Reduced Abundance of *Ixodes scapularis* (Acari: Ixodidae) and the Tick Parasitoid *Ixodiphagus hookeri* (Hymenoptera: Encyrtidae) with Reduction of White-Tailed Deer

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ABSTRACT The principal vector for the pathogens of Lyme disease, human granulocytic ehrlichiosis, and human babesiosis is the tick *Ixodes scapularis* Say. A chalcid wasp, *Ixodiphagus hookeri*, in the family Encyrtidae parasitizes populations of the tick on several islands or other geographically isolated sites in New England with high densities of these ticks and white-tailed deer (*Odocoileus virginianus*), the principal host for adult *I. scapularis*. Deer densities were reduced at a forested tract in Bridgeport and the Bluff Point Coastal Reserve in Groton, Connecticut, from levels exceeding 90 animals per km^2 in 1992 (Bridgeport) and 1994 (Bluff Point) to 17 and 10 animals per km^2, respectively, by fall 2001. Tick densities declined with sustained reductions in the population of white-tailed deer. Similarly, prevalence of tick parasitism by *Ixodes hookeri* declined at both sites from 30 to 25% to <1.0% and was significantly correlated with previous year's deer density at both sites ($r_s = 0.933$ and $r_s = 0.867$, $P \leq 0.0001$) and with nymphal tick densities at Bridgeport ($r_s = 0.867$, $P \leq 0.0001$), but was not as well correlated with tick densities in Groton. The virtual disappearance of *I. hookeri* in this study corresponds with a lack of *I. hookeri* in mainland *I. scapularis* at comparable deer and tick densities, suggesting that there is a threshold deer density of ≈10–20/km^2, with corresponding tick densities necessary for *I. hookeri* to successfully parasitize *I. scapularis*.

KEY WORDS *Ixodiphagus hookeri*, *Ixodes scapularis*, tick, parasitoid, deer reduction

TICKS ARE OBLIGATE hematophagous ectoparasites of humans, livestock, and wildlife associated with many zoonotic disease pathogens. Disease control, particularly for Lyme disease, has focused largely on vector control through chemical insecticides, habitat management, treating hosts, or influencing host abundance (Stafford 2002). Ticks have few natural enemies, but they are parasitized by seven known species of minute (2-mm) chalcid wasps in the family Encyrtidae (Ixodiphagini), which have been recovered from many species of ticks worldwide (Davis 1986, Hu et al. 1998). Two species occur in the United States, *Ixodiphagus* (*Hunterellus*) *hookeri* (Howard) and *I. texanus* Howard. The first species was mass released in the 1920s and 1930s on the Elizabeth Islands and Martha's Vineyard, Massachusetts, to control the American dog tick, *Dermacentor variabilis* (Say), and in Montana and other western states to control the Rocky Mountain wood tick, *D. andersoni* Stiles, a vector of Rocky Mountain spotted fever (Larrouse et al. 1928, Cooley and Kohls 1934, Smith and Cole 1943). No reduction in tick abundance caused by the parasitoids was observed, and few wasps were recovered after these releases, although the wasp apparently became established in the blacklegged tick, *Ixodes scapularis* Say on Naushon Island, Massachusetts (Larrouse et al. 1928, Cobb 1942, Mather et al. 1987). Similar releases of *I. hookeri* in Russia in the 1940s to control *I. ricinus* and *I. persulcatus* also were unsuccessful (Alfeev 1946). Failures of the previous releases decades ago may have been because of ecological constraints on the parasitoid, timing of the release, climatic incompatibility, or limitations on parasitoid reproduction in the targeted tick species.

Today, *I. scapularis* is of major concern as the vector of the pathogens for human babesiosis, human granulocytic ehrlichiosis, and Lyme disease, the leading arthropod-associated disease in the United States (CDC 2002). The rising incidence and geographical spread of Lyme disease are closely correlated with the

Research with laboratory and wild mice adhered to the Guide for the Care and Use of Laboratory Animals and approved protocols of the Experiment Station's Institutional Animal Care and Use Committee.

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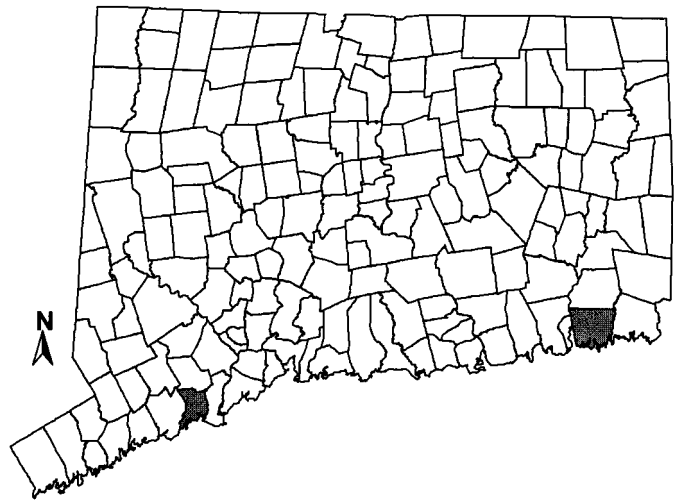

Fig. 1. Map of Connecticut towns showing Bridgeport (SW CT) and Groton (SE CT) (shaded), where the *Ixodiphagus* research sites are located.

distribution and annual abundance of ticks infected with the Lyme disease agent, *Borrelia burgdorferi* (Mather et al. 1996, Stafford et al. 1998). Increases in the tick population in recent decades have been linked to changing landscape patterns and the increasing population of white-tailed deer, *Odocoileus virginianus* (Zimmerman), which is the primary host for adult *I. scapularis* (Barbour and Fish 1993). The microgeographic distribution of immature *I. scapularis* is closely related to deer density (Wilson et al. 1990). Deer reduction or the acaricidal treatment of deer has been explored for the control of *I. scapularis.* The exclusion, elimination, or treatment of deer can significantly reduce tick abundance (Wilson et al. 1988, Daniels et al. 1993, Stafford 1993, Pound et al. 2000). A case also has been made for the control of *I. scapularis* by parasitoid augmentation with *I. hookeri* (Knipling and Steelman 2000). The parasitoid *I. hookeri* is established in *I. scapularis* at several insular locations in southern New England and New York, where deer and tick populations are extremely high, with parasitism rates in some cases ≈20–30% (Mather et al. 1987, Hu et al. 1993, Stafford et al. 1996, Hu and Hyland 1997). The fact that the wasp has been found only in areas with high tick densities suggests the wasp is strongly dependent upon tick or tick host densities and may require a threshold tick density for establishment. We previously reported the presence of *I. hookeri* in insular populations of the blacklegged tick in two locations in Connecticut (Stafford et al. 1996). Both were geographically isolated islands that had an overabundant tick population and deer densities in excess of 90 deer/km^2. In this study, we report on the effects of reducing white-tailed deer populations on the abundance of the tick host, *I. scapularis*, the prevalence of the wasp parasitoid, *I. hookeri*, and the implications for the use of the wasp for the control of the blacklegged tick.

Materials and Methods

Site Descriptions. The two study locations in Connecticut were Lake Success Business Park in Bridgeport and the Bluff Point Coastal Preserve in Groton (Fig. 1). Both sites supported a large population of deer and were heavily infested with *I. scapularis.* Lake Success Business Park, hereafter referred to as Bridgeport, is a privately owned, 176-ha largely mixed deciduous woodland tract with a lake, wetlands, and open fields. A fence (2.5 m high) separates the park from surrounding residential and commercial neighborhoods. This site is a focus for Lyme disease and ehrlichiosis (Magnarelli et al. 1995, Stafford et al. 1999). Many areas are dominated by dense undergrowth of barberry, *Berberis vulagaris* L., and greenbriar, *Smilax* spp. The annual incidence of Lyme disease in the city of Bridgeport itself is low, ranging from 2.1 to 29.4 cases per 100,000 population during the 11 yr from 1992 to 2002 (CT Department Public Health, www.dph.state.ct.us).

The Bluff Point Coastal Preserve is a 326-ha coastal peninsula in Groton, Connecticut, managed by the Connecticut Department of Environmental Protection (DEP). Isolated on the north by railroad tracks and housing development, the preserve is bounded by Mumford Cove to the east, the Poquonock River to the west, and Long Island Sound to the south. The preserve, hereafter referred to as Bluff Point, is 0.9 km wide and 2.9 km long, with mature open oak woodland in the northern half and a dense coastal-shrub community in the southern portion of the peninsula. A Lyme disease incidence rate is not directly available or perhaps relevant for these two nonresidential tracts, although thousands of hikers, joggers, bicyclists, and other visitors frequent Bluff Point each year. The annual incidence of Lyme disease in the town of Groton ranged from 28.2 to 155.4 cases per 100,000

population, 1992–2002 (CT Department Public Health, www.dph.state.ct.us).

Deer Reductions. The deer populations at both Bridgeport and Bluff Point exceeded 90 deer per km^2 in 1992 and 1994, respectively, when this study was initiated. Over one-half of the deer were removed at the Bridgeport site before deer reproductive control studies and additional deer were occasionally removed for research purposes. All animals were marked with ear tags, and all females were fitted with radio collars by summer 1992 (DeNicola et al. 1997). Each spring, all fawns were captured and tagged by midsummer to maintain a completely marked population. Supplemental feed was provided year around. The deer population at Bluff Point peaked in 1994 and was reduced by a controlled public hunt in January 1996 as part of an overall ecological management program developed by the Connecticut DEP (Kilpatrick et al. 1997). Additional animals were removed by the DEP in January 1997, 2000, 2001, and 2002. Deer at Bluff Point will be removed periodically by the DEP to maintain the deer population at the maximum habitat carrying capacity of ≈25 animals. Aerial winter surveys, spotlight counts, and number of deer removed were used to estimate deer densities at the preserve. Deer densities used in this study are fall season estimates because the major seasonal peak for adult *I. scapularis* activity and reproductive success is in the fall, although reductions in January would also impact the number of spring adult ticks feeding on deer.

Tick Sampling and Rearing of *I. hookeri*. Abundance of host-seeking subadult *I. scapularis* and percent parasitism by *I. hookeri* were monitored annually at Bridgeport and Bluff Point from 1993 to 2002, as described earlier (Stafford et al. 1996). Briefly, host-seeking larvae and nymphs of *I. scapularis* were collected roughly biweekly May through August by dragging the vegetation with a 1-m^2 flannel cloth at established 250-m^2 plots. Relative larval and nymphal tick abundance per 100 m^2 was calculated from seasonal cutoffs of mid-May through July for the nymphs and mid-July through August for the larvae. A total of 12 sample sites (10 × 25 m each) has been used at the Bridgeport site since 1997, an increase of 4 from earlier years (1993 through 1996, in which 7 plots were in the northern portion and 1 in the southern portion). Since 1997, there have been 6 plots in the northern portion and 6 in the southern portion of the Bridgeport site. One of the seven original northern sites was lost because of reclamation activity. A southern plot was lost part way through the 2000 season because of reclamation activity (n = 11 in 2001 and 2002). At Bluff Point, there are 5 sites in the southern portion of the peninsula and 2–4 sites in the northern area. Nymphal *I. scapularis* were placed in vials with grass for humidity and returned to the laboratory. Larvae were removed from the tick drag with tape, counted on site, and removed. A subsample of the nymphs was used to obtain estimates of parasitism rates by *I. hookeri*.

Annual estimates of wasp prevalence and fecundity were obtained by rearing *I. scapularis* nymphs from Bridgeport and Bluff Point on CD-1 or 3CH mice in the laboratory. Pools of no more than 30 nymphs collected during the same month at either Bridgeport or Bluff Point were placed on a mouse held in acrylic restrainers. After tick attachment (≈30 min), mice were then placed in cages held over trays of water to recover engorged ticks 3–5 d later. Food and water were provided ad libitum. Engorged nymphs were held at ≈20–22°C and 100% RH for signs of parasitism by *I. hookeri*. After 3 wk, potentially parasitized nymphs were segregated individually and monitored for the emergence of parasitoids. Adult wasps were counted, and many specimens were mounted on points. No wasps were reared from nymphs collected in 2001 because of construction of a new insectary facility. Average percent parasitism was based upon all nymphs showing evidence of parasitism and parasitoids obtained from nymphs collected during the period of nymphal tick activity during late May, June, and July. Voucher specimens of *I. hookeri* from earlier samples had been deposited at the Yale Peabody Museum of Natural History (New Haven, CT), as noted previously (Stafford et al. 1996).

Small rodents, especially white-footed mice, *Peromyscus leucopus* (Rafinesque), were live trapped at the Bridgeport site using Sherman box traps (7.6 × 8.9 × 22.9 cm; H.H. Sherman Traps, Tallahassee, FL) baited with peanut butter and apple in 1993, 1997–2000, and 2002. Two sample grids (3 traps × 8 traps, 10 m apart) had been established in 1993 in the northern portion of the site and were used for subsequent trapping from 1997 to 2002. Mice were ear tagged under anesthesia (methoxyflurane), ticks were removed and counted, and after recovery, the animals were released at the site of capture (Stafford et al. 1996).

Statistical Analysis. The relationship among deer density, tick abundance, and the rate of parasitism by *I. hookeri* over the 10-yr period was compared using the Spearman correlation on ranks, shifted 1 yr to correlate tick densities and wasp parasitism rates. Transformation of the data was insufficient in normalizing the data for a parametric analysis of variance (ANOVA). Therefore, differences between years in deer abundance and tick abundance using biweekly count data were compared with the nonparametric Kruskal-Wallis ANOVA on ranks with Dunn's method for multiple comparisons using SigmaStat 2.03 (SPSS, Chicago, IL) (Fox et al. 1995). Proportions of ticks infested with *I. hookeri* were compared using the z-test.

Results

Deer Reductions. Deer density at the Bridgeport site was reduced 60% from 171 animals (97.3/km^2 or 252/mi^2) in 1992 to 68 animals (38.6 deer/km^2) in 1993 (Fig. 2). From 1994 through 1999, the decrease in the deer population was more gradual, dropping to 34 animals in 1997 and only 23 animals (13.1/km^2 or 34/mi^2) by fall 1999. This deer density is comparable to that in several Connecticut shoreline communities (Old Lyme, 15.1 deer/km^2; Weston, 13.1/km^2) based

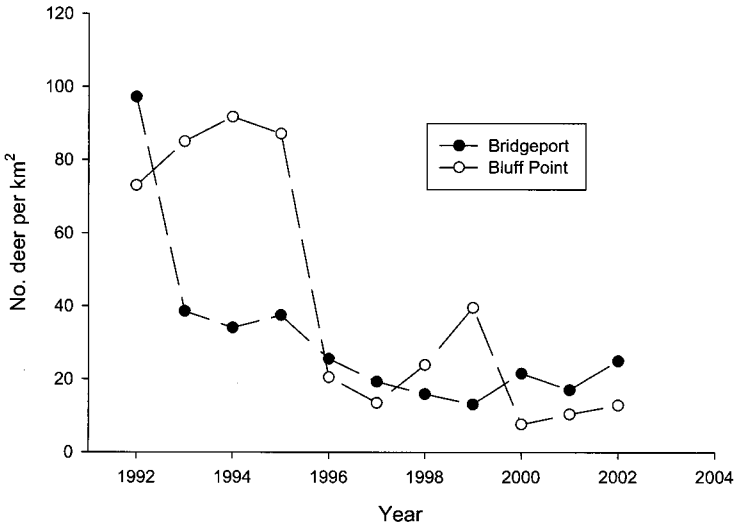

Fig. 2. Estimated density of deer per km^2 at Bridgeport and Bluff Point, 1992 through 2002, during the fall activity period for adult *I. scapularis*.

on aerial survey data (A.J.D. and K.C.S., unpublished data). Deer density was allowed to increase to 38 animals (21.6/km^2) by fall 2000 and 44 animals (25.0/km^2) by fall 2002, which is still only one-fourth of the 1992 population. Thirty animals (17.0/km^2) were present in fall 2001.

Bluff Point deer densities ranged from 73.4 to 92.3 deer/km^2 during 1992–1995, with nearly 300 animals in 1994. By fall of 1997, deer had been reduced 4-fold from that of 1995. The deer herd was reduced in January 1996 by 223 animals through the public-controlled hunt. The DEP removed an additional 35 animals in 1997. Aerial surveys before and after the initial 1996 management effort indicated that the herd was reduced from ≈284 deer (88 deer/km^2) to 55 deer (17 deer/km^2). There were an estimated 44 animals (13.5/km^2) in fall 1997, but the deer population had rebounded to 78 animals (23.9/km^2) a year later and 129 animals (39.6/km^2) by fall 1999 (Fig. 2). Another herd reduction program was conducted in January 2000, with 74 deer removed. The November 2000 population was estimated at 88 animals (55 deer remaining plus new fawn recruitment), and another removal program in January 2001 removed 63 deer (Kilpatrick 2001), resulting in an estimated fall 2001 population of 34 animals. In January 2002, 10 more deer were removed from Bluff Point by DEP staff.

Tick Reductions. A 10-fold decline from peak host-seeking nymphal tick densities and a 3- to 10-fold or more decline in larval tick densities were recorded with declining deer density. In Bridgeport, nymphal tick abundance declined significantly from a mean of 9.0–9.6/100 m^2 the first 2 yr to 2.5/100 m^2 by 2001 and 0.7/100 m^2 in 2002 ($H = 104.582$, df = 9, $P \leq 0.001$) (Table 1). Tick abundance in 2002 was significantly different from all previous years at $P = 0.05$. Larval abundance between years in Bridgeport was also significantly different ($H = 66.934$, df = 9, $P \leq 0.001$), dropping from 196 to 289 larvae per 100 m^2 to 37.2 and 45.6 larvae per 100 m^2 in 1999 and 2001, respectively.

Table 1. Mean (SEM) number of host-seeking nymphal and larval *I. scapularis* collected at Bridgeport and Bluff Point, 1993 through 2002

Year	Mean no. ticks (SEM) per 100 m^2							
	Bridgeport				Bluff Point			
	n	Nymphs	*n*	Larvae	*n*	Nymphs	*n*	Larvae
1993	40	9.0 (1.62)	32	196.5 (33.27)	38	8.8 (1.86)	22	176.1 (49.55)
1994	37	9.6 (1.71)	22	289.0 (76.93)	27	12.0 (2.84)	14	89.9 (36.88)
1995	48	4.6 (0.87)	23	101.4 (26.51)	24	7.6 (1.71)	25	153.6 (49.94)
1996	63	4.0 (0.72)	32	95.5 (21.58)	36	7.3 (0.80)	22	93.3 (29.59)
1997	60	3.4 (0.48)	36	162.0 (21.08)	33	7.9 (1.39)	27	41.0 (14.64)
1998	72	2.8 (0.29)	36	176.6 (35.75)	42	7.6 (1.42)	21	44.2 (19.34)
1999	60	3.3 (0.32)	36	37.2 (13.23)	42	4.5 (0.75)	21	37.4 (11.83)
2000	58	2.4 (0.27)	33	91.9 (19.00)	37	5.8 (0.78)	21	175.2 (41.26)
2001	22	2.5 (0.35)	33	45.6 (10.96)	28	9.0 (2.12)	14	28.6 (11.95)
2002	55	0.7 (0.11)	22	97.7 (37.54)	35	1.0 (0.19)	14	15.2 (5.58)

Sample size *(n)* is the number of visits × number of sites sampled during the period of nymphal or larval activity.

Larval activity declined by about one-third in 1995, 2 yr after the major reduction in deer numbers in 1993, but remained elevated (100–200/100 m^2) for 4 yr. When deer density was further reduced in 1997 by one-half, larval numbers dropped 2 yr later in 1999 and 2001 to <50 ticks/100 m^2. The low counts in 1999 and 2001 were significantly (at $P = 0.05$) different from 1993 to 1994, 1997 to 1998, and for 1999, from 2001. There was a significant correlation between deer density and declining nymphal abundance ($r_s = 0.867, P \leq 0.0001$) and larval numbers ($r_s = 0.673, P = 0.0290$) over the course of the study.

Because of the more intermittent nature of the deer reductions at Bluff Point, there was no direct correlation between deer densities and the abundance of nymphal *I. scapularis* ($r_s = 0.394, P = 0.243$), and nymphal tick abundance differed significantly from that observed from 1993 to 2001 only in 2002 ($H = 63.945$, df = 9, $P \leq 0.001$) (Table 1). By contrast, mean annual larval abundance was significantly correlated with the previous fall season's deer density ($r_s = 0.697$, $P = 0.0217$), and differences between years also were highly significant ($H = 42.864$, df = 9, $P \leq 0.001$). The abundance of *I. scapularis* larvae had dropped by over one-half in the year after the controlled hunt (41.0/100 m^2) and for 2 yr thereafter (Table 1). Because the Bluff Point hunt occurred in January 1996 after the fall adult tick season, but before the spring tick season, the full impact of the deer reduction on larval densities was probably not seen until the summer of 1998. Nymphs reached their lowest point the following year, declining from 8.8 to 12.0–4.5/100 m^2 by 1999, but increasing to 9.0/100 m^2 by 2001. The abundance of *I. scapularis* nymphs increased in 2001, after the substantial increase in the larval tick population the previous year. Larval tick densities rebounded to a high of 175.2/100 m^2 in 2000 as deer numbers increased in 1998 and 1999. This surge in the larval population was significantly different from that 2 yr before 2000 and 2 yr after 2000. Similarly, the full impact of deer reductions in January 2000 after the fall peak adult tick season would be expected 2 yr after the removal of the deer. Larval numbers were reduced significantly in 2001, and nymphal numbers reached their lowest point in 2002, with only one nymph per 100 m^2. Larval counts in 1998–99 and 2001–02 were significantly different from the first year ticks were collected, 1993 ($P = 0.05$).

Tick abundance on white-footed mice at Bridgeport also declined notably from that observed in 1993 to the latter half of the project period. Over 2,000 larvae and 64 nymphs were recovered from these animals in 1993, with a mean relative density of 40.3 larvae per mouse (Table 2). Relative density is the mean number of a parasite species recorded across all host individuals, infested and uninfested (Margolis et al. 1982). Many mice ($n = 9$) were infested with >100 larvae, with a maximum of 210 from one individual. By contrast, only one mouse had over 100 larvae ($n = 172$) during the 1997–2002 trapping period, and the mean relative density was significantly lower in 2000 ($H = 43.749$, df = 4, $P \leq 0.001$). The number of ticks on the *P. leucopus* during the 1997–2002 intervals closely matched host-seeking population during the same period.

Table 2. Number of mice captured and recaptured and the larvae and nymphs of *I. scapularis* recovered from those mice at Bridgeport May through August 1993, 1997–2002

Year	No. mouse captures	No. individual mice captured	Total no. nymphs	Total no. larvae	Mean (SEM)/mouse[a]	
					Nymphs	Larvae
1993	53	21	64	2,136	1.2 (0.3)	40.3 (6.8)
1997	42	20	33	683	0.8 (0.3)	17.2 (3.2)
1998	49	26	35	552	0.7 (0.2)	13.9 (3.9)
1999	66	26	83	378	1.3 (0.3)	6.4 (0.7)
2000	12	8	1	110	0.1 (0.1)	9.2 (5.7)
2001	-	-	-	-	-	-
2002	5	5	0	40	0.0 (0.0)	8.0 (5.1)

[a] Mean number of ticks on mice captured (= relative intensity), unadjusted for seasonal effect.

Parasitism by *I. hookeri*. The prevalence of tick parasitism by *I. hookeri* declined from 30 to 25% to <1.0%, and was highly correlated with previous year's deer density in both Bridgeport ($r_s = 0.933, P \leq 0.0001$) and Bluff Point ($r_s = 0.867, P \leq 0.0001$). Parasitoid emergence from nymphal *I. scapularis* at Bridgeport declined from 16.8 to 2.2% once deer densities dropped below 20/km^2, and below 1.0% when deer densities were reduced further to 13.1 animals per km^2 in 1999 (Table 3). Only 1 of 110 laboratory-reared engorged nymphs from Bridgeport in 1999 produced *I. hookeri*. The following year, no wasps emerged from 103 laboratory-reared Bridgeport nymphs collected in May and June, although adult *I. hookeri*, which failed to emerge, were detected in one dissected nymph. Rank order correlations over the 10 yr were significant between wasp parasitism rates and declining larval tick abundance ($r_s = 0.667, P = 0.0428$) and nymphal tick abundance ($r_s = 0.917, P \leq 0.0001$). There was a significant difference in the proportion of the nymphs parasitized by *I. hookeri* in 1993 and 1994 as compared with 1999–2000 and 2002 ($z = 7.447, P \leq 0.001$). No sample was available in 2001 and no wasps were re-

Table 3. Number of nymphs reared in the laboratory and percentage of nymphal ticks producing adult *I. hookeri* from collections at Bridgeport and Bluff Point from 1993 through 2002 (no data available for 2001)

Year	No. nymphs reared and no. nymphs parasitized (average %)			
	n	Bridgeport	*n*	Bluff Point
1993	146	37 (25.3)	38	11 (28.9)
1994	63	13 (20.6)	51	11 (21.6)
1995	137	20 (14.6)	40	40 (32.5)
1996	110	19 (17.3)	95	26 (27.4)
1997	94	16 (16.8)	60	11 (18.0)
1998	138	3 (2.2)	149	1 (0.7)
1999	110	1 (0.90)	96	15 (15.6)
2000	103	1 (0.98)[a]	100	11 (11.0)
2001	-	-	-	-
2002	25	0 (0.0)	14	1 (7.1)

[a] One engorged nymphal tick was found parasitized upon dissection, but adult wasps had failed to emerge. This gives a parasitism rate of <1.0%.

covered in 2002, although the sample size was small and rates below ≈5% may not be detected.

By contrast, the wasp is still present in the nymphs at Bluff Point, although the proportion of parasitized nymphs in 1999–2000 and 2002 was significantly lower than in 1993–1994 ($z = 2.363$, $P = 0.018$). Corresponding with the lowest deer density at Bluff Point in 1997 (13.5/km^2), the rate of parasitism the following year had dropped notably from 18% to only 0.7%. Mean parasitism rates were back up to 15.6% (of 96) and 11.0% (of 100) in 1999 and 2000, respectively, after the period of increased deer density. However, the parasitism rate had dropped to 7.1% (1 of 14) in 2002, after a decrease in deer density in 2000 and 2001 (Table 3). In 2000, 83 wasps emerged from 11 engorged nymphs from Bluff Point for a mean (SEM) of 7.5 (1.16) wasps per tick (range, 3–16).

Discussion

White-tailed deer density at the insular sites in Bridgeport and Groton was extremely high at the beginning of this study and well in excess of an estimated habitat carrying capacity of ≈8 deer per km^2. At Bluff Point, target of 25 animals was achieved in winter of 2000, 2001, and 2002, although the following fall populations upon which emerging adult *I. scapularis* feed were somewhat greater with the addition of newyear fawns. Animal assessments in 2002 found that the fat indices were higher than any previous years, herd health had improved, and damage to the vegetation had been greatly reduced (DEP 2002). Along with high deer densities, overabundant populations of *I. scapularis* were present at both sites and a relatively high parasitism rate in the ticks with the parasitoid *I. hookeri* was documented. Deer were reduced 7-fold in Bridgeport between 1992 and 1999. The removal of deer, either incrementally or through controlled hunts, has corresponded with a significant decline in the abundance of the blacklegged tick and presence of *I. hookeri* at both the Lake Success Business Park in Bridgeport and Bluff Point Coastal Preserve in Groton.

The reduction of *I. scapularis* after removal of deer from Bridgeport and Bluff Point supports observations from earlier studies (Wilson et al. 1988, Deblinger et al. 1993). The incremental removal of deer from a 567-ha coastal site in Ipswich, Massachusetts, over a period of 7 yr from ≈350 to ≈60 animals corresponded with a significant decline in the number of nymphal and larval ticks on white-footed mice (Deblinger et al. 1993), although the difference was less pronounced than the 4- to 6-fold decline in larvae observed on mice in Bridgeport in this study. Preintervention mean larval density in the Ipswich study was 20.8 larvae/mouse (versus 40.3 in Bridgeport), dropping by one-half to 10.3 after the deer reductions (versus a low of 6.4 in Bridgeport in 1999), but there was no detectable impact on *I. scapularis* on mice until 3–4 yr after the intervention. Mice were not trapped in Bridgeport during the interval from 1994 to 1996, so an appraisal of tick burdens on *P. leucopus* immediately after the intervention in Bridgeport could not be done. However, the abundance of host-seeking immature ticks appeared to respond within 2 yr to the initial 50% reduction in deer at Bridgeport. In the case of Bluff Point, an interim increase in deer density in 1998–1999 appears to have resulted in larval and nymphal numbers quickly increasing to preintervention levels in 2000 and 2001, respectively, after a 2-yr relaxation in the deer management program (possibly caused by a high residual adult tick population), but higher larval densities were not maintained as deer numbers were again reduced.

Unlike the nymphs and larvae at Bluff Point, larval ticks did increase dramatically in Bridgeport for 2 yr even as deer numbers continued to decline, before dropping to a significantly lower level. One possible cause is an increased tick infestation level on deer as deer densities decline. The intensity of infestation on deer by adult *I. scapularis* was not monitored at either Bridgeport or Bluff Point, but the female tick population on deer increased 4- to 6-fold as deer were reduced by 4- to 5-fold over the same period in the Ipswich study (Deblinger et al. 1993). Although quantitative comparisons were not made, annual collections of host-seeking adult ticks by flagging the vegetation at the Bridgeport site indicated that adult tick populations were high in 1999, with collection efficiency dropping from ≈300/h/individual or better to ≈150/h to ≈100/h or less in 2002, with a markedly fewer habitat foci with a concentration of adult ticks. A similar pattern was noted on Great Island with adult blacklegged ticks remaining abundant at least 3 yr after the deer were removed. Therefore, the number of adult ticks on the remaining deer in our study probably increased and was reflected in the prevalence of host-seeking larval ticks and moderate densities on the mice in 1997 and 1998. At Great Island, an insular peninsula off Cape Cod, Massachusetts, the virtual elimination of deer produced a significant reduction in larval tick densities on *P. leucopus* after 1 yr and a dramatic reduction 3 yr later (Wilson et al. 1988). Like the Bridgeport questing nymphal population, there was a generally decreasing pattern of nymphal abundance on mice over the 6-yr period of the study on Great Island. The exclusion of deer has been shown to dramatically increase the number of sampled adult ticks in the near term (Ginsberg and Zhioua 1999), although adult tick abundance will eventually decline when deer are removed from an area. When deer populations are excluded or reduced, more adult ticks may be available for flagging samples as these ticks are no longer picked up by deer and removed from the system, which may account, in part, for the high number of *I. scapularis* adults collected in Bridgeport in the late 1990s. Ginsberg and Zhioua (1999) found that a large proportion (>50%) of the questing adult tick population can successfully find a host when deer are overabundant.

The impact of moderate deer removal can be overlaid with normal interannual population cycles. Tick populations fluctuate annually, and samples may be impacted by other factors such as weather and alternative food sources that influence tick and host ac-

tivity. There was an increase in nymphal tick densities at both Bridgeport and Bluff Point in 1994, corresponding to a regional increase in tick abundance in Connecticut and New York that year (Ostfeld et al. 1996, Stafford et al. 1998). Part of the decrease in tick activity in 1995 and 1999 may be attributed to a drought in New England and its impact on questing activity and sampling success. For example, during the drought in 1999, a total of 1,940 larvae was collected in Bridgeport on 21 July, followed by only 15 larvae on 2 August, then 1,393 larvae on 16 August. The number of larvae recovered by dragging the vegetation dropped and rebounded in apparent response of emerging larvae to hot, dry conditions, which were relieved by some rain before the 16 August sample. Survival and consequently activity of immature *I. scapularis* are sensitive to humidity (Stafford 1994). Consequently, tick populations may not directly correspond to deer density as expected, although they ultimately fluctuate at a lower mean level after the deer reductions. Aside from deer density, the factors impacting tick populations are not well understood. Nevertheless, tick numbers at both sites were responsive to changes in deer density.

By contrast, tick parasitoid emergence rates were more highly correlated with deer densities than tick densities. This study suggests that while the successful parasitism of *I. scapularis* by *I. hookeri* is related to the density of the tick's host, white-tailed deer may have an even greater influence on *I. hookeri* parasitism. The wasp requires a certain threshold tick density for successful parasitism, an abundance of tick animal hosts to locate the ticks, and/or appropriate climatic conditions for survival. Deer density and tick abundance at Bridgeport dropped to or below that in mainland shoreline communities (2.68 and 3.42 in 1999, and 4.44 and 6.38/100 m^2 in 2000 in Old Lyme and Old Saybrook, CT, respectively; K.C.S., unpublished data). Deer density was estimated by aerial survey in a 5.2-km^2 area of Old Lyme in 1999 to be 15/km^2 (A.J.D. and K.C.S., unpublished data), a density comparable to that in Bridgeport in 1998 and 1999 and Bluff Point in 1997. Therefore, the threshold necessary for *I. hookeri* to successfully parasitize *I. scapularis* may be somewhere around 13–20 deer per km^2. This may account for the failure to recover *I. hookeri* on the mainland. However, there does not appear to be any change in the mean number of adult wasps emerging from a nymphal tick as the number of wasps produced per tick in Bluff Point in 2000 was similar to that obtained in 1993 and 1994 (Stafford et al. 1996).

Parasitoid reproductive success depends on the ability of a female wasp to find hosts. Little is known on how *I. hookeri* finds a tick host. Female *I. hookeri* deposit their eggs in engorged larvae or unfed nymphal ticks, although it is not clear whether *I. hookeri* naturally searches for and parasitizes ticks on or off the tick host (Fig. 3a) (Wood 1911, Hu et al. 1998). Parasitism rates in nymphs from *P. leucopus* and meadow voles, *Microtus pennsylvanicus*, are 4- to 5-fold lower than in host-seeking nymphs or in ticks removed from white-tailed deer (Stafford et al. 1996, Hu and Hyland 1997). In our earlier report on wasp parasitism at Bridgeport and Bluff Point, the rate in deer-derived nymphs (23.1% of 39) was substantially higher than in mouse-derived nymphs (6.7% of 30) (Stafford et al. 1996). No tick larvae from rodent hosts in Connecticut or Rhode Island were found parasitized by wasps, and only 1.2% (of 321) engorged *I. scapularis* larvae from *P. leucopus* on Nonamesset Island, Massachusetts (near Cape Cod), contained *I. hookeri* eggs (Lyon et al. 1998). Parasitoids usually restrict their search to microhabitats that have a particular common characteristic, and many use chemical cues that increase their chance of locating a host. For example, materials that contain or had contained house fly larvae are most attractive to the parasitoid *Spalangia endius*, increasing the chance of locating host fly puparia (Stafford 1984). *I. hookeri* apparently uses, at least in part, deer or deer bedding areas, to find its host, as deer densities in this study were strongly related to wasp parasitism success.

Embryonic development begins after nymphal attachment to a host and wasp larvae consumes the entire tissue and host blood content of the tick, which takes on a characteristic orange appearance (Fig. 3b) (Wood 1911, Hu 1990). According to Davis (1986), the ingestion of vertebrate blood by these wasps is unique among the Chalcidoidea. Adult parasitoids emerge from a single hole at the posterior end of the mummified nymph in ≈30–57 d after tick detachment from the host (Fig. 3c). Female wasps would emerge after the midsummer during the period of larval *I. scapularis* activity, attack host-feeding or fed larvae or remaining late season nymphs. It is likely that the wasp overwinters as nonembryonated eggs inside the nymph. The prevalence of wasp parasitism is highest in host-seeking nymphs in May, dropping in June as nymphal tick activity increases, and continuing to decline through August (Hu and Hyland 1997). Emergence of wasps from larval or adult ticks has not been reported, and only the nymphal stage of the tick is killed (Hu et al. 1998). There is probably only one generation per year for *I. hookeri* in *I. scapularis* in the northeastern United States. As parasitoids attack a targeted sample of available hosts, they can have a qualitative influence on the host population, or in this case the prevalence of a pathogen within the host. An increase in the prevalence of *B. burgdorferi* in the tick at these sites (K.C.S., unpublished data) may also be influenced indirectly by the decline in tick parasitism by *I. hookeri*. Fewer uninfected ticks from deer may be removed from the system by the parasitoid, increasing the prevalence of infection.

Parasitism rate appears to be influenced by a seasonal effect based on time of collection. The highest prevalence of *I. hookeri* in *I. scapularis* occurs in May and declines from June through August, which appears to be from increased mortality of parasitized ticks (Hu and Hyland 1997, Lyon et al. 1998). A series of samples may not represent the true generational rate of nymphal parasitism, and some differences between years could be influenced, in part, by when the majority of nymphs reared for parasitoids were col-

A

B

C

Fig. 3. *I. hookeri* lifecycle. (A) Female parasitoid, *I. hookeri* (right) with nymph of *I. scapularis* (left). Eggs are laid in engorged larval or unfed nymphal ticks; eggs are dormant until nymphal engorgement with a host bloodmeal. (B) Engorged *I. scapularis* nymphs with unparasitized nymph (right) and nymph parasitized by *I. hookeri* (left), showing orange color as parasitoid larvae consume the bloodmeal and internal contents of the tick. (C) After pupation, adult *I. hookeri* emerge from a hole in the posterior end of the mummified nymphal tick.

lected. In this study, most of the ticks reared for parasitoid emergence were collected during the month of June, although some ticks collected in May and July also were used. One-half of the parasitoids were recovered from June-collected ticks at Bridgeport (50.0%) and Bluff Point (47.4%). Our data may slightly underestimate true parasitism levels because they are based largely on June-collected ticks and adult wasp emergence (rather than the presence of eggs in the hemocoel). Nevertheless, prevalence of the wasp was obtained from consistent timing of tick collecting and rearing of the wasps each year. Therefore, the seasonality of tick collection on the estimate of *I. hookeri* parasitism was minimal and most likely did not impact the trend observed during the 10-yr study. The initial observed parasitism rates were consistent with that obtained from parasitoid egg counts in the studies from the northeastern United States cited previously.

Deer and tick densities would have to be considered in the feasibility of controlling ticks with parasitoid augmentation. The feasibility of controlling *I. scapularis* by rearing and releasing the parasitoid has been explored (Knipling and Steelman 2000), as augmentation is needed for most parasitoids to be used in pest host ecosystems (Knipling 1992). The authors note that theoretically 95% parasitism of *I. scapularis* could be achieved with a parasitoid/tick release ratio of 3:10, 12 times the number estimated to cause 25% parasitism. Each female parasitoid was estimated to normally parasitize 10 tick larvae. These estimates were based on coexistence of a stable natural population of the wasp and tick in areas in which both the tick and wasp were overabundant. As demonstrated by the low to extremely low parasitism rates following the deer and tick reductions in this study, these estimates may not hold for conditions typical of most Lyme endemic areas. It is not known whether large numbers of released *I. hookeri* could successfully locate and parasitize *I. scapularis* at free-ranging deer densities $\leq$20 per km^2. It is evident that the existing wasp population was unable to maintain high attack rates at lower host densities.

Only one recent published study has evaluated the release of *I. hookeri* for tick control. The release of 150,000 *I. hookeri* over a period of 1 yr in a 4-ha field of 10 cattle in Africa rapidly reduced nymphs of the tick *Amblyomma variegatum* from 44 to 2 ticks per animal (Mwangi et al. 1997). No parasitoids were present before the release. During the release, 51% of engorged ticks had parasitoids, while only 9% were found parasitized during the 3 mo after parasitoid augmentation ceased. Nevertheless, nymphal tick abundance remained at a low level for over 1 yr after the parasitoid releases. The adult tick population declined $\approx$6–7 mo after *I. hookeri* was released. With only a 51% parasitism rate in the nymphal ticks and 95% suppression in the tick population, it has been noted that most engorged larvae and unfed nymphs must have been parasitized off host (Knipling and Steelman 2000).

In Connecticut, the deer population has risen from an estimated 49,472 animals in 1993 to $\approx$76,000 in 1999–2000 (Gregonis 2000), with the highest densities in southwestern portion of the state, where deer management options are limited. The rising deer population has led to increased deer vehicle collisions and excessive deer damage to forests, agricultural crops, nursery stock, and landscape plantings (Warren 1997), but an increasing impetus for managing urban and suburban populations of deer may be the rising incidence of Lyme disease. The exclusion or reduction of deer has been shown to reduce tick abundance (Wilson et al. 1988, Daniels et al. 1993, Deblinger et al. 1993, Stafford 1993). In this study, a significant decline in tick density corresponded with reductions in deer density. However, because both tick and deer densities appear comparable to that typical of many Connecticut shoreline communities, ticks remain abundant at both Bridgeport and Bluff Point. The level at which reduced deer density impacts ticks sufficiently to virtually eliminate the risk of Lyme disease or break the epizootic cycle has not been firmly established. Based on long-term deer reductions at Great Island, Massachusetts, one estimate of the density of deer necessary to reduce the transmission of Lyme disease was 3.1 deer per km^2 (Telford 1993). With the exception of some islands and peninsulas, it would be difficult to attain and maintain deer densities that low. Conversely, little attention has been given to reversing the curve to examine how tick abundance and risk of Lyme disease would increase in the absence of a management program for deer. Both the Bridgeport and Bluff Point sites may illustrate what could happen if the curves were reversed, showing a steadily or rapidly increasing deer population. This study also indicates that the use of the parasitoid *I. hookeri* as a biological control agent in most Lyme disease endemic areas may not be feasible until questions concerning the ability of an augmented wasp population to locate tick hosts are answered. Assuming deer and tick numbers are maintained at or below the natural parasitoid threshold, the mass release of *I. hookeri* at either Bridgeport or Bluff Point could potentially address this question.

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References Cited

Alfeev, N. I. 1946. The utilization of *Hunterellus hookeri* Howard for the control of the ticks, *Ixodes ricinus* L. and *Ixodes persulcatus* P. Sch. with reference to peculiarities

of their metamorphosis under conditions of the Province of Lenningrad. Rev. Appl. Entomol. B. 34: 108–109.

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

[CDC] Centers for Disease Control and Prevention. 2002. Lyme disease: United States, 2000. Morbid. Mortal. Wkly. Rep. 51: 29–31.

Cobb, S. 1942. Tick parasites on Cape Cod. Science 95: 503.

Cooley, R. A., and G. M. Kohls. 1934. A summary of tick parasites. 5th Pacific Sci. Cong. Proc. 5: 3375–3381.

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.

Davis, A. J. 1986. Bibilography of the Ixodiphagini (Hymenoptera, Chalcidoidea, Encyrtidae), parasites of ticks (Acari, Ixodidae), with notes on their biology. Tijdschrift voor Entomologie 129: 181–190.

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.

DeNicola, A. J., D. J. Kesler, and R. K. Swihart. 1997. Remotely delivered prostaglandin F2a implants terminate pregnancy in white-tailed deer. Wildl. Soc. Bull. 25: 527–531.

[DEP] Department Environmental Protection. 2002. 2002 Bluff Point deer management. Connecticut Wildl. 22: 18.

Fox, E., K. Shotton, and C. Ulrich. 1995. SigmaStat statistical software user's manual. Jandel Corporation, San Rafael, CA.

Ginsberg, H. S., and E. Zhioua. 1999. Influence of deer abundance on the abundance of questing adult *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 36: 379–381.

Gregonis, M. 2000. Aerial deer survey results indicate population is increasing. Connecticut Wildl. 20: 12–13.

Hu, R. 1990. Identification of the wasp parasitoid of the deer tick, *Ixodes dammini*, in Rhode Island and its implication in the control of Lyme disease. University of Rhode Island, Kingston.

Hu, R., and K. E. Hyland. 1997. Prevalence and seasonal activity of the wasp parasitoid, *Ixodiphagus hookeri* (Hymenoptera: Encyrtidae) in its tick host, *Ixodes scapularis* (Acari: Ixodidae). Syst. Appl. Acarol. 2: 95–100.

Hu, R., K. E. Hyland, and T. N. Mather. 1993. Occurrence and distribution in Rhode Island of *Hunterellus hookeri* (Hymenoptera: Encyrtidae), a wasp parasitoid of *Ixodes dammini.* J. Med. Entomol. 30: 277–280.

Hu, R., K. E. Hyland, and J. H. Oliver. 1998. A review on the use of *Ixodiphagus* wasps (Hymenoptera: Encyrtidae) as natural enemies for the control of ticks (Acari: Ixodidae). Syst. Appl. Acarol. 3: 19–28.

Kilpatrick, H. J. 2001. Assessing deer management at Bluff Point, 2001. Connecticut Wildl. 21: 12.

Kilpatrick, H. J., S. M. Spohr, and G. G. Chasko. 1997. A controlled deer hunt on a state-owned coastal reserve in Connecticut: controversies, strategies, and results. Wildl. Soc. Bull. 25: 451–456.

Knipling, E. F. 1992. Principles of insect parasitism analyzed from new perspectives: practical implications for regulating insect populations by biological means. US Dep. Agric., Agric. Res. Serv. Handb. No. 693.

Knipling, E. F., and C. D. Steelman. 2000. Feasibility of controlling *Ixodes scapularis* ticks (Acari: Ixodidae), the vector of Lyme disease, by parasitoid augmentation. J. Med. Entomol. 37: 645–652.

Larrouse, F., A. G. King, and S. B. Wolbach. 1928. The overwintering in Massachusetts of *Ixodiphagus caucurteri.* Science 67: 351–353.

Lyon, S. M., R. V. Driesche, and J. D. Edman. 1998. Ecology of *Hunterellus hookeri* (Hymenoptera: Encyrtidae) and evaluation of its impact on *Ixodes scapularis* (Acari: Ixodidae) on Nonamesset Island in Massachusetts. Environ. Entomol. 27: 463–468.

Magnarelli, L. A., A. DeNicola, K. C. Stafford III, and J. F. Anderson. 1995. *Borrelia burgdorferi* in an urban environment: white-tailed deer with infected ticks and antibodies. J. Clin. Microbiol. 33: 541–544.

Margolis, L., G. W. Esch, J. C. Holmes, A. M. Kuris, and G. A. Schad. 1982. The use of ecological terms in parasitology. J. Parasitol. 68: 131–133.

Mather, T. N., J. Piesman, and A. Spielman. 1987. Absence of spirochetes (*Borrelia burgdorferi*) and piroplasms (*Babesia microti*) in deer ticks (*Ixodes dammini*) parasitized by chalcid wasps (*Hunterellus hookeri*). Med. Vet. Entomol. 1: 3–8.

Mather, T. N., M. C. Nickolson, E. F. Donnelly, and B. T. Matyas. 1996. Entomologic index for human risk of Lyme disease. Am. J. Epidemiol. 144: 1066–1069.

Mwangi, E. N., S. M. Hassan, G. P. Kaaya, and S. Essuman. 1997. The impact of *Ixodiphagus hookeri*, a tick parasitoid, on *Amblyomma variegatum* (Acari: Ixodidae) in a field trial in Kenya. Exp. Appl. Acarol. 21: 117–126.

Ostfeld, R. S., K. R. Hazler, and O. M. Cepeda. 1996. Temporal and spatial dynamics of *Ixodes scapularis* (Acari: Ixodidae) in a rural landscape. J. Med. Entomol. 33: 90–95.

Pound, J. M., J. A. Miller, and J. E. George. 2000. Efficacy of amitraz applied to white-tailed deer by the '4-poster' topical treatment device in controlling free-living lone star ticks (Acari: Ixodidae). J. Med. Entomol. 37: 878–884.

Smith, C. N., and M. M. Cole. 1943. Studies of parasites of the American dog tick. J. Econ. Entomol. 36: 569–572.

Stafford, K. C., III. 1984. Olfactory studies of host seeking by the parasitoid *Splangia endius* Walker (Hymenoptera: Pteromalidae). Environ. Entomol. 13: 228–231.

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. 1994. Survival of immature *Ixodes scapularis* (Acari: Ixodidae) at different relative humidities. J. Med. Entomol. 31: 310–314.

Stafford, K. C., III. 2002. Environmental management for Lyme borreliosis, p. 368. *In* J. Gray (ed.), Lyme borreliosis: biology and control. CABI Publishing, Oxon, United Kingdom.

Stafford, K. C., III, A. J. DeNicola, and L. A. Magnarelli. 1996. Presence of *Ixodiphagus hookeri* (Hymemoptera: Encyrtidae) in two Connecticut populations of *Ixodes scapularis* (Acari: Ixodidae). J. Med. Entomol. 33: 183–188.

Stafford, K. C., III, M. L. Cartter, L. A. Magnarelli, S. Ertel, and P. A. Mshar. 1998. Temporal correlations between tick abundance and prevalence of ticks infested with *Borrelia burgdorferi* and increasing incidence of Lyme disease. J. Clin. Microbiol. 36: 1240–1244.

Stafford, K. C., III, R. F. Massung, L. A. Magnarelli, J. W. IJdo, and J. F. Anderson. 1999. Infection with agents of human granulocytic ehrlichiosis, Lyme disease, and babesiosis in wild white-footed mice (*Peromyscus leucopus*) in Connecticut. J. Clin. Microbiol. 37: 2887–2892.

Telford, S. T., III. 1993. Forum: management of Lyme disease, pp. 164–167. *In* H. S. Ginsberg (ed.), Ecology and environmental management of Lyme disease. Rutgers University Press, New Brunswick, NJ.

Warren, R. J. (ed.). 1997. Deer overabundance. Wildl. Soc. Bull. Special Issue. 25(2): 1–595.

Wilson, M. L., S. R. Telford III, J. Piesman, and A. Spielman. 1988. Reduced abundance of immature *Ixodes dammini* (Acari: Ixodidae) following elimination of deer. J. Med. Entomol. 25: 224–228.

Wilson, M. L., A. M. Ducey, T. S. Litwin, T. A. Gavin, and A. Spielman. 1990. Microgeographic distribution of immature *Ixodes dammini* ticks correlated with that of deer. Med. Vet. Entomol. 4: 151–159.

Wood, H. P. 1911. Notes on the life history of the tick parasite, *Hunterellus hookeri* Howard J. Econ. Entomol. 4: 425–431.

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