

Marmota flaviventris. By Barbara A. Frase and Robert S. Hoffmann

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Marmota Blumenbach, 1779

Marmota Blumenbach, 1779:79. Type species *Mus marmota* Linnaeus, 1758, by original designation. *Marmota* Frisch, 1775, although sometimes cited, is unavailable (Bull. Zool. Nomencl., 4:547, 1950).

Arctomys Schreber, 1780:721, pl. 207. No type designated.

Lagomys Storr, 1780:39. No type designated.

Lipura Illiger, 1811:95. Type species *Hyrax hudsonius* Schreber (= *Mus monax* Linnaeus).

Marmotops Pocock, 1923:1200. Type species *Mus monax* Linnaeus, by monotypy. Reduced to subgeneric rank by Howell, 1938:38.

CONTEXT AND CONTENT. Order Rodentia, Suborder Sciuromorpha, Family Sciuridae, Subfamily Marmotinae. *Marmota* contains 14 living species, eight in Eurasia and six in North America (Hoffmann, 1968).

Key to North American Species of *Marmota*

1. Dorsal pelage soft; guard hairs black-tipped, with sub-terminal light band. Black "cap" on dorsal surface of head extending uninterrupted from nose to neck. Found only in northern Alaska and adjacent Yukon *M. broweri*
- Dorsal pelage coarse; many guard hairs with light tips (Fig. 1), or else uniform dark brown or black. Black or brown dorsal surface of head interrupted by white markings on face, or else top of head uniform brown or grizzled 2
- 2(1) Entire pelage dark brown; guard hairs without light tips; occasionally with white spots on ventral surface. Posterior border of nasals deeply V-shaped. Found only on Vancouver Island *M. vancouverensis*
- Not as above 3
- 3(2) Dorsal surface of head uniform grizzled blackish or dark brown; sides of neck grizzled brown, not different from rest of pelage on side. Upper tooth rows approximately parallel. Postorbital processes project along a line drawn across their bases at right angles to the long axis of the skull. Usually only four pair of mammae *M. monax*
- Dorsal surface of head black to brown, usually interrupted by white facial markings; sides of neck whitish to buffy, lighter than rest of pelage on side. Upper tooth rows more or less divergent anteriorly. Postorbital processes usually project back of a line drawn across their bases at right angles to the long axis of the skull (Fig. 2). Usually five pair of mammae 4
- 4(3) Sides of neck buffy to yellowish; feet hazel-brown to buffy; rarely dark brown and never black (except in melanistic specimens); pad in middle of sole of hind foot oval (Fig. 3; see also Howell, 1915; Hoffmann et al., 1979). Fronto-nasal and fronto-premaxillary sutures usually forming distinct arch across rostrum (Fig. 2) *M. flaviventris*
- Sides of neck whitish to gray or cream; never buffy; feet black to dark brown; pad on hind foot near edge of sole, subcircular. Fronto-nasal and fronto-premaxillary sutures usually forming a fairly straight line across rostrum 5
- 5(4) Head and forepart of body mainly black and white in color; feet black. Not found in Olympic Mountains of western Washington *M. caligata*
- Head and forepart of body mainly brown, mixed with white guard hairs. Feet dark brown. Found only in Olympic Mountains of western Washington *M. olympus*

Marmota flaviventris (Audubon and Bachman, 1841)

Yellow-bellied marmot

Arctomys flaviventer Audubon and Bachman, 1841:29. Type locality "Mountains between Texas and California," but fixed as Mount Hood, Oregon, by Howell (1915). Not *A. lewisii* Audubon and Bachman, 1848:pl. 107 (see Hoffmann, 1977).

Arctomys dacota Merriam, 1889:8. Type locality Black Hills at Custer, Custer Co., South Dakota.

Marmota flaviventer Trouessart, 1904:344.

Marmota engelhardti Allen, 1905:120. Type locality Briggs (= Britt's) Meadows, Beaver Range Mountains, Beaver Co., Utah.

Marmota flaviventris Howell, 1915:36.

CONTEXT AND CONTENT. Context noted in generic summary above. There are 11 recognized subspecies of *M. flaviventris* (Howell, 1915; Hall and Kelson, 1959). For complete synonymy of subspecies, see Hall and Kelson (1959).

M. f. avara (Bangs), 1899:68. Type from Okanagan, British Columbia.

M. f. dacota (Merriam), 1889:8, see above.



FIGURE 1. Adult female yellow-bellied marmot (*Marmota flaviventris*), Visitor Center, Grand Coulee, Grant Co., Washington, 990 m. Photo by J. M. Ward, Jr.

- M. f. engelhardti* J. A. Allen, 1905:120, see above.
M. f. flaviventris (Audubon and Bachman), 1841:29. Type locality "Mountains between Texas and California," but fixed as Mount Hood, Oregon, by Howell (1915).
M. f. fortirostris Grinnell, 1921:242. Type from McAfee Meadows, White Mountains, Mono Co., California.
M. f. luteola Howell, 1914:15. Type from Woods Post Office, Medicine Bow Mountains, Albany Co., Wyoming (*warreni* Howell and *campioni* Figgins are synonyms, Warren, 1936:392).
M. f. nosophora Howell, 1914:15. Type from Willow Creek, 7 mi E Corvallis, Ravalli Co., Montana.
M. f. notioros Warren, 1934:62. Type from near Marion Reservoir or Lake, Wet Mountains, Custer Co., Colorado.
M. f. obscura Howell, 1914:16. Type from Wheeler Peak, 5 mi S Twining, Taos Co., New Mexico.
M. f. parvula Howell, 1915:14. Type from Jefferson, Nye Co., Nevada.
M. f. sierrae Howell, 1915:43. Type from head of Kern River, Mount Whitney, Tulare Co., California.

Marmota flaviventris is closely related to the hoary marmot (*M. caligata*) and the ranges of the two species overlap in only a small area in northwestern Montana and western Washington.

DIAGNOSIS. Conspicuous buffy patches on side of neck; usually white markings between eyes (Fig. 1); color of belly yellow or orange to russet; color of upperparts some shade of yellow-brown to tawny, with many light-tipped guard hairs; feet buffy, hazel or dark brown (never black); 10 mammae, two pectoral, two abdominal, and one inguinal pair; interorbital region relatively narrow; postorbital processes projecting back of a line drawn across their bases and at right angles to the long axis of skull (Fig. 2); nasals no broader posteriorly than premaxillae; temporal ridges usually united in old age to form low, short sagittal crest; posterior border of palate beveled at an obtuse angle; incisive foramina constricted posteriorly or of equal width throughout; upper tooth row slightly divergent anteriorly; P4 as large or larger than M1; metaloph complete on each upper molar and on M3 turns posteriorly and joins posterior cingulum; P4 molariform, its protolophid a transverse crest between protoconid and parametaconid; m1 and m2 parallelogram-shaped in occlusal outline (from Howell, 1915; Hall and Kelson, 1959).

GENERAL CHARACTERS. Size small to medium; lean weight (posthibernation) of adult males averages 3.9 kg (range, 2.95 to 5.22) and for adult females 2.8 kg (1.59 to 3.97) (Armitage et al., 1976); body thickset, head short and broad. Underfur is soft, dense and somewhat woolly, chiefly on back and sides; longer, coarse outer guard hairs cover the entire body. Overall color yellow-brown to tawny, often with "frosted" appearance due to light tips and darker subterminal bands of many dorsal guard hairs; considerable variation in coloration occurs even within subspecies (see Howell, 1915; Warren, 1936; Armstrong, 1972). Partial to complete melanism is especially common in populations in the southern Rockies from Wyoming to New Mexico (Howell, 1915; Fryxell, 1928; Armitage, 1961). Ears are small and well-furred; tail is relatively long; feet have five digits; claws are stout and slightly curved; thumb is rudimentary, but bearing nail; palm with five pads (three at bases of digits), posterior pad on sole of hind foot oval in shape and situated near middle of sole (Fig. 3); dental formula $i\ 1/1, c\ 0/0, p\ 2/1, m\ 3/3$, total 22; cheek teeth high crowned; anterior face of incisors yellowish-white. Measurements (in mm) are: total length 470 to 700; length of tail 130 to 220; length of hind foot 70 to 90; condylobasal length 68.0 to 99.8; zygomatic breadth 42.6 to 66.4; interorbital breadth 14.1 to 24.2; mastoid breadth 33.2 to 46.2; length of nasal 29.0 to 42.9; alveolar length of maxillary tooth row 17.7 to 22.6 (in part from Howell, 1915; Hall and Kelson, 1959). Nee (1969) found adult males to have consistently longer total length than adult females. Armitage et al. (1976) determined that adult males were significantly heavier than adult females.

DISTRIBUTION. The yellow-bellied marmot is widely distributed in the western United States (Fig. 4). It extends as far north as southcentral British Columbia and extreme southern Alberta (Fig. 4) where it occurs only in relatively warm, arid habitats at low to mid-elevations (Cowan and Guiguet, 1956; Soper, 1964). Southward, the species occurs from semi-desert in the Columbia Plateau, Snake River Plains and Great Basin through woodland and forest openings to the alpine zone. The lower altitudinal limit of its range becomes progressively higher to the south. Where it reaches its southern range limits in the southern

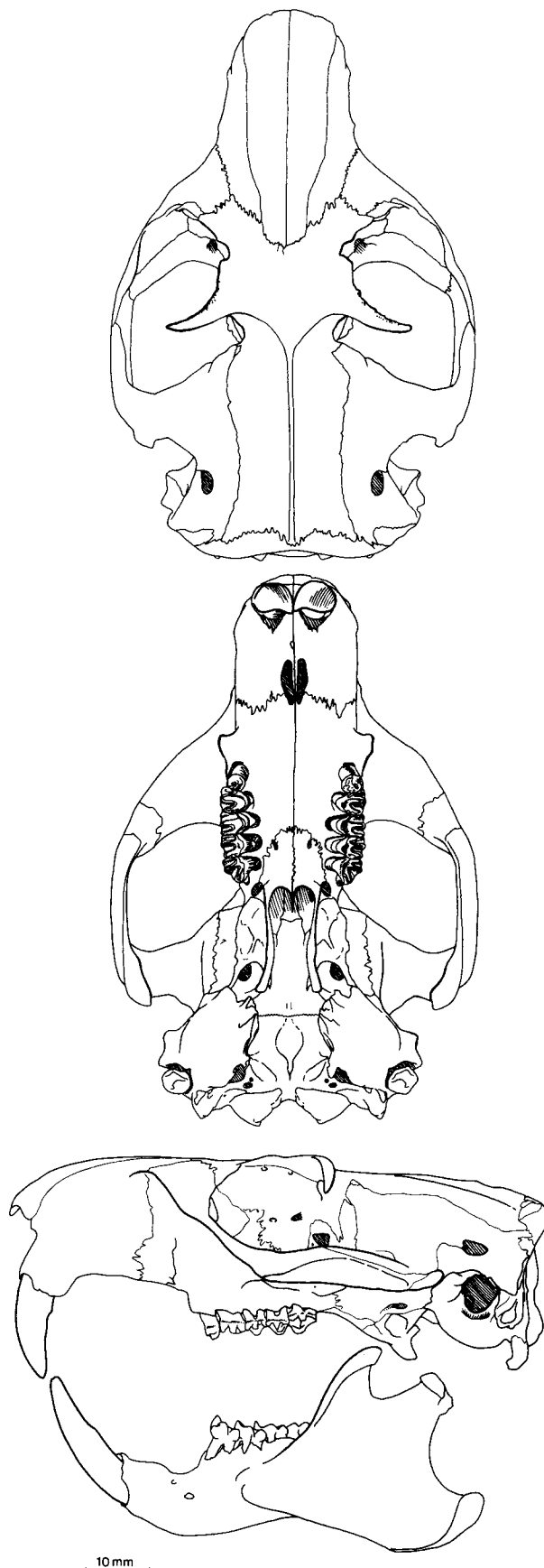


FIGURE 2. Lateral views of skull and dentary (lower), and ventral and dorsal views of skull (middle and upper, respectively) of male *Marmota flaviventris parvula* (MVZ 57476). After Hall and Kelson (1959), by permission.

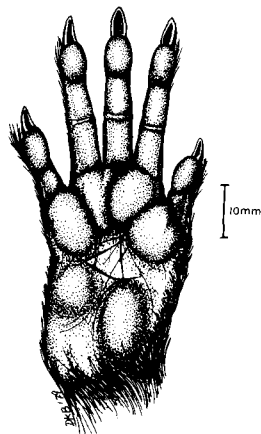


FIGURE 3. Ventral surface of sole of hind foot of *Marmota flaviventris*, showing oval shape of posterior pad.

Sierra Nevada and White Mountains of California, the Toquina and Pine Valley mountains in the Great Basin of Nevada, and the Sangre de Cristo Mountains in New Mexico, the yellow-bellied marmot is found only at higher elevations, usually above 2000 m.

Because of its absence from valleys, southern populations are in many cases isolated from one another, on a series of montane "islands." The yellow-bellied marmots of the Black Hills are probably also isolated (Fig. 4). The common feature of these different habitats is the presence of rocks sufficiently large to provide shelter (Hoffmann, 1974).

FOSSIL RECORD. Anderson (1974) listed six Pleistocene-Holocene localities for *M. flaviventris* in Wyoming, Colorado and Idaho, and Rasmussen (1974) reported records for Montana. Specimens have been collected from the Natural Trap Cave in Wyoming (L. D. Martin, pers. comm.), and from several sites in California and Washington (Sinclair, 1905; Hay, 1921; Merriam and Stock, 1925; Hall, 1946; Schultz and Howard, 1935). Of considerable interest to paleoecologists is the presence of fossil *M. flaviventris* far south of its present range (Howell, 1915; Hay, 1921; Schultz and Howard, 1935; Skinner, 1942; Stearns, 1942; Wilson, 1942; Harris and Findley, 1964; Lange, 1956; Jakway, 1958; Harris, 1970a) (Fig. 4). The presence of the yellow-bellied marmot in these fossil faunas suggests a cooler, more mesic Pleistocene environment (Murray, 1957; Van Devender et al., 1977; Van Devender and Spaulding, 1979). However, some extant populations do inhabit relatively xeric environments (K. B. Armitage, J. M. Ward, pers. comm.) and thus the fossils may indicate cooler, but not necessarily moist, conditions. Seasonal distribution of precipitation may be more critical than total annual rainfall, and a shift toward predominantly winter rainfall in the southwestern United States during the Holocene might have adversely affected *M. flaviventris* (Harris, 1970b).

FORM. Cheek glands and anal glands are present in both sexes (Armitage, 1974). Scent marking with cheek glands was seen in conflict situations (Armitage, 1976). It is probably an expression of dominance rather than territoriality, and also may have a reassurance function. Marking with anal glands has not been observed.

The baculum was described and figured by Burt (1960). He reported a small os clitorides in the female. Cranial measurements of subspecies can be found in Hall (1946) and Howell (1915). There is considerable geographic variation in size; specimens from populations in the arid central portion of the range are smaller than those from more mesic montane habitats (Blake, 1977). A description of the musculature can be found in Bryant (1945).

FUNCTION. There is a single annual molt in summer, the time varying with the timing of the annual cycle of reproduction and torpor (Howell, 1915). Individuals emerging from hibernation in late winter or spring are in full, long, and fairly fresh pelage. However, this fades rapidly through the spring and summer, and assumes a progressively coarser texture. Molt commences earlier in low altitude populations that emerge from hibernation before populations at higher elevations. Within a population, males and

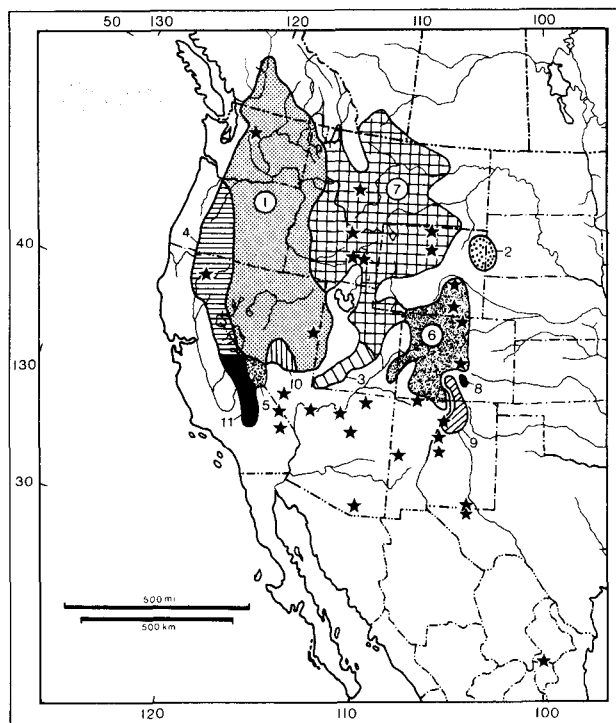


FIGURE 4. Distribution of *Marmota flaviventris*, modified from Hall (1980). Approximate ranges of recognized subspecies: 1) *M. f. avara*; 2) *M. f. dacota*; 3) *M. f. engelhardti*; 4) *M. f. flaviventris*; 5) *M. f. fortirostris*; 6) *M. f. luteola*; 7) *M. f. nosophora*; 8) *M. f. notioros*; 9) *M. f. obscura*; 10) *M. f. parvula*; 11) *M. f. sierrae*. Stars indicate localities of Pleistocene and sub-Recent occurrence (E. Anderson, pers. comm.; Colbert and Chaffee, 1939; Cragin, 1900; Guilday, 1969; Logan and Black, 1979; Mehlinger and Ferguson, 1969; Wells and Jorgensen, 1964; plus text references).

non-lactating females begin to molt before nursing females, who delay molt until weaning approaches. Most adults in the Ruby Mountains, Nevada, were in fresh winter pelage by the end of July (Borell and Ellis, 1934). There seems to be much variation in patterns of molting. However, some hairs on the rump and tail are often retained for more than one year, and become noticeably paler and coarser than the remainder of the hair, especially in the late summer and fall when the rest of the pelage is fresh.

Hock (1969) found that the approximate mean rate of metabolism (MR) of the yellow-bellied marmot was 0.54 ml O₂/g per hour at 30°C. During hibernation it dropped to 0.03 ml O₂/g per hour. Ward (1980) compared the MRs of marmots in a montane population with those of marmots in a population from a semi-arid region. The MRs of both groups increased linearly below 15°C but the montane marmots had significantly lower rates than the semi-arid group at 5 and 10°C. Above 25°C, the MRs of the montane group increased while the MRs of the semi-arid group remained constant from 25°C to 34°C. Ward suggested that reduced metabolism at low temperatures may represent an adaptation for conserving energy for the montane group while reduced metabolism at high temperatures in the semi-arid group may serve to conserve water.

Kilgore (1972) observed that yellow-bellied marmots had a relatively low metabolic rate compared to non-hibernators and were able to divert more energy to fat production. The marmots used only 77% of the assimilated energy in biomass maintenance. Efficiency of tissue growth averaged 16.8%, about five times greater than that in typical homeotherms (Kilgore and Armitage, 1978).

There have been a number of studies dealing with the physiology of hibernating *M. flaviventris*. Goodrich and Lyman (1971) reported that the arterial blood pH was 7.6 to 7.7 during hibernation, slightly above that of a normothermic animal, while pO₂ was 100 mm Hg and pCO₂ was 40 to 80 mm Hg. HCO₃⁻ levels were considerably higher in the hibernating marmot than in a normothermic one: 60 to 85 mm/kg H₂O and 25 to 33 mm/kg H₂O, respectively. The central nervous system, mediated by the hy-



FIGURE 5. Typical yellow-bellied marmot habitat at Gothic, Gunnison Co., Colorado, 2900 m. Photo by B. A. Frase.

pothalamus, controls body temperature throughout the marmot's entire annual cycle, including hibernation (Florant et al., 1978; South et al., 1975; Florant and Heller, 1977). Hypothalamic thermosensitivity is maintained throughout hibernation although the threshold for metabolic heat production decreases (Florant and Heller, 1977).

Downhower and Pauley (1970) recorded deep body temperatures of a free-ranging yearling female and an adult female using a radio-telemetric device. Their data showed a peak in body temperature about sunset followed by a precipitous drop (about 2°C). The yearling had a consistently higher temperature than the adult. Pattie (1967), taking rectal temperatures from marmots as captured, reported a peak around noon. This noontime peak may represent slight hyperthermia induced by restraint in the heat of the day.

Renal blood flow is reduced during hibernation and active transport in the glomerulus decreases (Zatzman and South, 1972). Similar changes occur during hypothermia in marmots; active transport is even lower than it is during hibernation. Non-hibernating mammals exhibit more extreme decreases in renal blood flow during hypothermia and recover more slowly than *M. flaviventris* (Zatzman et al., 1971).

ONTOGENY AND REPRODUCTION. Gestation in marmots requires about 30 days. Litter size ranges from 3 to 8 (Howell, 1915). Downhower and Armitage (1971) reported an average litter size at emergence of 4.32 for the Gothic, Colorado, area based on six years of data. Nee (1969) reported 4.8 embryos per female, whereas Hayward (1952) found a median of seven placental scars per female, and it is likely that litter size varies both geographically and from year to year. Nee (1969) also found that adult females had a mean corpus luteum count of 4.7, whereas in subadults (1- and 2-year-olds) the mean was 4.2.

Reproductive behavior is concentrated in the first two weeks after emergence from hibernation (Armitage, 1965; Nee, 1969). No female yearling at Gothic, Colorado (2900 m) was observed to produce a litter (Downhower, 1968) and only 25% of the two-year old females were reproductive (Armitage and Downhower, 1974). In contrast, Nee (1969) found 40% of the subadult females pregnant at Sagehen Creek, California (1700 to 2200 m). The testes of adult males were enlarged for several weeks post-emergence and then regressed to become the same relative size as those of subadults and juveniles (Nee, 1969).

Newborn young measure 111.0 mm in length and weigh 33.8 g ($n = 3$) (J. W. Koeppl, pers. comm.). The young remain in the burrow for 20 to 30 days, by which time they are nearly weaned. Body weights of the young at Gothic averaged 0.59 kg for males and 0.50 kg for females during the first week post-emergence (Armitage et al., 1976). Growth of young marmots was greater at 3400 m than 2900 m (Andersen et al., 1976). Growth coefficients for all age/sex/class groups were calculated by Kilgore and Armitage (1978) and Armitage et al. (1976). Most litters in the vicinity of Gothic are weaned in the first half of July, but emergence of young has been observed from mid-June to early August (Armitage et al., 1976).

ECOLOGY. Marmots are semi-fossorial and typically inhabit vegetated talus slopes or rock outcrops in meadows (Fig. 5).

Rocks serve as support for burrows and as sunning and observation posts (Borell and Ellis, 1934). The burrows are usually located on well-drained slopes. There were no marked differences in general configuration between the five burrows (including two thought to be used as hibernacula) excavated by Svendsen (1976). The main entrance of a marmot burrow (there may be up to three) extends to a depth of about 0.6 m and the main passageway extends another 3.8 to 4.4 m horizontally into the hillside. Several short blind tunnels branch from the main passageway and from the nest chamber, the latter located at the end of the burrow beneath a large rock. Burrows serve as nurseries, refuges from predators and conspecifics, and hibernacula (Svendsen, 1974). Well-defined trails connect the burrows (Armitage, 1962). In the vicinity of Gothic, Colorado, a marmot spends approximately 80% of its life in a burrow (Svendsen, 1976). The burrow environment is relatively stable; temperature within the burrow deviated little from 10°C June through October (Kilgore, 1972). Burrow availability may partially explain marmot distribution; hibernacula are probably a restricted resource (Andersen et al., 1976).

Yellow-bellied marmots live as members of a colony or as single or paired animals (Svendsen, 1973). Colonial animals are residents of harems, typically consisting of an adult territorial male, several adult females, and their offspring (Armitage 1962, 1965, 1974, 1975; Downhower and Armitage, 1971). Peripheral habitats in which the number of burrows are limited, termed "satellite sites" by Svendsen (1974), are occupied by single marmots, a pair, or a female and sometimes her young. There is probably a continuum of sites, ranging from those harboring one animal, through one-harem colonies, to contiguous multi-harem sites (Armitage and Downhower, 1974; Johns and Armitage, 1979). In the Gothic area, 75% of the marmots were colony residents, 16% were in "satellite sites," and 7% were transients (Svendsen, 1974). All colonial males and 41% of the females were recruited from outside the colony (Armitage and Downhower, 1974). The mean size of 24 typical territories was 0.67 ha (Armitage, 1975).

Reproductive rates at "satellite sites" were lower than in colonies, and such sites exhibited greater population fluctuations and shorter terms of individual residency. Using the observed number of yearling offspring of individual males and females living as monogamous pairs or in colonies of different sizes as a measure of fitness, Downhower and Armitage (1971) predicted that a harem composed of a male and two or three females should be the most fit. Elliott (1975) argued, however, that predator defense, rather than the mating system, was more likely to be the advantage derived from the polygynous group.

Hibernation lasts about eight months in the Gothic area, from early September to May, and represents around 60% of the total time spent underground (Svendsen, 1976). Young marmots lost about 50% of their body weight during hibernation (Armitage et al., 1976), and it is thus crucial that they obtain a threshold weight by fall. The earlier the young are weaned, the more they will weigh at the time of hibernation; the earlier the spring of the natal year, the greater the number of young surviving to become yearlings. Hibernation is probably the time of greatest mortality of all age-groups of marmots (Armitage and Downhower, 1974). Females living in a high subalpine meadow (3400 m), where the growing season was short, were not observed to produce litters in consecutive years. The shortness of the post-weaning period during which weight gain is possible may preclude sufficient fat deposition to provide energy for both overwintering and subsequent reproduction (Andersen, 1975; Johns and Armitage, 1979).

At lower elevations in the northwestern United States, marmots emerge from hibernation from late February to mid-March or later, depending upon the elevation (P. L. Wright, pers. comm.). Adults begin estivation in early June, and are followed by the young about 20 days later (Couch, 1930). A small percentage of a laboratory population originating from semi-arid eastern Washington became dormant in early August (Ward, 1980). Hall (1946) reported that in the Upper Sonoran, Transition, and lower Canadian zones of Nevada, marmots began estivation in June, while in the more boreal zones, they seemed to be active throughout the summer. He suggested that estivation at lower elevations was necessary due to the dearth of green vegetation in the summer, a problem not faced by marmots at higher elevations.

Marmots are herbivorous. They are probably not food limited, ingesting only 0.8 to 3.1% of the available net primary production (Kilgore and Armitage, 1978; see, however, Armitage, 1979). The reproductive success of emerging females may indeed be food-limited, however, in areas where snow cover persists in the spring (Andersen et al., 1976).

Marmots eat a wide variety of plant species including grasses, flowers, and forbs (Armitage, 1979; Svendsen, 1973; Andersen, 1975; Couch, 1930). In late summer, large numbers of seeds are eaten (Fraser, unpubl.). Armitage (1979) demonstrated experimentally that marmots feed selectively and exhibit preferences. He noted that the plants or plant parts that were rejected contain toxic compounds, and suggested that marmot density could be limited by the chemical defenses of their food *sensu* Freeland and Winter (1975). Bailey (1936) reported finding the stomach of one specimen filled with caterpillars of the sphinx moth, *Deilephila lineata*.

Interspecific competition may be a factor in determining the distribution and population density of *Marmota flaviventris*. In the absence of large grazing ungulates, productivity of plants favored by yellow-bellied marmots may be inhibited or prevented by growth of perennial grasses; moderate grazing may therefore favor marmot populations (G. Belovsky, pers. comm.). Conversely, heavy grazing may remove up to 40% of the standing crop biomass of vegetation in a short time (Andersen et al., 1979). Such a reduction in potential food supply during the period of fat accumulation prior to the onset of torpor might have a serious adverse effect on subsequent marmot survival.

Congeners may affect the distribution of yellow-bellied marmots, as they are nowhere sympatric with woodchucks (*M. monax*). In western Montana, where *M. flaviventris* is sympatric with the larger *M. caligata*, *M. flaviventris* is restricted to suitable habitat in intermontane valleys and the lower mountain slopes, while *M. caligata* is found in the subalpine and alpine (Hoffmann and Pattie, 1968; Hoffmann, 1974). South and east of the range of *M. caligata*, *M. flaviventris* occupies all suitable alpine meadows and talus slopes, suggesting that, in the presence of *M. caligata*, *M. flaviventris* is inhibited from colonizing habitats at higher elevations.

Predation on marmots has seldom been directly observed, even in the hundreds of hours of field observation compiled by Armitage and his students. Fryxell (1926) described the method employed by a gray wolf (*Canis lupus*) to kill a marmot. Armitage (pers. comm.) saw a coyote (*Canis latrans*) capture a yearling marmot, and Bond (1939) found *M. flaviventris* remains in coyote scats. Badgers (*Taxidea taxus*) prey on marmots (Bailey, 1936; Verbeek, 1965; Andersen and Johns, 1977). Couch (1930) and Bond (1939) list bobcats, hawks, and owls as additional predators. Skeletal fragments have been found in a golden eagle nest (Armitage and Downhower, 1974), and Knight and Erickson (1978) documented that marmots were a main prey item of golden eagles. Adult marmots have been observed to chase weasels (*Mustela frenata*) and marten (*Martes americana*), which may prey on pre-emergent young (Travis and Armitage, 1973; Waring, 1965). Three incidents of cannibalism were reported by Armitage et al. (1979). Predation appears to be a minor source of mortality for colonial animals, but may be of greater significance to peripheral populations. Losses of colonial animals have been attributed to mortality during hibernation and emigration (Armitage and Downhower, 1974; Johns and Armitage, 1979).

Marmots harbor fleas, lice, mites, and ticks (Eskey, 1936; Cooley and Kohls, 1938; Olson, 1938; Allred, 1961), as well as various internal parasites (Armitage and Downhower, 1974) including the cestode, *Diandrya composita* Darrach 1930 (Rausch and Rausch, 1971). *M. f. nosophora* serves as a host for the Rocky Mountain tick (*Dermacentor andersoni*), and thus aids in the dissemination of spotted fever (Howell, 1915). *M. flaviventris* also harbors fleas of the genera *Amphalius*, *Oropsylla* and *Thrassis* (Jellison, 1945; Senger, 1966; Kinsella and Pattie, 1967) which may be important vectors of sylvatic plague (Stark, 1957).

BEHAVIOR. The activity cycle of marmots is generally bimodal, with peaks in morning and late afternoon (Armitage, 1962). The animals typically emerge from their burrows soon after sunrise. They may defecate, and spend a short time sunning and grooming. Foraging activity peaks in mid-morning, followed by sunning, sometimes more grooming, and long intervals in the burrow. A second period of feeding occurs in late afternoon. Most above-ground behavior involves sunning with the head in an alert position (Armitage, 1962; Kilgore, 1972; Travis and Armitage, 1973). Sentinel behavior, in which some animals keep watch while others feed, does not occur in yellow-bellied marmot populations (Travis and Armitage, 1973). General activity patterns show seasonal variation, perhaps coinciding with changes in temperature and day-length (Armitage, 1962, 1965; Johns and Armitage, 1979). Sunning may have a thermoregulatory function.

Communication is chiefly auditory and visual (but see scent

marking in Form). According to Waring (1966), there are three basic vocalizations: the whistle (at roughly 4 kHz); the undulating scream; and the tooth chatter. Six different variant calls of the whistle are distinguishable. These may have more than one function including an alert, alarm, or threat. Screams are responses to either fear or excitement, and the tooth chatter is a threat. Other animals such as pikas (*Ochotona princeps*) and golden-mantled ground squirrels (*Spermophilus lateralis*) may respond to marmot alarm calls (Waring, 1966).

Social interactions can be categorized as amicable or agonistic. Play, some grooming, and greeting behavior are amicable. Play occurred frequently between young, between young and adults, and between yearlings, but was observed between adults in only one year (Armitage, 1962). Nowicki and Armitage (1980) analyzed play behavior in the young and suggested that play in *M. flaviventris* may function as a mechanism of social integration. Grooming may be amicable or have overtones of a dominance-subordination interaction. Greeting behavior was described by Armitage (1962) and Waring (1966).

Agonistic behavior includes some grooming, social mounting, alert behavior, chases, and flight (Armitage, 1962, 1974). Armitage and Downhower (1970) described several instances of interment behavior: the subordinate marmot would escape into a burrow and the excited, dominant marmot would plug the entrance with dirt and/or rocks.

The rates of all social interactions were highest in June and decreased thereafter (Armitage, 1962, 1973). Interactions between burrow mates tended to be amicable in contrast to the agonistic interactions between non-burrow mates and non-harem mates (Johns and Armitage, 1979). The rates of amicable and/or agonistic behaviors are not correlated with population density (Armitage and Downhower, 1974; Armitage, 1975) but were related to the behavioral profiles (see below) of individuals and the length of time the animals had lived together. Amicable behavior increased and agonistic behavior decreased when all marmots had been residents in the colony for more than one year (Armitage, 1977). Armitage (1975) found that recruitment of female yearlings into a colony was most likely when their home ranges overlapped those of adult females by more than 50%, an indication of social tolerance.

All male offspring disperse, as do many females (Downhower, 1968; Armitage and Downhower, 1974). Marmots usually disperse as yearlings; however, Johns and Armitage (1979) reported a tendency toward delayed dispersal of both sexes in alpine colonies at 3400 m. They suggested that since females at this elevation do not have consecutive litters, the yearlings can increase their fitness by remaining in their natal colony another year without interfering with their mothers' next litter of young. Shirer and Downhower (1968) indicated that dispersing individuals, initially at least, tended to inhabit marginal areas in spruce forests. Dispersal may take individual marmots several miles from suitable habitat (Anthony, 1923).

The aggressive behavior of females with litters may be partly responsible for dispersal by both sexes (Downhower, 1968). Agonistic behavior of the territorial male may enhance the dispersal of male yearlings but it is not necessary for dispersal (Armitage, 1973). The presence of burrows in inconspicuous areas may increase the time yearlings can remain in a colony.

Dispersal of male yearlings is delayed when many male yearlings are present, when they are underweight, and when the levels of amicable behavior between yearlings, males, and adults are high. Low levels of adult aggression and high amicability also delay female yearling dispersal. Interestingly, dispersal of female yearlings is independent of the number of females in the harem (Downhower and Armitage, pers. comm.).

Territorial males direct most of their aggression toward male yearlings and adults (Armitage, 1975). Some males patrol their territories with conspicuous tail flagging (Armitage, 1973), in which the extended tail is waved in an arc above and to the rear of the body. Anal glands may be used in this context to further advertise the male's presence.

The behavioral responses of individual marmots to their mirror images were recorded and subjected to factor analysis. Behavioral "profiles" were obtained from this analysis by plotting an "avoidance" axis against a "sociability" axis; observed field behaviors of these same individuals were consistent with these profiles (Svendsen and Armitage, 1973).

Barash (1974) has hypothesized that the degree of sociality in the genus *Marmota* is related to the harshness of the environment and the progressive shortening of the growing season with increasing altitude. Increased sociality in *Marmota* species at

higher elevations would allow dispersal to be delayed until the young had more than one growing season to gain weight and reach reproductive maturity. Barash (1973) found that *M. flaviventris* living at 3850 m were smaller and more sociable than those living at 2650 m. However, Andersen et al. (1976) showed that young *M. flaviventris* living at 3400 m grew at a faster rate than young living at 2900 m, and thus fully compensate for the shorter season. Furthermore, Armitage (1977) showed wide variation in social behavior from year to year in different colonies living at the same elevation. These data indicate that Barash's (1974) hypothesis of social evolution should be re-evaluated.

GENETICS. A diploid number of 42 chromosomes has been reported from *M. f. avara* (Rausch and Rausch, 1965, 1971) and *M. f. luteola* (Hoffmann and Nadler, 1968). In the *luteola* karyotype, 22 of the autosomes are metacentric and submetacentric and 18 are acrocentric. The X chromosome is metacentric and the Y chromosome minute. The number of autosomal arms (FN) is 62. The autosomes are indistinguishable from those of *M. caligata* and *M. vancouverensis*; however, the X chromosomes in the latter two species are submetacentric.

Genetic variation among marmot colonies in Gunnison County, Colorado was assessed by Schwartz (1979). Among blood proteins, eight of 20 loci examined were polymorphic (transferrin, leucineaminopeptidase, phosphoglucose isomerase, phosphoglucosmutase, and four esterases), while among ten tissue proteins, only two were variable (α glycerophosphate dehydrogenase and phosphoglucosmutase). C. Nadler (pers. comm.) also found malate dehydrogenase from liver to be polymorphic, while serum albumin was monomorphic (Hoffmann et al., 1979). Genetic disequilibrium (nonrandom association of alleles in gametes) between three loci, and significant heterogeneity in genetic dispersion between colonies was found, both of these perhaps related to genetic drift resulting from the population substructure (Schwartz, 1979; Schwartz and Armitage, 1980). An association between transferrin genotype and aggressiveness, and a weak correlation between leucineaminopeptidase gene frequency and density were reported, although no correlation was found between any gene frequency and other environmental or behavioral characters. Intercolony variance is significant and probably is the result of relatively low gene flow between colonies, coupled with genetic drift. As a result of the dispersal of most young away from their natal colonies, however, gene flow is sufficiently high to retard the fixation of genetic variants (op. cit.).

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