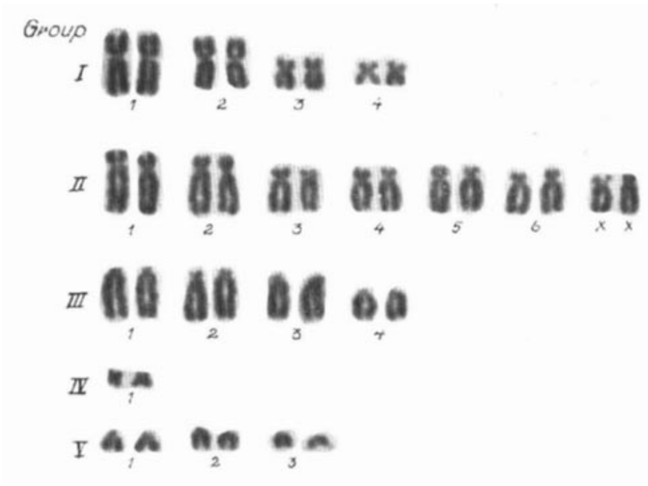

FIG. 5. Karyotype of a female *Tamias speciosus frater* from Chester, Plumas Co., California. Roman numerals indicate the type of chromosome: I, large metacentric; II, submetacentric; III, large acrocentric; IV, small metacentric; V, small acrocentric. The number of chromosomes of each type is noted (Nadler, 1964).

Of 20 allozymes examined, *T. speciosus* had an average heterozygosity of 0.0608 and four polymorphic loci (serum transferrin, serum leucine aminopeptidase, glucose-6-phosphate dehydrogenase, red cell phosphoglucomutase—Levenson et al., 1985). Based on allozymes, *T. speciosus* differs from *T. amoenus*, *T. merriami*, and *T. obscurus*, which do not possess esterase-1 (Blankenship and Bradley, 1985).

REMARKS. The fox sparrow (*Passerella iliaca*) occurs in the same geographic area as *T. speciosus*, and breeding ranges of subspecies of *P. iliaca* are similar to ranges of subspecies of *T. speciosus*. In each species, there is a wide ranging subspecies on both slopes of the northern and central Sierra Nevada, which is replaced in the vicinity of Kings River Canyon by a different form ranging only over the western slope of the southern Sierra Nevada and occurring on high mountains of southern California. In *P. iliaca*, all southern populations are of one subspecies, whereas in *T. speciosus* there are three subspecies. In *P. iliaca* and *T. speciosus*, the primary division occurs in the vicinity of Kings River Canyon; the range of *T. speciosus* is continuous around the head of the canyon (Johnson, 1943).

Studies to elucidate the relationship of *T. speciosus* to other species of *Tamias* have included examination of morphology (closest affinities are with *T. amoenus* and *T. ruficaudus*—Levenson et al., 1985), bacula (*T. bulleri*, *T. palmeri*, *T. panamintinus*, and *T. umbrinus*—White, 1953), chromosomes (*T. amoenus*, *T. dorsalis*, *T. quadrivittatus*, *T. senex*, and *T. townsendii*—Nadler, 1964), and allozymes (*T. minimus*, *T. quadrimaculatus*, and *T. ruficaudus*—Levenson et al., 1985).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Levenson et al., 1985; Nadler et al., 1969, 1977; Wilson and Reeder, 1993). However, indications that *Eutamias* and *Tamias* may be distinct genera include divergence in the late Miocene (Ellis and Maxson, 1979; Hafner, 1984), differences in pattern of dorsal stripes, structure of the hyoid, chromosomes, dental formulas, bacula (Hoffmeister, 1986), microcomplement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

Tamias is from the Greek *tamias* meaning a storer or distributor. The specific epithet is the Latin *speciosus* meaning showy or brilliant (Jaeger, 1955). Other common names include Sierra Nevada (Dolan and Moran, 1969), showy, related, beautifully garbed (Elliot, 1905), Tahoe, sequoia, San Bernardino, and Mount Pinos chipmunk (Howell, 1929).

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