

**Tamias minimus.** By B. J. Verts and Leslie N. Carraway

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***Tamias minimus* Bachman, 1839**

Least Chipmunk

*Tamias minimus* Bachman, 1839:71. Type locality “along the banks of the Rio Colorado.” Restricted to “not far from Green River City, [Sweetwater Co., Wyoming]” by Allen (1890:112) based on comments by Townsend (1839:72).

**CONTEXT AND CONTENT.** Order Rodentia, suborder Sciurognathi, family Sciuridae, subfamily Sciurinae, tribe Tamiini, genus *Tamias* (Black 1963; Hoffmann et al. 1993). *T. minimus* is in the subgenus *Neotamias* (Howell 1929). Twenty-one subspecies of *T. minimus* are recognized (Hall 1981; Jackson 1957; Sullivan and Petersen 1988; White 1953a).

- T. m. arizonensis* Howell, 1922:178. Type locality “Prieto Plateau at the south end of Blue Range, Greenlee County, Arizona.”
- T. m. atristriatus* (Bailey, 1913:129). Type locality “Sacramento Mountains, New Mexico, on Penasco Creek 12 miles east of Cloudercroft [Otero Co.], alt. 7400 feet.”
- T. m. borealis* Allen, 1877:793. Type locality designated as “Fort Laird, Mackenzie [Northwest Territories]” by Hall and Kelson (1959:299); no type designated with original description.
- T. m. cacodemus* (Cary, 1906:89). Type locality “Sheep Mountain, Big Bad Lands [Big Corral Draw, Washington Co.], South Dakota.”
- T. m. caniceps* (Osgood, 1900:28). Type locality “Lake Leberge, Northwest Territory, Canada.”
- T. m. caryi* (Merriam, 1908:143). Type locality “Medano Ranch, San Luis Valley [Alamosa Co.], Colorado.”
- T. m. chuskaensis* Sullivan and Petersen, 1988:21. Type locality “Arizona: Apache Co.: Chuska (Lukachukai) Mountains, View Point, Lukachukai Pass, 8.5 mi NE Lukachukai, T36N R30E, 2,900 m.”
- T. m. confinis* (Howell, 1925:52). Type locality “head of Trapper’s [=Trapper] Creek (8,500 feet altitude), west slope of Bighorn Mountains [Big Horn Co.], Wyoming.”
- T. m. consobrinus* Allen, 1890:112. Type locality “Wahsatch foothills near Salt Lake City [Salt Lake Co.], Utah” (*lectus* J. A. Allen and *clarus* Bailey are synonyms).
- T. m. griseceus* (Howell, 1925:52). Type locality “Farmer, Douglas County, Washington.”
- T. m. hudsonius* (Anderson and Rand, 1944:133). Type locality “Bird, Hudson Bay Railway, Mile 349, northern Manitoba, Canada.”
- T. m. jacksoni* (Howell, 1925:53). Type locality “Crescent Lake, Oneida County, Wisconsin.”
- T. m. minimus* Bachman, 1839:71, see above.
- T. m. neglectus* Allen, 1890:106. Type locality “eastern end of Lake Superior [Ontario, Canada].” Designated as “Montreal River, Ontario” by Hall and Kelson (1959:301).
- T. m. operarius* (Merriam, 1905:164). Type locality “Gold Hill (altitude 7,400 feet) [Boulder Co.], Colorado.”
- T. m. oreocetus* (Merriam, 1897:207). Type locality “timberline near Summit, Teton Mts. (main range Rocky Mts.) [Flathead Co.], Montana.”
- T. m. pallidus* Allen, 1874:289. Type locality designated as “Camp Thorne near Glendive [Dawson Co.], Montana” by Hall and Kelson (1959:302); no description or type designated with listing of name by Allen (1874).
- T. m. pictus* Allen, 1890:115. Type locality “Kelton [Box Elder Co.], Utah” (*melanurus* Merriam is a synonym).
- T. m. scrutator* (Hall and Hatfield, 1934:321). Type locality “10,500 ft. altitude, near Blanco Mtn., White Mts., Mono County, California.”
- T. m. selkirki* (Cowan, 1946:113). Type locality “Paradise Mine

near Toby Creek, 19 miles west of Invermere, B[ritish]. C[olumbia].”

*T. m. silvaticus* (White, 1952:261). Type locality “3 mi. NW Sundance, 5900 ft., Crook County, Wyoming.”

Hall (1981), following Anderson and Rand (1944), considered *jacksoni* a junior synonym of *neglectus* although he indicated that White (1953a) recognized *jacksoni* as a valid subspecies. Seemingly, he did not consider that Banfield (1974) recognized *jacksoni* or the rebuttal in which Jackson (1957:518) claimed that Anderson and Rand (1944) had “never seen specimens from Wisconsin, Michigan, or Minnesota!” Jackson (1957) made a strong argument for retaining *jacksoni* as a valid subspecies; we have followed his lead.

**DIAGNOSIS.** *Tamias minimus* (Fig. 1) is among the smaller chipmunks (Hall 1946, 1981). Although no character or group of characters serve to distinguish *T. minimus* from sympatric or parapatric chipmunks of similar size throughout its geographic range, at any one locality it usually can be distinguished readily from its congeners (Hall 1981). For example, skulls of the 2 small chipmunks that occur in Oregon are separable by use of a discriminant function equation: condylo-nasal length (40.3238) + palatal length (1.45163) + breadth of braincase (0.32907). Specimens with values  $\leq 39.8728$  are *T. minimus*; those with values  $\geq 40.3238$  are *T. amoenus*. Only 9 (1.7%) of 543 specimens could not be identified by use of the equation (Carraway and Verts 1995). In some areas, little or no ochre on the flanks, yellowish underside of the tail, rounded braincase, rounded zygomatic arches, short rostrum, and only slightly recurved upper incisors are characters that may serve to distinguish *T. minimus* from sympatric congeners (Hall 1981).

**GENERAL CHARACTERS.** *Tamias minimus* is a typical sciurid rodent with a spinelike postorbital process on each frontal bone (Fig. 2); a broad zygomatic plate that serves as the origin of the lateral masseter muscle; the 4th digit is the longest on both the manus and pes; a bushy, somewhat dorsoventrally flattened tail; and a small infraorbital foramen. Manus has 4 digits and pes has 5. Limb bones are unspecialized, and limb joints have unrestricted movement (McLaughlin 1984). Like other members of the subgenus *Neotamias*, *T. minimus* has internal cheek pouches, 2 upper premolars (anteriormost is peglike), a canal-like infraorbital foramen, and numerous microscopic longitudinal grooves in enamel faces of upper incisors (Howell 1929; Jones and Manning 1992).

Pelage on sides, rump, and thighs ranges from Pinkish Buff or Light Pinkish Cinnamon through Clay or Sayal Brown to Ochraceous Tawny (color names follow Ridgway 1912). Venter is whitish. Dorsum is marked with 5 dark and 4 light longitudinal stripes that extend from nape to base of tail. The dark stripes range from Pink-



FIG. 1. Photograph of an adult *Tamias minimus*. Used with permission of the photographer, Ronn Altig.

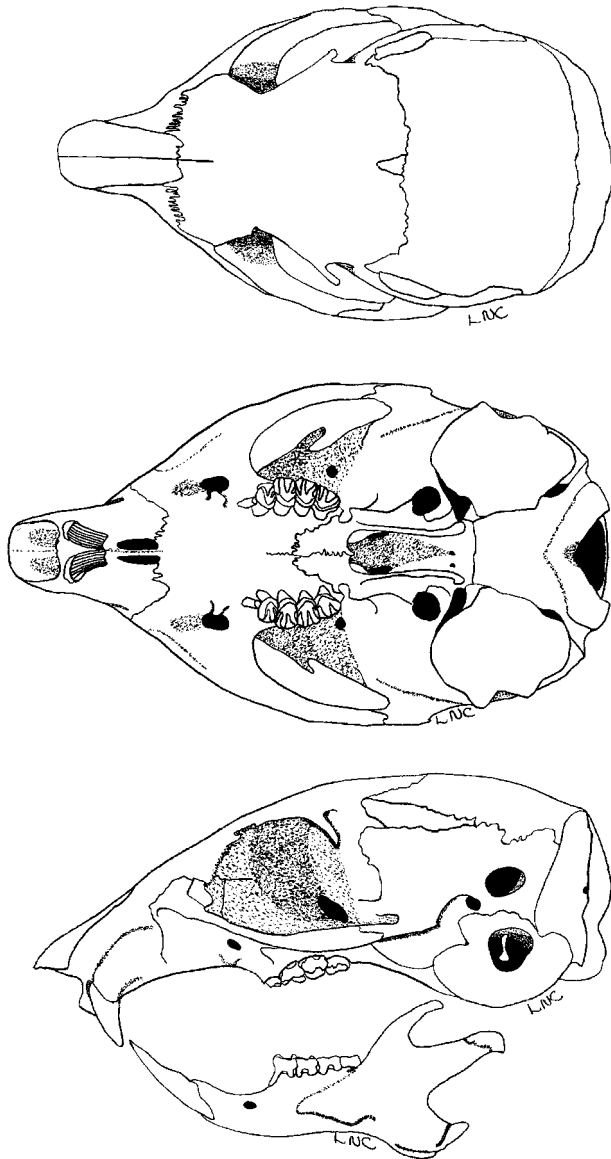


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral view of the mandible of an adult male *Tamias minimus* (Oregon State University Department of Fisheries and Wildlife mammal collection, OSUFW 3120; from 13 miles W Fields, Harney Co., Oregon). Greatest length of skull is 29.52 mm.

ish Cinnamon through Snuff Brown to Black. Innermost light stripes are whitish or grayish mixed with shades of brown; outermost light stripes are white or cream and usually not mixed with brown. Pate is grayish or brownish with colors often intermixed (Howell 1929). Face is marked with 2 light and 2 dark stripes extending from nosepad to ear; uppermost dark stripe passes through eye. Colors of stripes on face are similar to those on dorsum. *T. minimus* undergoes 2 annual molts; summer pelage is brighter than grayish winter pelage (Nowak 1991). In some regions, variation in pelage color is clinal; for example, east of the Rio Grande Valley, New Mexico, *T. minimus* exhibits a north-south latitude-pelage color relationship, with ventral surface of tail grading from reddish yellow to strong brown, pate grading from light brown to dark gray, and rump grading from medium gray to very dark gray (Sullivan 1985).

Ranges (in mm) in total length, length of tail, and length of hind foot, respectively, for adults (Howell 1929) were 212-222, 97-110, 31-32 in northern Alberta ( $n = 11$ ); 196-220, 87-97, 30-33.5 in Arizona ( $n = 11$ ); 203-225, 84-99, 33-34 in British Columbia ( $n = 5$ ); 184-212, 80-89, 30-32 in north-central Colorado ( $n = 20$ ); 186-200, 83-96, 29-31 in south-central Colorado ( $n = 12$ ); 197-223, 91-104, 32-34 in eastern Montana ( $n = 12$ ); 193-

201, 82-90, 31 in northwestern Montana ( $n = 4$ ); 203-220, 94-114, 31.5-32 in New Mexico ( $n = 4$ ); 210-225, 97-105, 34-35 in South Dakota ( $n = 7$ ); 175-200, 82-90, 27.5-30 in Utah ( $n = 10$ ); 167-188, 74-87, 26-28 in Washington ( $n = 7$ ); and 178-190, 80-90, 28-30 in Wyoming ( $n = 10$ ). The same dimensions were 202-220, 94-107, 30-33 in Minnesota ( $n$  not provided—Hazard 1982); 204-219, 89-100, 31-33 in Nebraska ( $n = 9$ —Jones 1964); 173-203, 71-90, 28-32 in Nevada ( $n = 20$ —Hall 1946); 157-250, 51-98, 24-34 in Oregon ( $n = 60$ —Verts and Carraway 1998); 196-219, 82-100, 29-33 in Wisconsin ( $n$  not provided—Jackson 1961); and 178-232, 69-112, 30-36 in Yukon Territory ( $n = 28$ —Youngman 1975). In California, averages and ranges (in parentheses) for the same dimensions were 191 (180-196), 81 (77-88), 28.6 (27.7-29.8) in females ( $n = 11$ ) and 181 (176-183), 77 (72-80), 28.1 (27.3-29.2) in males ( $n = 6$ —Johnson 1943). In Manitoba, averages and maxima (in parentheses) for the same dimensions were: 221, 100, 30.2 (234, 103, 33.5) for 15 males and 229, 102.7, 30.2 (233, 107, 32) for 15 females (Criddle 1943). In Minnesota, means ( $\pm SE$ ) for the dimensions were  $220.3 \pm 1.7$  ( $n = 17$ ),  $96.9 \pm 0.9$  ( $n = 17$ ),  $31.7 \pm 0.3$  ( $n = 20$ ) for females and  $213.7 \pm 1.1$  ( $n = 27$ ),  $95.2 \pm 0.8$  ( $n = 26$ ),  $31.3 \pm 0.2$  ( $n = 28$ ) for males (Forbes 1966c). Of 11 subspecies, females averaged larger than males in 10 and significantly larger in 6; for *T. m. minimus* males averaged larger than females but not significantly so (Levenson 1990).

Ranges in body mass (g) were 38.3-52.2 in Minnesota (Hazard 1982), 42.2-52.1 in Nebraska (Jones 1964), 30-54 in Nevada (Hall 1946), 31.0-54.4 in Oregon (Verts and Carraway 1998), 35-51 in Wisconsin (Jackson 1961), 29-53 in Wyoming (Clark and Stromberg 1987), and 43.4-65.8 in Yukon Territory (Youngman 1975). In Minnesota, mean ( $\pm SE$ ) body mass was  $48.33 \pm 1.29$  ( $n = 20$ ) for females and  $43.70 \pm 0.75$  ( $n = 28$ ) for males (Forbes 1966c). In Alberta, mean ( $\pm SE$ ) body mass of females increased from  $45.4 \pm 1.36$  ( $n = 17$ ) in May to  $50.5 \pm 0.54$  ( $n = 4$ ) in August, whereas that of males increased from  $38.8 \pm 0.62$  ( $n = 25$ ) to  $43.7 \pm 0.75$  ( $n = 5$ ) during the same period. Nonbreeding females and males did not exhibit a similar pattern (Sheppard 1968). In Manitoba, means and maxima (in parentheses) body masses were 41.16 g (51.63 g) for 15 females and 41.49 g (44.95 g) for 15 males (Criddle 1943).

Average ( $\pm SE$ ) skull dimensions (in mm) for adult females ( $n = 30$ ) and males ( $n = 30$ ) in Oregon (Verts and Carraway 1998) were: greatest length of skull,  $29.72 \pm 0.18$ ,  $29.37 \pm 0.15$ ; length of maxillary tooththrow,  $4.99 \pm 0.04$ ,  $4.93 \pm 0.03$ ; zygomatic breadth,  $16.70 \pm 0.13$ ,  $16.41 \pm 0.11$ ; breadth of braincase,  $14.92 \pm 0.10$ ,  $14.87 \pm 0.08$ ; breadth of molariform tooththrow,  $7.25 \pm 0.06$ ,  $7.09 \pm 0.04$ ; skull depth,  $12.38 \pm 0.08$ ,  $12.45 \pm 0.06$ ; and length of mandible,  $15.66 \pm 0.14$ ,  $15.48 \pm 0.12$ . In South Dakota, averages ( $\pm SD$ ) for females ( $n = 129$ ) and males ( $n = 54$ ) were as follows (Turner 1974): greatest length of skull,  $32.4 \pm 0.69$ ,  $32.6 \pm 0.48$ ; zygomatic breadth,  $18.4 \pm 0.36$ ,  $18.6 \pm 0.39$ ; breadth of braincase,  $15.7 \pm 0.39$ ,  $15.7 \pm 0.34$ ; rostral length,  $11.4 \pm 0.30$ ,  $11.5 \pm 0.28$ ; interorbital breadth,  $7.0 \pm 0.32$ ,  $7.0 \pm 0.27$ ; length of maxillary tooththrow,  $5.2 \pm 0.14$ ,  $5.3 \pm 0.15$ ; and cranial depth,  $13.2 \pm 0.27$ ,  $13.2 \pm 0.23$ . In Colorado, averages and ranges for females ( $n = 54$ ) and males ( $n = 49$ ) were (Armstrong 1972): greatest length of skull, 31.5 (29.0-33.0), 31.1 (29.7-32.4); condylobasal length, 28.9 (27.5-30.4), 28.4 (27.2-29.3); zygomatic breadth, 17.6 (16.6-18.7), 17.4 (16.1-18.2); interorbital constriction, 6.9 (6.2-7.8), 6.7 (5.9-7.6); length of mandibular tooththrow, 4.9 (4.5-5.5), 4.8 (4.4-5.5); and cranial depth, 16.5 (15.0-18.0), 16.3 (15.2-17.2). In California, averages and ranges for females ( $n = 10$ ) and males ( $n = 9$ ) were: greatest length of skull, 30.2 (29.7-30.5), 29.7 (29.2-30.3); zygomatic breadth, 16.7 (16.2-17.2), 16.6 (16.2-16.9); interorbital breadth, 6.9 (6.5-7.2), 6.8 (6.6-7.2); breadth of braincase, 14.8 (14.1-15.2), 14.7 (14.3-15.1); length of mandibular tooththrow, 4.6 (4.4-4.8), 4.6 (4.4-4.7); and cranial depth, 10.2 (9.8-10.5), 10.0 (9.6-10.5—Johnson 1943). The latter dimension seems particularly small suggesting that different morphological landmarks were used for cranial depth. Although Patterson (1983) reported that 12 (63.2%) of 19 cranial and 7 (77.8%) of 9 mandibular characters differed significantly among samples collected from 5 populations in New Mexico and Utah, he did not take into account the possible role of sexual dimorphism in the differences. Investigators who provided skull measurements for small samples from other localities also did not separate males and females (Hoffmeister 1986; Jones 1964; Youngman 1975).

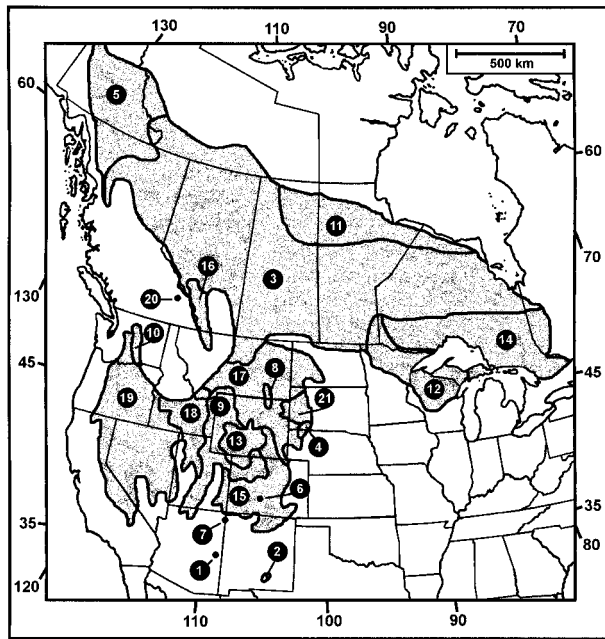


FIG. 3. Distribution of *Tamias minimus*. Subspecies: 1, *T. m. arizonensis*; 2, *T. m. atristriatus*; 3, *T. m. borealis*; 4, *T. m. cacodemus*; 5, *T. m. caniceps*; 6, *T. m. caryi*; 7, *T. m. chuskaensis*; 8, *T. m. confinis*; 9, *T. m. consobrinus*; 10, *T. m. griseocens*; 11, *T. m. hudsonius*; 12, *T. m. jacksoni*; 13, *T. m. minimus*; 14, *T. m. neglectus*; 15, *T. m. operarius*; 16, *T. m. oreocetus*; 17, *T. m. pallidus*; 18, *T. m. pictus*; 19, *T. m. scrutator*; 20, *T. m. selkirki*; and 21, *T. m. silvaticus*. Map redrawn from Banfield (1974:101, map 44), Hall (1981:345, map 236), Howell (1929:37, figure 4), and Sullivan and Petersen (1988:23, figure 7), with modifications.

**DISTRIBUTION.** *Tamias minimus* occurs from west-central Yukon Territory southward along the east base of the Rocky Mountains in British Columbia eastward to Hudson Bay and James Bay, southeastern Ontario, and the Upper Peninsula of Michigan. It also occurs in eastern Montana, South Dakota, Minnesota, southern Idaho, and eastern Washington southward to east-central California, southern Nevada, central Utah, northeastern Arizona, and northern New Mexico (Fig. 3). Disjunct populations occur farther south in New Mexico and Arizona. Least chipmunks have been recorded at elevations >3,500 m (Bole 1938; Findley and Negus 1953). *T. minimus* is the most widely distributed member of the subgenus *Neotamias* (Bergstrom and Hoffmann 1991; Sullivan 1985).

**FOSSIL RECORD.** Fossil remains of *T. minimus* dating from late Sangamonian to early Holocene were reported from Moonshiner (Idaho), Wasden (Idaho), Little Box Elder (Wyoming), and Silver Creek (Utah) cave deposits (Kurtén and Anderson 1980). Extralimital records for the species include remains from Peccary (Arkansas), Kokoweef (California), Back Creek No. 2 (Virginia), Clark's (Virginia), Baker Bluff (Tennessee), and Mandy Walters (West Virginia) caves, Daggett Solid-Waste Locality (California), Craigmile (Iowa), and North Cove (Nebraska—Faunmap Working Group 1994; Guilday and Hamilton 1978; Guilday et al. 1977). Mead et al. (1982) assigned remains of smaller chipmunks from  $\geq 12,000$ -year-old reddish brown silt in Smith Creek Cave, Nevada, to *T. minimus*. Remains identified only to genus have been recovered from cave deposits within and beyond the present range of *T. minimus* (Kurtén and Anderson 1980).

**FORM AND FUNCTION.** Relative brain size and length of vibrissae in sciurids tend to be correlated with arboreality (Ahl 1987; Meier 1983). Where *T. minimus* is associated with shrub-steppe, brain mass:body mass ratios are significantly less than those among the three congeners that occupy habitats that permit greater arboreality (Budeau and Verts 1986). The average ( $\pm$  SD) ratio of mystacial vibrissae length:head width in *T. minimus* ( $1.220 \pm 0.103$ ;  $n = 6$ ) was similar to that of *T. amoenus* ( $1.227$

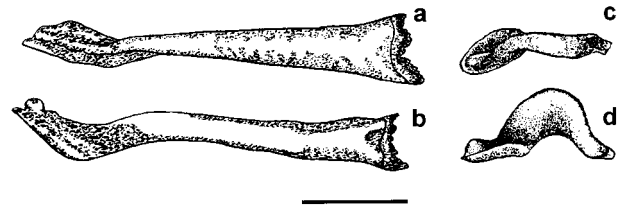


FIG. 4. Drawings of dorsal (a) and left lateral (b) views of the baculum (redrawn after Wade and Gilbert 1940) and dorsal (c) and left lateral (d) views of the os clitoridis (redrawn after Layne 1954) of *Tamias minimus*. Distal is to the left. Scale bar = 1 mm.

$\pm 0.119$ :1,  $n = 19$ —Ahl 1987). Dental formula is  $i$  1/1,  $c$  0/0,  $p$  2/1,  $m$  3/3, total 22. Females have 8 mammae: 2 pectoral, 4 abdominal, and 2 inguinal (Jackson 1961).

The os clitoridis (Fig. 4) of *T. minimus* is ca. 1.4 mm long and somewhat U-shaped, with the shaft slightly longer than either base or tip (Layne 1954). The base is rounded proximally and angled ca.  $30^\circ$  from the shaft. The tip bends to the right ca.  $9$ – $20^\circ$  (Sutton 1982). The os clitoridis varies in shape among nominal races (Sutton 1982:398, figure 3); the bone cannot be distinguished from that of *T. amoenus* (Sutton 1992).

The baculum (Fig. 4) has a thin shaft 2.44–4.35 mm long slightly compressed laterally in the distal one-half, a low keel about 20% the length of the tip, a tip 18–28% of the length of the shaft, and a  $125^\circ$  angle between the tip and shaft (Wade and Gilbert 1940; White 1953a). The tip:shaft ratio can be used to distinguish *T. minimus* (1:3.6–5.6) from *T. amoenus* (1:2.9–3.3—Sutton 1992).

Average diameter of erythrocytes of *T. minimus* from Colorado was  $6.5 \mu\text{m}$  (range,  $6.1$ – $8.3 \mu\text{m}$ ;  $n = 5$ ). Average ( $\pm$  SE) hemoglobin concentrations (g/100 ml), hematocrits (%), and corpuscular hemoglobin concentrations (%) for adult females ( $n = 4$ ) and males ( $n = 10$ ; in parentheses) were:  $13.3 \pm 1.3$  ( $14.7 \pm 0.5$ ),  $43.8 \pm 5.9$  ( $49.2 \pm 1.9$ ), and  $31.0 \pm 2.6$  ( $30.0 \pm 0.9$ ), respectively. Recent parturition suggested by uterine changes in some females was offered as a possible explanation for differences in values between sexes (Selander 1964).

In Alberta, average ( $\pm$  SE) mass (in mg) of paired adrenal glands of breeding females increased from  $19.4 \pm 0.90$  ( $n = 16$ ) in May to  $30.8 \pm 2.53$  ( $n = 4$ ) in August, and those of breeding males increased from  $12.7 \pm 0.40$  ( $n = 20$ ) in May to  $19.8 \pm 1.40$  ( $n = 3$ ) in August. Those of nonbreeding females increased from  $17.6 \pm 0.42$  ( $n = 12$ ) in June to  $21.8 \pm 1.23$  ( $n = 8$ ) in July, but declined to  $20.5 \pm 1.05$  ( $n = 4$ ) in August and those of nonbreeding males increased from  $17.5 \pm 1.24$  ( $n = 5$ ) in May to  $18.1 \pm 1.45$  ( $n = 7$ ) in August. Adrenal glands may undergo involution in September (Sheppard 1968). The cyclic nature of adrenal mass may be related to seasonal changes in social interaction, changes in activity (greater food gathering, foraging movements, and alertness), or the hibernation cycle (Sheppard 1968:473).

Under laboratory conditions (50–75% humidity,  $15^\circ\text{C}$ ), daily water consumption (ad lib.) by *T. minimus* ( $n = 9$ ) from the east slope of the Sierra Nevada, California, averaged ( $\pm$  SE)  $10.8 \pm 0.8\%$  of body mass, about one-third less than the amount consumed by *T. alpinus*, *T. speciosus*, and *T. amoenus* from higher elevations (Heller and Poulson 1972). The free water requirement of *T. minimus* exposed to  $35^\circ\text{C}$  and 11% relative humidity was  $0.1385 \text{ ml/h}$ , 38.0–58.5% less than that of the other 3 species examined by Heller and Poulson (1972).

Nine individuals from Minnesota (mean body mass =  $46.2 \pm 0.8$  g; range,  $42.0$ – $50.2$  g) consumed an average ( $\pm$  SE) of  $5.4 \pm 0.4 \text{ ml/day}$  or  $2.16 \text{ ml}$  ( $1.62$ – $2.96 \text{ ml}$ )/g body mass, about the same as *T. striatus* (Forbes 1967). Daily water consumption (ad lib.) among chipmunks from an arid region in South Dakota that were acclimated to room temperature ( $22^\circ\text{C}$ ) was greater (27.0% of body mass) than those from a montane region of Colorado (24.5% of body mass—Willems and Armitage 1975b). During acclimatization at  $26^\circ\text{C}$  and  $30^\circ\text{C}$ , daily water consumption was slightly less for chipmunks from both populations but still greater for those from South Dakota. However, at  $34^\circ\text{C}$ , daily water consumption was greater for chipmunks from Colorado (29.7%) than for those from South Dakota (20.3%—Willems and Armitage 1975b). Water intake of captives at  $21$ – $25^\circ\text{C}$  was highest during the reproductive season (minimum = 17.7% body mass/day), after which it began

to decrease, reaching a nadir during the season of torpor (minimum =  $8.05\% \pm 0.92$  *SD* body mass/day—Blake 1977).

Average ( $\pm$  *SE*, range) water content of feces of least chipmunks from California ( $n = 3$ ) was  $46.1 \pm 2.0\%$  (1.9–7.6% less than for the 3 other species of *Tamias*) and relative medullary thickness (relationship between longest loop of Henle and kidney mass;  $n = 15$ ) was  $12.08 \pm 0.35\%$  (7.7–22.8% greater than for the other species—Heller and Poulson 1972). Fecal water content of least chipmunks from South Dakota averaged 1.8% higher than those from Colorado when provided with water ad lib. but was 2.5% lower on restricted water rations (Willems and Armitage 1975b).

Average evaporative water loss for *T. minimus* was  $0.0049 \pm 0.0002$  ml  $g^{-1} h^{-1}$  ( $n = 4$ ) at an ambient temperature ( $T_A$ ) of 25°C,  $0.0045 \pm 0.0003$  ml  $g^{-1} h^{-1}$  ( $n = 8$ ) at 35°C, and  $0.0146 \pm 0.0013$  ml  $g^{-1} h^{-1}$  ( $n = 18$ ) at 40°C; at 40°C the value was 18.9–41.1% less than that for 3 other species of *Tamias* (Heller and Poulson 1972). Evaporative water loss per unit of body mass was significantly greater for *T. minimus* from South Dakota than for those from Colorado and remained relatively constant between 26°C and 34°C for animals from both populations. At 38°C, water loss increased threefold for Colorado animals but only slightly more than twofold for those from South Dakota (Willems and Armitage 1975b). Evaporative heat loss at 40°C averaged  $911.7 \pm 71.2$  J/h ( $n = 4$ ), 33.8–58.6% less than for 3 other species of *Tamias* from California (Heller and Poulson 1972).

Basal metabolic rate (mean  $\pm$  *SE*,  $n = 10$ ) for *T. minimus* from California was  $1.58 \pm 0.07$  ml  $O_2 g^{-1} h^{-1}$  (Heller and Gates 1971). Metabolic rates averaged  $1.81 \pm 0.02$  ml  $O_2 g^{-1} h^{-1}$  ( $n = 4$ ) at  $T_A = 25^\circ C$  and  $1.61 \pm 0.15$   $O_2 g^{-1} h^{-1}$  at  $T_A = 35^\circ C$  (Heller and Poulson 1972). At  $T_A$ 's of 22–38°C, average metabolic rates of least chipmunks from a site in South Dakota characterized by high temperatures and aridity were significantly lower than those of chipmunks from a montane site in Colorado. At  $T_A$ 's of 22–33°C, body temperatures ( $T_B$ ) of those from South Dakota after measuring metabolic rates were significantly lower than those of least chipmunks from Colorado. Average thermal conductance (rate of heat loss) between  $T_A$ 's of 18–26°C was equal to that predicted ( $2.93 J h^{-1} ^\circ C^{-1}$ ) based on body mass for least chipmunks from Colorado but was 10% less than predicted for those from South Dakota. These characteristics are adaptations to the semiarid environment that permit chipmunks in South Dakota, in comparison with those in Colorado, to be exposed to high environmental heat loads for longer periods before needing to dissipate excess heat (Willems and Armitage 1975a, 1975c). The maximum  $T_A$  that *T. minimus* can tolerate even at the lowest average absorbed radiation would be 36°C if it maintained a  $T_B$  of 40°C. Exposure to 38°C for 2 h was lethal for 3 of 9 individuals from Colorado, but caused no deaths among those from South Dakota (Willems and Armitage 1975a). A  $T_A$  of 36°C is common by 1100 h in arid, desert habitats occupied by *T. minimus* in many regions, a time corresponding to a rapid decline in activity in such areas. Least chipmunks probably adapt to such habitats by undergoing short periods of hyperthermia while active, then return to their burrow systems to dissipate the heat load (Heller and Gates 1971).

Based on kidney volume, relative medullary thickness (ratio of medullary thickness to the cube root of kidney size  $\times 10$ ) of the kidneys of least chipmunks ranged from 6.75 in moist habitats to 9.5 in arid habitats (Blake 1977). These values indicate an increasing ability to concentrate urine with increasing dryness of the habitat occupied (Blake 1977; Heller and Poulson 1972). Based on kidney mass, average relative medullary thickness ( $\pm$  *SE*) for *T. minimus* was  $12.08 \pm 0.35$  ( $n = 15$ ), greater than that of 3 congeners that occupied less arid habitats on the east slope of the Sierra Nevada, California (Heller and Poulson 1972). These same *T. minimus* had a urine concentration of  $>3,600$  mOsm/l (Blake 1977; Heller and Poulson 1972). On restricted water consumption, least chipmunks from an arid region of South Dakota excreted urine with significant lower osmolarity (mean = 2,241 mOsm/l) and chlorine-ion concentrations (mean = 336 mEq/l) than those from a montane region of Colorado (mean = 2,499 mOsm/l and 370 mEq/l, respectively), but differences were not significant when the least chipmunks were provided water ad lib. (Willems and Armitage 1975b).

Average ( $\pm$  *SE*) digestion efficiencies (digested proportion of ingested food) for *T. minimus* in the laboratory were  $90.3 \pm 1.0\%$  for sunflower seeds and  $90.4 \pm 0.3\%$  for rolled oats, but only  $79.0 \pm 1.7\%$  for the oil-rich seeds of Russian thistle (*Salsola iberica*).

In the wild, digestion efficiencies of natural foods were 91.5–98.4% in July–September, but only 77.8–83.3% in October–November when the least chipmunks shifted their diet to oil-rich seeds (Schreiber 1979).

Although some congeners develop fat deposits before becoming dormant in autumn (Tevis 1955), *T. minimus* seemingly does not. In Minnesota, average percent composition of body fat among adults was 4.4 (range, 3.1–5.3;  $n = 4$ ) in July and 6.2 (range, 5.0–7.4;  $n = 2$ ) in October. Values for subadults were 3.1 (range, 1.6–4.3) in July and 3.1 (range, 2.7–3.5) in August (Forbes 1966a). In Idaho, average body fat increased from ca. 2.2% of body mass in July to ca. 3.8% in November, and average water content decreased from 71.2% in July to 64.4% in November. Variation in the lean dry component was  $<1\%$  of body mass and contained  $20.47 \pm 0.08$  kJ/g (Schreiber and Johnson 1975).

**ONTOGENY AND REPRODUCTION.** In Wyoming, all males captured at onset of trapping in March through May possessed scrotal testes, but in June, some had scrotal testes and some had abdominal testes. Length and mass of testes were greatest in March and declined during spring and summer. Spermatogenesis was ongoing and spermatozoa were present in the epididymides in March–May, although specimens with testes of below-average mass produced no spermatids or spermatozoa and their epididymides usually were empty (Skryja 1974). Mating occurred from 8 April to mid-May, and the latest birth was on 16 June. At 3,018 m in Colorado, males emerged as snow-free areas appeared; at height of snowmelt in mid-May, 80% of 30 males were in breeding condition and were believed to be the only males that would attain breeding condition during the year. Spermatogenesis was ongoing in all reproductive males to mid-June, but only 25% of 12 taken in July had spermatozoa in the testes (Vaughan 1969). Mass of both testes can be calculated from linear dimensions of the organ by the formula: mass =  $1.027(\text{length} \times \text{width}^2) + 1.314$  (Kenagy 1979).

At 3,018 m in Colorado, females enter estrus within ca. 1 week of emergence, so their reproductive organs undergo preparation for breeding while they are still in their winter dens. Of 18 females taken at height of snowmelt in mid-May, 4 were pregnant, 9 were in estrus, and 5 were nonbreeders. Nine nonbreeding females averaged 7.3 g (16.0%) less than 26 breeding females (mean = 45.5 g); the nonbreeding females may have been yearlings that had not attained a critical mass before entering dormancy the previous autumn (Vaughan 1969).

Gestation reportedly is 28–30 days (Criddle 1943; Jackson 1961). Lactating females were observed from 6 May to 15 August in Wyoming (Skryja 1974), from 9 June to 5 August in Michigan (Manville 1949), but no later than early July in Minnesota (Forbes 1966b). In Alberta, the first record of a postpartum female was 5 June, the first young were seen above ground on 14 July, and the latest birth was on 24 June (Sheppard 1969). Only 1 litter is produced annually, although based on captives, females that lose a litter soon after birth may breed again (Criddle 1943; Skryja 1974). In Michigan, *T. minimus* was believed to produce 1 or 2 litters annually in the wild (Manville 1949).

In Manitoba, of 41 pregnant females, 4 carried 4 embryos, 21 carried 5, 9 carried 6, and 7 carried 7 (mean = 5.46 embryos—Criddle 1943). On Grand Mesa, Colorado, of 9 pregnant females, 2 carried 3 embryos, 5 carried 4, 2 carried 6, and 1 carried 7 (mean = 5.0 embryos—Anderson 1959). At 3,018 m in Colorado, both numbers of fetuses per gravida ( $n = 52$ ) and pigmented implantation sites in postpartum females ( $n = 97$ ) averaged ( $\pm$  *SE*)  $5.7 \pm 0.15$  (Vaughan 1969). In Alberta, average ( $\pm$  *SE*) litter size was  $4.54 \pm 0.12$  ( $n = 52$ ) corpora lutea,  $4.19 \pm 0.22$  ( $n = 21$ ) embryos, and  $4.03 \pm 0.18$  ( $n = 32$ ) pigmented implantation sites (Sheppard 1969). In Wyoming, averages based on the latter 2 methods were  $6.4 \pm 0.3$  ( $n = 11$ ) and  $5.4 \pm 0.3$  ( $n = 24$ ), respectively (Skryja 1974). In northeastern California, counts of embryos averaged 5.8 (range, 4–7;  $n = 4$ —Tevis 1955). Mean litter size based on pigmented implantation sites in Minnesota was 4.2 (range, 3–5—Timm 1975). Prenatal mortality was higher among yearlings than among adults (Sheppard 1969).

At birth, the skin is soft, smooth, hairless, and pinkish red; eyes are closed; and ears, although slightly raised, are covered with thin, tissue-like skin (Criddle 1943). Total length, length of tail, and length of hind foot (in mm) and mass (g) were: 51, 15, 6.5, and 2.21 for 1 female and 50, 16.5, 6.2, and 2.36 for 1 male (Criddle 1943).

Among 7 species of chipmunks, development of the ability to stand (27 days) and eruption of both upper and lower incisors (27 days) in *T. minimus* were delayed; opening of eyes and auditory meatuses (27 days) and weaning (36 days) were average; and eruption of cheek teeth (34 days) was early (Forbes 1966b; Hirshfeld and Bradley 1977). Average and ranges (in parentheses) of total length, length of tail, and length of hind foot (in mm) and body mass (g) for littermates born in captivity (Forbes 1966b) were: 117.2 (100–121), 47.2 (40–51), 21.8 (20–23), and 11.7 (9.5–12.7) at 27 days of age ( $n = 5$ ); 132.0 (127–138), 57.5 (54–61), 23.5 (23–24), and 13.2 (12.4–13.9) at 34 days ( $n = 4$ ); 146.3 (143–148), 60.8 (58–65), 25.0 (24–26), and 17.2 (16.3–18.4) at 40 days ( $n = 4$ ); and 159.3 (156–162), 67.0 (64–70), 26.7 (26–27), and 22.1 (20.7–23.1) at 55 days ( $n = 3$ ). Animals attain adult size in September (Forbes 1966b; Skryja 1974).

In Alberta, age at sexual maturity varied among years; only 26% of 23 yearling females and 28% of 39 yearling males bred in samples from 1961–1963, but in 1964, 52% of 25 yearling females and 86% of 22 yearling males bred (Sheppard 1969). Other investigators reported 9.4% (Skryja 1974) and 55% (Anderson 1959) of adult females failed to breed; whether yearlings were distinguished from adults  $\leq 2$  years old was not stated.

Sex ratios (females/male) in samples of *T. minimus* were 1.82:1 ( $n = 93$ —Erlien and Tester 1984) and 0.73:1 ( $n = 76$ —Forbes 1966c) from Minnesota and 0.89:1 from Alberta ( $n = 195$ —Sheppard 1968). The latter 2 ratios were not significantly different from 1:1. Average life span of male and female *T. minimus* combined, based on a 22-year sample, was 0.66 years (Erlien and Tester 1984). Maximum recorded longevity is 6 years 4 months for a captive least chipmunk (Cridle 1943).

**ECOLOGY.** On the eastern slope of the Sierra Nevada, California, *T. minimus* occupies “hot, arid sagebrush habitat” that excludes the aggressively dominant *T. amoenus*, which can displace *T. minimus* in areas where shade from piñon pines (*Pinus edulis*) is available (Heller and Poulson 1972:312). Farther east, *T. minimus* occupies arid valleys and alpine zones above tree line, but not the piñon pine zone occupied by *T. panamintinus* (Heller 1971). In central Oregon, most captures of *T. minimus* were in the shrub–steppe portion of grids that extended into coniferous forest with shrub understory; only 2–13% of captures of *T. minimus* were inside tree line (States 1976). On Steens Mountain, Oregon, *T. minimus* was the only chipmunk at elevations  $< 1,770$  m; it was associated with *T. amoenus* between ca. 1,770 m and ca. 2,745 m and was usually associated with aspen (*Populus tremuloides*) groves and rocky outcrops (Hansen 1956). At lower elevations in eastern Oregon, *T. minimus* was captured on trapping grids established in sagebrush (*Artemisia*) and greasewood (*Sarcobatus vermiculatus*) habitats, but not in grassland or marsh habitats (Feldhamer 1979). Density was correlated positively with soil depth, strength, and proportion of clay but overall comparable (2.0–13.9/ha and 1.7–16.9/ha, respectively) in occupied habitats (Feldhamer 1979). Least chipmunks selected habitats in which cover in the 1st 15 cm above the surface was sparse, permitting rapid escape and concealment from aerial predators (Feldhamer 1979). In the Uinta Mountains region, Utah and Wyoming, the species was considered to be restricted to stream side, rock cliff, rock slide, and alpine habitats in sagebrush, spruce–fir, and pine belts (scientific names not provided—Svihla 1931). In the Ruby Mountains, Nevada, it was “limited only by the absence of sagebrush” (Borell and Ellis 1934:26). In the Southwest, *T. minimus* is “restricted to more mesic, mountaintop habitats,” which invariably are “the largest and more mesic mountains” (Patterson 1982:396).

In Ontario, *T. minimus* was captured in grasses and sedges at the shoreline of a lake; Long (1964) claimed that the species was associated with *T. striatus* in open coniferous forest nearby. In northern Minnesota, *T. minimus* was associated with “recently logged or burned areas, in disturbed habitats around campsites and resorts, and along the rocky shore of Lake Superior” (Timm 1975:18). The species also was taken in early seral stands of black spruce (*Picea mariana*), black ash (*Fraxinus nigra*), and balsam fir (*Abies balsamea*) but was replaced by *T. striatus* in stands of mature pine. In the Upper Peninsula of Michigan, *T. minimus* occurs “in dense upland forest, hardwoods and conifers alike, but it also frequents swamps of white cedar, black spruce, alder, and leatherleaf, as well as rocky and sandy shores, recently burned or cutover areas, rocky mountain-tops, cleared lands, and openings in

the forest grown up to brambles and brush” (Manville 1949:56). However, in the same region, habitats with good horizontal visibility, medium to dense brush piles, and open canopies were occupied significantly more than habitats with other characteristics (Reilly 1971). In Idaho, the number of *T. minimus* captured on grazed plots in sagebrush (*Artemisia tridentata*) habitats was only slightly less than that captured on ungrazed plots. However, removal of sagebrush and reseeding with crested wheatgrass (*Agropyron cristatum*, *A. desertorum*) nearly eliminated the species (Reynolds 1980). In northern Alberta, *T. minimus* occurs in greatest numbers in “sunny aspen–spruce forests bordering the larger streams,” but not at all in extensive stretches of muskeg (Soper 1942:133–134). On the eastern slope of the Front Range in Colorado, *T. minimus* occurs “in most habitats from lower montane open woodland–scrub to alpine tundra” (Bergstrom and Hoffmann 1991:15). Farther west in the same state, the species was considered abundant in rocky meadows at forest edges to tree line, less so in “spruce–fir forests” (Findley and Negus 1953). In south-central Colorado, the species occupies “stabilized sand dunes and . . . pale, alkaline soils” vegetated by greasewood (Armstrong 1972:98).

In an alpine meadow in Colorado, densities of *T. minimus* ranged from 11.4 to 22.2/ha during a 3-year period. Its biomass averaged 469.3–922.5 g/ha and constituted 14.8–26.1% of the small-mammal biomass in the meadow (Vaughan 1974). In Utah, ranges in estimates of density in early summer were 0.3–1.8/ha in meadow and 1.0–4.6/ha in aspen, whereas those in late summer were 0.3–5.7/ha in meadow and 0.8–2.1/ha in aspen. Average daily biomass ( $\times 10^{-3}$  g/m<sup>2</sup>) of the species was 2.2–10.1 and constituted 1–8% of the total supplied by small mammals. The species was rarely taken in fir (*Abies lasiocarpa*) and spruce (*Picea engelmannii*) forests (Andersen et al. 1980). In the Raft River Valley, Idaho, average ( $\pm SE$ ) captures ( $n/100$  trap days) were 1.0  $\pm$  0.5 in sagebrush, 0.5  $\pm$  0.3 in healthy shadscale (*Atriplex confertifolia*), 4.6  $\pm$  0.7 in “depleted” shadscale, 0.4  $\pm$  0.3 in crested wheatgrass, 1.8  $\pm$  0.8 in kochia (*Kochia*), 2.4 (no SE) in greasewood, and 1.4 (no SE) in halogeton (*Halogeton glomeratus*). Relative abundance was greatest in depleted shadscale at all seasons during a 7-year study (Larrison and Johnson 1973).

The summer diet of *T. minimus* in an alpine meadow in Colorado based on analysis of stomach contents ( $n = 377$ ) consisted of 48.6–55.2% seeds, 6.5–23.0% arthropods, 8.3–9.9% leaves, 8.6–22.2% fruits and flowers, and 5.4–6.0% fungi (Vaughan 1974). Differences in diet were related to timing of onset of the growing season and seasonal changes in availability of various foods. Seeds were considered the most sought food, but other items supplemented the diet when seeds were not available. At snowmelt in May, fruits and flowers contributed most (58.2%) to the diet, but no other category ranked as high as 20% (Vaughan 1974). At this season, deer mice (*Peromyscus maniculatus*) and least chipmunks partition food resources, thereby avoid competing during the season of scarcity. In meadows farther south in Colorado, *T. minimus* consumed only 14% of the plant taxa available; dandelion (*Taraxacum officinale*) composed ca. 80% of the diet in June–August. Dandelion flower heads seemed particularly relished (Carleton 1966). In another study in the same state, arthropods composed 19.8% of the diet in June, 4.4% in July, and 2.2% in August (Vaughan and Weil 1980). In Minnesota, stomachs of adults contained animal material more frequently than did stomachs of either subadults or juveniles (Forbes 1966c).

In Minnesota, items of vegetative origin were present in 90.1% of least chipmunks taken in August and September. Items of animal origin were in 80.3% of 71 stomachs; vegetative material was found in 100% of cheek pouches of 30 individuals. None of the cheek pouches contained animal material (Aldous 1941). Of plant materials, creeping snowberries (*Chilogenes* [= *Gaultheria*] *hispidula*), raspberries (*Rubus idaeus*), and blueberries (*Vaccinium*) occurred in 22.5%, 28.1%, and 45.1% of the stomachs, respectively. Of animal materials, grasshopper eggs (Orthoptera), beetles (Coleoptera), caterpillars (Lepidoptera), and ants and bees (Hymenoptera) were found in 25.3%, 25.3%, 23.9%, and 21.1% of the stomachs, respectively. Smartweed and bindweed (*Polygonum*), cranesbill (*Geranium*), and raspberry composed 40.0%, 16.7%, and 16.7%, respectively, of plant materials carried in cheek pouches (Aldous 1941). Twenty-eight genera of seeds were consumed or were being transported by *T. minimus*; many of those in the stomachs of the chipmunks were unchewed. Thus, if seeds are undamaged by the digestive process, chipmunks may be partly responsible for regen-

eration of some species of plants (Aldous 1941). Pouches of *T. minimus* contained 16 species of plants, only 3 of which occurred in pouches of syntopic *T. striatus* (Aldous 1941). In Michigan, the least chipmunk was observed to consume "seeds of sugar maple [*Acer saccharum*], acorns [*Quercus*], leaves and seeds of dandelion, alder [*Alnus incana*] cones, leaves of the early saxifrage [*Saxifraga virginiana*], and red raspberries" (Manville 1949:56). In North Dakota, a least chipmunk was observed to feed on seeds of red osier dogwood (*Cornus stolonifera*) after it removed and discarded the fleshy outer layer of the fruit (Fox 1939). In Utah, chipmunks were observed to gather fruits of lady's-mantle (*Amelanchier* [= *Alchemilla oreophila*], snowberry (*Symphoricarpos vaccinioides* [= *oreophilus*]), and common chokecherry (*Prunus melanocarpa* [= *virginiana*])—Tanner 1927). In the same state, least chipmunks were considered 1 of the 3 dominant predators on dark-eyed juncos (*Junco hyemalis mearnsi*)—Smith and Andersen 1982). In late summer, these chipmunks sometimes leave shrub habitats to raid adjacent grain fields (Larrison 1947). In eastern California, *T. minimus* fed on fallen seeds ca. 40% of the time and on bitterbrush (*Purshia*) ca. 34% of the time (Chappell 1978). Of 19 *T. minimus* examined from eastern Oregon, 1 contained spores of the fungus *Glomus* (Zygomycetes) and 5 contained spores of unidentified fungi (Maser et al. 1988).

In western Alberta, minimum-area home ranges of *T. minimus* were  $1.22 \pm 0.32$  ha for males ( $n = 10$ ) and  $0.66 \pm 0.07$  ha for females ( $n = 19$ ). Average distances moved between captures were 105.5 m and 71.3 m for the males and females, respectively (Sheppard 1972). In Colorado, minimum-area home ranges for 3 individuals located 11–33 times by radiotelemetry (1.38–5.52 ha) were 3.49–6.27 times larger than those (0.22–1.06 ha) based on 5–8 captures each for the same individuals (Bergstrom 1988). In northern Michigan, home-range areas calculated by the exclusive boundary-strip method for *T. minimus* captured on an 11-by-11-trap grid (9.1 m between traps) averaged 0.09 ha (range, 0.06–0.11 ha;  $n = 3$ ) for males and 0.09 ha (range, 0.05–0.13 ha;  $n = 4$ ) for females (Manville 1949). In southern Alberta, a male and a female were observed 450 m and 530 m, respectively, outside a 3.7-ha trapping grid on which they were captured and marked (Meredith 1974). Observation of dye-marked chipmunks in Montana revealed that use of home-range areas of individuals changed greatly between seasons and years (Martinsen 1968).

In Colorado, where 60% of syntopic *T. umbrinus* exhibited evidence of bot fly (*Cuterebra fontinella*) myiasis, only 1 of 100 *T. minimus* was infested (Bergstrom 1992). Other external parasites of *T. minimus* include sucking lice (Anoplura): *Hoplopleura arboricola* and *Neohaematopinus pacificus* (Durden and Musser 1994; Emerson et al. 1984; Timm 1975); mites (Acarina): *Androlaelaps fahrenheitsi* (Timm 1975); and ticks (Acarina): *Dermacentor andersoni*, *Ixodes angustus*, and *I. eastoni* (Bishopp and Trembley 1945; Robbins and Keirans 1992). Fleas (Siphonaptera) known to infest least chipmunks include: *Aetheca wagneri*, *Ceratophyllus ciliatus kincaidi*, *Ctenophthalmus pseudagyrtus*, *Eumolpianus e. eumolpi*, *E. cyrturus*, *E. wallowensis*, *Megabothris acerbus*, *M. asio*, *M. clantoni*, *M. quirini*, and *Orchopeas caedens* (Lewis et al. 1988; Timm 1975; Traub et al. 1983).

In Rocky Mountain National Park, Colorado, the virus responsible for Colorado tick fever was isolated from 31 (18.3%) of 169 *T. minimus* examined; 64 (37.9%) contained antibodies to the virus. The highest rate of infection in *T. minimus* was in July (Bowen et al. 1981). Transmission among small-mammal hosts is by immature stages of *Dermacentor andersoni*. *T. minimus* and other small mammals are refractory to tick fever. Juvenile least chipmunks inoculated with *Borrelia burgdorferi* spirochetes (the causative agent of Lyme disease) maintained the organism for at least 72 days (Ubico et al. 1996).

**BEHAVIOR.** Although usually considered to be terrestrial, least chipmunks often climb or perch in shrubs (Borell and Ellis 1934; Larrison 1947) and may climb trees to nest or feed (Broadbooks 1974; Fox 1939; Harper 1932; Orr 1930). They usually are shy and, when approached, often keep vegetation between themselves and an observer as they scamper off to reappear 20 m or so farther away or disappear by entering burrow systems. They commonly do not respond to "lip squeaking," a technique that often prompts other species of chipmunks to reveal their presence (Larrison 1947:24). However, in campgrounds and parks they become

extremely bold and commonly pilfer food from campsites or otherwise become a nuisance (Banfield 1974; Cahn 1937).

Occasionally, in summer, least chipmunks appropriate nest cavities constructed by woodpeckers (Picidae) or even construct tree nests of leaves and grass (Banfield 1974; Broadbooks 1974). More commonly, they construct burrow systems. Tunnels are dug and excavated earth is pushed from the tunnel, then the "work" tunnel is plugged and a new opening to the system is constructed so that tell-tale spoil does not reveal the location of the entrance. A chamber ca. 15 cm in diameter in the burrow is filled with dry grass, bark, fur, feathers, and other fine materials for a winter nest. Nesting materials may be removed and replaced occasionally, possibly to reduce parasites (Criddle 1943). In Idaho, polyurethane casts of burrows used by *T. minimus* ( $n = 5$ ) averaged ( $\pm SE$ )  $1.7 \pm 0.6$  m (range, 0.4–3.5 m) long,  $17.5 \pm 1.2$  cm (range, 14.4–20.8 cm) below the surface,  $7.5 \pm 0.5$  cm (range, 6.5–8.7 cm) wide,  $4.2 \pm 0.3$  cm (range, 3.5–5.2 cm) tall, and displaced  $5.2 \pm 2.4$  l (range, 1.8–12.2 l). Burrow systems had an average ( $\pm SE$ ) of  $2.6 \pm 0.4$  (range, 2–4) openings (Laundré 1989). In a subalpine region of Colorado, entrances to burrows constructed by *T. minimus* were under large rocks more frequently than expected on the basis of the distribution of these features in habitats (Bihl and Smith 1998). Burrows ( $n = 34$ ) had an average ( $\pm SD$ ) of  $1.3 \pm 0.5$  entrances, with an average entrance diameter of  $3.7 \pm 1.1$  cm ( $n = 29$ ). Tunnels ( $n = 13$ ) averaged ( $\pm SD$ )  $59.2 \pm 35.2$  cm long, contained  $1.2 \pm 0.6$  chambers, and attained a maximum depth of  $31.5 \pm 17.6$  cm. Although entrances to 19 of 40 burrows faced 210–270°, Bihl and Smith (1998:356) claimed that they were "randomly placed." Burrows contained scattered seeds, fungi, fecal pellets, and some live invertebrates (including ectoparasites), but no large caches of food items.

Calls produced by *T. minimus* include a low "cluck" or a shrill, abrupt "psst"; the latter call is similar to that of the white-crowned sparrow (*Zonotrichia leucophrys*)—Harper 1932). Various other calls produced by the species include "trp trp trp" or "trk trk trk" (general alarm); "tsp tsp tsp" (greater alarm); a sharp explosive "tsk" followed by "tsk s-r-r-r" (sudden alarm); "tuk" or "tyuk" (low whispered alarm); "whirt," "pirt," or "whit" (dashing for cover); and "ts ts s-r-r-r" (when confined—Gordon 1938). The calls are ventriloquistic; thus, individuals making the calls commonly are difficult to locate (Bailey 1926).

*Tamias minimus* is considered subordinate to *Spermophilus lateralis* (Carey 1978) and to some congeners (Heller 1971). However, in habitats where predation is less of a risk, *T. minimus* can outcompete the spermophile through resource depletion; the reverse is true where predation is more of a risk (Smith 1995). Engaging in aggressive interactions may not be metabolically feasible for *T. minimus* in hot sagebrush desert (Heller 1971). In relatively rare instances of broad sympatry among members of the genus, 1 of the 2 smallest species (*T. minimus* and *T. amoenus*) and a larger congener usually are involved (Bergstrom and Hoffmann 1991). In interspecific encounters, *T. minimus* is subordinate to *T. amoenus*; where *T. amoenus* is removed, *T. minimus* can invade, but not vice versa (Chappell 1978). On the east slope of the Rocky Mountains in Alberta, *T. minimus* is restricted to the alpine zone above tree line because it is excluded from forested areas by aggressive interactions with *T. amoenus*. When cross-transplanted, *T. minimus* survived, but *T. amoenus* did not. Possibly because of its small size, *T. minimus* is better adapted to areas with limited resources (Sheppard 1971). Wild-caught individuals of both species selected talus significantly more frequently than trees in artificial habitats; captive-born *T. minimus* also selected talus significantly more frequently, but captive-born *T. amoenus* did not. Thus, the response of *T. minimus* was considered "innate" (Meredith 1976). In the wild, least chipmunks are believed to use "remembered metric relations between environmental cues to navigate" to locations at which they earlier had been fed (Devenport and Devenport 1994a: 728). Least chipmunks were believed to be capable of making decisions regarding which patch to visit based on the relative age of information available (Devenport and Devenport 1994b). In both laboratory and wild situations, least chipmunks marked, with copious quantities of urine, patches depleted or nearly depleted of food resources. Neither the individual that marked nor conspecifics revisited the patch, suggesting that foraging efficiency is improved by quick rejection of unprofitable sites (Devenport et al. 1999).

The least chipmunk is sprightly and agile (Banfield 1974); it "runs excitedly with its long tail vertical" (Jackson 1961:151). An

average maximal running speed of 2.13 m/s (ca. 7.7 km/h; range, 0.5–3.2 m/s;  $n = 27$ ) was recorded for individuals fleeing from a pursuing investigator, only 67.8% as fast as *Spermophilus lateralis*. The slower speed may prevent *T. minimus* from foraging as far from protective cover as *S. lateralis*, thereby permitting coexistence of the 2 species (Smith 1995). Smith (1995) believed the 16 km/h (4.4 m/s) reported for *T. minimus* (Cottam and Williams 1943), a speed 40% greater than the average she recorded for *S. lateralis*, to be unreliable because it was measured for 1 individual with the speedometer in an automobile from which it fled for 45 m. She further considered it the only other record of running speed for the species. However, in captivity, an average ( $\pm$  SD) maximal running speed of  $16.8 \pm 0.8$  km/h (range, 15.9–17.4 km/h;  $n = 3$ ) was recorded by Djawdan and Garland (1988), a speed almost identical with that recorded by Cottam and Williams (1943) and faster than all but 2 of 17 species of desert mammals tested.

Least chipmunks may be active at any time during daylight hours, but in Wisconsin, they seem to be most active during midday on warm days (Jackson 1961). In California, activity assessed between 0600 h and 1700 h peaked at 0700 h and declined to nearly zero by 1200 h; small amounts of activity were noted during the afternoon (Chappell 1978). When temperatures are high, least chipmunks frequently retire to their burrows to unload excess body heat (Heller and Poulson 1972). In autumn, they exhibit great activity in caching seeds, nuts, and grains that they transport in their cheek pouches. Much of this material is stored beneath stumps and logs or scatterhoarded in small pits to be retrieved and cached in the tunnel system later (Criddle 1943); caches may be in a separate compartment in the tunnel system or beneath the nest (Banfield 1974; Howell 1929; Jackson 1961). In Manitoba, Criddle (1943) found a cache containing 528.5 g of seeds and grain, another with 799.39 g of acorns, and a 3rd with 465 g of a variety of seeds. Because *T. minimus* does not fatten significantly in autumn (Forbes 1966a), in winter, it must depend on stored food, which it consumes between bouts of torpor (Bailey 1936). Timing of onset and cessation of bouts of torpor are dependent upon latitude and amount of snow cover. For example, in northern Alberta, aboveground activity was observed from 30 April to 17 October (Soper 1942), but in Manitoba, activity was noted from mid-April to November (Criddle 1943), and in Wisconsin, from mid-March to early November (Jackson 1961).

**GENETICS.** *Tamias minimus* has a modal fundamental number of  $2n = 38$  (Nadler 1964; Nadler et al. 1977; Sutton and Nadler 1969). Two karyotypes were identified in the species: karyotype A is characterized by 4 pairs of large metacentric (Group I), 6 pairs of submetacentric (Group II), 4 pairs of large acrocentric (Group III), and 3 pairs and an unpaired singleton of small acrocentric or submetacentric chromosomes (Group V—Nadler 1964). Karyotype B is nearly the same, except for more dense staining of 1 band in Group I (pair 3 chromosomes) and of 2 bands in Group III (pair 4 chromosomes); a pair of Group IV small metacentric chromosomes; and the lack of an unpaired chromosome in Group V. The former 2 characters may be the result of the slide preparation technique (Nadler et al. 1977). Within *T. minimus*, the subspecies *arizonensis*, *caryi*, *minimus*, *neglectus*, *operarius*, and *pallidus* have karyotype A, whereas the subspecies *cacodemus*, *confinus*, *scrutator*, and *silvaticus* have karyotype B. However, the subspecies *borealis* and *consobrinus* contain both karyotypes, and hybrids have been found among *pallidus* and *borealis* (Nadler et al. 1977). Both karyotypes A and B and the hybrid karyotype were presented in Nadler et al. (1977:345, 349, figures 1, 6, 7). The X chromosome is a Group II large submetacentric and the Y is a Group V small acrocentric.

Average heterozygosity was 0.008–0.1319 among subspecies throughout the geographic range of *T. minimus* (Levenson et al. 1985; Sullivan and Petersen 1988). Of 22 proteins encoded by 27 presumptive loci examined in 16 subspecies of *T. minimus*, Adh, Alb-1, Alb-2, Gd, Ald, Got-1, Got-2, Gpi, Hgb, Icd-2, Ldh-2, Mdh-1, Mdh-R, Sod, and Sordh were monomorphic; Est, Icd-1, Lap, Pgm-2, and Tf each had a rare allozyme that appeared with a frequency of <0.05; and G6Pd, 6Pgd,  $\alpha$ Gpd, Ldh-1, Mdh-L, Pgm-1, and Pgm-2 were polymorphic (Levenson et al. 1985; Sullivan and Petersen 1988). Adh was examined only by Levenson et al. (1985), and Gpi, Gd, Lap, Sod, and Sordh were examined only by Sullivan and Petersen (1988). Perault et al. (1997) examined 18 proteins encoded by 28 presumptive loci (misreported as 29 loci) in least

chipmunks from 10 localities in the Unita Mountains of northeastern Utah. Average heterozygosity was 0.060–0.096. Of these 28 loci, only Est-1, Est-2, Lap-2, Mpi, Pep-1, and Pep-2 were polymorphic; Ah, Adh, Est-3, Gdh, Gdh-1, Gdh-2, Got-1, Got-2, Gp, G6pd,  $\alpha$ Gpd-1,  $\alpha$ Gpd-2, Gpi, Idh-1, Idh-2, Pgm, Lap-1, Ldh-1, Ldh-2, Iddh, Me-1, and Me-2 were monomorphic. The most likely reason that G6pd and Ldh-1 were found to be monomorphic by Perault et al. (1997) was the more limited geographic distribution of populations examined.

Amplification of 4 of 9 microsatellite loci for alleles/number of base pairs of polymerase chain reaction products detected (GS3, 227/233; GS17, 159/161; GS20, 250/250; and GS34, 249/249, respectively) was accomplished with primers developed for *Spermophilus columbianus* (Stevens et al. 1997). The low success rate was believed to indicate a distant relationship between *T. mimimus* and *S. columbianus*.

**REMARKS.** In 1811, Illiger proposed the generic name *Tamias*. In 1880, Troussart proposed the subgeneric name *Eutamias* to include all ground squirrels with 2 premolars in each maxilla, as compared with the subgenus *Tamias* to include all sciurids with only 1. By 1897, Merriam had removed all sciurids except the chipmunks from *Eutamias* and elevated it to generic status (Merriam 1897:189); however, he presented no evidence in support of his contention. Subsequently, the genus *Eutamias* variously was divided into 2 subgenera, *Eutamias* and *Neotamias*, based on skull and baculum morphology; number of functional mammae; and fossil, karyotypic, biogeographic, and immunological data (Ellerman 1940; Ellis and Maxson 1979; Hafner 1984; Howell 1929; Moore 1961; White 1953b). *Eutamias* was subsumed into the genus *Tamias* and designated 1 of 3 subgenera (*Tamias*, *Eutamias*, and *Neotamias*) based on Giemsa-band patterns of chromosomes and on morphological, fossil, karyotypic, and electrophoretic data (Bryant 1945; Ellerman 1940; Levenson et al. 1985; Nadler 1964; Nadler and Block 1962; Nadler et al. 1969, 1977, 1985). Initial research revealed that chipmunks had 2 karyotypes, thus supporting the contention that *Tamias* and *Eutamias* were distinct genera. However, subsequent work revealed the presence of both karyotypes and hybrid karyotypes within some subspecies of *T. minimus* (Nadler et al. 1977); consequently, all chipmunks were placed within the genus *Tamias* where they remain at present.

The generic name *Tamias* is from the same Greek word meaning a storer or a distributor. The specific epithet *minimus* is from the same Latin word meaning least or smallest (Jaeger 1978).

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