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Thomomys mazama.

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Thomomys mazama Merriam, 1897

Western Pocket Gopher

Thomomys mazama Merriam, 1897:214. Type locality "Crater Lake, Mt. Mazama, [Klamath Co.,] Oregon. Exact locality, head of Anna Creek; altitude 6000 feet."
Thomomys nasicus Merriam, 1897:216. Type locality "Farewell Bend, Des Chutes River, [Deschutes Co.,] Oregon."
Thomomys melanops Merriam, 1899:21. Type locality "timberline at head of Soleduc River, Olympic Mts., [Clallam Co.,] Washington."
Thomomys hesperus Merriam, 1901:116. Type locality "Tillamook, [Tillamook Co.,] Oregon."
Thomomys niger Merriam, 1901:117. Type locality "Seaton [= Mapleton], near mouth of Umpqua River [= head tidewater, Siuslaw River, Lane Co.,] Oregon."
Thomomys helleri Elliot, 1903:165. Type locality "Goldbeach, mouth of the Rogue River, Curry County, Oregon."

CONTEXT AND CONTENT. Order Rodentia, family Geomyidae, genus *Thomomys,* subgenus *Thomomys* (Hall, 1981; Thaeler, 1980). The following 15 subspecies are recognized (Hall, 1981):

T. m. couchi Goldman, 1939:243. Type locality "4 miles north Shelton, Mason County, Washington."
T. m. glacialis Dalquest and Scheffer, 1942*a*:97. Type locality "two miles south of Roy, Pierce County, Washington."
T. m. helleri Elliot, 1903:165, see above.
T. m. hesperus Merriam, 1901:116, see above.
T. m. louiei Gardner, 1950:92. Type locality "twelve miles NNE of Cathlamet (Crown-Zellerbach's Cathlamet Tree Farm), altitude 2500 feet, Wahkiakum County, Washington."
T. m. mazama Merriam, 1897:214, see above.
T. m. melanops Merriam, 1899:21, see above.
T. m. nasicus Merriam, 1897:216, see above.
T. m. niger Merriam, 1901:117, see above.
T. m. oregonus Merriam, 1901:115. Type locality "Oregon City, Willamette Valley, [Clackamas Co.,] Oregon."
T. m. premaxillaris Grinnell, 1914:312. Type locality "two miles south of South Yolla Bolly Mountain, altitude about 7500 feet, in Tehama County, California."
T. m. pugetensis Dalquest and Scheffer, 1942*a*:96. Type locality "4 miles south of Olympia, Thurston County, Washington" corrected to "3 mi. S Olympia, Thurston County, Washington" by Lidicker (1971).
T. m. tacomensis Taylor, 1919:169. Type locality "six miles south of Tacoma, Pierce County, Washington." Probably extinct as a result of urbanization (Nowak, 1991).
T. m. tumuli Dalquest and Scheffer, 1942*a*:96. Type locality "7 miles north of Tenino, Thurston County, Washington."
T. m. yelmensis Merriam, 1899:21. Type locality "Tenino, Yelm Prairie, [Thurston Co.,] Washington."

DIAGNOSIS. *Thomomys mazama* (Fig. 1) can be distinguished from sympatric and parapatric congeners (*bottae, bulbivorus,* and *talpoides*) by one or more of the following characters: small size, a closed or slitlike sphenoidal fissure, presence of a wide (ca. 1.5 mm) flange projecting posteroventrally from the angle of the dentary (Fig. 2—Verts and Carraway, 1998), and a baculum 22–31 mm long in adult males (Johnson and Benson, 1960). *T. mazama* (2n = 40–58) also can be distinguished from *T. bottae* (2n = 74–82) and *T. bulbivorus* (2n = 76) by diploid number, but karyotypes of *T. mazama* and *T. talpoides* have overlapping diploid numbers (Thaeler, 1980). The subaricular dark patch of fur is five to six times as large as the ear in *T. mazama,* but only ca. three times larger in *T. talpoides* (Ingles, 1965). Smooth interparietal and frontoparietal sutures, longer and narrower interparietal, and divergent temporal ridges were considered useful for distinguishing *T. mazama* from its similar-sized congener, *T. talpoides,* by Ingles (1965) and Johnson and Benson (1960), but not by Verts and Carraway (1998).

GENERAL CHARACTERS. *Thomomys mazama,* like other members of the family (Hill, 1937; Hollinger, 1916), is highly adapted to a fossorial mode of life; body tapers from heavily muscled head and shoulders to relatively narrow hips. Legs are short. Five toes on the forefeet are equipped with long, tapering claws and fimbriae; five toes on rear feet have shorter, less-curved claws (Bailey, 1915). Eyes are small and ears are short. I1s are not highly procumbent, but are equipped with a shallow groove (suculus) in the enamel face near the inner edge (Ingles, 1965). Fur-lined cheek pouches open external to the mouth and extend posteriorly well beyond the margin of the skull. Base of M1 is not inclined posteriorly and base of I1 does not enter space between P4 and I1 (Thaeler, 1980). As in other members of the family, skull is flattened dorsally, zygomata are wide-spreading, and mandibles are heavy and irregular (Bailey, 1915).

Color of dorsal pelage ranges from a shiny black with purplish and greenish iridescence in *T. m. niger* to blackish brown in *T. m. tumuli* and *T. m. pugetensis* to dark brown in *T. m. fuscus* and *T. m. louiei* to reddish brown in *T. m. hesperus, T. m. mazama, T. m. helleri,* and *T. m. melanops* to reddish tan in *T. m. couchi* and *T. m. tacomensis* to light yellowish brown in *T. m. nasicus, T. m. premaxillaris,* and *T. m. glacialis* to light brown in *T. m. oregonus* and *T. m. yelmensis* (Bailey, 1915; Dalquest and Scheffer, 1942*a*; Taylor, 1919). Nose and face usually are dusky, plumbeous, or blackish; chin, feet, and tip of tail commonly are light gray, white, or buff; and the chest commonly contains white splotches (Bailey, 1915). Tip of tail may be naked or nearly so. In Washington, pelage color was considered to be "modified by the relative length of the sepia-colored proximal band of the fur" (Dalquest and Scheffer, 1944*b*:449).

Thomomys m. hesperus is dichromatic; most individuals are dark reddish brown, but some are black (Walker, 1949). Bailey (1915) speculated that the black subspecies in western Oregon, *T. m. niger,* was dichromatic, even though to that time only specimens of the black phase had been taken. Walker (1949) examined ca. 175 specimens from within the range of the latter race without finding other than black individuals; he further claimed that greenish iridescence in *T. m. niger* was lost in summer leaving a dull slaty-black pelage. Later Walker (1955) reported examining 23 specimens from Marys Peak (= Chintimini Mountain), Benton County, Oregon, 7 of which were black with most cranial characters referable to *T. m. niger* and 16 of which were brownish but with

FIG. 1. Photograph of *Thomomys mazama* from Rochester, Washington. Photograph courtesy of V. B. Scheffer.

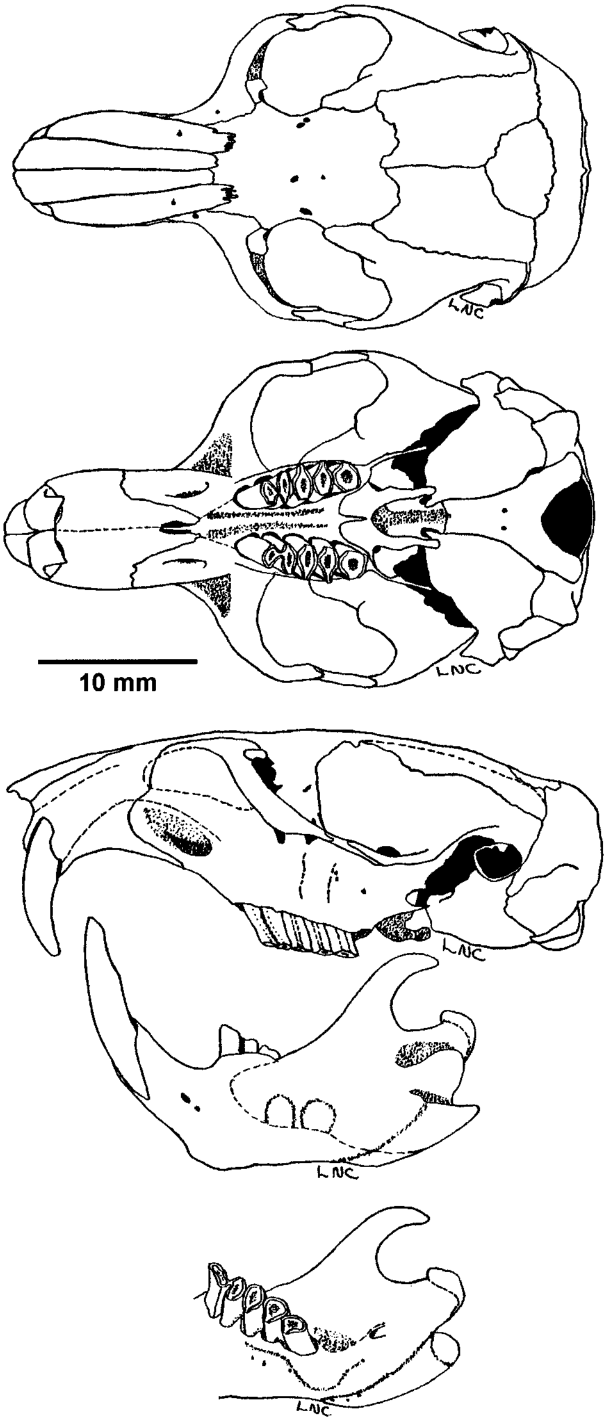

FIG. 2. Dorsal, ventral, and lateral views of the cranium and lateral and oblique views of the mandible of adult female *Thomomys mazama* (Oregon State University Department of Fisheries and Wildlife Mammal Collection [OSUFW] 5529) from 8 mi. E Upper Soda, Linn Co., Oregon. Condylonasal length is 36.06 mm.

some skull characters resembling more closely those of *T. m. niger* than those of the nearby brown race, *T. m. oregonus.* He considered the area from which the specimens were collected to have been invaded by the two colormorphs at different times and that the area was a zone of intergradation.

Ranges in average body dimensions (in mm) for adult female (*n* = 163) and male (*n* = 148, in parentheses) *T. mazama* from regions in Oregon depicted by Hall (1981:487, map 301) as occupied by six nominal subspecies were (Verts and Carraway, 1998): total length, 194–214 (204–222); length of tail, 56–68 (59–70); and length of hind foot, 27–28 (27–29). Means and ranges (in parentheses) for standard measurements of samples of female (*n* = 45) and male (*n* = 26) *T. m. niger* were (Walker, 1949): total length, 214 (203–226), 222 (210–232); length of tail, 65 (58–77), 67 (52–76); and length of hind foot, 28.5 (27–30), 29.5 (27–31). Ranges in averages of the same body dimensions for females (*n* = 123) and males (*n* = 121, in parentheses) of six subspecies in Washington were (Dalquest and Scheffer, 1944*b*): total length, 189–220 (196–225); length of tail, 53–71 (62–72); and length of hind foot, 26–30 (27–31). Dalquest and Scheffer (1944*b*:429, table II) reported average length of tail for 11 *T. m. tumuli* as 30 mm; we believe this value to be a typographic error. Ranges for total length, length of tail, and length of hind foot (*n* not reported) for female and male (in parentheses) *T. m. mazama* in California were (Thaeler, 1968): 188–218 (181–234), 52–78 (54–79), and 24–29 (24–29). Ranges in average body mass (g) for samples from Oregon (Verts and Carraway, 1998) were 82.5–92.2 for females (*n* = 59) and 97.8–112.5 for males (*n* = 57); for Washington (Dalquest and Scheffer, 1944*b*; Witmer et al., 1996) ranges were 79–126.7 for females (*n* = 153) and 87–146.7 for males (*n* = 147); and for California (Thaeler, 1968) ranges (*n* not reported) were 61.9–109.5 g for females and 60.7–135.0 g for males. Within two sites ca. 15 km apart in the Puget Sound, Washington region, body mass, length of tail, and length of ear for females and length of tail, length of ear, and length of hind foot for males were significantly different. Also, body mass, length of tail, length of ear, and length of hind foot were significantly different between the sites irrespective of sex (Witmer et al., 1996).

Ranges in average skull dimensions (in mm) for females (*n* = 132) and males (*n* = 127, in parentheses) from regions in Oregon depicted by Hall (1981:487, map 301) as occupied by six nominal subspecies were (Verts and Carraway, 1998): basilar length, 29.25–30.72 (30.57–32.21); length of nasals, 12.79–13.63 (13.43–14.28); zygomatic breadth, 19.46–20.95 (20.30–22.55); mastoid breadth, 16.50–17.31 (17.09–18.22); least interorbital breadth, 6.04–6.45 (6.14–6.54); length of maxillary toothrow, 7.71–8.45 (7.84–8.75); depth of skull, 12.32–13.08 (12.79–13.59); length of mandible, 20.66–22.31 (21.31–23.27); and length of mandibular toothrow, 7.51–8.12 (7.65–8.41). In general, those from the central, coastal region of Oregon were largest and those from the east-central slope of the Cascade Range were smallest (Verts and Carraway, 1998).

Ranges in skull dimensions (*n* not reported) for female and male (in parentheses) *T. m. mazama* in California (Thaeler, 1968) were: condylonasal length, 33.0–37.0 (33.5–40.0) and zygomatic breadth, 17.9–21.5 (18.4–23.7). In Washington, ranges in average skull dimensions for females (*n* = 132) and males (*n* = 128, in parentheses) of six subspecies (Dalquest and Scheffer, 1944*b*) were: condylobasal length, 33.7–37.1 (34.5–37.9); length of rostrum, 15.5–17.5 (16.4–17.9); zygomatic breadth, 19.5–22.2 (20.3–23.0); interorbital breadth, 6.0–6.8 (6.2–6.9); width of nasals, 3.8–4.6 (4.0–4.5); and width of rostrum, 7.1–8.0 (7.3–8.1). Largest and smallest races in Washington are <50 km apart. Dalquest and Scheffer (1944*b*:450) considered cranial dimensions of several races near Puget Sound, Washington, were "correlated [presumably positively] with the depth of the soil in the habitat occupied."

DISTRIBUTION. Disjunct populations of *T. mazama* occur south of Puget Sound and in the Olympic Mountains, Washington. In Oregon, the species occurs in the Coast Range south to Scottsburg, Douglas County, with coastal populations in Curry County, as well as in the Cascade Range east to Cascade Locks, Hood River County; Paulina Lake, Deschutes County; and Yamsey Mountain and Merrill, Klamath County. In California, the species occurs south to South Yolla Bolly Mountain, Tehama County, west to Poker Flat, Siskiyou County, and east to Dickson Flat, Shasta County (Fig. 3—Dalquest and Scheffer, 1944*b*; Hall, 1981; Thaeler, 1968; Verts and Carraway, 1998).

FOSSIL RECORD. No fossils of *T. mazama* are known. However, *T. microdon,* a fossil species from late Rancholabrean-age deposits from Potter Creek and Samwel caves in northern California, may be a subspecies of *T. mazama* (Anderson, in litt.; Kurtén and Anderson, 1980).

Dalquest and Scheffer (1944*a,* 1944*b*) attempted to reconstruct the biogeographical history of pocket gophers in Washington during the late Pleistocene based on the premise that all gophers in the state were *T. talpoides.* They believed that, at maximum

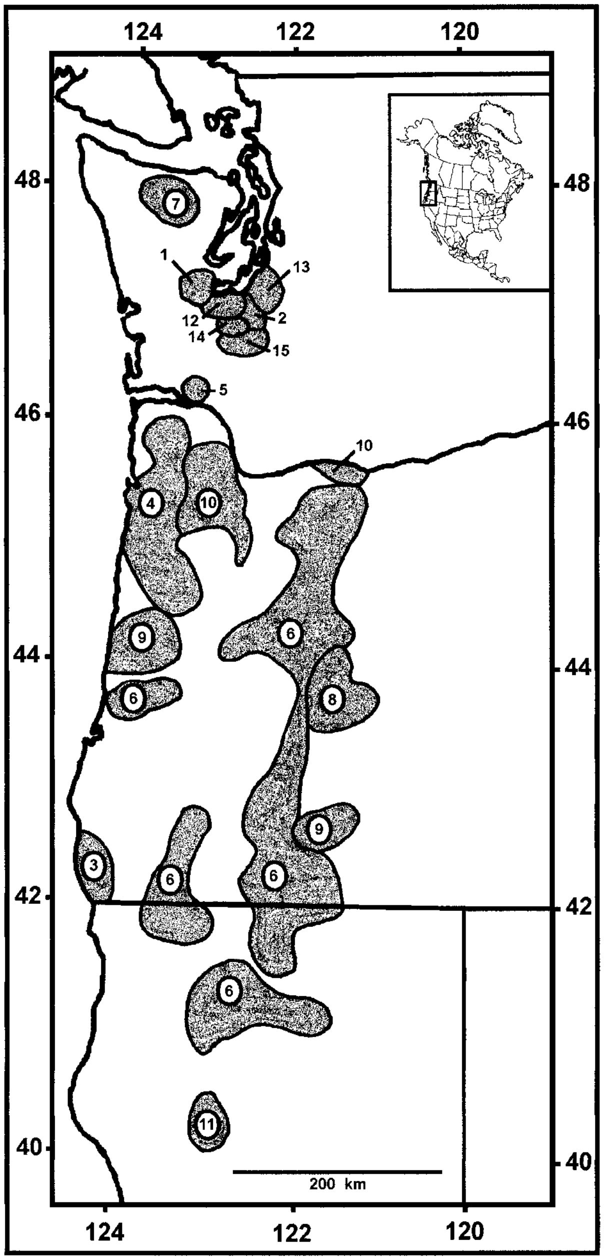

FIG. 3. Distribution of *Thomomys mazama.* Subspecies are: 1, *T. m. couchi*; 2, *T. m. glacialis*; 3, *T. m. helleri*; 4, *T. m. hesperus*; 5, *T. m. louiei*; 6, *T. m. mazama*; 7, *T. m. melanops*; 8, *T. m. nasicus*; 9, *T. m. niger*; 10, *T. m. oregonus*; 11, *T. m. premaxillaris*; 12, *T. m. pugetensis*; 13, *T. m. tacomensis*; 14, *T. m. tumuli*; 15, *T. m. yelmensis.* Map redrawn from Hall (1981:467, map 301) and Verts and Carraway (1998:232, figure 11-51) with modifications (E. Steinberg, in litt.).

extent of the Vashon–Wisconsin ice sheet, pocket gophers in Washington were present in the southern Cascade Range, in southeastern Washington, and on the Columbian Plateau. As the ice retreated, dark-colored gophers of southeastern Washington and southern Cascades became separated from light-colored gophers of the Columbian Plateau by habitat changes related to increasing aridity. Those in the southern Cascades spread westward to populate prairies and glacial outwashes in the Puget Sound, Olympic Mountain, and southwest Washington regions, areas now considered to be occupied by *T. mazama.*

For Oregon, Walker (1955) postulated that ancestral *T. m. mazama,* derived from *T. talpoides* stock, migrated westward through the Cascade Range into margins of the Willamette Valley during an interglacial period between the Illinoian and Wisconsinan glaciations, and differentiated to become *T. m. oregonus* and a proposed new subspecies. A somewhat later wave of *T. m. oregonus* stock may have migrated along the relatively low Calapooya Mountains at the south end of the Willamette Valley to invade regions along the coast and valleys of the west slope of the Coast Range. Populations from this invasion gave rise to *T. m. hesperus, T. m. niger,* and a second proposed new subspecies. To our knowledge, descriptions of the proposed new subspecies were not published.

FORM AND FUNCTION. Distal portions of phallus and baculum of *T. mazama* are long and slender and both are longest among all geomyid species. Tip and base of baculum are poorly defined. Phallus does not possess "a distinct collar, midventral raphae, or middorsal groove, and the constriction is not distinct," characters common to most geomyids (Williams, 1982:17). Bacula of *T. m. mazama* ($n = 25$) averaged (± *SD*) 26.12 ± 1.94 mm (Long and Frank, 1968), whereas those from two samples ($n = 10$ and $n = 17$) from Washington (subspecies not provided) averaged 24.3 ± 2.2 mm and 26.6 ± 1.9 mm, respectively (Witmer et al., 1996). Condylobasal length (an estimate of body size) for six adult *T. m. mazama* from northern California averaged only 1.2 (range, 1.1–1.3) times longer than distal tract of phallus and only 1.3 (range, 1.1–1.5) times longer than the baculum. For the same six individuals, length of distal tract ranged from 27.2 to 34.1 mm and length of baculum ranged from 24.9 to 32.9 mm (Williams, 1982). Other authors set minimum length of baculum for adults at 21–22 mm (Ingles, 1965; Johnson and Benson, 1960; Thaeler, 1968).

Dental formula is i 1/1, c 0/0, p 1/1, m 3/3, total 20; premolars are figure eight–shaped, almost appearing as two teeth. Alignment of enamel ridges on all upper cheek teeth of *T. mazama* deviated significantly from 90° to the midsagittal plane of the skull; angles ranged from 80.2° for the anterior column of the left upper premolar to 98.4° for the right M3. Alignment of scars on ridges resulting from wear deviated significantly from parallel to the midsagittal plane of the skull for all right upper cheek teeth, but only on the upper premolar in the left toothrow. Values ranged from −1.6° on M3 to −2.5° on the right upper premolar; the value on the left upper premolar was −1.7° (Wilkins, 1988). These values, combined with those for congeners, suggest that chewing in extant *Thomomys* is propalinal.

ONTOGENY AND REPRODUCTION. Male *T. m. niger* taken on 24 March and 10 April had enlarged testes, but genitals of a female taken on 21 March exhibited no evidence of reproductive activity. A female collected on 10 April had greatly enlarged external genitalia, thickened and enlarged uterine horns, and obvious nipples; no embryos were observed, but a female taken on 3 July contained three embryos (Walker, 1949). Embryo counts of three, four (Walker, 1955), four, four, and seven (Witmer et al., 1996) have been recorded. Average litter size for *T. mazama* in Oregon is 3.9 (range, 1–7, $n = 7$) based on counts of embryos and pigmented sites of implantation (Verts and Carraway, 1998). This was the smallest average among the five species of *Thomomys* in Oregon. In Washington, pregnant females were taken from 18 March to 15 May during one year, from 4 April to 15 June another year, and from 24 March to 26 May a third year. Except for the first year when 3 of 27 females collected 18–20 March contained embryos, no female examined before 21 March ($n = 50$) was pregnant. Average litter size based on counts of embryos ($n = 46$) and of pigmented sites of implantation ($n = 27$) was five (Scheffer, 1938).

ECOLOGY. Although distributions of various species of geomyids are allopatric or parapatric (Thaeler, 1968; Vaughan and Hansen, 1964), populations of *T. mazama* and *T. bulbivorus* likely occur as "adjacent interdigitating but not intermingling colonies" (Walker, 1955:104). *T. mazama* purportedly ranges to the edge of the Willamette Valley, Oregon, but does not enter it (Gabrielson, 1923); *T. bulbivorus* is endemic to the Willamette Valley (Verts and Carraway, 1987, 1998). Nevertheless, several museum specimens of the two species were listed with identical collection localities (Verts and Carraway, 1998). In northern California, *T. mazama* and *T. monticola* occurred within a few decimeters of each other, but areas occupied by the two species rarely overlapped (Thaeler, 1968).

Despite a broad overlap in habitat requirements and foods consumed, *T. mazama,* in general, occupies a narrower array of environments than either *T. talpoides* or *T. bulbivorus* (Thaeler, 1968; Walker, 1955). Thaeler (1968:42) concluded that sympatry occurred "only between morphologically divergent types and at least in some cases seems to be related to ability to make differential use of hard and soft soils." Forests were considered inadequate habitat for *T. m. niger,* but most of the area occupied is within a forest sere (Walker, 1949). Nevertheless, Walker (1955: 110) later suggested that juvenile *T. talpoides* must disperse into dense coniferous forests and that "To argue that the gopher cannot exist in these regions is unsound."

In coastal areas and valleys on the west slope of the Coast Range, *T. m. niger* occurred mostly on abandoned farms reverting to natural vegetation or in pastures where soils were silt loams or sandy loams (but usually not on red clay hillsides). Bracken fern (*Pteridium aquilinum*), blackberry (*Rubus ursinus*), and grasses with scattered small alder (*Alnus rubra*), big-leaf maple (*Acer macrophyllum*), and Douglas-fir (*Pseudotsuga menziesii*) trees were common plants on occupied areas (Walker, 1949).

In southern Oregon, the species "lives mainly in meadows and open, parklike habitats . . . [and] is also often found scattered in the more open timbered areas common to the ponderosa pine region" (Hooven, 1971:347). "Dense populations" (*n*/ha not provided) occurred on a Douglas-fir–white fir (*Abies concolor*) forest area logged three years earlier and in a mixed-conifer stand (76% white fir; 20% Douglas-fir; 3% incense cedar, *Libocedrus decurrens*; and a small amount of sugar pine, *Pinus lambertiana*) logged five years earlier (Hooven, 1971:349). Both areas were replanted to ponderosa pine (*Pinus ponderosa*). On the former area, vegetative cover was 10–25%; initially, dominant plants were common thistle (*Cirsium vulgare*), currant (*Ribes cereum*), and grass (*Bromus*), but these were replaced by miner's lettuce (*Montia perfoliata*), pussypaws (*Spraguea umbellata*), pink phlox (*Phlox gracilis*), and false Solomon's seal (*Smilacina sessilifolia*—Hooven, 1971). Vegetative cover on the latter area was 5–15% and initially consisted largely of common thistle and grass, but these were replaced by Canada thistle (*Cirsium arvense*), mullein (*Verbascum thapsus*), dandelion (*Taraxacum officinale*), western strawberry (*Fragaria cuneifolia*), and vetch (*Vicia*). Collinsia (*Collinsia*), bleeding heart (*Dicentra oregona*), phacelia (*Phacelia*), and red sorrel (*Rumex acetosella*) invaded still later. Soils on both areas were moderately deep clay loams over andesitic bedrock (Hooven, 1971).

Farther east in Oregon, where 110 *T. mazama* were removed from a 4-ha plot during a 14-month period (≤16 per 2-month period—Burton and Black, 1978), vegetation was dominated by annual and perennial grasses and annual forbs. Before a forest fire 14 years earlier, the area supported a ponderosa pine–bitterbrush (*Purshia tridentata*)–needlegrass (*Stipa occidentalis*) community, but subsequent to the wildfire the area was salvage-logged and replanted to ponderosa pine. Seral vegetation consisted of needlegrass, mountain brome (*Bromus carinatus*), cheatgrass (*B. tectorum*), groundsmoke (*Gayophytum diffusum*), willow-weed (*Epilobium paniculatum*), knotweed (*Polygonum douglasii*), bitterbrush, currant, and rabbitbrush goldenweed (*Haplopappus bloomeri*).

South of Puget Sound, Washington, estimated prerecruitment density (presumably based on counts of burrow systems and capture records) was 10/ha in an orchard with a mowed grass and forb understory and 60/ha in a Christmas tree plantation with an understory of orchard grass (*Dactylis glomerata*) and Scotch broom (*Cytisus scoparius*). The orchard population was subjected to control measures "on several occasions" during years before the study was conducted (Witmer et al., 1996:96).

In prairie areas south of Puget Sound, Washington, where soils are black silt and gravel over a bed of yellow stratified gravel (but not where soils are deep and rich), topography consists of 0.3- to 2.1-m-tall round or slightly oval mounds ca. 2.4–12.2 m (most ca. 6.1 m) in diameter. These mounds (Fig. 4), called Mima mounds, are attributed to burrowing activities of *T. mazama* because most, but not all, such areas are occupied by the species. Spacing of mounds is approximately the same as that of individual territories of *T. mazama* (Dalquest and Scheffer, 1942*b*). Other explanations for the origin of Mima mounds within the range of *T. mazama* and its congeners were largely refuted (Arkley and Brown, 1954; Cox, 1984; Dalquest and Scheffer, 1942*b*; Price, 1949).

Based on analysis of plant epidermal fragments, "Stomachs from 110 *T. mazama* contained 31 species of plants, or 67 percent of the plants occurring on the study area" (Burton and Black, 1978: 386–387). Grasses contributed most to the diet in winter (60.5% in January) and least in summer (16.5–17.4% in July); forbs contributed most in summer (41.7–60.4% in July) and least in winter (4.1% in March, 7.1% in December); and woody plants contributed most in winter (6.2% in January) and least in summer (trace–1.6% in July and September). On an annual basis, grasses composed 32% of the diet; however, consumption of grasses was related inversely to demand for water (Burton and Black, 1978). Ponderosa pine was the most commonly eaten woody plant. Roots comprised 11.2–44.2% of materials consumed with greatest amounts in autumn and spring (44.2% in March, 26.4% in November) and least amounts in winter and summer (11.2–23.1% in July, 16.4% in December). Overall, use of various species of plants as food corresponded closely with their phenology and abundance. In July, when all types of vegetation were available, most plants consumed by *T. mazama* were forbs (Burton and Black, 1978). Caches in burrow systems excavated in an orchard in western Washington contained root cuttings of either thistle (*Cirsium*) or scotch broom (Witmer et al., 1996).

FIG. 4. Mima mounds at Mima Prairie, Washington. Gravel pit, roads, and buildings in distance provide scale reference for size of mounds. Photograph courtesy of V. B. Scheffer.

Average (± *SD*) home ranges (method of calculating area not provided) of adult females (*n* = 4) and males (*n* = 4) followed by radiotelemetry during February–April in Washington were 97 ± 57.1 m^2 (range, 47–151 m^2) and 108 ± 37.9 m^2 (range, 73–143 m^2). Radios were removed by some individuals and other radio-tagged individuals were preyed upon (Witmer et al., 1996).

Within its range, *T. mazama* often contributes significantly to failure of forest plantings, especially in the ponderosa pine zone. Damage to seedlings primarily is by "root pruning" or "by a combination of stem girdling and clipping" (Barnes, 1973:1). In Oregon, two-thirds of damage and nearly all losses of 2.5- to 3-year-old seedlings were attributed to pocket gophers; most occurred during one winter when 52% of seedlings died. Burrow casts (Fig. 5) revealed most damage was caused by gophers burrowing through snow (Barnes, 1978). In another study, 87% of seedlings on areas free of gophers survived, whereas on areas occupied by gophers only 12% survived (Hooven, 1971). A variety of equipment, repellents, toxicants, and techniques were developed to reduce impact of *T. mazama* and congeners on forest plantings (Anthony et al., 1978; Barnes, 1973; Barnes et al., 1970; Sullivan et al., 1988, 1990; Wick and Landforce, 1962).

The adult : juvenile ratio in a sample of 127 *T. mazama* from Klamath County, Oregon, based on counts of periosteal zonations in mandibles, was in 94.5% concordance with those determined by reproductive-induced characters (pigmented sites of implantation, open or closed pubic symphyses, enlarged and pigmented nipples in females, and bacula >20 mm or <20 mm long in males—Livezey and Verts, 1979). Based on counts of periosteal zonations, 67 (52.8%) were young-of-the-year, 54 (42.5%) were ≥1 year old, 6 (4.7%) were ≥2 years old, and none was ≥3 years old. The sex ratio among young-of-the-year was nearly 1:1 (33 males, 34 females), but the sample of older animals was biased (but not significantly so) toward females (36 females, 24 males—Livezey and Verts, 1979). In Washington, sex ratio of a prerecruitment sample ($n = 57$) collected in February–April was 1:1.11 in favor of females (Witmer et al., 1996).

Mammals associated with eastern populations of *T. mazama* include *Dipodomys californicus, Microtus montanus, Perognathus parvus, Peromyscus maniculatus, Sylvilagus nuttalli,* and *Tamias amoenus* (Burton and Black, 1978). *Microtus oregoni* was captured in burrow systems of *T. m. niger* and *Neurotrichus gibbsii. P. maniculatus, Scapanus townsendii, Sorex bairdii,* and *S. vagrans* also may use these burrow systems (Walker, 1949). Other sympatric species that may use burrow systems of *T. mazama* include *Clethrionomys californicus, Microtus californicus, M. longicaudus, M. townsendii, Phenacomys albipes, Scapanus latimanus, S. orarius, Sorex pacificus, S. sonomae, S. trowbridgii, Spermophilus lateralis, Tamias senex, T. siskiyou, T. townsendii,* and *Zapus trinotatus.*

In Washington, a long-tailed weasel (*Mustela frenata*) left a tunnel carrying a dead western pocket gopher and another weasel was captured in a gopher tunnel (Scheffer, 1932). Other potential mammalian predators of *T. mazama* include *Lynx rufus, Mustela erminea, M. vison, Spilogale gracilis,* and domestic dogs and cats (Walker, 1949). However, none of 227 prey items identified in 143 fecal droppings of *L. rufus* from the Coast Range (presumably within the range of the gopher) was *T. mazama.* Only 3 prey items identified from 34 fecal droppings (Nussbaum and Maser, 1975) and 23 prey items identified from 494 fecal droppings (Toweill and Anthony, 1988*a*) from the Cascade Range were western pocket gophers. Remains of *T. mazama* were identified in 4% of 844 fecal droppings of coyotes (*Canis latrans*) from the Cascade Range; *T. mazama* was the second most common species of rodent identified (Toweill and Anthony, 1988*b*). East of the Cascade Range within the range of *T. mazama*, pocket gophers reported as *T. talpoides* occurred in ca. 5–20% of fecal droppings of coyotes during 8 of 12 months that droppings were collected (Van Vuren and Thompson, 1988).

Remains of *T. mazama* were identified among regurgitated pellets of spotted owls (*Strix occidentalis*) in both Cascade and Coast ranges (Forsman et al., 1984). Similar remains were not found in pellets of long-eared owls (*Asio otus*), barn owls (*Tyto alba*), or great horned owls (*Bubo virginianus*) from habitats in western Oregon occupied by *T. mazama* (Maser and Brodie, 1966). Gopher snakes (*Pituophis melanoleucus*), known to take other pocket gophers (Scheffer, 1932), probably also prey on *T. mazama.*

The fleas (Siphonaptera) *Foxella ignota recula* and *Spicata comis comis* were identified from *T. m. niger* (Walker, 1949; Whitaker et al., 1985). Lewis et al. (1988) listed *Spicata c. comis, S. c. scapoosei, S. c. tacomae, S. c. walkeri, S. m. moorei,* and *S. pacifica* from pocket gophers from areas within the range of *T. mazama.* The chewing lice (Mallophaga) *Geomydoecus betleyae, G. thaeleri,* and *G. thomomyus* and the mites (Acarina) *Androlaelaps geomys, Echinonyssus longichelae, E. thomomyus, Glycyphagus hypudaei, Haemogamasus onychomydis, H. reidi, H. thomomysis,* and *Laelaps alaskensis,* and an unidentified species of the family Histiostomatidae also were identified from *T. mazama* (Hellenthal and Price, 1989; Whitaker et al., 1985).

An oral dose of 30 mg/kg body mass of rhodamine B administered by gavage produced a band in vibrissae and claws of *T. mazama* that fluoresced under ultraviolet light. The marker lasted 5–6 weeks (Lindsey, 1983). Such a marker should be useful in evaluating various baits and baiting techniques for control of *T. mazama* and other pocket gophers (Sullins and Verts, 1978).

BEHAVIOR. Like its similar-sized congener, *T. talpoides*, the western pocket gopher is largely fossorial, spending most of the time in burrow systems it constructs itself or appropriates and refurbishes when conspecifics move or die. Burrow systems that become unoccupied or unused are invaded quickly by conspecifics. Reoccupation of eight burrow systems after removal of original occupants required 1–16 (mean = 8.4) days, but replacement after removal of invaders from four systems required only 4–8 (mean = 6.5) days, and removal of a second invader from one system resulted in reoccupation in 6 days. Two invaders were adults, seven were subadults, and four were of unknown age (Tunberg et al., 1984). In March in Washington, an adult male and female western pocket gopher were removed from each of several burrow systems, but interval between captures of the two individuals was not presented (Witmer et al., 1996). The latter authors believed that capture of the two sexes represented dual occupancy and was evidence of an ongoing mating season.

Burrows are ca. 3.8–4.4 cm in diameter and ca. 10–15 cm beneath the surface with a vertical tunnel to deeper burrows that include the nest (Walker, 1949). Typically, spoil mounds of earth are crescent-shaped and are produced when excavated earth is pushed from the tunnel opening onto the surface. Tunnel entrances are filled with earth from within producing a characteristically shaped plug at one side of the crescent (Walker, 1955). In Washington, ovoid nests ($n = 12$) ca. 25 cm in diameter and 15 cm high constructed at an average (± *SD*) depth of 88.5 ± 25.9 cm (range, 48–150 cm) were lined with "dry grass often with a few pieces of plastic and root cuttings" (Witmer et al., 1996:97). Feces were deposited in nearby chambers. In subnivian environments, excavated earth is packed into tunnels in the snow; at snowmelt, ropelike bands of soil are produced aboveground (Fig. 5).

In captivity, *T. mazama* is coprophagous. Fecal pellets are reingested after they are chewed thoroughly. Thus, distinct pellets are absent from stomach contents (Wilks, 1962).

In late evening, *T. mazama* sometimes forages aboveground. While aboveground, individuals stay close to openings to their burrows, cut vegetation, load their cheek pouches, and quickly disappear below ground. They commonly reappear later and repeat the process. Individuals remain aboveground for longer periods while they cut seed heads of grasses, but do not consume seeds while on the surface (Maser et al., 1981).

GENETICS. Diploid numbers for *T. mazama* range from 40 to 58. Washington subspecies, *T. m. glacialis* and *T. m. pugetensis,* have 2n = 44–46 and 2n = 46, respectively; western Oregon subspecies, *T. m. helleri, T. m. hesperus, T. m. niger,* and *T. m. oregonus,* have 2n = 40, 2n = 44, 2n = 42, and 2n = 44, respectively; and subspecies east of the Cascade Range in Oregon and in California, *T. m. mazama* and *T. m. nasicus,* have 2n = 58 and 2n = 56, respectively (Thaeler, 1980). Variation in diploid number (Thaeler, 1980) and postulated biogeographic origins (Dalquest and Scheffer, 1944*a*, 1944*b*; Walker, 1955) suggest that the species is polyphyletic.

Albinism, melanism, and dilution (absence of a dark color band on hairs) were recorded in *T. mazama* in Oregon. Some individuals have white splotches on the venter and a forehead blaze was noted in some specimens of *T. m. niger* and *T. m. oregonus* (Walker, 1955).

CONSERVATION STATUS. As of 28 October 1998, *T. mazama* was listed as a "candidate" species by the Washington Department of Fish and Wildlife and a "species of concern" by the U.S. Fish and Wildlife Service. The species was not included on lists of threatened or endangered species prepared by the Oregon

FIG. 5. Casts of *Thomomys mazama* burrows formed when snow that contained burrows packed with earth melted. Photograph from Verts and Carraway (1998).

Department of Fish and Wildlife or the California Department of Fish and Game.

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 mouselike body shape—Jaeger, 1955). The specific name *mazama* was derived from the type locality, Mount Mazama (= Crater Lake), Oregon (Merriam, 1897).

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