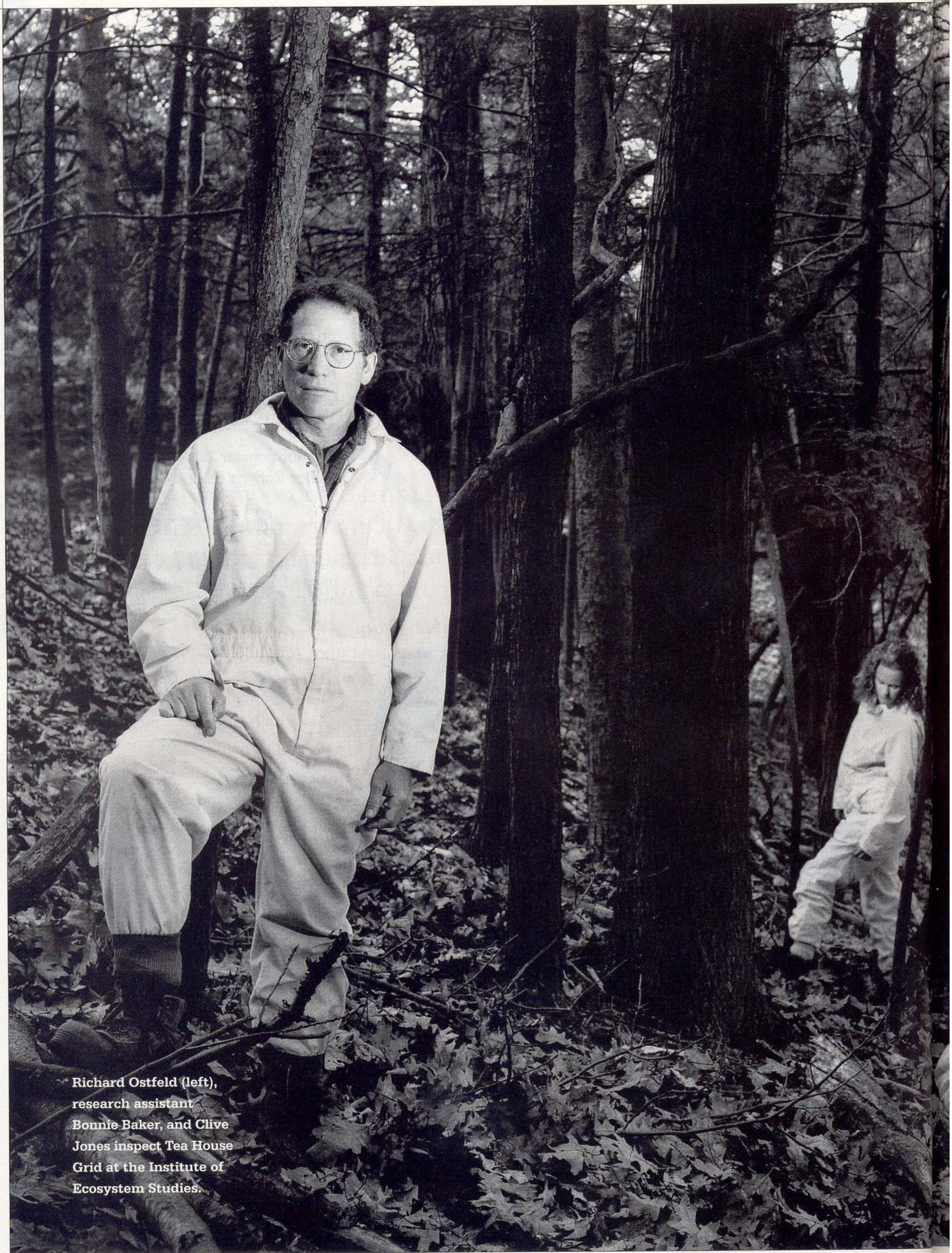
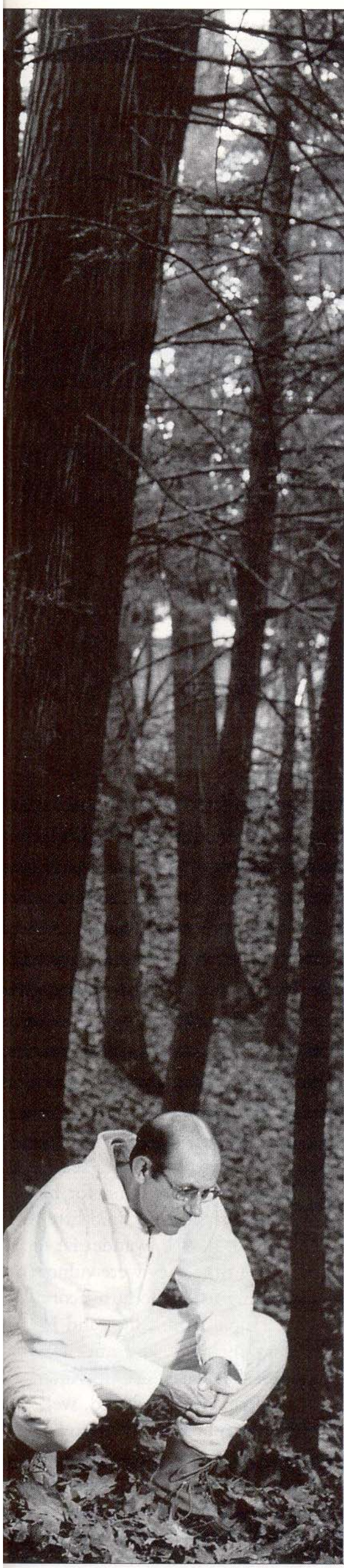


Richard Ostfeld (left), research assistant Bonnie Baker, and Clive Jones inspect Tea House Grid at the Institute of Ecosystem Studies.



PERIL *in the* UNDER-STORY

GRADUATE STUDENT ERIC SCHAUBER ENTERS TEA House Grid with three research technicians in tow. Once in this forested area they separate into teams of two, marching resolutely toward their coordinates. It's an August morning in 1998, already 70 degrees Fahrenheit even though the sun has been up less than an hour. Heavy dew drips from the forest understory. Despite the heat, Schauber and crew are dressed in white coveralls and latex gloves, with duct tape sealing the gaps at ankle and wrist. Schauber lifts a small metal box from the forest floor and dumps its contents into a plastic bag. After a quick examination he says, "Number 2864, lactating female, 26 grams, 9 left, 12 right." He then gently places Number 2864 on some leaf litter, and in three bounds she is gone down a hole.

SCIENTISTS ARE SAYING THIS SUMMER WILL BE ONE OF THE WORST YET FOR LYME DISEASE. HOW DO THEY KNOW? NEW ANSWERS LIE IN THE OAK FOREST.

by RICHARD S. OSTFELD *and* CLIVE G. JONES

This is not Chernobyl or a Superfund site, and Number 2864 is not some mutant radioactive creature with extra limbs. Tea House Grid is a five-acre forest plot in upstate New York, one of the most thoroughly studied in this part of the country. Number 2864 is a white-footed mouse (Schauber knows her identity from a numbered metal ear tag), and she is infested with black-legged ticks on both ears—their preferred sites of attachment. As Schauber has noted, there are 9 ticks on the left ear, 12 on the right. The metal box she was caught in is a live trap used to monitor natural populations of mice. Schauber and crew wear duct-taped white coveralls because these ticks are just as happy crawling up the leg of a graduate student as that of a mouse, and the ticks can transmit Lyme disease, ehrlichiosis, babesiosis (a malaria-like sickness), and other debilitating diseases.

Schauber is part of our ecological research team at the Institute of Ecosystem Studies, in Dutchess County. Over the past several years, the team's research has revealed remarkable connections among oak trees, mice, deer, ticks, human diseases, and gypsy moths, to name only the most prominent players. The ticks on the ears of Mouse Number 2864 are in the midst of an odyssey that began the previous autumn and may end as a case of human Lyme disease during the following summer.

BY STUDYING ACORNS AND WHITE-FOOTED MICE, ECOLOGISTS CAN PREDICT THE RISK OF EXPOSURE TO LYME DISEASE ALMOST TWO YEARS IN ADVANCE.

That odyssey began 10 months before, in the fall of 1997, when the red oak and chestnut oak trees on Tea House Grid (and throughout the northeastern United States) let loose with a bumper crop of acorns—something they usually do only every three or four years. Our co-worker Charles Canham determined that over a couple of months the trees dumped as many as 10 acorns per square foot of forest floor, providing a food bonanza for wildlife. One of the main beneficiaries of this bounty was the white-tailed deer. Bill McShea, a wildlife biologist with the Smithsonian Conservation Research Center, and his colleagues have shown that deer are among the first wildlife on the scene once acorns start hitting the ground, spending about half their waking hours eating.

As deer move through the forest in search of acorn-rich patches, they brush against understory seedlings and saplings, just as a human might when meandering off a trail. In such autumn wanderings deer encounter adult black-legged ticks. These ticks, about the size of a sesame seed, crawl up shrubs and saplings to a height of two or three feet and extend their sticky legs, waiting in suspended animation for something warm and furry to brush by. At that height, they avoid the smaller mammals and birds that are likely to groom them off and instead are much more likely to encounter a deer.

Once on a deer, the adult ticks roam about in search of a prime spot in which to embed their mouthparts and begin drinking blood. The females spend several days to a week taking a single long draft, during which they expand to the size of a small jelly bean. With mouthparts anchored firmly in the deer's skin, the immobile females are approached by males, and they mate. (The males drink deer blood only intermittently, maintaining their freedom to search for mates.) Although the males die shortly after mating, the female ticks eventually extract themselves, drop off the deer, and burrow into the leaf litter to await the warmth of the following summer. In the intervening winter and spring, they convert the energy and nutrients from ingested deer blood into the next generation: They lay about 2,000 tiny eggs in a single mass, then die. After incubating a month or so, the egg mass crawls to life as a horde of larval ticks.

Because of the insatiable appetite of deer for acorns and of ticks for deer blood, acorns determine where deer spend time in the fall, and thus where adult ticks mate and lay eggs. When acorn crops are heavy, larval ticks irrupt the next summer in the parts of the forest dominated by oaks. Schauber and crew typically find as many as 10 larval ticks per square yard of forest floor in the summer following an acorn boom. When acorn crops fail, deer eat woody browse, and they prefer maple browse to oak. As a result, the larval ticks show up in maple woods the next summer. But larval ticks, creepy and crawly though they may be, are not dangerous to people. Juvenile ticks hatch from eggs free of the bacterium that causes Lyme disease. So where do ticks get the bacterium that can make people sick? The answer lies with another acorn gourmand.

GIVEN THAT MOUSE NUMBER 2864 WAS NURSING her babies in August 1998, she was probably born in March or April of that year, the product of a particularly early breeding season for mice. The acorn crop of 1997 was a godsend for her parents. With so many morsels of protein and lipid littering the forest floor, the mice did not have to wander far in search of food, so they reduced the time they were vulnerable to swooping owls and pouncing foxes. Because acorns are rich in tannins that protect them from fungi and insects, they have an extraordinary shelf life, and mice take advantage of this to create hoards that may last all winter. Following a banner acorn year like 1997, well-fed, well-protected mice gain weight, and even breed, in winter—an impossibility in years when fewer acorns are available—and so their populations grow to a peak by the next summer. In their mouse-youths, the parents of 2864 undoubtedly enjoyed the windfall of 1997. They met and courted

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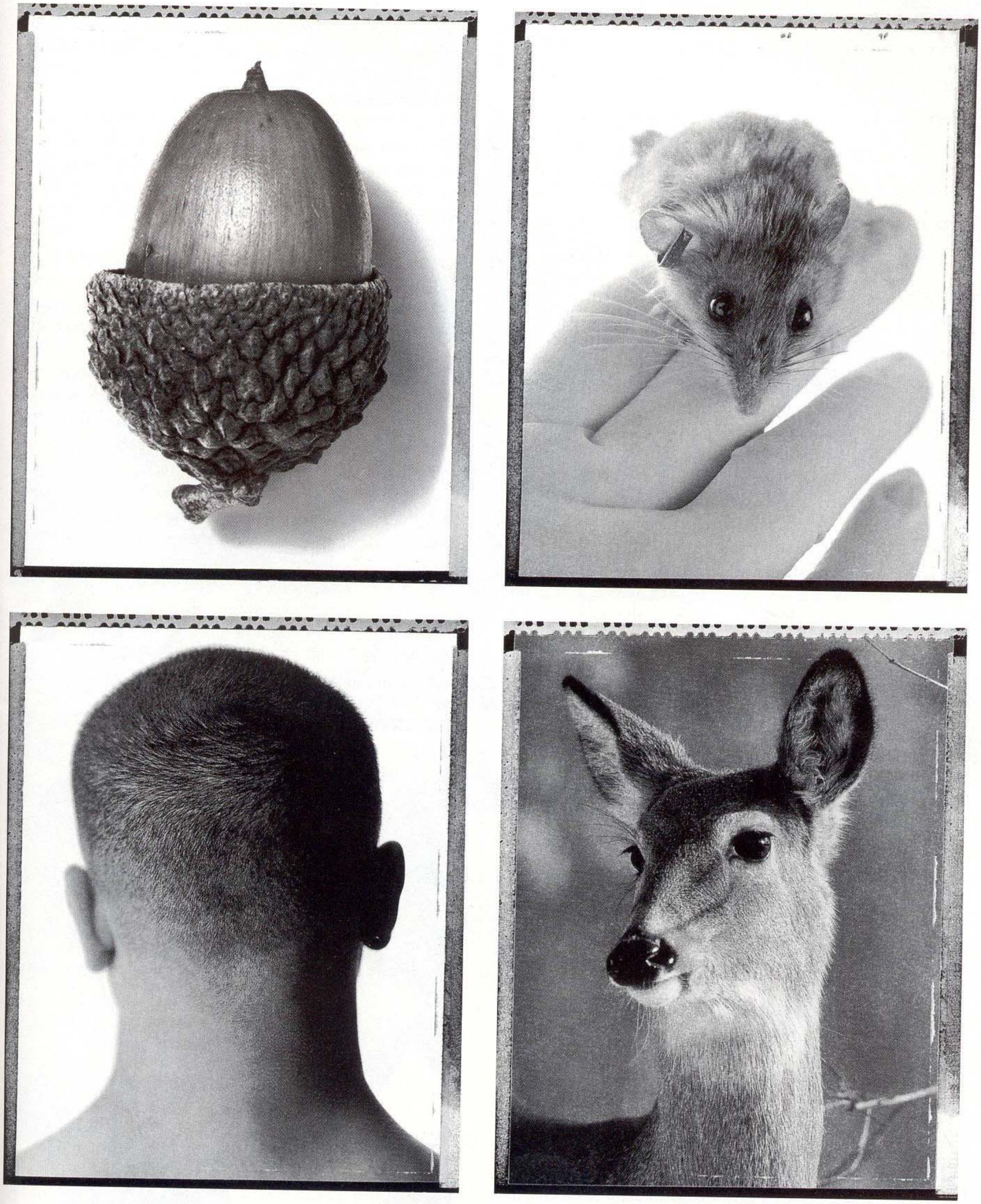
PREVIOUS PAGES FROM LEFT: ROBERT LEWIS FOR *AUDUBON*; PHOTOPIX/PHOTONICA



CLOCKWISE FROM TOP LEFT: DORLING KINDERSLEY LIMITED, LONDON/CORBIS; ROBERT LEWIS FOR *AUDUBON*; JIM BRANDENBURG/MINDEN PICTURES; ROBERT LEWIS FOR *AUDUBON*

Acorns are morsels of protein and lipid that provide ideal nourishment for the white-footed mouse, in whose blood Lyme disease bacteria thrive. In a year of abundant acorn output, mice don't have to scurry about excessively to find a meal and so are less vulnerable than they might ordinarily be to predators like owls and foxes. The black-legged ticks that attach themselves to the ears of the mice have an insatiable appetite for the blood of the white-tailed deer, whose numbers have increased tenfold in this country since the beginning of the century. The deer, the mouse, and the tick don't suffer from Lyme disease, but human beings do.

ONE ECOLOGIST BELIEVES THAT THE EXTINCTION OF THE PASSENGER PIGEON, 85 YEARS AGO, MAY HAVE INFLUENCED PRESENT-DAY INTERACTIONS AMONG ACORNS, MICE, TICKS, AND MOTHS. THE BIRDS ONCE SIPHONED OFF A MAJOR PART OF THE FOREST FOOD SUPPLY.

under some frozen log, and produced Mouse Number 2864 and her siblings a month or so later, thus contributing to the 1998 peak in mouse abundance.

White-footed mice are handsome and demure creatures with chestnut-brown backs, white bellies and feet, large black eyes, and active whiskers, but their bodies are an insidious breeding ground for various bacteria, viruses, and protozoans. These pathogens, although apparently benign to the mice, can be dangerous, even lethal, to humans. One such pathogen is the Lyme bacterium, which circulates harmlessly in mouse bloodstreams. From the point of view of a Lyme disease bacterium, a tick is just a vehicle for getting from one mouse to another. If juvenile ticks fed exclusively on mice, the cycle of transmission would proceed from mouse to tick and back to mouse, and Lyme disease would not plague humans. Unfortunately for us, juvenile ticks have catholic tastes and will attempt to feed on almost any warm-blooded animals, including people.

Once a tick hatches from an egg, it wanders several inches to a few feet away from the egg mass. Given that the tick is the size of the period at the end of this sentence, that is a considerable trek. It then stops, waits for something warm and furry or feathered to draw near, and climbs aboard. The tick goes on an extended walkabout in order to find the anatomically optimal spot into which to sink its mouthparts and commence sucking blood. If the first animal that happens along is a cottontail, an ovenbird, or almost any other species of mammal or bird, the tick will attach and feed to repletion. But because Lyme bacteria are very scarce in the blood of these animals, it is unlikely that the tick will ingest these bacteria. However, if the tick feeds on a white-footed mouse, where Lyme bacteria thrive in the blood, then bacteria are almost inevitably ingested, remaining within the tick for the rest of its life.

The surprising links among acorns, deer, mice, ticks, and Lyme bacteria mean that ecologists can look at acorn production and predict the risk of exposure to Lyme disease almost two years in advance. In 1994 there was heavy acorn production at our study sites, so the forest should have been crawling with both larval ticks and mice the following summer. This collision of ticks and Lyme-bearing mice in 1995 should have led to an outbreak of infected ticks in 1996. Sure enough, that's exactly what happened. The dense population of infected ticks that year corresponded to the highest number of Lyme cases reported to date in the northeastern United States. Acorn production at the sites was also high in 1997 and 1998, so Lyme disease risk may well be higher than normal in 1999 and 2000. A higher risk, however, may not result in an increase in the number of Lyme cases if the newly available Lyme vaccine is widely used and effective. (See "There's a Vaccine, but...," page 80.)

LYME DISEASE RISK IS NOT THE ONLY THING THAT acorns can predict. Strangely, they can also tell us when gypsy moth populations are likely to explode in the forest—another boon to mice. After all, if you were a mouse, you'd be foolish to restrict your diet to acorns, since they're abundant for only a few months every three to five years. But mice are not fools. They have an unusually indiscriminate palate and capitalize on various food items as they become available. When periodical cicadas emerge from the forest soil every 13 years, mice are among the first on the scene. When wild blueberry crops ripen, mice go on nocturnal raids, reducing the amount of fruit available to more civil songbirds the next morning. One key midsummer food source for white-footed mice is the pupal stage of the gypsy moth, an exotic pest well known for its ability to strip forests of leaves during outbreaks.

The gypsy moth was imported from Europe to Medford, Massachusetts, in 1869 by an entrepreneur hoping to make a killing with a new silk-producing moth. Unfortu-

ROBERT LEWIS FOR AUDUBON

Black-legged ticks such as these, reposing in a shot glass, attach themselves to mice and ingest Lyme disease bacteria.

nately, the gypsy moth was an utter failure as a silk producer but a smashing success as an invader of the oak forests of eastern Massachusetts. The incursion spread over the next decades into most of the northeastern United States, and in recent years gypsy moths have entered the forests and suburbs of the mid-Atlantic and midwestern regions.

In most summers the moths are hardly detectable—a few caterpillars quietly munching oak leaves overhead, a couple of white moths fluttering about in search of mates. But in some years, for reasons that until recently were mysterious, the caterpillars advance, denuding first oaks and then maples, elms, and pines, converting green leaf tissue into brown frass (a euphemism for caterpillar excrement) that rains down from the treetops. Most of the trees use their stored energy reserves to produce a new flush of leaves after the caterpillars become dormant for the year, but if the outbreak continues for a second or third summer, the leafless trees cannot photosynthesize and thus die.

Mouse Number 2864, nursing her babies in August, had been unconsciously planning her family in July. To satisfy her hunger, she undertook nightly reconnaissance of the forest floor, using her keen nose, whiskers, and eyes to leave no edible morsel undetected. Because the fall of 1997 was a bumper year for acorns, and the mouse population surged, competition among the mice was particularly acute in the summer of 1998. The mice had to crank up their foraging activities a notch to meet their dietary demands. Some spent more time than usual climbing trees and searching the bark crevasses for unsuspecting insects. On these tree trunks the cycles of mice and gypsy moths collided.

In early spring, in synchrony with budbreak, moth caterpillars began hatching en masse. The tiny caterpillars crawled up into the trees to feed, parachuting from tree to tree on silken threads (at least the silk is good for *something*) to find the best spots to feed. They settled down and spent the summer eating in the tree canopy, molting from one caterpillar stage to the next as soon as they could no longer fit inside their hairy skin. (These caterpillars are well protected against most predators; their hairy bodies reduce their appeal to most birds and mammals.) By July the caterpillars had finished eating, and they climbed down to the base of the trees, or even to the ground, seeking protected nooks and crannies in which to pupate.

At this point, the gypsy moths replaced their hirsute exoskeletons with smoother casings, starting the two-week vigil required to metamorphose into adults. Any moth pupa lucky enough not to be eaten by a mouse and to emerge from the pupal case immediately turns its attention to reproduction. The flightless females lure the flying males with a chemical scent, mate, lay eggs, and die. Because each female lays a mass of several hundred to more than 1,000 eggs, even a modest number of surviving pupae can result in rapid population growth.

Because of the bountiful 1997 acorn year, there were so many mice the next July that the moth pupae were devastated in 1998. But what happens in the summer following a poor acorn year? The fall of 1995 saw an acorn failure in the northeastern United States. White-footed mouse populations, which were booming earlier that summer because of the heavy acorn production in 1994, began to crash in September and continued their decline throughout the fall and winter of 1995–1996. Although the mice began breeding in the spring of 1996, they continued to experience high mortality and did not recover that summer.

In some temperate and boreal areas, peak populations of rodents like mice, voles, and lemmings fuel the breeding success of predators such as owls, kestrels, weasels, and foxes. The result is a predator-prey oscillation. Increasing numbers of rodents drive up the predator populations, but the rapidly growing raptor and mammal populations take a heavy toll on the rodents. Often the rodent population will crash within a single season, from a few hundred animals an acre to only three or four. Owls or foxes that breed when prey are legion may find that the bottom has fallen out of the food market by the time they fledge or wean their young. The newly fledged predators then put increasing pressure on the dwindling prey populations, driving them to great scarcity before themselves dying of starvation. This scenario may have been responsible for the extremely poor performance by mice in 1996. In any event, mice were rare that summer.

As Eric Schauber and crew have done each summer for the past several years, they tested the ability of the 1996 mouse cohort to keep gypsy moths in check. The research team does this by using beeswax to affix freeze-dried gypsy moth pupae to small burlap squares (we call these bug rugs) and stapling the burlap to tree trunks—a

THERE'S A VACCINE, BUT . . .

The US Food and Drug Administration recently approved a vaccine for Lyme disease. Produced by SmithKline Beecham, the vaccine consists of a genetically engineered protein identical to one found on the surface of the Lyme bacterium. This protein causes the human immune system to produce antibodies that attack and kill the bacterium wherever they find it, even inside the body of a tick that has begun to feed on human blood. Boosters may be necessary to keep antibody levels high. The vaccine is not approved for people younger than 15 or older than 70.

The vaccine does not protect people against other tick-borne illnesses, such as babesiosis and ehrlichiosis, which appear to be increasingly common in the northeastern and midwestern United States. Some individual ticks from New York study sites have tested positive for all three disease agents, demonstrating that people may become exposed to multiple diseases from a single tick bite. Even with a vaccine available, personal precautions are important in avoiding Lyme disease. Wear light-colored clothing (so the dark ticks are more visible) with long sleeves and pants; tuck pant legs into socks; apply insect repellent to shoes, socks, and pant legs; and carefully check clothing and skin for ticks. —*R. S. O.*

CLEARLY, EXTINCTIONS AND EXOTIC PESTS HAVE CHANGED OUR LANDSCAPE IN WAYS THAT INFLUENCE BOTH FOREST HEALTH AND HUMAN HEALTH.

technique invented by Harvey Smith, a colleague at the US Forest Service. We then examine the bug rugs for signs of attack by various predators. We use freeze-dried pupae because live pupae might survive and later reproduce, and it would be unseemly for a group of ecologists to accidentally set off a gypsy moth outbreak. We use beeswax because it tells us who visited the pupa—mice in particular leave characteristic tooth marks in the wax.

In most years, the vast majority of the pupae are attacked long before the two weeks required for moth pupation have elapsed. And the wax confirms that the predominant pupal predator is the white-footed mouse. But in 1996 about half the pupae remained untouched after two weeks. There simply weren't enough mice to keep the moth population in check. We have confirmed this result experimentally by deploying bug rugs in forest areas from which we had removed nearly all the mice.

A mouse crash means that moths will survive. It takes only a handful of female moth survivors per acre to start the population irrupting toward a peak, given their abundant egg production. Even though mice are voracious, each mouse can eat only four or five pupae a day. So once the forest is populated with the thousands of pupae per acre that characterize a moth outbreak, the mice become impotent control agents. When the gypsy moths reach outbreak levels, they may become infected by the fatal nuclear polyhedrosis virus, which, like many human viruses, does well only when its victims are crowded. But whenever moths are at low to moderate levels, mice are the key control agent.

Another consequence of the gypsy moth's culinary habits is that the defoliated forests turn rapidly from cool, dark, shady places to brighter, hotter, drier habitats. Although understory plants awash in new light will grow rapidly and thrive, other forest denizens may be damaged or killed by the penetration of light and heat. One creature quite sensitive to these conditions is the black-legged tick, which does not survive well in hot, dry places. Might gypsy moths be an indirect, inadvertent enemy of Lyme disease? Only further studies will tell.

UNANTICIPATED CONNECTIONS AMONG SPECIES appear to characterize ecological communities. The ecologist David Blockstein has conjectured that the extinction of the passenger pigeon, 85 years ago, may have influenced present-day interactions among acorns, mice, ticks, and moths. The passenger pigeon formed flocks of thousands to hundreds of thousands of birds, and these flocks descended on oaks as acorns began to ripen. Because passenger pigeons plucked fruits and seeds directly off the trees, they undoubtedly siphoned off a major part of the food supply from the wildlife restricted to the forest floor, keeping those populations in check. It seems quite possible that if passenger pigeons were extant, both the outbreaks of mice that lead to high Lyme disease risk and the crashes of mice that lead to gypsy moth outbreaks would be much less frequent today.

Changes in the populations of humans and other species in the past few centuries have probably changed the nature of our eastern forests in ways that influence Lyme disease risk and gypsy moth populations. The displacement of Native Americans and the disappearance of mountain lions and wolves from these forests have eliminated the major predators of white-tailed deer. As a result, deer populations have exploded, going from about 2 million in 1900 to between 15 and 20 million today, providing ticks with more than ample opportunities for feeding. In addition, the American chestnut, formerly a dominant tree species in our forests, has succumbed to the invasion of chestnut blight, a foreign fungus that kills the trees before they are old enough to reproduce. The demise of the American chestnut was apparently followed by an increase in the number of oaks. Clearly, extinctions and exotic pests have changed the nature of our landscapes in ways that influence both forest health and human health.

One goal of scientists is to understand nature well enough to predict events accurately. But prediction for an ecologist focuses on the most complex and inclusive of natural entities: the ecosystem. At first glance the forest ecosystems we study might seem unfathomably complex, but we've found that in fact they are understandable, at least in small pieces. Unfortunately, developing an understanding of some of the crucial connections in these forests requires an enormous investment of time in the field, in the lab, and in just plain thinking. The upside is that the better we understand these systems, the more likely we are to be able to predict gypsy moth outbreaks and Lyme disease. Forewarned about such challenges to human health and forest health, we are in a better position to avoid them. Mouse Number 2864 has no idea how important she is.

A FOCUS ON THE LONG TERM

The Institute of Ecosystem Studies, founded in 1983 as part of the New York Botanical Garden's Mary Flagler Cary Arboretum, has a scientific staff of 24; 23 of these scientists hold doctorates. The institute concentrates on long-term ecological studies in areas such as climate change and ecosystem interrelationships. Situated just west of Millbrook, New York, and about 80 miles north of New York City, the institute offers courses, workshops, seminars, and excursions with an ecological focus for the public. For information about the courses available, scheduling, and costs, call the institute at 914-677-5359, or visit its web site at <www.ecostudies.org>.