BURROW-BUILDING STRATEGIES AND HABITAT USE OF VOLES IN PACIFIC NORTHWEST ORCHARDS

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Seidel and Booth (1960) wrote that the "life histories of the genus Microtus are not numerous in the literature." In support of his observation he cited 6 publications, all dated between 1891 and 1953. Since then the literature has exploded with a proliferation of publications. An international literature review recently revealed over 3,500 citations for the genus. When Pitymys and Clethrionomys are included another 350 and 1,880, respectively, were found. Over the last 10 years approximately 3 new publications on voles appeared every 4 days; a significant output for what some would consider such an insignificant species.

Most of the publications were the result of graduate research projects on population dynamics and species ecology. As such, many do not explore more than the rudimentary ecological relationships between the animal and their environments. Unfortunate, as well, is that all but one confined their observations to only a small part of their total environment. For many of these animals, their life underground may be more important for their survival than that above ground.

Trapping studies conducted by Godfrey and Askham (1988) with permanently placed pitfall live traps in orchards revealed a significant inverse population fluctuation during the year. During the winter, when populations are expected to decrease, as many as 6 to 8 mature Microtus montanus were collected at any 1 time in the traps after several centimeters of snow accumulation. During the summer, when populations are expected to increase, virtually no animals were collected in the traps. According to current population dynamics theory, greater numbers of animals, including increasingly larger numbers of immature members of the community, should appear in any sample between the onset of the breeding period, generally in the spring, taper off during the latter part of the production season, usually late summer, and then decline as the limiting factors begin to take effect. For us, we trapped more animals in the fall and early winter than we did during the spring and summer. A review of the above literature did little to answer our question. Where are the animals going during the summer and why?
METHODS

The study was initiated by inventorying an apple orchard during the early spring with a 3-year history of Microtus montanus infestations. Within the block, 15, 1-m² samples were randomly placed, the number of open active holes counted, and the lengths of active runways between each hole measured. We then recorded the amount of cambium that had been removed from the base of each tree during the preceding winter and removed 5 trees, 1 from each damage class (none, 0-25%, 26-50%, 51-75% and 76% or more of the tree girdled).

The next phase of the project was to excavate what was believed to be an extensive burrow system within the orchard. A 10.98 x 10.98 m section of the orchard was subdivided into 144, 0.84 m² units. All of the holes were marked with a steel pen, and their positions, along with the runs connecting them, plotted. All of the vegetation, including dead material, was removed from the site. The top 2.54 cm of soil was then removed from each unit with an active burrow opening. As succeeding layers of soil were removed, 2.54 cm at a time, we marked where burrows were found, and plotted on separate pieces of graph paper the depth at which they were found. The process was then repeated until no more burrow systems could be located.

Data were then entered into an IBM compatible microcomputer with an 80386 or 80486 processor, a math co-processor, 4 Mb RAM, a Targa video graphics board, an analog monitor, digitizer, animation controller, and 1.37 cm (0.5-in.) tape deck. The Targa board provided adequate resolution and color palettes to capture the video, video and RGB output, compositing and retroscoping overlays. The data were modeled using Studio 31) (Autodesk), a 3-dimensional (3D) tool that provides sophisticated animation.

When the initial survey was tabulated we found that approximately 16,000 holes (approximately 39,000/ha) and 792,480 lineal cm (1,971,000 cm/ha) of above-ground runways dotted each 0.4 ha within the orchard. Densities, however, were not equally distributed throughout the area. More holes and runs were encountered between the tree rows than within the rows even though both were equally sampled. A little over 43% of trees were damaged. Of these, 5.5% were damaged enough (>50%) that they were effectively removed from production. All of the trees grafted to M27 root stocks were killed during the winter. Damage was also severe with M7A where 38% were dead the following spring. This rootstock also sustained significant damage with over 30% having 50% or more of the cambium removed from the base of the tree. Only 10% of the M106 root stock was damaged. No attempt was made to measure the amount of root damage to the trees removed but extensive feeding was noted for each.

Byers (1976) found that pine voles (Microtus pinetorwn) developed a system of underground burrows-some as deep as 46 cm below the soil surface-beneath the apple tree canopies he excavated in Virginia. In these excavations he found 4 general layers: 0-5.1 cm, 5.1-15.2 cm, 15.2-30.5 cm and 30.5-45.7 cm. He also found a nest, food caches, and several "breathing" holes within each system. He also found that most of the burrow system was confined to the region beneath the tree canopy.

In this study, the burrow systems were mainly confined to those regions of the orchard with the heaviest grass cover (Fig. 1). Few were found in the herbicide treated strips within the tree row. Shallow, depressed runways connected most of the
burrow openings. Most of these runways were about 5.1 cm wide and all of the vegetation was consumed within the pathway. Not all openings led to active burrows. Some extended only 7.6-10.2 cm into the soil (Fig. 2). The open burrows generally led to 3 distinctive activity levels at 5.1-15.2, 15.2-25.4 and 66.0-76.2 cm below the surface (Fig. 3). Within each level several food caches were found. Nests, burial sites, and fecal chambers, however, were only found in the second and third levels. At the second level (15.2-25.4 cm) nests were generally 15.2 to 22.9 cm in diameter and lined with fresh grass. At the lowest level, however, nests were much larger, around 25.4-38.1 cm in diameter, and lined with up to 5 years worth of dry grass. Measurements of each level within the burrow system produced some interesting results. The total amount of tunnels excavated within the first 15.2 cm of the soil was approximately 4 times as long as the runways measured above ground. The burrows within the next 10.2 cm were only about 10% of those encountered above ground and the deepest burrows were only about 2% as extensive.

The most time consuming task of building the computer program was constructing the 3D model that formed the foundation of the animation sequences. This consisted of creating simple geometric primitive shapes, such as rectangles, cylinders, and cones that were combined to create more complex objects, such as trees.

Each sequence required 30 frames for every second of animation. Each frame required approximately 500 K of storage space. To store 1 minute of animation required approximately 900 Mb (500 K/frame x 30 frames/sec. x 60 sec. = 900 Mb). Rendering one of these frames took 25 to 35 minutes per frame. Approximately 150 continuous hours of computer time were
needed to generate each minute of the animation sequence.

The complexity of the burrow systems made it difficult to visualize the data using traditional 2-dimensional graphics. To resolve this problem we used state-of-the-art computer technology to create 3D models.

From prior work we found that scientific and technical computing applications are migrating toward 3D animation "visualization." Computer animation, as many are aware, has evolved because much of the repetitive work associated with traditional cell animation can now be quickly accomplished with a few strokes of a mouse or digitizer. Computers not only simplify the animation process but dramatically speed up the creation process. Computer-based paint programs can also be used to create realistic effects, such as rain, snow, and fog, which are very difficult to create by traditional means.

The 3D models created from the field data, combined with animation sequences and paint programs, now provide us with a better understanding of the voles' use of their operational habitat. Most of the rodents' activity is confined to areas with the heaviest accumulation of biomass. Interconnecting runways between burrow openings were generally found only under dense litter accumulations. Shallow burrows were generally found within the actively growing root masses of the orchards' ground cover crop. Only 1 shallow burrow was found in the herbicide strip spray zone within a tree row. The burrow was plugged, however, and appears to have been used to connect 2 burrow systems during the previous season.

The second level of burrows appears to be the species' primary living chambers. Here, where temperatures are modified by the soil's insulating properties, most of the daily routines are carried out. The lack of large food caches and nest chambers indicate that they are used by a relatively small number of animals at one time. The presence

The lowest level of burrows came as a complete surprise. The existence of these burrows was first suspected when vertical holes were encountered during the second level excavations. Finding them tended to be a tedious job but when they were uncovered several important observations were made. First, the food caches were much larger than

These data, along with those collected in other studies over the years, now lead us to the hypothesis that voles, particularly Microtus montanus, exploit their resources to the fullest extent possible. In the spring, when the soil is loose and plants are rapidly producing vegetative growth, voles capitalize upon these resources by extending their above ground runways and burrows through the developing root masses. As both vegetative cover and root mass increase, runways and burrows are excavated to the fullest extent possible.

At some point, as ambient air temperatures increase and humidity decreases, their presence is harder to find and they become more difficult to catch even with permanently established pitfall live traps. Like pocket gophers, little activity is seen above ground. No new holes
appear. Cobwebs, leaves, and dead grass accumulate at the burrow openings and little feeding can be found in the runways. At this juncture it is difficult to say whether or not burrow-building continues but since food requirements remain unchanged, feeding must continue, presumably within the actively growing cover crop root mass.

As the weather cools and humidity increases, signs of their activity begin to appear and trapping success generally increases. Surprisingly, few juveniles are caught and many of the females appear not to have borne litters. By late fall population counts have again risen. In early winter these numbers sometimes exceed those of the previous year.

As winter approaches the ground begins to harden and freeze. Soon biomass production stops and the upper burrows become too cold to live in. Leaves and grass, as well as fallen fruit, now become the animals’ primary food source. Deeper burrows are either built, or if previously established, become the rodents’ living quarters. With the fall of snow, runways are extended further. As the biomass within the runs is depleted, new runs are forced through the snow. Often they are confined to existing ground cover but when populations become quite high, feeding begins on the living trees within the animal’s environment.

The cycle then repeats in the spring when the surviving animals again revert to the original foraging strategies. Old burrows are probably rebuilt and extended. Nests are again relined and the new crop of young born and nurtured.

These data, when viewed through 3dimensional computer generated animation graphics, help us visualize the probable use of the voles’ operational habitat. Much of what has been surmised, however, can only be confirmed, or denied, through additional deep research.

**LITERATURE CITED**

