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Marmots

Marmota monax and Allies

Kenneth B. Armitage

NOMENCLATURE

Scientific and Common Names. Six species of marmot occur in North America: yellow-bellied marmot (*M. flaviventris*), woodchuck (*M. monax*), hoary marmot (*M. caligata*), Olympic marmot (*M. olympus*), arctic or Alaskan marmot (*M. broweri*), and Vancouver Island marmot (*M. vancouverensis*); scientific names follow Hoffmann et al. (1993); nearly all marmots are called groundhogs, whistle pigs, or whistlers; those living in the mountains commonly are called rockchucks

Subspecies. No subspecies have been described for *M. broweri*, *M. olympus*, and *M. vancouverensis;* there are 11 recognized subspecies of *M. flaviventris* (Howell 1915; Frase and Hoffmann 1980): *M. f. avara*, *M. f. dacota*, *M. f. engelhardti*, *M. f. flaviventris*, *M. f. fortirostris*, *M. f. luteola*, *M. f. nosophora*, *M. f. notioros*, *M. f. obscura*, *M. f. parvula*, and *M. f. sierrae*. Nine subspecies of *M. monax* are recognized (Hall 1981): *M. m. bunkeri*, *M. m. canadensis*, *M. m. ignava*, *M. m. johnsoni*, *M. m. monax*, *M. m. ochracea*, *M. m. petrensis*, *M. m. preblorum*, and *M. m. rufescens*. Eight subspecies of *M. caligata* are recognized (Hall 1981): *M. c. caligata*, *M. c. cascadensis*, *M. c. nivaria*, *M. c. okanagana*, *M. c. oxytona*, *M. c. raceyi*, *M. c. sheldoni*, and *M. c. vigilis*

Other Marmots. Fourteen species of marmot are recognized worldwide (Barash 1989; Hoffmann et al. 1993); eight occur in Eurasia. Two species occur in Europe: the alpine marmot, *M. marmota*, in the Alps, Carpathians, Pyrenees, and Apennines; and the steppe marmot, *M. bobac*, in the steppe regions of Russia, Kazakhstan, and Ukraine. The other six species occur in the mountainous regions of Asia: the Himalayan marmot, *M. himalayana;* the tarbagan, *M. sibirica;* the black-capped marmot, *M. camtschatica;* Menzbier's marmot, *M. menzbieri;* the gray marmot, *M. baibacina;* and the red or long-tailed marmot, *M. caudata* (see Armitage [2000] for distribution of Eurasian species). Much of the Russian literature was summarized by Bibikow (1996). Information on marmots is available in the proceedings of three international conferences (Bassano et al. 1992; Le Berre et al. 1996; Armitage and Rumiantsev 2002) and in a comprehensive bibliography of 4034 entries complied by Ramousse (1997). Some of the recognized Eurasian subspecies may deserve specific status, such as *M. caudata caudata* and *M. c. aurea*.

PHYLOGENY

The first squirrel, *Protosciurus*, appeared in the Oligocene in North America and the first of the true ground squirrels, *Miospermophilus*, appeared in the late Oligocene (Black 1972). During the Miocene, well-developed genera of sciurids derived from *Miospermophilus* included *Marmota*, *Cynomys*, and *Spermophilus* (Hafner 1984). These modern genera are grouped in the Tribe Marmotini (Rodentia, Sciuridae). Within this tribe, the marmots form a monophyletic group (Kruckenhauser et al. 1998; Steppan et al. 1999) in subtribe Marmotina along with *Paenemarmota* from the middle or late Pliocene (Hafner 1984; Mein 1992). Cladistic analysis with allozyme data indicates that marmots were derived from *Spermophilus* (Hafner 1984). The first species, *M. vetus*, occurred in North America about 9.5 million years ago (Steppan et al. 1999). Marmots reached Eurasia at the beginning of the Quaternary via the Bering land bridge. Rapid divergence in the Pleistocene led to the present array of species.

Steppan et al. (1999) proposed that the 14 species of marmot be placed in two subgenera: (1) subgenus *Marmota*, which includes all the Eurasian species plus *M. monax* and *M. broweri*, and (2) subgenus *Petromarmota*, which includes *M. caligata*, *M. vancouverensis*, *M. flaviventris*, and *M. olympus*. This analysis, based on a complete cytochrome *b* sequence, rejects the two major hypotheses concerning the phylogenetic position of *M. broweri;* it is not related to *M. caligata* nor is it a sister species to *M. camtschatica* of eastern Siberia. However, this analysis does not explain how *M. broweri* came to host a flea, *Oropsylla silantiewi*, which otherwise occurs only on Palearctic marmots (Rausch and Rausch 1971). The presence of *O. silantiewi* on *M. broweri* supports the hypothesis that the arctic marmot reinvaded North America from Eurasia, but does not reject the hypothesis that *M. broweri* is a relict species, which was a member of a paraphyletic North American grade that was possibly sister to the Palearctic group (Steppan et al. 1999). *M. monax* probably represents a surviving member of the subgenus *Marmota*, which diverged from the *Petromarmota* in North America before crossing into and radiating in Eurasia.

DISTRIBUTION

The woodchuck, the widest ranging North American marmot, occurs at low elevations from eastern Alaska through southern Canada to southern Labrador and south across the eastern United States to northern Georgia and Alabama and west to eastern Kansas and Nebraska (Kwiecinski 1998). It is absent from the prairie regions of western Canada and the United States, but extends south from Alaska into northern Idaho (Fig. 9.1).

Yellow-bellied marmots are widely distributed in the western United States (Frase and Hoffmann 1980) and extend northward into south-central British Columbia and southern Alberta, where the species occurs at low to middle elevations in relatively warm, arid habitats. It also occurs in arid habitats in eastern Washington and Oregon and portions of northwestern Idaho and Nevada (Couch 1930). Its lower elevation limit becomes progressively higher to the south, where it reaches its range limits in the Sangre de Cristo Mountains in New Mexico, in the southern Sierra Nevada and White Mountains of California, and the Toquima and Pine Valley Mountains in the Great Basin of Nevada (Fig. 9.2). Because yellow-bellied marmots may occur only above 2000 m elevation, southern populations are likely isolated from each other, as intervening valleys act as dispersal barriers. These "island" populations may have been genetically isolated for thousands of years.

The hoary marmot occurs from central Alaska (south of the Brooks Range) and the Yukon and Northwest Territories of Canada southward to western and northeastern Washington, central Idaho, and western Montana. The Alaskan marmot occurs in the Brooks Range of northern Alaska and possibly also in the northern Yukon of Canada. Olympic marmots are restricted to the Olympic Mountains of western

FIGURE 9.1. Distribution of the woodchuck (*Marmota monax*). SOURCE: Adapted from Hall and Kelson (1959).

FIGURE 9.2. Distribution of the yellow-bellied marmot (*Marmota flaviventris*). SOURCE: Adapted from Hall and Kelson (1959).

Washington, whereas *M. vancouverensis* is endemic to Vancouver Island (Fig. 9.3).

DESCRIPTION

Marmots are the largest deep hibernator (Lyman et al. 1982). There are differences of 1.2 times in average body length and two times emergence mass between the smallest and the largest North American marmots. Typically, body mass is minimal at emergence from hibernation and maximal at the time of immergence (Table 9.1). Body length is significantly correlated with emergence mass ($p = .038$, $R^2 = .34$) and immergence mass ($p = .008$, $R^2 = .49$) (Armitage 1999). Males are

FIGURE 9.3. Distribution of the hoary marmot (*Marmota caligata*), Alaska marmot (*M. broweri*), Vancouver marmot (*M. vancouverensis*), and Olympic marmot (*M. olympus*).

larger than females (Armitage 1981). Yellow-bellied marmots from arid regions are smaller than those from more mesic montane habitats (Frase and Hoffmann 1980; Armitage et al. 1990).

The feet have five claw-bearing digits, although the thumb is rudimentary. The claws are thick and slightly curved; those in the front feet are heavier. The palms are naked with five pads, and the soles are naked with six pads. The head is short and broad; all legs are short and thick set, and the densely haired, slightly flattened tail is one-fifth to one-third the total length. The ears are short, broad, rounded, and well haired. The eyes are circular and small. *Marmota monax* has four pairs of mammae, whereas all other species have five pairs. A cheek pouch is present but is rudimentary and lacks retractor muscles. (Lee and Funderburg 1982:177–78).

Pelage and Molt. The color of marmot species varies, but shades of brown and gray, often with splotches or streaks of yellow, reddish-brown, white, or black, predominate on the dorsal surfaces (Barash 1989). Ventral areas are usually paler and are yellow in *M. flaviventris*. In some *M. vancouverensis*, white hairs form a streak on the center of the chest (Nagorsen 1987). White facial markings typically occur in *M. flaviventris* and *M. vancouverensis*. Although the rich, brown color of *M. vancouverensis* was interpreted as melanism (Hoffmann et al. 1979), the color is not black as it is in melanistic *M. flaviventris* (Fryxell 1928). In the Teton Range, Wyoming, melanistic individuals constituted 23% of the population (Armitage 1961). Melanistic *M. monax* also were reported (Anderson 1934). Fur texture ranges from coarse to soft; all North American marmots except *M. broweri* have a coarse pelage (Frase and Hoffmann 1980). Hair length, depth, density, and diameter probably also vary among species; these hair properties strongly affect heat loss (Melcher 1987) and energy use during hibernation in *M. flaviventris* (Armitage et al. 2003). A single, annual molt occurs during the summer (Bibikow 1996).

Molt patterns are highly variable and molts may only be partial. In woodchucks, new fur appears on the hind quarters and proceeds anteriorly (Hamilton 1934; Davis 1966). An animal in partial molt has bright, new fur caudally and old fur anteriorly, giving it a two-tone appearance. Partial molt or bleaching may account for the color pattern in *M. olympus*, although Barash (1973a) suggested that the Olympic marmot molted twice annually. Two annual molts seem unlikely because of the

TABLE 9.1. Standard measurements and mean body masses of North American marmots

Species	Length (mm)			Body Mass (g)	
	Total	Tail	Hind Foot	Immergence	Emergence
M. flaviventris[1]	470–700	130–220	70–90	3431	2422
M. monax[2,3]	510–700	100–180	68–88	4718	3356
M. broweri[4]	553–600	150–162	86–88	3500[a]	3414
M. caligata[3]	630–820	170–252	90–113	6187	3283
M. vancouverensis[5]	650–708	187–236	93–99	5328	3899
M. olympus[2,3]	670–785	180–252	91–112	7100	3350

SOURCES: For length, (1) Frase and Hoffmann 1980, (2) E. R. Hall 1981, (3) Howell 1915, (4) Bee and Hall 1956, and (5) Nagorsen 1987. Body mass values are modified from Armitage and Blumstein (2002).

NOTE: Species listed in order of increasing total length.

[a]This value undoubtedly is too low, but only one value, from a captive adult female, was available. Three adult males averaged 4260 g in early spring (Rausch and Bridgens 1989) and must have averaged at least 5400 g at immergence.

high energy costs of molting (Bibikow 1996). Nonreproductive marmots initiate molt in late spring or early summer, whereas reproductive females initiate molt at about the time of weaning. Marmots lose hair and increase conductance after emergence from hibernation. Reduced insulation apparently is essential for coping with the thermal load of summer (Melcher et al. 1989, 1990). After the molt, conductance and oxygen consumption decrease (Armitage and Salsbury 1993). Pelage of adult and juvenile *M. broweri* and *M. caligata* are described by Hoffmann et al. (1979).

Skull and Dentition. Descriptions and drawings are included in species accounts for *M. flaviventris* (Frase and Hoffmann 1980), *M. monax* (Kwiecinski 1998), and *M. vancouverensis* (Nagorsen 1987).

Photographs and cranial measurements of a series of North American species and subspecies are available in Howell (1915). Condylobasal length is normally 75–100 mm. Rostrum and cranium are subequal, with the interorbital region being much wider than the postorbital region (Fig. 9.4). On all marmots, the second upper premolar (p4) is as large as or larger than the first molar (m1). The cheek teeth are highly crowned and metaloph is complete on each upper molar. The dental formula is I 1/1, C 0/0, P 2/1, M 3/3. Hoffmann et al. (1979) provided comparative cranial dimensions for 24 characters for *M. camtschatica, M. broweri, M. caligata, M. olympus,* and *M. vancouverensis* and discussed cranial sexual dimorphism and geographic and interspecific variation. (Lee and Funderburg 1982:178)

GENETICS

The karyotypes of Eurasian marmots are similar, with a diploid number $2N = 38$, except for *M. camtschatica*, $2N = 40$. Karyotypes of North American marmots are diverse: *M. broweri*, $2N = 36$; *M. monax*, $2N = 38$; *M. olympus*, $2N = 40$; *M. flaviventris*, *M. caligata*, and *M. vancouverensis*, $2N = 42$. Apparently the fundamental number FN (the number of autosmal arms) is 66 in all species of marmots (Rausch and Rausch 1971).

Allozyme variation was explored in yellow-bellied marmot populations in Gunnison County, Colorado. Blood samples were collected from 88 marmots in North Pole Basin (3400 m elevation) and 203 marmots in the East River Valley. Tissue samples were obtained from 30 marmots each at elevations of 2680, 3170, and 3660 m (Schwartz and Armitage 1981). Allozyme variation occurred at 8 of 20 loci, whereas in *M. vancouverensis*, 4 of 22 loci were polymorphic (Bryant 1990). Neither gene frequencies nor heterozygosity were associated with age, altitude, habitat, litter size, sex, survivorship, and a suite of behavioral variables. There was significant heterogeneity in genetic variation among colonies (Schwartz and Armitage 1980). Heterogeneity among the social groups was promoted by the restriction of mating to those in the social group, the low rate of exchange between social groups, and the preferential recruitment of juvenile females from their natal colony.

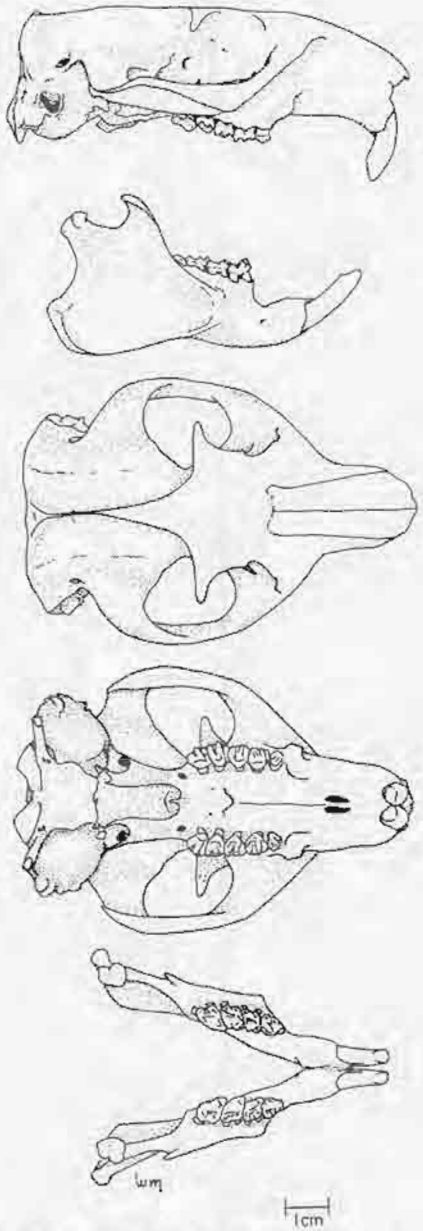

FIGURE 9.4. Skull of the woodchuck (*Marmota monax*). From top to bottom: lateral view of cranium, lateral view of mandible, dorsal view of cranium, ventral view of cranium, dorsal view of mandible.

Gene flow between colonies occurred primarily by male immigration, which prevents fixation of gene frequencies. By contrast, overall differentiation among colonies was much less in *M. vancouverensis* (Bryant 1990).

Genetic variation was examined in woodchuck populations with high and low prevalence rates of woodchuck hepatitis virus, which is endemic in areas of the mid-Atlantic states, but apparently is absent from populations in New York and much of New England. Eighteen monomorphic and six polymorphic loci were identified from blood samples from 40 woodchucks from New York and Delaware (Wright et al. 1987). Average heterozygosity of 0.066 in New York and 0.039 in Delaware was similar to the 0.073 for *M. vancouverensis* (Bryant 1990) and 0.075 for *M. flaviventris* (Schwartz and Armitage 1981). Significant heterogeneity between Delaware and New York samples was observed at two loci. It is not known whether the genetic differences were in response to the virus.

In general, studies of population variation in marmots are few. There is no explanation for the nature and pattern of subspecific variation, although Howell (1914) remarked that the subspecies of *M. flaviventris* are connected "by almost perfect series of intergrades." Physiological differences in montane and lowland yellow-bellied marmots were noted; because these differences persisted in animals maintained in the laboratory for ≥1 year, they may be genetic. The annual cycle of marmots in hot, dry areas may be shifted by several months; yellow-bellied marmots in Capitol Reef National Park in Utah emerge in March and hibernate in July (P. Hopkinson, pers. commun., 1999), whereas in eastern Washington, they emerge in late February and immerge in June (Couch 1930).

PHYSIOLOGY

The Circannual Cycle. The annual cycle consists of the heterothermal period when marmots hibernate and the homeothermal period in which mating, gestation, lactation, growth, and fattening occur. The sequence of events in the annual cycle is driven by an endogenous circannual clock (Davis 1976). Lack of activity in one phase of the cycle does not prevent activity in the next phase. For example, the cycles of testis size and testosterone concentrations are not altered in woodchucks by the absence of hibernation (Baldwin et al. 1985). Food consumption by wild woodchucks varies seasonally from low in March to a maximum in May and declines throughout the summer (Fall 1971). This annual rhythm of appetite is not altered by increasing the time in torpor or by early arousal; woodchucks adjust food intake and body mass to reassume the normal schedule (Davis 1970). Woodchucks maintained on restricted diet failed to gain mass until fed ad lib in August. Body mass did not reach the July peak of fed animals, but reached the mass of the fed animals in September (Young 1984). The circannual rhythm of mass gain and loss (Ward and Armitage 1981a), of reproductive cycles (Concannon et al. 1992), and of food and water consumption and urine production (Zatzman et al. 1984) persist under a constant photoperiod of 12 hr light:12 hr dark. Photoperiod is the likely environmental factor that entrains the rhythm. *M. monax* sent to Australia from Pennsylvania shifted the annual phase of maximum and of minimum body mass by 6 months (Davis and Finnie 1975). Reversal of daily changes in photoperiod can alter reproductive and metabolic cycles within 3–5 months in juveniles and within 6–8 months in adults and can reverse these cycles in 20–24 months (Concannon et al. 1993).

As might be expected, the annual cycle of mass gain and loss and of reproduction is associated with circannual rhythms in other physiological activities. For woodchucks, maximal values of serum blood fractions of total protein, prealbumin, and alpha and beta fractions occurred just before and into the hibernating period. Minimal values occurred just before and for a few weeks following emergence (Wenberg and Holland 1972). Most endocrine glands involute in preparation for hibernation. The 17-keto steroids have an annual cycle with low levels during hibernation; 17-hydroxy steroids have high values in spring and summer. There were no significant differences between males and females. Maximal values of urinary estrogen occurred from April to June, and epinephrine and norepinephrine were low during late summer, lowest in December and January, then increased in February and March to a peak in June (Wenberg and Holland 1973a). Epinephrine and norephinephrine concentrations did not differ between sexes nor between adults and young. In the spring, the thyroid gland of *M. monax* is extremely heterogeneous in appearance; some follicular and parafollicular cells appear quite active (Frink et al. 1977; Krupp et al. 1977). Iodine-131 uptake declines during the spring (Wenberg and Holland 1973b) and serum T_4 and T_3 and T_4-binding protein (TBG) are low (Young et al. 1986) and remain low during the summer, when the follicles are uniformly small. Plasma concentrations of T_4 and T_3 and T_4-binding protein levels peak in late winter and early postemergence (Wenberg and Holland 1973b; Young et al. 1986). Uptake levels of I^{131} are greatest during the late-winter months of hibernation and just before arousal. The increased serum T_4 and T_3 concentrations and increased T_4-binding protein in the winter may result, in part, from fasting (Young et al. 1986). High thyroid activity occurs at the same time of year as high metabolic activity, and nonhibernating, fed woodchucks have lowest metabolic rates during the normal hibernating season (Bailey 1965a). Fed woodchucks have lowest T_3 concentrations during the time of rapid mass gain (Young 1984). The thyroid gland seems to have a major role in the body mass cycle, but the significance of the pattern of thyroid activity and the thyroid-binding proteins is unclear. The circannual cycle may be driven by metabolic rate. In *M. flaviventris*, the maximum and minimum values of metabolic rate precede the maximum and minimum values of food consumption by at least 1 month and values of body mass by about 2 months (Ward and Armitage 1981a).

Hibernation. All species of marmots hibernate (Barash 1989; Bibikow 1996). Immergence occurs in autumn: *M. flaviventris* in late August to mid-September; *M. broweri*, *M. olympus*, and *M. caligata*, early to mid-September; *M. vancouverensis*, early October; and *M. monax*, early to late October. North American marmots hibernate for about 7–8 months, except for *M. monax*. Woodchucks hibernate for about 5.5 months in Canada (de Vos and Gillespie 1960; Ferron 1996), for about 5 months in upstate New York (Hamilton 1934), for about 4.0–4.5 months in Pennsylvania (Snyder et al. 1961) and Missouri (Twichell 1939), and for 3.5–4.0 months in Maryland (Grizzell 1955). Among free-ranging woodchucks with surgically implanted temperature sensitive radio transmitters, males had shorter hibernation periods (mean = 104.8 days) than females (mean = 121.8 days) (Zervanos and Salsbury 2003). When weather conditions are mild, woodchucks may be active in any month (Anthony 1962). Hibernation is an adaptation for conserving energy in response to a seasonal lack of food (Lyman et al. 1982; French 1986; Weiner 1989; Armitage et al. 2003). Thus, food-deprived woodchucks, but not fed woodchucks, become torpid (Davis 1967a). Yellow-bellied marmots in Colorado and Olympic marmots enter torpor when vegetation senesces (Wood 1973; Armitage 1996a). No food is stored; marmots rely on body fat as the source of energy during hibernation. All age classes of marmots gain mass during the homeothermal period. Mass gain may be delayed by cold and/or stormy weather in the spring; these conditions may cause mass loss after hibernation is terminated, as in *M. flaviventris* (Armitage 1996a), *M. monax* (Snyder et al. 1961), and *M. caligata* and *M. olympus* (Barash 1989). All age–sex groups gain mass linearly and it varies among years, among litters, between sexes, and at different elevations (Andersen et al. 1976; Armitage et al. 1976; Armitage 1996a; Lenihan and Van Vuren 1996). Mass gain for *M. monax* and *M. flaviventris* averages 11.5 to 13.0 g/day (Davis 1967b; Armitage et al. 1976). Mass gain in *M. flaviventris* does not occur throughout the active season and occurs for periods from about 43 days in postlactation females to about 93 days in yearling females. The period of stasis following mass gain may be as long as 5 weeks in adults. Yearling and 2-year-old females have longer growth periods than adults, probably because they increase size as well as accumulate fat (Armitage 1996a). Reproductive females fail to gain mass and may lose mass during lactation. When only the period of mass gain is considered, yellow-bellied marmots gain mass at the mean rate of 16–26 g/day. Summer drought reduces mass gain, which may result in

increased mortality during the subsequent hibernation (Hamilton 1934; Armitage 1994). Mass loss during hibernation varies among species; *M. flaviventris*, *M. monax*, and *M. vancouverensis* lose 26–30% of their immergence mass, whereas *M. caligata* and *M. olympus* lose 46–53%. Mass loss per day ranges from 3.9 g in *M. flaviventris* to 16.7 g in *M. olympus*. Mass specific loss (mg/g immergence mass per day) varies among species: 1.14 in *M. flaviventris*, 1.37 in *M. vancouverensis*, 2.14 in *M. monax*, 2.23 in *M. caligata*, and 2.35 in *M. olympus* (Armitage and Blumstein 2002). In Ontario, *M. monax* lose more mass during hibernation than woodchucks in Pennsylvania, but at about the same rate (Ferron 1996). Rates of mass loss are much greater in euthermic, food-deprived woodchucks (20.7 g/day) than in hibernating woodchucks (3.0 g/day). Most of the mass loss of hibernators occurs during arousal, 13.7–17.9 g/day (Bailey and Davis 1965). Energetic efficiency varies among species; during a torpor bout, metabolism is significantly less in *M. flaviventris* than in *M. monax* (Armitage et al. 2000). *M. flaviventris* spends significantly more time in torpor than does *M. monax*, as a consequence, energy savings for the entire hibernation period are 43.2% for *M. monax* and 83.2% for *M. flaviventris*. Both *M. monax* and *M. flaviventris* hibernate singly, although in *M. flaviventris*, littermates (Lenihan and Van Vuren 1996) and high-elevation populations (Johns and Armitage 1979) may hibernate in groups. All other North American species hibernate in groups (Blumstein and Armitage 1999) and may reduce energetic expenditures by social thermoregulation (Arnold 1993).

Energy savings are possible because of the marked decrease in metabolism during torpor. In *M. monax*, heart rate decreases from 80–95 beats/min in awake, fasting animals to 3/min in deep hibernation. Oxygen consumption decreases from 0.32 to 0.98 ml/g/hour to 0.01–0.05ml/g/hour (Lyman 1958). Body temperature decreases to 1–3° C above ambient temperature (Benedict and Lee 1938). Similar results were reported for *M. flaviventris* (Hock 1969). Frequency and duration of arousals progressively decrease in the autumn, remain low through most of dormancy, and increase toward the end of dormancy (Albert and Panuska 1981; French 1990). Male woodchucks maintained a higher body temperature and shorter torpor bouts than females; as a consequence, the cost of hibernation was greater for males (Zervanos and Salsbury 2003). Two polyunsaturated fatty acids, linoleic and linolenic, are essential for successful hibernation (Florant 1998). Yellow-bellied marmots on diets deficient in essential fatty acids have bout lengths of 6.3 days compared to 11.0 days for controls, and thus essential fatty acid-deficient marmots spend more time in the energetically costly euthermic condition (Florant et al. 1993). Furthermore, metabolic rate during entrance into torpor, during deep torpor, and during arousal is higher in essential fatty acid-deficient animals (Thorp et al. 1994).

Entrance into torpor in *M. monax* and *M. flaviventris* is initiated by a rapid decline in oxygen consumption followed by a slow decline in body temperature (Lyman 1958; Armitage et al. 2000; Woods et al. 2002). This pattern of decline suggests that metabolism is actively suppressed and heat is lost passively. Hibernation terminates spontaneously in adult marmots, but juveniles may continue to hibernate until they become emaciated from starvation or are fed (French 1990). Frequent arousals in the spring allow marmots to assess variable weather conditions (French 1986). Emergence of *M. monax* (Davis 1977) and *M. flaviventris* (Nee 1969) is correlated with periods of warm weather, and *M. broweri* emerge when the hibernation plug is thawed sufficiently to allow the animals to dig out (Rausch and Bridgens 1989). Yellow-bellied marmot emergence in Colorado has become significantly earlier from 1976 to 1999; the regressed values for first emergence have changed 23 days. Earlier emergence is significantly correlated with warmer temperatures in April (Inouye et al. 2000).

The shift from euthermic, fat-storing animals to torpid, fat-catabolizing animals is associated with numerous other physiological changes. The half-saturation pressure of oxygen for woodchuck blood decreased from an average of 23.4 to 22.3 mm Hg and 2,3-diphosphoglycerate decreased from 5.2 to 3.4 mmol/ml erythrocytes during hibernation. The oxygen equilibrium curve shifts further to the left and hemoglobin and hematocrit increase in early hibernation. Normal values are restored about 1 month after arousal (Hock 1967; Wenberg et al. 1973; Harkness et al. 1974). Carotid systolic blood pressure and cardiac temperature at cardiac arrest are lower and resistance to cooling is greater in hibernating than in nonhibernating woodchucks. Woodchucks selectively lower the temperature of certain tissues and thus retard cooling of essential tissues (Albert and Panuska 1978). During hibernation in *M. flaviventris*, the decline of mean arterial pressure and the heart rate and the almost fourfold increase in total peripheral resistance retard flow to peripheral areas and should greatly retard heat loss and conserve energy (Zatzman and Thornhill 1986). Arterial pH of *M. monax* and *M. flaviventris* is 7.52–7.75 during hibernation and 7.38–7.50 when they are euthermic. Standard bicarbonate values are twice as high in hibernators as in euthermic individuals (Goodrich 1973). The hypothalamic regulation of body temperature in *M. flaviventris* is active throughout hibernation; the threshold hypothalamic temperature probably rises gradually several hours to a day before actual arousal (Florant and Heller 1977). In euthermic woodchucks, the auditory brainstem response consists of four waves. In hibernating woodchucks, waves I and II were traced to the lowest body temperature. Activity remains in the VIII cranial nerve, and the functional integrity of the brainstem auditory pathway is restored during arousal. Woodchucks arouse quickly to auditory stimulation (Katbamna et al. 1992).

Reduction in renal blood flow during hibernation is not accompanied by a decrease in active transport; renal function is maintained at about 10% of its euthermic level (Zatzman and South 1972). Urine osmolalities of hibernating *M. flaviventris* are about half those of euthermic animals, but are hyperosmotic to plasma. Urine flow is about 0.05–0.1 ml/day. Excretion rates increased by several orders of magnitude when body temperature reached 32° C during arousal (Zatzman and South 1975). Insulin affects food intake during periods of mass gain and loss (Florant and Bauman 1985; Florant et al. 1991; Tokuyama et al. 1991), and plasma glucose appears to be regulated during hibernation (Florant and Greenwood 1986; Florant et al. 1986). Plasma levels of cortisol (Florant and Weitzman 1980) and catecholamines (Florant 1981) are related to arousal.

Marmots plug their burrows at the start of the hibernation period (Bibikow 1996); thus one can expect hypoxia to occur. A family (three adults and five young) of *M. broweri* that hibernated in artificial outdoor dens sealed their nest box and were exposed to carbon dioxide levels as high as 13.5% (CO_2 levels were usually below 4%) and oxygen levels as low as 4% (but usually above 15%). Levels of CO_2 and O_2 and temperature cycled, with peak changes occurring every 5–8 days (Williams and Rausch 1973). Temperature was high when concentration of CO_2 was high and that of O_2 was low. This pattern probably represented torpor bouts, with the peak temperature and CO_2 concentration occurring during arousal. The response of euthermic *M. monax* to induced hypoxia is similar to that during hibernation: decreased cardiac output and heart rate, increased total peripheral resistance, decreased blood flow in all tissues, and increased ventilation rate, which decreased alkalosis (Burlington et al. 1971). Hypoxic woodchucks have a large Bohr coefficient and low bicarbonate levels, they do not have an elevated buffering capacity, and they maintain a high arterial partial pressure of CO_2 associated with a low arterial pH (Boggs and Birchard 1989). Woodchucks have a reduced ventilatory responsiveness to CO_2. Because this response is ubiquitous among burrowing mammals (Boggs et al. 1984), all species of marmots likely have a similar response. The reduced ventilatory response could represent an energy-conserving tactic because increased ventilation is likely of little utility in a high-CO_2 environment (Boggs et al. 1984).

Blood characteristics of *M. monax* and *M. flaviventris* differ. Hemoglobin concentrations are higher in *M. flaviventris* than in *M. monax* (Hall 1965; Bullard et al. 1966; Armitage 1983). The hematocrit of woodchucks living at low altitudes (38.9%, Hall 1965; 39.4%, Boggs and Birchard 1989) is much lower than that of high-altitude yellow-bellied marmots (49.4%, Bullard et al. 1966; 50.8%, Armitage 1983). Yellow-bellied marmots acclimatized to low altitude have lower hematocrit values (sea level, 42.4%; high altitude, 47%; Winders et al. 1974). Hematocrn values of yellow-bellied marmots transported from

Colorado to Kansas were about 4.3% lower than the high-altitude values and did not differ significantly from values for marmots captured in Washington and maintained in the laboratory (Armitage 1983). Hematocrit levels are inversely related to body mass for 11 species of semifossorial sciurids. Hematocrit values of *M. monax* are about as predicted from body mass, but those of *M. flaviventris* are much higher than predicted. This difference, attributed to chronic exposure to hypoxia by *M. flaviventris*, persists when yellow-bellied marmots are acclimatized to sea level, which suggests that at least part of the difference is genetic (Armitage 1983). Hematocrit and hemoglobin values are lower in juvenile *M. monax* (Wenberg et al. 1973) and *M. flaviventris* (Armitage 1983), but are similar to adult values at the time of hibernation. In general, oxygen equilibrium curves of marmots are shifted to the left in comparison to nonhibernators, such as the laboratory rat (Hall 1965; Bullard et al. 1966). Electrophoresis of hemoglobin produces single and double bands in *M. caligata* (Blumberg et al. 1960) and single bands in *M. flaviventris* and *M. monax* (Harkness et al. 1974).

During hibernation, the fasting marmots are on a lipid metabolism. The major storage fatty acids are palmitic, oleic, and linoleic in yellow-bellied marmots (Florant et al. 1990) and palmitic, oleic, and linolenic in woodchucks (Davis and McCarthy 1965). Polyunsaturated essential fatty acids are metabolized more slowly than other fatty acids (Florant et al. 1990; Xia et al. 1993). Adipose mass in *M. flaviventris* may be controlled by the seasonal regulation of genes involved in lipid storage or use (Wilson et al. 1992).

Metabolism and Water Balance. Oxygen consumption of montane–mesic and lowland–xeric yellow-bellied marmots is significantly affected by ambient temperature. The shape of the metabolism–temperature curve differed from that of a typical mammal. A thermoneutral zone occurs between 15° C and 20° C. Decrease in metabolism at 25° C may represent thermal stress. Metabolism decreases at higher ambient temperatures except for montane–mesic marmots on ad lib water, for which metabolism increases at 30° C, then decreases at 34° C. Oxygen consumption increases linearly with decreasing ambient temperature below 15° C (Armitage et al. 1990). By contrast, minimal oxygen consumption of *M. monax* occurs at 28° C and increases linearly as temperatures decrease (Benedict and Lee 1938). However, the metabolism–temperature curve of posthibernation woodchucks was similar to that reported for *M. flaviventris* (Armitage et al. 2000). Lowland–xeric yellow-bellied marmot populations had a lower metabolic rate at high ambient temperatures and a higher metabolic rate at lower temperatures than montane–mesic animals. Oxygen consumption was lower on a restricted-water regimen. Body temperature was significantly affected by ambient temperature (it was high at low and high environmental temperatures), water regimen (higher on ad lib water), and habitat (higher in lowland–xeric marmots). Conductance generally was lower in the montane–mesic than in the lowland–xeric marmots. Both populations increased conductance at high ambient temperatures. Metabolic water production equaled or exceeded evaporative water loss at 5–20° C, which indicates that metabolic water could satisfy water requirements during hibernation (Armitage et al. 2000). Metabolic rates of wild-caught yellow-bellied marmots were lower for all ages and sexes than predicted from body-mass equations (Armitage and Salsbury 1992). Resting metabolic rates of adult males were higher than those of adult females in the first month following emergence and then declined throughout the summer.

Resting metabolic rates of lactating females were about 1.3 times greater than those of nonreproductive adult females at the same time of year. Mass-specific metabolic rates of young were much greater than those of adults. The decrease in resting metabolism in all age and sex groups following the annual molt reduced maintenance costs and permitted more energy to be allocated to fat production (Armitage and Salsbury 1993). Although resting metabolic rate of males decreased in early summer, field metabolic rates significantly increased through the season. High field metabolic rates coincided with the peak of intrusions by adult males into male territories (Salsbury and Armitage 1994a). Energy expenditure varied among adult males and increased with the number and dispersion of defended females (Salsbury and Armitage 1995). Daily energy expenditure, excluding production, of yellow-bellied marmots varied from 539 kJ/day for a yearling female in June to 1017 kJ/day for a lactating female in July. Foraging accounted for 11–51% of daily energy expenditure; sitting, for 1–28%; time in the burrow, for 41–60%; and thermoregulation, for 1–6% (Melcher et al. 1989). Yellow-bellied marmots conserve energy (Armitage 1998); energy conservation is reflected in the high tissue growth efficiency of 16.8%, about five times greater than that of typical homeotherms (Kilgore and Armitage 1978). Wood (1973) calculated a tissue growth efficiency of 4.3% for all age classes of *M. olympus*.

The major source of water for marmots under natural conditions is vegetation, but *M. olympus* will eat snow or drink water (Barash 1973a) and *M. monax* will occasionally drink water (Kwiecinski 1998). Water influx in *M. flaviventris* varied with age (body size), season, reproductive status, and site (Melcher et al. 1989). High mass-specific water influx occurred in lactating females. In general, mass-specific water influx was up to five times greater than the influx of laboratory-housed animals on *ad lib* water. The major source of water for laboratory populations of montane–mesic and lowland–xeric yellow-bellied marmots was drinking (about 74% of total water); metabolic water contributed 23%, and water from food, 3% (Ward and Armitage 1981b). Water output was primarily urine loss; urine concentration was higher and urine volume lower in the lowland–xeric population. When provided restricted amounts of water, both populations reduced urinary and fecal losses of water. The lowland–xeric marmots were adapted to dry conditions; they required significantly less total water and were more capable of mobilizing evaporative water when heat stressed than were montane–mesic marmots.

Endocrine Response. Christian (1962) measured the mass of adrenal glands of 872 woodchucks. Adrenal mass, considered a measure of stress, was linearly related to body length. Mean adrenal mass increased by 60% from early March (immediate posthibernation) to early July, then declined sharply. It increased again by 48% at the end of August, and finally declined by October (time of hibernation immergence) to 15% below the March level. The initial rise in spring coincided with a high level of aggressiveness, and the subsequent decline was associated with the end of the breeding season, when the level of aggressiveness was low. The August peak was associated with movement of young woodchucks, when the potential for conflict increased. Adrenal mass seemed most responsive to aggressiveness in the population; the physiological process of reproduction had no detectable influence on adrenal mass. Adrenals of females were about 8% heavier than those of males. When trapping and removal of woodchucks increased the percentage of young in the population, adrenal weight and cortical mass generally decreased. These decreases were attributed to decreased levels of social pressure (Lloyd et al. 1964).

Total corticosteroid concentrations of yellow-bellied marmots were highest in young, intermediate in yearlings, and lowest in adults. Neither sex nor reproductive status affected their concentrations. Population density was not consistently related to corticosteroid concentrations; when significantly related, only 22–34% of the variation was explained. Social behavior and social status were the major factors affecting corticosteroid concentrations (Armitage 1991a).

REPRODUCTION AND DEVELOPMENT

Marmots breed shortly after emerging from hibernation (Nee 1969). An exception is *M. broweri*, which mates in the burrow before coming aboveground when the stomach and intestine are empty and much contracted (Rausch and Rausch 1971). Young are born about 2 weeks after emergence (Rausch and Bridgens 1989). Males of *M. monax* (Kwiecinski 1998) and *M. flaviventris* (Armitage 1991b) emerge before females. Males of *M. olympus*, *M. caligata*, and *M. vancouverensis* probably emerge at the same time as the females because all group members of these species hibernate together (Blumstein and Armitage 1999). Because spermatogenesis in ground-dwelling squirrels occurs only during euthermy (Barnes 1996), euthermy probably is a requirement for

spermatogenesis in marmots. Probably all male marmots terminate heterothermy earlier than females and may spend part or all of this early euthermic period quiescent in their burrows. Early emergence aboveground in *M. monax* and *M. flaviventris* may be related to their requirement to locate females, which is unnecessary in the group hibernators.

Anatomy and Physiology. The male reproductive tract of *M. monax* was superficially described by Mossman et al. (1932). The apparently typical sciurid tract consists of a pair of coiled, relatively little branched seminal vesicles; a simple, compact, highly compound tubular prostate gland opening by a single pair of primary ducts; and a pair of very large compound tubular Cowper's glands. These glands have wide spiral ducts, which constrict as they enter the corpus spongiosum of the bulb, but then expand and unite to form the bulbar gland. This gland drains through a single glandular penile duct, which runs distalward through the corpus spongiosum ventral to the urethra to the ventral flexure of the penis, where it joins the urethra from the ventral side. The bulbar gland and penile duct are the most characteristic features of all sciurid genera except *Tamiasciurus*. In *M. monax*, the genital system is considerably smaller relative to body size than in *Spermophilus*, but the glands have the same relative size. The testes are abdominal most of the year. Three anal glands are present, but are not part of the reproductive system. Males can be distinguished from females at all ages by the distance between the anal and genital openings. The normal length of the perineum is ≥2 times longer in males than in females (Grizzell 1955); in yellow-bellied marmots, the perineum of males typically is 25–45 mm and that of females, 5–10 mm. Nipples of pregnant yellow-bellied marmots enlarge and reach maximal size during lactation (Armitage and Wynne-Edwards 2002). Nipples develop in females that initiate breeding but fail to wean a litter. Nipple size remains smaller than that of successful females, regresses sooner, and decreases to the size of nonreproductive females, whereas nipples of successful females remain large through the first 5 weeks of postlactation. Nipples of reproductive *M. monax* are swollen during lactation and diminish slowly thereafter (Snyder and Christian 1960).

Mean mass of testes in known-aged adult, wild *M. monax* is greatest at emergence from hibernation in February and declines thereafter to a low in September. Mean mass of testes in yearlings increases in the month following emergence to about one half the size of the adult testes, then declines slowly through August, when testes masses of adults and yearlings coincide (Christian et al. 1972). The size of the seminiferous tubules and spermatogenic activity is greatest at emergence and least during autumn. Decline in testes mass and maturation depletion is evident before reproductive activity in March. Mean testes mass declines less rapidly than tubule size and spermatogenic activity. In October, the size of the seminiferous tubules increases, the germinal epithelium is active, and primary spermatocytes at the pachytene stage are present. Mature spermatozoa are present in the testes of some yearlings at emergence. The testes of young have spermatogonia and primary spermatocytes appear by September. No spermatozoa are found at the time of hibernation, which implies that spermatogenesis is completed at the termination of the heterothermal period.

The estrous cycle of captive woodchucks was examined by taking daily vaginal smears for 2 consecutive months. Seven of 10 adult females exhibited readily identified estrus, in which 83% of the cells were cornified. The animals were monoestrous and remained in a prolonged estrous period, that ranged from 12 to 27 days, with a mean of 18.1 days (Sinha Hikim et al. 1991), then became anestrous. Levels of estradiol were elevated before and during estrus and declined significantly 1 week after termination of estrus. Elevated levels of estradiol preceded and coincided with the maximal degree of vaginal cornification. Females with predominantly cornified cells were always receptive to males regardless of the time interval from onset of estrus and mated within 24 hr of pairing (Sinha Hikim et al. 1992). Ovulation occurred 20–30 hr after copulation. Induction of ovulation was associated with a fourfold increase in progesterone. Although ovulation is induced, there is evidence that spontaneous ovulation also occurs (Sinha Hikim et al. 1991). Progesterone levels of wild and laboratory woodchucks are highest during midpregnancy and decrease about 25% in the last third of pregnancy. Postpartum progesterone levels are elevated above basal values in lactating and nonlactating animals for 2–3 months postpartum (Concannon et al. 1983, 1984). The corpora lutea are either maintained or rejuvenated during the postpartum period, and nonreproductive females spontaneously form multiple corpora lutea, which secrete progesterone when parturient females are lactating (Concannon et al. 1984). In wild yellow-bellied marmots, progesterone levels of nonreproductive females are low during the season of early gestation and slowly decline to basal levels at about the fourth week of the postlactation period. Progesterone levels of reproductive females and those that initiated reproduction but failed to wean a litter are high during gestation, decrease during late gestation, increase to a peak in midlactation, and then decline steadily until reaching basal levels about 4 weeks postlactation (Armitage and Wynne-Edwards 2002). Progesterone levels are correlated with nipple enlargement. High levels of progesterone occur in yearling females during the lactation season and in juveniles in the late postlactation season. The elevated progesterone levels in nonbreeding females may function to (1) prevent ovulation and/or mating at an inappropriate time of year (Concannon et al. 1990) and (2) integrate the reproductive cycle into the overall annual cycle or be involved in critical priming events that occur in the year before reproduction (Armitage and Wynne-Edwards 2002).

Age of First Reproduction. Only *M. monax* breeds as a yearling (that is, in its second summer of life). About 20% of yearling females reproduce, but the percentage increases to 42% when the proportion of adults in the population is decreased (Snyder 1962). The yellow-bellied marmot first breeds at 2 years of age, only 22.6% of 2-year-old females reproduce, and the median age of first reproduction is 3 years (Schwartz et al. 1998). No known 2-year-old female *M. vancouverensis* bred; 3-year-old females can reproduce, but the mean age of first reproduction is 4.3 years (Bryant 1996). Both *M. caligata* (Barash 1974a) and *M. olympus* (Barash 1973a) first breed at age 3 years. The age of first reproduction of *M. broweri* is unknown, but is likely 3 years. The age of first reproduction occurs in the year after the maturity index reaches 0.65. This index is calculated as the emergence mass of yearlings or 2-year-olds/emergence mass of adults (Blumstein and Armitage 1999). The maturity index indicates that all species of marmots could breed at 2 years of age; delay beyond age 2 years may represent reproductive suppression in social marmots (Armitage 1999; Blumstein and Armitage 1999).

Mating. Mating occurs early in the homeothermal period (Synder and Christian 1960; Armitage 1965; Nee 1969; Barash 1973a; Holmes 1984a; Rausch and Bridgens 1989; Bryant 1996). In yellow-bellied and Olympic marmots, a male usually approached a female by sniffing her face or rump; sniffing was often accompanied with pawing, especially near the rump. The "approach" usually was followed by a grasp in which the male seized the female with his forelegs placed anterior to her hind legs. Attempted copulation occasionally followed a grasp, and began when the male lunged quickly and seized with his jaw the skin in the middle of the female's back while simultaneously grasping her. Woodchuck behavior was similar (Hoyt and Hoyt 1950). The female's tail was pushed aside and the male extended his hindquarters up under the female and began thrusting. During attempted copulation the female crouched quietly (Armitage 1965). Copulation attempts lasted from 1 to 23 min in yellow-bellied marmots and 7 to 14 min in *M. monax* (Sinha Hikim et al. 1992). Two yearling woodchucks copulated three times for 8, 5, and 3 min, respectively (Hoyt and Hoyt 1950). Mounts never occurred in females that did not breed in that year (Barash 1973a). In *M. flaviventris* and *M. olympus*, the male sniff could be followed by agonistic behavior by the female, or she might move away and the male might follow. Often the female initiated contact with the male. Sometimes the male chased the female. Fights occurred between male and female Olympic marmots, but were not observed in yellow-bellied marmots. In both species, sexual behavior declined rapidly after the first or second week of reproductive activity.

Gestation. The gestation period of *M. monax* was reported as about 28 days (Hamilton 1934), 31 days in a yearling female (Hoyt and Hoyt 1950), and 30–32 days in a laboratory population (Sinha Hikim et al. 1992). Captive woodchucks had gestation periods of 31–32 days when artificially inseminated and 32–33 days when mated (Grizzell 1955). Gestation period was estimated at 30 days for yellow-bellied marmots (Nee 1969; Armitage and Downhower 1974). Probably the gestation period of other species of marmots is about 30–32 days.

Parturition and Lactation. Parturition occurs in the burrow. Newborn *M. flaviventris* are 111.0 mm long and weigh 33.8 g ($n = 3$) (Frase and Hoffmann 1980). Newborn *M. monax* weigh 23.7 g ($n = 22$) in Ontario (Ferron and Ouellet 1991), 26.5 g ($n = 20$) in central New York (Hamilton 1934), 32.3 g ($n = 3$) in central Pennsylvania (Snyder et al. 1961), and 27.2 g ($n = 11$) in Maryland (Grizzell 1955). Young *M. monax* are 105 mm long (Hamilton 1934). There is no sexual dimorphism in young woodchucks before weaning (Ferron and Ouellet 1991). Weaning in woodchucks occurs at 42 (Ferron and Ouellet 1991) to 44 days (Snyder and Christian 1960), in yellow-bellied marmots, at 25 (Armitage 1981) to 35 days (Nee 1969), in the hoary marmots, at 25–30 days (Holmes 1984a), and in the Olympic marmot, at about 30 days (Armitage 1981). Generally, weaning is essentially completed when young first appear aboveground, but some lactation may continue. Thus, total lactation time calculated by Nee (1969) is greater than the time of emergence. The lactation period is shorter in marmots that have a short active season compared to the woodchuck, which has a long active season.

Litter size at birth is known only for laboratory-held animals. In *M. monax*, litter size averaged 4.8 ($n = 5$) in Ontario (Ferron and Ouellet 1991), 4.5 ($n = 4$) in Illinois (Sinha Hikim et al. 1992), and 4.3 ($n = 7$) in New York (Concannon et al. 1984). Litter size in a captive colony of *M. broweri* varied from 3 to 7 and averaged 5 (Rausch and Bridgens 1989). Snyder and Christian (1960) calculated mean litter size at birth by counting embryos, fetuses, and placental scars of 382 necropsied *M. monax* and subtracting the average loss of embryos or fetuses. They estimated a mean value of 3.42 in 1957 and 3.97 in 1958. Litter size typically is determined at weaning. Mean litter sizes are as follows: *M. flaviventris*, 4.1 ($n = 265$) (Schwartz et al. 1998); *M. olympus*, 4.6 ($n = 14$) (Barash 1973a); *M. caligata*, 3.3 ($n = 6$) (Barash 1975); *M. vancouverensis*, 3.36 ($n = 36$) (Bryant 1996); *M. broweri*, about 4.0 (Rausch and Bridgens 1989); and *M. monax*, 4.6 ($n = 29$) in Maryland (Grizzell 1955) and 3.75 ($n = 18$) in Ontario (de Vos and Gillespie 1960). Litter size is smaller in yearling *M. monax*, which averaged 3.13 implantations, whereas adults averaged 4.54 (Synder and Christian 1960). Two-year-old *M. flaviventris* had a smaller mean litter size than older age classes (O. A. Schwartz et al. 1998).

Sex ratio at weaning does not differ from 1:1 in *M. monax* (Synder and Christian 1960; Ferron and Ouellet 1991), *M. vancouverensis* (Bryant 1996), and *M. flaviventris* (Schwartz et al. 1998). Sex ratio in *M. flaviventris* does not vary with density of adult females, litter size, stress, or social environments. It varies with age; young females wean significantly more females than males (Armitage 1987). Age and social structure interact; young females living with at least one additional female in the only matriline on a habitat patch produce about twice as many daughters as sons. These females recruit more daughters per litter, and more daughters per female young weaned than expected. The female-biased litters are produced by females with a high probability of successful recruitment of daughters into the local population.

Growth and Development. Postnatal preweaning physical and behavioral development were described in detail only for *M. monax* (Hamilton 1934; Ferron and Ouellet 1991). Young are born blind and naked with the ear pinnae up. Vibrissae (2.5 mm long) and short hair on the muzzle, chin, and head are present. The external auditory meatus is closed. Backward and forward linear crawling, circular crawling, righting motion, rooting, and teat seeking occur.

Physical development does not differ between the sexes. Increase in tail, body, and hind foot length are relatively constant. Instantaneous growth rates diminish continuously. Calculated from birth to weaning, growth rates were 0.072 in Pennsylvania, 0.058 in New York, and 0.056 in Ontario. Hair appears gradually from head to tail and more rapidly on the back than on the belly. Physical development precedes the appearance of social behavioral patterns, which appear in the last third of development (Table 9.2).

TABLE 9.2. Physical and behavioral development in *M. monax*

Age (days)	Development
12	Grasping by forepaws
20	Lower incisors erupt
21	Eyes partly open
25	Regular walking begins
26	Upper incisors erupt
26	Alert postures appear
26	Olfactory exploration begins
28	Body grooming activities begin
28	Whistling
31	Hearing occurs
32	Feeding on solid food
33	Emergence from the nest
33	Tooth chattering
35	Digging
37	Biting and nose-to-nose smelling
39	Jumping begins
39	Social grooming
41	Anal gland full evagination
42	Weaning occurs
42	Play-fighting

SOURCE: Data from Ferron and Ouellet (1991).

Mother–infant contact peaks when young woodchucks are about 1 week old and declines thereafter to no contact at weaning (Barash 1974b). Aggressive responses by the mother toward the young increase over the same time period. Adult woodchucks are agonistic to the young (Anthony 1962). Aggressiveness by the adult female is associated with early dispersal in this species (Barash 1989). By contrast, only amicable social interactions were observed between mother and young *M. flaviventris* (Webb 1981; Rayor and Armitage 1991), and social interactions of young *M. olympus* with adults were primarily amicable (Barash 1973a). Young of both species hibernate in their natal social groups.

ECOLOGY

The woodchuck is a forest-edge species. It occupies meadow hedgerows and lives in old field associations, pastures, or cultivated crops interspersed with small woodlots. Burrows may be in fields or woodland in well-drained soil (Hamilton 1934; de Vos and Gillespie 1960; Ferron and Ouellet 1989). Sixty-three percent of 132 burrows occurred on slopes of 30 deg or greater and most were in rocky soil (Twichell 1939). The yellow-bellied marmot occupies grass–forb meadows with a mean slope of 33 deg and with rock outcrops or talus. This species avoids meadows where rocks are too tightly packed for digging or where large subsurface rock volume occurs. Grassy meadows and flats are inhabited in lowland inland valleys (Couch 1930; Svendsen 1974; Carey 1985a). Hoary marmots may occupy rock ledges and talus slopes with adjacent subalpine meadows (Barash 1974a) or relatively flat meadows with short mesophytic grassland vegetation above timberline (Holmes 1984a). The Olympic marmot lives in subalpine to alpine meadows and talus slopes just above and below timberline at 1500–1750 m elevation. Most colonies are oriented between southeast and southwest (Barash 1973a). About 81% of Vancouver Island marmots live at elevations between 1000 and 1400 m in clearcuts or grass–forb alpine meadows. Most (74%) are on south- to west-facing slopes; natural habitat patches are small, scattered, and typically in avalanche bowls (Bryant and Janz 1996). The Alaskan marmot occupies precipitous sides of canyons and valleys and lives at the base of active talus with extensive meadows

(Bee and Hall 1956). Hibernacula are on exposed ridges that become snow-free relatively early in the spring (Rausch and Rausch 1971). In general, habitats of mountain-dwelling marmots have the following characteristics: (1) meadow or grassland for foraging, (2) steep to moderate slope with good drainage, (3) a southern to eastern exposure where snow melts early, (4) a soil structure that both permits burrowing and supports burrows, and (5) elevation above or near timberline or lower elevation forest openings (Armitage 2000).

Activity Cycles and Time Budgets. Marmots are typically diurnal, but some activity may occur at night (Hamilton 1934; Grizzell 1955; Hayes 1976). For *M. olympus*, early season activity is unimodal, with some tendency for a late afternoon peak (Barash 1973a). Early and late in the active season, activity cycles of *M. monax* and *M. flaviventris* are unimodal, with peaks occurring in early or late afternoon. During most of the season, the activity of all three species peaks in the morning and late afternoon and declines at midday (Anthony 1962; Armitage 1962, 1965; Pattie 1967; Hayes 1976). The afternoon peak may be much higher in *M. monax* (Bronson 1962) and some populations of *M. flaviventris*, but the peak is higher in the morning in other populations (Armitage et al. 1996). The reduced midday activity during the summer is a consequence of high ambient temperatures and heat stress (Webb 1980). Melcher et al. (1990) analyzed the thermal environments of microhabitats of yellow-bellied marmots in the Elk Mountains of Colorado using the standard operative temperature (T_{es}) method. Higher wind speeds over rocks produced T_{es} up to 10°C less than in meadows. Marmots responded to high, stressful T_{es} by reducing aboveground activity, reducing the length of foraging bouts, sitting on rocks, and tolerating transient increases in body temperature. When body temperature reached about 40°C, marmots ceased foraging. Because young were more affected by convection than adults, they could be more active at midday, but were less active early and late, when T_{es} was low. In general, marmots avoided foraging during stressful T_{es}, but sometimes did so when necessary to meet energy demands.

An extensive time budget is available only for yearling and adult *M. flaviventris* (Armitage et al. 1996), based on 17 behaviors for three colonies in the Upper East River Valley of Colorado. Marmots allocated 40–60% (110–265 min daily) of their aboveground activity to sitting/lying and 12–23% (37– 94 min daily) to foraging. Vigilance/alert varied from 1.1% to 14.5% (12.0–71.7 min) daily. Social status affected the time budget, and time allocated to vigilance/alert increased in subordinate yearlings. Locomotion, social behavior, play, grooming, chirping, digging, investigation, and gathering grass each used <5% of the time. The adult-male cohort spent significantly more time aboveground and reproductive females spent significantly more time foraging. Aboveground activity was lowest during gestation, increased during lactation, remained high during early postlactation, and declined during late summer. On average, 28.5% of each day was spent aboveground during the 4-month active period. Since marmots hibernate underground for 8 months, only about 9.5% of the year is spent aboveground. Significant relationships common to the three colonies suggest species characteristics or common environmental influences. More time is allocated to foraging in the afternoon, and more time to foraging/alert, alert, and locomotion during gestation and lactation than during postlactation. Feeding is minimal early after emergence (Snyder and Christian 1960; Rausch and Bridgens 1989), peaks during gestation, and then decreases progressively through postlactation and before immergence (Anthony 1962; Fall 1971; Barash 1976, 1989; Arsenault and Romig 1985; Concannon et al. 1990; Armitage et al. 1996). Because marmots allocate so much time to sitting/lying and being below ground in the burrow, energy budgets may be constrained by time required to process food and not by foraging time. Time spent vigilant/alert did not seem to constrain energy intake; marmots often were alert while chewing. Social behavior was not limited by time. Reproductive hoary marmot females spend more time foraging, forage more on bad-weather days, and feed significantly farther from the nearest burrow during gestation and lactation periods than do nonreproductive females during the same time periods (Barash 1980).

Home Range and Movements. Mean home range of adult female *M. flaviventris* varied from 0.13 to 1.02 ha (Armitage 1975). Within a locality, mean home range area varied at least 300% among years. Mean home range size was not related to the mean number of adult females, but the percentage overlap of home ranges was significantly and positively correlated with the number of adult females. The degree of home range overlap ($\bar{X} = 42.3\%$) was highest among females whose degree of kinship was 0.5; at all r values below 0.5, the degree of overlap was less than that predicted from the assumption that overlap is directly related to the degree of kinship (Armitage 1996b). For colonial male yellow-bellied marmots, home range size varied from 0.2 to 1.98 ha (Armitage 1974). Range was smaller when two or more males occupied a habitat patch and was larger when one male was present. There was virtually no overlap in adjacent home ranges. When noncolonial males are included, home range size varied from 0.06 to 47.5 ha (Salsbury and Armitage 1994b). Home range size of males was not significantly correlated with the number of adult females (range = 0–7), but was significantly correlated with the maximum distance between females within a male's home range. Female home ranges expand subsequent to mating to include newly available foraging areas or to avoid agonistic behavior with other females (Armitage 1965; Andersen et al. 1976).

Home ranges of adult female *M. monax* did not overlap in early spring, but overlapped minimally (<10%) in late spring and summer (Meier 1992). Home ranges of resident males did not overlap those of other males, but did overlap those of one to three adult females. Mean size of female home ranges was 0.25 ha and for resident males was 1.6 ha. In Connecticut, overlap of home ranges was 36% for reproductive females and males, 13.5% for reproductive females, and 31% among males (Swihart 1992). Home range area changed seasonally in Ontario. Before dispersal, mean home range, based on burrows occupied ≥2 times, was 11.6 ha for males, 0.1 ha for females with young, and 2.7 ha for females without young. Following natal dispersal, home ranges of males and females without young decreased to 1.9 and 0.6 ha, respectively. Mean home range of females with young increased to 0.7 ha (Ferron and Ouellet 1989). Home ranges of males (2.8 ha) were larger than those of females (0.83 ha) in Iowa (Trump 1950) and 1.8 times larger in Connecticut (Swihart 1992).

Although home ranges of male *M. flaviventris* and *M. monax* are larger than those of females, there is no difference between sexes in home range for species living in restricted family groups (Armitage 2000). For *M. caligata* (Holmes 1984a), *M. olympus* (Barash 1973a), and *M. vancouverensis* (Nagorsen 1987), home range is a family home range. The adults defend the family range (= territory); there is a tendency in *M. caligata* for resident females to respond to female intrusions and the resident male to respond to male intrusions (Holmes 1984a). Intruder males are repulsed by the resident male in *M. olympus* (Barash 1973a).

Size of home range is affected by food resources. For *M. monax*, adult feeding area was 0.92 ha in woodland, 0.09 ha in a clover field, and 0.3 ha in clover-brush (Anthony 1962). Mean movement of *M. monax* on marginal habitat was 337 m and was 246 m on good habitat (de Vos and Gillespie 1960). There apparently is an inverse relationship between home range area and vegetation biomass. For example, in habitat with a vegetation biomass of 383 g/m^2, *M. flaviventris* had a home range of ≤1.0 ha, whereas with a vegetation biomass of 117 g/m^2, *M. caligata* had a home range of 13.8 ha (Armitage 2000).

Woodchucks frequently move between burrows. Adults used an average of eight burrow systems in a Connecticut population. Mean duration at a burrow was 4.5 days for males and 5.8 days for females. Simultaneous use of a burrow usually involved an adult male and a reproductive female (Swihart 1992). In Ontario, before natal dispersal, the mean number of burrows used by adult males (20.5) was significantly greater than the 5.0 used by reproductive females (Ferron and Ouellet 1989). During natal dispersal, the mean number of burrows used did not differ significantly between males (8.7) and females (11). The mean number of burrows used daily ranged from 1.7–2.8. Distances traveled between burrows by males averaged 319 m before natal dispersal and 145 m during natal dispersal; for females, mean distances

were 45 m before natal dispersal and 118 m during natal dispersal. The increased movement by females during natal dispersal may be related to breaking the maternal bond, as distance is greater during the first 10 days of dispersal (Ferron and Ouellet 1989). Comparable movements are not recorded for other North American marmots. Female yellow-bellied marmots may move young to different burrows within their home range, but such movements are typically less than 30 m (K. B. Armitage unpublished data). Male yellow-bellied marmots (Salsbury and Armitage 1994b) and male hoary marmots (Barash 1981) may make short excursions (<1000 m) from their home ranges. Male excursions by yellow-bellied marmots occurred after the breeding season. Males did not seek extra copulations, but may have tried to locate nearby undefended females for an expanded harem. Excursions by hoary marmots occurred primarily during the mating season and presumably served to obtain extra copulations. Intruders were repulsed by residents, but successfully copulated when the colony male was removed (Barash 1981). Yellow-bellied marmots also made long excursions (>1000 m); the longest was about 4270 m. They occurred in mid- to late summer. Half the time, these males returned to their home range either before hibernation or at the start of the next active season; fates of those that did not return are unknown. The tendency to make long excursions was not related to the number of females in the male's home range. Since these males deserted established territories with reproductive females, the movements are an enigma.

Merriam (1963) used radiotelemetry to follow woodchuck movements. Most animals were juveniles, which almost always moved along permanent trails that interconnected most of the burrow systems. Some juveniles remained in a clump of burrows, whereas others wandered more widely. Dispersing young may occupy empty burrows (de Vos and Gillespie 1960; Anthony 1962). Repeated movements from the den to foraging areas or to other burrows result in the formation of trails (woodchucks, Hamilton 1934; Anthony 1962; yellow-bellied marmots, Armitage 1962; Olympic marmots, Barash 1989).

Marmots may move long distances from their hibernation sites to their summer dens. As the snow melted, a colony of *M. caligata* moved a distance of 500 m and an elevation of 200 m (Barash 1974a). When an outcropping of rock along a ridge became available because of the removal of the intervening forest, *M. flaviventris* adopted a pattern of long-distance movement (0.73–2.61 km) between the ridge and their summer food source (Thompson 1979b). *M. monax* regularly moved between summer and winter dens (Grizzell 1955). Marmots may disperse from their home ranges in time of drought (Armitage 2000).

Home range use is strongly influenced by foraging behavior and risk. *M. flaviventris* avoided areas where dense growth of avens (*Geum rossi*), a nonfood plant, was located (Andersen et al. 1976). Patch use by *M. flaviventris* in California was positively related to high food biomass and negatively related to soil moisture and vegetation height and volume (Carey 1985a) and associated with concentrations of clover (Stallman and Holmes 2002). Hoary marmots living on a talus slope associated with a meadow of herbs, grasses, and sedges overselected snow-free old-growth areas for foraging (Tyser and Moermond 1983). When foraging areas were fertilized, patch use by *M. caligata* increased by 62.5% (Holmes 1984b). When frequency of plants was chosen as the forage factor and number of burrows per patch and distance to talus served as risk factors, risk factor was more important (Holmes 1984b). Patch use by *M. flaviventris* shifted throughout the summer in response to plant phenology (Frase and Armitage 1984). In addition, use of space is influenced by kinship (only closely related animals share space) and individual behavioral characteristics. For example, subordinate individuals may be forced to a different burrow system or to a different foraging area (Frase and Armitage 1984).

Burrows. Burrows are a critical resource for marmots. Yellow-bellied marmots on large habitat patches (= colonies) use an average of 14 burrows, whereas those on small habitat patches (= satellites) use an average of 2.3 burrows (Svendsen 1974). The mean resident marmot population (3.16 at colonies, 1.39 at satellites) closely matches the number of resident burrows (3.0 at colonies, 1.14 at satellites). Burrows typically are located in rock outcrops, under boulders, in talus, and under tree or shrub roots. On a talus slope, nearly every suitable rock is used. For example, one colony had 78 burrows in various stages of use in an area of about 0.85 ha (Svendsen 1974), although only 6–8 burrows were used in each year (K. B. Armitage unpublished data). Burrows may be shared. Adult burrowmates consist of mother:daughter:sister kin groups. Burrows are of three types: home burrow or den, where a marmot spends the night, rears young, and retreats to when danger threatens; auxiliary, flight, or escape burrow, which serves as a refuge when the marmot cannot safely return to its home burrow (Armitage 1962); and hibernaculum, the burrow in which the marmot hibernates. The hibernaculum may be used as the home burrow or may be separate and located a considerable distance from the summer burrows (Thompson 1979b). The hibernaculum is shared by the entire social group in *M. olympus* (Barash 1973a), *M. caligata* (Holmes 1984a), *M. broweri* (Rausch and Bridgens 1989), *M. vancouverensis* (Bryant 1990; Bryant and Blood 1999) and populations of *M. flaviventris* at high elevation (Andersen et al. 1976; Johns and Armitage 1979). *M. monax* (Hamilton 1934; Ferron 1996) and *M. flaviventris* hibernate singly, although littermate young yellow-bellied marmots (Lenihan and Van Vuren 1996) and closely related members of a matriline (K. B. Armitage unpublished data) may hibernate together. Only certain burrows are suitable as hibernacula for *M. monax*. In Maryland, hibernacula are in woody or brushy habitats on well-drained sites on a southern exposure and, when possible, under the roots of a tree or stump (Grizzell 1955). In Ohio, hibernacula are usually located in areas of rock outcrops. Some young do not disperse in their first summer and probably share their mother's hibernaculum (Meier 1992). Some burrows are used repeatedly as hibernacula (de Vos and Gillespie 1960; Meier 1992).

Woodchuck burrows are located along woodland edges and brushy fence rows two to three times more often than expected based on availability (Swihart 1992). The spatial distribution of 112 woodchuck burrows was clustered. Part of the clustering resulted from a preference for steep slopes and well-drained soils; a greater area of imperfectly drained soils was available (Merriam 1971). Six hundred interburrow movements were recorded. Movements between burrows in a cluster are more frequent than movement between clusters. High levels of movement occur at midday and continue later in the evening than all other activity (Merriam 1966).

Burrow structure was described by Hamilton (1934), Grizzell (1955), Svendsen (1976), and Barash (1989). Burrows of *M. flaviventris*, *M. monax*, and *M. olympus* typically have dirt mounds formed by the excavated soil. Home burrows or dens usually have multiple entrances, up to 11 in *M. monax* (Merriam 1971). Only *M. olympus* and *M. monax* excavate burrows in meadows. However, *M. flaviventris* digs flight burrows in meadows when foraging areas are expanded (Armitage 1962). Digging is done with the forelegs; the dirt is thrown between the hind legs. Small rocks are carried to the surface in the mouth and dropped on the dirt mound. When dirt and rocks pile up at the entrance, the marmot lies at the edge of the pile and pushes the dirt away with its chest and forelegs (Armitage 1962). All species build a nest of grass and other vegetation and may also have latrine chambers (Grizzell 1955; Barash 1989). Yellow-bellied marmots gather nest material by tearing dry grass loose with the mouth and position it in their mouth with their forelegs. Gathering grass occurs frequently near the time of hibernation (Armitage 1962) and by reproductive females primarily during lactation (Armitage et al. 1996).

Yellow-bellied marmots rarely dig new burrows. In 40 years of marmot research, I observed that the same burrows are used year after year. As a result, burrows are renovated; soil, rocks, grass, and even marmot skulls are cast out on the surface. Merriam (1971), in a study of 99 burrow systems of woodchucks, reported only four new systems were dug in 4 years. New burrow systems may be dug primarily by juveniles or yearlings (de Vos and Gillespie 1960). Burrow design varies considerably. Flight burrows are short and shallow (Andersen and Johns 1977), whereas nest or home burrows are complex. There may be multiple nest chambers and blind pockets. The hibernation chamber may be so concealed that it and the hibernator may be missed by excavators

(Grizzell 1955). Woodchucks typically prepare wide entrance holes that narrow abruptly shortly below the surface. A second type of entrance, the plunge hole, descends vertically or near vertically and may terminate in less than 1 m in a turn-around chamber or connect to the shaft. The plunge hole is considerably smaller than the main entrance (Grizzell 1955). The main shaft may descend steeply or slope gently, and length varies, but is about 4 m for *M. flaviventris* (Svendsen 1976) and up to 15 m for woodchucks (Grizzell 1955). The main shaft may have multiple branches. Burrows of both species are shallow, usually about 1 m in *M. flaviventris* and 1–2 m in *M. monax*. The shaft usually is deeper than the nest chamber, which may function to drain water away from the nesting marmot. Temperature change is slow; in yellow-bellied marmot burrows, temperature increased from an average of 9.0°C in June to 11.3°C in late August, then declined to 9.1°C in early October (Kilgore and Armitage 1978). Probably all marmot species plug the hibernaculum chamber with a mixture of soil and feces (Bibikow 1996).

A population of yellow-bellied marmots used 11 standing and 1 fallen, horizontal cottonwood trees (*Populus* sp.) as burrow sites in Montana. Most of the marmots's vertical movements were made inside the trees. Most had entrances near the ground, and piles of dead grass and feces were found in several hollows (Garrott and Jenni 1978).

FEEDING HABITS

Marmots are herbivores but may eat some animal matter. June bugs (*Phyllophaga* sp.) occurred in the scat of *M. monax* (Gianini 1925); a *M. flaviventris* preyed on a pika, *Ochotona princeps* (Petterson 1992); and twice *M. olympus* was observed carrying a dead chipmunk, *Eutamias townsendi* (Barash 1973a). Marmots eat a variety of plants and are generalist herbivores (Frase and Armitage 1989; Swihart and Picone 1991a). *M. monax* ate 37 species of plants, of which 3 were grasses (Hamilton 1934). Woodchucks in Maryland consumed 24 different items; red clover (*Trifolium pratense*), white clover (*Trifolium repens*), grass, chickweed (*Stellaria media*), and alfalfa (*Medicago sativa*) were eaten most often and in large amounts (Grizzell 1955). Vancouver Island marmots ate 26 (grasses grouped as one species) of 88 available species. Four species accounted for 87.2% of the grazing: *Phlox diffusa* (42.2%), grasses (30.3%), carices (10.6%), and *Lupinus latifolius* (4.1%). Diet selection was not based on abundance (Milko 1984). The diet was similar among colonies; *Lupinus* spp. and *Eriophyllum lanatum* were major foods later in the summer (Martell and Milko 1986). For *M. caligata*, 28 species were identified, but vetches (*Oxytropis, Astragulus*), sedges, fleabanes (*Erigeron*), and fescues (*Festuca*) formed more than 80% of the diet (Hansen 1975). These hoary marmots also did not forage in proportion to relative abundance. Olympic marmots preferred new plant growth and the upper 6–10 cm of plants when feeding and selected inflorescences of most species when available (Wood 1973). Although grasses are important in marmot diets, forbs may be essential for a normal diet. Forbs were preferred over graminoids, especially in mid- and early summer, by *M. flaviventris* in California (Carey 1985b; Stallman and Holmes 2002) and in Colorado (Frase and Armitage 1989) and by *M. vancouverensis* in late summer (Martell and Milko 1986).

Woodchucks in Pennsylvania consumed 46 species of plants and selected dicots, especially clover, much more frequently than monocots (Arsenault and Romig 1985). Selectivity experiments support a preference for forbs. Woodchucks in Missouri selected wild lettuce (*Lactuca*), white clover, red clover, and grasses in that order (Twichell 1939); dandelion (*Taraxacum officinale*) and common plantain (*Plantago major*) were most commonly selected in cafeteria-style feeding trials (Swihart 1990). Woodchucks climb trees (Gianini 1925) and feed on leaves (Weeks and Kirpatrick 1978) of hackberry (*Celtis occidentalis*), red mulberry (*Morus rubra*), Norway maple (*Acer platanoides*), and peach (*Prunus persica*) (Swihart and Picone 1991a). I observed *M. caligata* feeding on leaves of cottonwood (*Populus trichocarpa*). Woodchucks housed in outdoor pens were presented five common components of orchard ground cover and leaves of four tree species. The percentage of foliage eaten by woodchucks varied from 100% for dandelion to 1.2% for orchard grass (*Dactylis glomerata*). Multiple comparisons indicated that dandelions, red clover, and red mulberry were most palatable; Norway maple and orchard grass were least palatable; and common strawberry (*Fragaria virginiana*), hackberry, bird-vetch (*Vicia cracca*), and peach were moderately palatable (Swihart and Picone 1991a).

Food choice is based on additional considerations. In food choice experiments, yellow-bellied marmots reject plants or parts of plants containing defensive compounds (Armitage 1979a). Food plants may be chosen to fill mineral needs. Yellow-bellied marmots were observed licking the mud surface at salt licks (Armitage 2000). Woodchucks use small mineral licks and lick road surfaces for residues of salt applied during winter. When they were provided with salt-impregnated wooden pegs, pegs containing sodium compounds were more highly gnawed than pegs with calcium, potassium, or magnesium. Water-soaked pegs were not gnawed (Weeks and Kirkpatrick 1978). A woodchuck feeding on aquatic plants may have been seeking salt (Fraser 1979). Two principal forbs eaten by *M. flaviventris* had a calcium content two to three times greater than any other plant species. Forbs are significantly higher in phosphorus, calcium, and sodium, and significantly lower in cellulose, than graminoids (Carey 1985b). Food choice may be based on protein content (Frase and Armitage 1989) or essential fatty acid content (Florant 1998; Frank et al. 1998). High concentrations of essential fatty acids occur in the leaves of dandelion, cinquefoil (*Potentilla gracilis*), cow parsnip (*Heracleum lanatum*), and grasses (Hill and Florant 1999), all of which are common elements in the diet of yellow-bellied marmots (Frase and Armitage 1989).

Marmots have a quantitative and qualitative impact on vegetation. Yellow-bellied marmots used only 2–6.4% of the available net primary production (Kilgore and Armitage 1978); however, a colony of *M. olympus* used 30.4% of the net production. Seasonal standing crop of vegetation was greater in enclosed versus open plots (Wood 1973). In an old field inhabited by *M. monax*, total plant cover increased with distance from burrows. Species richness was low near and distant from burrows and relatively high at intermediate distances (English and Bowers 1994). Horse nettle (*Solanum carolinense*), Kentucky bluegrass (*Poa pratensis*), and fescue (*Festuca elatior*) increased and orchard grass decreased with distance from burrows. The strongest effects were limited to a 4-m radius around the burrows. Woodchucks function as important agents in creating a vegetational mosaic. Species close to burrows tend to be early-successional, mostly unpalatable, and early-colonizing annual and biennial species (English and Bowers 1994). Around *M. flaviventris* burrows, unpalatable fireweed (*Epilobium angustifolium*), Rocky Mountain pentstemon (*Pentstemon stricta*), nettle (*Urtica dioica*), and composites are conspicuous (Armitage 2000). In hayfields, forb biomass increased and grass biomass decreased as a function of distance from *M. monax* burrows. In a grass hayfield, orchard grass increased about 2.6% because of woodchuck feeding (Swihart 1991a). In a hayfield with alfalfa, the biomass of alfalfa decreased by an average of 2.5% and orchard grass increased 7.4% because of woodchuck activity. In feeding trials, alfalfa was selected on average 10 times more often than orchard grass. Orchard grass was more lush around burrows and contained significantly greater levels of crude protein than orchard grass 15 m distant (Swihart 1991a). Alfalfa stem totals were about three times greater 6 m or more from a woodchuck burrow than they were within 1.5 m of a burrow. Because woodchucks prefer legumes, differences in alfalfa versus grass stems can be attributed to selective foraging (Merriam and Merriam 1965). A lush green zone occurred next to the burrow; soil nitrogen was 1.7 times more concentrated near the burrows than in the field. Feces, and probably urine, deposited in the burrow area are the likely source of nitrogen, producing lush growth.

In meadows used by *M. olympus*, primarily unpalatable plant species occur on burrow mounds. Overall species richness was greater

in the meadow than on mounds (Del Moral 1984). Marmots fed selectively, enhanced plot diversity, and reduced the dominance of common species.

DEMOGRAPHY AND MORTALITY

Population densities of yellow-bellied marmots are relatively stable (Armitage 1991b). Annual fluctuations occur primarily through reproduction and dispersal of yearlings. Populations increase when yearling daughters are recruited and decrease because of mortality during hibernation and predation (Armitage 1996c). Life-table statistics for a cohort of yellow-bellied marmots based on 1532 known-age individuals revealed that females had significantly better survivorship than males beyond the first-year age class. Thus, adult sex ratio became progressively female biased (Schwartz et al. 1998). Rates of survivorship were constant and the probability of mortality did not increase with age. Female generation length was 4.49 years. Reproductive values were approximately equal across reproductive age classes and the net reproductive rate was 0.85. There was significant yearly variation in births and deaths such that time-specific and cohort life tables were nonequivalent (Schwartz and Armitage 1998). Litter sizes were not equal among years, but were equal among age classes. Virtually all adult males were immigrants. The percentage of adult females that were immigrants varied from 16.7% at age 2 years to 40.6% at age 7 years (Schwartz et al. 1998). Immigrants varied from 22.3% to 96.9% among populations (Armitage 1988). Yellow-bellied marmot social systems are closed. Immigration occurs primarily when space is vacant because of overwinter mortality and no recruits are present. In only 5 of 141 colony-years did immigration and recruitment occur in the same colony. No introduction of adult female marmots into an occupied habitat patch was successful (Armitage 1991b).

Male survivorship appears to be lower than that of females for *M. olympus* (Barash 1973a) and *M. vancouverensis* (Bryant 1998). Survivorship is significantly greater at all ages beyond age 1 year for the Olympic and Vancouver Island marmots compared to yellow-bellied marmots (Armitage 1998; Blumstein et al. 2002). The difference probably results from dispersal at an earlier age in yellow-bellied marmots and the higher mortality of dispersers than of residents (Van Vuren and Armitage 1994). There may be a tradeoff between survival and reproduction, as yellow-bellied marmots reproduce at an earlier age than the other two species.

A woodchuck population on 4000 ha declined 80% between 1955, when the area was primarily grain and hay agriculture, and 1970, when the area became primarily old field. A low birth rate of 1.3 in (young per female in the population) 1955 was attributed to the small (20%) proportion of yearlings breeding. Birth rate increased to 1.7 by 1958, when 53% of the yearling females reproduced (Snyder and Christian 1960; Davis and Ludwig 1981). Rapid decline occurred from 1963 to 1966, when the survival of young declined. Drought occurred during this period, the vegetation dried prematurely, and young failed to gain the critical mass needed to survive hibernation. The population stabilized after 1967 (Davis and Ludwig 1981). Woodchucks were removed from two areas with mainly old-field vegetation to determine the effects of exploitation (Davis et al. 1964). The percentages of young and yearlings in the population increased greatly. High immigration of primarily young into one area, and the tendency of young animals born there to remain, resulted in an increase in the population despite removal of 1040 animals. Natality initially increased on this area, but then decreased because the proportion of adults declined and yearlings have a lower birth rate (Davis et al. 1964).

Weather affects survival and reproduction. For *M. flaviventris*, colony size, survival, and litter size were most affected by the length of winter, length of the growing season, and precipitation (Schwartz and Armitage 2002). Colony size was the larger, the earlier snowmelt occurred and the longer the growing season lasted. Extensive reproduction occurred in the year after a rainy year. Drought decreased survivorship of reproductive females and young in the following hibernation, and reproduction decreased the following summer (Armitage 1994). The effect of drought operates through reduced growth during the active season (Hamilton 1934; Davis and Ludwig 1981; Armitage 1994; Lenihan and Van Vuren 1996). The later snowmelt occurs, the fewer litters per female and fewer young per litter are produced (Van Vuren and Armitage 1991).

Dispersal. Typical age of dispersal is as follows: *M. monax*, young; *M. flaviventris*, yearling, *M. caligata* and *M. olympus*, age 2 years (Armitage 1999; Blumstein and Armitage 1999). Although dispersal reduces the density of the disperser's natal population, little is known about the fate of dispersers or the causes of dispersal. In yellow-bellied marmots, essentially all juvenile males and about one half of the females disperse (Armitage 1991b). Dispersal of yearling males was delayed when they were underweight, when the rates of amicable behavior between them and adults was high, and when there were many yearling males in the colony. Dispersal of yearling females was independent of the number of adult females present. It was delayed when rates of adult aggression were low and when adults behaved amicably toward them (Downhower and Armitage 1981). Dispersal probably is not genetically determined; when adults were removed from two populations, yearling females did not disperse (Brody and Armitage 1985). Dispersal is socially mediated by adults interacting with same-sex yearlings (Downhower and Armitage 1981). Dispersal distance is highly skewed; median dispersal distance for females was 400 m and for males was 1500 m (Van Vuren 1990). Marmots display three dispersal patterns: (1) 40% abandon their home range in a single, abrupt move to a new locality; (2) 33% gradually extend their home ranges until a new one is established; and (3) 27% disperse in two stages by first establishing new home ranges nearby and then, on average 41 days later, moving again. Females use the second pattern more than males and males move more often by the third pattern. Survival of dispersers was 0.73, not much less than that (0.87) of philopatric marmots; there was essentially no difference in survivorship (0.87 vs. 0.91) in the subsequent hibernation (Van Vuren and Armitage 1994).

Predation. The major predators of marmots are canids, mustelids, bears, and raptors. Predation rarely is observed, but coyotes (*Canis latrans*) and badgers (*Taxidea taxus*) were observed preying on yellow-bellied marmots (Verbeek 1965; Andersen and Johns 1977; Thompson 1979b; Armitage 1982). A coyote and a cougar (*Puma concolor*) were observed to prey on Olympic marmots (Barash 1973a). Predation by golden eagles (*Aquila chrysaetos*) was documented by examining prey remains at nests and in pellets. Yellow-bellied marmots contributed 71.4% (Knight and Erickson 1978) and 73.3% (Marr and Knight 1983) of the prey biomass found at golden eagle nests along the Columbia River, and 2.4% in southwestern Idaho (Collopy 1983). In these studies, biomass of marmots was estimated from mean weights of museum specimens. These estimates may be too high because yearlings were not distinguished from adults. All skulls and other remains of marmots found at an eagle nest in Colorado were yearlings (G. E. Svendsen, pers. commun., 1971) and a golden eagle was observed feeding on a yearling. Of six marmots with radio transmitters killed by eagles, three were yearlings and three were adults (Van Vuren 1990). Thus, the smaller yearlings seem to form a substantial proportion of marmots predated by eagles.

Van Vuren (1990) reported that 59% of the predator kills of yellow-bellied marmots with radio transmitters in Colorado were by coyotes; badgers were responsible for 13%. Other predators were eagles (11%), black bears (*Ursus americanus*, 7%), and martens (*Martes americana*, 5%). Yellow-bellied marmot remains occurred in 17% of 395 coyote scats collected during the summer in Colorado, thus verifying that marmots are frequent prey (Van Vuren 1991).

Golden eagles, wolves (*Canis lupus*), and cougars prey on the Vancouver Island marmot (Bryant 1998), and wolves, grizzly bears (*Ursus arctos*), red foxes (*Vulpes vulpes*), and golden eagles prey on the hoary marmot (Murie 1944). Hoary marmots were minor items in

the diet of bears and foxes, and occurred in 6% of eagle pellets and 8% of wolf scats. Marmots were more abundant in wolf scats (37%) when caribou (*Rangifer tarandus*) were scarce.

Marmots respond to some predators by chasing them. Yellow-bellied marmots chased long-tailed weasels (*Mustela frenata*) and marten (Travis and Armitage 1972). A marmot observed by Waring (1965) made one or two "barking whistle" sounds per second while chasing less than 1 m behind a marten. An adult woodchuck chased a fox (de Vos and Gillespie 1960). After coyote predation on a female yearling, yellow-bellied marmots modified their home ranges and spent less time in the area where predation occurred (Armitage 1982). Marmots typically respond to an approaching predator by emitting an alarm call, a high-pitched tone produced by the vocal cords (Barash 1989). Marmots also may run to a burrow without calling. Predators and nonpredators may evoke calls. For example, yellow-bellied marmots responded to deer (*Odocoileus hemionus*), moose (*Alces alces*), black bears, horses (*Equus cabellus*), coyotes, sandhill cranes (*Grus canadensis*), ravens (*Corvus corax*), great blue herons (*Ardea herodias*), swallows (*Tachycineta bicolor*), and northern harriers (*Circus cyaneus*) (Armitage 1962). Woodchucks when frightened aboveground fled to their burrow and had marked tachycardia; once in the burrow, the heart rate declined. When frightened in the burrow, there was an onset of bradycardia, which persisted as long as the stimulus lasted (Smith and Woodruff 1980).

Hoary marmots responded to a model golden eagle by giving an alarm call while simultaneously running to a burrow when >5 m away or called and visually tracked the model if <1 m from the burrow. Other marmots responded to the call by running to a burrow; 28% of these emitted a call after reaching a refuge. When at the refuge, all marmots tracked the model and 9 of 32 emitted calls (Noyes and Holmes 1979).

Marmots may flee from a predator at a distance that allows them to reach a refuge ahead of the predator with some margin of safety. An observer approached juvenile woodchucks from the direction opposite to the burrow. Flight distance increased directly with the distance to the burrow, but was not affected by the speed of approach. The rate of increase in flight initiation distance was higher when the burrow was between the observer and the woodchuck than when the woodchuck was between the observer and the burrow. Escape velocity was slower for woodchucks closer to the burrow. When distant, a woodchuck stopped before entering; when close, it usually entered directly (Bonenfant and Kramer 1996; Kramer and Bonenfant 1997).

Parasites and Diseases. Major external parasites of marmots are fleas, mites, and ticks; major internal parasites are tapeworms and roundworms (Bibikov 1992; Bibikow 1996; Bassano 1996). Ticks were almost always present on woodchucks in Missouri (Twichell 1939). Eight species of Protozoa were taken from the cecum of *M. flaviventris*; six were described from *M. monax* (Gabel 1961). Bassano (1996) summarized much of the information on the distribution of parasites among marmot species; additional information for the amphiberingian marmots is summarized by Rausch and Rausch (1971). Marmots may be widely infected with large cestodes and nematodes during autumn, but these are eliminated at hibernation when the stomach and intestines contract (Rausch and Rausch 1971). Incidence of parasitism may vary widely; one population of woodchucks was reported to be free of internal parasites (McTaggart-Cowan 1933). Although there is little evidence that internal parasites affect survival and reproduction, infected juvenile yellow-bellied marmots gain little or no mass and do not survive hibernation (Armitage 2000). Ectoparasites also may reduce fitness. Two seriously underweight woodchucks were heavily infected with mites, probably *Androlaelaps* sp. (Grizzell 1955). Yearling *M. flaviventris* with greater flea infestations grew more slowly, animals that died during hibernation had more fleas than survivors, and adult females that failed to reproduce had more fleas than those that reproduced (Van Vuren 1996).

Viral and bacterial diseases of North American marmots were described primarily for *M. monax* (Bassano 1996). Woodchuck hepatitis virus (WHV) was discovered in laboratory animals and subsequently found in wild animals in southeastern Pennsylvania, central New Jersey, and north-central Maryland (Tyler et al. 1981). Evidence of infection was not found in woodchucks <3 months old. No cases were reported from woodchucks captured in Vermont or Massachusetts (Young and Sims 1979). Because the virus belongs to the same class of viruses as hepatitis B, woodchucks serve as a laboratory model for the study of hepatitis. Other diseases reported from woodchucks are rabies, Rocky Mountain spotted fever, tularemia, leptospirosis, and human encephalitis (Young and Sims 1979).

Plague (*Yersinia pestis*) was reported in North American marmots (Bibikow 1996). The fleas *Thrassis acamantis* and *T. stanfordi* are primary vectors of plague. Both occur on *M. flaviventris*, but little is known about marmot susceptibility to plague (Stark 1970), which does not appear to have any significant demographic effects. In Eurasia, plague in *M. bobac*, *M. baibacina*, and *M. sibirica* typically occurs in localized areas (foci). In plague foci, only about 2% of the animals are infected. Rabies increased in woodchuck populations during 1980–1984 in association with an epizootic of rabies in raccoons (*Procyon lotor*). Although rabies in woodchucks may be a public health concern, there is no information on its effects on woodchucks (Fishbein et al. 1986).

Reproductive Success. Reproductive success should be measured as the number of reproductive descendants produced by an individual during its lifetime. However, lifetime reproductive success is usually unknown and this discussion will focus on annual reproductive success. Reproductive success of a male yellow-bellied marmot depends on the number of reproductive females and the length of time he is associated with them (Armitage 1991b); the numbers of both young and yearlings produced increase linearly with the number of females in the harem (Armitage 1986a). A male is resident for an average of 2.24 years (Armitage 1974), but residency may reach 4–6 years (Armitage 1984). An average resident male produces 11.1 young during his lifetime (Armitage 1991b).

Female reproductive success is affected by environmental harshness (Armitage 2000; Armitage and Blumstein 2002) and reproductive suppression by conspecifics (Wasser and Barash 1983; Blumstein and Armitage 1999). As a consequence of these two factors, the estimated percentage of adult females that breed is 72% for *M. monax* (Snyder and Christian 1960), 53% for *M. vancouverensis* (Bryant 1996), 52% for *M. flaviventris* (Armitage 1991b), 43% for *M. caligata* (Barash 1989), and 41% for *M. olympus* (Barash 1973a). No female yellow-bellied marmot living at a high elevation (3400 m) bred in successive years (Johns and Armitage 1979), whereas females at a lower elevation (2900 m) frequently breed in successive years (Armitage 1984). Hoary and Olympic marmots breed biennially (Barash 1973a, 1974a); in an Alaskan population, a mean of 3.3 years occurred between breedings (Holmes 1984a). The average time between breedings by female Vancouver Island marmots is 2 years (Bryant 1998).

Reproductive suppression occurs when mature females fail to breed in the presence of older, dominant individuals. Thus, in a captive population of *M. broweri* maintained in the laboratory for 6 years, only the dominant pair bred despite the presence of other individuals of both sexes up to 5 years of age (Rausch and Bridgens 1989). Occasionally a second nonparous female is present in a family of Olympic marmots (Barash 1973a), which suggests possible reproductive inhibition. In bigamous families of hoary marmots, females may skip an additional year when both would be expected to breed. When both females breed, the subordinate individual produces about one half as many young and one fifth as many yearlings as the dominant female (Wasser and Barash 1983). The frequency of reproduction by 2-year-old *M. flaviventris* is significantly lower when adult females, including their mothers, are present (Armitage 1998). Weaning success is lower in a single female living in proximity to a matriline of two or more females than when she lives solitarily or adjacent to a matriline of one female (Armitage 1986a). Net reproductive rate and survivorship increase with the increase in matriline size, then decrease in the largest groups (Armitage and Schwartz 2000). Females increase their reproductive success by leaving large matrilines.

Reproductive success of female *M. flaviventris* varies with behavioral phenotype. Over a 2-year period, submissive females produced few young, and social females produced about one third of the young (Svendsen 1974). Social females recruited more yearling daughters than did asocial females (Armitage 1984). Sociable females had higher lifetime values for number of female yearlings, number of recruits, and number of 2-year-old daughters than females categorized as "avoidance" or "approach" (Armitage 1986b).

BEHAVIOR

Basic behavioral patterns are common to all species of marmots, but the social context and frequency of expression vary among species (Barash 1989; Bibikow 1996). Social interactions may be broadly classified as amicable, which includes greeting and allogrooming, and agonistic, which includes chase, flight, fight, and avoidance (Armitage 1973; Johns and Armitage 1979). Sexual behavior includes genital sniffing, grasping, grappling, and mounting (Armitage 1965). Rates of amicable and agonistic behavior are related to population density, the age–sex structure of the population, length of shared residency, and individual behavioral phenotypes. Yearly changes in agonistic and amicable behavior among yellow-bellied marmots are not correlated within or among colonies (Armitage 1977). Barash (1973b) suggested that high-elevation colonies of *M. flaviventris* may be more social than medium elevation colonies as an adaptation to a shorter growing season. However, the age–sex structure and population density of these colonies varied and could account for the observed behavioral differences. Typically, social interactions are high in the spring and decline thereafter (Armitage 1962; Bronson 1964; Barash 1973a, 1974a; Heard 1977; Meier 1992). Social behaviors occurred more frequently in the morning and evening in Olympic and hoary marmots. In yellow-bellied marmots, social interactions occurred more frequently at midday in one colony and in the morning in another (Armitage et al. 1996). Social behaviors tended to be more frequent in the early postlactation period when young emerged and decreased by 3 weeks of postlactation.

Amicable Behaviors. A greeting occurs when two marmots approach head-on with tails arched followed by nose-to-nose, nose-to-cheek, or nose-to-mouth contact or when they "sniff" at each other without contact (Armitage 1962; Barash 1989). A greeting often is followed by allogrooming in which one marmot chews at the neck, back, or flanks of the other. Mutual allogrooming occurs when the "groomee" becomes the "groomer." Social interactions among woodchucks are rare (Bronson 1964; Ferron and Ouellet 1989). Amicable behavior occurs between all combinations of age and sex except among adult females or adult males (Barash 1989; Meier 1992). Adult males are more socially active in hoary (Barash 1974a; Holmes 1984a) and Olympic (Barash 1973a) marmots, but less active in yellow-bellied marmots (Armitage and Johns 1982). The rate of greetings is much greater in the restricted family groups of Vancouver Island, Olympic, and hoary marmots than in the matrilineal yellow-bellied marmot groups (Barash 1973a, 1974a; Armitage 1977; Heard 1977). Amicable behavior among yellow-bellied marmots varies with age–sex groups and kinship (Armitage and Johns 1982; Armitage 1986a, 1989). Amicable behavior predominates among females related by 0.5; and occurs much less than expected when relatedness is 0.25 or less. Female yearlings interact amicably with both parents, and male yearlings may behave amicably with their mothers (Armitage 1974; Armitage and Johns 1982).

Agonistic Behavior. Agonistic behavior characterizes social interactions among woodchucks (Bronson 1964). Subordinate penned woodchucks gain less body mass than the dominant animals (Bailey 1965b). Woodchucks may be organized into a complex of dominance–subordinate relationships that is maintained regardless of the location of the interaction. Yearlings are subordinate to adults. When a woodchuck threatens another animal, the tail is raised with hairs erect and often flipped up and down, the back is arched, and the head directed toward the opponent with mouth open and incisors showing (Bronson 1964). Home range size and social rank were not significantly related in woodchucks. Seasonal changes in aggressiveness were more significant than changes in population density (Bronson 1963). Agonistic behavior among Olympic marmots occurs primarily when the resident male chases intruders or when satellite males avoid the residents (Barash 1974a). Chases occurred among several age classes of Vancouver Island marmots, but were relatively rare (Heard 1977). Agonistic interactions characterize adult male–adult male and adult male–yearling male behavior in yellow-bellied marmots (Armitage 1974). Otherwise, agonistic behavior is strongly related to kinship. It occurs much less frequently than expected among kin related by 0.5 and more frequently than expected among more distant kin and unrelated individuals. However, adult females may be highly agonistic to yearlings that are nonlittermate full sibs and to nieces; some females are agonistic toward their daughters (Armitage and Johns 1982; Armitage 1986a). Agonistic behavior, especially among adult males, predominated in a captive population of *M. broweri*. Three adult females died and a fourth sustained serious injury; all had extensive wounds (Loibl 1983). This pattern of agonism is atypical for species with an extended family social system (Armitage 1996c). Perhaps confinement resulted in atypical behavior.

Infanticide can be considered an extreme expression of agonistic behavior and has been reported only for yellow-bellied marmots. Typically the young was either unrelated or distantly related to the adult perpetrator (Armitage 1979b; Brody and Melcher 1985).

Vigilance and Defense. Vigilance is characterized by a marmot sitting upright on its haunches, forelegs held in front of the chest, and surveying the surroundings (Armitage et al. 1996). All species of marmots express this behavior. Marmot defense also includes alert behavior in which the marmot has head up and looks around while sitting, lying, or foraging. Alert and vigilance combined occupied 1.1–14.5% and 12.0–71.7 min/day among three populations of *M. flaviventris* in Colorado (Armitage et al. 1996) and 10.2% of foraging time in a California population (Carey and Moore 1986). Reproductive females and adult males have high levels of vigilance (Barash 1973a; Armitage et al. 1996). Vigilance may be higher in marmots where human disturbance is frequent (Armitage et al. 1996) or when feeding near the periphery of a colony (Armitage 1962). It may be reduced when most individuals are members of a closely related kin group (Armitage et al. 1996). Woodchucks become vigilant and scan when in feeding areas (Anthony 1962). Adult and 2-year-old *M. caligata* were alert less often than yearlings. Marmots were alert less often when foraging near other individuals and when foraging near talus (Holmes 1984b). In yellow-bellied marmots, foraging group size, alarm call occurrence, and age significantly affected the time spent alert (Carey and Moore 1986). Young and yearlings were alert more while foraging than adults. Yellow-bellied marmots reduced the potential cost of time spent alert by chewing while alert or vigilant (Armitage et al. 1996).

Communication. Marmots use visual, auditory, and olfactory senses for communication. An individual running to the burrow frequently results in other marmots running to their burrows. Tail flicking, which frequently occurs when an animal is moving or initiating movement, may serve as an intention movement (Armitage 1962) or to coordinate group activities. Adults tail flick more frequently than young or yearlings (Barash 1973a). Adult male yellow-bellied marmots wave their tails conspicuously when patrolling their territories or when approaching another animal; tail flagging may signify dominance or serve to communicate presence (Armitage 1974).

All marmots have sudoriferous facial glands (Walro et al. 1983; Rausch and Bridgens 1989), which are used for scent marking by rubbing the cheeks and oral angles against rocks, tree roots, or other objects (Barash 1973a; Armitage 1976; Hebert and Prescott 1983; Taulman 1990; Brady and Armitage 1999). Scent marking rates do not differ between sexes for *M. monax* (Ouellet and Ferron 1988), but *M. flaviventris* males mark more frequently than females (Brady and Armitage 1999). Scent marking decreases significantly during the summer (Barash 1973a; Hebert and Prescott 1983; Brady and Armitage 1999). Both *M. flaviventris* and *M. monax* spend more time marking or investigating foreign than familiar scents (Hebert and

Barrette 1989; Meier 1991; Brady and Armitage 1999). Scent marking has multiple functions: territorial marking, dominance, burrow occupancy, individual identity, familiarity with the home range, and a possible self-reassurance role.

All marmots emit a variety of vocalizations including alarm calls, shrieks, tooth chattering, growls, and whines (Waring 1966; Lloyd 1972; Barash 1973a; Taulman 1977; Hoffmann et al. 1979; Blumstein and Armitage 1997a). Shrieks are heard during play of young or from a submissive animal during an encounter (Armitage 1962; Waring 1966). Tooth chattering occurs during agonistic encounters (Waring 1966; Taulman 1977). Growl and whine are directed at other marmots and represent threat and submissiveness, respectively (Armitage 1962; Taulman 1977). Alarm calling is the most intensively studied vocalization. Calls generally center on 2–4 kHz (Waring 1966; Hoffmann et al. 1979, Blumstein 1999). Yellow-bellied marmots produce three acoustically distinct alarm vocalizations: whistle, trill, and chuck (Blumstein and Armitage 1997a). The whistle is elicited by both aerial and terrestrial predators in addition to suddenly appearing birds. Submissive yellow-bellied marmots and woodchucks often call when chased (Anthony 1962; Armitage 1962). Trills are preceded by whistles. Marmots trill as they enter a burrow after being pursued by a predator, when suddenly surprised, or when fleeing a conspecific. Marmots chuck infrequently; chucks are produced when minimally alarmed and often follow whistles (Blumstein and Armitage 1997a). *M. monax* has a single whistle (Hamilton 1934; Lloyd 1972). *M. olympus* and *M. caligata* have four alarm vocalizations: ascending, flat, descending, and trill; *M. vancouverensis* produce those four sounds plus a fifth, the kee-aw (Blumstein 1999). Alarm calls in these species are elicited by a variety of birds and mammals and by conspecific aggression (Barash 1973a; Heard 1977; Blumstein 1999). About 54% of the variation in the repertoire size of marmot alarm calls was explained by a measure of social complexity, and significant variation was explained when controlling for phylogenetic effects (Blumstein and Armitage 1997b). Aerial and terrestrial stimuli do not elicit unique alarm calls in *M. flaviventris*, *M. olympus*, *M. caligata*, and *M. vancouverensis*. Rather, calls vary according to risk. In *M. flaviventris*, repetition rate increases with risk and this pattern does not vary geographically (Blumstein and Armitage 1997a). The other three species with similar vocalizations communicate relative predation risk differently. *M. olympus* varies the number and rate of alarm calling; *M. caligata* produces quickly paced calls in response to aerial stimuli and longer calls uttered at a slow rate, to terrestrial stimuli; *M. vancouverensis* varies call duration and bout (≥ 1) composition (Blumstein 1999).

After young are weaned, adult female *M. flaviventris* with young call more than other age–sex classes; before weaning, calling rate does not differ among age–sex groups. Over the entire study period, about 42% of the variation in rate of calling was attributable to females that weaned young and 13% to the presence of older offspring. Degree of relatedness is not a significant factor (Blumstein et al. 1997). Indirect fitness apparently played a minor role and direct fitness a major role in the evolution of alarm calling in *M. flaviventris*. Although calling may function to alert offspring and other conspecifics, alarm calls may be directed toward the predator (Blumstein and Armitage 1997a, 1997b).

Yellow-bellied marmots may respond to the alarm calls of golden-mantled ground squirrels (*Spermophilus lateralis*) (Shriner 1998) and rock squirrels (*S. variegatus*) (Blumstein and Armitage 1997a), but not to bird calls used as controls. *M. olympus* may call in response to hearing conspecific alarm calls (Blumstein 1999). Some individuals are more highly excited than others and continue calling for >30 min, long after other animals are alerted (Armitage 1962; Waring 1966). Finally, when detecting a predator, a marmot may flee silently to its burrow and not alarm call (Waring 1966; Blumstein 1999).

Grooming. Marmots may scratch an anterior part of their body with a hind foot or chew their fur, usually while sitting on their haunches. Among yellow-bellied marmots, grooming, including allogrooming, accounts for 0.8–3.4% of the time aboveground (Armitage et al. 1996). Grooming generally occurs throughout the day. Reproductive females and adult males tend to groom more than other age–sex groups. A greeting typically precedes grooming in yellow-bellied and Olympic marmots (Barash 1973a). Woodchucks also groom (Anthony 1962); probably all marmot species do.

Play. This behavior includes a variety of motor patterns, including hide/seek, grapple, chase/flee, and mouth-spar. Jamieson and Armitage (1987) described and illustrated play motor patterns, transition motor patterns such as escaping, and play-associated motor patterns, which include allogroom, approach, greeting, autogroom, social investigation, and withdraw. Play is often called play-fighting and may escalate into aggressiveness, especially in those species in which adults play. Thus, 39% of the upright play fights between adult *M. caligata* were followed by a chase (Barash 1974a) and adult play fights between *M. olympus* adults often were more characteristic of fights (Barash 1973a).

All species of marmots play. It typically occurs only among young *M. monax* for a few days after emergence (Barash 1989). However, four instances of play were observed between an adult female and yearling female and eight instances between an adult male and yearling female (Meier 1992). These play bouts may have been conflict. I have frequently observed conflict between two *M. flaviventris* that has some of the same behavioral motor patterns as play. Play in yellow-bellied marmots occurs among young and among yearlings; male young and yearlings play more than female young and yearlings (Armitage 1974; Nowicki and Armitage 1979; Jamieson and Armitage 1987). Both young and yearlings play with the same sex at rates higher than expected and males initiate play with females more than the reverse. Role reversal (or flips) occurs whenever animals exchange top and bottom positions in wrestling. Role reversal occurs more often when two males are involved and much less often when a male–female pair or two females are playing. Young males engage in mouth-spar, grapple, wrestle, and allogroom significantly more than females (Nowicki and Armitage 1979). Yearling females are more likely to be in the bottom or flee position, and males in the top or chase position. Females are more likely to terminate play. Pouncing occurs as a transition from one bout to another; males are responsible for about 70% of the pounces (Jamieson and Armitage 1987). Play rarely occurs between young and yearlings, does not occur among adult *M. flaviventris* (Nowicki and Armitage 1979), and rarely between mothers and their offspring (Armitage et al. 1996). Play occurs more frequently in the morning and early in the season (Armitage et al. 1996). Yearling play rarely occurs beyond mid-July. Play contains motor patterns similar to those observed in adults during agonistic behavior. These patterns, plus the differences in play activity between males and females, suggest that play functions in social integration by facilitating social dominance and the coordination of agonistic behavior.

Adult male *M. vancouverensis* play with adults, 2-year-olds, and yearlings; adult females play with 2-year-old females and yearlings, but not with adult females or infants. Infants play with other infants, and 2-year-old females play with yearlings (Heard 1977). Play is common among yearling and infant *M. olympus* and occurs in 2-year-olds and adults (Barash 1973a). Young, yearling, and 2-year-old *M. caligata* play most often; adults play at low rates (Barash 1974a). None of these studies analyzed play behavioral patterns.

Individuality. Yellow-bellied marmots can be broadly classified as social or asocial; the asocial animals are either submissive avoiders or aggressive. Behavioral phenotypes appear to be relatively stable among adults (Svendsen and Armitage 1973; Svendsen 1974), but may change during ontogeny (Armitage 1986c). Adult female hoary marmots transplanted to new colonies tend to maintain their pretransplant levels of aggressiveness (Barash 1989).

Social Organization. Marmots can be grouped into four social systems: solitary, female kin groups, restricted family, and extended family (Armitage 2000). Only *M. monax* is solitary. Adult and yearling females may share the same burrow in early spring, but not after adult females give birth (Snyder 1962; Meier 1992). Spatial structure of woodchuck

populations indicates a low degree of sociality: The frequency of burrow sharing is low, the degree of overlap between neighboring reproductive females is low, the presence of nonreproductive females at natal burrows is scarce, and juveniles disperse (Swihart 1992). The uniform spacing of burrows is attributed to agonistic behavior, primarily among juveniles during rapid invasion of new habitat (Hendersen and Gilbert 1978). Young may chase or fight with other young, and adults may chase young (Anthony 1962). The mating system is polygynous (Meier 1992).

Female yellow-bellied marmots are organized into mother: daughter:sister kin groups, which persist through time as matrilines (Armitage 1984, 1998). All male yearlings disperse. Adult males associate with ≥ 1 female matrilines to form a harem polygynous mating system. About 50% of the female yearlings are recruited into their natal matriline; the others disperse.

Olympic, hoary, and Vancouver Island marmots live in restricted family groups into which the male is integrated such that the social and mating systems are congruent (Armitage 2000). Family groups typically consist of an adult male, one or three females, yearlings, and one litter of young (Barash 1973a, 1974a; Heard 1977). Some populations of *M. caligata* are monogamous (Holmes 1984a). Dispersal is typically at age 2 years. An individual adult female typically is associated with either young or yearlings, but not both.

All remaining species of marmots form extended family groups; *M. broweri* is the only representative of this social system in North America. The typical family consists of an adult territorial pair that does all the breeding, subordinate nonbreeding adults ≥ 2 years old, yearlings, and young. Polyandry may occur. Dispersal occurs at age 3 years or older (i.e., beyond the age of first reproduction). Because all members of the family hibernate in the same burrow (Rausch and Rausch 1971), alloparental care may occur (Arnold 1993; Blumstein and Armitage 1999).

Barash (1974c) first pointed out the relationship between marmot sociality and the length of the growing season. These ideas were extended to all ground-dwelling sciurids (Armitage 1981). More recently, the following scenario was proposed for the evolution of marmot sociality (Armitage 1999, 2000). Marmots evolved in harsh landscapes and developed hibernation to cope with periods of food shortage or absence. The evolution of large body size as a means of maximizing the efficiency of storage and use of fat, coupled with a short active season, resulted in young requiring ≥ 1 years of additional growth to reach maturity. Young were retained in their natal area; retention of young within the parental home range formed social groups in all species except *M. monax*. Retention of young led to delayed dispersal, which provided the potential for cooperative breeding with its attendant alloparental care (Blumstein and Armitage 1999) and communal nesting (Armitage and Gurri-Glass 1994). Delayed dispersal probably evolved because habitats were saturated; marmots disperse at an older age, when the chances of success are greater (Armitage 1996c). Some consequences of increased sociality are a delay in the age of first reproduction, smaller litter size, and a smaller proportion of breeding females (Blumstein and Armitage 1998). At least some of the reproductive costs of sociality result from reproductive suppression.

AGE ESTIMATION

The most useful criterion for estimating age of marmots is body mass 30–60 days after emergence from hibernation, when body fat is minimal. Yearling, 2-year-old, and 3-year-old or older *M. flaviventris* (Armitage et al. 1976) and *M. olympus* (Barash 1973a) and yearling and adult *M. vancouverensis* (Bryant 1998) and *M. monax* (Davis 1964) can be distinguished by differences in body mass. Young of all species are easily identified because of their small size. In *M. monax*, the size difference between young and adults becomes less by late summer. Characteristics of pelage, shape and color of incisors, and shape of head are important for assessing chronological age and distinguishing yearlings from adults in the spring (Davis 1964). Older animals cannot be distinguished by length or body mass for any marmot species. Eye lens weight provides a good estimate of age of *M. monax*, but requires killing the animals. In *M. flaviventris*, premolar wear increases linearly with age through age 4 years, but is unsuitable for estimation beyond 3 years of age (Van Vuren and Salsbury 1992).

ECONOMIC STATUS, MANAGEMENT, AND CONSERVATION

Economic Status. Eurasian marmots are hunted for fur, fat, and flesh; during famines and World War II, marmots saved thousands of people from starvation (Bibikow 1996). Marmot fat is rendered to obtain oil, which is believed to be medicinal and is used to treat ailments such as burns and arthritis. In the former Soviet Union in 1991, a marmot was worth about 200 rubles, several times the monthly salary of a worker. No comparable economic use of North American marmots is known. Marmots are hunted for food (Bollengier 1994), and woodchuck fur and hide formerly were used for cheap coats, patching leatherwork, and straps (Schwartz and Schwartz 1981). Minor economic activity centers on the groundhog in Pennsylvania as a prognosticator of winter duration ("Punxsutawney Phil"). Marmots are used as symbols for commercial enterprises (Marmot Mountain Ltd.) and as characters in children's books. The hoary marmot was prized by northwest native Americans for clothing. Areas with marmots were privately owned, huts or cabins were built at the sites, and the marmots were hunted in the autumn after the molt (Drucker 1950). The hides were a chief article used in potlatches, and wealth among Tlingit and Gitksan was directly measured in hoary marmot skins. Okanagan Indians derived food and clothing from *M. c. okanagana* (Anderson 1934). Cut marks on bones and artifacts recovered from subalpine caves indicate that the Vancouver Island marmot was used as food by aboriginal peoples (Nagorsen et al. 1996). Native Americans in the Great Basin use marmots for food (C. Floyd, pers. commun., 2000). Marmots are a tourist attraction, especially in the western states, but this economic potential has not been developed to the extent that it has in Europe (Ramousse and Giboulet 2002). Woodchuck burrows are used by other small mammals of economic importance, such as skunks (*Mephitis mephitis*), cottontail rabbits (*Sylvilagus floridanus*), raccoons, and red fox (Eadie 1954; Grizzell 1955; Schmeltz and Whitaker 1977).

Only *M. flaviventris* and *M. monax* occur at elevations low enough to potentially negatively affect agriculture. Yellow-bellied marmots prefer alfalfa and may forage in irrigated meadows (Thompson 1979b) and consume much of the crop (Couch 1930). Marmots may also burrow into and cause breaks in levees and dikes (Eadie 1954). Damage by yellow-bellied marmots appears to be minimal, localized, and generally is not discussed in books on wildlife damage.

Woodchucks gnaw woody stems, primarily in the spring. There is greater stem mortality near burrows. Sugar maple was the species most severely gnawed, possibly because woodchucks may feed on the sap (Swihart and Picone 1991b).

Woodchucks may damage a variety of crops such as grains, clover, alfalfa, hay grasses, beans, peas, corn, and apple trees (Eadie 1954). In Connecticut, woodchucks damage apple trees near their burrows; 17% of trees within 1.5 m of a burrow were dead or recently replaced compared to none at distances greater than 12 m (Swihart and Picone 1994). Woodchucks gnawed 96% of 48 trees near their burrows; none were gnawed distant from burrows. Gnawed trees were smaller and produced 43% fewer apples, and individual apples were smaller. Up to 1.5% of the trees were affected by woodchucks, whose activity reduced the yield of apples by a minimum of 0.6%.

Both species may climb into automobiles and gnaw on electrical wiring or rubber hoses. They also cause electrical outages by gnawing on underground power cables (Bollengier 1994). Yellow-bellied marmots may excavate burrows under buildings, gnaw through a floor, and cause considerable disarray in a building. Usually, burrowing under a building is more of a nuisance because of odors from feces and rotting vegetation in the burrow than an economic liability.

Although marmots carry diseases, transmission of disease from marmots to humans or their domesticated animals is of little or no

importance. For example, leptospirosis in woodchucks in New York was not associated with bovine leptospirosis (Fleming 1979).

Management. Control of marmots falls into three categories: exclusion, removal, and killing. A fence about 1 m high that extends 23–30 cm in the ground and includes modifications that prevent marmots from climbing it is useful for home gardens and obviates the necessity of ongoing removal or killing of marmots (Bollengier 1994). Repellents were tried on several common garden crops (Swihart and Conover 1991). Consumption of acorn and zucchini squash treated with Hot Sauce Animal Repellent was slightly reduced, but more than two thirds of the foliage was consumed. Over an 11-day period, woodchucks gradually developed an aversion to tomatoes treated with emetine dihydrochloride, but the woodchucks sampled the vegetation daily and lost the aversion. Consumption of romaine lettuce was not affected by Hinder, Cygon, or Sevin. In general, repellents have minimal success and are most effective on plant species of lower palatability. Gnawing of fruit trees occurs primarily during the spring in Connecticut and is associated with scent-marking behavior. Providing hardwood stakes as alternative scent-marking substrates delayed the onset of damage, but did not reduce it (Swihart 1991b). Spraying bobcat urine weekly on the lower 75 cm of the fruit trees near woodchuck burrows greatly reduced the number of trees damaged and the extent of the damage. A single application of thiram was ineffective in reducing damage.

Marmots may be removed by livetrapping. Traps should be placed in a runway or at the opening of the burrow and baited with apple slices, lettuce, peanut butter, peanuts, or soybeans (Thompson 1979a). Traps can be set at any time of day and left open overnight (Davis 1982). During the hot part of the day, traps should be closed or checked hourly to prevent heat death. Captured animals may be released into suitable habitat where damage is not a problem.

Marmots may be killed with poisons, shooting, or trapping consistent with local regulations on such actions. Cartridges of carbon monoxide may be placed in a burrow and the entrances sealed. Bollengier (1994) provided detailed directions for this procedure. Other procedures, such as use of aluminum phosphide tablets, require a certified pesticide applicator. A cartridge with poisonous gas is highly effective. When 165 burrows were treated on a 40-ha area, all woodchucks were killed (de Vos and Merrill 1957). However, within 1 month, the area was repopulated. Ploughing the area was more effective; after 2 months, none of the burrows that were ploughed were opened up. Woodchucks rapidly recolonize a depauperated area (Davis 1962). General broad-scale removal may be ineffective and control should focus on individual woodchucks that are doing damage. Shooting may keep a population at an acceptably low level, but should not be used where safety is a concern. In general, control measures should not be initiated without consulting with the proper local authorities. Body-gripping kill traps kill the animal quickly, but should not be used where domestic or other wild animals might be captured. Use of body-gripping kill traps may be limited by state or local laws; local authorities should be contacted (Bollengier 1994).

Although management traditionally focuses on eliminating or reducing marmot populations, management in some areas is concerned with increasing populations or recolonizing areas where they have died out (Bibikow 1996). Since 1970, the Vancouver Island marmot has declined in numbers. Natural subalpine meadows are small and scattered. Recently, *M. vancouverensis* colonized logged habitats within five adjacent watersheds on south-central Vancouver Island (Bryant and Janz 1996). The initial colonization of logged habitats and ski runs increased marmot populations (Bryant 1998), but the population decreased to about 40 animals by 2000 (A. A. Bryant, Marmot Recovery Foundation, pers. commun., 2000). Persistence of marmots at natural sites is higher than at logged sites (65% vs. 48%). Females live longer on natural sites; maximum age was 9 years versus 5 years on logged sites. No adult female inhabiting a clearcut weaned more than one litter; 5 of 14 females in natural habitats produced at least two litters during the 9 years of the study (Bryant 1996). The logged sites may act as sinks, which capture dispersing marmots and prevent them from recolonizing natural habitats. Reasons for the rapid decline and extinctions on logged and natural habitats are unclear, but disease and predation, both of which may have been enhanced by human activities, are implicated (Bryant 1997). A recovery plan was developed by the Vancouver Island Marmot Recovery Team in 1994 and updated in 2000. An international workshop made recommendations for conserving the species (Elner 2000) and a captive breeding program was established in zoos in Toronto and Calgary (Canadian Wildlife Service 1999–2000).

RESEARCH NEEDS

The study of marmot biology has progressed considerably since 1980. However, little is known about the population and social biology of *M. broweri*. Other species require long-term research to determine the role of kinship in social organization, the relationship between life-table statistics and social organization, the effect of weather and climate change on survival and reproduction, and the factors that contribute to lifetime reproductive success in males and females. Other areas deserving investigation include the basis and importance of geographic variation, the role of nutrition in food choice and habitat selection, the extent and mechanism of reproductive suppression, the function of alarm calling (warn kin, talking to predators?) and the reason marmots frequently do not call, the significance of species-specific alarm calls, the importance of parasites and disease and the genetic and physiological mechanisms marmots use to combat them, and the annual profiles of hormones and their role in dominance relationships, reproductive and territorial behavior, and environmental stress.

Marmot body size is diverse. Little is known of the role of body size in the allocation of energy to maintenance during torpor or to euthermy in the burrow before emergence, or about the relationship between social organization and energetic efficiency and social thermoregulation during hibernation. Because marmots have low reproductive rates, it would be useful to know the energetic basis of reproductive skipping and how that might be managed to increase reproductive output in declining marmot populations.

Most economic problems appear to be local and are best managed at that level with the help of local authorities. Development of effective repellents could simplify control by eliminating the need for trapping and/or killing.

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KENNETH B. ARMITAGE, Department of Ecology and Evolutionary Biology, University of Kansas, Lawrence, Kansas 66045-7534. Email: marmots@ukans.edu.