

The background of the cover is a photograph of a forest floor. It is covered with numerous acorns, some whole and some broken, scattered among low-growing green plants with small, star-shaped leaves. Large, dark, lobed leaves, likely from oak trees, are also visible. The scene is set against a backdrop of a tree trunk with rough, textured bark.

BioScience

May 1996

American Institute of Biological Sciences

Vol. 46 No. 5

Ecological Connections—
Mast, Moths, Mice, and Malaise

Of Mice and Mast

Ecological connections in eastern deciduous forests

Richard S. Ostfeld, Clive G. Jones, and Jerry O. Wolff

A popular characterization of ecological systems is that everything is connected to everything else. Although in some metaphysical sense it may be true that influences experienced by a particular species are transmitted to all other species in the ecosystem, such pervasive connections have not been demonstrated scientifically. Instead, the focus of community ecology has been on pairwise interactions between species. The paradigm has been that the determinants of community structure can be elucidated by studies of direct effects of populations on one or a few other populations (Kareiva 1994).

To identify the role of predation or competition in structuring ecological communities, typically a predator or competitor is removed, and the responses of prey or other competitors are monitored (Connell 1983, Menge and Sutherland 1976, Schoener 1983, Sih et al. 1985). These studies reveal the importance of direct effects in ecological communities. However, such experiments often produce unexpected results,

Richard S. Ostfeld is an associate scientist and vertebrate ecologist and Clive G. Jones is a scientist and chemical ecologist at the Institute of Ecosystem Studies, Millbrook, NY 12545. Jerry O. Wolff is a research associate professor in the Department of Fisheries and Wildlife at Oregon State University, Corvallis, OR 97331, and a project leader in ecological risk assessment with the US Environmental Protection Agency, Corvallis, OR 97333. © 1996 American Institute of Biological Sciences.

In oak forests, both direct and indirect interactions among species have crucial consequences for the behavior of the entire ecosystem

for example, a prey population decreasing in density after removal of its predator (Holt 1977, 1984), or qualitatively different results among so-called replicates of the same experiment (Pimm 1991). Pimm (1991) argued that these unexpected changes in community dynamics are due to pervasive indirect effects of the removal ramifying through the community. If the structure and function of ecological communities are determined largely by indirect effects, then an exclusive focus on direct effects is misleading and counterproductive. Pimm's assertion is profoundly important to ecological theory and practice (Billick and Case 1994, Wootton 1993) but has not been adequately assessed.

We view the understanding of indirect interactions among species as a crucial development in ecology. Increasingly, ecological systems are experiencing disturbances from anthropogenic sources; and a critical role for ecologists is to predict the system-wide effects of these distur-

bances. Disturbances such as the exploitation of a commercially valuable species, a disease outbreak, or the introduction of an exotic species often have a direct impact on one or a few species. However, effects of the disturbance may permeate past the "target" species to its competitors, predators, parasites, and beyond.

The far-reaching effects of a disturbance depend on the nature and strength of the target species' connections to other species in the system. Indirect effects may or may not include strong feedback loops, which occur when the original target of the experiment or perturbation is affected as an indirect result of the perturbation. Feedback loops are governed by either positive or negative forces and therefore should result in either a propagation or dampening of the original disturbance. Some feedback loops (or any other indirect effects, for that matter) may be transient or highly contingent on other interactions in the system.

Without a better understanding of indirect interactions, ecologists' power to predict system-wide effects of a disturbance is likely to remain severely limited. In this article we describe an ecological system in which both direct and indirect interactions among species have crucial consequences for the behavior of the entire system.

A conceptual model of oak forest systems

We have been studying the consequences of episodic events (distur-

bances) in deciduous forests of the eastern United States. We have developed a conceptual model of this system based on our work and that of our colleagues (Figure 1). In recognition of the prominence of primary producers in ecological systems (Hunter and Price 1992), we base our model on the dominant organisms in our system—oak trees (genus *Quercus*). Many oaks are mast seeders, which means they produce large seed (acorn) crops every two to six years, with low production or total failure in the intervening years (Janzen 1971, Koenig et al. 1991, Silvertown 1980, Sork et al. 1993). Many animal species consume acorns, including weevils, birds (e.g., bluejays and turkeys), and several mammalian species. We focus predominantly on three consumer species: white-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), and white-tailed deer (*Odocoileus virginianus*). We chose these species because of their high biomass, high consumption rates, strong numerical response to resource availability, and/or demonstrated linkages to other species in our system.

White-footed mice, chipmunks, and white-tailed deer are the predominant hosts for larval, nymphal, and adult deer ticks (*Ixodes scapularis* [formerly *Ixodes dammini*], respectively Lane et al. 1991, Mannelli et al. 1993) and thus play crucial roles in the Lyme disease epidemic. Mice also are important predators on gypsy moth (*Lymantria dispar*) pupae (Bess et al. 1947, Campbell and Sloan 1977) and on nonoak seeds when acorns are not abundant. Chipmunks are known to be important predators on eggs and nestlings of ground-nesting birds (Leimgruber et al. 1994, Reitsma et al. 1990). Chipmunks and mice appear to be a limiting food resource for predators such as barred owls¹ and may compete with seed-eating birds for nonmast seeds. Browsing by deer strongly inhibits growth and survival of understory tree seedlings (McShea and Rappole 1992, Tilghman 1989), which in turn can re-

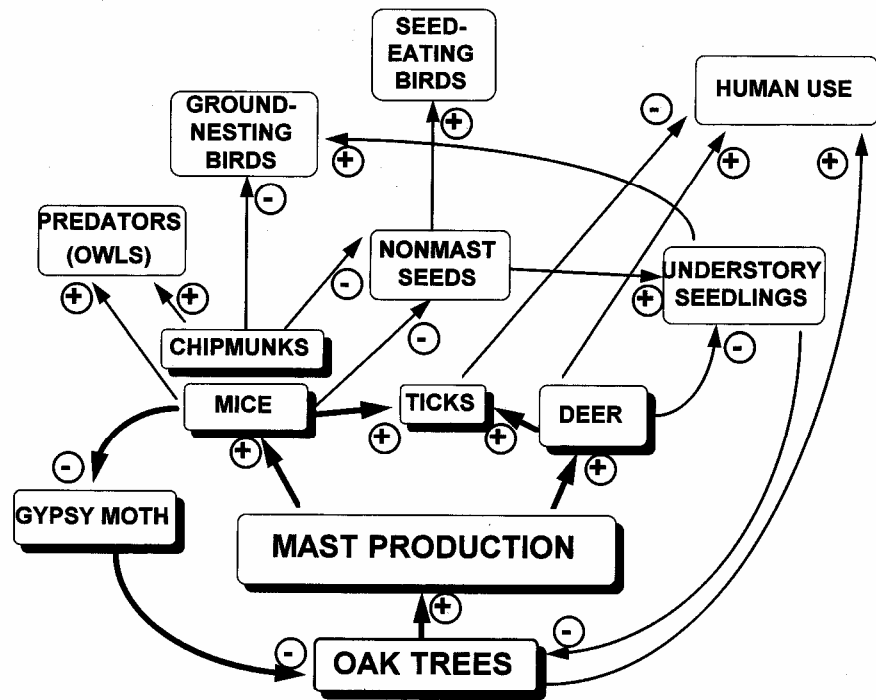


Figure 1. Conceptual model of the relationships among key functional units in the oak forests of eastern North America. Arrows represent directions of the predominant influence between pairs of units. Plus symbols indicate that an increase in density or biomass of the donor level results in an increase in the recipient level; minus symbols indicate a decrease in the recipient level. Shadows indicate the functional units emphasized in this article. Heavy lines represent connections well established by observational or experimental data; light lines represent relationships that are less well established or only postulated.

duce abundance and species richness of songbirds (deCalesta 1994). Songbird abundance is also reduced when gypsy moth defoliation increases the vulnerability of nests to predators (Thurber et al. 1994). Humans are affected by these forest interactions as well, as victims of Lyme disease, as hunters of deer, and as loggers of oak trees.

The oak forest system under study is exceedingly complex, and some of the linkages in Figure 1 are only postulated or are supported by incomplete evidence. In what follows, we focus on the better studied species and linkages (represented by shadowed boxes and heavy lines in Figure 1). We demonstrate that mast production sets off a chain of reactions that ramify throughout the system and affect both the functioning and appearance of these forest systems. We emphasize that the processes shown in Figure 1 operate on different time scales: For example, mouse and moth dynamics are relatively short and produce changes in

population density over several orders of magnitude, whereas tree dynamics operate over longer time scales involving much more gradual changes in abundance. For simplicity, we present a series of pairwise interactions but emphasize instances in which the occurrence or strength of an interaction depends on the existence of other interactions in the system; thus our model is fundamentally holistic.

Connections between mast and rodents

One of us (JOW) conducted studies of population dynamics of white-footed mice, deer mice (*Peromyscus maniculatus*), and chipmunks at the Mountain Lake Biological Station (MLBS) in southwestern Virginia from 1980 to 1994. At this site, the dominant oak species are red oak (*Quercus rubra*) and white oak (*Quercus alba*), which constitute 54% and 10% of the canopy tree community, respectively. We have

¹Jerry O. Wolff, 1994, unpublished data. Department of Fisheries and Wildlife, Oregon State University, Corvallis, OR.

also been monitoring population dynamics of white-footed mice at the Institute of Ecosystem Studies (IES) in southeastern New York since 1991. Forests in our New York plots are dominated by red oak, chestnut oak (*Quercus prinus*), and white oak. At both MLBS and IES we conducted live trapping on at least two trapping grids, each covering 1.0–2.25 ha. We trapped for three to four consecutive days every two to three weeks, generally from April to October or November. At MLBS, wooden nest boxes were used to examine acorn storage and breeding conditions of mice during winter. Nest boxes allowed us to sample the condition and behavior of mice during winter, when trapping is difficult and risky to rodents. Abundance of acorns was estimated by counting acorns on permanently marked trees (MLBS), counting fallen acorns in small quadrats (both sites), and using nylon mesh seed traps placed under the canopies of mature oaks (IES). Although the methods for determining acorn abundance varied between sites, we

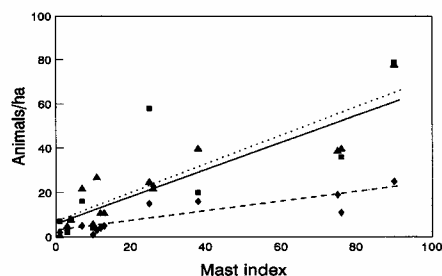


Figure 2. Correlations between mast index for each year and rodent densities for each following summer at the Mountain Lake Biological Station in Virginia. Data are from a 13-year study described in Wolff (in press). The mast index was derived from acorn counts on ten randomly selected branches on each of ten permanently marked red oak and white oak trees. It was converted to a semiquantitative scale in which 0–1 = failure, 2–5 = poor, 6–20 = fair, 21–35 = good, and 36+ = excellent. White-footed mice (*Peromyscus leucopus*), eastern chipmunks (*Tamias striatus*), and deer mice (*Peromyscus maniculatus*) are represented by the dotted line and triangles, solid line and squares, and dashed line and diamonds, respectively. Correlations between mast index and rodent density were 0.887, 0.799, and 0.751, for the three species, respectively; $p < 0.05$ in all cases.

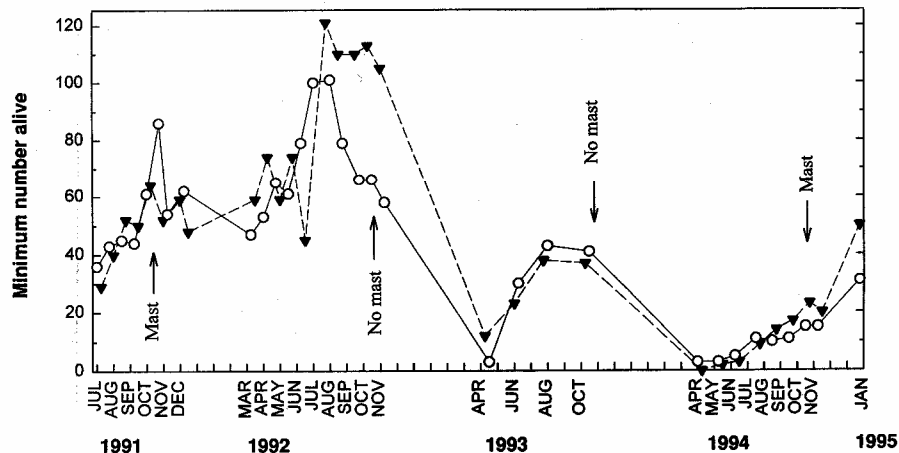


Figure 3. Time series of the density of white-footed mice in relation to mast production on two 2.4-hectare live trapping grids at the Institute of Ecosystem Studies. Triangles represent the Henry Farm grid, and circles represent the Tea House grid.

were able to generate qualitative or semiquantitative estimates that reflect the extreme variation in annual mast production.

Over the 15-year period of monitoring at MLBS, indices of acorn production showed peak years in 1980, 1985, 1988, and 1989. Over this period, densities of rodents were highly correlated with the previous year's mast index (Figure 2). Population densities of the three rodent species reached peaks in the summers of 1981, 1986, 1989, and 1990. Although *Peromyscus* typically do not breed during winter at MLBS (Wolff 1985, Wolff and Durr 1986), winter breeding was observed during each winter preceding a peak. Observations of nest boxes revealed that excess stored acorns remained throughout each winter in which winter breeding was observed, whereas stored acorns did not persist past January in other years (Wolff in press).

Although our IES data set covers only four years, it demonstrates a similar strong correlation between acorn abundance and mouse density (Figure 3). Heavy acorn production was noted in 1991² but not in the following two years.³ Densities of white-footed mice peaked in August

1992, achieving levels at least twice as high as in the summers of 1991, 1993, or 1994. In addition, the typical pattern for both MLBS and IES is that mouse density crashes to extremely low levels approximately 1.5 years after peak acorn abundance (Figure 3; Wolff in press). Thus we concluded that mouse and chipmunk density at our study sites is controlled largely by acorn abundance.

Similar relationships between seed crop and rodent density have been observed in Europe (Pucek et al. 1993). In these forests, the yellow-necked mouse, *Apodemus flavicollis*, which is similar to *Peromyscus* in diet and habitat choice, experiences high rates of overwinter survival and breeding following seasons of heavy acorn production and reaches peak density approximately one year following mast peaks. Mouse populations then decline rapidly to a nadir during the subsequent winter or spring.

Connections between mast and deer

The effect of mast seeding on white-tailed deer is less well understood than for rodents. Deer are voracious consumers of acorns (McShea and Rappole 1992) and may be more likely to produce twins following years of heavy acorn production than at other times.⁴ In addition, deer

²T. Coulson and C. Canham, 1991, unpublished data. Imperial College at Silwood Park, England, and Institute of Ecosystem Studies, New York.

³C. Canham, 1993, unpublished data. Institute of Ecosystem Studies, New York.

⁴R. Ostfeld, personal observation.

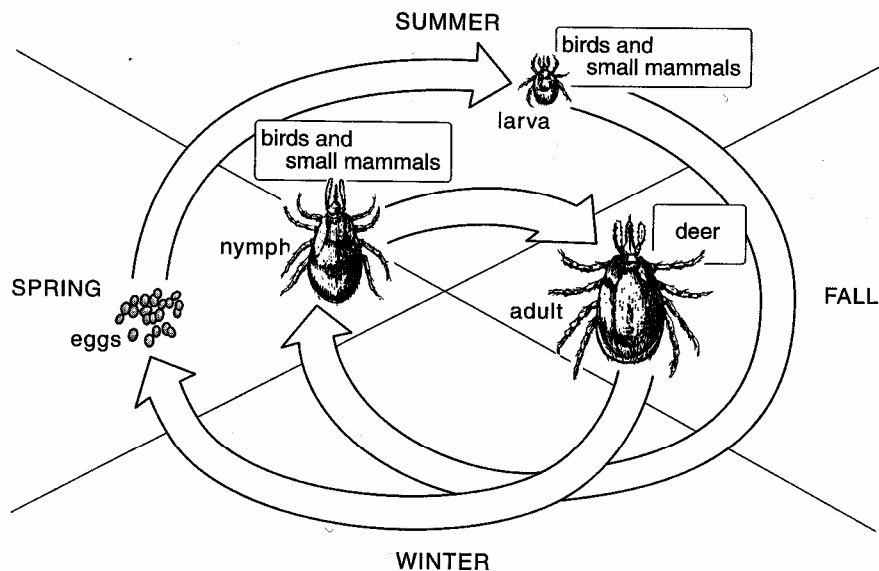


Figure 4. Life cycle of the tick *Ixodes scapularis* in the northeastern United States. Reprinted from Van Buskirk and Ostfeld (1995) with permission from the Ecological Society of America.

occupying patchy forest mosaics in the eastern United States spend more than 40% of their time in oak-dominated stands during the autumn of mast years but less than 5% of their time there in nonmast years, when they favor other patch types, such as stands dominated by maple (genus *Acer*; McShea and Schwede 1993).

Thus, the primary effect of acorn production on white-tailed deer is to shift their distribution during the autumn. During autumn and winter of mast years, deer may consume little besides acorns, and their browsing on tree seedlings and saplings may be lessened at these times.

Connections among mice, deer, ticks, and Lyme disease

Lyme disease is caused by the transmission of spirochetes (*Borrelia burgdorferi*) from ticks (genus *Ixodes*) to humans during blood meals. In the eastern and north central United States, the primary vector of Lyme disease is *I. scapularis*. The life cycle of this tick consists of four stages: egg, larva, nymph, and adult (Figure 4). During each stage except the egg, the tick takes a single blood meal from a vertebrate host before molting into the next stage. Any of these stages may feed on humans. Larvae, nymphs, and adults

are typically active at different seasons and show different degrees of host specificity (Figure 4). Adult deer ticks, however, are much more specialized than larvae or nymphs in their selection of hosts, occurring predominantly on white-tailed deer. After taking their final blood meal from a deer in the autumn, adult ticks drop off their hosts and overwinter in leaf litter before laying eggs early the next summer (Fish 1993). The dispersal capabilities of deer ticks (especially juvenile stages) are poor; thus the distribution of larval ticks appears to be determined by the distribution of white-tailed deer in the prior autumn.

Because 1991 was a year of heavy acorn production at IES, we expected that deer would be attracted to oak-dominated stands in the autumn and consequently would import their burdens of adult ticks into these habitat types. Because adult ticks lay eggs in whatever habitat types their hosts occupy in the autumn, we predicted that peak numbers of larval ticks should occur in oak-dominated habitats in the summer of 1992. To test this prediction, we established sets of transects at three replicate sites within each of five different habitat types at IES. We performed transect drag sampling (Ostfeld et al. 1995) to estimate the

abundance of host-seeking ticks at frequent intervals from spring to autumn each year.

As predicted, numbers of larval ticks peaked in oak sites the summer following mast production, reaching densities approximately ten times higher than in any other habitat type (Figure 5). Encouraged by this result, we further predicted that, because 1992 and 1993 were years of poor acorn production, deer would not aggregate in oak-dominated habitats in those autumns, but would select other habitat types instead. Our observation of peak densities of larval ticks in maple-dominated forest stands in both 1993 and 1994 strongly supported this prediction (Figure 5).

Larval ticks are relatively harmless to humans because they typically hatch devoid of Lyme disease spirochetes (Lane et al. 1991). However, larval ticks may acquire the disease agent during blood meals taken from an infected host and then molt into an infected nymph. The abundance of infected nymphal ticks is the primary ecological risk factor in the Lyme disease epidemic (Falco and Fish 1989). Various species of host differ widely in their likelihood of transmitting spirochetes to feeding larval and nymphal ticks (i.e., in their reservoir competence; Mather 1993). White-footed mice are the most competent reservoirs for the Lyme disease spiro-

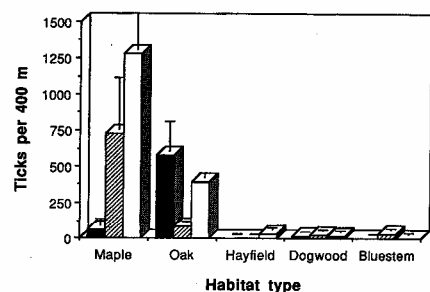


Figure 5. Abundance of host-seeking larval ticks in 1992 (black bars), 1993 (hatched bars), and 1994 (white bars), as determined by standard drag-sampling along 400-meter transects. Bars represent means (± 1 SE) of three replicate sites for each of the five habitat types at the Institute of Ecosystem Studies, New York. Reprinted from Ostfeld et al. (1995) with permission from the Ecological Society of America.

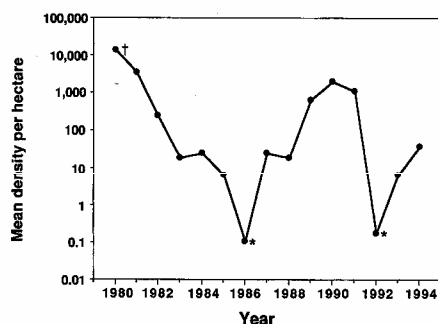


Figure 6. Long-term trends in density of gypsy moth egg masses (log scale) on plots (78.5 m², N = 20) at the Institute of Ecosystem Studies, New York. The dagger indicates that the data for 1980 were obtained by estimating from old egg mass remnants. The asterisks (*) indicate low-density censuses of 18.75 ha in 1986 and 11.0 ha in 1992.

chete, and in some regions the mice are responsible for infecting the majority of larvae (Mather 1993), which then molt into infected nymphs.

The independent effects of acorn production on density of mice and on distribution of larval ticks result in the coincidence in time and space of peak numbers of parasites and their most reservoir-competent host. We have demonstrated that feeding success of ticks (proportion of the population attached to hosts) is correlated positively with the density of white-footed mice (Ostfeld et al. 1995, in press). Abundant populations of tick larvae in 1992 presumably had an unusually high probability of feeding on a mouse host and thus of acquiring the Lyme disease spirochete. Because nymphs from that generation do not become active until the following spring or summer, we predicted that numbers of infected nymphal ticks would peak in oak habitats two years following peak acorn production (i.e., in 1993). We collected many nymphal ticks from various habitat types in 1993, and we will use long-term monitoring of ticks and mouse density to determine whether their spirochete infection rates are higher than those of tick generations feeding as larvae on sparse populations of mice.

Predicting the effects of mast production on abundance of infected nymphs two years later is made more complex by dispersal patterns of

mice in the patchy mosaic of habitats. The decline in mouse abundance at IES from their peak in August 1992 to their winter-spring low apparently was caused in part by emigration from oak-dominated sites (Ostfeld et al. 1995). Populations of nymphal ticks in shrubby or herbaceous habitat patches near the oak forest matrix were largely imported by mice dispersing from oak habitats (Ostfeld et al. 1995). Thus, because of the high reservoir competence of white-footed mice, these tick populations are expected to have particularly high infection rates. Ongoing studies are testing the effects of habitat patchiness and dispersal on the distribution and infection rates of ticks.

Connections between mice and gypsy moths

The gypsy moth was imported to the northeastern United States in the late nineteenth century as a potential silk producer (Forbush and Fernald 1896). Populations promptly escaped human control and invaded deciduous forests. Gypsy moths are one of the most conspicuous examples of herbivores that undergo outbreaks. Although the caterpillars can consume leaves of many plant species, they show strong preferences for oak leaves (Houston and Valentine 1977). When they reach outbreak levels (densities of more than 1000 egg masses per hectare), gypsy moth larvae often defoliate large expanses of forest and may cause the death of oak trees (Campbell and Valentine 1972). Typically, gypsy moth population dynamics are cyclic, with approximately nine to ten years between peaks (Figure 6).

Several factors appear to be important contributors to the cyclic dynamics of gypsy moth populations. The rapid growth phase from low (fewer than 100 egg masses per hectare) to high (more than 1000 masses per hectare) density is facilitated by the high fecundity of females (several hundred eggs per egg mass), which confers a high intrinsic rate of increase (Jones et al. 1990). Decline from the peak phase is affected by many factors, including food limitation following defolia-

tion; mortality from specialized enemies such as egg and larval parasites, a nuclear polyhedrosis virus, and fungal pathogens (Campbell 1975, Majchrowicz and Yendol 1973); and both immediate and delayed effects of poor maternal condition resulting from consumption of plant defensive chemicals (Rositer 1994). As gypsy moth populations decline from peak densities, defoliation, and hence food limitation, ceases, and negative maternal effects probably relax. The densities of specialist predators and pathogens decline sharply after a time lag because their gypsy moth prey have declined (Campbell 1967). Nevertheless, gypsy moth populations usually do not rebound immediately to high densities; instead, they rebound only after a low-density phase has elapsed. What prevents their immediate recovery?

Our data suggest that a generalized predator, the white-footed mouse, plays a key role in preventing low-density populations of gypsy moths from achieving rapid population growth toward a peak. Mice, as well as other rodents and shrews, eat gypsy moth pupae (Bess et al. 1947). Predation by small mammals may play only a minor role in regulating gypsy moth populations that have already achieved high density, because neither the consumption rates by individual mice and shrews nor the maximal growth rates of their populations are sufficient to keep pace with moth population growth at moderate to high density (Campbell 1967). However, we have found evidence that predation by white-footed mice maintains gypsy moth populations at low density and that when mouse populations collapse, gypsy moths are released from control.

To test the hypothesis that a decrease in mouse density is necessary and sufficient to restore low-density gypsy moth populations to outbreak levels, we performed predation experiments in which freeze-dried gypsy moth pupae were attached with beeswax to small squares of burlap. These pupal panels were placed on oak tree trunks 1.3 m above the ground or at the base of trees (both of which represent sites where natural pupation occurs) dur-

ing the period of natural pupation (late June–early August) at our study sites. Predation pressure on moth pupae was monitored by daily inspection for attack or disappearance. In most cases, we could classify predation as being caused by invertebrates, mice, or nonmouse vertebrates based on the occurrence of various types of damage pattern. Predation by mice was indicated by the presence of specific incisor marks on the wax; insect predation was indicated by the presence of drill holes in the pupal case; and predation by nonmouse vertebrates was suggested by damage without tooth marks. In 1993 and 1994, we introduced 400 and 1368 freeze-dried pupae, respectively, to our IES study site. Mouse density on two 2.25-hectare trapping grids averaged 17.9 mice per ha in July 1993 and 3.1 mice per ha in July 1994 (Figure 7).

In 1993 (a year of moderate mouse density), all of the introduced gypsy moth pupae were destroyed within eight days, and more than 90% of the damage was clearly due to white-footed mice. In 1994 (a year of low mouse density), approximately 50% of introduced pupae persisted after 18 days, and only approximately 20% of the destruction was attributable to mice (Figure 7). We have observed that naturally occurring female gypsy moths at IES typically require 12–16 days of pupation before eclosing to adulthood. Because in 1993 experimental pupae were completely eliminated before eclosion, the white-footed mice appear to have controlled the gypsy moth populations in that year. However, moths may have been released from control in 1994 because of the low pupal predation associated with the low density of white-footed mice. This low predation may have initiated a phase of rapid growth of the gypsy moth population to a peak, which we expect in three to four years due to time delays in population growth. Because population crashes of mice tend to be predictable, often occurring 1.5 years after mast production, it appears that the time of release of gypsy moth populations may be a predictable, indirect consequence of acorn production.

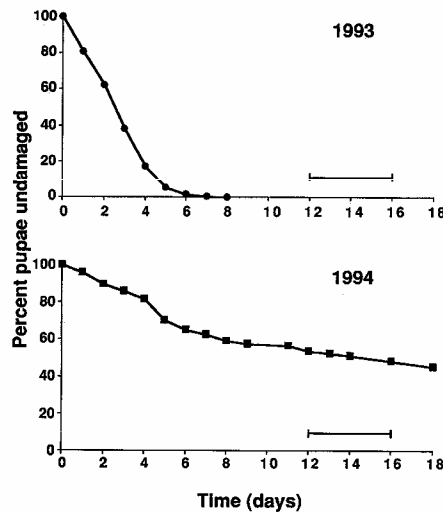


Figure 7. Persistence of freeze-dried gypsy moth pupae during field experiments at the Institute of Ecosystem Studies in 1993 and 1994. Pupae were attached to burlap panels that were placed on tree trunks 1.3 m above the ground. Average density of white-footed mice during the experiments was 17.9/ha in 1993 and 3.1/ha in 1994. Horizontal bar indicates typical onset of gypsy moth female pupal eclosion.

The feedback termini

How might the direct and indirect interactions among species in oak forests impinge on the oak trees at the base of the model (Figure 1)? Recent evidence suggests that oak species have different intrinsic rhythms of mast production that are determined by interactions between cumulative carbon storage and allocation strategies to growth versus reproduction (Sork et al. 1993). Weather patterns that may affect carbon storage appear to alter natural species-specific cycle lengths (Lalonde and Roitberg 1992, Sork et al. 1993). Defoliation of oaks during gypsy moth peaks has a clear effect on carbon balance, such that successive years of defoliation often result in reduced growth and tree death (Campbell and Valentine 1972). Defoliation by gypsy moths may alter the natural cycle of mast production, causing delays in or eliminating mast years (see also Gottschalk 1990). Moreover, because gypsy moth defoliation increases light penetration to the forest understory, results in a flush of understory saplings (Leonard 1981),

and causes death of oaks, we hypothesize that the feedback loop from acorns to mice to gypsy moths to acorn production may change the species composition of the forest.

Another possible feedback pathway in our model, which has not yet been tested, is from acorns to mice and other seed predators to the survival of oak and nonoak seeds to the species composition of regenerating forests. Note that the two feedback pathways share common elements that may affect system behavior (Figure 1). A spatially explicit model of transition oak–northern hardwood forests (SORTIE; Pacala et al. 1993) suggests that forest dynamics depend on demographic processes acting on the various tree species (primarily fecundity of mature trees and growth and mortality rates of immature stages). When rodents reach high densities, they are capable of virtually eliminating seed crops of species such as red maple (*Acer rubrum*; Ostfeld et al. 1994). Therefore, fluctuating rodent densities are expected to cause a periodic failure in recruitment of some non-oak species' seeds to seedlings and saplings, altering the species composition of the forest understory. High densities of deer or concentrated foraging activities can also change the species composition of saplings. Because defoliation, and consequent light penetration to the understory, may be necessary for seedlings to grow fast enough to survive deer browsing, the two feedback pathways interact. In both cases, the strength of the feedback pathway is expected to fluctuate considerably from year to year, even appearing and disappearing repeatedly through time.

Management implications

Our studies of forest dynamics have implications for management. Some forests are used for both recreation (e.g., hiking, bird watching, and deer hunting) and timber harvest. However, the complex interactions we have uncovered suggest that it is likely to be difficult or impossible to manage simultaneously for multiple uses (both recreational and industrial) of the forests.

For instance, timber production

from oaks and aesthetic attractiveness to recreational users could be increased by minimizing gypsy moth outbreaks. Thus, one management strategy might be to provide supplemental food for mouse populations in the postmast year, when mouse populations normally crash, thereby preventing gypsy moth populations from exploding and thus defoliating the forest. But this practice might also increase the risk of tick bites and Lyme disease. The health care costs of Lyme disease are substantial. Moreover, within Lyme disease-endemic areas, the epidemic has resulted in fear and distrust of nature and has decreased enthusiasm for recreational use of the forests (Barbour and Fish 1993). Another outcome of this management strategy might be a reduction in the density of understory seedlings (due to more intense seed predation) and hence forage quality for deer, thus reducing the attractiveness of the forest for hunting. If a single management option cannot simultaneously optimize multiple forest uses, then the set of management outcomes must be prioritized.

Conclusions

Fifteen years of monitoring interactions between mice and acorns and 16 years of studying the dynamics of gypsy moths have led to the conceptual models of direct and indirect interactions in the deciduous forests of the eastern United States. But even with the benefit of these long-term studies, many of the interactions we propose are still tentative and are likely to require considerable additional study. However, we believe we have identified some critical functional linkages in the web of connections that defines these forest ecosystems.

Our studies demonstrate the importance of embedding sets of pairwise interactions into a larger system context. Although the basic pairwise interactions may be predictable (e.g., more acorns consistently lead to more mice), the effects of a pairwise interaction on system behavior depend on other interactions within the system and thus may be unpredictable without a knowledge of system infrastructure.

For instance, a mouse increase during a gypsy moth peak is not likely to prevent defoliation, and thus current mouse density is likely to be essentially irrelevant to tree carbon storage, mastling, and light availability to tree seedlings. But a mouse increase during a gypsy moth nadir may delay or prevent a moth outbreak and avert an effect on acorn production and seedling growth and survival. We believe ecological systems generally are characterized by such contingencies, which may explain contradictory or inconsistent results of field experiments on pairs or small groups of species.

We have now entered the experimental phase of this research, in which we plan to manipulate the abundance of particular key entities (e.g., acorns and mice) and more rigorously test the accuracy of our model. If our conceptual model of the oak forest system is robust, we should be able to understand and predict the system-wide effects of changes in abundance within all of the taxa represented.

Acknowledgments

We gratefully acknowledge the excellent help of our many field assistants at IES and MLBS who have been involved since the inception of this research program. We are indebted to our colleagues Charlie Canham and Gary Lovett for intellectual stimulation. Research was supported by the General Reinsurance Corporation, the Plymouth Hill Foundation, The New York State Department of Environmental Conservation, the US Department of Agriculture Forest Service, the Mary Flagler Cary Charitable Trust, and the National Science Foundation (DEB-9419640). This article is a contribution to the program of the Institute of Ecosystem Studies.

References cited

Barbour AG, Fish D. 1993. The biological and social phenomenon of Lyme disease. *Science* 260: 1610-1616.
Bess HA, Spurr SH, Littlefield EW. 1947. Forest site conditions and the gypsy moth. *Harvard Forest Bulletin* 22: 1-56.
Billick I, Case TJ. 1994. Higher order interactions in ecological communities: what are they and how can they be detected? *Ecology* 75: 1529-1543.

Campbell RW. 1967. The analysis of numerical changes in gypsy moth populations. *Forest Science Monographs* 15: 1-33.
———. 1975. The gypsy moth and its natural enemies. *Agricultural Information Bulletin* 381: 1-27.
Campbell RW, Sloan RJ. 1977. Natural regulation of innocuous gypsy moth populations. *Environmental Entomology* 6: 315-322.
Campbell RW, Valentine HT. 1972. Tree condition and mortality following defoliation by the gypsy moth. USDA Forest Service Research Paper NE-236. Washington (DC): USDA Forest Service.
Connell JH. 1983. On the prevalence and relative importance of interspecific competition: evidence from field experiments. *American Naturalist* 122: 661-696.
deCalesta DS. 1994. Effect of white-tailed deer on songbirds within managed forests in Pennsylvania. *Journal of Wildlife Management* 58: 711-718.
Falco R, Fish D. 1989. Potential for exposure to tick bites in recreational parks in a Lyme disease endemic area. *American Journal of Public Health* 79: 12-15.
Fish D. 1993. Population ecology of *Ixodes dammini*. Pages 25-42 in Ginsberg H, ed. *Ecology and management of Lyme disease*. New Brunswick (NJ): Rutgers University Press.
Forbush EH, Fernald CH. 1896. The gypsy moth. Boston (MA): Wright and Potter.
Gottschalk KW. 1990. Gypsy moth effects on mast production. Pages 42-50 in McGee CE, ed. *Proceedings of the workshop, Southern Appalachian [sic] Mast Management*. Knoxville (TN): University of Tennessee.
Holt RD. 1977. Predation, apparent competition and the structure of prey communities. *Theoretical Population Biology* 12: 197-229.
———. 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124: 377-406.
Houston DA, Valentine HT. 1977. Comparing and predicting forest stand susceptibility to gypsy moth. *Canadian Journal of Forest Research* 7: 447-461.
Hunter MD, Price PW. 1992. Playing chutes and ladders: heterogeneity and the relative roles of bottom-up and top-down forces in natural communities. *Ecology* 73: 724-732.
Janzen DH. 1971. Seed predation by animals. *Annual Review of Ecology and Systematics* 2: 465-492.
Jones CG, Steininger MK, Luciano P, Moore KEB. 1990. Estimating gypsy moth fecundity in the field: a comparison between data from North America and Sardinia (Italy). *Environmental Entomology* 19: 108-110.
Kareiva P. 1994. Higher order interactions as a foil to reductionist ecology. *Ecology* 75: 1527-1528.
Koenig WD, Carmen WJ, Stanback MT, Mumme RL. 1991. Determinants of acorn productivity among five species of oaks in central coastal California. Pages 136-142 in USDA Forest Service Technical Report PSW-126. Washington (DC): USDA Forest Service.
Lalonde RG, Roitberg BD. 1992. On the evolution of masting behavior in trees: predation or weather? *American Naturalist* 139: 1293-1304.

- Lane RS, Piesman J, Burgdorfer W. 1991. Lyme borreliosis: relation of its causative agents to its vectors and hosts in North America and Europe. *Annual Review of Entomology* 36: 587-609.
- Leimgruber P, McShea WJ, Rappole JH. 1994. Predation on artificial nests in large forest blocks. *Journal of Wildlife Management* 58: 254-260.
- Leonard DE. 1981. Bioecology of the gypsy moth. In Doane CC, McManus ML, eds. *The gypsy moth: research toward integrated pest management*. USDA Forest Service 1584. Washington (DC): USDA Forest Service.
- Majchrowicz I, Yendol WG. 1973. Fungi isolated from the gypsy moth. *Journal of Economic Entomology* 66: 823-824.
- Mannelli A, Kitron U, Jones CJ, Slajchert TL. 1993. Role of the eastern chipmunk as a host for immature *Ixodes dammini* (Acari: Ixodidae) in northwestern Illinois. *Journal of Medical Entomology* 30: 87-93.
- Mather TN. 1993. The dynamics of spirochete transmission between ticks and vertebrates. Pages 43-62 in Ginsberg HS, ed. *Ecology and environmental management of Lyme disease*. New Brunswick (NJ): Rutgers University Press.
- McShea WJ, Rappole JH. 1992. White-tailed deer as a keystone species within forest habitats of Virginia. *Virginia Journal of Science* 43: 177-186.
- McShea WJ, Schwede G. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy* 74: 999-1006.
- Menge BA, Sutherland JP. 1976. Species diversity gradients: synthesis of the roles of predation, competition, and temporal heterogeneity. *American Naturalist* 110: 351-369.
- Ostfeld RS, Lewin N, Schnurr J, Canham CD, Pickett STA. 1994. The roles of small rodents in creating patchiness. *Polish Ecological Studies* 20: 265-276.
- Ostfeld RS, Cepeda OM, Hazler KR, Miller MC. 1995. Ecology of Lyme disease: habitat associations of ticks (*Ixodes scapularis*) in a rural landscape. *Ecological Applications* 5: 353-361.
- Ostfeld RS, Hazler KR, Miller MC. In press. Causes and consequences of tick (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy*.
- Pacala SW, Canham CD, Silander JA. 1993. Forest models defined by field measurements: I. The design of a northeastern forest simulator. *Canadian Journal of Forest Research* 23: 1980-1988.
- Pimm SL. 1991. The balance of nature? Ecological issues in the conservation of species and communities. Chicago (IL): University of Chicago Press.
- Pucek Z, Jedrzejewski W, Jedrzejewska B, Pucek M. 1993. Rodent population dynamics in a primeval deciduous forest (Bialowieza National Park) in relation to weather, seed crop, and predation. *Acta Theriologica* 38: 199-232.
- Reitsma LR, Holmes RT, Sherry TW. 1990. Effects of removal of red squirrels, *Tamiasciurus hudsonicus*, and eastern chipmunk, *Tamias striatus*, on nest predation in a northern hardwood forest: an artificial nest experiment. *Oikos* 57: 375-380.
- Rossiter M. 1994. Maternal effects hypothesis of herbivore outbreak. *BioScience* 44: 752-763.
- Schoener TW. 1983. Field experiments on interspecific competition. *American Naturalist* 122: 240-285.
- Sih A, Crowley P, McPeck M, Petranka J, Strohmeier K. 1985. Predation, competition, and prey communities: a review of field experiments. *Annual Review of Ecology and Systematics* 16: 269-311.
- Silvertown JW. 1980. The evolutionary ecology of mast seeding in trees. *Biological Journal of the Linnean Society* 14: 235-250.
- Sork VL, Bramble J, Sexton O. 1993. Ecology of mast-fruiting in three species of North American oaks. *Ecology* 74: 528-541.
- Thurber DK, McClain WR, Whitmore RC. 1994. Indirect effects of gypsy moth defoliation on nest predation. *Journal of Wildlife Management* 58: 493-500.
- Tilghman NG. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *Journal of Wildlife Management* 53: 524-532.
- Van Buskirk J, Ostfeld RS. 1995. Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecological Applications* 5: 1133-1140.
- Wolff JO. 1985. Comparative population ecology of *Peromyscus leucopus* and *Peromyscus maniculatus*. *Canadian Journal of Zoology* 63: 1548-1555.
- _____. In press. Population fluctuations of mast-eating rodents are correlated with acorn production. *Journal of Mammalogy*.
- Wolff JO, Durr DS. 1986. Winter nesting behavior of *Peromyscus leucopus* and *Peromyscus maniculatus*. *Journal of Mammalogy* 67: 409-411.
- Wootton JT. 1993. Indirect effects and habitat use in an intertidal community: interaction chains and interaction modifications. *American Naturalist* 141: 71-89.

BioScience is the monthly magazine for biologists in all fields. It includes articles on research, policy, computers, and education; news features on developments in biology; book reviews; meetings calendar. Published by the American Institute of Biological Sciences, 1444 Eye St. NW, Suite 200, Washington, DC 20005; 202/628-1500. 1996 membership dues, including *BioScience* subscription: Individual \$60.00/year; Student \$35.00/year. 1996 Institutional subscription rates: \$165.00/year (domestic), \$193.00/year (foreign).

**A CORRECTION TO
"OF MICE AND MAST"**

In the recent article "Of Mice and Mast: Ecological connections in eastern deciduous forests" by R. S. Ostfeld, C. G. Jones, and J. O. Wolff (*BioScience* 46: 323-330), the description of sampling methods for gypsy moth pupal predation and the discussion of mouse predation (pp. 327-328) inadvertently omitted two key references (Smith 1985, Yahner and Smith 1991). The authors regret the error. Readers may also be interested in some additional publications on these topics (Cook et al. 1994, 1995, Elkinton et al. 1989, Smith 1989).

CLIVE G. JONES
RICHARD S. OSTFELD
Institute of Ecosystem Studies
Millbrook, NY 12545

JERRY O. WOLFF
Department of Fisheries and Wildlife
Oregon State University
Corvallis, OR 97331
and
US Environmental Protection Agency
Corvallis, OR 97333

References cited

- Cook SP, Hain FP, Smith HR. 1994. Oviposition and pupal survival of gypsy moth (Lepidoptera: Lymantriidae) in Virginia and North Carolina pine-hardwood forests. *Environmental Entomology* 23: 360-366.
- Cook SP, Smith HR, Hain FP, Hastings FL. 1995. Predation of gypsy moth (Lepidoptera: Lymantriidae) pupae by invertebrates at low small mammal population densities. *Environmental Entomology* 24: 1234-1238.
- Elkinton JS, Gould JR, Liebhold AM, Smith HR, Wallner WE. 1989. Are gypsy moth populations in North America regulated at low density? Pages 233-249 in Wallner WE, McManus KA, eds. *Lymantriidae: a comparison of features of New and Old World tussock moths*. Northeastern Forest Experiment Station General Technical Report nr NE-123. Broomall (PA): USDA Forest Service.
- Smith HR. 1985. Wildlife and the gypsy moth. *Wildlife Society Bulletin* 13: 166-174.
- _____. 1989. Predation: its influence on population dynamics and adaptive changes in morphology and behavior of the Lymantriidae. Pages 469-488 in Wallner WE and McManus KA, eds. *Lymantriidae: a comparison of features of New and Old World tussock moths*. Northeastern Forest Experiment Station General Technical Report nr NE-123. Broomall (PA): USDA Forest Service.
- Yahner RH, Smith HR. 1991. Small mammal abundance and habitat relationships on deciduous forest sites with different susceptibility to gypsy moth defoliation. *Environmental Management* 15: 113-120.