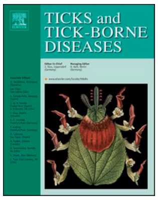
Ticks and Tick-borne Diseases 12 (2021) 101724

Contents lists available at ScienceDirect

Ticks and Tick-borne Diseases

journal homepage: www.elsevier.com/locate/ttbdis



Original article

Dilution and amplification effects in Lyme disease: Modeling the effects of reservoir-incompetent hosts on *Borrelia burgdorferi* sensu stricto transmission

Vardayani Ratti [a,*], Jonathan M. Winter [b], Dorothy I. Wallace [c]

[a] *Department of Mathematics and Statistics, California State University Chico, CA, United States*
[b] *Department of Geography, Dartmouth College, Hanover, NH, United States*
[c] *Department of Mathematics, Dartmouth College, Hanover, NH, United States*

ARTICLE INFO

Keywords:
Lyme disease
Dilution effect
Borrelia burgdorferi sensu stricto
Ixodes scapularis Say 1921
Mathematical model
Ticks

ABSTRACT

The literature on Lyme disease includes a lively debate about the paradoxical role of changing deer populations. A decrease in the number of deer will both (1) reduce the incidence of Lyme disease by decreasing the host populations for ticks and therefore tick populations, and (2) enhance the incidence of Lyme disease by offering fewer reservoir-incompetent hosts for ticks, forcing the vector to choose reservoir-competent, and therefore possibly diseased, hosts to feed on. A review of field studies exploring the net impact of changing deer populations shows mixed results. In this manuscript, we investigate the hypothesis that the balance of these two responses to changing deer populations depends on the relative population sizes of reservoir-competent vs. reservoir-incompetent hosts and the presence of host preference in larval and adult stages.

A temperature driven seasonal model of *Borrelia burgdorferi* sensu stricto (cause of Lyme disease) transmission among three host types (reservoir-competent infected and uninfected hosts, and reservoir-incompetent hosts) is constructed as a system of nonlinear ordinary differential equations. The model, which produces biologically reasonable results for both the tick vector *Ixodes scapularis* Say 1921 and the hosts, is used to investigate the effects of reservoir-incompetent host removal on both tick populations and disease prevalence for various relative population sizes of reservoir-competent hosts vs. reservoir-incompetent hosts.

In summary, the simulation results show that the model with host preference appears to be more accurate than the one with no host preference. Given these results, we found that removal of adult *I. scapularis*(Say) hosts is likely to reduce questing nymph populations. At very low levels questing adult abundance may rise with lack of adult hosts. There is a dilution effect at low reservoir-competent host populations and there is an amplification effect at high reservoir-competent host populations.

1. Background

Lyme disease is a common vector-borne disease caused by *Borrelia burgdorferi* sensu stricto in the U.S., characterized by an initial infection leading to later complications if not treated in its early stages (Ostfeld, 2011; Rosenberg et al., 2018). The tick, *Ixodes scapularis* Say 1921, is the primary vector in the Eastern United States, with the highest abundance of infectious ticks in the Northeast (Pepin et al., 2012).

The tick life cycle is complex, including three stages of maturation and molting, interrupted by periods of questing for a host and feeding. Dynamical models of these stages go back to the late 1990s and the subsequent work of Ogden and colleagues (Porco, 1999; Ogden et al., 2005). Maturation rates for these stages depend on temperature, and this dependency has been described by Ogden et al. (2004) and incorporated into models of the tick lifecycle with the goal of describing the observed seasonality of questing tick populations (Ogden et al., 2005; Wu et al., 2010; Dobson et al., 2011; Diuk-Wasser et al., 2010). Because temperature controls many aspects of the tick life cycle, many efforts have been made to link climate to the potential range of this vector. Some of these studies are empirical, some statistical, and some rely on dynamic models (Ogden et al., 2006, 2008a, b, 2014; Simon et al., 2014; Leighton et al., 2012; Brownstein et al., 2003; Wallace et al., 2019).

Some mammals (white footed mice, shrews) are reservoir-competent hosts for *B. burgdorferi* sensu stricto and others (deer, possums, raccoons)

---

* Corresponding author.
E-mail address: vratti@csuchico.edu (V. Ratti).

https://doi.org/10.1016/j.ttbdis.2021.101724
Received 5 October 2020; Received in revised form 28 March 2021; Accepted 29 March 2021

are not (LoGiudice et al., 2003). Competency for disease transmission may be present but low. For this study reservoir hosts with low competence are classified as reservoir-incompetent hosts (Levi et al., 2016; LoGiudice et al., 2003; Porco, 1999; Ogden et al., 2007; Ostfeld, 2011; Hamer et al., 2010; Rand et al., 2003). The prevalence of tick reservoir hosts varies with land use and human interventions, with consequences for both vector and disease.

Not only the number of ticks but also the fraction that carry disease, is an important determinant of disease risk. An abundance of infected ticks implies a higher contact rate of infected ticks with humans, reservoir hosts in particular. The number of infective bites per host per unit time, known as increasing the entomological inoculation rate (EIR), which is known to have a strong relationship with infection rates for other vector-borne diseases such as malaria (Beier et al., 1999; Smith et al., 2005). Tick reservoir hosts are not equally distributed throughout the landscape (Schulze and Jordan, 1996). This simple observation has led to several hypotheses about why *B. burgdorferi* sensu stricto is more prevalent in some locations than others, as well as suggestions for how to reduce or eliminate it in a region. One of the most frequently discussed reservoir hosts is white-tailed deer (*Odocoileus virginianus*). Because they are vector reservoir hosts, the reduction of deer could be expected to reduce overall incidence of *B. burgdorferi* sensu stricto while the increase of deer would increase incidence of the bacterium, called an “amplification effect” (Stafford III, 1993). On the other hand, it has been argued that because deer are incompetent disease reservoir hosts, their presence dilutes the transmission of disease and may be beneficial in reducing the incidence of *B. burgdorferi* sensu stricto (Levi et al., 2016). This second argument is referred to as “the dilution effect.” There are field studies that support and refute each argument. As no study has complete data on host populations, it remains a question whether the distribution of host populations accounts for wide discrepancies in the conclusions of these studies.

This study is based on a prior model used to investigate the impact of rising mean annual temperature on transmission dynamics of *B. burgdorferi* sensu stricto (Wallace et al., 2019). That model was parameterized with temperature-dependent maturation rates based on Ogden et al. (2004, 2005), annual temperature patterns for Hanover, NH, and host distributions from Levi et al. (2016). Winter et al. (2020) used the model of Wallace et al. (2019) calibrated over the Northeast to examine the sensitivity of *I. scapularis* abundance and timing to temperature and land cover. The influence of land cover, which impacted *I. scapularis* dynamics exclusively through differences in host populations, had a relatively weak effect (Winter et al., 2020). One key limitation to modeling the influence of reservoir hosts on *I. scapularis* abundance is the relative lack of observed data about *I. scapularis* and host (competent and incompetent) numbers across different land covers (Winter et al., 2020).

Our study considers a simplified situation with three host types: reservoir-competent hosts (based on infected or uninfected rodents) and reservoir-incompetent hosts (based on deer), at a range of population densities. In addition, a long day diapause for adults and short day diapause for nymphs were included (Belozerov, 2009; Belozerov et al., 2002b,a), leading to the observed double peak distribution of questing nymphs and adults (Ostfeld et al., 1995, 1996; Ogden et al., 2005; Lindsay et al., 1999b). We also considered an alternative scenario in which host preference plays a role, with larvae feeding only on rodents and adults feeding only on deer and nymphs feeding on both. The simulation results delineate circumstances under which reduction of deer is likely to have a noticeable impact on tick populations. The model also offers useful insight about what host distributions are likely to exhibit the dilution effects described in field studies, and whether or not these effects lead to reduced disease risk.

2. Methods

Fig. B.1 offers an overview of the relationships modeled in this study. System equations and parameter estimates are similar to those in Wallace et al. (2019) and are included in Appendix A. Simulations were run for 10 years using Matlab ode45 solver (MATLAB, 2018).

2.1. Equations and parameters.

All equations and parameters (see Appendix A) are taken from Wallace et al. (2019) with a few modifications. This model includes host distributions derived from field measurements in the Northeastern United States (LoGiudice et al., 2003). To simplify the question of dilution, the model considered only reservoir-incompetent deer and reservoir-competent rodents, as these two types of host are frequently cited as reasons for rise in tick populations and *B. burgdorferi* sensu stricto, respectively (Ostfeld, 2011). Default parameters and initial conditions for the remaining quantities are the same as in that paper (also given in Table B.1 in Appendix A). These include temperature related winter diapause. A bimodal distribution is often observed in the Northeastern U.S., as well as a two year life cycle (Lindsay et al., 1999a, b; Levi et al., 2016). The model produces such a distribution if a long day diapause is introduced such as the one observed (but not completely quantified) by Belozerov et al. (2002b). The default cutoff for both nymph and adult diapause was set at 0.555 day of light per day in order to produce the expected bimodal summer distribution of questing adult ticks, similar to the model in Winter et al. (2020).

2.2. Tick host preference

In a study of the dilution effect, Ogden et al. considered alternative reservoir hosts with differential contact rates and tick hosting capacities, as we do here (Ogden and Tsao, 2009). While those authors represent contact rates as a single parameter, here we expand the process to incorporate reported host densities and estimated on-host tick carrying capacities. Two processes are at work here, as the contact rate, or probability of encountering a specific host type, depends on the fraction of reservoir hosts of a given category, while the ability to remain on the host and feed depends on the overall tick capacity for that category. Several other models consider multiple host classes. Ogden et al. (2005) give a two-host model in which larvae and nymphs feed only on rodents or other small mammals, while adults feed only on deer. Hock et al. also create a two-host model with the same feeding assumptions. Lou and Wu extends this models by comparing host-seeking functional forms under the same assumption that smaller stages feed on rodents and the adult stage on deer (Lou and Wu, 2014). The basic assumptions about feeding preference in these models are not observed to hold in the field, where larvae are found on mammals of all sorts and birds, with over 200 larvae observed on deer (LoGiudice et al., 2003). Surveys of tick on deer show all three stages present (Lindsay et al., 1999b).

It is nonetheless believed that earlier life stages may be more likely to be picked up by small mammals, while larger mammals offer larger blood meals to later stages (Pfäffle et al., 2013). In practice, it is not known whether this is a small or large effect, and it has not been quantified by field data that would suggest electivity measures comparable to those for foraging animals (Jacobs, 1974; Chesson, 1983; Lechowicz, 1982). The first model constructed here embraces a form of the null hypothesis, by assuming that tick-host contact rates depend on population densities of reservoir hosts and ticks irrespective of life stage, and that all on-host ticks taken together are subject to a single on-host carrying capacity. As a second experiment, the model was altered so that questing larvae only feed on rodents and questing adults only feed on deer, while nymphs could feed on either type of host. This experiment represents an extreme version of parasite preference but may be closer to real observation than assuming no preference at all. Fig. B.2 and Fig. B.6 shows time series population dynamics for both scenarios at steady state, as well as a 10-year simulation to verify that both models arrive at steady state.

For both numerical experiments, carrying capacities of deer and rodents were reduced from default values (25 deer, 9335 rodents per km^2) reported in the literature (Levi et al., 2016). Probability of host to tick disease transmission was chosen to produce approximately 40% infected nymphs on average at steady state, as observed in some field measurements (Schmidt and Ostfeld, 2001).

Please refer to Fig. B.1 for symbols discussed in the following text. Average percent infected questing nymphs and average percent infected questing adults are calculated using the formulae

$$\frac{\int \frac{\mathrm{NI}_2}{\mathrm{NI}_2+\mathrm{NU}_2}\mathrm{dt}}{\mathrm{counter1}}$$

and

$$\frac{\int \frac{\mathrm{AI}_2}{\mathrm{AI}_2+\mathrm{AU}_2}\mathrm{dt}}{\mathrm{counter2}}$$

respectively, where counter1 is the number of days when $\mathrm{NI}_2 > 0$. Similarly, counter2 is the number of days when $\mathrm{AI}_2 > 0$. Note that questing infected and non-infected tick populations appear together, and any of these could have been tracked by the counter, to the same effect. In both cases, the integral is taken over the last (i.e., 10th) year.

Average percent of total feeding nymphs on deer is calculated using the following formula

$$\frac{\int \frac{\mathrm{FNU}_a+\mathrm{FNI}_a}{\mathrm{totalnymphs}}\mathrm{dt}}{\mathrm{counter3}}$$

where

$$\text{total nymphs} = \mathrm{FNU}_a + \mathrm{FNU}_b + \mathrm{FNU}_c + \mathrm{FNU}_d + \mathrm{FNU}_f + \mathrm{FNI}_a + \mathrm{FNI}_b + \mathrm{FNI}_c + \mathrm{FNI}_d + \mathrm{FNI}_f$$

and counter3 is the number of days when total nymphs is non-zero and one of the terms in the numerator (i.e., FNU_a or FNI_a) is non-zero. In this case also, the integral is taken over the last year. Similarly, average percent of total nymphs on mice is calculated using the following formula

$$\frac{\int \frac{\mathrm{FNU}_d+\mathrm{FNU}_f+\mathrm{FNI}_d+\mathrm{FNI}_f}{\mathrm{totalnymphs}}\mathrm{dt}}{\mathrm{counter4}}$$

where counter4 is the number of days when total nymphs is non-zero and one of the terms in the numerator (i.e., $\mathrm{FNU}_d, \mathrm{FNU}_f, \mathrm{FNI}_d, \mathrm{FNI}_f$) is non-zero.

Cumulative infected questing nymphs over the last year is calculated by $\int \mathrm{NI}_2\mathrm{dt}$ over the last year. Similar formulae are used to calculate cumulative infected adults. Total questing adults and total questing nymphs over the last year are calculated by $\int(\mathrm{AU}_2 + \mathrm{AI}_2)\mathrm{dt}$ and $\int(\mathrm{NU}_2 + \mathrm{NI}_2)\mathrm{dt}$ respectively.

To investigate the role of host distributions, the carrying capacities of reservoir-competent hosts (K_C) per square kilometer and reservoir-incompetent hosts (K_I) were varied from low to high. The default values producing the time series runs are in a high range for reservoir-competent hosts. Resulting quantities of questing nymphs and adults, as well as disease prevalence, are displayed as heat maps or scatter plots in Figs. B.3–B.6.

3. Results

Both models produce an annual pattern of emergence with two distinct peaks for questing adults, as seen in Fig. B.2. Fig. B.2a and b show the seasonal pattern for questing nymphs with and without host preference. Fig. B.2c and d show the bimodal pattern for adults with and without host preference. Fig. B.2e and f show the infected nymph compartment arriving at steady state for both models.

For scenarios with sufficient reservoir hosts present, both models reach steady state oscillating patterns. Also two runs of multiple years for both models just to illustrate that we get steady state with the default parameters.

3.1. Questing nymph abundance and feeding behavior

Whether host preference is included or not, the cumulative number of questing nymphs rises with both host categories at low reservoir-competent host (K_C) densities, as seen in Fig. B.3a and b. The cumulative number of questing nymphs rises with both host categories at high reservoir-competent host densities for the host preference case, as seen in Fig. B.3c. In the case of no host preference, this effect fades at high reservoir-competent host densities, and the cumulative questing nymph measure only rises noticeable with increased reservoir-competent hosts, seen in Fig. B.3d. Note also that the questing nymph population is similar both with and without host preference.

Feeding nymph behavior is similar for both models (with and without host preference) as the host distribution changes. In both cases one sees a gradual shift of host selection as the number of reservoir-incompetent hosts rises relative to the reservoir-competent host population, as in Figs. B.3e and f with low reservoir-competent host populations. At high reservoir-competent host populations, most feeding nymphs are on these reservoir-competent hosts, as seen in Figs. B.3g and h. Because the results are similar for both cases, the model suggests that host preference in larvae and adults does not create much difference in the distribution of feeding nymphs.

3.2. Questing adult abundance

Fig. B.4 shows the patterns of questing adult abundance with and without host preference. When there is no host preference for adults and larvae, the patterns of abundance are similar to those for nymphs. Fig. B.4b and d qualitatively resemble Fig. B.3b and d for nymphs.

In the case of host preference, the cumulative number of questing adults can be seen to decline as their host populations rise, reading a row left to right in Fig. B.4a. The cumulative number is in tick-days, and as the host populations rise the questing adult needs to spend less time questing, because the time required to find a host is inversely proportional to the size of host populations, resulting in more questing adults at any given time. When the number of reservoir-incompetent hosts rises sufficiently, the number of ticks rises so much that it outstrips the reduction in tick-days due to shorter questing. Even in the bigger range shown in Fig. B.4c this pattern persists, with cumulative adult questing tick-days dropping as the number of available reservoir hosts goes up and the questing time goes down.

3.3. Disease prevalence in questing nymphs

Because the population of questing nymphs is an order of magnitude greater than that of questing adults, it is worth considering the patterns of disease prevalence in this population in detail. Fig. B.5 shows cumulative questing tick-days and disease prevalence for both models. On a coarse grained big range of host values, one sees a pattern of infected questing tick abundance that is similar to overall questing tick abundance, in Fig. B.5a and b. Fig. B.5c and d show this relationship. Fig. B.5e and f illustrate that, in both models, disease rapidly establishes itself at a fixed prevalence as the number of reservoir-competent hosts increases. At all but the lowest reservoir-competent host value, there is only the slightest decline in infection prevalence with more reservoir-incompetent hosts.

The lowest level of reservoir-competence shown in Fig. B.5e and f does show a marked decline in disease prevalence with increasing reservoir-incompetent. This suggests that low levels of reservoir-competence should be investigated and may lead to conditions creating a dilution effect. Fig. B.5g and h show that, for both models, varying host distributions in a small reservoir-competent host range does show a decrease in prevalence as reservoir-incompetent populations rise. Disease prevalence is not a mark of the dilution effect, however. To have a dilution effect, the actual numbers of infected questing ticks would go down as the number of reservoir-incompetent hosts increases.

3.4. Dilution effects

For low reservoir-competent host populations, cumulative infected ticks are shown in Fig. B.6a–h. Fig. B.6b and f show no indication of any dilution effect for the model with no host preference. On the other hand, Fig. B.6a and e show a clear dilution effect for the model with host preference. Comparing Figs. B.5a and B.6 a, it is also clear that this dilution effect only holds at low levels of reservoir-competent hosts. At higher levels, by contrast, there is an amplification effect of adding more reservoir-incompetent hosts to the landscape.

The scatterplots shown in Fig. B.6b, c, f, and g show a general trend of more infected questing ticks when there are more questing ticks in general. This trend is more pronounced for the model with no host preference, in Fig. B.6d and h. The model with host preference shows a wide range of infected questing tick populations for a given total questing tick population, in Fig. B.6c and g.

For low reservoir-competent host populations, average percent infected ticks are shown in Fig. B.7a–h. Similar to Fig. B.6, the scatterplots shown in Fig. B.7b, c, f, and g also show a general trend of more infected questing nymphs when there are more questing nymphs in general. This trend is more pronounced for the model with no host preference, in Fig. B.7d and h. The model with host preference shows a wide range of infected questing nymph populations for a given total questing nymph population, in Fig. B.7c and g. This observation also translates to the case of high reservoir-competent host populations, in Fig. B.8.

4. Discussion

Two models were created according to the schematic diagram in Fig. B.1. One model assumes no host preference for ticks at any stage, while the other assumes extreme host preference with larvae feeding only on competent (infected or uninfected) reservoir hosts represented by a mix of rodent populations, and adults feeding only on reservoir-incompetent hosts represented by deer populations, with nymphs having no host preference. Both models produce steady state dynamics that represent the seasonal tick cycle well, as seen in Fig. B.2.

Although populations of questing nymphs are an order of magnitude larger than populations of questing adult ticks, the time series shown in Fig. B.2 gives questing periods that are somewhat disjointed for these populations, due to the diurnal diapause built into both models. In reality there may be more or less overlap in questing periods. In any case we consider both adult and nymph populations as both may provide evidence for preferring one of these models over the other, and both play a role in disease risk.

4.1. Evidence for host preference

With the model parameters, 1000 reservoir-competent hosts have a feeding tick capacity of 46,000 ticks, while 100 reservoir-incompetent hosts have a feeding tick capacity of 23,900 ticks, computed as number of hosts × per host carrying capacity. During the course of a single (simulated) season these capacities are not reached. However, encounter likelihood depends on numbers of reservoir hosts rather than capacity, so in both models, a nymph at any stage would be ten times more likely to encounter a reservoir-competent stationary host than a reservoir-incompetent mobile host, resulting in a higher fraction of feeding ticks on these smaller reservoir hosts. This shift can be seen in Fig. B.3e and f for low populations of reservoir-competent hosts. When a large number of reservoir-competent hosts is present, the feeding habits of nymphs shift to reservoir-competent hosts, as seen in Fig. B.3g and h.

In the model with no host preference, adults and larvae behave the same way. Thus, for all questing stages, removing a fraction of incompetent mobile reservoir hosts barely increases the likelihood of meeting competent immobile reservoir hosts, but does not necessarily reduce overall numbers of feeding ticks. For this model, as the number of reservoir-competent hosts rises, the relatively small number of reservoir-incompetent hosts becomes irrelevant. Although one sees a rise in questing nymph populations at low reservoir-competent host levels in Fig. B.3b, the pattern disappears with higher reservoir-competent host populations. Figs. B.3d and B.4 d show that when reservoir-competent host populations are large, little reduction of questing adult or nymph abundance results from removing the sparser but larger reservoir-incompetent hosts.

The model with host preference tells a different story. In this situation, as the number of reservoir-competent hosts becomes large, the smaller number of reservoir-incompetent hosts becomes the limiting factor for adults to mature and lay eggs, thus limiting populations at every stage. Fig. B.3c shows this limitation for questing nymph populations, which rise in response to an increase in reservoir-incompetent hosts. This reduction of questing nymph abundance is especially noticeable when the number of incompetent (adult) reservoir hosts is reduced to a very small amount, in some cases producing more than a 50% reduction in nymph abundance, seen in Fig. B.3c.

Numerous studies have found that the reduction of deer in a region causes the reduction of tick abundance, both for *Ixodes scapularis* Say 1921 (Stafford et al. in Table B.2), and other tick species as well (Tagliapietra et al., 2011).

Stafford III et al. (2003) conducted a study of deer and tick populations at two confined study areas in Connecticut from 1992 to 2002. The reduction in deer population at both sites went from over 90 deer per km^2 to 10–30 per km^2. At one site there was a clear correlation between nymph density and deer populations, while at the other site the relationship was not straightforward. The authors attributed this to the uneven drop in deer population at the second site. An earlier study, also in Connecticut, looked at two study areas after exclosure (deer fencing). Both areas showed approximately a 50% decrease in nymphal abundance compared to outside the exclosure (Stafford III, 1993). A 2003 study by Rand et al. (2003) of numerous sites in Maine showed a positive relationship between questing adult tick counts and deer counts, although the authors described the relationship as “weak”. Duffy et al. (1994) showed a 93% reduction in ticks after complete deer removal in a habitat on Long Island, NY. Daniels et al. (1993) studied five exclosure sites in Westchester County, NY and reported 83% fewer questing nymphs inside but comparable percentages of infected nymphs. A subsequent study by Daniels and Fish (1995) in the same of two exclosures found that densities of questing nymphs were significantly higher outside the exclosure than inside at one site but not significantly different at the other. Jordan et al. (2007) did not find any effect on tick density after reducing deer populations by 46% at a site in New Jersey. A recent multiyear study by Kilpatrick et al. (2014) of a site in Connecticut found a 76% reduction in tick abundance after reducing the deer herd from around 54 per km^2 to 5 per km^2.

The overall nature of these studies is summarized in Table B.2. In none of these studies was a survey taken of alternative reservoir hosts to deer. The presence of alternative reservoir hosts would be likely to make the reduction of deer less of a factor in tick populations.

These field studies are in regions that are likely to have high populations of reservoir-competent hosts, as in the default runs of the models, based on host populations estimated in the literature Levi et al. (2016), LoGiudice et al. (2003). The statements on reduction of nymph abundance coming from these studies show either a marked reduction in nymphs with reduced deer or no significant change. Comparing Fig. B.3c and d, which have high reservoir-competent host populations, it is clear that the model with host preference is a far better fit to this range of descriptions. For some host distributions, reducing the reservoir-incompetent hosts enough significantly reduces questing nymph abundance, and for other host distributions it does not. Without host preference incorporated into the model (Fig. B.3d) no change would be observed for any host distribution represented in this range. With host preference included, it is possible in Fig. B.3c to see even a 75% reduction in ticks as reservoir-competent hosts are reduced from their maximum to their minimum value in the heat map, as observed in one of the field studies (Kilpatrick et al., 2014).

A similar conclusion can be made for questing adult ticks, but with a twist. Ginsberg and Zhioua (1999), in a study of ticks in a deer exclosure on an island with abundant deer, noted that there appeared to be more questing adults inside the exclosure than outside. The model with host preference also displays this phenomenon at low reservoir-incompetent host density, seen at different scales in Fig. B.4a and c. In most rows, there is a point at which questing adult abundance drops as their reservoir host density rises, given a fixed density of the reservoir-competent host.

The authors proposed that this was due to the difficulty of adult ticks finding a suitable host, and therefore questing longer. This phenomenon is exactly what is driving our modeled differences in questing adults. As the number of reservoir-incompetent hosts rises, it takes less time for a questing tick to find a host and therefore the cumulative number of questing adult-days is lower, even though there are more ticks, easily validated by checking the numbers of feeding adults at the next stage. The model with host preference produces the same result as the field data, and for the very reason proposed by the researchers. Ginsberg and Zhioua (1999) also note that no difference was found in the abundance of questing nymphs. The model simulations disagree with this, and instead follow the rising pattern described in the studies in Table B.2. The response of questing tick populations to changes in host distribution suggest that the model that includes host preference is a better match to field observations in general.

4.2. Dilution and amplification effects.

At high densities of competent rodent reservoir hosts, little change in tick populations or disease incidence was produced by the model with no host preference in response to changes in reservoir-incompetent host population, seen in Fig. B.5b. On the other hand, the model with host preference showed an amplification effect, with more infected nymphs at higher reservoir-incompetent host populations, seen in Fig. B.5a. In both cases the disease prevalence in nymphs was more or less stable across high host populations, as seen in Fig. B.5c and d. At lower populations, prevalence was reduced with more reservoir-incompetent hosts for both models, as seen in Fig. B.5e and f, with a more pronounced effect in the model with host preference. All of this indicates that a dilution effect, if it exists, is to be found at low abundances of reservoir-competent hosts.

As reservoir-incompetent host populations rise under conditions of few reservoir-competent hosts, disease prevalence drops in both nymphs (Fig. B.5e and f, both models) and adults (as observed in field measurements) (Huang et al., 2019). However the number of ticks is rising overall. The result at low reservoir-competent host populations is shown in Fig. B.6. Here we see that the model with no host preference has no visible dilution or amplification effect for nymphs in Fig. B.7b, and an almost negligible amplification effect for adults in Fig. B.7f. By contrast, the model with host preference shows a clear dilution effect for both nymphs in Fig. B.7a and adults in Fig. B.7e.

Our results for low reservoir-competent host numbers are consistent with a recent agent-based model based on a diverse but low population of reservoir hosts (Halsey and Miller, 2020). The potential of a diverse ecological community to dilute the effect of zoonotic diseases has been proposed by various authors (Ostfeld, 2009; Ostfeld and Keesing, 2000). One literature review indicates a reduction of disease risk with higher host diversity (Keesing et al., 2006). A model by Ogden et al. indicates that either dilution or amplification could happen depending on various factors (Ogden and Tsao, 2009). Another recent study argues the opposite: that species richness is positively correlated with disease risk (Wood and Lafferty, 2013). This last study sparked a lively debate (Ostfeld and Keesing, 2013; Lafferty and Wood, 2013).

One potential source of confusion or disagreement is whether one measures disease prevalence in the vector, e.g. nymphal disease prevalence, or whether one measures abundance of infected questing ticks, e.g. the actual density in the environment of infected nymphs. The first of these two quantities (percent of questing ticks that are infected) is much easier to measure than the second. However, the second measure (actual density of infected questing ticks) is a better indicator of disease risk, because increasing this density increases the probability of human contact with a diseased questing tick.

A recent meta-analysis shows a weak and heterogeneous relationship between biodiversity and disease (Salkeld et al., 2013) and concludes that the specific composition of reservoir hosts and vectors determines disease risk, rather than actual species diversity. The models developed in this study, in particular the model with host preference included, supports this conclusion somewhat. In both models there are exactly two host species given and yet Fig. B.6c and g show a range of results in which, for a given abundance of questing ticks, a broad range of infected questing ticks could be present. This spread is smaller for the model with no host preference, as seen in Fig. B.6d and h. What determines the total infected questing tick abundance is the population numbers of each kind of host, that is, the specific numbers. For the model with host preference, a low population of reservoir-competent hosts will experience a dilution effect as reservoir-incompetent host numbers rise (Fig. B.6a and e), but a high population of reservoir hosts will experience an amplification effect with the same change in reservoir-incompetent host populations (Fig. B.5a).

Schmidt and Ostfeld (2001) attempt to estimate dilution effects at a New York site, claiming that the unexpected but observed nymphal infection rate of 37% and adult infection rate of 70.5% could be explained if fewer reservoir-competent hosts provided 61% of larval meals and 72% of nymphal meals, echoing an earlier estimate by LoGiudice et al. (2003). Simulations were parameterized so that the default host-to-tick transmission parameter produced a similar value for nymphal infection rate (37 to 40%), which persists across a range of host distributions, seen in Figs. B.7 and B.8 . With this parameter, the adult infection rate falls near the observed value for very different reasons than those given in Schmidt et al.

A questing tick that successfully finds a host will not necessarily attach immediately. After attaching, it may remain attached for as long as four days (Hojgaard et al., 2008). When it is finished feeding it may not drop off immediately. A decay constant for this compartment of 0.5 removes 95% of feeding ticks in six days. Duration of attachment and time sequence of infection are well known. Immatures stay attached to mice for three-four days and adults stay attached for about seven days. Timing of transmission of spirochetes from nymphs to mice has been described (Piesman et al., 1987, 1991), as has timing of acquisition of spirochetes by larvae feeding on infected mice (Couret et al., 2017). The host-to-tick infection rate used in simulations was 10% per day which, over the course of feeding produces a much higher probability of infection than is suggested by the 10%. It is known that tick-to-host transmission is not immediate (Hojgaard et al., 2008) and in the model it is also assumed that host-to-tick transmission is not immediate. Host-to-tick transmission in the model becomes more likely the longer the tick is feeding. With this assumption, the infection rates observed in Schmidt et al. are produced without requiring host preference on the part of questing nymphs, which are feeding predominantly on reservoir-competent hosts, as seen in Fig. B.3g and h for higher host populations. Simulations therefore suggest an alternative explanation to the one given by Schmidt et al. Which explanation is more accurate can only be sorted out by field data and experiments.

4.3. Directions for future research

The model currently assumes that ticks choose a host based on the probability of encounter, which is measured by relative density of a particular host type, or that host preference is extreme for both larvae and adults. The reality is likely to lie between these assumptions. A survey of feeding ticks on reservoir hosts of various types according to their life stage could shed light on this question and possibly offer an electivity index (Jacobs, 1974; Chesson, 1983) for each stage of questing tick, as has been done for some insects (Lechowicz, 1982).

In this model, animals are considered only as potential reservoir hosts for ticks and disease. The reality, of course, is more complex. Insectivorous birds, which are reservoir-competent hosts for *B. burgdorferi* sensu stricto, are also predators of these ticks. A study that describes how many ticks are consumed by various types of birds would be useful for developing a model that includes predation on ticks. It would be particularly interesting to know if birds that consume ticks are also at risk of hosting them or *B. burgdorferi* sensu stricto, or whether these are two distinct bird populations.

The analysis of the dilution effect included only two host categories. Once again, this oversimplified the true distribution of hosts, which includes multiple hosts of varying reservoir-competence and size. If further hosts were included it is likely that any dilution effect would diminish, as it is only present when few reservoir-competent hosts are present. The two types of host most widely blamed for both tick increases and *B. burgdorferi* sensu stricto were chosen as categories for simulation (Ostfeld, 2011). Competent stationary reservoir hosts, which include mice, carry a large tick population in the synthetic landscape we have used based on (Levi et al., 2016). Deer are reservoir-incompetent hosts widely credited with the potential for a dilution effect. Under the assumption of no host preference, no noticeable dilution effect is observed. With host preference, the effect is visible at low reservoir-competent host abundance. It is possible that this effect would persist even with the addition of some alternative adult reservoir hosts to the model.

5. Conclusion

The two models of tick populations and *B. burgdorferi* sensu stricto transmission developed in this study are based on earlier work by Ogden et al. (2005, 2004) and extended by Wallace et al. (2019). The models here incorporate temperature-dependent maturation rates, day length related diapause, and three categories of tick host populations based on whether they are incompetent or competent *B. burgdorferi* sensu stricto reservoir hosts and whether the reservoir-competent host is susceptible or infectious. The two models differ by the use or omission of host preference for larvae and adults. The results of both models were compared with field data taken from a variety of studies in the Northeast U.S. To investigate the proposed dilution effect, the model included two categories: competent stationary reservoir hosts, which include small rodents, and incompetent mobile reservoir hosts, which are represented exclusively by deer. The small rodents are a relatively large population of individuals compared to the deer for default runs.

The models produce, on the whole, biologically reasonable results, including the seasonality of tick populations, observed on-host tick burdens, and disease prevalence at steady state (Wallace et al., 2019). The introduction of day-length related diapause gave seasonal patterns of questing ticks observed in the Northeastern United States.

A host model based on small rodents and deer was tested for the effect of reservoir-incompetent host densities on cumulative populations of questing nymphs and adults by varying number of reservoir-competent hosts (small rodents) and reservoir-incompetent hosts (deer). The version of the model that included extreme host preference for adults and larvae did a better job of matching the overall range of observations of questing tick abundance with varying numbers of adult hosts. Nymph populations rose with increased hosts of all types. For some host population ranges, questing adult tick populations dropped with increased adult hosts due to shortened questing times, as one field study found.

The results suggest that if there is any dilution effect by reservoir-incompetent hosts going on, it will most likely occur at low reservoir-competent host populations and will require some form of host preference. At high reservoir-competent host populations there will be an amplification effect of increasing reservoir-incompetent hosts, assuming a fairly extreme host preference is at work. These observations have implications for local deer control measures if few alternative adult tick hosts are present.

In summary, the simulation results show that the model with host preference appears to be more accurate than the one with no host preference. Given this assumption, we have that

- removal of adult hosts is likely to reduce questing nymph populations.
- at very low levels of reservoir hosts, questing adult abundance may rise with lack of adult hosts.
- there is a dilution effect at low reservoir-competent host populations.
- there is an amplification effect at high reservoir-competent host populations.

Conflict of interest

The authors declare no conflict of interest.

Acknowledgements

We thank the Neukom Institute for Computational Science at Dartmouth College for its financial support of the undergraduate students involved in the early stages of this project.

Appendix A. Equations and parameters

Fig. B.1 shows eggs developing into hardening larvae followed by a questing stage:

$$\begin{aligned}
\dot{E} &= b * A_4 - m_{\mathrm{Etemp}}E - d_eE,\\
\dot{L_1} &= m_{\mathrm{Etemp}}E - d_1L_1 - m_1L_1,\\
\dot{L_2} &= m_1L_1 - d_2L_2 - m_2L_2.
\end{aligned}$$

In all relevant equations, the attachment process for successful feeding is described by an expression that is the product of maturation rate, prior population, a functional form W_X approaching zero as the total on-host carrying capacity is reached, and a ratio Q describing the probability of finding a host of the given type. Notice that the functional form W_X reduces the attachment rate of questing tick to host as the total on-host carrying capacity for host category X is approached (see detailed expression in (A.53)). In the case of no host preference, larvae could feed on host type I, giving

$$\dot{\mathrm{FL}}_I = m_2L_2F_IQ_{\mathrm{LI}} - d_I\mathrm{FL}_I - m_3\mathrm{FL}_I. \tag{A.4}$$

In the case of extreme host preference, no larvae feed on host I, giving

$$\dot{\mathrm{FL}}_I = 0. \tag{A.5}$$

In both the no-host-preference and the host-preference model,

$$\begin{aligned}
\dot{\mathrm{FL}}_{\mathrm{CU}} &= m_2L_2F_{\mathrm{CU}}Q_{\mathrm{LCU}} - d_C\mathrm{FL}_{\mathrm{CU}} - m_3\mathrm{FL}_{\mathrm{CU}},\\
\dot{\mathrm{FL}}_{\mathrm{CI}} &= m_2L_2F_{\mathrm{CI}}Q_{\mathrm{LCI}} - d_C\mathrm{FL}_{\mathrm{CI}} - m_3\mathrm{FL}_{\mathrm{CI}}.
\end{aligned}$$

At this point, disease transmission may occur, giving two categories of engorged larvae followed by questing nymphs.

$$\begin{aligned}
\dot{\mathrm{NU}}_1 &= m_3L_I + m_3\mathrm{FL}_{\mathrm{CU}}, +(1-p_L)(m_3\mathrm{FL}_{\mathrm{CI}}) - d_{n1}\mathrm{NU}_1 - m_{\mathrm{Ntemp}}\mathrm{NU}_1,\\
\dot{\mathrm{NI}}_1 &= p_L(m_3\mathrm{FL}_{\mathrm{CI}}) - d_{n1}\mathrm{NI}_1 - m_{\mathrm{Ntemp}}\mathrm{NI}_1,\\
\dot{\mathrm{NU}}_2 &= m_{\mathrm{Ntemp}}\mathrm{NU}_1 - d_{n2}\mathrm{NU}_2 - m_{n2}\mathrm{NU}_2,\\
\dot{\mathrm{NI}}_2 &= m_{\mathrm{Ntemp}}\mathrm{NI}_1 - d_{n2}\mathrm{NI}_2 - m_{n2}\mathrm{NI}_2.
\end{aligned}$$

Populations of infected and uninfected nymphs are tracked separately as they feed on the three host categories, as follows:

$$\begin{aligned}
\dot{\mathrm{FNU}}_I &= m_{n2}\mathrm{NU}_2F_IQ_{\mathrm{NI}} - d_I\mathrm{FNU}_I - m_3\mathrm{FNU}_I,\\
\dot{\mathrm{FNU}}_{\mathrm{CU}} &= m_{n2}\mathrm{NU}_2F_{\mathrm{CU}}Q_{\mathrm{NCU}} - d_C\mathrm{FNU}_{\mathrm{CU}} - m_3\mathrm{FNU}_{\mathrm{CU}},\\
\dot{\mathrm{FNU}}_{\mathrm{CI}} &= m_{n2}\mathrm{NU}_2F_{\mathrm{CI}}Q_{\mathrm{NCI}} - d_C\mathrm{FNU}_{\mathrm{CI}} - m_3\mathrm{FNU}_{\mathrm{CI}},\\
\dot{\mathrm{FNI}}_I &= m_{n2}\mathrm{NI}_2F_IQ_NI - d_I\mathrm{FNI}_I - m_3\mathrm{FNI}_I,\\
\dot{\mathrm{FNI}}_{\mathrm{CU}} &= m_{n2}\mathrm{NI}_2F_{\mathrm{CU}}Q_{\mathrm{NCU}} - d_C\mathrm{FNI}_{\mathrm{CU}} - m_3\mathrm{FNI}_{\mathrm{CU}},\\
\dot{\mathrm{FNI}}_{\mathrm{CI}} &= m_{n2}\mathrm{NI}_2F_{\mathrm{CI}}Q_{\mathrm{NCI}} - d_C\mathrm{FNI}_{\mathrm{CI}} - m_3\mathrm{FNI}_{\mathrm{CI}}.
\end{aligned}$$

Disease transmission also occurs during nymphal feeding, giving two categories of engorged nymph and questing adult.

$$\begin{aligned}
\dot{\mathrm{AU}}_1 &= m_3(\mathrm{FNU}_I + \mathrm{FNU}_{\mathrm{CU}}) + m_3(1-p_n)(\mathrm{FNU}_{\mathrm{CI}}) - d_{A1}\mathrm{AU}_1 - m_{\mathrm{Atemp}}\mathrm{AU}_1,\\
\dot{\mathrm{AI}}_1 &= m_3(\mathrm{FNI}_I + \mathrm{FNI}_{\mathrm{CU}} + \mathrm{FNI}_{\mathrm{CI}}) + m_3(p_n)(\mathrm{FNU}_{\mathrm{CI}}) - d_{A1}\mathrm{AI}_1 - m_{\mathrm{Atemp}}\mathrm{AI}_1,\\
\dot{\mathrm{AU}}_2 &= m_{\mathrm{Atemp}}\mathrm{AU}_1 - d_{A2}\mathrm{AU}_2 - m_{A2}(T)\mathrm{AI}_2,\\
\dot{\mathrm{AI}}_2 &= m_{\mathrm{Atemp}}\mathrm{AI}_1 - d_{A2}\mathrm{AI}_2 - m_{A2}(T)\mathrm{AI}_2.
\end{aligned}$$

The following describe feeding adults, uninfected and infected:

$$\begin{aligned}
\dot{\mathrm{FAU}}_I &= m_{A2}\mathrm{AU}_2F_IQ_AI - d_I\mathrm{FAU}_I - m_3\mathrm{FAU}_I,\\
\dot{\mathrm{FAI}}_I &= m_{A2}\mathrm{AI}_2F_IQ_AI - d_I\mathrm{FAI}_I - m_3\mathrm{FAI}_I.
\end{aligned}$$

In the case of no host preference, adults may also feed on reservoir-competent hosts, giving;

$$\begin{aligned}
\dot{\mathrm{FAU}}_{\mathrm{CU}} &= m_{A2}\mathrm{AU}_2F_{\mathrm{CU}}Q_{\mathrm{ACU}} - d_C\mathrm{FAU}_{\mathrm{CU}} - m_3\mathrm{FAU}_{\mathrm{CU}},\\
\dot{\mathrm{FAU}}_{\mathrm{CI}} &= m_{A2}\mathrm{AU}_2F_{\mathrm{CI}}Q_{\mathrm{ACU}} - d_C\mathrm{FAU}_{\mathrm{CI}} - m_3\mathrm{FAU}_{\mathrm{CI}},\\
\dot{\mathrm{FAI}}_{\mathrm{CU}} &= m_{A2}\mathrm{AI}_2F_{\mathrm{CU}}Q_{\mathrm{ACI}} - d_C\mathrm{FAI}_{\mathrm{CU}} - m_3\mathrm{FAI}_{\mathrm{CU}},\\
\dot{\mathrm{FAI}}_{\mathrm{CI}} &= m_{A2}\mathrm{AI}_2F_{\mathrm{CI}}Q_{\mathrm{ACI}} - d_C\mathrm{FAI}_{\mathrm{CI}} - m_3\mathrm{FAI}_{\mathrm{CI}}.
\end{aligned}$$

In the case of extreme host preference, adults feed only on reservoir-incompetent hosts, giving

$$\mathrm{FA\dot{U}}_{\mathrm{CU}} = \mathrm{FA\dot{U}}_{\mathrm{CI}} = \mathrm{FA\dot{I}}_{\mathrm{CU}} = \mathrm{FA\dot{I}}_{\mathrm{CI}} = 0. \tag{A.28}$$

In the case of no host preference, fed adults come from all feeding compartments, giving

$$\dot{A_4} = m_3(\mathrm{FAU}_I + \mathrm{FAU}_{\mathrm{CU}} + \mathrm{FAU}_{\mathrm{CI}} + \mathrm{FAI}_I + \mathrm{FAI}_{\mathrm{CU}} + \mathrm{FAI}_{\mathrm{CI}}) - d_{A4}A_4. \tag{A.29}$$

In the case of extreme host preference, fed adults come only from reservoir-incompetent hosts, giving

$$\dot{A_4} = m_3(\mathrm{FAU}_I + \mathrm{FAI}_I) - d_{A4}A_4. \tag{A.30}$$

Host populations and disease dynamics:

$$\dot{I} = b_I I\left(1 - \frac{I}{K_I}\right) - d_I I \tag{A.31}$$

In the case of no host preference, disease may be transmitted by both nymphs and adults in a prevalence dependent fashion, giving:

$$\mathrm{C\dot{U}} = b_C(\mathrm{CU} + \mathrm{CI})\left(1 - \frac{\mathrm{CU} + \mathrm{CI}}{K_C}\right) - d_C\mathrm{CU} - p_C\frac{\mathrm{FNI}_{\mathrm{CU}} + \mathrm{FAI}_{\mathrm{CU}}}{T_{\mathrm{CU}} + \epsilon}\mathrm{CU},$$
$$\mathrm{C\dot{I}} = p_C\frac{\mathrm{FNI}_{\mathrm{CU}} + \mathrm{FAI}_{\mathrm{CU}}}{T_{\mathrm{CU}} + \epsilon}\mathrm{CU} - d_C\mathrm{CI}.$$

In the case of extreme host preference, only infected nymphs transmit disease to reservoir-competent hosts, giving

$$\mathrm{C\dot{U}} = b_C(\mathrm{CU} + \mathrm{CI})\left(1 - \frac{\mathrm{CU} + \mathrm{CI}}{K_C}\right) - d_C\mathrm{CU} - p_C\frac{\mathrm{FNI}_{\mathrm{CU}}}{T_{\mathrm{CU}} + \epsilon}\mathrm{CU},$$
$$\mathrm{C\dot{I}} = p_C\frac{\mathrm{FNI}_{\mathrm{CU}}}{T_{\mathrm{CU}} + \epsilon}\mathrm{CU} - d_C\mathrm{CI}.$$

For each respective host type, we have the following equations describing Q_x, the fraction of available hosts of a given type x, including a negligible number ϵ in the denominator for numerical stability. As there are two models being compared, we consider first the model with no host preference. As any tick may alight on any host, we have that Q_x is the same across questing tick categories:

$$Q_{\mathrm{AI}} = Q_{\mathrm{LI}} = Q_I = I/(I + \mathrm{CU} + \mathrm{CI} + \epsilon)$$
$$Q_{\mathrm{ACU}} = Q_{\mathrm{LCU}} = Q_{\mathrm{CU}} = \mathrm{CU}/(I + \mathrm{CU} + \mathrm{CI} + \epsilon)$$
$$Q_{\mathrm{ACI}} = Q_{\mathrm{LCI}} = Q_{\mathrm{CI}} = \mathrm{CI}/(I + \mathrm{CU} + \mathrm{CI} + \epsilon)$$

In the case of extreme host preference, the denominator of Q_x only includes hosts that the category of questing ticks will accept. This assumption gives

$$Q_{\mathrm{LI}} = 0$$
$$Q_{\mathrm{LCU}} = \mathrm{CU}/(\mathrm{CU} + \mathrm{CI} + \epsilon),$$
$$Q_{\mathrm{LCI}} = \mathrm{CI}/(\mathrm{CU} + \mathrm{CI} + \epsilon),$$
$$Q_{\mathrm{NI}} = I/(I + \mathrm{CU} + \mathrm{CI} + \epsilon),$$
$$Q_{\mathrm{NCU}} = \mathrm{CU}/(I + \mathrm{CU} + \mathrm{CI} + \epsilon),$$
$$Q_{\mathrm{NCI}} = \mathrm{CI}/(I + \mathrm{CU} + \mathrm{CI} + \epsilon),$$
$$Q_{\mathrm{AI}} = 1,$$
$$Q_{\mathrm{ACU}} = Q_{\mathrm{ACI}} = 0.$$

Let T_i be the total ticks on hosts of type i for the case of no host preference. Then

$$T_I = \mathrm{FL}_I + \mathrm{FNU}_I + \mathrm{FNI}_I + \mathrm{FAU}_I + \mathrm{FAI}_I,$$
$$T_{\mathrm{CU}} = \mathrm{FL}_{\mathrm{CU}} + \mathrm{FNU}_{\mathrm{CU}} + \mathrm{FNI}_{\mathrm{CU}} + \mathrm{FAU}_{\mathrm{CU}} + \mathrm{FAI}_{\mathrm{CU}},$$
$$T_{\mathrm{CI}} = \mathrm{FL}_{\mathrm{CI}} + \mathrm{FNU}_{\mathrm{CI}} + \mathrm{FNI}_{\mathrm{CI}} + \mathrm{FAU}_{\mathrm{CI}} + \mathrm{FAI}_{\mathrm{CI}}.$$

Let T_i be the total ticks on hosts of type i for the case of extreme host preference. Then

$$T_I = \mathrm{FNU}_I + \mathrm{FNI}_I + \mathrm{FAU}_I + \mathrm{FAI}_I,$$
$$T_{\mathrm{CU}} = \mathrm{FL}_{\mathrm{CU}} + \mathrm{FNU}_{\mathrm{CU}} + \mathrm{FNI}_{\mathrm{CU}},$$
$$T_{\mathrm{CI}} = \mathrm{FL}_{\mathrm{CI}} + \mathrm{FNU}_{\mathrm{CI}} + \mathrm{FNI}_{\mathrm{CI}}.$$

In this model, tick populations are bounded by the total on-host carrying capacities, $C_X X$ where X represents populations of the three host categories I, CU, and CI respectively, and C_X is a per-host maximum capacity.

The functional form W_X is given as the fraction of on-host space available for further attachments and feeding:

$$W_X = \max\left(\frac{C_X X - T_X}{C_X X} + \epsilon), 0\right) \tag{A.53}$$

Appendix B

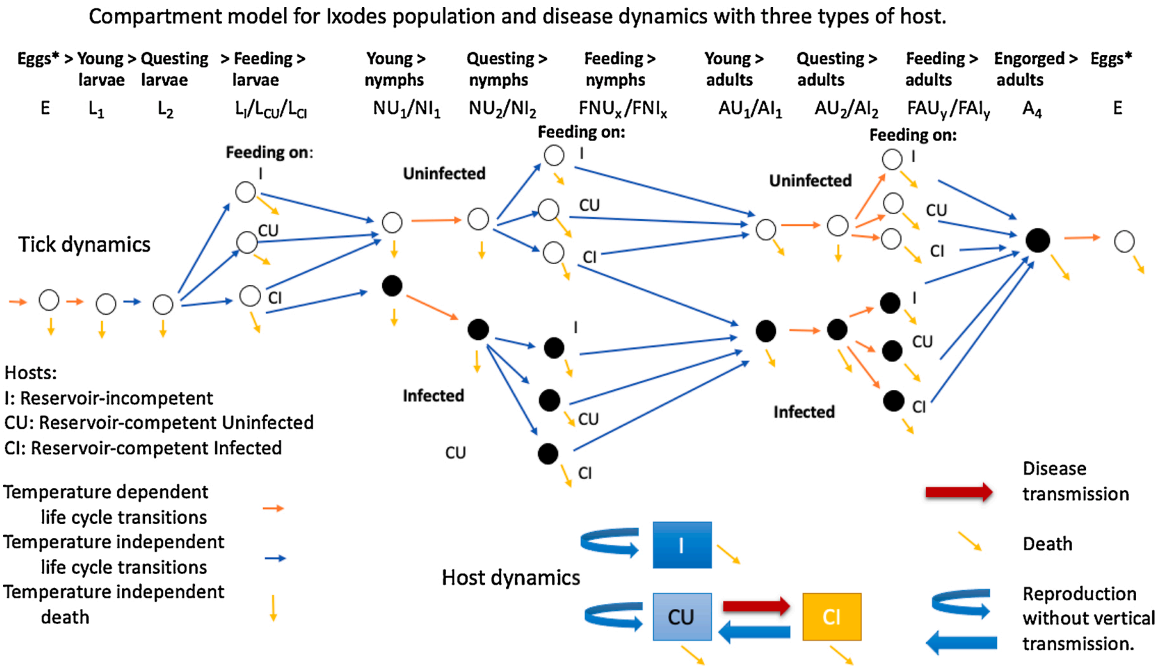
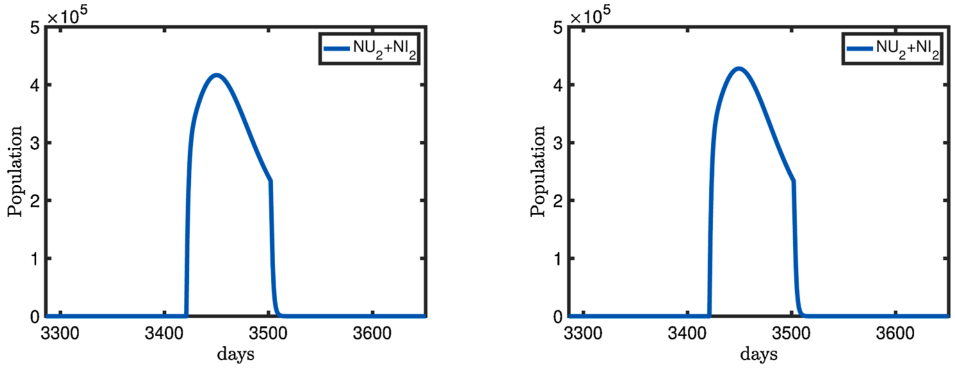
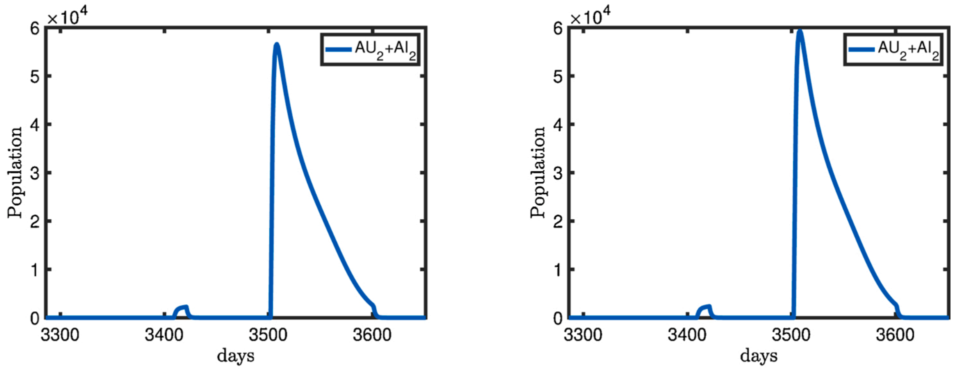


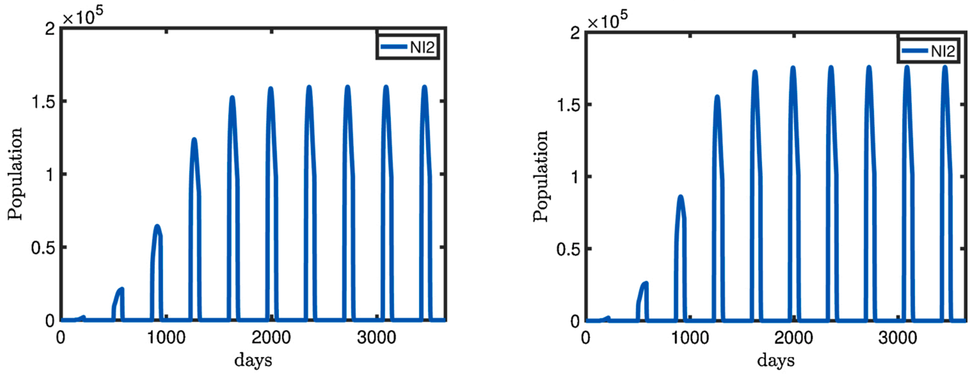
Fig. B.1. The life cycle and disease dynamics of *Ixodes scapularis* Say 1921 as described by equations in Wallace et al. (2019). Feeding populations are split according to host type. Temperature dependent maturation transitions are indicated in orange. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)



(a) With HP (b)Without HP

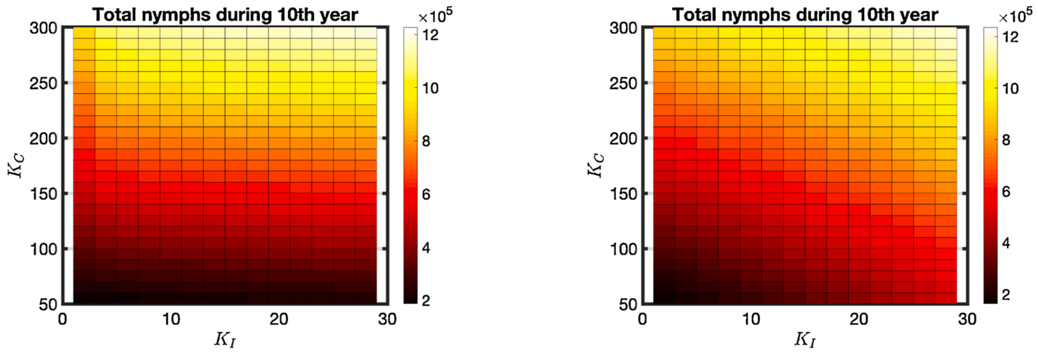


(c)With HP (d)Without HP

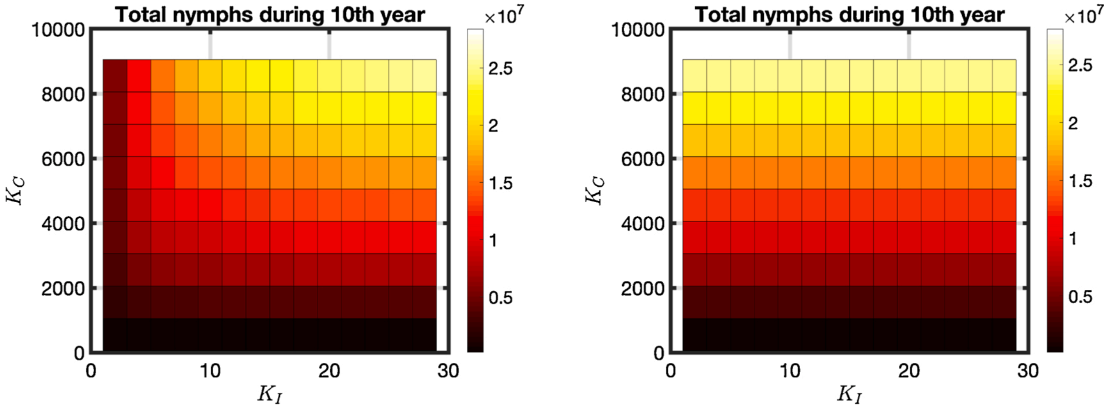


(e)With HP (f)Without HP

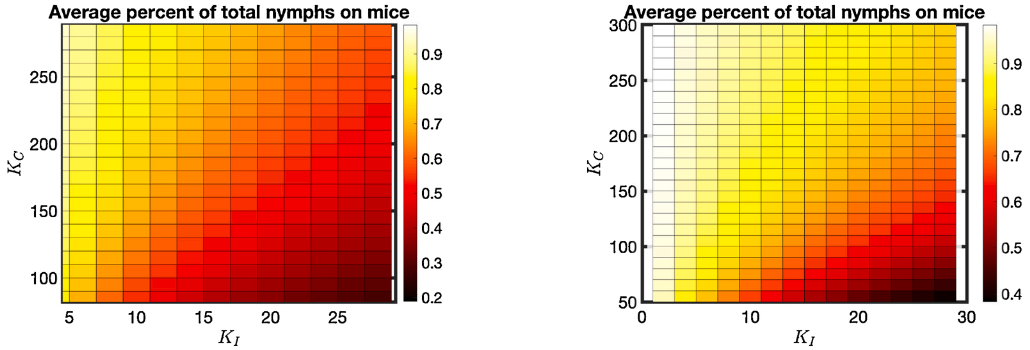
Fig. B.2. Figure represents steady state population with HP using default parameters for 10 years. Panels (a) and (b) represent questing nymphs over the 10th year with and without HP respectively. Panels (c) and (d) represent adults over the 10th year with and without HP respectively. Panels (e) and (f) represent infected nymph population at steady state. Note that HP stands for host preference.



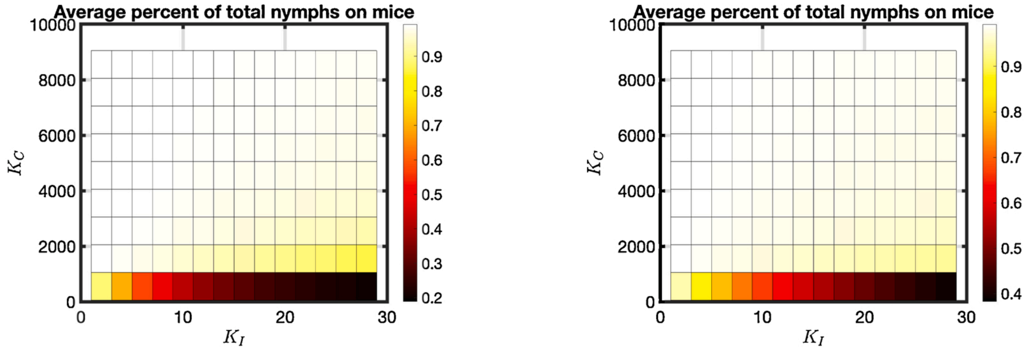
(a) With HP (b) Without HP



(c) With HP (d) Without HP

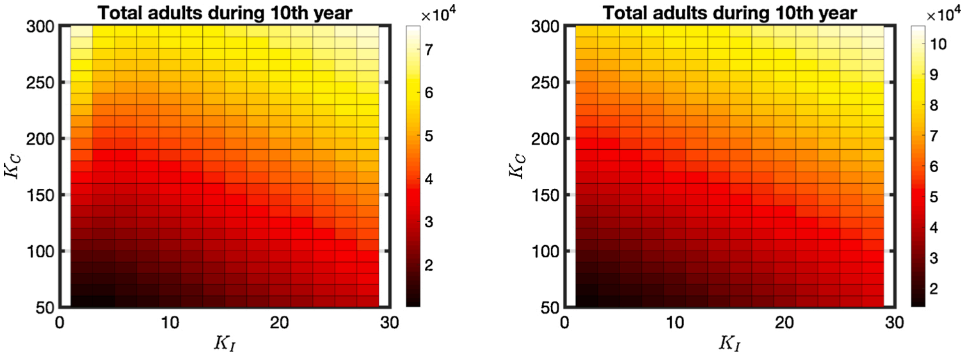


(e) With HP (f) Without HP

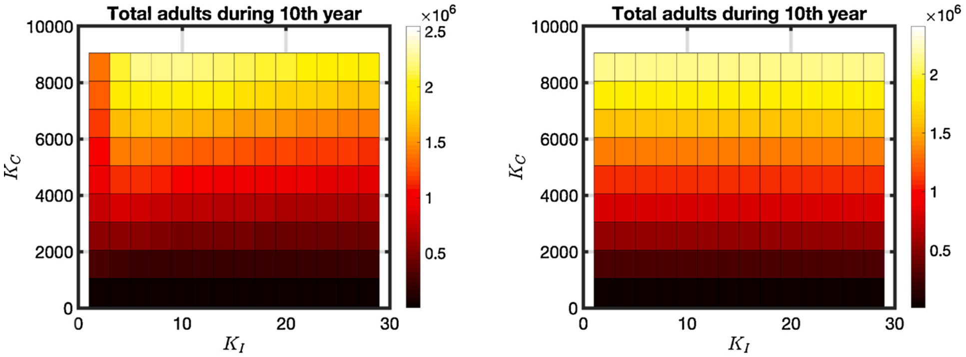


(g) With HP (h) Without HP

Fig. B.3. Questing nymph abundance and feeding nymph behavior: Panels (a) and (b) represent total nymph population on the smaller range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer) with and without HP respectively. Panels (c) and (d) represent total nymph population on the bigger range of K_I and K_C with and without HP respectively. Panels (e) and (f) represent average percent total nymphs on mice on the smaller range of K_I and K_C with and without HP respectively. Panels (g) and (h) represent average percent total nymphs on mice on the bigger range of K_I and K_C with and without HP respectively. Note that HP stands for host preference.

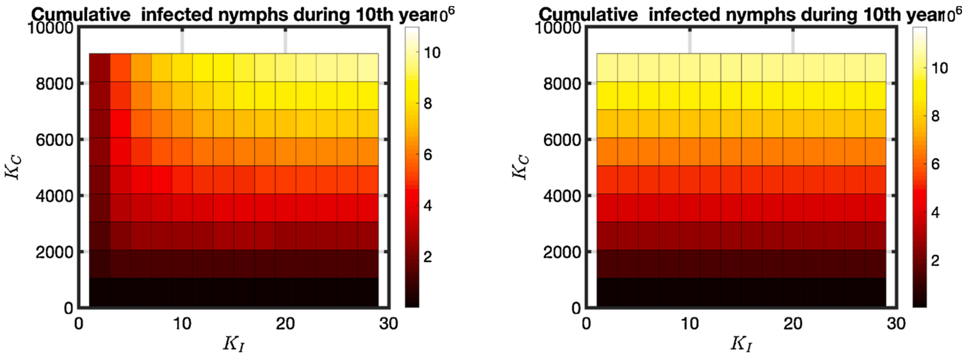


(a) With HP (b) Without HP

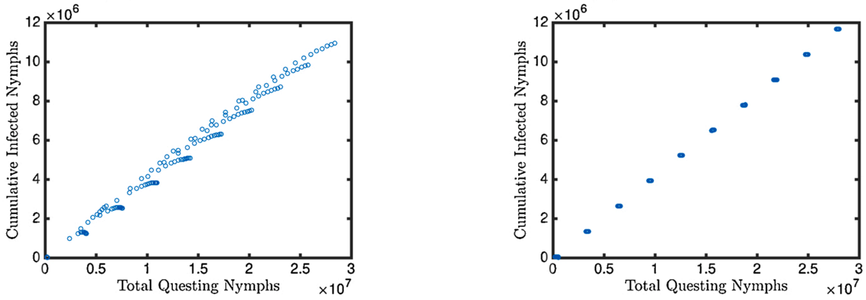


(c) With HP (d) Without HP

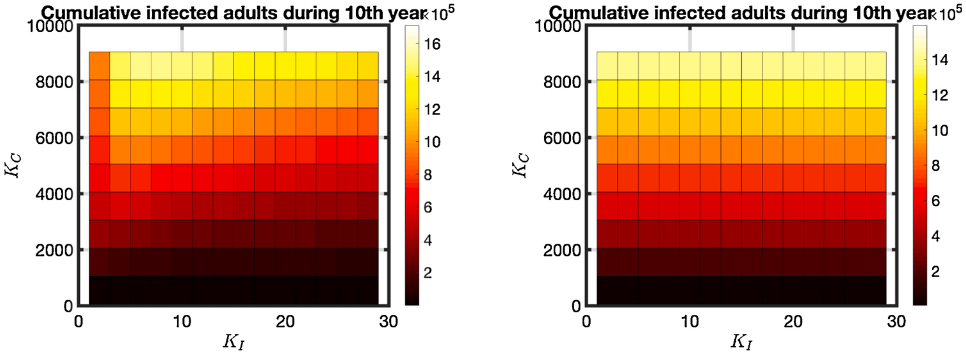
Fig. B.4. Questing adult abundance: Panels (a) and (b) represent smaller range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer) with and without HP respectively. Panels (c) and (d) represent bigger range of K_I and K_C with and without HP respectively. Note that HP stands for host preference.



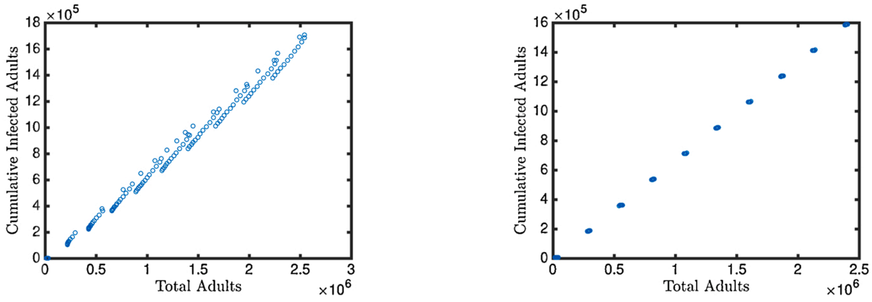
(a) With HP (b) Without HP



(c) With HP (d) Without HP

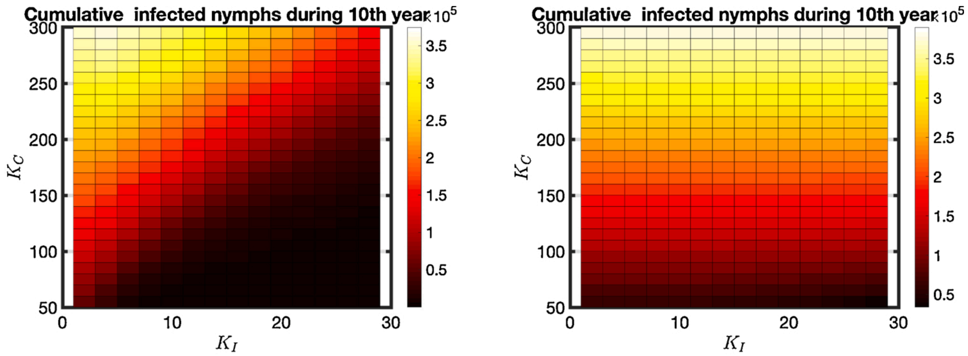


(e) With HP (f) Without HP

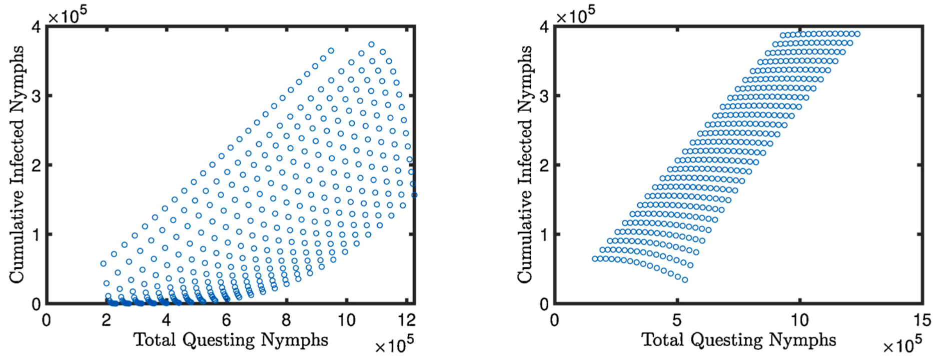


(g) With HP (h) Without HP

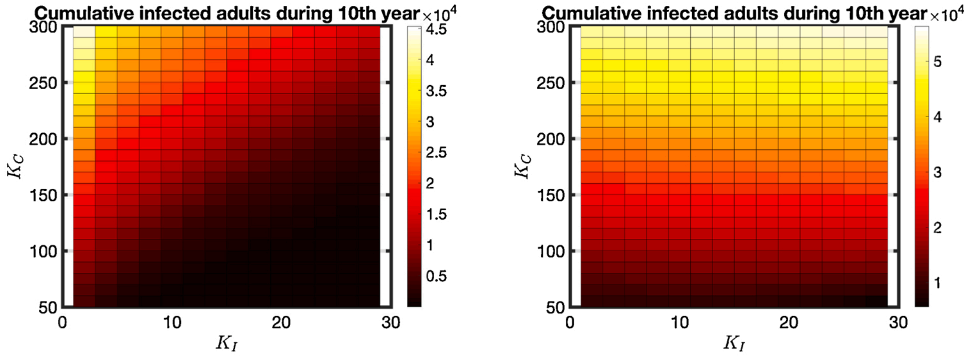
Fig. B.5. Bigger range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer): (a) Heat map of cumulative infected nymphs with HP; (b) Heat map of cumulative infected nymphs without HP; (c) Scatter plot of cumulative infected nymphs vs. total nymphs with HP; (d) Scatter plot of cumulative infected nymphs vs. total nymphs without HP; (e) Heat map of cumulative infected adults with HP; (f) Heat map of cumulative infected adults without HP; (g) Scatter plot of cumulative infected adults vs. total adults with HP; (h) Scatter plot of cumulative infected adults vs. total adults without HP. Note that HP stands for host preference.



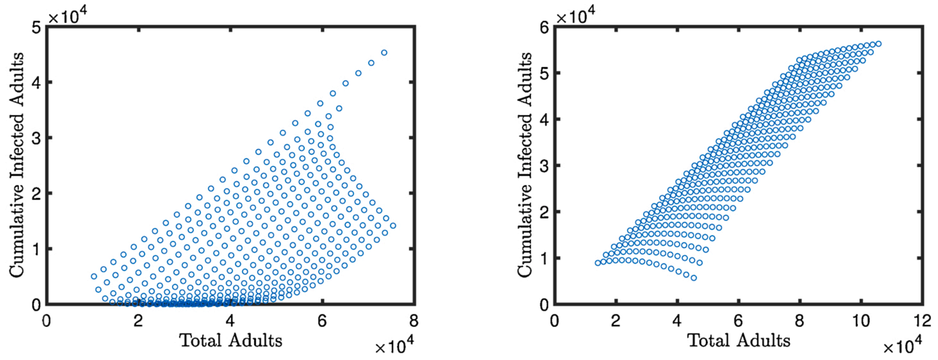
(a) With HP (b) Without HP



(c) With HP (d) Without HP

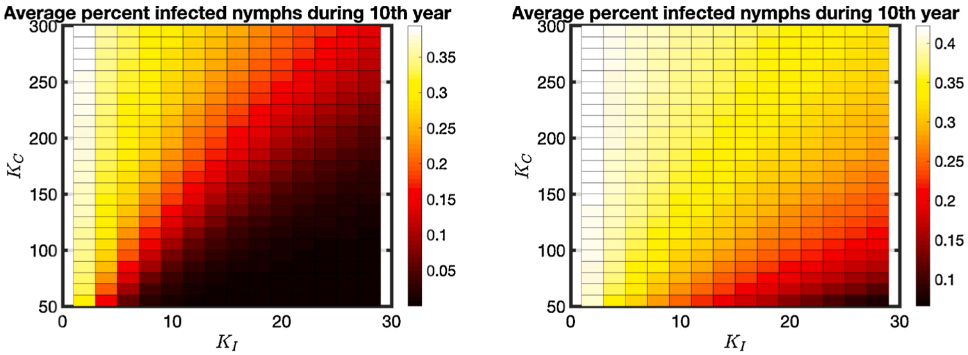


(e) With HP (f) Without HP

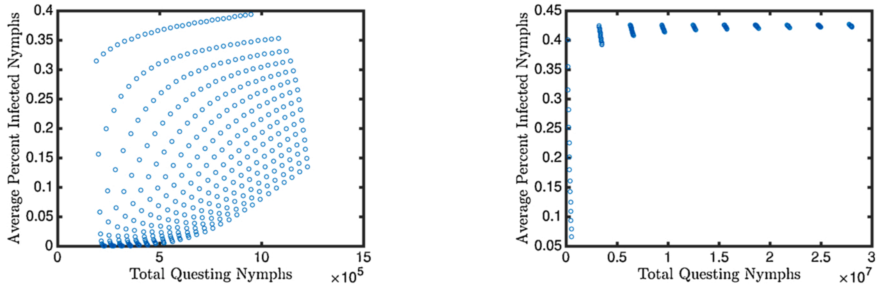


(g) With HP (h) Without HP

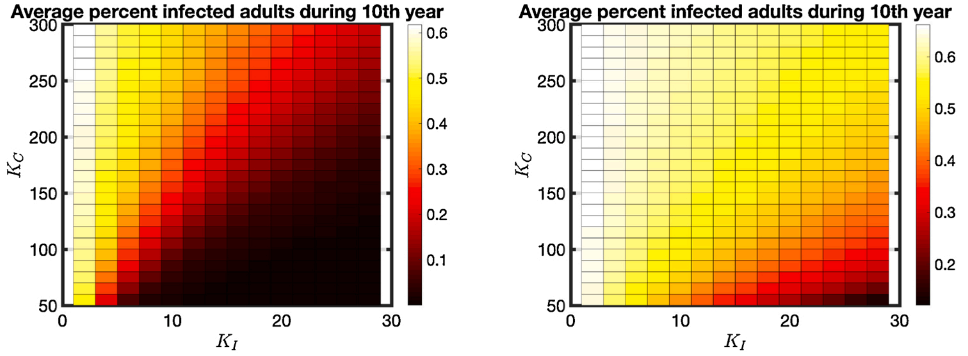
Fig. B.6. Smaller range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer): (a) Heat map of cumulative infected nymphs with HP; (b) Heat map of cumulative infected nymphs without HP; (c) Scatter plot of cumulative infected nymphs vs. total nymphs with HP; (d) Scatter plot of cumulative infected nymphs vs. total nymphs without HP; (e) Heat map of cumulative infected adults with HP; (f) Heat map of cumulative infected adults without HP; (g) Scatter plot of cumulative infected adults vs. total adults with HP; (h) Scatter plot of cumulative infected adults vs. total adults without HP. Note that HP stands for host preference.



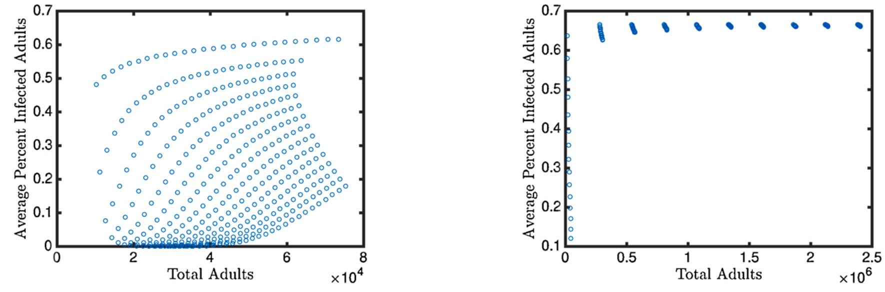
(a) With HP (b) Without HP



(c) With HP (d) Without HP

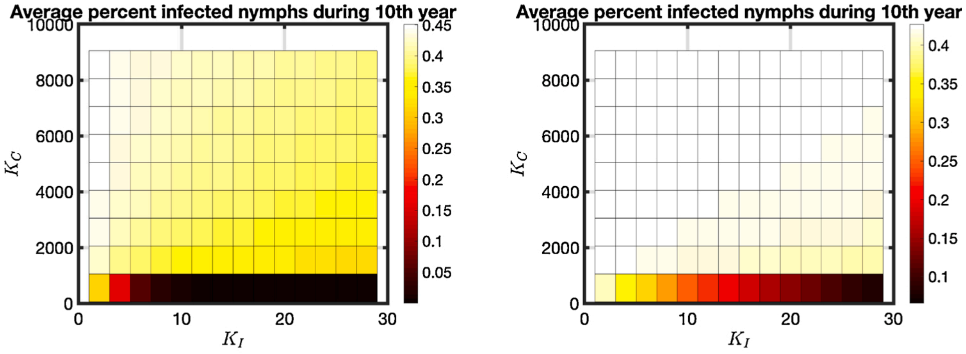


(e) With HP (f) Without HP

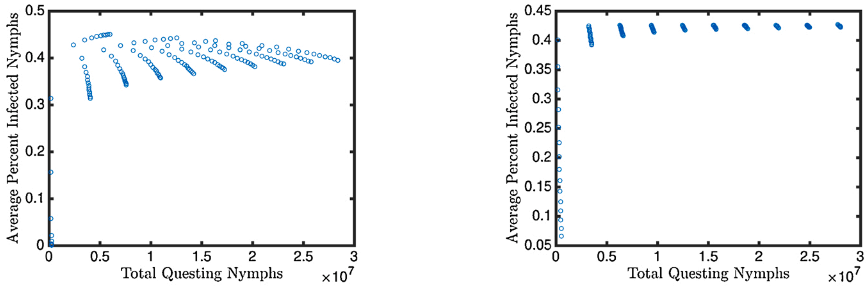


(g) With HP (h) Without HP

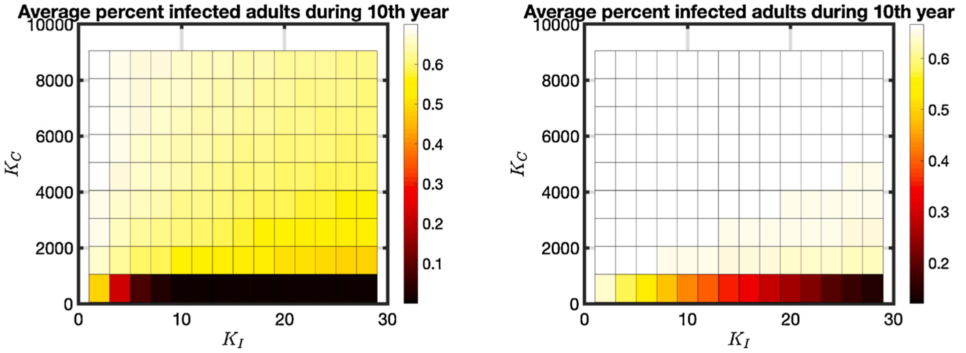
Fig. B.7. Smaller range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer): (a) Heat map of average percent infected nymphs with HP; (b) Heat map of average percent infected nymphs without HP; (c) Scatter plot of average percent infected nymphs vs. total nymphs with HP; (d) Scatter plot of average percent infected nymphs vs. total nymphs without HP; (e) Heat map of average percent infected adults with HP; (f) Heat map of average percent infected adults without HP; (g) Scatter plot of average percent infected adults vs. total adults with HP; (h) Scatter plot of average percent infected adults vs. total adults without HP. Note that HP stands for host preference.



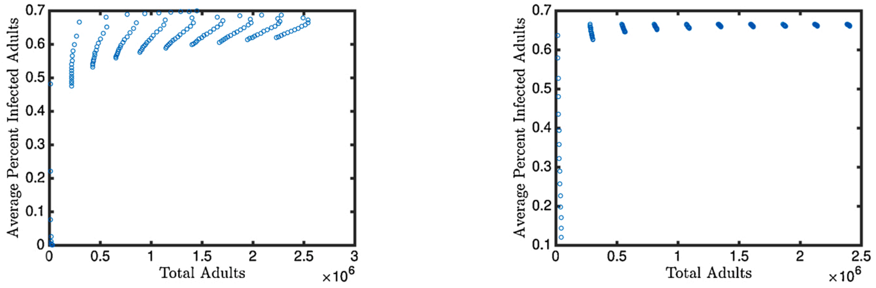
(a) With HP (b) Without HP



(c) With HP (d) Without HP



(e) With HP (f) Without HP



(g) With HP (h) Without HP

Fig. B.8. Bigger range of K_I (number of reservoir-incompetent deer per square kilometer) and K_C (number of reservoir-competent rodents per square kilometer): (a) Heat map of average percent infected nymphs with HP; (b) Heat map of average percent infected nymphs without HP; (c) Scatter plot of average percent infected nymphs vs. total nymphs with HP; (d) Scatter plot of average percent infected nymphs vs. total nymphs without HP; (e) Heat map of average percent infected adults with HP; (f) Heat map of average percent infected adults without HP; (g) Scatter plot of average percent infected adults vs. total adults with HP; (h) Scatter plot of average percent infected adults vs. total adults without HP. Note that HP stands for host preference.

Table B.1
Default parameter values used in the numerical simulations unless otherwise mentioned.

Parameter	Value	Description
b	300	Egg production
m_{Etemp}	Varying	Temperature-dependent maturation of larvae
d_e	0.015	Egg death rate
d_1	0.01	Hardening larva death rate
m_1	0.033	Hardening larvae maturation to questing
d_2	0.094	Death rate of questing larvae
m_2	0.5	Success rate of questing larvae
d_I	0.51	Death of feeding ticks on host I
m_3	0.5	Dropoff rate of feeding ticks, all stages, all hosts
d_C	0.72	Death of feeding ticks on hosts CU, CI
P_L	0.5	Daily probability of on host transmission to larvae
d_{n1}	0.001	Death rate of engorged larvae/ young nymphs
m_{Ntemp}	Varying	Temperature-dependent maturation of engorged larvae/ young nymphs
d_{n2}	0.094	Death rate of questing nymphs
m_{n2}	0.5	Success rate of questing nymphs
d_{A1}	0.001	Death rate of engorged nymphs/young adults
m_{Atemp}	Varying	Temperature-dependent maturation of engorged nymphs/young adults
d_{A2}	0.094	Death rate of questing adults
m_{A2}	0.5	Success rate of questing adults
d_{A4}	0.006	Death rate of engorged adults
b_I	0.00261	Birth rate of host I
d_I	0.000609	Death rate of host I
k_I	25	Default carrying capacity per km^2 for host I
C_I	239	Tick capacity per host type I
b_C	0.0176	Birth rate of CU and CI hosts
d_C	0.00345	Death rate of CU and CI hosts
K_C	9335	Default carrying capacity per km^2 for hosts $CU + CI$
C_C	46.84	Tick capacity per host types CU and CI
p_C	0.6635	Rate of CU host infection per infectious feeding tick per day
ϵ	0.001	Numerical stability
E_0	10^7	Initial number of eggs
$NU1_0$	5×10^6	Initial uninfected nymphs
$NI1_0$	10^4	Initial infected nymphs
$AU1_0$	3×10^5	Initial uninfected adults
I_0	25	Initial hosts of type I
CU_0	9335	Initial hosts of type CU
X_0	0	All other initial conditions

Table B.2
Summary data on the effect of deer removal, exclosure, or population comparison across sites, indicating strong, weak, or little to no reduction in ticks after deer removal.

Deer study	Strong effect	Weak effect	Little to no effect
Stafford III et al. (2003)	One site		One site
Stafford III (1993)	Two sites		
Duffy et al. (1994)	One site		
Rand et al. (2003)		Eight sites	
Daniels et al. (1993)	Five sites		
Daniels and Fish (1995)	One site		One site
Jordan et al. (2007)			One site
Kilpatrick et al. (2014)	One site		

References

Beier, J.C., Killeen, G.F., Githure, J.I., 1999. Entomologic inoculation rates and *Plasmodium falciparum* malaria prevalence in Africa. Am. J. Trop. Med. Hyg. 61, 109–113.

Belozerov, V., 2009. Diapause and quiescence as two main kinds of dormancy and their significance in life cycles of mites and ticks (chelicerata: Arachnida: Acari). part 2. parasitiformes. Acarina 17, 3–32.

Belozerov, V.N., Fourie, L.J., Kok, D.J., 2002a. Photoperiodic control of developmental diapause in nymphs of prostriate ixodid ticks (acari: Ixodidae). Exp. Appl. Acarol. 28, 163–168.

Belozerov, V.N., Naumov, R.L., et al., 2002b. Nymphal diapause and its photoperiodic control in the tick *Ixodes scapularis* (Acari: Ixodidae). Folia Parasitol. 49, 314–318.

Brownstein, J.S., Holford, T.R., Fish, D., 2003. A climate-based model predicts the spatial distribution of the Lyme disease vector *Ixodes scapularis* in the United States. Environ. Health Perspect. 111, 1152–1157.

Chesson, J., 1983. The estimation and analysis of preference and its relationship to foraging models. Ecology 64, 1297–1304.

Couret, J., Dyer, M., Mather, T., Han, S., Tsao, J., Lebrun, R., Ginsberg, H.S., 2017. Acquisition of *Borrelia burgdorferi* infection by larval *Ixodes scapularis* (Acari: Ixodidae) associated with engorgement measures. J. Med. Entomol. 54, 1055–1060.

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.

Daniels, T.J., Fish, D., Schwartz, I., 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease risk by deer exclusion. J. Med. Entomol. 30, 1043–1049.

Diuk-Wasser, M.A., Vourc'h, G., Cislo, P., Hoen, A.G., Melton, F., Hamer, S.A., Rowland, M., Cortinas, R., Hickling, G.J., Tsao, J.I., et al., 2010. Field and climate-based model for predicting the density of host-seeking nymphal *Ixodes scapularis*, an important vector of tick-borne disease agents in the eastern United States. Global Ecol. Biogeogr. 19, 504–514.

Dobson, A.D., Finnie, T.J., Randolph, S.E., 2011. A modified matrix model to describe the seasonal population ecology of the European tick *Ixodes ricinus*. J. Appl. Ecol. 48, 1017–1028.

Duffy, D.C., Campbell, S.R., Clark, D., Dimotta, C., Gurney, S., 1994. *Ixodes scapularis* (Acari: Ixodidae) deer tick mesoscale populations in natural areas: effects of deer, area, and location. J. Med. Entomol. 31, 152–158.

Ginsberg, H.S., Zhioua, E., 1999. Influence of deer abundance on the abundance of questing adult *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 36, 376–381.

Halsey, S.J., Miller, J.R., 2020. Maintenance of *Borrelia burgdorferi* among vertebrate hosts: a test of dilution effect mechanisms. Ecosphere 11.

Hamer, S.A., Tsao, J.I., Walker, E.D., Hickling, G.J., 2010. Invasion of the Lyme disease vector *Ixodes scapularis*: implications for *Borrelia burgdorferi* endemicity. EcoHealth 7, 47–63.

Hojgaard, A., Eisen, R.J., Piesman, J., 2008. Transmission dynamics of *Borrelia burgdorferi* s.s. during the key third day of feeding by nymphal *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 45, 732–736.

Huang, C.I., Kay, S.C., Davis, S., Tufts, D.M., Gaffett, K., Tefft, B., Diuk-Wasser, M.A., 2019. High burdens of *Ixodes scapularis* larval ticks on white-tailed deer may limit Lyme disease risk in a low biodiversity setting. Ticks Tick-borne Dis. 10, 258–268.

Jacobs, J., 1974. Quantitative measurement of food selection. Oecologia 14, 413–417.

Jordan, R.A., Schulze, T.L., Jahn, M.B., 2007. Effects of reduced deer density on the abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease incidence in a northern New Jersey endemic area. J. Med. Entomol. 44, 752–757.

Keesing, F., Holt, R.D., Ostfeld, R.S., 2006. Effects of species diversity on disease risk. Ecol. Lett. 9, 485–498.

Kilpatrick, H.J., Labonte, A.M., Stafford III, K.C., 2014. The relationship between deer density, tick abundance, and human cases of lyme disease in a residential community. J. Med. Entomol. 51, 777–784.

Lafferty, K.D., Wood, C.L., 2013. It's a myth that protection against disease is a strong and general service of biodiversity conservation: Response to ostfeld and keesing. Conserv. Biol. 14, 722–728.

Lechowicz, M.J., 1982. The sampling characteristics of electivity indices. Oecologia 52, 22–30.

Leighton, P.A., Koffi, J.K., Pelcat, Y., Lindsay, L.R., Ogden, N.H., 2012. Predicting the speed of tick invasion: an empirical model of range expansion for the Lyme disease vector *Ixodes scapularis* in Canada. J. Appl. Ecol. 49, 457–464.

Levi, T., Keesing, F., Holt, R.D., Barfield, M., Ostfeld, R.S., 2016. Quantifying dilution and amplification in a community of hosts for tick-borne pathogens. Ecol. Appl. 26, 484–498.

Lindsay, L., Mathison, S., Barker, I., McEwen, S., Gillespie, T., Surgeoner, G., 1999a. Microclimate and habitat in relation to *Ixodes scapularis* (Acari: Ixodidae) populations on Long Point, Ontario, Canada. J. Med. Entomol. 36, 255–262.

Lindsay, L., Mathison, S., Barker, I., McEwen, S., Surgeoner, G., 1999b. Abundance of *Ixodes scapularis* (Acari: Ixodidae) larvae and nymphs in relation to host density and habitat on Long Point, Ontario. J. Med. Entomol. 36, 243–254.

LoGiudice, 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. USA 100, 567–571.

Lou, Y., Wu, J., 2014. Tick seeking assumptions and their implications for lyme disease predictions. Ecol. Complex. 17, 99–106.

MATLAB, 2018. Version 9.5.0 (R2018b). The MathWorks Inc., Natick, Massachusetts.

Ogden, N., Bigras-Poulin, M., Hanincova, K., Maarouf, A., O'callaghan, C., Kurtenbach, K., 2008a. Projected effects of climate change on tick phenology and fitness of pathogens transmitted by the North American tick *Ixodes scapularis*. J. Theor. Biol. 254, 621–632.

Ogden, N., Bigras-Poulin, M., O'callaghan, C., Barker, I., Lindsay, L., Maarouf, A., Smoyer-Tomic, K., 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., Lindsay, L., Beauchamp, G., Charron, D., Maarouf, A., O'callaghan, C., Waltner-Toews, D., Barker, I., 2004. Investigation of relationships between temperature and developmental rates of tick *Ixodes scapularis* (Acari: Ixodidae) in the laboratory and field. J. Med. Entomol. 41, 622–633.

Ogden, N., Maarouf, A., Barker, I., Bigras-Poulin, M., Lindsay, L., Morshed, M., O'callaghan, C., Ramay, F., Waltner-Toews, D., Charron, D., 2006. Climate change and the potential for range expansion of the Lyme disease vector *Ixodes scapularis* in Canada. Int. J. Parasitol. 36, 63–70.

Ogden, N., Tsao, J., 2009. Biodiversity and lyme disease: dilution or amplification? Epidemics 1, 196–206.

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.

Ogden, N.H., Radojevic, M., Wu, X., Duvvuri, V.R., Leighton, P.A., Wu, J., 2014. Estimated effects of projected climate change on the basic reproductive number of the Lyme disease vector *Ixodes scapularis*. Environ. Health Perspect. 122, 631–638.

Ogden, N.H., St-Onge, L., Barker, I.K., Brazeau, S., Bigras-Poulin, M., Charron, D.F., Francis, C.M., Heagy, A., Lindsay, L., Maarouf, A., et al., 2008b. Risk maps for range expansion of the Lyme disease vector, *Ixodes scapularis*, in Canada now and with climate change. Int. J. Health 7, 1–15.

Ostfeld, R., 2011. Lyme Disease: The Ecology of a Complex System. OUP USA.

Ostfeld, R.S., 2009. Biodiversity loss and the rise of zoonotic pathogens. Clin. Microbiol. Infect. 15, 40–43.

Ostfeld, R.S., Cepeda, O.M., Hazler, K.R., Miller, M.C., 1995. Ecology of Lyme disease: habitat associations of ticks (*Ixodes scapularis*) in a rural landscape. Ecol. Appl. 5, 353–361.

Ostfeld, R.S., Keesing, F., 2000. Biodiversity and disease risk: the case of lyme disease. Conserv. Biol. 14, 722–728.

Ostfeld, R.S., Keesing, F., 2013. Straw men don't get lyme disease: response to wood and lafferty. Trends Ecol. Evol. 28, 502–503.

Ostfeld, R.S., Miller, M.C., Hazler, K.R., 1996. Causes and consequences of tick (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). J. Mammal. 77, 266–273.

Pepin, K.M., Eisen, R.J., Mead, P.S., Piesman, J., Fish, D., Hoen, A.G., Barbour, A.G., Hamer, S., Diuk-Wasser, M.A., 2012. Geographic variation in the relationship between human Lyme disease incidence and density of infected host-seeking *Ixodes scapularis* nymphs in the Eastern United States. Am. J. Trop. Med. Hyg. 86, 1062–1071.

Pfäffle, M., Littwin, N., Muders, S.V., Petney, T.N., 2013. The ecology of tick-borne diseases. Int. J. Parasitol. 43, 1059–1077.

Piesman, J., Mather, T.N., Sinsky, R., Spielman, A., 1987. Duration of tick attachment and *Borrelia burgdorferi* transmission. J. Clin. Microbiol. 25, 557–558.

Piesman, J., Maupin, G.O., Campos, E.G., Happ, C.M., 1991. Duration of adult female *Ixodes dammini* attachment and transmission of *Borrelia burgdorferi*, with description of a needle aspiration isolation method. J. Infect. Dis. 163, 895–897.

Porco, T.C., 1999. A mathematical model of the ecology of lyme disease. Math. Med. Biol.: J. IMA 16, 261–296.

Rand, P.W., Lubelczyk, C., Lavigne, G.R., Elias, S., Holman, M.S., Lacombe, E.H., Smith, R.P., 2003. Deer density and the abundance of *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 40, 179–184.

Rosenberg, R., Lindsey, N.P., Fischer, M., Gregory, C.J., Hinckley, A.F., Mead, P.S., Paz-Bailey, G., Waterman, S.H., Drexler, N.A., Kersh, G.J., et al., 2018. Vital signs: trends in reported vectorborne disease cases-united states and territories, 2004-2016. Morb. Mortal. Wkly. Rep. 67, 496.

Salkeld, D.J., Padgett, K.A., Jones, J.H., 2013. A meta-analysis suggesting that the relationship between biodiversity and risk of zoonotic pathogen transmission is idiosyncratic. Ecol. Lett. 16, 679–686.

Schmidt, K.A., Ostfeld, R.S., 2001. Biodiversity and the dilution effect in disease ecology. Ecology 82, 609–619.

Schulze, T.L., Jordan, R.A., 1996. Seasonal and long-term variations in abundance of adult *Ixodes scapularis* (Acari: Ixodidae) in different coastal plain habitats of New Jersey. J. Med. Entomol. 33, 963–970.

Simon, J.A., Marrotte, R.R., Desrosiers, N., Fiset, J., Gaitan, J., Gonzalez, A., Koffi, J.K., Lapointe, F.J., Leighton, P.A., Lindsay, L.R., et al., 2014. Climate change and habitat fragmentation drive the occurrence of *Borrelia burgdorferi*, the agent of Lyme disease, at the northeastern limit of its distribution. Evol. Appl. 7, 750–764.

Smith, D., Dushoff, J., Snow, R., Hay, S., 2005. The entomological inoculation rate and *Plasmodium falciparum* infection in African children. Nature 438, 492–495.

Stafford III, K.C., 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) with exclusion of deer by electric fencing. J. Med. Entomol. 30, 986–996.

Stafford III, K.C., Denicola, A.J., Kilpatrick, H.J., 2003. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and the tick parasitoid *Ixodiphagus hookeri* (Hymenoptera: Encyrtidae) with reduction of white-tailed deer. J. Med. Entomol. 40, 642–652.

Tagliapietra, V., Rosà, R., Arnoldi, D., Cagnacci, F., Capelli, G., Montarsi, F., Hauffe, H., Rizzoli, A., 2011. Saturation deficit and deer density affect questing activity and local abundance of *Ixodes ricinus* (Acari: Ixodidae) in Italy. Vet. Parasitol. 183, 114–124.

Wallace, D., Ratti, V., Kodali, A., Winter, J.M., Ayres, M.P., Chipman, J.W., Aoki, C.F., Osterberg, E.C., Silvanic, C., Partridge, T.F., et al., 2019. Effect of rising temperature on Lyme disease: *Ixodes scapularis* population dynamics and *Borrelia burgdorferi* transmission and prevalence. Can. J. Infect. Dis. Med. Microbiol. 2019.

Winter, J.M., Partridge, T.F., Wallace, D., Chipman, J.W., Ayres, M.P., Osterberg, E.C., Dekker, E.R., 2020. Modeling the Sensitivity of Blacklegged Ticks (*Ixodes scapularis*) to Temperature and Land Cover in the Northeastern United States. J. Med. Entomol.

Wood, C.L., Lafferty, K.D., 2013. Biodiversity and disease: a synthesis of ecological perspectives on lyme disease transmission. Trends Ecol. Evol. 28, 239–247.

Wu, X., Duvvuri, V.R., Wu, J., 2010. Modeling dynamical temperature influence on tick *Ixodes scapularis* population. International Congress on Environmental Modelling and Software 2272–2287.