

CAUSES AND CONSEQUENCES OF TICK (*IXODES SCAPULARIS*) BURDENS ON WHITE-FOOTED MICE (*PEROMYSCUS LEUCOPUS*)

RICHARD S. OSTFELD, MICHAEL C. MILLER, AND KIRSTEN R. HAZLER

Institute of Ecosystem Studies, Box AB, Millbrook, NY 12545

White-footed mice (*Peromyscus leucopus*) are the principal hosts responsible for infecting ticks (*Ixodes scapularis*) with the spirochete that causes Lyme disease. In a 3-year field study, we examined the effects of density of mice and ticks on burdens of ticks per mouse and the proportion of the tick population successfully attaching to mouse hosts. We found that burdens of ticks per mouse were lowest in the year (1992) of highest densities of both mice and unattached (host-seeking) ticks. Movements by mice and presumably encounter rates with ticks, were suppressed at high density of mice. However, at high density of mice the population of ticks had a higher success rate in attaching to mice. Persistence of individual mice was positively correlated with burdens of ticks, indicating that heavy infestations of ticks do not reduce fitness of mouse hosts. Fluctuating densities of mice and ticks should strongly affect risk of exposure of humans to Lyme disease.

Key words: enzootic cycle, ectoparasites, epizootiology of Lyme disease, parasite-host interactions, Lyme disease

Lyme disease is a rapidly growing zoonotic disease in the United States and parts of Europe (Barbour and Fish, 1993). In the eastern and central United States, the disease is acquired when infected nymphal or adult ticks (*Ixodes scapularis*) transmit a spirochete *Borrelia burgdorferi* to human hosts. The density of infected, host-seeking nymphs has been identified as the primary risk factor to humans in the Lyme disease epidemic (Falco and Fish, 1989).

Typically, *I. scapularis* hatch devoid of *B. burgdorferi*. To become infected nymphs, they must obtain the spirochete during their larval blood meal (Anderson, 1988; Lane et al., 1991). Although larval ticks feed on a wide variety of vertebrate hosts, *Peromyscus leucopus* is the most efficient source on which ticks become infected with *B. burgdorferi* (Anderson and Magnarelli, 1993). Therefore, the factors that influence the number of larval ticks feeding on *P. leucopus* should be crucial determinants of the abundance of infected nymphs, and therefore of the risk to humans of Lyme disease (Van Buskirk and Ostfeld, in press).

Densities of *P. leucopus* and *I. scapularis* fluctuate substantially in time and space (Fish, 1993; Krohne et al., 1988; Ostfeld et al., 1995; Wolff, 1985a), and the interactions between populations of these two species are likely to be key determinants of the risk of Lyme disease. In addition, the dynamics of Lyme disease should be affected if heavy tick burdens reduce the fitness of mouse hosts. We have begun long-term studies of dynamics of rodents and ticks in an area with a high incidence of Lyme disease in southeastern New York to understand the ecological basis for the enzootic cycle. In this study, we tested the hypotheses that: tick burdens per mouse increase with increasing density of host-seeking ticks; tick burdens per mouse decrease with increasing density of mice; the proportion of the tick population that attaches to mice (tick-success index) increases with density of mice; heavy tick burdens reduce fitness, or fitness correlates, of individual mice. Our ultimate goal is to forecast relative risk to humans among years as a function of density of mice and tick burdens per mouse.

MATERIALS AND METHODS

In June 1991, we established two 2.25-ha grids at the Institute of Ecosystem Studies near Millbrook, Dutchess Co., New York (41°50'N, 73°45'W). The grids at the Tea House and Henry Farm sites occur in forest dominated by red oak (*Quercus rubra*) and chestnut oak (*Q. prinus*), with sugar maple (*Acer saccharum*) and white pine (*Pinus strobus*) well represented in the understory. Both samplings of ticks and small mammals occurred predominantly on the two grids. However, in 1992 we established three additional grids in red oak-dominated stands to supplement sampling of ticks. All five grids were within a 5-km radius and occurred in generally continuous forest. In both the Tea House and Henry Farm sites we established a grid of points in an 11-by-11 array, with 15-m spacing. These grid points formed the coordinates for the tick-sampling and mammal-trapping efforts. In the three satellite plots, we established four parallel 100-m transects, with each 10-m interval marked by flagging.

We used transect drag-sampling to estimate the abundance of unattached (host-seeking) ticks. In the drag-sampling method, the investigator pulls a piece of cloth over low vegetation while walking the transects to collect host-seeking ticks (Falco and Fish, 1992). We used a 1-m² piece of white-corduroy cloth sewn at one end to a wooden dowel for support, and weighted at the opposite, free end by small lead weights sewn into the cloth. The drag cloth was examined and ticks were counted every 30 m along a 500-m transect on Tea House and Henry Farm grids, and every 20 m along a 400-m transect on the satellite grids. Ticks removed from the investigator's clothing during sampling also were counted. Because transects were 1-m wide, we converted counts into an estimate of ticks/m² for analysis. In the 1st 2 years of the study (1991 and 1992), all ticks collected were removed with fine forceps and preserved in 70% ethanol for later identification. We removed, but did not preserve, ticks in 1993. From 1991 through 1993, drag sampling was performed on the main study grids weekly or every 2nd week from May through October, with the following exceptions. In 1991, sampling did not begin until early July. In 1992, sampling was performed only on the satellite plots from late July through October.

Small mammals were censused for 3 consecutive nights every 3 weeks from July to Decem-

ber 1991, and from March to November 1992. From April to November 1993, we censused for 4 consecutive nights every 8 weeks. We set one large (7.6 by 8.9 by 22.9 cm) and one small (5.1 by 6.4 by 15.2 cm) Sherman trap at each station. Traps were baited with crimped oats; during cold periods they also were supplied with sunflower seeds and cotton batting. Traps were closed during the day and between trapping sessions. In 1991, we marked all small mammals (except shrews) with uniquely numbered metal ear tags (size 1, Monel fish fingerling tags; National Band and Tag Company, Newport, KY) upon first capture. However, we discovered that ear tags cause about a two-fold increase in numbers of ticks attached to mice (Ostfeld et al., 1993). To examine the effects of toe-clipping versus ear-tagging on burdens of ticks, in 1992 and 1993, we tagged mice on one-half of each grid and toe-clipped mice on the other one-half. Toe-clipping caused a similar increase in total numbers of ticks on mice (R. Ostfeld and M. Miller, in litt.); therefore, differences among years in loads of ticks were not due to marking techniques. Upon capture, we recorded tag number or toe-clip number, gender, age class, reproductive status, mass, and capture location of each individual. In addition, upon first capture of individual rodents during each trapping session, we counted all ticks located on the auditory pinnae (the primary site of attachment—Main et al., 1982). We used the minimum-number-alive method (Krebs, 1966) to estimate density of mice. Incorporating a 7.5-m boundary strip, which is one-half the distance between grid points, grids effectively sampled an area of 2.4 ha.

Our primary statistical approach was to determine the effects of variation in density of host-seeking ticks and of mice (independent variables) on burdens of ticks per mouse using linear regression. Because seasonal activity peaks in *I. scapularis* are well documented (Fish, 1993), it was necessary in some analyses to distinguish between seasonal and interannual variation in abundance of ticks. To isolate the effects of interannual variation in abundance of ticks, we used yearly samples on each grid, either averaged or integrated, as independent units ($n = 2$ grids \times 3 years = 6). In other cases, we were interested in both seasonal and interannual fluctuations and, thus, used sequential trapping or dragging sessions as sampling units. Examples

TABLE 1.—Sample sizes for host-seeking ticks, ticks attached to mice, and total number of mice examined during the study, 1991–1993.

Year	Grid	Host-seeking ticks	Attached ticks	Mice examined
1991	Henry Farm	3,670	2,103	377
	Tea House	4,018	2,436	319
1992	Henry Farm	720	3,349	674
	Tea House	512	6,161	738
	Satellites	3,349	—	—
1993	Henry Farm	2,459	1,467	111
	Tea House	3,967	1,321	111

include effects of density of mice on movement distances and on tick-success index.

To analyze effects of gender of mice on burdens of ticks, we used analysis of variance on yearly average burden of ticks on each study grid. To describe statistically the spatial pattern of host-seeking ticks (random, clumped, or overdispersed) we used chi-square analysis of observed distributions against the expectation of a Poisson distribution.

RESULTS

In each of the 3 years, we collected >4,500 host-seeking ticks, >2,700 attached ticks, and examined >100 white-footed mice (Table 1). In 1991 and 1992, peaks in abundance of larval ticks attached to white-footed mice occurred in August and early September. However, in 1993, heavy infestation began in spring on both grids, and the peak in per capita burden of ticks occurred in June on Tea House grid and in August on Henry Farm grid (Fig. 1). Peaks in per capita burdens of ticks were 1.5–2× greater in 1991 than in the other years. However, mice were infested over a longer period in 1993 than in the other 2 years. To determine the mean numbers of ticks feeding on individual mice each year, we integrated the area under the curves in Fig. 1 to generate estimates of burdens of ticks per mouse over the entire season during which mice were parasitized. For this analysis, we assumed a 48-h attachment period for larval ticks (Piesman et al., 1987). Total burdens of ticks per mouse, integrated over the en-

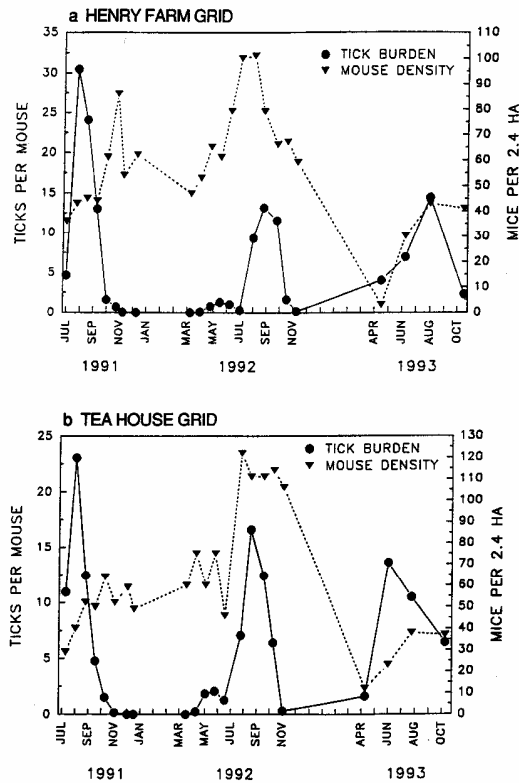


FIG. 1.—Tick burdens (mean numbers of ticks per mouse) and density of mice (minimum number alive per 2.4 ha) in Henry Farm grid (a) and Tea House grid (b).

tire season, were similar in 1991 and 1993, and lowest in 1992. Because densities of mice during summer were 2–4× higher in 1992 than in the other 2 years, there was a negative relationship between peak density of mice and integrated per capita tick load ($y = -0.26x + 77.19$, $r^2 = 0.643$, $d.f. = 1,4$, $P < 0.05$).

The reduction in per capita tick load at high density of mice may have been due to density-dependent reduction in movement distances of mice. For both genders and on both grids, movement distances between successive captures 3 weeks apart (an approximation of size of home range) tended to be negatively correlated with population density (Table 2). In addition, males moved longer distances than females at any given

TABLE 2.—Regression statistics for analysis of the effects of population density of white-footed mice on movement distances of individuals during successive trapping sessions; n = the number of mice in each category that were captured on successive trapping sessions three weeks apart. Individual mice were included only once in the analysis.

Grid	Sex	Regression equation	n	r^2	P
Henry Farm	M	$y = -0.32x + 32.00$	17	0.262	0.041
	F	$y = -0.11x + 19.24$	17	0.133	0.189
Tea House	M	$y = -0.22x + 29.30$	16	0.303	0.015
	F	$y = -0.27x + 27.13$	16	0.541	0.001

population density, as determined by the y intercepts of the regression equations (Table 3), and had significantly higher tick loads on both grids during 1991 and 1992 (Fig. 2). Host-seeking larval ticks were highly clumped in space (Fig. 3), and apparently they were more likely to be contacted by individual mice that moved over larger areas.

Annual variation in burdens of ticks per mouse was not positively associated with annual variation in abundance of host-seeking ticks. Host-seeking ticks were most abundant in 1992 (Fig. 4), the year in which burden of ticks per mouse was lowest (Fig. 1).

Individual ticks had a higher probability of finding a mouse host at higher densities of mice. As density of mice increased, a higher proportion of the total number of ticks was found attached to mice (Fig. 5). We defined a new term, the tick-success index, as (number of ticks attached to mice) / [(number of host-seeking ticks) + (number

attached to mice)]. The correlation between tick-success index and density of mice was statistically significant on Tea House grid ($r^2 = 0.55$, $d.f. = 1,11$, $P < 0.005$), but not on Henry Farm grid ($r^2 = 0.25$, $d.f. = 1,11$, $P > 0.1$). However, the range in variation in tick-success index on Henry Farm grid was only a fraction of the range observed on Tea House grid (Fig. 5), and therefore, the lack of a correlation in the former was not surprising.

To test the hypothesis that greater burdens of ticks reduce survival probabilities of mice, we regressed the mean number of ticks per individual mouse against persistence time (weeks) on the grid. We assumed that persistence times of adult mice are roughly equivalent to longevity, and therefore correlated with individual fitness. We performed analyses only in 1991 and 1992, because trapping sessions in 1993 were 8 weeks apart, too long for meaningful persistence estimates to be generated. Because longevity of male and female *P. leucopus*

TABLE 3.—Regression statistics for analysis of the effects of maximum tick burden on persistence (= longevity on the grid) of individual white-footed mice; n = the number of mice in each category for which we documented persistence.

Year	Grid	Sex	Regression equation	n	r^2	P
1991	Henry Farm	M	$y = 0.11x + 20.08$	34	0.319	0.001
		F	$y = 0.53x + 17.53$	38	0.247	0.002
	Tea House	M	$y = 0.11x + 20.08$	38	0.072	0.10
		F	$y = 0.53x + 6.96$	29	0.563	0.001
1992	Henry Farm	M	$y = 0.12x + 15.21$	60	0.136	0.005
		F	$y = 0.401x + 4.05$	56	0.602	0.001
	Tea House	M	$y = 0.38x + 14.37$	78	0.369	0.001
		F	$y = 0.47x + 5.01$	77	0.407	0.001

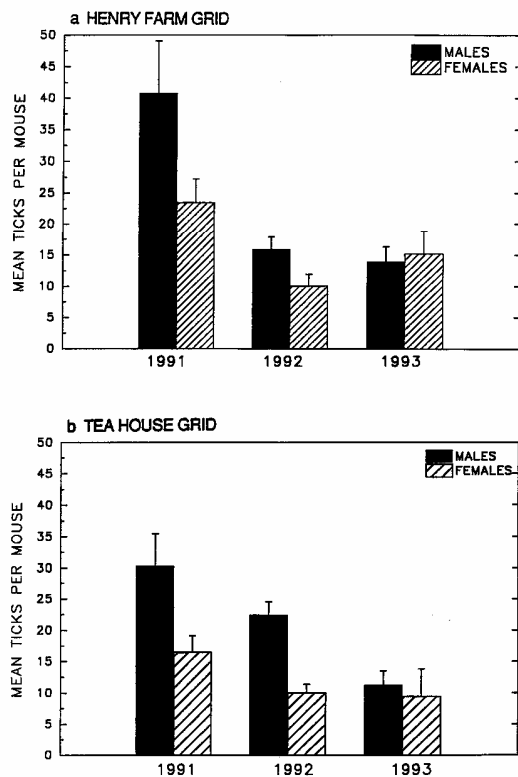


FIG. 2.—Tick burdens (mean \pm SE) for males and females in all 3 years on both study sites. Tick burdens varied significantly between sexes and among years at both sites (ANOVA, Henry Farm grid, for sex, $F = 6.39$, $d.f. = 1$, $P = 0.013$, for year, $F = 17.85$, $d.f. = 2$, $P < 0.001$; Tea House grid, for sex, $F = 15.68$, $d.f. = 1$, $P < 0.001$, for year, $F = 8.31$, $d.f. = 2$, $P = 0.0004$).

sometimes are different (Wolff, 1985a), we examined the genders separately. For both genders, mean tick load and persistence were positively correlated (Table 2), indicating that heavy burdens of ticks did not reduce fitness, and, in fact, may have been associated with greater fitness.

DISCUSSION

Risk to humans of exposure to Lyme disease is a function of the density of nymphal *I. scapularis* infected with *B. burgdorferi* (Falco and Fish, 1989; Piesman et al., 1987). Because *P. leucopus* is the most

competent reservoir for *B. burgdorferi*, the total number and the proportion of larval ticks feeding on white-footed mice will be key determinants of the risk of Lyme disease. Our goal was to accurately forecast risk of Lyme disease in different years and habitat types. Our approach was to examine determinants of tick loads per individual mouse and total numbers of ticks feeding on the population of mice.

From our initial 3 years of study, we reject the hypothesis that larval tick loads per mouse are correlated with the overall abundance of host-seeking larval ticks. Behavioral features of mice and ticks appear to be responsible for this lack of correlation. Larval *I. scapularis* are weakly motile and remain within a few meters of the egg mass after hatching (Daniels and Fish, 1990; Stafford, 1992), as was indicated by the extreme spatial clumping of host-seeking larval ticks (Fig. 3). Exposure of individual mice to larval ticks should be affected by both the density of aggregations of ticks and the amount of space used by mice. In the year of highest density of ticks (1992), mice had the smallest movement distances due to density-dependent reduction of size of home range, which also has been observed by Wolff (1985b). Thus, although host-seeking larval ticks and white-footed mice were most abundant in 1992, individual mice had low burdens of ticks probably due to their reduced probability of contacting aggregations of ticks.

Perhaps more important to the enzootic cycle of Lyme disease than tick load per mouse, is the total number or proportion of ticks feeding on *P. leucopus* (Fish, 1993; Van Buskirk and Ostfeld, in press). We found that, at the population level, ticks had higher success in attaching to mice at higher densities of mice (Fig. 5). Although individual mice use less space at higher densities, it is likely that at higher densities the population of mice occupies a greater proportion of total space, and therefore, host-seeking ticks have higher success in finding a host.

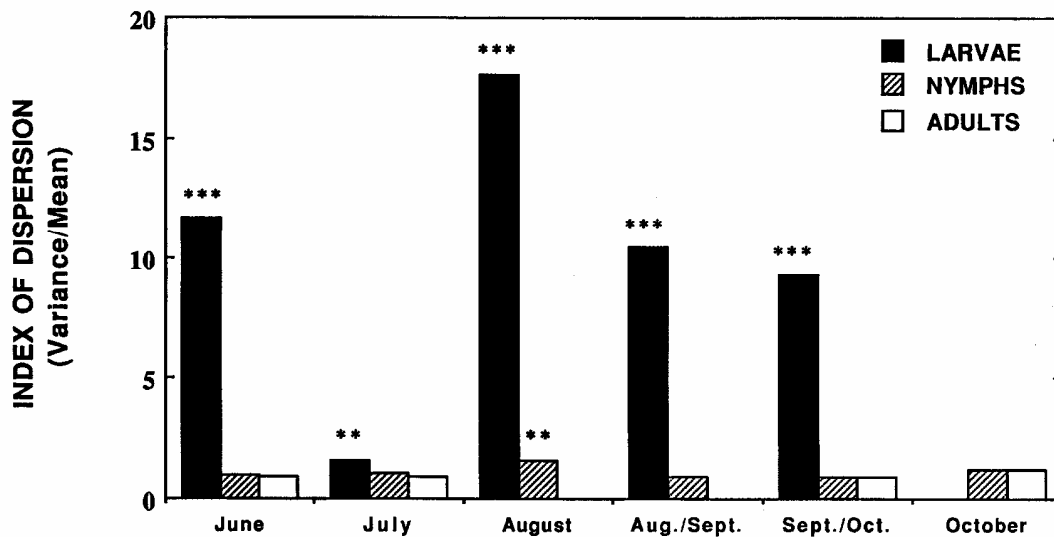


FIG. 3.—Degree of aggregation (variance/mean) of host-seeking ticks as determined by transect drag sampling. Spatial units were 20-m lengths of transect in oak-dominated habitats in 1993. Statistically significant χ^2 values, indicating aggregated distributions, are indicated by ** ($P < 0.01$) and *** ($P < 0.001$).

Viitala et al. (1986) found that infestation of ixodid ticks dramatically increased mortality rates in a population of gray-sided voles (*Clethrionomys rufocanus*). In addition, nymphal ticks attached to mice are responsible for transmitting *B. burgdorferi* to mice, and infection with *B. burgdorferi* can cause systemic disease in captive *P. leucopus* (Burgess et al., 1990). Therefore, heavy infestation by both the tick and the pathogen may reduce survival of free-ranging mice. If survival of mice was negatively affected by burdens of ticks, then the enzootic cycle could be inhibited or disrupted. However, our evidence suggests that mice with high burdens of ticks do not exhibit higher rates of mortality (Table 2), and in fact, seem to persist longer than less infested mice. A similar relationship between burdens of ticks (*Aponomma hydrosauri* and *Amblyomma limbatum*) and longevity of lizards (*Tiliqua rugosa*) was discovered recently in South Australia (Bull and Burzacott, 1993). Because we do not believe that burdens of ticks actually are beneficial to hosts, we suspect that high tick loads are

correlated with, but do not themselves cause, high survival probability in *P. leucopus*.

In conclusion, fluctuating populations of mice probably play an important role in the enzootic cycle of Lyme disease. Prior studies (Ostfeld et al., 1995; J. O. Wolff, in litt.) indicate that populations of *P. leucopus* in oak-dominated forests fluctuate with acorn production, reaching peaks the summer following good mast years. Our studies also show that in patchy successional landscapes, abundance of larval ticks shifts to oak forests in the summer following a good mast year (Ostfeld et al., in press) due to acorns attracting white-tailed deer (*Odocoileus virginianus*) and their attached adult ticks in autumn (McShea and Schwede, 1993). Thus, peaks in population levels of mice in stands of oak-dominated forest should typically coincide with peaks in population levels of ticks. Because larval ticks are both more abundant and more successful in attaching to *P. leucopus* in the summer following mast production, we predict that risk of Lyme disease should fluctuate

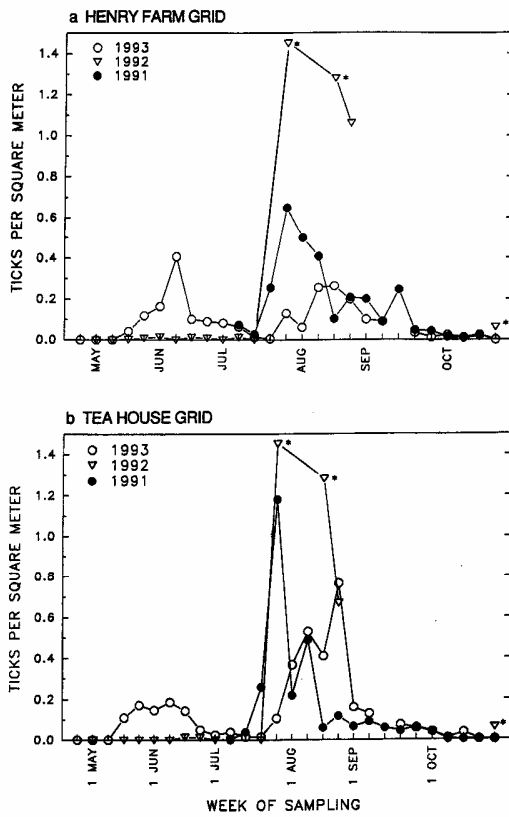


FIG. 4.—Numbers of host-seeking larval ticks per square meter on Henry Farm grid (a) and Tea House grid (b), 1991–1993. Asterisks indicate samples taken from the satellite sites in 1993.

tuates substantially, reaching a peak two summers following good mast years, when the nymphs that fed as larvae on abundant mice become active.

Future studies should focus on whether the density of infected nymphs in any given year can be predicted from the integrated product of density of mice and larvae per mouse in the prior year. If so, studies of mammalian population dynamics will contribute strongly to an understanding of the epidemiology of Lyme disease.

ACKNOWLEDGMENTS

We are grateful to V. Braslau, H. Rigney, A. Ruesink, J. Schnurr, and G. Vaters for excellent assistance in the field. Research was supported

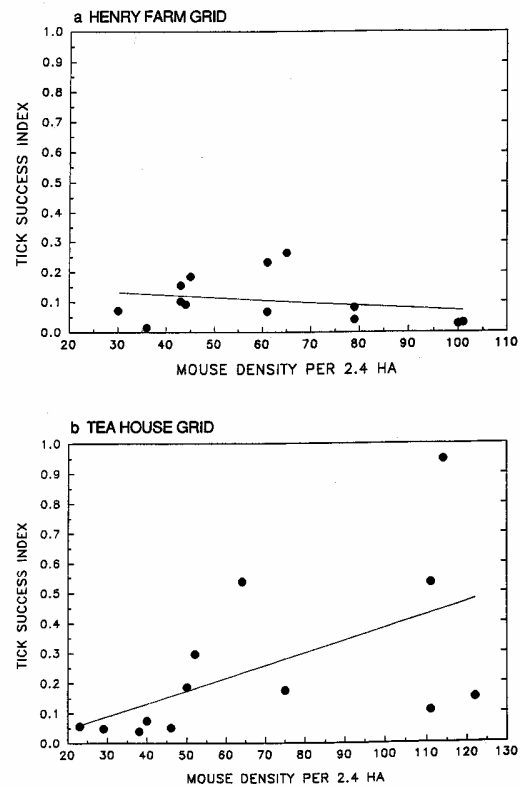


FIG. 5.—Tick-success index as a function of density of mice on Henry Farm grid (a) and Tea House grid (b). Tick-success index was calculated as (number of ticks attached to mice)/[(number of host-seeking ticks) + (number attached to mice)]. Density of mice was calculated as minimum number alive per 2.4 ha.

by grants from the General Reinsurance Corporation, the David Goodstein Family Foundation, the Plymouth Hill Foundation, and The National Science Foundation (DEB-9419640). This is a contribution to the program of the Institute of Ecosystem Studies.

LITERATURE CITED

- ANDERSON, J. F. 1988. Mammalian and avian reservoirs for *Borrelia burgdorferi*. *Annals of the New York Academy of Sciences*, 539:180–191.
- ANDERSON, J. F., AND L. A. MAGNARELLI. 1993. Natural history of *Borrelia burgdorferi* in vectors and vertebrate hosts. Pp. 11–24, in *Ecology and environmental management of Lyme disease* (H. S. Ginsberg, ed.). Rutgers University Press, New Brunswick, New Jersey, 224 pp.
- BARBOUR, A. G., AND D. FISH. 1993. The biological

- and social phenomenon of Lyme disease. *Science*, 260:1610–1616.
- BULL, C. M., AND D. BURZACOTT. 1993. The impact of tick load on the fitness of their lizard hosts. *Oecologia* (Berlin), 96:415–419.
- BURGESS, E. C., J. B. J. FRENCH, AND A. GENDRON-FITZPATRICK. 1990. Systemic disease in *Peromyscus leucopus* associated with *Borrelia burgdorferi* infection. *American Journal of Tropical Medicine and Hygiene*, 42:254–259.
- DANIELS, T. J., AND D. FISH. 1990. Spatial distribution and dispersal of unfed larval *Ixodes dammini* (Acari: Ixodidae) in southern New York. *Environmental Entomology*, 19:1029–1033.
- FALCO, R. C., AND D. FISH. 1989. Potential for tick exposure in recreational parks in a Lyme disease endemic area. *American Journal of Public Health*, 79:12–15.
- . 1992. A comparison of methods for sampling the deer tick, *Ixodes dammini*, in a Lyme disease endemic area. *Experimental and Applied Acarology*, 14:165–173.
- FISH, D. 1993. Population ecology of *Ixodes dammini*. Pp. 25–42, in *Ecology and environmental management of Lyme disease* (H. S. Ginsberg, ed.). Rutgers University Press, New Brunswick, New Jersey, 224 pp.
- KREBS, C. J. 1966. Demographic changes in fluctuating populations of *Microtus californicus*. *Ecological Monographs*, 36:239–273.
- KROHNE, D. T., J. F. MERRITT, S. H. VESSEY, AND J. O. WOLFF. 1988. Comparative demography of forest *Peromyscus*. *Canadian Journal of Zoology*, 66:2170–2176.
- LANE, R. S., J. PIESMAN, AND W. BURGENDORFER. 1991. Lyme borreliosis: relation of its causative agent to its vectors and hosts in North America and Europe. *Annual Review of Entomology*, 36:587–609.
- MAIN, A. J., A. B. CAREY, M. G. CAREY, AND R. H. GOODWIN. 1982. Immature *Ixodes dammini* (Acari: Ixodidae) on small animals in Connecticut, USA. *Journal of Medical Entomology*, 19:655–664.
- MC SHEA, W. J., AND G. SCHWEDE. 1993. Variable acorn crops: responses of white-tailed deer and other mast consumers. *Journal of Mammalogy*, 74:999–1006.
- OSTFELD, R. S., M. C. MILLER, AND J. SCHNURR. 1993. Ear tagging increases tick (*Ixodes dammini*) infestation rates of white-footed mice (*Peromyscus leucopus*). *Journal of Mammalogy*, 74:651–655.
- OSTFELD, R. S., O. M. CEPEDA, K. R. HAZLER, AND M. C. MILLER. 1995. Ecology of Lyme disease: habitat associations of deer ticks (*Ixodes dammini*) in a rural landscape. *Ecological Applications*, 5:353–361.
- PIESMAN, J., T. N. MATHER, R. J. SINSKY, AND A. SPIELMAN. 1987. Duration of tick attachment and *Borrelia burgdorferi* transmission. *Journal of Clinical Microbiology*, 25:557–558.
- STAFFORD, K. C. 1992. Oviposition and larval dispersal of *Ixodes dammini* (Acari: Ixodidae). *Journal of Medical Entomology*, 29:129–132.
- VAN BUSKIRK, J., AND R. S. OSTFELD. In press. Controlling Lyme disease by modifying the density and species composition of tick hosts. *Ecological Applications*.
- VIITALA, J., T. KOJOLA, AND H. YLÖNEN. 1986. Voles killed by ticks—an unsuccessful attempt to introduce north Finnish *Clethrionomys rufocanus* into an enclosure in central Finland. *Annales Entomologici Fennici*, 52:32–35.
- WOLFF, J. O. 1985a. Comparative population ecology of *Peromyscus leucopus* and *P. maniculatus*. *Canadian Journal of Zoology*, 63:1548–1555.
- . 1985b. The effects of density, food, and interspecific interference on home range size in *Peromyscus leucopus* and *P. maniculatus*. *Canadian Journal of Zoology*, 63:2657–2662.

Submitted 9 May 1994. Accepted 17 May 1995.

Associate Editor was Karen McBee.