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Marmota monax.

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Marmota monax (Linnaeus, 1758)

Woodchuck

[Mus] monax Linnaeus, 1758:60. Type locality, Maryland.

[Glis] canadensis Erxleben, 1777:363. Based on the Quebec marmot of Pennant. Type locality fixed as Quebec, Quebec, Canada, by A. H. Howell, 1915:31.

Mus empetra Pallas, 1778:75. Type based on the Quebec marmot of Pennant.

Arctomys sibila Wolf, 1808:481 (name proposed to include *Arctomys empetra* Pallas and *Arctomys pruinosa* Gmelin, 1788, supposed to be the same, thus, in part based on Quebec marmot of Pennant).

Arctomys melanopus Kuhl, 1820:64. Type locality, Canada.

Arctomys ignavus Bangs, 1899:13. Type locality, Black Bay, Strait of Belle Isle, Labrador.

[Marmota] monax Trouessart, 1904:344. First use of current name combination.

Marmota ochracea Swarth, 1911:203. Type locality, Forty-mile Creek, Alaska.

CONTEXT AND CONTENT. Order Rodentia, Family Sciuridae, Genus *Marmota*. Nine subspecies of *Marmota monax* are currently recognized (Hall, 1981):

M. m. bunkeri Black, 1935:319. Type locality, seven miles SW of Lawrence, Douglas Co., Kansas.

M. m. canadensis Erxleben, 1777:363, see above (*empetra* Pallas, *melanopus* Kuhl, *sibila* Wolf, are synonyms. For complete synonymy of subspecies see Howell, 1915).

M. m. ignava Bangs, 1899:13, see above (for complete synonymy of subspecies see Howell, 1915).

M. m. johnsoni Anderson, 1943:53. Type locality, Percé, Gaspé Co., Quebec.

M. m. monax Linnaeus, 1758:370, see above.

M. m. ochracea Swarth, 1911:203, see above.

M. m. petrensis Howell, 1915:33. Type locality Revelstoke, British Columbia.

M. m. preblorum Howell, 1914:14. Type locality, Wilmington, Middlesex Co., Massachusetts.

M. m. rufescens Howell, 1914:13. Type locality, Elk River, Sherburne Co., Minnesota.

DIAGNOSIS. The following descriptions are summarized from Howell (1915) and Hall (1981). Of the North American marmots, *M. monax* (total length 418–665 mm) is smaller than *M. flaviventris* (470–700 mm) and *M. caligata* (533–820 mm). Tail is black or dark brown, bushy, almost flattened, and is short, being 20–25% total length. By contrast, in *M. flaviventris* the tail is 25–30% total length, and in *M. Caligata* , 27–33% total length. Head is without the white markings (except around nose) that are present in congeners. Sides of the neck are the same color as upper parts, whereas *M. flaviventris* has conspicuous buffy patches. Ears are small, but larger than in congeners. Forelegs are overlaid with deep reddish brown hairs that are not present in congeners. Feet are black, blackish brown, or (in *M. m. ochracea*) pinkish cinnamon, but are buffy, hazel or tawny in *M. flaviventris* and either mixed black and white or solid brown in *M. caligata.* Posterior pad on sole of hind foot is oval in shape and situated near the middle of the sole, similar to *M. flaviventris,* whereas that of *M. caligata* is near the edge of the sole. Mammae are p 2/2, a 1/1, i 1/1, total 8; all other marmots have five pairs (with two abdominal pairs). Upper tooth rows are parallel, whereas in other marmots they diverge anteriorly.

GENERAL CHARACTERS. Year-round weight (in g) for adult males averages 3,826, $n = 433$ (minimum in April, mean 3,116, $n = 45$; maximum in September, mean 5,066, $n = 21$). For adult females, year-round weight averages 3,526, $n = 410$ (minimum in April, mean 3,084, $n = 64$; maximum in September, mean 4,804, $n = 14$—Snyder et al., 1961). Yearling male weights average 2,719, $n = 250$; yearling females average 2,656, $n = 269$; male young of the year average 1,957, $n = 373$; and female young of the year average 1,779, $n = 356$ (Snyder et al., 1961). External measurements (in mm) are as follows: total length 418–665, length of tail 100–155, length of hind foot 68–88. Ears are broad, rounded, well-furred and can close over external auditory canal (Hall, 1981; Howell, 1915).

Adult coloration does not differ between the sexes and varies from upperparts grayish- or reddish-brown (in *M. m. ochracea* vinaceous-cinnamon); head without white markings except around nose; sides of neck same colors as upper parts; feet black or dark brown; forelegs overlaid with deep reddish hairs (hazel to burnt sienna); tail black, dark brown, or pinkish cinnamon; wooly underfur confined to back and sides while longer guard hairs cover whole body; guard hairs with white tips yield frosted or grizzled appearance. Young are black then grayish and acquire adult pelage as yearlings (Howell, 1915).

The skull (Fig. 2) has a nearly-straight superior outline, occipital region slightly depressed; rostrum considerably, but not abruptly, depressed near posterior border of maxillae; braincase broad and flattened; interorbital region broad; postorbital processes projecting at right angles to long axis of skull or slightly forward of right angle; nasals at posterior end usually wider than premaxillae; incisive foramina widest posteriorly and narrowest anteriorly; maxillary tooth-rows nearly parallel; anterior face of incisors white or yellowish white or ivory yellow to pale orange-yellow (Hall, 1981; Howell, 1915). Averages and ranges (Howell, 1915) of cranial measurements (in mm) for six adult male *M. monax monax* from Maryland, Pennsylvania, Virginia, and West Virginia are as follows: condylobasal length, 97.8 (97.3–102.5); palatal length, 57.4 (55–59.5); postpalatal length, 36.2 (34.5–37.7); length of nasals, 40.8 (39.7–41.8); zygomatic breadth, 65.9 (63–69.2); breadth across mastoids, 46.9 (44.5–50.2); least interorbital breadth, 27.1 (25–29.2); breadth of rostrum, 21.7 (20.6–23.7); maxillary tooth row, 21.3 (21–21.9); for five adult females from District of Columbia, Pennsylvania, and Virginia: condylobasal length, 91.2 (90.4–91.8); palatal length, 53.1 (50.2–56); postpalatal length, 34.9 (33.7–36.3); length of nasals, 38.7 (36.8–40.6); zygomatic breadth, 61.2 (59.5–62); breadth across mastoids, 44.7 (44–45.8); least interorbital breadth, 24.9 (23.5–26.5); breadth of rostrum, 20.5 (19.7–21.3); maxillary tooth row, 21.2 (20.5–22.4).

DISTRIBUTION. Woodchucks are the widest ranging of North

FIG. 1. Adult *Marmota monax* from Pennsylvania. Photograph by G. L. Twiest.

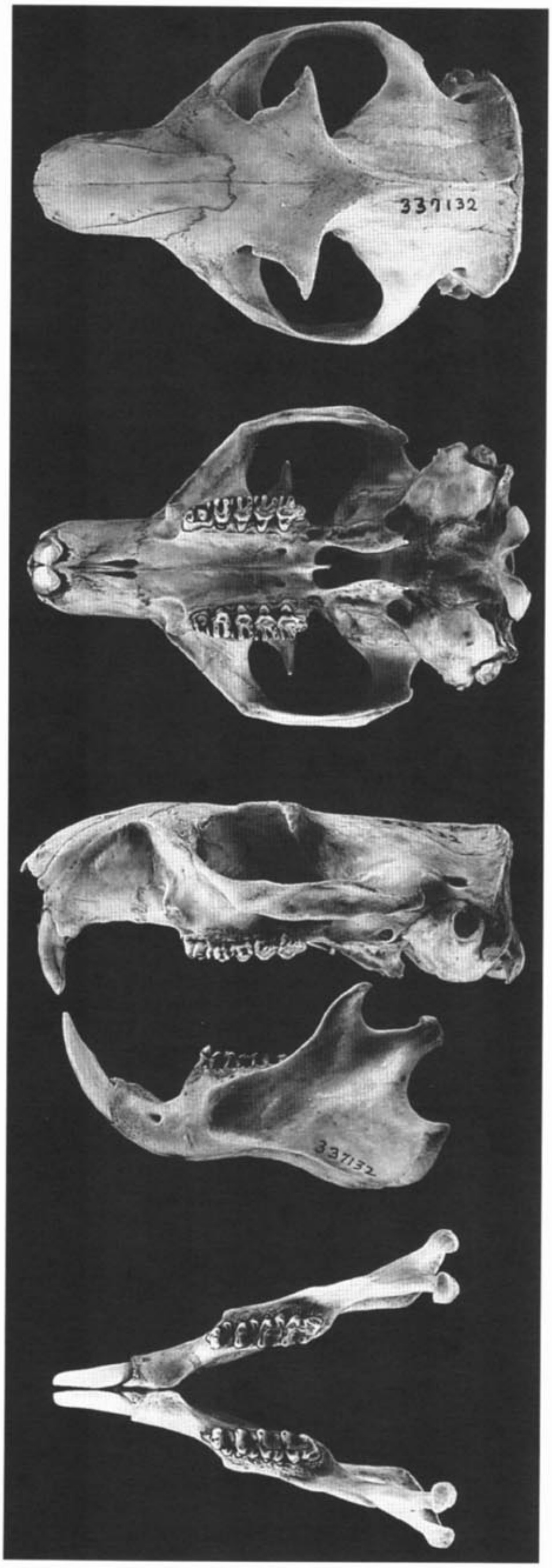

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral and occlusal views of mandible of *Marmota monax* (United States National Museum of Natural History 337132). Greatest length is 102.5 mm (Howell, 1915).

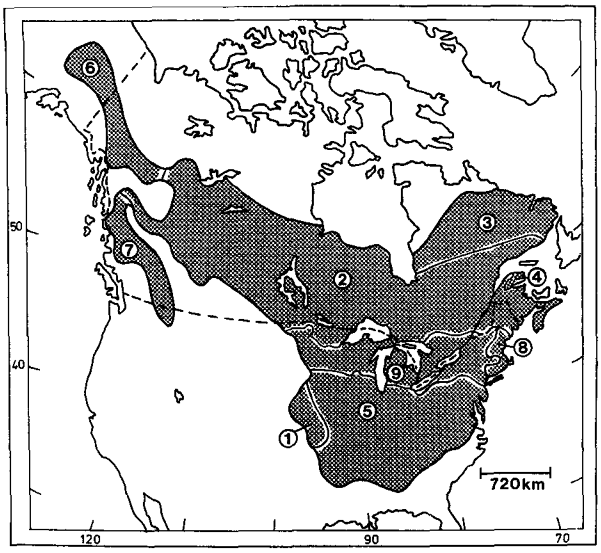

FIG. 3. Distribution of *Marmota monax* (modified from Hall, 1981): 1, *M. m. bunkeri*; 2, *M. m. canadensis*; 3, *M. m. ignava*; 4, *M. m. johnsoni*; 5, *M. m. monax*; 6, *M. m. ochracea*; 7, *M. m. petrensis*; 8, *M. m. preblorum*; 9, *M. m. rufescens.*

American marmots, being distributed from eastern Alaska to Great Slave Lake, the south shore of Hudson Bay and along the East Main and Hamilton Rivers, Quebec. *M. m. ignava* occurs in eastern Labrador. The range extends from Nova Scotia south to Georgia, Alabama, northwestern Louisiana, and Arkansas. From western Canada, the range extends southward into the Rocky Mountains to northern Idaho and east of the Great Plains to eastern Oklahoma (Fig. 3).

FOSSIL RECORD. Stratigraphic range of the extant Holarctic genus *Marmota* extends back to the Clarendonian in North America, the Villafranchian in China, and the late Middle Pleistocene in Europe. With a Nearctic origin indicated, the Hemphillian *Marmota minor* (Kellogg) may be ancestral, since it is structurally intermediate between the Clarendonian *Marmota vetus* (Marsh) and the recent *Marmota monax* (Black, 1963). Subsequent differentiation involved chromosome fission and/or fusion, a general increase in size, enlargement of the fourth lower premolar, modification of the molars, and fossorial specializations (Kurtén and Anderson, 1980). *Marmota monax* has been identified at 25 localities from Arkansas to Pennsylvania (Kurtén and Anderson, 1980), with the earliest occurrences being late Irvingtonian (Conard Fissure, Cumberland, Trout). Varying degrees of adaptation occurred among North American marmots, with the woodchuck remaining the least specialized (Hoffmann and Nadler, 1968).

FORM AND FUNCTION. The single annual molt lasts ca. one month and usually occurs between May and August (Howell, 1915). Cheek pouches are rudimentary and lack retractor muscles (Hall, 1981; Howell, 1915). A bilateral pair of large, palpable, buccal glands occurs near the oral angle (Walro et al., 1983). These multilobular apocrine sudoriferous glands drain into anastomosing ducts to form a primary duct that opens at the base of a flap formed by the folding of skin lateral to the boundary between oral and cutaneous epithelia. The secretions emit a pungent odor, are active in woodchucks of both sexes and all ages, and serve a marking function (Meier, 1991). Three white, nipple-like, anal glands (Grizzell, 1955) can be everted to disseminate a musky odor. Anal gland secretions are not sprayed as in skunks and may not have repelling qualities. They may play a role in social communication.

Dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Jaw movements and muscle activities of mastication differ from those during incisal biting. Mastication is strongly asymmetrical with chewing being on one side for long sequences. Mandibles deviate to one side and then move anteriorly and toward the midline during closing. Movements during incisal biting are primarily along the midline and are accompanied by symmetrical activity of jaw adductor muscles. Most biting cycles do not end with contact between upper and lower incisors. During sharpening cycles, at 8 cycles/s, the lingual surface of the lower incisor is dragged across the tip of the upper incisor producing a lingual wear facet (Druzinsky, 1995).

Seasonal changes in weights indicate circannual deposition and use of fat. Weight gain (20 g/day for young males, 18 g/day for young females, 14.7 g/day for yearlings of both sexes, 13.0 g/day for adult males, 11.5 g/day for adult females) occurs during summer (Snyder, 1961). Weight loss (2.4 g/day for young males, 4.3 g day for young females, 6.5 g/day for adult males, 8.7 g/day for adult females) occurs during hibernation and spring arousal (Snyder et al., 1961). These cycles continue under constant photoperiod and reverse within 2 years when animals are sent to the southern hemisphere (Davis, 1976). Young of the year and yearlings undergo body growth in spring before fat deposition begins. Woodchucks attain progressively higher weights each year for the first 2–3 years, then weights plateau. An endogenous circannual metabolic rate parallels the weight cycle. Maximal metabolic rate occurred in May (3.22 g CO_2/h) and slowly declined until minimal levels (1.60 g CO_2/h) occurred in February (Bailey, 1965a).

Adults gain weight by increasing fat in existing cells (Young, 1975). Fatty acid depots in adipose tissue are proportionally uniform throughout the year. Serum fatty acid concentration increases during hibernation without change in fatty acid composition (Davis and McCarthy, 1965; Young, 1975). Plasma free fatty acids, insulin, and insulin/glucose ratios increase while glucose remains unchanged as animals gain weight, indicating development of insulin resistance during fat deposition (Young, 1975).

To hibernate, woodchucks seek hedgerows, woods, steep inclines in stony ground, haystacks, or sites with adequate drainage and a southern exposure (Davis, 1976; de Vos and Gillespie, 1960; Grizzell, 1955; Hamilton, 1934; Twitchell, 1939). Timing of the entrance into, and arousal from, hibernation varies with ambient temperature, season, and latitude. In Ithaca, New York, at 42°N, 76°W, adults enter hibernacula near the autumnal equinox and emerge 4–5 months later. Hibernation consists of 4–10 day bouts of torpor interrupted by 1–5 days arousal with torpor bouts becoming progressively longer (Concannon et al., 1990). In Sainte-Luce, Quebec, at 48°N, 68°W, hibernation began 13 October ± 18.5 days (n = 11) and lasted 167 ± 18.7 days (Ferron, 1996). During torpor, body temperature is maintained at 2–3°C above burrow temperatures (2–4°C) in New York (Concannon et al., 1990), but in Quebec, body temperatures are 4–14°C above burrow temperatures (2–7°C—Ferron, 1966).

Typically, adult males emerge from hibernation before females. For example, in Pennsylvania (Snyder and Christian, 1960), adult males emerge in February, females and subadults in March. They do not come to the surface every day after their first emergence, but remain underground during cold spells (Davis, 1967; de Vos and Gillespie, 1960; Grizzell, 1955; Hamilton, 1934; Twitchell, 1939).

Physiologically, entrance into hibernation involves a drop in body temperature to as low as 2°C, with increased blood oxygen, carbon dioxide, magnesium, potassium, and hematocrit, but decreased blood glucose (Concannon et al., 1990; McBirnie et al., 1953). Entry into hibernation is accompanied by a rapid fall in heart rate (minimum ca. 10 beats/min at 10°C) and contractile force. During deep hibernation, the ventricular myocardium generates a force of contraction equal to the non-hibernating heart. During the initial phase of arousal, force capabilities, rate of contractile force development, and heart rate greatly increase (maximum ca. 220 beats/min at 20°C), and then decrease until body temperature reaches 37°C and heart rate settles at ca. 130 beats/min (Armour et al., 1974).

A blood-borne substance or substances may induce natural mammalian hibernation. Serum from woodchucks, when transfused into ground squirrels, induces hibernation (Dawe and Spurrier, 1972). This blood-borne "trigger" promotes earlier hibernation in recipients when derived from long-term hibernating donors. A woodchuck in summer that receives its own frozen and thawed serum drawn during the winter-hibernation period, hibernates within 3 days and for up to 3 months (Dawe and Spurrier, 1972).

Morphologically, thyroid follicular cells and pituitary thyrotrophs are most active in spring, with secretory activity decreasing in summer and autumn, until quiescence occurs in early winter (Krupp et al., 1977). Serum concentrations of thyroxine (T_4) and triiodothyronine (T_3) are highest during the breeding season at the end of winter (T_4, 12.6 ± 2.2 μg/dl; T_3, 299 ± 57 ng/dl) and lowest during fat accumulation in summer and autumn (T_4, 4.6 ± 0.2 μg/dl; T_3, 79 ± 7 ng/dl). The level of serum thyroxine-binding globulin is highest during winter (binds 80% T_4, compared to 32% in summer) and is partly responsible for increased levels of T_4 and T_3 (Young et al., 1986). Seasonal variations in morphology of thyroid calcitonin-secreting cells show a cyclic pattern of activity consistent with most hibernating mammals, i.e., increased synthetic activity in spring/summer and relative inactivity during autumn/winter (Frink et al., 1978).

The male reproductive tract is typical for sciurids. An os penis is present, and accessory sexual glands include a pair of coiled branched seminal vesicles, a single compound tubular prostate, and a pair of compound tubular Cowper's glands (Mossman et al., 1932). Testes of adults are regressed and abdominal before hibernation, and testicular recrudescence occurs near the end of hibernation. Spermatogenic activity and size of seminiferous tubules are greatest in adults at emergence from hibernation. Maturation depletion and a decline in mean testis weight occurs prior to overt reproductive activity. Mean testis weight declines less rapidly than testicular size and spermatogenic activity because interstitial tissue increases as tubule size shrinks (Baldwin et al., 1985; Christian et al., 1972). Adult male serum testosterone (T) levels are minimal (≥0.1 ng/ml) in December, and April through August, and maximal (5.2 ± 0.5 ng/ml) early January to late March (Baldwin et al., 1985). In yearlings, maximum testis volume and serum T levels (0.9 ± 0.2 ng/ml) occur later (April or May) than in adults. Annual cycles of T production and testes recrudescence and regression are parallel, maximal during breeding, and are not altered by absence of hibernation or by captivity (Baldwin et al., 1985).

The woodchuck uterus is duplex, with two complete cervices and separated horns, precluding transcornual migration of blastocysts. The estrous cycle is a single, prolonged estrous period (18.1 ± 2.1 days, n = 7) during the brief spring mating season (Sinha Hikim et al., 1991). During the estrous cycle (in captive woodchucks), circulating estradiol was elevated before (34.4 ± 2.1 pg/ml) and during (31.4 ± 2.8 pg/ml) estrus at the time of maximal vaginal cornification, but progesterone (P) levels (0.04–0.09 ng/ml) did not change significantly (Sinha Hikim et al., 1991). Number of implantations is always equal to or less than the number of corpora lutea in the ipsilateral ovary (Concannon et al., 1983). Corpora lutea are maintained or rejuvenated following parturition and, independent of suckling, secrete amounts of P (23–61 ng/ml) for 2–3 months during postpartum anestrum equal to or greater than those during pregnancy (8–44 ng/ml). All corpora lutea retrogress by September (Concannon et al., 1983; Rasmussen, 1918; Snyder and Christian, 1960). Barren or unmated females, including yearlings, spontaneously form P-secreting corpora lutea during the lactational period of parturient females (Concannon et al., 1984).

A positive linear relationship between adrenal weight and body length exists, and female adrenal glands are ca. 8% heavier than those of males of equal length (Christian, 1962). Peak adrenal weights occur at mid-summer and mid-autumn and are not correlated with reproduction, but instead with aggressive behaviors (Christian, 1962). Urinary excretion of epinephrine, norepinephrine, and vanilmandelic acid indicates that activity of the adrenal medulla is low during early hibernation, increases three-fold during late hibernation, and remains high into summer (Wenberg and Holland, 1973). Urinary adrenocortical steroid (17-keto, 17-hydroxy, and total estrogens) levels are low during winter, but prior to and during arousal they increase, peaking in early summer (Wenberg and Holland, 1973).

ONTOGENY AND REPRODUCTION. Females are monoestrous and enter estrus, mate, and conceive soon after emergence from hibernation. In autumn, a number of large Graafian follicles develop which persist throughout hibernation (Rasmussen, 1918). Young females have many polyovular follicles (Christian, 1950). Males are promiscuous and mate after emergence from hibernation (Grizzell, 1955). Copulation occurs near burrow entrances or in nearby grass or brush. Ovulation is induced (Concannon et al., 1997), although it has occurred spontaneously in captivity (Sinha Hikim et al., 1992). Timing of breeding is influenced by latitudinal variations, local conditions, and arousal times. In New York (Hamilton, 1934) and Pennsylvania (Snyder and Christian, 1960), mating occurs late February through March and in Ontario, Canada (de Vos and Gillespie, 1960), during March and April. Circannual reproductive cycles persist in captive animals maintained in constant

(12L:12D) photoperiods. Responsiveness to altered photoperiods is greater in immature than mature animals. In the absence of strong photoperiodic cues and hibernation, reproductive cycles become free running at 10–11 month intervals (Concannon et al., 1992).

Pregnancy rates for adult females average 72–80% but can be as low as 56% (Concannon et al., 1997; Snyder and Christian, 1960). Some yearling females breed (6 of 21 in New York—Hamilton, 1934; 8 of 15 in Pennsylvania—Snyder and Christian, 1960; and 6 of 14 in Virginia—Ruckel et al., 1976), but the gravidum is smaller than that of adults (Snyder and Christian, 1960). Counts of corpora lutea indicate that the mean number of ovulations per female is 4.7–5.5, $n = 237$, whereas the mean number of implantations is 4.0–4.7, $n = 291$ (Snyder and Christian, 1960). Fetal atrophy often reduces the original number of fetuses, and total prenatal mortality ranges from 24 to 37% of shed ova (Snyder and Christian, 1960). Gestation length is 31–32 days (Grizzell, 1955; Hamilton, 1934; Hoyt, 1952). Litter size usually varies from one to eight but Howell (1915) and Young and Sims (1979) noted litters of nine. Average litter size is 3.8 ($n = 18$) in Ontario (de Vos and Gillespie, 1960); 3.4 ($n = 76$), 3.5 ($n = 50$), and 4.0 ($n = 145$) in Pennsylvania (Snyder and Christian, 1960), 4.0 ($n = 6$) in Virginia (Ruckel et al., 1976), 4.1 ($n = 49$) in New York (Hamilton, 1934), and 4.6 ($n = 29$) in Maryland (Grizzell, 1955). In Pennsylvania, average litter size of yearlings is 3.1 (Snyder and Christian, 1960). Reproductive rate (number of young born per female in the population) ranged from 2.6 to 3.2 for 3 years in Pennsylvania (Snyder and Christian, 1960).

In New York (Hamilton, 1934) and Maryland (Grizzell, 1955), young are born from early April until mid-May. In Pennsylvania mean date of birth is April 10 (Snyder and Christian, 1960) whereas in Ontario the first litter is born mid-May (de Vos and Gillespie, 1960). Parturition occurs in burrows. Average weight of young <24 hours old is 27.2 g ($n = 11$) in Maryland (Grizzell, 1955) and 26.5 g ($n = 20$) in New York (Hamilton, 1934). Average external measurements (in mm) are as follows: total length, 105; length of tail, 16; length of hindfoot, 13 (Hamilton, 1934). Litter weight and litter size are not correlated. Sex ratios are ca. 1:1 (Snyder and Christian, 1960).

Young are born with the external auditory meatus closed (Hamilton, 1934) and ear pinnae erect (Ferron and Ouellett, 1991). Eyes appear as darkened areas on the face. Neonates are almost naked (vibrissae 2.5 mm long and short hair is present on muzzle, chin, and head) and the skin is wrinkled with a pink-reddish tinge. Forelegs are better developed than hindlegs, and no teeth are erupted (Hamilton, 1934). Although neonates are quite active, motor movements are poorly coordinated. Developmental stages are as follows: at 1 week skin becomes pigmented; at 2 weeks a covering of short black hair is acquired; at ca. 3 weeks crawling begins; at ca. 4 weeks eyes open and feeding on solid material begins; and at ca. 5–6 weeks whistling and tooth chattering occur and emergence from the burrow begins. If a young wanders, the mother will carry it back in her mouth (Hamilton, 1934). Growth is completed late in the second year or during the third year. Details of growth and development are provided by Hamilton (1934) and Ferron and Ouellett (1991).

Females stand on four legs while nursing, and young are weaned after a lactation of ca. 44 days (Concannon et al., 1983; Hamilton, 1934; Snyder and Christian, 1960). Survival of young depends on previous history of the mother. Females born in captivity or captured shortly after weaning did not raise litters successfully, but all females captured as yearlings or adults subsequently raised young (Young and Sims, 1979).

Most males mature sexually as 2-year-olds (Christian et al., 1972). As the breeding season progresses, an increasing number of yearling males show enlarged, descended testes and possibly engage in breeding activity (Hamilton, 1934). Most females first reproduce as 2-year-olds: 47% in Pennsylvania (Snyder and Christian, 1960); 74% in New York (Hamilton, 1934); 75% in Maryland (Grizzell, 1955); 88% in Ohio (Meier, 1992).

The life-span of woodchucks is 4–6 years (Grizzell, 1955; Hamilton, 1934). One lived in the National Zoological Park, Washington, DC for 9 years, 3 months (Mann, 1930) and the longevity record (9 years, 8 months) is in the London Zoological gardens (Flower, 1931). Flooding and heavy rains may drown young and hibernating woodchucks in burrows (Grizzell, 1955; Hamilton, 1934). Incisor malocclusions can cause starvation, and continuously growing incisors may penetrate the skull and cause death (Hamilton, 1934).

ECOLOGY. In general, *M. monax* occupies low elevation woodland-field ecotones, preferring wooded areas for hibernation and fields for breeding and foraging. It also occurs near fence rows, vegetated gullies, banks of streams or lakes, near human structures, and other sites suitable for burrow construction (Grizzell, 1955; Hamilton, 1934; Howell, 1915).

Woodchucks are generalists and choose a variety of plant materials. Extensive lists of taxa consumed by woodchucks are provided by Hamilton (1934) and Arsenault and Romig (1985). Alfalfa and clover are among favorite foods, and fields of such are the most desirable habitat. Woodchucks easily switch food choices depending on local vegetation, seasonal availability, and individual preferences. They eat June bugs (species not identified—Gianini, 1925), snails (*Heliosoma anceps*—Hamilton, 1934), and grasshoppers (*Malanophus femur-rubrum*—Hamilton, 1934). Arboreal foraging of hackberry *(Celtis occidentalis)*, Norway maple *(Acer platanoides)*, peach *(Prunus persica)* and red mulberry *(Morus rubra)* leaves occurs (Swihart and Picone, 1991). Among captive animals, preference order for wild foods is wild lettuce *(Lactuca scariola)*, white clover *(Trifolium repens)*, red clover *(T. pratense)*, grasses *(Poa)*, and sweet clover (*Melilotus alba*—Twitchell, 1939). Water requirements are normally satisfied by dew and succulent vegetation but animals occasionally drink free water (Grizzell, 1955).

Woodchuck populations are loosely structured. They occupy burrow systems not clustered spatially, are asocial and territorial, and their associations are limited to reproductive efforts. Population density averages 3.3 woodchucks/ha in Ohio (Meier, 1985), 1.6 to 2.2 woodchucks/ha in Connecticut (Swihart, 1992), 1.2 woodchucks/ha in Ontario (de Vos and Gillespie, 1960), 0.9 woodchuck/ha in Pennsylvania (Bronson, 1963), and 0.1 woodchuck/ha in Quebec (Ferron and Ouellett, 1989). Spatial relationships change because of seasonal levels of aggression, dispersion of young, and shifting of home ranges. Adult males are classified as residents when their activity is confined to a well defined area or as transients when they spend only short periods of time in any one area (Meier, 1992). Following dispersal, females are transient until establishing a burrow system, and reproductive females are widely dispersed (Meier, 1992; Swihart, 1992). Adults of high relative rank normally do not contribute to the transient population (Meier, 1992) but shifts in home ranges occur; for example, in Connecticut (Swihart, 1992), 38% of adult males and 20% adult females relocated. In Pennsylvania (Bronson, 1964), adult males and females do not associate beyond the breeding season, but in Ohio (Meier, 1985), they associate with each other throughout the year and often from year to year. Yearling males, who are always low in dominance status, are usually transients (Bronson, 1964; Swihart, 1992). Rather than maintain exclusive use of one or two burrows, frequent and extensive movements occur during the post-reproductive period, presumably to avoid conspecifics (Bronson, 1964; Meier, 1992; Swihart, 1992). Studies using telemetry indicate post-reproductive woodchucks use a mean of 7.4 burrows in Ohio (Meier, 1985), 5.9 burrows in New York (Merriam, 1971), 7.5 in Connecticut (Swihart, 1992), and 5.1 burrows in Quebec (Ferron and Ouellett, 1989).

In general, male and female associations are limited to copulation and the mother-young nexus which terminates at weaning and dispersal (Barash, 1974b). In Pennsylvania (Bronson, 1964) and Quebec (Ferron and Ouellett, 1991), all juveniles disperse, but in Ohio (Meier, 1985), 35% of juvenile females and 9% of juvenile males remain in their natal home range until the next year. Offspring of adults disperse later than offspring of yearlings (Hamilton, 1934; Meier, 1985). Young disperse by one of three methods: follow their mother to another burrow system either voluntarily or under inducement, follow trails of their mother or others, or use random (chance) movements (de Vos and Gillespie, 1960; Grizzell, 1955; Hamilton, 1934). In response to removal of woodchucks from a population (Davis et al., 1964), a sustained decline did not occur; instead, birth, mortality, and movement rates compensated for losses.

Predators of woodchucks include humans, dogs, foxes, hawks, owls, bobcats, mink, weasels, and occasionally large rattlesnakes (species not identified—Grizzell, 1955; Hamilton, 1934). Woodchucks can climb trees to escape predators (Howell, 1915). Cottontail rabbits *(Sylvilagus floridanus)*, opossums *(Didelphis virginiana)*, raccoons *(Procyon lotor)*, and skunks *(Mephitis)* may den with hibernating woodchucks (Grizzell, 1955; Linduska, 1947). Foxes (species not identified) will excavate woodchuck burrows for use as natal dens and interspecific competition for burrows between woodchucks and raccoons occurs (Grizzell, 1955). River otters *(Lutra canadensis)*, domestic cats *(Felis catus)*, chipmunks *(Tamias striatus)*, meadow voles *(Microtus pennsylvanicus)*, short-tailed shrews *(Blarina brevicauda)*, house mice *(Mus musculus)*, jumping mice *(Zapus hudsonius)*, white-footed mice *(Peromyscus leucopus noveboracensis)*, and pine voles *(Pitymys pinetorum scalopsoides)*, as well as unidentified species of ground squirrels, weasels, snakes, and birds use abandoned or vacated woodchuck burrows (Grizzell, 1955; Hamilton, 1934).

Marmota monax is susceptible to arteriosclerosis, botfly larvae, fibroma, fleas, hepatitis, hepatoma, mites, nematodes, protozoa, roundworms, ticks, tularemia (rabbit fever), and rabies (Gabel, 1954; Grizzell, 1955; Hamilton, 1934). Taxonomy of intestinal protozoa is provided by Gabel (1954) and helminths by Rausch and Tiner (1948). Out of 40 woodchuck stomachs examined by Grizzell (1955), two contained the roundworm *Obeliscoides cuniculi*, and Hamilton (1930) reported finding a stomach nearly full of them. Among ticks, *Ixodes cookei* Packard (Ko, 1971) and *Ixodes hexagenia* var. *cookei* Pack (Hamilton, 1934), and among fleas, *Ceratophyllus arctomys* Baker (Hamilton, 1934), have been identified. Ectoparasites such as fleas, ticks, lice, flies, and mites occur on wild but not captive-born animals (Young and Sims, 1979). Woodchuck infection with hepatitis virus is endemic in the mid-Atlantic states but absent from populations in New York and much of New England (Wright et al., 1987). Tularemia and Rocky Mountain spotted fever can be transmitted from *M. monax* to humans by ticks, e.g., by *Ixodes cookei* (Ko, 1971). Bacterial infections are common in captive animals and streptomycins are toxic to woodchucks (Young and Sims, 1979).

Marmota monax has been used as a biomedical model for obesity, energy balance, reproduction, endocrine and metabolic functions, central nervous system control mechanisms, and cardiovascular, cerebrovascular and neoplastic disease (Christian et al., 1965; Concannon et al., 1997; Davis and McCarthy, 1965; Ganem, 1990; Young and Sims, 1979). A variety of virus particles very similar to those of human hepatitis B were found in woodchucks with woodchuck hepatitis virus (Summers et al., 1978), providing an experimental system for investigating human hepatocellular carcinoma (Cote et al., 1984; Ganem, 1990).

Common human complaints against woodchucks include its garden depredations. They are hunted occasionally by humans but with no apparent impact on their numbers (Grizzell, 1955). Seasons for hunting depend on state game laws. The most successful trapping method has been to live-trap. To handle animals, wire cones, gunny sacks, and cotton mesh bags are commonly used. Trapped animals have been marked with lacquer, dyes, and ear tags (de Vos and Gillespie, 1960; Grizzell, 1955; Hamilton, 1934; Young and Sims, 1979). Pens and cages for captive studies have been described (Albert et al., 1976; Grizzell, 1955; Hamilton, 1934; Young and Sims, 1979). Young animals, taken before weaning, accept captivity well, but wild-caught adults are aggressive (Young and Sims, 1979).

BEHAVIOR. Social organization differs among populations of woodchucks, with some studies suggesting some degree of sociality (Bailey, 1965b; Hamilton, 1934; Meier, 1992; Merriam, 1971; Swihart, 1992), while other studies suggest woodchucks are asocial (Barash, 1974b; Bronson, 1963, 1964; Davis, 1981; Ferron and Ouellett, 1989; Snyder et al., 1961). The social behavior of woodchucks in Pennsylvania was described as agonistic (Bronson, 1964). Of 66 observed interactions, 27 were chases, 13 were threats, and 26 were passive where only one individual overtly displayed. In contrast, in Ohio (Meier, 1992), 29 of 102 interactions were nonagonistic between siblings and their mother before weaning, and after weaning four observations of chasing and fighting were observed between two adult females, but all other observations between siblings and their mother or between adult males and females or subadults were nonagonistic. Frequent interactions include greetings (nuzzling), visual threats (back arched, tail erect and often flipped up and down, tail piloerection, and head directed towards opponent with mouth open and incisors obvious), tooth chattering, fights, and subtle avoidances ranging from simple crouching in a hole to a slight turning of the head (Bronson, 1964; Ferron and Ouellett, 1991; Hamilton, 1934; Meier, 1992).

Active scent marking with glands located in the oral angle has been described (Ouellett and Ferron, 1988; Walro et al., 1983). Cheek and chin rubbing behavior associated with scent marking is highest in frequency during breeding and minimal in summer (Hébert and Prescott, 1983). Agonistic interactions and scent markings are positively correlated. Scent marking occurs during exploration and all individuals mark burrow entrances and paths between burrows, suggesting territorial and self-assurance roles (Meier, 1991; Ouellett and Ferron, 1988).

Post-emergence weight loss in males is due to energetic demands of competition in establishing dominance/subordinance relationships that lead to reproductive success (Meier, 1985). Male woodchucks fight during early spring (Ferron and Ouellett, 1989; Hamilton, 1934), as indicated by a high frequency of scarring (Bronson, 1964). Male reproductive strategies include resident males defending hibernacula of females and transient males searching for estrous females (Meier, 1992). Post-reproductive behavior includes maintaining dominance/subordinance relationships with neighbors, and reacting agonistically to transients (Bronson, 1964). Summer ranges of adult males change little, but females increase ranges, indicating males are defending hibernacula and not females (Meier, 1985).

Behavioral development is summarized by Ferron and Ouellett (1991). Behaviors present at birth and associated with lactation include rooting, a "crawling under" reaction (Ferron and Ouellett, 1991:1043), teat seeking, an oscillation of the head from side to side, a righting motion, circular crawling, and forward linear crawling. Grasping begins at ca. 11 days, climbing at ca. 23 days, jumping at ca. 39 days, and the transition from crawling to walking at ca. 22 days. The first alert posture is standing on all fours (ca. 26 days) with forelegs stretched, the sitting alert posture follows at ca. 32 days, and the upright alert posture begins at ca. 37 days. Digging, a behavior associated with exploration, first appears at ca. 32 days. Scratching with the hind paw is the first grooming to appear (ca. 1–4 days) and grooming is organized into a sequence of care of different body parts at ca. 33 days. From their first day, young sleep in a curled position on one side and at ca. 30 days they can sleep in a curled sitting posture.

Social behaviors appear at ca. 6 days when defensive postures are first observed as they turn on their back or side when disturbed. Undirected defensive jumps begin at ca. 21 days and directed defensive jumps begin at ca. 26 days. First appearance of tail piloerection occurs at ca. 35 days, anal gland evagination at ca. 37 days, biting at ca. 38 days, and pulling food from siblings at ca. 42 days. Social grooming and play fighting are the only cohesive behavior patterns recorded in young woodchucks (Ferron and Ouellett, 1991) and appear shortly after initial emergence from the burrow. Play near the den is frequently exhibited in young animals, and less often, between young and mother. It may be preceded by nose-to-nose smelling (Ferron and Ouellett, 1991). As young mature, mother-young associations and solicitous behavior decline, and aggressive behavior increases. Of all marmot species, *M. monax* is the most aggressive and solitary at weaning (Barash, 1974a; Bronson, 1964).

Woodchucks are primarily diurnal, but they may be active at night (Howell, 1915). During the height of spring and summer activity, adult woodchucks spend only 1–5 hours each day above ground (Bronson, 1962; Hamilton, 1934). Many factors alter daily activity (Grizzell, 1955; Hamilton, 1934; Meier, 1985), but typically patterns consist of a unimodal activity peak at midday in early spring, late summer before hibernation, and during inclement weather, and a bimodal activity pattern with morning and late afternoon peaks during midsummer (Bronson, 1962; Meier, 1985).

Free-living woodchucks depend on olfactory, auditory, and visual clues to determine the presence of others (Bronson, 1963). Woodchucks have a well-developed voice (Hamilton, 1934; Lloyd, 1972) heard occasionally from distances up to 200–300 m. Infants at birth frequently utter high-pitched squeaks (solicitations) that increase in frequency until declining at weaning. The common whistle (alarm call—2.7–4.8 kHz) is often heard as a two-part whistle (Lloyd, 1972). Another noise (tooth chattering), made by grinding the cheek teeth together, denotes anger or fear (Ferron and Ouellett, 1991). Muffled barks, not unlike those of dogs, and soft purring noises occur (Hamilton, 1934; Lloyd, 1972).

The normal gait of the undisturbed woodchuck is a waddling walk with pauses to nibble vegetation or to rise to scan its surroundings. In walking, its feet are spread wide, its body is hung low, and it progresses up to 3 km/hr, but when alarmed or chased, it can lope or gallop up to 16 km/hr (Hamilton, 1934). Hibernating woodchucks ($n = 14$) vary their posture but most often lie on their sides with abdomen exposed (Albert and Panuska, 1979).

Although primarily terrestrial, woodchucks can climb trees, and they swim with head and tail above water (Hamilton, 1934; Howell, 1915; Merriam, 1884). *Marmota monax* digs simple and complex burrow systems with no uniformity of structure. Excavations are accomplished with alternate strokes of fore and hind limbs. Stones ($\geq$1 kg) are pushed with their head. A burrow system may be >2 m deep in loose, sandy soil, or less deep in gravelly soil, and usually is parallel to the surface, varying in length from 1 to 13 m or longer (Fisher, 1893; Hamilton, 1934). Usually there is provision for freshet by having the lowest part of the shaft midway between the entrance and nest chamber (Grizzell, 1955). Numbers of entrances vary from 1 to 11 (Grizzell, 1955; Merriam, 1971). Hibernation sites are usually in wooded areas, often on sloping, well-drained ground, and may be used throughout the year. Summer burrows, preferred for breeding and foraging activities, are usually in open, flat, or gently rolling areas, and are occupied from spring to early autumn. They are characterized by a main entrance with a mound of fresh earth and a small plunge (escape) hole. Plunge holes are concealed in vegetation and dug from within the main tunnel system, leaving little soil on the surface (Grizzell, 1955; Hamilton, 1934; Twitchell 1939). Most burrows have an enlarged hibernation or nest chamber, lined with dead leaves and dried grass. Nests are seldom >38 cm in diameter and are constructed of the nearest available plant material (Grizzell, 1955). Scats are deposited in a dry pocket off the main burrow tunnel or buried in the entrance mound. Burrows frequently have several blind pockets containing fecal remains partially covered with dirt. Females cover their young's waste with fresh bedding placed directly over the old, and occasionally matted material is removed and replaced (Grizzell, 1955; Hamilton, 1934; Merriam, 1971).

The greatest amount of food is consumed by woodchucks in the afternoon, but young animals growing rapidly feed at any time. They employ forepaws in food handling and do not cache food (Grizzell, 1955; Hamilton, 1934). An endogenous annual rhythm of appetite parallels weight gain and is independent of day length, temperature, and other demonstrable factors (Davis, 1970). Lack of torpor does not alter the endogenous annual rhythm of appetite and feeding (Davis, 1970). Mean food consumption (Fall, 1971) of recently-trapped adults in May was 254 g/day ($n = 15$), and steadily declined until October, when consumption was 146 g/day ($n = 15$). Juveniles consumed an average of 107 g/day ($n = 16$) in June, 260 g/day ($n = 4$) in July, and 122 g/day ($n = 13$) in October.

Predator-antipredator vigilance includes alert postures and interruption of foraging to look up. Average aggressive-interaction rates are about one per day per animal (Bronson, 1964). Maximum aggressiveness occurs when yearlings make their appearance from hibernation (Bronson, 1963, 1964). Threats, including vocalizations, are often given by high-ranking animals. When alarmed, woodchucks use paths worn in vegetation between burrows and feeding spots instead of taking shorter routes through vegetation (Hamilton, 1934).

Home range size varies with locality, with estimates of 0.39–1.00 ha in New York (Merriam, 1971), 1.10 ha in Pennsylvania (Bronson, 1963, 1964), 1.48 ha in Missouri (Twitchell, 1939), and 1.99 ha in Arkansas (Hayes, 1977)—with no reference made to sex or age class. Mean home range of six radio-tagged females in Ohio (Meier, 1992) after emergence from hibernation was 0.25 ha ($SD = 0.08$). After young were born in mid-April, 13 females expanded their home range (1.35 ha, $SD = 0.24$) which overlapped ranges of other females. In Ohio (Meier, 1992), the home range of radio-tagged resident adult males ($n = 8$) in the spring was 85% of the size of the summer home range (1.61 ha, $SD = 0.29$). Resident adult males in Ohio have home ranges containing hibernacula of 1–3 adult females, home ranges do not overlap with other males, and home ranges are stable during and between years (Meier, 1992). Because of aggressive interactions and scent marking, woodchucks are territorial, defending areas that were exclusive (with regard to sex—Meier, 1992). In Connecticut (Swihart, 1992), mean home range of nine radiocollared adult males was 4.0 ha ($SE = 0.88$) and of 18 radiocollared females was 1.96 ha ($SE = 0.38$). Mean overlap among home ranges of adult males was 31.2%, among males and reproductively active females was 33.5%, and among adult females was 13.5%. Although rare, simultaneous use of a burrow usually involved adult male and female. Space use was determined by dominance hierarchies among neighbors, and reproductively active females were intolerant of each other. In Quebec, prior to dispersal, mean home range of 10 radiocollared males was 55.6 ha and of eight radiocollared females was 0.6 ha, and male home ranges overlapped those of females but not those of other males (Ferron and Ouellett, 1989). After dispersal mean home ranges for males was 7.6 ha and for females was 4.9 ha. Spatial organization is territorial, but unlike Ohio and Connecticut populations, home ranges of adult males and adult females do not overlap after dispersal of young. In Pennsylvania (Bronson, 1964), overlap of home ranges (36%) does not differ among woodchucks of different age or sex, but decreases with lower population density. Space use is determined by dominance relationships, and residents react agonistically to neighbors and transients.

GENETICS. Based on one male *Marmota monax ochracea* from central Alaska and one female *Marmota monax preblorum* from New Hampshire, Rausch and Rausch (1971) reported a diploid number of 38 and a fundamental number of 66 (62 major autosomal arms). The karyotype has four metacentric, four submetacentric, five subtelocentric, and five acrocentric pairs of autosomes. The X chromosome is a medium-sized submetacentric and the Y chromosome is subtelocentric. Distinctive chromosomal characteristics separate *M. monax* from members of the *caligata*-group. In a study of whether genetic variability between woodchuck populations in the mid-Atlantic states could account for high and low rates of infection with woodchuck hepatitis virus, Wright et al., (1987) found significant heterogeneity between samples from New York and Delaware for two genetic loci.

REMARKS. Marmots of the *monax* group are known in northern states as woodchucks, in southern states as ground hogs, in eastern Canada, among French Canadians, as *siffleur,* and in central Canada, by the Cree Indian name *wenusk* (Howell, 1915). According to Grizzell (1955), the name woodchuck is not a compound word of wood and chuck; instead it is a corruption of Native American Indian words *wejack, woodshaw,* or *woodchoock,* a name applied to this animal by hunters, trappers, and traders in the Hudson Bay region. Supposedly, woodchuck is derived from the Cree *otcheck* or Chippewa *otchig,* which was applied to the fisher by Native American Indians but was transferred to the woodchuck by Europeans.

The American commemoration of Ground Hog Day originates from Candlemas Day, initiated in the 4th or 5th century by the Catholic church to commemorate the purification of the Virgin Mary 40 days after the birth of Christ (Reichmann, 1942). In addition to being a holy day, Candlemas marked the halfway point through winter and took on significance in European agricultural fairs in preparation for spring planting. Traditionally, local hedgehogs and badgers emerged from their dens to predict the coming of spring. A clear and cold February 2 meant a continuation of winter, but an overcast day meant spring was at hand. When early European colonists found neither hedgehog nor badger, the mid-sized day-active herbivore that happened to be handy became the animal of prophet.

Skull photographs courtesy of D. E. Wilson. Artwork courtesy of M. Howland and P. Morton.

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