Passive Surveillance in Maine, an Area Emergent for Tick-Borne Diseases

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ABSTRACT In 1989, a free-of-charge, statewide tick identification program was initiated in Maine, 1 yr after the first *Ixodes scapularis* Say (=*I. dammini* Spielman, Clifford, Piesman & Corwin) ticks were reported in the state. This article summarizes data from 18 continuous years of tick submissions during which >24,000 ticks of 14 species were identified. Data provided include tick stage, degree of engorgement, seasonal abundance, geographical location, host, and age of the person from whom the tick was removed. Maps depict the distributions of the three major species submitted. *I. scapularis* emerged first along the coast, and then it advanced inland up major river valleys, *Dermacentor variabilis* Say slowly expanded centrifugally from where it was initially reported in southwestern Maine, and the distribution of long-established *Ixodes cookei* Packard remained unchanged. Submissions of nymphal *I. scapularis* closely correlated with reported Lyme diseases cases at the county level. Annual fluctuations of nymphal submissions in Maine correlated with those of Lyme disease cases for New England, supporting the possibility of a regional influence on tick abundance. More ticks were removed from people ≤14 and ≥30 yr of age, and their degree of engorgement was greatest in people ≤20 yr of age and progressively increased in people ≥30 yr of age. This study demonstrates the usefulness and potential of tick identification programs.

KEY WORDS *Ixodes scapularis*, *Ixodes cookei*, *Dermacentor variabilis*, lyme disease, passive tick surveillance

In the late 1970s, Steere et al. (1978) provided evidence that an inflammatory arthritis reported previously in Lyme, CT, was transmitted by a tick vector and that cases occurred within the distribution of the blacklegged tick, *Ixodes scapularis* Say (Steere and Malawista 1979). Since that time, the range of this tick has expanded into northern New England, and reported Lyme disease cases in this region have increased, rapidly so in the last decade. In addition, two more diseases carried by *I. scapularis* have emerged in Maine in recent years: human granulocytic anaplasmosis and babesiosis. Furthermore, five cases of another tick-born disease, Powassan encephalitis, also have been reported in Maine and Vermont (CDC 2001, 2006b). This last disease is transmitted primarily by *I. cookei*, but also by *Ixodes marxi* Banks (Artsob 1988), and potentially by *I. scapularis* (Telford et al. 1997). Because awareness of risk is an essential element of disease prevention, maps indicating current tick distributions and the inherent threat from tick-borne diseases are needed.

At a statewide scale, data on tick distribution and prevalence may be obtained by systematic methods involving consistent sampling and standardized collection protocols, such as multisite flagging efforts (Bunnell et al. 2003, Diuk-Wasser et al. 2006) or surveys of ticks removed from hosts (Wallis et al. 1978, Daniels et al. 1993, Mather et al. 1996, Rand et al. 2003). These methods, however, require large outlays of personnel, time, and funds, and collections may be hampered by unfavorable weather events. Perhaps more pertinent from a public health standpoint are maps showing where Lyme disease is being transmitted, which may be derived from canine serosurveys (Lindenmeyer et al. 1991, Rand et al. 1991, Guerra et al. 2001, Stone et al. 2005). This methodology remains valuable, but is increasingly compromised where large portions of the dog population have been vaccinated or treated with topical acaricides.

More economically, information directly related to exposure to vector ticks may be obtained by offering free tick identification to the public. Although maps developed from these passively derived data are limited to the distribution of the tick submitters themselves, within those bounds their value has been dem-

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onstrated in mapping the distribution and diversity of tick species (Walker et al. 1988, Smith et al. 1992), relating tick prevalence to the incidence of Lyme disease (Johnson et al. 2004), and, by spatial statistics, correlating satellite-derived vegetative indices to tick prevalence (Ogden et al. 2006). In addition, information about population segments at risk and the sources of ticks encountered can be gained from questionnaires completed by submitters. Moreover, with several years of data, the timing and size of the seasonal peaks of each life stage can be described, providing patterns which, when analyzed with relevant biotic and abiotic data, may lead to regional predictive models.

Thus, in the late 1980s, after the first reports of *I. scapularis* in Maine (Anderson et al. 1987, Ginsberg and Ewing 1988) and a detailed report of an outbreak of Lyme disease in Ipswich, MA, 48 km south of the Maine border (Lastavica et al. 1989), our laboratory established a statewide tick identification service open to the general public (Smith et al. 1992). With 18 yr of data (1989–2006), the principal objectives of this article were to describe 1) the array of tick species and their hosts in Maine, 2) the phenology of the three major human-biting ticks in Maine, 3) the spatial and temporal trends and fluctuations in *I. scapularis* as they relate to Lyme disease cases reported in Maine and New England, and 4) the age distribution of tick attachment and degree of engorgement.

Materials and Methods

Study Area. Maine, the most northeastern of the United States, encompasses 86,542 km^2 and more than three degrees of latitude (43.1–47.3° N, 67.0–71.0° W). Within its southern half, abundant deciduous vegetation, a moist climate, and an ample population of white-tailed deer (*Odocoelius virginianus* Zimmerman) provide a favorable environment for *I. scapularis* and other tick species. With the exception of agricultural land along its eastern border with Canada, the northern half of the state is primarily commercial forests of spruce and fir (*Picea* and *Abies* spp.) being gradually supplanted by hardwood stands, principally of maple and oak (*Acer* and *Quercus* spp.). A series of higher elevations (600–1,600 m) occupies the northwestern half of the state. The majority of its human population of 1.3 million resides in its southern half (Fig. 1), generally within an 80-km-wide coastal plain with elevations <150 m.

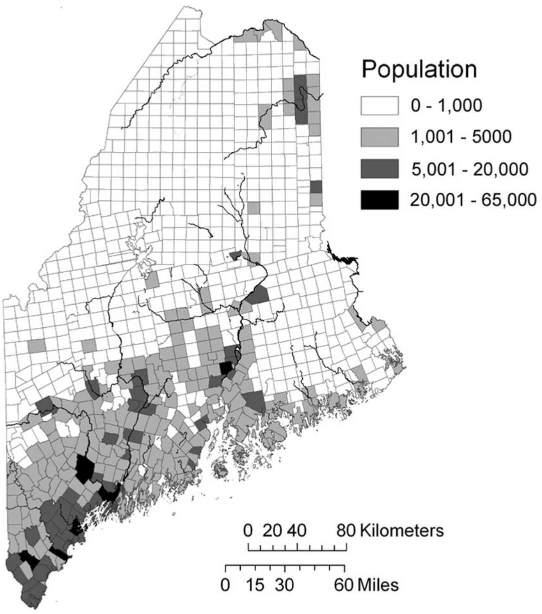

Fig. 1. Populations ranges of Maine towns, 2000 (U.S. Census Bureau 2005).

Tick Submission Program. Initially (1989), we announced the identification service in lectures to the general public, in the media, in public health and veterinary newsletters, and in communications with hospitals, physicians, game biologists and others (e.g., surveyors, linemen). In a few cases, to gather information from the sparsely populated areas of Maine, we contacted specific groups, such as summer camp and hunting camp operators, providing vials and postage prepaid mailing labels to facilitate cooperation. With these exceptions, ticks have been passively submitted. Since the first of a series of canine seroprevalence surveys in 1989 (Rand et al. 1991), veterinary clinics have been important contributors. In addition, an entomologist for the Maine Forest Service (RD), who had been identifying ticks submitted by the general public, shared his data with us through 2002. Together, our two laboratories have been virtually the public's only resource for tick identification in Maine. Ticks from our field study sites or other organized collections are not included in the data presented here. Those submitting ticks were asked to complete a form giving their name and address, where the tick was thought to have been acquired, the date found, the attachment site, any related symptoms, and, if on a person, the age and sex.

Laboratory Analysis. For *I. scapularis*, we described four levels of engorgement, determined subjectively: unengorged, slightly engorged, moderately engorged, or very engorged, and we provided an interpretation relating the degree of engorgement to the risk of transmission. We identified ticks to species and stage following standard keys and taxonomic references (Cooley and Kohls 1945, Cooley 1946, Clifford et al. 1965, Keirans and Litwak 1989, Durden and Keirans 1996), and we submitted unusual specimens to the U.S. National Tick Collection, Institute of Arthropodology and Parasitology, Georgia Southern University, Statesboro, GA, for confirmation.

Lyme Disease Case Data. For estimates of Lyme disease transmission throughout Maine, 1989–2006, we obtained annual reported cases data from the Maine Center for Disease Control and Prevention (G.A.B., unpublished data). For estimates of Lyme disease transmission throughout New England, we obtained annual Lyme disease case data for 1989–2005

Table 1. Maine-acquired ticks, identified to species, in order of frequency, 1989–2006

Tick species	Yr																		
	1989	1990	1991	1992	1993	1994	1995	1996	1997	1998	1999	2000	2001	2002	2003	2004	2005	2006	Total
I. scapularis	120	253	344	290	294	493	597	525	495	823	871	1,305	1,039	1,146	1,314	820	851	1,316	12,896
D. variabilis	135	314	533	235	459	524	602	402	229	370	305	637	205	478	158	298	94	241	6,219
I. cookei	376	228	305	262	169	345	239	368	176	224	149	290	125	127	83	102	72	56	3,696
D. albipictus	37	38	91	61	19	78	53	107	28	45	85	16	60	2	10	11	5	7	753
H. leporispalustris	8	14	6	6	91	233	14	2	0	7	2	4	6	3	0	0	1	0	397
I. marxi	9	22	18	12	16	2	8	11	10	3	11	12	6	7	10	4	8	3	172
I. muris	10	18	9	11	4	7	23	23	6	6	16	10	7	2	2	5	1	0	160
A. americanum	3	3	6	6	9	5	9	7	2	8	12	17	8	5	1	1	1	7	110
R. sanguineus	1	5	3	4	7	19	12	7	4	4	1	5	20	6	0	1	1	0	100
I. angustus	6	0	1	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	8
I. dentatus	0	0	0	0	0	0	2	0	0	0	0	0	0	0	1	0	0	0	3
I. gregsoni	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	2	0	0	2
A. maculatum	0	0	0	0	0	0	1	0	0	1	0	0	0	0	0	0	0	0	2
I. uriae	0	0	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0	0	2
Total	705	895	1316	887	1,069	1,708	1,560	1,452	950	1,491	1,452	2,296	1,476	1,776	1,579	1,244	1,034	1,630	24,520

from the website of the Centers for Disease Control and Prevention (CDC 2006a).

Data Analysis. We summarized tick counts and Lyme disease cases to the level (town, county, or year) appropriate for specific analysis. For *I. scapularis, I. cookei,* and *D. variabilis,* we 1) summarized by week across years to examine phenology, 2) summarized attachment by age of human host, and 3) constructed maps indicating the total number of ticks submitted from each town. We also summarized engorgement by age of human host for *I. scapularis.* In addition, to demonstrate that the increasing submissions of *I. scapularis* were not due to increased public awareness, we compared the number of submissions of that tick with those of *I. cookei.* The latter tick is widespread, has been recognized in the state for over a century (Banks 1908), and cannot reliably be distinguished from *I. scapularis* macroscopically. Submissions, rather than the number of ticks submitted, were used in this comparison because numerous *I. cookei* were frequently removed from a single host. Furthermore, to demonstrate where the advance of *I. scapularis* was taking place, we divided the state geographically into towns that were 0–7.4, 7.5–32.0, and ≥32.1 km (0–4.9, 5.0–19.9, and ≥20 miles, respectively), from the coast, and then we summed the numbers of annual submissions per town of the two tick species in each sector.

Statistical Analysis. We summarized tick counts and Lyme disease cases (where applicable) to the level appropriate for the specific analysis. To analyze the temporal and spatial relationships between Lyme disease cases and *I. scapularis* ticks, we natural log-transformed the summarized data. For the time series analysis, we used the 14-yr interval 1992–2005, for which Maine case data were available. We examined trends over time on annual series through simple linear regression and, given the absence of serially autocorrelated errors in all series (all $P > 0.05$), we examined the correlation between nymph submissions and Lyme disease cases over time in the upward-trending and detrended series (Spearman correlation coefficient, ρ_s). We considered significant correlations ($P < 0.05$) to be moderate where $0.30 < \rho_s < 0.50$ and strong where $\rho > 0.50$, and we considered significant linear relationships ($P = 0.05$) in the regressions to be moderate where $0.040 < R^2 < 0.70$ and strong where $R^2 > 0.70$.

Results

Species Identified. From 1989 through 2006, 24,519 Maine-acquired ticks representing 14 species have been identified (Table 1). By far, the most commonly identified ticks have been *I. scapularis,* followed by *Dermacentor variabilis* Say and *I. cookei.* Of the remaining 11 species listed in Table 1, five (*Ixodes angustus* Neumann, *Ixodes dentatus* Marx, *Ixodes gregsoni* Lindquist, Wu & Redner, *Ixodes uriae* White, and *Amblyomma maculatum* Koch) are rarely submitted by the public. With the exception of *A. maculatum,* however, they are regularly encountered in our fieldwork and other targeted programs (Keirans and Lacombe 1998, Smith et al. 2006, Lubelczyk et al. 2007). The sources of submitted ticks are listed in Table 2. Observations for each species follow.

I. scapularis. Through the 1990s, the number of blacklegged ticks submitted for identification increased slowly at first, and then rapidly after 1997, exceeding 1,000/yr from 2000 to 2003. Although submissions declined in 2004–2005, they reached a new peak in 2006, as did the number of reported Lyme disease cases in the state (Fig. 2). A map showing the total number of *I. scapularis* submitted by town over the period 1989–2006 is included in Fig. 3. As ticks became established, the distribution of reported Lyme disease cases followed that of submitted *I. scapularis* (Fig. 4). During the first 2 yr of this study, the small numbers of these ticks that were submitted were from towns primarily within 32 km of Maine's southern and mid-coast (Smith et al. 1992). Subsequently, *I. scapularis* has intensely colonized this zone, has become established as well in inland areas along major river valleys, and it is now submitted even from Maine's northernmost Aroostook County. In contrast, submissions of macroscopically similar *I. cookei* have shown no increase over the period of the study (Fig. 5).

Submissions of adult *I. scapularis* have followed a bimodal pattern, with a sharp fall peak in mid-October followed by a secondary peak of the overwintered

Table 2. Sources of ticks submitted for identification

	I. scapularis	*D. variabilis*	*I. cookei*	*D. albitpictus*	*H. leporispalustris*	*I. marxi*	*I. muris*	*A. americanum*	*Rhipicephalus sangui neus*	*I. angustus*	*I. dentatus*	*I. gregsoni*	*A. maculatum*	*I. uriae*
Human														
Homo sapiens	6,704	3,870	1,554	347	10	141	39	95	18	0	3	0	2	2
Dog														
Canus familiaris	3,701	1,839	732	93	2	1	61	10	80	1	0	0	0	0
Cat														
Felis catus	1,898	153	719	11	21	6	51	1	2	3	0	0	0	0
Ferret														
Mustela furo	0	2	375[a]	0	0	0	0	0	0	0	0	0	0	0
Bird														
Passeriformes	3	0	0	0	234[b]	1	2	0	0	0	0	0	0	0
Fisher														
Martes pennanti	0	0	204[c]	0	0	1	0	0	0	0	0	0	0	0
Deer														
Odocoileus virginianus	34	9	2	141	0	0	0	0	0	0	0	0	0	0
Rabbit														
Silvilagus transitionalis	0	1	0	0	122[d]	0	0	0	0	0	0	0	0	0
Moose														
Alces alces	1	14	0	71	0	0	0	0	0	0	0	0	0	0
Horse														
Equus caballus	25	2	4	7	0	0	2	0	0	0	0	0	0	0
Woodchuk														
Marmota monax	0	0	17	0	0	0	0	0	0	0	0	0	0	0
Squirrel														
Sciurus carolinensis	0	0	0	0	0	10	0	0	0	0	0	0	0	0
Mouse														
Peromyscus spp.	5	0	0	0	0	0	0	0	0	4	0	0	0	0
Cow														
Bos taurus	2	0	3	0	0	0	0	0	0	0	0	0	0	0
Goat														
Capra hircus	1	0	2	0	0	0	1	0	0	0	0	0	0	0
Mink														
Mustela vison	0	0	4	0	0	0	0	0	0	0	0	2	0	0
Harbor Seal														
Phoca vitulina	0	1	2	0	0	0	0	0	0	0	0	0	0	0
Fox														
Vulpes vulpes	1	0	1	0	0	0	0	0	0	0	0	0	0	0
Rat														
Rattus spp.	1	0	0	0	0	0	0	0	0	0	0	0	0	0
Mole														
Parascalops breweri	0	1	0	0	0	0	0	0	0	0	0	0	0	0
Raccoon														
Procyon lotor	0	0	1	0	0	0	0	0	0	0	0	0	0	0
Sheep														
Ovis aries	0	0	0	0	0	1	0	0	0	0	0	0	0	0
No Host	63	63	12	0	0	3	0	0	0	0	0	0	0	0

[a] 19 ferrets.
[b] 2 birds.
[c] 23 fishers.
[d] 24 rabbits.

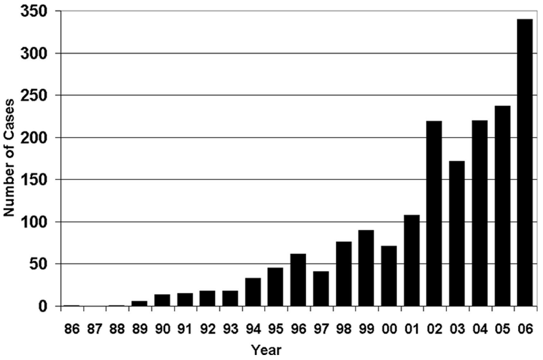

Fig. 2. Number of Maine-acquired cases of Lyme disease as reported to the Maine Centers for Disease Control and Prevention, 1986–2006.

residual of this cohort in early May (Fig. 6). Over the course of study, nymphal submissions described a single peak, the greatest numbers being submitted during the 25th week of the year, approximately the third week of June. The relationship between cumulative Lyme disease cases and nymph submissions at the county level was strong and the regression significant ($n = 16$ counties, $R^2 = 0.77$, $P < 0.0001$) (Fig. 7). At the town level, the regression of cases on nymphs was significant, but the strength of the relationship was moderate ($n = 368$ towns, $R^2 = 0.41$, $P < 0.0001$). Over the period of the study the upward trend in nymph submissions with time was significant (1992–2005: $R^2 = 0.52$, $P = 0.004$), as were the upward trends in Lyme disease cases for both Maine ($R^2 = 0.89$, $P < 0.0001$) and New England ($R^2 = 0.51$, $P = 0.004$). Although none of the series was periodic, the cases series were characterized by high and low years that corresponded roughly with highs and lows in the Maine nymph submission series (Fig. 8). The correlation between cases and submitted nymphs in the upward-trending series was strongly significant for both Maine and New England ($\rho_s = 0.88$, $P < 0.0001$ and $\rho_s = 0.78$, $P = 0.001$, respectively), and in the detrended series was insignificant for Maine ($\rho_s = 0.42$, $P = 0.14$), but strongly significant for New England ($\rho_s = 0.61$, $P = 0.02$). The lack of significance in the Maine series was due to 2000, a year with very high nymph submission but low cases.

Of the 4,361 *I. scapularis* that were reported to have been attached to people, 39.4% were removed from the 0–14 yr age group, whereas, remarkably, only 7.7% were submitted from those 15–29 yr of age (Fig. 9). Those within the broader age group of 30–59 provided almost as many ticks (36.8%) as did the 1–14 age group. For comparison, the proportions of the total Maine population in 2000 represented by the three age groups were, respectively, 19.3, 18.1, and 43.9% (U.S. Census Bureau 2005). The degree of engorgement of submitted ticks also varied among age groups. By decade, 10.9 and 13.2% of ticks were reported as moderately or very engorged in the 0–10 and 11–20 age groups, respectively, but only 2.1% were so engorged in the 21–30 age group. Thereafter, the percentage of

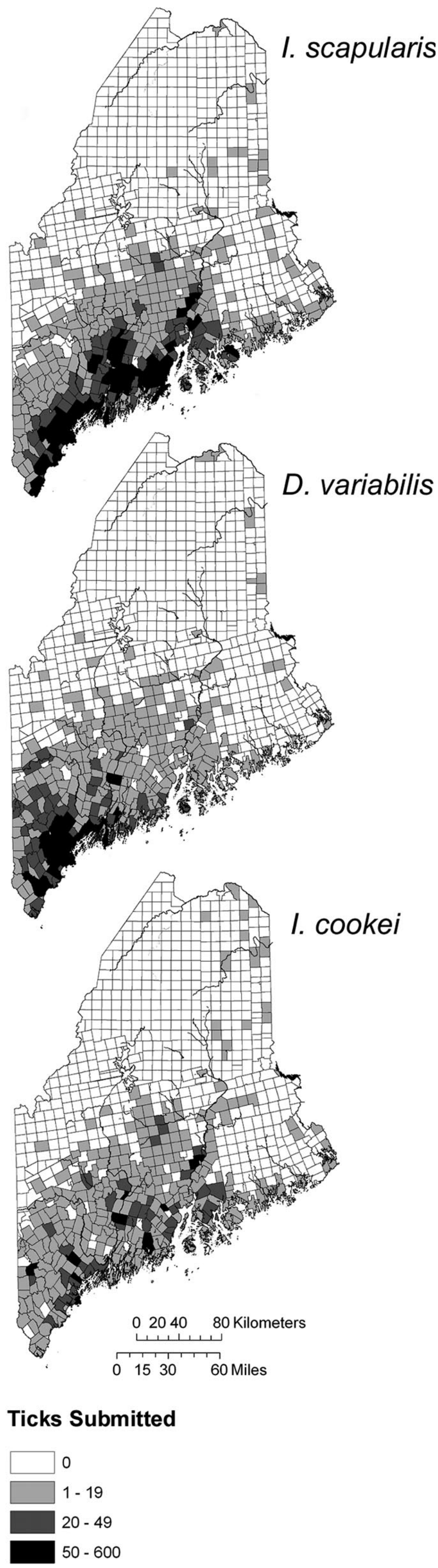

Fig. 3. Numbers of *I. scapularis*, *D. variabilis*, and *I. cookei* submitted per Maine town, 1980–2006.

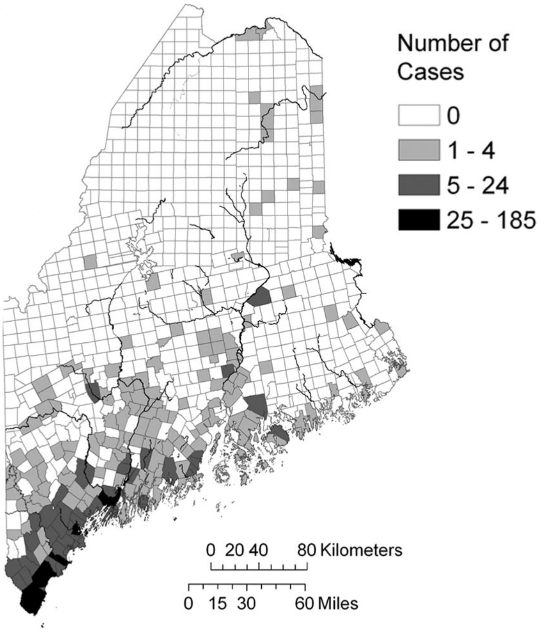

Fig. 4. Reported Lyme disease cases by town in Maine, 1989–2006.

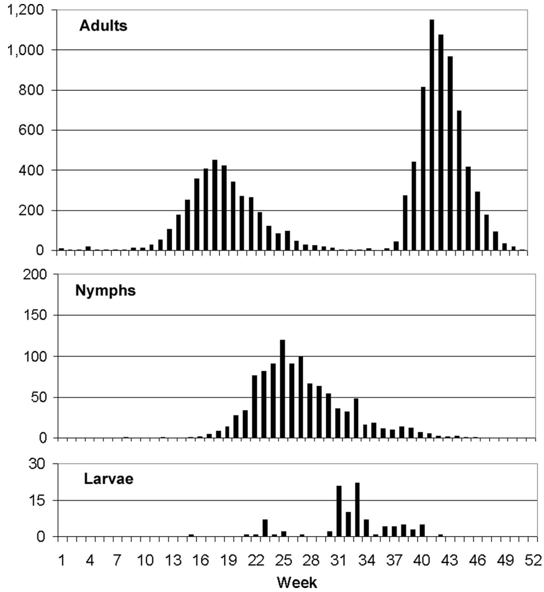

Fig. 6. Weekly submissions of *I. scapularis* adults, nymphs and larvae, 1989–2006.

moderately or very engorged submitted ticks increased linearly with each decade of age to 18.9% between ages 71–80 ($P < 0.0001$; Cochran–Armitage Trent test). Of a sample of 1625 *I. scapularis* removed from humans 2004–2006, 51.4% were from males.

D. variabilis. Compared with maps of submissions of *D. variabilis* in the first 2 yr of this study (Smith et al. 1992), the range of this tick has now increased to encompass the southern half of the state, including towns distant from the coast. (Fig. 3). Of 6,219 submitted, 97% were adults which first appeared in April, peaked near the first of June, and virtually disappeared by early August (Fig. 10). Of note were 14 *D. variabilis* found on two moose examined during the summer, and one removed from a harbor seal. Overwhelmed by dog tick submissions, in 2000, we encouraged submitters not to send specimens they could identify from descriptions we provided. Subsequent data, therefore, may not reflect the continuing increase in this tick. As with *I. scapularis*, a large proportion (41.4%) of *D. variabilis* were removed from children 0–14 yr of age, few (8.2%) in the 15–29 yr age group, and 32.1% on those 30–60 yr of age ($n = 993$).

I. cookei. Initially, more *I. cookei* than *I. scapularis* were removed from humans. Although called the "woodchuck tick," it also heavily infests other mid-sized mammals, including mustelids, as evidenced by large numbers found by trappers on fishers and by their owners on pet ferrets that had ventured outside. Frequent specimens were sent from dogs and cats, and two were removed from a harbor seal (Table 2). Submissions of *I. cookei* have been relatively constant, falling slightly in recent years, and they have been distributed throughout the southern half of the state,

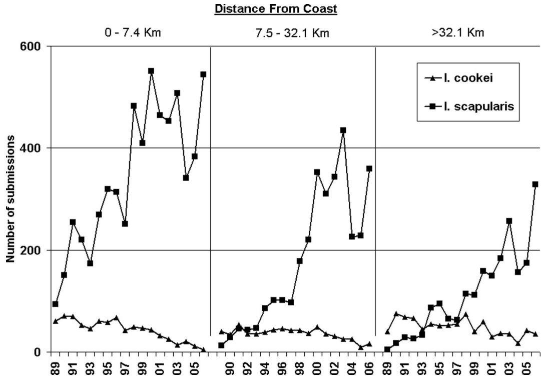

Fig. 5. Annual submissions of *I. scapularis* versus *I. cookei* in three sectors increasingly distant from the coast of Maine, 1989–2006.

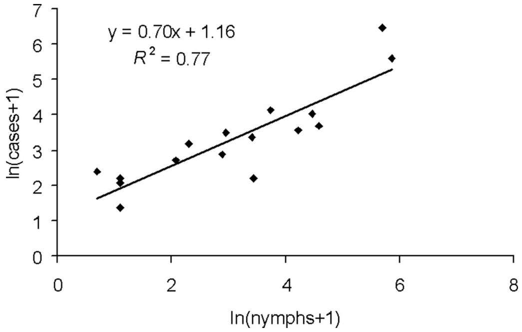

Fig. 7. Reported Maine Lyme disease cases by county ($n = 16$) versus submissions of nymphal *I. scapularis*, 1989–2006.

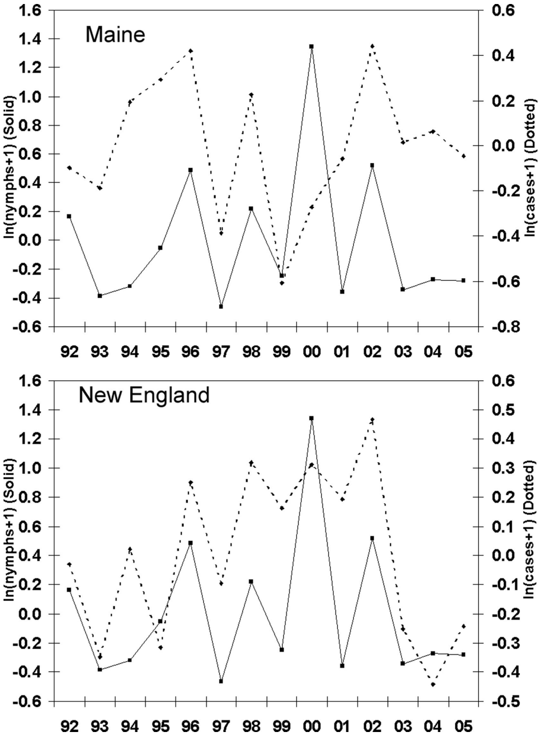

Fig. 8. Maine annual *I. scapularis* nymph submissions, detrended, versus Maine and New England reported Lyme disease cases, 1992–2005.

more closely reflecting that of the human population than *I. scapularis.* Of the 570 attached *I. cookei* removed from humans in this project, more than half (56.3%) were from children under 15 yr of age (Fig. 9). Unlike the separate seasonal patterns for the stages of *I. scapularis,* all stages of *I. cookei* (17% adults, 56% nymphs, and 27% larvae) follow a more unimodal distribution, peaking in midsummer (Fig. 10).

Ixodes muris Bishopp & Smith. Although primarily a tick of rodents, in our study 39 *I. muris* were removed from humans, but most were found on dogs and cats. We have previously reported that as the female *I. muris* becomes increasingly engorged on unnatural hosts an extremely painful reaction occurs characterized by edema, loss of appetite, lethargy, and fever as high as 41°C (Lacombe et al. 1999). Although swelling and inflammation have been reported by human hosts, ticks were usually discovered and removed before they became engorged. Initially, *I. muris* was found throughout Maine, but it is now rarely submitted. Most *I. muris* submissions have been adult females, and they have occurred at two times during the year, a lesser peak in late June and a main peak in late August and September.

Other Ixodes Ticks Submitted. I. marxi is usually found on sciurids, but it also is quite commonly found on people, particularly in the spring and summer when owners return to seasonal dwellings that have been occupied by squirrels during the winter. *I. angustus* is frequently encountered in our field studies, but infrequently submitted for identification, being rarely found on any but rodent hosts. *I. dentatus,* although common in southern New England states, has rarely been submitted for identification, and it is only occasionally collected from diverse sites in our field studies. *I. gregsoni* has recently been identified as a new species of the genus *Ixodes* found in Canada on the mustelids mink, weasels, and American marten (Lindquist et al. 1999). It was first found in Maine on a mink, and in Vermont on fisher and a domestic cat (Lubelczyk et al. 2007). The *I. uriae* listed in Table 1 were submitted in 1994 by an observer of a puffin colony on an offshore Maine island. Subsequently, this tick has been collected from other island nesting sites on the Maine coast and specimens collected from seabird colonies on the coast of Newfoundland and Labrador have been shown to harbor the neurotropic

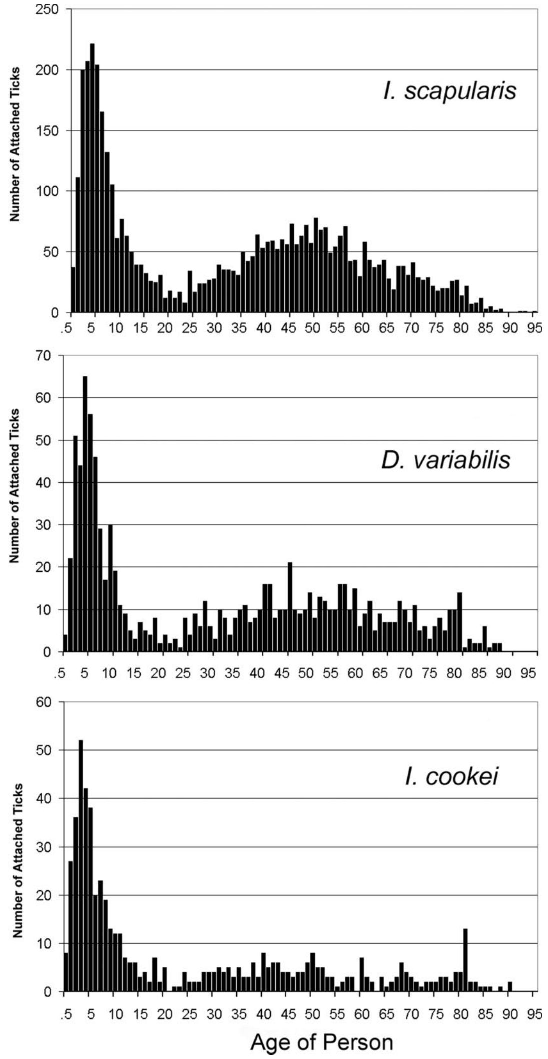

Fig. 9. Age distribution of individuals from whom *I. scapularis*, *D. variabilis* and *I. cookei* were removed, 1989–2005.

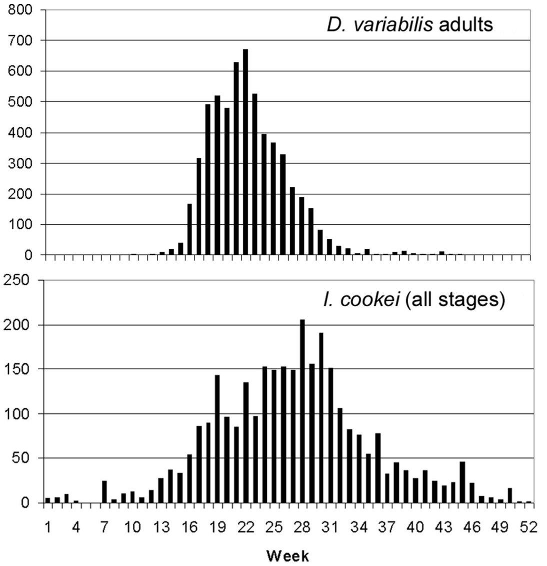

Fig. 10. Weekly submissions of *D. variabilis* and *I. cookei* of all life stages, 1989–2005.

European Lyme disease pathogen *Borrelia garinii* (Smith et al. 2006).

Other Tick Species. Submissions of *Dermacentor albipictus* Packard have shown this tick to be widely distributed throughout Maine. Although considered a "one-host tick" and primarily found on moose and deer, all stages have been submitted from cats, dogs, horses, and people. Hunters have reported encountering numerous *D. albipictus* larvae while walking through fern fields or even in tree stands. Clumps of larval ticks more than an inch in diameter have been reported on clothing. When attached, they have caused what has been variously described as a "rash," "small red dots," or "red sores." *D. albipictus* larvae have been found from early September through December; nymphs from October into January, and adults from November into May. *Haemaphysalis leporispalustris* Packard, although widespread in nature, is rarely submitted from any hosts other than rabbits and birds on which it can occur in overwhelming numbers. It is occasionally found on people and domestic animals. In 1998, we first reported *A. americanum* in Maine from ticks submitted by individuals verified to have had no out-of-state exposure (Keirans and Lacombe 1998). Not included in Table 1 are 244 specimens submitted by travelers returning to Maine from the south where this tick is common. *Rhipicephalus sanguineus* Latreille, the brown dog tick or kennel tick, found commonly on dogs, in our study has frequently been associated with recently adopted greyhounds. It is the vector of *Ehrlichia canis,* but this disease is not commonly seen in Maine. It occasionally bites people. Two adult *Amblyomma maculatum* Koch, the Gulf Coast tick, have been submitted by nontraveled Maine residents.

Discussion

This study has shown a close association between the numbers of *I. scapularis* nymphs submitted in Maine and reported Lyme disease cases not only within the state over the duration of the project but also across New England from year to year, where the numbers of cases in most states have oscillated annually during the 1990s (Fig. 8). Although some correlations have been found between indices of moisture over the minimal 2-yr life cycle of the tick and the abundance of ticks (Jones and Kitron 2000) or the incidence of Lyme disease (Subak 2003, McCabe and Bunnell 2004), a recent study, in which four weather variables were compared with Lyme disease cases in seven northeastern states (not including Maine) over 10 years, failed to demonstrate consistent relationships that could be applied across the region (Schauber et al. 2005).

There have been few multiyear studies comparing tick abundance with Lyme disease cases, and none that we are aware of that have made regional comparisons. Falco et al. (1999) found a strong correlation between annual flagged nymph densities and locally diagnosed cases of erythema migrans over a 6-yr period during which cases and nymphal abundance synchronously fluctuated from year to year. In a 10-yr comparison of passively submitted *I. scapularis* nymphs and Lyme disease cases in Rhode Island towns, Johnson et al. (2004) found a high correlation between submitted ticks and Lyme cases by town, but they were unable to show a correlation between tick submissions and human cases from year to year. Our finding of a statistical correlation between annually submitted nymphs in Maine with New England-wide Lyme disease cases invites further study.

The age distribution of individuals in Maine from whom attached *I. scapularis* were removed is similar in pattern to the age distribution of Lyme disease cases reported nationally (Dennis and Hayes 2002), but it is striking in the high numbers of ticks removed from children below 15 yr of age and the few ticks from individuals in their late teens and twenties. In the first instance, the high numbers can easily be explained by the greater proximity of children to the zone of questing ticks and to the frequency with which they are checked by concerned parents. Explanations for the low numbers of ticks submitted for identification by young adults might include diminished exposure resulting from educational pursuits, employment, competing interests that reduce opportunities for outdoor activities, or a greater acceptance of risk by that age group (Liang et al. 1999). In a survey of Lyme disease prevention behaviors in a hyperendemic area, Phillips et al. (2001) reported statistically less avoidance of tick areas, wearing protective clothing, and application of repellents by respondents under 30 yr of age.

Although the duration of attachment has been related to the risk of transmission of Lyme disease (Sood et al. 1997), we are unaware of previously reported data relating the degree of engorgement of *I. scapularis* ticks to the age of their human hosts. Although

≈8% of *I. scapularis* ticks had fed long enough to become at least moderately engorged on individuals during the first two decades of life, only 1% removed from people in their twenties were similarly engorged. Thus, although few ticks were submitted from the latter age group, the majority of those we did receive had been discovered within 2 or 3 d of attachment. With each subsequent 10-yr cohort, the percentage of submitted ticks that were at least moderately engorged increased linearly, reaching 18.9% in the 70s. Although this apparent decreasing awareness of attached ticks might relate to an aging-related loss of visual acuity, this finding, because of its usefulness in targeting populations at particular risk, needs further evaluation. Although it is generally assumed that, because of their size, adult ticks are found early and therefore present an insignificant risk (CDC 2005), very engorged adults were frequently submitted, particularly from children and the elderly.

Because the 18 yr of this study coincided with the advance of *I. scapularis* into a previously uninfested area, the geographic pattern of tick submissions provided clues to the environmental influences that foster the tick's establishment. At least two aspects of the tick's ecology may be involved: its reported intolerance to desiccation and the important role played by birds in its long-distance dispersal. Stafford (1994) has reported that survival of subadult stages falls off significantly below 93% RH, and we have shown in Maine, as have others elsewhere, that ground-associating, migrating passerines provide both long-range dispersal and serve as competent reservoir hosts of the agent of Lyme disease (Smith et al. 1996, Rand et al. 1998, Ginsberg et al. 2005, Morshead et al. 2005). Thus, as subadult *I. scapularis* have been dispersed by Neotropical songbirds during their coastal migration along the Atlantic flyway, this species has first become established within a few miles of the Maine coast, where maritime air maintains high humidity, then up river valleys into the interior. This association of *I. scapularis* with rivers has been documented previously at a noncoastal site (Kitron et al. 1991).

D. variabilis, however, is more tolerant of mesic conditions (Knulle 1966), and it rarely parasitizes birds (we reported only a single *D. variabilis* found on >20,000 mist-netted birds examined in a previous study; Smith et al. 1996). Although southern New England and southern Nova Scotia were thought to be the northeastern limits of the range of the American dog tick in 1979 (Sonenshine 1979), occasional specimens were received from towns in the southern half of Maine in the past by the Maine Forest Service Insect and Disease Laboratory and a "heavy infestation" was documented in south central Maine in 1951 (Nutting 1952). The tick's subsequent slow and diffuse spread in Maine, relative to that of *I. scapularis,* may reflect its lack of an avian long-distance transporter and a greater tolerance of drier conditions. *I. cookei,* meanwhile, which has been well established in Maine for at least a century (Banks 1908), showed no change in its distribution during the course of this study.

As *I. scapularis* advances into higher northern latitudes, thermal constraints make survival through the stages of its minimally 2-yr life cycle increasingly precarious (Lindsay et al. 1995, Rand et al. 2004). In this Maine study, the greatest number of nymphs was submitted in the third week of June, a date 2 to 4 wk later than nymphal peaks described earlier from New Jersey (Schulze et al. 1986), New York (Falco and Fish 1988), and Massachusetts (Wilson and Spielman 1985), where annual mean daily temperatures are 3–4°C warmer. This delay in nymphal peaks between Maine and sites in Massachusetts and southern New York is consistent with the findings of a recent survey encompassing the eastern United States (Diuk-Wasser et al. 2006).

The fact that the submissions of macroscopically similar *I. cookei* have shown no increase over the period of this study (Fig. 5) confirms that the rising numbers of *I. scapularis* submissions were not simply a reflection of the public's increased concern about ticks and Lyme disease. *I. cookei* is the primary vector of Powassan virus, first isolated from an Ontario child with fatal encephalitis (McClean and Donahue 1958). An outbreak of this disease in Maine and Vermont was reported in 2001 (CDC 2001), and a subsequent case was reported in Maine in 2004 (CDC 2006b). These cases may have been recognized, however, as a result of a recently implemented laboratory screen for West Nile virus; thus, previous cases may have gone undiagnosed. Although these cases were all adults, Powassan virus frequently infects children, a fact consistent with our finding that more than half of the total *I. cookei* removed from humans came from children under the age of 15. Unlike the agents of Lyme disease and human granulocytic anaplasmosis, there is no delay in the transmission of Powassan virus by feeding ticks (Ebel and Kramer 2004), nor is a specific vaccine or drug available for its prevention or treatment. Thus, reports of Powassan encephalitis are yet another reason for people in the northeastern and central United States to remain vigilant about protecting themselves from tick bites. Fortunately, the incidence of clinical cases remains low. Little is known about the prevalence of infection among the several potential mammalian reservoir hosts, nor in the tick vectors.

I. muris has been reported to have widespread distribution in the United States and Canada (Durden and Keirans 1996), and although not a common tick, it is surprising that the acute reaction associated with its bite has not been more frequently reported. The mechanism of this reaction remains unclear. Yearly fluctuations in numbers of this tick may be explained by its dependence on mice or other small mammals, but it seems to be no longer found where *I. scapularis* is established. In noting a similar decrease in southern New England, Spielman (1988) hypothesized: "with the colonization of *I. dammini,* the common mouse tick *I. muris* has reciprocally become exceedingly scarce–perhaps reflecting some form of competitive displacement". How ticks of one species might compete with, and displace those of another, remains a question for further study. *I. muris* has been reported to be at least a weak vector of Lyme disease (Dolan et al. 2000). Because of the discomfort associated with its bite, however, human hosts may have become aware of the tick before transmission could have occurred, even if the tick were infected.

The role of other native *Ixodes* ticks in disease transmission may expand as these species share hosts with *I. scapularis*, an aggressive human biter. *I. marxi* is a vector for Powassan virus (Artsob 1988); from our trapping studies, we know it may be found with *I. scapularis* on the same squirrel. Although *I. angustus* has been shown to be a competent vector of *B. burgdorferi* in the laboratory (Peavey et al. 2000) and it has been reported to have possibly transmitted Lyme disease to a person (Damrow et al. 1989), none of this species submitted to us for identification was removed from humans. *I. angustus* also has been implicated in the enzootic transmission of babesiosis (Goethert et al. 2006).

D. albipictus, the "winter tick", has been submitted from all counties in Maine, a distribution corroborated by our deer tagging station surveys (Smith et al. 1990, Rand et al. 2003). Both moose and deer are major hosts of this tick, and both *D. albipictus* and *I. scapularis* are often found on the same deer where the two species overlap. *D. albipictus* are also found in large numbers on sick moose throughout the winter, contributing to mortality from anemia and hair loss (McLaughlin and Addison 1986).

The range of *A. americanum*, the vector of *Ehrlichia chaffiensis* and *Borrelia lonestari*, seems to be expanding, increasing the likelihood that the diseases caused by these agents may be seen in northern New England, either from ticks acquired locally or from out of state travel. The submission of *A. maculatum* from two untraveled Maine residents is of interest considering the recent report of *Rickettsia parkeri* in Gulf Coast ticks (Sumner et al. 2007).

Maine has provided a unique and valuable place for this study because of its size, its extension across three degrees of latitude, and the variations of elevation and habitat within its borders. The project has had the advantage of a large and diverse sampling pool that included humans, domestic animals, and wildlife. Despite the disadvantages of passively submitted data, the project has demonstrated the advance of a vector tick along ecologically supportive corridors and has correlated patterns of its abundance with those of Lyme disease incidence far beyond the state in which it was conducted. This finding supports the suggestions of others (Ginsberg et al.1998, Ostfeld et al. 1998, Schauber et al. 2005) that as yet poorly understood broad regional shifts of abiotic and biotic cycles influence tick populations over the northeastern United States. More observations and analyses of long-term trends are needed to give better understanding of the natural vulnerabilities of *I. scapularis*.

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