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The Ecology of Lyme-Disease Risk

Complex interactions between seemingly unconnected phenomena determine risk of exposure to this expanding disease

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In the past two decades, people living in the northeastern, north-central and western United States have unwittingly entered a dangerous enzootic cycle—a cycle of disease that typically is restricted to wildlife. Wild mammals and birds host a wide variety of disease agents, with effects ranging from mild symptoms to mortality, but in most cases the pathogen affects only one or a few host species and never causes disease in people. However, as the result of a complicated sequence of events, people have become frequent accidental hosts for ticks and the disease agents they carry, including a corkscrew-shaped bacterium called *Borrelia burgdorferi*, the agent of Lyme disease. As of 1995, cases of Lyme disease had been reported in 48 of the 50 states and appear to be increasing, both in numbers of people affected and in geographic distribution.

Where does this disease come from, why has it emerged so rapidly, and what can people do to reduce their risk of exposure? It is possible to address these questions not from a medical point of view, but rather from an ecological one. All living organisms—from the *B. burgdorferi* bacterium and the ticks they infect to the mice and deer on which the ticks feed—form an ecological relationship with their habitats. Understanding the complex interactions between plant and animal species within those habitats may help people to predict the places where they are most likely to encounter disease-bearing ticks and become infected. Thus armed, individuals may ultimately be able to protect themselves from Lyme disease.

Currently, to prevent Lyme disease people wear protective clothing when they are in wooded areas and perform "tick checks" after leaving the woods. One underemphasized means to avoid exposure to Lyme disease, however, is avoiding the most heavily tick-infested habitats at the times of year when ticks are most abundant or most dangerous. Recent research performed in my laboratory, as well as in others, has suggested that such habitats can be predicted, often well in advance. Ultimately, it is the hope of ecologists studying this problem that we can use our expertise in pinpointing these habitats to warn the public away from areas that are likely to contain an abundance of disease-carrying ticks.

Diagnosing the Disease

To the average physician, Lyme disease is suspected when a patient arrives at a clinic or hospital complaining of a strange bull's-eye-shaped rash, known as erythema migrans, or EM, together with one or more flu-like symptoms, such as fever, chills, muscle aches or lethargy. The doctor will take a blood sample for laboratory confirmation, but will feel quite confident to make a diagnosis of Lyme disease after noting the telltale combination of symptoms, as well as the circumstances surrounding the infection. The patient will undoubtedly have been bitten by the black-legged tick *Ixodes scapularis*, formerly called the deer tick, or a close relative, which transferred to him or her the *B. burgdorferi* bacterium. Most likely, the doctor will prescribe an oral course of antibiotics and will duly report the case to the county or state health department, which will include it in the morbidity statistics for Lyme disease.

Accurate diagnosis and effective treatment of Lyme disease is not always so straightforward, particularly in regions of the country newly invaded by the epidemic. In these regions, health-care professionals and the public need to be educated about the confusing and generalized symptoms, the generally poor, albeit growing, accuracy of lab tests and the efficacy of various antibiotic treatments. If Lyme disease is left untreated for some time, *B. burgdorferi* may persist in the patient's tissues and can migrate to the central and peripheral nervous system or to joints and cause more-severe late-stage symptoms, which include arthritis and neurological disorders, such as dizziness, memory loss and disorientation. Vaccines that protect against Lyme disease are now being field-tested by pharmaceutical companies, but none has yet been approved by the Food and Drug Administration for public use. Even if an effective vaccine were certified and marketed, the primary means that individuals have of protecting themselves against the disease is avoiding the tick in the first place. To do that, ecologists are trying to understand the natural history of Lyme disease and the life history of the black-legged tick.

Natural History of Lyme Disease

Lyme disease is mistakenly thought by many to be a new disease that first ap-

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William S. Lea

Figure 1. Nature's serenity draws millions of people into the forest throughout the spring, summer and fall. But by entering the forest, people are also unwittingly entering a cycle of disease that would otherwise be restricted to wildlife. In the forest people frequently become accidental hosts for ticks and the disease agents they carry, including the corkscrew-shaped bacterium that causes Lyme disease. In the absence of any generally available vaccine against the disease, the best strategy for avoiding Lyme disease is to avoid habitats that are likely to have an abundance of disease-carrying ticks during any particular year. Ecologists are starting to discern the factors that may facilitate such predictions.

peared late in the 1970s. In reality the erythema migrans syndrome—now recognized as indicative of Lyme disease—was described in Europe more than 80 years ago. At the time, it was correctly linked to bites from the tick *Ixodes ricinis*, although the causative microbial agent had not been established. In 1975 health specialists were called in to investigate a peculiar cluster of childhood arthritis cases in Lyme, Connecticut, and they found that many of the cases had been preceded by EM. Allan Steere at Tufts University and his colleagues suspected a link between the Connecticut EM cases and the earlier European ones, causing them to search for and eventually find highly abundant populations of ticks. At first, it was thought that the ticks represented a newly discovered species, which was named *Ixodes dammini*, but later evidence indicated that the specimens were simply members of northern populations of the previously described species *Ixodes scapularis*. Further medical detective work by Willy Burgdorfer at Rocky Mountain Labs and colleagues revealed that both the European and Connecticut ticks played host to *B. burgdorferi*, which had been previously undescribed.

Even in North America, Lyme disease almost certainly existed for thousands of years before its discovery in the 1970s. Native Americans and European colonists probably experienced the disease in the forested landscapes of the northeastern and north-central United States and the West Coast, but the symptoms went largely unrecognized, perhaps because of the prevalence of more serious, debilitating diseases. Early symptoms of Lyme disease are rather mild compared with those of cholera, typhus, tuberculosis and others that plagued early Americans, and acute Lyme disease is often a brief and self-limiting ailment. However, several weeks or months after initial infection, bacteria may begin dispersing away from the bite to distant sites in the body, to the knees and shoulders or to the central and peripheral nervous systems, where they can wreak havoc on joints and nerves, causing serious arthritic and neurological disorders.

Since 1990, between 9,000 and 14,000 cases of Lyme disease have been reported annually to federal health officials, although the true number of cases is unknown. The Lyme-disease epidemic has caused hysteria in some areas, which probably leads to the false reporting of some cases. But it is also likely that many cases of Lyme disease go unreported each year because health-care

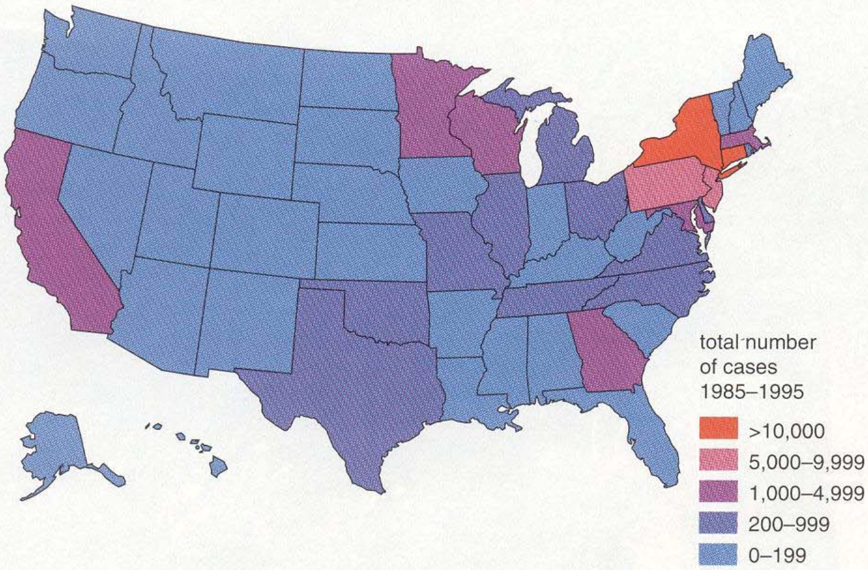

Figure 2. Lyme disease had been reported in 48 of the 50 states as of 1995. This map showing the number of cases reported to the Centers for Disease Control and Prevention in each state since 1985 demonstrates that the regions most seriously affected are the northeastern, north-central and western United States. The geographic range continues to increase, as does the number of cases.

workers and patients are unfamiliar with the symptoms. In any event, Lyme disease is by far the most common vector-borne disease in the United States, surpassing malaria, yellow fever, dengue fever, Rocky Mountain spotted fever, plague and others. Although Lyme disease is widespread in the United States, the northeastern seaboard from Maryland to Massachusetts, the upper Midwest and California have the highest numbers of cases.

Life Cycle of the Tick

Lyme disease is virtually restricted to forested landscapes, since these are the habitats in which *Ixodes* ticks find hosts and complete their life cycles. Several species of *Ixodes* ticks have recently been found to transmit Lyme disease, and each species has a somewhat different life cycle as well as a slightly different menagerie of vertebrate hosts. The following generalized life cycle pertains to *I. scapularis* in the northeastern and midwestern United States. Larval ticks hatch from eggs in midsummer, and newly emerging larvae seek a host at that time. Because the larvae are about the size of the period at the end of this sentence, they are virtually impossible to detect when they are crawling on or embedded in one's skin. These ticks are weak crawlers and cannot hop or fly; therefore a warm-blooded vertebrate must pass extremely close for a larval tick to climb aboard. Larval ticks have catholic tastes and will feed readily on a wide variety of species of small mammals and birds (and lizards in the southern and western United States). The ticks locate a suitable site on the host and anchor their mouth parts for a single two-to-three-day blood meal, after which they drop off the host. Within about a month, the larval tick molts into the second post-egg stage, the nymph, and remains quiescent on or just beneath the forest floor for all of the following winter.

Late the next spring or early in the summer, the nymphs, now about the size of a poppyseed, actively search for a host. They either remain on the surface or climb into low vegetation to await the close passage of almost any species of warm-blooded vertebrate. Again, the tick inserts mouth parts into the host and feeds for about three to five days. Once it has become engorged with blood, the nymph drops off, and after approximately three months, molts into the adult stage.

The peak season for adult-tick activity is midautumn. An adult tick, about the size of a sesame seed, is somewhat more mobile than a juvenile tick and typically climbs as high up as one meter on vegetation to seek hosts. The result of its upward mobility is that the adult tick usually encounters and parasitizes large mammals, particularly the white-tailed deer *Odocoileus virginianus*. The specificity of the adult-stage tick for white-tailed deer is the reason why *I. scapularis* was formerly called the deer tick.

Adult ticks use deer not only as their terminal host but also as their mating grounds. Male ticks, which wander

Larry Mulvehill (Photo Researchers, Inc.)

Figure 3. Bull's-eye-shaped rash, known as erythema migrans, is often one of the first indicators of Lyme disease. Symptoms of the disease at first mimic the flu and include fever, chills, muscle aches and lethargy. If the disease is left untreated, more serious symptoms appear, including arthritis and neurological disorders, such as dizziness, memory loss and disorientation.

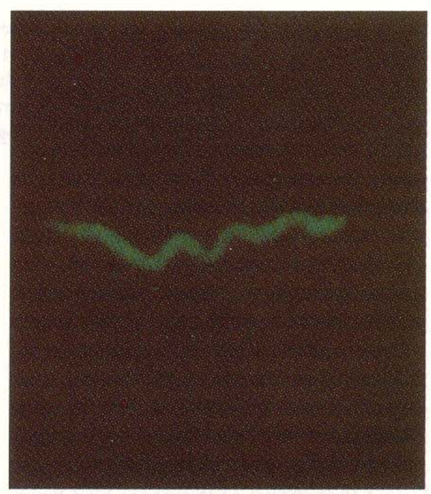

Figure 4. Corkscrew-shaped bacterium, *Borrelia burgdorferi*, that causes Lyme disease can be seen in this photomicrograph. Discovered in the late 1970s, these bacteria are extremely widespread in populations of black-legged ticks, *Ixodes scapularis*, but can be found in other tick hosts as well. The presence of these bacteria can be established by incubating suspensions of dissected ticks with anti-*Borrelia* antibodies linked to a fluorescent stain. (Photograph courtesy of the author.)

about the deer and feed only intermittently, often mate with feeding females, whose mouth parts are embedded in the deer's skin. Females feed steadily for four to five days, after which they drop off the deer and overwinter in an engorged state, seeking shelter from extreme weather conditions beneath leaf litter in the forest. The following spring the engorged females lay eggs in masses of several hundred to a few thousand, and these eggs hatch a few weeks later into a new cohort of larvae.

The vast majority of larval ticks—well over 99 percent—hatch from eggs free of the Lyme-disease bacterium, indicating that the disease agent does not pass readily from adult through the ova to her offspring. However, larval ticks may become infected if they feed on an infected host, and these acquired infections are retained through the molts from larva to nymph and from nymph to adult. Work by Thomas Mather at the University of Rhode Island, Joseph Piesman at the Centers for Disease Control and Prevention and their colleagues have revealed that the white-footed mouse *Peromyscus leucopus* is the host primarily responsible for infecting larval ticks with the Lyme spirochete, and thus the mouse is considered the principal natural reservoir for the disease agent.

In Lyme-disease-endemic areas, approximately 25 to 35 percent of nymphs and 50 to 70 percent of adult ticks are infected with *Borrelia burgdorferi*. Because nymphal ticks are much smaller than adults and hence more difficult to detect on one's clothing or skin, and because their peak activity period is from May to July, when most people also spend a lot of time outdoors, most cases of Lyme disease are probably caused by bites from nymphs rather than from adult ticks. Research by Durland Fish at Yale University and colleagues indicates that the primary ecological risk factor in the Lyme-disease epidemic is the number of infected nymphs within areas people use recreationally or domestically from late spring to midsummer.

The Acorn Connections

Since the number of infected nymphs emerging in any given season has some bearing on the number of people potentially exposed to the bacterium, it is important to determine how many infected nymphs emerge within a given habitat type in any given year. Recent research in my laboratory reveals that one of the most powerful predictors of nymph numbers is the number of acorns in a particular area. The episodic or periodic production of bumper crops of acorns, a phenomenon known as "masting" behavior by oak trees, sets off an ecological chain reaction that influences distribution and infection rates of ticks, and hence risk of Lyme disease. White-tailed deer consume woody browse during much of the year, but

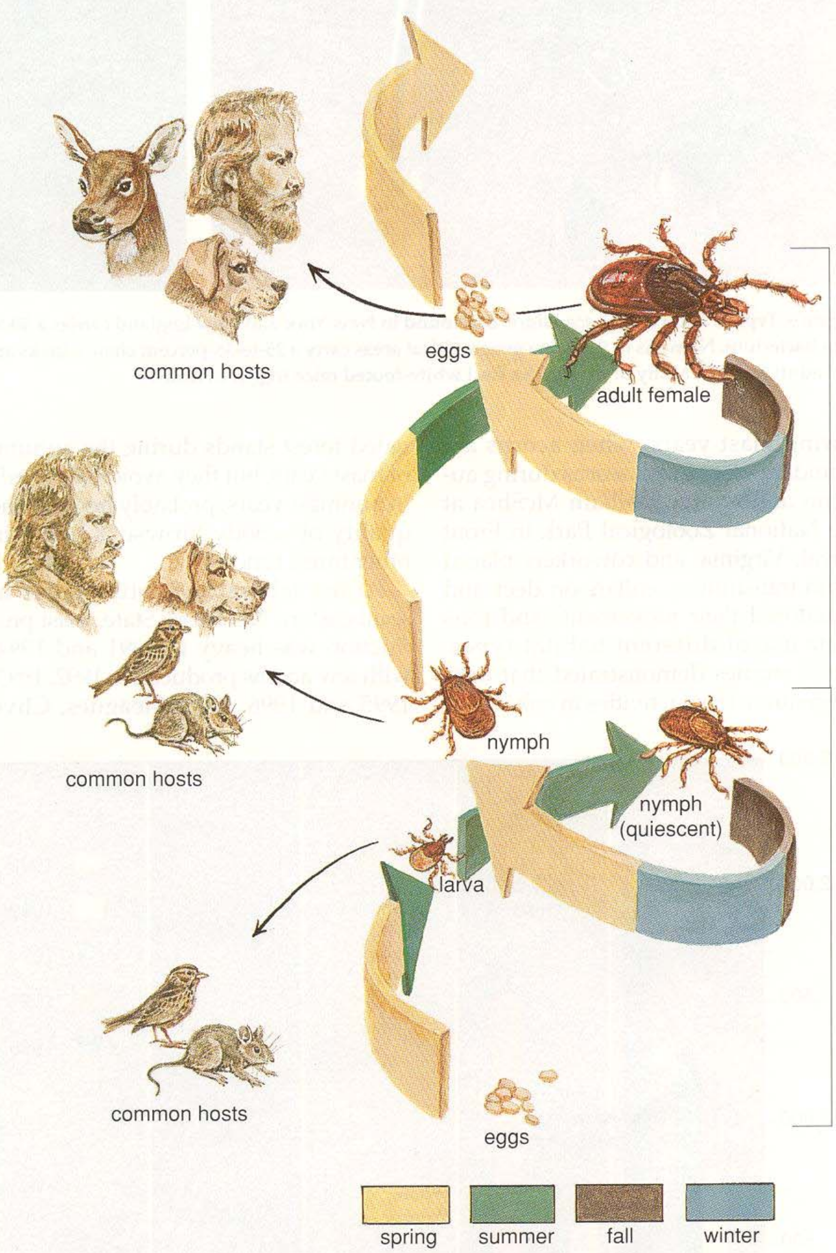

Figure 5. Generalized life cycle of the black-legged tick in the northeastern and north-central United States is illustrated in this schematic. (The timing of the molts between stages and the identities of predominant hosts differ somewhat in *I. scapularis* from the southeastern United States and in related Lyme disease-bearing ticks from the western United States, Europe and Asia.) Larval ticks hatch from eggs in the midsummer and seek a host, generally a small vertebrate, such as a mouse or a bird. After feeding on the blood of this host for two to three days, the tick drops off. Within a month, the larval tick molts and becomes a nymph, and in this stage remains quiescent on or just beneath the forest floor for all of the following winter. Late in the spring or early in the summer of the following year, the nymph seeks a new host on which to feed and prepare for the final molt into an adult-stage tick about three months later. The peak season for adult-tick activity is midautumn. At this time, the adult and fully mobile tick has access to its preferred host, the white-tailed deer, on which the tick both feeds and mates. Adult females lay their eggs the following spring, and the cycle starts all over again. When people substitute for animal hosts, they risk becoming infected with the *Borrelia* bacterium.

Scott Camazine (Photo Researchers, Inc.)

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Figure 6. Typical adult *Ixodes scapularis* tick found in New York and New England carries a 50-to-70-percent chance of being infected with the *Borrelia* bacterium. Nymphs in the same geographical areas carry a 25-to-35-percent chance (ticks are, clockwise from bottom right, nymph, adult male and adult female). Many of these ticks find white-footed mice *(right)* as hosts.

during mast years, when acorns are abundant, deer favor acorns during autumn and winter. William McShea at the National Zoological Park in Front Royal, Virginia, and coworkers placed radio transmitting collars on deer and monitored their movements and thus their use of different habitat types. These studies demonstrated that deer concentrate their activities in oak-dominated forest stands during the autumn of mast years, but they avoid oak stands in nonmast years, probably because the quality of woody browse is better in other forest types.

At my laboratory's study sites in southeastern New York State, mast production was heavy in 1991 and 1994, with few acorns produced in 1992, 1993, 1995 and 1996. My colleagues, Clive Jones of the Institute of Ecosystem Studies and Jerry Wolff at Oregon State University, and I therefore expected that in the autumns of 1991 and 1994, deer would concentrate their activities in oak-dominated patches, that they would import their burdens of adult ticks into oak stands, and that oak forests would be the primary sites where the ticks would mate and lay their eggs. We predicted that oak stands would be infested with newly hatched larval ticks in the summers of 1992 and 1995—that is, the summers following heavy mast production. In contrast, for the summers following mast failure, we predicted that larval ticks would be most abundant in other habitat types, since we also predicted that deer would avoid oak forests in nonmast autumns.

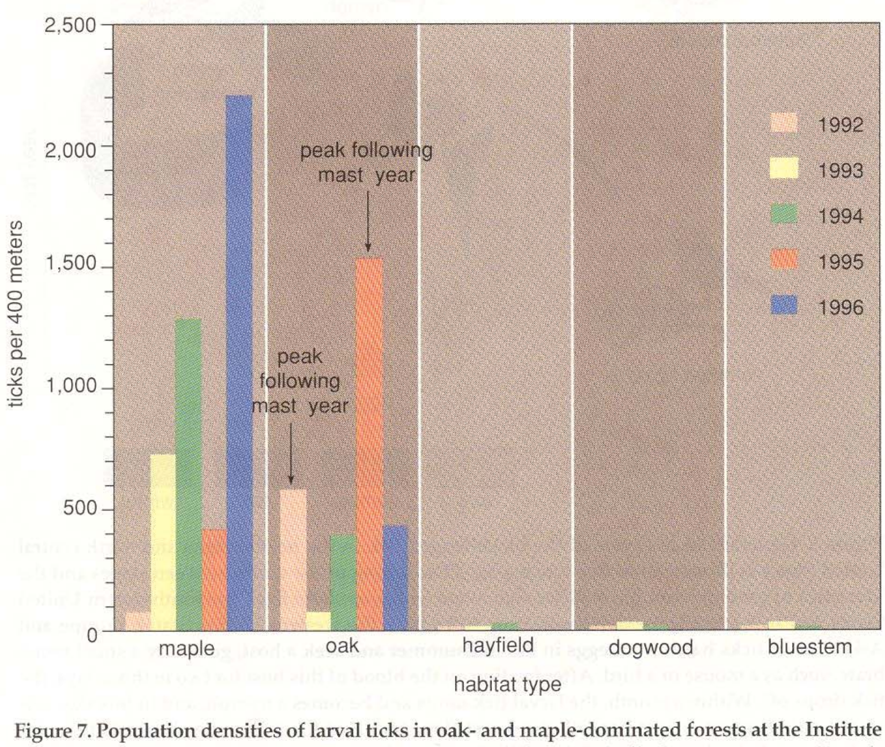

Figure 7. Population densities of larval ticks in oak- and maple-dominated forests at the Institute of Ecosystem Studies (IES) in southeastern New York shift dramatically from year to year. Larval-tick densities are especially high in oak forests following years in which the oaks have produced a particularly high number of acorns—a phenomenon known as masting. Following nonmast years, when acorn production has been average or below average, tick populations are most dense in maple forests. Observations such as these have suggested that mast production may be a useful predictor of habitats in which Lyme-disease risk may be particularly high.

To test this prediction, we made estimates of relative tick populations in five different habitats (two forest types and three types of open fields, with three replicate sites for each type) based on samples we culled from each. To sample tick abundance, we used a standard technique that involves dragging a one-square-meter piece of white corduroy cloth along premeasured lines 100 meters long and stopping every 15 meters to count the ticks that attach to the cloth.

We found that the location of peak abundance of larval ticks shifts dramatically from year to year, coinciding with the presence or absence of acorns in oak stands the prior fall. Oak forests were the sites of larval-tick outbreaks in the summers following acorn years, whereas maple forests were most heavily infested in summers following acorn failure. Subsequently, together with Clive

Jones, Jerry Wolff and several technicians, I added almost 1 million acorns to three 2.25-hectare forest plots during the autumn of a year of very poor natural-acorn production. As a control, we monitored three matched plots to which no acorns were added. The following summer we observed that densities of larval ticks were approximately 10 times higher in acorn-supplemented plots than in control plots. This result supports our proposed link between acorn availability, space use by white-tailed deer and location of larval-tick outbreaks.

Deer are not the only wildlife species that rely strongly on acorns as a food resource. Long-term studies of population dynamics of white-footed mice, conducted by Jerry Wolff in Virginia, by Steven Vessey at Bowling Green State University in Ohio, by Joseph Merritt at the Powdermill Biological Station in Pennsylvania, and by ourselves in New York, reveal that the abundance of mice in a particular area is closely tied to acorn production. In the fall of a mast year, mice both consume and store acorns in large numbers. Consequently, during the winters following mast production, mice tend to experience higher-than-normal survival rates. Winter breeding by white-footed mice almost never takes place when acorns are unavailable. In contrast, mice breed rampantly during postmast winters and begin the normal spring-breeding season at high density and in good physiological condition. Mouse populations then reach peak density by the middle of the summer following a mast year.

By influencing the use of space by deer and the population dynamics of mice, acorn production is tied to peaks in abundance of both larval ticks and mice, the most reservoir-competent host, in oak forests during the summer following a mast year. Currently, my colleagues and I are testing the prediction that, because of greater densities of mice in the postmast year, larval ticks have a higher probability of feeding on this reservoir species and consequently of acquiring the Lyme-disease-causing bacterium. If this is true, we expect bacterial-infection rates of nymphal ticks to be highest two years following heavy acorn production, an expectation that is currently being tested by dissecting ticks and examining their tissues for the presence of *B. burgdorferi*. Because the abundance of infected nymphal ticks is the primary ecological risk factor in the Lyme-disease epidemic, it is clear that masting behavior by oaks may have crucial consequences for Lyme-disease epidemiology.

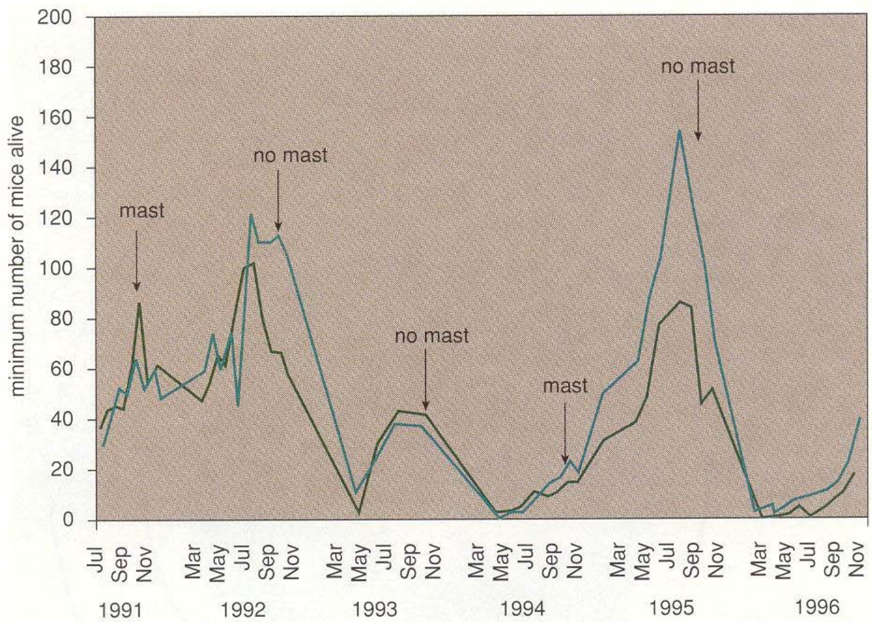

Figure 8. Densities of white-footed mice are also affected by mast production. The author and his colleagues tracked the population density of white-footed mice on two 2.25-hectare trapping grids at separate oak-dominated locations near the IES. In the winter following autumns of good acorn (mast) production, mice survive well, breed and reach peak populations the following summer. Declines rapidly follow the peaks (1993 and 1995) as mice die or disperse, probably because of the increased competition and predation within the area. In summers following mast failure, mouse populations are considerably lower in density. Understanding the dynamics of mouse populations may add accuracy to predictions of high-risk habitats.

Based on heavy acorn production in 1991 and 1994, we predicted that 1993 and 1996 would be years of particularly high incidence of Lyme disease. Statistics from the county health departments in southeastern New York state indicate that, although 1993 was an average year for Lyme disease, 1996 saw an unusually high number of cases. A robust test of our model's accuracy will require at least several more years of monitoring mast production and Lyme disease cases. In addition, it will be important to determine over how large an area oak trees are synchronized in their mast production, because it is only within these areas that we expect Lyme disease risk to be correlated with acorn production two years earlier.

The role of the population dynamics of white-footed mice in determining the risk of Lyme disease is complicated by the tendency of mice to emigrate in large numbers during population peaks, probably to avoid intraspecific aggression and a buildup of predators in high-density areas. Work in progress in my lab indicates that almost immediately after reaching peak density the summer following mast production, mouse populations begin to decline rapidly, and that this decline is a result of both mortality and emigration from oak-dominated habitats. Emigration rates appear to be highest during the peak season of infestation of mice with larval ticks, so that dispersing mice may be responsible for transporting attached larval ticks from patch to patch within the landscape. Mice typically move from oak forests into suboptimal, but less crowded, habitat types such as maple-dominated forests or shrub-dominated fields; therefore they may be responsible for our observation that, two years following mast production, maple forests and fields have denser-than-usual populations of highly infected nymphal ticks. In most years, maple forests and open fields are relatively safe, but two years following acorn production they are much riskier. Note, however, that these habitat types become risky as a result of immigration by mice that are infested with ticks. Areas that are distant from oak forests or that are of poor quality for mice may never attract large numbers of vagrant mice.

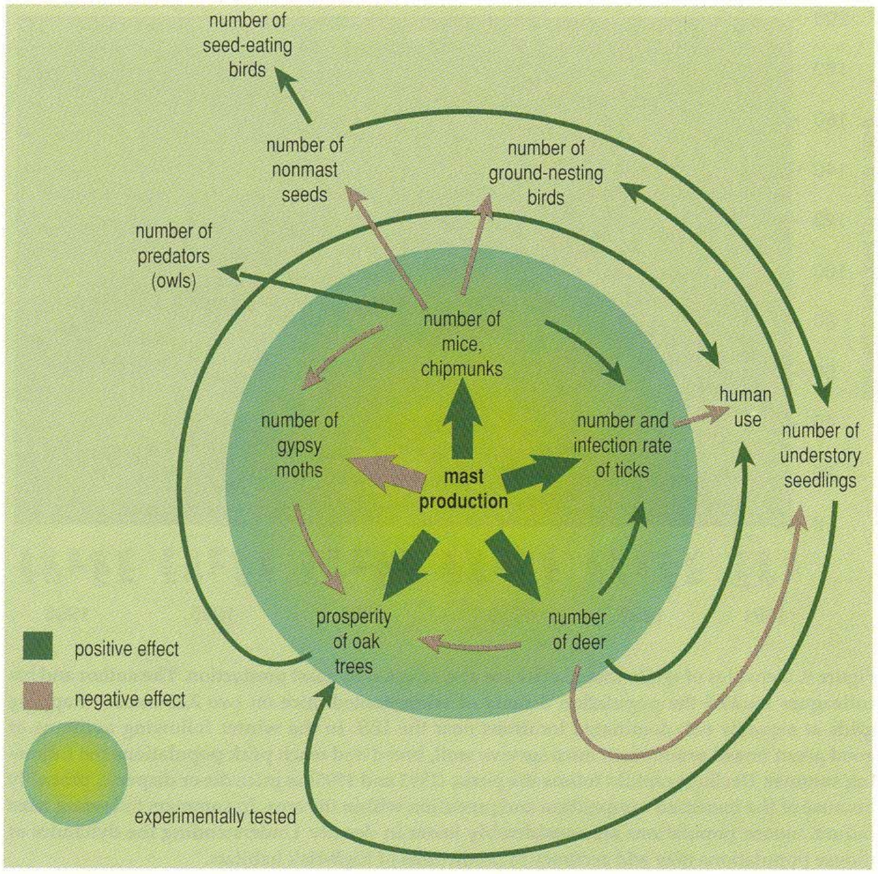

Figure 9. Factors within oak-forest ecosystems that influence risk of Lyme disease are summarized in this model. Arrows indicate the primary direction of effects. For example, the numbers of mice influence the numbers (or *Borrelia*-infection rates) of ticks, but not vice versa. Green arrows indicate a positive effect; red arrows indicate a negative one. Interactions within the shaded area have been verified by recent studies. The model demonstrates that the ecological interactions affecting risk of Lyme disease also influence gypsy-moth outbreaks and other forest problems.

The studies summarized above are ongoing, but they provide hope that various forest and field types can be risk-rated for Lyme disease well in advance. Ultimately, we expect that, just as fire risk is posted at many national and state parks and forests each season, further studies of links between acorns, deer, mice, ticks and spirochetes will allow us to warn the public which areas to avoid and when to avoid them.

Controlling Ticks and their Hosts

Ecologists and entomologists have searched unsuccessfully for biological agents that might control populations of black-legged ticks. Natural enemies of ticks, such as parasitic wasps, wolf spiders and foraging guinea fowl, have been found to be either highly localized in their impacts on tick survival or ineffective. Although further studies of the potential effectiveness of parasites, pathogens and predators as control agents are warranted, the biological control of ticks appears elusive. In many animals, population control is imposed naturally by crowding, which reduces reproduction rates or increases mortality, but whether this mechanism of control operates for ticks and, if so, in which life stages, is largely unknown.

My former student Kirsten Hazler, currently at North Carolina State University, and I designed a study to determine whether crowding of larval ticks on *Peromyscus* mice reduces the tick's ability to survive, feed successfully and molt into viable nymphs. We placed varying numbers of ticks on captive mice and followed their feeding and molting success. We found that the same proportion of larval ticks fed successfully on mice and molted into nymphs when the mice were heavily infested at 100 ticks per mouse as when they were lightly infested with only 5 ticks per mouse. Thus, at the densities we used, tick populations do not appear to be regulated by crowding on their most important host. In fact, our experiments suggested that ticks fed more successfully when they were more crowded on mice, a result that would be expected if the anticoagulants and immunosuppressive agents in tick saliva are more effective at higher doses.

A recent effort in our laboratory to create computer models of the dynamics of Lyme disease revealed that the degree of species diversity in the community of hosts for ticks may have a strong impact on the risk of Lyme disease. This simulation model, devised by Josh Van Buskirk at the Zoologisches Institut, University of Zurich, created a habitat in which ticks encounter host species in proportion to the population density of the host. As in nature, the computer-created hosts varied in their likelihood of infecting feeding juvenile ticks with bacteria, but did not vary substantially in the probability that a tick feeding on that host species would gain a full blood meal and molt into the next stage.

The model suggested that reducing the density of deer, which serve as hosts for adult ticks, would have only a modest effect on tick density, and that nothing short of the near eradication of these hosts would substantially reduce tick numbers. This result is supported by empirical data collected by Mark Wilson at the University of Michigan and his coworkers indicating that deer hunting has little if any effect on tick numbers, whereas eliminating deer by fencing them or removing them from islands drastically reduces tick density. On the other hand, the model suggested that the number of ticks can be reduced steadily by gradually reducing the density of hosts for juvenile ticks (that is, rodents and lizards), a prediction that has not yet been tested rigorously.

Perhaps most interesting, the model suggested that infection rates of juvenile ticks, and hence the risk of Lyme disease, are lower when the host community is highly diverse than when only a few species of hosts are available. Because only one species of host, the white-footed mouse, is a highly competent reservoir for *B. burgdorferi*, any increase in the species diversity of hosts will dilute the effect of mice by offering ticks alternative, reservoir-incompetent hosts from which to feed. This result is consistent with empirical results obtained from the southeastern and western United States by Robert Lane of the University of California at Berkeley and his colleagues. In these areas the host community includes several species of reservoir-incompetent rodents and lizards, and the infection rate of *Ixodes* ticks is much lower than in the northeastern and north-central United States. A key implication of the model is that maintaining high species diversity in vertebrate communities, for instance by maintaining high habitat diversity or high predator density, may reduce the risk of Lyme disease.

Recently Josh Van Buskirk and I extended the simulation model to a landscape consisting of several different types of habitat patches among which both rodent and deer hosts were able to move. We arranged these habitat patches according to our understanding of the nature of semirural and suburban landscapes in Lyme-disease-endemic areas of the northeastern United States. In these areas, patches are relatively small compared to the dispersal capabilities of mammals, and some habitat types constitute "source patches," as they are net exporters of emigrants, whereas others constitute "sink patches" because they are net importers of immigrants.

One key result of the model was that considerable densities of highly infected ticks can be maintained in "sink" habitats even when the average density of rodent hosts is low. The density of infected ticks in any particular habitat type is a consequence of the proximity of other patch types and the dispersal patterns of rodent and deer hosts, which our empirical studies demonstrate are affected by acorn availability. Thus, our model and field data indicate that the local risk of Lyme disease cannot be predicted simply by focusing on conditions within the local habitat. Rather, land-use policy makers must also consider the dynamics of mice and ticks in the surrounding landscape.

Figure 10. White-footed mice disperse from oak-dominated forests to other habitat types during and preceding peaks in mouse abundance. Mice and hitchhiking ticks disperse more readily into small shrub-dominated and mixed shrub and grassy patches that are surrounded by an oak forest than they do into larger patches, grass-dominated patches and patches distant from oak forests. The risk of acquiring Lyme disease in one of these latter habitats is expected to be lower than the risk of acquiring the disease in small patches surrounded by oak forest. Part of a Lyme-disease prevention strategy would be to know which habitats to avoid and when to avoid them. (Larger migratory movements are indicated by thicker arrows; smaller migratory movements, by thinner arrows.)

Societal Attitudes toward Nature

It is ironic that, just as human societies are becoming increasingly aware of the intrinsic value of nature and wilderness, the Lyme-disease epidemic has caused people to fear and mistrust nature within endemic areas. Other emerging tick-borne diseases, such as human babesiosis and human granulocytic ehrlichiosis (HGE), add to the real and perceived risks of encountering a tick while outdoors. Hikers and others entering forests are either annoyed or frightened by the measures they must take to avoid contact with ticks. These include wearing light-colored clothing, tucking pant legs into socks, wearing long-sleeved shirts, applying insect repellents and conducting thorough tick checks after leaving the woods. Parents are often reluctant to allow children to play in the forest, and when such latitude is given, it is often accompanied by the admonition to remain on trails at all times. In sum, our current battery of Lyme-disease prevention strategies relies almost wholly on avoiding ticks and tick bites. Unfortunately, this situation is unlikely to change in the near future.

Some steps are being taken to boost people's immunity to the bacterium, should they encounter it. At least two vaccines have recently been tested in large-scale field trials with volunteer human subjects, and preliminary evidence suggests that they will be relatively safe and effective in preventing Lyme disease. However, an effective vaccine may not be the panacea that some people expect. On a population-wide level, the risk of Lyme disease remains remarkably low. For instance, in Lyme-disease-endemic counties in the northeastern and north-central states, the number of cases remains about 10 to 30 per 100,000 individuals, and in the rest of the United States, cases per 100,000 are well below 10. Given this relatively low risk at the population level, it remains to be determined whether widespread use of a vaccine is warranted even if it is relatively safe.

For example, the question of who needs to take the vaccine becomes an issue. Should physicians urge that the general population throughout states having high Lyme-disease incidence be given vaccine? Should vaccines be made available only to people who are particularly at risk owing to their profession (for example, landscape gardeners, foresters and park rangers)? Apparently, the effectiveness of the vaccine declines dramatically after one year, and annual booster administrations are needed to maintain an effective response. Will patients and their doctors be responsible about sustaining their immunizations every year? Will vaccinated people believe that they do not have to avoid tick bites, relax their vigilance and become exposed more readily to other, potentially more deadly, tick-borne diseases, such as HGE, from which they are not protected?

It appears likely that, even with a widely available vaccine and a public and health-care community that are well educated about its use, avoidance of tick bites will remain the primary means of preventing Lyme disease. If so, the primary responsibility for prevention will continue to rest with individuals, rather than with the health-care community. Avoiding tick bites requires knowledge about some fundamental aspects of the natural history of Lyme disease, and about the ecological interactions that determine where and when risk is high. Thus, ecological studies on acorn production, on population dynamics of mice, deer, other hosts and their predators, and on the biology of ticks and *B. burgdorferi* bacteria will continue to be of primary importance in efforts to reduce the incidence of Lyme disease. If ecologists are to use acorn production to predict areas that are likely to be infested with disease-carrying ticks, various measures can be taken to reduce the risk. These measures include boosting public-education efforts in the months preceding an expected increase in local risk, posting warning signs in high-risk areas and alerting health-care specialists whose patients live or work in high-risk regions. The interface between ecology and human health is both broad and deep.

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