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Marmota olympus.

By Andrew J. Edelman

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Marmota olympus (Merriam, 1898)

Olympic Marmot

Arctomys olympus Merriam, 1898:352. Type locality "From Timberline at head of Soleduc [= Sol Duc] River, Olympic Mountains, [Olympic National Park] Washington."

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

CONTEXT AND CONTENT. Order Rodentia, suborder Sciurognathi, family Sciuridae, subfamily Sciurinae, tribe Marmotini, genus *Marmota*. Fourteen species of *Marmota* are recognized, 6 occur in North America (Wilson and Reeder 1993). Similarities in morphology, chromosomes, and behavior place *M. caligata*, *M. olympus*, and *M. vancouverensis* in the superspecies *caligata* group (Hoffmann et al. 1979; Howell 1915). *Marmota olympus* is monotypic.

DIAGNOSIS. *Marmota olympus* is the only species of *Marmota* on the Olympic peninsula. Marmots of the *caligata* group are distinguished from other North American *Marmota* (*M. broweri*, *M. flaviventris*, and *M. monax*) by nearly circular shape of 2 posterior pads on sole of hind foot (Hall 1981; Hoffmann et al. 1979). *Marmota olympus* differs from both *M. caligata* and *M. vancouverensis* by having yellow-brown pelage upon emergence from hibernation, brown feet, larger body length (>7% larger), skull broader interorbitally with narrower zygomatic and postorbital regions, and U-shaped posterior border of nasals (Hall 1981; Hoffmann et al. 1979; Howell 1915).

GENERAL CHARACTERS. *Marmota olympus* (Fig. 1) is a large marmot that exhibits sexual dimorphism in body size. Means (ranges) of post- and prehibernation body mass (in kg), respectively, are: adult males, 4.1 (4.1–4.3, $n = 6$), 9.3 (8.5–11.0, $n = 5$); adult females, 3.1 (2.7–3.5, $n = 4$), 7.1 (6.7–7.5, $n = 6$); 2-year-old males, 3.0 (2.7–3.5, $n = 4$), 6.6 (6.4–6.8, $n = 5$); 2-year-old females, 2.7 (2.5–3.0, $n = 4$), 4.9 (4.5–5.1, $n = 5$); 1-year-old males, 1.5 (1.4–1.6, $n = 4$), 4.3 (4.0–4.7, $n = 4$); 1-year-old females, 1.3 (1.1–1.4, $n = 4$), 3.3 (3.1–3.6, $n = 4$—Barash 1973). Means (ranges) of adult body measurements (in mm) for males ($n = 3$) and females ($n = 2$), respectively, are total length, 740 (720–750), 680 (670–690); length of tail, 219 (210–237), 186 (180–192); length of hind foot, 106 (100–110), 95.5 (91–100—Howell 1915).

Pelage consists of 2 types of fur: a dense, soft underfur along back and sides and long, coarse guard hairs along entire body (Howell 1915). Tail is densely haired (Hoffmann et al. 1979). A white patch of fur occurs in front of eyes. Nose, lips, and chin are also white (Howell 1915). Upon spring emergence, pelage is yellow-brown in color. A molt begins during midsummer changing pelage to nearly black by hibernation (Barash 1973). One-year-olds have grayish brown pelage with a light brown rump; infants have dark gray pelage (Wood 1973).

Ears are small, rounded, and covered in fur. Legs are short; feet have 5 digits with curved fossorial claws; 3rd digit is longest, 2nd and 4th subequal, 5th smaller, and thumb is rudimentary with nail; palms of fore feet are hairless with 5 pads, 3 below digits and 2 posterior; soles of hind feet are hairless except for heel with 6 pads, 4 below digits and 2 posterior (Howell 1915). Cheek pouch is rudimentary and lacks retractor muscles (Hall 1981).

Skull (Fig. 2) has an almost straight and superior outline (Howell 1915). Rostrum and cranium are subequal; interorbital region is wider than postorbital region (Hall 1981). Nasals narrow posteriorly ending slightly wider than premaxilliae; U-shaped notch marks posterior border of nasals (Hall 1981; Howell 1915). Anterior floor of basioccipital is almost flat and bordered by 2 low processes that meet at center of basioccipital and continue as a ridge to foramen magnum. Palate is beveled along posterior border. In older adults, temporal ridges combine to form a pronounced sagittal crest (Howell 1915). Means (*SD*) of cranial measurements (in mm) for adult males ($n = 12$) and females ($n = 12$), respectively, are: condylobasal length, 103.27 (2.68), 99.83 (4.41); length of maxillary toothrow, 23.34 (0.77), 22.97 (0.80); nasal length, 43.23 (1.55), 41.98 (2.02); rostral width, 22.56 (1.11), 21.69 (0.98); zygomatic width, 64.22 (2.11), 62.76 (2.73); interorbital width, 27.53 (2.08), 25.76 (1.25); length of angular process, 54.93 (1.96), 52.98 (2.35); width of mastoid, 45.49 (1.59), 44.55 (2.20—Hoffmann et al. 1979).

Dental formula is i 1/1, c 0/0, p 2/1, m 3/3, total 22. Upper toothrows diverge anteriorly; P4 is equal or slightly larger than M1; cheek teeth are high-crowned; metaloph is complete on upper molars and on M3 turns posteriad and joins posterior cingulum; p4 is molariform, and its protolophid is a transverse crest between protoconid and parametaconid; m1 and m2 are parallelogram-shaped in occlusal outline (Hall 1981). Color of incisors is dull white in 1-year-olds and dull yellow to dark orange in adults and 2-year-olds (Barash 1973).

DISTRIBUTION. *Marmota olympus* is endemic to the Olympic peninsula in Washington, United States (Fig. 3). Their 1,800-km^2 range falls almost completely within Olympic National Park (Barash 1973). Colonies are typically found at altitudes of 1,500–1,750 m, although some are located as low as 920 m or as high as 1,990 m (Barash 1973; Wood 1973). Rare occurrences of individuals near sea level (30–200 m) have been observed (Scheffer 1995). No fossils are known.

FORM AND FUNCTION. Unlike other marmots (Barash 1989), 2 molts per year are reported for *M. olympus*. The 1st molt begins in July with 2 black patches of new fur first appearing on the back. Pelage growth then moves to the tail and haunches, finally covering shoulders, upper back, and head (Barash 1973). Completeness of molt is highly variable (from patches of black to all black) between individuals (Barash 1973; Elliot 1899). On rare occasions, an individual will not molt during the summer. Molting occurs earlier and more extensively in older animals and males. Young-of-the-year do not experience the summer molt. The 2nd molt has not been observed, but is suggested to occur during hibernation because the pelage is yellow-brown at spring emergence (Barash 1973).

Marmota olympus has 10 paired mammae (4 pectoral, 4 abdominal, 2 inguinal), although 1 individual with 9 mammae was

FIG. 1. Adult *Marmota olympus*. Photograph by G. L. Twiest, courtesy of the Mammal Images Library of the American Society of Mammalogists.

FIG. 2. Dorsal, ventral, and lateral views of cranium and lateral view of mandible of *Marmota olympus* (female from Deer Park, Olympic National Park, Callum County, Washington; University of Puget Sound, James R. Slater Museum of Natural History, 14760). Greatest length of skull is 104.0 mm. Photographs by R. Walker.

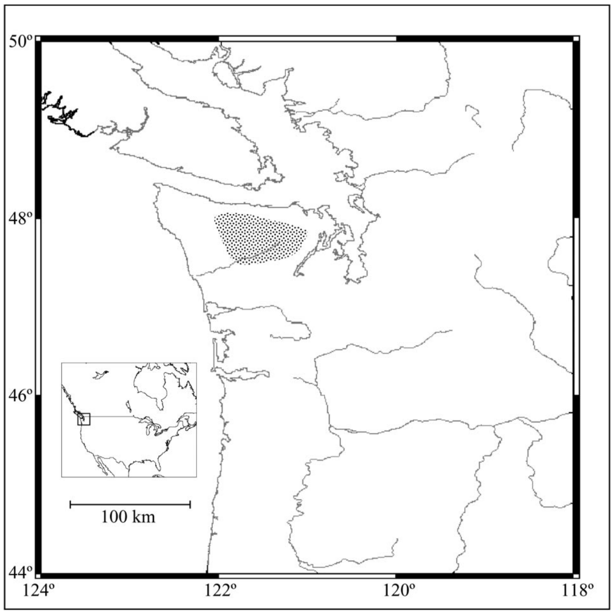

FIG. 3. Distribution of *Marmota olympus*.

recorded (Hoffmann et al. 1979; Howell 1915). Cheek and anal glands are present (Barash 1973).

Marmota olympus hibernates for 7–8 months per year (Barash 1973; Wood 1973). Adults emerge from hibernation during May, while 1-year-olds generally appear 1 month later. Snow cover does not affect the date of emergence. Individuals typically begin gaining weight immediately after emergence. The onset of hibernation is characterized by lethargic behavior and a decline in social interactions. Adult males and nonparous females enter hibernation in early September; 1-year-olds, infants, and parous females enter hibernation several weeks later. All colony members hibernate in the same burrow (Barash 1973), and the entrance is plugged with dirt (Wood 1973).

During the short active season, body mass is doubled regardless of age or sex (Barash 1973). Average daily weight gains (g/day, measure of variation not provided) for various age classes are as follows: young-of-the-year ($n = 2$), 28.9; 1-year-old ($n = 2$), 32.2; 2-year-old ($n = 2$), 23.8; adult female ($n = 1$), 22.9; adult male ($n = 1$), 16.1. Mean assimilation efficiency (range) of ingested food is 75 (61–90%, $n = 31$) for all age classes combined. Means ± *SE* of ingested energy and metabolized energy (cal/g/day), respectively, for various age classes are as follows: young-of-the-year ($n = 2$), 562 ± 35, 451 ± 34; 1-year-old ($n = 2$), 500 ± 52, 442 ± 55; 2-year-old ($n = 2$), 342 ± 17, 306 ± 17; adult female ($n = 1$), 665 ± 19, 593 ± 17; adult male ($n = 1$), 270 ± 38, 237 ± 36. Mean tissue growth efficiency and ecological growth efficiency ± *SE* for all age classes combined ($n = 31$) are 4.3% ± 0.8 and 3.6% ± 0.6, respectively (Wood 1973). Approximately 53% of body mass is lost during hibernation, which is the largest amount known for any *Marmota* (Armitage and Blumstein 2002).

ONTOGENY AND REPRODUCTION. Sexual maturity is reached at 3 years (Barash 1973). Sexual maturity is probably delayed to 3 years because the short growing season (40–70 days) prevents attainment of adult body size until the 4th summer (Barash 1974). Ovaries in 2-year-old females ($n = 2$) are mature except for the presence of medullary cords and the lack of corpora lutea. Sexual maturity may be variable among 3-year-old females because only 10 of 24 individuals were known to produce young. Two-year-old males have moderately enlarged testes (two-thirds of adult size) during the reproductive season but exhibit no sexual behavior. Breeding males have enlarged and descended testes (Barash 1973).

Females typically produce young every other year. Occasionally, a female will not reproduce for 2 years in a row. In a year of nonreproduction, the ovaries of an adult female lacked corpora lutea, and nonparous females exhibited no overt sexual behavior (Barash 1973).

Based on sexual behavior, estrus occurs the 2nd week after emergence. Gestation is ca. 4 weeks. Birth occurs underground, probably in late June (Barash 1973). Average litter sizes (ranges) are 3.7 (2–6, $n = 10$—Wood 1973) and 4.0 (2–6, $n = 25$—Barash 1973) young. Infants emerge from natal burrows during the 3rd or 4th week of July (Barash 1973; Wood 1973). Weaning likely coincides with emergence because infants begin foraging for food immediately after leaving the natal burrow (Barash 1973). The reproductive cycle (copulation to weaning) takes ca. 10 weeks (Barash 1989). Offspring stay with their mother until the start of their 3rd summer. Means (ranges) of infant body mass (in kg) several weeks after emergence and prehibernation, respectively, are male, 1.5 (1.5–1.6, $n = 3$), 1.6 (1.4–1.8, $n = 7$); female, 1.4 (1.2–1.6, $n = 5$), 1.6 (1.4–1.8, $n = 4$—Barash 1973).

ECOLOGY. *Marmota olympus* is commonly found near timberline on subalpine and alpine meadows and talus slopes of the Olympic Mountains. Many colonies are located on south-facing slopes, where food availability is probably greater because of earlier snowmelt (Barash 1973). Colonies typically encompass several plant communities with tall sedge, mesic grass, dwarf sedge, and *Valeriana* forb types being the most common (Wood 1973; for a complete description of plant communities see Kuramoto and Bliss 1970).

Marmota olympus is a diurnal herbivore that eats a variety of meadow flora including grasses, sedges, roots, and flowers. Plant species eaten varies depending on the plant communities available within the colony's range and changes throughout the summer as snow melts and different plants become available. Some of the most frequently eaten plant species include *Arenaria capillaries*, *Campanula rotundifolia*, *Erythronium montanum*, *Festuca idahoensis*, *Lilium columbianum*, *Lupinus latifolius* var. *subalpinus*, and *Polygonum bistortoides*. The inflorescences and upper 6–10 cm of new growth on plants are typically eaten (Wood 1973). Bark and cambium of *Abies lasiocarpa* and *Pinus monticola* are occasionally gnawed (Barash 1973; Watson 1976; Wood 1973). Dry grass is collected and placed in burrows for food or bedding. Parous females gather considerably more grass before emergence of litters than other colony members (Barash 1973).

Occasional carnivorous and cannibalistic behaviors occur. Two occurrences of individuals carrying dead chipmunks (*Tamias townsendii*) have been observed. Adult marmot bones were found in *M. olympus* scats in early June. Beef hearts placed at colonies were eaten when snow covered the ground but ignored after snowmelt (Barash 1973).

Snow is eaten after spring emergence, and water is drunk when available. In many colonies, standing water is not present, and moisture is likely derived from vegetation and dew (Barash 1973).

Grazing of subalpine meadows by *M. olympus* reduces the dominance of common plant species resulting in higher plant community diversity. Marmot herbivory around burrows reduces the abundance of palatable plant species and increases the abundance of unpalatable species present (del Moral 1984). Total impact of *M. olympus* and other herbivores is 30.4% of the net primary production in subalpine meadows (Wood 1973).

Marmota olympus is a polygynous colonial animal (Armitage 1981; Barash 1973). A typical colony consists of 1 adult male, 2 adult females (no more than 3), and varying numbers of 2-year-olds, 1-year-olds, and young-of-the-year. A 2nd adult male who is subordinate to the dominant male may live on the periphery of a colony. If the dominant male dies, the subordinate male can replace him. Because of alternating years of reproduction, each adult female is usually associated with either 1-year-olds or young-of-the-year. Within a colony, only 1 of the adult females typically gives birth each year. Occasionally, 2 females in a colony will reproduce during the same year. Nonreproducing females generally give birth the following year (Barash 1973).

Colonies contain several separate burrows used by colony members for shelter, hibernation, raising of young, and escape. Burrows are located in open meadows with slopes of 15–50 degrees (Barash 1989). Burrows are widely distributed throughout the colony area and range from 13–79 per colony. Individuals mainly forage ≤15 m from a burrow to allow quick escape from predators (Wood 1973). Burrow locations and landmarks of the colony must be relearned every spring. Upon spring emergence, all colony members (excluding subordinate adult males) usually cohabitate in the same burrow. Later in the season, varying groups of colony members will reside in several burrows. Parous females occupy their own burrow after mating. Large burrows with several openings are used as sleeping dens; trails run between the most frequently used burrows (Barash 1973; Elliot 1899). Large burrows have several chambers lined 30–38 cm deep with plant material (Beltz and Booth 1952). A dirt mound composed of excavated material averaging 0.8 m^2 is located below the burrow entrance and used as a lookout and resting spot (Barash 1973; Wood 1973). Smaller burrows scattered throughout the colony are used as temporary refuges or latrines and are shallow (120–180 cm deep) with usually only 1 opening (Barash 1973; Beltz and Booth 1952).

Known predators are coyote (*Canis latrans*) and puma (*Puma concolor*—Barash 1973, 1975). Other possible predators that elicit alarm calls include black bear (*Ursus americanus*), bobcat (*Lynx rufus*), fisher (*Martes pennanti*), bald eagle (*Haliaeetus leucocephalus*), golden eagle (*Aquila chrysaetos*), gyrfalcon (*Falco rusticolus*), northern harrier (*Circus cyaneus*), common raven (*Corvus corax*), and red-tailed hawk (*Buteo jamaicensis*—Barash 1973, 1975; Blumstein 1999; Watson 1976).

Ectoparasites include the fleas *Oropsylla* (*Oropsylla*) *eatoni* and *Oropsylla* (*Thrassis*) *spenceri spenceri* (Hubbard 1954; Lewis et al. 1988). The cestode *Diandrya composita* is a common endoparasite (Rausch and Rausch 1971).

Survivorship of male and female young-of-the-year is 55% and 52%, respectively and increases in 1-year-olds to 84% and 86%, respectively (sample size not provided—Barash 1989). Survivorship among 2-year-olds is unknown because many individuals disperse. In adults (≥3 years) mortality is lower among females than males. Longevity of individuals in the wild is unknown. Winter mortality is the primary source of death for *M. olympus*. In years with heavy snow cover, winter mortality is very low among all age classes. In years of light snow cover, winter mortality is high especially among young-of-the-year (50%). This high mortality rate is probably due to the lack of insulating snow, which increases the susceptibility of hibernating Olympic marmots to starvation, hypothermia, and disease. Young-of-the-year have higher surface-area-to-mass ratios and less insulation and fat reserves, making them more vulnerable to winter mortality (Barash 1973).

Olympic marmots acclimate quickly to human intrusion into colonies and allow observation of behavior. Differences in pelage, molt patterns, incisor color, and body size allow for individual recognition of adults and most 2-year-olds (Barash 1973; Wood 1973). This technique is difficult to use with 1-year-olds and young-of-the-year that are more homogeneous in color (Barash 1973). Marmots are live-trapped using box traps baited with peanut butter or salted oats (Armitage 1982; Barash 1973). Handling is possible by placing marmots in a cone-shaped bag with zippers that allows access for marking animals (Armitage 1982). Individuals can be marked with semipermanent ear tags (Wood 1973), permanent ear notching (Barash 1973), or hair dye (Armitage 1982).

BEHAVIOR. Activity is bimodal during June, July, and August, with most aboveground activity occurring in the morning and afternoon. Typical behavior consists of foraging or resting in or directly outside burrows. During midday most time is spent in the burrow. Before the morning and afternoon feeding periods, colony members engage in intense social interactions and enter all burrows in the colony. During periods of rain, snow, and fog, activity begins later and ends earlier, distance traveled is restricted, and no midday lull occurs. Just prior to hibernation, low levels of social and feeding behaviors are exhibited; most time is spent resting (Barash 1973).

Vocalizations include whistles, teeth chatter, growls, and yips. Vocalizations vary in length, interval, and harmonic structure, but all have a fundamental frequency ca. 2,700 Hz (Barash 1973). The following 4 distinctive alarm vocalizations are given in response to dangerous stimuli: ascending, flat, descending, and multiple-note trills. Ascending calls end >10% higher in frequency; flat calls begin and end at frequencies that differ no more than ±10%; descending calls end >10% lower in frequency; the multiple-note trill is a series of sort ascending calls repeated rapidly. The trill is an infrequently used call that denotes a high-risk situation (Blumstein 1999). The flat call is the most commonly used alarm call (Daniel and Blumstein 1998). Alarm calls are usually given once but occasionally >100 times. During these extended calling bouts, the duration of the calls remains unchanged, but the interval between calls decreases as the bout proceeds and increases toward the end. Alarm calls are not used to distinguish between predator types but can communicate relative risk by varying the number and rate. They are also given in response to conspecific alarm calls (Blumstein 1999). Alarm calls are sometimes given without apparent reason and in response to nonpredatory animals such as mule deer (*Odocoileus hemionus*), elk (*Cervus elaphus*), and mountain goats (*Oreamnos americanus*—Barash 1973; Blumstein 1999). When an alarm call is given, most colony members run to burrow entrances and enter or scan the area (Barash 1973). *Marmota olympus* alarm calls do not transmit optimally through their habitat (Daniel 1998; Daniel and Blumstein 1998).

Cheek glands are used by both sexes to scent mark rocks and vegetation. This behavior is most prominent during periods of intense social interactions and is seasonal in occurrence (June and July). Use of anal glands is unknown, but everted papillae have been observed in frightened individuals caught in traps (Barash 1973).

Marmota olympus is highly social and has the highest social complexity index (1.46) of any sciurid (Blumstein and Armitage 1997, 1998). Two common social behaviors are greeting and play-fighting. Greeting consists of nose-to-nose or nose-to-mouth contact initiated by 1 individual toward another. This behavior typically occurs among separated individuals after emerging from the burrow in the morning and afternoon. During longer greeting sessions, nose-to-cheek, ear chewing, and neck chewing may occur. Recipients of greetings respond by standing still, ignoring, or returning the greeting. The recipient may also growl or nip the initiator. These aggressive behaviors increase with the length of the greeting. Greeting rates are highest for adults in June and decline drastically as the summer progresses. During August, the recently emerged infants have the highest greeting rates. Play-fighting consists of 2 individuals standing on their hind legs and boxing or pushing against each other while their heads are thrown back. Play-fights are usually concluded when 1 animal runs away. All individuals engage in play-fighting, but the behavior becomes more aggressive as the age of the participants increases. Rates of play-fighting are highest in adults after emergence and decline thereafter. Upon emergence, infants engage in high levels of play-fighting, but the frequency of this behavior declines by the 3rd week aboveground (Barash 1973).

Reproductive behavior begins immediately following emergence from hibernation and peaks during the 2nd 10-day period after emergence (Barash 1973). Copulation occurs aboveground but may also take place below ground (Barash 1973, 1989). The adult male in the colony attempts to copulate with parous and nonparous females, although more frequently with the former. Mating behavior involves the male sniffing the female's genitals and chewing on her back or neck; the male mounts the female and grasps her around the middle and bites her neck; a receptive female responds by arching her tail and holding it to one side (Barash 1973).

Movement is characterized as a discontinuous series of steps often preceded by a flick of the tail. The pauses in movement may allow scanning of the area for conspecifics or predators (Barash 1973).

Feeding groups of ≤ 8 individuals are common until late summer and frequently change in composition (Barash 1973). Regardless of group size, foraging Olympic marmots spend a large percentage of time looking up (ca. 35%, $n = 20$) for predators (Blumstein et al. 2001). Foraging individuals ($n = 5$) averaged less time per minute looking up when in a group (14.8 s) than alone (33.1 s) allowing more foraging time (Barash 1973).

Dispersal of male and female 2-year-olds occurs in mid-July and is density dependent. In colonies with high winter mortality, few 2-year-olds disperse. In colonies with low winter mortality, almost all 2-year-olds disperse. Increased social interactions (greeting and play-fighting) at larger colonies may trigger dispersal of 2-year-olds. Dispersing 2-year-olds may establish new colonies usually in old colony sites with burrows (Barash 1973).

A general trend in dominance during social encounters exists between age and sex classes as follows (most dominant to least): adult male, adult females, 2-year-olds, 1-year-olds, and infants. Tail raising preludes aggressive behavior during greetings and play-fights. Aggressive behavior occurs by parous females toward adult males until emergence of litters and by resident males toward subordinate males. Subordinate males actively avoid resident males and are frequently chased from the main colony area. This aggression decreases throughout the active season, and by August the subordinate male is permitted to live with the rest of the colony (Barash 1973).

No territoriality exists within the colony. Individuals enter all burrows and move freely within the colony (Barash 1973). The home range of a colony averages 5.35 ha (2.0–8.7 ha), beyond which members rarely stray (Barash 1973; Blumstein et al. 2001). Several colonies may exist in close proximity (<500 m). Rates of agonistic encounters (fighting and chases) between residents of adjoining colonies are low, while those between more distant colonies are higher. Resident males aggressively chase off other adult males that enter colonies (Barash 1973).

GENETICS. The $2n = 40$ (Rausch and Rausch 1965, 1971); $FN = 66$ with 62 major autosomal arms. Autosomal pairs consist of 4 metacentric, 3 submetacentric, 5 subtelocentric, and 7 acrocentric chromosomes. The Y chromosome is subtelocentric, and the X chromosome is submetacentric (Rausch and Rausch 1971). Portions of the cytochrome *b* gene and pseudogenes are sequenced and registered with GenBank under the following accession numbers: AF100723, AF111182, AF143935, and AF143936 (Kruckenhauser et al. 1999; Steppan et al. 1999). Blood serum albumin is monomorphic (Hoffmann et al. 1979).

CONSERVATION STATUS. Barash (1989) believed the entire population of *M. olympus* consisted of <2,000 individuals. Most of the Olympic marmots' habitat is protected in Olympic National Park. A systematic parkwide survey was initiated in 2002, and preliminary results indicate that the total population of marmots may be higher than previously believed; however, sharp declines and local extirpations have occurred at several colony sites since the late 1980s, although other colonies appear to be stable in number. Predation by coyotes and tree encroachment into subalpine meadows may be responsible for these local declines (S. C. Griffin, pers. comm.). In Washington State, *M. olympus* is listed as a protected species, and hunting is prohibited by law (Washington Administrative Code 232-12-011).

REMARKS. *Marmota* is derived from the Latin words *mus* meaning "mouse" and *montis* meaning "mountain" (Jaeger 1944); *olympus* refers to the Olympic Mountains, to which the species is endemic. Other common names include whistler, whistling marmot (Scheffer 1995), and Olympic mountain marmot (Hall 1981).

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Associate editors for this account were Elaine Anderson and Lui Marinelli. Editor was Virginia Hayssen.

A. J. Edelman, School of Renewable Natural Resources, University of Arizona, 325 Biological Sciences East, Tucson, Arizona 85721, United States.