

Supporting Information

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SI Text

Parameters and Derivations. Although our analysis is qualitative and we produce closed-form solutions, we nevertheless find plausible parameter values to see if reasonable levels of predation can influence Lyme disease.

$M(N_m)$. We model predation with a type III functional response, but our results can also be obtained by combining a type II functional response with a numerical response.

For example, if we instead model predation with a type II functional response

$$M(N_m) = \frac{aPN_m}{b + N_m},$$

but also note that predator density, P , should increase and eventually saturate with prey density, then we obtain

$$P = \frac{\alpha N_m}{\beta + N_m}.$$

Combining these two equations yields

$$M(N_m) = \frac{a\alpha PN_m^2}{(b\beta + 2b\beta N_m + N_m^2)},$$

which is simply a more general form of the type III functional response that has the same sigmoid shape and qualitative properties (this can be understood intuitively by recognizing that the squared-term dominates the expression in the denominator). **F .** We estimate the density of noncompetent dilution hosts following LoGiudice et al. (1). We sum the density estimates of dilution hosts to obtain $F \sim 4,120$. We ignore the fact that dilution hosts are somewhat reservoir competent because of evidence that 80–90% of ticks are infected by a few small-mammal species (2). We thus consider a class of dilution hosts rather than considering

Following LoGiudice et al. (1), the reservoir-competent small-mammal density (N_m) ranges from 5,000 to 200,000 km^{-2} . To estimate b_0 , we use an intermediate (nonresource pulse) value of 10,000 km^{-2} . Substituting in F and solving for b_0 , a reasonable estimate of b_0 is $\sim 80,000$, meaning that half of ticks are expected feed if the total host population ($N_m + F$) is 80,000 km^{-2} .

aP and c . One classic study (4) quantified the impact of generalist predators on two species of small mammals over 40 km^2 in southern Sweden. This study found that generalist predators were responsible for far more predation on voles and wood mice than specialist predators. We use predation rate data from this study to fit the parameters aP and c . A precise estimate of aP is not necessary because we explore the steady states of the differential equations as a function of a variable maximum predation rate, aP (Fig. 1 *B* and *C* and Fig. S2). We thus only need a reasonable half-saturation parameter. Although this study comes from Sweden, the predator community is similar to that of the northeastern United States, with red foxes being the dominant predator of small mammals.

We fit the per capita predation rate $\frac{aP \cdot N}{c^2 + N^2}$ (a type III functional response divided by N) to the data with and without two potential outliers. These data come from monthly predation rates that should show considerably more variation than annual predation rates because annual measures smooth over seasonal and stochastic variability. The best estimate of aP is 241,391 per 40 km^2 , which is equivalent to 6,034 annual kills per km^2 .

Steady-State Solutions. Eqs. 1–6 can be solved for steady-state solutions that depend only on the steady-state small-mammal density, \bar{N}_m . The steady states are given by

$$\bar{S}_t = \frac{\nu(b_0 + \bar{N}_m + F)}{\bar{N}_m + F + \mu_l(b_0 + \bar{N}_m + F)}, \quad [\text{S1}]$$

$$\bar{I}_t = \bar{N}_m(b_0 + \bar{N}_m + F) \left(\frac{T_{m\nu}}{(\bar{N}_m + F + \mu_l(b_0 + \bar{N}_m + F))(\bar{N}_m + F + \mu_n(b_0 + \bar{N}_m + F))} - \frac{aP}{T_{mt}(c^2 + \bar{N}_m^2)} \right), \quad [\text{S2}]$$

$$\bar{J}_t = \bar{N}_m(b_0 + \bar{N}_m + F) \left(\frac{\nu \left(1 - T_{tm} + \frac{F}{\bar{N}_m} \right)}{(\bar{N}_m + F + \mu_l(b_0 + \bar{N}_m + F))(\bar{N}_m + F + \mu_n(b_0 + \bar{N}_m + F))} + \frac{aP}{T_{mt}(c^2 + \bar{N}_m^2)} \right), \quad [\text{S3}]$$

the variability among hosts. The nonzero infectiousness of dilution hosts can prevent complete *Borrelia* extinction even when small mammals are rare, but this does not impact the qualitative relationship between predation and Lyme disease risk.

b_0 . We use tick densities estimated with mark-recapture techniques (3) to estimate the half-saturation parameter of the tick functional response, b_0 .

Daniels et al. (3) found larval densities of ~ 11.5 million km^{-2} and nymph densities of 1.2 million km^{-2} . The nymph population was $\sim 10\%$ of the larva population. We reason that at least 10% of larva successfully fed, allowing us to estimate b_0 .

$$\beta(N_m + F) = \frac{N_m + F}{b_0 + N_m + F} = 0.10$$

$$\bar{S}_m = \frac{(\bar{N}_m + F + \mu_l(b_0 + \bar{N}_m + F))(\bar{N}_m + F + \mu_n(b_0 + \bar{N}_m + F))aP\bar{N}_m}{(c^2 + \bar{N}_m^2)T_{mt}T_{m\nu}}, \quad [\text{S4}]$$

and

$$\bar{I}_m = \bar{N}_m \left[1 - \frac{aP(\bar{N}_m + F + \mu_l(b_0 + \bar{N}_m))(\bar{N}_m + F + \mu_n(b_0 + \bar{N}_m))}{(c^2 + \bar{N}_m^2)T_{mt}T_{m\nu}} \right]. \quad [\text{S5}]$$

All quantities are restricted to be nonnegative, and the abundance of any one class of either hosts or ticks is restricted to be less than the total abundance of hosts or ticks.

The infection prevalence of hosts (HIP) and nymphs (NIP) can be derived from the steady states

$$HIP = 1 - \frac{aP(\overline{N}_m + F + \mu_l(b_0 + \overline{N}_m + F))(\overline{N}_m + F + \mu_n(b_0 + \overline{N}_m + F))}{(c^2 + \overline{N}_m^2)T_{mt}T_{m\nu}} \quad [S6]$$

and

$$NIP = \frac{\overline{I}_t}{\overline{I}_t + \overline{J}_t} = T_{im} \frac{\overline{N}_m}{\overline{N}_m + F} \left(1 - \frac{aP(\overline{N}_m + F + \mu_l(b_0 + \overline{N}_m + F))(\overline{N}_m + F + \mu_n(b_0 + \overline{N}_m + F))}{(c^2 + \overline{N}_m^2)T_{mt}T_{m\nu}} \right). \quad [S7]$$

Combining Eqs. S6 and S7, we recover the intuitive result that relates the nymphal infection prevalence to the infection prevalence of hosts,

$$NIP = \frac{\overline{I}_t}{\overline{I}_t + \overline{J}_t} = T_{im} \frac{\overline{N}_m}{\overline{N}_m + F} HIP. \quad [S8]$$

The fraction of hosts that are reservoir competent determines the relationship between host infection prevalence and nymphal infection prevalence.

The steady-state solutions provide a framework for understanding the role of the known multiple drivers of Lyme disease risk. For example, the steady-state densities of sus-

ceptible and infected hosts and ticks can be assessed as a function of predation, aP , relative to the density of the tick birth rate, ν (Fig. S4), or dilution hosts, F (Fig. S5). Increasing both predation and the density of dilution hosts reduces Lyme disease risk as long as the tick birth rate, ν , remains constant. However, by reducing the density or activity level of small mammals, predation likely reduces the tick birth rate if a larger fraction of immature ticks cannot find the hosts necessary to

transition into reproductively mature adult ticks. In contrast, increased density of dilution hosts takes blood meals away from disease-amplifying small mammals, but by supplying blood meals, dilution hosts can increase the tick birth rate if hosts for immature ticks are limiting.

Thus, predation is always expected to reduce the density of infected nymphs, but the magnitude of this reduction in Lyme disease risk depends on how much predation of small mammals reduces the tick birth rate (Fig. S4, black arrows). In contrast, increasing the density of dilution hosts is expected to lower nymph infection prevalence but may have minimal impact on the density of infected nymphs (Fig. S6, black arrows) (5).

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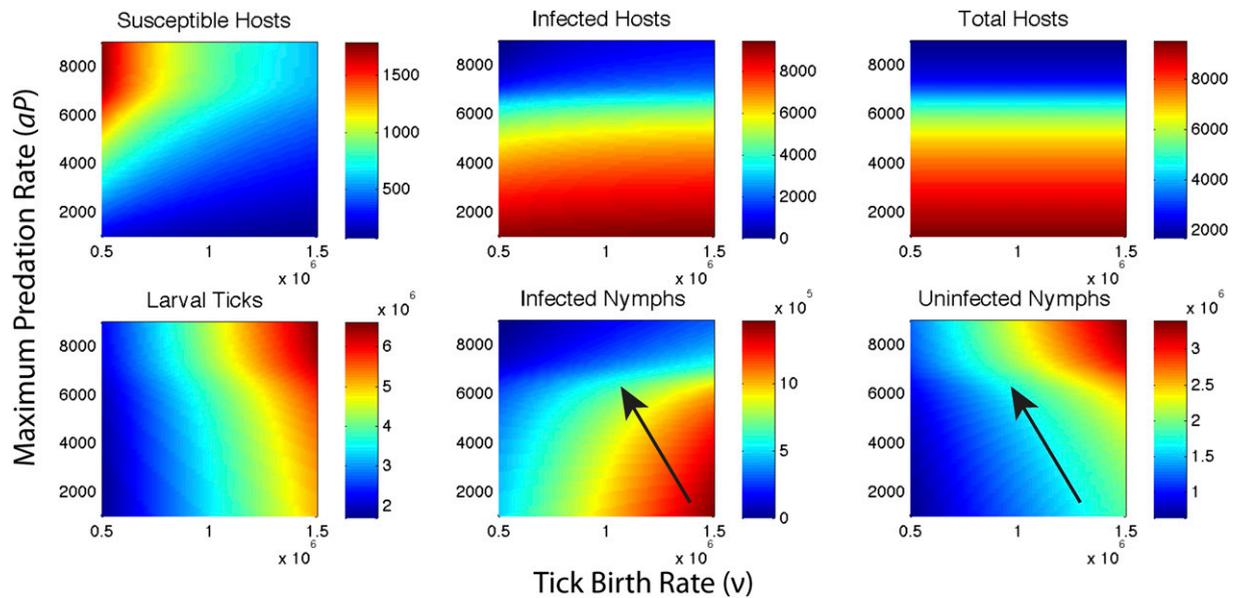


Fig. 54. Color plot of the steady states of the different equations as a function of the tick birth rate, ν , and the asymptotic maximum predation rate, aP . Black arrows signify the qualitative impact of predation on tick density when expected changes to the tick birth rate are accounted for. The density of infected nymphs is expected to decline substantially with the combined effect of predators on aP and ν .

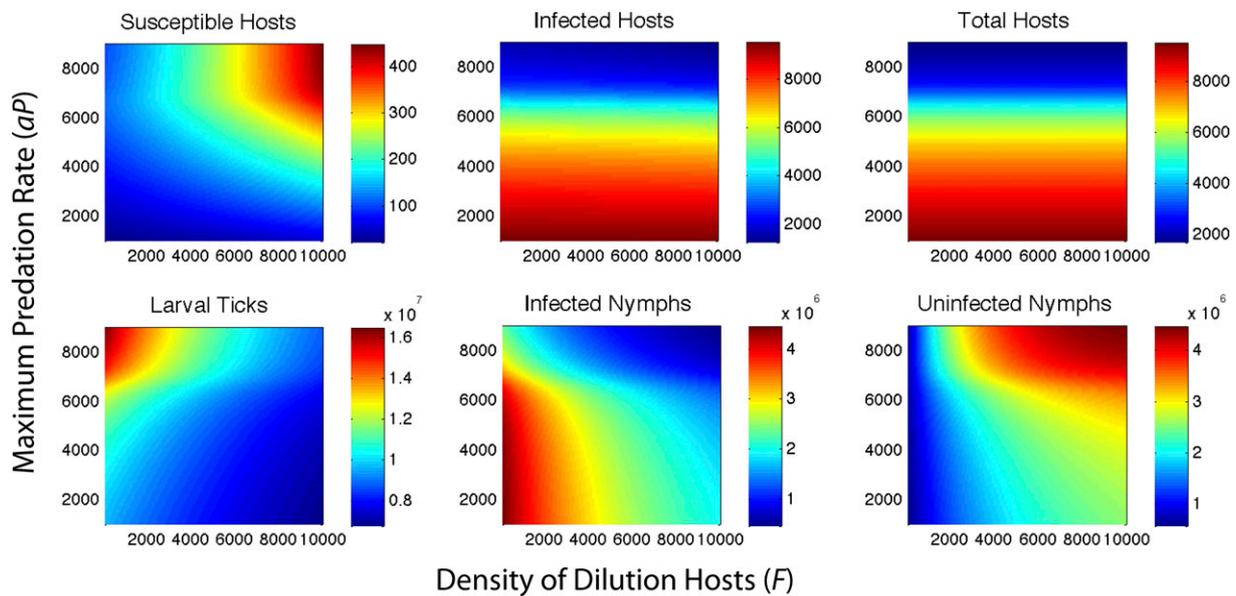


Fig. 55. Color plot of the steady states of the different equations as a function of F , dilution host density (km^2), and aP , the asymptotic maximum predation rate.

Table S1. Summary of studies measuring or manipulating deer populations and the corresponding response of ticks

Location	Island or mainland	Summary	Ref.
Montgomery County, MD	Mainland	Very low tick density found despite hyperabundant deer	1
Westchester County, NY	Mainland	After 25 y of deer exclusions, fewer nymphs inside most exclusions, but more nymphs inside in one site. No change in nymphal infection prevalence.	2
Westchester County, NY	Mainland	Differences in tick density inside and outside enclosure decline with successive tick developmental stages.	3
Ipswich, MA	Island	A 40% harvest rate of deer reduced population by 75% on an island. Larva per mouse falls substantially, and nymphs per mouse falls somewhat. Additionally, tick burdens on deer increase as deer density decreases.	4 (data presented in Fig. S1)
Long Island, NY	Island	<i>Ixodes scapularis</i> nymphs present at sites without deer but at low abundance.	5
Galway, Ireland	Mainland	Ticks much more abundant outside enclosure fence.	6
Sweden	Island	<i>Borrelia</i> and <i>Ixodes</i> ticks are both maintained in the absence of deer by hare populations.	7
Somerset County, NJ	Mainland	Deer culling by 47% produced no effect on tick abundance.	8
Monmouth County, NJ	Mainland	No relationship between ticks and deer pellet counts or browse damage.	9
Helsinki, Finland	Mainland	Ticks and <i>Borrelia</i> present without deer or any other ungulates.	10
Coastal Maine	Mainland	Deer pellet group and tick abundance are correlated.	11
Dutchess County, NY	Mainland	No relationship between deer and tick nymphs, but a strong relationship between ticks and rodents.	12
Italian Alps	Mainland	Small deer enclosure amplifies nymph intensity on rodents and increases infection prevalence but no change in larval intensity.	13
Various sites in Maine	Mainland	Adult tick abundance and deer pellet groups are positively correlated.	14
Monhegan Island, ME	Island	Complete removal of deer from small island with no other medium or large vertebrate hosts greatly reduced tick abundance.	15
Lyme, CT	Mainland	Deer exclusions greatly reduce larval and nymphal tick abundance. Adult tick results are mixed.	16
Bridgeport, CT, and Groton, CT	Mainland	Tick densities are reduced substantially by severe reduction in deer densities, but the effect saturates (Fig. S6).	17 (data presented in Fig. S2)
Mendocino, CA	Mainland	Nymphal density higher with deer at one site but not at another.	18
Great Island, MA	Island	A 70% reduction in deer did not reduce larval ticks per mouse the following year.	19
Great Island, MA	Island	On 13 islands, larval ticks are significantly correlated with deer but nymphs are not.	20
Great Island, MA	Island	Great reduction in larva and mild reduction in nymphs after complete removal of deer from island.	21

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Table S2. List of parameters and variables

	Interpretation	Value
Parameters		
μ_l, μ_n	Mortality rate of larva and nymphs	0.2
F	Density of dilution hosts	4,120
b_0	Half-saturation parameter of tick functional response	80,000
aP	Asymptotic number of hosts killed annually by predators with population, P	1,000–9,000
c	Mouse population where the predation rate reaches half of the maximum	2,500
T_{mt}	Probability that an infected tick biting a susceptible host transmits <i>Borrelia</i>	0.9
T_{tm}	Probability that an infected host bitten by a susceptible tick transmits <i>Borrelia</i>	0.9
r	Maximum intrinsic growth rate of hosts	2
K	Carrying capacity of hosts	10,000
ν	Birth rate of larval ticks	500,000, 1 million, 1.5 million
Variables		
S_m	Density of susceptible small mammals	
I_m	Density of infected small mammals	
N_m	Total density of small mammals	
S_t	Density of larval ticks, which are all susceptible	
I_t	Density of infected nymphal ticks	
J_t	Density of susceptible nymphal ticks	

Table S3. Model comparisons of three hunter-harvest predictors in explaining the number of annual Lyme disease cases (log transformed) in four states

State	Variable	R^2	AICc	Δ AICc	n	Model weight
MN	Deer + coyote + fox	0.85	30.21	0.00	21	0.89
	Coyote + fox	0.79	34.43	4.22	21	0.11
	Deer + fox	0.64	45.23	15.02	21	0.00
	Fox	0.58	45.45	15.25	21	0.00
	Deer + coyote	0.45	54.14	23.93	21	0.00
	Coyote	0.32	55.64	25.43	21	0.00
	Deer	0.13	60.69	30.48	21	0.00
WI	Coyote	0.73	39.66	0.00	27	0.37
	Coyote + fox	0.75	39.77	0.11	27	0.35
	Deer + coyote	0.74	41.13	1.47	27	0.18
	Deer + coyote + fox	0.76	42.21	2.55	27	0.10
	Fox	0.47	57.60	17.94	27	0.00
	Deer + fox	0.47	60.37	20.71	27	0.00
	Deer	0.02	74.04	34.37	27	0.00
PA	Coyote	0.53	28.62	0.00	18	0.51
	Deer + coyote	0.58	29.89	1.27	18	0.27
	Coyote + fox	0.54	31.30	2.68	18	0.13
	Deer + coyote + fox	0.60	32.71	4.09	18	0.07
	Fox	0.28	36.05	7.43	18	0.01
	Deer + fox	0.29	39.37	10.75	18	0.00
	Deer	0.09	40.31	11.69	18	0.00
VA	Coyote + fox	0.83	27.05	0.00	14	0.86
	Deer + coyote + fox	0.84	31.85	4.80	14	0.08
	Coyote	0.66	33.06	6.01	14	0.04
	Deer + coyote	0.72	34.57	7.53	14	0.02
	Fox	0.47	39.12	12.07	14	0.00
	Deer + fox	0.50	42.38	15.33	14	0.00
	Deer	0.25	44.02	16.97	14	0.00

Harvests are not scaled by license sales. MN, Minnesota; PA, Pennsylvania; VA, Virginia; WI, Wisconsin.

Table S4. Model comparisons of three predictors in explaining the number of annual Lyme disease cases (log transformed) in four states with deer, coyote, and fox scaled by big-game hunting license sales

State	Variable	R^2	AICc	Δ AICc	n	Model weight
MN	Coyote + fox	0.79	34.40	0.00	21	0.83
	Deer + coyote + fox	0.79	37.86	3.46	21	0.15
	Deer + fox	0.67	43.50	9.10	21	0.01
	Fox	0.63	42.67	8.27	21	0.01
	Deer	0.34	55.00	20.61	21	0.00
	Deer + coyote	0.36	57.36	22.96	21	0.00
WI	Coyote	0.12	61.05	26.65	21	0.00
	Coyote + fox	0.76	39.32	0.00	27	0.40
	Coyote	0.72	39.88	0.56	27	0.30
	Deer + coyote	0.74	40.93	1.61	27	0.18
	Deer + coyote + fox	0.76	41.62	2.30	27	0.13
	Fox	0.46	57.99	18.67	27	0.00
PA	Deer + fox	0.46	60.69	21.36	27	0.00
	Deer	0.07	72.85	33.53	27	0.00
	Deer + coyote	0.59	29.36	0.00	18	0.42
	Coyote	0.50	29.74	0.38	18	0.35
	Deer + coyote + fox	0.60	32.69	3.33	18	0.08
	Coyote + fox	0.50	32.93	3.57	18	0.07
VA	Fox	0.38	33.42	4.06	18	0.06
	Deer + fox	0.42	35.48	6.12	18	0.02
	Deer	0.00	42.07	12.71	18	0.00
	Coyote + fox	0.83	27.56	0.00	14	0.32
	Deer	0.76	28.19	0.63	14	0.24
	Deer + coyote	0.82	28.37	0.81	14	0.21
VA	Deer + coyote + fox	0.86	29.24	1.68	14	0.14
	Deer + fox	0.78	31.18	3.62	14	0.05
	Coyote	0.69	31.94	4.38	14	0.04
	Fox	0.29	43.23	15.67	14	0.00

MN, Minnesota; PA, Pennsylvania; VA, Virginia; WI, Wisconsin.