



Biodiversity and Lyme disease: Dilution or amplification?

N.H. Ogden^{a,*}, J.I. Tsao^{b,c}

^a Centre for Foodborne, Environmental and Zoonotic Infectious Diseases, Public Health Agency of Canada—Agence de la santé publique du Canada, 3200 Sicotte, C.P. 5000, Saint-Hyacinthe, Québec, Canada J2S 7C6

^b Department of Fisheries and Wildlife, Michigan State University, East Lansing, MI 48824, USA

^c Department of Large Animal Clinical Sciences, Michigan State University, East Lansing, Michigan, USA

ARTICLE INFO

Article history:

Received 14 May 2009

Revised 12 June 2009

Accepted 15 June 2009

Keywords:

Biodiversity

Dilution effect

Lyme disease

Ixodes scapularis

Borrelia burgdorferi

Mathematical model

ABSTRACT

Reduced Lyme disease risk by the 'dilution effect' is often cited as an example of biodiversity providing 'ecosystem services' to public health. Using a mechanistic model we investigated how transmission of the Lyme disease agent, *Borrelia burgdorferi*, by *Ixodes scapularis* ticks amongst highly efficient reservoir mice is affected by varying the abundance of a less efficient reservoir host. Simulations indicated either amplification or dilution may occur, with the outcome depending precisely on mechanisms of competition, host contact rates with ticks, and acquired host resistance to ticks. Quantifying these mechanisms will be crucial to predicting how biodiversity affects Lyme disease risk.

Crown Copyright © 2009 Published by Elsevier Inc. All rights reserved.

Introduction

Norman et al. (1999) described the term 'dilution effect' as the theoretical inhibitory effect on enzootic pathogen transmission cycles maintained by one competent reservoir host species, when reservoir-incompetent host species are added to the host community. By definition, the dilution effect occurs when the addition of one or more host species to a community makes a pathogen less abundant and less likely to persist than in the presence of one highly competent reservoir host species alone (Begon, 2008). Mechanistically, 'dilution' occurs when a transmission event that previously might have linked infectious and susceptible individuals of the reservoir-competent host species, instead links infectious individuals to susceptibles of a less reservoir-competent species. This diversion of transmission from highly competent reservoir host species (also called 'encounter reduction' in Keesing et al. (2006)) results in fewer new infections, and thus reduces R_0 , the basic reproductive number of the pathogen. We term this a 'direct dilution effect', as Keesing et al. (2006) also consider a number of 'indirect' ways in which biodiversity could negatively impact transmission cycles, for example, if susceptible host populations are reduced via competition or predator–prey interactions. By extension, increased biodiversity (a combination of species richness and species evenness as defined by Ostfeld and Keesing (2000a,b) and Keesing et al. (2006)) should lead to reduced pathogen abundance (Dobson et al., 2006) and would have great consequences

for land use and natural resource management decisions: anthropogenic impacts that reduce diversity may have direct and calculable public health costs.

It has been suggested that community effects on Lyme disease transmission may provide a working example of the dilution effect in nature (Ostfeld and Keesing, 2000a,b; Dobson et al., 2006). This is highly relevant to public health because the agent of Lyme disease, *Borrelia burgdorferi*, which is transmitted by the blacklegged tick *Ixodes scapularis*, is emerging in Canada (Ogden et al., 2008a) and the United States (Diuk-Wasser et al., 2006). Lyme disease is the commonest vector-borne zoonosis in the northern temperate zone (Kurtenbach et al., 2006) and incidence is rising, in large part because the geographic range of vector ticks is expanding (Diuk-Wasser et al., 2006; Ogden et al., 2008a,b). The pathogen must be transmitted between the tick population and reservoir-competent vertebrate hosts in order to persist in nature. *I. scapularis* has three post-egg stages that are obligate parasites. Although the larval and nymphal stages feed on a very wide range of host species including mammals, lizards, and birds (Keirans et al., 1996), the white-footed mouse, *Peromyscus leucopus*, has been considered the primary reservoir host for *B. burgdorferi* because of its abundance, its importance as a host for immature *I. scapularis* ticks, the efficiency with which infected *P. leucopus* transmits infection to uninfected feeding ticks, and the often lifelong infectivity of infected individuals (Donahue et al., 1987; Thompson et al., 2001). The adult stage of *I. scapularis* requires a large host on which to feed. In North America this often means the white-tailed deer, which are largely reservoir incompetent.

* Corresponding author. Fax: +1 450 778 8120.

E-mail address: nicholas_ogden@phac-aspc.gc.ca (N.H. Ogden).

The hypothesis that biodiversity may cause a dilution effect for Lyme disease was introduced in two modeling studies (Van Buskirk and Ostfeld, 1995; Schmidt and Ostfeld, 2001). Two field studies (Allan et al., 2003; LoGiudice et al., 2003) further provide evidence, but cast-iron support of a dilution effect in nature is still elusive (Begon, 2008). A number of metrics for measuring a dilution effect have been proposed (Keesing et al., 2006), but here, we argue that to demonstrate a dilution effect of public health and ecological significance, the actual number of infected host-seeking nymphal *I. scapularis* per unit area of habitat (density of infected nymphs or DIN) must decrease (Begon, 2008), because the majority of Lyme disease cases are transmitted by nymphs (Falco et al., 1999). If nymphal infection prevalence (NIP) were low, but the overall density of infected ticks were high, epidemiological risk would still be significant. Therefore, we consider that, until proven otherwise, reduction in NIP alone, without reference to changes in nymphal tick abundance (e.g. LoGiudice et al., 2003), does not constitute evidence of a dilution effect.

A dilution effect is a less likely consequence of increasing biodiversity if pathogen transmission is dominated by density-dependent, rather than frequency-dependent, interactions amongst vertebrate hosts (Schmidt and Ostfeld, 2001; Dobson, 2004; Keesing et al., 2006). In contrast to adult mosquito abundance, determined mainly by the survival of non-parasitic immature life stages (Reiter, 2001), tick abundance is determined importantly by host abundance because all post-egg life stages are obligate parasites (Wilson et al., 1984; Randolph and Steele, 1985; Daniels and Fish, 1995; Jones et al., 1998; Ostfeld et al., 2001, 2006; Rand et al., 2003; Randolph, 2004). In this circumstance, were diversity to increase not only by increasing species richness, but also overall abundance of hosts, the dilution effect might not occur. Even if the additional species were less efficient reservoirs and reduced NIP, the increased density of hosts might increase tick survival and abundance, which in turn could increase DIN even though NIP decreases, causing amplification rather than dilution of transmission cycles.

In this study we investigated the effect of increasing host biodiversity on transmission cycles of the Lyme disease agent via direct (direct impact on DIN) or indirect (by competition) mechanisms. We used a model that incorporates mechanistic representations of observed seasonality in tick vector abundance (i.e. seasonal transmission: Keeling and Grenfell, 2002) and rodent reservoir demographic processes (i.e. seasonal breeding with seasonal input of susceptibles: Hosseini et al., 2004) because of their potential importance for transmission. Furthermore, temporal dynamics of the tick life cycle, particularly seasonal variations in the duration of development of ticks, also determine tick vector survival (Ogden et al., 2005) and thus the potential for alternative hosts to impact tick abundance, which has not been accounted for in studies to date. To account for these factors, the model used is parameterized from a synthesis of published field and laboratory data. First, we investigated the effects of interspecific variation in host–parasite interactions (i.e., tick–host attachment rates and tick feeding success) that may determine the effects of biodiversity in nature. Second, we investigated the possibility for indirect versus direct dilution effects. Third, using parameter values derived from published field studies, we evaluated the potential for, and generality of, the dilution effect in nature in northeastern North America.

Methods

Model structure

The model is based on that previously described (Ogden et al., 2007), which models transmission between a seasonally dynamic reservoir host population and a seasonally dynamic vector tick population. The *P. leucopus* model is constructed as a susceptible–

infected (SI) model of *B. burgdorferi* transmission, i.e. we are implicitly considering the transmission of those *B. burgdorferi* genotypes that are transmitted lifelong by *P. leucopus* (Donahue et al., 1987; Derdáková et al., 2004), and which are common where Lyme disease is endemic in the northeastern USA (Hanincová et al., 2006). The abundance of infected nymphs depended on transmission from infected animals, processes affecting tick survival, and seasonality in tick development and activity as determined by a population model of *I. scapularis* (Ogden et al., 2005, Fig. 1). The model contained several key elements of realism via parameterization from field and laboratory studies on *I. scapularis*, *P. leucopus*, and *B. burgdorferi* infection in, and transmission from, *P. leucopus*: i) contact rates between ticks and *P. leucopus* hosts that are equivalent to those seen in the field in northeastern North America; ii) seasonality in tick abundance due to climate-dependent and climate-independent influences on interstadial tick development and tick activity; iii) seasonality in *P. leucopus* abundance driven by seasonality in population processes (mortality and birth rates) and regulation as observed at the northern edge of the range of this rodent or in experimental studies; iv) a realistic, climate-dependent time lag between larval ticks acquiring infection and the emergence of nymphal ticks capable of transmitting infection with field-observed tick mortality rates; v) density-dependent rates of mortality of on-host ticks; and vi) dependence of tick survival and abundance on the abundance of *P. leucopus* and reservoir-incompetent deer that also act as hosts for immature and adult *I. scapularis* in the model (Ogden et al., 2007).

For this study the model was modified by including an additional host for immature ticks, the potential diluting host (as defined by LoGiudice et al., 2003), hereafter called by us the alternative host, because most of these hosts are competent reservoirs. As for *P. leucopus*, this host was modeled in a simple two-compartment SI model (Fig. 1). Mean survival for the alternative host was 265 days, a value between that for medium-sized mammals such as squirrels and chipmunks (approximately 1 year: Barkalow et al., 1970; Tryon and Snyder, 1973), and ground feeding passerines such as American Robins (approximately 150 days from hatching: Young, 1955), both of which have been considered as dilution hosts (LoGiudice et al., 2003). The total alternative host population size remained constant during simulations by balancing births with mortality. For simplicity there was no seasonality to birth and mortality rates in the alternative host.

Susceptible hosts (either alternative hosts or *P. leucopus*) acquired infection at a rate determined by the rate at which infective nymphs attached to that host species. In turn, the nymphal attachment rate was a function of the abundance of host-seeking nymphs, intrinsic host-finding rates for nymphs that are host species-specific, and an adjustment for non-linear relationships between host abundance and host-finding rates (Mount et al., 1997).

Infected *P. leucopus* and alternative hosts infected larvae at host species-specific rates determined by i) the host-to-tick transmission coefficient, and ii) the abundance of larvae feeding per host. The transmission coefficient was defined as the proportion of uninfected ticks that acquire infection while feeding on an infected host, which for the alternative host was always set lower than that for *P. leucopus*. Transmission coefficients were obtained from laboratory and field studies as previously described (Ogden et al., 2007) or as described in the following. In nature ticks are usually highly aggregated on a small subset of the host population (Davidar et al., 1989; Kitron et al., 1991; Randolph et al., 1999); however, given the lack of data on aggregation for multiple species, for simplicity it was assumed here that the distribution of ticks amongst hosts was even and the same for both host species.

Engorged larvae from alternative hosts, *P. leucopus*, and deer, regardless of infection status, were assumed to be dispersed homogeneously in the environment. Thus, once these larvae molted into nymphs, the total abundance of host-seeking nymphs in the

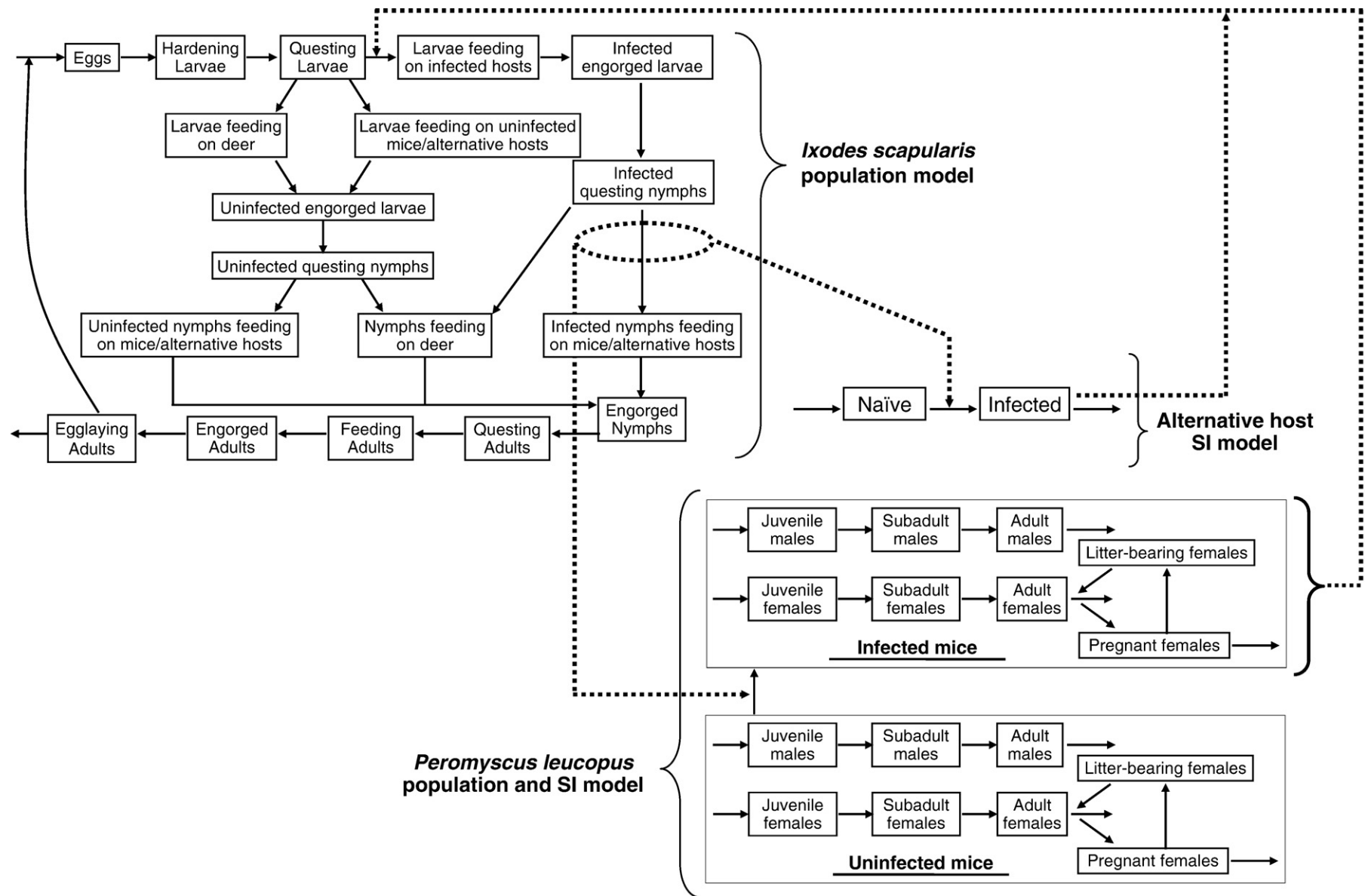


Fig. 1. A diagram of the combined model comprising sub-models of *Ixodes scapularis*, *Peromyscus leucopus* (an SI model) and the alternative host (also an SI model). The bold dotted lines indicate infection transmission between ticks and mice and alternative host populations. For simplicity, not all flows to indicate mortality, nor linkage of *I. scapularis* abundance to host-finding and feeding success of immature ticks, are shown.

model was the sum of that arising from all three hosts. The abundance of infected host-seeking nymphs, however, was derived only from *P. leucopus* and the alternative host.

The abundance of ticks in the model was regulated by on-host mortality, which was dependent on the density of immature ticks feeding on the host (Levin and Fish, 1998). The nature of the on-host density-dependent mortality was identical for *P. leucopus* and the alternative host (Ogden et al., 2005).

Variables in the model that are new to, or modified from, Ogden et al. (2007) are shown in Table 1, while new and modified equations are shown in Appendix A. The model was pre-loaded with 100 infected and 20 uninfected *P. leucopus* and 10,000 uninfected questing adult *I. scapularis* as previously described (Ogden et al., 2007). The model was stable to multiple starting conditions (Ogden et al., 2007). The starting number of naive alternative hosts is specified in the following scenarios. The *I. scapularis* model was run using data on tick activity and development duration calculated as described previously (Ogden et al., 2005) from monthly temperature data (1971 to 2000) for Chatham, Ontario (close to a site where *I. scapularis* are endemic) obtained from Environment Canada (see Ogden et al., 2005).

For each simulation using a particular set of parameters, the model was run for 40 simulated years with a 1-day timestep, although in all cases the model reached a stable annually cyclic equilibrium within 11 simulated years. For analysis, we used output data obtained in the last year of each simulation for the various scenarios described in the following section.

Scenarios without interspecific host competition

The first two scenarios assume that additional hosts can be added to the system without affecting the abundance of the *P. leucopus* population (i.e. there is no interference, exploitative, or apparent competition between hosts). We further assumed that alternative hosts would vary in their relative capacity to host larval or nymphal ticks, because of differential rates at which they contact (i.e., encounter or attract) these ticks, which may be due to a number of mechanisms (Shaw et al., 2003; Bown et al., 2003; Sonenshine, 2004; Randolph, 2004; Crooks and Randolph, 2006).

Table 1

Parameters in the model additional to, or modified from, those in Ogden et al. (2007).

A	Total number of alternative hosts (default value 20)
A_i	Total number of infected alternative hosts (initial value 0)
A_u	Total number of uninfected alternative hosts (initial value 8 to 50 in simulations)
B_a	Per capita daily birth rate of alternative hosts (which equals the total daily mortality rate of all alternative hosts)
μ_a	Per capita mortality rate of alternative hosts (= 0.0089)
λ_{ia}	Per capita daily rate at which alternative hosts acquired an infected nymph
λ_{qlia}	Per capita daily rate at which questing larvae found an infected alternative host
λ_{qlua}	Per capita daily rate at which questing larvae found an uninfected alternative host
λ_{na}	Per capita daily rate at which questing nymphs found an alternative host
HFRLA	Basic rate at which questing larvae found alternative hosts
HFRNA	Basic rate at which questing nymphs found alternative hosts
TE_a	Infection transmission efficiency from infected alternative hosts to uninfected feeding larvae
FN^a	Number of nymphs feeding on alternative hosts (initial value 0)
EN	Number of engorged nymphs (initial value 0)
FL	Number of feeding larvae (initial value 0)
EL	Number of engorged larvae (initial value 0)
Superscripted ia, and ua	Indicates whether feeding or engorged larvae are feeding or have fed, on infected or uninfected alternative hosts, respectively
Subscripted $t-x$	Indicates the number of ticks in that state x days before the present day; x is a time delay in the lifecycle of the tick determined empirically (Ogden et al., 2005)

Scenario 1: variable larval contact rates, but equal nymphal contact rates

In this scenario nymphs contacted alternative hosts and *P. leucopus* at the same rate. Contact rates of questing larvae, however, for an alternative host (HFRLA) varied from 0.125 to 8 times the basic rate that they contacted a *P. leucopus* (HFRL).

Scenario 2: equal larval contact rates but variable nymphal contact rates

In this scenario the rate that questing nymphs contacted an alternative host (HFRNA) varied from 0.125 to 8 times the basic rate that they contacted a *P. leucopus* (HFRN), while the basic rates that larvae contacted alternative hosts and *P. leucopus* were the same.

In addition to varying HFRLA and HFRNA, we varied the abundance of alternative hosts. Specifically, for each value of HFRLA or HFRNA in these scenarios, 22 simulations were run with values of alternative host abundance from 8 to 50. Throughout these simulations, the proportion of larvae infected by an infected *P. leucopus* (i.e., the transmission efficiency) was set at 0.6 (see Ogden et al. (2007) for justification for these values). The proportion of ticks infected by an alternative host was 0.1 (approximately the transmission efficiency quoted for potential dilution hosts such as squirrels and birds by LoGiudice et al. (2003)). Once infected, both *P. leucopus* and alternative hosts were infective for life. To investigate the potential for dilution at more extreme values for transmission coefficients, simulations for the above scenarios were repeated with the transmission efficiencies for *P. leucopus* and the alternative host set at 0.9 and 0.02 respectively.

Scenarios with interspecific host competition

In the next two scenarios, the addition of alternative hosts to the model reduced the abundance of *P. leucopus* through interspecific competition. This was achieved by using the alternative host abundance to add to *P. leucopus* numbers in density-dependent regulation of reproduction rates of *P. leucopus* (see Ogden et al., 2007):

Scenario 3: strong interspecific competition

The simulations for Scenario 2 above were repeated with a range of alternative host numbers that almost completely competed with *P. leucopus*. To do this, the effect of alternative host numbers on *P. leucopus* reproduction was set so that introduced alternative hosts reduced *P. leucopus* abundance on a one-for-one basis, and the total number of hosts remained constant across most values for the numbers of alternative hosts.

Scenario 4: moderate interspecific competition

Simulations for Scenario 2 were also run with a range of alternative hosts that partially competed with *P. leucopus*. To do this, the effect of alternative host numbers on *P. leucopus* reproduction was set so that three introduced alternative hosts reduced *P. leucopus* abundance by one.

We measured three response variables. The first key outcome measure was the total annual number of infected engorged larvae (IL) that dropped off all hosts at equilibrium, compared to that when the model was run with no alternative hosts. Molting rates for infected and uninfected engorged larvae were equal and were the same for all larvae regardless of host species. This variable is equivalent to DIN because it gave a precise value for the number of infected and uninfected engorged larvae that were simulated to be seeded into the 'environment' to become questing nymphs. Furthermore, direct interpretation of values from the model compartments for infected and uninfected questing nymphs was more difficult because the ticks remained for multiple time steps in these compartments, the number of which depended on-host density and season. Second, we measured the abundance of all engorged larvae dropping from all the hosts (L) to investigate how different

scenarios of tick attachment to alternative hosts could affect the overall abundance of ticks. Finally, we measured the infection prevalence in engorged larvae dropping from all the hosts, which is equivalent to NIP.

Investigating field evidence for a dilution effect

To investigate whether the dilution effect may occur in nature, we ran model simulations using values obtained from nature for key parameters: i) densities of alternative hosts, ii) the numbers of larvae and nymphs they feed compared to *P. leucopus*, iii) the transmission efficiency from host-to-larva, and iv) the proportion of larvae that survive after feeding on the hosts. We used the data from [LoGiudice et al. \(2003\)](#), to our knowledge the only study in which *I. scapularis* tick infestations, transmission efficiencies and host densities were estimated contemporaneously in North America, to provide data on-host density and relative importance of species as hosts for larvae. Data on nymphal infestations of alternative hosts and *P. leucopus* were not recorded in [LoGiudice et al. \(2003\)](#), so we obtained mean values for the relative importance of potential alternative hosts and *P. leucopus* as hosts of nymphs from field studies at other sites ([Table 2](#)). In these studies larval and nymphal *I. scapularis* infestations of *P. leucopus* and alternative hosts were estimated contemporaneously, but host densities were not assessed or quoted. We assumed that birds can carry twice as many nymphs as do *P. leucopus* as suggested by the studies of [Rand et al. \(1998\)](#) and [Battaly and Fish \(1993\)](#).

In our model, only one alternative host species was included for computational simplicity, so using the methodology described in [Appendix B](#) we collapsed the community of alternative host species into one alternative host species. All the alternative host species in [LoGiudice et al. \(2003\)](#) were included in these calculations with the exception of deer, which are already in the model, and shrews, which may actually be amplifying hosts ([Brisson et al., 2008](#)). Parameters for the alternative host community were also estimated for a community that excluded chipmunks, because transmission efficiency from this species can be high (>50% in [LoGiudice et al., 2003](#)) and they occur at high densities (approximately half that of *P. leucopus*: [LoGiudice et al., 2003](#)). Hence, by excluding the latter species, our model was biased towards revealing a dilution effect and against an amplification effect, based on-host reservoir capacities. The parameter values for alter-

native hosts were: density = 66.3/hectare (41.3 without chipmunks), HFRNA and HFRNA = 1.29 and 3.85 times these values for *P. leucopus* (HFRNA = 4 times without chipmunks, which carry many nymphal ticks: [LoGiudice et al., 2003](#)), host-to-larva transmission efficiency = 0.1 (0.45 with chipmunks), 50% of engorged larvae survived the molt (55.4% without chipmunks, on which engorged survival is slightly lower than other alternative hosts: [LoGiudice et al., 2003](#)) versus 41.5% for *P. leucopus*. The model was run with and without alternative hosts across a range of mean *P. leucopus* numbers (for the period 1 May to 30 September when most larvae are actively attaching to hosts in the model) from 6 to 212. In addition, the model was run using alternative host values for individual alternative host species described in [Table 2](#) (using density estimates for those species in [LoGiudice et al. \(2003\)](#)) to assess how individual host species may contribute to an outcome of dilution or amplification.

Results

Scenarios without interspecific host competition

Effects on abundance of all larvae (L) dropping from the hosts

In all simulations the inclusion of alternative hosts increased the number of engorged larvae produced by all hosts due to the positive effect of alternative hosts on tick survival. Both the number of alternative hosts in the model and the relative rates at which they acquired immature ticks, however, influenced the total numbers of engorged larvae (L) dropping off the hosts ([Figs. 2a](#) and [b](#)).

Given equal contact rates with nymphs, variations in larval contact rates resulted in a non-linear response in L ([Fig. 2a](#)). The increase in L was maximal ([Fig. 2a](#)) when alternative hosts and *P. leucopus* acquired larvae at the same rate. To either side of this value, introduction of alternative hosts had a lesser effect on boosting L either because they contacted fewer larvae, or because they attracted many larvae but also killed many due to increasing density-dependent, per capita mortality rates of larvae on alternative hosts ([Figs. 2c](#) and [d](#)).

When contact rates with larvae were equal between *P. leucopus* and alternative hosts, low rates of contact between nymphs and alternative hosts resulted in an expected small effect of introducing alternative hosts on L ([Fig. 2b](#)). Increasing the rate at which nymphs contacted alternative hosts increased L across the range of values for

Table 2
The ratio of mean *I. scapularis* infestations of alternative hosts to infestations of *P. leucopus*, as observed in field studies in the USA and Canada in which infestations of potential alternative hosts and of *P. leucopus* were estimated contemporaneously.

Study	Potential alternative host species	Ratio for larvae	Ratio for nymphs	Density estimates used in simulations	Effect
Hanincová et al., 2006	Pine vole	0.6	0.5	4*	Amplification
	Gray squirrel	0.6	9.7	8.1	Dilution
	Raccoon	8.5	5.3	0.2	Dilution
	Virginia opossum	8.6	3.9	1	Dilution
Brisson and Duykhuizen, 2004 Mannelli et al., 1993, 1994^a	Gray squirrel	1.3	4.4	8.1	Amplification
	Raccoon	6.1	65.5	0.2	Dilution
	Virginia opossum	7.2	36.9	1	Dilution
	Fox squirrel	1.5	22.1	(1)	Dilution
Levin et al., 2002	Cottontail rabbit	4.2	3.1	4	Amplification
	Gray Squirrel	1.8	6.9	8.1	Amplification
	Virginia opossum	7.6	8.0	1	Dilution
	Raccoon	18.5	5.6	0.2	Dilution
Schmidt et al., 1999 Slajchert et al., 1997	Striped skunk	10.9	8.0	0.05	Dilution
	Chipmunk	0.4	3.5	25	Amplification
Mather et al., 1989 Lindsay, 1995	Raccoon	1.3	11.1	0.2	Dilution
	Meadow vole	0.19	(1)	4*	Dilution
	Raccoon	0.2	0.4	0.2	Dilution
	Virginia opossum	0.1	2.9	1	Amplification

Also shown are the density estimates (numbers per hectare) used in simulations that were obtained from [LoGiudice et al. \(2003\)](#) unless otherwise stated, and the effect of introducing these alternative hosts individually in simulations.

^a The studies of [Manelli et al. in 1993 and 1994](#) were conducted contemporaneously but data on infestations of *P. leucopus* and medium-sized mammals appeared in different publications.

* Density estimates from our own unpublished studies. Values in parentheses are those ascribed in simulations when we have no field observations.

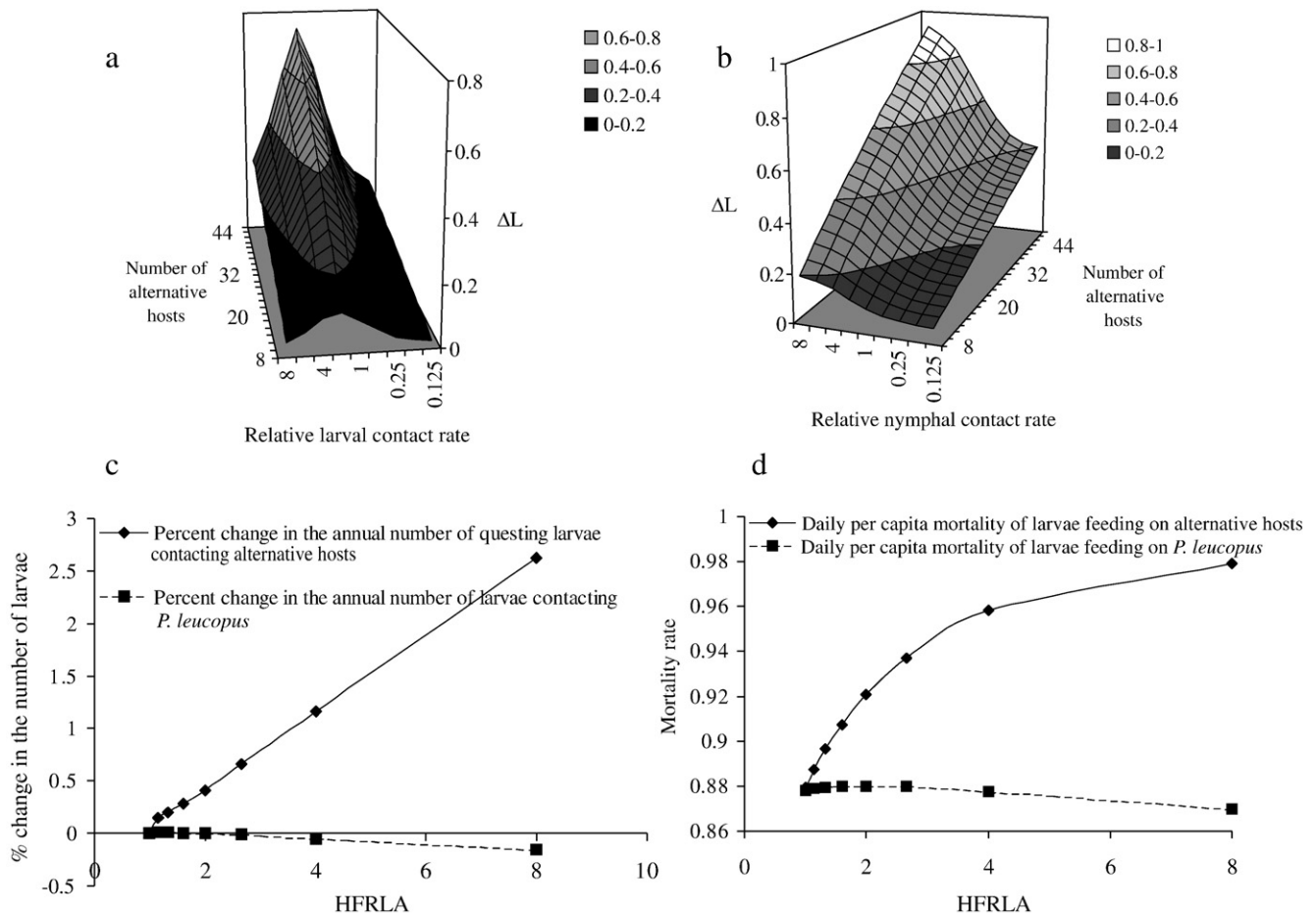


Fig. 2. Changes in the annual total number of engorged larvae dropping from all hosts at model equilibrium (ΔL), relative to the number obtained in simulations in which the alternative host was not included, in Scenarios 1 and 2 (see [Methods](#)) are shown in graphs a and b respectively. At point $\Delta L = 0$ there is no difference relative to the baseline scenario (i.e. no alternative hosts). Alternative host abundance is on the y-axis in both graphs. On the x-axis are the factors by which the basic rate at which questing larvae contacted alternative hosts (HFRLA) was increased or decreased above that for *P. leucopus* (graph a), or the factors by which the basic rate at which questing nymphs found alternative hosts (HFRNA) was increased or decreased above that for *P. leucopus* (graph b). Graphs c and d show, respectively, the change in contact rates of larvae with, and per capita daily larval mortality rates on, alternative hosts and *P. leucopus* as larval contact rates with alternative hosts increased in Scenario 1.

nymphal contract rates simulated. Increasing nymphal contract rates to alternative hosts had much smaller direct positive effects on tick infestations than did increasing the rate larvae contacted alternative hosts: in the model, as in nature, the abundance of nymphs was always approximately an order of magnitude lower than the abundance of larvae.

Effects on the prevalence of infection in engorged larvae dropping from the hosts

In all simulations that included an alternative host, the prevalence of infected engorged larvae dropping from all hosts (i.e., *P. leucopus*, alternative hosts, and deer) was lower than that when simulations were run with only *P. leucopus* and deer (Figs. 3a and b). The negative effect on prevalence increased with alternative host abundance and higher relative rates at which alternative hosts contacted ticks. Variation in nymphal contact rates had much stronger effects on reducing prevalence than did variation in larval contact rates (Figs. 3a and b).

Effects on abundance of infected engorged larvae (IL) dropping from the hosts

There was a non-linear response in the numbers of engorged infected larvae (IL) dropping from all hosts when the abundance of alternative hosts and contact rates of immature ticks were varied (Fig. 3). The majority of equilibrial outcomes resulted in amplification, rather

than a direct dilution effect. This was due to the increased production of ticks in the system, some of which became infected when feeding either on infected *P. leucopus* or alternative hosts, to a degree that more than compensated for any fall in prevalence. Changes in IL were maximal when contact rates with immature ticks were similar for alternative hosts and *P. leucopus*. Whether dilution or amplification was the outcome depended on the balance between the number of ticks added to the system by including alternative hosts, and the degree to which alternative hosts diverted infected nymphs from *P. leucopus*.

Direct dilution was more likely to occur by three mechanisms. First, when alternative hosts contacted larvae at much higher rates than did *P. leucopus*, high density-dependent mortality of larvae on alternative hosts limited the number of extra ticks alternative hosts added to the system. Second, when alternative hosts contacted too few larvae, that also limited the number of extra ticks alternative hosts added to the system. Third, when alternative hosts contacted nymphs at much higher rates than *P. leucopus* did, the diversion of infected nymphs from *P. leucopus* reduced the prevalence of infection in *P. leucopus* to the extent that overcame any boosting in tick numbers. The mechanisms behind these observations are described in detail in [Appendix C](#).

As expected, in simulations in which dilution occurred, increased abundance of alternative hosts increased the magnitude of the dilution effect. Furthermore, the dilution effect occurred over a wider range of parameter values when the difference in transmission efficiencies

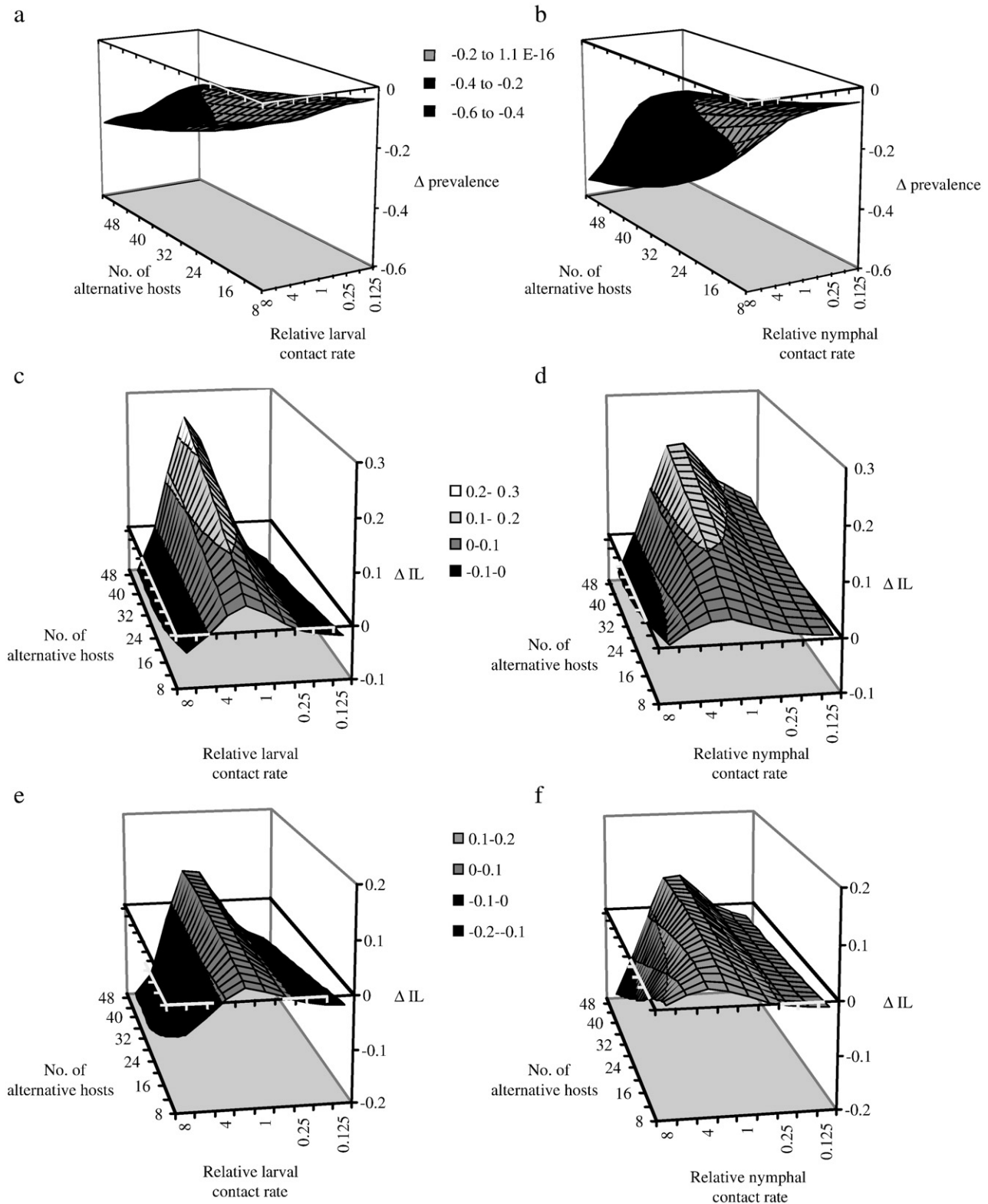


Fig. 3. The annual mean prevalence of infection in engorged larvae (graphs a and b), or the actual annual total of infected engorged larvae (graphs c and f), dropping from all hosts at model equilibrium in Scenarios 1 and 2 (see [Methods](#)). In all cases, the difference in prevalence (Δ prevalence) or numbers (Δ IL), from the same values obtained in a simulation in which no alternative hosts were included, are shown as a proportion of the value obtained with no alternative hosts. At point Δ IL or Δ prevalence = 0 there is no difference relative to the baseline scenario (i.e. no alternative hosts). Values for the difference in the number of infected engorged larvae dropping from hosts that are lower than zero (the darkest areas of the graphs) indicate that a dilution effect occurred when the model was set with the combined parameter values on the x- and y-axes. Alternative host abundance is on the y-axis in all graphs. On the x-axis are the factors by which the basic rate at which questing larvae found alternative hosts (HFRLA) was increased or decreased above that for *P. leucopus* (graphs a, c and e), or the factors by which the basic rate at which questing nymphs found alternative hosts (HFRNA) was increased or decreased above that for *P. leucopus* (graphs b, d and f). In graphs c and d, transmission efficiencies from infected hosts to larvae were 0.6 and 0.1 respectively for *P. leucopus* and the alternative host, while in graphs e and f these values were 0.9 and 0.02.

between alternative hosts and *P. leucopus* was increased (compare graphs in Figs. 3c and 3d, with 3e and 3f).

Scenarios with interspecific host competition

With strong interspecific competition, i.e., when alternative hosts replaced *P. leucopus* in the model almost one-for-one, (Fig. 4a), indirect dilution occurred in all simulations (Fig. 4c). Even with more moderate interspecific competition, i.e. when alternative hosts replaced *P. leucopus* in the model on approximately a three-for-one basis (Fig. 4b), indirect dilution still occurred in all simulations, although the effect was less pronounced (Fig. 4d).

Local sensitivity analyses to other model parameters

Analyses of the sensitivity of the model outcomes (the abundance of infected engorged larvae produced by the system per year at model equilibrium) to changes in parameter values that were not directly investigated in the aforementioned simulations, are presented in Appendix D. The outcome was most sensitive to variables affecting the survival of tick vectors and the abundance of *P. leucopus* relative to alternative hosts, which was consistent with the findings of simulations described above.

Investigating field evidence for a dilution effect

When simulations were run using an alternative host representing the community of alternative hosts in LoGiudice et al. (2003), the

infection prevalence in engorged larvae dropping from the hosts (equivalent to NIP) was lower when the alternative host was included across the range of *P. leucopus* numbers in the model (Fig. 5a). This reduction in NIP was similar, but more pronounced, when chipmunks (a moderately reservoir-competent host) were excluded from the alternative host community (Fig. 5b). These results are consistent with the model results of LoGiudice et al. (2003) when the alternative host community was “added” to the mouse population. However, the difference in the actual numbers of infected engorged larvae dropping from all hosts (IL) indicated an amplification effect at all *P. leucopus* densities investigated, which still occurred, although less markedly, when chipmunks were excluded (Figs. 5c, d).

When simulations were run with values of HFRLA and HFRNA from the range of field observations, the individual mammalian alternative host species were predicted in many cases to cause a dilution effect (Table 2). Although not shown in this table, birds were predicted to cause a dilution effect because they carry many nymphs but relatively few larvae according to the tick infestation data quoted in LoGiudice et al. (2003), which were used in the simulations.

Discussion

In this study we have investigated the possible effects of host biodiversity on *B. burgdorferi* transmission cycles, and thus on Lyme disease risk. To do this we used a mechanistic model that accounted for seasonal transmission and introduction of susceptible rodent hosts, and incorporated our most realistic estimates of the effect that

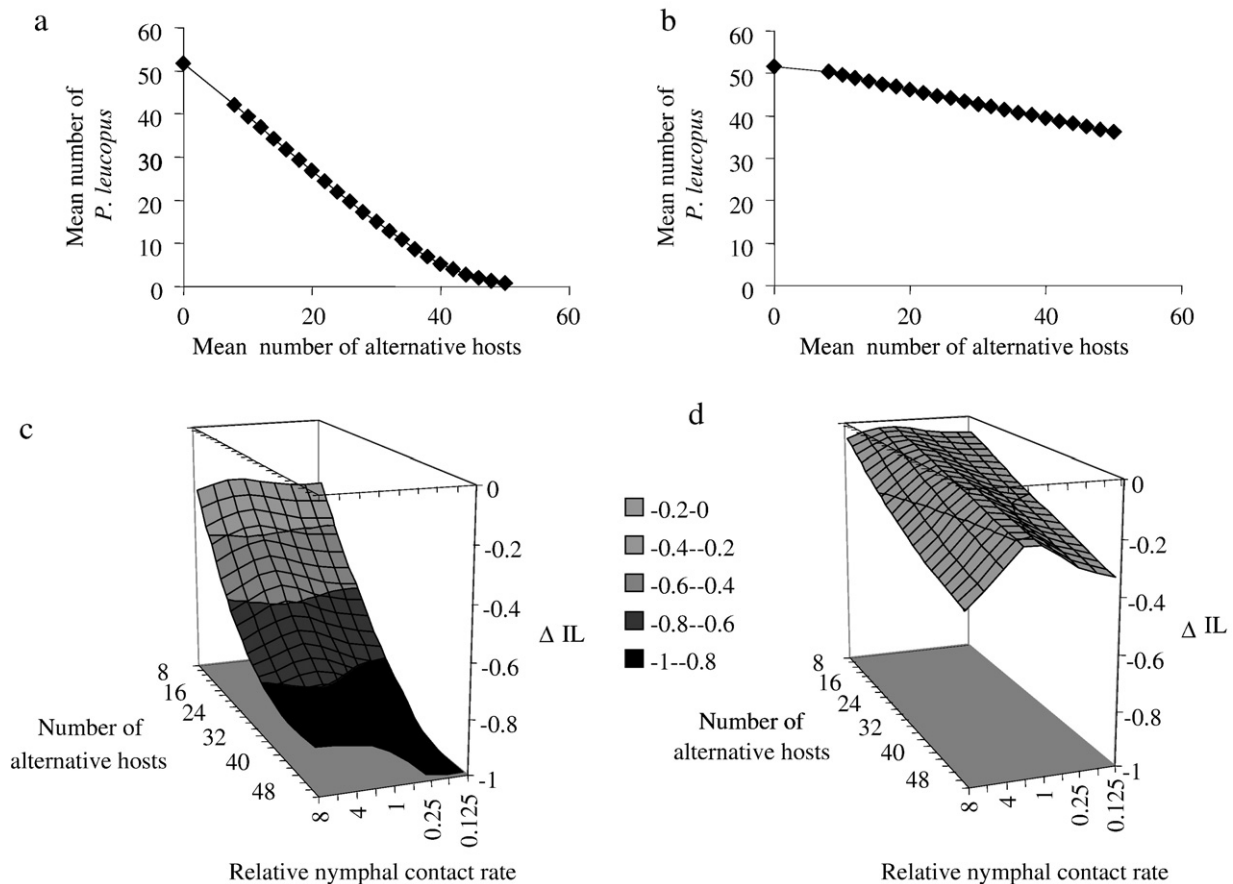


Fig. 4. Effects of ‘competition’ between *P. leucopus* and alternative hosts on changes in the annual total number of infected engorged larvae dropping from all hosts at model equilibrium (ΔIL), relative to the number obtained in simulations in which the alternative host was not included. At point $\Delta IL = 0$ there is no difference relative to the baseline scenario (i.e. no alternative hosts). Graph a shows the effect of almost one-to-one replacement of *P. leucopus* with alternative hosts, while graph b shows the effect of three-to-one replacement of *P. leucopus* with alternative hosts. Under these conditions respectively, changes in the annual total number of infected engorged larvae dropping from all hosts at model equilibrium, relative to the number obtained in simulations in which the dilution host was not included, are shown in graphs c and d.

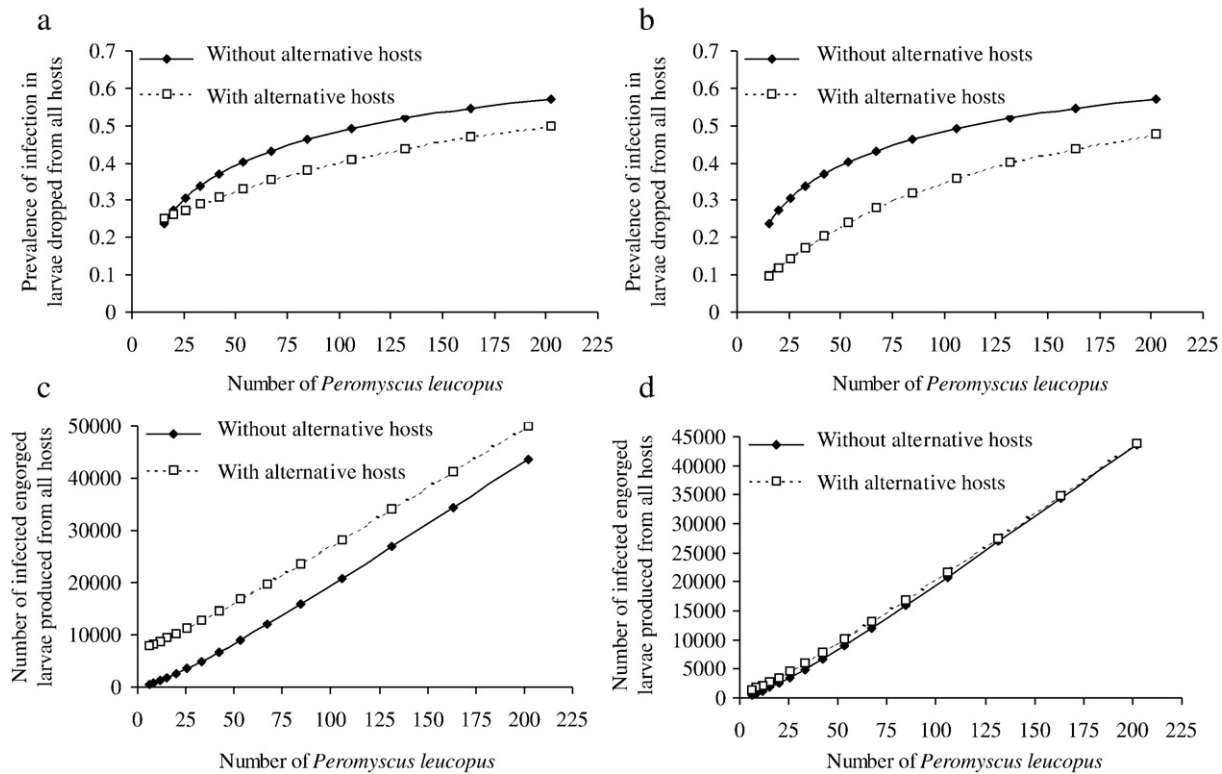


Fig. 5. A comparison of the infection prevalence in engorged larvae dropping from all hosts (graphs a and b) and the number of infected engorged larvae droppings from all hosts (graphs c and d) when the model was run with and without an alternative host representing actual densities and tick infestation levels seen in the field (Lo Giudice et al., 2003). Graphs a and c show the results of simulations using data from all hosts in Lo Giudice et al. (2003) except shrews and chipmunks. In graphs a and b, reduction in prevalence was consistent across most values for the number of *P. leucopus* in the model. In graphs c and d an amplification effect occurred at all values for *P. leucopus* numbers.

increasing host abundance may have on the number of tick vectors in the system. Our model simulations indicated that the dilution effect is not an axiom of Lyme disease ecology, but we identify specific circumstances under which dilution may well occur: i) if diversity negatively impacts *P. leucopus* density (via any form of competition: direct, indirect or apparent) causing an indirect dilution effect, ii) if the alternative host community feeds proportionately more nymphs than larvae compared to *P. leucopus*, and/or iii) if tick mortality is higher on alternative hosts. Significantly though, if these effects are not present, the more likely outcome of introducing hosts of another species is not a neutral effect, but amplification of transmission cycles.

Ticks are very different from mosquitoes (Randolph, 1998), with which they are often lumped for convenience as 'arthropod vectors'. Pathogen transmission by mosquitoes is effectively frequency-dependent (i.e. independent of host abundance) because adult mosquito density is determined mostly by host-independent factors (such as climate) on survival of free-living immature mosquito stages (Reiter, 2001; Dobson, 2004). However, because all feeding stages of ticks are parasitic, tick density depends much more on host density (e.g. Wilson et al., 1984; Randolph and Steele, 1985; Daniels and Fish, 1995; Jones et al., 1998; Ostfeld et al., 2001, 2006; Rand et al., 2003; Randolph, 2004). Thus, pathogen transmission by tick vectors comprises elements of both frequency-dependency (being dependent on biting rates of infected vectors rather than on the immediate abundance of infected hosts) and density-dependency (via time-lagged effects of host abundance on vector abundance). Our study illustrates the need to study tick-borne pathogens in models that account for effects of host density on both vector and pathogen abundance.

If transmission of tick-borne zoonoses comprises an element of density-dependence then dilution of tick-borne zoonoses is less likely to occur per se, as pointed out by Dobson (2004). In the model,

amplification was the default because adding alternative hosts to the system increased tick abundance, and increased numbers of infected engorged larval ticks were produced from both alternative hosts and *P. leucopus*, even though the prevalence of infection in engorged larvae fell. This is conceptually similar to the 'rescue effect' of adding reservoir-incompetent hosts that boost tick numbers and enhance transmission amongst reservoir hosts when their density would be too low to sustain transmission cycles (Norman et al., 1999; Ogden et al., 2007). However, dilution occurred when model parameters were set to constrain the effect alternative hosts had on amplifying tick abundance, while maintaining the effect they had on diverting infective nymphs from *P. leucopus* reservoirs, i.e. dilution occurred if the positive effects of adding alternative hosts on tick survival were minimised. Because mosquito abundance is much less dependent on host density the dilution of mosquito-borne pathogens by diverse host communities may be a more certain outcome (Ezenwa et al., 2006).

We used a mechanistic model to explore explicitly the effects of alternative hosts on tick survival and account for the effects of seasonality on transmission from *P. leucopus*. Complex mechanistic models comprise many parameters, and many different potential output values can be obtained by altering the parameter values. We have striven, however, to ensure that the model does represent nature in key respects relevant to the study, and that comparisons amongst simulations are valid. This was ensured by ascribing precisely the same parameter values for both *P. leucopus* and the alternative host, except for parameters of interest (i.e. different abundance, host-to-tick transmission efficiency, and, in some simulations, rates that immature ticks found the hosts). In particular, on-host tick mortality and post-prandial survival rates of ticks on alternative hosts and *P. leucopus* were identical, such that increasing the abundance of alternative hosts had precisely the same effect on tick abundance as increasing the abundance of *P. leucopus*, except when contact rates

with ticks were explicitly changed. Also, the model was structured so that infected and uninfected nymphs arising from all hosts mixed homogeneously and could not affect infection prevalence in *P. leucopus* or alternative hosts disproportionately to the relative rates at which the ticks attached to these hosts. Lastly, while alternative host abundance did not vary seasonally as did that of *P. leucopus* (via seasonally variable birth and death rates), infected and uninfected ticks from alternative hosts were subject to identical seasonality as ticks from other hosts in the model. Therefore, changes to infection rates of *P. leucopus* in the model were simply due to changes in abundance of infected and uninfected ticks, rather than alteration of the simulated seasonality of infection of *P. leucopus*.

Our findings were consistent with the broad findings of the models of Schmidt and Ostfeld (2001) and Van Buskirk and Ostfeld (1995). In the former, reductions in DIN were obtained when the default for the model was competition between *P. leucopus* and other less competent species. In the latter, in the absence of competition, increasing abundance of an alternative host reduced NIP but increased DIN and thus induced amplification. Our model also reproduced the reduction in NIP consistent with the model of LoGiudice et al. (2003). While these researchers emphasize the effect of dilution with increased biodiversity, our results instead suggest a predominance of amplification.

However, the main objective of our study is to further enlighten as to whether or not increasing diversity in natural communities of North America really reduces Lyme disease risk to the public. Our modeling study suggests that a more mechanistic understanding of the effect of diversity in this context becomes important in three key respects.

First, empirical studies have already shown that an indirect dilution effect will result if a 'monoculture' of a highly efficient reservoir species, is changed by simply replacing (by interspecific competition) one or more efficient reservoir individuals with those of a species that is a less efficient reservoir, assuming that the two species are equally efficient hosts for tick vectors (Tsao et al., 2004). Complete competition amongst possible reservoirs of *B. burgdorferi* with increasing biodiversity seems unlikely in nature because *P. leucopus* can be a very invasive species (Long, 1996). Partial competition, however, may occur in some circumstances (Schulte-Hostedde and Brooks, 1997; Nupp and Swihart, 2001; Schmidt et al., 2005; Smith and Carpenter, 2006), in which case our model indicates that dilution would be a highly likely response, even if total host abundance, and therefore tick abundance, increased.

Second, a dilution effect can be simply concluded if the introduced host species acts as a 'sink' for ticks and has a net negative effect on tick population abundance even if it is equally efficient as a reservoir (i.e. infected individuals of both species infect a high proportion of ticks that feed on them). In this case the introduced host species kills ticks more efficiently either by virtue of more efficient grooming or a more efficient acquired immune response to feeding ticks (Dizij and Kurtenbach, 1995; Craig et al., 1996; Levin and Fish, 1998). The existence of 'sink' species for *I. scapularis* is possible. For example, raccoons and perhaps opossums acquire measurable resistance to *I. scapularis*, whereas *P. leucopus* do not (Craig et al., 1996 and Slajchert et al., 1997 versus Levin and Fish, 1998). This potential mechanism for dilution remains to be investigated empirically in most species.

Third, as already stated and demonstrated in the field (Table 2), if alternative hosts acquire ticks at a higher rate than *P. leucopus*, and have equal or greater density-dependent effects on tick mortality, then dilution is more likely.

In previous reviews, these factors have been considered as theoretically possible methods whereby biodiversity could produce a dilution effect (Ostfeld and Keesing, 2000a,b; Keesing et al., 2006). Here we show through modeling that these comprise the precise mechanisms whereby increasing biodiversity could produce a dilution effect on Lyme disease risk, and that without them, an amplification of Lyme disease risk is more likely.

Our simulations produced the same results as LoGiudice et al. (2003) regarding effect of increasing biodiversity on NIP. Our study suggests that without accounting for any competition, the net effect of the whole alternative host community would be to increase the numbers of infected engorged larvae produced in the system and thus increase Lyme disease risk. However, while our simulations illustrate that amplification is a plausible outcome of increased biodiversity, a dilution effect still may have operated at the study site used by LoGiudice et al. (2003). Our study shows that the occurrence of dilution or amplification depends on three key parameters: tick attachment rates to alternative hosts and *P. leucopus*, direct and density-dependent mortality of ticks on different host species, and competition amongst alternative hosts and *P. leucopus*. Parameterization of our model using means for these values resulted in amplification rather than dilution, but field observations are scant and use small sample sizes with correspondingly large errors around the estimates: dilution could have resulted were the parameters only slightly different. Furthermore, different constructions of the community could produce a dilution effect. Importantly however, the result of changes to all the parameters including host densities would be dilution or amplification and not a neutral middle ground.

If biodiversity can lead to a significant dilution effect for *B. burgdorferi*, then this is of considerable public health significance, not only where Lyme disease is endemic, but particularly where it is emerging. However, our conclusion is that, in contrast to current dogma, transmission cycles of the agent of Lyme disease, and possibly agents of other tick-borne zoonoses, may not easily be diluted by increasing biodiversity. This is because, in contrast to mosquito-borne zoonoses, vector abundance is highly dependent on host density, so transmission of tick-borne diseases is very dependent on the density of all tick hosts regardless of their reservoir competence. Dilution of tick-borne zoonoses, however, may well occur in nature via mechanisms of competition between reservoir-competent and less competent hosts, interspecific differences in contact rates with different tick instars, and acquired resistance to ticks. Empirical research on these mechanisms are needed, therefore, to help clarify whether, and under what circumstances, diverse host communities may dilute the agent of Lyme disease in nature.

Acknowledgments

We thank Graham Hickling and two anonymous reviewers for providing constructive comments on previous drafts that have improved the manuscript.

Appendix A. Supplementary data

Supplementary data associated with this article can be found, in the online version, at doi:10.1016/j.epidem.2009.06.002.

References

- Allan, B.F., Keesing, R.S., Ostfeld, F., 2003. Effects of habitat fragmentation on Lyme disease risk. *Conserv. Biol.* 17, 267–272.
- Barkalow Jr., F.S., Hamilton, R.B., Soots Jr., R.F., 1970. The vital statistics of an unexploited gray squirrel population. *J. Wildlife Manage.* 34, 489–500.
- Battaly, G.R., Fish, D., 1993. Relative importance of bird species as hosts for immature *Ixodes dammini* (Acari: Ixodidae) in a suburban residential landscape of southern New York State. *J. Med. Entomol.* 30, 740–747.
- Begon, M., 2008. Effects of host diversity on disease dynamics. In: Ostfeld, R.S., Keesing, F., Eviner, V. (Eds.), *Infectious Disease Ecology: Effects of Ecosystems on Disease and of Disease on Ecosystems*. Princeton University Press, Princeton, pp. 12–29.
- Bown, K.J., Begon, M., Bennett, Z., Woldehiwet, M., Ogden, N.H., 2003. Seasonal dynamics of *Anaplasma phagocytophila* in a rodent-tick (*Ixodes trianguliceps*) system, United Kingdom. *Emerg. Infect. Dis.* 9, 63–70.
- Brisson, D., Dykhuizen, D.E., 2004. ospC diversity in *Borrelia burgdorferi*: different hosts are different niches. *Genetics* 168, 713–722.
- Brisson, D., Dykhuizen, D.E., Ostfeld, R.S., 2008. Conspicuous impacts of inconspicuous hosts on the Lyme disease epidemic. *Proc. Biol. Sci.* 275, 227–235.

- Crooks, E., Randolph, S.E., 2006. Walking by *Ixodes ricinus* ticks: intrinsic and extrinsic factors determine the attraction of moisture or host odour. *Exp. Biol.* 209, 2138–2142.
- Craig, L.E., Norris, D.E., Sanders, M.L., Glass, G.E., Schwartz, B.S., 1996. Acquired resistance and antibody response of raccoons (*Procyon lotor*) to sequential feedings of *Ixodes scapularis* (Acari: Ixodidae). *Vet. Parasitol.* 63, 291–301.
- Daniels, T.J., Fish, D., 1995. Effect of deer exclusion on the abundance of immature *Ixodes scapularis* (Acari: Ixodidae) parasitizing small and medium-sized mammals. *J. Med. Entomol.* 32, 5–11.
- Davidar, P., Wilson, W., Ribeiro, J.M.C., 1989. Differential distribution of immature *Ixodes dammini* (Acari: Ixodidae) on rodent hosts. *J. Parasitol.* 75, 898–904.
- Derdáková, M., Dudišák, V., Brei, B., Brownstein, J.S., Schwartz, L., Fish, D., 2004. Interaction and transmission of two *Borrelia burgdorferi* sensu stricto strains in a tick–rodent maintenance system. *Appl. Env. Microbiol.* 70, 6783–6788.
- Dobson, A., 2004. Population dynamics of pathogens with multiple host species. *Am. Nat.* 164, S64–S78.
- Dobson, A., Cattadori, I., Holt, R.D., Ostfeld, R.S., Keesing, F., Krichbaum, K., Rohr, J.R., Perkins, S.E., Hudson, P.J., 2006. Sacred cows and sympathetic squirrels: the importance of biological diversity to human health. *PLoS Med.* 3, e231.
- Donahue, J.G., Piesman, J., Spielman, A., 1987. Reservoir competence of white-footed mice for Lyme disease spirochetes. *Am. J. Trop. Med. Hyg.* 36, 92–96.
- Diuk-Wasser, M.A., Gatewood, A.G., Cortinas, M.R., Yaremych-Hamer, S., Tsao, J., Kitron, U., Hickling, G., Brownstein, J.S., Walker, E., Piesman, J., Fish, D., 2006. Spatiotemporal patterns of host-seeking *Ixodes scapularis* nymphs (Acari: Ixodidae) in the United States. *J. Med. Entomol.* 43, 166–176.
- Dizij, A., Kurtenbach, K., 1995. *Clethrionomys glareolus*, but not *Apodemus flavicollis*, acquires resistance to *Ixodes ricinus* L., the main European vector of *Borrelia burgdorferi*. *Parasite Immunol.* 17, 177–183.
- Ezenwa, V.O., Godsey, M.S., King, R.J., Guptill, S.C., 2006. Avian diversity and West Nile virus: testing associations between biodiversity and infectious disease risk. *Proc. Biol. Sci.* 273, 109–117.
- Falco, R.C., McKenna, D.F., Daniels, T.J., Nadelman, R.B., Nowakowski, J., Fish, D., Wormser, G.P., 1999. Temporal relation between *Ixodes scapularis* abundance and risk for Lyme disease associated with erythema migrans. *Am. J. Epidemiol.* 149, 771–776.
- Hanincová, K., Kurtenbach, K., Diuk-Wasser, M., Brei, B., Fish, D., 2006. Epidemic spread of Lyme borreliosis, northeastern United States. *Emerg. Infect. Dis.* 12, 604–611.
- Hosseini, P.R., Dhondt, A.A., Dobson, A., 2004. Seasonality and wildlife disease: how seasonal birth, aggregation and variation in immunity affect the dynamics of *Mycoplasma gallisepticum* in house finches. *Proc. Biol. Sci.* 271, 2569–2577.
- Jones, C.G., Ostfeld, R.S., Richard, M.P., Schaubert, E.M., Wolff, J.O., 1998. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. *Science* 279, 1023–1026.
- Keeling, M.J., Grenfell, B.T., 2002. Understanding the persistence of measles: reconciling theory, simulation and observation. *Proc. Biol. Sci.* 269, 335–343.
- Keirans, J.E., Hutcheson, H.J., Durden, L.A., Klompen, J.S.H., 1996. *Ixodes (Ixodes) scapularis* (Acari: Ixodidae): redescription of all active stages, distribution, hosts, geographical variation, and medical and veterinary importance. *J. Med. Entomol.* 33, 297–318.
- Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. *Ecol. Lett.* 9, 485–498.
- Kitron, U., Jones, C.J., Bouseman, J.K., 1991. Spatial and temporal dispersion of immature *Ixodes dammini* on *Peromyscus leucopus* in northwestern Illinois. *J. Parasitology* 77, 945–949.
- Kurtenbach, K., Hanincová, K., Tsao, J., Margos, G., Fish, D., Ogden, N.H., 2006. Key processes in the evolutionary ecology of Lyme borreliosis. *Nat. Rev. Microbiol.* 4, 660–669.
- Levin, M.L., Fish, D., 1998. Density-dependent factors regulating feeding success of *Ixodes scapularis* larvae (Acari: Ixodidae). *J. Parasitol.* 84, 36–43.
- Levin, M.L., Nicholson, W.L., Massung, R.F., Sumner, J.W., Fish, D., 2002. Comparison of the reservoir competence of medium-sized mammals and *Peromyscus leucopus* for *Anaplasma phagocytophilum* in Connecticut. *Vector Borne Zoonotic Dis.* 2, 125–136.
- Lindsay, L. R., 1995. Factors limiting the density of the black-legged tick, *Ixodes scapularis*, in Ontario, Canada. PhD Thesis, University of Guelph.
- Lo Giudice, K., Ostfeld, R.S., Schmidt, K.A., Keesing, F., 2003. The ecology of infectious disease: effects of host diversity and community composition on Lyme disease risk. *Proc. Natl. Acad. Sci.* 100, 567–571.
- Long, C.A., 1996. Ecological replacement of the deer mouse, *Peromyscus maniculatus*, by the white-footed mouse, *P. leucopus*, in the Great Lakes region. *Can. Field Nat.* 110, 271–277.
- Mannelli, A., Kitron, U., Jones, C.J., Slajchert, T.L., 1993. *Ixodes dammini* (Acari: Ixodidae) infestation on medium-sized mammals and blue jays in northwestern Illinois. *J. Med. Entomol.* 30, 950–952.
- Mannelli, A., Kitron, U., Jones, C.J., Slajchert, T.L., 1994. Influence of season and habitat on *Ixodes scapularis* infestation on white-footed mice in northwestern Illinois. *J. Parasitol.* 80, 1038–1042.
- Mather, T.N., Wilson, M.L., Moore, S.I., Ribeiro, J.M., Spielman, A., 1989. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). *Am. J. Epidemiol.* 130, 143–150.
- Mount, G.A., Haile, D.G., Daniels, E., 1997. Simulation of blacklegged tick (Acari: Ixodidae) population dynamics and transmission of *Borrelia burgdorferi*. *J. Med. Entomol.* 34, 461–484.
- Norman, R., Bowers, R.G., Begon, M., Hudson, P.J., 1999. Persistence of tick-borne virus in the presence of multiple host species: tick reservoirs and parasite-mediated competition. *J. Theor. Biol.* 200, 111–118.
- Nupp, T.E., Swihart, R.K., 2001. Assessing competition between forest rodents in a fragmented landscape of midwestern USA. *Mammalian Biology* 66, 345–356.
- Ogden, N.H., Bigras-Poulin, M., Barker, I.K., Lindsay, L.R., Maarouf, A., O Callaghan, C.J., Smoyer-Tomic, K.E., Waltner-Toews, D., Charron, D., 2005. A dynamic population model to investigate effects of climate on geographic range and seasonality of the tick *Ixodes scapularis*. *Int. J. Parasitol.* 35, 375–389.
- Ogden, N.H., Bigras-Poulin, M., O Callaghan, C.J., Barker, I.K., Kurtenbach, K., Lindsay, L.R., Charron, D.F., 2007. Vector seasonality, host infection dynamics and fitness of pathogens transmitted by the tick *Ixodes scapularis*. *Parasitology* 134, 209–227.
- Ogden, N.H., Lindsay, R.L., Sockett, P.N., Morshed, M., Artsob, H., 2008a. The rising challenge of Lyme disease in Canada. *Can. Comm. Dis. Rep.* 34, 1–19.
- Ogden, N.H., St-Onge, L., Barker, I.K., Brazeau, S., Bigras-Poulin, M., Charron, D.F., Francis, C.M., Heagy, A., Lindsay, L.R., Maarouf, A., Michel, P., Milord, F., O Callaghan, C.J., Trudel, L., Thompson, R.A., 2008b. Risk maps for range expansion of the Lyme disease vector, *Ixodes scapularis*, in Canada now and with climate change. *Int. J. Hlth. Geogr.* 7, 24.
- Ostfeld, R.S., Keesing, F., 2000a. Biodiversity and disease risk: the case of Lyme disease. *Conserv. Biol.* 14, 722–728.
- Ostfeld, R.S., Keesing, F., 2000b. The function of biodiversity in the ecology of vector-borne zoonotic diseases. *Can. J. Zool.* 78, 2061–2078.
- Ostfeld, R.S., Schaubert, E.M., Canham, C.D., Keesing, F., Jones, C.G., Wolff, J.O., 2001. Effects of acorn production and mouse abundance on abundance and *Borrelia burgdorferi* infection prevalence of nymphal *Ixodes scapularis* ticks. *Vector Borne Zoonotic Dis.* 1, 55–63.
- Ostfeld, R.S., Canham, C.D., Oggenfuss, K., Winchcombe, R.J., Keesing, F., 2006. Climate, deer, rodents, and acorns as determinants of variation in Lyme disease risk. *PLoS Biol.* 4, e145.
- Rand, P.W., Lacombe, E.H., Smith Jr., R.P., Ficker, J., 1998. Participation of birds (*Aves*) in the emergence of Lyme disease in Southern Maine. *J. Med. Entomol.* 35, 270–276.
- Rand, P.W., Lubelczyk, C., Lavigne, G.R., Elias, S., Holman, M.S., Lacombe, E.H., Smith Jr., R.P., 2003. Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). *J. Med. Entomol.* 40, 179–184.
- Randolph, S.E., 1998. Ticks are not insects: consequences of contrasting vector biology for transmission potential. *Parasitol. Today* 14, 186–192.
- Randolph, S.E., 2004. Tick ecology: processes and patterns behind the epidemiological risk posed by ixodid ticks as vectors. *Parasitology* 129, S37–S65.
- Randolph, S.E., Steele, G.M., 1985. An experimental evaluation of conventional control measures against the sheep tick *Ixodes ricinus* (L.) (Acari: Ixodidae). II. The dynamics of the tick–host interaction. *Bull. Entomol. Res.* 75, 501–518.
- Randolph, S.E., Mikšlová, D., Rogers, D.J., Labuda, M., 1999. Incidence from coincidence: patterns of tick infestations on rodents facilitate transmission of tick-borne encephalitis virus. *Parasitology* 118, 177–186.
- Reiter, P., 2001. Climate change and mosquito-borne disease. *Environ. Health Persp.* 109, S141–S161.
- Schmidt, K.A., Ostfeld, R.S., 2001. Biodiversity and the dilution effect in disease ecology. *Ecology* 82, 609–619.
- Schmidt, K.A., Ostfeld, R.S., Schaubert, E.M., 1999. Infestation of *Peromyscus leucopus* and *Tamias striatus* by *Ixodes scapularis* (Acari: Ixodidae) in relation to the abundance of hosts and parasites. *J. Med. Entomol.* 36, 749–757.
- Schmidt, K.A., Manson, R., Lewis, D., 2005. Voles competing with mice: differentiating exploitative, interference and apparent competition using patch use theory. *Evol. Ecol. Res.* 7, 273–286.
- Schulte-Hostedde, A.I., Brooks, R.J., 1997. An experimental test of habitat selection by rodents of Algonquin Park. *Can. J. Zool.* 75, 1989–1993.
- Shaw, M.T., Keesing, F., McGrail, R., Ostfeld, R.S., 2003. Factors influencing the distribution of larval blacklegged ticks on rodent hosts. *Am. J. Trop. Med. Hyg.* 68, 447–452.
- Slajchert, T., Kitron, U.D., Jones, C.J., Mannelli, A., 1997. Role of the eastern chipmunk (*Tamias striatus*) in the epizootiology of Lyme borreliosis in northwestern Illinois, USA. *J. Wild. Dis.* 33, 40–46.
- Smith, K.F., Carpenter, S.M., 2006. Potential spread of introduced black rat (*Rattus rattus*) parasites to endemic deer mice (*Peromyscus maniculatus*) on the California Channel Islands. *Diversity Distrib.* 12, 742–748.
- Sonenshine, D.E., 2004. Pheromones and other semiochemicals of ticks and their use in tick control. *Parasitology* 129, S405–S425.
- Thompson, C., Spielman, A., Krause, P.J., 2001. Coinfecting deer-associated zoonoses: Lyme disease, Babesiosis, and Ehrlichiosis. *Clin. Infect. Dis.* 33, 676–685.
- Tryon, C.A., Snyder, D.P., 1973. Biology of the eastern chipmunk, *Tamias striatus*: life tables, age distributions, and trends in population numbers. *J. Mammal.* 54, 145–168.
- Tsao, J.I., Wootton, J.T., Bunikis, J., Luna, M.G., Fish, D., Barbour, A.G., 2004. An ecological approach to preventing human infection: vaccinating wild mouse reservoirs intervenes in the Lyme disease cycle. *Proc. Natl. Acad. Sci. U. S. A.* 101, 18159–18164.
- Van Burskirk, J., Ostfeld, R.S., 1995. Controlling Lyme disease by modifying density and species composition of tick hosts. *Ecol. Appl.* 5, 1133–1140.
- Wilson, M.L., Levine, J.F., Spielman, A., 1984. Effect of deer reduction on abundance of the deer tick (*Ixodes dammini*). *Yale J. Biol. Med.* 57, 697–705.
- Young, H., 1955. Breeding behavior and nesting of the eastern robin. *Am. Midl. Nat.* 53, 329–352.