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Spermophilus beldingi.

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Spermophilus beldingi Merriam, 1888

Belding's Ground Squirrel

Spermophilus beldingi Merriam, 1888:317. Type locality Donner, Placer County, California.
Spermophilus oregonus Merriam, 1898:69. Type locality Swan Lake Valley, Klamath Basin, Oregon.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Genus *Spermophilus*, Subgenus *Spermophilus*. Three subspecies are recognized (Hall, 1981):

S. b. beldingi Merriam, 1888:317, see above.
S. b. creber (Hall, 1940:59). Type locality Reese River Valley, 7 mi N Austin, Lander County, Nevada (*crebrus* Hall a synonym).
S. b. oregonus (Merriam, 1898:69), see above.

DIAGNOSIS. *Spermophilus beldingi* lacks stripes, spots, and variegated coloration, as found in the subgenera *Callospermophilus*, *Ictidomys*, and *Otospermophilus*, respectively. It differs from the subgenus *Poliocitellus* in size (230 to 300 mm total length as opposed to 381 to 397 mm for *S. franklinii*). It differs from the subgenus *Xerospermophilus* in tail shape (moderately bushy and somewhat flattened in *S. beldingi*; round and short-haired in *S. tereticaudus*) or color (reddish beneath in *S. beldingi*; whitish beneath in *S. mohavensis*). The subgenus *Spermophilus* (*sensu* Hall, 1981) also is characterized by hypsodont molars, in contrast with all other subgenera except *Ictidomys*; and a continuous metaloph on P4, in contrast with *Ictidomys*. No members of the subgenera *Ictidomys*, *Poliocitellus*, or *Xerospermophilus* are sympatric with *S. beldingi* (Hall, 1981).

S. beldingi differs from other Nearctic representatives of the subgenus *Spermophilus* in having a tail that is reddish beneath, hindfeet longer than 39 mm, and no spotting or mottling on the back (Fig. 1). The mid-dorsal area often is darker reddish-brown than the sides, although the conspicuousness of this trait varies geographically (Davis, 1939; Hall, 1981). Multivariate analysis of skull measurements allows clear separation of *S. beldingi* from other members of the subgenus *Spermophilus* (Robinson and Hoffmann, 1975). Also, *S. beldingi* has the lowest chromosome number ($2n = 30$, $FN = 56$) of its subgenus (Nadler, 1966). *S. beldingi* is most similar to *S. armatus* morphologically (Robinson and Hoffmann, 1975) and biochemically (Nadler et al., 1982), prompting Nadler et al. (1982) to place the two species together in a single superspecies.

GENERAL CHARACTERS. *Spermophilus beldingi* is a medium-sized ground squirrel with a relatively short tail, short limbs, and small ears (Fig. 1). The pelage is gray, grading to cinnamon ventrally and to reddish-brown dorsally. The dark mid-dorsal region is most conspicuous in the subspecies *S. b. beldingi* and least so in *S. b. creber* (Davis, 1939; Hall, 1946). There are three color bands (red, black, and white) on distal hairs of the tail (Davis, 1939; Turner, 1972*a*). Adult sizes (in mm) are: total length, 230 to 300, tail length, 44 to 76, length of hindfoot, 39 to 47, ear length, 7 to 11 (Grinnell and Dixon, 1918; Hall, 1981; Morton and Tung, 1971). Hall (1946) reported that body masses of adult specimens representing all three subspecies ranged from 126 g (Grinnell and Dixon, 1918) to 550 g. As in other hibernators, masses vary seasonally; they are lowest in spring and greatest just before entry into hibernation (McKeever, 1963; Morton, 1975). In a population of *S. b. beldingi* at an elevation of 3,020 m in the southern Sierra Nevada (hereafter referred to as the Tioga Pass population), adults of each sex weighed significantly more than yearlings of the same sex throughout the active season. Adult males weighed more than adult females at emergence from and entry into hibernation, although masses of males and females were similar while females were pregnant. Yearling males weighed more than yearling females during the latter part of the active season (Morton and Parmer, 1975). Approximate mean body masses for this population were: adult males in May, 235 g; adult females in May, 215 g; yearling males in May, 160 g; yearling females in May, 150 g; adult males in August and September, 385 g; adult females in August and September, 305 g; yearling males in August and September, 355 g; yearling females in August and September, 280 g (estimated from Morton and Parmer, 1975:306, Fig. 1).

The skull of *S. beldingi* is moderately convex in dorsal profile (Fig. 2). The rostrum is short and its depth approximately equals its width. The cranium is subglobular in dorsal view and moderately deep in comparison with other sciurids. The postorbital constriction is narrow and the zygomatic arches expand posteriorly and converge anteriorly (Bryant, 1945; Howell, 1938). Auditory bullae are small, broad, and low (Howell, 1938). The dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Upper incisors are slender and slightly curved, P3 is moderately large in comparison with other sciurids, occlusal outlines of M1 and M2 are narrowly triangular, and M3 is much larger than M2. Lower incisors are slender, p4 is molariform, and p4 through m2 appear as parallelograms in occlusal outline (Bryant, 1945, Hall, 1981). Means and ranges of cranial measurements (in mm) of adults ($n = 36$) are: greatest length of skull, 44.6 (41.3 to 46.3); palatilar length, 21.6 (19.8 to 23.0); zygomatic breadth, 28.6 (24.8 to 30.1); cranial breadth, 19.5 (18.2 to 20.6); interorbital breadth, 10.6 (9.0 to 11.9); postorbital constriction, 11.6 (10.4 to 12.7); nasal length, 16.5 (15.0 to 18.2); maxillary toothrow, 9.3 (8.6 to 10.1) (Howell, 1938). Means for males are greater than or equal to those of females for all measurements; nasal length shows the greatest difference (5.0%).

DISTRIBUTION. The geographic range of *Spermophilus beldingi* extends from northeastern Oregon south to California, southwestern Idaho, north-central Nevada, and extreme northwestern Utah (Fig. 3). Hall (1946) described intergradation between the subspecies *S. b. oregonus* and *S. b. creber* in southeastern Oregon and northwestern Nevada. There is a 40-km gap between known ranges of *S. b. oregonus* and *S. b. beldingi* in California. Howell (1938) reported intergradation of characters between these two forms despite this gap. Davis (1939) considered the Snake River as the northern boundary for the species in Idaho, but Durrant and Hansen (1954) reported *S. beldingi* north of the river. Populations

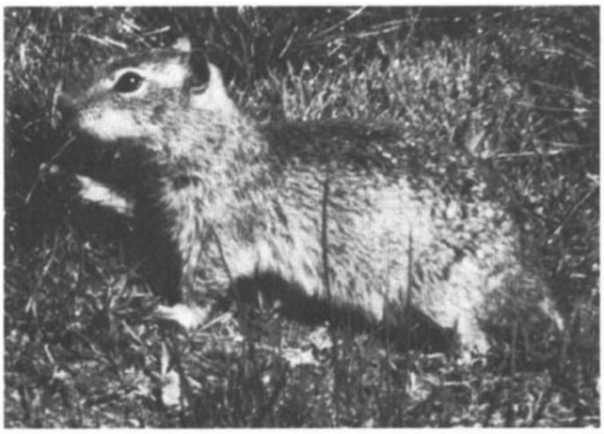

FIGURE 1. Belding's ground squirrel (*Spermophilus beldingi beldingi*). Photographed at the George Whittell Forest and Wildlife Area (Little Valley), Washoe County, Nevada, by K. A. Loehr.

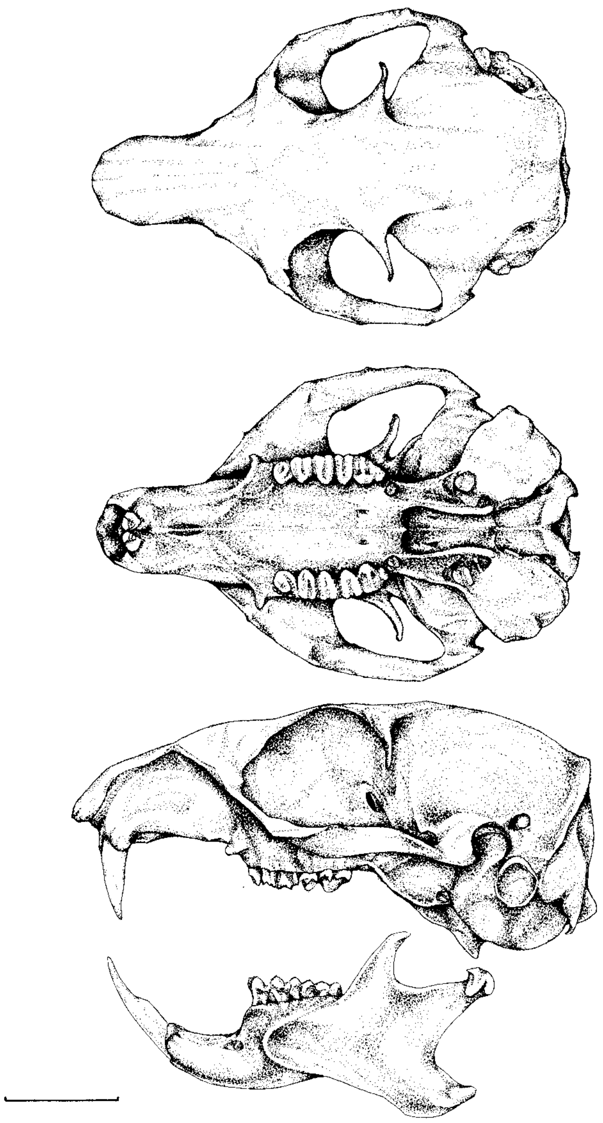

FIGURE 2. Skull of *Spermophilus beldingi* (Univ. of Nevada Mus. Biol. no. T94). Drawn by C. Evans. Scale represents 10 mm.

of Belding's ground squirrels occur at elevations from 550 m (Sullins and Verts, 1978) to 3,020 m (Morton, 1975).

FOSSIL RECORD. The genus *Spermophilus* evolved in North America from the more primitive *Miospermophilus* during the Miocene, as climates became dryer and grassland habitats spread in the Great Plains. The subgenus *Spermophilus* first appeared for certain in the Hemphillian period of the Pliocene (Black, 1963, 1972). *Spermophilus beldingi* seemingly differentiated from its closest nearctic relatives in the late Pleistocene (Nadler et al., 1982). It has not been found in any Pleistocene fauna.

FORM. The pelage of Belding's ground squirrel is short and soft (Bailey, 1936; Morhardt and Gates, 1974). The soles of the feet are bare or sparsely haired; the tail is fully haired (Grinnell and Dixon, 1918). Adults molt twice a year, shortly after parturition and a few weeks before hibernation (Sherman, 1976; Turner, 1972*a*). There are typically five pairs of mammae: one inguinal, two abdominal, and two pectoral (Bailey, 1936; Moore, 1961), although intraspecific variation in number of mammae is common in sciurids (Bryant, 1945). According to McKeever (1966), mammary glands remain visible externally after lactation. In comparison with other terrestrial sciurids, internal cheek pouches of *S. beldingi* and other members of the subgenus *Spermophilus* are moderate in size (Bryant, 1945).

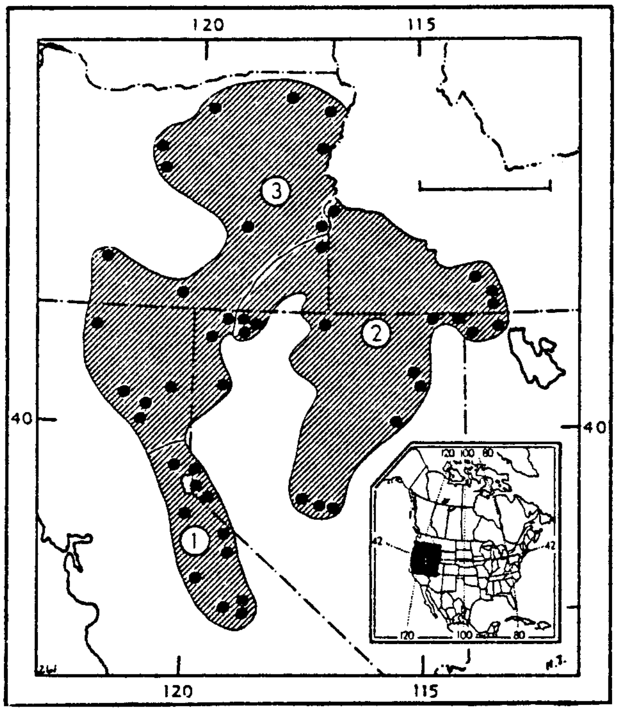

FIGURE 3. Distribution of *Spermophilus beldingi* (Hall, 1981). Subspecies ranges are shown as follows: 1, *S. b. beldingi*; 2, *S. b. creber*; 3, *S. b. oregonus*. Dots are marginal records. Scale represents 240 km. Reproduced from Hall (1981) with permission of John Wiley and Sons, Inc.

The baculum of one specimen of *S. beldingi*, illustrated by Howell (1938), was 3.5 mm long. The shaft is slightly curved and broader at the base than at the tip. The tip is spoon-shaped and has divergent rows of spines on its margins. The apex of the shaft is a short process that extends from the lower surface of the terminal disk (Bryant, 1945; Howell, 1938).

Morton and Gallup (1975) reported that paired testicles of sexually active *S. b. beldingi* weighed 2 to 3 g. McKeever (1966) reported average testicular masses for sexually active *S. b. oregonus* of 0.79 g (maximum = 1.8 g). Minimum mass of testes is 0.13 g, and occurs within 6 to 8 weeks of emergence from hibernation (McKeever, 1966; Morton and Gallup, 1975). Seminiferous tubules of sexually active animals are 150 to 250 μ in diameter (Morton and Gallup, 1975), one-quarter to one-half of which is lumen (McKeever, 1966). Minimum size of seminiferous tubules of adults is 60 μ (Morton and Gallup, 1975). Seminal vesicles of adults have a maximum size of 0.36 g and a minimum of 0.009 g, and the epithelium of these glands does not stratify (McKeever, 1966).

For the first 6 weeks after emergence from hibernation, ovaries of adult females weigh 20 to 30 mg. Ovaries of postpartum females weigh 8 to 15 mg (Morton and Gallup, 1975). Mature follicles average 0.38 mm in diameter. Corpora lutea, found either on the periphery or in the interior of the ovary, average 0.85 mm in diameter (McKeever, 1966).

Adrenal glands of females are heavier than those of males, average maxima being 49 and 39 mg, respectively. Maximum masses of the pituitary are 3.8 mg for males and 4.5 mg for females (McKeever, 1963). These endocrine glands, as well as the spleen and thyroid, vary in size throughout the year (McKeever, 1963; Morton et al., 1974). McKeever (1966) suggested that these patterns may be associated primarily with seasonal cycles of activity and hibernation, rather than with reproductive cycles as in nonhibernating mammals.

FUNCTION. Much physiological work with *S. beldingi* has focused on seasonal changes in body composition and tissue characteristics in relation to the extremely long hibernatory period of the species. Fat stores of adults are about 40% of lean dry body mass at emergence from hibernation, decrease to a minimum of about 10% in midsummer, and are 125% of lean dry mass just before entry into hibernation (Morton, 1975). Fat stores of juveniles are about 80% of lean dry body mass at the end of their first summer of life (Morton et al., 1974). Brown fat and white fat show similar seasonal patterns of change in mass (Morton, 1975). The large amounts of body fat retained by individuals until the end of hibernation (up to 30% of pre-immergence body fat) enable them to fast for about 9 days at standard rate of metabolism, possibly necessary for survival under adverse weather conditions in late spring (Morton and Sherman, 1978). Fattening occurs rapidly at the end of the active period; Morton (1975) reported average gains in mass of 43% in 21 days for females and 54% in 36 days for males. In females, fattening begins about 2 weeks after the end of lactation (Morton, 1975). Morton (1975) hypothesized that prehibernatory fattening depends on an intrinsic annual rhythm of appetite rather than on seasonal changes in types of food available, as suggested by Turner (1972*a*). Durations of periodic arousals during hibernation are correlated with ambient temperature and body mass, consistent with the hypothesis that such arousals function to restore homeostasis in hibernating animals (French, 1982*a*).

Surprisingly little research has been conducted on digestive physiology in Belding's and other ground squirrels. At least in *S. beldingi*, liver masses increase rapidly following emergence; this is more rapid in females than in males and hypertrophy is coincident with lactation (Morton and Parmer, 1975). There is no significant catabolism of basic body components such as bone and muscle during hibernation (Morton, 1975).

Mean hematocrit of the blood for a high-altitude population at time of emergence from hibernation was approximately 52%, but it decreased initially to about 44%, then stabilized at 50% for the remainder of the active season. This variation was considered a function of both erythropoietic activity and erythrocyte storage (Huang and Morton, 1976). No sexual differences were noted for plasma protein components (Huang and Morton, 1976), but plasma lipid concentrations tended to be higher in females than males throughout the season. Maximum levels of plasma lipids of 825 and 700 mg%, for females and males respectively, were recorded just before immergence in late August. Plasma lipid concentration is related directly to seasonal energy storage and possibly influenced by altitude (Huang and Morton, 1976). Albumin varied inversely with lipid concentration during most of the active season (Huang and Morton, 1976). Relative lipid and water contents of individuals were correlated negatively at emergence from hibernation but correlated positively during the fattening period in late summer (Morton, 1975). Morton (1975) suggested that individuals lost some of their lean dry body mass and became somewhat dehydrated during hibernation. When derived of water, *S. beldingi* lost a significantly smaller percentage of plasma volume than of body mass (Hartman and Morton, 1973). However, the desert-adapted *Ammospermophilus leucurus* retained greater relative plasma volume than *S. beldingi* under these conditions. Water deprivation also resulted in decreases in total intravascular potassium and sodium in *S. beldingi* (Hartman and Morton, 1973).

Body temperatures of nonhibernating animals in the field ranged from about 36 to 40°C (Morhardt and Gates, 1974). Mean body temperature of animals in captivity was 37.7°C in summer, slightly lower for active animals during winter (Morhardt and Gates, 1974). Body temperatures were correlated positively with ambient temperatures, at least during summer (Hudson and Deavers, 1972; Morhardt and Gates, 1974). Hudson and Deavers (1972:6, Table 2) reported a circadian rhythm in body temperatures of Belding's ground squirrels, but their captive animals seemingly were exposed to different ambient temperatures during day and night so the reality of this circadian rhythm is not clear. Preoptic and hypothalamic tissues of the brain are more sensitive to experimentally induced temperature reduction than in a nonhibernating species (*Canis familiaris*), indicating that Belding's ground squirrels (and presumably other hibernators) have effective thermoregulatory mechanisms (Heller et al., 1974). Hudson and Deavers (1973:98, Table 1) reported that the highest temperature tolerated without extreme stress by *S. beldingi* in captivity was 41°C, although they stated later in the same paper that some animals tolerated 43.0°C. Morhardt and Gates (1974) reported that temperatures above 34°C produced stress under their experimental conditions. The thermal neutral zone is poorly defined in *S. beldingi* (Morhardt and Gates, 1974), although Hudson and Deavers (1972) implied that the upper critical temperature was about 35°C and Morhardt and Gates (1974) showed that the lower critical temperature was about 28°C, substantially higher than expected from Morrison's (1960) allometric equation for mammals.

Morhardt and Gates (1974) reported a minimum metabolic rate for *S. beldingi* of 1.19 ml O_2 g^{-1} h^{-1} at 28°C, whereas Hudson and Deavers (1972) reported a diurnal value of 0.55 ml O_2 g^{-1} h^{-1} at 30°C, and suggested that nocturnal metabolic rates were even lower, although precise values per unit body mass cannot be computed from their published data (Hudson et al., 1972). Basal metabolic rates of 0.91 and 0.82 ml O_2 g^{-1} h^{-1} for typical mammals of 200 g and 300 g, respectively, are predicted from Kleiber's allometric equation (McNab, 1983). Whether or not Belding's ground squirrels have basal rates of metabolism above or below Kleiber's predicted value, it is clear that their rates vary substantially with body temperature, time of day, and time of year, even under presumably normothermic conditions (Hudson and Deavers, 1972).

Minimal thermal conductance of *S. beldingi* is 0.0123 cal cm^{-2} min^{-1} $°C^{-1}$, about twice the value predicted by use of Herreid and Kessel's (1967) allometric equation for mammals, presumably because *S. beldingi* has relatively thin fur for its size (Morhardt and Gates, 1974). Measurements of thermal conductance above 28°C ambient temperature are variable (Hudson and Deavers, 1972; Morhardt and Gates, 1974). Evaporation accounts for 4.5 to 6.0% of total heat loss at temperatures of 10 to 20°C, and 100% of metabolic heat produced can be dissipated by evaporation at 40°C. *S. beldingi* is similar to other montane ground squirrels in evaporative heat loss (Hudson et al., 1972). Squirrels increase evaporation by drooling at high ambient temperatures (Hudson and Deavers, 1972). Morhardt and Gates (1974) found that the cutaneous portion of evaporative water loss increases from 29% of total evaporative water loss at 5°C to 41% at 30°C. Absorptivity of solar radiation by the darker dorsal fur of *S. beldingi* was 79.1%, compared with 68.9% for the lighter-colored sides of these animals (Morhardt and Gates, 1974).

Respiratory rate is approximately 75 breaths/min at a typical body temperature (Hudson and Deavers, 1973), about the same as predicted by use of Stahl's (1967) allometric equation for mammals. Respiratory rates increase with body temperature and ambient temperature to a maximum of 260 breaths/min at an ambient temperature of 40°C. Hudson and Deavers (1972, 1973) considered this a form of panting, although not as strong a response as occurs in canids under similar conditions.

ONTOGENY AND REPRODUCTION. Male Belding's ground squirrels (at least high-elevation populations of *S. b. beldingi*) reach adult body size and become sexually mature as 2-year-olds (Morton and Gallup, 1975). The testes of adult males are scrotal at the time of emergence in early spring (McKeever, 1966; Morton and Gallup, 1975). Adverse weather conditions or a scarcity of females or both can suppress temporarily the reproductive readiness of the males by causing the testes to re-ascend (Morton and Sherman, 1978). Males are sexually active for about 1 month. Spermatogenic activity begins in early autumn while animals are in hibernation (McKeever, 1966).

Adult females emerge shortly after males and are sexually receptive within 4 to 5 days. Yearling females emerge and reproduce slightly later than adults (Morton and Gallup, 1975). Immediately before the breeding season, the vagina becomes spirally thickened (McKeever, 1966). Mating periods last about 2 weeks in the Tioga Pass population; individual females are receptive for 4 to 6 h (Morton and Sherman, 1978; Sherman, 1977). Sherman and Morton (in press) reported frequencies of reproduction in this population at 3,020 m of about 65% for yearling females and almost 100% for females in older age classes, based on appearance of weaned young above ground. Costain and Verts (1982) indicated that 90% or more of both yearlings and adults reproduced in populations at 1,700 m in Oregon, based on examination of reproductive tracts.

Belding's ground squirrels have one litter per year. Yearlings have smaller litters than adults, both in Oregon (Costain and Verts, 1982) and in the high Sierra of southern California (Morton and Gallup, 1975). Mean litter sizes of pregnant females based on counts of viable embryos were reported as 7.1 (n = 37) in Lassen County, California (McKeever, 1966), 7.4 (n = 175) in north-central Oregon (Sullins and Verts, 1978), 4.8 (n = 60) for yearlings and 5.8 (n = 49) for adults in central Oregon (Costain and Verts, 1982), and 4.8 (n = 20) for yearlings and 6.3 (n = 21) for adults in the Tioga Pass population near Yosemite National Park, California

(Morton and Gallup, 1975). Embryo resorption ranged from 1% (McKeever, 1966) to 4% (Costain and Verts, 1982; Morton and Gallup, 1975). Poor quality and quantity of food may have a negative effect on litter size (Morton and Sherman, 1978). Most litters are multiply sired; multiple matings usually result in multiple paternity (Hanken and Sherman, 1981).

Gestation lasts 23 to 28 days, young first emerge above ground at 25 to 28 days after birth, and lactation lasts 26 to 31 days (Holekamp, 1983; Sherman, 1980). At birth the young are hairless and no eye slits are present. Average body mass is 6.9 g (range 5.4 to 8.0 g). By day 10, the body is covered with hair and young can thermoregulate to a limited extent (Maxwell and Morton, 1975). At day 13 to 14, the incisors erupt, and by day 20, the eyes and ears are open. Shivering was first noted on day 15. Captive juveniles were capable of full homeothermy at day 25, when mean mass was 69 g, 30% of adult body mass (Maxwell and Morton, 1975). Feral juveniles weigh about 35 g at emergence (Morton et al., 1974). The growth rate constant in captivity was calculated as 0.066 for days 0 to 50 (Morton and Tung, 1971), similar to values for other species of *Spermophilus* (range = 0.053 to 0.092, n = 13) but greater than growth rates of *Eutamias* (range = 0.033 to 0.52, n = 5 species; Levenson, 1979).

ECOLOGY. Estimated population densities of Belding's ground squirrels range from 1.2/ha in an alpine meadow in the southern Sierra Nevada (Holekamp, 1983) to 304/ha in an alfalfa field in northern California (Sauer, 1976). The former estimate was based on a complete count of squirrels in a circumscribed area; the latter on Lincoln Index calculations for a plot, with edge effects ignored. Therefore, maximum densities probably are less than 304/ha, although the range of values for different habitat types undoubtedly is large. Cox (1980) suggested that population densities may be limited by the availability of suitable sites for hibernacula, based on analysis of local distribution patterns in relation to water table depths in the central Sierra Nevada.

Belding's ground squirrels occur in alpine and subalpine meadows, sagebrush flats, mixed brush and grass habitats, agricultural fields, and pastures (Costain, 1978; McKeever, 1966; Sherman and Morton, 1979; Turner 1972*b*). They seem to be limited to relatively open habitats where either succulent vegetation or standing water is available, as they usually are not found in forests or on rocky slopes (Turner, 1972*a*). Durrant and Hansen (1954) suggested that various species of ground squirrels have different tolerances to aridity that could account for differences in distribution patterns. Turner (1972*b*) documented such distributional differences on a local scale in Oregon; where sympatric, *S. beldingi* occurred in more mesic habitats than *S. columbianus.* Turner (1972*b*) also provided indirect evidence for competition between the two species; where allopatric, they occupied a broader range of habitats than where sympatric. Competition between *S. beldingi* and representatives of other subgenera of *Spermophilus* (e.g., *S. lateralis*, *S. beecheyi*) probably is minimal because of more fundamental habitat differences, and differences in food habits and seasonal activity patterns. None of the microhabitats available to a Sierra Nevada population at 2,700-m elevation seemed to be used mainly for thermoregulation (Morhardt and Gates, 1974). In the microhabitat used most (green grass, for feeding), squirrels were closer to their upper limits of ambient temperature and absorbed radiation than to their lower limits, suggesting that these environmental factors might limit habitat distribution and microhabitat use at lower elevations (Morhardt and Gates, 1974).

Major predators of Belding's ground squirrels are coyotes (*Canis latrans*), badgers (*Taxidea taxus*), long-tailed weasels (*Mustela frenata*), various species of raptors, and possibly gopher snakes (*Pituophis melanoleucus*) and rattlesnakes (*Crotalis viridis*) (Robinson, 1980; Sherman, 1977; Sherman and Morton, 1979). Pine martens (*Martes americana*), mink (*Mustela vison*), and Clark's nutcrackers (*Nucifraga columbiana*) also were reported to prey on *S. beldingi* (Mulder et al., 1978; Robinson, 1980; Sherman, 1977). Sherman and Morton (1979) estimated that predation accounted for 4 to 11% of the annual mortality of the Tioga Pass population. However, severe winter weather and other unknown events during hibernation were the major causes of mortality for this population. Morton and Sherman (1978) documented the impact of an unusually late spring snowstorm on animals that already had emerged from hibernation; about 60% died during the 1-month storm.

Sherman (1976) and Holekamp (1983) listed seven species of fleas (*Diamanus montanus*, *Opisocrostis oregonensis*, *Opisocrostis tuberculatus*, *Monopsyllus eumopli*, *Oropsylla idahoensis*, *Hystrichopsylla occidentalis*, and *Thrassis francisi sierrae*) collected from *S. beldingi* in the southern Sierra Nevada, four of which are known vectors of plague. Sherman (1976) found that numbers of fleas per individual were highest just after emergence from hibernation, but Holekamp (1983) found more variable seasonal patterns. Both reported no sexual differences in flea loads. Although large-scale plague epizootics caused widespread die-offs of *S. beldingi* in northeastern California during the 1930's and 1940's, no known human cases of plague in California were associated with this squirrel or its fleas (Nelson, 1980). Mites, lice, and ticks also are common ectoparasites in some populations (Holekamp, 1983; Turner, 1972*a*). During hibernation, *Entamoeba citelli* was consistently lost from the caecum but *Entamoeba* sp. (similar to *E. muris* from *Eutamias speciosus*) was not (Davis, 1969). Davis (1969) suggested that ground squirrels became reinfected with the former species by eating cyst-containing feces after emergence.

Belding's ground squirrels are primarily herbivorous, although insects, other vertebrates, carrion, and conspecifics also are eaten (Morton, 1975; Sherman and Morton, 1979; Turner 1972*a*). Morton (1975) found that arthropods constituted less than 10% of stomach contents throughout the active season, although 32 to 45% of the stomachs examined at two sites contained them. Seeds constituted more of the diet as the summer progressed, undoubtedly because of increased availability (Turner, 1972*a*; Morton, 1975). Lists of plant species eaten (Docekal, 1978; Holekamp, 1983; Loehr, 1974; Sherman, 1976) indicate that Belding's ground squirrels are generalized herbivores. Based on observations of animals foraging in the field, Docekal (1978) and Holekamp (1983) reported that leaves, stems, and seeds of grasses composed most of the diet. This does not necessarily indicate selection for grasses over forbs, because availabilities of various potential foods were not reported. Eshelman (1982) showed that a grass, *Agropyron trachycaulum*, and a sedge, *Carex nebrascensis*, were never eaten by squirrels in cafeteria-style feeding experiments when certain forb species also were provided. *Taraxacum officinale* (common dandelion), *Agoseris glauca* (mountain dandelion), and *Lupinus sellulus* (lupine) were highly preferred. Nutritional attributes of the plants most clearly associated with preference were protein and water content. Turner (1972*a*) stated that dandelions make good bait for trapping ground squirrels, and suggested that squirrels may eliminate dandelion flowers from the vicinity of their burrows by selectively foraging on them. Sauer (1977) and Kalinowski and deCalesta (1981) found that dense populations of Belding's ground squirrels were capable of harvesting 35 to 61% of vegetative biomass in alfalfa-brome grass or pure alfalfa stands. Overall impacts on vegetation in natural habitats undoubtedly are much less (Holekamp, 1983; Sherman, 1976), although ground squirrels may influence species composition of plants in meadows by selective feeding.

Females typically live longer than males (life expectancies at birth = 1.33 and 1.07 years, respectively, for the Tioga Pass population; Sherman and Morton, in press). Among females in this relatively undisturbed population, 16% were greater than 4 years old and maximum age of individuals marked at birth was 11 years; among males, 4% were older than 4 and maximum age was 6. By contrast, Costain and Verts (1982) found no animals over 3 years old in populations in Oregon more disturbed by human activities (e.g., sport hunting and control by poisoning). Sex ratios at birth are 1:1 (Morton et al., 1974), but may approach 3 females: 1 male among adults (Morton and Parmer, 1975). This is caused fundamentally by differential mortality of the sexes, particularly after males reach reproductive maturity (Sherman and Morton, in press). For example, in the Tioga Pass population, survival probabilities were not significantly different for male and female juveniles or male and female yearlings but, for older age classes, were an average of 44% less for males than females. Spatial and temporal differences in activity may also influence sex ratios estimated from trapping data (Morton and Parmer, 1975).

Differences in sizes of home ranges between sexes and age classes of Belding's ground squirrels were reported by Docekal (1978) and Cox (1980), based on observational and trapping data, respectively. Cox (1980) also found year-to-year differences in sizes of home ranges for certain age-sex classes. Ranges are poorly defined for adult males, because their home burrows in a specific year may be at substantial distances from mating sites used the same year ($\bar{X} = 242$ m, n = 12; Sherman, 1976). Also, adult males often move large distances between years, whereas adult females usually are sedentary (Sherman, 1980). Holekamp (1983) found that females ranged a maximum of 80 m from their home burrows during the week before and week after emergence of their litters. Sherman (1976) reported a median territory size for females at this time of 500 m^2, but females were outside of their territories for half of the time they spent foraging. All males disperse from the vicinity of their natal burrows, 90% as juveniles and 10% as yearlings, but only about 10% of females disperse during this interval. Juvenile females that disperse move similar distances as juvenile males (250 to 500 m), much farther than nondispersers (8 to 25 m; Holekamp, 1983). These movement and dispersal patterns are typical of terrestrial squirrels, although dispersing Belding's ground squirrels move relatively short distances compared with some other species (Boag and Murie, 1981; Holekamp, 1983; Quanstrom, 1971). Also, under certain conditions males of some other species may settle in their natal areas (Michener and Michener, 1977; Pfeifer, 1982).

Spermophilus beldingi is an agricultural pest in parts of its range, especially northeastern California and eastern Oregon (Sullins and Verts, 1978; White, 1972). A variety of methods have been used for ground squirrel control during the past 100 years, but distribution of poisoned bait is the major control method used today (Tomich, 1982). Kalinowski and deCalesta (1981) showed that two applications per year of oat groats treated with compound 1080 (sodium monofluoroacetate) were more effective at reducing ground squirrel damage to alfalfa than the more commonly employed single yearly application, and that distributing poisoned bait in a 60-m border around alfalfa fields gave even better control. Strychnine and zinc phosphide also can produce significant population reductions of squirrels (O'Brien, 1978). Sullins and Verts (1978) assayed various baits for acceptability by ground squirrels. Succulent baits generally were preferred to dry baits (e.g., grain), although the total amount of bait eaten varied with availability of forage crops and natural vegetation.

BEHAVIOR. Like other ground squirrels, adult male *S. beldingi* emerge from hibernation before adult females, an average of 10 days earlier in the Tioga Pass population. Yearling females emerge after adult females, and yearling males emerge last. Time of emergence varies by as much as 1 month in successive years at the same location, and is correlated roughly with snow depth, although there is not a particular snow depth at which emergence consistently occurs (Morton and Sherman, 1978). In the laboratory, large adult males arouse spontaneously in spring whereas females and yearling males do not terminate hibernation unless food is available. Spontaneous arousal and reproductive development in males depends on body mass rather than age (French, 1982*b*). At Tioga Pass, adult males enter hibernation first in late summer or early fall, followed by adult females and yearlings of both sexes, then juveniles (Sherman, 1976). This sequence is consistent with patterns found in other ground squirrels. Although Costain (1978) and Sullins and Verts (1978) suggested that adult males may remain above ground later in summer than adult females in Oregon, yearlings seemingly were included in the adult age class in their studies. In the Tioga Pass population, adult males hibernate for about 280 days, adult females for 269, yearling males for 262, and yearling females for 269 (Morton, 1975). Duration of hibernation is shorter for populations at 550 to 1,220 m elevation in Oregon (Sullins and Verts, 1978).

Belding's ground squirrels are strictly diurnal. On clear days, they do not come above ground until burrow entrances are in full sunlight, although this is not a necessary condition for activity because they emerge on cloudy days (Docekal, 1978; Loehr and Risser, 1977; Morhardt and Gates, 1974). The proportion of a population active above ground may decrease gradually as the day progresses (Turner, 1972*a*), or show a bimodal pattern with a dip during the hottest part of the day (Docekal, 1978; Loehr and Risser, 1977).

Ethograms for *S. beldingi* (Turner, 1972*a*; Holekamp, 1983) are similar to those for other ground squirrels (e.g., *S. columbianus* Betts, 1976). Time budgets change seasonally, with feeding behavior increasing substantially as the summer progresses (Eshelman, 1982; Loehr and Risser, 1977; Morton, 1975). Eshelman (1982) and Holekamp (1983) also demonstrated differences between populations in relative frequencies of behaviors such as feeding, vigilance, grooming, and social interactions. Elaborate evolutionary hypotheses were constructed to account for these types of differences in other situations (e.g., Barash, 1974), but Armitage's (1977) long-term marmot (*Marmota flaviventris*) study suggested that such differences should not be attributed to ecological factors without also considering age-sex structures of the populations and individual differences in behavior.

Burrows of *S. beldingi* are 4.5 to 9 cm in diameter and some reach depths of 115 cm (Grinnell and Dixon, 1918). Turner (1973) classified burrows as short with single entrances, or long with more complex tunnel systems and multiple entrances. He showed that the former were used for quick escapes from aerial predators. *S. beldingi* seemingly rarely used burrows for more than 1 year. In addition to digging new burrows of their own each spring, they may usurp pocket gopher (*Thomomys* spp.) burrows (Sherman, 1976). Groups of two or three females often hibernate together, but males hibernate alone and multiple use of burrows during the active season does not occur at all except during prolonged inclement weather (Morton and Sherman, 1978; Sherman, 1976).

Unlike most other ground squirrels, *S. beldingi* copulates above ground, a great advantage for studying mating behavior under natural conditions. At Tioga Pass, males gather on ridge tops where female hibernacula are concentrated several days before females begin to emerge. Individual males do not establish territories at these sites, nor do they return consistently to the same site in successive breeding seasons or even on successive days within the same breeding season. Males that mate most often at one site are less likely to be found at that site the following year than less successful males. Males fight vigorously and sustain major injuries during the breeding season, and most such fights occur in close proximity to estrous females. Female behavior before and during estrus suggests that females actively select mating partners. Copulations usually are interrupted, and each female copulates with an average of 2.8 males during her estrous period (Sherman, 1976; Hanken and Sherman, 1981). There is substantially greater variance in reproductive success among males than among females, and the heaviest males are the most successful (Sherman, 1976).

One of the most striking forms of agonistic behavior in this species is infanticide. Juveniles are vulnerable until about the time of weaning; yearling males and adult females do most of the killing. Infanticide accounted for at least 29% of all mortality of juveniles before their first winter in the Tioga Pass population (Sherman, 1981*a*). Sherman (1981*a*) suggested that yearling males kill infants for food because weight gain is necessary for reproductive success of these animals the following year; indeed, yearling males are more carnivorous in general than other age and sex classes. Adult females only kill infants after emigration of the females to a new location and before production of their first litter at the new location, and adult females do not eat the infants they kill. Infanticide by nonresident adult females may reduce future competition for favorable burrow sites (Sherman, 1981*a*). Reproductive females defend territories of 100 to 1,600 m^2 from shortly after mating until young are weaned. They scent-mark along territorial boundaries and chase or fight with intruders. Other types of individual Belding's ground squirrels, including adult males, defend at most a few square meters around home burrows. Territorial females are more aggressive toward certain types of intruders than others; in particular, nonrelatives, especially nonresident adult females and yearling males (prominent perpetrators of infanticide), are chased and attacked more often than close kin. Female relatives also cooperate in territorial defense (Sherman, 1976, 1980, 1981*a*, 1981*b*).

Belding's ground squirrels give two basic types of alarm calls: a brief chirp that usually consists of a single note, and a more extended trill or churr that consists of several notes in rapid succession (Robinson, 1980; Sherman, 1977; Turner, 1973). Chirps are associated more often with aerial predators or close terrestrial predators, that is, more dangerous situations. They are typically accompanied by evasion such as running or entering a burrow, whereas trills are accompanied by erect alert postures (Robinson, 1980, 1981). Turner (1973) found that squirrels usually responded to a trained dog by trilling and running to a burrow with two openings, perhaps bypassing several with only one opening, whereas they responded to a trained hawk by entering the nearest burrow. Females give alarm calls much more often than males, and reproductive females with close kin nearby (not only offspring but also littermate sisters) call more often than females without close kin nearby (Sherman, 1977, 1980). Sherman (1977) considered several explanations for these patterns and argued that kin selection was the most likely mechanism for the evolution of alarm calling in Belding's ground squirrels.

Belding's ground squirrels play (Holmes and Sherman, 1982; Holekamp, 1983), but play behavior has not been described in detail. Juvenile males are less fearful and show more exploratory behavior than juvenile females, particularly near the time of dispersal (Holekamp, 1983). Surprisingly, no differences in social behavior toward or by juveniles of the two sexes could account for the much greater tendency of males than females to disperse. Perinatal exposure of females to androgens caused masculine dispersal behavior by these individuals, but castration of juvenile males or ovariectomy of juvenile females shortly after weaning did not change their dispersal behavior (Holekamp, 1983). In laboratory studies, nonsibs reared together were less agressive toward one another in later tests (after hibernating separately for several months) than sibs or nonsibs reared apart. Sisters reared apart showed less agonistic behavior than nonsibs reared apart. In the field, littermate sisters with the same father showed more cohesive and less aggressive behavior toward each other than littermate sisters with different fathers (Holmes and Sherman, 1982). There seem to be fairly sophisticated mechanisms associated with kin recognition in this species. Situations eliciting alarm calls and responses to alarm calls of conspecifics change with age. Juveniles, unlike adults, call as often when harmless stimuli are present as when predators are present, and juveniles respond equally often to adult and juvenile calls, whereas adults tend to ignore juvenile calls (Robinson, 1981).

GENETICS. *Spermophilus beldingi* has $2n = 30$ and a fundamental number of 56 (Nadler, 1965, 1966). The karyotype contains eight pairs of metacentric and six pairs of submetacentric autosomes, a pair of medium-sized submetacentric X chromosomes in females, and a tiny metacentric Y chromosome. Karyotypes of the three subspecies are grossly similar (Nadler, 1965). Aberrant karyotypes not obviously affecting the phenotype were observed in three members of a sample of *S. beldingi* from Oregon. All individuals containing this aberration possibly were related, although two were caught at a distance of 1.6 km from the third. The karyotype contained an unpaired submetacentric and a minute metacentric chromosome. This aberration probably involved the familial X chromosome (Nadler, 1965; Nadler and Hughes, 1966*a*).

Protein polymorphisms in various populations of Belding's and other ground squirrels were demonstrated by use of starch-gel electrophoresis (Hanken and Sherman, 1981; Marsh et al., 1969; Nadler, 1968; Nadler and Hughes, 1966*b*; Nadler et al., 1974, 1982). A sample of 27 *S. beldingi* had a mean heterozygosity of 2.8%, equal to the median value for 25 taxa of ground squirrels (Nadler et al., 1982). However, Hanken and Sherman's (1981) much larger sample ($n = 250$) had a mean heterozygosity of 10.7%. Nadler and Hughes (1966*b*) reported subspecific differences in allele frequencies, and Nadler et al. (1982) presented dendrograms for the genus *Spermophilus* based on electrophoretic data. Turner (1972*a*) reported both albinism and melanism in *S. beldingi*.

REMARKS. Sciurids in general, and Belding's ground squirrels in particular, have been the subjects of some of the best tests to date of various sociobiological hypotheses. *S. beldingi* appears to be about average among terrestrial sciurids in most life history traits and in degree of sociality (Armitage, 1981; Michener, 1983). However, detailed studies of social behavior were conducted only at high elevation sites in the southern Sierra Nevada. Perhaps social behavior of Belding's ground squirrels differs in more dense populations that inhabit agricultural areas at lower elevations.

The length of the active season of Belding's ground squirrels, at least at Tioga Pass, is shorter than that of all species reviewed by Armitage (1981) except *S. columbianus*. Digestive and metabolic adaptations that enable Belding's ground squirrels in this population to reproduce, grow, and gain weight for hibernation in only 3 months deserve further study.

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LITERATURE CITED

Armitage, K. B. 1977. Social variety in the yellow-bellied marmot: a population-behavioral system. Anim. Behav., 25:585–593.

— 1981. Sociality as a life-history tactic of ground squirrels. Oecologia, 48:36–49.

Bailey, V. 1936. The mammals and life zones of Oregon. N. Amer. Fauna, 55:1–416.

Barash, D. P. 1974. The evolution of marmot societies: a general theory. Science, 185:415–420.

Betts, B. J. 1976. Behavior in a population of Columbian ground squirrels, *Spermophilus columbianus columbianus*. Anim. Behav., 24:652–680.

Black, C. C. 1963. A review of the North American Tertiary Sciuridae. Bull. Mus. Comp. Zool., 130:109–248.

— 1972. Holarctic evolution and dispersal of squirrels (Rodentia: Sciuridae). Pp. 305–322, *in* Evolutionary biology (T. Dobzhansky, M. K. Hecht, and W. C. Steere, eds.). Meredith Corp., New York, 6:1–445.

Boag, D. A., and J. O. Murie. 1981. Population ecology of Columbian ground squirrels in southwestern Alberta. Canadian J. Zool., 59:2230–2240.

Bryant, M. D. 1945. Phylogeny of nearctic Sciuridae. Amer. Midland Nat., 33:257–390.

Costain, D. B. 1978. Dynamics of a population of Belding's ground squirrels in Oregon. Unpubl. M.S. thesis, Oregon State Univ., Corvallis, 66 pp.

Costain, D. B., and B. J. Verts. 1982. Age determination and age-specific reproduction in Belding's ground squirrels. Northwest Sci., 56:230–235.

Cox, S. 1980. Population structure and dynamics of Belding's ground squirrel, *Spermophilus beldingi beldingi* in Little Valley, Nevada. Unpubl. M.S. thesis, Univ. Nevada, Reno, 107 pp.

Davis, S. D. 1969. Hibernation: intestinal protozoa populations in ground squirrels. Exp. Parasitol., 26:156–165.

Davis, W. B. 1939. The Recent mammals of Idaho. Caxton Printers, Ltd., Caldwell, Idaho, 400 pp.

Docekal, E. M. 1978. Home range, activities, and diet of the Belding's ground squirrel, *Spermophilus beldingi beldingi*, at Sagehen Creek, California. Unpubl. M.A. thesis, San Francisco State Univ., San Francisco, California, 58 pp.

Durrant, S. D., and R. M. Hansen. 1954. Distribution patterns and phylogeny of some western ground squirrels. Syst. Zool., 3:82–85.

Eshelman, B. D. 1982. Components of Belding's ground squirrel foraging behavior. Unpubl. M.S. thesis, Univ. Nevada, Reno, 114 pp.

French, A. R. 1982*a*. Effects of temperature on the duration of arousal episodes during hibernation. J. Appl. Physiol.: Respirat. Environ. Exercise Physiol., 52:216–220.

— 1982*b*. Intraspecific differences in the pattern of hibernation in the ground squirrel *Spermophilus beldingi*. J. Comp. Physiol., 148B:83–91.

Grinnell, J., and J. Dixon. 1918. Natural history of the ground squirrels of California. Bull. California State Comm. Horticulture, 7:597–708.

Hall, E. R. 1940. A new race of Belding ground squirrel from Nevada. Murrelet, 21:59–61.

— 1946. Mammals of Nevada. Univ. California Press, Berkeley, 710 pp.

— 1981. The mammals of North America. Second ed. John Wiley and Sons, New York, 1:1–600 + *90*.

Hanken, J., and P. W. Sherman. 1981. Multiple paternity in Belding's ground squirrel litters. Science, 212:351–353.

Hartman, L. A., and M. L. Morton. 1973. Plasma volume changes in ground squirrels during water deprivation. Comp. Biochem. Physiol., 46A:79–94.

Heller, H. C., G. W. Colliver, and P. Anand. 1974. CNS regulation of body temperature in euthermic hibernators. Amer. J. Physiol., 227:576–582.

Herreid, C. F., II, and B. Kessel. 1967. Thermal conductance in birds and mammals. Comp. Biochem. Physiol., 21:405–414.

Holekamp, K. E. 1983. Proximal mechanisms of natal dispersal in Belding's ground squirrel (*Spermophilus beldingi beldingi*). Unpubl. Ph.D. dissert., Univ. California, Berkeley, 288 pp.

Holmes, W. G., and P. W. Sherman. 1982. The ontogeny of kin recognition in two species of ground squirrels. Amer. Zool., 22:491–517.

Howell, A. H. 1938. Revision of the North American ground squirrels, with a classification of the North American Sciuridae. N. Amer. Fauna, 56:1–256.

Huang, S. N-Y., and M. L. Morton. 1976. Seasonal changes in plasma proteins and lipids in the Belding ground squirrel (*Spermophilus beldingi beldingi*). Comp. Biochem. Physiol., 54A: 239–243.

Hudson, J. W., and D. R. Deavers. 1972. Thermoregulation of ground squirrels from different habitats. Proc. Internatl. Congr. Zool., 17:1–35.

— 1973. Thermoregulation at high ambient temperatures of six species of ground squirrels (*Spermophilus* spp.) from different habitats. Physiol. Zool., 46:95–109.

Hudson, J. W., D. R. Deavers, and S. R. Bradley. 1972. A comparative study of temperature regulation in ground squirrels with special reference to the desert species. Symp. Zool. Soc. London, 31:191–213.

Kalinowski, S. A., and D. S. deCalesta. 1981. Baiting regimes for reducing ground squirrel damage to alfalfa. Wildl. Soc. Bull., 9:268–272.

Levenson, H. 1979. Sciurid growth rates: some corrections and additions. J. Mamm., 60:232–235.

Loehr, K. A. 1974. Body weights, torpor, and activity patterns in the Belding ground squirrel, *Spermophilus beldingi beldingi*. Unpubl. M.S. thesis, Univ. Nevada, Reno, 85 pp.

Loehr, K. A., and A. C. Risser, Jr. 1977. Daily and seasonal activity patterns of the Belding ground squirrel in the Sierra Nevada. J. Mamm., 58:445–448.

Marsh, R. E., W. E. Howard, and H. Bongardt. 1969. Some serum transferrins in California ground squirrels (*Spermophilus*). J. Mamm., 50:649–652.

Maxwell, C. S., and M. L. Morton. 1975. Comparative thermoregulatory capabilities of neonatal ground squirrels. J. Mamm., 56:821–828.

McKeever, S. 1963. Seasonal changes in body weight, reproductive organs, pituitary, adrenal glands, thyroid gland, and spleen of the Belding ground squirrel (*Citellus beldingi*). Amer. J. Anat., 113:153–173.

— 1966. Reproduction in *Citellus beldingi* and *Citellus lateralis* in northeastern California. Symp. Zool. Soc. London, 15: 365–385.

McNab, B. K. 1983. Ecological and behavioral consequences of adaptation to various food resources. Pp. 664–697, *in* Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Spec. Publ., Amer. Soc. Mamm., 7:1–753.

Merriam, C. H. 1888. Description of a new spermophile from California. Ann. New York Acad. Sci., 4:317–321.

— 1898. Descriptions of six new ground squirrels from the western United States. Proc. Biol. Soc. Washington, 12:69–71.

Michener, G. R. 1983. Kin identification, matriarchies, and the evolution of sociality in ground-dwelling sciurids. Pp. 528–572, *in* Advances in the study of mammalian behavior (J. F. Eisenberg and D. G. Kleiman, eds.). Spec. Publ., Amer. Soc. Mamm., 7:1–753.

Michener, G. R., and D. R. Michener. 1977. Population structure and dispersal in Richardson's ground squirrels. Ecology, 58:359–368.

Moore, J. C. 1961. Geographic variation in some reproductive characteristics of diurnal squirrels. Bull. Amer. Mus. Nat. Hist., 122:1–32.

Morhardt, S. S., and D. M. Gates. 1974. Energy-exchange analysis of the Belding ground squirrel and its habitat. Ecol. Monogr., 44:17–44.

Morrison, P. 1960. Some interrelations between weight and hibernation function. Bull. Mus. Comp. Zool., 124:75–91.

Morton, M. L. 1975. Seasonal cycles of body weights and lipids in Belding ground squirrels. Bull. S. California Acad. Sci., 74: 128–143.

Morton, M. L., and J. S. Gallup. 1975. Reproductive cycle of the Belding ground squirrel (*Spermophilus beldingi beldingi*): seasonal and age differences. Great Basin Nat., 35:427–433.

Morton, M. L., and R. J. Parmer. 1975. Body size, organ size, and sex ratios in adult and yearling Belding ground squirrels. Great Basin Nat., 35:305–309.

Morton, M. L., and P. W. Sherman. 1978. Effects of a spring snowstorm on behavior, reproduction, and survival of Belding's ground squirrels. Canadian J. Zool., 56:2578–2590.

Morton, M. L., and H-C. L. Tung. 1971. Growth and development in the Belding ground squirrel (*Spermophilus beldingi beldingi*). J. Mamm., 52:611–616.

Morton, M. L., C. S. Maxwell, and C. E. Wade. 1974. Body size, body composition, and behavior of juvenile Belding ground squirrels. Great Basin Nat., 34:121–134.

Mulder, B. S., B. B. Schultz, and P. W. Sherman. 1978. Predation on vertebrates by Clark's nutcrackers. Condor, 80: 449–451.

Nadler, C. F. 1965. Chromosomes of the ground squirrel *Spermophilus beldingi* and report of an aberrant karyotype in a phenotypically normal female. Cytogenetics, 4:37–44.

— 1966. Chromosomes and systematics of American ground squirrels of the subgenus *Spermophilus*. J. Mamm., 47:579–596.

— 1968. The serum proteins and transferrins of the ground squirrel subgenus *Spermophilus*. Comp. Biochem. Physiol., 27:487–503.

Nadler, C. F., and C. E. Hughes. 1966*a*. Chromosomal aberrations in a population of ground squirrels. Science, 151:579–580.

— 1966*b*. Serum protein electrophoresis in the taxonomy of some species of the ground squirrel subgenus *Spermophilus*. Comp. Biochem. Physiol., 18:639–651.

Nadler, C. F., et al. 1974. Evolution in ground squirrels. I. Transferrins in Holarctic populations of *Spermophilus*. Comp. Biochem. Physiol., 47A:663–681.

Nadler, C. F., et al. 1982. Evolution in ground squirrels. II. Biochemical comparisions in Holarctic populations of *Spermophilus*. Z. Saugetierk., 47:198–214.

Nelson, B. C. 1980. Plague studies in California—the roles of various species of sylvatic rodents in plague ecology in California. Proc. Vert. Pest Conf., 9:89–96.

O'Brien, J. 1978. Chopped cabbage baits for ground squirrel control in Nevada. Proc. Vert. Pest Conf., 8:25–27.

Pfeifer, S. 1982. Disappearance and dispersal of *Spermophilus elegans* juveniles in relation to behavior. Behav. Ecol. Sociobiol., 10:237–243.

Quanstrom, W. R. 1971. Behavior of Richardson's ground squirrel, *Spermophilus richardsonii richardsonii*. Anim. Behav., 19:646–652.

Robinson, J. W., and R. S. Hoffmann. 1975. Geographical and interspecific cranial variation in big-eared ground squirrels (*Spermophilus*): a multivariate study. Syst. Zool., 24:79–88.

Robinson, S. R. 1980. Antipredator behavior and predator recognition in Beldings ground squirrels. Anim. Behav., 28:840–852.

— 1981. Alarm communication in Beldings ground squirrels. Z. Tierpsychol., 56:150–168.

Sauer, W. C. 1976. Control of the Oregon ground squirrel (*Spermophilus beldingi oregonus*). Proc. Vert. Pest Conf., 7:99–109.

— 1977. Exclusion cylinders as a means of assessing losses of vegetation due to ground squirrel feeding. Pp. 14–21, *in* Test methods for vertebrate pest control and management materials (W. B. Jackson and R. E. Marsh, eds.). Spec. Tech. Publ., Amer. Soc. Testing and Materials, 625:1–258.

Sherman, P. W. 1976. Natural selection among some group-living organisms. Unpubl. Ph.D. dissert., Univ. Michigan, Ann Arbor, 254 pp.

— 1977. Nepotism and the evolution of alarm calls. Science, 197:1246–1253.

— 1980. The limits of ground squirrel nepotism. Pp. 505–544, *in* Sociobiology: beyond nature/nurture? Reports, definitions and debate (G. W. Barlow and J. Silverberg, eds.). Westview Press, Inc., Boulder, Colorado, 627 pp.

— 1981*a*. Reproductive competition and infanticide in Belding's ground squirrels and other animals. Pp. 311–331, *in* Natural selection and social behavior: recent research and new theory (R. D. Alexander and D. W. Tinkle, eds.). Chiron Press, New York, 532 pp.

— 1981*b*. Kinship, demography, and Belding's ground squirrel nepotism. Behav. Ecol. Sociobiol., 8:251–259.

Sherman, P. W., and M. L. Morton. 1979. Four months of the ground squirrel. Nat. Hist., 88(6):50–57.
— In press. Demography of Belding's ground squirrels. Ecology.
Stahl, W. R. 1967. Scaling of respiratory variables in mammals. J. Appl. Physiol., 22:453–460.
Sullins, G. L., and B. J. Verts. 1978. Baits and baiting techniques for control of Belding's ground squirrels. J. Wildl. Mgmt., 42: 890–896.
Tomich, P. Q. 1982. Ground squirrels: *Spermophilus beecheyi* and allies. Pp. 192–208, *in* Wild mammals of North America (J. A. Chapman and G. A. Feldhamer, eds.). Johns Hopkins Univ. Press, Baltimore, Maryland, 1147 pp.
Turner, L. W. 1972*a*. Autecology of the Belding ground squirrel in Oregon. Unpubl. Ph.D. dissert., Univ. Arizona, Tucson, 149 pp.
— 1972*b*. Habitat differences between *Spermophilus beldingi* and *Spermophilus columbianus* in Oregon. J. Mamm., 53: 914–917.
— 1973. Vocal and escape responses of *Spermophilus beldingi* to predators. J. Mamm., 54:990–993.
White, L. 1972. The Oregon ground squirrel in northeastern California: its adaptation to a changing agricultural environment. Proc. Vert. Pest Conf., 5:82–84.

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