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Spermophilus columbianus.

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Spermophilus columbianus (Ord, 1815)

Columbian Ground Squirrel

Arctomys columbianus Ord in Guthrie, 1815:303. Ord's description was based on Lewis and Clark's description of animals taken on a camas prairie between forks of Clearwater and Kooskooskie rivers, Idaho.

Anisonyx brachiura Rafinesque, 1817:45. Also based on Ord's description.

Spermophilus columbianus Merriam and Stejneger, 1891:39. First use of current name combination.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Sciurinae, Tribe Marmotini, Genus *Spermophilus*, Subgenus *Spermophilus*. Two subspecies are recognized (Hall, 1981; Howell, 1928):

S. c. columbianus (Ord in Guthrie, 1815:303), see above (*brachiura* Rafinesque is a synonym).

S. c. ruficaudus (Howell, 1928:212). Type locality Wallowa Lake [Wallowa Co.], Oregon.

DIAGNOSIS. The subgenus *Spermophilus* differs from other subgenera by having the metaloph of P4 continuous and the upperbody parts with reddish or fine, white spots on a gray background. Within the subgenus, *S. columbianus* differs from other species by having buffy dorsal spots and hind feet longer than 43 mm. The skull resembles that of *S. richardsonii*, but is longer, the zygomatic arches are less expanded posteriorly, it is more nearly flat in dorsal outline, the supraorbital margins of frontals are not elevated or thickened, the rostrum and nasals are longer, and the upper toothrows are nearly parallel (Hall, 1981).

GENERAL CHARACTERS. *Spermophilus columbianus* is a stout-bodied ground squirrel with relatively short, dense pelage (Fig. 1). The nose and front of the face are tawny and the dorsum tends to be cinnamon buff, shaded with darker brown of the underfur. The eye ring is pale buff, and sides of neck a pale gray. Flanks tend to be grayish or buffy white; legs, feet, and venter are a cinnamon buff. Tail is black, rather than cinnamon buff above, fuscous-black and grayish-white below (Howell, 1938). Molt pattern is "diffuse" without an external molt line (Hansen, 1954). Upper side of tail in *S. c. ruficaudus* is more tawny (not gray), sides of face and throat a deeper shade of tawny, and legs and feet darker than *S. columbianus*. Albinism has been observed (Svihla, 1933). Skull of *S. c. ruficaudus* is relatively broader, jugal wider, and zygomata more heavily built than *S. c. columbianus* (Fig. 2; Howell, 1938).

Spermophilus columbianus is one of the largest members of the subgenus *Spermophilus*, being second in body length to *S. parryii* (Hall, 1981). External measurements (in mm) range as follows: total length, 325–410; length of tail, 80–116; length of hind foot, 47–57; length of ear, 16–22.5 (Elliott and Flinders, 1984; Hall, 1981). Ranges for cranial measurements (in mm) of 94 *S. c. columbianus* (Elliott and Flinders, 1984) are: length of diastema, 9.9–11.8; occipitonasal length, 46.9–51.3; palatilar length, 24.3–25.6; zygomatic breadth, 28.9–32.6; mastoidal breadth, 23.4–25.9; interorbital breadth, 9.9–10.9; nasal length, 16.1–18.2; length of maxillary toothrow, 11.3–11.8. Average cranial measurements (in mm) of 12 *S. c. ruficaudus* (Howell, 1938) are: greatest length of skull, 51.7; palatilar length, 25.1; zygomatic breadth, 31.8; cranial breadth, 20.8; interorbital breadth, 10.6; postorbital constriction, 11.3; length of nasals, 19.4; length of maxillary toothrow, 10.9.

DISTRIBUTION. The distribution of *S. columbianus* (Fig. 3) includes the Rocky Mountain region of western Montana, Idaho, northeastern Washington, southeastern British Columbia, and western Alberta. They also occur on the plains of eastern Washington and in the mountains of east-central Oregon (Hall, 1981). Fossils of *S. columbianus* have been identified only at the Wasden Site (Owl Cave), a late Pleistocene (Rancholabrean) deposit in Bonneville County, Idaho (Kurtén and Anderson, 1980).

FORM AND FUNCTION. Columbian ground squirrels possess sebaceous glands associated with hair follicles and gland complexes found in the oral angle, dorsal, and anal regions. The gland at the oral angle is an apocrine-type consisting of three lobes; each drained by a separate duct. Approximately 60 oval-shaped glands, extending posteriorly from the scapular region, compose the dorsal gland field. Anal glands are located in retractable papillae near the anal aperture, one median-ventral and two lateral. Sweat glands are found on the volar surface of foot pads (Kivett, 1978). The location and histology of integumentary glands in *S. columbianus* are similar to those in other *Spermophilus* (Kivett et al., 1976).

Spermophilus columbianus attains full adult mass in its fourth summer (at 3 years of age). Males are usually heavier than females, but the amount of mass gained is affected by environmental conditions of that particular year (Boag and Murie, 1981*a*).

Physiological preparations for hibernation appear to be completed when body mass ceases to increase, plateaus, and begins to decrease in late summer or early autumn. Individuals periodically arouse from winter torpor, urinate, then re-enter torpor. The frequency with which they arouse from torpor is regulated by environmental temperature (Twente et al., 1977). Glomerular filtration ceases during torpor and most residual urine in the bladder is formed after the initial urination following arousal, and as the animal reenters torpor (Moy, 1971; Pengelley and Fisher, 1961). Urine flow does not begin until the animal has warmed (Lesser et al., 1970; Moy, 1971; Moy and Pfeiffer, 1971; Moy et al., 1972). Passmore et al. (1975) noted urea accumulated in blood of torpid animals is excreted in urine during arousal. Hematocrit increases and total leucocyte concentration decreases in torpid individuals. Percent of lymphocytes increases, whereas percentage of neutrophils decreases during torpor. Red cell counts do not change during torpor or arousal (Nansel and Knoche, 1972). Clotting time of blood is prolonged in torpid *S. columbianus*. Prolonged clotting may serve to prevent thrombosis during winter torpor (Svihla et al., 1951). At ambient temperatures similar to nest temperatures, injection of noradrenaline increases heat production, rectal temperature, and axillary temperature in neonates. Heat production increases with increasing age. At low air temperatures, injections of noradrenaline have no effect on heat production (Glass and Wang, 1978).

Average brain cholinesterase activity of *S. columbianus* is 16.51 milliunits/mg. After being sprayed with the organophosphorus insecticide acephate, brain cholinesterase activity is inhibited for 3–6 days after application (Zinkl et al., 1980).

Fig. 1. Yearling female *Spermophilus c. columbianus* from Banff National Park, Alberta, Canada. Photograph by D. R. Wiggett.

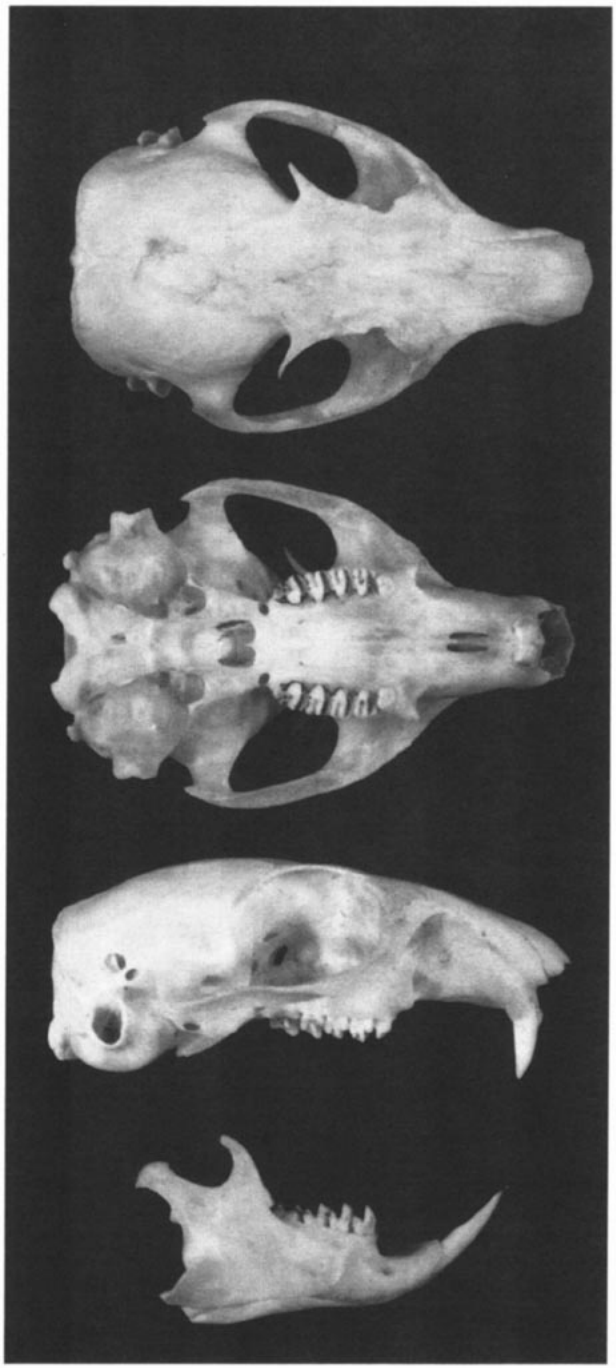

Fig. 2. Dorsal, ventral, and lateral views of the skull and lateral view of mandible of *Spermophilus c. columbianus* (Eastern Kentucky University 1458, male, Rush Point, Big Creek Ranger District, Valley Co., Idaho). Greatest length of cranium is 52 mm.

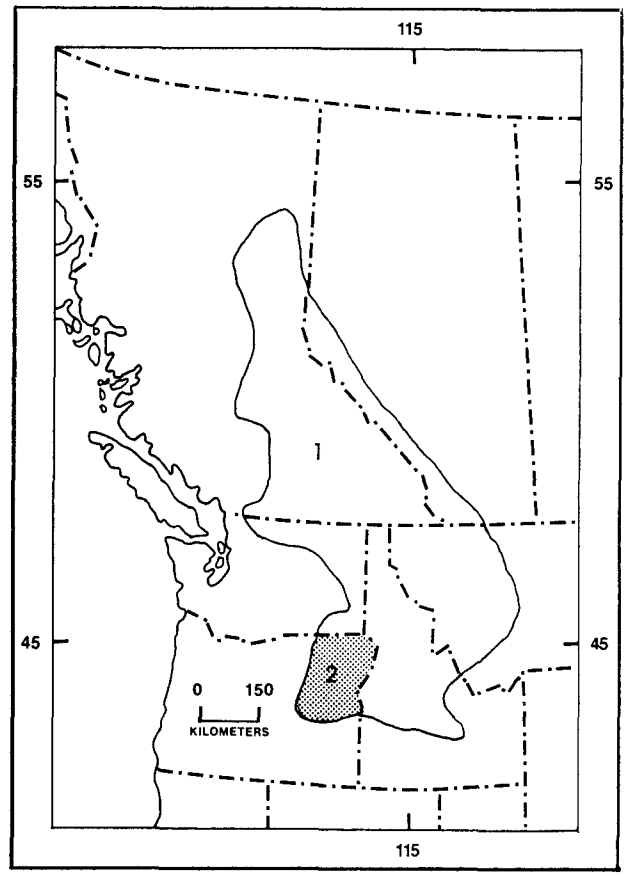

Fig. 3. Distribution of *Spermophilus columbianus* (Hall, 1981): 1, *S. c. columbianus*; 2, *S. c. ruficaudus*.

The enlarged basal end of the baculum in *S. columbianus* is nearly round in cross section. The shaft narrows abruptly, with a slight twist, then expands again into a distal scooplike-end studded with toothlike projections, and is more horseshoe shaped than any other in the genus. These projections number from 12 to 20, usually of unequal number on the two sides. There is a median, keel-like projection on the ventral border of the distal end. Ranges of measurements (in mm) of 18 specimens from Montana are: length, 4.3–5.5; width of base, 0.7–1.3; width of distal end, 1.4–1.8 (Burt, 1960). Females have a small os clitoridis that resembles a teardrop-shaped disc. The disc bears prominent, regularly spaced projections on its margin. Dimensions (in mm) are: length, 2.4; greatest width of disc, 1.0 (Layne, 1954).

Average mass (in g) of liver (10.8 and 6.9, for adult and juvenile *S. columbianus*, respectively), lung (4.8, 2.8), heart (2.0, 1.1), spleen (0.7, 0.3), right kidney (0.9, 0.6), and left kidney (1.0, 0.7) is not different between sexes or age categories (Elliott, 1980). The brain of *S. columbianus* weighs approximately 4.1 g (Mace et al., 1981).

Cell counts have indicated typical mitosis occurs in somatic tissue of the embryo of *S. columbianus*. There is an intermediate stage of specialization that occurs between typical and modified mitosis (Nunemarker, 1933). Development of the central nervous system is similar to processes found in other mammals (Stone, 1925). The testis undergo an annual cycle of spermatogenesis with greatest activity occurring during hibernation (Howard, 1924).

ONTOGENY AND REPRODUCTION. The active season of female *S. columbianus* is about 90–100 days each year, during this period they mate, gestate, lactate, and fatten for a subsequent period of hibernation that lasts for about 70% of the year (Dobson and Murie, 1987). Breeding in *S. columbianus* commences shortly after adult females emerge from hibernation and continues for a period of about 3 weeks. Adult males emerge 1–2 weeks before yearling males (Murie and Harris, 1982; Shaw, 1924, 1925*a*). Testes mature during hibernation and are at maximum size when animals emerge (Shaw, 1926*a*). All stages of spermatogenesis are present at this time; regression of the tract commences soon after emergence. Reproductive tracts of juvenile males are small and, except for the vasa deferentia, show little change during the summer. Among juveniles, spermatogenic activity does not progress beyond the spermatogonial stage during the first summer (Smith, 1947). Males observed in Alberta did not breed until they were 3 years of age (Murie and Harris, 1978).

Columbian ground squirrels undergo one estrus shortly after emergence from hibernation (Murie and Harris, 1982). As a female approaches estrus, her vulva becomes enlarged and swollen and there is an odorous discharge. Male *S. columbianus* can discriminate estrus status of females from vaginal odors (Harris and Murie, 1982, 1984*a*). Gestation period is 24 days, there is one litter/year (Mich-

ener, 1977; Shaw, 1924, 1925*b*). Michener (1977), Murie et al. (1980) and Murie and Harris (1982) noted female *S. columbianus* delay breeding until 2 years of age, but Festa-Bianchet (1981) observed females may breed as yearlings. If a female does not mate during the rut, she will return to estrus in 2 weeks (Shaw, 1925*b*). Shaw (1925*b*) observed animals breeding 6 weeks after initial mating activity. Breeding success affects the time of entry into hibernation, but apparently not the time of emergence from hibernation (Michener, 1977). The date of breeding varies with elevation, with greater variability being noted at higher elevations (Murie and Harris, 1982). Body mass appears to influence reproduction, with heavier females having larger litters (Dobson and Kjelgaard, 1985*a*, 1985*b*; Murie and Dobson, 1987).

Mean counts of embryos and placental scars are correlated inversely with elevation. Rates of preimplantation loss in *S. columbianus* vary from 7 to 13%, and in utero loss after implantation, 3 to 9% (Murie et al., 1980). Reports of mean litter sizes, based on counts of embryos and placental scars vary from 2.7 (Murie et al., 1980) to 7.0 (Zammuto, 1984). Average litter size at birth of captive animals ranges from 3.0 (Murie et al., 1980) to 4.6 (Shaw, 1925*a*). Average litter size of wild populations ranges from 2.1 to 4.2 (Murie and Dobson, 1987).

At birth, Columbian ground squirrels are naked, flesh colored or slightly pinkish, blind, toothless, and apparently have closed external auditory meatuses (Shaw, 1925*b*). Average mass at birth ranges from 6.8 to 11.4 g (data includes captive-raised animals; Koeppl and Hoffmann, 1981; Wroot et al., 1987). The nursing period usually lasts 30 days (Shaw, 1925*b*). Shaw (1925*b*) and Ferron (1981) noted adult-like vocalizations at 14 days of age, hearing at 19–21 days, eyes open at 21–23 days, incisors erupting at 16–20 days, hair development at 3 days and shedding of initial coat by day 56, walking at 15–16 days, climbing at 18–19 days, gnawing at 21–22 days, digging at 23–24 days, drinking at 28–29 days, ingesting solid food at 23–24 days, and grooming at 23–25 days. The growth curve for *S. columbianus* shows an initial linear segment of relatively long, uniformly rapid growth, a transition from 42 to 46 days during which growth diminishes, followed by a second linear segment of relatively long, uniform but slower growth. Body mass as a function of age also seems to exhibit a three-part curve, with *S. columbianus* displaying an initial transition at day 24. When compared with other species, linear characters (lengths of body, tail, and hind foot) of *S. columbianus* and *S. armatus* generally were larger at equivalent ages than in either *S. elegans* or *S. richardsonii* (Koeppl and Hoffmann, 1981). Early growth rate of *S. columbianus* is similar to *S. beldingi, S. lateralis,* and *S. tereticaudus* (Levenson, 1979). Litter sizes and preweaning growth rates of *S. columbianus* differ in different parts of their geographical range. Litter size is negatively correlated with latitude, while median birth date is positively correlated with elevation (Wroot et al., 1987).

Spermophilus columbianus does not reach adult physical dimensions until its second season (Shaw 1925*b*). The hind foot achieves 98% of adult size in the first summer; length of ear, 89%; length of tail, 89%; total length of body, 86%; zygomatic breadth, 89%; and condylobasal length, 88% (Elliott and Flinders, 1980*a*). Juveniles do not attain full cranial dimensions until their second season. By the end of their first summer, length of maxillary toothrow in juveniles closely approximates adult dimensions (Elliott and Flinders, 1984).

Michener (1977) reported juvenile *S. columbianus* attain about 60% of adult prehibernation mass before entering hibernation, whereas young of *S. richardsonii* attained 80–90% of adult prehibernation mass. Although juvenile *S. columbianus* entered hibernation at a smaller mass (in proportion to adult mass) and at a younger age than juvenile *S. richardsonii, S. columbianus* exhibited a greater over-winter survival rate (87%) as yearlings. Murie and Boag (1984) found significantly more large-mass than small-mass juveniles survived to the next summer.

ECOLOGY. The Columbian ground squirrel is a colonial sciurid typically found in alpine or subalpine meadows (Steiner, 1970*a*). In Oregon, *S. columbianus* occurs in the Hudsonian, Canadian, and upper levels of the Transition life zones, but rarely in heavy timber (Bailey, 1936). Thus, their distribution usually is discontinuous. Similar habitat is occupied in Idaho (Elliott and Flinders, 1980*b*), Montana (Manville, 1959), and Washington (Larrison, 1970). In the subalpine areas of the Blue and Wallowa mountains of Oregon, *S. columbianus* occupies edges of meadows and mounds within meadows where flooding is frequent (Turner, 1972). In alpine regions of the Pacific Northwest, *S. columbianus* is found most often in wet meadows and grasslands and less often in rock, fellfield, heather, and herbfield habitats (Reichel, 1986). *S. columbianus* also readily uses modified habitats such as clear-cuts (Ramirez and Hornocker, 1981). Where *S. columbianus* and *S. beldingi* are sympatric, *S. beldingi* occupies lower, more arid habitats often associated with sagebrush (*Artemisia*), whereas *S. columbianus* occupies higher, wetter habitats (Turner, 1972). Durrant and Hansen (1954) ranked *S. columbianus* second to *S. beldingi* as the ground squirrel least adapted to dry conditions.

Shaw (1920) reported *S. columbianus* population densities of 24.7/ha on wheatfields and 61.7/ha on agricultural bottomlands in Washington. Lambeth and Hironaka (1982) reported 32/ha on subalpine rangeland in central Idaho. In Alberta, Adams (1961) recorded 34.6/ha, and Boag and Murie (1981*b*) reported density of yearling and adult squirrels ranged from 11.6 to 16.1/ha; density of juveniles was from 4.6 to 20.7/ha.

Boag and Murie (1981*b*) noted *S. columbianus* were concentrated in certain parts of their southwestern Alberta study area, and that areas where density was greatest were consistent among years. The density of animals within densely populated areas was three times that within sparsely populated areas. The sex ratio within densely populated areas averaged 1:2.3 in favor of females, whereas in sparsely populated sites it was 1:1.2. The uneven distribution was thought to reflect a selection for drier parts of the habitat. The densely populated sites were situated on well-drained, south-facing slopes. Shaw (1925*c*) noted south-facing slopes accumulated less snow and postulated this allowed squirrels to emerge from hibernation sooner.

The placement of *S. columbianus* burrows has been postulated to be influenced by soil moisture (Elliott, 1983), aspect (Shaw, 1924), drainage (Boag and Murie, 1981*b*), slope (Murie et al., 1980), and social or historical factors such as the presence of other *S. columbianus* or their burrows (Weddell, 1989). Based on the amount of soil transported (4–12.3 kg/year) to the surface, 4–7 m of tunnel are added to *S. columbianus* burrow systems annually. Newly constructed burrows result in the transfer of 25–50 kg of soil to the surface (Smith and Gardner, 1985). Entrances to Columbian ground squirrel burrows are of two types. One is small and round, not much larger than the burrow itself; the other is a larger, funnel-shaped opening (Shaw, 1924).

The summer burrow often is used for hibernation. In some instances, a separate summer den is used then joined to a hibernation den. An "exit shaft" connects the hibernation cell (a circular cavity in the den where the hibernation nest is placed) with the surface (Shaw, 1925*a*, 1926*b*). Hibernation dens also have drains to keep water from entering the nest. The hibernation nest is dome shaped, the lining made of finely-shredded grass. Within the nest the hibernating animal lies on its sacrum, curled vertically so the nose is against the diaphragm and the skull parallel with the bottom of the nest (Shaw, 1925*a*). The hibernation den of adult males often has a cache of food in it (Shaw, 1926*c*). The food generally is used in spring when the earlier emerging males often find the ground snow-covered and food scarce (Shaw, 1925*d*, 1926*c*). When ready for hibernation, squirrels close their dens with an earthen plug (Shaw, 1925*a*, 1925*e*). Squirrels at high elevations use hibernacula that are larger and shallower than those found at lower elevations. The size of the hibernaculum is proportional to the weight of the occupant except that adult males use hibernacula larger in proportion to their weight than do adult females or juveniles. Juveniles usually hibernate close to their mother and siblings (Young, 1990).

Summer dens often are used as brood dens (Shaw, 1924). A small, separate tunnel connecting the brood den to the outside may be constructed. These entrances are well-hidden and frequently plugged at night and reopened in the morning. McLean (1978) postulated plugging did not serve as protection from predators or weather, but as protection from wide-ranging adult males. Harris (1985) noted unplugged burrows already stocked with nest material might be a desirable resource for other females or members of other sympatric species, such as pocket gophers (*Thomomys talpoides*), deer mice (*Peromyscus maniculatus*), or meadow voles (*Microtus pennsylvanicus*).

Spermophilus columbianus exhibits *K*-strategies in high-elevation environments and *r*-strategies in low-elevation environments. Most data show a pattern reversed to that predicted by bet-hedging theory (Dobson et al., 1986; Murie, 1985; Zammuto and Millar, 1985*a*, 1985*b*). Life expectancy at birth for *S. armatus, S. beldingi, S. columbianus, S. lateralis,* and *S. parryii* is lower than life

expectancy at maturity. Of these species, *S. columbianus* has the greatest life expectancy at both birth and maturity, whereas *S. parryii* has the lowest at both ages (Zammuto, 1983). Reproductive value at maturity for *S. columbianus* was greater than the residual reproductive value at maturity, suggesting a daughter in an average female's first litter was more likely to replace her mother than daughters in subsequent litters (King and Murie, 1985; Zammuto, 1983).

Columbian ground squirrels eat a variety of flowers, seeds, bulbs, and fruits (Howell, 1938; Manville, 1959; Martin et al., 1951; Shaw, 1925*f*, 1925*g*). On domestic sheep range in Idaho, *S. columbianus* mainly consumed silky lupine (*Lupinus sericeus*; Lambeth and Hironaka, 1982). Animals on pastures grazed by cattle in British Columbia selected clover (*Trifolium*) and dandelion (*Taraxacum officinale*; Harestad, 1986). Adult *S. columbianus* on a mountain meadow in Idaho ate mainly clover, yarrow (*Achillea millefolium*), and alpine timothy (*Phleum alpinum*). Juvenile animals on the same site consumed fleabane (*Erigeron speciosus*) and clover during July and, like adults, eliminated clover from the August diet concentrating instead on fleabane and yarrow. Adult and juvenile *S. columbianus* inhabiting south-facing mountain slopes in Idaho ate balsamroot (*Balsamorhiza saggittata*), bluebunch wheatgrass (*Agropyron spicatum*), and silky lupine during summer (Elliott and Flinders, 1985). *S. columbianus* also consume animal matter (Manville, 1959; Tyser and Moermond, 1983), including others of their own species (Betts, 1976; Elliott, 1978). Infanticide has been observed (Balfour, 1983; Waterman, 1984).

Shaw (1916) reported 385 *S. columbianus* consumed as much forage per day as one cow; 96 animals consumed as much food as one sheep. Because of possible competition with livestock, *S. columbianus* has been the subject of control efforts. Record (1978) and Albert and Record (1982) found sodium floroacetate more effective than zinc phosphide, gas cartridges, or strychnine as a control technique. Matschke et al. (1988) found *S. columbianus* may be controlled using strychnine bait concentrations of 0.20–0.35%. Askham (1985) tested two anticoagulant rodenticides (chlorophacinone and bromadiolone), determining mid-season and late-season applications could achieve 70–80% and 100% mortality, respectively.

Columbian ground squirrels are hosts of the Rocky Mountain spotted fever tick, *Dermacentor andersonii* (Bacon et al., 1959; Birdseye, 1912; Bishopp and Trembley, 1945). Other external parasites recorded include: the lice *Enderleinellus suturalis* and *Neohaematopinus laeviusculus*; the fleas *Neopsylla inopina, Opisocrostis tuberculatus*, and *Oropsylla idahoensis*; and the mites *Dermacarus heptneri, Androlaelaps fahrenholzi, Macrocheles* sp., and *Pygmephorus erlangensis* (Hilton and Mahrt, 1971*a*). Internal parasites include *Trypanosoma otospermophili, Eimeria bilamellata, E. callospermophili*, and *E. lateralis* (Hilton and Mahart, 1971*b*, 1972*a*, 1972*b*). Plague (*Yersinia pestis*) was reported by Twigg (1978). McLean et al. (1970) detected hemagglutinin-inhibiting antibodies to Powassan or St. Louis encephalitis viruses in *S. columbianus* from British Columbia, and postulated they may function as a natural reservoir for the viruses. Wobeser and Gordon (1969) observed *S. columbianus* exhibiting dermatitis caused by *Dermatophilus congolensis*.

Columbian ground squirrels are prey for the brown bear (*Ursus arctos*; Taylor, 1964), coyote (*Canis latrans*; Elliott and Guetig, 1990), marten (*Martes americana*; Koehler and Hornocker, 1977; Weckwerth and Hawley, 1962), badger (*Taxidea taxus*; Rust, 1946), lynx (*Felis lynx*; Barash, 1971), weasel (*Mustela*; Murie, 1985), and mountain lion (*Felis concolor*; Seidensticker et al., 1973). The golden eagle (*Aquila chrysaetos*; Boag, 1977), red-tailed hawk (*Buteo jamaicensis*; Miller, 1931; Munro, 1929), and goshawk (*Accipiter gentilis*; Festa-Bianchet and Boag, 1982) are the principal avian predators.

BEHAVIOR. The total time *S. columbianus* spends above ground decreases through the season. Daily activity patterns depend on seasonal changes in average temperatures at various times of the day. During early days of summer, morning temperatures are cool and animals are not very active, activity increases as the day warms. As the season progresses, they tend to avoid the heat of the day and are more active in morning and late afternoon hours (Betts, 1976; Elliott and Flinders, 1980*b*). Because abundance of forage as well as risk of predation increases with increasing distance from burrows, the feeding behavior of *S. columbianus* is mediated by time budgeting and differs with distance from burrows (Andrusiak and Harestad, 1989).

Columbian ground squirrels enter hibernation with adult males entering first, then adult females, yearlings, and juveniles (Betts, 1976). Adult males emerge from hibernation before adult females; yearlings emerge later than adults, but time of emergence does not differ by sex (Murie and Harris, 1982). Emergence of adult and juvenile *S. columbianus* occurs later in the season with increasing altitude and latitude (Michener, 1977; Moore, 1937; Murie and Harris, 1982).

Male and female *S. columbianus* exhibit territoriality and dominance. Adult males have overlapping home ranges (mean size, 4,200 m^2). Within these home ranges are smaller core areas (mean size, 460 m^2) defended more than other parts of the home range. Murie and Harris (1978) considered core areas to be approximations of territories. Males within their core areas exhibit dominance over other *S. columbianus*. Dominant males defend their core areas, but a male's dominance will shift to a subordinate status outside its core area. This type of territory is classified as "spatiotemporal." Resources within the territory that are defended appear to be females with which to breed. Aggressive interactions between males decline after the breeding period, remaining at a low level for the rest of the summer (Betts, 1976; Murie and Harris, 1978).

Adult females exhibit strong site fidelity. Adult *S. columbianus* that successfully establish themselves in a colony are resident for >3 years (Murie and Harris, 1984). The combination of site attachment and longevity may result in a high potential for inbreeding among fathers and daughters and an increased likelihood for familiarity. Long-term familiarity may affect patterns of social relations among both male and female squirrels (that is, reducing the time and energy spent in territorial defense; Murie and Harris, 1984).

Adult females establish a home range of about 1,000 m^2 near the nest burrow and will actively defend part of it as a territory (Festa-Bianchet and Boag, 1982). Adult males establish territories farther from their natal dens than do females (Murie and Harris, 1984). Overlap between home ranges of adult females is great following emergence, decreases to a minimum during late gestation, and increases again after parturition (Festa-Bianchet and Boag, 1982). King and Murie (1985) postulated high survival and recruitment rates are important factors influencing temporal overlap of female kin in *S. columbianus*. The establishment of a territory by adult females is thought to help defend juveniles from other adults, particularly during the time between parturition and emergence (Festa-Bianchet and Boag, 1982).

Sex differences in use of space and social behavior develop early (Waterman, 1986). Differences between sexes in the movement of juveniles is apparent after the first 10 days of emergence from the natal burrow. Juvenile males travel farther from their natal burrow, have larger home ranges, and shift their activity centers more than do juvenile females. Juvenile females remain close to the natal burrow and in many cases will inherit the nest burrow of their mother when they breed (Harris and Murie, 1984*b*).

Columbian ground squirrels undertake two types of movements, excursions, which are temporary absences from the home range, and dispersal movements. Excursions are commonly undertaken by yearling females. Dispersal mainly occurs immediately before and after juveniles emerge (Boag and Murie, 1981*b*; Shaw, 1945). A greater proportion of yearlings disappear during the active season than any other age class (Elliott and Flinders, 1980*a*; Festa-Bianchet and King, 1984). The loss results from dispersal movements, with more males leaving an area than females (Boag and Murie, 1981*b*; Murie and Harris, 1984). Adult animals behave aggressively toward yearlings, particularly yearling males (Festa-Bianchet and King, 1984). Boag and Murie (1981*b*) suggested numbers of *S. columbianus* are regulated by a density-dependent mechanism, where an increase in density may promote a decline in numbers of juveniles produced and their subsequent survival.

Columbian ground squirrels walk in a quadrupedal gait, but usually bound when moving >1 m (Betts, 1976). They have been observed to leap over a 2-m-wide stream (Steiner, 1970*a*). Individuals will climb trees and shrubs to feed on buds and fruits (Manville, 1959; Steiner, 1970*a*). They use all four legs for propulsion when swimming, covering 1 m of open water in 2.5 s (Dagg and Windsor, 1972).

Foraging behavior is meticulous and area-intensive (Tyser and Moermond, 1983). The typical feeding pattern is a repeated sequence of walking a few steps and pausing to take a bite (Betts, 1976; Tyser and Moermond, 1983). Squirrels may chase and catch insects, pouncing on them or knocking them out of the air (Betts, 1976).

Over a portion of its range, *S. columbianus* occurs in sympatry with hoary marmots (*Marmota caligata*) and pikas (*Ochotona princeps*). Barash (1973) noted a differential foraging radius where the species coexisted near talus slopes. He suggested a niche differentiation existed on feeding areas; with pikas feeding nearest talus slopes, *S. columbianus* feeding farthest from slopes, and hoary marmots feeding in between.

Ferron (1984) considered *S. lateralis* more precocial than *S. columbianus* in development of many agonistic patterns, but noted *S. columbianus* develop cohesive and neutral patterns of social behavior earlier. He postulated that the difference in relative timing of social behavior development was related to differences in social organization of the species. He suggested it would be more beneficial for the asocial species, *S. lateralis*, to possess its behavioral signals before emergence from the nest, whereas such would not be necessary for the more social *S. columbianus*.

Columbian ground squirrels exhibit two types of self-grooming behavior, ordinary grooming and displacement grooming. Ordinary grooming, which is exhibited by both sexes, is a relaxed activity and involves typical body maintenance activities (for example, licking and cleaning the fur; Steiner, 1973). Mean bout lengths of ordinary grooming are shorter in adults than in young (Ferron and Lefebvre, 1982). Displacement grooming is evident in adult males and appears to reach a peak during breeding. Courtship bouts and chases of females are interspersed with bouts of hurried grooming motions (Steiner, 1973).

Allogrooming, though rare in nature, occurs between females and pups and between littermates. In juveniles and yearlings, allogrooming occurs during bouts of play, particularly during or after play-fighting and play-wrestling (Steiner, 1970*a*, 1970*b*). Grooming among adults appears to be affected by social status. Dominant animals initiate grooming more frequently and consistently than subordinate individuals. Dominance expressed in allogrooming appears to be situation-dependent (Steiner, 1973, 1975).

Columbian ground squirrels often seek places to bask, particularly in spring. They sprawl on dirt mounds with hind legs fully extended so the plantar surfaces are turned upward. Animals dust by sliding on their belly through the dirt, the hind legs giving a forward push. The sequence ends with a vigorous shaking of the body (Steiner, 1970*a*).

Greeting behavior, referred to as "kissing," involves a slight sidetilting of the head to facilitate simultaneous sniffing of the oral-gland region (Betts, 1976; Kivett et al., 1976; Steiner, 1970*b*, 1975). The animal that initiates contact usually is dominant. The recipient may exhibit a wide range of responses; active participation, passive submission, some form of opposition, or a refusal of mouth contact and escape (Steiner, 1970*b*). Greeting contact is more frequent among members of the same social group and essentially is a cohesive activity between the animals (Kivett et al., 1976). Greeting behavior may be ontogenetically linked with, or derived from, food-seeking and food investigation behaviors (Steiner, 1975). Shaw (1925*b*) suggested female *S. columbianus* regurgitate food for their young. He also noted neonates apparently show food-begging behavior by vibrating their lips in contact with the mother's mouth. Such behavior may promote scent-sharing, olfactory imprinting, or scent preference, between mother and young. In this way, scent of infants may be integrated into the "scent pool" of adult squirrels (Steiner, 1975). The process could be essential to prevent young squirrels from being attacked by adults, as observed in some populations (Steiner, 1972).

Agonistic encounters between males begins with one animal bounding toward another. The approaching male is almost always the dominant. At any time during the approach, the subordinate male may turn and bound away, whereupon the dominant male usually stops. If contact is initiated, a fight results. Such fights appear to be free-flowing, unpatterned interactions (Betts, 1976).

Before mating, females rarely chase males and show little reaction to being approached and sniffed by males. After breeding, however, females chase males regularly, and become dominant over males until late in lactation. Lactating females exhibit greater dominance over males than females not lactating. Although the overall trend is for female dominance over males after breeding, the strength of the domination depends on the territorial-dominance status of the males and the spatial relationship of males to a female (Murie and Harris, 1988).

Aggressive interactions between adult females are essentially like those between adult males and females (Betts, 1976). Interactions between adults and yearlings or juveniles often consist of greeting behavior. Later in the season greeting behavior may be followed by the adult attacking the younger animal, especially if the adult is a male (Betts, 1976; Steiner, 1972).

During the breeding season, males will approach receptive females and nose their ano-genital region. The male then mounts from behind, clasping the flanks of the female with his forelegs. The pair will fall on their sides until copulation ends. The majority of copulations take place underground (Steiner, 1970*b*).

Young *S. columbianus* spend considerable time playing together. Play invitations and play signal patterns can be interpreted in terms of intention movements and attention getting devices (Steiner, 1971). Waterman (1988) found differences among age, sex, and littermate-non-littermate play in *S. columbianus*. She noted play is more than just physical training, but may have different functions in the socialization of males and females.

Females with young exhibit a behavior termed the "follow-me" posture. The female assumes a position in which the hindquarters rest on the ground with the forequarters elevated and forelimbs extended, touching the ground. The activity begins with a period of grooming after which the female moves away and assumes the "follow-me" posture; the young then respond by following (Koeppl, 1980).

Columbian ground squirrels exhibit behavior patterns that function as forms of visual communication. Upright postures indicate greater alarm than horizontal postures. The direction that an erect, calling squirrel faces conveys to its conspecifics the general direction of the detected threat (Betts, 1976).

Seven types of vocalizations occur in *S. columbianus*. Shrill chirps, soft chirps, and churrs function as alarm calls (Betts, 1976; Harris et al., 1983). Tooth clatter, made by rapid clicking of teeth, functions as a threat, possibly to inhibit the approach of another squirrel. Squawks and squeals are loud calls given in response to pain or fear. Growls are low-pitched, guttural calls given by females mounted by males. Growls seem to function as threats (Betts, 1976). *S. columbianus* give different alarm calls in response to aerial and terrestrial predators. Aerial predators elicit a multiple series of calls given in rapid succession; terrestrial predators generate fewer, more widely spaced calls (Lickley, 1984). *S. columbianus* exhibits a more varied acoustical repertoire than *S. armatus*, *S. elegans*, or *S. richardsonii* (Koeppl et al., 1978).

Columbian ground squirrels exhibit two types of scent marking behavior, mouth–cheek rubbing, where the oral gland contacts the substrate; and twist-marking, a forward spiral movement in which oral, head, and dorsal glands are rubbed on the ground. Scent-marking is usually demonstrated by dominant males (Kivett et al., 1976; Steiner, 1974). Marking is directed at dirt mounds or den entrances and prominent landmarks (Thiessen and Rice, 1976). The development of marking behavior is important for young *S. columbianus*. Among male littermates, the individual who marks most frequently becomes dominant (Steiner, 1974).

GENETICS. The diploid number of chromosomes is 32, with 12 submetacentrics, a submetacentric X, and a minute metacentric Y chromosome (Nadler, 1966; Pechanec, 1926). Within embryos, a dimorphic condition exists in chromosome number of male and female somatic cells. Embryos with 33 chromosomes are male; those with 34 are female (Schwarz, 1927). Based on serum proteins and transferrins, *S. columbianus* can be distinguished from other members of the subgenus *Spermophilus* by the number of albumins, number and configuration of a group of characters (called Character II) that migrate slower than albumin, and number of arclike fractions (*S. columbianus* has three arc fractions, all other species have one; Nadler, 1968). Electrophenograms of *S. columbianus*, *S. lateralis*, and *S. saturatus* serum exhibit similar double albumins and dense globulin patterns (Johnson and Wicks, 1964). Zammuto (1983) determined the genetic variability in breeding females is lowest at intermediate elevations and highest at high and low elevations. Of five species examined (*S. armatus*, *S. beldingi*, *S. columbianus*, *S. lateralis*, *S. parryii*), *S. columbianus* had a lower degree of polymorphism and heterozygosity than *S. beldingi*.

REMARKS. Rand (1954) postulated a close relationship between *S. parryii* and *S. columbianus*, suggesting the species evolved from common ancestral stock as a result of separation by a continental glacier during the Pleistocene. Examination of fleas, giemsa-band patterns, chromosomes, transferrins, serum proteins, and location of scent glands tend to support the hypothesis that *S. columbianus* is closely related to *S. parryii* (Holland, 1958; Kivett et al.,

1976; Lyapunova and Vorontsov, 1970; Nadler et al., 1975, 1982, 1984). Separation of the *S. parryii-columbianus* ancestor into separate species may have occurred in the middle to late Pleistocene, about 0.47 mya (Nadler et al., 1984). Using mitochondrial DNA, MacNeil and Strobeck (1987) indicated *S. parryii* and *S. richardsonii* are more closely related to each other than either is to *S. columbianus*. They concluded colonization by female founders of *S. columbianus* populations occurred after deglaciation along eastern ranges of the Rocky Mountains, while colonies on western ranges may have been present before extensive deglaciation occurred, having existed in refugia in northwestern Alberta.

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