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SUBNIVEAN ROOT CACHING BY A MONTANE VOLE (*MICROTUS MONTANUS NANUS*), COLORADO FRONT RANGE, USA

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Key words: montane vole, Microtus montanus, *pygmy bitterroot,* Oreobroma pygmaea, *caching behavior, snow, Colorado Rocky Mountains.*

Food hoarding is a common winter-survival strategy of cold-climate animals (Smith and Reichman 1984), including many microtines. Voles store grasses, leafy vegetation, and twigs primarily in piles on the ground surface. They store epiphytic lichens in tree cavities and bird nests above the level of the snow. And they store roots, rhizomes, and tubers belowground or in subnivean chambers, where the food remains fresh for months (Vander Wall 1990). Subnivean caches are among the least-studied storage facilities due to the difficulty of observing activities that occur entirely beneath the snow. Caches are established after snow blankets the ground. Their contents are ordinarily consumed before meltout, and the chambers themselves are transient features. To our knowledge the only published observations of subnivean caching by microtines are those of Formozov (1966) in northern Kazakhstan and Gates and Gates (1980) in western Maryland.

Snow arrived early in the mountains of western Boulder County, Colorado, during the autumn of 1996. Heavy upslope snowstorms and downslope redistribution events between 17 and 27 September created a snowpack that gave every indication it would remain for the duration of winter. Conditions then turned warm and dry. By 9 October an elaborate system of root caches, runways, foraging trenches, and surface ball nests had begun to emerge from beneath the snow in a meadow above timberline in Indian Peaks Wilderness Area. By 12 October the entire meadow had become exposed, providing a snapshot of what a vole can accomplish in unfrozen soil beneath a continuous snowpack in about 3 weeks' time.

The meadow is at an altitude of 3410 m in the forest-tundra ecotone of Fourth of July valley. Beginning at the base of a low cliff, it slopes gently southeastward to the North Fork of Middle Boulder Creek. Snow blankets the meadow from October until early or mid-July of most years, supplying moisture that encourages lush plant growth. Caching activities reported in this paper occurred in a plant community dominated by sibbaldia (*Sibbaldia procumbens*) and fern-leaved lovage (*Ligusticum tenuifolium*). Other species include *Deschampsia cespitosa, Bistorta bistortoides, Erigeron peregrinus, Viola labradorica, Castilleja rhexifolia, Vaccinium myrtillus, Vaccinium scoparium, Gaultheria humifusa, Phleum commutatum, Carex nigricans,* and *Juncus drummondii.* Of special interest is the locally high density of pygmy bitterroot (*Oreobroma pygmaea* [Gray] Howell, formerly *Lewisia pygmaea*), a species that elsewhere in the Front Range reaches greatest percentage cover where maximum winter snow depths average 2 to 3 m (Walker et al. 1993).

Two grass ball nests were present in the meadow (Fig. 1), only one of which had been recently occupied. The other was faded and partially flattened, as though it had been built during the preceding winter. We identified the builder of the younger nest as a montane vole (*Microtus montanus nanus*), based on the characteristics of dorsal guard hairs shed in its nesting chamber. The hairs have brown to black tips, yellowish ivory bands confined to the central portions of shields, and black lower shields that terminate in subshield strictures. Restriction of the color band to the central

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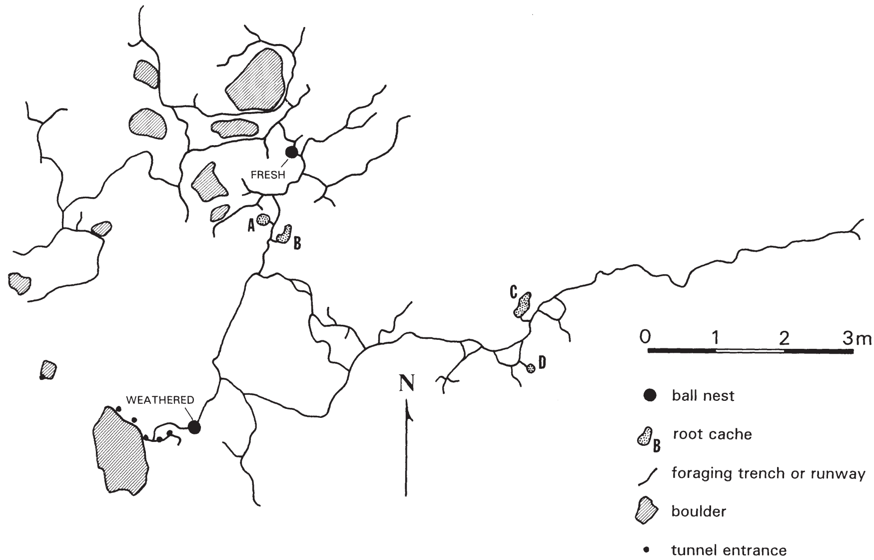

Fig. 1. Tape-and-compass map of runways, tunnel entrances, ball nests, and root caches.

portion of the shield (as opposed to extending downward to the subshield stricture) distinguishes the dorsal guard hairs of *M. montanus* from those of *M. longicaudus, Phenacomys intermedius,* and *Clethrionomys gapperi* (Moore et al. 1974)—other vole species that occur above timberline in western Boulder County. Supporting this identification is the vole's choice of habitats. During 10 years of trapping in a tundra saddle 8 km northeast of the valley, *M. montanus* was the only vole species captured in snowbed communities dominated by *Sibbaldia procumbens,* and the most numerous vole species in moist-meadow communities dominated by *Deschampsia cespitosa* (Armstrong et al. in press).

The ball nest was made from stems and leaves of *D. cespitosa,* clipped to lengths of 7 cm or less. Leaves of *Carex nigricans* and leaves and twigs of *Gaultheria humifusa,* still fresh and green, were present in trace quantities. The nest was globular in shape, with a height of about 8 cm. Its exterior diameter (19 cm) was larger than has been generally reported for *M. montanus,* but extra-thick insulative walls may be required in such a low-temperature environment. Two entrances led to a snug, central chamber barely large enough for a single individual. Field and laboratory studies (Jannett 1982, McGuire and Novak 1986) indicate that adult montane voles nest individually rather than in pairs or colonies.

Ball nests at the study site were connected to root caches and subsurface tunnels by a network of branching runways and foraging trenches with an aggregate length of about 60 m (Fig. 1). Runways and trenches were 2.5 to 4.0 cm wide and up to 3.0 cm deep. Foraging trenches were flanked with levees of earth and of cut rootlets, stems, and leaves piled to the side during the harvesting process. Five small-diameter (2.5 to 3.5 cm) holes near a boulder at the southwest end of the runway network (Fig. 1) appeared to be tunnel entrances, such as might lead to a summer nesting chamber. A 6th entrance occurred nearby, at the edge of a smaller boulder. The older of the 2 ball nests, the tunnels, and several runways are thought to predate the 1996 caching event.

Four root caches were present in the meadow, each linked to the trench network by a short runway (Fig. 1). Caches consisted of roots that had been heaped on the ground surface in chambers beneath the snow, forming circular mounds or irregularly elongated ridges. Table 1 summarizes cache dimensions and contents. Tuberous roots of pygmy bitterroot (*Oreobroma pygmaea*) were the only food items represented. Roots of this species grow in the meadow at depths of 0.6 to 3.4 cm, the approximate depth range explored by the foraging vole. Fleshy rhizomes of *Bistorta bistortoides,* another potential food source, begin below the bases of the trenches, at depths of

TABLE 1. Dimensions and contents of root caches.

Cache	Length (cm)	Width (cm)	Number of roots	Aggregate weight (g)[a]
A	9	8	139	17.0
B	24	18	432	70.4
C	37	18	290	45.9
D	5	4	26	7.4
TOTALS			887	140.7

[a]Field-moisture content, 12 October 1996

4.7 to 8.7 cm. They were not represented in the caches, although their upturned tips sometimes penetrate the foraging zone from below. Rather than selecting for robust plants with large roots, the vole appears to have stored all *O. pygmaea* roots it encountered, regardless of size. Rootlets, stems, and foliage were trimmed and discarded before caching. Altogether, caches contained 887 roots ranging from 5 to 27 mm in maximum dimension, with an aggregate fresh weight of 140.7 g. Assuming that roots from the caches were similar in caloric value and macronutrient content to a sample of fresh roots dug at the site in late August 1998 and analyzed by Warren Analytical Labs (Greeley, Colorado), the caches represented 395 kcal of stored energy. They contained 40.4 g of moisture, 95.1 g of carbohydrate, 3.5 g of protein, 0.1 g of fat, and 1.6 g of ash.

How many roots would the vole have collected if snowmelt had not interrupted its activities? Wolff (1984) found that underground food caches of taiga voles (*Microtus xanthognathus*) in central Alaska held up to 3.6 kg dry weight (about one bushel) of horsetail (*Equisetum* sp.) and fireweed (*Epilobium angustifolium*) rhizomes, but these were communal caches made in late summer by 5 to 10 individuals. Formozov (1966) reported that *Microtus brandti*, a field vole of the Mongolian steppes, stored up to 30 kg of stems, leaves, and whole plants, including their roots. Plants were collected in autumn, usually by 10 to 12 voles, and were stored in underground chambers, where they provided food for a wintering colony of up to 20 individuals. Formozov (1966) described caches of rhizomes made by mole-voles (*Ellobius* sp.) in snow passageways, but gave no details concerning their weights or numbers. Gates and Gates (1980) studied the subnivean food cache of a meadow vole (*Microtus pennsylvanicus*) in western Maryland. Exposed by springtime snowmelt, the cache contained 1655 food items with an aggregate oven-dry weight of 0.31 kg. Rhizomes of *Potentilla canadensis* were especially numerous, but underground parts of 3 other plant species were also represented. The authors calculated that the cache could support a single average-sized vole for 86.8 days. On a per-animal basis, weights reported by these authors are at least 3 times the oven-dry weight of roots in Fourth of July valley caches. The animal may have intended to continue harvesting until the ground froze or a winter's food supply had been stashed away, or the caches may have been meant merely to supplement other diet items available beneath the snow. Small hoards, reserved for times of great need, can make critical contributions to winter survival, even though they fall far short of meeting total nutritional requirements (Hitchcock and Houston 1994).

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