

Ochotona princeps. By Andrew T. Smith and Marla L. Weston

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Ochotona princeps (Richardson, 1828)

American Pika

- Lepus* (*Lagomys*) *princeps* Richardson, 1828:520. Type locality "Rocky mountains." Further restricted by Preble (1908:198) to "near the sources of Elk (Athabaska) River [Alberta]."
Lagomys minimus Lord, 1863:98. Type locality "Ptarmigan Hill." Further restricted by Howell (1924:28) to "near head of Ashnola River, Cascade Range, British Columbia."
[Ochotona] princeps Trouessart, 1897:648. First use of current name combination.
Lagomys schisticeps Merriam, 1889:11. Type locality "Donner [=Summit, Placer Co.], California."
Ochotona schisticeps: Merriam, 1897:223. Name combination.
Ochotona minimus: Bangs, 1899:39. Name combination.
Ochotona cuppes Bangs, 1899:40. Type locality "Monishee Divide, Gold Range, B[ritish] C[olumbia], altitude 4000 feet."
Ochotona saxatilis Bangs, 1899:41. Type locality "Snowy Range, Montgomery, Park Co., Colorado."
Ochotona cinnamomea Allen, 1905:121. Type locality "Briggs [=Britt's] Meadows, (alt. 11,000 ft.). Beaver Range, Beaver County, Utah."
Ochotona figginsi Allen, 1912:103. Type locality "Pagoda Peak, Routt County [Rio Blanco Co.], Colorado."
*Ochotona albatu*s Grinnell, 1912a:125. Type locality "near Cottonwood Lakes, 11,000 feet, Sierra Nevada Mountains, Inyo County, California."
Ochotona taylori Grinnell, 1912b:129. Type locality "Warren Peak, 9000 ft. alt., Warner Mts., Modoc Co., Calif[ornia]."
Ochotona levis Hollister, 1912:57. Type locality "Chief Mountain [=Waterton] Lake, [Glacier Co.], Montana."
Ochotona uinta Hollister, 1912:58. Type locality "Uintah Mountains, [Summit Co.], Utah."
Ochotona nigrescens Bailey, 1913:133. Type locality "Jemez Mts., [Sandoval Co.], New Mexico (alt. 10,000 feet)."
*Ochotona fenise*x Osgood, 1913:80. Replacement name for *Lagomys minimus* Lord (preoccupied by *Lagomys minimus* Schinz).

CONTEXT AND CONTENT. Order Lagomorpha, Family Ochotonidae. The genus *Ochotona* includes 14 to 18 extant species (Corbet, 1978; Corbet and Hill, 1986; Honacki et al., 1982; Weston, 1982), although as many as 25 species names are in current usage. These species are sometimes divided into subgenera, however, there appear to be no grounds for subgeneric divisions (Corbet, 1978; Honacki et al., 1982). *O. princeps* is most similar to the only other North American ochotonid, *O. collaris*, and the Asian *O. alpina* and *O. hyperborea*. Broadbooks (1965) and Youngman (1975) considered *O. collaris* and *O. princeps* to be one species, and Gureev (1964) and Corbet (1978) considered all four forms to be one species (*O. alpina*). Weston (1981, 1982) evaluated the relationships among these forms using 25 cranial and 17 mandibular measurements and concluded that the North American pikas each merited specific status. Hall (1981) recognized 36 subspecies of *O. princeps*, as follows:

- O. p. albata* Grinnell, 1912a:125, see above.
O. p. barnesi Durrant and Lee, 1955:6. Type locality "Johnson's Reservoir, 8,800 feet, 15 miles north of Loa (Fishlake Plateau), Sevier County, Utah."
O. p. brooksi Howell, 1924:30. Type locality "Sicamous, British Columbia."
O. p. brunescens Howell, 1919:108. Type locality "Keechelus, [Kittitas Co.], Washington."
O. p. cinnamomea Allen, 1905:121, see above.
O. p. clamosa Hall and Bowlus, 1938:335. Type locality "N rim Copenhagen Basin, 8400 ft., Bear Lake County, Idaho."
O. p. cuppes Bangs, 1899:40, see above.

- O. p. fenise*x Osgood, 1913:80, see above.
O. p. figginsi Allen, 1912:103, see above.
O. p. fumosa Howell, 1919:109. Type locality "Permelia [=Pamelia?] Lake, west base Mt. Jefferson, [Linn Co.], Oregon."
O. p. fuscipes Howell, 1919:110. Type locality "Brian Head, Parawan Mts., [Iron Co.], Utah."
O. p. goldmani Howell, 1924:40. Type locality "Echo Crater, Snake River Desert, [Butte Co.], Idaho (20 miles southwest of Arco)."
O. p. howelli Borell, 1931:306. Type locality "summit of Smith Mountain, Adams Co., Idaho, altitude 7500 feet (near head of Bear Creek, south end of Seven Devils Mountains)."
O. p. incana Howell, 1919:107. Type locality "Pecos Baldy, [Santa Fe Co.], New Mexico, altitude 12,000 feet."
O. p. jewetti Howell, 1919:109. Type locality "head of Pine Creek, near Cornucopia, south slope Wallowa Mts., Baker County, Oregon."
O. p. lasalensis Durrant and Lee, 1955:4. Type locality "Warner Ranger Station, 9750 feet, La Sal Mountains, Grand County, Utah."
O. p. lemhi Howell, 1919:106. Type locality "Lemhi Mountains, 10 miles west of Junction, [Lemhi Co.], Idaho."
O. p. littoralis Cowen, 1954:22. Type locality "Hagensborg, B[ritish] C[olumbia]."
O. p. lutenscens Howell, 1919:105. Type locality "Mt. Inglesmaldie, near Banff, Alberta."
O. p. moorei Gardner, 1950:344. Type locality "1 mile northeast of Baldy Ranger Station, Manti National Forest, altitude 10,000 feet, Sanpete County, Utah."
*O. p. mui*ri Grinnell and Storer, 1916:6. Type locality "9300 feet altitude near Ten Lakes, Yosemite National Park, Tuolumne County, California."
O. p. nevadensis Howell, 1919:107. Type locality "Ruby Mountains, southwest of Ruby Valley P.O., [Elko Co.], Nevada, altitude 10,500 feet."
O. p. nigrescens Bailey, 1913:133, see above.
O. p. obscura Long, 1965:538. Type locality "Medicine Wheel Ranch, 28 miles east of Lovell, 9000 ft., Big Horn County, Wyoming."
O. p. princeps (Richardson, 1828:520), see above (*levis* Hollister is a synonym).
O. p. saturata Cowen, 1954:23. Type locality "Mount Huntley in Wells Gray park, B[ritish] C[olumbia]."
O. p. saxatilis Bangs, 1899:41, see above.
O. p. schisticeps (Merriam, 1889:11), see above.
O. p. septentrionalis Cowen and Racey, 1946:102. Type locality "Itcha Mountains, British Columbia, altitude 6500 feet."
O. p. sheltoni Grinnell, 1918:429. Type locality "11,000 feet altitude, near Big Prospector Meadow, White Mountains, Mono County, California."
O. p. taylori Grinnell, 1912b:129, see above.
O. p. tutelata Hall, 1934:103. Type locality "Monitor Mountains, Greenmonster Canyon, 8150 feet, Nye County, Nevada."
O. p. uinta Hollister, 1912:58, see above.
O. p. utahensis Hall and Hayward, 1941:107. Type locality "2 miles west of Deer Lake, Garfield County, Utah."
O. p. ventorum Howell, 1919:106. Type locality "Fremont Peak, Wind River Mountains, [Fremont Co.], Wyoming."
O. p. wasatchensis Durrant and Lee, 1955:2. Type locality "10 miles above lower powerhouse, road to Cardiff Mine, Big Cottonwood Canyon, Salt Lake County, Utah."

DIAGNOSIS. *Ochotona princeps* may be distinguished from *O. collaris* using the following characters: 1) underparts have a buffy wash in contrast to the white underparts of *O. collaris*; 2) *O. princeps* lacks the grayish collar found on the shoulders of *O. collaris*; and 3) length of the tympanic bullae is generally <25% of the total skull length in *O. princeps* and >27% in *O. collaris*.

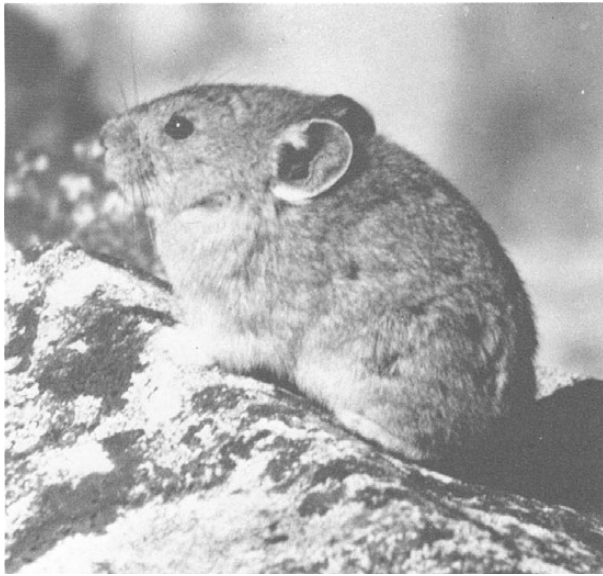


FIG. 1. Adult *Ochotona princeps* from Gunnison County, Colorado. Photograph by A. T. Smith.

GENERAL CHARACTERS. Overall body form of *O. princeps* is typical of that of ochotonids: small, short-legged, apparently tailless, and egg-shaped (Fig. 1). Actually, pikas have a "buried" tail that is longer relative to length of body than any other lagomorph. Moderately large suborbicular ears are haired on both surfaces and normally dark in color with white margins. The digitigrade hind limbs are not appreciably longer than the forelimbs, and the hind feet are relatively short among lagomorphs. Soles of the feet are densely furred except for small black naked pads at the end of the toes (Severaïd, 1955). There are five toes in front and four behind.

Within the ochotonids, *O. princeps* is intermediate in size, and there is considerable interpopulation variation. Length of body ranges from 162 to 216 mm; length of hind foot, from 25 to 35 mm (Hall, 1981); and mean body mass, from 121 to 176 g (Hall, 1981; Smith, 1978). Intrapopulation sexual dimorphism in size, when present (males larger than females), is slight (Brunson, 1973; Millar, 1971; Smith, 1981). Measurements of skulls of American pikas older than 1 year indicate no size differences between sexes (Weston, 1981; Wiseley, 1973). The skull (Fig. 2) is slightly rounded in profile, and the interorbital region is broad and flat. The rostrum is slender, and the nasals are widest anteriorly. The maxilla has one large fenestra, and the elongated jugals project far posterior to the zygomatic arm of the squamosal. The frontals lack postorbital processes. Average and extreme cranial measurements (in mm) of 225 specimens from throughout the range of *O. princeps* are: greatest length of skull, 43.6 (38.8–47.3); zygomatic width, 21.5 (19.6–23.1); breadth of braincase, 17.3 (15.9–18.5); least interorbital width, 5.3 (4.2–6.5); length of diastema, 10.0 (8.2–11.8); length of maxillary tooth row, 8.3 (7.4–9.0); palatal length, 7.4 (6.4–8.2); length of nasals, 13.5 (11.9–15.5); length of tympanic bulla, 11.0 (8.0–12.5); width of tympanic bulla, 9.7 (8.0–13.0; Weston, 1982). The dental formula is $i\ 2/1, c\ 0/0, p\ 3/2, m\ 2/3$, total 26. Molars have a simple enamel pattern, and the re-entrant enamel ridges on the upper cheekteeth are straight. The second upper premolar is decidedly smaller than P3, M2 has a projecting enamel loop on the interoposterior border, m3 is reduced to a single prism (not double), and the cutting edge of I1 has a V-shaped notch (Howell, 1924).

DISTRIBUTION. *Ochotona princeps* is distributed discontinuously in mountainous areas throughout western North America (Fig. 3). In the northern part of its range it is found at elevations ranging from sea level to 3,000 m. To the south the lower elevational limit of its range becomes progressively higher, as American pikas cannot tolerate high diurnal temperatures found at lower elevations (Grinnell, 1917; Smith, 1974a). Near the southern limits of its distributional range it is uncommon to find American pikas at elevations lower than 2,500 m.

FOSSIL RECORD. North American ochotonids probably arose from one or more Siberian immigrant ancestors (Dawson,

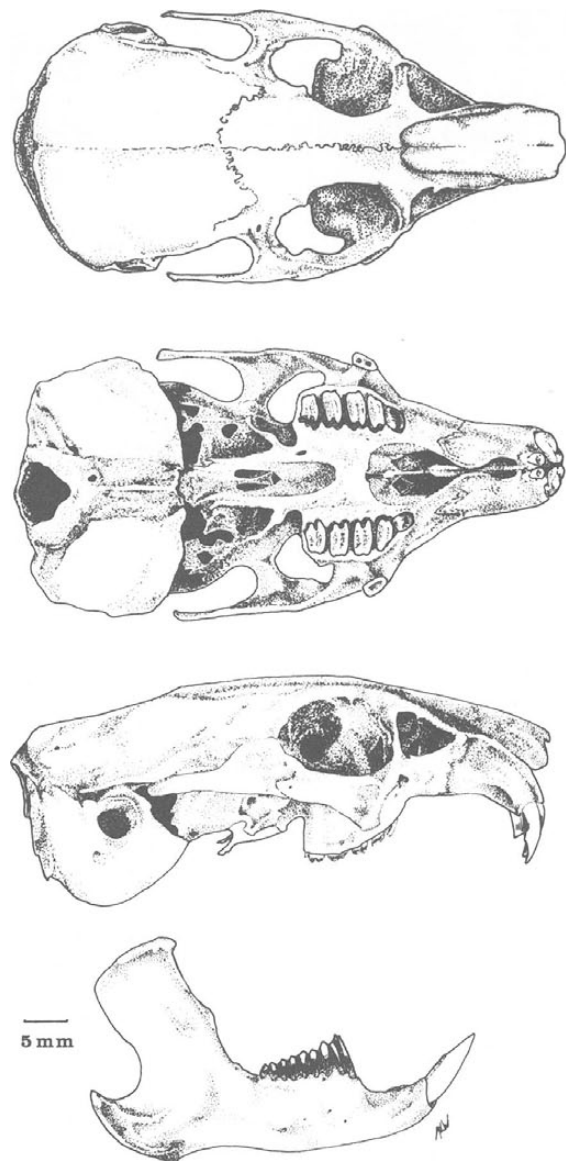


FIG. 2. Dorsal, ventral, and lateral views of the skull, and lateral view of the mandible of an adult *Ochotona princeps* (Cowen Vertebrate Museum 1086, male) from Alta Lake, British Columbia. Greatest length of cranium is 44.9 mm.

1967; Kurtén and Anderson, 1980). Mead (1987) reviewed the 46 Quaternary fossil and sub-fossil localities of *Ochotona* in North America. Of these, 36 contain specimens assigned to *O. princeps*. In general, fossil and Recent ochotonids appear to be morphologically conservative. The dental pattern that has proven useful in distinguishing among other lagomorphs varies little throughout the known Pliocene to Recent history of the genus *Ochotona* (Guilday, 1979; Weston, 1982).

Most of the fossil remains of *O. princeps* date the the Rancholabrean land mammal age, the last 500,000 years (Mead, 1987). By the Wisconsinan glacial period *O. princeps* was apparently restricted to the intermontane region of western North America. Geographic separation between *O. princeps* in the south and *O. collaris* in the north is probably the result of the Wisconsinan glaciation (Guthrie, 1973). It is likely that the range of *O. princeps* was pushed south with the advancing ice and cold temperatures, while *O. collaris* remained in the Bering refugium. Morphological differences between these two species have been attributed to character displacement during a period of pre-Wisconsinan sympatry (Weston, 1982).

Wisconsinan-age remains of *O. princeps* document that its geographic range extended 100 km south of its present distribution, and that it occurred at elevations lower than where it is currently found (Grayson, 1987; Mead, 1987). This record also indicates that

O. princeps did not always live in rocky or talus habitats. Throughout much of the Quaternary pikas apparently lived in valley-bottoms in steppe or grassland habitat (Mead, 1987), similar to many of the current *Ochotona* species in Asia (Smith, 1988). Throughout the Wisconsinan late glacial and into the Recent, summer temperatures increased and American pikas became isolated on suitable montane islands (Brown, 1971, 1978; Grayson, 1977, 1987). Continued warming and catastrophic events coupled with the demographic consequences of decreasing population sizes on mountaintop islands were responsible for extirpation of many isolated populations, and these conditions further prohibited re-colonization of these habitats (Brown, 1971, 1978; Grayson 1977, 1987; Thompson and Mead, 1982). By 7,500 years ago populations of *O. princeps* had apparently retreated up slope on isolated mountains and become habitat specific to talus, or become locally extirpated (Mead, 1987). Sub-specific differentiation within *O. princeps* may be due to the strong isolating role of these post-Pleistocene, low-latitude montane refugia (Guilday, 1979).

FORM AND FUNCTION. Pelage coloration is similar between the sexes, but varies with subspecies and season. There are two annual molts (Howell, 1924; Krear, 1965). Initiation of the summer molt of females is delayed about 2 weeks beyond that of males, apparently due to the costs of pregnancy and lactation (Krear, 1965; Severaid, 1955). Male molt begins at the head region and progresses steadily backwards and downwards over the sides, whereas female molt is of a more scattered or patchy nature (Krear, 1965). Midsummer pelage is worn a comparatively short time, generally for <2 months (Howell, 1924). Autumn molt appears to be the same for all American pikas, regardless of size or age; new winter hair appears first over the head region followed by the back, sides, and ventral regions. Autumn molt occurs much more rapidly than summer molt. In summer, dorsal pelage ranges from grayish to cinnamon-brown, often richly colored with tawny or ochraceous. Juveniles do not have a summer molt, but their soft gray coloration gradually matures into the adult color pattern by late summer. In winter, pelage is grayer and nearly twice as long as the summer pelage (Krear, 1965). The dense underfur is usually slate-gray or lead colored. Ventral pelage is predominantly whitish with a buffy wash. Vibrissae are conspicuously long (40–77 mm; Severaid, 1955).

Males do not possess a scrotum or a baculum; females do not possess a vulva (Duke, 1951). In both sexes, the rectal canal and urogenital canal are separated by a septum terminating 2 to 3 mm from the single "pseudocloacal" opening, which must be everted to expose the penis (long and pointed) or the clitoris (broad, with a shallow groove; Duke, 1951; Krear, 1965). Females have three pairs of mammae: one pectoral, one abdominal, and one inguinal. The mammae do not enlarge greatly during lactation (Smith, 1981). Unlike other lagomorphs, ovarian corpora lutea remain functional throughout lactation (Kirkpatrick and Satterfield, 1973). Testis length of adult males varies seasonally from 6 to 15 mm (Johnson, 1967). Males are considered sexually active (viable sperm in the testes and epididymides) when their testes are 11 mm in length or greater (Millar, 1972).

American pikas of both sexes possess an apocrine gland complex in the lower cheek (Harvey and Rosenberg, 1960), and they frequently deposit scent marks by rubbing the gland area on rocks. American pikas are able to discriminate among individuals by the odors emitted from these scent marks (Meaney, 1986, 1987). Scent marking occurs throughout the home range, but more frequently in areas of overlap with conspecifics of the opposite sex (Meaney, 1983, in press; Svendsen, 1979). American pikas cheek-rub throughout their active season, although the frequency of this behavior may be elevated during the breeding season or upon the colonization of a vacant territory (Meaney, 1983, in press; Smith and Ivins, 1984). When apocrine glands are experimentally removed, individuals have more difficulty keeping trespassers out of their territories than sham-operated American pikas (Reynolds, 1975). Thus, there may be a dual function to this behavior: territory advertisement or maintenance (Stewart et al., 1982), and sexual advertisement leading to mating (Meaney, 1986).

Adrenal mass of female American pikas ($\bar{X} = 31.8$ mg/100 g body mass) is significantly larger than that of males ($\bar{X} = 17.4$). For males, adrenal mass varies little with season, whereas female adrenals increase in mass in relation to pregnancy and lactation (Brunson, 1973; Millar, 1970).

American pikas are generalized herbivores, and the digestive system constitutes much of their body mass. American pikas deposit

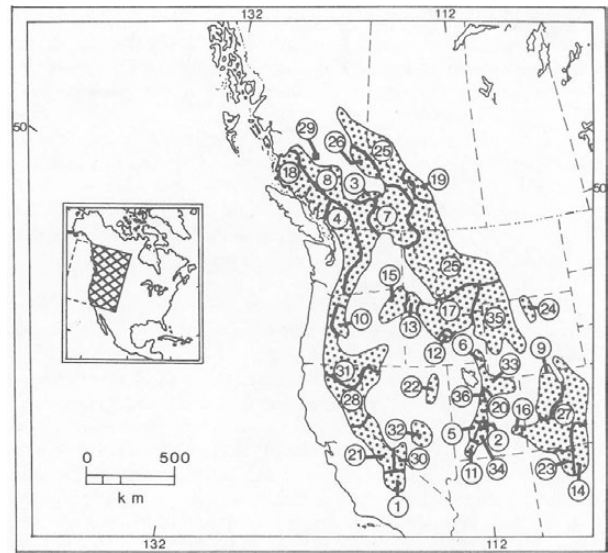


FIG. 3. Geographic distribution of *Ochotona princeps* based on Hall (1981): 1, *O. p. albata*; 2, *O. p. barnesi*; 3, *O. p. brooksi*; 4, *O. p. brunnescens*; 5, *O. p. cinnamomea*; 6, *O. p. clamosa*; 7, *O. p. cuppes*; 8, *O. p. fenissex*; 9, *O. p. figginsi*; 10, *O. p. fumosa*; 11, *O. p. fuscipes*; 12, *O. p. goldmani*; 13, *O. p. howelli*; 14, *O. p. incana*; 15, *O. p. jewetti*; 16, *O. p. lasalensis*; 17, *O. p. lemhi*; 18, *O. p. littoralis*; 19, *O. p. lutescens*; 20, *O. p. moorei*; 21, *O. p. muiri*; 22, *O. p. nevadensis*; 23, *O. p. nigrescens*; 24, *O. p. obscura*; 25, *O. p. princeps*; 26, *O. p. saturata*; 27, *O. p. saxatilis*; 28, *O. p. schisticeps*; 29, *O. p. septentrionalis*; 30, *O. p. sheltoni*; 31, *O. p. taylori*; 32, *O. p. tutelata*; 33, *O. p. uinta*; 34, *O. p. utahensis*; 35, *O. p. ventorum*; 36, *O. p. wasatchensis*.

two types of fecal droppings: a hard brown round pellet and a soft black shiny string of material formed in the caecum (Krear, 1965; Severaid, 1955). American pikas normally do not deposit their caecal pellets at the same localities where they urinate and drop hard pellets. Unlike other lagomorphs that void caecal pellets at night, American pikas may deposit these throughout the day (Johnson, 1967; Krear, 1965; Severaid, 1955). Some lagomorphs ingest all caecal pellets directly (coprophagy), whereas American pikas may either ingest them directly or store them for later consumption (Krear, 1965; Severaid, 1955). Caecal pellets have a higher energy value and protein content than plant food stored in haypiles. The daily energy intake of a non-gravid, non-lactating, adult American pika (171 g) has been estimated at 54.8 kcal (equivalent to filling a stomach nine times), of which about 68% is assimilated. Food intake, and perhaps caecal pellet reingestion, is increased during pregnancy and lactation (Johnson and Maxell, 1966).

There are a few detailed studies on the anatomy or physiology of *O. princeps*. Most studies have concentrated on adaptations to short summer seasons and extremes of temperature and elevations faced by American pikas. Like other pikas, *O. princeps* does not hibernate (Krear, 1965). Values for hematocrit, hemoglobin concentration, and erythrocyte count are low when American pika blood is compared with both the entire range of mammalian values as well as high-elevation species of similar body size (Brunson, 1973).

Ochotona princeps has a high body temperature ($\bar{X} = 40.1^{\circ}\text{C}$) and a relatively low upper lethal temperature ($\bar{X} = 43.1^{\circ}\text{C}$; MacArthur and Wang, 1973, 1974; Smith, 1974a). These temperatures may be respectively attributed to the high basal metabolic rate (1.53 cc O_2 g^{-1} h^{-1} ; 143% of the predicted weight-specific value) and low thermal conductance (0.096–0.050 cc O_2 g^{-1} h^{-1} ; 101–53% of the predicted values; MacArthur and Wang, 1973). The low thermal conductance indicates a reduction of energy consumption at ambient temperatures below the lower critical temperature of 21°C , thus favoring overwinter survival. Most thermoregulation in response to high ambient temperatures is behavioral rather than physiological, as hyperthermia and death may occur after brief exposures to moderate (25.5–29.4 $^{\circ}\text{C}$) ambient temperatures (MacArthur and Wang, 1973, 1974; Smith, 1974a). American pikas are relatively inactive on warm days, and near the lower altitudinal range of the species where temperatures may be hot, they shun activity throughout the midday hours (Smith, 1974a).

ONTOGENY AND REPRODUCTION. The pattern of reproduction in *O. princeps* is remarkably constant throughout the range of the species (Smith, 1978). Like other lagomorphs, American pikas are believed to be reflex ovulators (Kirkpatrick and Satterfield, 1973). Gestation is 30 days (Severaid, 1950). American pikas first breed as yearlings and are seasonally polyestrous. All adult females have two litters per year with a postpartum estrus (Kirkpatrick and Satterfield, 1973; Markham and Whicker, 1973; Millar, 1972, 1973, 1974; Severaid, 1950, 1955; Smith, 1978; Smith and Ivins, 1983a). Litter size (based on embryo counts) does not vary with age, habitat productivity, or between first and second litters (Millar, 1973, 1974; Smith, 1978).

Timing of reproduction in *O. princeps* is highly seasonal. First litters are conceived as early as will allow nursing under favorable feeding conditions (Millar, 1972; Smith, 1978; Smith and Ivins, 1983a). Timing of initiation of first litters at any site is a compromise between two conflicting demands. First, it is advantageous for a female to wean her litter early so as to ensure placement of her offspring on territories left vacant by overwinter adult mortality (Smith, 1978; Smith and Ivins, 1983a). Second, weaning is energetically taxing to females. During lactation, fat reserves are depleted (Millar, 1973) and rate of foraging is increased (Huntly et al., 1986; Sharp, 1973; Smith and Ivins, 1984). First litters tend to be conceived 1 month before snowmelt so that the spring flush of alpine vegetation is available to lactating females (Millar, 1972; Smith, 1978). Parturition occurs as early as March at some low-elevation sites, whereas throughout most of the range of *O. princeps*, parturition first occurs in May with a peak in June. Breeding this early is possible because American pikas do not hibernate and have access to food stored in their haypiles and on nearby meadows through the use of snow tunnels. As American pikas cannot determine in advance when snowmelt will occur in any given year, the variance of initiation of first litters is directly related to the long-term variance of snowmelt at a locality. Phenology of reproduction is more synchronous where snowmelt is predictable than at comparatively unpredictable sites (Smith, 1978).

Most females only wean one of the two litters they initiate, and one important contrast in reproductive performance within populations is the differential weaning success between first and second litters. In most populations <10% of weaned juveniles can be assigned to second litters (Kreier, 1965; Millar, 1973, 1974; Smith, 1978). Apparently, the demands of weaning the first litter compromise the ability of a mother to wean her second litter. When first litters are lost (due to predation or poor physiological condition of mothers), females are capable of weaning second litters (Smith and Ivins, 1983a).

Average litter size, as determined from counts of embryos, ranges from 2.34 to 3.68 throughout the range of *O. princeps*. Most populations living in typical high-elevation habitats have an average litter size from 3.0 to 3.1 (Millar, 1973; Smith, 1978). Predictability of adult mortality largely determines litter size at any particular locality through feedback from the average number of vacant territories available per year for settlement by juveniles (Smith, 1978).

The average number of young weaned per mother is often less than potential litter size as determined by mean ovulation rate. Millar (1973, 1974) documented a steady erosion in litter size due to preimplantation, postimplantation, and postnatal losses. Of all ova shed, 13% are lost before birth, while losses between birth and weaning are estimated at 21%. Relatively heavy losses occur among the largest potential litter sizes, and none of these losses appear to vary in relation to environmental parameters (Millar, 1973, 1974). For females successful at weaning at least one offspring, resorption occurs prior to mid-gestation and is limited to one embryo (Millar, 1973). Resorption of entire litters may also occur under conditions of extremely adverse weather conditions (Millar, 1974).

American pikas are among the fastest growing species within the Lagomorpha; they may reach minimum adult mass within 3 months of birth (Whitworth and Southwick, 1981). At birth, American pikas are altricial; they are slightly haired, eyes are closed, there are fully erupted teeth, and they have an average individual mass of 10 to 12 g (Millar and Tapper, 1973; Whitworth, 1984; Whitworth and Southwick, 1981). Eyes of young open at an average of 9 days of age (Whitworth, 1984). Mothers are away from the nest for extended periods. Females visit the nest once every 2 h and nurse for an average of 10 min each visit (Sharp, 1973; Whitworth, 1984). Captive young cannot survive independently of their

mother prior to 18 days of age (Whitworth and Southwick, 1981). The earliest adult-like behaviors to develop in young animals are those related to aggression and territoriality (agonistic behavior, scent-marking, and alarm-calling; Conner and Whitworth, 1985; Whitworth, 1984; Whitworth and Southwick, 1984). By the fourth week of age young are intolerant of, and spend little time in contact with, siblings and their mother (Whitworth, 1984). Weaning occurs as early as 3 to 4 weeks of age and after the young are surface-active (Millar and Tapper, 1973; Severaid, 1955; Smith and Ivins, 1987).

Ages of young American pikas may be determined accurately from their mass using a von Bertalanffy growth curve adapted to a particular population (Golian and Whitworth, 1985; Millar and Tapper, 1973). Millar and Zwickel (1972a) present a method for age determination of American pikas by counting the adhesion lines in the periosteal bone of the lower jaw. Annual mortality rates (average, 37–46%) are similar throughout the range of *O. princeps* (Millar and Zwickel, 1972a; Smith, 1974b, 1978). American pikas attain a maximum age of 7 years, and age-specific mortality rates are greatest in the birth–1- and 5–7-year age groups (Millar and Zwickel, 1972a; Smith, 1974b). Annual mortality of adults does not differ between males and females (Millar and Zwickel, 1972a).

ECOLOGY. *Ochotona princeps* is habitat specific to talus or piles of broken rock fringed by suitable vegetation. Given a range of rock sizes, American pikas select those from 0.2 to 1 m in diameter (Tyser, 1980). However, they often sit on larger, more prominent rocks, and haypiles (caches) are often situated under large boulders. American pikas are most commonly found near the talus–meadow interface, although their presence has been noted frequently on barren expanses of talus. American pikas occasionally inhabit man-made substrate such as mine tailings (Severaid, 1955; Smith, 1974a, 1974b) or piles of lumber or scrap metal (Lutton, 1975; Smith, 1974b). Talus habitat occupied by American pikas often is distributed patchily, leading to a local population structure that is island-like (commonly termed a metapopulation; Smith, 1974b, 1980, 1987). In general, American pikas do not dig burrows, however they may be capable of enlarging den and nest sites beneath the talus by digging (Markham and Whicker, 1972).

American pikas share their habitat with a variety of alpine mammals. Depending on the geographic area, American pikas are commonly sympatric with the following diurnal mammals: a marmot (*Marmota*), one or more chipmunks (*Tamias*), and one or more ground squirrels (*Spermophilus*; Barash, 1973a, 1973b; Broadbooks, 1965; Kreier, 1965; Smith, 1979; Tyser, 1980). Of these species, American pikas seem to be the most obligate residents of talus habitat (Barash, 1973a, 1973b). American pikas also share their habitat frequently with the ecologically similar, but nocturnal, bushy-tailed woodrat (*Neotoma cinerea*; Smith, 1974b). There are no data to indicate that any interspecific competition occurs between American pikas and any of these species.

Foraging follows a similar pattern throughout the range of *O. princeps*: 1) differences in species composition of plants harvested are frequent and reflect variation in the composition of plant communities; 2) at any locality some plants are selected over others, and some are not harvested at all; and 3) selected plants are commonly harvested in a definite sequence that normally corresponds to their seasonal phenology (Broadbooks, 1965; Conner, 1983a; Elliott, 1980; Huntly, 1987; Huntly et al., 1986; Kreier, 1965; Millar and Zwickel, 1972b; Smith, 1974a; West, 1981). Apparently, American pikas assess the nutritional value of available food and harvest accordingly. Selected plants have a significantly higher caloric, protein, lipid, and water content than nonselected plants (Millar and Zwickel, 1972b; Smith, 1974a; West, 1981). Avoidance of some abundant plants may also be due to the presence of toxic chemicals (Smith, 1974a; West, 1981).

American pikas execute two discretely different modes of foraging: direct consumption of food (feeding) and the caching of vegetation in haypiles for later use (haying). Whereas feeding occurs throughout the year, haying is confined to the summer months following the breeding season (Conner, 1983a; Huntly et al., 1986; Smith and Ivins, 1984). Adult males begin to hay earlier than adult females, and adults begin haying earlier than young of the year (Huntly et al., 1986; Kreier, 1965; Smith and Ivins, 1984). Feeding rates of adult females are greater than those of adult males during the reproductive season (Huntly et al., 1986; Smith and Ivins, 1984). American pikas are central-place foragers. When haying, American

pikas travel significantly farther into the meadow from the talus border than when feeding. Higher proportions of forbs and tall grasses are hayed than eaten directly; the most common plant type eaten is short alpine grasses (Huntly et al., 1986). The result of this selectivity and the differential in distance from talus between haying and feeding is a gradient of plant abundance and species richness that increases with distance from the talus. Unlike most forbs, cushion plants are characteristically maintained close to the talus-meadow interface where it is believed they form an important food for American pikas foraging during winter from snow tunnels (Huntly, 1987; Huntly et al., 1986). Lichens may also be an important source of winter food (Conner, 1983a).

Haypiles may be constructed on the surface of the talus or tucked under rocks leaving little vegetation exposed. A common, but untrue, myth (Seton, 1937) is that American pikas dry or "cure" their hay on the surface of the talus and then furtively store it in their haypiles when it begins to rain. Hay is stored directly in the haypile. Most haypiles are constructed near the talus-meadow interface in traditional localities (Broadbooks, 1965; Smith, 1974b; Tapper, 1973). Amount of vegetation stored in haypiles may vary with sex (males more than females), age (adults more than juveniles), forage availability on nearby meadows (more luxuriant meadows yield larger haypiles), and with distance vegetation has to be transported (the greater the distance, the smaller the haypile; Millar and Zwicker, 1972b). American pikas appear to collect as much vegetation as possible during the haying season, but this amount apparently is insufficient to provide an exclusive source of food during winter. Millar and Zwicker (1972b) experimentally removed entire haypiles in autumn, and survivorship to the following spring did not differ from the control group in which haypiles were left intact. The adaptive significance of haypiles is apparently related to the need to serve as a potential winter food supply during years when the winter season is unusually harsh or prolonged (Conner, 1983a; Millar and Zwicker, 1972b).

Territory size (defended area) and home range size (total area used; definitions in Smith, 1981) are correlated, with territory size averaging about 55% of home range size (Ivins, 1984; Kawamichi, 1982; Smith and Ivins, 1986). Measurements of territory and home range size appear remarkably constant throughout the range of *O. princeps*. Territory sizes have been reported as 709 m² (Kawamichi, 1976, 1982), 527 m² (Smith and Ivins, 1986), and 410 m² (Svendsen, 1979). Home range sizes are dependent upon methods of analysis and number of independent spatial observations (Kawamichi, 1982; Smith and Ivins, 1984; Tapper, 1973). Using data from the same study a bivariate normal home range program yielded average August home range sizes from a saturated population of 2,182 m² (males) and 1,782 m² (females), whereas cumulative counts of utilized 5- by 5-m quadrats yielded values of 1,059 m² (males) and 861 m² (females; Smith and Ivins, 1984). Kawamichi (1982) determined home range sizes of 1,149 m² by including the area inside the periphery of travel routes and of 1,579 m² by counting the number of utilized 5- by 5-m quadrats. Space use by American pikas also may be determined by measuring the nearest-neighbor distance between haypiles or centers of activity of individuals. The following average nearest-neighbor measurements between haypiles have been reported: 32.6 m in Washington (Broadbooks, 1965); 28.4 m in the Sierra Nevada, California; 21.8 m at Bodie, California (Smith, 1974b); and 14 m in Colorado (Smith and Ivins, 1984).

Ochotona princeps adults are individually territorial, and the sex ratio of adults has been close to unity in all studies of fully-marked populations. Average territory sizes of males and females are equivalent (Smith and Ivins, 1984; Tapper, 1973). Territory size and shape may vary locally as a result of different configurations of talus (small rock slides have smaller territory sizes than larger ones; Kawamichi, 1982), varying distance from the territory to vegetation (territory size increases with distance from vegetation; Krear, 1965; Tapper, 1973), and quality of vegetation (territory size increases as habitat quality decreases; Millar and Zwicker, 1972b). Territory size also varies seasonally, being significantly larger in early summer than in late summer (Smith and Ivins, 1984; Tapper, 1973).

Spacing of males and females on the talus is non-random; adjacent home ranges tend to be occupied by American pikas of the opposite sex (Brandt, 1989; Krear, 1965; Sharp, 1973; Smith and Ivins, 1984; Tapper, 1973). In addition, this paired spacing pattern persists in time because home ranges are usually occupied sequentially by animals of the same sex as the previous occupant (Krear,

1965; Sharp, 1973; Smith and Ivins, 1983b, 1984; Tapper, 1973). Overlap of home ranges is greater and nearest-neighbor distances are less between paired adults than between nearest-neighbors of the same sex (Smith and Ivins, 1984; Svendsen, 1979). Spatial overlap between paired adults is greatest in early to mid-summer and significantly reduced in late summer to early autumn (Meaney, 1983, in press; Smith and Ivins, 1984). Population size in American pikas is stable among years (Smith, 1978; Southwick et al., 1986). Estimates of population density are 2.2 to 7.4/ha (Kawamichi, 1982), 4.0 to 8.6/ha (Smith and Ivins, 1983b), and 3.4 to 9.9/ha (Southwick et al., 1986).

Potential predators of American pikas include coyotes (*Canis latrans*), longtail weasels (*Mustela frenata*), shorttail weasels (*M. erminea*), and pine martens (*Martes americana*; Ivins and Smith, 1983; Krear, 1965; Lutton, 1975; Murie, 1961; Quick, 1951). Larger predators are less successful than weasels in their ability to capture American pikas; weasels can follow American pikas into the talus interstices where coyotes and martens cannot go (Ivins and Smith, 1983). All American pika skulls found in coyote scats by Krear (1965) were juveniles, indicating young animals are vulnerable to predation and may be caught while trying to disperse between patches of talus. A variety of predatory birds occur in the habitat of American pikas, but these probably do not kill many individuals (Krear, 1965; Severaid, 1955).

Severaid (1955) lists 37 genera and 66 species of ectoparasites harbored by *O. princeps* and reviews the prevalence of endoparasites and disease in the species. Coccidia (Protozoa, Eimeriidae) and gastrointestinal helminths in American pikas have been investigated by Hobbs (1976, 1980) and Hobbs and Samuel (1974). Both coccidia and helminth faunas in *O. princeps* (and *O. collaris*) are shared with *O. hyperborea* of Asia, leading Hobbs (1976) to conclude that both North American species of pika are derived from one ancestral species that migrated across Beringia.

BEHAVIOR. American pikas are surface active about 30% of daylight hours (Smith and Ivins, 1986). The most pronounced behaviors of American pikas are 1) surveillance (or musing, sitting on a prominent rock), which may account for as much as one-half of the time an animal is surface active; 2) haying or feeding; 3) vocalizing; and 4) engaging in activities related directly to territory establishment or maintenance (including vocalizing, cheek rubbing, aggression and social tolerance; Smith and Ivins, 1984).

Ochotona princeps has two frequently used characteristic vocalizations (the short call and the long call or song), although several other distinct acoustic signals have been recorded and classified (Conner, 1985a). The short call varies geographically, but is uniform within populations (Conner, 1982, 1983b; Somers, 1973). Short calls are given in two contexts: as an alarm-call to both potential terrestrial and avian predators and to discourage conspecifics from intruding on one's territory (Conner, 1983b, 1984, 1985a; Ivins and Smith, 1983; Kawamichi, 1976; Kilham, 1958; Sharp, 1973; Smith and Ivins, 1984; Svendsen, 1979). Territorial and alarm short calls produced by the same individual may be differentiated by call structure, but there is no single call characteristic or set of characteristics that varies together among all individuals in a population (Conner, 1985a). American pikas respond differently to calls uttered by different individuals, and the strength of response appears related to the relative threat that the conspecific represents (Conner 1984, 1985b). Short calls are uttered most frequently during mid-summer (when juveniles are attaining adult size and becoming potential competitors for territories, and when adults are at their peak of haying activity; Conner, 1985a; Sharp, 1973; Smith and Ivins, 1984). Alarm-calls are generally repetitive short calls. American pikas utter alarms less frequently and delay the initiation of calling more often when they detect weasels than pine martens, presumably to avoid detection by weasels (Ivins and Smith, 1983). Long calls are given almost exclusively by adult males (Conner, 1985a; Krear, 1965; Smith and Ivins, 1984; Tapper, 1973; West, 1981). These calls are most common during the breeding season, although both males and females may give long calls in autumn (Conner, 1985a).

Territories are primarily defended by aggression (chases and fights between conspecifics). Aggressive acts occur rarely (Smith and Ivins, 1984) and normally occur between animals of the same sex (Krear, 1965; Smith and Ivins, 1984). A hierarchy may exist within the territorial system such that certain individuals are aggressive and dominant over others (Kawamichi, 1976; Sharp, 1973; Tapper, 1973). The highest frequency of aggressive acts occurs when un-

familiar animals of the same sex, for example a resident and an immigrant, come into contact (Smith and Ivins, 1984). American pikas frequently intrude on the territories of conspecifics (usually neighbors), but they usually do so when the resident is inactive (Smith and Ivins, 1987).

Social cohesion among nearest-neighbor American pikas of the opposite sex (pair-mates) is maintained by exhibiting social tolerance and engaging in short call duets. The mating system of *O. princeps* is classified as facultatively monogamous based on the paired configuration, its persistence in time, and the interplay of aggression and social tolerance behaviors (Smith and Ivins, 1984). Females may exhibit mate choice when more than one potential mate is available (Brandt, 1989).

Juveniles are born into the relatively permanent and static social organization of adult territory holders. The probability of a juvenile living to adult age is directly contingent on its finding a vacant territory to occupy. The appearance of a vacancy is neither frequent nor predictable in time and space (Smith, 1978, 1987; Smith and Ivins, 1983b). Juveniles face high rates of aggressive behavior by unfamiliar adults should they disperse (Smith and Ivins, 1983b, 1984). Also, the likelihood of successful dispersal across non-talus habitat is low (Smith, 1974a, 1974b, 1978, 1980). As a result, most young are philopatric, remaining on their natal or an adjoining home range (Brandt, 1985; Smith and Ivins, 1983b; Tapper, 1973). Only 25% of all juvenile American pikas may attempt to disperse (Smith, 1987). Brandt (1985) and Tapper (1973) noted that the few animals dispersing >100 m tended to be females. There was no sex bias in dispersal in the study of Smith and Ivins (1983b). While living on their natal home range, juveniles occupy areas as widely separated as possible from their mother, putative father, and siblings. In addition, philopatric juveniles are most likely to be active when their parents are inactive (Smith and Ivins, 1987).

GENETICS. The diploid number of chromosomes is 68; there are four submetacentric autosomes and 62 acrocentric and subtelocentric autosomes. Both the X and Y chromosomes are submetacentric; however, the Y chromosome can be distinguished by its smaller size (Hsu and Benirschke, 1971; Wurster et al., 1971). The diploid number of *O. princeps* is the same as the North American *O. collaris* (MacDonald and Jones, 1987; Rausch and Ritter, 1973) and *O. pusilla* from the Palearctic steppes (Vorontsov and Ivanitskaya, 1973). The two Asian species most similar to *O. princeps*, *O. alpina* and *O. hyperborea*, have diploid numbers of 42 and 40, respectively (Vorontsov and Ivanitskaya, 1973).

Ochotona princeps has low levels of genetic heterozygosity based on electrophoretic analysis (Brunson et al., 1977; Glover et al., 1977; Tolliver et al., 1985; Wiseley, 1973). Estimates of mean heterozygosity range from 0.5 to 1.4%. These values are among the lowest estimates reported for a mammal having a broad distribution and the lowest reported for a lagomorph.

REMARKS. *Ochotona* stems from the Mongolian name "ochodona," and *princeps* is a Latinized form of "chief" from the Chipewyan Indian name for pika, "little chief hare" (Seton, 1937). The name pika comes from the vernacular "piika" of the Tunguses, a tribe from northeastern Siberia (Gotch, 1979; Howell, 1924). The designation "American pika" follows Gotch (1979) and Corbet and Hill (1986). *O. princeps* has also been called the "Rocky Mountain" or "southern pika." Other common names for pikas are rock rabbit, piping hare, hay-maker, mouse-hare, whistling hare and cony (not the biblical "coney," which refers to hyraxes).

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