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HABITAT HETEROGENEITY, DISPERSAL, AND LOCAL RISK OF EXPOSURE TO LYME DISEASE

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Abstract. Spatial heterogeneity presents a fundamental challenge to conventional ecological theory. Although ecological systems are usually heterogeneous, it is not clear how often heterogeneity fundamentally alters their behavior. We addressed this issue with a study of the infection of ticks (*Ixodes scapularis*) by the causative agent of Lyme disease (the spirochete *Borrelia burgdorferi*) in multiple habitats within a semirural landscape, combining both field and modeling approaches. We sampled the densities and infection prevalences of ticks in five habitats over two years in southeastern New York. There were consistent differences among habitats in adult infection prevalence, which was unrelated to tick density, suggesting that local habitat features exert some control over local risk of exposure to infected ticks. Other results underscored the importance of processes taking place on larger scales. We observed a positive relationship between the change in tick density within a cohort from the nymphal to adult stages, and changes in prevalence over the same period. Habitats with many adults relative to the number of nymphs several months earlier showed increasing prevalence of *B. burgdorferi.* Presumably these habitats were receiving immigrating ticks that became infected on their dispersing hosts.

We designed a computer model, patterned after the life cycle of *I. scapularis,* to determine whether patterns observed in the field could be explained by dispersal among habitats differing in host species composition. The model showed that habitat-related variation in tick density and spirochete prevalence was maintained even with moderate dispersal, as long as the different habitats supported distinct assemblages of hosts. Dispersal produced nonlinear or threshold responses under many conditions, due to positive and negative feedbacks. Such feedback is a general feature of many ecological systems, which implies that the behavior of heterogeneous systems will very often be unpredictable from an understanding of isolated components.

Key words: Borrelia; *disease; dispersal; habitat heterogeneity; host-parasite model;* Ixodes; *landscape ecology; Lyme disease; New York, USA;* Peromyscus leucopus; *simulation model; ticks.*

INTRODUCTION

Classic ecological theory assumes spatial homogeneity to ensure analytical simplicity and broad applicability, and for most of the history of modern ecology simple models have profoundly influenced the way ecologists think about natural systems (MacArthur 1972, Kingsland 1985). Recently, the discovery of important spatial variation in ecological processes has been forcing a close inspection of the assumption of spatial homogeneity that forms the theoretical and conceptual basis for much of ecology (Turner 1989, Levin 1992, Pickett et al. 1997). It is not yet clear whether spatial heterogeneity will require a revision of theory, but the question of whether the dynamics of complex systems can be understood by studying the behavior of their component parts is of broad importance in many areas of ecology (e.g., Vandermeer 1969, Levin 1992, Pickett and Cadenasso 1995). In landscape ecology, the issue is whether the behavior of a spatially heterogeneous system can be approximated by combining the behavior of separate regions, or whether ecological processes exert fundamentally different effects when they take place in a heterogeneous context. We have addressed this issue with a study of tick density, infection, and Lyme disease risk in habitats having different ecological properties. We focus on two questions: (1) is the local risk of exposure to Lyme disease determined primarily by local process?, and if not (2) can one predict local disease risk by studying each of the nearby habitats and combining the results?

The Lyme disease system may be especially likely to exhibit unexpected ''emergent properties'' in a landscape context because the biological interactions involved are complex and take place on a variety of spatial scales. Lyme disease is caused by the spirochete *Borrelia burgdorferi*, and exists naturally in North America in an enzootic cycle involving black-legged ticks, *Ixodes scapularis* (formerly *I. dammini*), and their vertebrate hosts. Juvenile ticks feed on small mammals, birds, and reptiles, while adult ticks typically feed on white-tailed deer, *Odocoileus virginianus.*

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Each tick parasitizes three different hosts during its complete life cycle (one each for the larval, nymphal, and adult stages), which requires at least 2 yr to complete. Infection of humans usually results from blood meals taken by nymphs, because at this stage the ticks are small and difficult to see, and their peak questing period in early summer coincides with human outdoor activity (Falco and Fish 1989, Barbour and Fish 1993).

The majority of dispersal by *Ixodes* ticks takes place while feeding on a host, because free-ranging ticks can move only a few meters at best (Falco and Fish 1991, Carroll and Schmidtmann 1996). The dispersal capabilities of the vertebrates that are parasitized by ticks differ considerably, both among the various hosts used by juveniles and between hosts used by juvenile vs. adult ticks (M'Closkey and Lajoie 1975, Gaines and McClenaghan 1980). This suggests that the scale of tick movement will be sensitive to the choice of hosts and the life stage of the tick. For example, white-footed mice, *Peromyscus leucopus,* the most common host for juvenile *I. scapularis,* move considerably shorter distances and are more restricted in their habitat distribution than the much larger deer parasitized by adult ticks. Thus, we anticipate that most movement among habitats occurs in the adult stage, but this expectation may not be upheld if juvenile ticks feed on more mobile hosts such as songbirds or medium-sized mammals, or if habitats occur in small, closely adjacent patches.

What factors account for spatial variation in the risk of contracting Lyme disease? In Lyme disease endemic areas of New England and the midwestern United States, there exists enormous variation among habitats in the abundance of vertebrates that serve as hosts for ticks (Anthony et al. 1981, Wilson et al. 1988*a*), and in the density of questing ticks themselves (Maupin et al. 1991, Stafford and Magnarelli 1993, Ostfeld et al. 1995). These observations imply that the risk to humans of encountering ticks and contracting Lyme disease also varies across the landscape. From the standpoint of human health, the importance of spatial variation could be addressed empirically by sampling tick density and spirochete prevalence, and issuing recommendations concerning habitats that should be avoided by people. More generally, though, we would like to understand how ecological processes and landscape features interact to generate spatial variation in disease risk. Results that have been derived theoretically may suggest ways in which the architecture of a landscape could be modified to minimize disease exposure in areas occupied by humans, and will be of general interest to landscape ecologists. In this study, we begin by reporting results from a field sampling program to illustrate the extent of spatial variation in the density of ticks and prevalence of *B. burgdorferi* in a semirural landscape. We then present a model of tick population dynamics, incorporating multiple habitats and dispersal of ticks on vertebrate hosts, to explore the processes that give rise to uneven landscape-level patterns of tick density and infection. Throughout the paper we assume that the risk of exposure to Lyme disease within a habitat is proportional to the density of infected questing nymphs in that habitat (Mather 1993), since most cases result from parasitism by nymphal *I. scapularis* (Barbour and Fish 1993).

Field Studies

We established a field sampling program to determine the distribution of ticks among habitats and the prevalence of *Borrelia burgdorferi* infection within ticks. Earlier results for *Ixodes scapularis,* obtained by sampling ticks either questing for hosts or already attached to hosts, suggest that ticks are unevenly distributed among habitats (e.g., Wilson et al. 1988*a*, Ostfeld et al. 1995). Data on spatial variation in prevalence are scarce (Telford et al. 1992), so we designed a sampling protocol to address the question of whether patterns of abundance and infection within habitats are determined primarily by local processes, or whether host movement from other habitats must also be considered.

Field methods

We sampled the *Borrelia*-infection prevalence of *I. scapularis* in five habitat types at the Institute of Ecosystem Studies (IES) in Dutchess County, southeastern New York (41°50′ N, 73°45′ W). The landscape at IES consists of a matrix of oak- and maple-dominated forest within which are embedded relatively small patches of other forest types and old fields. The patches vary in size from ~0.5 ha for some old-field types, to ~75 ha for patches of oak forest. The size and juxtaposition of patches within this landscape mosaic afford mobile vertebrates relatively easy access to several potential destinations during dispersal events, yet are orders of magnitude larger than the dispersal distances of ticks.

Five habitat types were chosen to represent some of the most common distinct plant communities in rural southeastern New York and much of the northeastern United States. The dominant canopy trees in the oak habitat type were 80–130-yr-old chestnut oaks (*Quercus prinus*) and red oaks (*Q. rubra*). Both oak species, as well as sugar maple (*Acer saccharum*) and eastern hemlock (*Tsuga canadensis*), were common in sapling and understory layers. The maple habitat type consisted of young (60–80 yr old), relatively even-aged stands of sugar maple, which had developed following abandonment of cultivated fields. The dogwood and bluestem habitat types were both old fields ~40–60 yr old (Glitzenstein et al. 1990). The dogwood habitat consisted of dense thickets of gray dogwood (*Cornus racemosa*), whereas the bluestem habitat, which occurred on somewhat drier sites, was dominated by little bluestem grass (*Schizachyrium scoparium*). The hayfield habitat type consisted of lowland fields abandoned from corn cultivation 15–20 yr ago (Glitzenstein et al.

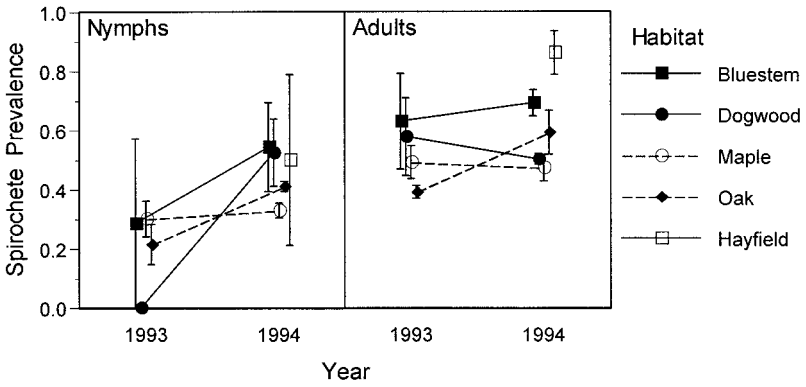

FIG. 1. The proportion of nymphal and adult *Ixodes scapularis* ticks infected with *Borrelia burgdorferi* spirochetes in five habitat types at the Institute of Ecosystem Studies, New York. Each point shows the mean ± 1 SE of three replicate plots. The figure is based on analysis of 1892 individual ticks, including 1362 nymphs (sample sizes by habitat, in 1993/1994: bluestem, 8 infected/31 nymphs; dogwood, 1/40; maple, 77/821; oak, 61/299; hayfield, 0/4) and 530 adults (bluestem, 21/83; dogwood, 28/80; maple, 61/97; oak, 57/109; hayfield, 0/14).

1990) that have been managed since then as hayfields with annual or biannual mowing.

We collected ticks at three replicate sites in each habitat type in 1993 and 1994; three samples occurred during the peak of nymphal activity (10 June–15 July), and two samples were during the fall activity period of adults (10–31 October). Replicates of any given habitat type were separated by 100–2500 m. At each site we established a set of parallel line transects totaling 400 m. Transects were 10 m apart and varied from 40 to 100 m in length. We used a standard drag-sampling technique (e.g., Falco and Fish 1992) to determine the density of ticks among habitat types and to collect ticks for determination of spirochete prevalence. The drag-sampling method has been demonstrated to be both reliable and efficient in censusing *I. scapularis* (Falco and Fish 1992), and to minimize biases among habitat types in sampling effectiveness (Ostfeld et al. 1995). We constructed a drag cloth from a $1-m^2$ piece of white corduroy cloth sewn at one end to a wooden dowel for support and pressed down at the opposite, free end by gravity acting on small lead weights sewn into the cloth. The cloth was dragged the length of each transect, held as close to the ground as possible. We stopped to examine the cloth every 20 m, and all ticks were removed with fine forceps and either maintained alive until dissection, or preserved in 70% ethanol for later identification.

Nymphal and adult ticks were examined for the presence of *Borrelia burgdorferi* using immunofluorescence microscopy. Ticks were washed once in 70% ethanol and twice in deionized water, placed in an Eppendorf tube, and ground in phosphate buffered saline (PBS). Three 5-mL aliquots of tick suspension were placed in separate wells in multiwell slides, air-dried, and fixed in cold acetone for 10 min. Fluorescent rabbit anti-*Borrelia* conjugate was added to wells and incubated for 45 min at 37°C. Slides were then washed in PBS, dried, and placed in fluorescent-antibody mounting medium. We examined the slides under an Olympus BH-2 binocular microscope. If spirochetes were not detected immediately, the three wells per individual tick were examined systematically. Each individual tick was categorized as positive or negative for *B. burgdorferi*.

We used analysis of variance to test whether the proportion of nymphs and adults that were infected varied among habitats and between years. A repeated-measures design was not possible because four of the 12 sites sampled in 1993 were replaced in 1994 by other sites within the same habitat. Our approach therefore treated the annual samples as independent observations, which was not strictly true. We do not consider this a problem because we are not using the data to test rigorous hypotheses, but instead to provide an indication of how strongly prevalence varies among habitats. Proportions were arcsine square-root transformed before analysis.

Data on the density of ticks in our study area have been reported elsewhere (Ostfeld et al. 1995, 1996*a*). We used data from these sources to ask whether tick density was associated with disease prevalence within habitats.

Field results: variation among habitats in spirochete prevalence

The prevalence of *B. burgdorferi* in adult ticks (40–80%) was generally higher than that in nymphs (0–50%, Fig. 1). This is typically the case, because adult ticks have parasitized at least two hosts and therefore have experienced twice as many opportunities to become infected as have nymphs. The spirochete prevalence within nymphs increased from 1993 to 1994, but did not differ among habitats (Fig. 1, Table 1). Adult prevalence varied significantly among habitats but did not change between years. In general, adult ticks in the bluestem habitat had high prevalence of *Borrelia* infection in both years (Fig. 1), although their

TABLE 1. Analyses of variance for differences among years (1993 and 1994) and habitats (five vegetation types) in the proportion of nymphal and adult *Ixodes scapularis* infected with *Borrelia burgdorferi*. The analysis treats each year–habitat combination as an independent observation.

Source of variation	df	MS	*F*	*P*	% variance explained
Response: prevalence of infection in nymphs					
Year	1	0.625	4.90	0.0427	18.5
Habitat	4	0.027	0.21	0.9270	3.2
Year × Habitat	3	0.109	0.86	0.4855	9.7
Error	23	0.127			68.6
Response: prevalence of infection in adults					
Year	1	0.009	0.28	0.6024	0.8
Habitat	4	0.132	4.34	0.0125	48.6
Year × Habitat	3	0.023	0.77	0.5280	6.4
Error	18	0.031			44.2

population densities were consistently low (Ostfeld et al. 1996*a*). The adult prevalence in the maple habitat was relatively low, although tick densities were high (Ostfeld et al. 1996*a*). Nearly half of the variation in adult prevalence was attributable to differences among habitats, and most of the remainder was due to variation among sampling sites within habitats (Table 1). Of course, these analyses are insensitive to small-scale spatial variation in prevalence within habitats (Ostfeld et al. 1996*a*).

There was a positive relationship between the change in prevalence within habitats, occurring between nymphal and adult stages from the same cohort, and the change in tick density during the same period (Fig. 2), suggesting that dispersal among habitats may influence prevalence within habitats. The data for nymphal infection and density came from three sampling periods between mid-June and mid-July, when nymphs were most abundant. The data for adult infection and density came from two sampling periods shortly after nymphs had molted into the adult stage, in mid- and late October.

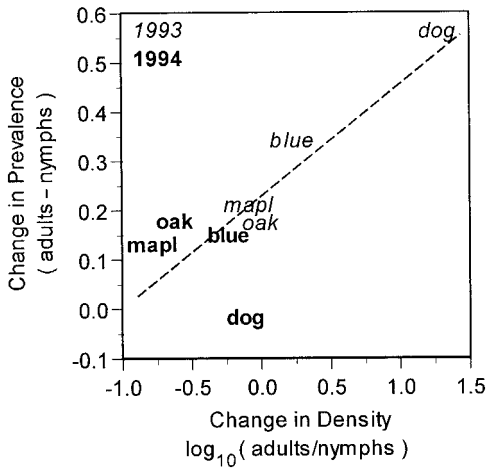

FIG. 2. Changes in the infection prevalence and density of *Ixodes scapularis* between the nymphal stage and adult stage, for four habitat types sampled over two years at the Institute of Ecosystem Studies, New York (1993 = italicized, 1994 = boldface; blue = bluestem, dog = dogwood, mapl = maple). Density is the average number of ticks per 400-m transect (three replicates in each habitat type; Ostfeld et al. 1996*a*). Prevalence is the proportion of ticks infected with *Borrelia burgdorferi*. Increases in density between nymphal and adults stages (presumably due to immigration) were accompanied by relatively large increases in prevalence (r_s = 0.81, P = 0.0149).

In bluestem and dogwood habitats during 1993, the density of adult *Ixodes* was higher than the density of nymphs several months earlier (Fig. 2), even though juvenile ticks undergo high mortality rates (Fish 1993). At least three processes could account for this result. It is possible that our drag cloth undersampled nymphs relative to adults, but data from earlier studies and other habitats suggest that this bias is small (Maupin et al. 1991, Falco and Fish 1992, Ostfeld et al. 1995). Second, perhaps uninfected ticks experienced lower survival than infected ticks within certain habitats in certain years, but this too seems unlikely because there is no evidence that tick survival is associated with infection status. Third, it is possible that nymphal ticks moved into the dogwood and bluestem habitats as their hosts dispersed out of other nearby habitats, causing an increase in adult density when they molted into the adult stage. This hypothesis is supported by long-term population data on *Peromyscus leucopus* at the Institute of Ecosystem Studies (Ostfeld et al. 1996*b*). Densities of white-footed mice in forested habitats during the summer of 1993 were high relative to the most important food source (acorns), so many mice presumably dispersed out of forests and into other habitats. During 1994 mouse numbers were low (Ostfeld et al. 1996*b*), which corresponds well with our lack of evidence for immigration and decreased nymph-to-adult survival in all habitats (Fig. 2). In any case, as ticks dispersed into the dogwood and bluestem habitats in 1993, there were associated increases in spirochete prevalence within adults compared with the nymphal cohort from which they molted (Fig. 2). Rising prevalences are consistent with the hypothesis that ticks moved while parasitizing mice, because *P. leucopus* has the highest reservoir competence of any host used regularly by *I. scapularis* (Mather et al. 1989).

These results, together with our earlier work (Ostfeld et al. 1995, 1996*a*), support two conclusions. First, tick densities and adult infection prevalence varied significantly among habitats, and there was no obvious relationship between the two. Second, both densities and prevalences appeared to change dramatically within habitats between nymphal and adult stages, and the pattern of change suggested that the underlying mechanism may involve tick dispersal upon vertebrate hosts. Both conclusions highlight the importance of landscape structure and dispersal dynamics for *I. scapularis* populations and Lyme disease exposure, and they formed the backdrop against which we designed our tick population model.

Modeling Studies

Earlier ecological models of tick population dynamics assume spatial homogeneity (Mount and Haile 1989, Mount et al. 1991, Porco 1991, Awerbuch and Sandberg 1995, Van Buskirk and Ostfeld 1995), although field data suggest that neither ticks nor their hosts are distributed homogeneously among habitats. In our study area juvenile and adult stages of *Ixodes scapularis* are unevenly distributed among habitats (Ostfeld et al. 1995), and the proportions of adult ticks infected with *Borrelia burgdorferi* varied among habitats (Fig. 1). Although the abundance of *I. scapularis* is sometimes related to local host densities (Maupin et al. 1991, Ostfeld et al. 1995, 1996*b*), there is no known stable relationship between the availability of vertebrate hosts for ticks in a particular habitat and the density and spirochete prevalence of the ticks. The goal of our modeling was to ask whether variation in density and species composition of vertebrates among habitats, coupled with dispersal by vertebrates, might lead to the sorts of patterns we have observed in the field. More generally, we were interested in exploring how heterogeneous components of a landscape combine to determine local ecological patterns.

Model of tick population dynamics

We begin with a computer model of a tick population infected with *B. burgdorferi* (Van Buskirk and Ostfeld 1995), and introduce multiple habitat types, which can support different densities and species compositions of vertebrate hosts. Within each habitat type, tick population dynamics were as described in Van Buskirk and Ostfeld (1995), except that individuals moved among habitats if their hosts dispersed (Fig. 3). Our analyses focus on the consequences of dispersal among habitats for the dynamics and proportion of infection of ticks within each habitat type.

The model tracks infected and uninfected individuals for each of the three stages of the *I. scapularis* life cycle. We designate the densities (number per hectare) of female ticks within the three stadia by the letters *L*, *N*, and *A*, corresponding to larvae, nymphs, and adults. Infected and uninfected populations within each stage

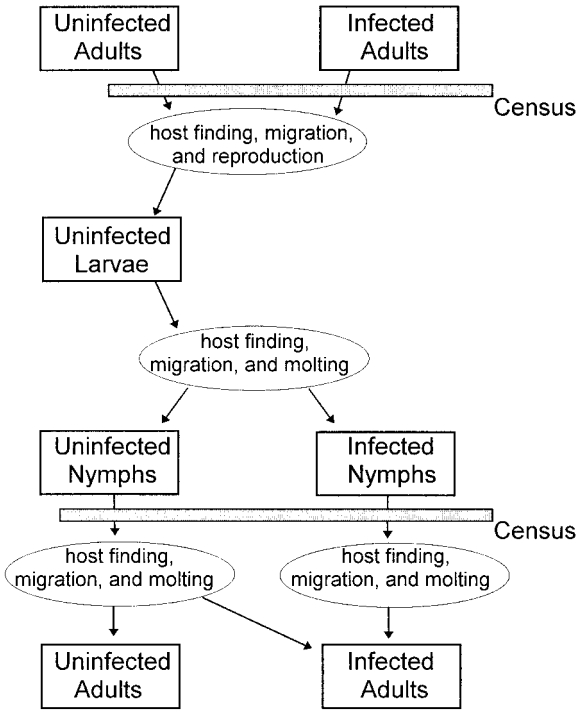

FIG. 3. Flow chart for the Lyme disease model with dispersal among habitats. A full generation takes 2 yr to complete, but the program counts nymphs and adults in every year.

are represented by *u* and *i* following the capitalized stage designation. The model is written as follows:

$$L_{t+1} = fR(Au_t + Ai_t) \quad (1)$$

$$Nu_{t+1} = sPL_{t+1}(1 - c) \quad (2)$$

$$Ni_{t+1} = sPL_{t+1}c \quad (3)$$

$$Au_{t+1} = sPNu_t(1 - c) \quad (4)$$

$$A_{t+1} = sP(Ni_t + cNu_t) \quad (5)$$

where *f* represents the survival and fecundity of adult females, *s* is the annual survival of ticks, and *c* is the reservoir competence of vertebrate hosts. Subscripts refer to time steps of 1 yr. The model reflects the 2-yr life cycle of *I. scapularis* in nature, because nymphs are produced from larvae without changing the value of *t*. Densities of nymphs and adults are counted during each year as the ticks are questing for hosts (Fig. 3).

The density of larvae depends on the product of adult tick density during the previous year, the proportion that locate a host (*R*), and the fecundity of engorged adults (*f*, which incorporates adult and egg survival as well as the number of eggs produced by an average female). The probability of locating a host depends on deer density according to an exponential function:

$$R = 1 - \exp(-\delta D) \quad (6)$$

where *D* is the density of hosts for adults (deer), and

δ is a constant that determines the efficiency of host-finding. The shape of this function and the value of the constant δ have not been estimated for *I. scapularis,* although there is evidence from other tick species that host-finding depends on host density (e.g., Smart and Caccamise 1988). We introduced competition among ticks for access to hosts by imposing a limit to the number of ticks that could be supported by each individual adult deer during one year. Thus, we used Eq. 6 as long as the number of ticks per deer did not exceed the limit $k_a = 1000$ adult ticks/host, and assumed that all hosts were saturated with ticks otherwise. The importance of density-dependent interference among feeding ticks or host immune responses in nature is not clear (Brown 1988, Davidar et al. 1989, Randolph 1994, Hazler and Ostfeld 1995), but it certainly represents one of the more likely sources of population regulation in the life cycle (Randolph 1979).

The production of nymphal ticks (Eqs. 2 and 3) depends on the density of larvae, their probability of locating a host (P), and their density-independent survival (s).

The density of adults (Eqs. 4 and 5) depends on the density of nymphs during the previous year, their probability of locating a host (P), and their survival (s). For both larval and nymphal ticks the probability of locating a host is an exponential function of the summed densities of all potential host species within the habitat

$$P = 1 - \exp\left(-\eta \sum^{n} H\right) \tag{7}$$

where H is the density (number per hectare) of the hosts parasitized by juvenile *Ixodes*, n is the number of host species available to juveniles, and η is a constant reflecting the efficiency of host-finding. We imposed a ceiling on the potential number of ticks that could be supported by each host, by using Eq. 7 when the number of ticks per host was less than $k_j = 200$ juvenile ticks/host, and assuming that all hosts were saturated otherwise.

We used published data to select values for survival ($s = 0.15$; Fish 1993), fecundity ($f = 600$ female larvae/female, including 50% mortality and an average clutch size of 2400; Daniels and Falco 1989, Fish 1993), and the relative numbers of ticks supported by deer and small vertebrates (Piesman et al. 1979, Levine et al. 1985, Fish and Daniels 1990, Wilson et al. 1990). Adjusting fecundity and survival had a quantitative but no qualitative impact on the results.

We define the reservoir competence of hosts as $c = \gamma r$, the product of the proportion of hosts that is infected with spirochetes (γ) and the proportion of uninfected juvenile ticks that becomes infected when they parasitize an infected host (the transmission rate, r). The reservoir competence of deer is irrelevant to the dynamics of Lyme disease, because adult ticks do not seek another host after parasitizing a deer, and do not transmit *B. burgdorferi* to larval ticks. Reservoir competence of hosts for juvenile ticks varies among seasons and years, owing in part to a positive feedback loop between tick infection and *B. burgdorferi* prevalence in hosts. Increasing numbers of juvenile ticks become infected as the incidence of spirochetes in the host population increases, which in turn allows the spirochete to be transmitted to an increasing number of hosts (Mather 1993, Tälleklint et al. 1993). Our model incorporates this mechanism because the prevalence within juvenile hosts increases with the density of infected nymphs:

$$\gamma = 1 - \exp(-\varepsilon N i_{t-1}), \tag{8}$$

where Ni_{t-1} is the density of infected nymphs in the previous generation, and ε is a constant that controls the efficiency of the feedback process.

Dispersal among habitats takes place while ticks are parasitizing a host. The model contains parameters that control both the proportion of hosts that disperses out of each habitat per year, and the proportion of dispersing hosts that enters each habitat. After all successful ticks have attached to their hosts, those ticks that have found a host enter a pool of dispersing individuals if their host is chosen to enter that pool. The fraction of ticks that disperses is identical to the fraction of hosts that disperses, since we assume that dispersing hosts are an unbiased sample of the host population with respect to tick burden. Ticks drop off their hosts only after entering a new habitat. Although vertebrate hosts move among habitats in this model, and tick densities can be dramatically altered by dispersal, the density of hosts is assumed to be an unchanging characteristic of a habitat that is not affected by dispersal (i.e., net movement of hosts balances over the course of 1 yr).

Our analyses focus on the responses of ticks to three kinds of variation among habitats and dispersal schedules: (1) variation in host density and reservoir competence, (2) variation in dispersal rate, and (3) variation in the age at which dispersal takes place. Habitats in natural landscapes often differ in the density and species composition of vertebrates they support, creating variation in the availability of hosts for ticks and the competence of vertebrate reservoirs for *B. burgdorferi.* We manipulated host density and reservoir competence in our model to explore the consequences of this variation. Likewise, we manipulated dispersal rate to investigate the effect of patch size and proximity of habitats in the landscape, under the assumption that dispersal among habitats occurs at high rates when patch sizes are small and closely adjacent. We assessed the impact of tick dispersal in both adult and juvenile stages because the vertebrate hosts of the different stadia display differing propensities to disperse. In all cases we were interested in responses in the density of infected nymphs, which we interpret as a measure of

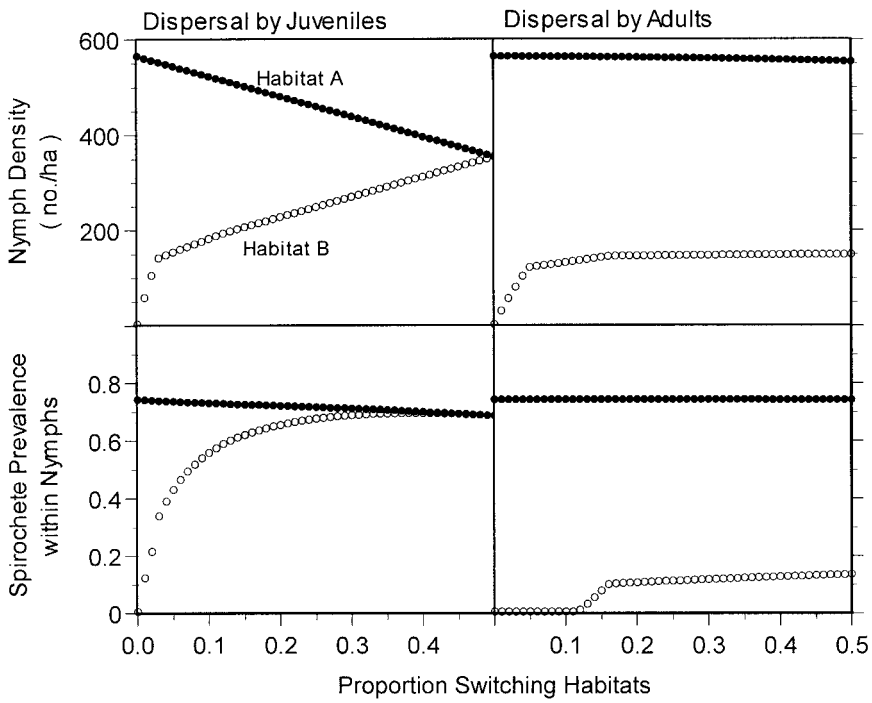

FIG. 4. Impact of dispersal by juvenile and adult ticks on the equilibrium density and infection prevalence of nymphs when habitats differ in density of hosts for juveniles. Habitat A contains 20 hosts/ha for juvenile ticks and 5 hosts/ha for adults; habitat B host densities are 5 individuals/ha for both juveniles and adults. Each point represents the results of a single simulation. A small amount of juvenile dispersal established a population of highly infected ticks in the less favorable habitat, whereas only high levels of dispersal by adult ticks established a population of infected ticks, and prevalence was always much lower.

the risk to humans of exposure to *B. burgdorferi* (Mather 1993).

Modeling results

First we describe the general behavior of the system when two habitats exist; then we analyze a model system patterned after the habitats on our study area, to determine what mechanisms are needed to produce the patterns we observed in the field.

Two habitat types.—We began with a system of two habitats to explore the impact of variation in habitat quality and dispersal in the simplest case. One habitat (habitat A) was always established to be favorable for maintaining a highly infected tick population, due to its high densities of hosts (20 hosts/ha for juveniles, 5 hosts/ha for adults; Van Buskirk and Ostfeld 1995) and high reservoir competence of hosts for juveniles (transmission rate, $r = 0.75$). Figs. 4–6 show the impact of dispersal when the second habitat (habitat B) was of lesser quality, either because of its low host densities or low reservoir competence of hosts.

When habitat B had too few hosts for juveniles to support an *Ixodes* population (5 hosts/ha), symmetrical dispersal between habitats strongly affected tick density and spirochete prevalence (Fig. 4). A dispersal rate of only ~2%/yr was sufficient to establish a tick population in habitat B, but the impact of higher dispersal levels depended on which hosts were moving. When juveniles dispersed, high rates of larval movement while attached to their hosts effectively homogenized densities in the two habitats. Prevalence in habitat B also climbed rapidly under juvenile dispersal due to the positive feedback involving tick density, *B. burgdorferi* incidence in hosts, and tick infection (Eq. 8). However, when tick dispersal took place only during the adult stage (on deer), the maximum nymph density that could be supported in Habitat B was constrained by the limited availability of hosts for larval ticks. At high adult dispersal rates, many eggs were produced in habitat B but relatively few larvae located a host, so the density of questing nymphs was held to ~30% of that in habitat A. Likewise, spirochete prevalence in habitat B remained low in spite of high adult dispersal, because densities of juvenile ticks were never sufficient to support high levels of *B. burgdorferi.*

When habitat B had too few adult hosts to support an *Ixodes* population (1 host/ha), a very low level of dispersal by either juveniles or adults had a dramatic impact on tick density and spirochete prevalence in habitat B (Fig. 5). Even if only 2–3% of hosts switched habitats each year, densities and prevalences in habitat B rose rapidly to levels similar to those found in habitat A. This pattern occurred in spite of the difficulty experienced by adults in locating deer in habitat B. Al-

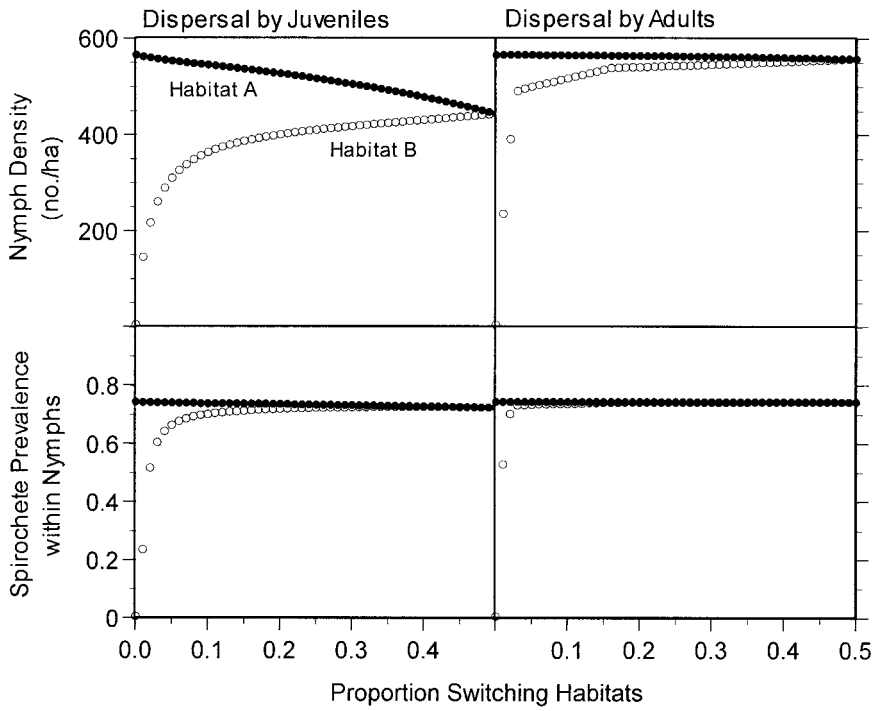

FIG. 5. Impact of dispersal by juvenile and adult ticks on the equilibrium density and prevalence of *Borrelia burgdorferi* within nymphs when habitats differ in density of hosts for adults. Habitat A contains 20 hosts/ha for juvenile ticks and 5 hosts/ha for adults; habitat B host densities are 20 individuals/ha for juveniles and 1 individual/ha for adults. A small amount of dispersal by juveniles or adults established a dense population of highly infected ticks in the less favorable habitat.

though they were unable to complete their entire life cycle because of the scarcity of deer, adult ticks entering habitat B on dispersing deer reproduced normally and their offspring found hosts effectively during the juvenile stages.

The impact of dispersal was less dramatic, and less likely to produce threshold effects, when the two habitats had identical host densities but differed in the reservoir competence of hosts. We explored the situation in which hosts for juvenile ticks in habitat B were only 10% as capable of transmitting *B. burgdorferi* to uninfected ticks as they were in habitat A (Fig. 6). Densities of ticks in the two habitats were identical and unaffected by symmetrical dispersal. Movement of juveniles introduced some spirochetes into habitat B, but *B. burgdorferi* did not become established there in an enzootic cycle, and most infected ticks recorded there had immigrated from habitat A. *Borrelia* did not occur in habitat B when only adults dispersed because the immigrants produced eggs that were free of infection.

Four habitat types.—The preceding results illustrate general dynamical features of a tick population in an environment with habitat structure, but they do not provide an explanation for the habitat-related patterns of density and prevalence we have observed in the field (Figs. 1 and 2; Ostfeld at al. 1995, 1996*a*). We therefore explored a model system of four habitat types to discover what circumstances are necessary to produce the two patterns we noted earlier (see *Field studies: Field results*): (1) independent variation of density and infection across habitats, and (2) correlated changes in the density and spirochete prevalence of successive stages within the same cohort. We selected host densities so that one or two habitats acted as sources of dispersing individuals and the others acted as sinks, to simulate the dispersal process we hypothesize was taking place in our study area. The model was capable of reproducing the observed patterns under a wide range of conditions.

Variation among the four habitats in host density and reservoir competence led to habitat differences in tick abundance and infection that persisted in spite of moderate, symmetrical dispersal (Fig. 7). Regardless of the exact values of the parameters, the density of nymphs was always related to the availability of hosts for juveniles, whereas the prevalence of *B. burgdorferi* depended more closely on the local average reservoir competence. Fig. 7 depicts a case in which the density of hosts and their reservoir competence were negatively related across habitats, illustrating that tick density and disease prevalence need not increase in tandem. This result closely matches the first pattern we observed in our field survey.

The impact of dispersal among the four habitats depended strongly on which life stage was moving (Fig. 7). When ticks dispersed on their juvenile hosts the effect was to homogenize densities across habitats, as was true for the two-habitat case discussed earlier

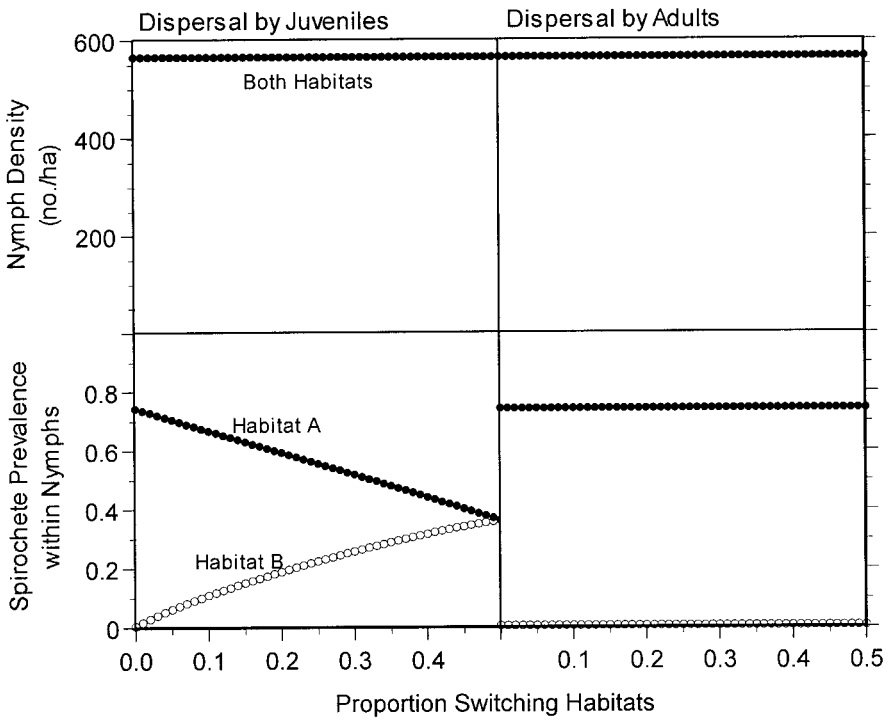

FIG. 6. Impact of dispersal by juvenile and adult ticks on the equilibrium density and infection prevalence of nymphs when habitats differ in the reservoir competence of hosts for juveniles. Both habitats contain identical host densities (20 individuals/ha for juveniles and 5 individuals/ha for adults), but the transmission rate (r) from hosts to juvenile ticks is 0.75 in Habitat A and 0.075 in Habitat B. In general, dispersal by nymphs evenly mixed the ticks in the two habitats and gradually introduced spirochetes into the less favorable habitat. Dispersal by adults alone could not establish Lyme disease in a habitat in which juvenile hosts have low reservoir competence.

(Figs. 4 and 5). Moderate levels of dispersal tended to decrease prevalence in the habitat with the highest incidence of *B. burgdorferi* infection (habitat C), because infected ticks were being exported and uninfected ticks were moving in from other habitats. At the same time, dispersal initially increased the spirochete prevalence in the habitat with the lowest density (habitat D), simply due to immigration of infected larvae from habitat C. Very high levels of juvenile dispersal eliminated *B. burgdorferi* from the system, because all habitats were heavily influenced by the influx of ticks riding hosts with low reservoir competence from the two high-density patches.

The system of four habitats behaved quite differently when dispersal occurred during the adult stage (Fig. 7, right side). There was almost no impact on nymph density, which is regulated primarily by availability of hosts for larvae. The infection rate in habitat C, which had the highest prevalence of *B. burgdorferi* under all conditions, showed a slight decrease under low dispersal rates in response to an increasing number of ovipositing females moving in from more crowded habitats. The uninfected offspring produced by these females claimed a larger fraction of available hosts, interfering with the ability of infected nymphs to find hosts and transmit spirochetes. This sort of interference among juvenile stages is not known to occur in nature, except perhaps through immune responses of hosts to the early summer cohort of larvae. Tick density in the habitat with the fewest hosts for juveniles (habitat D) climbed slightly under very high dispersal rates, and that increase in density allowed *B. burgdorferi* to become established in an enzootic cycle.

The general lesson from Fig. 7 is that both *Ixodes* density and the proportion of ticks infected can vary dramatically among habitats, and the most crowded habitats do not necessarily support the largest number of infected ticks. This pattern occurred whenever there was a negative correlation across habitats between the density of hosts for juveniles and their reservoir competence.

When we introduced asymmetric dispersal the model also reproduced the second pattern we noted in the field (Fig. 2). Within habitats that served as sinks for dispersing juveniles, changes in *Ixodes* prevalence between the nymphal and adult stage of a cohort were positively correlated with the change in density over the same period (Fig. 8). All four habitats in Fig. 8 had identical densities of hosts for adult ticks (5 individuals/ha), but the three ''sink habitats'' had substantially fewer hosts for juveniles than the ''source habitat'' (5 vs. 30 individuals/ha). The sink habitats differed in the extent to which they attracted dispersing ticks: the habitat to the lower left had the lowest immigration rate,

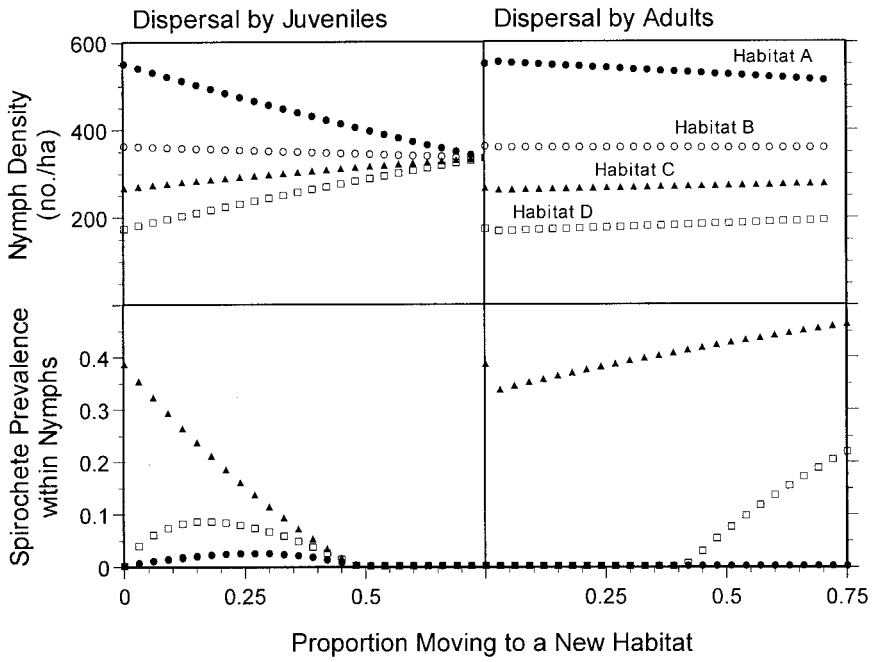

FIG. 7. Impact of dispersal on equilibrium densities and infection prevalence of nymphs in an environment with four kinds of habitats having different host compositions. The habitats with the lowest densities of hosts for juvenile ticks also have hosts with the highest reservoir competence. The densities of hosts for juveniles and transmission rates (r) in the four habitats are: 30 hosts, $r = 0.05$ (habitat A); 20 hosts, $r = 0.10$ (habitat B); 15 hosts, $r = 0.75$ (habitat C); 10 hosts, $r = 0.75$ (habitat D). Tick density and the prevalence of *Borrelia burgdorferi* varied independently in this system, and habitat-related variation in density and prevalence was maintained even in the face of moderate dispersal.

and therefore experienced the greatest reduction in density between nymphal and adult stages. Positive correlations among sink habitats such as that in Fig. 8 were a universal outcome of simulations in which there was asymmetric dispersal, the source habitat had host species with relatively high reservoir competence, and sink habitats differed slightly in their immigration rates. In all simulations the source habitat lost numerous ticks between nymphal and adult stages, but it always had fairly high spirochete prevalence, which was higher in adults than in nymphs (Fig. 8).

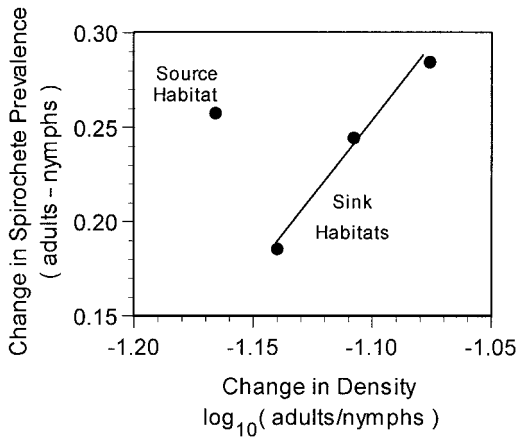

FIG. 8. Changes in the prevalence of infection and density of ticks between the nymphal stage and adult stage, for a model system of four habitats in which all dispersing individuals originate from a single source habitat. Dispersal is by juvenile ticks. The sink habitats have lower tick density and prevalence of *Borrelia burgdorferi* than the source habitat, and under these conditions there was always a positive relationship within the sink habitats between change in prevalence and change in density.

DISCUSSION

This study combined field sampling and modeling approaches to assess the likely influence of habitat heterogeneity on the enzootiology of *Borrelia burgdorferi* in tick populations. Our results provided clear answers to the two questions we set out to address: (1) the local risk of human exposure to infected ticks cannot be predicted simply by focusing on conditions within the local habitat, and (2) local dynamics of tick populations and spirochete prevalence often did not result from an additive combination of conditions in nearby habitats. These answers emerged from field data collected in several kinds of habitats, and from analysis of a tick population model that incorporates multiple habitat types. In addition, our analyses pointed out general features of spatially heterogeneous systems that have important implications for understanding population dynamics, species interactions, and disease ecology in the context of natural landscapes.

Causes of natural variation in density and prevalence

Our earlier tick population model (Van Buskirk and Ostfeld 1995) was successful in capturing general fea-

tures of numerical dynamics and *B. burgdorferi* infection, but it failed to explain certain field observations. For example, ticks are never evenly distributed at either local or regional scales (Patrick and Hair 1978, Wilson et al. 1988*a*, Maupin et al. 1991, Ostfeld et al. 1995), and we found that spirochete prevalence varied significantly among habitats on our study area in southeastern New York over 2 yr (Fig. 1). These habitat differences are usually attributed to variation in host density and species composition (Ostfeld et al. 1995), but in the absence of manipulating hosts in natural settings (e.g., Wilson et al. 1988*b*) it is difficult to judge whether differences could persist in the face of host dispersal. We therefore used the model to ask whether habitat-related variation in tick abundance and infection might persist in spite of the tendency of dispersal to homogenize tick densities and prevalences. Analysis of a four-habitat system patterned after our study area indicated that, while high levels of dispersal will reduce variation among habitats, this variation can persist even when 10–20% of juvenile ticks switch to a new habitat each time they parasitize a host (Fig. 7). The model therefore establishes the plausibility of the interpretation that characteristics of the local host assemblage are reflected in local tick density and spirochete prevalence (Ostfeld et al. 1995).

Field data further suggested that tick density and infection are not necessarily correlated, and therefore may be causally independent. There was no clear relationship between the densities reported by Ostfeld et al. (1996*a*) and prevalences we found in the same habitats (Fig. 1). The model shows how such a result can occur, since density and prevalence are controlled by different factors. Tick density is always a function of host density in the model, whereas spirochete prevalence depends on the reservoir competence of hosts (as long as sufficient numbers of hosts are available to support the enzootic cycle). In the four-habitat scenario, the strong signature of local host abundance and reservoir competence persisted even with moderate dispersal rates. This result provides a basis for interpreting the habitat-related variation on our study area in terms of the habitat preferences of species of small mammals and birds that differ in their reservoir competence (Ostfeld et al. 1995).

The model also reproduced a pattern of changing infection and density within tick cohorts that was visible in the field data. Across four habitats and two years, we observed a positive relationship between the change in density between nymphal and adult stages, and the change in prevalence of *B. burgdorferi* over the same period (Fig. 2). Biases in our field sampling methods and survival differences between infected and uninfected nymphal ticks seem unlikely to account for this result. Instead, the pattern may have resulted from dispersal of juvenile ticks among habitat types while parasitizing *Peromyscus leucopus,* the most highly competent reservoir species in our study area (Donahue et al. 1987, Mather et al. 1989). We propose that infected mice dispersing out of source habitats carried nymphal ticks with them to surrounding habitats and infected them at the same time. The ticks dropped off the dispersing mice, molted, and a few months later caused simultaneous increases in both the proportion infected and density of questing adults in their new habitat.

Patterns similar to that seen in the field were always obtained in the four-habitat model system, whenever one habitat acted as a source of dispersing ticks and also contained hosts with relatively high reservoir competence. Sink habitats with high rates of immigration or low capacities to support ticks showed the largest increases in both density and infection. If similar mechanisms were operating in the field, then during 1993 the Dogwood and Bluestem habitats should have been receiving numerous ticks dispersing on highly competent reservoir species such as *P. leucopus.* We do not have direct evidence of such dispersal from marked mammals, but other evidence from field studies of small-mammal densities and tick burdens suggests that mice have engaged in large-scale asymmetric dispersal among habitats in our study area several times in the past 5 yr (Ostfeld et al. 1996*b*). One such period of mass movement may have been during the spring and early summer of 1993, just after a poor acorn crop in 1992 forced an unusually high density of *P. leucopus* in oak habitats to seek food in marginal habitats. The timing of mouse movement during spring may also explain why we found habitat-related variation in spirochete incidence within adults but not nymphs. Large-scale dispersal of mice probably was completed by the time the peak larval questing period commenced in August, so mice were presumably more evenly distributed among habitats by that time, and the hosts that the larvae parasitized would have been primarily non-dispersing individuals.

It is unclear exactly what habitats on our study area correspond to the single ''source'' habitat in the four-habitat model system. None of the habitats behaved exactly like the source habitat in Fig. 8, with its heavily infected adults and high loss rate of ticks. It is possible that our field sampling failed to include some other habitat with very high densities of infected ticks, although our familiarity with the area suggests that this is unlikely. Also, the hypothesis that dispersing *P. leucopus* was involved strongly suggests that oak forest was a source of dispersers. We suspect that the oak habitat did not show the pattern exhibited by the source habitat in the model because dispersal in nature involves a shift in the distribution of host individuals, whereas the model assumes that host densities remain constant within habitats. On the study area there appeared to be a major exodus of mice from oak forest in early 1993, which means that oak forest probably functioned as a source habitat only temporarily, until its host populations became depleted. A more realistic

representation of host movements might alter the position of the source in Fig. 8.

Our explanations for changing patterns of density and infection in the field have revolved around dispersal during juvenile stages. The model suggests that this emphasis on juveniles is warranted under many conditions. The importance of dispersing juveniles arises because they have the potential to be infected and to carry *B. burgdorferi* with them to their new habitat, whereas adults produce uninfected larvae regardless of whether they themselves are infected. One important exception occurs when hosts for adults are locally scarce, in which case even a small amount of immigration of adult ticks and subsequent oviposition can produce high tick population densities. The local abundance of juvenile ticks in habitats frequented by deer may provide an example of this phenomenon (Wilson et al. 1988*a*, Ostfeld et al. 1996*b*).

Although the model does not incorporate numerous processes known to influence tick demography, we found the general agreement between field results and model results to be reassuring in that it encourages confidence in the basic framework of the model. We have shown that only a few simple elements need be invoked to explain landscape-level patterns in Lyme disease risk. These include variation in density and reservoir competence of hosts among habitats, dispersal between habitats, some form of density-dependent access to hosts, and positive feedback between the infection prevalence of ticks and hosts. Most of these appear to be present in nature, and the model shows that they are sufficient to produce the patterns occurring in nature.

Implications for managing Lyme disease

The study of the population dynamics of *Ixodes* ticks is directly relevant for controlling human exposure to Lyme disease because humans contract the disease after being bitten by an infected tick, usually a nymph (Barbour and Fish 1993). We focused on the processes that influence the density and infection prevalence of nymphs because these two responses together determine the probability of exposure to Lyme disease. Our results suggest that a landscape-level perspective will be needed to effectively decrease human risk by means of habitat management.

One approach currently favored by many involves altering vegetation structure to reduce suitability of local habitats for ticks and their hosts (Wilson et al. 1988*a*, Jaenson et al. 1991, Wilson and Deblinger 1993). This method apparently helps somewhat, but its beneficial effects are vulnerable to being overcome by dispersal into the modified habitat from elsewhere. Awareness of the identity and proximity of other habitats, their suitability for *Ixodes* hosts, and temporal patterns of host movement would help managers predict the benefit to be expected from local habitat management, and to anticipate when it is likely to fail. In the absence of information about surrounding habitats, our model suggests that local habitat modification is more likely to work when habitat patches are large and dispersal is relatively low.

Van Buskirk and Ostfeld (1995) noted that steps to increase diversity of small vertebrates could mitigate the overwhelming impact of the highly reservoir-competent *Peromyscus leucopus* in this system, simply by dilution with other less-competent species. Leaving aside the practical challenges associated with managing habitats to promote small-vertebrate diversity, the present results strengthen the earlier recommendation but also draw attention to the issue of the scale at which habitat management must be implemented. Obviously, local reduction in average reservoir competence can help reduce risk, even though it is unlikely to have much benefit beyond the limits of the habitat being manipulated. On the other hand, management strategies could prove mysteriously ineffective if they ignored the species composition of hosts in nearby habitats. If the managed habitat acts as a dispersal sink, relatively small amounts of movement by hosts can establish populations of infected hosts even if the management strategy is working properly on a local scale.

The importance of spatial heterogeneity in ecology

The model and field data both underscore the importance of landscape heterogeneity in this system: it is clear that we require information on more than just local host abundances to understand causes of local variation in tick density, and to predict local risk of Lyme disease. But our results go beyond this particular system in their implications for the study of spatial heterogeneity in landscape ecology.

Nonlinear or threshold responses to increasing dispersal rates were a conspicuous feature of this system, originating from both positive and negative feedbacks, which are ubiquitous attributes of ecological systems. Two kinds of feedback are operating. First, there is density-dependent interference competition among adults and juveniles for hosts. This kind of feedback affects nonlinear responses in tick density to changes in dispersal rate. For example, although low levels of dispersal established dense tick populations in habitats with relatively few hosts for adults, moderate or high levels of dispersal caused little further increase in numbers due to negative density dependence. Second there is positive feedback between the proportions of ticks and hosts that carry *B. burgdorferi*, mimicking a well-known feature of the natural history of Lyme disease (Mather 1993). This kind of feedback only affects spirochete prevalence, and is responsible for the threshold sensitivity of *B. burgdorferi* infection to very small levels of dispersal.

The implications of nonlinear combination of landscape components are general and far-reaching, and studies such as ours provide both practical and conceptual justification for attention to larger scales in

ecology. On a practical level, the results imply that the system cannot be understood by simply averaging across its separate components. For example, we argue above that Lyme disease cannot be managed appropriately by treating habitats as independent entities. On a more general level, our results challenge the validity of reducing ecological systems to their component parts (be they individuals, species, or habitats) for study in isolation (Vandermeer 1969, Schoener 1986). If the objective is to understand the processes that produce patterns in real systems, then it is essential for a complete research program to pay attention to those real systems in natural context, in which nonlinear processes can potentially be expressed (Werner 1998).

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