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Research Paper

Spatiotemporal Variation in a Lyme Disease Host and Vector: Black-Legged Ticks on White-Footed Mice

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ABSTRACT

We monitored population density of white-footed mice (*Peromyscus leucopus*), burdens of immature black-legged ticks (*Ixodes scapularis*) on mice, and infection prevalence of host-seeking ticks on six forest plots in southeastern New York State from 1995 through 1999. Despite densities of mice that fluctuated two orders of magnitude, average larval and nymphal tick burdens per mouse remained remarkably constant. Spatial variability in mouse density and tick burdens was modest. The total number of larval and nymphal ticks that fed on the mouse population each year depended strongly on population density of mice; a steady increase was observed in both mouse density and total tick meals on mice from 1996 through 1999. The result was a steady increase in the infection prevalence of nymphal and adult ticks with the etiological agent of Lyme disease, *Borrelia burgdorferi*, over this time. We suggest that fluctuations in population density of mice, combined with possible regulation of tick burdens on mice, may influence risk of human exposure to Lyme disease. Key Words: Lyme disease—White-footed mouse—Black-legged tick—Vector—Disease reservoir. Vector Borne Zoonotic Dis. 1, 129–138.

INTRODUCTION

LYME DISEASE (LD) is a zoonosis in which the etiological agent (*Borrelia burgdorferi*) cycles between tick vectors and their vertebrate hosts. In the eastern and central United States, the primary vector is the black-legged tick (*Ixodes scapularis*), and dozens of species of vertebrates serve as hosts for both *I. scapularis* and *B. burgdorferi* (Lane et al. 1991, Barbour and Fish 1993, Mather 1993). Larval black-legged ticks typically hatch uninfected with *B. burgdorferi* but may acquire an infection when feeding from a reservoir host (Piesman et al. 1986, Patrican 1997). Tick infections are maintained between life stages. Risk of human infection depends on the abundance and infection prevalence of host-seeking ticks, especially nymphs, in outdoor areas that people use (Barbour and Fish 1993).

Factors that can affect the abundance and infection prevalence of nymphs include (1) the abundance of larvae in the prior year, (2) the availability of suitable hosts, and (3) survival rates both during and after the larval blood meal. Spatiotemporal variation in abundance of ticks has been well described at both very large (e.g., continental) and small (e.g., Maupin et al. 1991, Ginsberg 1993, Ostfeld et al. 1996a, Dister et al. 1997, Dennis et al. 1998, Wilson 1998, Jones and Kitron 2000) scales. Similarly, host abundance and community composition can vary dramatically in space and time (Van Buskirk and Ostfeld 1995, Giardina et al. 2000). However, the causes of spatiotemporal variation in abundance and infection prevalence of ticks are not well understood.

Plentiful evidence indicates that the white-footed mouse (*Peromyscus leucopus*) plays a key

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role as both a preferred host for immature black-legged ticks and the principal natural reservoir for *B. burgdorferi* in eastern and central North America (Anderson and Magnarelli 1984, Levine et al. 1985, Mather et al. 1989, Fish 1993, Mather and Ginsberg 1994, Keirans et al. 1996, Donahue et al. 1997, Giardina et al. 2000, Jones and Kitron 2000). Additionally, in forested landscapes of the northeastern United States white-footed mice are typically the most abundant vertebrate host for black-legged ticks (Schmidt et al. 1999, Giardina et al. 2000, and references therein). However, white-footed mouse density may vary dramatically over time and in space (Kaufman and Kaufman 1989, Wolff 1996, McCracken et al. 1999).

Our purpose in this study is to assess the effects of both temporal and spatial variation in mouse density on several factors relevant to LD risk to humans. We report on the impacts of fluctuating mouse density on (1) larval and nymphal black-legged tick burdens on white-footed mice, (2) population-level estimates of the total number of larval and nymphal meals taken from mice, and (3) infection prevalence of nymphal and adult ticks.

MATERIALS AND METHODS

Our study was conducted between 1995 and 1999 on six 2.25-ha plots in oak-dominated forest at the Institute of Ecosystem Studies in Millbrook, NY. The six plots were established as three pairs of plots, with ~100 m between members of a pair and 500–1,500 m between pairs. Thorough descriptions of the study site are given in Jones et al. (1998) and Ostfeld et al. (2001).

Mouse trapping and tick burdens

Mark-recapture live-tapping was conducted between April or May and November of each year. In each plot, an 11 × 11 (for one plot, 12 × 10) array of trap stations was established with 15 m between stations and two Sherman live traps per station, for a total of 242 traps per 2.25-ha plot. Trapping was conducted for two

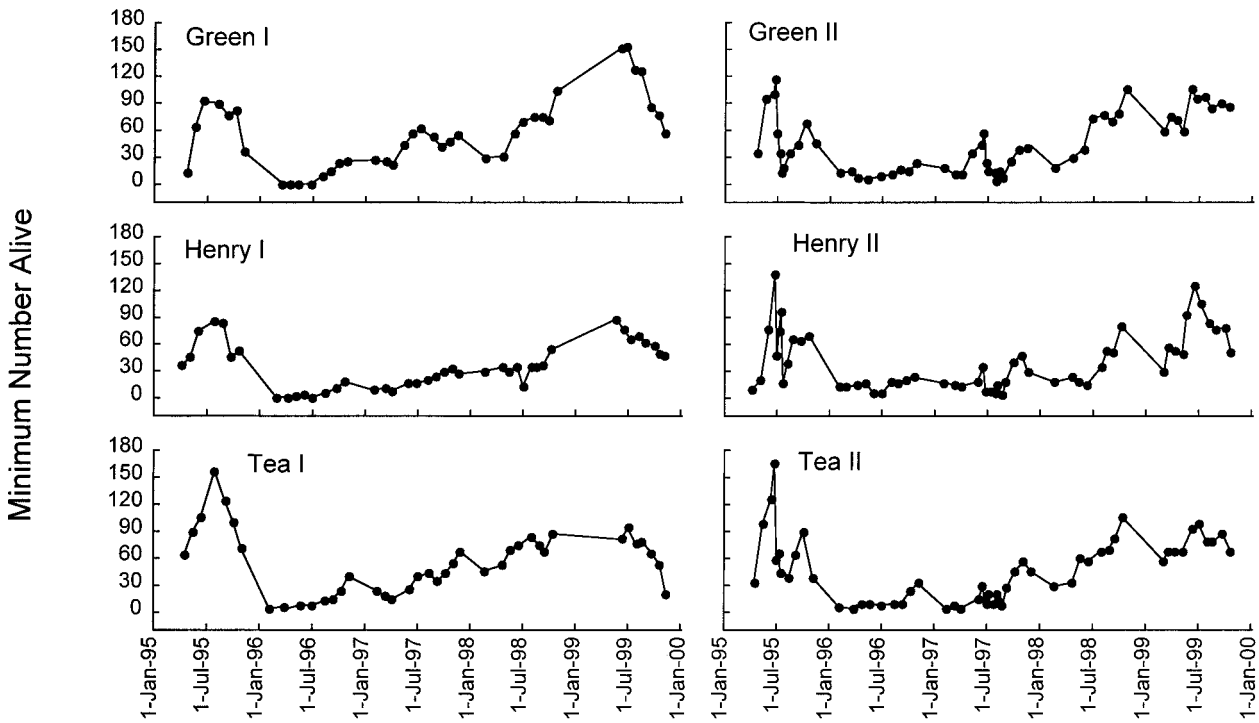

FIG. 1. Minimum number of white-footed mice alive on each of the six trapping grids for 1995–1999. All six grids are 2.25 ha.

consecutive nights every 3–4 weeks. Traps were covered with boards, baited with crimped oats, set in late afternoon, and checked and closed early the following morning. All captured animals were given uniquely numbered metal eartags for identification on first capture and released after brief examination. We estimated mouse density on each plot and trapping session using the minimum number alive (MNA). We selected MNA because high capture probabilites (>0.80) increased the accuracy of this method (Hilborn et al. 1976) and because "robust" estimators are subject to overestimation bias with short trapping sessions [e.g., two or three capture events (Slade and Blair 2000)].

Upon first capture in each trapping session, the ears and head of each mouse were inspected carefully for the presence of embedded larval and nymphal ticks, which concentrate on the ears and face. To account for the possibility that direct counts of tick burdens underestimate true burdens, in 1998 we performed an experiment to compare direct tick counts and actual tick burdens (see Schmidt et al. 1999, for details). For both larvae and nymphs, actual counts of ticks detaching from mice were significantly, and for larvae strongly, correlated with direct visual counts from the field ($r = 0.89$, $df = 40$, $p < 0.0001$ and $r = 0.43$, $df = 32$, $p = 0.012$, respectively). Because this experiment was performed near the end of the nymphal activity season, average nymph burdens were low, limiting the range of variation in that data. The y-intercept for the regression of actual counts on visual counts was positive for both larvae (4.67 ± 1.75 [S.E.]) and nymphs (1.46 ± 0.28), indicating that visual counts typically underestimated true burdens. The slope of the regression was not significantly different from 1.0 for larvae (1.11 ± 0.09) or nymphs (0.67 ± 0.25). Based on these results, we conclude that visual counts are reliable indices of true tick burdens on white-footed mice, especially for larvae, and we report visual counts on field-caught animals throughout this paper.

Tick infection prevalence

Host-seeking ticks were regularly collected during drag-sampling of all six plots. Briefly, every 3–4 weeks between April or May and November of each year, three 150-m transects on each plot were sampled with a 1-m^2 drag cloth. The cloth was examined after every 30 m of transect, and all nymphs and adults were placed in humidified glass vials and returned to the lab for analysis (see Ostfeld et al. 2001, for details).

Prevalence of infection with *B. burgdorferi* was determined with direct immunofluorescence assay. Nymphs and adults for assay were selected haphazardly from the total collected throughout the season. Ticks were washed once in 70% ethanol and twice in deionized water

Table 1. CV of Mean White-Footed Mouse MNA and Integrated Average Larval and Nymphal Black-Legged Tick Blood Meals per White-Footed Mouse

	Average mouse MNA	*Average larval tick blood meals per mouse*	*Average nymphal tick blood meals per mouse*
a. Temporal variability			
Green I	23.19	8.72	1.14
Green II	16.93	21.79	4.44
Henry I	18.06	22.25	3.92
Henry II	15.80	15.47	3.02
Tea I	19.83	19.60	2.86
Tea II	19.29	25.12	5.76
b. Spatial variability			
1995	4.15	1.37	0.99
1996	1.03	13.07	1.29
1997	4.73	1.69	0.27
1998	4.34	0.56	0.46
1999	3.74	0.41	0.83

CVs were determined (a) between years for each of the six grids and (b) between grids in each of the 5 years.

and ground in phosphate-buffered saline (PBS) in Eppendorf tubes. Three 5-μl aliquots of tick suspension were placed in separate wells of a multiwell slide, air-dried, and fixed in cold acetone for 10 min. Fluorescein rabbit anti-*B. burgdorferi* conjugate was incubated in wells at 37°C for 45 min, after which slides were washed in PBS, dried, and placed in mounting medium. 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 positive or negative. The number of ticks tested for any given grid on any given year was quite variable, but on average 58 nymphs (minimum = 10, maximum = 95) and 35 adults (minimum = 6, maximum = 135) were tested for any one grid in any year.

Statistical analysis

We assessed spatial and temporal variation in mouse density by calculating an annual average MNA for each trapping grid and then determining the coefficient of variation (CV) for all the grids within a year (spatial variation) or all the years on a grid (temporal variation). To assess variation among years in tick burdens on mice, it was necessary to account for seasonal patterns of tick activity and the timing of sampling, which differed somewhat both among grids and among years. By integrating the area under the tick burden curves (see Figs. 2 and 3) we estimated the grid-specific average number of larval and nymphal blood meals per mouse per year. Spatial and temporal variability was determined for the average number of larval and nymphal blood meals per mouse per year using the area under the curve values. Similarly, by integrating the area under curves of the total number of ticks on all mice caught (not shown) we estimated the grid-specific total number of larval and nymphal blood meals per year. We assumed that tick burdens were 0 between the third week in November and the first week in April. We evaluated the impact of grid and/or year on the integrated average and total tick blood meals using a two-way ANOVA. We did not evaluate any interactions between grid and year because there were insufficient degrees of freedom. We assessed the influence of year on tick infection using a lo-

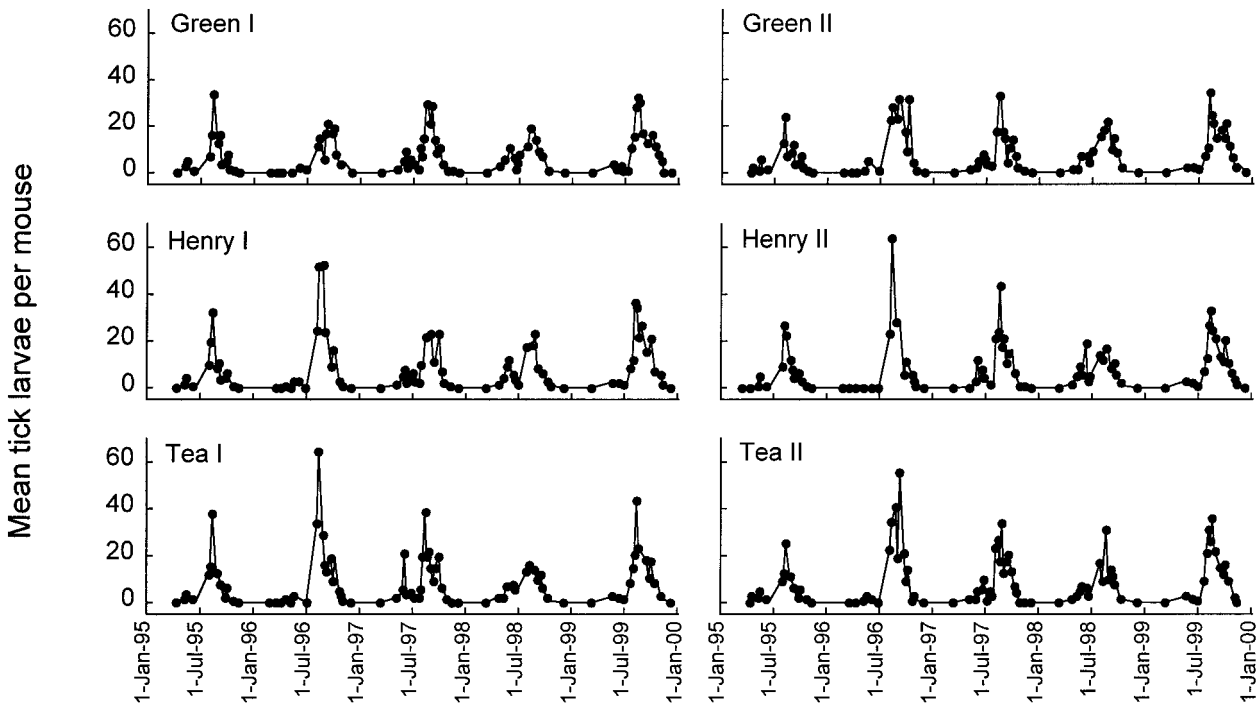

FIG. 2. Mean larval black-legged tick burden for white-footed mice captured on each of the six trapping grids for 1995–1999.

TABLE 2. DATE OF THE MAXIMUM PEAK FOR THE MEAN (A) LARVAL AND (B) NYMPHAL BLACK-LEGGED TICK BURDEN ON WHITE-FOOTED MICE FOR EACH OF THE SIX TRAPPING GRIDS FOR EACH OF THE 5 YEARS

	Green I	*Green II*	*Henry I*	*Henry II*	*Tea I*	*Tea II*
a. Larvae						
1995	13 Aug	6 Aug	13 Aug	6 Aug	13 Aug	13 Aug
1996	8 Sep	1 Sep	25 Aug	11 Aug	11 Aug	8 Sep
1997	10 Aug	10 Aug	31 Aug	17 Aug	10 Aug	24 Aug
1998	2 Aug	16 Aug	23 Aug	7 Jun	16 Aug	16 Aug
1999	8 Aug	1 Aug	1 Aug	8 Aug	8 Aug	15 Aug
b. Nymphs						
1995	14 May	1 Oct	4 Jun	10 Sep	24 Sep	10 Sep
1996	2 Jun	4 Aug	30 Jun	30 Jun	4 Aug	19 May
1997	11 May	15 Jun	27 Jul	13 Jul	27 Jul	22 Jun
1998	10 May	17 May	7 Jun	17 May	17 May	17 May
1999	6 Jun	4 Jul	16 May	16 May	27 Jun	27 Jun

gistic regression, since the data fit a binomial experiment design. All statistical analyses were conducted using SAS (1999).

RESULTS

Mouse numbers fluctuated two orders of magnitude over the 5 years of monitoring (Fig. 1). In general, mice were at high densities in 1995, but the population crashed in 1996 and increased steadily from 1996 to 1999. These temporal fluctuations resulted in a great deal of temporal variation on all six of the trapping grids (Table 1a). Although the six grids showed similar overall patterns in mouse density, considerable variation from grid to grid existed within some years (Table 1b). For example, mouse densities on all grids increased during the early summer of 1997, but across the grids mouse densities in July 1997 ranged from four to 61 mice per 2.25 ha.

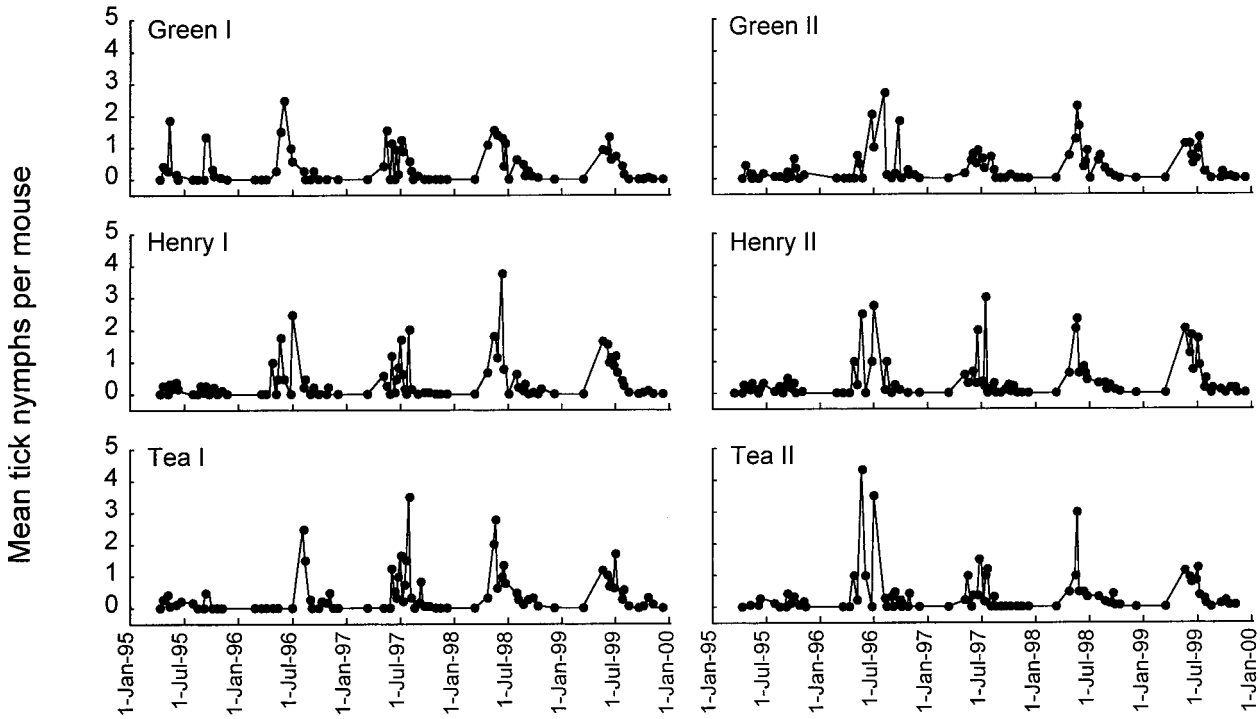

FIG. 3. Mean nymphal black-legged tick burden for white-footed mice captured on each of the six trapping grids for 1995–1999.

As has been demonstrated in previous studies (e.g., Kitron et al. 1991, Ostfeld et al. 1996a), mean larval tick burdens on mice were highly seasonal (Fig. 2). All grids had a substantial peak in larval tick burdens, up to 65 larvae per mouse, which consistently occurred in August/early September (Table 2a). Additionally, in most years and on most grids there was an earlier, smaller peak in tick burdens. Only once (Henry II grid in 1998) was the small peak larger, only by two ticks per mouse, than the later peak. Temporal variation in integrated larval tick burdens was similar to that in mouse MNAs (Table 1a). With the exception of 1996, spatial variation in integrated larval tick burdens was one-third to one-ninth that in mouse MNA (Table 1b). The height of the peak larval tick burden was not significantly different between grids ($F_{5,20} = 1.69$, $p = 0.1833$) but did vary significantly between years ($F_{4,20} = 7.21$, $p < 0.0009$). Seasonal variation in mean nymphal tick burdens on mice was not as consistent. There was a general pattern of a large peak in nymphal tick burdens early in the summer (Fig. 3), but the date of this peak was highly variable from grid to grid and year to year (Table 2b), and the height of that peak varied roughly 11-fold while the height of the larval burden peak varied only threefold. However, average nymphal blood meals per mouse had much less temporal variability than either tick larvae or mouse MNAs (Table 1a) and similar spatial variability as tick larvae (Table 1b).

For both larval and nymphal ticks, signifi-

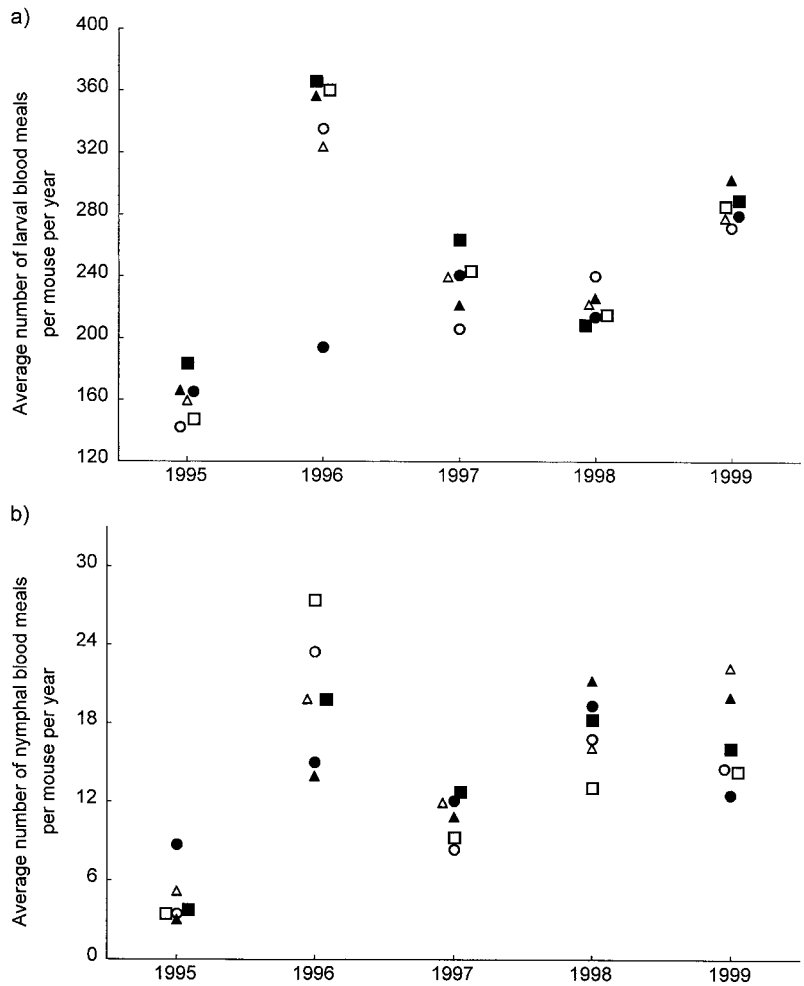

FIG. 4. Average number of (a) larval or (b) nymphal black-legged tick blood meals taken per white-footed mouse per year for each of the 5 years that trapping was conducted. Symbols differentiate among the trapping grids [Green I (●), Green II (○), Henry I (▲), Henry II (△), Tea I (■), Tea II (□)] and have been offset horizontally if overlapping.

cant differences existed among years in the average number of blood meals per mouse ($F_{4,20} = 23.42$, $p < 0.0001$ and $F_{4,20} = 17.15$, $p < 0.0001$, respectively), but no significant differences existed among grids ($F_{5,20} = 1.15$, $p = 0.3652$ and $F_{5,20} = 0.15$, $p = 0.9766$, respectively). For both tick life stages, 1995 had low mean annual blood meals per mouse, which sharply increased in 1996 and then settled at midrange values for the remaining years (Fig. 4). Over the six grids and 5 years of sampling the average number of larval and nymphal blood meals fluctuated by ~2.6- and ninefold, respectively, which is primarily driven by the high values in 1996.

In contrast to the patterns for average numbers of blood meals, the total numbers of both larval and nymphal blood meals per grid per year increased dramatically from 1996 to 1999 (Fig. 5). Total blood meals for both tick larvae and nymphs differed significantly among years ($F_{4,20} = 59.92$, $p < 0.0001$ and $F_{4,20} = 28.88$, $p < 0.0001$, respectively). Also, significant variation existed among grids in the annual total blood meals taken by larvae ($F_{5,20} = 4.34$, $p = 0.0077$). A similar but nonsignificant level of variability among grids existed for the annual total blood meals taken by nymphs ($F_{5,20} = 2.34$, $p = 0.0791$). The grid effect seemed to be driven primarily by the Henry II grid having higher annual total blood meals and the Tea II grid having lower annual total blood meals.

The increasing annual total blood meals from mice we observed between 1995 and 1999 was

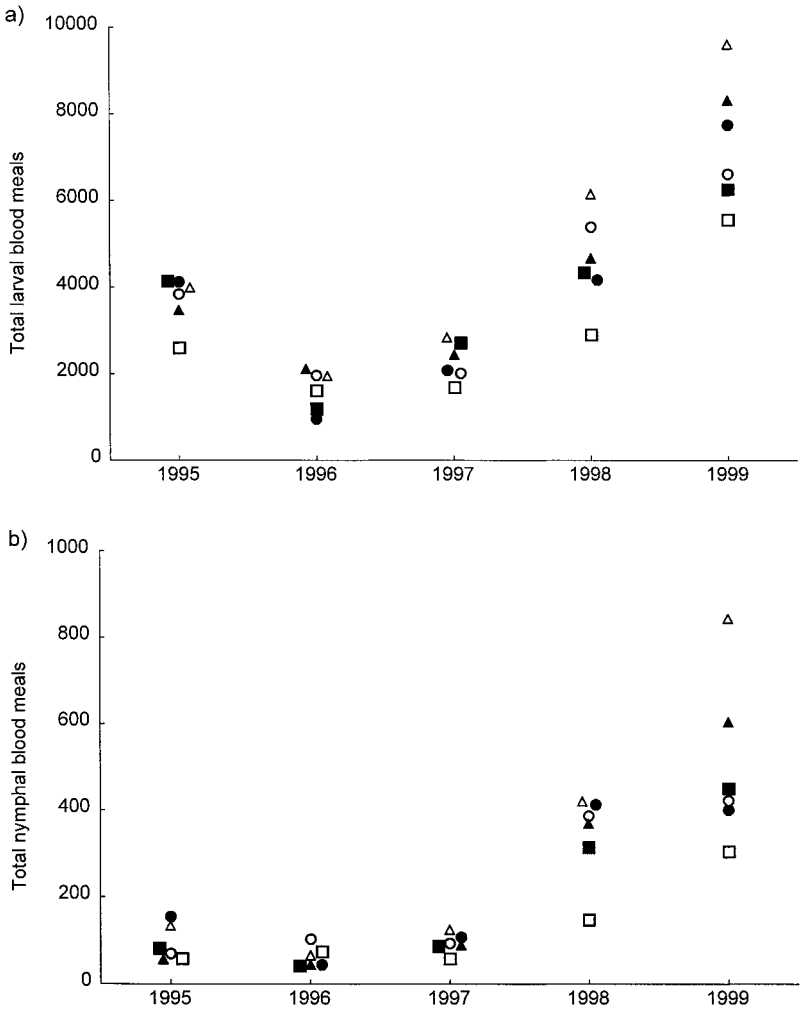

FIG. 5. Total number of (a) larval or (b) nymphal black-legged tick blood meals taken from white-footed mice per grid for each of the 5 years that trapping was conducted. Symbols differentiate among the trapping grids [Green I (●), Green II (○), Henry I (▲), Henry II (△), Tea I (■), Tea II (□)] and have been offset horizontally if overlapping.

reflected in *B. burgdorferi* infection prevalence in nymphal and adult questing ticks. For both questing nymphs and adults, a logistic regression indicates that the proportion of individuals infected was significantly influenced by year ($\chi^2 = 5.15$, $p = 0.0233$ and $\chi^2 = 9.22$, $p = 0.0024$ for nymphs and adults, respectively). Despite substantial variability in infection among grids, we observed a significant increase in infection prevalence over time (Fig. 6).

DISCUSSION

The dramatic interannual fluctuations in population density of white-footed mice that we observed in this study are typical of this species (e.g., Ostfeld 1988, Kaufman and Kaufman 1989, Elkinton et al. 1996, Wolff 1996). Our data from six trapping grids in similar oak-dominated forest indicate that although some variation in mouse density among grids existed, spatial variability was substantially lower than temporal variability (Fig. 1 and Table 1). Despite mouse densities that fluctuated two orders of magnitude among years, average larval and nymphal tick burdens per mouse fluctuated only 2.6- and ninefold, respectively, among years. Moreover, these relatively constant tick burdens occurred despite strong variation in the abundance of questing larval and nymphal ticks at these same sites

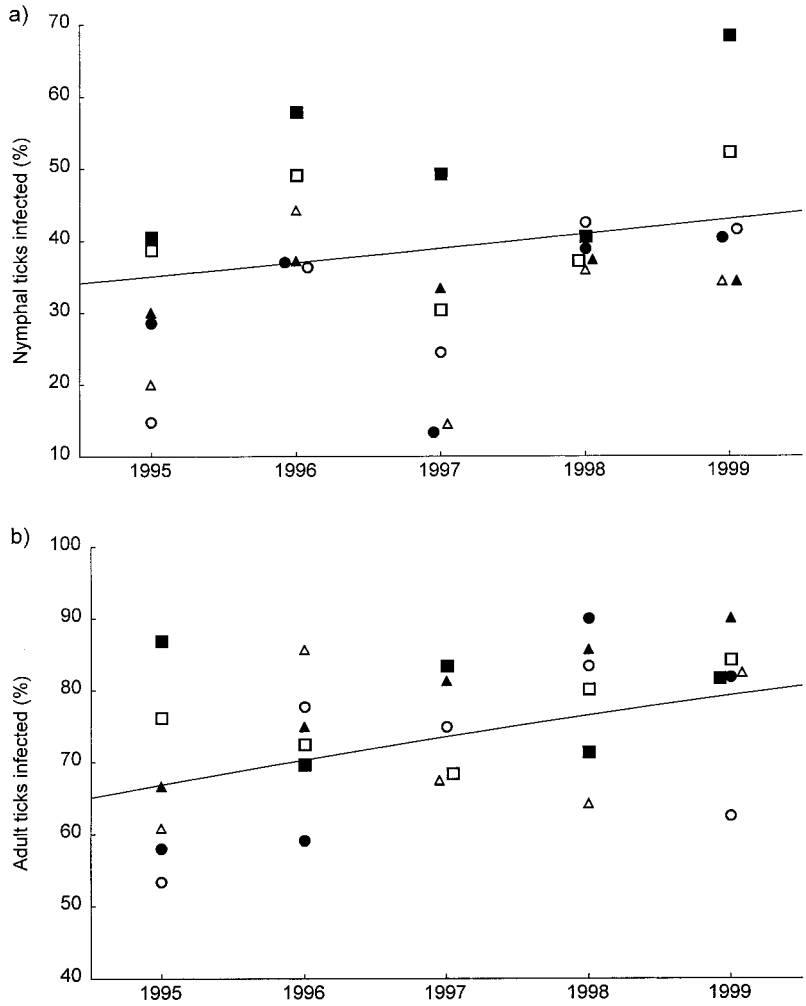

FIG. 6. Percent of (a) nymphal or (b) adult questing black-legged ticks infected with *B. burgdorferi*. Symbols differentiate between the trapping grids [Green I (●), Green II (○), Henry I (▲), Henry II (△), Tea I (■), Tea II (□)] and have been offset horizontally if overlapping. The solid lines show a logistic regression model fitted to the data: $\ln(p/1 - p) = 0.0896$ Year $- 167.4$ for the nymph infection and $\ln(p/1 - p) = 0.1595$ Year $- 317.5$ for the adult infection, where p is the proportion of individuals infected.

(Ostfeld et al. 1996b, 1998). Such constancy in average tick burdens despite fluctuating hosts and host-seeking ticks suggests strong regulation of tick numbers on hosts (e.g., Levin and Fish 1998; cf. Hazler and Ostfeld 1995). Alternatively, because acorn availability influences densities of both larval ticks and mice the following summer (Ostfeld et al. 1996b, Jones et al. 1998), constant tick burdens on mice may result from covariation among years in densities of host-seeking larvae and their mouse hosts.

Given that average tick burdens on mice remained fairly consistent among years and grids, the total number of blood meals taken by larval and nymphal ticks in any given year should be determined largely by the abundance of hosts. Indeed, we found that the integrated annual totals of larval blood meals on the mouse population were synchronous with fluctuating mouse density, with total larval blood meals being high in 1995, declining in 1996, and then steadily increasing over the next 3 years (Figs. 1 and 5a). Integrated total of nymphal blood meals showed a similar pattern of temporal increase, except that no peak in 1995 was evident (Fig. 5b).

The interannual pattern of total of blood meals taken by larval and nymphal ticks on mice was reflected strongly in the infection prevalence of host-seeking nymphal and adult ticks, respectively, in the following year (Fig. 6). Evidently, the steadily increasing densities of white-footed mice from 1996 through 1999 facilitated the gradual increase in total numbers of immature ticks feeding from the mouse population, which in turn resulted in steadily increasing infection prevalence in the nymphal and adult tick population over this time.

Infection prevalence of host-seeking ticks measures the risk of human exposure to LD given a tick bite (Ostfeld and Keesing 2000). Results of this study suggest that, despite evidence for constancy of tick burdens on one of their key hosts, the white-footed mouse, the total number of tick meals on the mouse population, and therefore the infection prevalence of questing ticks, increases with increasing mouse density. We suggest that further studies should focus on the causes of larger-scale spatial variation in mouse abundance and the potential roles played by fluctuations in the population density and community composition of nonmouse hosts for immature black-legged ticks.

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ABBREVIATIONS

CV, coefficient of variation; LD, Lyme disease; MNA, minimum number alive; PBS, phosphate-buffered saline.

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