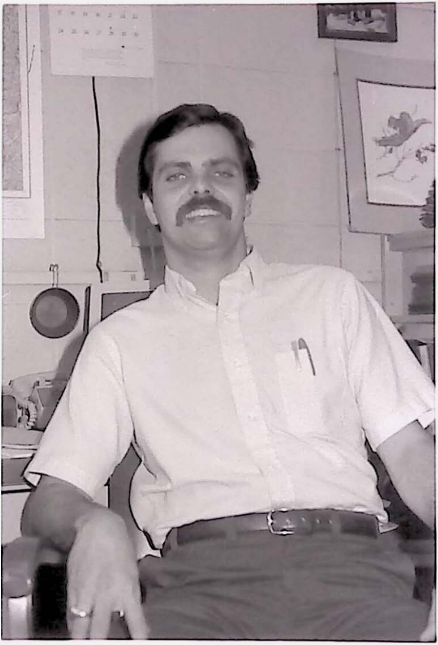


(the late)
Wm and Hilda

CURRICULUM VITAE

lives in WB

PERSONAL:

Name: Michael Alan Steele
Place and Date of Birth: Lancaster, Pennsylvania, 13 November, 1959 Lanc New Era
SSN: [redacted]
Marital Status: Married (Margaret Ann Steele) 2 children (Micahel A. Steele, Jr., 10 yrs.; Tyler W. E. Steele, 3 yrs.)

EDUCATION:

Millersville University of Pennsylvania, B.S. Biology
(Honors/Magna Cum Laude), May 1982
Wake Forest University, Ph.D. Biology, May, 1988
Dissertation: Patch use and foraging behavior in the fox squirrel: tests of theoretical predictions.

PROFESSIONAL EXPERIENCE:

Teaching Experience:

1989- Assistant Professor of Biology (Biological Principles, Human Biology, General Biology, Vertebrate Zoology, Animal Behavior, Parasitology, Ecology, Evolution), Wilkes University, Wilkes-Barre PA
1988 Visiting Lecturer in Biology (Zoology), Salem College, Winston-Salem, NC.
1987 (Summer) Teaching Assistantship (General Biology), Wake Forest University
1987 Teaching Assistantship (Organismic Biology), Wake Forest University.
1986 Teaching Assistantship (Ecology), Wake Forest University
1985-86 Co-director of a graduate study group in Evolutionary Ecology.
1985-89 Occasional lectures in Vertebrate Zoology and Ecology.
1983 Teaching Assistantship (Organismic Biology), Wake Forest University.
1982 Teaching Assistantship (Biological Principles), Wake Forest University.
1979-82 Undergraduate Teaching Assistant and Tutor, Millersville University of Pennsylvania

Research Experience:

1991-92 Collaborative research with Dr. Gordon Kirkland, Shippensburg University:
Small mammal communities of northeastern Pennsylvania

1989-92 Faculty-student research, Wilkes University:
Caching strategies of gray squirrels
Effects of plant toxins on parasite infections in a mammalian host
Chemical and physical adaptations of acorns for dispersal by seed predators
Response of seed predators to tannins in acorns
Biogeography of small mammals on islands in the Susquehanna river

1989-92 Collaborative research with Dr. Robert Brown, Wake Forest University:
Population Genetic of small mammals on mountains in the southern Appalachians

1988-89 Postdoctoral Research Associate, joint position between North Carolina State University (Dr. Roger Powell) and Wake Forest University (Dr. Peter Weigl):
Studies of biogeography of small mammal communities in southern, high-elevation spruce-fir forests.

1987-88 Research Associate, Wake Forest University:
Survey of rare, threatened and endangered vertebrate species in the mountains of North Carolina (results published in management handbook) Studies of habitat use

and distribution of northern flying squirrel (*Glaucomys sabrinus*) in the Great Smokies National Park.

1985-87 Research Associate , Wake Forest University:
Project leader for North Carolina Fox Squirrel Study (Funded by North Carolina Wildlife and Pittman Robertson Fund): Duties included demographic studies, radiotelemetry, habitat analyses, foraging experiments in the field, food analyses (Chemical analyses, calorimetry), behavioral experiments in the laboratory and museum studies.

1983-85 Student Curator of Mammal Collections, Wake Forest University.

1983-85 Research Assistantship, Wake Forest University:
Duties included studies of habitat use, activity and movement patterns of fox squirrels and gray squirrels, and competitive interactions between these two species.

1979-82 Undergraduate Research:
Habitat segregation between *Microtus pennsylvanica*, *Clethrionomys gapperi*, and *Peromyscus leucopus*; The status of the fox squirred (*Sciurus niger*) in Pennsylvania; Population ecology of the fox squirrel (*Sciurus niger*) in Pennsylvania.

AWARDS:

1992	Carpenter Oustanding Teaching Award (given to top faculty member)
1992	Who's Who in Science and Technology
1991	Outstanding Teaching Designation Award (given to Top 10% of faculty per year)
1990	~~Presidential Young Investigator Award (NSF) Nomination~~
1990	Full Member Sigma Xi Honor Society
1987	Elton C. Cocke Outstanding Graduate Student Award Nomination
1987	Sigma Xi Outstanding Graduate Research Award in Biological Sciences
1987	Outstanding Graduate Research Award in Biological Sciences, Benkman Scientific/WFU Graduate Student Association
1985	Wake Forest University Graduate Scholarship
1985	Associate Member Sigma Xi Honor Society
1982	Phi Kappa Phi Honor Society
1982	Outstanding Senior Biology Award (in dept. of 450 majors), The Assoc. of State College and University Biology Faculty
1982	Outstanding Young Men of America

GRANTS AND SCHOLARSHIPS:

1992	Wilkes University Faculty Development Grant ($1200.00)
1991	National Science Foundation (ILI) Grant ($57,000, pending)
1991	Pennsylvania Wildlife Conservation Fund Grant (with G. Kirkland, $13,100.00)
1991	Wilkes University Faculty Development Grant ($2450.00)
1990	Pennsylvania Wildlife Conservation Fund Grant (with G. Kirkland, $21,000.00)
1990	Highlands Biological Station Visiting Scientists Research Grant ($600.00)
1990	North Carolina Non-Game Research Grant ($3000.00)
1990	North Carolina Non-Game Research Grant ($2000.00)
1989	Highlands Biological Station Postdoctoral Research Grant ($200.00)
1987	Wake Forest University Summer Research Fellowship ($800.00)
1986	American Society of Mammalogists Research Grant ($500.00)
1986	North Carolina Wildlife Federation Scholarship and Research Grant ($500.00)
1985	Sigma Xi Grant-In-Aid of Research (National Chapter) ($250.00)
1983-87	Five Wake Forest University Travel Grants for paper presentations ($1200.00)
1983	Wake Forest University Summer Research Fellowship ($500.00)
1981	Millersville University Alumni Soc. Research Grant ($350.00)

RESEARCH INTERESTS:

Behavioral, population and community ecology of vertebrates
Foraging behavior
Plant-herbivore interactions
Seed predation and seed dispersal

PROFESSIONAL SOCIETIES:

American Society of Zoologists
American Society of Mammalogists
Ecological Society of America
Sigma Xi Honor Society
Phi Kappa Phi Honor Society
International Society for the Study of Ecology
Association of Southeastern Biologists
Pennsylvania Academy of Science
International Society of Behavioral Ecologists
Pennsylvania Biological Survey Committee

PUBLICATIONS:

Recent Papers:

Steele, M. A. and P. D. Weigl. (In Press). Patch use by the fox squirrel: responses to variation in patch density and prey profitability. American Midland Naturalist.

Steele, M. A. (1991). Learning. *In McGill's Life Science Survey.* Salem Press.

Steele, M. A. (In Press). The Hardy Weinberg Law. In *McGill's Life Science Survey.* Salem Press.

Steele, M. A., T. W. Knowles, K. Bridle, and E. Simms. (In Review). Tannins and partial consumption of acorns: evidence for a new mechanism of seed dispersal. Oecologia.

Weigl, P. D., M. A. Steele, L. J. Sherman, J. C. Ha and T. S. Sharpe. 1989. The ecology of the fox squirrel in North Carolina: Implications for survival in the southeast. Bulletin of Tall Timbers Research Station. 27: 1-95.

Steele, M. A. (In Press) Ethology. In *McGill's Survey of Psychology.* Salem Press.

Steele, M. A. (In Press) Habituation and Sensitization. In *McGill's Survey of Psychology.* Salem Press.

Knowles, T., M. A. Steel, P. D. Weigl. 1989. Survey of Rare and Endangered Vertebrates in North Carolina. Report to National Park Service. 1-173 pp.

Steele, M. A. and P. D. Weigl. Sampling behavior and selective foraging by the fox squirrel (*Sciurus niger*). (Manuscript).

Steel, M. A. and P. D. Weigl. Temporal and spatial patterns of patch use by the fox squirrel. (Manuscript).

Book Review:

The Naturalist History of Tree Squirrels. By John Gurnell. Facts on File Publ. New York, N.Y., and Oxford U.K. 1989. J. Wildlife Management. 53:273-274. (with P. D. Weigl)

Recent Abstracts:

Bachman, W. and M. A. Steele. 1991. The effects of tannins on partial acorn consumption by mammals. J. Pennsylvania Academy of Science. 64:181.

Bachman, W. and M. A. Steele. 1991. The effects of tannins on partial acorn consumption by mammals. Bulletin of the Ecological Society of America.

Steele, M., T. Knowles, W. Bachman. 1991. Tannins and partial consumption of acorns by mammals: evidence for a new mechanism of seed dispersal. Abstracts of the 71st Annual Meeting of the American Society of Mammalogists.

Steele, M. and R. Powell. 1991. Biogeography of small mammals in the southern Appalachians: patterns of local and regional abundance. J. Pennsylvania Academy of Science. 64: 207.

Steele, M. A., T. W. Knowles, and K. Bridle. 1990. Tannins in acorns: A new look at predator defense. Abstracts of the Sixth Internation Congress of Systematic and Evolutionary Biology.

Steele, M. A. , T. W. Knowles, and K. Bridle. 1990. Tannins in acorns: A new look at predator defense. Journal of the Pennsylvania Academy of Science. 63:105.

Steele, M. A., and R. Powell. 1990. Biogeography and community ecology of small mammals in the Southern Appalachians. Abstracts of the 70th Annual Meeting of the American Society of Mammalogists.

Steele, M. A., M. Bowen, P. D. Weigl. 1989. Body size, predation risks, and foraging efficiency in fox (*Sciurus niger*) and gray squirrels (*Sciurus carolinensis*) Amer. Zool:28-48A.

Weigl, P. D., M. A. Steele, T. W. Knowles, L. J. Krebs and T. M. Goater. 1989. The northern flying squirrel (*Glaucomys sabrinus*) in the Southern Appalachians: a victim of biological warfare? Abstracts of the 69th Annual Meeting of the American Society of Mammalogists.

Steele, M. A., T.W. Knowles and K. Bridle. 1989. Partial consumption of acorns by vertebrate predators: the role of tannins. ASB Bulletin. 36:89.

Steele, M. A. and P. D. Weigl. 1988. The energetics of patch use in the fox squirrel: trade-offs between prey profitability and prey density. Abstracts of 68th Annual Meeting of the American Society of Mammalogists.

Steele, M. A. and P. D. Weigl. 1987. Sampling behavior and patch-use in the fox squirrel (*Sciurus niger*). Abstracts of the 67th Annual Meeting of the American Society of Mammalogists.

Weigl, P. D. and M. A. Steele. 1987. Fox squirrel color polymorphism: an evolutionary riddle and ecological indicator. Abstracts of the 67th Annual Meeting of the American Society of Mammalogists.

Steele, M. A. and P. D. Weigl. 1986. Patch use and selective foraging by the fox squirrel (*Sciurus niger*) when feeding on the cones of the longleaf pine (*Pinus palustris*) Amer. Zool. 26:104A

Weigl, P. D. and M. A. Steele. 1986. The geographic variation of the fox squirrel (*Sciurus niger*): The influence of pleistocene vegetation patterns. Abstracts of the 66th Annual Meeting of the American Society Mammalogist.

seven additional abstracts prior to 1986

INVITED PRESENTATIONS:

1992 Millerville University of Pennsylvania, Millersville PA
1991 Pennsylvania State University, College Park PA
1991 East Stroudsburg University, East Stroudsburg PA
1990 Clemson University, Clemson SC
1990 Villanova University, Villanova PA.
1989 Wilkes University, Wilkes-Barre PA
1989 Salem College, Winston-Salem NC
1988 Millersville University of Pennsylvania, Millersville PA
1986 Sigma Xi Research Award Presentation, Bowman Gray School of Medicine, Wake Forest University, Winston-Salem NC

PROFESSIONAL REVIEWS:

Various textbook publishers
Journal of Wildlife Management
Journal of Mammalogy
Pennsylvania Academy of Science
American Midland Naturalist

SUPERVISION OF STUDENT PROJECTS AND HONORS RESEARCH:

1991-92 Kimberly Gavel, Physical and chemical adaptations of acorns for dispersal by seed predators; research grant from Sigma Xi

1991-92 Kathleen Flaim, The effects of dietary tannin on mammalian gut morphology, research grant from Pennsylvania Academy of Science

1991-92 Donna Zurawski, The effects of dietary tannin on helminth infections in a mammalian host

1990-91 Wendy Bachman (Ph.D. student, University of Illinois, Chicago), The effects of tannins on partial consumption of acorns by small mammals; research grant from the Pennsylvania Academy of Science

1990-91 John Daley (Ph.D. students, Lehigh University), The distribution of *Cuculio* larvae in *Q. alba* and *Q. rubra* acorns

1989-90 Bernard Novabilski (Medical Student), The biogeography of small mammals on islands in the Susquehanna River

DR. MICHAEL A. STEELE
BIOGRAPHY

Assistant Professor of Biology Dr. Michael A. Steele of Wilkes-Barre has been a member of the Wilkes University faculty since 1989. Steele specializes in plant/animal interactions and small mammal communities. He has directed numerous research projects with collegues and undergraduate students which include the physical and chemical adaptations of acorns for dispersal by seed preditors, the effects of dietary tannin on mammalian gut morphology, and the biogeography of small mammals on islands in the Susquehanna River.

"Research programs are an important part of my teaching activities," commented Steele. "The search for solutions to the environmental problems we face today can begin by intstilling the importance of basic research skills in our students. My contribution to science lies not only in research, but in the development of new scientists."

Author of numerous papers and abstracts, Dr. Steele's research interests include behavioral population and community ecology of vertebrates, foraging behavior, plant-herbivore interactions and seed predation and dispersal.

Active in local conservation efforts, Steele is also a member of several professional societies including the Ecological Society of America, the American Society of Zoologists Sigma Xi Honor Society, and the International Society for the Study of Ecology.

Steele received the Carpenter Oustanding Teacher Award for the 1991-92 academic year.

The Lancaster native holds a Ph.D. in Biology from Wake Forest University in in Winston-Salem, North Carolina. Steele is also a magna cum laude graduate of Millersville University with a B.S. in Biology.

The son of William and the late Hilda Steele of Lancaster , Dr. Steele and his wife, Margaret Ann have three children, Michael, Jr., Tyler, and Emily. The couple reside in Wilkes-Barre.

-30-

110293

ESSAY

Ecological degradation starts at the top and works its way down.

Peaks in Decline

by Robert A. Browne

203NW

IN MOST OF North Carolina, spring arrives early. On the Wake Forest campus, daffodils bloom in late February, tulips and dogwood trees in March, and by April even the frost-fearing oaks are in full leaf.

But on this mid-April day the scene before me is that of Maine or Quebec, not North Carolina, with two feet of old snow blanketing the ground. The climate and vegetation here should resemble what ecologists refer to as the Canadian zone. But I am at the top of Mount Mitchell, approximately a hundred miles west of Winston-Salem and, at 6,684 feet, the highest point in eastern North America.

Working silently as the sun sets in a saddle between two peaks, I set eighty small mammal live-traps, baited with peanut butter and a bit of apple. At first light I'll return to check the traps as part of a research project investigating the genetic variation of the small mammal populations inhabiting the spruce-fir zones that crown the southern Appalachian mountains.

At approximately 5,000 feet in elevation the southeast forests change from hardwoods such as oak, hickory, and maple to conifers, primarily red spruce and Fraser fir (a close relatent of the spruce-fir forests range from a 420-acre plot atop Grandfather Mountain to the thousands of acres straddling the ridge line of the Great Smoky Mountains.

Although some of the areas, such as Mount Mitchell, were extensively timbered at the turn of the century, much of the area is protected as national or state parks. However, park status has not protected the habitats from two serious problems.

In the late fifties, an insect pest introduced from northern Europe, the adelgid (also known as the woolly aphid), was first reported on Mount Mitchell, from there spreading to the other peaks. The insect attacks mature Fraser firs, eventually girdling and killing the trees. Airborne pollutants, such as sulfuric acid and heavy metal particles, also appear to have contributed to the decline of the spruce-fir forests. Twenty years ago, when I hiked the 2,000-mile Appalachian Trail, the southern spruce fir forests were a solid canopy above the trail. The effect was that of a darkened medieval cathedral with only scattered rays of light reaching the forest floor. Now, many of the mountain tops have been transformed into a graveyard of bare trunks, studded with trees so devoid of needles they are nearly transparent.

In addition to their fragile ecology, the southern high-peak coniferous forests can be thought of as islands surrounded by a sea of hardwoods. Habitat fragmentation, combined with the fact that many of the species are at the extreme southern limit of their range, means that many of the high-peak plant and animal species are rare and/or endangered. Some are relicts from the last glacial epoch of approximately 10,000 years ago, when spruce-fir forests covered much of the Southeast.

My interest focuses on how much genetic variability occurs in the small mammal species which inhabit the spruce-fir forests. Like the forests, their populations are fragmented, with some

(311

of the species threatened by extinction. I and my colleagues would like to know how much genetic variability exists in each population and the extent of variability between populations on each mountain top island. Since some of the populations may soon go extinct, we would like to know how much of a loss (in terms of the overall genetic variability) the extinction of a particular population would represent. We also are looking for evidence that corridors of immigration occur between some peaks and for the extent of isolation for different species.

To address these questions we've been trapping and conducting genetic analyses of three species. The deer mouse (Peromyscus maniculatus) occurs over much of the United States, but in the Southeast is usually restricted to areas above 2,500 feet (it is also the species that carries the deadly hantavirus, but fortunately the virus has never been reported in the East). Although it is common in the spruce-fir forests, it also does well in hardwoods, and hence the range is relatively continuous in the southern Appalachians. In contrast, the red-backed vole (*Clethrionomys gapperi*) is a larger rodent much more tightly linked to the spruce-fir ecosystems. Although it can live in some of the hardwood "gaps" between peaks, the river valleys present formidable, if not impassable, barriers between peaks. The third species, the northern flying squirrel (*Glaucomys sabrinus*), is most closely tied to the spruce-fir ecosystem. It also occurs in low densities and is officially classified as endangered in the Southeast.

Our project involves trapping all three species at night from eight peaks (see map). Since we try to obtain fifteen to forty individuals for each species from each peak, this entails numerous trapping nights in all types of weather. (I must admit, however, that the visits to the peaks are a welcome respite from laboratory work or grading papers back at the Wake Forest campus.) The field work is also markedly different from my other research project investigating the genetics of pathenogenetic (all-female) reproduction in brine shrimp, which are found in salty lakes and coastal lagoons, especially in the Mediterranean basin.

After trapping, tissue, and blood samples are taken from the mice and voles (only blood is taken from the flying squirrels since they are endangered), placed on dry ice, and returned to the laboratory at Wake Forest. Via a technique known as allozyme electophoresis, the genetic patterns controlling twenty to thirty enzymes are ascertained. In this way we can estimate the amount of genetic variability for each population.

***Top:* Red-back vole.**
***Bottom:* Northern flying squirrel.**

Many of the mountain tops have been transformed into a graveyard of bare trunks, studded with trees that are nearly transparent.

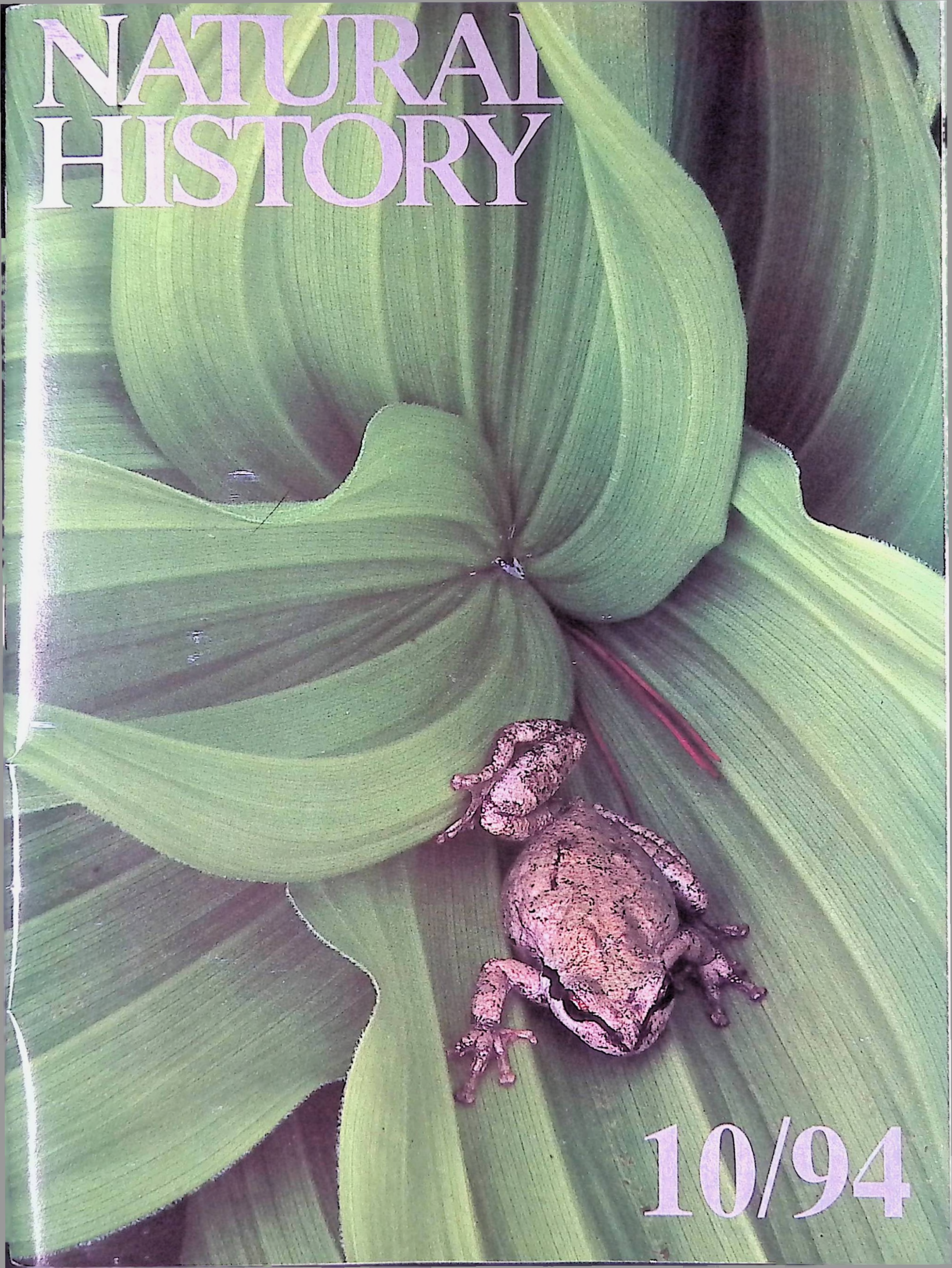
The study is a cooperative effort, with funding provided by the National Park Service, the U.S. Fish and Wildlife Service, the state of North Carolina, and Sigma Xi. Mike Steele, who received his doctorate in biology at Wake Forest in 1988 and is now an assistant professor at Wilkes College in Pennsylvania, has done part of the trapping of mice and voles, while Peter Weigl, a biology professor at Wake Forest, has done much of the trapping of flying squirrels, which he has studied for the last twenty-five years. Numerous Wake Forest undergraduates have been involved in both the field and laboratory analyses of the 400 animals sampled to date.

Our study, though not complete, has produced a number of preliminary findings. Deer mice, as expected, show extensive genetic variation, with few barriers to gene flow found among populations. Voles, which have only one-half the genetic variation of mice, with extensive barriers occurring between peaks, appear to be Pleistocene relicts, with the populations forced into drastically smaller areas since the last glacial epoch. The corridors between peaks also appear to be much more restricted for voles than mice. Although we have the least amount of data for flying squirrels, it is the most provocative. For example, for the ten squirrels we have sampled from Roan Mountain, we have found no detectable genetic variation. This flying squirrel population appears to be very isolated, with sporadic severe population declines to just one or two breeding pairs (the current population on Roan is estimated to be about fifty individuals). This lack of genetic variability may leave them susceptible to diseases and ill-equipped to adapt to habitat changes. As we collect more data we should soon know if flying squirrels from other peaks are also genetically uniform and whether significant genetic variability exists between populations.

I spent part of the summer trapping in northern New England where the spruce-fir forest are continuous. By comparing the genetic variation of the New England samples with those from the South, we should be able to measure how much, if any, loss of genetic variability has occurred in the fragmented relict populations of the southern Appalachians.

And what about the future of the southern high-peak fir forests? I'm afraid the prognosis is not an optimistic one. Each year the impact zone of the insect pests and anthropogenic pollution becomes more extensive. Yet there is a bit of hope. Due to changes in bark morphology with age, the adelgids only attack mature trees. Thousands of juvenile trees grow in the slim shadows of the ghostly trunks. Currently, as soon as they mature, they are doomed. But amidst that multitude may be the one or two genetic variants that are immune to adelgids and can tolerate acidic soils. ■

Robert A. Browne is a professor of biology at Wake Forest.


NATURAL HISTORY
10/94

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.

Rob Simpson

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

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. □