

Chapter 13

Ecological Webs Involving Acorns and Mice

Basic Research and Its Management Implications

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The disciplines of ecology and natural resource management have many parallels, including the use of both community and ecosystem perspectives. Decades ago, ecologists recognized a distinction between population ecology, in which the focus was on properties of single species, and community ecology, in which the focus was on interactions among species. More recently, community ecologists have expanded their focus to include interaction networks among species and the existence of both direct and indirect effects of species on one another (e.g., Wootton 1993, Holt 1984, Pimm 1991). Similarly, management of natural resources can be divided into approaches that focus on single species and those that target more inclusive entities, such as diversity or productivity. The latter is typically called ecosystem management (e.g., Grumbine 1994).

Natural resource managers have traditionally focused on single species of commercial or conservation importance. Such efforts to manage single species often fail, either because they are ineffectual or because they have unanticipated results (Pickett et al. 1997). For instance, the management of freshwater fisheries is often compromised because the fish participate in a "trophic cascade" (Carpenter et al. 1985) that complicates simplistic management approaches. Stocking of lakes with top predators can result in either suppression of primary production or in algal blooms, depending on the number of trophic levels in the lake (Carpenter and Kitchell 1988). Fisheries management has failed repeatedly because of poor information on species interactions and trophic

structure in freshwater and marine ecosystems (Walters 1998). The ecosystem management approach, on the other hand, explicitly recognizes that species exist in webs of trophic and nontrophic interactions and that these interactions have strong implications for the performance of both individual species and the entire ecosystem. Moreover, this approach is required when community diversity, stability, or ecosystem processes, rather than single species, are the target of management efforts.

The oak forests of the eastern United States are being modified and degraded by human activities, and sound management approaches are needed (Healy et al. 1997). Oak forests are highly complex ecosystems

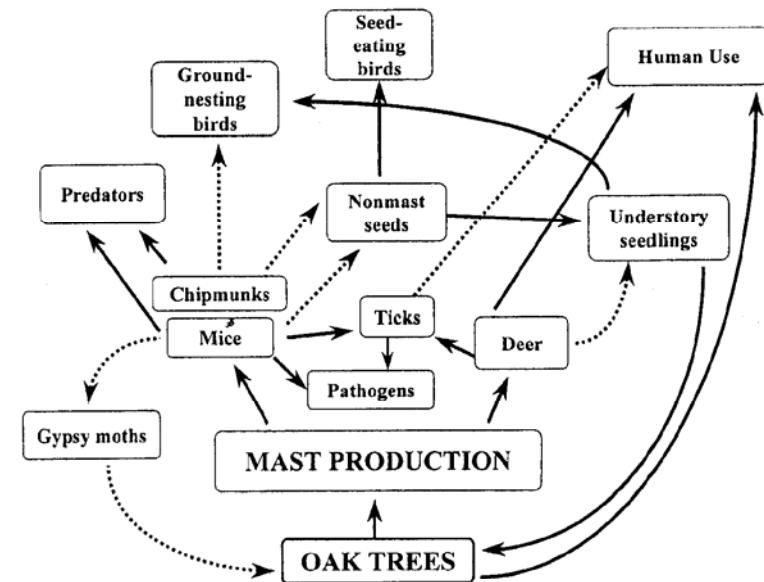


FIGURE 13.1. Conceptual model describing interacting taxa in oak forests of the eastern United States. Arrows indicate the direction of the primary interaction between taxa, for instance, mast production affects mice, but mice do not affect mast production. Solid arrows indicate that the effect of one taxon on another is positive (e.g., more mice leads to more ticks), and dashed arrows represent a negative effect of one taxon on another (e.g., more mice leads to fewer gypsy moths). The nature and strength of most interactions, and contingencies involved in the outcomes of interactions, are described in the text. (Adapted from Ostfeld, Jones, and Wolff 1996.)

with many interacting species and processes. Some of these interactions are conspicuous, for example, the overbrowsing of tree seedlings by dense populations of white-tailed deer (Healy 1997a). But others are subtle and cryptic, for example, the interactions between nocturnal rodents, such as white-footed mice, and their predators and prey. In this chapter, I describe some recently documented interconnections among oak trees, acorn production, wildlife populations, gypsy moth dynamics, and Lyme-disease risk (see Figure 13.1). I then describe the implications of these interconnections for human use of oak forests. Finally, I advance some possible management options and anticipate their consequences in light of the complex web of interactions within these ecosystems.

MAST SEEDING BY OAKS

Masting—the episodic or periodic production of large crops of fruits or seeds by a population of plants, punctuated by one to several years of low production—is characteristic of trees that bear large seeds and is believed to have evolved as a means of escaping seed predation (e.g., Janzen 1971). During mast years, so many seeds are produced that seed predators cannot consume them all, and this leads to successful recruitment of seedlings by the masting trees. In contrast, seedling recruitment may be minimal or nonexistent following years of low seed production, because virtually all seeds are consumed (Kelly 1994, Sork et al. 1993). Seed consumers often respond to mast production by increasing population density; therefore, selection may favor trees that produce large seed crops after several years have elapsed since the previous mast year, resulting in high seed production when populations of seed predators are at a nadir.

For the past few decades, plant ecologists and evolutionary biologists have been interested in both the proximate and the ultimate causes of masting (Chapter 9). Proximally, masting may occur because pollen production or pollen dispersal is limiting in some years but not others (Lalonde and Roitberg 1992). Alternatively, seed crops may be initiated only after sufficient carbon has been stored by trees to allow them to allocate stored resources to reproduction rather than to growth and maintenance (Lalonde and Roitberg 1992). Because by definition masting behavior involves simultaneous seed production by many or most members of a plant population, plant biologists are interested in discovering the environmental cues that trigger synchronous seed production within a

population. Whether individual plants respond to local or regional environmental cues, such as cumulative degree-days or seasonal rainfall, or to chemical signals produced locally or regionally by conspecifics is unknown. Plant ecologists appear to be in general agreement that the main ultimate cause of masting is the satiation of seed predators, to produce seedling recruitment (Janzen 1971, Kelly 1994, Silvertown 1980).

Until recent years, much less attention had been devoted to understanding the consequences of masting than its causes. However, the consequences of masting to the structure and function of forest ecosystems can be profound (Ostfeld and Keesing 2000b). Masting tree species are common in boreal, temperate, and tropical forests, so the cascade of effects of masting on wildlife, and the implications of this ecological cascade for both human health and forest health, may be widespread.

ECOLOGICAL CONSEQUENCES OF OAK MASTING

Effects of Masting on Rodents

Mast production provides an enormous flush of resources for seed consumers in forests dominated by masting trees. In the oak-dominated forests of the eastern United States, as well as those of eastern Europe, mast production causes high overwinter survival rates, and occasionally winter breeding, in both murid and sciurid rodents (Pucek et al. 1993, Ostfeld, Jones, and Wolff 1996, Jones et al. 1998, Wolff 1996). Abundant acorns may improve survival rates by allowing rodents to reduce foraging activities and home range sizes, thereby diminishing their vulnerability to predators. In addition, consuming an abundance of food allows storage of body fat, which may buffer rodents against harsh winter conditions. As a result of high overwinter survival and winter breeding following mast production, rodent populations begin the spring breeding season already at moderate to high density. Several studies have now demonstrated that forest rodent populations reach multiannual peaks in density in the springs or summers following mast production (Pucek et al. 1993, King 1983, Ostfeld, Jones, and Wolff 1996, Ostfeld et al. 1998, Wolff 1996, McShea 2000). Experimental simulation of masting, by providing abundant acorns on three 2.4-ha forest plots, reduced the rate of overwinter decline in white-footed mouse (*Peromyscus leucopus*) populations and resulted in spring-summer densities that were approximately

5 times higher than those on unsupplemented control plots (Jones et al. 1998). Studies in Virginia (Wolff 1996) and New York (Ostfeld et al. 1998) have demonstrated that the size of the acorn crop in the fall explains about 80% of the interannual variation in density of white-footed mice in summer.

Effects of Masting on Deer

Many studies have demonstrated the importance of acorns to the autumn and winter diets of white-tailed deer (*Odocoileus virginianus*) (Healy 1997a, Chapter 14). Although acorn availability does exert demographic effects on deer, as on rodents, population fluctuations among deer are largely independent of variations in acorn production, because of their longer mortality and natality schedules. However, recent studies have revealed a pronounced behavioral response by deer to acorn production. In the autumn of a mast year, deer are attracted to oak-dominated stands and spend a considerable portion of their daily time budgets there. In contrast, during autumns of poor acorn production, deer avoid oak-dominated stands, aggregating instead in forest of other types, such as those dominated by maples (McShea and Schwede 1993; Ostfeld et al. 1998). Because of interactions between mammals and both disease vectors and forest pests, the numerical response to acorns by rodents and the behavioral response by deer have profound implications for human health and forest health (Figure 13.1).

Interaction of Rodents and Deer with Ticks and Lyme Disease

Rodents and deer are crucial hosts for ticks of the genus *Ixodes*, which are the vectors of the Lyme-disease agent, a spirochete bacterium (*Borrelia burgdorferi*). Lyme disease is a zoonotic disease, which means that the bacterial pathogen is maintained in wildlife populations and occasionally is transmitted to humans. Unlike some other vector-borne diseases, such as malaria, humans are irrelevant to the maintenance of the Lyme-disease enzootic cycle and only become involved "accidentally" when ticks, which normally feed on wildlife, attack people. *Borrelia* infections in wildlife hosts, including rodents and deer, appear to be rather benign, resulting in no obvious symptoms and having no detectable effect on survival or reproduction. Because of the mammalian hosts' role in feeding

and infecting ticks, the population dynamics and space use of the hosts are critical to the epidemiology of this expanding disease (Lane et al., 1991, Piesman and Gray 1994, Ostfeld 1997).

Lyme disease is by far the most common vector-borne disease in the United States and is increasingly common in Europe. Over the past decade in the United States, between 8,000 and 16,000 cases have been reported to the Centers for Disease Control and Prevention (CDC) each year (Ostfeld 1997). In the United States, Lyme disease is particularly common in the northeastern and northcentral states, where the vector is the black-legged tick, *I. scapularis*.

Ixodes scapularis typically undergo a two-year life cycle that includes four stages: egg, larva, nymph, and adult (Fish 1993). In autumn of each year, adult ticks feed predominantly on white-tailed deer, mating during a single 3–4-day blood meal. Females drop off after engorging and overwinter in a quiescent state on the forest floor at the site of detachment from the deer. The following late spring or early summer, engorged females produce an egg mass before dying, and the eggs hatch in mid-summer into tiny (~0.5 mm) larvae. Because the adult stage of the tick is specialized to deer, the location of deer in autumn determines the location of newly hatched larvae the following summer. Larvae remain within a few meters of the site of hatching and wait for a host to wander near enough to permit attachment, a behavior called host seeking or questing. Unlike adult ticks, larvae are not specialized in their choice of hosts and may feed from any of a wide array of mammalian, avian, or reptilian hosts.

Because transovarial transmission of *B. burgdorferi* from female to offspring is highly inefficient, the vast majority of larval ticks hatch from eggs free of the Lyme disease spirochete (Piesman et al. 1986). Therefore, larval ticks are generally harmless. Larvae may become infected with *B. burgdorferi* if they feed on an infected vertebrate host, but the probability of becoming infected varies strongly with the species of the host. In the northeastern and north central United States, blood meals taken from white-footed mice are by far the most likely to result in infection of the feeding larval tick (e.g., Levine et al. 1985, Magnarelli et al., 1988, Mather 1993). It is for this reason that *P. leucopus* is considered the principal natural reservoir for Lyme disease in North America. In Europe, several mammalian and avian hosts may be competent reservoirs, resulting in more complex ecological dynamics (Randolph and Craine 1995). Once a larval tick becomes infected, it maintains the in-

fection through later molts and is capable of transmitting bacteria to subsequent hosts, including humans. Therefore, the population density of white-footed mice in summer, when larval ticks are active, strongly influences the number of ticks that become infected with *B. burgdorferi* (Mather and Ginsberg 1994). Because the density of infected ticks within areas that people use domestically and recreationally is the primary risk factor for Lyme disease, understanding the dynamics of white-footed mice may allow ecologists to predict and prevent human exposure to the disease (Ostfeld 1997).

After a single 2–3-day blood meal, larval ticks drop off the host and molt into the nymphal stage, which remains quiescent for 10 months or so, only becoming active the following late spring or early summer. Nymphs that acquired *B. burgdorferi* during their larval meal may transmit the disease agent to their human or nonhuman host during their nymphal meal. Because nymphs are small (~1 mm) and therefore difficult to detect, and because their season of peak activity coincides with that of humans, this life stage is probably responsible for transmitting the majority of Lyme disease cases (Barbour and Fish 1993). At forested sites in southeastern New York State, 25%–35% of nymphs are infected with the Lyme disease spirochete (Van Buskirk and Ostfeld et al., 1998, Ostfeld, unpublished data). Similar to larvae, nymphs do not specialize on any particular host species but instead feed on a wide variety of vertebrates. Feeding to repletion requires 2–3 days, after which nymphs drop off the host and molt into the adult stage, which seeks a deer host a few months later in the fall of the same year.

Acorn production influences Lyme disease risk through two different pathways, one involving deer and the other involving mice. In the autumn of a good mast year, when white-tailed deer are attracted to oak-dominated forest stands, they import their burdens of adult ticks into these habitat types, resulting in peak densities of newly hatched larval ticks the following summer (Ostfeld, Jones, and Wolff 1996, Jones et al. 1998). Because heavy acorn production also causes white-footed mouse populations to reach peaks in density the following summer, mast production results in simultaneous and syntopic peaks of ticks and the most competent natural reservoir for *B. burgdorferi*. These concurrent events result in a high probability that larval ticks will acquire the Lyme disease agent and molt into an infected nymph. The outcome is a higher than usual risk of Lyme disease during the second summer following heavy masting, given the 1-year delay before larvae that fed on abundant mice become active as infected nymphs.

Effects of Mice on Gypsy Moths

The density of white-footed mice is important not only to their parasites and pathogens but also to their prey, which include the gypsy moth (*Lymantria dispar*). The gypsy moth is a European invader of North American oak forests. In parts of the eastern United States, this species periodically undergoes population outbreaks during which it may defoliate large expanses of oak forest (Chapter 7). Gypsy moth populations tend to remain at low densities for several years before beginning a phase of rapid increase, often spanning five orders of magnitude in egg mass density over 2–3 years (Chapter 7, Campbell 1967, Ostfeld, Jones, and Wolff 1996). After one to several years of peak density, the moth populations then decline steeply, reentering a prolonged low-density phase.

Much attention has been devoted to understanding the causes of fluctuations in gypsy moth populations (Campbell and Sloan 1977, 1978, Doane and McManus 1981, Chapter 7). During the peak phase, moth populations may be regulated by their food supply, particularly when outbreaks result in massive defoliation of oak forests. Evidence indicates that the decline phase is caused by viral pathogens and parasitoids that specialize on gypsy moths and that exhibit a delayed density-dependent response to their moth hosts (Elkinton and Liebhold 1990). Other factors, such as induced chemical defenses by host trees, the use by moths of plant secondary chemicals for defense against pathogens, and delayed effects of high population density on maternal condition and fecundity, are also known to influence gypsy moth populations during both the peak and decline phases (Rossiter et al. 1988, Rossiter 1994, Hunter and Dwyer 1998).

After several larval instars, gypsy moths pupate for about two weeks in midsummer and then eclose into adults. It has long been known that white-footed mice eat gypsy moth pupae, which are a large (~2–3 cm), immobile, undefended food source, highly accessible to mice by virtue of their location on the forest floor or low on trunks of trees (Smith 1985, Yahner and Smith 1991). Despite their propensity to attack pupae, however, mice appear to be unimportant in regulating high-density moth populations, largely because neither the functional response nor the numerical response of mice to moths is sufficiently rapid. Nevertheless, recent research has generated strong evidence that mice, via predation on pupae, are responsible for regulating moth populations during the low-density phase (Elkinton et al. 1996, Ostfeld, Jones, and Wolff 1996, Jones et al. 1998).

Studies examining predation on freeze-dried gypsy moth pupae show that mice are the predominant predator in most years and that the proportion of pupae attacked is strongly correlated with mouse density (Elkinton et al. 1996, Ostfeld, Jones, and Wolff 1996). When mouse density exceeds 10–15 individuals ha^{-1} , virtually 100% of the experimentally deployed moth pupae were attacked by mice within the 2-week window necessary for eclosion (Ostfeld, Jones, and Wolff 1996). In an experimental field study in which mouse density was reduced by trapping and removal, survival of both experimentally deployed and natural pupae was dramatically higher than in control sites in which mouse density was high. The result was an enormous increase in density of egg masses and caterpillars the following year on plots from which mice had been removed (Jones et al. 1998). Essentially, the reduction of mouse density during the low phase of a gypsy moth cycle released the moth population from regulation by mice and allowed it to begin a phase of rapid growth (Jones et al. 1998). This study, combined with other observational and experimental studies (e.g., Elkinton et al. 1996, Ostfeld, Jones, and Wolff 1996), indicates that moderate- to high-density mouse populations are sufficient to maintain moth populations at low densities in perpetuity, and that a crash in the mouse population when moth populations are sparse is both necessary and sufficient to cause rapid growth toward an outbreak of moths (Jones et al. 1998, Ostfeld and Keesing 2000b). Because crashes in mouse populations are predictable based on mast production (Wolff 1996, Ostfeld and Keesing 2000b), moth outbreaks and defoliation events also may be predictable well in advance.

Gypsy moths do not have a reciprocal effect on population dynamics of white-footed mice. Because moths pupate in midsummer, when food is not limiting to populations of mice (Hansen and Batzli 1978, Wolff 1996), mice do not appear to be affected by the density of gypsy moths.

The potential exists for a positive feedback loop from acorns to mice to gypsy moths to oak trees and masting (Figure 13.1). Gypsy moth defoliation of oaks may delay or prevent the production of mast crops by existing oaks and/or reduce the community dominance of oaks (reviewed by Healy et al. 1997). Temporary or long-term reductions in mast crops are expected to reduce average population densities of white-footed mice (Ostfeld, Jones, and Wolff 1996, Elkinton et al. 1996, Jones et al. 1998), which will relax the suppressive effects of mice on gypsy moths. This in turn will increase the probability of moth outbreaks and defoliation events. The existence of feedback loops adds a level of complexity to forest management, because the impacts of a particular management action may become strongly amplified.

Effects of Mice on Ground-Nesting Songbirds

In oak forests of the eastern United States, several species of songbirds, including ovenbirds, worm-eating warblers, veeries, wood thrushes, and dark-eyed juncos, nest at or near ground level. Nests of these species may be vulnerable to attack by various mammalian and avian predators, especially during incubation. Indeed, many studies using artificial ground nests suggest the potential for these predators to cause nest failure and even population declines of some passerines (e.g., Leimgruber et al. 1994, Martin 1993). Deployment of artificial ground nests, typically baited with both quail eggs and clay eggs (the latter for acquiring tooth or bill prints useful in identifying nest predators), has suggested that mammals such as raccoons and opossums, and birds such as bluejays and crows, are the principal predators. However, because quail eggs are larger and have thicker shells than typical songbird eggs, this approach may bias results against the detection of smaller predators such as mice and chipmunks (Maxson and Oring 1978), which typically are unable to handle quail eggs.

Recent studies in southeastern New York State using passerine eggs revealed that the white-footed mouse was responsible for the majority of attacks on artificial ground nests and that eastern chipmunks were the second most frequent predator. Medium-sized mammals and birds were infrequent predators on these nests (K. Schmidt, R. Naumann, J. Goheen, R. Ostfeld, E. Schaubert, and A. Berkowitz, unpublished data). In oak-forest plots in which mouse populations were maintained at low densities via removal trapping, attack rates on artificial nests were significantly lower than on control plots supporting high mouse density. In contrast, experimental manipulation of chipmunk densities had no effect on nest-predation rates.

Studies of nest predation using artificial nests have a number of well-recognized potential weaknesses, including lack of parental defense, poor placement by the experimenter, and elevated attractiveness due to scent contamination. Therefore, additional studies, particularly examining attacks on natural nests, will be necessary to determine whether artificial nest experiments accurately represent rates and perpetrators of natural nest predation. However, some evidence suggests that results from artificial-nest studies may accurately reflect processes affecting success of natural nests. In a long-term study of nesting performance of dark-eyed juncos in oak forests of Virginia, Ketterson et al. (1996) showed that the proportion of nests failing to fledge young was strongly correlated with summer density of *Peromyscus* populations. At these same

sites, density of mice in summer was highly correlated with acorn production the prior autumn (Wolff 1996).

The density and structure of understory vegetation may influence the survival of eggs and nestlings of ground-nesting songbirds. Because browsing by deer on forest understories may affect protective cover and the suitability of nesting sites, population size and space use of deer may also strongly influence bird populations indirectly (McShea and Rappole 1997). When acorns are abundant, impacts by deer on understory vegetation in the autumn and winter may be relaxed, due to reduced browsing, which in turn may enhance protective cover for birds the following summer. On the other hand, dense populations of deer when no acorns are available may have a strongly destructive influence on protective understory vegetation (McShea and Rappole 1997).

Potential Interactions between Mice and Their Predators

Interactions between white-footed mice and their avian and mammalian predators in oak forests have not been well studied. Despite anecdotal reports, ecologists have not yet determined whether raptor or carnivore populations experience unusually high reproductive success during years of high mouse densities. Similarly, little evidence exists to evaluate the possibility that predation by raptors and carnivores is responsible for mouse population declines from high densities. In oak-hornbeam forests of eastern Europe, acorn-caused increases in the population density of rodents, particularly *Apodemus sylvaticus* and *A. flavicollis*, appear to induce population growth by their predators, especially mustelids and owls (Jędrzejewska and Jędrzejewski 1998). These predators, in turn, attack alternative prey, such as nesting songbirds, when rodent populations collapse.

MANAGEMENT OPTIONS AND POSSIBLE OUTCOMES

The ecological studies summarized above demonstrate that a network of species of plants, vertebrates, invertebrates, and microbes interact strongly in oak forests of the eastern United States. Masting behavior by the ecosystem dominant—oak trees—sets off an ecological chain reaction mediated by behavioral and numerical responses of white-footed

mice and white-tailed deer, which in turn cause changes in the dynamics of their prey (e.g., gypsy moths, songbirds), pathogens, parasites, and possibly their predators. A practical benefit of understanding the nature and strength of these ecological interactions may be the ability to predict Lyme disease risk, gypsy moth outbreaks, and nesting success of songbirds and owls, all of which are matters of practical or aesthetic importance to people. Beyond prediction, it may be possible to manage populations of deer or mice, directly or indirectly, in order to meet desired management goals. In the following section, I discuss some of the more obvious options concerning the management of vertebrate populations or the landscapes in which they occur, and speculate on the possible outcomes of these management schemes. Although the focus of management may often be a single species, the outcomes of management will almost certainly involve a number of interacting species and processes within a landscape.

Reduction or Elimination of Deer

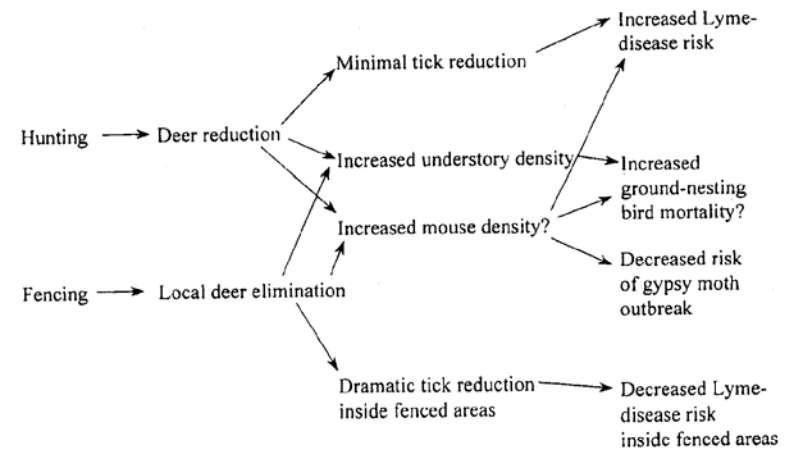
The primary means of managing deer populations are hunting and fencing. Hunting may reduce density and population growth rates of deer, particularly if the hunting program is of appropriate scale and intensity and if it includes the taking of does (Knox 1997, Winchcombe 1993). Hunting programs rarely if ever cause dramatic reductions or local extinctions in deer populations, unless those populations are isolated, for instance, on islands. Fencing may eliminate deer completely from enclosed areas, but typically this can be accomplished only in small tracts.

Is it possible to diminish population density of black-legged ticks, and therefore the risk of Lyme disease, via moderate reductions in populations of deer? The answer appears to be no. Recent modeling efforts have addressed this question by creating mathematical simulations of tick populations that feed as adults on deer and as juveniles on rodents, and then manipulating the simulated host populations to determine potential consequences for tick density and infection prevalence (Van Buskirk and Ostfeld 1995). The model predicted that incremental reductions in deer density would not result in similar reductions in tick density. Instead, it suggested that the relationship between deer and tick abundance was strongly nonlinear, with a threshold effect on tick density only at very low deer density. The intuitive reason for this nonlinearity is that, because each individual deer may host hundreds to thousands of adult ticks in a given season, and because each female tick may

lay more than 1000 eggs, even a modest population of deer may be able to support a dense population of ticks (Van Buskirk and Ostfeld 1995). Therefore, a small to moderate reduction in deer density probably will cause a trivially small reduction in tick density.

Empirical results generally are consistent with predictions of this model. Tick populations may be enormously high in areas where a hunting program results in moderate reductions in deer populations (Ostfeld, Hazler, and Cepeda 1996), as well as in places where deer populations are modest even without hunting (Wilson et al. 1988, 1990). However, on some Massachusetts islands from which deer were nearly extirpated and in mainland sites from which deer were excluded by fencing, populations of black-legged ticks experienced a dramatic reduction (results reviewed in Wilson and Childs 1997). Because of practical limitations to the installation and maintenance of fencing, this method of managing deer populations may be feasible only on a very local scale, but it could reduce Lyme disease risk around individual residential properties (Figure 13.2). In conclusion, large-scale reduction of deer density via hunting would appear to be an ineffective method of controlling Lyme disease risk, whereas fencing may be effective at small scales.

Despite the low likelihood of reducing Lyme disease risk by managing deer, there are other potential effects of deer management on the function of oak forest ecosystems, such as the nesting success of ground-dwelling songbirds. If reduction of deer density results in greater density of understory vegetation, which in turn results in higher attack rates by white-footed mice (R. Naumann, R. Ostfeld, and A. Berkowitz, unpublished data), deer management may reduce recruitment of ground-nesting songbirds. In contrast, because attack rates by raccoons and opossums often are higher in sparse than in dense understory, deer reduction could protect nests in areas where the predominant predators are medium-sized mammals (deCalesta 1994). Predicting the net effect of a deer reduction on nesting success is problematical because of incomplete knowledge of interactions between deer and other mast consumers (e.g., mice, raccoons) and of interactions between understory vegetation and susceptibility of nests to predation. For instance, if reduction of deer causes increased availability of mast for mice and raccoons, and these mast consumers increase in density, then songbird nests may be at high risk (McShea 2000). Clearly, understanding the net effects of deer management on songbirds requires additional empirical and modeling studies.



Possible deer management outcomes

FIGURE 13.2. Methods and possible consequences of managing populations of white-tailed deer. Postulated consequences are limited to disease risk, gypsy moth dynamics, and nesting success of ground-dwelling songbirds (see Figure 13.1). Those that are highly speculative are indicated with question marks. Arrows point to the likely consequences of each phenomenon.

Reduction of White-Footed Mice

A second potential target of oak forest management is the white-footed mouse. Because white-footed mice are the principal reservoir of the Lyme disease spirochete and may be major predators on songbird nests, reducing mouse densities might have benefits for both human and forest health. On the other hand, reducing density of mice will cause relaxation of predation on gypsy moths, thereby increasing the likelihood of moth outbreaks, oak tree defoliation, and potential declines in the abundance and productivity of oaks. These conflicting probable outcomes of a single management action emphasize the crucial importance of understanding interaction webs within ecological communities.

Irrespective of the desired management outcome, managing populations of white-footed mice, particularly at scales larger than individual residential properties, probably will be much more difficult than man-

aging deer. Reducing mouse populations directly, for instance by baiting with rodenticides, is infeasible except in small areas and may adversely affect nontarget organisms. As a consequence, the most viable means of controlling mouse populations probably will be to manage their habitats or landscapes.

Populations of *P. leucopus* often reach their highest densities in small isolated woodlots (Vessey 1987, Kaufman and Kaufman 1989, Cummings and Vessey 1994, Nupp and Swihart 1998). Several factors appear to be responsible for these high and relatively stable densities. First, in landscapes composed of woodlots within an agricultural, suburban, or urban matrix, populations of mouse predators, such as barred owls, bobcats, coyotes, foxes, and long-tailed and short-tailed weasels, may be insufficient to regulate mouse populations. Second, in some isolated forest patches, particularly those smaller than several hectares, populations of sciurid rodents (e.g., chipmunks and tree squirrels) are sparse or nonexistent, which may release mice from competitive suppression (Nupp and Swihart 1998). Third, when woodlots occur in a matrix that is inhospitable for mice, emigration is curtailed, thus negating the potential for dispersal to regulate population density. Populations of rodents in which dispersal is prevented often reach unusually high densities, which may be sustained for long periods (Ostfeld 1994).

For these reasons, it appears that management of landscapes of which oak forests are a component may be a viable option for controlling mouse populations. Larger, more continuous, or more interconnected forest patches are less likely to maintain excessively high populations of white-footed mice than are smaller, more fragmented patches (Nupp and Swihart 1996, 1998). Both extrinsic factors (predators and competitors) and intrinsic factors (dispersal) may be affected by patch size, disturbance, and the structure and composition of the nonforest matrix (Dooley and Bowers 1996). All of these features of forested landscapes can be managed by controlling the spatial arrangement of forestry practices, agricultural fields, and residential development. It should be noted that fragmentation of forested landscapes often optimizes the population performance of deer as well as that of mice, apparently because of the juxtaposition of different food types (e.g., young vs. old forests, forest vs. oldfield vegetation; Sinclair 1997).

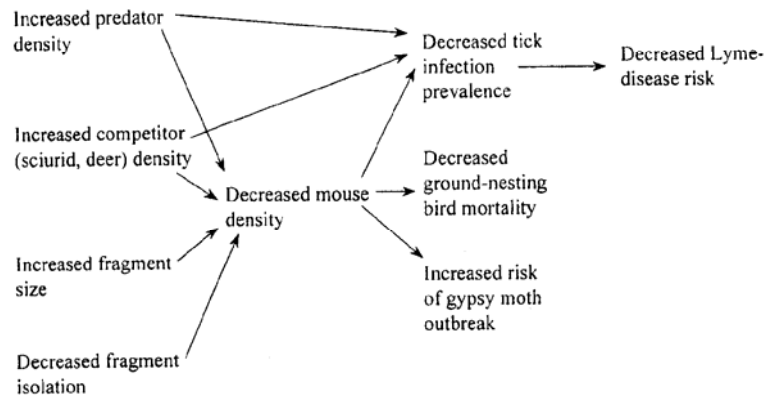
What are the likely outcomes for Lyme disease of reducing mouse populations? Van Buskirk and Ostfeld's (1995) model predicted that the density of juvenile black-legged ticks would be linearly (or log-linearly)

dependent on density of mice. Each mouse hosts about 50–100 larval ticks and 10–50 nymphal ticks in any given season (Ostfeld, Hazler, and Cepeda 1996), and each successful blood meal for a juvenile tick promotes survival to the next stage. Questing juvenile ticks that fail to find a host within a short activity season die, and empirical evidence suggests that mouse density is an important determinant of the proportion of the juvenile tick population that is able to find a host, feed, and molt to the next stage, resulting in an approximately linear relationship between mouse density and that of juvenile ticks (Van Buskirk and Ostfeld 1995).

Because of the role of the mouse as natural reservoir for the Lyme disease microbe, their density is also a key determinant of the number of juvenile ticks that become infected with *B. burgdorferi*. Empirical studies in oak forests of both Rhode Island and New York show that the density of white-footed mice in summer is a significant predictor of the infection prevalence of nymphal ticks the following year (Mather and Ginsberg 1994, Ostfeld et al., unpublished data). Thus, the lower the density of mice, the lower the number of larval ticks that will feed on mice and molt into infected nymphs that become active the next year.

The results of the Van Buskirk and Ostfeld (1995) model suggest a means of effectively reducing the influence of mice on infection prevalence of nymphal ticks. Managing habitats to enhance populations of species that compete with or prey on mice may not only influence the density of mice but also may dilute the impact of mice on infection prevalence of ticks (Ostfeld and Keesing 2000a). Van Buskirk and Ostfeld (1995) predicted that the higher the diversity in the community of hosts for juvenile ticks, the lower the infection prevalence of ticks, and therefore the lower the risk to humans of contracting Lyme disease. In a highly diverse community of ground-dwelling vertebrates, a high proportion of larval ticks will encounter a poor Lyme disease reservoir and molt into uninfected nymphs. Thus, high vertebrate diversity dilutes the influence of *P. leucopus* on disease risk (Ostfeld and Keesing 2000a) (see Figure 13.3). Although the presence of a diverse community of vertebrates may not reduce the opportunity for ticks to successfully obtain a blood meal, the proportion of ticks becoming infected, and therefore dangerous to humans, will likely decrease with increasing host diversity (Ostfeld and Keesing 2000a).

Although directly or indirectly diminishing the density of white-footed mice reduces Lyme disease risk for humans, reducing mouse densities increases the probability of a gypsy-moth outbreak (Figure 13.2).



Possible mouse management outcomes

FIGURE 13.3. Methods and possible consequences of decreasing population density of white-footed mice. Postulated consequences are limited to disease risk, gypsy moth dynamics, and nesting success of ground-dwelling songbirds (see Figure 13.1). Arrows point to the likely consequences of each phenomenon.

Experimental reductions in mouse density in 2.4-ha oak-forest plots in New York resulted in tenfold to thirtyfold increases in density of gypsy moth egg masses and caterpillars the following year (Jones et al. 1998). Densities of mice below approximately 10 ha^{-1} appear to be necessary to release gypsy moths from regulation and allow growth toward outbreak levels (Ostfeld, Jones, and Wolff 1996, Ostfeld et al. 1998). Consequently, the optimal management goal may be to avoid reducing the absolute abundance of mice but instead to reduce the abundance of mice relative to that of other species. Species diversity has two components: species richness (the number of species in the community) and species evenness (the relative abundance of each species). The higher the species diversity in the vertebrate community, by definition, the lower the relative abundance of mice will be. Thus, vertebrate diversity may be a desirable endpoint of management action for both practical and aesthetic reasons. Ecologists and managers may together be able to devise forest and landscape management options to be tested for their effectiveness in increasing diversity of vertebrates.

CONCLUSIONS

An intricate web of connections exists among species in oak forests. The nature and strength of these interactions, as well as their net effects on community and ecosystem dynamics, are still being uncovered. Our growing knowledge of these interactions facilitates scientifically sound management of oak forests and their components.

White-footed mice in the eastern United States, and their ecological counterparts in oak forests elsewhere, clearly are the hub of the highly interconnected oak-forest system. White-footed mice are among the most abundant of all vertebrates in oak forests, are quintessential generalist consumers, and may regulate populations of insects and birds, as well as of forest trees via seed predation (Ostfeld et al. 1997). They also interact strongly with parasites and zoonotic pathogens, and probably with their mammalian and avian predators. Because of this network of ecological connections, the net effects of managing mouse populations may be multifaceted and may result in conflicting outcomes for human users of oak forests. The tentative conclusion to arise from the studies described above is that high species diversity of vertebrate communities in oak forests is beneficial for both human health and forest health. High diversity of species that compete with or prey on mice will probably regulate mouse populations, directly reducing disease risk and possibly predation on songbird nests. These vertebrate predators and competitors also will dilute the influence of mice on infection prevalence of ticks (Ostfeld and Keesing 2000a, Schmidt and Ostfeld 2001).

However, the web of connections centered on white-footed mice will probably necessitate management tradeoffs. For instance, although reducing populations of mice may decrease Lyme disease risk and increase songbird nesting success, population declines of mice also increase the probability of a gypsy moth outbreak (Ostfeld, Jones, and Wolff 1996, Jones et al. 1998). Reducing the *relative* abundance of mice without dramatically decreasing their *absolute* abundance may preserve their positive effect on the regulation of gypsy moths.

Because of the benefits of reducing the abundance of white-footed mice relative to other vertebrate species, the most appropriate target of management efforts appears to be diversity rather than the population status of single species. Both species richness and species evenness appear to be enhanced in large and well-connected forested landscapes. Therefore, appropriate management efforts probably will involve features of landscapes, such as patch size, shape, and connectedness. Stud-

ies of the effects of landscape management on mouse populations and of the ecological and epidemiological consequences of any community changes that ensue will be important for wisely managing oak forests in the coming decades.

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