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2004-07-13

## Zapus princeps

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## **Zapus princeps**

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Source: Mammalian Species, 2004(749) : 1-7

Published By: American Society of Mammalogists

URL: <https://doi.org/10.1644/749>

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*Zapus princeps*. By E. Blake Hart, Mark C. Belk, Eralee Jordan, and Malinda W. Gonzalez

Published 13 July 2004 by the American Society of Mammalogists

*Zapus princeps* Allen, 1893

Western Jumping Mouse

*Zapus princeps* Allen, 1893:71. Type locality “Florida, La Plata Co., Colorado.”

*Zapus pacificus* Merriam, 1897:104. Type locality “Prospect, Rogue River Valley, Jackson Co., Oregon.”

*Zapus saltator* Allen, 1899:3. Type locality “Telegraph Creek, British Columbia.”

**CONTEXT AND CONTENT.** Order Rodentia, suborder Myomorpha, superfamily Dipodoidea, family Zapodidae, subfamily Zapodinae, genus *Zapus*. Three species of *Zapus* are recognized: *Zapus princeps*, *Zapus hudsonius*, and *Z. trinotatus* (Hall 1981; Krutzsch 1954). Eleven subspecies of *Z. princeps* are recognized (Hafner et al. 1981; Hall 1981; Krutzsch 1954).

*Z. p. chrysoyenus* Lee and Durrant, 1960:171. Type locality “2 mi. NE La Sal Peak, La Sal Mountains, 8500 ft., Grand Co., Utah.”

*Z. p. cinereus* Hall, 1931:7. Type locality “Pine Canyon, 6600 ft., Raft River Mountains, 17 mi. NW Kelton, Boxelder Co., Utah.”

*Z. p. curtatus* Hall, 1931:7. Type locality “Head of Big Creek, 8000 ft., Pine Forest Mountains, Humboldt Co., Nevada.”

*Z. p. idahoensis* Davis, 1931:221. Type locality “5 mi. E Warm Lake, 7000 ft., Valley County, Idaho.”

*Z. p. kootenayensis* Anderson, 1932:108. Type locality “Near summit Green Mountain, head of Murphy Creek, about 10 mi. N Rossland, West Kootenay District, British Columbia at about 6000 ft., latitude 49 degrees 13 minutes north, longitude 117 degrees, 52 minutes west.”

*Z. p. minor* Preble, 1899:23. Type locality “Wingard, near Carlton House, Saskatchewan.”

*Z. p. oregonus* Preble, 1899:24. Type locality “Elgin, Blue Mountains, Union Co., Oregon.”

*Z. p. pacificus* Merriam, 1897:104, see above.

*Z. p. princeps* Allen, 1893:71, see above.

*Z. p. saltator* Allen, 1899:31, see above.

*Z. p. utahensis* Hall, 1934:3. Type locality “Beaver Creek, 19 mi. S Manila, Daggett County, Utah.”

**DIAGNOSIS.** *Zapus princeps* (Fig. 1), *Z. hudsonius*, and *Z. trinotatus* have similar color patterns. When *Z. princeps* molts, new hair 1st appears on mid-dorsal surface between scapulae and then progresses anteriorly, laterally, and posteriorly. New hair of *Z. hudsonius* and *Z. trinotatus* appears simultaneously on anterior dorsal surface of nose and on middorsal surface between scapulae, migrating posteriorly and anteriorly, respectively (Krutzsch 1954).

Total lengths of *Z. princeps* (range, 216–247 mm) and *Z. trinotatus* (221–238 mm) overlap. In contrast, the length of *Z. hudsonius* (188–216 mm) is less than and overlaps little with *Z. princeps*. Diameter of guard hair is similar in *Z. princeps* (140  $\mu$ ; range, 130–168  $\mu$ ) and *Z. trinotatus* (141  $\mu$ ; 133–155  $\mu$ ), both having larger diameters compared to *Z. hudsonius* (115  $\mu$ ; 96–140  $\mu$ —Jones 1981; Krutzsch 1954).

Bacula of *Z. princeps* are longer (>5.1 mm) and more robust than bacula of *Z. hudsonius* (<5.1 mm—Krutzsch 1954). Width of bacular tips of *Z. princeps* is 0.2–0.9 mm and width of bases is 0.6–1.0 mm; bacular dimensions and extent of spatulation vary among members of interior populations. Bacula of *Z. hudsonius* are similar in form, but smaller than those of *Z. princeps*, with total lengths of 4.5–4.9 mm, tip widths averaging 0.28 mm (0.1–0.4 mm), and width of bases averaging 0.74 mm (0.5–1.0 mm). Bacula of *Z. trinotatus* are larger, with total lengths of 6.7–7.4 mm; broader

dorsal, spade-shaped, bases tilting upward from 0.7 to 0.9 mm, and tips 0.44–0.57 mm wide (Jones 1981).

Skull of *Z. princeps* is large with incisive foramina >4.7 mm and condylobasal length >21 mm (Fig. 2). Rostrum is broad but tapering; pterygoid fossa are moderately narrow; anterior ramus of zygomatic process usually is broadly rounded and elongate; auditory bullae are moderately inflated; and coronoid process of mandible is relatively short. Base of zygomatic process of squamosal is narrow and coronoid process of mandible is short and relatively weak (Krutzsch 1954). Skulls of *Z. hudsonius* are smaller and relatively narrow when compared to length; rostrum is pointed and short; incisive foramina are <4.6 mm and condylobasal length averages <20 mm; mastoid region is relatively narrow; and teeth are generally shorter and narrower with a strongly inflected mandible. *Z. trinotatus* has a large, broad, and deep skull in relation to length. Pterygoid fossa is broad and anterior ramus of zygomatic process of maxillary and coronoid process of mandible are elongate (Krutzsch 1954).

Length of maxillary toothrow of *Z. princeps* averages >3.8 mm and palatal breadth at M3 is >4.4 mm compared to length of maxillary toothrow of *Z. hudsonius* with an average of <3.7 mm (variation and *n* not available). Palatal breadth at M3 is <4.2 mm in *Z. hudsonius*. In *Z. trinotatus*, upper premolars are large (mean length, 0.70; mean width, 0.75 mm; variation and *n* not available) and have a crescentine fold on occlusal outside. M3 is relatively large and elongated and M1 is broadly elongated and rounded anteriorly (Krutzsch 1954). *Z. princeps* has a 4th upper premolar (4 upper cheek teeth—Jones 1981). Occlusal patterns within *Zapus* are not useful (Krutzsch 1954). M1 and M2 are consistent within species (Klingener 1963). Compared to *Z. princeps*, *Z. hudsonius* has an anteromedian fold of anteroconid of M1 and the presence of a free paracone in M1 and M2 (Jones 1981; Klingener 1963).

In zones of sympatry, paracone of M1 and M2 of *Z. hudsonius* is not connected to occlusal pattern, although 1st primary and 1st secondary folds are continuous medially. In *Z. princeps*, paracone is broadly connected and 1st primary and 1st secondary folds do not converge (Jones 1981).

*Zapus princeps* has a vertebral formula of 7 C, 12–13 T, 6–7 L, 4–5 S, 33–40 ca., total 62–72. *Z. hudsonius* is similar, except with 6–8 L and 33–38 ca. vertebrae. Numbers of caudal vertebrae in *Z. princeps* tend to increase towards northwest portions of its range (Jones 1981).

**GENERAL CHARACTERS.** *Zapus princeps* is mouse-like in appearance and of medium size. Total length is 216–247 mm and tail (129–148 mm) is longer than length of head and body (*n* not available). Measurements of *Z. princeps* adults throughout their range are as follows: length of tail, 118–160 mm; length of hind foot, 25–35 mm; mass, 17–40 g; condyloincisive length, 19.4–22.8 mm; greatest braincase breadth, 9.4–11.3 mm; and zygomatic breadth, 10.9–13.7 mm (Jones 1981). Although not uniform, exter-



FIG. 1. Photograph of adult *Zapus princeps*. Photograph by R. Hunter.



FIG. 2. Dorsal, ventral, and lateral views of skull and lateral views of mandible of an adult male *Zapus princeps* (Brigham Young University, Monte L. Bean Museum #6569) from Eccles Canyon, Carbon Co., Utah. Occipitonasal length is 24.6 mm. Photograph by M. Belk.

nal dimensions generally decrease from north to south. The smallest individuals are found in the southernmost range extremes, whereas the largest are found in the Great Basin near the geographic center of the distribution of the species (Kruttsch 1954).

Western jumping mouse bicolored pelage is coarse, pale to grayish-brown above, white to yellowish-white below, and variable from yellowish gray to salmon-brown and ochraceous on the dorsum, with sides paler than back (Jones 1981; Kruttsch 1954). A wide dark dorsal stripe has a broad lateral band that is yellow, brown, or red. At lower edge of lateral band is a narrow lateral line of brighter color, similar to ground color of lateral band. Ears are dark and often fringed with color patterns ranging from no color to heavy washes of side color. *Zapus princeps* generally has a non-white tail tip, compared to a generally white tip in *Napaeozapus* (Jones 1981). However, white tail tips are common in some areas of New Mexico and also often occur in populations along the periphery of the range (Jones 1981). Other anomalies of color include white dorsal spots and partial albinism, though no geographical pattern is apparent. Guard hairs are elliptical to circular in cross section, taper at both ends, and have discontinuous medullae (Kruttsch 1954).

Three basic combinations of color occur in the western jumping mouse. Yellow-sided, dark backed (*Z. p. idahoensis*, *Z. p. kootenayensis*, and *Z. p. utahensis*) in the eastern Rocky Mountains; reddish brown-sided, brown-backed (*Z. p. pacificus*) found west of

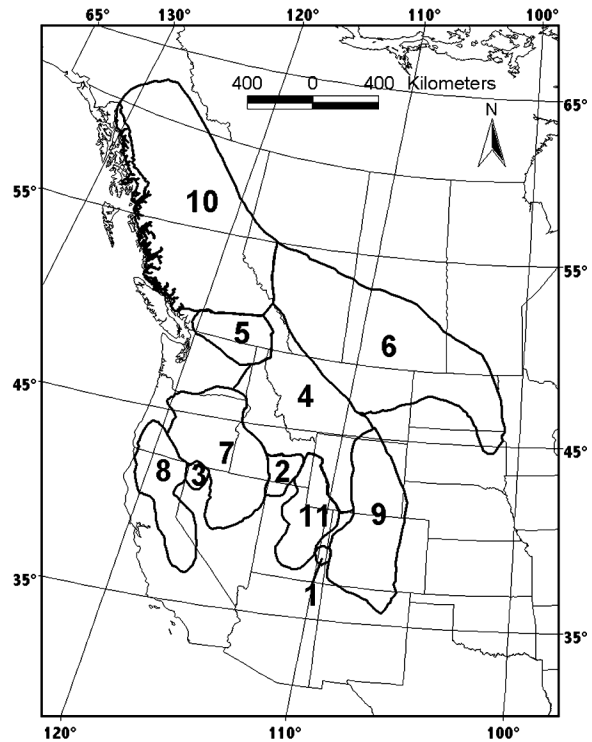


FIG. 3. Distribution of extant subspecies of *Zapus princeps*: 1, *Z. p. chrysogenys*; 2, *Z. p. cinereus*; 3, *Z. p. curtatus*; 4, *Z. p. idahoensis*; 5, *Z. p. kootenayensis*; 6, *Z. p. minor*; 7, *Z. p. oregonus*; 8, *Z. p. pacificus*; 9, *Z. p. princeps*; 10, *Z. p. saltator*; and 11, *Z. p. utahensis*. Adapted from Hall 1981 and Hafner et al. 1981 by G. Wein.

the Sierra Nevada; and yellow buff or pink-buff sided and light backed (*Z. p. cinereus*, *Z. p. curtatus*, and *Z. p. oregonus*) in the intervening Great Basin (Davis 1939; Hall 1931).

Forelimbs are reduced and hind feet are long. Both fore and hind feet have 5 digits with reduced pollex. Eyes are of medium size and set ca. one-half the distance between tip of nose and ears. Ears are medium size with small tragus and large antitragus. Upper lip has a median groove. No cheek pouches are present. The 4 pairs of mammae include 2 abdominal, 1 pectoral, and 1 inguinal. Sexes are not dimorphic. Tail is attenuate, subcylindrical, annulate, and bicolored (dark above and light below—Jones 1981; Kruttsch 1954).

Skull is mouse-like in general appearance, but with large infraorbital foramina reminiscent of hystricomorphs. Sides of incisive foramina are parallel with average distance between them 2.56 mm (range, 2.25–2.97; *n* not provided—Smith 1993). A small foramen occurs at ventral edge of skull. Pterygoid fossa is moderately narrow (Kruttsch 1954). Rostrum is broad but tapers. Nasals project beyond incisors and a large premaxillary plate protrudes between incisors. Palate is short with posterior edge variable in shape. Mandible is squirrel-like in that the angular process is more or less in line with the rest of jaw (Wood 1974); coronoid processes are weak and angular processes extend medially. Basihyals, hypohyals, and thyrohyals are fused in adults. A stylohyal is present (Jones 1981; Kruttsch 1954).

**DISTRIBUTION.** *Zapus princeps* is distributed south from the Yukon through much of British Columbia, Alberta, and Saskatchewan, and south into South Dakota (Fig. 3). It ranges through the Rocky Mountains into the Great Basin of Nevada and Utah, peripherally into northern New Mexico and Arizona. Westward, it ranges through the Cascade and Sierra Nevada ranges and eastward from Pacific Coast of California throughout much of Wyoming and Colorado (Hall 1981; Kruttsch 1954). In the Great Basin, *Z. princeps* occurs in only 6 of 16 mountain ranges (Lawlor 1998). Distribution of *Z. princeps* is not severely limited by altitude. In Nevada, western jumping mice occur from 1,980–2,900 m (Borell and Ellis 1934).

**FOSSIL HISTORY.** The subfamily Zapodinae is known from Pliocene (*Macrogathomys*, *Pliozapus*) and Pleistocene deposits of North America. Extant representatives presently occur in North America and China. The fossil history of the genus *Zapus* is fragmentary; mountainous habitats occupied by *Zapus* are generally not conducive to fossil formation (Smith 1993). Known fossils are represented by mandibles of Pleistocene age. *Zapus rinkeri*, the oldest known *Zapus*, is from the Rexroad formation of Blancan age, Meade Co., Kansas (Hibbard 1951; Krutzsch 1954). Teeth of *Z. rinkeri* are morphologically similar to those of individuals from extant peripheral populations of *Z. princeps* (Krutzsch 1954). *Zapus sandersi* is known from 7 late Blancan-early Irvingtonian Great Plains faunas (Hibbard 1956). *Zapus sykesae* is known from the early Irvingtonian in South Dakota (Martin 1989). *Zapus burti*, known from late Blancan Borchers fauna, Meade County, Kansas (Krutzsch 1954), might have been ancestral to *Z. princeps*, or *Z. princeps* and *Z. trinotatus* might represent a separate clade (Hibbard 1941). *Z. burti* is most similar to the Recent central forms of *Z. princeps* (Klingener 1963).

*Zapus princeps* might have been derived from *Z. burti* sometime during the Wisconsin glacial (Hibbard 1941) or during or after the Yarmouth Interglacial period in the far Midwest of montane western United States (Jones 1981). One of the interior populations, probably within a central portion of its range in the central Rocky Mountains, might have speciated into *Z. princeps* (Jones 1981; Klingener 1963).

*Zapus* materials were found in the Moscow Fissure, Late Pleistocene (Woodfordian) from the driftless area of southwest Wisconsin. Molar specimens from the Moscow fissure were not *Nepaeozapus* because of a relatively uncomplicated enamel pattern on any of the 3 molars. The anteroconid of M1 and M2 are separated from the metalophid by the confluent preprotoconid and premetaconid folds atypical of *Z. hudsonius* (Foley 1982).

**FORM.** *Zapus princeps* dental formula is: i 1/1, c 0/0, p 1/0, m 3/3, total 18 (Jones 1981; Krutzsch 1954). Tooth occlusal patterns are variable. Individuals of interior populations have attached paracone on M1 and M2, whereas individuals of peripheral populations usually have free paracones. The most common individual variation is from 1 to 6 cusplets on the teeth. Other morphologic anomalies can be present (Jones 1981). Western jumping mice have 8 palatal rugae (Jones 1981). Oral sebaceous glands are enlarged and oral epocrine sudoriferous glands are lacking (Quay 1965).

Male western jumping mice have broad-based bacula with converging shaft tips, most often spatulate, and usually curved dorsally. Bacula dimensions (in mm) are: width of tip, 0.2–0.9; width of base, 0.6–1.0; and total length, 5.0–7.1. Bacula of jumping mice in coastal populations are largest and have broadly-spatulate distal ends. Baculum is shorter and narrowly spatulate in individuals from interior populations; some have a baculum with a straight shaft without the spatulate tip. Female os clitoridi are similar in general appearance to baculae. Coastal populations have os clitoridi that are broadly spatulate, with variability in degree of curvature and length (Jones 1981).

In Utah and montane California, sperm head lengths (in  $\mu$ ) are 4.5–5.4, mean 5.1, width 0.97 ( $n = 6$ ). British Columbia individuals have slightly longer sperm heads, 4.9–5.5, mean 5.2 ( $n = 6$ —Jones 1981).

Tooth occlusal patterns are variable. Individuals of interior populations have attached paracone on M1 and M2, whereas individuals of peripheral populations usually have free paracones. The most common individual variation in *Z. princeps* is from 1 to 6 cusplets on the teeth. Other morphologic anomalies can be present (Jones 1981).

**FUNCTION.** Periods of torpor and euthermia in *Z. princeps* are inversely dependent on body mass. *Z. princeps* spends less time at high body temperatures following each arousal and arouses less frequently (French 1985). In Wyoming, western jumping mice spend two-thirds to five-sixths of their lives in hibernation (Brown 1967a). In Utah, the mean active cycle length was  $87.0 \pm 2.28$  days ( $SD$ ; range, 81–91) for all populations over all elevations ( $n$  not provided—Cranford 1977).

Seed abundance affects prehibernation deposition of fat, as does green vegetation (Cranford 1977, 1978; Muchlinski 1980). Dicotyledenous seeds produced the most favorable weight gains.

Distribution of *Z. princeps* is correlated with dicot seed plant abundance (Cranford 1977).

*Zapus princeps* has a well-defined pattern of nocturnal activity prior to hibernation, with occasional short bursts of daylight activity. Amount of activity decreases gradually over the 4 days prior to commencement of hibernation (Stebbins 1983). Rapid deposition of body fat reserves of up to two-thirds of dry body mass is initiated by *Z. princeps* when plant seeds are available 4 weeks before hibernation. Field animals enter hibernation with 62–70% of dry body mass in fat. In the laboratory, this phase can be accelerated and animals attain 65–80% of dry body mass in only 20 days (Cranford 1977). However, some animals lose weight just prior to hibernation (Cranford 1978).

Hibernating *Z. princeps* rely solely on body fat reserves for energy; no food caches are used. In Utah, fat reserves began to increase from 20–64% of dry body mass only after the 50th day of the active cycle. Animals feeding on a seed diet gained  $0.78 \pm 0.15$  g/day ( $SD$ ;  $n$  not provided). Mean rate of weight gain was 0.65 g/day with several instances of 1.3 g/day ( $n$  not provided). Weight at onset of hibernation was  $36.2 \pm 3.5$  g ( $SD$ ;  $n = 252$ ). Average loss of weight for a field population during 292 days was 0.07 g/day or total of 12 to 16 g ( $n = 50$ —Cranford 1977). Ca. 55–70% of dry body mass is equivalent to 12–14 g of fat (Brown 1967a; Cranford 1978, 1983a). At onset of hibernation in Wyoming, mean mass of adult males is 37 g; at emergence, when subcutaneous fat layer is mostly gone, average mass is 27 g ( $n$  not provided—Brown 1967a).

Juveniles enter their 1st hibernation with significantly lower body weights  $30.1 \pm 5.4$  g ( $SD$ ; range, 26–34;  $n$  not provided) and lower fat reserves than adults. Varying environmental extremes in 2 different years resulted in differential mortality in Utah. During the longer winter of 1974–1975,  $284 \pm 10$  days ( $SD$ ), 70% of juveniles ( $n = 64$ ) were not recaptured in the spring (compared to adult disappearance of 28%). During a milder winter in 1975–1976, only 41% of juveniles disappeared compared to adult disappearance of 24% ( $n$  not given—Cranford 1978, 1983a). In Wyoming, the overwinter disappearance of juveniles averaged 55.6% ( $SD$ ; range, 44.5–62.5;  $n = 36$ —Brown 1970).

In Wyoming, aboveground activity ceases from 1 September at higher elevations to 17 September at lower elevations. Males are active at lower elevations for 4 months, whereas females are active for 3.5 months. At 3,200 m, the active season is ca. 2.5 months for males and 2.25 months for females ( $n$  not given—Brown 1967a).

In Utah, initiation of hibernation occurred 1–7 September at 2,010 m, 6–7 September at 2,500 m, and on 29 September and 22 October at 2,900 m (Cranford 1978). In the Medicine Bow Mountains of Wyoming, late dates of occurrence were 1 September (3,200 m) and 17 September (2,590 m—Brown 1967a). Late dates of 13 September were recorded in northern California (Grinnell et al. 1930) and 20 September in New Mexico (Bailey 1931). The 1st snowfall can initiate hibernation, whether in August or September. Subsequent warm days do not bring animals out (Brown 1967a).

Laboratory experiments with captive animals indicated that increased frequency of arousals is energetically costly. Weight loss of animals above 32 g may allow minimal exposure to environmental factors due to tightly coiled postural configuration. (Cranford 1977). During hibernation, fat losses of 9.5–11.1 g in laboratory animals compares closely to a calculated fat loss of 8.97 g, based on 18,020 cc of oxygen consumed during a 295-day hibernation. A normothermic (nonhibernating) western jumping mouse uses an equivalent amount in just 14 days (Cranford 1983b).

Hibernation has 2 phases. Phase I varies from 90 to 120 days during which mean weight loss per day averaged 0.20 g ( $n > 27$ ). Use of Phase II (end of Phase I to 270–315 days to emergence), using the same groups at the same temperatures, averaged 0.06 g/day. Body weight loss levels out in Phase II. Arousals occurred more often during Phase I ( $\bar{X}$ , 17) than during Phase II ( $\bar{X}$ , 11;  $n$  not provided—Cranford 1977). During hibernation in the laboratory at 40°C, animals awoke every 38 days (Brown 1967b).

In Utah, mean terminal spontaneous arousal weight was  $18.7 \pm 1.2$  g ( $SD$ ;  $n$  not provided). This compares closely with animals maintained in 10 ( $n > 9$ ) and 15°C ( $n > 9$ ), whose mean weights at arousal were  $18.9 \pm 0.9$  g and  $17.8 \pm 1.1$  g, respectively. In the laboratory, 3 mice died without experiencing spontaneous arousal. Usually, when body mass dropped below 20 g, spontaneous terminal arousals occurred (Cranford 1977). Juvenile males, weighing 36.7 g going into hibernation, lost most of the subcutaneous fat

layer and weighed an average of 27.2 g at normal arousal ( $n$  not provided—Brown 1967a).

The hibernaculum of *Z. princeps* in the wild reaches and maintains a stable temperature of 4–6°C after the animals have been in hibernation from 50 to 120 days. *Z. princeps* are refractory to temperature-cued arousals up to 180 days with arousal responses occurring after that point. These adaptations allow *Z. princeps* to emerge from hibernation in favorable conditions from 200 to 300 days after hibernation has begun (Cranford 1978, 1981).

Body temperature in nocturnal normothermic western jumping mice is cyclic, ranging from 35.8–38.2°C, averaging 37.8°C during the nocturnal active phase and 36.6°C during the diurnal inactive phase, ambient temperature of 18°C. Maximum change in body temperature is only 0.25°C through 75% of the hibernation period ( $n = 25$ —Cranford 1977, 1978).

Oxygen consumption of western jumping mice at 30°C is 1.95 ml<sup>-1</sup> h<sup>-1</sup> g<sup>-1</sup>; at 18°C is 12.65, and is 6.20 when *Z. princeps* is normothermically inactive. During hibernation at 4.5°C, oxygen consumption is 0.042 ml<sup>-1</sup> hr<sup>-1</sup> g<sup>-1</sup> during the first 90 days and 0.024 during the later phase. During the normothermic phase prior to hibernation, oxygen consumption dropped to 5 ml<sup>-1</sup> h<sup>-1</sup> g<sup>-1</sup> ( $n = 25$ —Cranford 1977, 1983b). Increases of body temperature are slower during arousal than are increases in heart rate and oxygen consumption. During reentrance into hibernation state, heart rate and oxygen consumption decrease rapidly, while body temperature decreases more slowly. At emergence from hibernation, oxygen consumption increases to an average of 9.5 ml<sup>-1</sup> h<sup>-1</sup> g<sup>-1</sup> ( $n = 10$ ;  $SD = 0.75$ ) and body temperature increases at an average rate of 0.50°C/min ( $n = 3$ —Cranford 1977).

During the first 90 days of hibernation, heart rate of western jumping mice is 24 beats/min; subsequently, during day 160–210, heart rate is 14 beats/min ( $n = 22$ ). At emergence, heart rates increase from 14 to 580 beats/min in the first 45 min of arousal. Heart rates of inactive normothermic mice vary from 395–460 beats/min ( $\bar{X}$ , 420—Cranford 1977, 1983b).

When soil temperature increases to 8.0–9.5°C, arousal occurs ( $n = 42$ —Cranford 1978). When temperature does not change, hibernating western jumping mice do not end hibernation and die if body weight drops below 18–19 g. Fat stores of most juveniles usually dissipate before those of adults (Cranford 1977).

Infrequent waking behavior has been observed in *Z. princeps* once they have begun hibernation; average arousal time is 38 days in laboratory simulated hibernacula. In 3 laboratory groups held at 4.5, 10, and 15°C, average number of days between arousals was 6 for Phase I animals and 14 days for Phase II animals ( $n \pm 27$ —Cranford 1977). One jumping mouse remained in full hibernative torpor for 5 months; it was aroused by elevating temperature to 10°C, after which the mouse behaved normally (Brown 1967a).

Arousal of laboratory jumping mice was not synchronous with wild counterparts. Seven experimental animals hibernated through much of the active cycle of the wild populations. The activity cycle of laboratory animals was 38.7  $\pm$  21 days ( $SD$ ;  $n = 27$ —Cranford 1977). Laboratory animals ended hibernation within a 4-day period as temperatures within hibernacula exceeded 8.5°C in late May, although control animals remained in hibernation ( $n = 27$ ). Comparable field populations did not arouse in late May. Arousal occurred in the field when soil temperatures reached 8.3–8.8°C (Cranford 1977).

In Utah, males and females emerged at the same time except above 2,200 m where males emerged 3–9 days before females. Emergence timing varies widely among the same sites in different years depending when soil temperatures reach 8.5–9.5°C. Temperatures directly cue spring arousal (Cranford 1978). In the Medicine Bow Mountains of Wyoming, at 2,590, 2,900, and 3,200 m elevations, males aroused ca. May 16 (after 267 days of hibernation), 1 June (296), and 15 June (244), respectively. Females awoke 9–12 days later than males at similar elevations (Brown 1967a). In the Teton Mountains of Wyoming, earliest date of arousal was 24 May. Males emerged 5 days earlier than females (Clark 1971). Early arousal dates of 2 June and 28 May were reported in British Columbia (Cowan 1939).

Year, site, and elevation influence emergence. Arousal time differed by 7 days at 2 sites 300 m apart at the same elevation with the same vegetation components. This was due to blockage of sunlight which delayed snowmelt on 1 site due to a dense stand of alpine fir (*Abies lasiocarpa*) and Englemann spruce (*Picea engel-*

*mannii*). Two identical sites separated by 500 m had differences in emergence of 16, 14, and 10 days in 1974–1976. One of the sites had both western and southern exposures blocked by trees that cast deep shade by midafternoon and delayed snowmelt (Cranford 1983a). The range of variation in emergence dates was from 27 to 33 days ( $\bar{X}$ , 29.8  $\pm$  1.88  $SD$ ) from May 1 to July 22 over a 3-year period (Cranford 1977). Shallow nest sites (<30 cm deep) insulated by substantial winter snow cover prevents lowering of hibernacula temperatures to freezing levels (Brown 1967a).

Vegetative development of plant (common to different sites) heights from 7 to 17 cm best predicted arousal of *Z. princeps* from hibernation. The best predictor for all sites was *Mertensia arizonica*, which reached 12–16 cm by emergence of mice (Cranford 1983a).

An adult male and pregnant female western jumping mouse captured at 3,166 m in central Colorado, respectively, had a mean mass of 24.6 g, 26.0 g; hemoglobin (g/100 ml) of 17.8, 17.9; percent hematocrit, 53.2, 54.7; and percent mean corpuscular hemoglobin concentrations, 33.5, 32.7. Erythrocyte diameters of adults ( $n = 8$ ) averaged 6.3  $\mu$  (5.8–7.0—Sealander 1964). Seasonal variation in hemoglobin and hematocrit did not differ significantly between summer and winter (Sealander 1964). A correlation of  $r = 0.601$  for the regression of body mass on oxygen capacity was found. In Wyoming, 3 *Z. princeps* had mercury concentrations of 0.3, 0.7, and 0.8 ppm in their hair (Huckabee et al. 1973).

**REPRODUCTION.** In Wyoming, adult male testes are well developed at emergence from hibernation from various elevations ( $\bar{X}$  testis mass, 42–44 mg), although mature spermatozoa are not present until 7–12 days following capture of 1st males. Males are fully fertile 2–3 weeks prior to peak testis mass. Testis regression occurs in late summer. Deterioration of spermatozoa begins 2–3 weeks after peak testis development (Brown 1967a).

Juveniles weighing less than average adults all exhibited active spermatogenesis, indicating sexual readiness in the spring of the year following birth. Peak testicular mass in Wyoming was followed by rapid size decrease. Histological regression of testicular development is uniform. At 2,600 m, a statistically significant increase in mean testicular mass occurs in early September. No significant change in testis appearance at 2,900 m occurs just prior to hibernation and testicular mass gradually and steadily increases during hibernation. *Z. princeps* maintained in the laboratory at 4°C during winter and sacrificed at regular intervals had slightly accelerated testis development through April. In March, spermatogonial activity was present in the seminiferous tubule, and by April, mean testis mass had increased to 40.1  $\pm$  3.4 mg ( $SD$ ;  $n = 5$ —Brown 1967a).

Peak of maximal seminal vesicle length lags behind testis peak mass by ca. 2 weeks. Regression begins later at higher altitudes, but once begun, progresses more rapidly. Lowest testicular mass occurs at about the same time (Brown 1967a).

Development and regression of the male epididymis is similar to testicular changes at each elevation (Brown 1967a). Three to 4 weeks following peaks in testicular mass, spermatogonial deterioration occurred in the epididymal lumina. Also, a gradual shrinkage of luminal diameter occurred together with a marked decrease in epithelial cell height. Length of seminal vesicles followed a curve corresponding to testis mass, with the peak length (8.1–8.4 mm) lagging behind mass by ca. 2 weeks at each elevation. Minimal increase in length of seminal vesicles occurred late August or early September at altitudes of 2,600, 2,900, and 3,200 m ( $\bar{X}$  range, 3.3 mm). By March and April, a slight increase in length occurred (Brown 1967a).

Adult female western jumping mice in Wyoming start estrus and can breed within the 1st week they become active. Ovulation coincides with the 1st appearance of quantities of sperm in epididymis of males. Juvenile females do not mature during their 1st summer (Brown 1967a).

In Utah, full reproductive potential occurs in males and females when they emerge from hibernation (Cranford 1983a). Based on 2 individuals, average length of gestation is 18 days. Lactation is 28–35 days (Brown 1967a; Cranford 1977).

East of the Sierra and Cascade ranges, no females were pregnant after 13 July (Jones 1981). A few females were pregnant on 10 August from the Sequoia National Park area and Mount Rainier, Washington (Sumner and Dixon 1953; Taylor and Shaw 1927). In British Columbia, timing of mating varies from year to year, but averages 21 June ( $n = 52$ —Falk and Millar 1986). Females with

embryos are present late May to mid-July. Lactating females occur until late August (Kruttsch 1954).

In Wyoming, following birth, corpora lutea are replaced rapidly by connective tissue. At the end of lactation, only small corpora albacantia remain. No further follicular development occurs in the autumn prior to hibernation. The largest follicles present are in the solid growing stage, though small primary follicles are more abundant. Comparison of corpora lutea of pregnant females to numbers of visible embryos suggests a small loss of 2.3% of ova ovulated. No evidence of embryo resorption was noted ( $n = 33$ —Brown 1967a).

Body mass apparently influences reproduction. Yearling females with low body weights (21–25 g), undergoing initial reproduction, generally breed about a week later than larger females. Large females (>26 g) have litters born from mid- to late June at 2,600 m; at 2,900 m, litters arrive from early to mid-July; and at 3,200 m, litters arrive from mid- to late July ( $n$  not available—Brown 1967a). At 2 locations in Wyoming, 45% and 30% of overwintering females, respectively, did not breed each year (Clark 1971).

In British Columbia, ca. 59% of yearling females do not breed; those that breed do so later than older females, though litter size is not significantly smaller. Similarly, some 30% of females age 2 to 6 do not breed ( $n = 22$ ). This low rate of reproduction compares to relatively low rates of mortality among 1- and 2-year-old *Zapus princeps* with longevity of up to 6 years of age. Average rate of reproduction among all overwintering females was 58% ( $n = 52$ ). Forty-one percent of 1-year-old overwintering females and 70% of older overwintering females bred during 1 summer ( $n = 52$ —Falk and Millar 1986).

In Wyoming, average litter size based on embryo counts was 5.4 ( $SD$ , 1.7; range, 4–8;  $n = 33$ ). Numbers of embryos per female does not correlate to elevation. Larger females produce significantly more embryos than smaller females. Mean embryo counts of females weighing >26 g averaged  $6.7 \pm 1.1$  ( $SD$ ), whereas females averaging <25 g averaged only  $4.8 \pm 0.6$  embryos ( $n = 33$ —Brown 1967a).

In British Columbia, mean litter size of 1-year-old and 2+ year-old mice were:  $4.13 \pm 0.23$   $SD$ ;  $n = 8$ ; and  $4.64 \pm 0.33$ ;  $n = 14$ , respectively. Mean litter size among all breeding females was  $4.46$  ( $0.23 \pm n = 22$ —Falk and Millar 1986).

Average numbers of embryos from several localities were as follows: Arizona, 6 ( $n = 1$ ); Alberta, 5.5 ( $n = 2$ ; range, 5–6); British Columbia, 4.3 ( $n = 4$ ; range, 2–6); California, 7 ( $n = 2$ ); Colorado, 6 ( $n = 4$ ; range 5–7); Idaho, 5.8 ( $n = 4$ ; range, 4–7); Nevada, 5.8 ( $n = 5$ ; range, 4–7); Utah, 5 ( $n = 1$ ); and Wyoming, 5.3 ( $n = 20$ ; range, 3–7). For 43 females, the mean embryo count for interior populations was 5.4 (range, 2–7—Jones 1981). Twenty-five pregnant females, locale not specified, averaged 5 embryos (range, 2–7—Kruttsch 1954).

Six neonate *Z. princeps* from Clallam County, Washington, weighed an average of 0.8 g (range, 0.7–0.9). They were pink and hairless with their ears folded and eyes closed. No vibrissae were visible (Svihla and Svihla 1933).

Adults typically live from 35 to 48 months, during which time 3 or more reproductive bouts may occur (Brown 1970; Cranford 1977). Female *Z. princeps* have only 1 litter per year in the Wyoming Central Rockies due to the abbreviated activity cycle. Only 1 litter per summer occurs in Utah (Cranford 1983a).

**ECOLOGY.** *Zapus princeps* most commonly occurs in mesic, montane habitats. It occupies plant communities dominated by alder (*Alnus*) or aspen (*Populus tremuloides*), stands of willow (*Salix*), and meadows where forbs and grasses are abundant. Typically they are found in close proximity to water in areas of dense vegetation along streams (Armstrong 1977; Brown 1967b; Davis 1934; Kruttsch 1954; Svihla 1931). *Z. princeps* also can be found away from watercourses if soil moisture levels are high enough to support a diverse herbaceous plant community (Belk et al. 1988; Kruttsch 1954; Wrigley et al. 1991). Plants frequently associated with *Z. princeps* include *Agropyron*, *Carex*, *Erigeron*, *Hackelia*, *Lupinus*, *Mertensia*, *Poa*, *Potentilla*, *Rubus*, and *Rudbeckia* (Belk et al. 1988; Brown 1967b; Cranford 1977; Jones et al. 1978).

*Zapus princeps* is primarily a granivore. Seeds from forbs and grasses form the largest part of its omnivorous diet (Anderson et al. 1980). Less frequent food items include arthropods, subterranean fungi (*Endogone*), green vegetation, and fruit, red huckleberry

(*Vaccinium parviflorum*), salmonberry (*Rubus spectabilis*), and thimbleberry (*R. parviflorus*—Vaughn and Weil 1980; Williams and Finney 1964). Proportions of these components vary according to availability throughout the active season (Clark 1971; Cranford 1977; Stinson 1977). Spores of the fungus *Endogone pulvinata* Henn. were found in the stomach of a jumping mouse near Banff, Alberta (Dowling 1955). In Colorado, during June and July, forb seeds, as well as arthropods—mainly beetles (Coleoptera), dipterans, and larval lepidopterans—were the most common components of diets, with green vegetation consumed infrequently.

Feeding grounds can be identified by small heaps of grass stems 4–5 inches long left after the seeds have been removed (Bailey 1930). In August, seed and arthropod consumption decreased and green vegetation became predominant in the diet. It is suggested that this decline in seed consumption was the result of competition with other vertebrates, though a Wyoming study found little overlap between the diet of *Z. princeps* and other small mammals in the area, including *Clethrionomys gapperi*, *Microtus montanus*, *Mustela frenata*, *Peromyscus maniculatus*, *Sorex vagrans*, *Spermophilus armatus*, *Tamias minimus*, and *Thomomys talpoides* (McGee 1982; Vaughn and Weil 1980). Intensified consumption of seeds by *Z. princeps* in late summer is associated with rapid weight gain and fat deposition preparatory to hibernation. Indices of habitat quality on 8 grids were significantly correlated with density of animals ( $r_s = 0.98$ ) and with home range size (Cranford 1977).

Population densities of western jumping mice ranged from 2.0 to 38.5/ha over 3 years in 8 sites ( $n = 346$ ). Higher population densities were observed during juvenile dispersal (Cranford 1977). *Z. princeps* do not exhibit predictable cycles in population numbers (Brown 1970).

Overwintering loss of juveniles was 55.6% and that of adults in Wyoming was 16.5%. Summer disappearance rates for adults and young adults averaged 27.3% and 30%, respectively ( $n = 106$ —Brown 1970).

*Zapus princeps* competitively excludes the deer mouse, *Peromyscus maniculatus*, in the field (Cranford 1977). Other small mammals commonly associated with *Z. princeps* include: *Clethrionomys gapperi*, *Microtus montanus*, *Perognathus parva*, *Peromyscus maniculatus*, *Sorex vagrans*, *Sorex cinereus*, *Spermophilus armatus*, *Tamias minimus*, *Tamias ruficaudus*, and *Thomomys talpoides* (Belk et al. 1988; Brown 1967b, 1970; Cranford 1977; Negus and Findley 1959; Scrivner and Smith 1984).

Predators of *Z. princeps* include: *Lynx rufus* (bobcats), *Mustela* (weasels and skunks), *Procyon lotor* (raccoons), *Thamnophis sirtalis* (garter snakes), and various raptors (Brown 1970; Kruttsch 1954).

Ectoparasites of *Z. princeps* include: *Androlaelaps fahrenheitsi* (laelapid mites), *Dermacarus newyorkensis* (hypopial glycyphagid mites), *Gliricoptes zapi* (mycococtid mites), *Ixodes angustus* (ticks), and *Neotrombicula microti* (chiggers). Endoparasites include: *Cuterebra* (larval fly) and *Eimeria zapi* (coccidian eimerian—Duszynski et al. 1982; Kruttsch 1954; Whitaker 1979).

*Zapus princeps* are most commonly captured by snap and Sherman live traps, and less often with pitfall traps (Belk et al. 1988; Brown 1967b; Clark, 1971; Hoffman 1960; Negus and Findley 1959; Scrivner and Smith 1984; Stinson 1977; Williams and Braun 1983; Wrigley et al. 1991). The smoked-paper tracking technique and unbaited tracking boards have been used for home range analysis (Cranford 1977; Myers 1969).

Estimated mean life span of 28 jumping mice in Wyoming was 16.5 months. Population turnover time was estimated at 4 years (Brown 1970). Survivorship in Utah was calculated as 37 months ( $n = 53$ ), a significant survivorship for a rodent (Cranford 1983a).

**BEHAVIOR.** The shape of *Zapus princeps* home range is typically elongate along stream banks (Brown 1970), but is more elliptical, ca. 50 m from a linear reference point. Changes in home-range size were due to investigator disturbance, high densities of *Spermophilus armatus*, and disturbance of vegetation and mound construction by *Thomomys*. Home range size is negatively correlated with population density (Cranford 1977, 1983a).

In Colorado, home range size for *Z. princeps* varied from 1,743–3,075 m<sup>2</sup> for males and 1,041–2,350 m<sup>2</sup> for females ( $n = 11$ , both sexes—Myers 1969). In the Colorado Rocky Mountains, more male mice had overlapping (inclusive) home ranges than females, and average distance between centers of activity for males

was 11.1 m and for females was 15.3 m ( $n$  not provided—Stinson 1977).

In Wyoming, mean adult home range ( $n = 32$ ) was 173 m; average for males ( $n = 17$ ) was 209 m and females ( $n = 15$ ) was 155 m (variation not provided). Juveniles ( $n = 5$ ) averaged 144 m (range, 44–170 m). Some adult males (ca. 25–40%) showed a tendency to shift home ranges, whereas only 14% of females shifted home range (Brown 1970).

In Utah, *Z. princeps* home range sizes varied from 0.17 to 0.61 ha ( $n = 163$ ) over 3 years and was shown to have a negative correlation with population density. At one site, males occupy ranges 20% larger than females. From June to July, *Z. princeps* shifts habitat use to areas with a greater density of herbaceous cover (Belk et al. 1988).

*Zapus princeps* move with a series of zig-zag hops and horizontal leaps of ca. 36 cm (Kruttsch 1954). Escape behavior of *Z. princeps* consists of an individual executing several rapid bounds and then briefly remaining immobile, after which it resumes the quick jumps. In areas with more ground cover, it utilizes crawl as well as the bound-sit behavior to escape beneath vegetation (Belk et al. 1988; Jones and Jones 1985). When startled, leaps range from 36–72 cm long, ca. 30 cm high (Jones and Jones 1985; Kruttsch 1954). *Z. princeps* uses plainly visible runways, usually strewn with grass clippings as a result of foraging activities (Kruttsch 1954; Moore 1927). *Z. princeps* can swim well (Kruttsch 1954).

In an enclosed arena with *Peromyscus maniculatus*, *Z. princeps* individuals kick with hind limbs, push with front limbs, chatter teeth, and rattle their tails (Cranford 1977). Western jumping mice squeak when fighting (Jones and Jones 1985). Nests are constructed from bits of grass and are concealed beneath surface litter or vegetative cover (Bailey 1930; Kruttsch 1954). Although these mice can be observed during daylight hours, they are mostly nocturnal (Kruttsch 1954; Wrigley et al. 1991).

**GENETICS.** *Z. princeps* has  $2n = 72$  chromosomes, and FN = 82 (Meylan 1968). Normal XO females are known (Wrigley 1972). Where *Z. princeps* and *Z. trinotatus* occur sympatrically, fertile intergrades occur (Jones 1981).

Monomorphic loci were the most common of 21 presumptive loci encoding 15 proteins in *Z. princeps* (Hafner et al. 1981). Glyceral-3-phosphate dehydrogenase (G3PDH, 1.1.1.8), lactate dehydrogenase-2 (LDH, 1.1.1.27), malate dehydrogenase-1 (MDH, 1.1.1.37), and phosphoglucosyltransferase (PGM, 5.4.2.2) were monomorphic in all populations. Nine loci were fixed for different alleles in different populations: albumin (Alb), alcohol dehydrogenase (ADH, 1.1.1.1), esterase-2 and 3 (EST, 3.1.1.1), glucose-6-phosphate dehydrogenase (G6PDH, 1.1.1.49), glutamic oxalacetic transaminase-1 (GOT, 2.6.1.1), malic enzyme (ME, 1.1.1.40), 6-phospho-glucuronate dehydrogenase (PGDH, 1.1.1.44), and phosphoglucose isomerase (PGI, 5.3.1.9). Eight loci were polymorphic in at least 1 sample: esterase-1.4 (EST, 3.1.1.1), glutamic oxalacetic transaminase-2 (GOT, 2.6.1.1), isocitrate dehydrogenase-1 and 2 (ICDH, 1.1.1.42), lactate dehydrogenase-1 (LDH, 1.1.1.27), leucine aminopeptidase-2 (LAP), and tetrazolium oxidase-1 and 2 (SOD, 1.15.1.1).

**REMARKS.** The genus name *Zapus* is derived from the Greek root *za* meaning very or more, and the Greek root *pus* meaning foot. The species name *princeps* is derived from the Latin root *princ* meaning 1st or major. Conspecificity of *princeps* and *trinotatus* is recommended by Jones (1981).

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