

Thomomys talpoides. By B. J. Verts and Leslie N. Carraway

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Thomomys talpoides (Richardson, 1828)

Northern Pocket Gopher

Cricetus talpoides Richardson, 1828:518. Type locality “banks of the Saskatchewan” restricted to “near Fort Carlton (Carlton House) on the Saskatchewan River, Saskatchewan” by Bailey, 1915:97.

Geomys talpoides Richardson, 1829:204. Renaming of *Cricetus talpoides*.

Geomys borealis Richardson, 1837:150. Renaming of *Cricetus talpoides*.

Pseudostoma talpoides Audubon and Bachman, 1854:43. Renaming of *Geomys borealis*.

Thomomys talpoides Baird, 1858:403. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Family Geomyidae, Genus *Thomomys*, Subgenus *Thomomys* (Hall, 1981; Thaeler, 1980). Fifty-six subspecies are recognized currently (Patton, 1993):

- T. t. aequalidens* Dalquest, 1942:3. Type locality “Abel Place, elev. 2200 ft., 6 mi. SSE Dayton, Columbia Co., Washington.” (1)
- T. t. agrestis* Merriam, 1908:144. Type locality “Medano Ranch, San Luis Valley, Colorado.” (2)
- T. t. andersoni* Goldman, 1939:235. Type locality “Medicine Hat, on the South Saskatchewan River, Alberta, Canada.” (3)
- T. t. attenuatus* Hall and Montague, 1951:29. Type locality “3½ mi. W Horse Creek Post Office, 7,000 ft., Laramie Co., Wyoming.” (4)
- T. t. bridgeri* Merriam, 1901:113. Type locality “Fort Bridger, [Uinta Co.,] Wyoming.” (5)
- T. t. bullatus* Bailey, 1914:115. Type locality “Powderville, [Custer Co.,] Montana.” (6)
- T. t. caryi* Bailey, 1914:115. Type locality “head of Trapper Creek, at 9,500 feet altitude in the Bighorn Mountains, [Bighorn Co.,] Wyoming.” (7)
- T. t. cheyennensis* Swenk, 1941:5. Type locality “Two miles south of Dalton, Cheyenne County, Nebraska.” (8)
- T. t. cognatus* Johnstone, 1955:163. Type locality “Crowsnest Pass, British Columbia.” (9)
- T. t. columbianus* Bailey, 1914:117. Type locality “Touchet, Walla Walla County, Washington.” (10)
- T. t. confinus* Davis, 1937:25. Type locality “Gird Creek, near Hamilton, Ravalli County, Montana.” (11)
- T. t. devexus* Hall and Dalquest, 1939:3. Type locality “one mile WSW Neppel, Grant County, Washington” (*ericaeus* Goldman is a synonym). (12)
- T. t. douglasii* (Richardson), 1829:200. Type locality “near mouth of Columbia [River],” probably near Vancouver, Washington. (13)
- T. t. durranti* Kelson, 1949:143. Type locality “Johnson Creek, 14 mi. N Blanding, 7,500 ft., San Juan County, Utah.” (14)
- T. t. falcifer* Grinnell, 1926:180. Type locality “Bells Ranch, 6,890 feet altitude, Reese River Valley, Nye County, Nevada.” (15)
- T. t. fisheri* Merriam, 1901:111. Type locality “Beckwith, Sierra Valley, Plumas County, California.” (16)
- T. t. fossor* J. A. Allen, 1893:51. Type locality “Florida, La Plata Co., Colorado (altitude 7200 feet).” (17)
- T. t. fuscus* Merriam, 1891:69. Type locality Summit Creek “in mountains at head of Big Lost River, [Custer Co.,] Idaho” (*myops* Merriam is a synonym). (18)
- T. t. gracilis* Durrant, 1939a:3. Type locality “Pine Canyon, 6600 ft., 17 mi. NW Kelton, Box Elder County, Utah.” (19)
- T. t. immunis* Hall and Dalquest, 1939:4. Type locality “5 miles south of Trout Lake, Klickitat County, Washington.” (20)

- T. t. incensus* Goldman, 1939:240. Type locality “Shuswap, Yale District, British Columbia.” (21)
- T. t. kaibabensis* Goldman, 1938:333. Type locality “De Motte Park, Kaibab Plateau, Coconino County, Arizona (altitude 9,000 feet).” (22)
- T. t. kelloggi* Goldman, 1939:237. Type locality “West Boulder Creek, Absaroka Mountains, 18 miles southeast of Livingston, Park County, Montana.” (23)
- T. t. levis* Goldman, 1938:336. Type locality “Seven Mile Flat, 5 miles north of Fish Lake, Fish Lake Plateau, Sevier County, Utah (altitude 10,000 feet).” (24)
- T. t. limosus* Merriam, 1901:116. Type locality “White Salmon, Gorge of the Columbia [River, Klickitat Co.,] Washington.” (25)
- T. t. loringi* Bailey, 1914:118. Type locality “South Edmonton, Alberta.” (26)
- T. t. macrotis* Miller, 1930:41. Type locality “D’Arcy Ranch, 2 miles north of Parker, Douglas Co., Colorado at approximately 5,700 feet altitude.” (27)
- T. t. medius* Goldman, 1939:241. Type locality “Silver King Mine, summit Toad Mountain, 6 miles south of Nelson, Kootenay District, British Columbia.” (28)
- T. t. meritus* Hall, 1951:221. Type locality “8 mi. N and 19½ mi. E Savery, 8800 ft., Carbon County, Wyoming.” (29)
- T. t. monoensis* Huey, 1934:373. Type locality “Dexter Creek Meadow, Mono County, California (. . . Kuhlee Ranch, at confluence of Dexter and Wet creeks), altitude 6,800 feet.” (30)
- T. t. moorei* Goldman, 1938:335. Type locality “one mile south Fairview, Sanpete County, Utah (altitude, 6,000 feet).” (31)
- T. t. nebulosus* Bailey, 1914:116. Type locality “Sand Creek Canyon, Black Hills, [15 miles NE Sundance, Crook Co.,] Wyoming (Jack Boyden’s Ranch, 5 miles above mouth of canyon at 3,750 feet altitude).” (32)
- T. t. ocius* Merriam, 1901:114. Type locality “Fort Bridger, [Uinta Co.,] Wyoming.” (33)
- T. t. oquirrhensis* Durrant, 1939b:3. Type locality “Settlement Creek, Oquirrh Mountains, 6,500 feet, Toole County, Utah. (34)
- T. t. parowanensis* Goldman, 1938:334. Type locality “Brian Head, Parowan Mountains, Iron County, Utah (altitude 11,000 feet).” (35)
- T. t. pierreicolus* Swenk, 1941:2. Type locality “Wayside, Dawes County, Nebraska.” (36)



FIG. 1. Drawing of *Thomomys talpoides quadratus* by Bob Hines, reprinted from Moore and Reid (1951:6, fig. 3) with approval of Publishing and Information Service, United States Department of Agriculture.

- T. t. pryorii* Bailey, 1914:116. Type locality "Pryor Mountains, [Carbon Co.,] Montana at 6,000 feet on head of Sage Creek." (37)
- T. t. pygmaeus* Merriam, 1901:115. Type locality "Montpelier Creek, [ca. 10 miles NE Montpelier, Bear Lake Co.,] Idaho (alt. 6,700 ft.)." (38)
- T. t. quadratus* Merriam, 1897:214. Type locality "The Dalles, [Wasco Co.,] Oregon." (39)
- T. t. rarus* Durrant, 1946:15. Type locality "19 mi. N Vernal, 8,000 feet, Uintah County, Utah." (40)
- T. t. relicinus* Goldman, 1939:239. Type locality "Twin Springs, 20 miles north of Minidoka, Snake River Desert, [Minidoka Co.,] Idaho." (41)
- T. t. retrorsus* Hall, 1951:83. Type locality "Flagler, Kit Carson County, Colorado." (42)
- T. t. rostralis* Hall and Montague, 1951:27. Type locality "1 mi. E Laramie, 7164 feet, Albany County, Wyoming." (43)
- T. t. rufescens* Wied-Neuwied, 1839:378. Type locality "in der Nähe der Mandan- und Mönnitarri-Dörfer," restricted to "The Minnetaree Village' now Old Fort Clark, Oliver County, North Dakota (about 6 miles south of Stanton) on the west side of the Missouri River" by Bailey, 1915:98. (44)
- T. t. saturatus* Bailey, 1914:117. Type locality "Silver (near Saltese), in the western corner of Missoula County, Montana at 4300 feet altitude in the Couer d'Alene Mountains." (45)
- T. t. segregatus* Johnstone, 1955:161. Type locality "Goat Mountain, on the east side of the Kootenay River, near Wynndel, British Columbia." (46)
- T. t. shawi* Taylor, 1921:121. Type locality "Owyhigh Lakes, 5,100 feet, Mount Rainier, [Pierce Co.,] Washington." (47)
- T. t. talpoides*, see above. (48)
- T. t. taylori* Hooper, 1940:11. Type locality "New Mexico, Valencia County, six miles northeast of the summit Mount Taylor, [ca. 8,000 feet,] near Fernandez summer camp." (49)
- T. t. tenellus* Goldman, 1939:238. Type locality "Whirlwind Peak, Absaroka Range, Park County, Wyoming (altitude 10,500 feet)." (50)
- T. t. trivialis* Goldman, 1939:236. Type locality "near head Big Timber Creek, [ca. 15 miles NW Big Timber,] Crazy Mountains, [Sweetgrass Co.,] Montana (altitude 5,200 feet [aneroid reading])." (51)
- T. t. uinta* Merriam, 1901:112. Type locality "Uinta Mountains, [Summit Co.,] Utah. Altitude 10,000 feet." (52)
- T. t. wallowa* Hall and Orr, 1933:41. Type locality "Catherine Creek, seven miles E Telocaset, 3,500 feet altitude, Union County, Oregon." (53)
- T. t. wasatchensis* Durrant, 1946:8. Type locality "Midway, 5,500 ft., Wasatch County, Utah." (54)
- T. t. whitmani* Drake and Booth, 1952:52. Type locality "Whitman National Monument, 750 feet above sea level, 6 miles west Walla Walla, Walla Walla County, Washington." (55)
- T. t. yakimensis* Hall and Dalquest, 1939:4. Type locality "Selah, Yakima County, Washington" (*badius* Goldman is a synonym). (56)

Hall (1981) recognized 58 subspecies, but *clusius* Coues and *idahoensis* Merriam earlier were re-elevated to species level by Thaeler and Hinesley (1979) and Thaeler (1972), respectively. Interpopulation morphological differences within nominal geographic races of pocket gophers often are as great or greater than those between some described races (Davis, 1938; Smith and Patton, 1988), and chromosomal differentiation between geographic forms of *T. talpoides* is sufficient to suggest that "more than one biological species is currently included under the name *talpoides*" (Patton, 1993:475). Thaeler (1968b, 1974a, 1974b, 1976) consistently referred to these pocket gophers as the *Thomomys talpoides* complex.

DIAGNOSIS. *Thomomys talpoides* (Fig. 1) can be distinguished from most sympatric and parapatric congeners (*bottae*, *monticola*, *umbrinus*, *townsendii*, *bulbivorus*, *idahoensis*, and *mazama*) by one or more of the following characters: small size; posterior portion of skull projecting well beyond lambdoidal crests (Thaeler, 1972); closed or slitlike sphenoidal fissures; presence of a narrow flange projecting posteriorly and ventrally at the angle of the dentary (Fig. 2; Verts and Carraway, 1998); ear from notch ≥ 8 mm and pointed; nasals squarish posteriorly, not V-shaped (Jameison and Peeters, 1988); concave enamel plate on the anterior-lin-

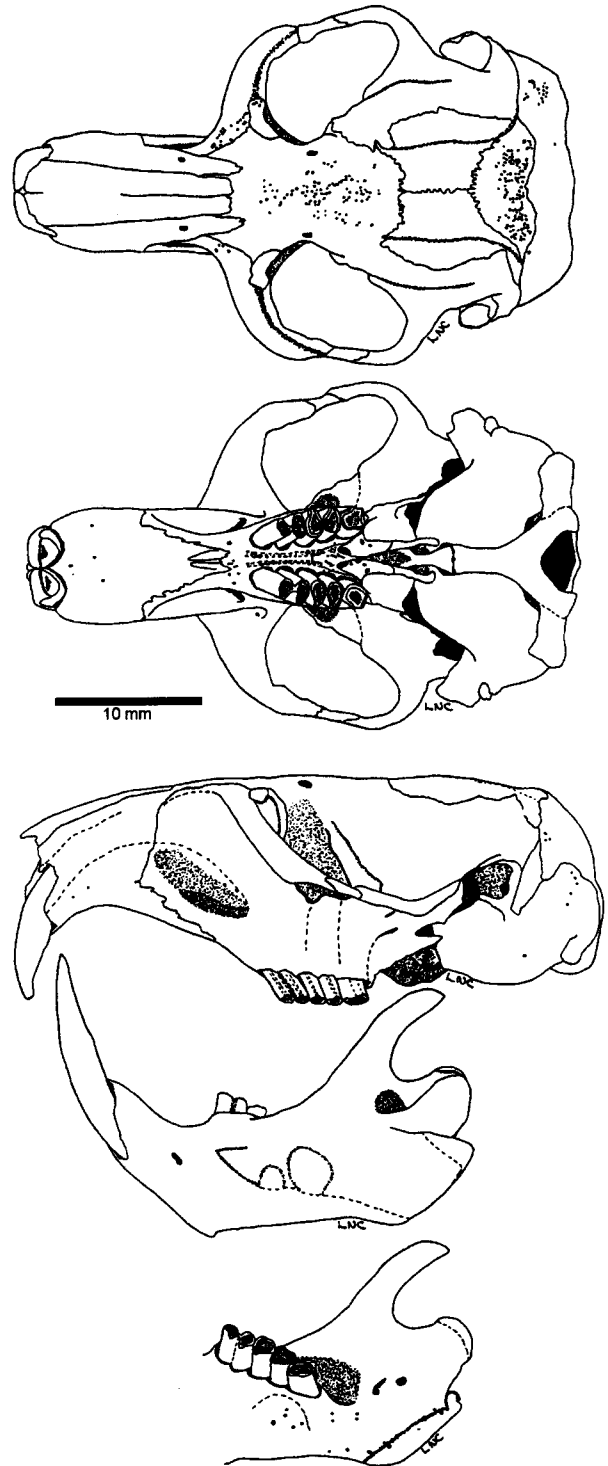


FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral and oblique views of the mandible of adult female *Thomomys talpoides* (OSUFW 5090) from Glendive, Dawson Co., Montana. Greatest length of skull is 38.96 mm.

gual face of p4 (Fig. 2; Thaeler, 1980); anterior prism of P4 triangular (Fig. 2; Durrant, 1946); incisive foramina anterior to infra-orbital canal (Hoffmeister, 1986); and a baculum 12–17 mm long (Johnson and Benson, 1960). Specimens of *T. talpoides* from nearby populations, at least, can be distinguished from *T. clusius* by 48 or 56 chromosomes (as opposed to 46 in *clusius*) and presence of dark periauricular patches (Thaeler and Hinesley, 1979). Serrate interparietal and fronto-parietal sutures, a shorter and wider interparietal, and parallel temporal ridges were considered useful for dis-

tinguishing *T. talpoides* from its similar sized congener, *T. mazama* by Ingles (1965) and Johnson and Benson (1960), but not by Verts and Carraway (1998).

GENERAL CHARACTERS. As in other members of the family (Hill, 1937; Holliger, 1916), *T. talpoides* is a powerfully built mammal adapted to fossorial environments and characterized by heavily muscled head and shoulders without a noticeable neck, body tapering posteriorly to relatively narrow hips, short legs, and small eyes and pinnae. Toes on the forelegs have long, tapering claws and are equipped with fimbriae; incisors are not highly procumbent; fur-lined cheek pouches open external to the mouth; and vibrissae extend well beyond the width of the head (Merriam, 1895). The lips close behind the incisors.

The skull (Fig. 2) is flattened dorsally; zygomata are wide-spreading; mandibles are heavy and irregular (Bailey, 1915); nasals, frontals, and parietals form nearly a straight line; jugals are restricted to the horizontal part of zygomata (Merriam, 1895). Temporal and lambdoidal ridges are prominent in older individuals. As in other members of the subgenus *Thomomys*, bases of M1s are not inclined posteriorly and bases of I1s do not enter the space between P4 and M1 (Thaeler, 1980). Although enamel faces of upper incisors of *Thomomys* usually are classified as asaculate, Akersten (1973) found all 266 *T. talpoides* that he examined to possess a lingual groove, 32 (12.0%) to possess a medial groove, and 6 (2.3%) to possess an atypical groove. W. A. Akersten (in litt., 28 July 1997) indicated that grooves he described as "lingual" and "medial" were those nearest the point of appression of the incisors and the midline of face of the incisor, respectively.

The pelage of *T. talpoides* is long, fine, and silky in winter, thin and harsh in summer (Bailey, 1915). The underfur is plumbeous, but the dorsal overpelage is rich brownish or brownish gray grading to buff on the venter. The chin is white and postauricular patches blackish or grayish black. The naked tail commonly is brownish with a white tip and the feet commonly are white or partly white (Durrant, 1952; Hall, 1946; Verts and Carraway, 1998). One or more molt lines commonly dissect the pelage.

Ranges in average values of external measurements (total length, length of tail, and length of hind foot, in mm) were as follows: 180–227, 52–72, and 25–30 for 11 currently recognized subspecies of *T. talpoides* in Washington (Dalquest, 1948); 131–246, 49–73, and 25–30 for 10 subspecies in Utah (Durrant, 1952); 173–216, 48–61, and 24–28 for 5 subspecies in Nevada (Hall, 1946); 205–229, 61–70, and 26–31 for 3 subspecies in Idaho (Davis, 1939); 210–236, 55–60, and 29–32 for 3 subspecies in Colorado (Warren, 1942); 200–266, 54–67, and 27–29 for 3 subspecies in the Black Hills of South Dakota and Wyoming, and surrounding areas (Turner, 1974); 185–212, 55–62, and 25–28 for 3 subspecies in Oregon (Verts and Carraway, 1998); 201–210, 61–62, and 27–28 for 2 subspecies in Arizona (Hoffmeister, 1986); and 220–250, 58–80, and 29–33 for 1 subspecies in Minnesota (Hazard, 1982). Ranges in dimensions for individuals recorded in these studies (except those of Turner, 1974 and Warren, 1942) are 160–253, 43–80, and 20–33. For studies in which dimensions for the sexes were reported separately, averages for total length, length of tail, and length of hind foot were 0–9.9, 0–9.4, and 0–8.3% greater for males than females, respectively. Body mass for adults ranged from 64.3 to 99.7 g in Oregon (Verts and Carraway, 1998), 75.1–131.4 g in Nevada (Hall, 1946), and 75–180 g in Wyoming (Clark and Stromberg, 1987). In Utah, average ($\pm SE$) body mass for 14 adult females was 91.4 ± 1.6 g and 104.4 ± 3.4 g for five adult males (Andersen, 1978). Turner (1974:85, Table 14) recorded an average ($\pm SD$) body mass of 140.6 ± 19.8 g for *T. talpoides* in the Black Hills, and Banfield (1974) recorded an individual 257 mm long that weighed 209 g in Canada. In general, among subspecies, *talpoides*, *ravus*, and *nebulosus* are largest, and *wallowa* and *quadratus* are smallest.

Ranges in average values of selected skull measurements (basilar length, zygomatic breadth, mastoid breadth, interorbital breadth, and length of maxillary tooththrow, in mm) were the following: 28.1–35.2, 19.2–24.7, 17.3–21.4, 6.0–6.9, and 6.9–8.3 for nine currently recognized subspecies in Utah (Durrant, 1952); 28.2–33.7, 19.9–24.3, 16.9–19.4, 6.2–6.5, and 6.8–7.8 for four subspecies in Nevada (Hall, 1946); 28.6–34.0, 19.7–22.3, 16.8–19.4, 6.3–7.5, and 7.2–7.8 for three subspecies in Oregon (Verts and Carraway, 1998); and 32.1–32.2, 21.0–21.1, 18.4, 6.1, and 7.5–7.6 for two subspecies in Arizona (Hoffmeister, 1986). For

studies in which dimensions for the sexes were reported separately, averages for basilar length were from 0.6% smaller to 10.9% larger, for zygomatic breadth from 2.4% smaller to 13.6% larger, for mastoid breadth from 3.4% smaller to 12.1% larger, for interorbital breadth from 3.2% smaller to 3.5% larger, and for length of the maxillary tooththrow from 1.4% smaller to 8.8% larger in males. The common pattern of larger size in males was reversed in several dimensions in *durranti* (Durrant, 1952).

Northern pocket gophers at higher elevations and on thinner soils are smaller and exhibit less sexual dimorphism (Davis, 1938), likely a reflection of habitat quality as body size of this and other species of pocket gophers is related to nutritional quality of available vegetation (Hansen and Bear, 1964; Smith and Patton, 1988; Tryon and Cunningham, 1968).

DISTRIBUTION. The distribution of *Thomomys talpoides* (Fig. 3) extends southward from a line connecting the following: Salmon Arm, British Columbia; Edmonton, Alberta; Prince Albert, Saskatchewan; and Swan River and Winnipeg, Manitoba along the east side of the Cascade and Sierra Nevada ranges in Washington, Oregon, and California, then eastward to extreme northwestern Minnesota, eastern North Dakota and South Dakota, southwestern Nebraska, and eastern Colorado. Southward extensions and disjunct populations occur in Arizona, Nevada, New Mexico, and Utah (Fig. 3).

We did not demarcate ranges for nominal subspecies (Hall, 1981) because of evidence that the taxon includes more than one species (Patton, 1993; Smith and Patton, 1988; Thaeler, 1968b, 1974a, 1974b, 1976). Instead, to illustrate geographic variation, we provide maps of type localities for nominal subspecies and diploid (2n) chromosome numbers (Fig. 3).

FOSSIL RECORD. *Thomomys talpoides* possibly descended from *T. gidleyi* (Kurtén and Anderson, 1980), an extinct species recorded in the Hemphilloblancon (Pliocene) and occurring in early Blancan mammal faunas (Savage and Russell, 1983). The earliest record of *T. talpoides* is from Sangamonian (late Pleistocene) deposits along the South Saskatchewan River near Medicine Hat, Alberta (Kurtén and Anderson, 1980). Later records of Wisconsinian age within the present-day range are from cave deposits in Alberta, Colorado, Idaho, Nevada, Utah, Washington, and Wyoming (Burns, 1987; Harris, 1985); extralimital records are known from Iowa, Kansas, Missouri, Montana, New Mexico, Oklahoma, and Texas (Dalquest and Baskin, 1992; Faunmap Working Group, 1994; Kurtén and Anderson, 1980; McMullen, 1978; Rhodes, 1984).

FORM AND FUNCTION. Ranges of dimensions (in mm) of the phallus among nine subspecies of *T. talpoides* are as follows: length of distal tract, 14.0–26.2; length of glans, 6.6–13.0; length of protractal tip, 3.1–5.9; width of glans across collar, 1.7–3.2; width of glans across base, 1.7–2.4; length of baculum, 12.3–22.6; width of base of baculum, 1.1–2.4; and height of base of baculum, 1.1–1.9. Western races tend to have smaller bacula than those in the eastern portion of the range (Williams, 1982), but the relationship between body size and size of the baculum is not significant (Patterson and Thaeler, 1982).

Where *T. talpoides* is parapatric with *T. mazama*, a congener of similar body size, the baculum is short and thick in comparison; among adults in the region it is only 12–17 mm long (Johnson and Benson, 1960). It is slightly curved and tapers from a slightly bulbous base to a thin point that becomes somewhat spatulate in older individuals. In autumn and winter, baculum length in prepubertal male *T. mazama* may fall within the 12–17 mm range of *T. talpoides* in this region, but length in relation to diameter of the base in the latter species is much less. Johnson and Benson (1960) described a juvenile *T. mazama* with a baculum 0.65 mm in diameter at the base and 13.3 mm long; they indicated that the baculum with the same basal diameter in a juvenile *T. talpoides* would be <10 mm long.

Growth of upper incisors of samples of two nominal races of *T. talpoides* from Colorado maintained in captivity averaged ($\pm SE$) 0.54 ± 0.017 mm/day and 0.58 ± 0.24 mm/day; growth of lower incisors averaged ($\pm SE$) 0.92 ± 0.13 mm/day and 1.08 ± 0.05 mm/day. Rates of the two samples are significantly different. Greatest rates of growth among individuals in the samples were 0.68 mm/day for upper incisors and 1.22 mm/day for lower incisors, or nearly 25 and 45 cm/year, respectively. Growth rates of both upper and lower incisors were significantly correlated positively with body

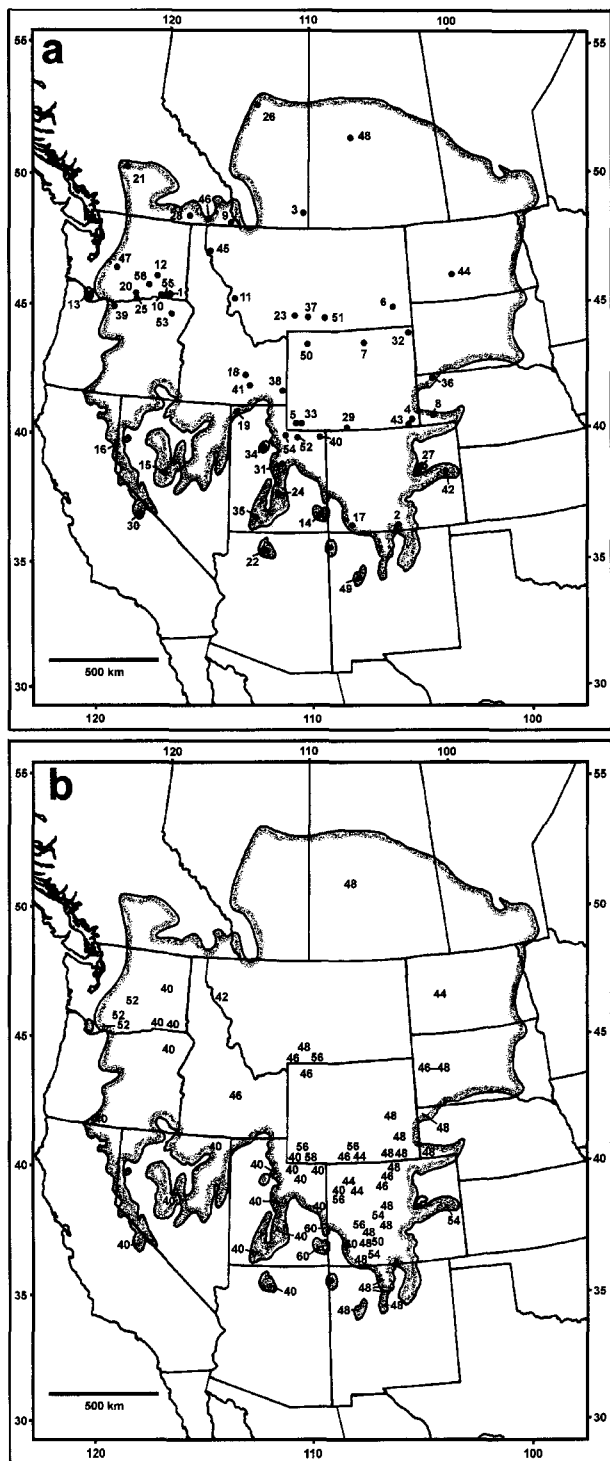


FIG. 3. Distribution of the *Thomomys talpoides* complex modified from Hall, 1981: a, type localities of nominal subspecies (numerals correspond to those following subspecies listed in Context and Content); and b, diploid ($2n$) chromosome numbers reported for specimens from various localities (Nevo et al., 1974; Thaeler, 1968b, 1974b, 1976, 1980).

mass (Miller, 1958). Dental formula is $i\ 1/1$, $c\ 0/0$, $p\ 1/1$, $m\ 3/3$, total 20; premolars are 8-shaped, almost appearing as two teeth (Verts and Carraway, 1998). Mammal formula varies by nominal subspecies: seven pairs (2-2 inguinal, 2-2 abdominal, 3-3 pectoral) in *ocius*; six pairs (2-2, 2-2, 2-2) in *columbianus*, *devexus*, *nebulosus*, *pygmaeus*, *rufescens*, and *talpoides*; five pairs (2-2, 0-0, 3-3) in *bridgeri*, *fisheri*, *fossor*, *quadratus*, and *uinta*; and four pairs

(2-2, 0-0, 2-2) in *douglasii*, *fuscus*, *incensus*, *kelloggi*, *medius*, *relicinus*, *tenellus*, and *trivialis* (Bailey, 1915; Goldman, 1938).

Alignment of enamel ridges on all upper cheek teeth of *T. talpoides* deviated significantly from 90° to the midsagittal plane of the skull; angles ranged from 76.6° to the left anterior column of P4 to 98.9° for the right M2 and M3. Alignment of scars on ridges, resulting from wear, deviated significantly from parallel to the midsagittal plane of the skull for all upper cheek teeth; values ranged from -1.3° on right M1 and M3 to -3.3° on left M3 (Wilkins, 1988). These values, combined with those for congeners, led to the conclusion that chewing in extant *Thomomys* is propalinal.

Body temperatures of *T. talpoides* averaged ($\pm SE$) $36.9 \pm 0.1^\circ C$ at ambient temperatures of 1.0 – $30.0^\circ C$, but at ambient temperatures above $32.0^\circ C$, body temperatures increased dramatically, and exposure to ambient temperatures $>37.5^\circ C$ for 1 h often was fatal. Thermoneutrality was ca. 26.0 – $32.0^\circ C$ (Gettinger, 1975). Metabolic rates of *T. talpoides* at rest as determined by oxygen consumption were related inversely to ambient temperature. Within the thermoneutral zone, oxygen consumption averaged ($\pm SE$) $1.33 \pm 0.03\ ml\ g^{-1}\ h^{-1}$ and was 124% of that predicted; thermal conductance was 84% of that predicted (Gettinger, 1975). During burrowing, oxygen consumption averaged $16.3\ ml\ g^{-0.75}\ h^{-1}$, but was not related to physical property or temperature of soil (Andersen and MacMahon, 1981). Evaporative water loss increased with ambient temperatures, but not logarithmically as in many species of small mammals; panting or salivation was not noted at higher temperatures (Gettinger, 1975).

For *T. talpoides* taken at 2,900 m in Colorado, hemoglobin concentration was $13.7\ g/100\ ml$, hematocrit was 45.2%, and mean corpuscular hemoglobin concentration was 30.3%. In a positive relationship between hemoglobin concentration and hematocrit plotted for 36 taxa of small mammals, that of *T. talpoides* was in the lowest quartile (Sealander, 1964).

ONTOGENY AND REPRODUCTION. At Livermore, Colorado (ca. 1,800 m elevation), monthly average ($\pm SE$) widths (in mm) of uterine horns of adult females attained a peak in May (4.3 ± 0.3 ; range, 2.0–6.0; $n = 20$) and a nadir in November (1.9 ; range, 1.5–2.0; $n = 5$ —Hansen, 1960). Average lengths (in mm, $\pm SE$) of testes of adult males during the same months peaked in March (22.9 ± 0.3 ; range, 20–25; $n = 24$) and was lowest in November (11.3 ± 0.2 ; range, 10–13; $n = 6$ —Hansen, 1960). At 3,020 m elevation in Colorado, average lengths (in mm, $\pm SE$) of testes during May–September were 19.0 ± 0.54 , 16.8 ± 0.33 , 14.5 ± 0.45 , 11.3 ± 0.42 , and 9.7 ± 0.95 , respectively (Vaughan, 1969).

Hansen (1960) cited Scheffer (1938) in speculating that the gestation period of *T. talpoides* was ca. 28 days. However, Andersen (1978) reported that a female, placed with a male three times commencing 24 h after capture and observed to copulate 48 h after capture, gave birth 18 days later. Reid (1973) estimated a gestation period of 19 days, the same that Schramm (1961) estimated for *T. bottae*.

The breeding season extends from ca. mid-March to ca. mid-June in Colorado (Hansen, 1960), Washington (Scheffer, 1938), and Oregon (Moore and Reid, 1951). Vaughan (1969) claimed that *T. talpoides* at 3,020 m in Colorado bred in May or June, but indicated (p. 63, fig. 6) that one taken in August was pregnant.

Litter size in *T. talpoides* is highly variable. Reported averages ($\pm SE$) based on counts of embryos during different years at different localities in Colorado (Hansen, 1960) were 6.4 ± 0.2 ($n = 88$), 4.4 ± 0.2 ($n = 33$), 4.7 ± 0.2 ($n = 33$), and 4.9 ± 0.1 ($n = 12$). Also, in Colorado, average ($\pm SE$) litter size based on counts of embryos and pigmented sites of implantation ranged from 3.3 ± 0.3 to 4.6 ± 0.2 during a 6-year period (Hansen and Ward, 1966). Averages in other regions were 4.8 in Wyoming (Wirtz, 1954), 5.2 (Andersen, 1978) and 4.9–5.6 in Utah (Andersen and MacMahon, 1981), 4.4 in Montana (Tryon, 1947), 6.3 (Wight, 1930) and 6.6 (Moore and Reid, 1951) in Oregon, 6.3 in Washington (Scheffer, 1938), and 2.9 in Manitoba (Criddle, 1930). In Oregon, repeated trapping within individual burrow systems revealed an average of 2.8 young, causing Wight (1930) to suggest that young experienced heavy mortality or some young dispersed before sampling commenced; he favored the latter explanation. Proportion of females producing litters also varies. In Utah, 62.5–100% of small samples bred annually during a 4-year period, but differences among years were not significant (Andersen and MacMahon, 1981). In Oregon,

all of 32 captured 1–10 May were either pregnant, recently parturient, or in breeding condition (Moore and Reid, 1951). Because of the short gestation and relatively long breeding season, a sample of adult females collected during a short period within this season likely would contain a proportion without evidence of reproductive activity. Indeed, Wight (1930) reported that only 79% of 112 mature females collected from 14 March to 11 April were reproductively active.

Synchronous capture of pregnant females and juveniles in burrow systems was suggested to indicate that some females produce more than one litter annually (Burt, 1933; Wight, 1930). However, Hansen (1960:332) found “no evidence of more than one annual litter per female . . . in the Rocky Mountain region” and suggested that capture of pregnant females and young in the same burrow system was not a reliable indicator of brood frequency.

In Utah, average ($\pm SE$) mass of neonates was 3.58 ± 0.09 g in five litters of five but 2.77 ± 0.14 g in a litter of six, a significant difference. However, total mass of the six litters averaged 17.65 ± 0.46 g and that of the litter of six was not significantly different from those of five (Andersen, 1978). Increase in body mass with age was exponential ($r^2 = 0.97$) with mass = $3.652^{0.0828X}$ for ≤ 30 days of age but followed the cubic model ($r^2 = 0.85$) with mass = $-52.95 + 4.42(X) - 0.0444(X^2) + 0.000147(X^3)$ at ≥ 30 days of age (where X is age in days—Anderson, 1978).

Neonates at 1 day of age are hairless; eyes appear as pigmented spots beneath closed lids and pinnae appear as tiny protrusions in the skin (Andersen, 1978). Young thought to be 2–3 days old were “semi-transparent dark pink color, naked, blind and toothless” (Criddle, 1930:269); the body was thick; tail and legs were short; and cheek pouches were shallow. They produced a “squawk” when handled (Criddle, 1930:270). At 9 days, grayish-black dorsal and sparse, whitish ventral pelages are evident; both upper and lower incisors are separated by a gap; and the young can crawl backwards. At 16 days, incisors are appressed, claws on front feet are prominent, pinnae are distinct, and young move about readily. Young commence to eat solid food by day 17, but at day 20, eyes, pockets, and auditory meatuses remain closed. Eyes and meatuses open by day 26, and by day 39 young carry foodstuff in their pouches (Andersen, 1978). Young reproduce in the calendar year following birth (Moore and Reid, 1951).

In captivity, disturbance caused by weighing young caused maternal females to abandon nests, whereupon young crawled about the cage. Although maternal females did not overtly reject the young, they did not retrieve them and most died (Andersen, 1978; Criddle, 1930). Young remain with the maternal parent for 6–8 weeks (Criddle, 1930).

ECOLOGY. Distributions of various species of Geomyidae, with few exceptions, are allopatric or parapatric (Thaeler, 1968a; Vaughan and Hansen, 1964). In Minnesota, *T. talpoides* and *Geomys bursarius* reportedly were separated by soil type, with the former occupying clays, the latter occupying lighter soils (Quimby, 1942). In a region of parapatry with *T. bottae* in Colorado, mixed populations established experimentally in three areas originally occupied by either one or the other, or both species, revealed that *T. talpoides* and *T. bottae* could live and reproduce side-by-side in all three areas. However, *T. talpoides* was able to occupy a greater variety of soil types and soil depths, and was able to reproduce and survive better than *T. bottae* in areas where it originally occurred alone or with *T. bottae*, but not where *T. bottae* originally occurred alone. Vaughan and Hansen (1964) believed that *T. talpoides* held a competitive advantage because of its greater dispersal capabilities and greater environmental tolerances. Average distance dispersed by *T. talpoides* was 239 m; maximum distance was 790 m (Vaughan, 1963). Long-distance dispersal commonly is beneath the snow (Marshall, 1941).

Miller (1964:256) claimed that all four species of pocket gophers in Colorado “prefer” deep light soils, but the greatest factors in relationships among the four species were soil tolerance and competition. He indicated that the species with the strictest niche requirements was the superior competitor and was able to displace others to less favorable habitats. On this basis, *T. talpoides* was considered subordinate to the other species (Miller, 1964). However, in paired encounters, Baker (1974) found that *T. talpoides* was dominant to *T. bottae*, one of the species with narrower niche requirements. He concluded that aggression may not be the mode

of competitive interference among different species of pocket gophers.

In many regions, *T. talpoides* occupies a unique topography consisting of 25–50 mounds/ha, each ca. 2 m high and 20–30 m in diameter (Cox and Hunt, 1990). These mounds, called “Mima mounds,” are thought by many (Arkley and Brown, 1954; Cox, 1984, 1990a, 1990b, 1990c; Cox and Allen, 1987a, 1987b; Cox and Gakahu, 1986; Cox and Hunt, 1990; Cox et al., 1987; Dalquest and Scheffer, 1942; Murray, 1967; Price, 1949) to be formed by burrowing activities of pocket gophers, although others believe the mounds result from seismic activity (Berg, 1990a, 1990b) or other, largely refuted, inanimate forces (Cox, 1984, 1990c; Dalquest and Scheffer, 1942). No Mima-mound areas are known from east of the Mississippi River where areas occupied by pocket gophers are limited (Price, 1949). Most Mima-mound areas are in grasslands on “poorly drained soils with a shallow basement layer or permanent water layer” (Cox, 1984:1397). Cox (1989) believed that Mima mounds are formed by soil being gradually displaced backward toward well-drained sites with deep soils as gophers burrow outward from their centers of activity. Mounds occupied by only one gopher tend to be small, smooth, relatively tall, and dome-shaped, whereas larger, flatter mounds are occupied by two or more individuals. Therefore, size of mounds and number of pocket gopher territories per mound are correlated strongly ($r = 0.935$ —Cox and Hunt, 1990). Areas between mounds have thin soils containing beds of sorted stones thought to be produced by the burrowing activities of pocket gophers. In Oregon, bluebunch wheatgrass (*Agropyron spicatum*) and Idaho fescue (*Festuca idahoensis*) predominate on Mima mounds, and stiff sagebrush (*Artemisia rigida*), pine bluegrass (*Poa scabrella*), bitterroot (*Lewisia rediviva*) and biscuit-root (*Lomatium*) dominate intermound areas (Cox, 1989). In Colorado, Mima mounds usually are occupied by adult *T. talpoides*, whereas juveniles tend to occur on intermound areas; thus, “high-ground” provided by mounds differentially favors survival of adults during snowmelt (Hansen, 1962).

In four stages of the spruce (*Picea engelmannii*)-fir (*Abies lasiocarpa*) climax sere in Utah in which 77–95% of aboveground biomass of herbaceous vegetation was forbs, ranges in densities of *T. talpoides* were 6.2–22.9/ha in spring and 12.5–62.5/ha in autumn in meadow, 2.1–16.7/ha in spring and 2.1–33.3/ha in autumn in aspen (*Populus tremuloides*), 0–4.2/ha in spring and 0–10.4/ha in autumn in fir, and 0–1.0/ha in spring and 0–1.0 in autumn in spruce (Andersen and MacMahon, 1981). Also, in Utah, estimates of density for populations of *T. talpoides* in early summer were 5.3–16.9/ha (2 years) in meadow, 2.1–14.4/ha (3 years) in aspen, 6.3/ha (1 year) in fir, and 0.4/ha (1 year) in spruce. In late summer, estimates in the same communities were 14.4–54.4/ha (3 years), 4.4–33.1/ha (3 years), 6.2–12.5/ha (2 years), and 4.4/ha (1 year). The contribution by *T. talpoides* to the total biomass of mammals (ungulates excluded) in each of the four mammal communities was 83, 70, 20, and 7%, respectively, in 1976, and 81, 67, 5, and 2%, respectively, in 1977 (Andersen et al., 1980). During a 3-year study at 3,020 m in subalpine parks in Colorado, densities in early summer were 6.2–12.4/ha and 14.8–34.6/ha in late summer; much variation in late summer was attributed to differences in survival of young (Vaughan, 1969). Hansen and Remmenga (1961) recorded a density of 91.6/ha on rangeland in Colorado. Dispersion at low densities tended to be clumped in optimal habitats, but at high densities it became more uniform (Hansen and Remmenga, 1961).

In a 930-m² enclosure in Colorado, mortality in introduced populations was ca. 10% per month during June–September and ca. 13% per month during September–June; 63% survived the summer period, but only 17% survived the winter (Hansen, 1965). Similarly, weekly survivorship in Utah was greater in summer than winter; annual survival rates were ≥ 0.27 , 0.18, 0.23, and 0.70 during a 4-year period (Andersen and MacMahon, 1981). Some *T. talpoides* survived the explosive eruption of Mount St. Helens, Washington, on 18 May 1980, but reproductive output or survival of young was low as most individuals captured were adults. Survival to the following year was ca. 10%, a value considered extremely low (Andersen, 1982).

In Oregon, *T. talpoides* probably eats most species of succulent plants within its range. It probably selects dandelions (*Taraxacum officinale*) over other species, but roots and tubers of bluegrass (*Poa*), oniongrass (*Melica fugax*), yampa (*Perideridia gairdneri*), American bistort (*Polygonum bistortoides*), agoseris (*Agoseris*), onion (*Allium*), yellow fritillary (*Fritillaria pudica*), fawnlily

(*Erythronium grandiflorum*), and brodiaea (*Brodiaea*) also were consumed (Moore and Reid, 1951). In Montana, spring foods of *T. talpoides* consisted primarily of *Geranium*, *Trifolium*, *Vicia*, *Achillea*, *Phleum*, *Frititaria*, and *Balsamorhiza* (Tryon, 1947). In a short-grass prairie region in Colorado, *T. talpoides* consumed 67% forbs, 30% grasses, and 3% shrubs; the major components of the diet were *Opuntia polyacantha* (49.9%), *Stipa comata* (12.1%), *Sphaeralcea coccinea* (10.3%), *Agropyron smithii* (10.1%), *Bouteloua gracilis* (3.0%), and *Atroplex canescens* (2.5%)—Vaughan, 1967). In a subalpine area in Colorado (elevation = 3,020 m), 87% of the summer diet consisted of leaves of forbs, 1% grasses, and 12% roots (Vaughan, 1974). Also in Colorado, where the vegetation was composed of 50% grasses, 42% forbs, and 8% shrubs, the summer diet of *T. talpoides* was composed of 6% grasses, 93% forbs, and 1% shrubs; 74% of the diet was aboveground parts of plants and only 26% consisted of roots. Plant species that composed most of stomach contents (percent volume in parentheses) were *Erigeron speciosus* (24.2), *Chrysopsis villosa* (16.4), *Lupinus* (15.4), *Lathyrus leucanthus* (7.5), *Collomia linearis* (6.7), *Geranium fremonti* (5.5), *Potentilla pulcherrina* (4.1), *Achillea lanulosa* (3.8), *Taraxicum officinale* (2.9), and *Agoseris* (1.6—Ward and Keith, 1962). At elevations of 2,750–3,050 m in Utah, species consumed most frequently and in greatest amounts were dandelion, penstemon (*Penstemon rydbergii*), sweet sage (*Artemisia discolor*), meadowrue (*Thalictrum fendleri*), and slender wheatgrass (*Agropyron trachycaulum*); these species composed 71.9% of the dry mass of plants eaten (Aldous, 1951). *T. talpoides* is capable of selecting plants with higher levels of protein and fat from among those available (Tryon and Cunningham, 1968).

In addition to consuming roots and tubers encountered underground, aboveground plants near burrow entrances also are cut and pulled into burrow systems; some plants are cut into small pieces and carried in cheek pouches to the nest where they are consumed. In a Colorado short-grass prairie region, 70% of foods consumed by *T. talpoides* were aboveground parts of plants (Vaughan, 1967), but in montane regions of Utah, most foods eaten were underground parts of plants encountered during excavation of tunnels (Aldous, 1951). In Montana, consumption of belowground parts of plants was $\geq 80\%$ during September–April, declined to 0% in June, and fluctuated irregularly during July–August (Ward, 1960).

During tunneling, a population of 10.2–40.6 northern pocket gophers/ha in Utah excavated ca. 11.5 metric tons of earth/ha to form mounds that covered 3.5% of the surface (Ellison, 1946). On subalpine grassland, quantity of vegetative production was not affected by removal of *T. talpoides*, but where the species was not removed, abundance of dandelions declined and abundance of grasses and sedges increased (Ellison and Aldous, 1952). Soils were softer and looser where pocket gophers were present. On aspen range in Utah, mounds created during excavation of burrows were bare during the 1st year, dominated by annuals with a few seedlings of perennials during the 2d year, and dominated by perennials (especially coneflower, *Rudbeckia*) with annuals in peripheral areas during 3d and 4th years after construction (McDonough, 1974). *Rudbeckia* had high mortality as a result of foraging by pocket gophers where aspen was removed (Marston and Julander, 1961). Pocket gophers, especially *T. talpoides*, interfere significantly with regeneration of ponderosa pine (*Pinus ponderosa*), and to a lesser extent, lodgepole pine (*P. contorta*) forests (Barnes, 1973). Removal of pine seeds possibly was the work of *Peromyscus maniculatus* that traveled along tunnels constructed by *T. talpoides* (Moore, 1943). A variety of equipment, repellents, toxicants, and techniques were developed to reduce the real or presumed impact of *T. talpoides* on forest and range resources (Anthony et al., 1978; Barnes, 1973; Barnes et al., 1970; Keith et al., 1959; Richens, 1965a; Sullivan et al., 1988, 1990; Ward and Hansen, 1962; Ward et al., 1967; Wick and Landforce, 1962).

In a Mima-mound area, underground parts of plants occurred in 12 of 15 stomachs of *T. talpoides* collected in early summer in Oregon, composing an average of 20.7% (range, 0–100%) of stomach contents. Shoots composed 79.1% of the contents of which 2.4% was grasses and 97.0% was forbs. *Lupinus caudatus* (56.1% of stomach contents), *Erigonum heracleoides* (12.5%), and *Achillea millefolium* (4.6%) composed most of the diet (Cox, 1989). In cafeteria-style tests of 14 potential food items conducted in a Mima-mound area, species typical of mounds were taken significantly less

frequently than those typical of intermound areas. Grasses were not considered an adequate diet for *T. talpoides* (Cox, 1989).

In subnivean environments, *T. talpoides*, in addition to consuming forbs and grasses, feeds on various trees and shrubs, sometimes, depending upon depth of the snow, at considerable height above the surface of the ground. Cuttings on trees 1–2 m above the ground by pocket gophers often are attributed erroneously to porcupines (*Erethizon dorsatum*)—Moore, 1940; Moore and Reid, 1951).

In Utah, five food caches of *T. talpoides* collected in late summer contained an average of 380 g (range, 164–611 g) of stored foodstuff; composition of stored materials was 70.9% dandelion, 18.5% tuber starwort (*Stellaria jamesiana*), 2.9% dogtooth violet (*Erythronium*) bulbs, and 7.6% lanceleaf springbeauty (*Clatonia lanceolata*) bulbs (Aldous, 1945). A winter cache in the snow contained 320 g of dandelion plus three shoots and one bulb of dogtooth violet; another was much more diverse with 2 g of oniongrass, 23 g of tuber starwort, 3 g of peavine (*Lathyrus*), 249 g of spring beauty, 8 g of saxifrage (*Saxifrage*), 18 g of Indian potato (*Orogenia*), and a trace of miscellaneous stems (Aldous, 1945). Materials cached in snow provided more energy than protein in terms of maintenance requirements, but they permitted survival during commonly encountered adverse environmental conditions (Stuebe and Andersen, 1985). *T. talpoides* ate high-protein items as they encountered them, but cached foodstuffs with lower protein content. *T. talpoides* in Oregon may not cache food (Moore and Reid, 1951).

Energy requirements estimated for individual *T. talpoides* in Utah were 161.5 kJ/day plus 7.1 kJ day⁻¹ °C⁻¹ when ambient temperatures are below thermoneutrality. At high density, estimated requirements were 1,087 MJ ha⁻¹ year⁻¹, or considerably greater than that reported for most populations of nonfossorial rodents (Andersen and MacMahon, 1981). High-density populations of *T. talpoides* may consume >30% of the net annual primary production allocated to below ground plant parts (Andersen and MacMahon, 1981). Vaughan (1974:793) claimed that pocket gophers were the dominant mammals in Colorado subalpine ecosystems and that "... not only the character of the vegetation but the distribution and abundance of several small mammals and the local patterns of movements of some migrating birds were seemingly strongly influenced by the activities" of *T. talpoides*. Andersen (1987) concurred by indicating that pocket gophers and other fossorial animals influenced the structure and function of natural biotic communities.

On an area treated with the herbicide 2,4-D in Colorado that reduced production of forbs by 83% and increased production of grasses by 37%, the diet of *T. talpoides* shifted from 82% forbs and 18% grasses to 50% each forbs and grasses. Tietjen et al. (1967) reported that *T. talpoides* lost body mass when forced to eat grasses. Also, the population of *T. talpoides* on a treated area declined by 87% (Keith et al., 1959), but the following year the population on a nearby control area declined by 74% (Hansen and Ward, 1966). As treated rangeland vegetation reverted to the perennial forb type, the population of *T. talpoides* became more dense than on untreated areas (Hansen and Ward, 1966).

Mammals associated with *T. talpoides* include *Brachylagus idahoensis*, *Canis latrans*, *Clethrionomys gapperi*, *Dipodomys ordii*, *Erethizon dorsatum*, *Glaucomys sabrinus*, *Lemmys curtatus*, *Lepus americanus*, *L. californicus*, *L. townsendii*, *Lynx rufus*, *Marmota flaviventris*, *Mephitis mephitis*, *Microtus longicaudus*, *M. montanus*, *Mustela frenata*, *M. erminea*, *Neotoma cinerea*, *Onychomys leucogaster*, *Perognathus parvus*, *Peromyscus maniculatus*, *P. truei*, *Phenacomys intermedius*, *Reithrodontomys megalotis*, *Sorex merriami*, *S. nanus*, *S. preblei*, *S. vagrans*, *Spermophilus armatus*, *S. elegans*, *S. lateralis*, *Spilogale gracilis*, *Sylvilagus nuttallii*, *Tamias umbrinus*, *T. minimus*, *T. amoenus*, *T. quadrivittatus*, *Tamiasciurus hudsonicus*, *Taxidea taxus*, and *Zapus princeps* (Andersen et al., 1980; Belk et al., 1988; Borell and Ellis, 1934; Thompson, 1977; Vaughan, 1961; Williams, 1984). Many of these species use burrow systems excavated by *T. talpoides*.

Gopher snakes (*Pituophis catenifer*) prey on *T. talpoides*, and rattlesnakes (*Crotalus viridis*) and long-tailed weasels (*Mustela frenata*) were taken within their burrow systems (Vaughan, 1961). Known or suspected mammals that prey on *T. talpoides* are *Canis latrans* (Hansen and Ward, 1966; Wells and Bekoff, 1982), *Lynx rufus* (Koehler and Hornocker, 1991; Young, 1958), *Martes americana* (Weckwerth and Hawley, 1962), *Mustela frenata* (Criddle, 1930; Hansen and Ward, 1966), and *Taxidea taxus* (Criddle,

1930). Foxes and skunks (species not specified) sometimes take gophers (Criddle, 1930).

In Oregon, remains of *T. talpoides* occurred in 6.6% of 347 regurgitated pellets of burrowing owls (*Speotyto cunicularia*—Maser et al., 1971) and 56% of 1,128 pellets of long-eared owls (*Asio otus*—Bull and Wright, 1989); 29% of prey items in 1,923 pellets of great gray owls (*Strix nebulosa*) were *T. talpoides* (Bull et al., 1989). In Colorado, *T. talpoides* comprised 56 (33.7%) of 166 mammals identified in regurgitated pellets of great horned owls (*Bubo virginianus*), 120 (15.0%) of 798 in those of barn owls (*Tyto alba*), 1 (5.3%) of 19 in those of burrowing owls, and 1 (0.1%) of 993 in those of long-eared owls (Marti, 1969). Mean body mass of *T. talpoides* consumed by three species of owls was related to the size of the predator: 67.9 g by great horned owls, 63.3 g by barn owls, and 41.0 g by long-eared owls (Janes and Bars, 1985). In Washington where 5 cm of tephra fell after eruption of Mount St. Helens, *T. talpoides* appeared in small numbers ($\leq 1\%$ of prey items) in pellets of the burrowing owl collected June–August in 1980 and in 1981 (Grimm et al., 1985).

Parasites of *T. talpoides* include the fleas (Siphonaptera) *Foxella ignota recula*, *F. i. utahensis*, *Spicata c. comis*, *Spicata m. moorei*, *S. nuditenacula*, *Epitedia scapani*, *Meringis hubbardi*, *Orchopeas sexdentatus cascadenis*, and *Micropsylla sectilis* (Hubbard, 1941, 1943; Lewis et al. 1988; Miller and Ward, 1960; Tryon, 1947; Whitaker et al., 1985) and the chewing lice (Mallophaga) *Geomydoecus thomyus*, *G. duchesnensis*, *G. dakotensis*, and *G. wardi* (Miller and Ward, 1960; Price and Emerson, 1971; Whitaker et al., 1985). *G. geomydis* and *G. chapini* also were reported from *T. talpoides* (Miller and Ward, 1964; Tryon, 1947), but Price and Emerson (1971) considered these species to be parasites of *Geomys* and *Orthogeomys*, respectively. Rates of infestation by lice and fleas are related significantly to body mass of *T. talpoides* (Miller and Ward, 1964). Also parasitizing *T. talpoides* were mites (Acarina) of the genera *Proctolaelaps* (Ascidae) and *Macrocheles* (Macrochelidae) and members of the family Laelapidae: *Echinonyssus femoralis*, *E. longichelae*, an *E. longichelae* variant, *E. thomomys*, *E. utahensis*, *Eulaelaps stabularis*, *Haemogamasus ambulans*, *H. onychomydis*, *H. reidi*, *H. thomomys*, *Haemolaelaps geomys*, and *Histionyssus geomydis* (Miller and Ward, 1960; Whitaker et al., 1985). A mite (Sarcoptidae) and a nonparasitic predatory mite on plants (*Garmania ponocum*: Phytoseidae) each were reported from one individual (Miller and Ward, 1960). Ticks (*Metastigmata*: Ixodidae) on *T. talpoides* were *Ixodes sculptus* and *I. kingi* (Miller and Ward, 1964). *T. talpoides* sometimes is infested with warbles of the botfly (*Cuterebra*—Tryon, 1947); occasionally, infestations involve 25–37% of populations and are sufficiently intense to cause mortalities (Richens, 1965b). Tryon (1947) reported that a fly (Diptera) of the genus *Pegomya* flew from each tunnel as it was opened.

Endoparasites identified from *T. talpoides* were *Eimeria thomomys* and *E. fitzgeraldi* (Sporozoa: Coccidia); *Ascaris laevis*, *Capillaria hepatica*, *Longistriata vexillata*, *Protospirura ascaroidea*, *Nippostrongylus muris*, *Ransomus rodentorum*, and *Trichuris fossor* (Nematoda: Trichinellida); and *Cittotaenia praecoquis*, *Hymenolepis citelli*, *H. horrida*, *Paranoplocephala infrequens*, *P. variabilis*, and *Taenia mustelae* (Cestoda—Frandsen and Grundmann, 1961; Lubinsky, 1957; Todd et al., 1971). A trypanosome (*Grahamella*: Protista) was identified in the blood from one specimen (Frandsen and Grundmann, 1961).

Traps designed for live capture of *T. talpoides* and pocket gophers of similar size include those of Baker and Williams (1972), Hansen (1962), and Howard (1952).

BEHAVIOR. *Thomomys talpoides* is an accomplished excavator. Each individual maintains ca. 45–60 m of tunnel system; tunnels usually are ca. 30–40 cm below the surface (Tryon, 1947). New tunnels are constructed and excavated soil pushed to the surface to produce characteristic fan-shaped spoil mounds. Waste materials such as old nesting materials, uneaten cached food, and feces are packed into specially dug chambers or abandoned tunnels. *T. talpoides* is capable of rapid and extensive tunneling; an adult male released into a vegetable garden with compact clay-loam soil constructed nearly 0.5 m of tunnel in ca. 15 min, then plugged the entrance and produced a mound 0.76 m from the release point in <1 h. In 8 days, the gopher excavated 32 m of tunnel and in ca. 4 months produced a 119-m burrow system; by 6 months the system had grown to 146 m (Richens, 1966). In a montane sere in

Utah, *T. talpoides* burrowed at nearly a constant rate of 1.85–1.87 cm/min, but it was either unable or unwilling to dig when soils were extremely dry or extremely wet. Radiotracked individuals were active ca. 50% of each day (Andersen and MacMahon, 1981). Some aboveground activity was inferred from the occurrence of skulls of the species in regurgitated pellets of great horned owls (Fassler and Leavitt, 1975) and by capture of individuals in pitfalls (Verts and Carraway, 1998). Although reported for congeners, swimming (Best and Hart, 1976) and coprophagy (Douglas, 1969; Wilks, 1962) have not been recorded for *T. talpoides*.

Mound-building activity is low in summer when soils are dry, but peaks in autumn when soil moisture is 9–18% and dispersing juveniles are constructing their own burrow systems (Laycock, 1957; Reid et al., 1966; Tryon, 1947). In Colorado, daily production of mounds was lowest in June, increased through August, and declined in September, and was related to “behavioral changes induced by the breeding cycle,” not to precipitation (Miller and Bond, 1960:473). At some seasons, number of individuals captured and number of mounds or earth plugs were correlated positively; thus, counts of mounds and earth plugs may provide reliable estimates of relative abundance (Reid et al., 1966; Scrivner and Smith, 1981).

In winter, in areas covered with snow, excavated soil and other unwanted materials are packed into tunnels in the snow. At snowmelt, these form snakelike casts on the surface of the ground (Warren, 1937). In Colorado, during excavation of tunnels, rocks >2.5 cm in diameter tended to be avoided, but those 0.6–2.5 cm in diameter were more abundant in mounds and casts than in topsoil (Hansen and Morris, 1968).

Considerable controversy has centered on the influence of burrowing and foraging activities of pocket gophers on depth, tilth, moisture content, fertility, and aeration of soils; on quantity, quality, and rate of regeneration of forage; on establishment of forage grasses; and on survival of seedlings planted for reforestation (Anderson, 1977; Barnes, 1973; Barnes et al., 1970; Dingle, 1956; Ellison and Aldous, 1952; Garrison and Moore, 1956; Hansen and Morris, 1968; Jutlander et al., 1959; Keith et al., 1959; Larrison, 1942; Laycock and Richardson, 1975; Long, 1940; Moore, 1940, 1943; Moore and Reid, 1951; Scheffer, 1948). *T. talpoides* on Colorado rangelands was responsible for increasing soil depth and loss of moisture, did not affect rate of recycling of nutrients or fertility, improved aeration and tilth, and moved small rocks to the surface where their decomposition was accelerated (Hansen and Morris, 1968). Levels of organic matter, nitrogen, and phosphorus were higher in soils in a subalpine grassland where pocket gophers were present than where they were controlled (Laycock and Richardson, 1975).

Individual *T. talpoides*, like other pocket gophers, vigorously defend territories from conspecifics and commonly maintain exclusive burrow systems except during the breeding season and during the period of maternal care of young. However, use of burrow systems by other species of small mammals is not restricted (Jannett, 1982). During the breeding season, agonistic behavior, especially that of adult females toward conspecifics, is relaxed (Hansen and Miller, 1959). In a sample of 881 *T. talpoides* captured in Colorado, 133 individuals were involved in 63 plural captures in 10 different sex and age combinations. Plural captures increased from 24.4% in early June to 41.7% by mid-July, then declined to 13.0% in late July–early August; only one plural capture involving two juveniles was recorded after mid-August (Hansen and Miller, 1959). Sex and age combinations of gophers simultaneously occupying the same burrow system during the breeding season (Wight, 1930) differed greatly from that after the breeding season (Hansen and Miller, 1959). Reoccupation of burrow systems by dispersing individuals was greater in Wight's (1930) study.

In captivity, young exhibit increasingly agonistic behavior at 5 weeks of age (Andersen, 1978). Wild-caught adults placed together in neutral arenas first explored, attempted to climb its walls, and dug briefly in litter. When two individuals contacted each other, both “froze” momentarily, often jerked backwards, and usually commenced to spar. During sparring contests, both individuals raised their forelegs and “pawed” at each other with open mouths. Often, contact terminated after a brief period of sparring, although occasionally the two individuals lunged and bit at each other. Fights that lasted more than a few seconds required that participants be forcibly separated, but more often fighting terminated with one individual in a defensive pose and the other poised over it. Shortly, the subordinate individual turned upright and retreated, and the

dominant individual resumed exploration of the arena (Andersen, 1978).

GENETICS. Diploid chromosome numbers in the *T. talpoides* complex vary regionally (Fig. 3) with populations of $2n = 40, 42, 44, 46, 48, 50, 52, 54, 56, 58,$ and 60 represented (Nevo et al., 1974; Thaeler, 1968b, 1974b, 1980). Fundamental number ranged from 70 to 84 (Patton and Sherwood, 1982; Thaeler, 1974b). Hybrid individuals with $2n = 47, 49, 51,$ and 53 were reported to occur in contact zones between some populations (Thaeler, 1974b, 1976). Instances of limited or no hybridization based on karyology combined with claimed morphological differences sufficient to distinguish between parental forms were interpreted as evidence of reproductive isolation, thus absence of introgression (Thaeler, 1974b, 1976). However, at other localities intrapopulation polymorphism in chromosome number was indicated with a relatively broad zone in which chromosome numbers gradually changed, suggesting that two chromosome forms were representative of the same species (Thaeler, 1974b).

Extensive karyotypic variation observed in the *T. talpoides* complex is characterized by Robertsonian changes (Sherwood and Patton, 1982). In *T. t. fossor*, C-band positive chromatin is restricted to the centromeric region irrespective of chromosome morphology; in some chromosomes centromeric regions are weakly C-band positive (Patton and Sherwood, 1982).

Both albinism and melanism occur in *T. talpoides*; the latter is more common. Other colormorphs have been recorded (Bailey, 1915).

REMARKS. The generic name *Thomomys* was derived from the Greek *thomos* meaning "a heap" (probably in reference to mounds of earth produced in tunneling) and the Greek *mys* meaning "mouse" (probably in reference to the somewhat mouse-like body shape). The specific name *talpoides* was derived from the Latin *talpa* meaning "mole" (probably in reference to its fossorial mode of life—Jaeger, 1955).

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B. J. VERTS AND L. N. CARRAWAY, DEPARTMENT OF FISHERIES AND WILDLIFE, NASH 104, OREGON STATE UNIVERSITY, CORVALLIS, OREGON 97331-3803.