

Managing Japanese Barberry (*Ranunculales: Berberidaceae*) Infestations Reduces Blacklegged Tick (*Acari: Ixodidae*) Abundance and Infection Prevalence With *Borrelia burgdorferi* (*Spirochaetales: Spirochaetaceae*)

SCOTT C. WILLIAMS,^{1,2} JEFFREY S. WARD,¹ THOMAS E. WORTHLEY,³
AND KIRBY C. STAFFORD III⁴

Environ. Entomol. 38(4): 977–984 (2009)

ABSTRACT In many Connecticut forests with an overabundance of white-tailed deer (*Odocoileus virginianus* Zimmermann), Japanese barberry (*Berberis thunbergii* DC) has become the dominant understory shrub, which may provide a habitat favorable to blacklegged tick (*Ixodes scapularis* Say) and white-footed mouse (*Peromyscus leucopus* Rafinesque) survival. To determine mouse and larval tick abundances at three replicate sites over 2 yr, mice were trapped in unmanipulated dense barberry infestations, areas where barberry was controlled, and areas where barberry was absent. The number of feeding larval ticks/mouse was recorded. Adult and nymphal ticks were sampled along 200-m draglines in each treatment, retained, and were tested for *Borrelia burgdorferi* (Johnson, Schmid, Hyde, Steigerwalt, and Brenner) presence. Total first-captured mouse counts did not differ between treatments. Mean number of feeding larval ticks per mouse was highest on mice captured in dense barberry. Adult tick densities in dense barberry were higher than in both controlled barberry and no barberry areas. Ticks sampled from full barberry infestations and controlled barberry areas had similar infection prevalence with *B. burgdorferi* the first year. In areas where barberry was controlled, infection prevalence was reduced to equal that of no barberry areas the second year of the study. Results indicate that managing Japanese barberry will have a positive effect on public health by reducing the number of *B. burgdorferi*-infected blacklegged ticks that can develop into motile life stages that commonly feed on humans.

KEY WORDS blacklegged tick, Japanese barberry, Lyme disease, white-footed mouse, white-tailed deer

Japanese barberry (*Berberis thunbergii* DC) is a thorny, perennial shrub native to southern and central Japan (Ohwi 1965). Japanese barberry was first planted in North America in the late 1800s (Harrington et al. 2003) and has since escaped from cultivated landscapes. It is now established in 31 states of the continental United States, the District of Columbia, and five Canadian provinces (USDA–NRCS 2008). Dense barberry stands are associated with a paucity of desirable tree regeneration and herbaceous plants (Harrington et al. 2003). Barberry may alter nitrogen cycling, affecting soil biota (Kourtev et al. 1999, Ehrenfeld et al. 2001), as well as soil structure and function (Kourtev et al. 2003). A Maine study reported blacklegged ticks (*Ixodes scapularis* Say) were twice as numerous in barberry-infested forests

than in adjacent forests without barberry (Elias et al. 2006). Blacklegged ticks are the major vector for the agents that cause Lyme disease, human granulocytic anaplasmosis, and human babesiosis (Magnarelli et al. 2006); thus, barberry infestations may have an indirect, adverse effect on human health.

Throughout the region, especially where white-tailed deer (*Odocoileus virginianus* Zimmermann) populations are high, dense barberry stands can develop in the forest understory (Ehrenfeld 1997, Silander and Klepeis 1999). Barberry is generally classified as a browse-resistant species (Silander and Klepeis 1999, Rutberg et al. 2004), because deer seldom eat its foliage. However, white-tailed deer have been witnessed consuming barberry fruits in late winter in southern Connecticut, when other available food sources were depleted (S.C.W., personal observation). However, Japanese barberry did not germinate from deer fecal samples gathered in Connecticut (Williams et al. 2008). Therefore, it is unlikely that white-tailed deer play a major role in the dispersal of Japanese barberry seeds, although they are known dispersers of other species of *Berberis* in western

¹ The Connecticut Agricultural Experiment Station, Department of Forestry and Horticulture, PO Box 1106, New Haven, CT 06504.

² Corresponding author, e-mail: scott.williams@po.state.ct.us.

³ University of Connecticut, Department of Extension, 1066 Saybrook Rd., Box 70, Haddam, CT 06438.

⁴ The Connecticut Agricultural Experiment Station, Department of Entomology, PO Box 1106, New Haven, CT 06504.

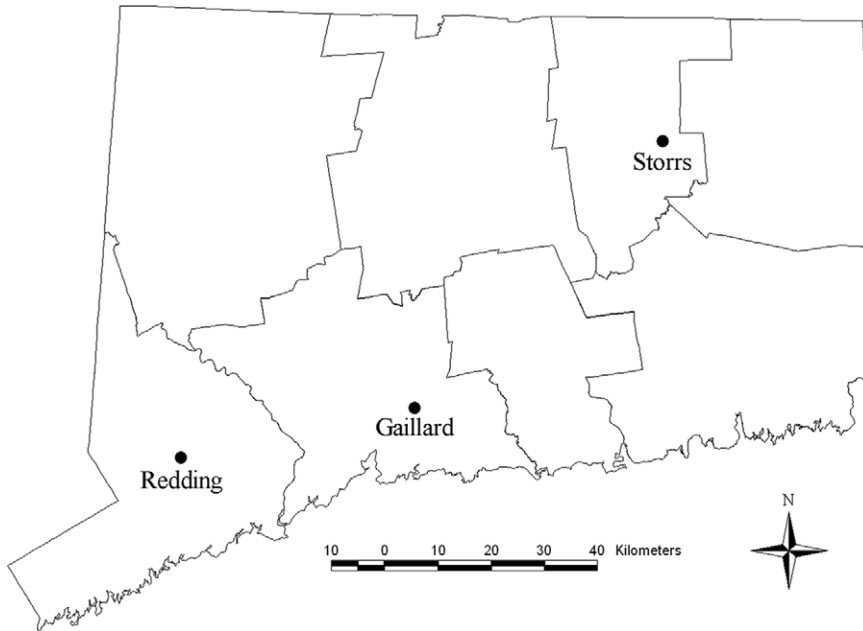


Fig. 1. Plot locations in Connecticut.

North America (Martin et al. 1951). It is likely that increased browsing of palatable species gives less palatable species, such as Japanese barberry, a competitive advantage (Tilghman 1989, Silander and Klepeis 1999, Elias et al. 2006). In addition, white-tailed deer are the primary host for adult blacklegged ticks, and their relative abundances are highly correlated (Daniels et al. 1993, Deblinger et al. 1993, Stafford 1993, Daniels and Fish 1995).

Anecdotal observations of severely browsed forests in southern Connecticut with deer densities as high as 40 deer/km² (Williams and Ward 2006) have shown a dearth of tree saplings and virtually no shrub layer other than dense Japanese barberry infestations. Such barberry stands may serve as refugia for small woodland rodents, specifically white-footed mice (*Peromyscus leucopus* Rafinesque) (Elias et al. 2006, Prusinski et al. 2006), providing increased protection from both avian and terrestrial predators. In addition, barberry is used as a questing habitat by blacklegged ticks because little other suitable vegetation exists in severely browsed forests. Because white-footed mice are the primary reservoir for the spirochete *Borrelia burgdorferi* (Johnson, Schmid, Hyde, Steigerwalt, and Brenner) (Anderson et al. 1987, Magnarelli et al. 2006), the causal agent of Lyme disease in humans, it is likely that infection prevalence in blacklegged ticks would be elevated where high mouse abundances exist.

We hypothesized that densities of white-footed mice and blacklegged ticks and associated *B. burgdorferi* infection prevalence were higher in wooded areas with dense Japanese barberry infestations than in adjacent wooded areas with no barberry. We also hypothesized that controlling barberry would result in a reduction in mouse and tick densities and potentially

B. burgdorferi infection prevalence. Data presented are from the first 2 yr of a multiyear study.

Materials and Methods

Study Areas. Three replicate study areas were established in geographically separate areas within Connecticut: in south-central Connecticut on South Central Connecticut Regional Water Authority property in the town of North Branford (Gaillard), in western Connecticut on Aquarion Water Company property in the town of Redding (Redding), and in northeastern Connecticut on the University of Connecticut Forest in Storrs (Storrs) (Fig. 1). All study areas had remnant stone walls running throughout and were once agricultural fields or pastures; Storrs and Gaillard were abandoned in the early 1900s and Redding in the 1940s.

Management was negligible (fuelwood harvests of declining and subcanopy trees), except at Gaillard where $\approx 70\%$ of eastern hemlock [*Tsuga canadensis* L. (Carrière)] were removed during a salvage harvest in the early 1990s. The remaining upper canopy of Gaillard was primarily sugar maple (*Acer saccharum* Marsh.) with mixed oak (*Quercus* spp.), white ash (*Fraxinus americana* L.), American beech (*Fagus grandifolia* Ehrh.), and scattered yellow poplar (*Liriodendron tulipifera* L.). Upper canopies of Storrs and Redding were characterized by a predominance of white ash, red maple (*Acer rubrum* L.), oak, yellow poplar, and some black cherry (*Prunus serotina* Ehrh.). All study areas had medium to dense stands of mature Japanese barberry that were excluding desirable forest regeneration and native herbaceous vegetation.

Table 1. Description of study area locations and soil types

Study area	Soil classification	Elevation (m)	Latitude	Longitude
Redding	Canton and Charlton	150	41.28	-73.37
Gaillard	Cheshire-Holyoke complex	85	41.37	-72.77
Storrs	Paxton and Montauk	190	41.82	-72.25

Soil classifications, elevations, and coordinates of study areas are shown in Table 1. Elevations ranged from 55 to 355 m above mean sea level. Climatic data (NOAA 1991) were from Hartford, CT, geographically centered among the study areas, which are within the northern temperate climate zone. Mean monthly temperature ranged from -3°C in January to 23°C in July. There was an average of 176 frost free days per year. Average annual precipitation was 1,128 mm/yr, evenly distributed over all months.

Plot Design and Japanese Barberry Control. Three treatment plots were established each at Gaillard, Storrs, and Redding. These included an intact barberry infestation where barberry was not manipulated (full barberry), an area where barberry was managed by a series of control methods (controlled barberry), and an area where barberry was minimal or absent (no barberry). The understory of full and controlled barberry areas also contained Oriental bittersweet (*Celastrus orbiculatus* Thunb.), winged euonymus [*Euonymus alatus* (Thunb.) Siebold], wine raspberry (*Rubus phoenicolasius* Maxim.), northern spicebush (*Lindera benzoin* L.), American witchhazel (*Hamelis virginiana* L.), and occasional common barberry (*Berberis vulgaris* L.), but were dominated by Japanese barberry. Because of severe browsing, little understory vegetation was present in no barberry areas except for unpalatable species such as northern spicebush, winged euonymus, American witchhazel, and an occasional Japanese barberry plant. Treatment plots within the three barberry cover types corresponded to mouse trapping areas, were ≈ 45 by 60 m, and were ≤ 250 m from one another at Gaillard, Storrs, or Redding. Barberry cover was estimated by sampling 100 0.5-m^2 areas at 3-m spacing within each treatment plot. The 0.5-m^2 sampling instrument consisted of a 4 by 4 grid with which percent barberry cover was determined by presence/absence within each cell.

In controlled barberry plots, initial control was accomplished by mechanical cutting and shredding of the above-ground portion of the plant and was completed in March 2007. We used a hydraulically driven rotary wood shredder (model BH74FM, Bull Hog; Fecon, Lebanon, OH) mounted to a compact track loader (model T300; Bobcat, West Fargo, ND) for initial control. Barberry clumps missed by the wood shredder (adjacent to trees, stone walls, or large rocks) were cut with a brush saw. Follow-up methods used to control resprouting ramets (individual stems) were directed flame with a propane torch (model BP 223 C Weed Dragon; Flame Engineering, LaCrosse, KN) and foliar applications of glyphosate and triclopyr. Follow-up control methods were completed in

late June 2007. Total area where barberry was controlled averaged $4,500\text{ m}^2$ each at Gaillard, Storrs, and Redding. More details on treatment specifics can be found in Ward et al. (2009).

Mouse Trapping and Larval Ticks. Mice were trapped using folding Sherman live traps (H. B. Sherman Traps, Tallahassee, FL) from July to September 2007 and July to August 2008. Twenty traps were set in permanent grids with 15-m spacing at each of the three treatment plots ($n = 60$) at each replicate study area and baited with peanut butter. Traps were set at each replicate study area on five different trapping events in 2007 and three different trapping events in 2008, resulting in a total of 480 trap nights/treatment ($n = 1440$ trap nights). Captured mice were temporarily sedated using the inhalant anesthetic isoflurane. Each mouse received a uniquely numbered ear tag (National Band and Tag, Newport, KY), and the number of larval ticks feeding on mice was recorded without removal.

Sedated mice were allowed to recover from the effects of isoflurane and were released into the plot from which they were originally captured. Mouse capture and handling protocols were approved by the Wildlife Division of the Connecticut Department of Environmental Protection and The Connecticut Agricultural Experiment Station's Institutional Animal Care and Use Committee in accordance with the American Society of Mammalogists guidelines for the use of wild animals in research (Gannon et al. 2007). Based on pelage and morphological characteristics, it was assumed that all captured mice were white-footed mouse rather than deer mice (*Peromyscus maniculatus* Wagner). Although deer mice are difficult to distinguish from white-footed mice based on appearance, the known range of deer mice in Connecticut is restricted to the northwestern portion of the state (DeGraaf and Rudis 1986), which was outside our study areas.

Population estimates were originally derived using the Jolly-Seber model (Jolly 1965, Seber 1965), but resulted in unacceptably high error because of inconsistent recaptures across treatments. Therefore, we used counts of first-captured mice to compare estimated population densities between treatments, which have been shown to be good indices of estimating intraspecific population size using our trapping protocols (Slade and Blair 2000).

One-way analysis of variance (ANOVA) was used to determine differences between treatments for first-captured mice for both years. One-way ANOVA was also used to test difference of feeding larval ticks/mouse between treatments for all captured mice, which included recaptures for both years. Tukey honestly significantly different (HSD) test was used to maintain α levels at $P < 0.05$ for multiple comparison tests of differences between treatments.

Adult Tick Sampling. Each treatment was sampled (with removal) 27 times (9 times at each of the three replicate sites) for adult blacklegged ticks from November 2007 to November 2008 using standard flagging techniques when adults were active (Stafford

2007). A 1-m² white canvas cloth attached to a dowel was used to flag vegetation or the forest floor over established transects totaling 200 m in each treatment. Flags were checked for ticks every 15 m. Gathered ticks were relocated to a laboratory, stored in a hydrator, and incubated at 10°C. Samples were pooled to determine the effect of Japanese barberry control on adult tick abundances immediately after (fall 2007/spring 2008) and 1 yr after management (fall 2008). Nymphal ticks also were retained, but sample sizes were too small to conduct meaningful density estimates. One-way ANOVA was used to determine differences in adult tick counts between treatments for each sampling interval. Tukey HSD was used to maintain α levels at $P < 0.05$ for multiple comparison tests of differences between treatments.

***Borrelia burgdorferi* Testing and Health Risk.** Gathered tick midguts were dissected under a stereo microscope and contents were smeared on 12-well glass microscope slides (30-103HTC; Thermo Fisher, Portsmouth, NH). *B. burgdorferi* spirochetes were identified in midgut contents by using indirect fluorescent antibody (IFA) staining methods with monoclonal antibody H5332, which is specific for outer surface protein A of *B. burgdorferi* (Magnarelli et al. 1994). Fluorescein isothiocyanate-conjugated goat anti-mouse immunoglobulins (KPL, Gaithersburg, MD) were diluted 1:40 in phosphate-buffered saline solution and used as a second antibody. Procedural details followed established protocols (Anderson et al. 1991; Magnarelli et al. 1994, 1997).

Borrelia burgdorferi infection prevalence data were pooled for adult and nymphal ticks as both stages were found in treatment plots, commonly feed on humans, and are capable of transferring spirochetes. When *B. burgdorferi* infection prevalence differed between treatments, the following procedures (Neter et al. 1982, pp. 325–329) were used to determine which treatments differed:

$$p' = \frac{n_1\bar{p}_1 + n_2\bar{p}_2}{n_1 + n_2}$$

$$s^2\{\bar{p}_2 - \bar{p}_1\} = p'(1 - p')\left(\frac{1}{n_2} + \frac{1}{n_1}\right)$$

$$z^* = \frac{(\bar{p}_2 - \bar{p}_1)}{s^2\{\bar{p}_2 - \bar{p}_1\}}$$

where n_i ($i = 1, 2$) is the sample size of treatment i , \bar{p}_i = number of infected ticks in treatment i , and z^* is the standardized test statistic. Differences for all comparisons were considered significant at $P < 0.05$. We used Bonferroni-adjusted probabilities to maintain $P < 0.05$ for all comparisons. This is a very conservative standard and may have excluded some significant differences.

To assess relative risk to public health, the estimated density of infected ticks per hectare was determined for each of the three treatments by taking the product of infection prevalence (%) and relative tick density (including nymphs for fall 2008) for each sampling interval. One-way ANOVA was used to determine

Table 2. Percent Japanese barberry cover at each replicate site for no barberry (No Barb.), controlled barberry pretreatment (Pre-treat), controlled barberry post-treatment (Post-treat), and full barberry (Full Barb.) by study area by year

Study Area	No Barb.	Controlled Barberry		Full Barb.
		Pre-treat	Post-treat	
Redding 2007	5.2	52.0	2.6	63.5
Redding 2008	5.3	—	1.1	61.0
Gaillard 2007	0.6	63.7	7.2	44.5
Gaillard 2008	1.4	—	4.9	45.9
Storrs 2007	1.9	70.8	0.3	23.9
Storrs 2008	0.8	—	2.8	25.8
Mean	2.9	62.2	3.2	44.1

differences in relative density of infected ticks between treatments for each sampling interval. Tukey HSD was used to maintain α levels at $P < 0.05$ for multiple comparison tests of differences between treatments.

Results

Japanese Barberry Control. Virtually all cut and shredded Japanese barberry clumps produced new ramets after initial mechanical control. Although the initial control did not kill all barberry genets (the entire plant), mechanical control was successful in reducing the size of barberry clumps. All follow-up control methods resulted in both increased mortality of barberry genets and smaller clump sizes (Ward et al. 2009). The control methods were successful in reducing Japanese barberry cover from 62% pretreatment to 3% post-treatment in controlled barberry areas. Japanese barberry cover estimates for treatments for both years are shown in Table 2. For a more detailed account of results of Japanese barberry management, see Ward et al. (2009).

Mouse Trapping and Larval Ticks on Mice. In 2007, there was minimal disturbance of traps; a few were triggered prematurely and moved several meters from their original locations, likely by raccoons (*Procyon lotor* L.). For 2007, we assumed equal disturbance across treatments and study areas. However, major trap disturbance occurred at all three treatments at Redding in 2008, and as a result, we were unable to obtain any usable data for mouse abundances or for larval ticks feeding on mice.

A total of 269 captures of 149 first-captured mice occurred in 2007. Counts of first-captured mice did not differ between treatments ($F = 0.01$; $df = 2, 3$; $P = 0.98$): full barberry ($n = 51$), controlled barberry ($n = 49$), and no barberry ($n = 49$). In 2008, there were 133 captures of 84 first-captured mice. Counts of first-captured mice did not differ between treatments ($F = 0.24$; $df = 2, 3$; $P = 0.80$): full barberry ($n = 27$), controlled barberry ($n = 22$), and no barberry ($n = 24$). However, mean feeding larval ticks per captured mouse did differ between treatments and were greatest in full barberry in both 2007 ($F = 3.37$; $df = 2, 265$; $P < 0.04$) and 2008 ($F = 3.10$; $df = 2, 128$; $P < 0.05$; Fig. 2). It was assumed that all larvae feeding on mice were blacklegged ticks

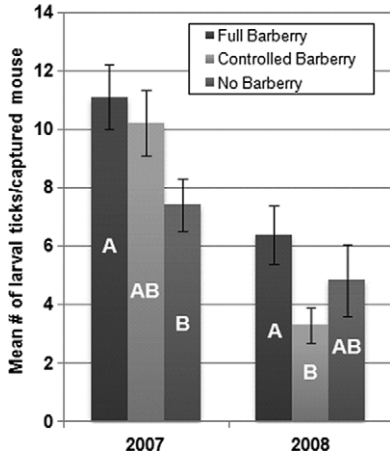


Fig. 2. Mean number of feeding larval ticks/mouse for Gaillard, Redding, and Storrs in 2007 and for Gaillard and Storrs in 2008. Means with the same letter within the same series are not significantly different. Error bars represent SEM.

because the only other tick species we encountered throughout the entire study were a few adult dog ticks (*Dermacentor variabilis* Say) ($n = 8$).

Adult Tick Sampling. A total of 525 adult blacklegged ticks (245 males, 280 females) were collected throughout all treatment areas: 23 (15 males, 8 females) in no barberrry, 76 (21 males, 55 females) in controlled barberrry, and 221 (103 males, 118 females) in full barberrry in fall 2007/spring 2008 and 26 (11 males, 15 females) in no barberrry, 35 (18 males, 17 females) in controlled barberrry, and 144 (77 males, 67 females) in full barberrry in fall 2008. Mean tick densities were consistently greater in full barberrry areas for both sampling intervals: fall 2007/spring 2008 ($F = 13.67$; $df = 2,42$; $P < 0.01$) and fall 2008 ($F = 7.39$; $df = 2,33$; $P < 0.01$). Full barberrry tick densities differed significantly from both controlled and no barberrry treatments for both sampling intervals (Fig. 3).

***Borrelia burgdorferi* Prevalence and Health Risk.** A total of 342 (132 males, 155 females, 55 nymphs) blacklegged ticks were tested for *B. burgdorferi* presence: 108 (47 males, 61 females) from the fall 2007/spring 2008 sampling interval and 234 (85 males, 94 females, 55 nymphs) from fall 2008. For fall 2007/spring 2008, infection prevalence was equal for ticks from full and no barberrry areas (44%) and was lower in ticks gathered from no barberrry areas (10%), but did not differ from full barberrry ($z = 2.04$; $df = 2$; $P > 0.10$) or controlled barberrry treatments ($z = 1.97$; $df = 2$; $P > 0.10$), likely because of low sample size in no barberrry ($n = 10$). After the second growing season postbarberrry control (fall 2008), infection prevalence in controlled barberrry (45%) was lower than full barberrry (63%) but did not differ ($z = 2.21$; $df = 2$; $P = 0.08$). Controlled barberrry tick infection prevalence did not differ from no barberrry areas either (39%) ($z = 0.51$; $df =$

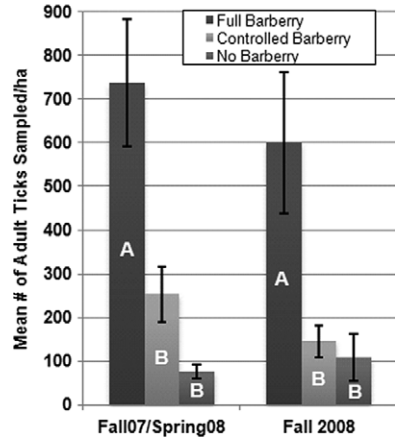


Fig. 3. Estimated adult blacklegged tick density (ticks/ha) based on 200-m² sampling areas. Means with the same letter within the same series are not significantly different. Error bars represent SEM.

2; $P > 0.90$). Full barberrry areas did have significantly higher infection prevalence than ticks in no barberrry areas ($z = 2.60$; $df = 2$; $P < 0.03$).

Estimated *B. burgdorferi* infected tick densities differed between treatments for both fall 2007/spring 2008 ($F = 15.91$; $df = 2,42$; $P < 0.001$) and fall 2008 ($F = 12.22$; $df = 2,33$; $P < 0.001$). There were an estimated 324 infected ticks/ha in full barberrry in fall 2007/spring 2008, which differed from both controlled barberrry (111 infected ticks/ha; $P = 0.002$) and no barberrry (8 infected ticks/ha; $P < 0.001$). The estimated number of infected ticks/ha did not differ between controlled barberrry and no barberrry ($P = 0.18$; Fig. 4). In fall 2008, there were an estimated 496 infected ticks/ha in full barberrry, which differed from both controlled barberrry (137 infected ticks/ha; $P = 0.001$) and no barberrry (89 infected ticks/ha; $P < 0.001$).

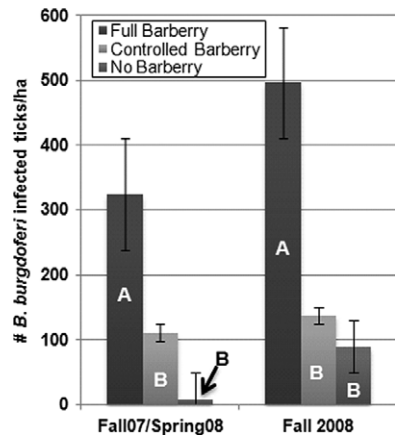


Fig. 4. Estimated number of blacklegged ticks infected with *B. burgdorferi* based on percent infection prevalence and estimated tick density for each treatment. Means with the same letter within the same series are not significantly different. Error bars represent SE.

Estimated infected ticks per hectare did not differ between controlled barberry and no barberry ($P = 0.86$; Fig. 4).

Discussion

The white-tailed deer density in portions of Connecticut is exceedingly high; an aerial survey conducted in 2003 indicated densities exceeding 40 deer/km² in portions of the Gaillard study area (Williams and Ward 2006). Continual browsing by white-tailed deer compromises the health and competitiveness of native shrubs, thus creating conditions favorable for Japanese barberry establishment (Tilghman 1989, Silander and Klepeis 1999). Ginsberg and Ewing (1989) reported that ticks were common in the shrub layer that provides physically higher questing habitat for ticks to find suitable hosts. Elias et al. (2006) found that in the 0.5- to 1.5-m height class, exotic-invasive shrub stem density was twice that of native shrubs in southern Maine. In some Connecticut forests, the only remaining suitable questing habitat for ticks is Japanese barberry.

Questing adult blacklegged tick abundances were greatest in areas dominated by Japanese barberry (Fig. 3). This relationship was also noted in southern Maine, at the northern extent of the blacklegged tick's range (Lubelczyk et al. 2004). Elias et al. (2006) reported a positive relationship between questing nymphal and adult blacklegged ticks and exotic-invasive shrubs, including Japanese barberry. We found a greater abundance of larval blacklegged ticks feeding on white-footed mice in barberry-dominated understories compared with areas where barberry was virtually absent. These collective results indicate that dense Japanese barberry infestations can be favorable habitat for all three life stages of the blacklegged tick.

By controlling Japanese barberry, we reduced the number of questing adult blacklegged ticks to densities statistically equal that of areas with no barberry for both years. This result was likely caused by the mechanical removal of the aboveground portion of barberry, effectively eliminated questing habitat, which corroborates Wilson (1986). The abundance of larval blacklegged ticks feeding on mice differed initially only between full barberry and no barberry treatment areas. In fall 2008 where barberry was controlled, feeding larval tick abundances were significantly lower than full barberry areas. We suspect this was a result of fewer available egg-laying adult females and that this trend will continue as the 2-yr life cycle of the blacklegged tick progresses.

Prusinski et al. (2006) emphasized the importance of the relationship between preferred small mammal habitat (food resources and protection from predation) and ideal tick habitat (questing areas, host availability, suitable microclimate). The dense growth form of Japanese barberry provides increased protection from predation, its abundant fruits provide a potential food source, and it may provide other yet unrecognized ecosystem services benefitting mouse

populations (Seagle 2008). Japanese barberry leafs out ~1 mo before overstory trees and most native shrubs (Silander and Klepeis 1999, Xu et al. 2007). This timing directly corresponds to the peak of spring activity of adult blacklegged ticks in Connecticut (Stafford 2007). We believe that the dense canopy of Japanese barberry infestations retains humidity better than surrounding areas, thus creating a favorable microsite for blacklegged tick survival (Rodgers et al. 2007). As a result, adult ticks may be concentrated in barberry infestations in early spring during barberry leaf-out, when limited forest overstory canopy allows for increased sunlight penetration, creating less than favorable conditions for tick survival by lowering soil moisture and relative humidity. Japanese barberry also provides excellent questing habitat as its height (upwards of 3 m) is ideal for blacklegged ticks to attach to white-tailed deer, which readily incorporate barberry infestations in their home ranges.

Prusinski et al. (2006) found that small mammals had higher *B. burgdorferi* infection prevalence in areas where shrub density was higher. We originally hypothesized that a higher percentage of blacklegged ticks found in barberry infestations would be infected with *B. burgdorferi* because increased white-footed mouse densities would serve as a larger reservoir. Although mouse densities were similar across treatments, infection prevalence was consistently higher in barberry infestations than in areas without barberry. This, combined with higher abundances of ticks found in barberry infestations, resulted in significantly more questing ticks infected with *B. burgdorferi* (Fig. 4), which poses a considerable threat to public health. By controlling Japanese barberry, we reduced adult blacklegged tick densities, *B. burgdorferi* infection prevalence, and resulting estimated number of *B. burgdorferi*-infected ticks to equal that of areas where barberry was absent (Figs. 3 and 4).

It is clear that dense Japanese barberry infestations provide highly favorable habitats for small mammals, deer, and tick development and survival. Removal of Japanese barberry will significantly decrease the abundance of ticks, their infection prevalence with *B. burgdorferi*, and the environmental risk of Lyme disease. It is also clear that Japanese barberry infestations pose an indirect threat to public health. We suggest that municipalities, forest managers, and private landowners with Japanese barberry infestations on their properties take immediate management action in the interest of preserving both forest and public health.

Acknowledgments

We thank Aquarion Water Company, CT Chapter-The Nature Conservancy, South Central Connecticut Regional Water Authority, and Weed-It-Now Program-The Nature Conservancy for financial and technical assistance and providing study sites. The Connecticut Department of Environmental Protection-Division of Forestry provided personnel assistance. J. P. Barsky, R. M. Cecarelli, R. J. Hannan, Jr., M. R. Short, G. M. Picard, E. A. Kiesewetter, D. V. Tompkins, R. A.

Wilcox, T. M. Blevins, H. Stuber, C. Ariori, K. Drennan, F. Pacyna, and J. Bravo assisted with plot establishment, treatments, data collection, and tick IFAs. Monoclonal antibody H5332 was provided by A. Barbour of the Department of Microbiology and Molecular Genetics at the University of California, Irvine's School of Medicine.

References Cited

- Anderson, B. E., J. E. Dawson, D. C. Jones, and K. H. Wilson. 1991. *Ehrlichia chaffeensis*, a new species associated with human ehrlichiosis. *J. Clin. Microbiol.* 29: 2838–2842.
- Anderson, J. F., R. C. Johnson, L. A. Magnarelli, F. W. Hyde, and J. E. Myers. 1987. Prevalence of *Borrelia burgdorferi* and *Babesia microti* in mice on islands inhabited by white-tailed deer. *Appl. Environ. Microb.* 53: 892–894.
- Daniels, T. J., and D. Fish. 1995. Effect of deer exclusion on the abundance of immature *Ixodes scapularis* (Acari: Ixodidae) parasitizing small and medium-sized mammals. *J. Med. Entomol.* 32: 5–11.
- Daniels, T. J., D. Fish, and I. Schwartz. 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) and Lyme disease risk by deer exclusion. *J. Med. Entomol.* 30: 1043–1049.
- Deblinger, R. D., M. L. Wilson, D. W. Rimmer, and A. Spielman. 1993. Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following incremental removal of deer. *J. Med. Entomol.* 30: 144–150.
- DeGraaf, R. M., and D. D. Rudis. 1986. England wildlife: habitat, natural history, and distribution. Gen. Tech. Rep. NE-108. U.S. Department of Agriculture, Forest Service, Northeastern Forest Experimental Station, Broomall, PA.
- Ehrenfeld, J. G. 1997. Invasion of deciduous forest preserves in the New York metropolitan region by Japanese barberry (*Berberis thunbergii* DC). *J. Torr. Botan. Soc.* 124: 210–215.
- Ehrenfeld, J. G., P. Kourtev, and W. Huang. 2001. Changes in soil functions following invasions of exotic understory plants in deciduous forests. *Ecol. Appl.* 11: 1287–1300.
- Elias, S. P., C. B. Lubelczyk, P. W. Rand, E. H. LaCombe, M. S. Holman, and R. P. Smith, Jr. 2006. Deer browse resistant exotic-invasive understory: an indicator of elevated human risk of exposure to *Ixodes scapularis* (Acari: Ixodidae) in southern coastal Maine woodlands. *J. Med. Entomol.* 43: 1142–1152.
- Gannon, W. L., R. S. Sikes, and The Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild animals in research. *J. Mammal.* 88: 809–823.
- Ginsberg, H. S., and C. P. Ewing. 1989. Habitat distribution of *Ixodes dammini* (Acari: Ixodidae) and Lyme disease spirochetes on Fire Island, New York. *J. Med. Entomol.* 26: 183–189.
- Harrington, R. A., R. Kujawski, and H.D.P. Ryan. 2003. Invasive plants and the green industry. *J. Arbor.* 29: 42–48.
- Jolly, G. M. 1965. Explicit estimates from capture-recapture data with both death and immigration–stochastic model. *Biometrika* 52: 225–247.
- Kourtev, P., J. G. Ehrenfeld, and M. Hagglom. 2003. Experimental analysis of the effect of exotic and native plant species on structure and function of soil microbial communities. *Soil Biol. Biochem.* 35: 895–905.
- Kourtev, P., W. Z. Huang, and J. G. Ehrenfeld. 1999. Differences in earthworm densities and nitrogen dynamics in soils under exotic and native plant species. *Biol. Invasions* 1: 237–245.
- Lubelczyk, C. B., S. P. Elias, P. W. Rand, M. S. Holman, E. H. LaCombe, and J.R.P. Smith. 2004. Habitat associations of *Ixodes scapularis* (Acari: Ixodidae) in Maine. *Environ. Entomol.* 33: 900–906.
- Magnarelli, L. A., J. F. Anderson, and K. C. Stafford III. 1994. Detection of *Borrelia burgdorferi* in urine of *Peromyscus leucopus* by inhibition enzyme-linked immunosorbent assay. *J. Clin. Microbiol.* 32: 777–782.
- Magnarelli, L. A., J. F. Anderson, K. C. Stafford III, and J. S. Dumler. 1997. Antibodies to multiple tickborne pathogens of babesiosis, ehrlichiosis, and Lyme borreliosis in white-footed mice. *J. Wildlife Dis.* 33: 466–473.
- Magnarelli, L. A., K. C. Stafford III, J. W. IJdo, and E. Fikrig. 2006. Antibodies to whole-cell or recombinant antigens of *Borrelia burgdorferi*, *Anaplasma phagocytophilum*, and *Babesia microti* in white-footed mice. *J. Wildlife Dis.* 42: 732–738.
- Martin, A., H. S. Zim, and A. L. Nelson. 1951. American wildlife and plants: a guide to wildlife food habits. Dover Publications, New York.
- National Oceanic and Atmospheric Administration [NOAA]. 1991. Local climatological data 1990. National Oceanic and Atmospheric Administration, Hartford, Connecticut.
- Neter, J., W. Wasserman, and G. A. Whitmore. 1982. Applied statistics, 2nd ed. Allyn and Bacon, Boston, MA.
- Ohwi, J. 1965. Flora of Japan. Smithsonian Institution, Washington, DC.
- Prusinski, M. A., H. Chen, J. M. Drobnack, S. J. Kogut, R. G. Means, J. J. Howard, J. Oliver, G. Lukacik, P. B. Backenson, and D. J. White. 2006. Habitat structure associated with *Borrelia burgdorferi* prevalence in small mammals in New York State. *Environ. Entomol.* 35: 308–319.
- Rodgers, S. E., C. P. Zolnik, and T. N. Mather. 2007. Duration of exposure to suboptimal atmospheric moisture affects nymphal blacklegged tick survival. *J. Med. Entomol.* 44: 372–375.
- Rutberg, A. T., R. E. Naugle, L. A. Thiele, and I.K.M. Liu. 2004. Effects of immunoneutralization on a suburban population of white-tailed deer (*Odocoileus virginianus*). *Biol. Conserv.* 116: 243–250.
- Seagle, S. W. 2008. Ecosystem ecology of the golden mouse, pp. 81–97. In G. W. Barrett and G. A. Feldhamer (eds.), *The golden mouse: ecology and conservation*. Springer, New York.
- Seber, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52: 249–259.
- Silander, J. A., and D. M. Klepeis. 1999. The invasion ecology of Japanese barberry (*Berberis thunbergii*) in the New England landscape. *Biol. Invasions* 1: 189–201.
- Slade, N. A., and S. M. Blair. 2000. An empirical test of using counts of individuals captured as indices of population size. *J. Mammal.* 81: 1035–1045.
- Stafford, K. C., III. 1993. Reduced abundance of *Ixodes scapularis* (Acari: Ixodidae) with exclusion of deer by electric fencing. *J. Med. Entomol.* 30: 986–996.
- Stafford, K. C., III. 2007. Tick management handbook: an integrated guide for homeowners, pest control operators, and public health officials for the prevention of tick-associated diseases. Connecticut Agricultural Experiment Station, New Haven, CT.
- Tilghman, N. G. 1989. Impacts of white-tailed deer on forest regeneration in northwestern Pennsylvania. *J. Wildlife Manag.* 53: 524–532.
- [USDA–Natural Resources Conservation Service] U.S. Department of Agriculture. 2008. The PLANTS database. (<http://plants.usda.gov>).

- Ward, J. S., T. E. Worthley, and S. C. Williams. 2009. Controlling Japanese barberry (*Berberis thunbergii* DC) in southern New England, USA. *Forest Ecol. Manag.* 257: 561–566.
- Williams, S. C., and J. S. Ward. 2006. Exotic seed dispersal by white-tailed deer in southern Connecticut. *Nat. Area J.* 26: 383–390.
- Williams, S. C., J. S. Ward, and U. Ramakrishnan. 2008. Endozoochory by white-tailed deer (*Odocoileus virginianus*) across a suburban/woodland interface. *Forest Ecol. Manag.* 255: 940–947.
- Wilson, M. L. 1986. Reduced abundance of adult *Ixodes dammini* (Acari: Ixodidae) following destruction of vegetation. *J. Econ. Entomol.* 79: 693–696.
- Xu, C. Y., K. L. Griffin, and W.S.F. Schuster. 2007. Leaf phenology and seasonal variation of photosynthesis of invasive *Berberis thunbergii* (Japanese barberry) and two co-occurring native understory shrubs in a northeastern United States deciduous forest. *Oecologia (Berl.)* 154: 11–21.

Received 27 October 2008; accepted 6 April 2009.
