

*Spermophilus saturatus*. By Stephen C. Trombulak

Published 27 December 1988 by The American Society of Mammalogists

*Spermophilus saturatus* (Rhoads, 1895)

Cascade Golden-mantled Ground Squirrel

*Tamias lateralis saturatus* Rhoads, 1895:43. Type locality "Lake Kichelos [=Keechelus], Kittitas Co., Washn. (elevation 8,000 ft.)."

**CONTEXT AND CONTENT.** Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Callospermophilus*. Considered monotypic by Hall (1981).

**DIAGNOSIS.** *Spermophilus saturatus* is the largest of the three species in the subgenus *Callospermophilus*. It is distinguished from *S. madrensis* by having a poorly-defined russet-colored mantle on head and shoulders and a length of body >286 mm; in *S. madrensis* the mantle is almost completely lacking and the length of body is <243 mm (Hall, 1981). *S. saturatus* is less reliably distinguished from *S. lateralis*; *S. saturatus*, however, has a less-developed mantle and all but the smallest individuals are larger than *S. lateralis*.

**GENERAL CHARACTERS.** *Spermophilus saturatus* has a stocky body and relatively long hair (Fig. 1). The top and sides of the head and shoulders have a poorly-defined russet mantle. The eyes are surrounded by a pinkish-buff ring and the ears are tawny. The remainder of the dorsum is dark gray-brown with a white stripe on each side that runs from shoulder to hip. White stripes are bordered above and below by poorly-defined black stripes (Hall, 1981; Howell, 1938). Tail, feet, and venter are buff colored.

Howell (1938) listed the following mean (range) measurements (in mm) of 10 males and 10 females, respectively, taken from the Cascade Mountains of Washington: total length, 305 (287 to 315), 300 (286 to 312); length of tail, 110.9 (100 to 118), 106.5 (92 to 116); length of hind foot, 46.5 (44 to 49), 45.4 (43 to 48); length of ear, 17 (16 to 18), 17.8 (17 to 18.5); greatest length of cranium, 46.4 (44.0 to 48.3), 45.2 (43.9 to 46.3); palatal length, 21.4 (20.0 to 22.5), 20.8 (20.0 to 21.3); zygomatic breadth, 28.9 (27.7 to 30.4), 28.1 (27.2 to 28.6); cranial breadth, 20.4 (19.5 to 20.9), 19.9 (19.5 to 20.2); interorbital breadth, 11.5 (10.9 to 12.3), 11.0 (10.6 to 11.6); postorbital constriction, 13.4 (12.9 to 14.2), 13.3 (12.4 to 14.0); length of nasals, 16.8 (15.8 to 17.7), 16.0 (15.6 to 16.6); length of maxillary tooth row, 8.9 (8.1 to 9.5), 9.0 (8.6 to 9.6). The dental formula is  $i\ 1/1, c\ 0/0, p\ s/1, m\ 3/3$ , total 22 (Fig. 2).

**DISTRIBUTION.** *Spermophilus saturatus* is found in the Cascade Mountains in Washington as far south as the Columbia River and in southern British Columbia as far north as the Tulameen River and east to the Similkameen River (Hall, 1981; Howell, 1938; Fig. 3); Cowen and Guiget (1960) state that the northern limit of the range is not known. No fossils of *S. saturatus* are known.

**FORM AND FUNCTION.** The annual molt takes place in June or July with molt beginning at the head and shoulders (Howell, 1938). They have a diamond-shaped glandular area of thickened skin between their shoulders and an anal gland composed of three papillae (Banfield, 1977).

Gut mass is 50% greater in pregnant and lactating females than in males and nonreproductive females. Monthly coefficients of variation for gut mass of males are near 10% (Kenagy and Barnes, 1988).

When *S. saturatus* is held at 23°C in 12:12 LD (light : dark) for 21 months, testes mass shows an endogenous circannual cycle with a 327-day period (Kenagy, 1980). Barnes (1986) observed maximum testes mass in January for animals at 23°C and 10:14 LD. It took 3 to 3.5 months for testes to reach maximum size and only a little longer for regression (Kenagy, 1980). Average testes mass was 2.3 g or 1.01% of total body mass. Actual testes mass of

*S. saturatus* relative to that predicted by the allometric equation describing testes mass for all mammals is 1.32. Testes grow at 0.042 g/day requiring 0.192 kJ (kilojoules)/day, which represents 0.26% of basal metabolic rate (Kenagy and Trombulak, 1986).

At emergence in early April, free-living males have enlarged testes (about 2,000 mg) and seminal vesicles (about 100 mg), plus abundant motile sperm. Epididymides contain motile sperm in late June, 3 weeks after the last successful mating (Kenagy and Barnes, 1988). Nonreproductive-yearling males have smaller testes at emergence (0.303 g vs. 1.736 g) and a smaller percentage have pigmented scrota (0 vs. 100%) than do reproductive-yearling males (Barnes, 1984). Testes and seminal vesicles rapidly regress to near 0 mg after mating. In females, ovaries are large at emergence (about 30 mg) and remain large with conspicuous corpora lutea during pregnancy (Kenagy and Barnes, in press).

Male *S. saturatus* held in captivity at 23°C and 10:14 LD show circannual cycles of FSH (follicle-stimulating hormone), LH (luteinizing hormone), T (testosterone), and DHT (dihydrotestosterone). FSH reaches a peak of 250 ng (nanograms)/ml in January and then declines to baseline (50 ng/ml) by June. LH is undetectable during the fall, increases to 30 ng/ml in March, and declines to baseline by summer. T and DHT peak at 3 ng/ml in March and parallel the pattern for LH. A few females have detectable levels of LH in February and March (Barnes, 1986).

Reproductive males have maximum levels of FSH and LH in March of 300 and 50 ng/ml and maximum T levels of 8.8 ng/ml after arousal. Maximum levels are 20 to 50% less in nonreproductive males. Both groups show FSH and LH levels in the autumn of 50 and 0 ng/ml, respectively, and T levels increase during periodic arousal from 0.063 to 0.534 ng/ml (Barnes, 1986).

In the field, adult males have high LH levels (600 ng/ml) after emergence from hibernation that decrease to basal level (1 ng/ml) by June. T levels peak in mid-April at the time of maximum testes and seminal vesicle mass. All three decrease in parallel and reach minimum by June. DHT is always low and is <10% of T levels. FSH is about 70 ng/ml throughout the active season. Corticosterone increases from 3 to 10 ng/ml between April and June and remains elevated until immergence. Adult females in the field have elevated LH levels only in early May, corresponding to the time of mating. FSH is maximum at 125 in April and decreases to 60 ng/ml by August. Juvenile males in the field have basal levels of FSH through-



FIG. 1. Adult male *Spermophilus saturatus* from 25 km S Trinity, Chelan Co., Washington.

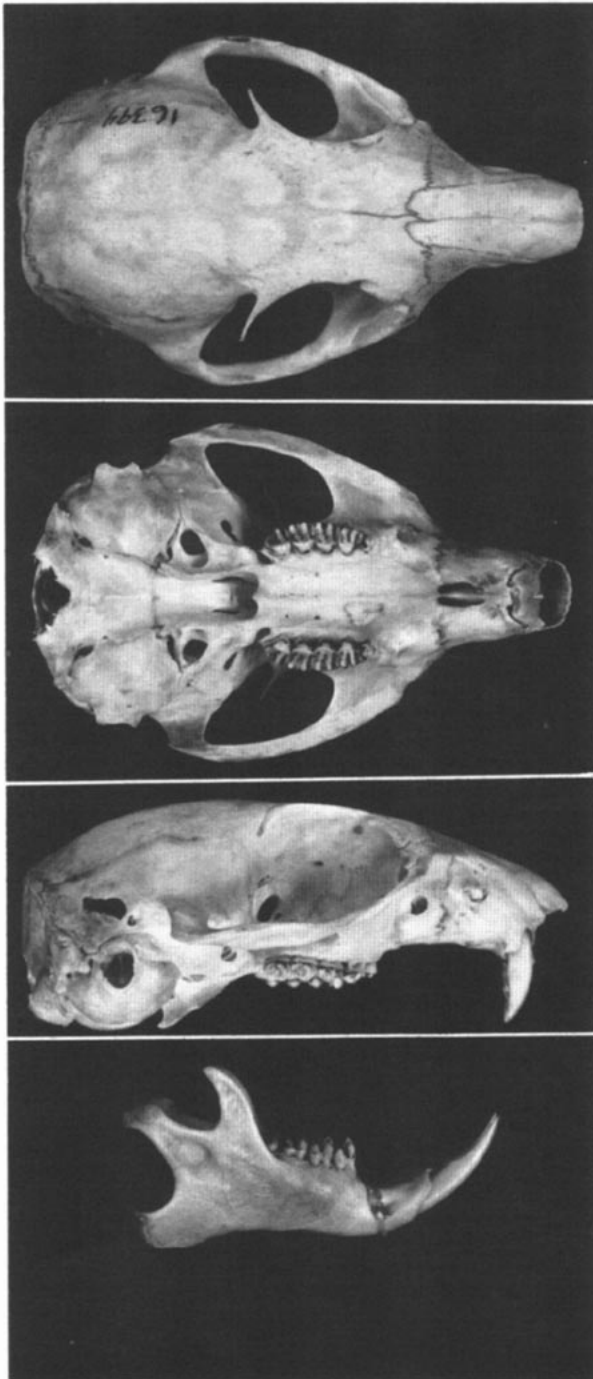


FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of an adult male *Spermophilus saturatus* collected 18 km N Cashmere, Chelan Co., Washington. Greatest length of cranium is 45.4 mm (16394 Thomas Burke Memorial Washington State Museum, Univ. of Washington).

out their first summer. LH, T, and corticosterone increase from near 0 to 25, 3, and 10 ng/ml, respectively, between emergence in July and immersion in September (Barnes, 1983).

At 23°C and 12L:12D, *S. saturatus* has an endogenous circannual cycle of body mass with a period of 327 days. The mean date of peak body mass is later than for animals in the field; when held in captivity for 21 months the first peak was 24 December and the second peak was 14 November (Kenagy, 1980).

Body mass in the field increases from emergence to immersion and ranges from 200 to 350 g. Adults weigh more than yearlings and yearlings weigh more than juveniles throughout the active season (Trombulak, 1987). Kenagy and Barnes (1988) found adult males

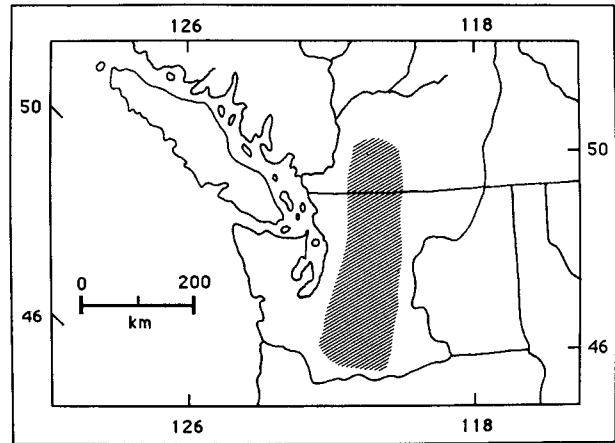


FIG. 3. Distribution of *Spermophilus saturatus* in western North America (modified from Banfield, 1977, and Hall, 1981).

to weigh 6% more than adult females although Trombulak (1987) found no difference. Body mass differs for *S. saturatus* in different habitats. Those that live in a meadow weigh up to 15% more than those in a forest. Body mass also differs as much as 20% among years, perhaps related to variation in time of snow melt (Trombulak, 1987).

Body mass of adults and yearlings increases at 0.93 g/day in meadow habitat and 0.58 g/day in forest. Growth rates of juveniles do not differ between habitats and average 2.5 g/day. Adult males do not gain weight at a constant rate during the active season. From mid-May to mid-June and from mid-August to mid-September they gain an average of 1.03 g/day. From mid-June to mid-August they gain only 0.39 g/day (Trombulak, 1987).

Body fat is 10% of body mass (without gut) in adults at emergence, declines to 2.5% during May and June, and then increases to a mean of 15% in September. Maximum body-fat content in September is 31.4%. Fat deposits in gonads peak at 4% of body mass in April. Much of the increase in body mass during the active season is due to the deposition of fat for hibernation. Body fat in juveniles increases from a basal level of 3.9% at emergence to 8.6% at immersion (Kenagy and Barnes, 1988).

Nonreproductive males are below reproductive males in body mass throughout the active season and in body fat during April (Kenagy and Barnes, 1988). Body fat of nonscrotal yearlings is 25.5% in late March (Barnes, 1984).

When held at 23°C and 12L:12D, *S. saturatus* has an endogenous circannual cycle of water consumption with a period of 347 days. Maximum and minimum consumption is 175 and 2 ml/day. The minimum is in mid-February, halfway between the maxima of body and testes mass. The endogenous rhythms of testes mass, body mass, and water consumption do not become internally desynchronized (Kenagy, 1980).

Normothermic, fasting animals in thermal neutrality (29.5°C), constant light, and available water show metabolic rates that differ between day and night and between times of year. Animals at the end of the hibernation have daytime metabolic rates of 116.3 ml/h and nighttime rates of 122.1 ml/h. Later in the spring these rates increase to 178.6 and 163.0 ml/h for day and night, respectively. The ratio of day to night metabolic rate in the spring (1.14) does not differ from that for 18 other species of small mammals. In the spring, metabolic rate has two daily peaks, one at the beginning of the activity period and one at the end (Kenagy and Vleck, 1982).

Normothermic body temperatures are 36 to 38°C (Barnes, 1986). In lethargic animals, rectal temperatures are as low as 24°C (Kenagy, 1980). Held in captivity at 4°C, *S. saturatus* enters torpor. When held at 23°C, animals are only occasionally hypothermic. While in torpor, animals arouse and return to normothermic temperatures every several days to 2 weeks (Barnes, 1986). Energy content of *S. saturatus* measured by bomb calorimetry is 3.4 kJ/g of wet mass; 86.7% of wet mass is water (Kenagy and Trombulak, 1986).

Daily energy expenditure in free-ranging *S. saturatus* measured with doubly-labeled water is greatest for lactating females

(Kenagy, 1987). They expend 289 kJ/day, which is 3.1 times greater than basal metabolic rate and represents an 82% increase over daily energy expenditure during the mating season. The maximum mass-specific metabolic rate is  $1.33 \text{ kJ g}^{-1} \text{ day}^{-1}$ , measured for lactating females. Energy expended during June represents 30% of the annual energy budget; 8,055 kJ are turned over as metabolism and 4,431 kJ are exported as milk and embryos. This level of expenditure is 55% greater than for males at the same time of year. The exported energy contained in embryos and milk plus their cost of synthesis is 5,908 kJ and is a 90% addition to energy metabolized for other needs. Females with an average size litter at weaning (2.7) face a 24% increase in energy commitment, including the energy exported in milk and young. Females weaning 5 young increase energy commitment by 44%. The greater mass of males in this population offsets the increased energetic cost of reproduction in females and the total annual energy expenditures of males and females are the same: 42.1 and 41.9 MJ (megajoules), respectively. Hibernation accounts for only 18% of the annual energy expenditure (Kenagy, 1987).

*Spermophilus saturatus* has three gaits (Hoyt and Kenagy, 1988). From 0.3 to 0.8 m/s they walk; all four legs move asynchronously with the left and right sides  $180^\circ$  out of phase. From 0.8 to 1.2 m/s they trot; each front foot is synchronous with the contralateral rear foot and the two pairs are  $180^\circ$  out of phase. At  $>1.2 \text{ m/s}$  they gallop; all four feet move asynchronously and the spine undergoes considerable flexion and extension. At 2.6 m/s, *S. saturatus* is near the maximum limit of aerobic metabolism. At speeds  $>4.2 \text{ m/s}$  they primarily are using anaerobic metabolism. At speeds  $<0.8 \text{ m/s}$ :  $\text{ml O}_2 \text{ g}^{-1} \text{ h}^{-1} = 2.91 + 3.80 \text{ speed}$ ; at speeds  $>0.8 \text{ m/s}$ :  $\text{ml O}_2 = 5.76 + 1.41 \text{ speed}$ . Energy expenditure increases less with increasing speed when running than when walking (Hoyt and Kenagy, 1988).

**ONTOGENY AND REPRODUCTION.** Mating occurs within a few days after female emergence in mid- to late-April and lasts about 2 weeks. Gestation is 28 days and parturition occurs in late-May. Twenty percent of observed pregnancies involve reabsorption of embryos. Average litter size at birth is 4.1 with a range of one to five (Kenagy and Barnes, 1988). The breeding season is highly synchronous; *S. saturatus* have one litter/year in the early summer (Kenagy and Barnes, 1988; Trombulak, 1987). Year-to-year differences in the time of breeding are as great as 15 days (Trombulak, 1987). Individual mass at birth is 6.0 g (representing 3% of maternal mass) and litter mass is 24.8 g (12% of maternal mass; Kenagy and Barnes, 1988).

Juveniles develop in underground nests for 36 days before emergence in early April. At emergence, average juvenile mass is 85 g (44% of maternal mass) and average litter mass is 352 g (170% of maternal mass). Mothers continue a low level of lactation for at least 1 week after juveniles emerge and begin eating solid food (Kenagy and Barnes, 1988).

Incidence of breeding is 100% for adult females, and from 54 to 100% for yearling females (Kenagy and Barnes, 1988; Trombulak, 1987). All adult males develop scrotal testes and yearling males may become scrotal. Age of first reproduction in males is variable. Twenty-two percent of yearlings in forest and 0% in meadow habitat are scrotal. Scrotal and nonscrotal yearlings do not differ in body mass at emergence (Trombulak, 1987). However, scrotal yearlings have greater body masses than nonreproductive yearlings at their maxima (311 vs. 254 g), first day of hibernation (274 vs. 224 g), and throughout hibernation (Barnes, 1984, 1986). *Spermophilus saturatus* lives to be at least 4-years old (Trombulak, 1983).

**ECOLOGY.** *Spermophilus saturatus* is common on eastern slopes of the Cascade Mountains from alpine to yellow pine (*Pinus ponderosa*) belts, but is only found occasionally on western slopes (Booth, 1947). In alpine habitat *S. saturatus* primarily is found in krumholtz and areas where talus  $\geq 75\%$  of the total cover (Reichel, 1986). At 800 m they are found in closed-coniferous forests as well as open meadows and clearcuts (Trombulak, 1987). Broadbooks (1958) observed several *S. saturatus* among scattered yellow pines above sage (*Artemisia tridentata*) and grassland at 1,000 m, but rarely in the open away from the cover of trees and logs.

*Spermophilus saturatus* is preyed upon by great-horned owls (*Bubo virginianus*) and probably goshawks (*Accipiter gentilis*), red-tailed hawks (*Buteo jamaicensis*), merlins (*Falco columbarius*), long-eared owls (*Asio otus*), coyotes (*Canis latrans*), red foxes (*Vulpes vulpes*), long-tailed weasels (*Mustela frenata*), martens (*Martes*

*americana*), and bobcats (*Lynx rufus*; Dalquest, 1948; Trombulak, 1983). *S. saturatus* does not use the same food as do other species that live in the same area, including *Eutamias amoenus* (Broadbooks, 1958; Trombulak, 1983). *S. saturatus* tolerates without aggression *E. amoenus* that forage within 5 cm and nest within 10 m (Broadbooks, 1958, 1970). Aggressive interactions over food are avoided by the use of different plant parts; *S. saturatus* eats more leaves and stems and *E. amoenus* eats more seeds (Broadbooks, 1958; Trombulak, 1983).

In areas with both forest and meadow, *S. saturatus* move freely between habitats. As many as 15% of juveniles, 14% of yearlings, and 7% of adults resident in either meadow or forest are born in the other habitat. Adult *S. saturatus* range widely during the breeding season. As many as 46% of adults resident in a forest are found in an adjacent meadow during April and May. Sex ratio does not differ from 1:1 for juveniles, yearlings, or adults. The combined density of adults and yearlings exceeds 4.5 individuals/ha in open meadows and 2.0/ha in closed-coniferous forest (Trombulak, 1983). Along the talus embankments of railroads they average one squirrel/90 m (Dalquest, 1948).

Distance of juvenile dispersal from the natal burrow is affected by habitat; average dispersal distance in forested habitat is 54.8 m, whereas in a meadow it is 231.0 m (Trombulak, 1983). Both males and females tend to disperse from the natal burrow; males disperse an average of 181.8 m and females disperse 157.5 m (Trombulak, 1987).

*Spermophilus saturatus* primarily is a mycophile and herbivore. In meadows, the proportion of feeding time spent consuming hypogeous fungi is 44%, leaves of vetch (*Vicia*) 21%, bark 10%, grasses (seeds and leaves) 6%, and conifer seeds 1%. In forests, the proportion of feeding time spent on hypogeous fungi is 63%, and as a result, a smaller proportion of time is spent on plant parts (Trombulak, 1983). *S. saturatus* eats more herbs in the spring and more fungi in the fall (Kenagy, 1987). In other locations the diet of *S. saturatus* includes dandelion heads (*Taraxacum*), corms, fungi, seeds of lupine (*Lupinus*) and pine (*Pinus*), and the berries of salal (*Guaytheria shallon*), huckleberry (*Vaccinium*), and mountain-ash (*Sorbus*; Dalquest, 1948; Broadbooks, 1958). Although *S. saturatus* occasionally climbs 3 to 5 m up into bushes and conifers, it generally forages on the ground for pine cones dropped by Douglas squirrels (*Tamiasciurus douglasii*). *S. saturatus* also eats the flesh of road kills, including their own species (Dalquest, 1948).

Trombulak (1983) used wire-mesh live traps (14 by 14 by 41 cm) baited with peanut butter to catch adult *S. saturatus* and aluminum-sided live traps (7.5 by 9 by 23 cm) baited with mixed birdseed to catch juveniles. Animals were transferred to a pillow case for subsequent handling. Toe clipping was used for permanent identification of individuals; this method does not affect survival. Kenagy and Barnes (1988) successfully used wire-mesh traps baited with 1 to 2 g of bacon.

Adults, yearlings, and juveniles can be distinguished at all times of the year based on mass and pelage condition as long as comparisons are made within the same habitat (Trombulak, 1983). Parasites of *S. saturatus* have not been described.

**BEHAVIOR.** *Spermophilus saturatus* is a diurnal and semifossorial species that begins to emerge from hibernation in spring. Adult males emerge up to 1 week before adult females (Kenagy and Barnes, 1988; Trombulak, 1987), although males and females do not differ in the time at which 50% of the individuals in each group emerge (Trombulak, 1987). Males patrol the areas where females will emerge (Kenagy, 1987). Timing of emergence varies among years from mid-April to mid-May (Trombulak, 1987) and is correlated with the time at which the soil temperature at 50 cm exceeds  $5^\circ\text{C}$  (Kenagy, 1987). Time of adult emergence is the same in a forest and adjacent meadow. Yearling females emerge 1 to 2 weeks after adults and yearling males emerge 1 week later (Trombulak, 1987). A substantial fraction of males emerge more than 2 weeks after the first males and are nonreproductive (Kenagy and Barnes, 1988). Nonreproductive-yearling males end hibernation later than reproductive-yearling males (17 May and 12 April, respectively; Barnes, 1984).

Populations are active aboveground for about 4.5 months. Adults and yearlings enter hibernation from mid-August to late-September. Females may enter hibernation before males (Trombulak, 1987) or males before females (Kenagy, 1987). Juveniles immerse 1 to 3 weeks after adults and yearlings. Juveniles that will reproduce

as yearlings enter hibernation later than those that will not (9 December and 2 November, respectively; Barnes, 1984).

The majority of time an individual is aboveground is spent sitting, followed by feeding, grooming, and searching for food. The proportion of time spent sitting decreases from 83% in May to 51% in July and increases again to 75% in September. The amount of time spent feeding and searching increases from 10% in May to 25% in July and decreases again to 8% in September (Trombulak, 1987). During lactation, feeding composes 17 to 18% of daily activity (Kenagy, 1987).

Habitat structure influences foraging behavior. In a meadow, the ratio of time spent feeding to search time is 0.55, whereas in a forest it is 0.42. The average length of a feeding bout in a meadow is 53.2 s with a search time of 20.6 s. In a forest, length of a feeding bout and search time is 26.5 s and 33.6 s, respectively (Trombulak, 1987).

*Spermophilus saturatus* use underground burrows for hibernation, sleeping, refuge, and raising young (Broadbooks, 1958). Entrances are usually placed beside rocks, stumps, logs, or among the roots of bushes. Tunnels go at least 1 m underground through dirt and clefts in boulders to a nest cavity. The nest is a matted cup of dry grass with fresh vegetation lying loose on the cup. Multiple tunnels lead to the nest cavity (Dalquest, 1948).

**REMARKS.** No published information exists on the genetics of *S. saturatus*. Some authors have placed *S. saturatus* as a subspecies of *S. lateralis* (Elliot, 1901, 1905; Miller, 1912) or have referred to *S. saturatus* as *S. lateralis* (Broadbooks, 1970; Ingles, 1965). Gromov et al. (1965) arrange *Callospermophilus* as a subgenus of *Otospermophilus*.

I thank B. M. Barnes, G. J. Kenagy, and E. Rickart for comments on the manuscript, and J. Rozdilsky and the Thomas Burke Memorial Washington State Museum, University of Washington, for providing the specimen depicted in Fig. 2.

#### LITERATURE CITED

- BANFIELD, A. W. F. 1977. The mammals of Canada. Univ. Toronto Press, Toronto, 438 pp.
- BARNES, B. M. 1983. The reproductive endocrinology of the golden-mantled ground squirrel. Unpubl. Ph.D. dissert., Univ. Washington, Seattle, 71 pp.
- . 1984. Influence of energy stores on activation of reproductive function in male golden-mantled ground squirrels. *J. Comp. Physiol.*, 154:421–425.
- . 1986. Annual cycles of gonadotropins and androgens in the hibernating ground squirrel *Spermophilus saturatus*. *Gen. Comp. Endocrinol.*, 62:13–22.
- BOOTH, E. S. 1947. Systematic review of the land mammals of Washington. Unpubl. Ph.D. dissert., Washington State Univ., Pullman, 646 pp.
- BROADBOOKS, H. E. 1958. Life history and ecology of the chipmunk, *Eutamias amoenus*, in eastern Washington. *Misc. Publ. Mus. Zool., Univ. Michigan*, 103:1–42.
- . 1970. Home ranges and territorial behavior of the yellow-pine chipmunk, *Eutamias amoenus*. *J. Mamm.*, 51: 310–326.
- COWEN, I. M., AND C. J. GUIGET. 1960. The mammals of British Columbia. Second ed. British Columbia Provincial Museum Handb., 11:1–413.
- DALQUEST, W. W. 1948. Mammals of Washington. *Univ. Kansas Publ., Mus. Nat. Hist.*, 2:1–444.
- ELLIOT, D. G. 1901. A synopsis of the mammals of North America and the adjacent seas. *Field Columbian Mus. Publ. Zool. ser.*, 2:1–471.
- . 1905. A checklist of mammals of the North American continent, the West Indies and the neighboring seas. *Field Columbian Mus. Publ. Zool. ser.*, 6:1–192.
- GROMOV, I. M., D. I. BIBIKOV, N. I. KALABUKHOV, AND M. N. MEIER. 1965. *Nazemnye belichii (Marmotinae)*. *Fauna SSSR, Mlekopitayushchie*, Nauka, Moscow-Leningrad, 3:1–466.
- HALL, E. R. 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1–606 + 90.
- HOWELL, A. H. 1938. Revision of the North American ground squirrels with a classification of North American Sciuridae. *N. Amer. Fauna*, 56:1–256.
- HOYT, D. F., AND G. J. KENAGY. 1988. Energy costs of walking and running gaits and their aerobic limits in golden-mantled ground squirrels. *Physiol. Zool.*, 61:34–40.
- INGLES, L. G. 1965. Mammals of the Pacific states. Stanford Univ. Press, Stanford, California, 506 pp.
- KENAGY, G. J. 1980. Interrelation of endogenous annual rhythms of reproduction and hibernation in the golden-mantled ground squirrel. *J. Comp. Physiol.*, 135:333–339.
- . 1987. Energy allocation for reproduction in the golden-mantled ground squirrel. *Symp. Zool. Soc. London*, 57:259–273.
- KENAGY, G. J., AND B. M. BARNES. 1988. Seasonal reproductive patterns in four coexisting rodent species from the Cascade Mountains, Washington. *J. Mamm.*, 69:274–292.
- KENAGY, G. J., AND S. C. TROMBULAK. 1986. Size and function of mammalian testes in relation to body size. *J. Mamm.*, 67: 1–22.
- KENAGY, G. J., AND D. VLECK. 1982. Daily and temporal organization of metabolism in small mammals: adaptation and diversity. Pp. 322–338, in *Vertebrate circadian systems* (J. Aschoff, S. Daan, and G. Groos, eds.). Springer-Verlag, Berlin, 340 pp.
- MILLER, G. S. 1912. List of North American land mammals in the United States National Museum, 1911. *Bull. U.S. Nat. Mus.* 79:1–455.
- REICHEL, J. D. 1986. Habitat use by alpine mammals in the Pacific Northwest USA. *Arctic Alpine Res.*, 18:111–119.
- RHOADS, S. N. 1895. New subspecies of the gray fox and Say's chipmunk. *Proc. Acad. Nat. Sci. Philadelphia*, 1895:42–44.
- TROMBULAK, S. C. 1983. The ecology of montane sciurids: pattern and process in population and community structure. Unpubl. Ph.D. dissert., Univ. Washington, Seattle, 78 pp.
- . 1987. Life history of the Cascade golden-mantled ground squirrel (*Spermophilus saturatus*). *J. Mamm.*, 68:544–554.

Editors of this account were TROY L. BEST and SYDNEY ANDERSON. Managing Editor was CARLETON J. PHILLIPS.

S. C. TROMBULAK, DEPARTMENT OF BIOLOGY, MIDDLEBURY COLLEGE, MIDDLEBURY, VERMONT 05753.