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Lagurus curtatus.

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Lagurus Gloger, 1841

Lagurus Gloger, 1841:97. Type species *Lagurus migratorius* Gloger (=*Mus lagurus* Pallas).
Eremiomys Poliakoff, 1881:34. Type species *Mus lagurus* Pallas.
Lemmiscus Thomas, 1912:401. Type species *Arvicola curtata* Cope.

CONTENT AND CONTEXT. Order Rodentia, Suborder Myomorpha, Family Muridae (*sensu lato*, including the Cricetidae), Subfamily Microtinae. The genus *Lagurus* includes three species. Two of these have Eurasian distributions, and one, *Lagurus curtatus* (treated below), inhabits parts of western North America.

Lagurus curtatus (Cope, 1868)

Sagebrush Vole

Arvicola curtata Cope, 1868:2. Type locality Pigeon Spring, Mt. Magruder, Nevada, near boundary between Inyo Co., California, and Esmeralda Co., Nevada.
Arvicola pauperrima Cooper, 1868:535. Type locality plains of the Columbia, near the Snake River, southwestern Washington.
Arvicola pallidus Merriam, 1888:704. Type locality Fort Buford, Williams Co., North Dakota.
Microtus intermedius Taylor, 1911:253. Type locality head of Big Creek, 8,000 ft, Pine Forest Mountains, Humboldt Co., Nevada.

CONTEXT AND CONTENT. Context noted in generic summary. Six subspecies are currently recognized, as listed below:

L. c. curtatus (Cope, 1868:2), see above.
L. c. intermedius (Taylor, 1911:253), see above.
L. c. levidensis (Goldman 1941:70). Type locality 5 mi E Canadian River, west base Medicine Bow Range, about 8,000 ft, east of Walden, North Park, Jackson Co., Colorado.
L. c. orbitus Dearden and Lee, 1955:271. Type locality Steep Creek, 15 mi N Boulder, 8,500 ft, Garfield Co., Utah.
L. c. pallidus (Merriam, 1888:704), see above.
L. c. pauperrimus (Cooper, 1868:535), see above. [*Microtus* (*Lagurus*) *curtatus artemisiae* Anthony, 1913:14 is a synonym.]

DIAGNOSIS. *Lagurus curtatus* differs from Old World *Lagurus* in the following characters: m3 with four (rather than five) prisms, consisting of two terminal transverse loops and two median triangles (Fig. 1); cement present in the reentrant angles of molars; antitragus present; ears over one-half the length of the hind foot; conspicuous dorsal stripe absent. Its pale coloration, short tail (about the same length as the hind foot), large bullae, and the structure of the m3 distinguish it from other North American microtines (Davis, 1939).

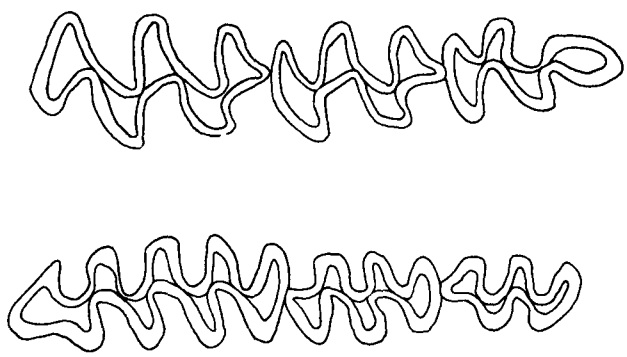

FIGURE 1. Occlusal view of upper (above) and lower (below) left molars of *Lagurus curtatus* from 2 mi SE Cross Mt., Moffat Co., Colorado (CM 15988). Anterior is to the left and posterior is to the right. Drawn by Nancy J. Perkins.

GENERAL CHARACTERS. Pelage is long, lax, and dense; bases of hairs are plumbeous gray; upper parts vary from pale buffy gray to ashy gray; ears and nose are often tinged with buff; sides are paler; venter is silvery white to pale buffy; tail is indistinctly bicolor, with dusky line above, silvery white to buffy below; feet are white or light gray to pale buffy (Fig. 2). Mammae: two pairs inguinal and two pairs pectoral. Hip glands are present in males. Soles of feet are densely furred posteriorly (Bailey, 1900; Anthony, 1928; Hall and Cockrum, 1953; Banfield, 1974) and have six plantar tubercles (Johnson et al., 1948; James and Booth, 1952; Maser et al., 1974). Skull (Fig. 3) is typically microtine in structure but decidedly flattened and angular; frontal region is often depressed; rostrum is short; zygomata are heavy and wide spreading; tympanic and mastoid bullae are inflated, cancellous and foamlike in structure, and project posteriorly beyond plane of occiput; stapedial canal is complete; squamosal crests are prominent and peglike; supraorbital ridges, although strong, are not fused in interorbital region (Bailey, 1900; Davis, 1939; Durrant, 1952; Hall and Cockrum, 1953; Banfield, 1974). Molars are rootless, with tightly enclosed triangles and wide intervening reentrant angles (Banfield, 1974), and inner and outer reentrant angles are of nearly equal depth (Dalquest, 1948; Durrant, 1952). Incisors are normally ungrooved (Hooper and Hart, 1962; Armstrong, 1972); lower incisors pass from lingual to labial side of molars between bases of m2 and m3 and ascend behind molars to terminate within or near condylar processes (Hall and Cockrum, 1953). For additional description of dentition, see Cope (1868), Bailey (1900), and Hooper and Hart (1962); for cranial characters, see Merriam (1891) and Hooper and Hart (1962).

Maser and Storm (1970) gave the following range of external measurements (in millimeters) for *Lagurus curtatus*: total length, 103 to 142; length of tail, 16 to 30; length of hind foot, 14 to 18; length of ear, 9 to 16; weight, 17.5 to 38 g. Averages and ranges of measurements of 10 males and 10 females of *L. c. curtatus*, and 7 males and 10 females of *L. c. intermedius* (in that order), as given by Hall (1946), are as follows: total length, 128 (119 to 132), 127 (121 to 135), 123 (109 to 142), 119 (108 to 134); tail, 22.9 (18 to 28), 21.7 (20 to 25), 20.4 (15 to 23), 21.0 (18 to 26); hind foot, 18.0 (17 to 19), 17.2 (16 to 18), 17.0 (16 to 17), 16.5 (15 to 18); weight, 29.4 (27.9 to 30.5), 24.4 (23.0 to 25.6), -, -; condylobasal length, 24.1 (23.1 to 24.6), 23.6 (22.3 to 24.5), 23.0 (21.5 to 24.0), 22.9 (22.0 to 24.0); occipitonasal length, 23.6 (22.8 to 24.3), 23.4 (22.2 to 24.0), 22.7 (21.4 to 23.9), 22.9 (21.8 to 23.7); nasal length, 6.5 (6.2 to 6.8), 6.5 (6.0 to 6.7), 6.2 (5.8 to 6.3), 6.3 (5.8

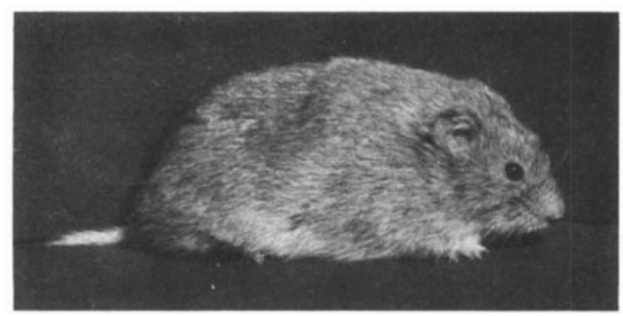

FIGURE 2. Photograph of an adult *Lagurus curtatus*. Photograph supplied by Murray L. Johnson, Puget Sound Museum of Natural History.

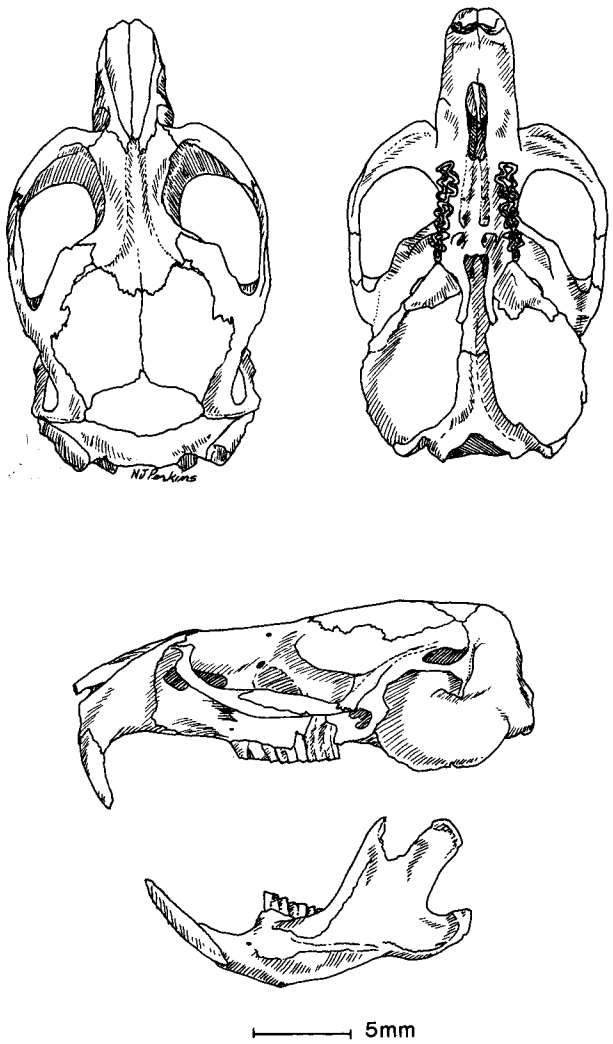

FIGURE 3. Dorsal, ventral, and lateral views of cranium and lateral view of lower jaw of *Lagurus curtatus*, CM 15988, male, 2 mi SE Cross Mt., Moffat Co., Colorado. Drawn by Nancy J. Perkins.

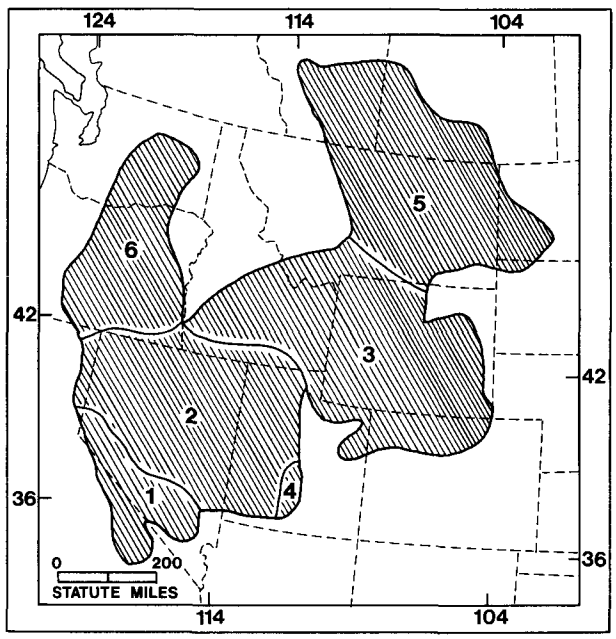

FIGURE 4. Geographic distribution of *Lagurus curtatus* and its subspecies as follows: 1, *L. c. curtatus*; 2, *L. c. intermedius*; 3, *L. c. levidensis*; 4, *L. c. orbitus*; 5, *L. c. pallidus*; 6, *L. c. pauperrimus* (modified from Hall and Kelson, 1959, using Soper, 1964; Long, 1965; Banfield, 1974; Hammer, 1971; Genoways and Jones, 1972; Birney and Lampe, 1972).

to 7.1); zygomatic breadth, 14.1 (13.6 to 14.5), 13.9 (13.4 to 14.6), 13.5 (13.2 to 14.2), 13.6 (13.2 to 14.4); interorbital breadth, 3.4 (3.2 to 3.5), 3.4 (3.1 to 3.6), 3.3 (3.1 to 3.4), 3.2 (3.1 to 3.4); mastoid breadth, 12.1 (11.2 to 12.6), 11.9 (11.5 to 12.3), 11.8 (11.3 to 12.6), 11.7 (11.3 to 12.1); alveolar length of upper molar row, 5.8 (5.4 to 6.1), 5.8 (5.4 to 6.1), 5.5 (5.1 to 6.0), 5.8 (5.5 to 6.2); width of rostrum, 4.3 (4.1 to 4.6), 4.5 (4.2 to 4.7), 4.2 (4.0 to 4.3), 4.2 (4.1 to 4.3); palatilar length, 12.1 (11.5 to 12.8), 11.9 (11.3 to 12.4), 11.6 (10.8 to 12.1), 11.7 (11.1 to 12.3).

DISTRIBUTION. The present distribution of *L. curtatus* in the western United States and adjacent Canada is shown in Fig. 4. *L. curtatus* occurs locally in sagebrush regions of the Upper Sonoran and semi-arid Transition zones, at elevations of from 305 m (Johnson et al., 1948) to 3,780 m (Dunmire, 1961). Dalquest (1948) believed the distribution of this species had probably changed little, if any, since the late Pleistocene. Hoffmann and Jones (1970), however, suggested that *L. curtatus* was able to spread from the Great Basin onto the northern Great Plains as non-forested connections between the Great Basin and the northern Great Plains were established in the Holocene.

FOSSIL RECORD. Dentaries and teeth of *Lagurus* cf. *curtatus* have been reported from deposits at Isleta Cave, Bernalillo Co., and Dry Cave, Eddy Co., New Mexico, more than 480 and 805 km, respectively, outside its present distribution (Harris and Findley, 1964; Harris, 1970, 1977). Anderson (1968) reported late Pleistocene remains of *Lagurus curtatus* (minimum number = 72) from Little Box Elder Cave, Converse Co., Wyoming.

FORM AND FUNCTION. There are two molts per year. The summer pelage is slightly darker than the winter pelage, and the first juvenile coat is marked by long dusky-tipped hairs (Bailey, 1900; Banfield, 1974). Taylor (1911) observed that the molt on two specimens began on the head and proceeded dorsoposteriorly along the median line; the new winter pelage was darker than that being replaced.

Reports of five plantar tubercles (Bailey, 1900; Anthony, 1928; Davis, 1939) and of absence of hip glands (Hall, 1946) may have been due to the examination of immature specimens. Johnson et al. (1948) and James and Booth (1952) each examined large series of adult specimens and found that six plantar tubercles were usual in adults, although juveniles and occasional adults showed only five. Both found hip glands in adult males. These occur on the sides immediately anterior to the hind legs, and appear internally as a solid black circle, measuring about 10 mm in diameter. Externally they are more obscure, but the hair over the gland is usually shorter and finer.

Dearden (1958) compared the bacula of the six subspecies of *L. curtatus* (see Fig. 5) with those of *L. lagurus*, *L. luteus*, and six other species of microtines. The baculum of *L. curtatus* is located in the glans penis, and is composed of a basal shaft, markedly enlarged and widened proximally, and three digit-like processes distally. The base of the shaft is slightly to moderately concave on the ventral surface, with a poorly developed keel (usually) on the dorsal surface. He found geographic variation in size and proportions of bacula of the different subspecies (Fig. 5); for additional description of the baculum of *L. c. levidensis*, see Anderson, 1960.

The baculum develops from a cartilaginous precursor; after birth, ossification centers become identifiable—one in the base of the shaft, and two in each digit. Ossification proceeds from the base of the shaft distally, and is complete in the adult (Dearden, 1958).

Hooper and Hart (1962) have described the glans penis. The short dorsal lobe of the glans penis is not well elevated above the papillose ventrolateral sectors of the rim, but is defined laterally by notches in the crater rim. Each ventrolateral sector carries four short fingers and there may be additional less distinct ones. The dorsal papilla has one or two short conules. The lateral bac-

ular mounds may be lobulate distally. The urethral process is stocky and compact, and divided into three subequal lobes.

Hooper (1968) found the tympanomastoid mass of *L. curtatus* was larger relative to skull size than in other species of microtines studied. Mastoid and tympanic parts are externally similar in texture; a suture clearly marks the boundaries between them. The mass is situated posteriad and ventrad; it extends behind the anterior edge of the foramen magnum and below the occlusal plane of the molar row. The external walls of both mastoid and tympanic are thick masses of cancellous bone. *Porus acusticus* is small, slightly tubular, and directed dorsoposteriad over a broad notch in its rim; the dorsomedial wall of *recessus meatus* is bony, and *pars flaccida* is a slim crescent. In the tympanic cavity, ribs and struts extend from the cochlear mass to the walls of the bulla. Some of these ribs terminate at the prominent tympanic annulus which contains a well-defined crest and groove.

Dearden (1959) found that the Meibomian glands in *L. curtatus* differed from those in *L. lagurus* in having less palmate tarsal glands, more extensive glandular tissue toward the inner margin of the eyelid, and extrapalpebral glands which open by a single duct (rather than separate ducts) into either the posterior corner of the eyelids or into the distal end of the duct of the exorbital lacrimal gland. He found considerable variation among the subspecies of *L. curtatus*, as well. The average and range of numbers of tarsal glands for each subspecies were as follows: *L. c. curtatus* (N = 6), 22.5 (21 to 25); *L. c. intermedius* (N = 6), 21.3 (21 to 23); *L. c. levidensis* (N = 7), 18.0 (14 to 21); *L. c. orbitus* (N = 5), 20.0 (20), *L. c. pallidus* (N = 12), 21.9 (18 to 25); *L. c. pauperrimus* (N = 5), 21.7 (20 to 25).

The histology of the gastroesophageal junction in *L. curtatus* shows that an abrupt transition from esophageal-type epithelium to gastric mucosa occurs within the pylorus at a point considerably removed from the corpopyloric fold. The sphincter and its action extend from above the cardia to well below the cardia (Dearden, 1966). The stomach consists of a forestomach, a narrow glandular zone, and pylorus. The majority of the stomach including the forestomach and pyloric antrum is lined with cornified stratified squamous epithelium. A narrow zone of glandular mucosa lies largely on and lines about a quarter of the greater curvature and is completely surrounded by cornified stratified squamous epithelium. The lesser omentum attaches the superior duodenum to the liver. The superior duodenum is descending and lacks a prepyloric pouch, with a possible resultant reduction in the amount of sphincteric muscle on the lesser curvature aspect of the lesser sphincter. On the greater curvature, however, the junction of the pyloric stomach and descending duodenum forms a tight inverted-U shaped configuration, thus insuring a markedly thickened muscular sphincter at this point (see Dearden 1969*a* for description of microscopic anatomy).

No studies have been made of the excretory system of *L. curtatus*; however, Maser et al. (1974) noted that urinary output is very low compared with other microtines. James and Booth (1952) found that these animals died if left in the trap without moist vegetation for more than five or six hours.

ONTOGENY AND REPRODUCTION. *Lagurus curtatus* appears to breed year-round (Moore, 1943); embryos have been found in every month except September (Maser et al., 1974). In the northern part of its geographic range, the breeding season may be restricted to March through early December (Banfield, 1974). James and Booth (1952) found most pregnant females in March through early May and October through December, and fewest in late summer; they also noted a marked decrease in size of testes during the summer months, and suggest *L. curtatus* has a summer period of sexual quiescence. Maser et al. (1974) cited a six-year study by Clanton et al. (1971), who also found increased reproduction in spring and autumn, corresponding with the growth of green vegetation, and decreased reproduction corresponding with summer drought and winter precipitation. Maser, in his own study, observed no reduction in breeding in summer, either because the population was at a peak, or because available moisture was not a limiting factor. Material obtained by Soper (University of Alberta Collection) indicates that at least three litters may be produced in a season (Moore, 1943). James and Booth (1952) reported up to three litters in succession for captive females, and one had a total of six litters in a year. Clanton (*in* James and Booth, 1952) had one female in captivity that produced eight litters in succession.

The gestation period averages 25 days (24 to 25) (James and Booth, 1952; Maser et al., 1974). Postpartum estrus occurs within 24 hours of parturition. The estrus cycle appears to be about 20 days (James and Booth, 1952).

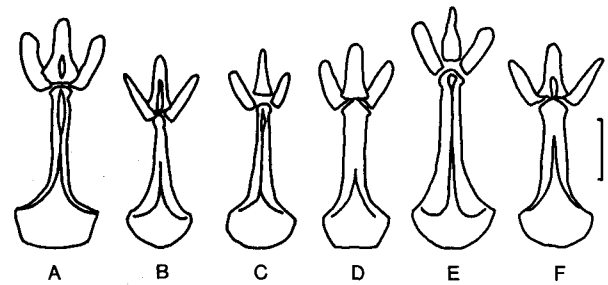

FIGURE 5. Dorsal view of the bacula of six subspecies of *Lagurus curtatus* as follows: A, *L. c. pallidus*; B, *L. c. levidensis*; C, *L. c. orbitus*; D, *L. c. intermedius*; E, *L. c. curtatus*; F, *L. c. pauperrimus* (adapted from Dearden, 1968). Scale is 1 millimeter long.

Means and ranges of numbers of embryos per pregnant female are as follows (for N = 42, 66, and 281 females, respectively): 4.4 (2 to 13) (Maser et al., 1974); 6.1 (4 to 10) (Moore, 1943); 5.26 (1 to 11) (Clanton *in* James and Booth, 1952).

Newborn *L. curtatus* are naked, blind, and helpless, with wrinkled bright pinkish skin; pinnae are folded flat; toes with claws are completely formed but still held together by interdigital membranes; and the dorsal surface darkens as pigment granules are deposited in the medullae of developing hairs. Measurements at birth are as follows: total length, 32 mm; tail, 5 mm; hind foot, 3 mm; weight, 1.5 g. Day 2: vibrissae begin to form, toes begin to separate. Day 3: pinnae begin to unfold. Day 4: dark hair appears first about the head and shoulders; fine black hairs appear on back and sides, while underparts remain naked and pinkish. Day 5: body is fully haired. Day 7: light gray hairs become mixed with the black hair on sides and around ears; underparts are covered with fine white hairs. Days 9–13: eyes open at an average of 11 days. Day 15: young are no longer wobbly on their feet, but rarely leave the female, and usually remain attached to mammae when she leaves the nest. Day 21: young are weaned and independent, and build their own nests. Day 25+: steady growth occurs up to about day 60. Females become sexually mature at about day 60 (although one female became pregnant at day 47), and males mature between days 60 and 75 (James and Booth, 1952). Maser et al. (1974) made the following additions to these observations: Day 3: young respond to vibrations, but not to lip-squeaking noises. Day 8: young move well in a semi-walk, and leave nest under their own volition. Day 10: young jerk in response to lip-squeaking. Day 11: young can detect odors of dog or weasel musk and react by moving away; they crawl rapidly out of the nest if it is disturbed. Day 15: most young scatter from the nest as soon as the mother leaves it. Days 17–19: young are completely weaned and independent of adults. Morphological maturity was not attained by either sex until sometime after 90 days of age.

ECOLOGY. *Lagurus curtatus* is generally restricted to semi-arid prairies, rolling hills, or brushy canyons, with loose, well-drained soil (although the surface may be rocky). Vegetation is usually dominated by sagebrush (*Artemisia* spp.) and bunchgrasses, especially crested wheatgrass (*Agropyron* spp.) (Hall, 1928; Moore, 1943; James and Booth, 1952; Rickard, 1960; O'Farrell, 1972, 1975*a*, 1975*b*). Rabbitbrush (*Chrysothamnus* spp.) may also be a dominant component of the vegetation (Cary, 1911; Dunmire, 1961; O'Farrell, 1975*a*, 1975*b*; Maser et al., 1974). Atypical habitats lacking sagebrush and dominated by grasses and various annuals were described by Cooper (1868), Cary (1911), Moore (1953), Dunmire (1961), Maser et al. (1974), and Maser and Strickler (1978). Maser et al. (1974) stressed the importance of sagebrush and/or rabbitbrush, whether alive or dead, in providing essential cover for the voles, although voles were also found where the only cover was dense grasses.

Lagurus curtatus is entirely vegetarian, and will eat almost anything green. Maser et al. (1974) found the following plants were heavily utilized as food in Oregon from May through July, until they matured with ripe seeds: *Bromus tectorum* (which appeared to be the main food), *Agropyron desertorum*, *Poa bulbosa*, *Holcus lanatus*, *Stipa spartea*, *Elymus caput-medusae*. Tender leaves, nodes, and young culms were eaten. Seedheads were routinely discarded, except for *Agropyron* seeds, which were eaten to some extent while they were in the soft "dough" stage. Also consumed

were leaves, flowers, and terminal portions of stalks of *Eriogonum strictum* (June through September); seeds of *Sisybrium altissimum* (late autumn and winter); stems, leaves, and green seeds of *Alyssum alyssoides* (April); leaves of *Thelypodium lasiophyllum* (April and May); leaves and parts of smaller stems of *Medicago sativa* (July); green seed pods and smaller leaves of *Lupinus wyethi* (July); leaves and tender stems and possibly green seed pods of *Astragalus cusickii* (June); green seeds of *Erodium cicutarium* (April and June); leaves of *Lomatium nevadense* (June); leaves from small terminal branches of *Chrysothamnus viscidiflorus*, which became important in the diet as *Bromus tectorum* matured (March and June); leaves of *Achillea millefolium* (June); and inflorescences (primarily) of *Artemisia tridentata* (heavily utilized from October through January). Maser et al. (1974) found that the latter had actually been clipped by deer mice, and that *L. curtatus* had been "stealing" from the piles accumulated by deer mice. They also suggested that stripping of the bark and cambium of *A. tridentata* under snow cover in winter, and severe defoliation in summer, attributed to *L. curtatus* by Hall (1928) and James and Booth (1952), may have been due to the action of deer mice. Moore (1943) found that *L. curtatus* in Oregon fed upon *Poa secunda*, *Sitanion hystrix*, and *Collinsia parviflora*, and attributed severe defoliation of sagebrush to the activity of ants. In Utah, Presnall (1937) found three seeds of *Pinus ponderosa* in the mouth of one sagebrush vole. In Colorado, greasewood was eaten (Miller, 1930). In North Dakota, flowers of *Artemisia frigida*, flowers and bulbs of *Liatris graminifolia*, and heads and seeds of *Eurotia lanata* were consumed (Bailey, 1926). In Washington, leaves of *Artemisia* sp., *Allium* sp., *Sisymbrium altissimum*, and *Bromus tectorum* (Johnson et al., 1948), and *Artemisia tridentata*, *Agropyron spicatum*, *Allium* sp., and *Descurainia pinnata* (=*Sisymbrium longipedicellatum*) (James and Booth, 1952), were eaten. In Canada, sagebrush voles fed upon grasses and *Selaginella densa* (Moore, 1953), *Chrysothamnus* sp., flowers of *Artemisia frigida* and *Liatris graminifolia*, heads and seeds of *Eurotia lanata* (Soper, 1931), and *Glomus fasciculatus* (=*Endogone fasciculata*) (Dowding, 1955; Maser et al., 1978). Birney and Lampe (1972) found the percent density of stomach contents of two sagebrush voles taken in mid-July in South Dakota to be as follows: Leguminosae, 78.6%, 34.0%; Cyperaceae, 0.0%, 58.6%; *Agropyron*, 10.8%, 0.0%; *Artemisia*, 9.8%, 0.7%; seeds, 0.0%, 3.0%; *Atriplex*, 0.0%, 3.0%; *Bouteloua*, 0.8%, 0.0%; Cruciferae, 0.0%, 0.7%.

The burrows of *L. curtatus* usually occur in clusters or "colonies" with from eight to 30 entrances each. Entrances tend to be located under cover, especially under sagebrush, but sometimes are in the open, or in rockpiles (Hall, 1928, 1946; Soper, 1931; Moore, 1943; Johnson et al., 1948; James and Booth, 1952; Maser et al., 1974). Abandoned *Thomomys* tunnels were often incorporated into the burrow system (Miller, 1930; Warren, 1942; Moore, 1943; Maser et al., 1974). Dearden (1969*b*) observed that vole entrances were 40 to 50 mm in diameter and led to a short shelf just below the surface, then continued downward in a sigmoid pattern to an average depth of 355 mm, where horizontal connecting passages were numerous. James and Booth (1952) reported that burrows ranged from 100 to 460 mm deep. They are often paved with clippings of sage and grass (Johnson et al., 1948; Dearden, 1969*b*; Banfield, 1974).

Maser et al. (1974) found that nest chambers of *L. curtatus* had two or three (or as many as six) entrances each; they were located 80 to 250 mm underground, and ranged in size from 100 by 100 mm to 130 by 180 mm in open ground, and up to 200 by 250 mm when the nest was in a rockpile. Nests were constructed almost exclusively of leaves, stems, and sometimes seedheads of grass; some contained feathers or paper, but none contained shredded sagebrush bark; nests containing sagebrush bark were those of *Microtus montanus*. Moore (1943), Johnson et al. (1948), and James and Booth (1952) attributed nests containing sagebrush bark to *Lagurus*, however.

Runways are 60 to 80 mm wide (wider than those of most *Microtus*), and are usually indistinct, especially where vegetative cover is sparse (Hall, 1928, 1946). Runways located under cover are relatively unkempt and may be obstructed by pieces of grass. In winter, tunnels under the snow are more often used than runways over the snow (Maser et al., 1974). Fresh cuttings of vegetation may be located in protected places and at the entrances to burrows (Johnson et al., 1948). Feces may be found in runways but are not as numerous as those in *Microtus* runways; often they are deposited in piles outside burrow entrances, whereas the burrows themselves are very clean. Scat piles measuring 100 to 200 mm long, 50 to 100 mm wide, and 25 to 80 mm deep may also be found along runways or under cover. Short, blind tunnels 25 to 50 mm deep and 150 to 200 mm long frequently open off runways; these and fallen fenceposts, rocks, and cavities or runways dug or eaten into cow dung, may serve as escape burrows and feeding stations where cover is lacking (Hammer and Maser, 1969).

Predation by a rattlesnake has been reported by Anthony (1913) and by Preble (*in* Bailey, 1926). However, owls seem to be the most important predators of *L. curtatus*. Moore (1943) observed large numbers of Short-eared Owls (*Asio flammeus*) during a peak vole population period. Owl pellets containing the remains of these voles have been reported by Long (1965) and Hoffmann et al. (1969). Analysis of the contents of numerous pellets showed that *L. curtatus* composed 25.6% of the diet of Burrowing Owls (*Speotyto cunicularia*) (Maser et al., 1971), 3.7% of the diet of Great Horned Owls (*Bubo virginianus*), 3.7% of the diet of *Asio flammeus*, and 3.6% of the diet of Long-eared Owls (*A. otus*) (Maser et al., 1970). Of twelve pellets from a Pygmy Owl (*Glaucidium gnoma*), one contained the remains of *L. curtatus* (Maser et al., 1974). Moore (1953) reported predation by a shrike, *Lanius ludovicianus*. Hall (1946) reported predation by a bobcat. Maser et al. (1974) found scats of *Mustela frenata* amidst *L. curtatus* colonies, next to runways and burrows, and all were composed primarily of sagebrush vole hairs.

Maser et al. (1974) reported that lice, mites, ticks, and fleas were common on *L. curtatus*. They also found cestodes (*Andrya* sp.) occurring singly in the small intestines of three of 37 voles examined. No larval cestodes were found in wild specimens. Moore (1953) found that two voles (N = 14) had diseased livers due to moderate infestation by nematodes. Maser et al. (1974) found two voles with enlarged spleens, and suggested possible infestation by a piroplasm, *Babesia* sp.

The following species of fleas have been reported from *L. curtatus*: *Amphypsylla sibirica* (Egoscue, 1966); *Atyphloceras multidentatus multidentatus* (Maser et al., 1974); *Catallagia decipiens* (Hubbard, 1949*a*, 1949*b*; Maser et al., 1974); *C. sculleni* (Maser et al., 1974); *Malaraeus telchinum* (Hubbard, 1949*a*, 1949*b*; Egoscue, 1966; Maser et al., 1974); *Megabothris clantoni clantoni* (Hubbard, 1949*b*); *M. clantoni johnsoni* (Hubbard, 1949*a*, 1949*b*; Moore, 1953; O'Farrell, 1975*a*); *M. princei* (Hubbard, 1949*b*; Maser et al., 1974); *Meringis shannoni* (Hubbard, 1949*a*, 1949*b*; Maser et al., 1974; O'Farrell, 1975*a*); *M. hubbardi* (Egoscue, 1966); *Monopsyllus wagneri* (Moore, 1953; Maser et al., 1974); *Opisodasys keeni keeni* and *Rhadinopsylla sectilis* (Maser et al., 1974); *Thrassis bacchi johnsoni* (O'Farrell, 1975*a*); *T. gladiolus johnsoni* (Hubbard, 1949*a*, 1949*b*). Two of these fleas, *Megabothris clantoni johnsoni* and *Thrassis bacchi johnsoni*, are apparently specific to *L. curtatus*, and because of their high infection rate and high blocking-survival rate, they play an important role in the maintenance of sylvatic plague (*Pasturella pestis*) in *L. curtatus* colonies. Maser et al. (1974) found no transfer of these two species to other hosts, and their specificity probably mitigates the likelihood of transmission to other species (see Maser et al., 1974, for discussion of the vector efficiency of other fleas for the plague organism). Data collected during a 1947–1953 plague survey by Clanton et al. (1971) (cited by Maser et al., 1974) indicate that *L. curtatus* is the principal, if not the sole, reservoir responsible for the maintenance of sylvatic plague in Washington.

Lagurus curtatus populations fluctuate, sometimes occurring in small, isolated colonies, and at other times occurring in abundance (Hall, 1928; Soper, 1946; Banfield, 1974). Moore (1943) observed a population which peaked in May–June and died off in late July. Three factors appear to be associated with peak populations of sagebrush voles: (1) a winter with above-normal temperatures and without excess moisture; (2) a summer with above-normal precipitation; (3) early onset of autumn rains (Clanton et al., 1971, quoted by Maser et al., 1974).

Moore (1943) found that of 25 embryos, 36% were male; Maser et al. (1974) found a ratio of 51.5% males for 33 embryos. Sex ratios of trapped animals have been reported as 56% male (N = 77) (Hall, 1928); 62% male (N = 84) (Johnson et al., 1948); 52% male (N = 1,094) (Clanton *in* James and Booth, 1952); and 56% male (N = 153) (Maser et al., 1974). However, the sex ratio of trapped animals may be affected by the population cycle; during a peak period, Moore (1943) caught three females for every male, but found that the trend reversed as density decreased. Trapping technique may skew the sex ratio. James and Booth (1952) caught 60% males in kill traps, but only one male to every eight females in live traps.

BEHAVIOR. *Lagurus curtatus* is essentially active 24 hours a day, year-round. The main activity periods are from two to three hours before sunset until two or three hours after full darkness,

and again in the early morning from one to two hours before daylight to one to two hours after sunrise. Wind velocity at ground level influences activity above ground, and the voles are only active above ground when there is little or no detectable wind at ground level. In winter, activity continues under snow cover (Maser et al., 1974).

Lagurus curtatus does not store food, except for pulling freshly cut food into burrows, which reduces desiccation (Maser et al., 1974). They are extremely clean animals; in captivity they defecate and urinate as far as possible from their nest area (James and Booth, 1952; Maser et al., 1974). They will dig as deep as 460 mm to find dry soil (James and Booth, 1952).

James and Booth (1952) observed mating behavior in a captive pair, where the male chased the receptive female around the cage for three to four hours, mounting her many times. In the wild, after parturition, the female closes the nest entrances and goes in search of a male, presumably aided by his scent. In captivity, after postpartum mating, the male is excluded from the nest; if it cannot be defended, he may kill and eat the young. Maser et al. (1974) found that captive females would share nests and suckle each other's young.

On the basis of lacerations and bites observed by Maser et al. (1974) breeding males accounted for most aggressive conflicts. In addition, James and Booth (1952) observed aggression under the following circumstances: (1) between a strange male and a non-receptive female at first encounter, but, unless she had young, they became acquainted quickly; (2) between females when a strange female was introduced to a mated pair; (3) among females and a lone male until they accepted him, which took about three days.

GENETICS. Wurster et al. (1971) found a diploid number of 54 chromosomes and a fundamental number of 58 chromosomal arms for *L. curtatus*. The autosomal complement consists of 50 acrocentric elements, graded in size, and one pair (next to the smallest in the complement) of submetacentrics. The X chromosome is submetacentric and as large as the largest autosome. The Y is a medium-small subacrocentric. The autosomes and one X chromosome replicate fairly synchronously, some being slightly later than others. The second X in the female is late replicating. Hsu and Benirschke (1971) found the identification of the Y chromosome was subjective, as only one pair of autosomes could be separated from the remainder. They identified the Y as an acrocentric, but in other respects their description concurred with that of Wurster et al. (1971).

REMARKS. Extreme care should be used in handling these animals because of the possibility of infestation with plague-positive fleas which could transmit the disease to humans. Fleas should be killed by fumigation, and rubber gloves should be worn while preparing specimens (Johnson et al., 1948; James and Booth, 1952).

Care of *L. curtatus* in captivity was described by James and Booth (1952) and Maser et al. (1974). They survive and reproduce on a diet of carrots, but colonies tend to lose vigor and cease breeding unless this diet is supplemented by various other foods. Dried alfalfa, rolled oats, and green vegetation are accepted. If an excess of carrots is supplied, water is not necessary. Nest boxes should be provided within the enclosure.

Lagurus: Greek for hare-tail. *Curtatus*: Latin *curtus*, shortened. The sagebrush vole, or campagnol des sauges, has often been referred to as the sage vole (or sage meadow mouse), pygmy vole, pallid vole, short-tailed vole, intermediate meadow mouse, and variations on these names.

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