VECTOR BORNE AND ZOONOTIC DISEASES
Volume 1, Number 1, 2001
Mary Ann Liebert, Inc.

Research Paper

Effects of Acorn Production and Mouse Abundance on Abundance and *Borrelia burgdorferi* Infection Prevalence of Nymphal *Ixodes scapularis* Ticks

RICHARD S. OSTFELD,[1] ERIC M. SCHAUBER,[1] CHARLES D. CANHAM,[1] FELICIA KEESING,[1,2] CLIVE G. JONES,[1] and JERRY O. WOLFF[3]

ABSTRACT

Risk of exposure to Lyme disease is a function of the local abundance of nymphal *Ixodes* ticks that are infected with the etiological agent, the spirochete *Borrelia burgdorferi*. We monitored abundance of white-footed mice (the principal *B. burgdorferi* reservoir in the eastern and central United States) and acorns (a critical food resource for mice), and *Ixodes scapularis* ticks, as well as ambient temperature (cumulative growing degree days) and growing season precipitation, in a forested landscape of southeastern New York State from 1994 to 2000. We found that acorn production in autumn strongly influenced abundance of white-footed mice the following summer and that abundance of mice in summer, when larval ticks are active, influenced the abundance of infected nymphs the following year. Consequently, the abundance of infected nymphal ticks can be predicted from acorn production 1.75 years earlier. Monitoring of natural fluctuations in acorn production thus supports results of prior acorn addition experiments that were conducted at small spatial scales. Growing degree days and precipitation either had no significant effect on density of nymphs or marginally increased the explanatory power of models that included acorns or mouse density as independent variables. We conclude that, at our study site in New York, the risk of human exposure to Lyme disease is affected by mouse density in the prior year and by acorn production 2 years previously. Vector Borne Zoonotic Dis. 1, 55–63.

INTRODUCTION

LYME DISEASE is the most common vector-borne disease in the United States and parts of Europe (Lane et al. 1991, Barbour and Fish 1993). In the northeastern and north-central United States, Lyme disease is primarily vectored by the blacklegged tick (*Ixodes scapularis*), which has three active life stages: larva, nymph, and adult, each of which takes a single blood meal before molting to the next stage (in the case of larvae and nymphs) or reproducing and dying (adults). Larvae hatch and feed in midsummer (year 1), molt into nymphs that feed the following early summer (year 2), and finally molt into adults that feed predominantly on white-tailed deer (*Odocoileus virginianus*) the following autumn or spring (year 2 or 3) (Fish 1993, Ostfeld 1997). Nearly all larval *I. scapularis* ticks hatch free of infection (Piesman et al. 1986, Patrican 1997) and are not known to transmit *Borrelia burgdorferi*. If a tick acquires *B.*

[1]Institute of Ecosystem Studies, Millbrook, NY.
[2]Department of Biology, Bard College, Annandale, NY.
[3]Department of Biology, University of Memphis, Memphis, TN.

burgdorferi during its larval meal, it may then transmit the infection during its nymphal meal. Indeed, most human cases of Lyme disease are thought to be transmitted by nymphs, owing to their minute size, summer activity, and potentially high infection prevalence (Barbour and Fish 1993). The local abundance of infected nymphs, therefore, is the primary ecological risk factor for human populations (Barbour and Fish 1993).

Within Lyme disease endemic areas, white-footed mice (*Peromyscus leucopus*) are heavily parasitized by larval ticks (Mather and Ginsberg 1994, Ostfeld et al. 1996a, Schmidt et al. 1999), are frequently infected (Donahue et al. 1987, Hofmeister et al. 1999), and are highly efficient at transmitting *B. burgdorferi* to feeding larval ticks (Levine et al. 1985, Mather et al. 1989). However, the impact of mouse abundance on abundance and infection prevalence of nymphal ticks, and hence on risk of human exposure to Lyme disease, is controversial (Mather and Ginsberg 1994, Ginsberg et al. 1998, Ostfeld et al. 1998a, Randolph 1998). Abundance of nymphs may be influenced by weather factors, especially temperature and precipitation, which can affect larval survival during the prior year and survival of nymphs in the current year (Lindsay et al. 1995, Jones and Kitron 2000). Assessing the relative importance of biotic factors, such as the abundance of larval hosts and of resources for hosts, and abiotic factors, such as weather effects, in determining population density and infection prevalence of nymphal ticks is important for predicting Lyme disease risk to humans.

In a prior study, we found that experimental autumnal addition of acorns (*Quercus rubra*), which are a crucial fall and winter food source for mice and deer (Ostfeld et al. 1996b, Wolff 1996), increased abundance of both host-seeking blacklegged tick larvae and white-footed mice the following summer (Jones et al. 1998). As a consequence, larval tick burdens on individual mice the summer following treatment were significantly higher on acorn addition plots than on control plots (Jones et al. 1998). We postulated that the acorn enrichment should therefore increase the abundance of nymphal ticks and the fraction of nymphal ticks infected with *B. burgdorferi* two summers after supplementation. Testing this hypothesis experimentally is infeasible owing to logistic limitations on the spatial extent over which acorns can be supplemented. Because mice (and attached larval ticks) disperse between supplemented and adjacent unsupplemented areas following acorn depletion (Ostfeld et al. 1998b), nymphal ticks present in experimental plots two summers following acorn addition did not necessarily acquire their larval meal in the same plots.

In this paper, we describe an alternative, observational approach to analyzing the relative importance of natural acorn production, mouse abundance, and weather, both on abundance of nymphal *I. scapularis* and on *B. burgdorferi* infection prevalence in the tick population. Our general approach was to use regression models to assess the explanatory power of specific biotic and abiotic factors in predicting density of infected nymphs (DIN) in any given year.

MATERIALS AND METHODS

Study sites and acorn sampling

Field studies were conducted at the Institute of Ecosystem Studies in Dutchess County, southeastern New York, in a postagricultural landscape consisting of an oak forest matrix (57–70% oak relative basal area) (Ostfeld et al. 1998b). Six plots (five 150×150m, one 165×120m), separated by >100 m, were established in oak-dominated sites. Four of these plots were added in 1995 to two previously existing plots. In the two longer-term plots, one 0.5-m^2 seed trap was deployed beneath each of five randomly chosen, mature specimens of each of the four dominant canopy trees, oak (*Q. rubra*, *Quercus prinus*, *Quercus alba*) and hickory (*Carya glabra*), for a total of 20 traps per plot. Acorns were collected weekly from September to December each year, and total acorn counts were divided by total seed-trap area to create a mast index (acorns m^{-2}). The mast index provided a single, landscape-scale measure of acorn production each autumn. We tested the mast indices from 1993 to 1998 as predictors of abundance of white-footed mice the next year and of abundance and infection prevalence of nymphs 2 years later (1995–2000).

Rodent, tick, and Borrelia *sampling*

On each of the six plots, either an 11 × 11 or a 12 × 10 grid of Sherman live traps was established, with two traps per station and 15 m between stations (240–242 traps per grid). Trapping was conducted each year for 2–3 consecutive nights every 3–4 weeks from April or May to November of 1994–2000 on the original two plots and of 1995–2000 for the remaining four plots. Each captured white-footed mouse was uniquely marked by a numbered metal eartag. In 1994 (two grids only), sampling effort for estimating mouse density was ~10,650 trap nights. In 1995–2000, with six grids, sampling effort was ~32,000 trap nights per year, for a total of ~202,650 trap nights for the entire study. Owing to high capture probabilities (>0.80), population density was estimated using the minimum number alive (Hilborn et al. 1976, Slade and Blair 2000).

Mouse density during the seasonal peak in host-seeking activity of larval *I. scapularis* [mid August-early September at our sites (Ostfeld et al. 1996c)] is relevant to assessing the impacts of white-footed mice on abundance and infection prevalence of nymphs the following year. Therefore, we estimated mouse density on September 1 of each year by interpolating between sequential mouse density estimates.

We monitored abundance of nymphs in each individual year (1995–2000) by dragging 1-m^2 white corduroy drag cloths along 450 m of transects in each of the six oak plots. For each drag sample, a set of three 150–m rows within the 11 × 11 or 10 × 12 grid was selected randomly. Drag sampling was conducted on all plots every 2–4 weeks from April to November each year. Drag cloths were examined, and all ticks were counted and removed every 30 m. Similar methods of sampling blacklegged ticks have been validated at sites ~100 km south of our study site (Daniels et al. 2000). The peak period of nymphal activity each year was identified as the sampling week with maximum nymphal abundance values averaged across all six grids. As we found earlier from a smaller sample of years (Ostfeld et al. 1996c), nymphal ticks at our sites reach their annual activity peak in late June to early July.

Infection of individual ticks with *B. burgdorferi* was determined using DFA. Ticks were washed once in 70% ethanol and twice in deionized water and ground in phosphate-buffered saline (PBS) in Eppendorf tubes. Three 5-ml aliquots of tick suspension were placed in separate wells of a multiwell slide, air-dried, and fixed in cold acetone for 10 minutes. Fluorescein rabbit anti-*B. burgdorferi* conjugate was incubated in wells at 37°C for 45 minutes, after which slides were washed in PBS, dried, and mounted with a coverslip. Slides were examined at ×400 magnification under UV light. If spirochetes were not detected immediately, the three wells per individual tick were examined systematically to categorize each tick as either infected or uninfected. Altogether, 146, 442, 271, 398, 404, and 322 nymphs were examined for spirochete infection in 1995–2000, respectively. For each grid and year separately, we estimated DIN by multiplying peak nymphal density by infection prevalence (proportion of nymphs from that grid that tested positive).

Weather variables

We focused on the same weather variables recently described by Jones and Kitron (2000) as influencing abundance of blacklegged ticks in Illinois. We determined temperature and precipitation values for both the current (year t) and prior (year $t-1$) years, to reflect potential weather effects on survival during the nymphal stage and survival during the preceding larval stage, respectively. In the case of temperature data, we included only those months from the beginning of the growing season through the end of the activity period for the appropriate tick life stage [July for nymphs, September for larvae (Ostfeld et al. 1996c, Jones and Kitron 2000)]. Similarly, for precipitation data, we included only those months from the onset of potential soil moisture limitation (May) to the end of the appropriate activity period (Jones and Kitron 2000). We assessed the following weather parameters, which we downloaded from the Institute of Ecosystem Studies environmental monitoring station (http://www.ecostudies.org/research/emp/emppurp.html), located <1.5 km from our rodent, tick, and acorn sampling plots: (1) cumulative growing degree days (GDD) for March 1

through June 30 of year t; (2) cumulative GDD for March 1 through September 30 of year $t - 1$; (3) total precipitation (PPT; in mm) for May 1 through June 30 of year t; and (4) PPT for May 1 through September 30 of year $t - 1$.

Data analysis

Our general approach was to use linear regression models to determine the degree to which interannual variation in tick density and infection prevalence can be explained by a series of independent variables. Because our primary interest was in predicting Lyme disease risk at a scale that would be relevant epidemiologically, we focused on providing a single, landscape-scale estimate of both the independent and dependent variables for each year. Therefore, we averaged grid-specific mouse and tick data from the six grids each year. We focused initially on testing the hypothesis that density of nymphs (DON) and nymphal infection prevalence (NIP) are related to mouse density 1 year previously (mouse model) and acorn abundance 2 years previously (acorn model). We then conducted two follow-up analyses. First, to address smaller-scale spatial variation, we assessed the relationship between prior-year mouse density and nymph parameters for each grid separately. Second, to include abiotic variables, we analyzed two forward, stepwise multiple regression models: one using mouse density in year $t - 1$ and the four weather variables as determinants of the DIN (mouse model), and the other using the acorn index in year $t - 2$ and the four weather variables as determinants of DIN (acorn model).

Because measurements of some dependent and independent variables were temporally separated by up to 2 years, our sample size for some of the regressions was relatively small (n = 6 years). Therefore, to increase our power to detect the effect of the independent variables, we a priori set $\alpha = 0.15$ for entrance into the multiple regression models.

RESULTS

Simple regression models

Averaging across the six study plots, DON, NIP, and their product, DIN, all increased with increasing prior-year mouse density ($R^2 > 0.80$, $p \leq 0.02$; Fig. 1). Results at the landscape scale were supported by finer scale analyses of individual plots. DIN, DON, and NIP on individual plots were significantly positively related to prior-year mouse density on those plots ($p \leq 0.0002$ for all three response variables), with similar slopes among grids (Fig. 2). We found a strong positive relationship between acorn production in autumn and white-footed mouse density the following summer ($R^2 = 0.85$, $p = 0.001$), extending our prior findings (Wolff 1996, Ostfeld et al. 1998b). The lagged impacts of acorns on mice, and of mice on ticks, led to a significant positive relationship between acorn production in autumn and DON and DIN, but not NIP, two summers later (Fig. 3).

Multiple regression models

For the stepwise regression model of DIN, with mouse density in year $t - 1$ and the four weather factors as independent variables, mouse density entered the model first, explaining 83% of the variation in DIN ($F = 26.0$,

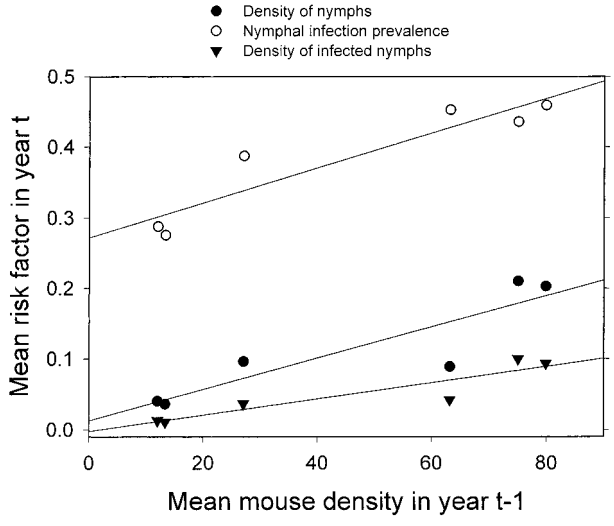

FIG. 1. Effects of population density of white-footed mice (minimum number alive per 2.25-ha grid) on three Lyme disease risk factors, measured during the annual peak in questing activity of nymphal *I. scapularis* ticks the following June–July. Values for mouse density are averages across the six grids for Sept 1 of each year, representing the peak larval activity period at the study sites. DON and DIN are expressed as individuals $\times$ m^{-2}, and NIP is expressed as a proportion of nymphs infected with *B. burgdorferi*. Regression statistics for risk factors against mouse density are: DON, $R^2 = 0.80$, $p = 0.02$; DIN, $R^2 = 0.83$, $p = 0.01$; NIP, $R^2 = 0.87$, $p = 0.01$.

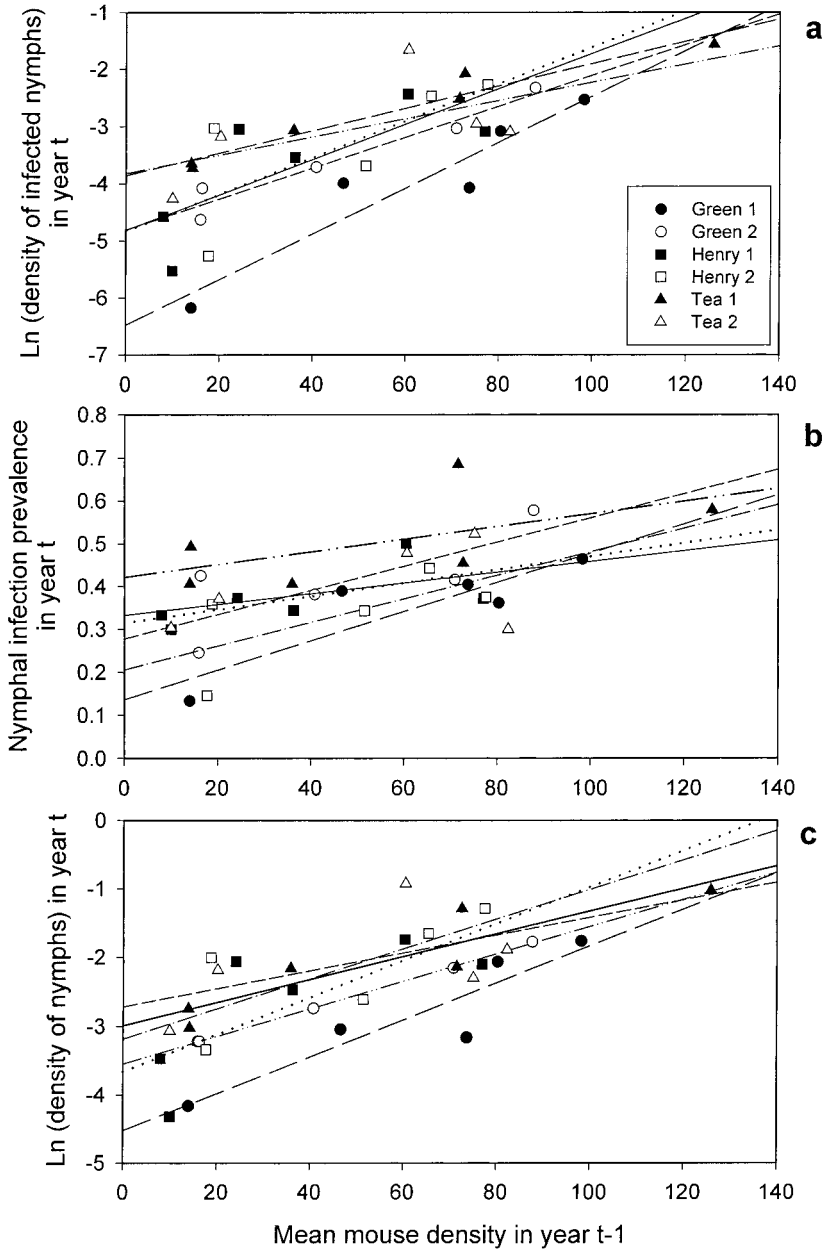

FIG. 2. Effects of population density of white-footed mice (minimum number alive per 2.25-ha) on three Lyme disease risk factors, measured during the annual peak in questing activity of nymphal *I. scapularis* ticks the following June–July. Values for mouse density are extrapolated values corresponding to Sept 1 and are specific to each of the six trapping grids, with different symbols and lines representing each grid. DON and DIN were ln-transformed before analysis to stabilize variances. ANCOVA revealed significant effects of mouse density on (**a**) DIN ($F_{1,20} = 44.61$, $p = 0.0001$), (**b**) NIP ($F_{1,20} = 20.90$, $p = 0.0002$), and (**c**) DON ($F_{1,20} = 37.65$, $p = 0.0001$), as well as homogeneity of slopes among grids (grid × mouse density) interaction; for all three risk factors, $F_{5,20} < 0.80$, $p > 0.56$.

$df = 1$, $p = 0.007$; Table 1). The only other variable entering the model was GDD in year t ($F = 6.65$, $df = 1$, $p = 0.01$), which increased the model R^2 value to 0.96. For DON, mouse density in year $t - 1$ was the only explanatory variable entering the model, and for NIP, mouse density entered first ($R^2 = 0.87$), followed by GDD in year $t - 1$, which increased the model R^2 value to 0.94 (Table 1).

For the stepwise regression model of DIN using acorns in year $t-2$ and the four weather variables, acorns entered the model first ($R^2 = 0.86$, $F = 24.45$, $df = 1$, $p = 0.008$), followed by PPT in year t, which improved the model R^2 to

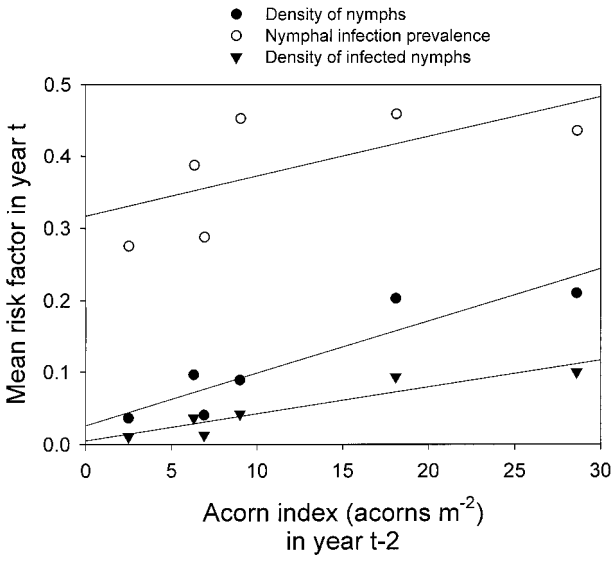

FIG. 3. Effects of acorn production in autumn on three Lyme disease risk factors, measured during the annual peak in questing activity of nymphal *I. scapularis* two summers later. Acorn production is expressed as the total density of acorns (number $\times$ m^{-2}) collected in 40 seed traps placed under the canopies of dominant tree species in oak-dominated forest. DON and DIN are expressed as individuals $\times$ m^{-2}, and NIP is expressed as the proportion of nymphs infected with *B. burgdorferi*. Regression statistics for risk factors against acorn production are: DON, $R^2 = 0.84$, $p = 0.01$; DIN, $R^2 = 0.86$, $p = 0.01$; NIP, $R^2 = 0.45$, $p = 0.15$.

0.95 (Table 1). The effect of acorn production on combined DON and NIP was due primarily to an effect on density. Acorn production was not a significant determinant of NIP; only GDD in year t entered the model for NIP ($R^2 = 0.48$, $F = 3.65$, $df = 1$, $p = 0.129$; Table 1). For the model of DON, acorn production was the first variable entering ($R^2 = 0.84$, $F = 21.27$, $df = 1$, $p = 0.010$), with PPT in year t entering second and improving model R^2 to 0.94 (Table 1).

To assess the possibility that the inclusion of mice and acorns in the regression models might have masked effects of weather on nymphal ticks, we ran regression models that included only the four weather variables as determinants of nymphal abundance or infection. Only PPT in year $t - 1$ entered the models as a determinant of DIN and DON (for DIN, $R^2 = 0.58$, $p = 0.135$; for DON, $R^2 = 0.67$, $p = 0.088$). In no other case did any weather variable enter the model (Table 1).

To assess the possibility that the mouse–DIN and acorn–DIN relationships are the spurious results of independent effects of weather variables on mouse density, acorn production, and

TABLE 1. RESULTS OF FORWARD, STEPWISE MULTIPLE REGRESSION MODELS ASSESSING THE INFLUENCE OF BOTH BIOTIC AND ABIOTIC VARIABLES ON DIN, NIP, AND DON

Model, parameter	*Standard coefficient*	df	F	P	R^2
Acorn					
DON					0.943
Acorns	0.99	1	162.69	0.006	
May–June PPT	0.42	1	31.33	0.030	
May–Sept PPT	0.28	1	10.42	0.084	
NIP					0.000
(no variables enter model)					
DIN					0.947
Acorns	0.89	1	43.56	0.007	
May–June PPT	0.30	1	4.94	0.113	
Mouse					
DON					0.803
Mouse density	0.90	1	16.30	0.016	
NIP					0.943
Mouse density	1.09	1	48.97	0.006	
GDD to Oct	−0.39	1	6.22	0.088	
DIN					0.959
Mouse density	0.78	1	34.87	0.010	
GDD to July	0.34	1	6.65	0.082	

"Mouse model" refers to the regression model in which mouse density in year $t - 1$ is one of the independent variables. "Acorn model" refers to the regression model in which acorn production in year $t - 2$ is one of the independent variables. May–June PPT and GDD to July pertain to year t, whereas May–Sept PPT and GDD to Oct pertain to year $t - 1$. Criterion for inclusion in the models was $\alpha = 0.15$. Nonsignificant independent variables are excluded here.

nymphal ticks, we ran additional regression analyses to determine if any of the weather variables were significant determinants of either mouse density or acorn production. In the case of the model of mouse density, we used GDD and precipitation data for both year t and year $t - 1$, to reflect the possibility of both a current-year and prior-year effect of weather on mice. Similarly, in the case of the acorn model, we used GDD and precipitation data for both year t and year $t - 1$, to reflect the fact that the dominant oak species on our sites (*Q. rubra*) requires 2 years to mature acorns after flowering (Fowells 1965). None of the weather variables was a significant determinant of either acorn production or mouse density.

DISCUSSION

Results of monitoring naturally fluctuating abundances of acorns, mice, ticks, and Lyme disease bacteria in ticks support the hypothesis, derived from experimental acorn additions (Jones et al. 1998), that high availability of acorns leads to high density of infected nymphal ticks two summers later. This delayed effect of acorn production appears to result from two pairwise, causal interactions. First, acorn production in autumn is the primary determinant of the population size of white-footed mice the following summer (Elkinton et al. 1996, Ostfeld et al. 1996b, 1998a, Wolff 1996, McCracken et al. 1999, this study). Second, because white-footed mice are both the preferred host for larval ticks and the principal natural reservoir for *B. burgdorferi*, abundant numbers of mice in summer (when larval ticks seek hosts) provide increased opportunities for larvae to feed successfully and to acquire an infection. The high abundance of mice in the summer following heavy acorn production thus results in both high densities and high infection prevalence of nymphal ticks the next year.

In Illinois, population densities of both larval and nymphal blacklegged ticks can be influenced by abiotic factors, such as temperature and precipitation (Jones and Kitron 2000). Our analyses indicated that the same temperature and precipitation variables used by Jones and Kitron (2000), in both the current and prior year, had little influence on abundance or infection prevalence of nymphs in southeastern New York. In the mouse model assessing DIN, inclusion of GDD in the current year marginally increased explanatory power over that provided by mouse density in the prior year. Similarly, acorns in year $t - 2$ but no weather variables was significant in explaining variation in DIN. We conclude that, at our sites in southeastern New York, the impact of weather was restricted to the relatively small amount of the interannual variation in nymph density not explained by mouse abundance or acorn production. The lack of any significant correlations between weather variables and either acorn production or mouse density rules out the possibility that the correlations between acorn production and nymphal ticks, and between mouse density and nymphal ticks, are spurious.

The current results, combined with prior analyses (Jones et al. 1998, Ostfeld et al. 1998a,b), suggest that acorn production has multiple effects on DIN two summers later. First, both observational and experimental studies indicate that acorn masting events attract white-tailed deer and their attached adult ticks into oak-dominated forest stands, increasing the density of larval ticks in oak forests the following summer. Second, the same masting events produce abundant populations of white-footed mice the next summer, when these larval ticks begin seeking hosts. The presence of abundant mice, in turn, appears to increase both the density (Figs. 1 and 2c) and infection prevalence (Figs. 1 and 2b) of the next year's nymphal population. Monitoring over much longer periods would allow us to assess (1) whether these interactions are linear or nonlinear and (2) the degree of temporal autocorrelation of the data. Nevertheless, the current observational data, combined with prior experimental results (Jones et al. 1998), indicate that heavy acorn production and resulting high mouse density can predict unusually high densities of infected nymphal ticks. Yet, the ability of forest ecologists to predict accurately masting events in eastern U.S. oak populations will remain poor until long-term data on acorn production and its possible causes allow empirical models to be produced.

ACKNOWLEDGMENTS

We thank the many field and lab assistants who helped in sampling seeds, mammals, ticks, and spirochetes. This work was funded by the National Science Foundation (DEB 9605414), the National Institutes of Health (R01 AI40076), and the General Reinsurance Corp., and is a contribution to the program of the Institute of Ecosystem Studies.

ABBREVIATIONS

DIN, density of infected nymphs; DON, density of nymphs; GDD, growing degree days; NIP, nymphal infection prevalence; PBS, phosphate-buffered saline; PPT, total precipitation.

REFERENCES

Barbour, AG, Fish, D. The biological and social phenomenon of Lyme disease. Science 1993; 260:1610–1616.

Daniels, TJ, Falco, RC, Fish, D. Estimating population size and drag sampling efficiency for the blacklegged tick (Acari: Ixodidae). J Med Entomol 2000; 37:357–363.

Donahue, JG, Piesman, J, Spielman, A. Reservoir competence of white-footed mice for Lyme disease spirochetes. Am J Trop Med Hyg 1987; 36:92–96.

Elkinton, JS, Healy, WM, Buonaccorsi, JP, Hazzard, AM, et al. Interactions among gypsy moths, white-footed mice, and acorns. Ecology 1996; 77:2332–2342.

Fish, D. Population ecology of *Ixodes dammini*. In: Ginsberg, H, ed. *Ecology and Environmental Management of Lyme Disease.* New Jersey: Rutgers University Press; 1993:25–42.

Fowells, HA. *Silvics of Forest Trees of the United States. USDA Forest Service Agricultural Handbook.* Washington, DC: U.S. Government Printing Office; 1965; no. 271.

Ginsberg, HS, Hyland, KE, Hu, R, Daniels, TJ, et al. Tick population trends and forest type. Science 1998; 281:349–350.

Hilborn, R, Redfield, JA, Krebs, CJ. On the reliability of enumeration for mark and recapture census of voles. Can J Zool 1976; 54:1019–1024.

Hofmeister, EK, Ellis, BA, Glass, GE, Childs, JE. Longitudinal study of infection with *Borrelia burgdorferi* in a population of *Peromyscus leucopus* at a Lyme disease-enzootic site in Maryland. Am J Trop Med Hyg 1999; 60:598–609.

Jones, CG, Ostfeld, RS, Richard, MP, Schauber, EM, et al. Chain reactions linking acorns to gypsy moth outbreaks and Lyme disease risk. Science 1998; 279:1023–1026.

Jones, CJ, Kitron, UD. Populations of *Ixodes scapularis* (Acari: Ixodidae) are modulated by drought at a Lyme disease focus in Illinois. J Med Entomol 2000; 37:408–415.

Lane, RS, Piesman, J, Burgdorfer, W. Lyme borreliosis: relation of its causative agents to its vectors and hosts in North America and Europe. Annu Rev Entomol 1991; 36:587–609.

Levine, JR, Wilson, MW, Speilman, A. Mice as reservoirs of the Lyme disease spirochete. Am J Trop Med Hyg 1985; 34:355–360.

Lindsay, LR, Barker, IK, Surgeoner, GA, McEwen, SA, et al. Survival and development of *Ixodes scapularis* (Acari: Ixodidae) under various climatic conditions in Ontario, Canada. J Med Entomol 1995; 32:143–152.

Mather, TN, Ginsberg, HS. Vector–host–pathogen relationships: transmission dynamics of tick-borne infections. In: Sonenshine, DE, Mather, TN, eds. *Ecological Dynamics of Tick-Borne Zoonoses.* New York: Oxford University Press; 1994:68–90.

Mather, TN, Wilson, ML, Moore, SI, Ribeiro, JMC, et al. Comparing the relative potential of rodents as reservoirs of the Lyme disease spirochete (*Borrelia burgdorferi*). Am J Epidemiol 1989; 130:143–150.

McCracken, KM, Witham, JW, Hunter, ML, Jr. Relationships between seed fall of three tree species and *Peromyscus leucopus* and *Clethrionomys gapperi* during 10 years in an oak–pine forest. J Mammal 1999; 80:1288–1296.

Ostfeld, RS. The ecology of Lyme-disease risk. Am Sci 1997; 85:338–346.

Ostfeld, RS, Miller, MC, Hazler, KR. Causes and consequences of tick (*Ixodes scapularis*) burdens on white-footed mice (*Peromyscus leucopus*). J Mammal 1996a; 77:266–273.

Ostfeld, RS, Jones, CG, Wolff, JO. Of mice and mast: ecological connections in eastern deciduous forests. Bioscience 1996b; 46:323–330.

Ostfeld, RS, Hazler, KR, Cepeda OM. Temporal and spatial dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a rural landscape. J Med Entomol 1996c; 33: 90–95.

Ostfeld, RS, Jones, CG, Richard, MP, Schauber, EM, et al. Tick population trends and forest type. Science 1998a; 281:350–351.

Ostfeld, RS, Keesing, F, Jones, CG, Canham, CD, et al. Integrative ecology and the dynamics of species in oak forests. Integr Biol 1998b; 1:178–186.

Patrican, LA. Absence of Lyme disease spirochetes in larval progeny of naturally infected *Ixodes scapularis* (Acari: Ixodidae) fed on dogs. J Med Entomol 1997; 34:52–55.

Piesman, J, Donahue, JG, Mather, TN, Spielman, A. Transovarially acquired Lyme disease spirochetes (*Borrelia burgdorferi*) in field-collected larval *Ixodes dammini* (Acari: Ixodidae). J Med Entomol 1986; 23:219.

Randolph, SE. Mighty theories from little acorns grow: is Lyme disease risk predictable from mast-seeding by oak trees? Trends Ecol Evol 1998; 13:301–303.

Schmidt, KA, Ostfeld, RS, Schauber, EM. Infestation of *Peromyscus leucopus* and *Tamias striatus* by *Ixodes scapularis* (Acari: Ixodidae) in relation to the abundance of hosts and parasites. J Med Entomol 1999; 36:749–757.

Slade, NA, Blair, SM. An empirical test of using counts of individuals captured as indices of population size. J Mammal 2000; 81:1035–1045.
Wolff, JO. Population fluctuations of mast-eating rodents are correlated with production of acorns. J Mammal 1996; 77:850–856.

Address reprint requests to:
Dr. Richard S. Ostfeld
Institute of Ecosystem Studies, Box AB
Millbrook, NY, 12545
E-mail: Rostfeld@ecostudies.org