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Tamias ruficaudus.

By Troy L. Best

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Tamias ruficaudus (A. H. Howell, 1920)

Red-tailed Chipmunk

Eutamias ruficaudus A. H. Howell, 1920:91. Type locality "Upper St. Mary's Lake [Glacier Co.—Miller, 1924:204], Montana."

Tamias ruficaudus: Ellerman, 1940:434. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae. The genus *Tamias* contains ca. 25 species (Honacki et al., 1982; Patterson, 1984). *T. ruficaudus* is in the subgenus *Neotamias* (Levenson et al., 1985). Two subspecies of *T. ruficaudus* are recognized (Hall, 1981):

T. r. ruficaudus (A. H. Howell, 1920:91), see above.

T. r. simulans (A. H. Howell, 1922:179). Type locality "Coeur d'Alene [Kootenai Co.—Miller, 1924:204], Idaho."

DIAGNOSIS. In parts of its range, *T. ruficaudus* (Fig. 1) may be sympatric with *T. amoenus* and *T. minimus*. Compared with *T. amoenus ludibundus*, *T. r. simulans* is larger, the tail and ears are longer, and the upperparts, especially the head, shoulders, and rump, are more tawny in summer (Howell, 1929). *T. amoenus felix* of the coastal region of British Columbia is similar to *T. r. simulans*, but may be distinguished from that taxon by its larger size, larger skull, longer and paler tail, whiter underparts, paler sides of the body and face, and more tawny head (Howell, 1922, 1929). *T. r. ruficaudus* can be distinguished from *T. a. felix* by its whiter belly, more reddish tail, more whitish dorsal stripes, and particularly by its larger skull and longer rostrum (Fig. 2; Howell, 1929). There are distinct differences in habitat where *T. r. simulans* and *T. amoenus* are found in the same area. *T. r. simulans* occurs in forest cover, whereas *T. amoenus* is found in more open areas. Bacula of the two are different, and the bell-like call note of *T. r. simulans* may be distinctive (Johnson and Ostenson, 1959).

Tamias r. ruficaudus is similar to *T. umbrinus*. However, the upperparts and sides of *T. r. ruficaudus* are more tawny, head and face are more ochraceous (less grayish), postauricular patches (posterior to ears) are more buffy (less whitish), dark dorsal stripes are more blackish (less brownish), pale dorsal stripes are less whitish and more mixed with ochraceous tawny, ventral surface of the tail is deeper red, skull averages larger, and zygomata are more expanded posteriorly (color nomenclature follows Ridgway, 1912—Howell, 1929).

GENERAL CHARACTERS. 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). *T. ruficaudus* is a large, dark-colored chipmunk. The general tone of the back is deep orange-brown, the five dark stripes are black to fuscous, and the four pale ones are grayish to tawny and creamy white. The underparts of the body are creamy white and washed with pale pinkish-buff. The underside of the tail is brilliant rufous and bordered with black and pale pinkish-cinnamon. The top of the head is cinnamon and fuscous sprinkled with grayish white (Soper, 1964).

No information has been published on summer pelage of *T. r. ruficaudus*. Summer pelage (August) of *T. r. simulans* has cinnamon or ochraceous tawny mixed with fuscous and white on top of the head, bordered on each side with a fuscous stripe. The ocular (eye) stripe is fuscous black, shaded posteriorly with ochraceous tawny. The submalar stripe (below eye) is fuscous and washed with cinnamon or clay color. The sides of the nose and face are washed with clay color. The ears are chaetura drab and broadly bordered posteriorly with pinkish buff. The dark dorsal stripes are black or fuscous black. The median pair of pale stripes is grayish white and mixed with ochraceous tawny, and the outer pair is creamy white; the lateral stripes are fuscous or fuscous black. The shoulders and sides are ochraceous tawny (sometimes nearly tawny). The rump and thighs are mixed-clay color and fuscous. The hind feet are pinkish cinnamon and the front feet are pale pinkish-cinnamon. Dorsally, the tail is fuscous black overlaid with pinkish buff. Ventrally, the tail is ochraceous tawny, bordered with fuscous black and tipped with pinkish buff. The underparts are grayish white and washed with pale pinkish-buff (Howell, 1929).

Worn winter pelage (April) of *T. r. simulans* is similar in color to summer pelage, but the upperparts are paler and grayer (much less tawny). The sides are cinnamon or pale ochraceous tawny and the tail is edged with tilleul buff or pale smoke-gray. In winter pelage (May and June), the sides of the nose of *T. r. ruficaudus* are pinkish cinnamon or cinnamon buff; the top of the head is mixed cinnamon and fuscous, sprinkled with grayish white, and bordered with an indistinct fuscous stripe. The pale facial stripes are grayish white and shaded with buff. The submalar stripe is fuscous to bister mixed with tawny, and the ocular stripe is fuscous black. The ears are fuscous black; their posterior margins have a broad band of buffy white or pinkish buff. The inside of the ear is clothed with cinnamon hairs. The postauricular patches are buffy white, rather small, and inconspicuous. The dark dorsal stripes are black or fuscous black. The median pair of pale stripes is grayish white, mixed with cinnamon or tawny and shading anteriorly into the color of the crown. The outer pair of pale stripes is creamy white. The lateral stripes are fuscous black, overlaid with tawny; often these are indistinct. The rump and thighs are mouse gray, mixed with cinnamon. The sides are ochraceous tawny, and the feet are pinkish cinnamon. Dorsally, the tail is fuscous black mixed with orange cinnamon; ventrally, the tail is amber brown, bordered with fuscous black, and edged with pale pinkish-cinnamon. The underparts are creamy white and washed with pale pinkish-buff (color nomenclature follows Ridgway, 1912—Howell, 1929).

Coloration of *T. r. simulans* is similar to *T. r. ruficaudus*, but in *T. r. simulans* the color of the sides of the body (at least in winter pelage), ventral surface of the tail, and tail edgings are paler (Howell, 1929). *T. r. simulans* has a shorter baculum (os penis) than *T. r.*

FIG. 1. A young *Tamias ruficaudus simulans* in Pend Oreille Co., Washington. Photograph courtesy of H. E. Broadbooks.

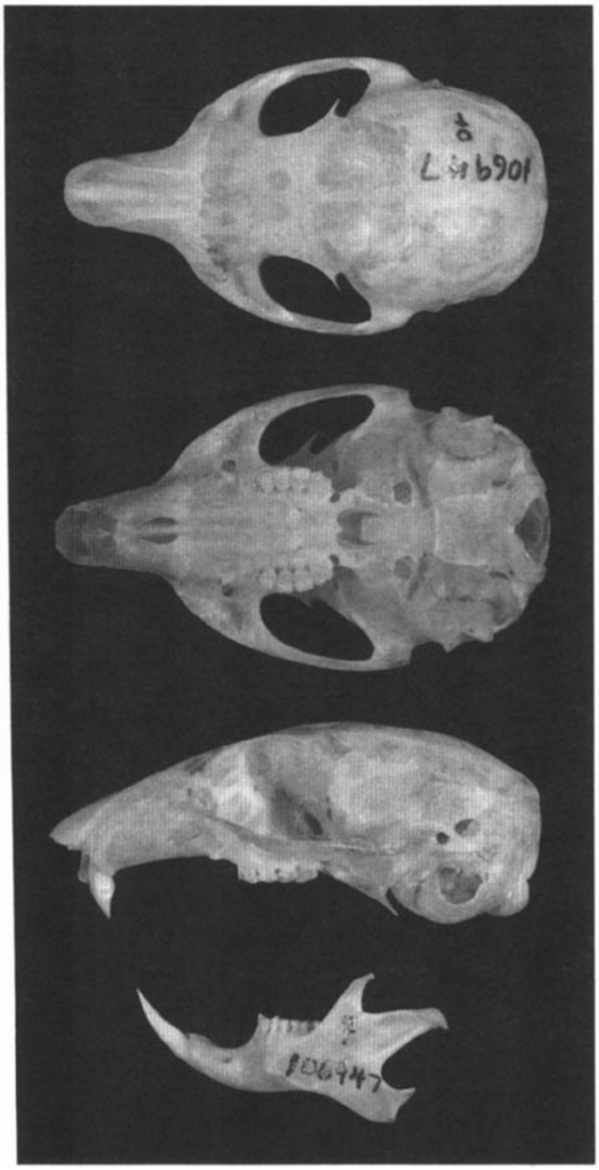

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Tamias r. ruficaudus* from Birch Creek, 2,130 m, 28.8 km NW Dillon, Beaverhead Co., Montana (female, Museum of Vertebrate Zoology, University of California, Berkeley 106947). Greatest length of cranium is 34.9 mm. Photographs by T. H. Henry.

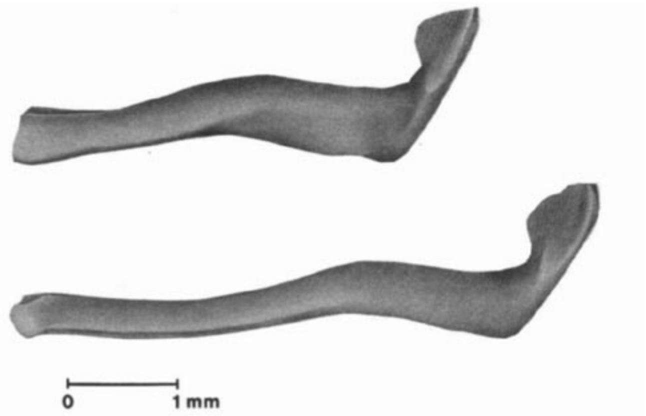

FIG. 3. Right lateral views of bacula of *T. r. simulans* (above) from near Mt. Spokane, Spokane Co., Washington, and *T. r. ruficaudus* (below) from near Lolo Pass, Missoula Co., Montana (Patterson and Heaney, 1987).

ruficaudus (Fig. 3). Individual bacula of *T. r. simulans* are 4.02–4.71 mm in length; *T. r. ruficaudus* scarcely overlaps this distribution, with bacula 4.65–5.55 mm in length. Opposite relationships were shown by length of tip and bend of shaft, characters in which *T. r. simulans* is larger than *T. r. ruficaudus*. Unlike patterns of bacular variation, the existence of discrete eastern and western morphs is not apparent in cranial morphology. *T. r. ruficaudus* averages larger than *T. r. simulans* in cranial dimensions (Patterson and Heaney, 1987). Average and range of measurements (in mm) of *T. r. ruficaudus* and *T. r. simulans*, respectively, are: total length, 231 (223–244), 238 (224–248); length of tail, 106 (101–118), 113 (103–121); length of hind foot, 35.0 (33.5–36.0), 33.6 (32.0–35.0); length of ear from notch, 14.4 (13.0–15.5), 13.9 (13.0–14.5—Howell, 1929). Average and range of averages of cranial measurements (in mm) for five populations each of *T. r. ruficaudus* and *T. r. simulans*, respectively, are: greatest length of cranium, 34.7 (34.5–34.9), 34.4 (34.0–34.8); zygomatic breadth, 19.4 (19.3–19.7), 19.1 (19.0–19.4); breadth of cranium, 14.3 (14.1–14.9), 14.6 (14.5–14.7); length of mandible, 20.2 (20.0–20.5), 19.7 (19.3–19.9); nasal length, 9.9 (9.4–10.2), 9.6 (9.3–9.8); length of maxillary toothrow, 5.6 (5.5–5.7), 5.5 (5.4–5.7); interorbital breadth, 7.7 (7.6–7.9), 7.3 (7.2–7.8); nasal width, 3.4 (3.2–3.6), 3.2 (2.9–3.7); diagonal length of orbit, 9.0 (8.9–9.2), 8.8 (8.7–8.9); length of premaxilla, 10.9 (10.7–11.2), 10.5 (10.2–10.7); depth of cranium, 15.1 (15.0–15.2), 15.1 (15.0–15.2—Patterson and Heaney, 1987).

Males average ca. 3% smaller than females in length of head and body (males, 122.2 mm; females, 126.7 mm—Levenson, 1990), and males have narrower skulls than females (Beg and Hoffmann, 1977). In Montana, breeding females average heavier during pregnancy, lactation, and until ca. 1 month after lactation, but average mass of non-breeding adult females and adult males is about the same in any particular month. Average mass of adults varies by month. Although adults average heavier in October, gains in mass over September are insignificant. For males and females (nonpregnant), respectively, average mass (in g) is: April, 53.7, 54.7; May, 53.8, 53.8; June, 54.9, 55.1; July, 58.0, 57.8; August, 58.2, 58.6; September, 57.1, 59.5; October 59.4, 61.5 (Beg, 1972).

DISTRIBUTION. The red-tailed chipmunk is restricted to southeastern British Columbia, southwestern Alberta, northeastern Washington, northern Idaho, and western Montana (Fig. 4; Hall, 1981). It occurs in transition, Canadian, and Hudsonian life zones at elevations of 720–2,400 m (Howell, 1929; Soper, 1964, 1973).

FOSSIL RECORD. *Tamias* evolved by the early Miocene (Black, 1972). Chipmunks of the *quadrivittatus* species group (*T. bulleri, T. canipes, T. cinereicollis, T. durangae, T. palmeri, T. quadrimaculatus, T. quadrivittatus, T. ruficaudus, T. speciosus,* and *T. umbrinus*—Howell, 1929; Patterson, 1980; White, 1953) exhibit allopatric (occasionally parapatric) distributions. However, vegetational displacements during the Pleistocene brought adjacent allopatric populations into contact. Thus, although now allopatric, chipmunks of the *quadrivittatus* group were periodically exposed to potential interbreeding with other members of the group and apparently have undergone bacular divergence that promoted species integrity. Members of this group that presumably were apposed by Pleistocene vegetational displacements (e.g., *T. ruficaudus–T. umbrinus*) all show significant bacular differences, whereas distant taxa that presumably never contacted one another (e.g., *T. ruficaudus–T. cinereicollis*) show bacular similarities, befitting a common ancestral genome without contrary selection pressures (Patterson, 1980; Patterson and Thaeler, 1982).

Tamias ruficaudus and *T. townsendii* may have shared a common ancestor in the early Pleistocene. *T. townsendii* became established in the Cascade Mountains and *T. ruficaudus* became established in the Rocky Mountains. During glacial substages, *T. ruficaudus* was restricted to a refugium in Idaho and subsequently expanded its range when climates warmed and became less severe. Both species adapted to similar environments and evolved similar characters. *T. townsendii* survived along coastal Oregon during Wisconsinan glaciation, whereas *T. ruficaudus* inhabited the Clearwater River drainage in Idaho (Gambs, 1965). No fossils of *T. ruficaudus* are known.

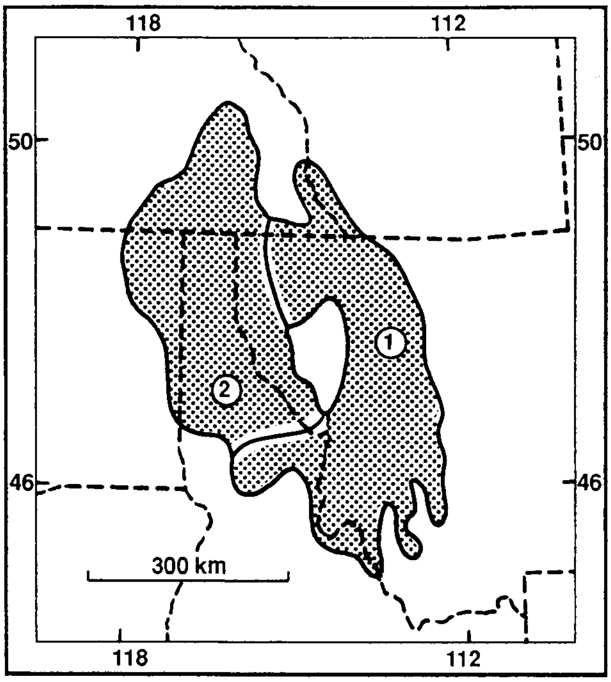

FIG. 4. Distribution of *Tamias ruficaudus* in British Columbia, Alberta, Washington, Idaho, and Montana (modified from Hall, 1981, and Patterson and Heaney, 1987): 1, *T. r. ruficaudus*; 2, *T. r. simulans*.

FORM AND FUNCTION. An adult male *T. ruficaudus* from Thompson Pass, Idaho, had nearly completed summer molt in early August. The new pelage covered the anterior one-half of the body and nearly all of the sides to the flanks (Howell, 1929).

The baculum is heavily constructed throughout, the base is nearly twice as wide as it is high and usually is bifid, the keel on the tip is prominent and notched at the base, and the tip and distal part of the shaft form an angle >90° (Burt, 1960). Average and range of averages of bacular measurements (in mm) for five populations each of *T. r. ruficaudus* and *T. r. simulans*, respectively, are: total length, 5.13 (4.97–5.12), 4.41 (4.27–4.58); length of tip, 1.59 (1.57–1.69), 1.66 (1.64–1.68); height of keel, 0.54 (0.53–0.56), 0.59 (0.55–0.60); width of tip, 0.53 (0.47–0.59), 0.52 (0.51–0.53); width of neck, 0.29 (0.28–0.33), 0.32 (0.31–0.35); width of base, 0.84 (0.82–0.93), 0.93 (0.89–1.04); bend of shaft, 0.72 (0.71–0.75), 0.88 (0.85–0.91); angle of tip, 119.90° (119.00–120.50°), 117.66° (114.75–119.58°—Patterson and Heaney, 1987). Bacula of juveniles of *T. ruficaudus* are similar in size to those of adults (Beg and Hoffmann, 1977).

The baubellum (os clitoris) of *T. ruficaudus* is similar to those of *T. minimus* and *T. umbrinus*, which are bent almost into a U-shape in lateral aspect, and join an asymmetrical spoon at a slight angle. The dorsal surface of the spoon is concave and is divided by a prominent crest that extends longitudinally and somewhat obliquely from close to the insertion of the shaft almost to the end of the bone. The margins of the spoon are flared. A large opening at the base of the shaft leads into a narrow canal that extends distad through the center of the shaft (Layne, 1954). Average and range of measurements (in mm) of the baubellum are: length of base, 1.04 (0.78–1.30); length of shaft, 1.17 (1.10–1.30); depth of shaft, 0.57 (0.36–0.65); length of tip, 1.12 (0.98–1.30); length of keel, 0.42 (0.39–0.46); angle of the tip-shaft, 122.1° (111–130°). The baubellum of *T. ruficaudus* has the longest shaft and largest keel of any species of *Tamias*. Length of base is exceeded only by *T. senex* and length of tip only by *T. siskiyou*. The base equals the shaft in depth and has no taper. The proximal end has two divergent knobs separated by a notch of ca. 0.3 mm. The shaft is uniformly deep and the shaft-base angle is ca. 90°. The tip is large and long, with thin flanges that curve on each side only on the distal 75% of the tip. The tip bends to the right ca. 20° and has no counterclockwise rotation. One of two specimens had the shaft bent to the right ca. 20°, but the other had no such shaft bend (Sutton, 1982).

FIG. 5. Karyotypes of a male (above) and female (below) *Tamias ruficaudus* from Missoula Co., Montana (Hsu and Binirschke, 1971).

ONTOGENY AND REPRODUCTION. In Montana, 89% of males had scrotal testes 7 April–30 May. The remaining 11% were juveniles. In sexually active males, testes were 12–15 mm in length and seminal vesicles 7–10 mm in length. The bulbourethral glands of these males were firm and the epididymal tubules were distinct. Sperm were present in testes and cauda epididymides (Beg, 1971*a*).

Date of conception varied among localities in Montana. At lower elevations insemination occurred 28 April–13 May and at higher elevations 6–24 May (Beg, 1971*a*). In southern Canada, a female had five small embryos on 19 August (Crowe, 1943). At low elevations in Montana, 65–67% of females were pregnant each year and at higher elevations 50–73% became pregnant. Pregnancy rates varied among age groups. Females that were 10–16 months of age were pregnant less often than older females; 11–15% of these younger females were pregnant. However, 36–100% of females 22–64 months of age were pregnant. Overall, rate of pregnancy was 68–83% for the population when females 10–16 months of age were not considered (Beg, 1971*a*).

In Montana, there is a significant difference in ovulation rates, estimated by counts of corpora lutea, at lower (5.52) compared with higher elevations (4.87). Younger females tended to have a lower rate of ovulation than older females. Those females >2 years of age had larger litters. However, variation among years of the study was not significant. Prenatal mortality was 6.5 and 7.5% during 2 years at lower elevations, and 5.9, 8.5, and 14.6% during 3 years at higher elevations (Beg, 1971*a*).

There are four to six young per litter (Rand, 1948). In Montana, litter size in lower elevations was 5.16, and 4.54 for higher elevations. These differences were not significant; pooled data indicated that average litter size was 4.85. At lower elevations, an average of 3.1–3.2 young were produced by females that had a litter each year, compared with 2.4–3.5 at higher elevations (Beg, 1971*a*).

The gestation period is unknown, but probably is ca. 31 days. Embryos of 25 mm in head-rump length are considered full term. At lower elevations in Montana, parturition occurred 29 May–15 June, lactation 10 June–25 July, and the first young appeared 11

July, compared with 7–25 June, 14 June–29 July, and 21 July, respectively, at higher elevations. Based upon patterns of tooth eruption, young were 39–45 days of age at first emergence (Beg, 1971*a*).

Lower incisors erupt at 23–25 days of age, and upper incisors at 30–32 days of age. Upper cheekteeth reach occlusal level as follows: deciduous P4, 28 days; deciduous P3 and M1, 34 days; M2, 39 days; M3, 45–52 days. At 39–45 days of age, M1 and M2 are fully grown, M3 is at or below bone level and covered by the gum, and most young appear aboveground at this stage (occasionally M2 may not be erupted at this age). At 45–67 days of age, molars are fully grown and deciduous premolars are present. At ca. 79 days of age and older, permanent upper premolars are present. At 10–16 months, P3 does not show wear through its enamel. At 22–28 months, P3 may show slight wear. At 34–40 months, P3 is worn. At 46–52 months, the top of P3 is flattened by increased wear. At 58–64 months or more, all cheekteeth show extensive wear; M2 and M3 show the greatest wear (Beg and Hoffmann, 1977).

Some individuals of *T. ruficaudus* may live 6–7 years. One lived 8 years in the wild (Beg, 1971*b*).

ECOLOGY. *Tamias ruficaudus* inhabits dense coniferous forests (Howell, 1929), and is most abundant in forest openings or edges, where shrubby undergrowth is abundant (Hoffmann and Pattie, 1968). It occurs in forests of western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*), Douglas fir (*Pseudotsuga menziesii*), and Englemann spruce (*Picea englemanni*). Along the western edge of its range, *T. ruficaudus* is limited by open Ponderosa pine (*Pinus ponderosa*) forests (Gambs, 1965). In British Columbia, it occupies clumps of stunted pine and spruce trees (*Picea*), and mountain rhododendron (*Rhododendron*) and blueberry bushes (*Vaccinium*) that constitute the margins of timberline meadows (Cowan and Guiguet, 1978). In the Pend Oreille Mountains, Washington, *T. ruficaudus* occurs in mixed second-growth forests of lodgepole pine (*Pinus contorta*), western larch (*Larix occidentalis*), Englemann spruce, Douglas fir, grand fir (*Abies grandis*), and aspen (*Populus tremuloides*—Broadbooks, 1974).

The red-tailed chipmunk may be the most plentiful and widely distributed chipmunk in northern Idaho (Rust, 1946). It is abundant higher in the mountains, and is a common resident of the Englemann spruce and alpine fir association (Orr, 1943). In northern Idaho, it can be found in sunny openings in the Ponderosa pine zone where boulders and low brush are present, particularly along old roadways and at the lower edge of foothills. In forests of the Canadian zone, it usually can be found around fallen logs and brush piles (Rust, 1946).

In Montana, *T. ruficaudus* occurs in subalpine coniferous forest (Hoffmann et al., 1969). It occupies habitats ranging from xeric Ponderosa pine forests to hydric riparian communities. Ponderosa pine and Ponderosa pine-Douglas fir savannahs occur on drier sites. In the Douglas fir zone, western larch and Ponderosa pine are primary constituents. On moist slopes near the upper edge of this zone, grand fir and Englemann spruce also are present. In the subalpine forest zone, subalpine fir (*Abies lasiocarpa*) and Englemann spruce are dominant. Lodgepole pine occupies upper elevations, and aspen and willow (*Salix*) are common in its habitat (Beg, 1971*b*). Common understory plants of Ponderosa pine forest are arnica (*Arnica cordifolia*), balsam-root (*Balsamorhiza sagittata*), sedge (*Carex geyeri*), field chickweed (*Cerastium arvense*), strawberry (*Fragaria bracteata*), and snowberry (*Symphoricarpos occidentalis*). Common understory plants of Douglas fir forest are spiraea (*Spiraea betulifolia*), arnica, field chickweed, glacier lily (*Erythronium grandiflorum*), nine-bark (*Physocarpus malvaceus*), and wild rose (*Rosa*). Common understory plants in subalpine forest are grouse whortleberry (*Vaccinium scoparium*), big whortleberry (*Vaccinium membranaceum*), arnica, prince's pine (*Chimaphila umbellata*), wintergreen (*Pyrola secunda*), bear grass (*Xerophyllum tenax*), and rattlesnake plantain (*Goodyera oblongifolia*). *T. ruficaudus* occurs in areas with whitebark pine (*Pinus albicaulis*), western birch (*Betula papyrifera*), western red cedar, western white pine (*Pinus monticola*), willows, mountain maple (*Acer glabrum*), Rocky Mountain juniper (*Juniperus scopulorum*), dwarf juniper (*Juniperus communis*), and chokecherry (*Prunus virginiana*—Beg, 1969).

In Montana, the habitat of *T. ruficaudus* is sharply seasonal. There is snow on the ground for 6 months. Snowmelt begins in late March and April, depending on exposure and elevation. Average annual precipitation is 34.3–40.4 cm, but greater amounts occur at higher elevations. The wet season is in May and June, with drier conditions in July and August. Most precipitation falls during winter as snow (ca. 120 cm—Beg, 1971*a*).

In Montana, males were predominant in samples obtained in April and May (sex ratio, 4 males : 1 female); later in the season, the sexes were present in nearly equal numbers. The population was low following hibernation (May) and reached a maximum size in August. After the peak in August, the population declined rapidly. By October, the population was comprised almost entirely of young-of-the-year (Beg, 1971*b*).

In Montana, average distances between captures for adult males, adult females, and juveniles were 76.8, 58.5, and 51.6 m, respectively. Only 18.8% of adult males, 11.3% of adult females, and 7.0% of juveniles had an average distance between captures >120 m. Most animals moved 30–120 m; only 15.5–21.1% had an average distance between captures <30 m. The longest movements between captures were 265.8, 240.0, and 195.0 m, made by an adult male, an adult female, and a juvenile, respectively. Average distance between captures of males (79.8 m) for May to August was greater than that for breeding females (56.1 m), but not different from that of nonbreeding females (59.7 m). There was no significant difference in range of movement of breeding and nonbreeding females. Average distance between captures of adult males and females and juveniles were not different after July. Average maximum distance moved between captures for adult males, adult females, and juveniles were 115.2, 79.8, and 69.6 m, respectively. Only 15.6% of adult males, 9.0% of adult females, and 4.2% of juveniles travelled a maximum distance >180 m. The majority travelled 30–180 m; only 3.4–11.5% moved a maximum distance <30 m. Longest maximum distances moved were 450, 255, and 285 m for adult males, adult females, and juveniles, respectively. Observations indicated that *T. ruficaudus* usually made daily movements of 90–150 m, although occasionally individuals moved 180–270 m (Beg, 1969).

The red-tailed chipmunk eats seeds of fir trees, honeysuckles (*Lonicera*), locusts (*Robinia*), and cranberries (*Vaccinium oxycoccus*—Van Dersal, 1938). In Idaho, two had their cheek pouches filled with seeds of Douglas knotweed (*Polygonum douglasii*—Orr, 1943). In Montana, it eats fruits and seeds of nine-bark, wild rose, Ponderosa pine, snow brush (*Ceanothus sanguineus*), Douglas fir, serviceberry (*Amelanchier alnifolia*), big whortleberry, buckbrush (*Symphoricarpos rivularis*), knotweed, grass (Gramineae), huckleberry (*Vaccinium ovalifolium*), mountain maple, and bull thistle (*Cirsium vulgare*), and leaves and flowers of dandelion (*Taraxacum officinale*), arnica, currant (*Ribes inerme*), balsam-root, glacier lily, oyster plant (*Tragopogon dubius*), willow herb (*Epilobium*—Beg, 1969), and tarweed (*Madia glomerata*—C. B. Henderson, pers. comm.). In captivity, *T. ruficaudus* ate sunflower seeds and corn (Beg and Hoffmann, 1977). In addition, this species has been caught in steel traps baited with meat (Orr, 1943) and in snap traps baited with peanut butter mixed with rolled oats (Beg, 1971*a*).

In northeastern Washington, three tree nests of *T. ruficaudus* were in Englemann spruce trees (late July) that stood among lodgepole pines, other conifers, and aspens. All rested on limbs close to or touching the trunk. Their heights above ground were 5.8, 7.6, and 18.3 m in trees that were 12, 12, and 24 m in height, respectively. All three nests were beneath dense growths of small branches and dry dead twigs. One of these shelters was 1 m in height and 45 cm in width. Nests were made of dry grasses. One was a compact structure 28.0 by 17.8 cm with a room on top that was 8.9 by 6.4 by 6.4 cm. Thinly roofed and partly broken down, the cavity was half-open above. Two ground dens in the same area were tunnels 90 cm in length and 28 cm in depth, with nests of dry grass and lichen at the ends (the same as burrows of *T. amoenus*). The tunnel near one of the tree nests was used by a mother and young. Apparently, the litter was born underground and then transferred to the tree nest when the young were capable of climbing and independent feeding, but not completely weaned. They may use the tree den until they disperse and each establishes an individual home range and digs a burrow in which to build a nest and store seeds for winter (Broadbooks, 1974).

In northern Idaho, a red-tailed chipmunk had a grass nest fastened in a crotch of a bush along the shore of a small lake on 15 June. The nest was oval and made of dry grass blades, measured 17.8 by 25.4 cm in outside dimensions, and had a small entrance at one end. It contained four young about one-third grown, well furred, but with their eyes unopened. The usual nesting site for this species in the transition zone is in crevices in large boulders or under old log piles (Rust, 1946).

Along with *T. umbrinus*, *T. ruficaudus* forms part of a series of closely related allopatric species that geographically replace one another throughout the central and southern Rocky Mountains. *T. ruficaudus* is the northernmost link in this chain of species (Hoffmann and Pattie, 1968). Although primarily found at lower elevations than *T. minimus*, the range of *T. ruficaudus* overlaps the altitudinal range of *T. minimus* in some areas of the upper slopes and near timberline (Hoffmann and Pattie, 1968; Howell, 1929; Soper, 1964, 1973). *T. ruficaudus* chiefly inhabits elevations above those of *T. amoenus* (Rand, 1948); *T. amoenus* inhabits aspen-parkland to the exclusion of *T. ruficaudus* (Cowan, 1946). Although *T. amoenus* and *T. ruficaudus* do not occupy the same spectrum of habitats, overlap of their habitats seems broad. For example, both species occupy Douglas fir forest, subalpine forest, and alpine tundra. Their association with altitude and plant communities seems to be determined by presence and absence of congeners. In the presence of *T. ruficaudus*, *T. amoenus* is restricted to open dry forests. In the absence of *T. ruficaudus* and *T. minimus* in central Montana, *T. amoenus* ranges from valley bottoms to alpine tundra, but in Glacier National Park in northwestern Montana in the presence of the other two species it inhabits only Ponderosa pine and Douglas fir forest; *T. minimus* and *T. ruficaudus* occupy alpine tundra and subalpine forest, respectively. In the Waterton Park area of Alberta, in the absence of *T. amoenus*, *T. ruficaudus* inhabits the Canadian zone and *T. minimus* occurs in the Hudsonian zone and timberline. Although *T. amoenus* and *T. ruficaudus* do not seem to differ appreciably in foraging and feeding habits, they have different breeding times. When ranges of the two come in contact, they maintain a relationship of contiguous allopatry by occupying specific habitats and they do not form mixed-species populations. Almost the entire fundamental niche of *T. ruficaudus* seems to be a subset of the fundamental niche of *T. amoenus* (Beg, 1969; Soper, 1964).

In Montana, *T. ruficaudus* occupies the same habitat as *Sorex vagrans*, *S. cinereus*, *Microsorex hoyi*, *Lepus americanus*, *T. amoenus*, *Spermophilus columbianus*, *Tamiasciurus hudsonicus*, *Glaucomys sabrinus*, *Clethrionomys gapperi*, *Microtus longicaudus*, *M. pennsylvanicus*, *Peromyscus maniculatus*, *Neotoma cinerea*, *Erithizon dorsatum*, *Mustela erminea*, *M. frenata*, *Mephitis mephitis*, *Canis latrans*, *Ursus americanus*, *Odocoileus hemionus*, and *O. virginianus* (Beg, 1969; Halvorson, 1981; Johnson, 1963). The only ectoparasite known from *T. ruficaudus* is the flea *Ceratophyllus ciliatus* (Traub et al., 1983). No internal parasites are known.

BEHAVIOR. *Tamias ruficaudus* is diurnal and easily tamed for laboratory study (Lockner, 1968). In late September, when the weather becomes quite cold, there is a noticeable decrease in the number of red-tailed chipmunks (Orr, 1943). During cold days from mid-November to late March, *T. ruficaudus* stays in its burrow and rarely is seen outside. It is active as early as 29 March and as late as 4 December, but the primary season of activity is April to October. Apparently, males become active earlier in spring than females (Beg, 1971*a*).

When sandbathing, the ventral surface of the body and head touch the substrate, and the line of the back is concave rather than convex. The body is rolled from side to side in the sand and the animal may even move forward while half-buried in the sand (Lockner, 1968).

On sunny mornings on densely forested mountain slopes, *T. ruficaudus* often comes out into clearings and onto fallen trees (Rand, 1948). In spring, it forages mostly on the forest floor, moving through ground vegetation nibbling seedlings, leaves, and flowers, and often stopping to search among leaves and litter. The red-tailed chipmunk may forage a distance of 45–60 m within 3–4 min. In summer, foraging in shrubs increases. Trees are foraged more frequently in autumn than in any other season. In one study, Ponderosa pine and Douglas fir were the only trees in which it was seen (Beg, 1969).

The red-tailed chipmunk is more arboreal in habits than *T. amoenus*. Much foraging by *T. ruficaudus* is in trees, and it has nest holes in living or standing-dead trees. Although usually forest-dwelling, many marginal habitats of brushland with standing-dead trees are inhabited. In one place, a broken, dead fir 5.4 m in height housed six individuals. Each chipmunk seemed to possess a separate hole in the main trunk in which it would take refuge. On 14 September, two were observed picking up feathers in a camp. These were placed in their cheek pouches and later carried to their burrows where they served as nest material (Orr, 1943).

In captivity, *T. ruficaudus* persistently hoarded food. When housed in small cages (45-cm square), red-tailed chipmunks piled food in corners of the cage and in their small nest box. When deprived of food for 23 h, the times required to complete hoarding trips were reduced. However, when sated they continued to hoard, but at reduced rates. They cached more food outside of the nest (scatter hoarding) when sated than when deprived of food (Lockner, 1972).

In captivity, hoarding consisted of four discrete acts; approaching, picking up, running with, and caching the food. The first approach to the food source was in a head-down foraging posture (the head was extended, the nose and belly were close to the ground, and the back was arched so that the shoulders were level with the top of head). On subsequent trips, red-tailed chipmunks ran directly to the food source (not in the head-down posture). When running, neither the body nor head was as close to the substrate as when foraging. Food always was picked up in the mouth. Occasionally, a chipmunk attempted to pick up a second food item with the forepaws while holding the first item in its mouth. This second food item always was dropped. Food was pushed into the mouth and held between the teeth when the chipmunks ran. To bury a food item, they stopped, lowered the head (with the food still held in the teeth), and scooped out a hole with the forepaws. Shavings in the nest box were moved back under the body and behind the widely placed hind legs by alternate movement of the forelegs. The back was arched and the abdomen elevated from the substrate. After the hole was dug, the animal pushed its head into it. When the substrate was soft, chipmunks often pushed the entire front one-half of the body under the surface. They then tapped the food object (which still was held between the teeth) against the substrate five or six times with the head push (the snout was lowered and the neck was alternately extended and flexed). The food was then released and the chipmunk filled the hole without moving its hind feet. Initially, a chipmunk placed its forelegs on the far side of the hole, then pulled both of its forepaws straight back toward the body or moved them toward the midline of the body as it moved material into the hole. The animal then turned the ventral surface of the paws forward and pushed material forward into the hole. After the food was covered, the area was raked over with more shavings. When raking, it stood on both hind feet and one forefoot. The free forepaw was used to drag shavings over the buried food. The chipmunk then placed the free forepaw down and patted the area simultaneously with both forepaws. After burying or caching, it returned to the food pile and picked up more food. Although this hoarding sequence was typical, time required to complete each trip varied considerably (Lockner, 1972).

Manipulation of food by *T. ruficaudus* is related to size and shape of the food item. When gnawing, the mouth must be opened so that the chipmunk can position its lower incisors against the food. Small food items (4-mm cubes, 5.6-mm spheres) can be held against the upper incisors, while the lower incisors gnaw off fragments. Larger food items cannot be placed in the mouth in their entirety. However, if there is a corner or an edge on the food, the chipmunk can fit it between the upper and lower incisors. When offered large cubes, it begins gnawing on one of the edges. After one edge has been eaten, the food is rotated to another edge. When an animal is offered a large sphere, it cannot begin gnawing on an edge because none is available; the chipmunk rapidly rotates the sphere in an apparent attempt to find an edge. It then begins eating, thus creating a flat surface on the sphere. Food is then repositioned so that this edge between the flat surface and the rest of the sphere can be gnawed. Thus, food manipulation in *T. ruficaudus* probably is to position food so the lower incisors can gnaw off pieces, while it holds the item against the upper incisors (Lockner, 1970).

The red-tailed chipmunk feeds in discrete bouts that are confined to the daylight hours. Within the activity period, the feeding bouts are randomly distributed in time. In the laboratory, there is a temporal relationship between feeding and drinking; $>75\%$ of feeding bouts occur within 5 min of a drinking bout. *T. ruficaudus* is able to discriminate between food and non-food items on the basis of olfaction alone, to use its olfactory ability to find buried food items, and to orient to a potential food object on the basis of visual clues alone (Lockner, 1968).

At a tree nest in northeastern Washington, red-tailed chipmunks left in the morning and came back at night. They visited the tree nest only once in late morning for nursing. The mother left the tree nest well before sunrise (before 0540 h), but the young waited until the sun warmed the nest and left at 0710–0800 h. The young descended quietly and without delay. During the morning, the mother foraged alone, while the young fed or explored within 30 m of the nest tree. At 1015 h they began climbing the den tree. The young appeared hungry as they nuzzled the mother's belly. The mother returned to the ground, foraged awhile, then entered the tree nest at 1030–1110 h. Apparently, nursing took place at this time. Early in the afternoon, the mother fed periodically on the ground and in trees. Arboreal foraging primarily was for tiny resinous tips at ends of live twigs of Englemann spruce. This occupied 47% of her time for 1 h after nursing and 24% of her time for 2 h after nursing. For 260 min of observations, time aloft totaled 16 min. For 0.5 h before going into the nest, mother and young gathered near the tree nest to eat and interact. The mother nuzzled her young and ran about with them. Several young smelled each other near the anus, ran in circles together, and occasionally tried mounting each other. The mother steadily called during this time (Broadbooks, 1974). Vocalizations of *T. ruficaudus* include scolding notes that may run together and produce a trill (Rand, 1948).

GENETICS. *Tamias ruficaudus* has a type B karyotype (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).

Based upon analyses of 20 allozymes, two populations of *T. r. ruficaudus* had a mean heterozygosity of 0.0950 and 0.0889, each had four polymorphic loci (glucose-6-phosphate dehydrogenase, 6-phosphogluconate dehydrogenase, red cell phosphoglucomutase-1 and -2), and there were no fixed allelic differences between populations (Levenson et al., 1985). Although reported as a comparison of *T. r. ruficaudus* and *T. r. simulans* (Levenson et al., 1985), both of these samples came from within the range of *T. r. ruficaudus* (B. D. Patterson, in litt.; Patterson and Heaney, 1987).

REMARKS. In a phenetic analysis of morphologic characters, *T. ruficaudus* grouped in a cluster with *T. amoenus* and *T. speciosus*. A cladistic analysis of electrophoretic data placed *T. ruficaudus* with *T. minimus*, *T. quadrivittatus*, and *T. speciosus* (Levenson et al., 1985; Nadler et al., 1985). *T. ruficaudus* has been placed in the *quadrivittatus* species group with *T. bulleri*, *T. canipes*, *T. cinereicollis*, *T. durangae*, *T. palmeri*, *T. quadrimaculatus*, *T. quadrivittatus*, *T. speciosus*, and *T. umbrinus* (Howell, 1929; Patterson, 1980; White, 1953), in the *townsendii* species group with *T. townsendii* (Gambs, 1965), and in the *minimus* species group with *T. alpinus*, *T. minimus*, and *T. speciosus* (Levenson et al., 1985).

Based upon differences in bacular (Fig. 3) and cranial morphology, the two subspecies of *T. ruficaudus* may represent different species (Patterson and Heaney, 1987; White, 1953). However, there is evidence of interbreeding between these taxa. Across the range, color of the undertail varies from pale red or buffy to brick-red. Races from the ends of this cline are most contrasting, but toward the center the races become increasingly difficult to distinguish. Except for some local isolates, there seems to be considerable gene flow (assessed by pelage) throughout the species (Gambs, 1965).

Currently, chipmunks previously assigned to the genus *Eutamias* are included in the genus *Tamias* (Honacki et al., 1982; Levenson et al., 1985; Nadler et al., 1969, 1977). 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), micro-complement-fixation reactions, and allozymes (Ellis and Maxson, 1979; Hafner, 1984).

Tamias is from the Greek *tamias* meaning a storer or distributor. The specific epithet *ruficaudus* is from the Latin *rufus* meaning reddish and *cauda* meaning tail (Jaeger, 1955). It also has been referred to as rufous-tailed and Coeur d'Alene chipmunk (Howell, 1929).

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Editors of this account were J. ALDEN LACKEY and KARL F. KOOPMAN. Managing editor was JOSEPH F. MERRITT.

T. L. BEST, DEPARTMENT OF ZOOLOGY AND WILDLIFE SCIENCE AND ALABAMA AGRICULTURAL EXPERIMENT STATION, 331 FUNCHESS HALL, AUBURN UNIVERSITY, ALABAMA 36849-5414.