The tastes of two small rodents—the meadow vole and the white-footed mouse—can determine what trees grow in a forest. ***By Richard S. Ostfeld***

Little Loggers Make a Big Difference

A hundred years ago in the northeastern United States, farms covered one-half to three-quarters of what is today forested land. But working the thin, rocky soils of the Northeast was a marginal existence, and after the opening of the Erie Canal in 1825, farming shifted to the more fertile ground of the Ohio River Valley and the Midwest. Since then, northeastern woods have been regrowing—creating new habitats for forest wildlife, satisfying a human yearning for unmediated natural beauty, and possibly even helping to reduce global warming (young trees have enormous potential to remove carbon dioxide, the primary greenhouse gas, from the atmosphere by capturing the carbon in their burgeoning tissues).

But while some tracts of abandoned farmland became overgrown with woody plants in only a few years, others resisted colonization by trees for decades, and scientists eventually began to wonder what accounted for the difference. The wind would have blown in myriad seeds from the maples, pines, ashes, and other trees bordering all of these "old fields"; were quick-growing grasses outcompeting tree seedlings by creating too much shade and appropriating the available water and nitrogen? Two plant ecologists in upstate New York tried to test this supposition in the 1980s by planting seedlings in areas dense with grasses as well as in areas dominated by taller, slower-growing herbs such as goldenrod—only to have some mysterious nocturnal visitors clip the seedlings, killing them and ruining the experiment. A bit of detective work revealed the unexpected culprits: meadow voles *(Microtus pennsylvanicus)*, small herbivorous rodents that are ubiquitous in North American old fields. The ecologists promptly fenced out the pesky saboteurs and resumed their investigation of plant competition.

Voles are common denizens of virtually every habitat (other than dry desert) in the temperate, boreal, and arctic zones of the Northern Hemisphere. Of the roughly 120 species of voles worldwide, about a dozen are notorious for their boom-and-bust population fluctuations; one of these is the meadow vole. But unlike the populations of some of their more famous relatives (more famous to ecologists, at least), whose population fluctuations follow a regular, three-year cycle, some meadow vole populations irrupt sporadically and others almost always stay high or low. Biologists interested in the radical population swings of voles and their close relatives, the lemmings, have focused almost exclusively on why such fluctuations occur rather than on what the wider impact is. Hearing of the devastation of the researchers' experimental tree seedlings by marauding rodents, my plant ecologist colleague Charles Canham and I decided to investigate whether the fluctuations in vole populations might be important in determining when and whether tree seedlings are able to invade old fields: we wondered whether trees can establish themselves only when the voles go bust. If so, it could be that the old fields that resist tree invasion for decades are those in which the vole populations are chronically high,

Red maple seedlings, opposite, are inviting targets for a hungry meadow vole like the one below. Several weeks old, this rodent has most likely already reached maturity.


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and those that get overgrown quickly are able to do so because their vole populations crash frequently.

Canham and I established nine enclosures in a grassy field on the grounds of the Institute of Ecosystem Studies in Millbrook, New York. We chose a typical northeastern hayfield—habitat that's wonderful for voles but also likely to get rapidly overgrown if left unmown. The enclosures were each about a third of an acre, and wire-mesh fencing more than three feet high kept all but the most intrepid voles from moving between them. For two years we kept track of the populations every other week by livetrapping and marking each individual with a numbered ear tag. Within each enclosure, we kept the vole population at one of three density levels: about 400, 175, and 80 voles per hectare. We chose such distinct levels to match what happens naturally. To maintain these vole densities over the course of the experiment, we had to keep removing individuals from the lower-density enclosures. (We released these animals in another field about a mile away. Some voles, we learned, can navigate their way home from this distance—even wading through streams, crossing paved roads, and scaling fences to get there.)

Inside the enclosures we planted small seedlings of several tree species that commonly colonize old fields in the eastern United States, Quebec, and Ontario, and we monitored their fates for up to a year. In that time, the densest vole populations eliminated about 95 percent of seedlings, whereas medium- and low-density populations killed about 80 and 65 percent, respectively. The voles, it turned out, preferred red maple, white ash, and tree-of-heaven seedlings and turned up their noses at those of white pine and red oak. Such high levels of destruction, combined with such clear food preferences, suggest that these animals control the species composition of regrowing forests.

Were the voles searching for food—or managing their habitat by keeping woody plants out of the grassy fields?

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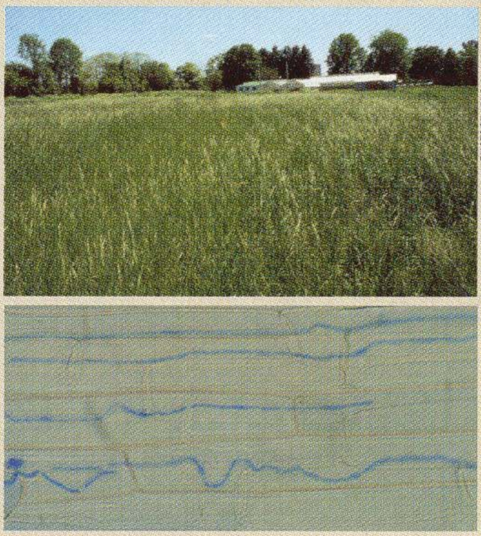
Home and away: The entryway to a meadow vole's nest, right. "Runways" dug by voles, below, leave a lasting impression on their grassland habitat.

Seedlings killed by voles are easy to identify: the stems are clipped near ground level, leaving tiny, diagonally cut stumps. We were puzzled to find that about a third of the clippings went uneaten and were left to rot. Were the voles not searching for food but instead managing their habitat by keeping woody plants from invading the grassy fields that voles prefer? After all, other animals appear to engineer their environment for their own future benefit—beavers create wet meadows by damming streams, elephants aid grasses by destroying savanna trees. But individual beavers and elephants live long enough to benefit from the work, so the evolutionary rewards plausibly outweigh the costs. A vole lives no more than a year, and it is hard to

The Fescue, the Fungus, and the Prairie Vole

The prairie vole *(Microtus ochrogaster)*—a close relative of the meadow vole and one of North America's most prolific mammals—lives in the grasslands of the central United States, building elaborate paths and fibrous nests under the elfin canopy. Tall fescue, a vigorous Old World grass introduced to the New more than a century ago, now reigns over much of this region. Farmers and others planted it widely in the Midwest and Southeast, where it invaded natural communities and displaced native species. Its success results in part from its beneficial relationship with a fungal endophyte—a symbiont living within the plant—that was discovered and quickly forgotten in New Zealand in the 1940s and then redescribed by Charles W. Bacon and colleagues at the USDA's Agricultural Research Service and the University of Georgia in the mid-1970s. They found the fungus after noting that cows grazing on tall fescue were prone to infertility and spontaneous abortion; the endophyte produces toxic alkaloids that sicken and thus discourage grazers, allowing the grass to grow unmolested (see "Trespassers Will Be Poisoned," September 1989).

In 1994, aided by a small army of undergraduates, researcher Jennifer Holah and I planted a series of plots at Indiana University with either infected or uninfected tall fescue to determine how the endophyte affects competition between the grass and other plants. Compared with the plots planted with fungus-free grass, the plots containing the endophyte had fewer different plant species, and tall fescue accounted for a higher proportion of the individual plants. However, we didn't know why.


PHOTOGRAPHS BY KEITH CLAY

Tall fescue grass, top, and the fungus within it, below

For some time, I had been noting dead patches of tall fescue in my research plots. I thought they were succumbing to disease, so I decided to show them to a colleague. To my surprise, the whole mass of dead leaves lifted cleanly off the ground. The grass had been cut near ground level as if with a machete. My colleague, Gary Fortier, of Delaware Valley College, quickly recognized this as the work of voles. I was also puzzled by the toothpicklike segments of grass stems littering our plots, until another small-mammal ecologist explained: Voles like to eat the succulent, nutritious tips of leaves, not the tough bases, but getting hold of leaves twenty inches off the ground requires some effort for a creature that's only two inches high. To feed, a vole bites a stem off at the bottom, pulls it downward, bites off a piece and discards it, pulls the stem down farther, bites off another piece, and so on, until the good parts are within reach. Like the cartoon carrots pulled down into Bugs Bunny's burrow, the grass is eaten from the bottom up.

Although, as a botanist, I have tended to discount mammals as minor components of most plant communities, my research team expanded our study to look at how tall fescue's endophyte might affect vole populations. In the first year, vole density started out low and increased quickly. We found a significantly higher proportion of male voles in endophyte-infected plots than in uninfected ones, suggesting that female voles were avoiding the infected fescue. In the second year of our study, as the population became denser, the ratio between males and females in infected areas evened. Perhaps increasing competition for food and territory had forced females into less desirable habitat. Females in infected plots were older and bigger when they began to reproduce than were their counterparts in uninfected plots; ingesting the fungus seemed to delay puberty.

When vegetation is lush and prairie vole populations are small, little prevents the voles from increasing rapidly. But as their numbers rise, so does competition for the best food plants or, indeed, for any plants whatsoever. Though the voles prefer uninfected tall fescue, they do eat other grasses while trying to avoid the infected plants. In our infected plots, the proportion of tall fescue plants rose as the vole population—and hence the consumption of other grasses—increased. The opposite occurred in uninfected plots. Voles, then, are unwitting accomplices in tall fescue's competitive strategy: the fungus redirects the rodents' appetite toward other plants, sparing its host the cost of being eaten and also eliminating the competition.—*Keith Clay*

S. T. A. PICKETT/BUELL-SMALL SUCCESSION STUDY; I. E. S.

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Good vole habitat, the field above has been clear for about a year and is dominated by plants such as mustard and foxtail grass. The "field" at right, after twenty-eight years of regrowing, has been overrun by red maple.

imagine an individual vole reaping much benefit from killing a several-inch-tall seedling that is years away from shading out grasses and eliminating vole habitat. Only if the voles' descendants, several generations later, lived in the same area could there be an evolutionary benefit from clipping seedlings, and the propensity of the voles' offspring to disperse makes that unlikely. Perhaps, we speculated, voles constantly explore potential new foods, and the few surviving seedlings belonged to species that proved bad tasting.

If noxious taste might protect seedlings, what else would have the same effect? Canham and I tried our best to think like meadow voles. We knew that various hawks, owls, snakes, and mammals prey on the voles and that these rodents have a number of adaptations to compensate for their popularity as food. One is reproductive—females reach sexual maturity at three to four weeks of age and become sexually receptive within a day of giving birth. One litter of approximately four to five young is suckled while the next brood is gestating. Other adaptations include selecting safe haunts and being discreet. It's easy for vole aficionados to impress the uninitiated by predicting which spots in a field are best for finding voles: simply parting the tallest, densest patches of grass will more than likely reveal vole feces, as well as small piles of grass clippings characteristic of vole activity (see "The Fescue, the Fungus, and the Prairie Vole," page 67) and narrow "runways." In shorter, sparser vegetation or near the bare dirt around woodchuck or gopher mounds, such signs will be rare. Canham and I planted seedlings down the middle of small clearings that were intended to simulate woodchuck mounds or other disturbances; in keeping with our expectations, the voles almost never touched these seedlings, even when their populations were quite dense. Lingering in the open, it seems, is not worth the risk of being killed by a sharp-eyed predator, especially an aerial one.

Tall grass is no perfect refuge, however. Mammalian carnivores such as weasels and foxes catch voles by chasing or pouncing and are probably just as dangerous in dense cover as in sparse. Perhaps, I thought, mammalian predators indirectly protect tree seedlings in all habitats—not just in clearings—by trimming the vole populations or at least scaring them into inactivity. My colleague Jyrki Pusenius and I got the idea of tricking the voles into perceiving that they were in danger. We created an audiotape with the sounds of a weasel calling and a weasel catching a vole. With speakers wired to a van parked on the study site, we played the tape every night for two weeks inside some of the enclosures while we monitored the fate of seedlings. To our amazement, voles clipped more seedlings in enclosures where they heard taped weasel sounds than in those where no tapes were played. The same thing happened when we placed a caged weasel inside one enclosure. And neither the feces of bobcats nor the urine of foxes, coyotes, and bobcats discouraged voles from attacking seedlings. The smells of these predators had no more effect than the odor of dilute vinegar. Only when these carnivores actually *eat* voles do they become accidental allies of the little trees.

Most of the trees that invade old fields have fairly large seeds that don't fall far from the parent plant. Even maple and ash seeds, with their helicopter-like samaras, may float only a few dozen yards on the wind, while larger seeds, such as acorns, beechnuts, and hickory nuts, drop like stones. (Exceptions do exist: tiny, winged aspen and birch seeds may float thousands of yards, and cherry and red cedar seeds are swallowed by fruit-eating birds and defecated at some distant spot.) Because of this modest dispersal distance, the invasion of old fields by trees usually proceeds most rapidly near forest edges, where the influx of seeds can be tremendous. Several colleagues and I therefore decided to establish our next generation of experiments at the boundary between forests and fields. Two students, Robert Manson and Jaclyn Schnurr, had already demonstrated that the ubiquitous white-footed mouse is a seed predator extraordinaire, and we thought that mice and voles might provide a one-two punch that could undermine tree colonization of old fields. While meadow voles rarely leave grassy fields to enter forests, white-footed mice are generalists, preferring forests but frequenting old fields as well.

Tall grass is no perfect refuge for voles. Weasels and foxes, which hunt by pouncing and chasing, can catch voles anywhere.

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The white-footed mouse, left, and the meadow vole, below, reproduce frequently and prolifically, adaptations that helps keep them a step ahead of their many predators.

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This time, our enclosures extended five and a half yards into the forest and thirty-eight yards into the field. Each enclosure had three walls and was open on the forest side. We suspected that the voles would treat the forest edge like a fourth wall but that the mice would freely enter the old fields. Again we created vole populations of differing density levels. As before, attack rates on tree seedlings correlated well with vole density. However, we found that wherever vole density was high, mouse density was low, and wherever we kept voles scarce, mice thrived. We don't know exactly how voles deter mice, but we suspect that voles, which are twice the size of mice and about ten times as pugnacious, may attack and chase any mice they encounter. Whatever the mechanism, the result was that enclosures with a high vole density had low seedling survival but high seed survival, whereas those with a low vole density had good seedling but poor seed survival.

A crucial twist is that not only do voles eat seedlings while mice eat seeds, but voles and mice have different food preferences. Mice avoid the smaller and less protein-rich seeds of maples, ashes, and trees-of-heaven but devour the larger, more nutritious seeds of pines and oaks. Pines and oaks, then, should invade old fields dominated by voles (assuming that parent trees reside somewhere nearby), and maples and ashes should colonize old fields dominated by mice. But since few, if any, long-term records are available to tell us which types of old fields each animal inhabits, testing this expectation is difficult.

However, because we maintained the high and low vole population levels within our three-walled enclosures for about four years, we were able to observe which species of rodent had the stronger net impact on tree invasion. Manson surveyed all the experimental plots and found very few naturally occurring seedlings where voles were abundant and mice were scarce. On the other hand, many more natural seedlings flourished where voles were kept rare and mice were plentiful. It makes sense that, as seedling predators, voles have a greater impact on tree regeneration than do seed-eating mice. Any individual forest tree can produce tens of thousands of seeds (or more) in any given autumn, and even if the mice consume 95 percent of those seeds, a healthy number of seedlings could survive. On the other hand, after everything else that may kill seeds—fungi, bacteria, insects, birds, mice, infertility—has had its way, far fewer seedlings than seeds will be present. So a dense vole population that kills almost every tree seedling can strongly inhibit the regrowth of forests.

When mice dominate a field, pines and oaks can't grow there; voles prevent maples and ashes from colonizing.

The life of the meadow vole has wider implications than I suspected the first time my cat bestowed upon me a small, brown, and very dead one. Its targeting of seedlings has prompted some utilities, as an alternative to using herbicides or machinery to control trees, to look into making their power-line corridors favorable to voles. These rodents also play a strong role in preserving attractive vistas and maintaining the open habitats favored by such other wildlife as deer, turkeys, woodcocks, and bluebirds. And meadow voles, by excluding white-footed mice from some habitats, may reduce the risk of Lyme disease, which is carried by ticks that feed off (and are infected by) these mice. Nearly omnipresent, these voracious killers of tree seedlings might even affect the global climate by delaying or preventing the expansion of woods at a time when the absorption of carbon would be very helpful. All these wider implications are nearly invisible—until you push back the tall grass and have a look. □

A weasel, below, indirectly protects seeds and seedlings only when it catches and kills rodents. Death from above: An American kestrel, opposite, swoops down on a vole.

STOUFFER PROD.; ANIMALS ANIMALS

ANTHONY MERCIECA; PHOTO RESEARCHERS, INC.