

Tamias alpinus. By Robin G. Clawson, Joseph A. Clawson, and Troy L. Best

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Tamias alpinus Merriam, 1893

Alpine Chipmunk

Tamias alpinus Merriam, 1893:137. Type locality "Big Cottonwood Meadows, High Sierra [Tulare Co.—Miller, 1912:307], California, just south of Mount Whitney (altitude, 3,050 meters or 10,000 feet)."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains 25 species (Wilson and Reeder, 1993); *T. alpinus* is in the *minimus* group of the subgenus *Neotamias* (Levenson et al., 1985). *T. alpinus* is monotypic (Hall, 1981).

DIAGNOSIS. *Tamias alpinus* is sympatric or parapatric with *T. amoenus*, *T. minimus*, *T. quadrimaculatus*, *T. senex*, *T. speciosus*, and *T. umbrinus* (Callahan, 1976). In the Yosemite region of the Sierra Nevada, *T. alpinus* (Fig. 1) is one of the palest-colored chipmunks (Grinnell and Storer, 1924). It is smaller than other *Tamias* in the same area, except *T. minimus*, from which *T. alpinus* differs in possessing a shorter tail that is flatter in cross section (Hall, 1981), larger ears, a skull (Fig. 2) that is larger and broader inter-orbitally (Howell, 1929), a larger and more flattened braincase, a longer and blunter rostrum, a wider palate, shorter incisors (Hall, 1981), longer nasals, and longer nasal branches of premaxillaries. The length of the nasals equals or exceeds the combined length of the basioccipital and basisphenoid; in *T. minimus* the nasals fall short of this measurement (Merriam, 1893). Compared with *T. minimus*, *T. alpinus* has bright orange instead of dull-grayish yellow on its underside, longer and finer fur, paler dorsal coloration, and more ochraceous in the pale dorsal stripes (Hall, 1981). In all pelages, *T. alpinus* may be distinguished from *T. minimus* by the tail, which is hoary above (rarely yellowish), is broader and more bushy, and has a black terminal part that is longer. The outer pair of white dorsal stripes also is broader, as in *T. speciosus*. In spring and early summer, before the postbreeding molt, *T. alpinus* is paler than the palest *T. minimus*. In midsummer pelage, the sides and dark stripes are deeper ferruginous than in the brightest summer pelage of *T. minimus*, and in some individuals even the inner pair of pale stripes is sometimes obscured by rusty (Merriam, 1893). In winter pelage, coloration is more buff and less gray, and the sides are darker than in *T. minimus* (Howell, 1929).

Along the eastern margin of the range of *T. alpinus*, *T. amoenus* is found; a species of larger size, but of somewhat more brilliant coloration (Grinnell and Storer, 1924). Compared with *T. amoenus* in summer pelage, the upperparts are similar, but *T. alpinus* may be distinguished by its smaller size, paler colors, paler (more grayish) hind feet, and the tail has more black at the tip. The dark stripes are less blackish and the outer pair of pale stripes is broader and more prominent. The head, rump, sides of body, hind feet, and underside of the tail of *T. alpinus* are paler (Howell, 1929). Both may be seen among rocks, and then only close scrutiny of individuals will enable an observer to distinguish between the two. However, *T. alpinus* has not been found east of Warren Fork of Leevining Creek and Mono Pass and *T. amoenus* is not known to occur west of these locations (Grinnell and Storer, 1924).

At Glen Aulin, the range of *T. senex* meets that of *T. alpinus*. *T. alpinus* is only about one-half the mass of *T. senex* and its coloration is paler, so there is no difficulty in distinguishing these species (Grinnell and Storer, 1924).

The baculum of *T. alpinus* (Fig. 3) differs from *T. bulleri*, *T. palmeri*, *T. panamintinus*, *T. speciosus*, and *T. umbrinus* in that the base is not markedly widened and the shaft is thinner. *T. alpinus* differs from *T. cinereicollis*, *T. quadrimaculatus*, *T. quadrivittatus*, and *T. ruficaudus* in that the shaft is thinner and the baculum is shorter. *T. alpinus* differs from *T. townsendii* in that the base is

not dorsoventrally thickened and is not as widened. *T. alpinus* differs from *T. sonomae* in that the ridges on either side of the tip are not enlarged and the base is not dorsoventrally thickened. *T. alpinus* differs from *T. amoenus*, *T. dorsalis*, and *T. minimus* in that the keel is lower and the angle formed by the tip and the shaft is more distinct. *T. alpinus* differs from *T. merriami* in that the baculum is shorter and the base is not incised dorsally (White, 1953).

GENERAL CHARACTERS. In autumn pelage, the upperparts of the alpine chipmunk are hoary gray, suffused on the flanks with ochraceous buff. The median dorsal stripe is dusky and is obscured by pale rusty. The lateral dorsal dark stripe is pale ferruginous and the inner pair of white stripes is hoary gray. The outer pair of stripes is white and broad (as in *T. speciosus*). The postauricular patches are whitish, and are not sharply defined. The facial stripes are pale. The ear stripes are indistinct and the legs and feet are gray. Dorsally, the tail is hoary (rarely yellowish), becoming black toward the tip (individual hairs are buff gray sub-basally, then black, and broadly tipped with pale buff-gray or yellowish). Ventrally, the tail is pale buff-fulvous, bordered and broadly tipped with black, and broadly edged laterally with pale buff (Merriam, 1893).

Winter pelage (October) is similar to summer pelage, but the upperparts are more grayish and less tawny. The sides are pinkish buff. In summer pelage (August), the head is smoke gray and washed with pale pinkish-cinnamon. The stripe on each side of the head is pale fuscous mixed with sayal brown. The ocular stripe is fuscous and the submalar stripe is snuff brown. The pale facial stripes are grayish-white. The ears are chaetura drab or dark brown anteriorly and buff white posteriorly. The postauricular patches are rather large and creamy white. The dark dorsal stripes are tawny and mixed with fuscous black; the median one is darkest and usually is blackish. The median pair of pale dorsal stripes is smoke gray and sometimes sprinkled with tawny. The outer pair is broader and creamy white. The sides are clay color with an indistinct patch of smoke gray on the shoulders. The rump and thighs are smoke gray, sprinkled with clay color. Dorsally, the tail is fuscous black, overlaid with clay color. Ventrally, the tail is clay color and pinkish-cinnamon, bordered with fuscous black and edged with clay color. The tip of the tail is fuscous black for ca. 20 mm. The forefeet and hind feet are pale smoke-gray, washed with pale pinkish-buff, and the underparts are



FIG. 1. A subadult *Tamias alpinus* at Bullfrog Lake, Fresno Co., California. Photograph by J. S. Dixon; courtesy of the Museum of Vertebrate Zoology, University of California, Berkeley.

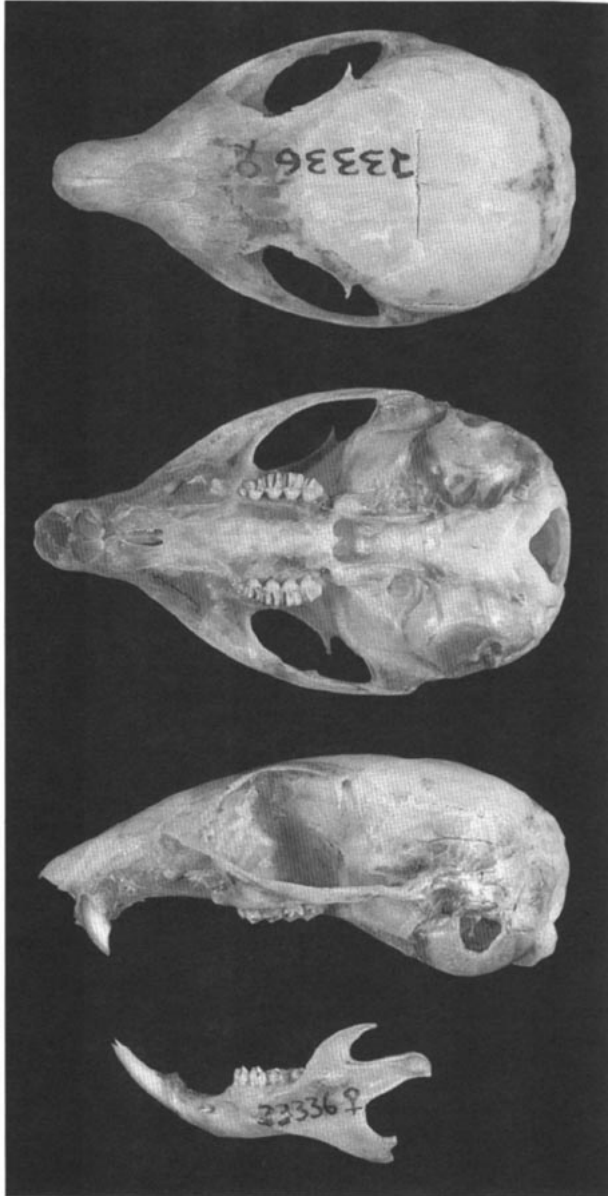


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias alpinus* from Warren Fork, Leeving Creek, 3,000 m, Mono Co., California (female, Museum of Vertebrate Zoology, University of California, Berkeley 23336). Greatest length of cranium is 29.7 mm. Photographs by T. H. Henry.

creamy white (color nomenclature follows Ridgway, 1912—Howell, 1929).

Average and range of measurements (in mm) of *T. alpinus* from Mariposa, Mono, and Tuolumne counties, for males and females, respectively, are: total length, 174 (166–184), 177 (169–181); length of head and body, 103 (87–115), 105 (98–112); length of tail, 71 (63–81), 72 (63–76); length of hind foot (dry), 28.0 (26.6–29.0), 28.1 (27.1–29.3); condylobasal length of cranium, 26.5 (25.8–27.2), 26.7 (26.1–27.5); greatest length of cranium, 29.8 (28.9–30.4), 30.0 (29.3–31.0); zygomatic breadth, 16.9 (16.3–17.6), 17.1 (16.5–17.6); breadth of cranium, 14.6 (14.3–14.9), 14.7 (14.1–15.0); depth of cranium, 9.9 (9.6–10.2), 9.9 (9.5–10.2); interorbital breadth, 7.2 (6.8–7.3), 7.2 (7.0–7.7); length of nasals, 9.3 (8.9–9.8), 9.5 (9.1–9.8); depth of rostrum, 4.3 (3.9–4.6), 4.3 (4.1–4.5); length of incisive foramina, 2.2 (1.7–2.5), 2.3 (2.1–2.5); length of lower toothrow, 4.5 (4.4–4.6), 4.7 (4.6–4.8—Johnson, 1943). Average length of ear from notch is 13 mm (genders combined; range, 12–14—Howell, 1929). Body mass averages 34.0–



FIG. 3. Baculum of *Tamias alpinus* from Big Cottonwood Meadow, Tulare Co., California. The bar represents 1 mm (modified from White, 1953).

39.1 g (genders combined; range, 27.5–45.5—Heller and Gates, 1971; Heller and Poulson, 1972; Howell, 1929; Johnson, 1943). Length of hind foot is 27.5% of the length of head and body (Johnson, 1943).

The restricted range of the alpine chipmunk, general uniformity of its habitat, and absence of barriers separating populations are factors that should tend to make this species uniform in characters. However, specimens from the northern part of the range have smaller skulls and shorter tails than those from southern localities. These differences are not sufficient to warrant subspecific designation of a northern race and there seem to be no correlated color differences (Johnson, 1943).

Average length of head and body of females (107.3 mm) is larger than that of males (103.9 mm). In addition, there is geographic variation in sexual dimorphism between the central and southern Sierra Nevada, California. The average length of head and body (in mm) of populations in the central and southern Sierra Nevada, respectively, is 102.8 and 104.6 for males and 106.5 and 107.8 for females (Levenson, 1990).

DISTRIBUTION. *Tamias alpinus* occurs in the Sierra Nevada of California (Fig. 4; Hall, 1981). It occupies the Hudsonian, Arctic alpine, and Canadian life zones, with an altitudinal range from ca. 2,300 (Johnson, 1943) to 3,900 m (Swarth, 1919). The alpine chipmunk ranges higher in elevation than any other *Tamias* in the Sierra Nevada (Howell, 1929); it seldom occurs at <2,500 m (Grinnell and Storer, 1924). *T. alpinus* appears to have developed within the Arctic-alpine region in the range it now inhabits (Merriam, 1906). No fossils of *T. alpinus* are known.

FORM AND FUNCTION. Physical and physiological parameters of *T. alpinus* include: total surface area, 87 cm²; effective surface area for the emission and absorption of long-wave radiation, 109 cm²; absorptivity, 73%; evaporative water loss at 25°C, 1.21 calories/min; evaporative water loss at 30°C, 2.34 calories/min; evaporative water loss at 40°C, 8.76 calories/min; coefficient of convection, 0.070(flow rate) + 3.22 calories min⁻¹ cm⁻² °C⁻¹ × 10²; length of pelage, 0.96 cm; thickness of pelage, 0.33 cm (Heller and Gates, 1971).

The pale color of *T. alpinus* is similar to the gray granite boulders where it lives (Elliot, 1904). The dorsal guard hairs have a distal dark band 1 mm in length and a width to 51 μm (Mayer, 1952). The summer and winter pelage is long, fine, and silky (Johnson, 1943). In late June and early July, the alpine chipmunk changes from the worn and dulled winter pelage into the more brightly colored summer coat. By October, the longer, denser, and grayer winter pelage is present (Grinnell and Storer, 1924). On 19 June, an alpine chipmunk from Mount Whitney, California, was molting into summer pelage. The new pelage was coming in irregularly on the anterior part of the back. Another from the east fork of the Kaweah River had nearly completed its molt on 4 August; only the rump retained winter pelage. At Alta Peak on 10 August, an adult male had summer pelage that was just beginning to appear on the head and middle of the back and a breeding female showed no signs of molt (Howell, 1929).

As in all members of the subgenus *Neotamias*, the dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22 (Howell, 1929; Ingles, 1965). The incisors are short and the rows of cheekteeth are bowed outward. Average nasal measurements are ca. 9.5 mm or ca. 35% of the condylobasal length of cranium. The skull is broad, flattened, and large in proportion to the body size. The zygomatic arches are moderately appressed to the skull. Their outer edges are straight, nearly parallel, convergent anteriorly, and narrow at the base. The braincase is broad, nearly vertical-sided, flat topped, and depressed medially at the frontoparietal suture. The auditory bullae are small and recessed. The foramen magnum is high and

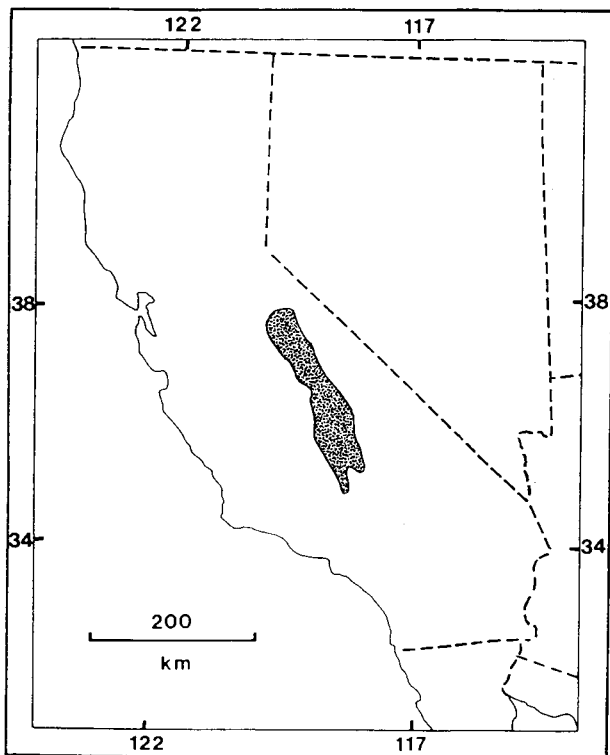


FIG. 4. Distribution of *Tamias alpinus* in California (Hall, 1981).

narrow and its dorsolateral margins are concave. The palate is broad and flat (Johnson, 1943).

Metabolic rates for *T. alpinus* are: basal metabolic rate, $1.48 \text{ ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$; metabolic rate below thermoneutrality (in $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1}$), $-0.121(\text{ambient temperature in } ^\circ\text{C}) + 4.871$; surface-area specific rate of metabolism below the thermoneutral zone (in $\text{calories cm}^{-2} \text{ min}^{-1}$), $-0.0047(\text{ambient temperature in } ^\circ\text{C}) + 0.180$. 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 from the larger body size 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. Average values of insulation of live *T. alpinus* at an ambient temperature of 30°C are: net heat production, $0.031 \text{ calories min}^{-1} \text{ cm}^{-2}$; body temperature minus the surface temperature, 3.7°C ; quality of insulation of fat and pelage, $119.35 \text{ cm}^2 \text{ } ^\circ\text{C}^{-1} \text{ min}^{-1} \text{ calorie}^{-1}$ (Heller and Gates, 1971).

In the laboratory, internally heated, metal casts covered with pelts of *T. alpinus* were used to measure the coefficient of convection and the effective surface area for the emission and absorption of thermal radiation. The casts were suspended in a vacuum and the effective radiating surface area was calculated from the wattage necessary to maintain a constant cast-radiating surface temperature and surface temperature of the chamber. The casts were placed in a wind tunnel and the coefficients of convection at different wind speeds were calculated from the wattage necessary to maintain a constant cast-radiating surface temperature, air temperature, tunnel-wall temperature, and total surface area of cast. The coefficient of convection (in $\text{watts cm}^{-2} \text{ } ^\circ\text{C}^{-1} \times 10^3$) of *T. alpinus* (0.0049) approximates those of *T. amoenus* (0.0053) and *T. minimus* (0.0044); *T. speciosus* was lower (0.0037). These results correspond with the relative surface areas of the four species (Heller, 1972).

In the laboratory, water relationships of the alpine chipmunk include: consumption of water ad lib., 16.1% of body mass/day; minimum consumption of water, 7.2% of body mass/day; water content of feces, 49.9% wet weight; relative medullary thickness, 11.15 mm. When deprived of water, concentrated urine is produced. The average extent to which this species can decrease its water requirement when stressed is 55%. The relative medullary thickness of *T. alpinus* is less than that of *T. minimus*, but it is greater than

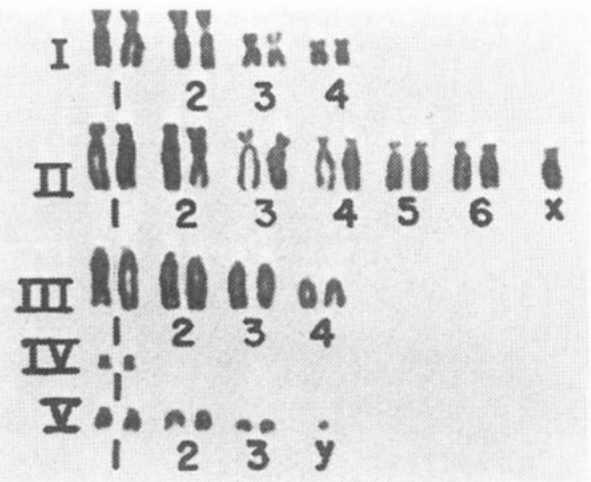


FIG. 5. Karyotype of a male *Tamias alpinus* from Tioga Pass, Mono Co., California. Roman numerals indicate the type of chromosome: I, large metacentric; II, submetacentric; III, large acrocentric; IV, small metacentric; V, small acrocentric. The number of chromosomes of each type is noted (Sutton and Nadler, 1969).

T. amoenus and *T. speciosus*. There is no difference between the mass-specific rates of evaporative water loss of *T. alpinus*, *T. amoenus*, and *T. speciosus*, at 25°C , but *T. minimus* shows a higher value than any of these species (Heller and Poulson, 1972).

Average evaporative water loss at ambient temperatures of 25, 35, and 40°C , respectively, is 3.2, 6.2, and $24.8/\text{ml} \times 10^3 \text{ g}^{-1} \text{ h}^{-1}$. At 40°C , the alpine chipmunk exhibits hyperthermia and the rate of evaporative heat loss is 393.5 calories/45 min. The proportion of heat production dissipated by water loss is 23.5% at an ambient temperature of 25°C and 50.7% at 35°C . Rate of rise in body-heat content at an ambient temperature of 40°C is 2.29 calories $\text{g}^{-1} \text{ 45 min}^{-1}$; the total is 93.2 calories/45 min (Heller and Poulson, 1972).

The relative importance of endogenous control and the sensitivity to environmental stimuli differ among species of *Tamias* from rigorous and predictable climates (*T. alpinus* and *T. speciosus*), and those from less rigorous and less predictable climates (*T. amoenus* and *T. minimus*). Habitat differences are reflected by differences in endogenous and exogenous control of circannian rhythms of *Tamias* in the laboratory. Under constant conditions, *T. alpinus* and *T. speciosus* show an endogenous rhythm, and when exposed to low ambient temperature or dehydration, they have longer inactive times and higher incidence of torpor than do either *T. amoenus* or *T. minimus*. The circannian rhythm is related to the size of the animal, predictability and availability of food, and predictability and rigor of winter environment (Heller and Poulson, 1970).

The shaft of the baculum is thin (Hall, 1981), the distal 33% of the shaft is laterally compressed, and the base is wider than the shaft. The ridges on either side of the tip are neither enlarged nor partially obscure the lateral view of the keel. The height of the keel is one-seventh of the length of the tip. The shaft is 2.17 mm in length, the tip is 39% of the length of the shaft, and the shaft is not incised on the dorsal side of the base. The angle formed by the tip and shaft is 135° (White, 1953).

ONTOGENY AND REPRODUCTION. Although no nests have been found, *T. alpinus* probably has dens among rocks or in the ground beneath them (Grinnell and Storer, 1924). The usual number of young per litter is four or five (Sumner and Dixon, 1953). Two females on 30 June had four and five large embryos, respectively. Females had been suckling young 5–17 July. In July, males were not sexually active. On 30 July, young individuals were observed. On 20 August, a young female with a body mass of 19.5 g, which is ca. 50% of the body mass of an adult, was present at 3,150 m elevation. On 22 August, two individuals were about two-thirds grown. By early October, young-of-the-year are about the size of adults (Grinnell and Storer, 1924). *T. alpinus* shows a trend towards breeding later at higher elevations (Hirshfeld, 1975).

ECOLOGY. *Tamias alpinus* occurs on rock-bordered alpine

meadows and talus slopes (Cade, 1963) from near timberline to near the summits of the highest peaks of the Sierra Nevada (Stephens, 1906). It usually inhabits either large masses of slide rock on canyon sides or scattered boulders within open stands of lodgepole pines (*Pinus contorta*). Frequently, it is seen scampering over and around logs lying on the ground. Individuals traverse rock piles with great facility, and venture farther into such places than does *T. speciosus* (Grinnell and Storer, 1924).

The habitat of *T. alpinus* has ca. 42% cover, the majority of which is rocks. A stretch of boulder fields offers more escape routes and more protection from predators than would the same length of solid rock. The habitat also includes clumps of whitebark pine (*Pinus albicaulis*), which the animals occasionally visit, but do not appear to spend much time foraging there (Heller, 1971).

Ambient temperatures are never high in the alpine habitat of *T. alpinus*, but levels of incident radiation are high and in late summer this habitat becomes quite arid (Heller and Poulson, 1972). Maximum daily temperatures in the habitat of *T. alpinus* generally do not exceed 20°C, but most of its habitat is exposed to full sun. *T. alpinus* forages among rocks where the air is quite still in spite of breezes of 100–500 cm/s above the rocks. In full sun and still air, 20°C is too high an ambient temperature for *T. alpinus*. Around midday, *T. alpinus* may forage between the rocks for short periods and then run to the top of a rock and sit in the full sun. Even at maximum absorption of radiation, moving from still air (10 cm/s) to a gentle breeze (100 cm/s) is sufficient to allow *T. alpinus* to endure an ambient temperature >20°C (Heller and Gates, 1971).

The food of *T. alpinus* chiefly consists of the small seeds of sedges and other alpine plants (Sumner and Dixon, 1953). It also eats seeds of many kinds of forbs and grasses and may gather fungi (Jameson and Peeters, 1988). New Jersey tea (*Ceanothus*), bitter cherry (*Prunus emarginata*), currant (*Ribes*), and blueberries or huckleberries (*Vaccinium*) are eaten (Van Dersal, 1938). In Yosemite, cheekpouches of nine individuals of *T. alpinus* contained: fragments of a brown fungus; two seeds of pine; 47 seeds of grass (*Stipa*); 324 seeds of sedge and one of grass; 165 seeds of sedge and 24 of galingale; 388 seeds of sedge and 1 of pussy-paws (*Spraguea umbellata*); 1,113 seeds of willow-herb, 1 of pussy-paws, 19 of grass, and 36 of galingale; 27 seeds of pussy-paws, 1 of rush, 1,080 of small unidentified seeds; 1,550 seeds of sedge and 5 of grass; 4,796 seeds of pussy-paws and 174 seeds of sedge. The seeds of pussy-paws seem to be preferred by alpine chipmunks. These seeds are small (0.7–1.2 mm in diameter), flattened, smooth, and glistening black. The mass of seeds in cheekpouches is free of chaff or any other material. Cheekpouches of one alpine chipmunk contained ca. 5,000 seeds (Grinnell and Storer, 1924).

Alpine chipmunks gather grass seeds by pulling the stalks to reach the heads and then stuffing their cheekpouches. They also have been seen in pine trees (9–12 m from the ground) removing seeds from cones (Swarth, 1919). However, seeds of pines do not constitute a major source of food since this species dwells at elevations where conifer growth is sparse (Jameson and Peeters, 1988).

Tamias alpinus gathered and ate all edible items from a refuse pile at a camp. Favorite items included prune seeds and trout skeletons (Swarth, 1919). In captivity, it favored sunflower seeds, but apples, peanut butter, and oatmeal also were eaten. Shelled sunflower seeds were stored in the bottom of the cotton lining of the nest box (Cade, 1963).

Circumstantial evidence points to *T. alpinus* as a robber of nests of the rosy finch (*Leucosticte arctua*) and white-crowned sparrow (*Zonotrichia leucophrys*). Eggs in many nests were missing or young were found dead and partially eaten. This predation may limit the breeding range of the rosy finch to the vicinity of the highest cliffs (Twining, 1940).

In the timberline area, the alpine chipmunk is the most abundant mammal (Gordon, 1943). However, it may be rare at some localities, such as near Mammoth, Mono Co. (Howell, 1924). It occupies the same habitat as the pika (*Ochotona princeps*), yellow-bellied marmot (*Marmota flaviventer*), and bighorn sheep (*Ovis canadensis*—Merriam, 1893). In addition, one *T. alpinus* was active under a den tree of a short-tailed weasel (*Mustela erminea*—Ingles, 1942). Geographically, *T. alpinus* overlaps the ranges of *T. amoenus*, *T. minimus*, *T. speciosus*, *T. umbrinus* (Howell, 1929), and *T. senex* (Grinnell and Storer, 1924). Its range is separated from that of *T. minimus* by part of the transition and Canadian life zones (Howell, 1929). Only one chipmunk, *T. speciosus*, regularly is found within the territory inhabited by *T. alpinus*. *T. alpinus*

shows a marked affinity for rocks compared with *T. speciosus*. Furthermore, *T. alpinus* shows less curiosity than *T. speciosus*. If an observer makes a squeaking noise, *T. speciosus* usually will be attracted to investigate, whereas *T. alpinus* will either pay no attention or hasten away (Grinnell and Storer, 1924).

No predators have been reported. Bold displays and extensive behavioral interactions do not make *T. alpinus* seriously vulnerable to predation because the rocky habitat provides escape routes and refuges. Also, the line-of-sight at ground level is limited in the alpine-boulder fields making it practically impossible for most predators to stalk *T. alpinus*. In addition, the lack of tree cover in the alpine habitat means that aerial predators can be seen at a considerable distance (Heller, 1971).

Ectoparasites include the lice *Neohaematopinus pacificus* and *Hoplopleura arboricola* (Ferris, 1916) and the mite *Ornithonyssus sylviarum* (Whitaker and Wilson, 1974). Plague, caused by the bacterium *Yersinia pestis*, has not been found in *T. alpinus* (Nelson, 1980).

BEHAVIOR. *Tamias alpinus* typically forages in open, non-forested areas, such as talus slopes at the bases of canyon walls and rocky borders of meadows and lakes (Johnson, 1943). It is terrestrial, but it may climb trees (Grinnell and Storer, 1924; Howell, 1929; Johnson, 1943; Sumner and Dixon, 1953) including whitebark pine and lodgepole pine (Johnson, 1943).

The call of *T. alpinus* is a thin, high-pitched, repeated sweet, sweet (Sumner and Dixon, 1953). This sometimes is modified to whit when uttered more slowly and with emphasis. When frightened, it will utter a startled whip-per'r as it runs to shelter. On occasion, a low chuckling note is given, similar to the hollow-sounding barks of larger species (Grinnell and Storer, 1924). During vocalization, *T. alpinus* uses the chip, chipping, chuck, agonistic chattering (when chased by another chipmunk), and a whistle. The vocalization rate recorded near Tioga Pass, Mono Co., was 144 chips/min (range, 56–210), 1 chip/burst, 144 bursts/min (56–210), and length of syllable was 0.025 s (0.015–0.035). Frequency ranges (in kilocycles/s) were: bottom of upsweep, 1.5 (1.0–2.5); top of upsweep, 9.5 (6.5–12.5); bottom of downsweep, 6.5 (4.0–11.0—Brand, 1976).

Tamias alpinus is extremely agile. When running on the ground, it usually holds the tail vertically. When an alpine chipmunk is perched on some rock and calling, its tail usually is jerked upward at the instant each note is given (Grinnell and Storer, 1924). This distinctive tail action consists of quick, upward jerks, that are consistently repeated (Swarth, 1919).

The habit of pursuing one another is conspicuous. A pair will go at great speed, one individual after the other, up over logs and rocks and down through crevices, the two keeping only a few centimeters apart. This behavior occurs long after the mating season (Grinnell and Storer, 1924).

Intraspecific competition exists; for example, several alpine chipmunks were seen contesting for possession of some scraps of bread. At first, only one chipmunk was present, another arrived shortly, then a third, and a fourth. Only one chipmunk ate from a particular piece of bread at one time. If another attempted to join in, a contest would ensue (Grinnell and Storer, 1924).

In mid-September the alpine chipmunk will take cover during storms, but it reappears as soon as snowfall ceases. Individuals may be observed running across the snow banks. It seems probable that weather other than temperature alone is the determining factor in limiting the season of activity (Grinnell and Storer, 1924). In view of the high elevation, the hibernation period is relatively brief (Sumner and Dixon, 1953). Alpine chipmunks remain active until near the middle of October and appear to emerge again in June (Grinnell and Storer, 1924). In September, *T. alpinus* was observed gathering willow down, presumably as a nest lining. It also was observed taking cotton batting and hiding objects in the soil; behaviors that possibly were related to hibernation. It also dug in search of items already buried. When an item was found it would be carried ca. 1 m away and buried again. The objects were buried just beneath the surface of the ground, and only one piece in any one place. At other times, it worked in a more methodical fashion. A hole would be excavated at the base of a stump or a rock to some depth. After the cache was made, the hole was refilled with the removed dirt by extending the forepaws and shoving the dirt back in with the forward thrust of the whole body (Swarth, 1919).

Tamias alpinus emerges from its hibernaculum while its habitat

primarily is snow covered. It has an opportunity to establish territories and dominance relationships before the period of maximal availability of food. This is necessary because the proportion of alpine habitat that supports vegetation is small and the growing season is short. A food supply is assured with the minimum sacrifice of foraging time for aggressive interactions (Heller, 1971).

The fundamental niche of *T. alpinus* includes the habitat of *T. speciosus*, but the presence of *T. speciosus* may reduce its success in this habitat. The aggression of *T. alpinus* is ineffective in limiting the activity of *T. speciosus*, i.e., where *T. speciosus* can take cover in dense vegetation or trees. In these areas of dense vegetation, repeated encounters with *T. speciosus* may be detrimental to *T. alpinus* in that its foraging time is decreased (Heller, 1971).

The vegetational zone occupied by *T. alpinus* is the alpine zone beginning at ca. 3,000 m at the upper edge of the effective range of *T. speciosus*. In encounters with *T. speciosus*, the smaller *T. alpinus* almost always is defeated suggesting that its lower limit is due to aggressive exclusion. *T. speciosus* is dominant in natural situations, but in laboratory situations *T. alpinus* is dominant to *T. speciosus* (Chappell, 1978). In laboratory interactions between male *T. alpinus* and *T. speciosus*, *T. alpinus* was dominant seven times with no aggression displayed during one trial. In interactions between male *T. alpinus* and female *T. speciosus*, *T. speciosus* was dominant twice out of five trials, *T. alpinus* was dominant twice, and no aggression was displayed in one trial. In interactions between female *T. alpinus* and *T. speciosus*, *T. alpinus* was dominant in seven trials, *T. speciosus* in one, and no aggression occurred in one trial. Aggression was displayed in all intraspecific tests of *T. alpinus* (Heller, 1971).

GENETICS. *Tamias alpinus* has a type B karyotype of *Tamias* (Fig. 5). The diploid karyotype contains 38 chromosomes 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).

REMARKS. *Tamias alpinus* is not closely related to any other *Tamias* (Howell, 1929; Johnson, 1943; Merriam, 1893). Externally, *T. alpinus* resembles *T. minimus* rather closely in winter pelage and *T. panamintinus* in summer pelage (Howell, 1929). Based upon phenetic analysis of morphologic characters, *T. alpinus* and *T. minimus* were grouped in a cluster separate from other taxa (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, there are indications that *Eutamias* and *Tamias* may be distinct genera, e.g., 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 *alpinus* is from the Latin *alpinus* referring to its alpine habitat (Jaeger, 1955). Another common name is mountain chipmunk (Ferris, 1916).

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