

Spermophilus lateralis. By Molly A. Bartels and Doug P. Thompson

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Spermophilus lateralis (Say, 1823)

Golden-mantled Ground Squirrel

Sciurus lateralis Say, 1823:46. Type locality "Arkansas River, near Canyon City [Fremont Co.], Colorado." Restricted to "about 26 miles below the present Canyon City" by Merriam (1905:163).

Spermophilus lateralis Cuvier, 1831:335. First use of current name combination.

Tamias castanurus Merriam, 1890:19. Type locality "Park City, Wasatch Mountains [Summit Co.], Utah."

Tamias chrysodeirus Merriam, 1890:19. Type locality "Fort Klamath [Klamath Co.], Oregon."

Tamias cinerascens Merriam, 1890:20. Type locality "Helena, [Lewis and Clark Co.], Oregon."

Tamias wortmani Allen, 1895:335. Type locality "Kinney Ranch, Bitter Creek, Sweetwater Co., Wyoming."

Spermophilus (Callospermophilus) bernardinus Merriam, 1898:782. Type locality "San Bernardino Peak [San Bernardino Co.], California."

Callospermophilus trepidus Taylor, 1910:283. Type locality "head of Big Creek, (altitude 8000 feet), Pine Forest Mountains, Humboldt County, Nevada."

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Tribe Marmotini, Subtribe Spermophilina (Hafner, 1984), Subgenus *Callospermophilus* (Hall, 1981). The genus *Spermophilus* contains about 36 species (Honacki et al., 1982). There are 13 subspecies of *S. lateralis* (Hall, 1981).

S. l. arizonensis (Bailey, 1913:130). Type locality "near Little Spring (8252 ft.), San Francisco Mts. [Coconino Co.], Arizona."

S. l. bernardinus Merriam, 1898:782, see above.

S. l. castanurus (Merriam, 1890:19), see above.

S. l. certus (Goldman, 1921:232). Type locality "Charleston Peak (north base), Charleston Mountains [Clark Co.], Nevada."

S. l. chrysodeirus (Merriam, 1890:19), see above.

S. l. cinerascens (Merriam, 1890:20), see above.

S. l. connectens (Howell, 1931:161). Type locality "Homestead [Baker Co.], Oregon."

S. l. lateralis (Say, 1823:46), see above.

S. l. mitratus (Howell, 1931:161). Type locality "South Yolla Bolly Mountain [Tehama Co.], California."

S. l. tescorum (Hollister, 1911:2). Type locality "head of Moose Pass branch of the Smoky River, Alberta (near Moose Pass, B.C.), at 7000 feet."

S. l. trepidus (Taylor, 1910:283), see above.

S. l. trinitatis (Merriam, 1901:126). Type locality "Trinity Mountains east of Hoopa Valley, California (altitude 5700 feet)."

S. l. wortmani (Allen, 1895:335), see above.

DIAGNOSIS. *Spermophilus lateralis* is distinguished from other *Spermophilus* species by a longitudinal white stripe on either side of the back, bordered on each side by a pronounced black stripe, and by a golden brown to a tawny or russet mantle over the head and shoulders (Fig. 1; Cowan and Guiguet, 1965; Gordon, 1943). The lateral stripes of *S. lateralis* are similar to those of *Tamias* but do not extend through the eye and lack the median dark stripe (Hatt, 1927). The tail is less bushy and shorter than in *Tamias* (Gordon, 1943). *S. lateralis* is distinguished from *S. saturatus* by its mantle color, strongly marked inner black stripe, pale yellowish-white sides, and larger skull (39.6-45.6 mm vs. 44.0-48.3 mm; Hall, 1981). In addition, only *S. saturatus* occurs in the Cascade Mountains of southern British Columbia and Washington (Cowan and Guiguet, 1965; Hall, 1981; Howell, 1938). *S. lateralis* is distinguished from *S. madrensis* by its longer tail (61-120 mm

[Long, 1965] vs. 52-66 mm [Hall, 1981]), the presence of a mantle, longer and strongly marked black stripes and shorter white stripes, and its less highly arched skull. In addition *S. madrensis* occurs in Mexico; *S. lateralis* does not occur in Mexico (Hall, 1981).

GENERAL CHARACTERS. Whitish fur rings the eyes. The underparts are whitish or yellowish-gray. The tail is brownish black above, edged with buff, and yellow-gray or reddish-brown below. Winter pelage is grayer than in summer and the mantle is dull (MacClintock, 1970). The dorsal guard hairs have a distal dark band 4 mm in length (Mayer, 1952). *S. lateralis* exhibits sexual dimorphism in the brightness of the mantle (males are redder) and depth of skull (Hoffmeister, 1986; Merriam, 1890). Total length ranges from 235 to 295 mm (females, 238-295 mm—Hall, 1946; Howell, 1938; males, 235-293 mm—Howell, 1938; Taylor, 1910) and body mass ranges from 120 to 394 g (Hatt, 1927; McKeever, 1964). Other measurements (in mm) are: length of tail vertebrae, 61-120 (Long, 1965); length of hind foot, 35-46 (Howell, 1938); length of ear, 12-24; length of nasal, 13.1-17.5; length of maxillary toothrow, 7.1-9.4 (Howell, 1938; Long, 1965); zygomatic breadth, 23.8-29.4 (Hall, 1946; Hollister, 1911); cranial breadth, 18.1-21.9; palatal length, 18-22.2 (Hall, 1946; Hoffmeister, 1986); interorbital breadth, 8.2-12; postorbital breadth, 11.2-14.4 (Hoffmeister, 1986; Howell, 1938). Subspecies differ in pelage color and markings, body size, and cranial and dental characters (Howell, 1938; Merriam, 1901).

DISTRIBUTION. *Spermophilus lateralis* occurs in the mountains of the western United States and Canada (Fig. 2; Hall, 1981), and ranges from Upper Sonoran to boreal zones (Armstrong, 1972; Grinnell, 1913). It ranges in elevation from 1,220 m in the northern Sierra Nevada of California to 3,965 m at Pikes Peak, Colorado (Hatt, 1927; Tevis, 1952).



FIG. 1. *Spermophilus lateralis* from Lake Louise, Alberta, Canada. Photograph by F. S. Dobson.

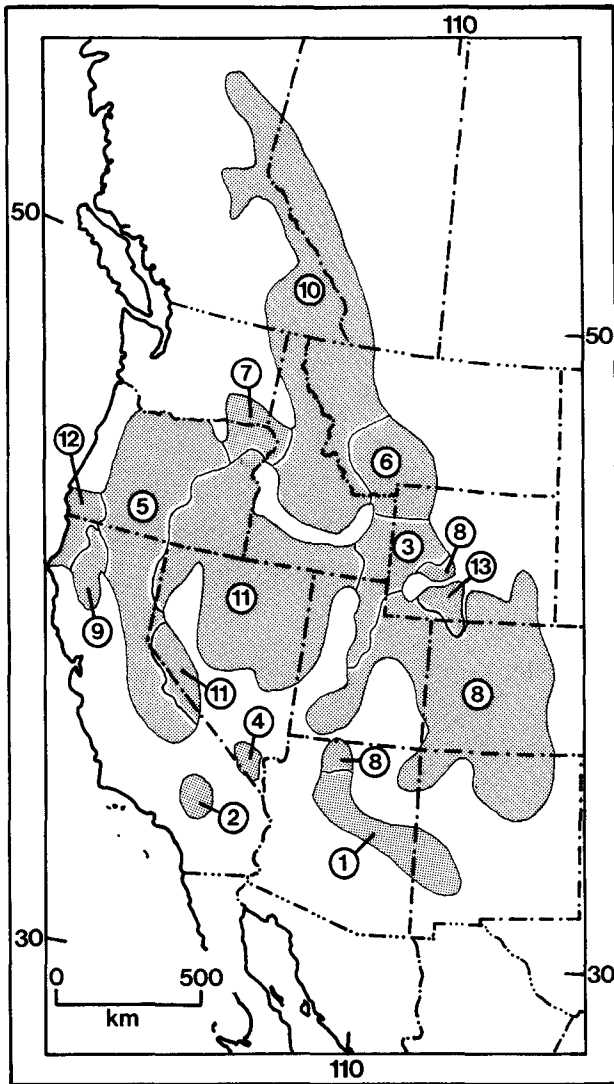


FIG. 2. Distribution of *Spermophilus lateralis* in western North America (Hall, 1981): 1, *S. l. arizonensis*; 2, *S. l. bernardinus*; 3, *S. l. castaneus*; 4, *S. l. certus*; 5, *S. l. chrysodeirus*; 6, *S. l. cinerascens*; 7, *S. l. connectens*; 8, *S. l. lateralis*; 9, *S. l. mitratus*; 10, *S. l. tesorum*; 11, *S. l. trepidus*; 12, *S. l. trinitatis*; 13, *S. l. wortmani*.

FOSSIL RECORD. Fossils of *S. lateralis* have been found in late Pleistocene deposits (Bryant, 1945). Currently, *S. lateralis* is absent from mountain ranges south of the Mogollon Rim in Arizona and those ranges that are both east of the Rio Grande and south of the Sangre de Cristo Mountains in New Mexico. Pleistocene occurrences outside the present distributional range presumably imply greater moisture in the past (Harris, 1985). The occurrence of *S. lateralis* at Ventana Cave, Pima Co., Arizona, is of particular interest because the nearest present-day occurrence is 260 km north of the cave at elevations >2,150 m (1,400 m higher than Ventana Cave; Kurtén and Anderson, 1980). It has been found in caves in Wyoming, Colorado, Idaho, Montana, California, Nevada, and Arizona, and identified from the late Wisconsinian and the mixed provenience, late Pleistocene/Holocene (Harris, 1985; Kurtén and Anderson, 1980). *S. saturatus* was isolated from *S. lateralis* in the southern Cascades during Vashon-Wisconsin time (Dalquest, 1948).

FORM AND FUNCTION. Skulls of adults have well-developed sagittal crests, while subadult skulls do not (Fig. 3; Tevis, 1955). The postorbital constriction is relatively broader than in the subgenera *Spermophilus* and *Poliocitellus* and the genera *Cynomys*, *Marmota*, and *Glaucomys*. The postorbital processes proper are farther posteriad in *S. lateralis*, the subgenera *Ictidomys* and *Xe-*

rospermophilus, and the genus *Ammospermophilus* than in other sciurids. The anterior cranial fossa is relatively larger in *S. lateralis*, the subgenus *Otospermophilus*, and the genus *Tamias* than in other sciurids. The skull of *S. lateralis* is smaller than that of *Otospermophilus* with the origin of the temporalis less extensive, the angular process of the mandible relatively shorter, and the interorbital region relatively narrower in comparison with width at the postorbital constriction. The cheek pouch extends posteriad to the level of the manubrium sterni. The ears resemble those of *Otospermophilus*, but the conchal lobe is smaller and the intertragal notch is deep and narrow (Bryant, 1945).

The dental formula is $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22. The upper incisors are slender, moderately curved, and perpendicular to the basicranial axis. The teeth resemble those of the subgenus *Otospermophilus*, but differ in that the metaloph of M1 and M2 joins the protocone and a small protolophid is present on P4 (Bryant, 1945). Molariform teeth of adults are conspicuously worn (Tevis, 1955).

Golden-mantled ground squirrels have one annual molt, which occurs in males when the sexual organs involute and in females usually after lactation. Young begin to molt after they begin to forage for themselves (Tevis, 1955). At the beginning of the molt the mantle and black lateral stripes appear faded. The molt begins on the nose and head, then rapidly progresses caudally and ventrally. If the skin is stretched out flat, the line of molt forms a distinct "V" with the open portion directed cephalad (Burt, 1934). Individuals in molt may have a patchy coat, with areas of dense new hair on the head or back surrounded by old worn hair (Grinnell and Dixon, 1918). Hairlessness has been reported (DuBowy and DuBowy, 1988).

Sudoriferous glands occur in a spatulate area of skin on the back and secrete strong-smelling sweat that may be used to mark. These glands are more prominent in spring and summer, are stimulated by excitement, and are more developed in adult males. When an animal is frightened, a milky secretion with a weak odor is emitted from three nipple-like anal glands that protrude from the anus (Hatt, 1927).

There are 18–20 caudal vertebrae and the fifth transverse process often is lost; 60% of individuals have four sacral vertebrae. The lateral fossa of the tibia is flatter in *S. lateralis* and *Otospermophilus* than in other ground squirrels. The fourth metatarsal is longer than the second. The slip of the serratus posterior, inferior to the eighth rib, is absent. There are seven or eight slips to the ribs of the levator scapulae and serratus anterior (Bryant, 1945).

Fat begins to accumulate in July with a three-fold increase from August to September. It is deposited subcutaneously between the shoulders, about the kidneys, and on the mesenteries (Hatt, 1927; Jameson and Mead, 1964; McKeever, 1964). Body size and fat storage is greater in squirrels at higher altitudes; males store more fat than females, regardless of altitude (Blake, 1972). Seasonal variation in fat content is greatest in young adults and lowest in juveniles and old animals (Aloia, 1981). Lipectomized squirrels can restore fat deposits (Forger et al., 1986).

Normal body temperature of *S. lateralis* ranges from 31.4 to 40.2°C (Blake, 1971; Mullally, 1953) and varies with altitude, ambient temperature, season, and time of day (Blake, 1971; Hudson and Deavers, 1973). In females, the reproductive stage coincides with highest mean body temperature; in males, highest body temperature occurs during the involution stage following the reproductive stage (Blake, 1971). Conductance decreases as ambient temperature rises from 37 to 39°C. Drooling occurs at 40°C and the maximum respiratory rate occurs at 38°C (Hudson and Deavers, 1973).

Water requirement of animals that are laboratory-acclimated and recently trapped from the field is 10 and 5 ml of water 100 g⁻¹ day⁻¹, respectively, when given water ad libitum (Bintz, 1969). Water requirements are greatest during the reproductive season declining immediately afterwards to as low as 29–50% of the maximum level. Water requirements are lowest during hibernation (2% of body mass/day—Blake, 1977). When deprived of water, only blood is consistently dehydrated; water content of the liver increases (Bintz and Riedesel, 1967). The greatest concentration of sodium chloride on which water balance can be maintained is 200–300 μM. When deprived of water, field-adapted animals are better able to conserve body sodium than laboratory-acclimated animals (Bintz, 1969).

Golden-mantled ground squirrels have dichromatic color vision with spectral neutral points centered at 507.5 nm. Their retinas contain a small number of functional rods in addition to a much

more obvious population of cones. Cone pigments found in the retina have peaks of sensitivity at about 440 and 525 nm (Jacobs, 1978).

Adrenal glands of mature males are heavier than those of females, except in May–July and January. Adrenal glands of males are heaviest at the peak of the breeding season, whereas adrenals of females are heaviest during the reproductive period. There is little difference in histology or relative width of the three zones of the adrenal cortex of sexually active males and females (McKeever, 1964).

In the second year after a pinealectomy, *S. lateralis* lacks the progressive increase in length of hibernating bouts characteristic of intact and sham-operated animals. Pinealectomized males have an accelerated loss of body mass and show early onset of testicular development compared with intact and sham-operated males (Phillips and Harlow, 1982).

Mass of pituitary glands increases in summer and decreases in autumn. Minimum mass of pituitary glands is attained by adults and nonadults from December to January. Maximum mass and activity of pituitary glands occurs during the peak of the breeding season. Little secretory activity occurs in summer and autumn, except in juvenile animals, which have a burst of secretory activity in June coinciding with attainment of maximum relative body mass. Secretory activity is pronounced in December and January. Colloid inclusions can occur in the anterior pituitary (McKeever, 1964). Size of kidneys increases and protein levels in kidneys change significantly relative to control levels after both cold (5°C) and heat (35°C) acclimation, but enzyme activities of kidneys do not change (Balcer and Chaffee, 1984). Liver mass does not change due to chronic temperature stress, but liver protein content increases at 5°C and decreases at 35°C (Balcer and Chaffee, 1982).

Golden-mantled ground squirrels exhibit an endogenous circannual cycle, with hibernation occurring in winter (Blake, 1972). Maximum body mass is closely correlated with the onset of the heterothermic period, but is not a prerequisite for hibernation (Pengelley, 1968). Ambient temperature and food supply are potential circannual entraining agents. For females, entraining agents are gestation and lactation. It requires >1 year for light to show any appreciable effect on the free-running period (Pengelley and Asmundson, 1974). Forebrain structures are implicated in induction and maintenance of hibernation (Kilduff et al., 1985). A relative increase in cholecystokinin in the cerebral cortex with onset of hibernation may be responsible for inhibiting feeding (Muchlinski et al., 1983). The reticular formation of the brain stem area may modulate sensitivity and responsiveness to stimulation during hibernation (Toth, 1978). Hypothalamic neurotensin and bombesin may be involved in the reduction of body temperature during hibernation (Muchlinski et al., 1983). Hibernation is actively maintained through parasympathetic suppression of sympathetic stimuli (Twente and Twente, 1978).

Body temperature of hibernating animals approximates ambient temperature (Pengelley and Kelly, 1966). Periods of hibernation are shorter at higher body temperatures and are extended by cold temperatures (Mrosovsky, 1980; Twente et al., 1977). Mean metabolic rate at an ambient temperature of 30°C is 1.60 ml of oxygen $g^{-1} h^{-1}$, dropping to 0.066 ml of oxygen $g^{-1} h^{-1}$ during hibernation at an ambient temperature of 6°C. The respiratory quotient varies by season (Hock, 1969). Hibernating golden-mantled ground squirrels display a periodic respiratory pattern characterized by a variable breathing frequency (0–15 breaths/min) and tidal volume (1–4 ml). Apneic periods average 5–15 min (Steffen and Riedesel, 1982). Heart rate decreases to 6–13 beats/min and heartbeats frequently occur in duplicates and triplicates. In some animals, the heart rate accelerates near the end of periods of apnea. Cardiac arrests of 8–10 s are frequent during bouts of breathing and during periods of apnea (Steffen and Riedesel, 1979).

During hibernation, the pancreatic content of insulin, glucagon, somatostatin and pancreatic polypeptide are reduced and pancreas mass decreases to 57% of the nonhibernating mass (Bauman et al., 1987). The lipid phosphatidyl choline increases in the kidney, while sphingomyelin decreases. This may enhance membrane fluidity and contribute to low-temperature membrane function (Aloia, 1978). Glycogen granules of the liver are more abundant in hibernating animals (McKeever, 1964).

The stomach and small intestine of hibernating animals are empty, except for a small amount of clear liquid in the stomach. Some material remains in the caecum and large intestine throughout the winter. Except for the greater folding of the intestinal wall and

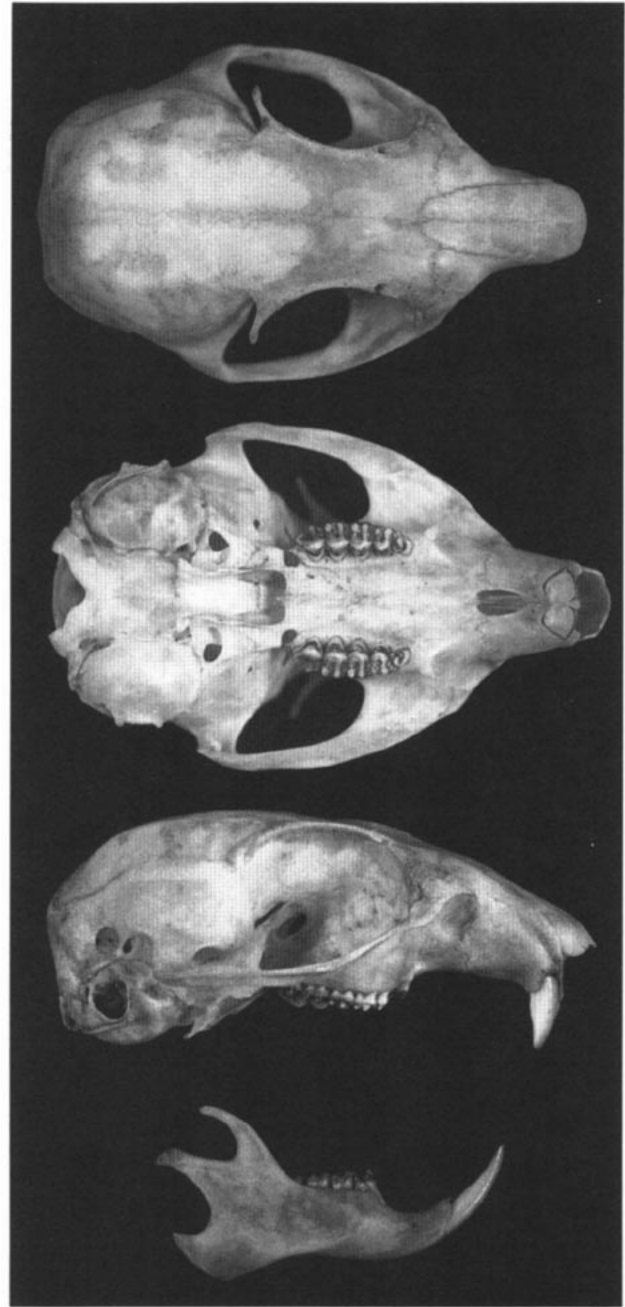


FIG. 3. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Spermophilus lateralis* (female from Taos County, New Mexico). Greatest length of cranium is 43.2 mm. Photographs by T. H. Henry.

the thicker surface epithelium in hibernating animals, there is no difference in the appearance of the large intestine in hibernating and nonhibernating animals. The caecum of hibernating animals has more mucous-filled goblet cells than in active animals (McKeever, 1964). Crypt cells in the small intestine, especially Paneth cells, undergo pronounced morphological changes during hibernation (Toth, 1981). Average mass loss during the entire hibernating period is 13.8% of the body mass or 0.26% loss of body mass per day (McKeever, 1964).

Hibernating golden-mantled ground squirrels have lower plasma potassium and higher plasma magnesium concentrations than active squirrels (Pengelley and Chaffee, 1966; Pengelley and Kelly, 1967). The concentrations of sodium, potassium, and calcium remain constant in the blood between periodic arousals and during hibernation (Pengelley and Asmundson, 1971). During torpor, the levels of total protein, globulin, amylase, lactate dehydrogenase, creatinine kinase,

cholesterol, and triglycerides decrease in the blood. Phosphate increases and levels of glucose, urea, creatinine, sodium, potassium and calcium are stable. These trends are reversed during the arousal phases of hibernation. Build up of toxic metabolic by-products does not trigger arousal (Andrews and Taylor, 1988). Urination takes place during every arousal, while defecation is rare during the hibernation period (Pengelley and Fisher, 1961).

Arousal from torpor starts with the activation of an intense oxidative source of heat. It takes an average of 3.5 h for the body temperature to rise from 4 to 38°C, while an average of 13 h is required for the body temperature to drop back to 4°C to re-enter torpor (Grodums et al., 1966; Hammel et al., 1968). Arousal is accompanied by a return to continuous ventilation, a 25-fold increase in ventilation rate in the first h, and a marked decrease in the ratio of heartbeats to breaths (Steffen and Riedesel, 1979, 1982). At emergence from hibernation golden-mantled ground squirrels possess reserve retroperitoneal fat, but by June these reserves have been depleted (Skryja and Clark, 1970). Northern and southern subspecies show no physiological differences in hibernation (Pengelley and Kelly, 1966).

Arousal is stimulated through a sympathetic reflex and is metabolically driven and expressed through progressive irritability (Twente and Twente, 1978). The reticular formation of the mesencephalon may be involved in the activation of arousal from torpor (Beckman et al., 1974). The amount of epinephrine required to evoke arousal decreases as the period of torpor progresses (Twente and Twente, 1968).

Males have circannual rhythms in plasma testosterone and levels of luteinizing hormone. Testosterone levels are lowest from October to January and peak during April and May. Peaks of luteinizing hormone are reached from March to July (Licht et al., 1982). The onset and termination of release of luteinizing hormone may be mediated by a circannual rhythm in the central nervous system (Zucker and Licht, 1983). Gonadal hormones secreted during the early postnatal period induce the seasonally recurring sex differences in body mass and some aspects of luteinizing hormone secretion (Smale et al., 1985).

During the reproductive stage, males have enlarged scrotal testes, which reach maximum mass and length in March when the scrotum and sheath of the penis are darkly pigmented (Blake, 1972). The baculum is about 2 mm in length. The spoon joins the shaft at an angle of about 135° and bears spines continuously around the sides and the distal margin (Bryant, 1945). The seminal vesicles continue to enlarge from March to April (McKeever, 1965). Mature sperm are present in the tubules from March to May (Skryja and Clark, 1970).

After the breeding season, the gonads and secondary sexual organs of both sexes atrophy. During testicular regression, Leydig cells undergo structural changes and may be steroidogenically active (Pudney, 1986). When not in reproductive condition, males have small abdominal testes (Blake, 1972). They begin redeveloping in the autumn (McKeever, 1965). During the hibernation season, the secondary sexual organs continue to develop (McKeever, 1965). Average gonadal mass nearly doubles in males, but spermatogenesis does not advance beyond pachytene spermatocytes which are present before hibernation. This increase in testicular mass represents only 20% of the eventual growth to an average mass of 3.5 g. Growth of testes is restricted to intervals of normothermy during and after the hibernation season. During the month following hibernation, testes increase rapidly in mass, and after 31 days, spermatozoa are found in the epididymides (Barnes et al., 1986).

In females, reproductive condition is characterized by a swollen vulva and perforate vagina (Blake, 1972). Ovaries are largest during April and May (McKeever, 1965). The mammae usually are in five pairs; one inguinal, two abdominal, and two pectoral. In 1-year-old females, the anterior pair of pectoral mammae usually are undeveloped (Bailey, 1936).

ONTOGENY AND REPRODUCTION. The breeding season of *Spermophilus lateralis* begins shortly after emergence from hibernation in March or April. Almost all males are in breeding condition when they emerge from hibernation. Males are sexually active for about 2 months. There is a delay of 2–3 weeks before some females enter breeding condition, and a few females are sexually active after the reproductive organs of males have atrophied. Corpora lutea involute rapidly during lactation and disappear by August.

Follicles begin enlarging in December and by February consist mostly of liquid (McKeever, 1964, 1965).

The gestation period is 26–33 days with the young usually born in July. However, births may occur as early as the last week of June at the lowest altitudes and as late as the first week of August at the highest altitudes (Cameron, 1967; Grinnell and Dixon, 1918; Pengelley, 1966). There may be two to nine placental scars (McKeever, 1964; Skryja and Clark, 1970), but these are reliable indicators of litter size only for 2 weeks after parturition (Tevis, 1955). Embryo resorption occurs in 11–12% of reproductive females (McKeever, 1964; Skryja and Clark, 1970). Implantation is equally distributed in both uterine horns (McKeever, 1964). Embryo mortality rates increase (0–19%) with decreasing altitude (Bronson, 1979). Litter size ranges from two to eight with an average of five. Litter size is greater at lower elevations, and for younger or heavier mothers (Bronson, 1979; Gordon, 1943; McKeever, 1965). The sex ratio (males : females) of litters is about 1:1, but favors females in adulthood possibly due to the greater exposure to risks of the more mobile males (Bronson, 1979).

Rates of growth and development are inversely related to litter size (Phillips, 1981). The body mass of neonates is 6.1 g (Meier, 1983). At birth, young are pink and hairless except for the mystacial vibrissae, which are 2 mm long, and minute hairs on top of the head. The lateral stripe pattern is not evident; ears and eyes are closed. All toes are fused and claws are barely discernable (McKeever, 1964). During the first 3 days, cranial suture lines and internal organs are barely visible through the skin. The claws of the forefeet are pigmented at their bases. The young are unable to right themselves when placed on their backs, and activity is limited to random leg movements and trunk twistings. Squeaks are emitted. The dorsal body area and head are pale and the eye regions are much darker (Clark and Skryja, 1969). By day 4, the skin of the dorsal body area is pale; vibrissae and head hair have not grown, and pinnae are evident (McKeever, 1964). By day 5, the claws of the forefeet are fully pigmented, while those of the hind feet are black at the bases only. The pinnae extend laterally. Pups are able to right themselves (Clark and Skryja, 1969). The lateral stripes appear on the shoulder area on days 4–6. By day 7, the lateral stripes are fully evident and all claws are fully pigmented. The vibrissae are 3–5 mm in length. By day 15, the front digits have separated and the hair is well developed on the entire dorsum, but sparse on the tail and ventor. The vibrissae are 5–10 mm in length, and the lower incisors are fully erupted. On days 15–19, a chucking note is uttered, which is the call until the young are nearly grown. The hind toes separate on days 14–18 (Clark and Skryja, 1969; McKeever, 1964). The ears open on days 14–20 (Ferron, 1981; Pengelley and Asmundson, 1966). At 18 days, the cheeks, neck, and foreshoulders have the characteristic golden color (Clark and Skryja, 1969). The upper incisors erupt on days 20–30 (Clark and Skryja, 1969; Ferron, 1981). Eyes open on days 22–31. The grooming sequence is first seen on days 23–25. Ingestion of solid food begins at 28–40 days, after which rate of growth accelerates from 1.2 to 3.7 g/day (Ferron, 1981; McKeever, 1964). Young are weaned at a minimum of 29 days (Pengelley and Asmundson, 1966). At 35 days, they defecate solid, black pellets (Clark and Skryja, 1969). At 40 days, they show a typical adult hair pattern over the entire body and tail, and vibrissae are 27 mm in length. The body form and proportions closely resemble those of adults (McKeever, 1964). Young emerge from the burrow when they are as small as 25% of adult size (Grinnell and Dixon, 1918). These young are the last to enter hibernation in the autumn (Yousef and Bradley, 1971). *S. lateralis* has a life span of 5 years in captivity (Pengelley and Asmundson, 1969) and of at least 7 years in the wild (Bronson, 1979).

ECOLOGY. *Spermophilus lateralis* is found in sunny habitats and inhabits forested or sparsely brushy territory from the upper edge of the pinyon belt to above timberline. It occurs on rocky slopes adjoining grasslands and also on forest floors, areas of scattered chapparal, and margins of mountain meadows. *S. lateralis* ranges down into sagebrush country and even out into meadows, but only if there are rocks for shelter. It also inhabits recently burned pine forests where an abundance of stumps and fallen tree trunks provide shelter and the open habitat produces an abundance of berry-bearing shrubs and flowering plants (Burt, 1934; Cowan and Guiguet, 1965; Gordon, 1943; Grinnell, 1918). *S. lateralis* commonly is found in pure and mixed stands of *Pinus ponderosa*, *P. flexilis*, *P. contorta*,

Picea engelmannii, *Pseudotsuga menziesii*, and *Populus tremuloides*, but is either absent or only forages through dense stands of *Picea* or *Abies* (Hatt, 1927; McKeever, 1964). It will invade logged timber stands (McKeever, 1964). *S. lateralis* also is found on dry, open, gravelly hillsides with sparse oak chaparral or seedling growth with an abundance of *Arctostaphylos uvaursi*, *Odostemon fremontii*, grasses, and other herbs and shrubs. It also occurs around campgrounds and buildings (Hatt, 1927).

Spermophilus lateralis is an omnivore. Fungi (Gasteromycetes and Tuberales) included in the diet (Tevis, 1952) apparently are detected by smell and recovered by digging (McKeever, 1964). Seeds of *Pinus ponderosa*, *P. monticola*, *Pseudotsuga menziesii*, and *Picea* and acorns of various *Quercus* (Gordon, 1943; Grinnell and Dixon, 1918; Hoffmeister, 1986) are consumed. *S. lateralis* occasionally makes heavy use of nuts of *Pinus* (Warren, 1942). Shrubs eaten include *Rosa*, *Amelanchier*, *Rubus parviflorus*, *Ribes*, *Grossularia*, *Purshia*, *Prunus virginiana*, and *Ceanothus cordulatus* (Gordon, 1943; Mullally, 1953). Herbs consumed include *Lupinus*, *Capsella bursa-pastoris*, *Penstemon azureus*, *Verbascum*, *Fritillaria*, *Galium aparine*, *Swertia radiata*, *Cirsium lanceolatum*, *Ceanothus cordulatus*, *Bromus*, *Aconitum columbianum*, *Menzelia multiflora*, and *Trifolium repens* (Carleton, 1966; Gordon, 1943; Grinnell and Dixon, 1918; Hatt, 1927; Hoffmeister, 1986; Tevis, 1952, 1953). Animal foods include insects such as Orthoptera, Coleoptera, Diptera, Formicidae, Lepidoptera, and Lepidoptera larvae (Gordon, 1943; Tevis, 1953). Eggs and young birds may be eaten, including mountain bluebirds (*Sialia currucoides*—Warren, 1942), and Oregon juncos (*Junco oreganus*—Tevis, 1953). Young *Microtus*, entrapped yellow-pine chipmunks (*Tamias amoenus*—Cameron, 1967), lizards (*Sceloporus gracilis*—Tevis, 1953), and carrion, including road-killed conspecifics, may be consumed (Gordon, 1943). *S. lateralis* will take almost any handouts including bacon, macaroni, bread, pancakes, cake, and cereals (Gordon, 1943).

Ectoparasites include fleas (*Oropsylla idahoensis*, *Orchopeas sexdentatus*, *Thrassiss howelli*, *Diamanus montanus*, *Monopsyllus ciliatus*, *Peromyscopsylla selenis*, *Monopsyllus eumolpi*, *Hoplopyllus anomalus*, *Ceratophyllus*, *Catathagia sculleni*, and *Malareus telchinum*—Hatt, 1927; Hubbard, 1947; Tevis, 1955), ticks (*Dermacentor andersoni* and *Ornithodoros*—Gordon, 1943), and, in burrows, possibly sandflies (*Phlebotomus vexator*, *P. stewarti*, *P. californicus*—Chaniotis and Anderson, 1968). Internal protozoans in the caecum include *Chilomastix magna*, *Monocercomonoides pilleata*, *Tritricomonas muris*, and *Hexamastix muris* (Kirby and Honigberg, 1949). The bacteria *Eimeria bilamellata*, *E. callospermophili*, and *E. morainensis*, occur in the feces (Torbett et al., 1982). Laboratory infections of *Trypanosoma* (Hilton and Mahrt, 1972), disseminated *Staphylococcus aureus* (Campbell et al., 1981), and the nematode *Oxyuris triradiata* also have been found (Gordon, 1943). *S. lateralis* is commonly infected with plague, *Yersinia pestis*, which is transmitted to it by fleas (Gordon, 1943). Mammalian predators include *Canis latrans*, *Felis rufus*, *Mephitis mephitis* and *Mustela*. Avian predators include *Buteo jamaicensis* and *Accipiter gentilis* (Gordon, 1943).

Spermophilus lateralis is trapped with Sherman live traps, snap traps, or number 0 steel traps set in burrow openings (Hubbard, 1947; McKeever, 1964; Tevis, 1952). Oatmeal and walnut kernels may be used as bait (McKeever, 1964). It is difficult to keep golden-mantled ground squirrels away from traps baited with bodies of various birds and small mammals (Grinnell and Dixon, 1918).

Because coniferous seeds can constitute about 33% of the diet in September and October, *S. lateralis* can be a threat to reforestation when it is abundant. It destroys young seedlings by eating the newly emerged cotyledons along with the remaining endosperm (McKeever, 1964). It is otherwise of little economic importance to agriculture due to its selection of habitats (Gordon, 1943). *S. lateralis* is not bothered by human presence; it often is fed and becomes tame (Hatt, 1927).

BEHAVIOR. Golden-mantled ground squirrels usually are silent, but make a variety of calls from a "querulous" high-pitched call to a "tk tk tk" and a "tsp." Different calls are given in situations of nervousness or fear, fighting, alarms, chasing, and human encounters. Some calls are accompanied by tail jerks (Gordon, 1943; Hatt, 1927). Squirrels often spread and relax the hairs along the tail when they are excited, especially in social encounters (Gordon, 1943).

Spermophilus lateralis customarily sits on its haunches leaving

its forefeet free for manipulating food. Food or bedding material is packed into the cheeks or mouth for transport to the den. Grass stems are pulled down hand-over-hand until the heads are within reach of the teeth. The species stores food, especially in late summer and early autumn. Local or temporary caches often are made, particularly where food is unusually abundant. Permanent stores are made in or near the home burrow (Gordon, 1943).

Frequent dry baths are taken in dust or fine powder from rotting wood (Gordon, 1943). Most grooming activity consists of scratching with the hind legs (41.3%), followed by grooming of the head and forepaws (10.8%), the hind feet (4.9%), and the tail (3.5%). Grooming acts increase from 1.98 acts/bout at 31–35 days of age to 3.99 acts/bout in adults (Ferron and Lefebvre, 1982). The head is groomed with the front feet, which are licked and then rubbed against the face. The neck and thoracic regions are groomed in a similar manner using the hind feet. The abdomen, hind legs, tail, and the posterior part of the back are groomed by licking (Torke and Twente, 1977).

The running gait is clumsy. The tail often is displayed over the back, or, when running, either held vertically or frisked violently fore and aft. Golden-mantled ground squirrels can climb trees. They generally only ascend rocks or logs when seeking a lookout station (Grinnell and Dixon, 1918). When their usual position of attention does not give them a clear enough view of possible danger, they assume an erect pose, although this is uncommon (Gordon, 1943).

There are no records of activities that are directly cooperative, except in the case of females with young. There is no cooperation or interdependence, other than that involved in alarm vocalization. Golden-mantled ground squirrels compete with each other for food, shelter, territory, homesites, and mates. They gather quickly where food is abundant and develop a social hierarchy, which is divided into groups rather than a straight line or circular dominance (Gordon, 1943). Agonistic interactions among conspecifics are common for all age and sex groups, except among littermates before dispersal (Wirtz, 1967). Males do not take part in family life. The female is solicitous about the young when they are helpless, but after they leave the den she becomes less attentive. After 2–3 weeks the female becomes antagonistic towards her offspring (Gordon, 1943). In adults, interindividual smelling is primarily performed between males and females. All smelling by adults and young occurs between mother and young (Ferron, 1985).

Spermophilus lateralis enters hibernation as early as late August at higher elevations or as late as November at lower elevations (Tevis, 1955; Yousef and Bradley, 1971) and emerges from hibernation in late March to May (Gordon, 1943). Both entrance and emergence from hibernation vary with the amount of snowfall and altitude (Phillips, 1984). The free-running circannual period does not differ between sexes, adults and juveniles, castrated and intact animals, or laboratory-born and wild juveniles (Pengelley and Asmundson, 1974).

Spermophilus lateralis orients during hibernation to expose the least possible surface area (Hatt, 1927). It curls itself into a ball with the back situated vertically and the posterior one-third of the body folded under so that the tail extends under and beyond the head. The head is buried under the chest, close to the belly with the nose extending posterior to the anal region. The front legs are folded across the chest and the hind legs are drawn up so that the hind feet rest in the bottom of the nest or turn inward toward the body. The ears are pressed flat against the head (McKeever, 1964; Torke and Twente, 1977).

Spermophilus lateralis is difficult to arouse from torpor early in the period of hibernation; later, less stimuli are required to provoke premature arousal (Twente and Twente, 1978). The initial five or six torpor bouts in the autumn progressively increase in duration and the body temperature progressively decreases. After the fifth or sixth torpor bout the winter pattern is established (Twente and Twente, 1967). Few animals consume food during hibernation (McKeever, 1964). In the laboratory, aroused animals either stay in the nest and look about and sniff the air, or move slowly around the cage and sniff the contents (Torke and Twente, 1977). In natural habitats, some squirrels come above ground (McKeever, 1964). The average durations of these active periods for males and females are 11 h and 10.3 h, respectively. They devote 93.4% of this time to posturing, 3.7% to arranging bedding, 1.8% to grooming, 0.9% to exploratory behavior, and 0.2% to feeding (Torke and Twente, 1977).

Females have significantly longer total hibernating periods than

males, but males have longer bouts of continuous torpor. There is no significant difference between circannual periods of males and females (Pengelley et al., 1978). Jameson (1965) reported females having longer hibernation periods at higher elevations than at lower elevations. Pengelley and Fisher (1961) reported males with more frequent arousals than females. Twente and Twente (1967) reported that males handled when aroused tended to cease hibernating; females showed no effect or reiterated the autumn pattern.

Rapid-eye-movement sleep occupies about 20% of sleep, while slow-wave sleep occupies 80%. These proportions remain constant throughout the year. Seasonal changes in the daily percent of time asleep under constant environmental conditions constitutes an endogenous rhythm with its maximum coinciding with hibernation (Walker et al., 1980).

Golden-mantled ground squirrels dig their own burrows beneath rocks, stumps, logs, next to large objects, in banks, along washes, at bases of trees, and beneath cabins and rock piles. They also inhabit modified gopher holes or partially decomposed logs or stumps (Burt, 1934; Gordon, 1943; Mullally, 1953). Golden-mantled ground squirrels stay in burrows at night and use them for hibernation, shelter from unfavorable weather, and as protection from pursuing enemies (Hatt, 1927). When pursued, they may run down the nearest available hole (Mullally, 1953). Little or none of the excavated earth is left near the burrow entrance (Gordon, 1943). Squirrels keep a series of trails in their feeding grounds and in the vegetation near their burrows (Hatt, 1927). The burrow may have one or more entrances that are 5–6.3 cm in diameter and descend steeply for about 30 cm or more (Grinnell and Dixon, 1918; Mullally, 1953). Burrows are 20–90 cm deep depending on location and 46–183 cm long with several side passages including a nest cavity in large, well-established burrows and those with young in them (Hatt, 1927; Mullally, 1953). Nest cavities may contain dry leaves, shredded grasses, dry stems of other plants, dead pine needles, small rootlets, fragmented paper or cloth, shredded bark, and feces. The latter may bear fruiting fungus and various invertebrates (Hatt, 1927; Gordon, 1943). Nests also may be made in crevices of ledges or rock slides and even roofs of houses (Gordon, 1943).

GENETICS. *Spermophilus lateralis* has a diploid number of 42 chromosomes. The X chromosome is submetacentric and the Y chromosome is acrocentric (Hsu and Benirschke, 1971; Nadler, 1966). Hsu and Benirschke (1971) report 40 metacentric and submetacentric autosomes, while Nadler (1966) reports 2 acrocentric, 22 metacentric, and 16 submetacentric autosomes. Its fundamental number is 78 (Nadler, 1966).

REMARKS. Using albumin as a molecular dating device, *Tamias*, *Ammospermophilus*, and *S. lateralis* separated from *S. tridecemlineatus* about 2.0×10^7 years ago in the early Miocene. Using this technique, there is a closer relationship between *Ammospermophilus* and *S. lateralis* than either of these two with *S. tridecemlineatus*. Also, *Marmota* and *Tamias* are more closely related to *S. lateralis* than any of these are to *S. tridecemlineatus* (Maxson et al., 1981). Among the Nearctic Sciuridae, *S. lateralis* is closest to *S. otospermophilus*, originating in the Pleistocene (Hafner, 1984).

Common names for *S. lateralis* include rock squirrel, callo, and copperhead (Bailey, 1936; Dalquest, 1948; Hatt, 1927).

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