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Rob Simpson

What Are Squirrels Hiding?

Their half-eaten acorns are clues to a complex relationship with oaks

by Michael Steele and Peter Smallwood

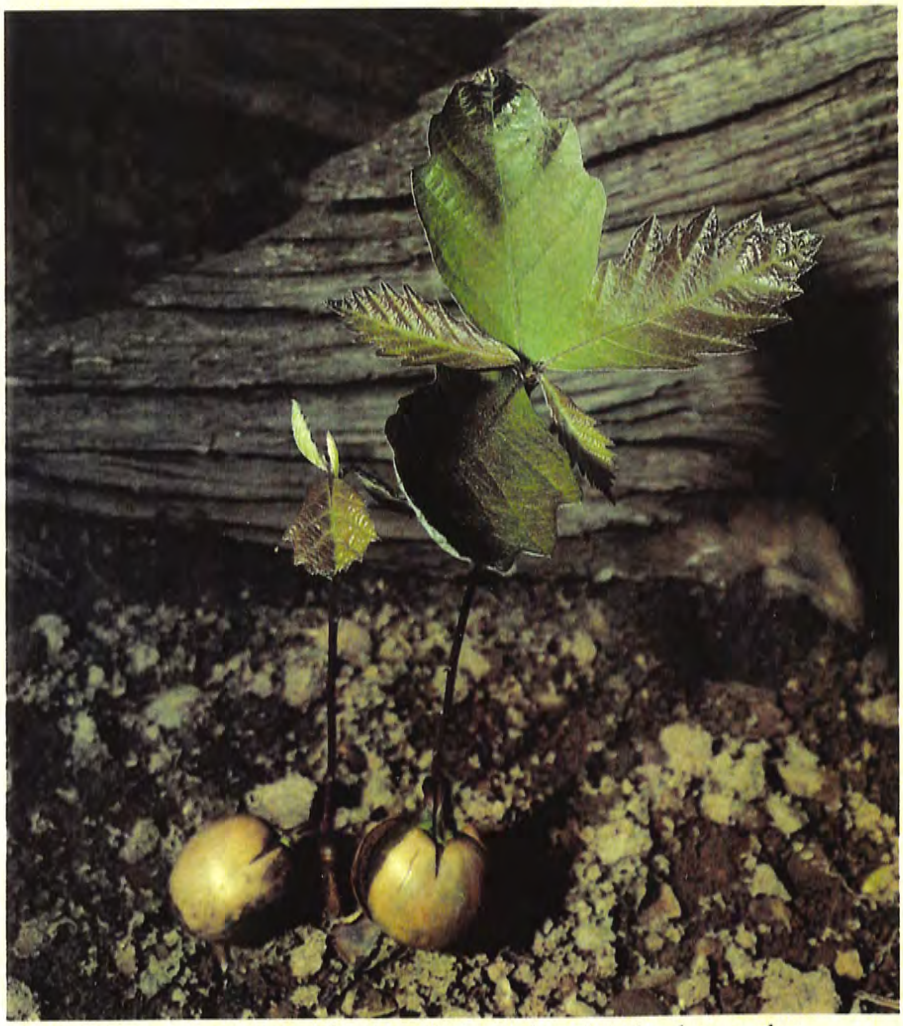
Naturalists and casual observers alike have been struck by the special relationship between squirrels and acorns. As ecologists, though, we cannot observe these energetic mammals scurrying up and down oak trees and eating and burying acorns without wondering about their complex relationship with the trees. Are squirrels dispersers and planters of oak forests or pesky seed predators? The answer is not a simple one. Gray squirrels may devour many acorns, but by storing and failing to recover up to 74 percent of them (as they do when seeds are abundant), these arboreal rodents can also aid regeneration and dispersal of the oaks.

Their destructive powers are well documented. According to one 1908 report, squirrels destroyed tens of thousands of fallen acorns from an oak stand on the University of Indiana campus. A professor there estimated that each of the large white oaks had produced between two and eight thousand acorns, but within weeks of seed maturity hardly an acorn could be found among the fallen leaves.

Deer, turkeys, wild pigs, and bears also feed heavily on acorns, but do not store them, and are therefore of no benefit to the trees. Flying squirrels, chipmunks, and mice are also unlikely to promote tree dispersal, as they often store seeds in tree cavities and underground burrows. Only tree squirrels—whose behavior of caching below the leaf litter often promotes successful germination of acorns—and perhaps blue jays, important long-distance dispersers (see *Natural History,* October 1986), seem to help oaks spread and reproduce.

Early in our study, we observed one particularly puzzling behavior pattern. Squirrels would pry off the caps of acorns, bite through the shells to get at the nutritious inner kernels, and then discard them half eaten. Moments later, they would seize another acorn and repeat the routine. The ground under the towering oaks was littered with thousands of half-eaten acorns, each one bitten only from the top. Why would any animal waste so much time and energy and risk exposure to such predators as red-tailed hawks only to leave a large part of each acorn uneaten?

Gray squirrels are generally opportunistic in their feeding habits, but at other times they are picky. They often eat a variety of budding leaves, flowers, and spring twigs, and even the pupae of giant silk



After sprouting from acorns, red oak seedlings produce their first leaves, above. Acorns of red oaks are more often cached by squirrels, while those of white oaks are immediately eaten. Right: Before caching it for use in winter, a gray squirrel nips an acorn's tip, killing the oak embryo so the seed cannot sprout.

E. R. Degginger; Bruce Coleman, Inc.

An acorn weevil feeds on oak seeds, below. Female weevils may deposit their eggs in them, and squirrels will frequently eat such infested acorns, larvae and all. Right: Two young squirrels venture from their natal nest in the spring or early summer. Within days they will be weaned and left by their mother to forage for themselves.

Mark Moffett; Minden Pictures

Rob Simpson

moths, carrion, a bird's egg or two—and, rarely, nestling chicks. During the autumn and winter months, however, their main diet consists of nuts and seeds, and at this time squirrels readily distinguish between various species, and even parts, of acorns. Active throughout the year, the squirrels store large quantities of seeds and nuts to see them through the winter. These caches usually include acorns of some of the thirty-two oak species that grow in the squirrel's range in eastern North America.

An oak seed, or acorn (really a fruit), consists of an outer shell enclosing two young, energy-rich seed leaves (or cotyledons) that meet to surround a tiny embryo at the apex, or tip. To a squirrel, the acorn is a package of energy (between five and twenty kilocalories) that can be easily opened and eaten in less than half the time needed for other, harder nuts or stored for use up to ten months later.

Not all acorns are the same. The two major groups of oaks—red and white—have seeds that differ generally in chemical makeup. Red oak acorns are rich in fats (18 to 25 percent of dry weight) but are laced with 6 to 10 percent tannins (the bitter-tasting, water-soluble compounds used to tan hides). White oak acorns are less fatty (5 to 10 percent) and lower in tannins (less than 2 percent). The two groups of trees also differ in when they germinate. Red oak acorns lie dormant in winter and sprout in spring; white oak seeds usually sprout soon after falling to the ground in autumn.

We knew that more fat enhances the seeds' energy value, but we also suspected that high tannin levels make them less palatable and digestible to squirrels. Tannin in oak leaves repels many insects, and some trees may even increase their tannin concentrations as a natural pesticide. Do these chemicals also repel squirrels or do the squirrels rely on them to protect their own acorn caches from insects and other pathogens? How do tannins and other acorn chemicals influence the squirrels' feeding and caching decisions? And do these behaviors, in turn, affect the distribution of oaks? These were but a few of the questions we sought to answer with a series of field experiments.

In 1980, zoologist Alan R. Lewis studied the dietary preferences of squirrels in the winter by identifying the remains of acorns left behind after squirrels had eaten from their caches. Lewis demonstrated that squirrel preferences depend not only on the energy content of the acorns but also on their relative abundance. Sometimes as many as six species of oaks grow within the range of a single gray squirrel. Lewis found that when faced with these choices, the squirrels ate more fatty acorns, except when the lower-energy acorns were more numerous. Other researchers have shown that squirrels are generally efficient in their feeding habits, expending the least amount of energy to obtain the most nutritious foods (see *Natural History*, October 1989). Ecologist Christopher C. Smith, of Kansas State University, and others had shown that given a choice, squirrels preferred to take mostly the high-fat red oak acorns.

To further analyze the squirrels' preferences, Peter Smallwood and David Peters, of Ohio State University, created "artificial acorns" with measured chemical additives. After shelling and processing white oak acorns into a dough, they added various levels of tannin and fat to simulate those in real acorns. The squirrels consistently chose to eat the acorns with lower tannin levels, particularly in autumn—even those acorns with low fat content.

These results seemed to contradict such earlier studies of squirrels' food preferences as Smith's. After wrestling with this inconsistency, however, Smallwood and

Peters realized that squirrels may exhibit different preferences for caching and eating. Perhaps squirrels use one kind of acorn for immediate consumption and another for storing. When white oak acorns germinate in the fall, they concentrate much of their nutrients in a taproot, which squirrels find unpalatable. We wondered whether squirrels might eat white oak acorns immediately because their early germination renders them unsuitable for caching, and store the red oak acorns, which germinate later, for consumption in winter and spring.

To test this idea, we presented gray squirrels in Ohio and Pennsylvania parks and campuses with both red oak and white oak acorns. In each of more than 1,200 feeding trials, we recorded whether the acorn was eaten or stored, the distance it was dispersed, and the amount of time the animal took to eat or bury the acorn. Unambiguously, squirrels cached more red oak acorns (60 percent) and consistently ate those of the white oaks (more than 85 percent).

In a second group of experiments we attempted to determine the squirrel's role in dispersing trees—this time in mature oak forests in Pennsylvania's Pocono region. But we often failed to find the buried acorns, even after watching a squirrel only ten feet away shove a nut into a shallow hole, cover it, and brush debris over the top. Clearly, we needed a more sophisticated approach. Following the lead of botanist Victoria Sork, we tagged thousands of red and white acorns with small metal labels and, after the animals dispersed the seeds, used metal detectors to recover them. Again, the results were clear. Squirrels either ate white oak acorns on the spot or carried them only short distances before eating them. Red oak acorns were generally carried farther away and cached intact.

Other factors besides germination schedules and seed chemistry affect the seeds' perishability. Might squirrels also respond to these in deciding whether to cache? Many acorns become infested with insect larvae, particularly weevils of the genus *Curculio*. During spring, females of several species of these beetles bore into acorns to deposit their eggs. By early fall, the maggot-sized larvae have often destroyed more than 60 percent of the crop of single trees. Would squirrels avoid wormy acorns as less suitable for storing?

We identified batches of infested acorns

Preparing to cache an acorn, a gray squirrel excavates a hole in the soil. Often squirrels go through the motions of burying acorns, only to store the seeds elsewhere.
E. A. Janes; NHPA

by having them X-rayed at a local hospital, then offered them to the squirrels. Consistently, they selected noninfested seeds for caching, but opened and consumed the infested ones, eating the weevils as well. In nearly 300 tests, the squirrels readily ate the high-protein larvae.

Sometimes squirrels kill the early-sprouting white oak acorns by excising the seed embryos just before burying them, as John Fox reported in 1982. If an acorn germinates before the squirrel can recover it, up to half its stored energy goes to the seedling rather than the squirrel. A few quick scrapes of the squirrel's incisors across the bottom of the acorn kills the embryo and preserves the seed's nutrients intact.

While this notching behavior underscores the importance of seed perishability, it does not explain the habit of biting and discarding acorns that so intrigued us at the beginning of our study. Those squirrels ate only from the acorn's top half—the end farthest from the embryo. And the acorns were of red oaks, not white. As we moved our research from parks and campuses to rural woodlands, from the scrub-oak forests of the southeastern coastal plain to the oak-hickory forests of the Middle Atlantic States, we saw the same pattern. Squirrels bit off the tops of acorns of at least seven red oak species. We also found that blue jays and common grackles did the same. Squirrels, jays, and grackles each employed a different technique to open an acorn, but all consumed only 30 to 60 percent of the kernel—and always from the top of the seed. Later we discovered that weevil larvae were found in the top of the acorn two to three times more often than in the bottom.

Our first guess, that higher levels of noxious tannins are located near the bottom of the acorn, where the embryo is located, was borne out by chemical tests. But we also found, in more than seventy-five trials, that squirrels frequently cached partly eaten seeds, which raises the possibility that the acorns may have become adapted to withstand such attacks. Because their embryos were not destroyed, these seeds germinated about as often as undamaged ones. Perhaps for the oak, the half-palatable acorn is an effective strategy for survival. Maybe acorns benefit from being chosen by squirrels for burial and dispersal, as long as they are not totally destroyed.

We still wondered what factors other than tannin content influenced the squirrels' choices. What about the acorn's shape, for instance, or the toughness of its shell? In pursuit of these questions, we offered gray squirrels their choice of whole acorns, shelled acorns, and shelled acorns in which the bottom and top ends were carved to resemble the opposite ends. Squirrels ate just the top portion of both whole and shelled seeds, indicating that the shell was not the determining factor. But when we presented squirrels with carved seeds, we found that they were fooled into eating in reverse, feeding only on the disguised bottom half. Next we presented squirrels with artificial acorns that contained varying amounts of tannin. Consistently, when given those seeds with the highest tannin concentration, squirrels ate from the top half but consumed only a small amount.

Ecologist Joseph Grinnell, in a 1936 paper, pondered how oaks could colonize hilltops, since acorns are too heavy for wind dispersal and do not roll uphill. He concluded that animals must carry them to such sites. Although we are only just begining to grasp some of the complexities of the squirrels' relationship with oak forests, we agree with Grinnell's early assessment. By dispersing red oak acorns more often and farther than white oak acorns, by excising the embryo of white oak acorns and storing primarily sound acorns, we suspect that gray squirrels can strongly influence the distribution and range of various oak species. Indeed, evidence is accumulating that along with jays, squirrels are crucial in regenerating second-growth oak forests and may even have been responsible for spreading the vast stands of oak throughout North America after the last retreat of the glaciers 10,000 years ago. □