

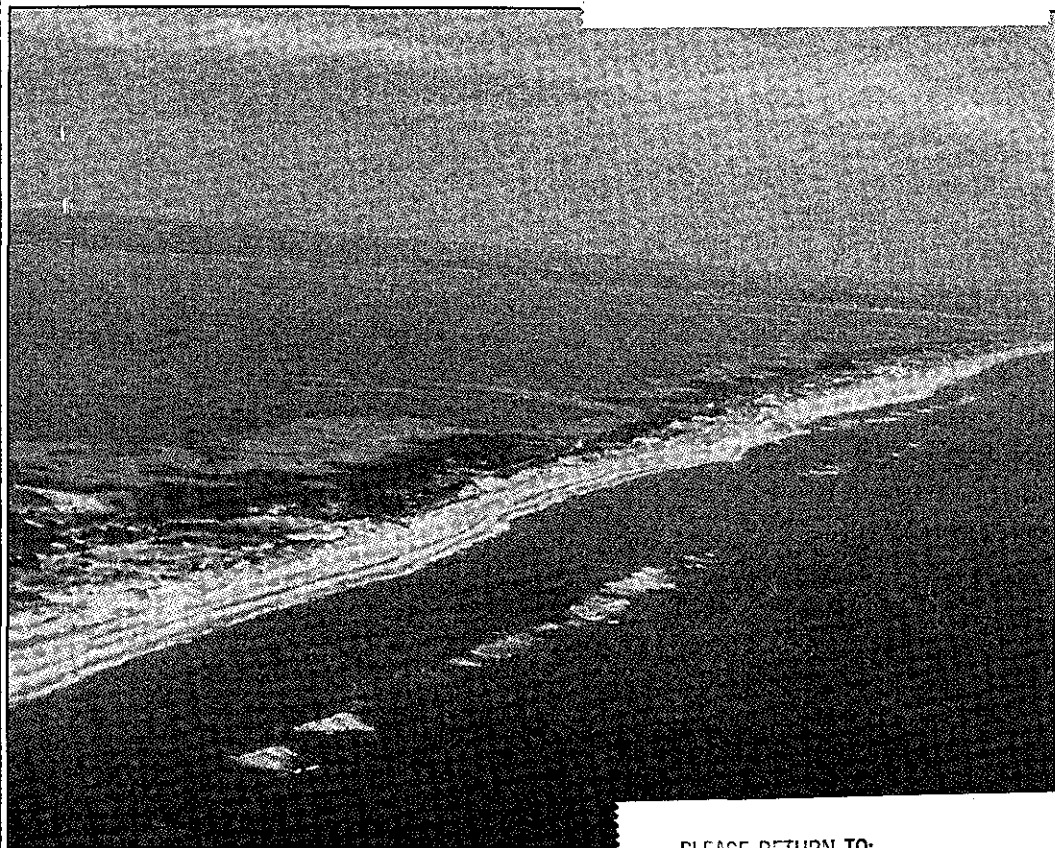
Ecology and Management of Ticks and Lyme Disease at Fire Island National Seashore and Selected Eastern National Parks

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Ecology and Management of Ticks and Lyme Disease at Fire Island National Seashore and Selected Eastern National Parks

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SUMMARY

The distributions of ticks and Lyme disease spirochetes were studied at 16 National Park System units in the eastern United States. Habitat distribution was studied at Fire Island National Seashore, New York, by collecting specimens from the clothes of investigators and from muslin drags and by running tick traps at several sites along Fire Island. The ticks were returned to the lab where they were dissected and examined for spirochetes.

Adult deer ticks were most abundant in the spring and fall. They were more common in high shrub habitats than in grassy and low shrub habitats at both times of the year. In the fall, they were also common in the woods. Adults were more abundant on trails than in nearby areas off the trails.

Nymphs and larvae were far more common in leaf litter in the woods than in open grass-shrub habitats. Trap captures of nymphs on trails were not significantly larger than trap captures off trails. Immature *Ixodes dammini* were commonly collected in clusters, while adults were mostly collected singly.

During the spring and fall, activities that take place in high shrub areas or in the woods (e.g., landscaping, trail or brush clearing, patrolling trails through thickets or woods) involve a high risk of exposure to adult ticks infected with Lyme disease. From spring through midsummer, any activity involving close contact with leaf litter (e.g., playing in the leaves, gathering leaves for bedding, picnicking on leaf litter) results in a high risk of exposure to infected nymphs.

Of the 16 national park sites sampled in the North Atlantic, Mid-Atlantic, National Capital, and Southeast regions of the National Park System, the number of infected ticks captured per unit sampling effort was greatest at Fire Island National Seashore, followed by Assateague Island National Seashore, Cape Cod National Seashore, and Acadia National Park. Overall, an average of 51.5% of the adult *Ixodes dammini* and 28.0% of the nymphs were infected with spirochetes.

Lyme disease can potentially spread rapidly through animal populations because generally several ticks attach to each host, resulting in a high probability that at least one of those ticks carries spirochetes. Therefore, most host individuals in a typical endemic area are exposed to spirochetes. However, many tick host species are inefficient or incompetent reservoirs, and ticks might immigrate on host animals that are inefficient reservoirs. These host-related factors could slow down the spread of Lyme spirochetes in animal host and tick populations and lower the prevalence of spirochetes in questing ticks.

Treatment with permethrin-treated cotton balls did not consistently lower densities or spirochete prevalence levels of northern deer ticks in field trials on Fire Island. This technique effectively removed ticks from white-footed mice at fully treated experimental sites. The densities and spirochete preva-

lence levels of questing ticks in the subsequent stage were lower in treated than untreated sites in some trials, but not in others. This method shows promise as an approach to tick management, with relatively little environmental impact (compared to broadcast spraying and other high-impact approaches), especially if the sources of infected ticks (other than local white-footed mice) can be identified and managed. Applying this material by itself would probably lower the overall number of cases of Lyme disease. However, since results varied in different trials, people should continue to follow precautions to avoid tick bites, even in fully treated areas.

INTRODUCTION

Lyme disease is a tick-borne bacterial illness that is currently the most commonly reported arthropod-borne disease in the United States (Centers for Disease Control 1989). Most human cases occur in the northeastern and north-central states, especially New York State (mainly Westchester and Suffolk counties), including Shelter Island (Bosler et al. 1983, 1984) and Fire Island (Hanrahan et al. 1984b).

The northern deer tick, *Ixodes dammini* Spielman, Clifford, Piesman, and Corwin (Acari: Ixodidae), is the vector species responsible for most human cases of Lyme disease in the northeastern United States. This tick was separated from a similar southern species, *I. scapularis* (Say) in 1979 (Spielman et al. 1979). Similarly, *Borrelia burgdorferi* Johnson, Schmid, Hyde, Steigerwalt, and Brenner, the spirochete that causes Lyme disease, was identified as the etiologic agent (Burgdorfer et al. 1982; Benach et al. 1983; Steere et al. 1983a) and named (Johnson et al. 1984) recently. Therefore, a great deal remains to be learned about the ecology and management of these species. We are still in the early stages of describing the ecological interactions among spirochetes, ticks, and their vertebrate hosts.

This report covers four major aspects of the ecology of Lyme disease in eastern national parks. The first section reports field results on the habitat distributions of *Ixodes dammini*, *Amblyomma americanum*, *Dermacentor variabilis*, and *Borrelia burgdorferi* on Fire Island and identifies human activities that involve a high risk of exposure to infected ticks. The second section is a study of the geographical distribution of *I. dammini* and Lyme spirochetes in eastern national parks. The third section is a theoretical study of the spread of Lyme spirochetes through natural populations. Mathematical models are used to explore the potential influence of reservoir competence of alternative host species and of tick immigration on spirochete prevalence in questing ticks. The final section discusses methods to manage ticks and reports results of a field trial of permethrin-treated cotton balls on Fire Island.

Background Information

Distribution and Symptoms of Lyme Disease

As stated earlier, Lyme disease is an illness caused by a spirochete, *Borrelia burgdorferi*, that is transmitted to humans by the bite of an infected tick. The disease was first recognized in 1975 when a cluster of cases with arthritis-like symptoms appeared in the vicinity of Old Lyme, Connecticut (Steere et al. 1976, 1977b). The disease has been present in Europe at least since 1909 when the characteristic rash was first recognized (Afzelius 1921),

but it was not then identified as part of a more extensive disease syndrome. Lyme disease is now known in North America, Europe, Asia, Australia, and possibly elsewhere (Steere et al. 1983b; Schmid 1984, 1985; Ai et al. 1988). In this country Lyme disease is most common in the Northeast (especially Connecticut, Massachusetts, New Jersey, New York, and Rhode Island) and is also found in the north-central United States (Minnesota and Wisconsin), western coastal states (California and Oregon), and Texas, with scattered cases in other states (Dryer et al. 1979; Steere and Malawista 1979; Osterholm et al. 1984; Spielman et al. 1985; Ciesielski et al. 1988). Locally acquired cases have now been reported in 43 states (Centers for Disease Control 1989).

The symptoms of Lyme disease vary from patient to patient and often mimic other conditions (Steere et al. 1977a; Centers for Disease Control 1982). Early symptoms (a few days to a few weeks after being bitten by an infected tick) include an expanding circular rash or lesion that clears at the center (*Erythema chronicum migrans*, or ECM), often accompanied by flu-like symptoms including headache, fever, stiff neck, muscle aches, and sore throat. Treatment with appropriate antibiotics is effective at this stage (Steere et al. 1983b, 1984). Unfortunately, the rash can vary, ranging from blotchy in appearance to red throughout. Furthermore, many patients display only some of these symptoms, or none of them, and progress directly to the later manifestations of the disease. Therefore, early diagnosis can be difficult.

Later symptoms (a few weeks to over a year after the tick bite) can be severe and include arthritic, neurological, and cardiac problems. Episodic bouts of arthritis in the large joints are common (Steere et al. 1977a, 1977b). Possible neurological problems include numbness, tingling in the extremities, lethargy, stiff neck, temporary loss of control of one side of the face, and memory problems (Reik et al. 1979, 1985; Pachner and Steere 1985). Cardiac problems such as palpitations and heart block are somewhat less common (Steere et al. 1980). The occurrence and severity of these later symptoms differ markedly in different patients. Treating these later manifestations (Steere et al. 1983c, 1985) is far more difficult than treating the early stages, and often requires hospitalization. Many cases have resisted all currently available antibiotics. Therefore, early diagnosis and treatment are important.

Vectors of Lyme Disease

The primary vector of Lyme disease in North America is the northern deer tick, *Ixodes dammini*. This species extends north to Massachusetts (McEnroe 1977b, 1984, 1985) and Maine (Anderson et al. 1987; Ginsberg and Ewing 1988) and has been reported in Ontario, Canada (Spielman et al. 1985). This species has been reported as far south as Assateague Island in Maryland (Coan and Stiller 1986) but is replaced to the south by a similar species, *I. scapularis*. The apparent parapatric distribution of these species suggests that they may actually be geographical subspecies (McEnroe 1985). Furthermore, *I. scapularis* is also capable of transmitting Lyme disease (Piesman and Sinsky 1988). On the West Coast, the California black-legged

tick, *I. pacificus* Cooley and Kohls, can transmit Lyme disease (Burgdorfer et al. 1985). Finally, the lone star tick, *Amblyomma americanum* (Linnaeus), which is most common in the southern states (Strickland et al. 1976) but extends into New England, can apparently also transmit Lyme disease (Schulze et al. 1984a). The common American dog tick, *Dermacentor variabilis* (Say), can carry *B. burgdorferi* (Piesman and Sinsky 1988) but has not been implicated in Lyme disease transmission (*D. variabilis* is a major vector of Rocky Mountain spotted fever).

Magnarelli and coworkers (1986) recently isolated Lyme disease spirochetes from tabanid flies (Diptera: Tabanidae) and mosquitoes (Diptera: Culicidae). This isolation does not necessarily mean that these insects can transmit Lyme disease, because dipteran hosts present numerous barriers to survival, reproduction, and subsequent transmission of pathogens. Furthermore, the geographical distribution of Lyme disease fits well with that of the tick vectors (Steere and Malawista 1979), rather than with those of biting flies. Nevertheless, anecdotal accounts of ECM appearing at the sites of mosquito bites (e.g., Hard 1966) suggest that mosquitoes can occasionally transmit the disease (perhaps passively on the mouthparts). If they can transmit Lyme disease at all, mosquitoes are probably only secondary vectors (Magnarelli et al. 1986).

Natural History of Ixodes dammini and Lyme Spirochetes

Adult *I. dammini* are active in the fall through the spring (sometimes even on warm winter days) during which time they seek a blood meal, overwinter, and lay eggs. They attach mostly to white-tailed deer (*Odocoileus virginianus*), but are also found on humans, domestic dogs and cats, foxes (*Vulpes vulpes*), raccoons (*Procyon lotor*), opossums (*Didelphus virginiana*), gray squirrels (*Sciurus carolinensis*), and other species (a total of 13 mammal hosts have been reported; Anderson 1989).

Larvae appear around midsummer and are found mostly on white-footed mice, but also on gray squirrels, eastern chipmunks (*Tamias striatus*), deer, raccoons, opossums, meadow voles (*Microtus pennsylvanicus*), eastern cottontails (*Sylvilagus floridanus*), meadow jumping mice (*Zapus hudsonius*), masked shrews (*Sorex cinereus*), and northern short-tailed shrews (*Blarina brevicauda*). They molt and overwinter, appearing as nymphs the following spring and early summer (May–July). The nymphs have a similar host range to the larvae (Wallis et al. 1978; Piesman and Spielman 1979; Spielman et al. 1979; Anderson and Magnarelli 1980; Carey et al. 1980, 1981; Main et al. 1981, 1982; Bosler et al. 1984; Schulze et al. 1986). Immatures are also found on various species of birds (McEnroe 1977a; Anderson and Magnarelli 1984; Anderson et al. 1986). Immature *I. dammini* have been recorded from a total of 29 species of mammals and 49 species of birds (Anderson 1989).

After feeding, the nymphs molt to the adult stage, completing the two-year life cycle (Spielman et al. 1985). Therefore, during any one year adults are active in fall and spring, nymphs in early summer, and larvae from mid- to

late summer. Thus nymphs are active earlier in the year than larvae (an earlier stage of a later generation). However, small numbers of ticks in each stage are found at other times of the year, probably because immature ticks that fail to attach to a host can survive the winter and quest the following spring. In contrast, adults that fail to attach apparently die during the summer (Yuval and Spielman 1990).

Wilson and coworkers (1985) found a correlation between larval tick abundance (density on white-footed mice) and deer abundance (estimated from pellet counts, spottings, and tracks) on 13 islands in Massachusetts. However, the correlation did not hold for nymphal abundance. The authors argued that deer numbers influenced the numbers of adult ticks feeding and laying eggs (and thus influencing the number of larvae), but that nymphs dispersed between islands, perhaps on birds (McEnroe 1977a; Anderson and Magnarelli 1984; Anderson et al. 1986). However, in New Jersey, Schulze and coworkers (1984b, 1984c) found that ticks were absent from the northern part of the state where deer density was greatest, and that elevation best explained tick distribution. Furthermore, Wilson and coworkers (1984) did not find a marked decrease in tick abundance one year after removing 70% of the deer from part of Great Island, Massachusetts. When the rest of the deer were removed (Wilson et al. 1988), larval densities on mice declined sharply. This result suggests that deer were initially a superabundant resource for ticks on Great Island (because thinning the deer population did not influence tick densities), but that when deer were completely removed, hosts for adult ticks became a limiting factor. Unfortunately, the results are inconclusive because they do not take possible time delays (due to tick migration or survival over more than one season) into account, and because tick density on mice is a problematic estimator of tick abundance (the number of ticks per mouse is ambiguous because it depends on tick densities, mouse densities, and densities of alternate hosts). Therefore, the role of deer in the population dynamics of *I. dammini* remains poorly understood.

Transovarial transmission of Lyme disease spirochetes occurs but is rare in *I. dammini*. In Massachusetts, less than 1% of field-caught questing larvae were infected with spirochetes (Piesman et al. 1986). Therefore, ticks pick up the disease primarily by feeding on infected hosts. Since immature *I. dammini* commonly feed on *P. leucopus* (a competent reservoir of Lyme disease; Donahue et al. 1987), this mouse species is probably the major reservoir of Lyme disease in nature (Bosler et al. 1984; Spielman et al. 1984; Levine et al. 1985; Mather et al. 1989b). However, immatures feed on numerous other host species as well. Deer and catbirds appear to be incompetent as reservoirs of Lyme disease (Mather et al. 1988; Telford et al. 1988a, 1988b), while voles, chipmunks, raccoons, shrews, rabbits, and some birds apparently can serve as reservoirs with varying degrees of efficiency (Mather et al. 1989a, 1989b; Weisbrod and Johnson 1989; Telford and Spielman 1989; Fish and Daniels 1990; Telford et al. 1990). Unfortunately, the reservoir competence of many vertebrate host species is unknown. The roles of these various species as Lyme disease reservoirs need further study.

CHAPTER 1. Habitat Distribution of Ticks and Spirochetes on Fire Island



Information about the habitat distribution of *Ixodes dammini* and *Borrelia burgdorferi* can be used to target self-protection efforts at habitats where a high risk of encountering infected ticks exists. Habitat distribution data also provide basic natural history information about this tick, which contributes to our understanding of the epizootiology of Lyme disease. The purpose of this chapter is to describe the habitat and spatial distribution of *I. dammini* and Lyme spirochetes on Fire Island.

Methods

General sampling methods and a description of the study area are provided in the following sections. Details of techniques that are specific to each section are given in the appropriate subsections.

Study Area

Fire Island is a barrier island off the south shore of Long Island, New York, that stretches 55 km from Democrat Point (near Fire Island Inlet) on the west to Moriches Inlet on the east. Sample sites were selected to include major visitor areas, a diversity of habitat types, and several human residential areas. From east to west, the eight sample sites were Hospital Point, Watch Hill, Talisman, Fire Island Pines, Sailors Haven–Sunken Forest, Point O' Woods, Ocean Beach–Robbins Rest, and the Lighthouse (Fig. 1).

The beach on Fire Island faces the Atlantic Ocean to the south, with primary dunes to the north. Behind these dunes lies an area of secondary dunes and swales (Fig. 2). The vegetation is primarily beach grass (*Ammophila breviligulata*) on the primary dunes, with low patches of beach plum (*Prunus maritima*). The secondary dune area includes creeping mats of beach heather (*Hudsonia tomentosa*) and, in places, bearberry (*Arctostaphylos uva-ursi*). Beach grass meadows and low shrub areas of beach plum, bayberry (*Myrica pensylvanica*), and various ericaceous shrubs grade into high shrub thickets (1 m and taller) of these same species, along with poison ivy (*Rhus radicans*) and black cherry (*Prunus serotina*), often tangled with vines of greenbrier (*Smilax rotundifolia*). Farther north are wooded areas that vary in tree height and dominant species and that commonly include pitch pine (*Pinus rigida*), black cherry, holly (*Ilex opaca*), shadbush (*Amelanchier canadensis*), and sassafras (*Sassafras albidum*).

A belt of reeds (*Phragmites communis*) fringes the salt marsh to the north of the forest. Upland marsh species include marsh elder (*Iva frutescens*) and sea myrtle (*Baccharis halimifolia*), which grade into black rush (*Juncus gerardii*), salt grass (*Distichlis spicata*), and saltmeadow hay (*Spartina patens*) on the marsh proper. Saltmarsh cordgrass (*S. alterniflora*) predominates lower in the intertidal. The vegetation of Fire Island has been described in greater detail by Art (1976) and Stalter and coworkers (1986).

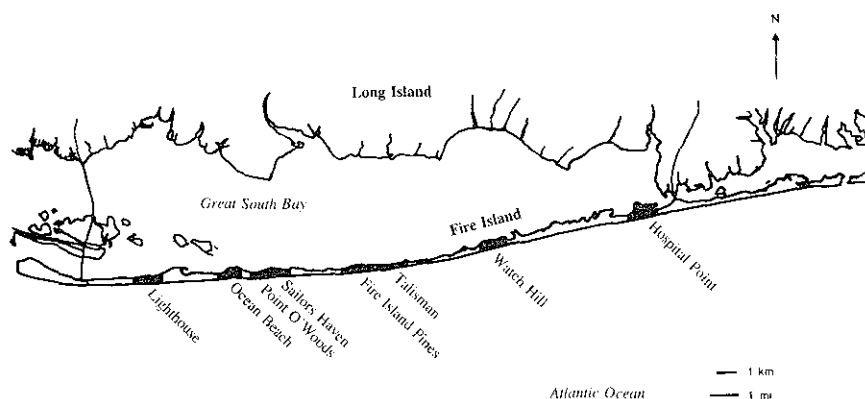


Fig. 1. Study area (from Ginsberg and Ewing 1989a). Reprinted by permission of the Journal of Medical Entomology.

Adult Ticks

Transect Samples

Adult ticks were sampled by an investigator walking random transects (2-m-wide strips) in the eight sample sites on Fire Island. Each sample site was measured east-west along the primary dune crest using maps and aerial photographs (sample sites ranged from 1,219 m to 1,463 m in length along the dune). Strips (transects) for sampling each site were selected with a random number table. Every odd number of meters along the primary dune crest represented the center of a 2-m-wide north-south strip.

Transects were sampled by walking due north and collecting ticks while pulling a tape measure that was attached at the south end of the transect, at the

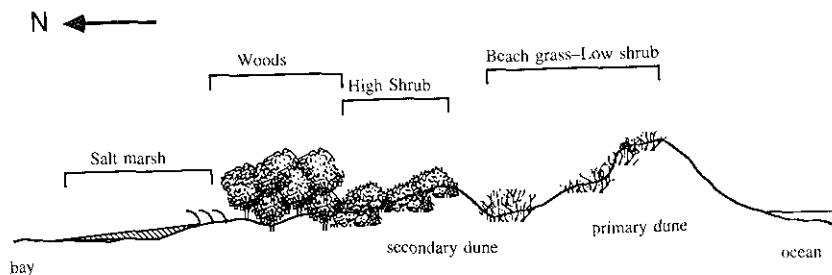


Fig. 2. Cross section of Fire Island showing typical distribution of habitats (from Ginsberg and Ewing 1989a). Reprinted by permission of the Journal of Medical Entomology.

inland base of the primary dune. The distance walked through each habitat type (Fig. 2) was recorded. Habitats were designated as follows:

1. beach grass meadow—low shrub (less than 1 m tall)
2. high shrub (1 m and taller)
3. woods (closed tree canopy)

Ticks were collected and recorded as they were found clinging to the investigator's clothing (occasionally they were found on his skin). He wore standard field clothes consisting of tan chino pants, an off-white cotton shirt with a faded light-brown corduroy field jacket, khaki sneakers with white socks (pant legs were tucked into the socks), and a tan fishing hat. The vast majority of the ticks were collected from the pants and socks. They were placed alive into vials and returned to the lab. The ticks were stored in a refrigerator in sealed vials with pieces of moist paper towel. They were later dissected in phosphate-buffered saline, pH = 7.4 (PBS), and examined for spirochetes under dark-field. Adult *I. dammini* were sampled on transects in the spring (4 April–6 May) and fall (20 October–24 November) 1986.

During the fall adult samples, sheets of muslin were dragged through the vegetation along each transect after the regular transect sample was taken. Five-minute drag samples were taken in each habitat (beach grass meadow—low shrub, high shrub, and woods) in the vicinity of each transect (a total of three drag samples with each transect). Both large and small muslin drags (see Drag Samples section) were used simultaneously. Ticks were collected from the drags as well as from the investigator's clothing and were returned to the lab for dissection.

Path—No Path Samples

The tendency of adult dog ticks (*Dermacentor variabilis*) to quest for hosts along trails was examined by walking on and off trails at Watch Hill, Sailors Haven—Sunken Forest, Ocean Beach, and the Lighthouse from 12 to 29 May 1986. A starting point was selected at random, and the investigator walked the nearest trail for 30 min, recording the number of ticks he found clinging to his clothes in that time. He then walked for 30 min in the same vicinity, but not on the trail, and recorded the number of ticks. A new starting point was randomly selected for each trail sample.

Similar samples were taken for adult *I. dammini* on 29 October (near Ocean Beach) and 10 November (at Watch Hill) 1986. In these samples, the trail nearest a random starting point was walked for 5 min. Then the area in the vicinity but off the trail was walked for 5 min. The ticks were then collected and returned alive to the lab. Additional samples were taken on the same trail, starting at the point where the previous sample had ended. The samples on 29 October were taken by Curtis Ewing, the field assistant. I took all other adult samples. Path—no path samples of immature ticks were taken with tick traps (see next section).

Immature Ticks

Drag Samples

Questing larval and nymphal ticks were collected with a dragging method that was modified from the flagging technique of Clymer et al. (1970). The terms *drag* and *flag* are used interchangeably in this report. The small drag (or flag) consisted of a piece of off-white, lightweight muslin, 30×116 cm (12×46 inch), stapled at the middle to a 122-cm (48-inch) wooden rod (Fig. 3A). The muslin hung like two flags on either side of the rod, which was used to stir up the vegetation and litter, and then drag the muslin through. The large drag consisted of a 76×112 -cm (30×44 -inch) piece of muslin stapled to a wooden base with a rope handle (Fig. 3B). This piece was dragged through the vegetation behind the investigator. Drags were taken throughout the study (1986–89) by myself and in 1986 by Curtis Ewing.

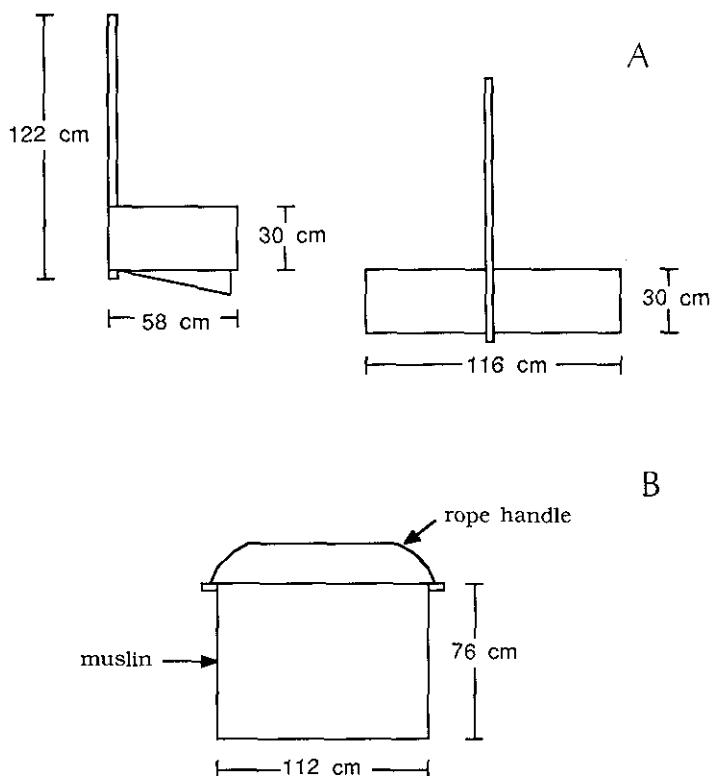


Fig. 3. Devices for tick drag samples (from Ginsberg and Ewing 1989b). A. Small drag (or flag); B. large drag. Reprinted by permission of Experimental and Applied Acarology.

Nymphs were sampled by dragging at the eight sample sites from 1 to 10 July 1986. Preliminary random samples at Ocean Beach on 26 June produced few ticks, apparently because of the highly clustered distribution of the nymphs. Therefore, favorable tick habitats were selected at each site for drag samples. The amount of time dragging, the habitat type, and the information on the ticks collected were recorded. Subsequent to 1986, standard 5-min drag samples were taken. The understory and leaf litter in the woods, and grassy-shrubby vegetation in the open were sampled for comparative purposes. The large and small drags were used simultaneously in nymph samples.

Larvae were collected from 14 July to 18 September 1986 using tick traps (see Tick Traps section) and drag samples. The small drag was used in most samples because of the difficulty and time required to search the entire large drag for the very small larvae (about 0.8 mm in length). On 24 July, drags were taken in the yards of 10 houses in Ocean Beach. The houses were selected with a random number table from a plot map of the village. Houses were excluded from the sample if residents could not be located or were unwilling to let us on their property. Presumably, the exclusion of some houses did not introduce any important bias into the sample. In each yard, Ewing and I each took a 5-min drag sample (with the small drag). Drags were also taken in the woods to the west of Ocean Beach.

From 8 to 18 September, I sampled larvae with the small drag in the eight sample sites along Fire Island. At each site, one drag was taken along a broad sand road (e.g., the Burma Road), one in open shrub and beach grass, and four in leaf litter in the woods. The drags were 5 min each.

Tick Traps

Ticks were collected with dry ice-baited traps that were modified from the designs of Wilson and coworkers (1972) and Gray (1985). Each trap consisted of a 1.9-L (2-quart) lidded plastic tub mounted on a wooden base (Fig. 4). The base was approximately 4 cm thick with angled edges that formed ramps toward the center. Each tub had a hole (approximately 6.5 mm diameter) drilled facing each edge of the base (total of four holes) to allow carbon dioxide to escape. Each sample night, 1.1 kg of dry ice were wrapped in newspaper and placed into the tub. Masking tape was placed at the top of the wooden base, overlapping the ramp, sticky side down. The next day, ticks that had climbed the ramp were collected from the masking tape (Ginsberg and Ewing 1989b).

Tick traps were set on and off trails in the woods west of Talisman on 14 July 1986. Trails were selected by using the trail nearest a random point on Burma Road. Each trap was set on a distinct trail, 3 m from Burma Road. An off-trail trap was set 3 m to the west of each trail trap (direction parallel to Burma Road). The traps were collected on 15 July (Ginsberg and Ewing 1989b).

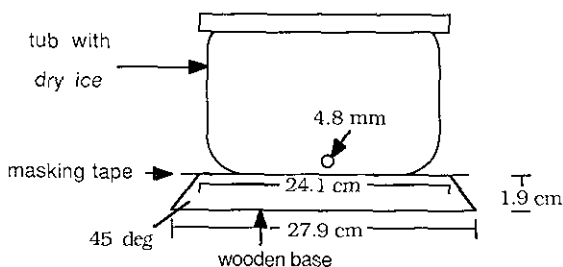


Fig. 4. Tick trap (from Ginsberg and Ewing 1989b). Reprinted by permission of Experimental and Applied Acarology.

Mouse Samples

In 1986, ticks were collected from white-footed mice (*Peromyscus leucopus*) captured at Watch Hill, Sailors Haven–Sunken Forest, and the natural area between Ocean Beach and Robbins Rest. The mice were caught in Sherman traps that were set in 5×5 grids (25 traps) with 20 m between grid points. The traps were baited with a mixture modified from that used in the *North American Census of Small Mammals* (Calhoun 1951). The bait consisted of 2 parts (by weight) beef suet, 2 parts peanut butter, 2 parts raisins, 2 parts oatmeal, and 1 part paraffin. The suet and paraffin were melted and the ingredients were combined, mixed well, and allowed to cool. In samples taken from 1987 to 1988, the Sherman traps were set in grids with 10 m between traps and were baited with a 3:1 mixture (by volume) of rolled oats and peanut butter.

Traps were collected at Watch Hill on 12 June, 22 July, and 28 August; at Sailors Haven–Sunken Forest on 18 June, 30 July, and 4 September; and at Ocean Beach on 26 June, 6 August, and 11 September 1986. Additional samples were taken in subsequent years (see Chapter 4). The mice were returned to the Talisman lab where they were anesthetized, measured, and marked by toe-clipping, and where their ticks were removed. The mice were anesthetized by placing them in quart plastic bags with a screened vial that contained cotton moistened with methoxyflurane. After recovering from the anesthesia, the mice were released (the same day) in the capture area.

Determining Spirochete Prevalence

Questing ticks were examined for spirochetes by dark-field microscopy. Ticks were refrigerated alive in vials with moist paper toweling until dissection. Each tick was bathed in merthiolate and rinsed twice in phosphate-buffered saline, pH = 7.4 (PBS), then dissected in PBS under a dissecting microscope. The gut was placed on a slide in PBS, flattened by gently pressing under a

cover slip, and examined for spirochetes under dark-field (Leitz Laborlux 11 compound microscope with a dark-field adapter). A slide was considered negative if spirochetes were not found after examining 100 fields of view at $\times 400$.

Selected slides (with large numbers of spirochetes) were air-dried, then fixed in methanol for 10 min, air-dried again, and stored dry. They were later taken to the New York State Health Department lab at the Health Sciences Center at Stony Brook, New York, where the slides were incubated in murine monoclonal antibody 11G1 (Benach et al. 1988), which is specific to an antigenic determinant in Osp-A, a 31-kilodalton outer surface protein specific to the Lyme disease spirochete (*B. burgdorferi*). The slides were then rinsed in fluorescein isothiocyanate-conjugated antimouse IgM and examined under an ultraviolet microscope. The presence of *B. burgdorferi* was indicated by glowing spirochetes on the slide. The spirochetes from ticks collected on Assateague Island were identified with a similar technique by E. M. Bosler (New York State Health Department) using a rabbit-derived polyclonal antibody and a fluorescein isothiocyanate-antirabbit conjugate.

Statistical Methods

Tick abundances in different habitat types were analyzed with a three-way Model I ANOVA (habitat type $\times$ site on Fire Island $\times$ time of year) when the variances could be stabilized by transforming the data. Otherwise, non-parametric tests were used (Siegel 1956; Rohlf and Sokal 1981; Sokal and Rohlf 1981).

Spatial distribution data were tested for randomness with goodness-of-fit tests to a Poisson distribution, and by testing the significance of the variance-to-mean ratio (Southwood 1978; Sokal and Rohlf 1981). Statistical tests were performed with the BIOM statistical package (see Sokal and Rohlf 1981), the StatView 512+ package (D. S. Feldman and J. Gagnon, 1986, Abacus Concepts, Inc.), or on a hand calculator.

Distribution of *Ixodes dammini*

Ixodes dammini Adults

Habitat Distribution

Figure 5 shows the number of ticks captured per kilometer of transect walked through each major habitat type. Adults were less commonly encountered in beach grass-low shrub areas than in areas with higher vegetation. The number of ticks encountered in each habitat differed from the expected number based on an assumed uniform distribution among vegetation types in both the spring and the fall (Ginsberg and Ewing 1989a).

A three-way ANOVA was performed on the number of adult ticks per kilometer transect in each habitat type, in spring versus fall, at each of the

sample sites along Fire Island. (Watch Hill and the Lighthouse were excluded because transects at these sites did not include forested areas during some samples.) The interaction between season (spring versus fall) and habitat distribution was significant at $P < 0.01$, but adult tick abundance did not differ significantly among sites on Fire Island (Ginsberg and Ewing 1989a).

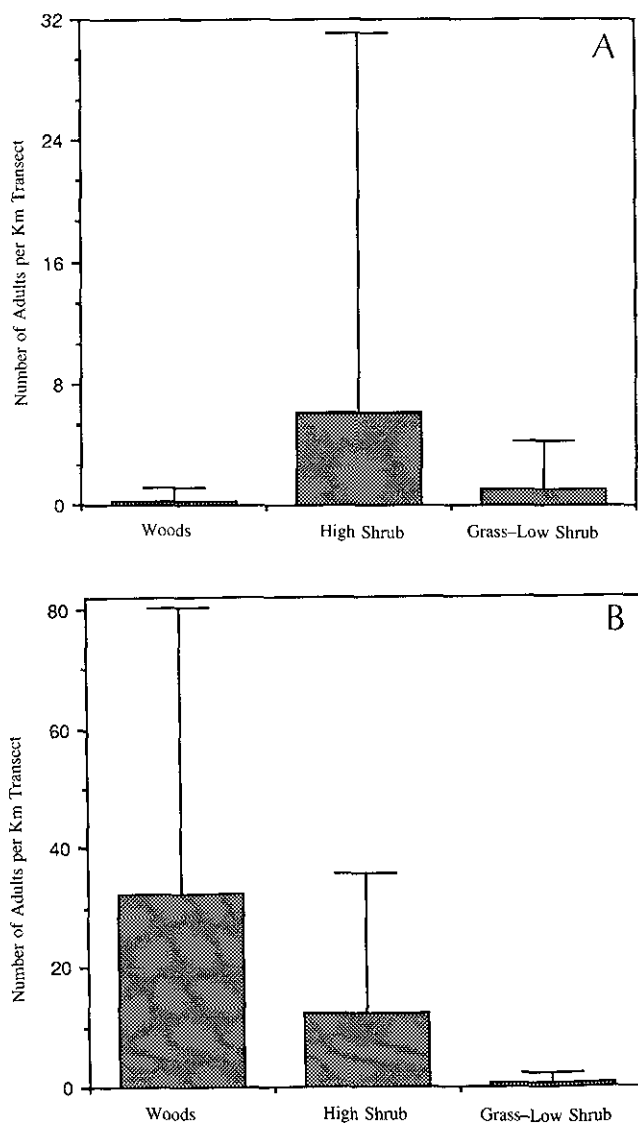


Fig. 5. Mean number of adult *Ixodes dammini* in samples from different habitats, 1986 (from Ginsberg and Ewing 1989a). Means are backtransformed geometric means; error bars are upper 95% confidence limits. A. Habitat distribution of adults, spring 1986; B. habitat distribution of adults, fall 1986.

Therefore, the distribution of adult ticks among habitats differed in the fall from that in the spring but did not differ at different localities along Fire Island (Figs. 5 and 6).

This picture of habitat distribution of adult *I. dammini* could be influenced by biases in the sampling procedure (Ginsberg and Ewing 1989a, 1989b). The data provided estimates of the likelihood of tick encounters by a person walking through different habitats, which is relevant to the risk of tick bite, but may not reflect the actual abundance of ticks in each habitat type. For example, a person contacts a greater surface area of vegetation when walking through a high thicket than through low brush and may therefore encounter more ticks, even if ticks are equally abundant in each habitat.

To test this hypothesis, ticks were sampled with muslin drags after walking each transect in the fall. Drags were placed down in the vegetation (grass, forest understory, leaf litter, etc.) where they could contact a roughly equal surface area of vegetation in each habitat type. The number of ticks collected in each habitat by muslin drags differed significantly from the number expected based on transect samples in the same areas (chi-square = 18.018, $df = 2$, $n = 45$, $P < 0.001$). However, during the drag samples, the habitat distribution of ticks collected from drags was the same as that collected from the investigator's clothing (Ginsberg and Ewing 1989b). Furthermore, like transect samples, the drag samples showed greatest tick abundance

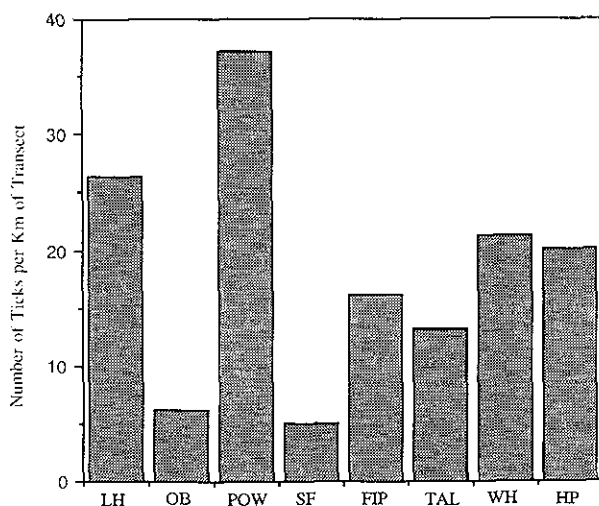


Fig. 6. Number of adult *Ixodes dammini* captured per kilometer transect at sample sites on Fire Island. Abbreviations refer to natural areas in and near the sites: LH = Lighthouse; OB = Ocean Beach; POW = Point O' Woods; SF = Sunken Forest; FIP = Fire Island Pines; TAL = Talisman; WH = Watch Hill; HP = Hospital Point.

in high shrub and woods (Fig. 7), with numbers significantly different from a uniform distribution among habitats (chi-square = 20.81, $df = 2$, $n = 45$, $P < 0.001$).

This habitat distribution has implications for the likelihood of encountering ticks as one moves from south to north on Fire Island. Beach grass-low shrub vegetation predominated in the southern one-third of each transect, near the primary dune, and ticks were relatively rarely encountered. High shrub and woods composed a greater proportion of the vegetation on the northern two-thirds of each transect, and there ticks were frequently encountered (Figs. 8 and 9).

Spatial Distribution

The distribution of the numbers of adult ticks found on the investigator at any one time (excluding times when no ticks were present) did not differ significantly between the spring and fall or between males and females (Ginsberg and Ewing 1989a).

The variance-to-mean ratio of adults in drag samples in the fall (variance-to-mean ratio = 2.538) indicated a clumped distribution (Ginsberg and Ewing 1989a). However, in most collections during transect samples, only one tick was found on the investigator at a time (Table 1). Data from eight 5-min samples taken on trails and nearby off-trails in the fall indicated that adult *I. dammini* were significantly more commonly encountered on trails than off (Ginsberg and Ewing 1989a).

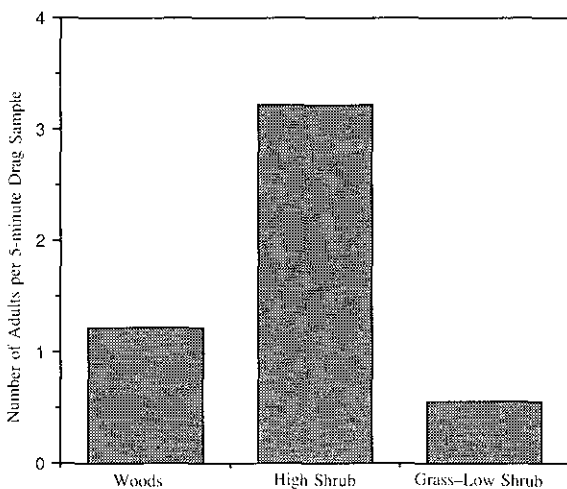


Fig. 7. Average number of adults per drag sample in different habitats. Data untransformed.

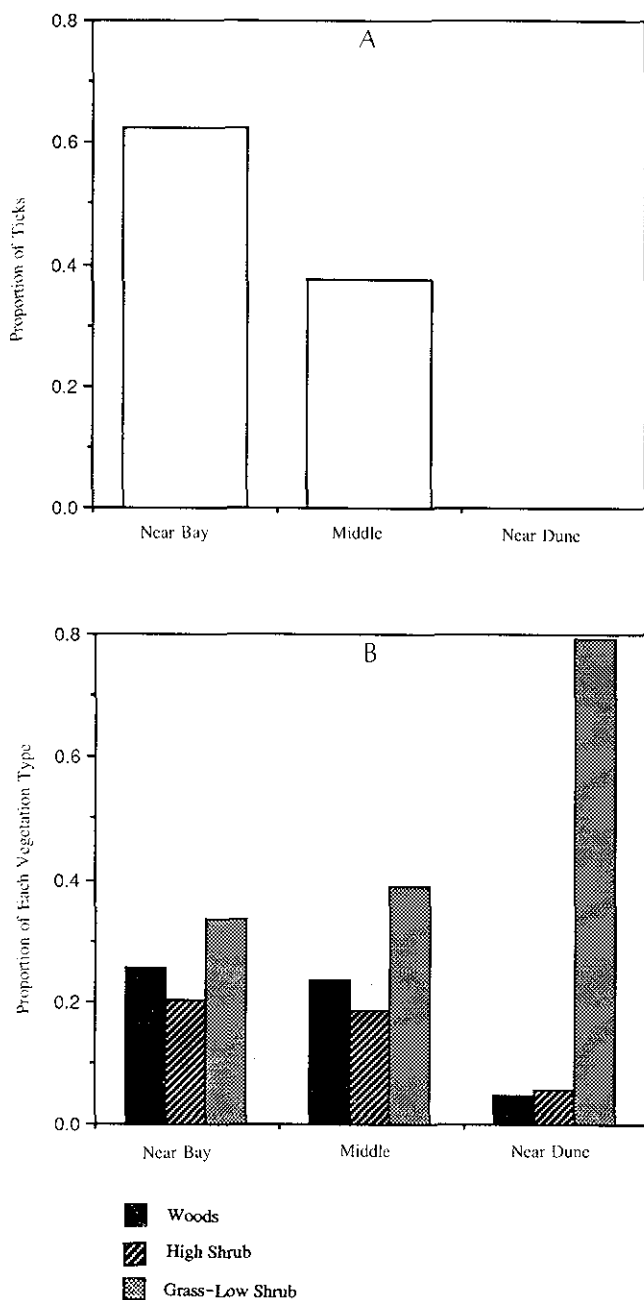


Fig. 8. Relation of adult tick abundance to habitat types along north-south transects on Fire Island. Spring samples, 1986. A, North-south distribution of spring adults; B, north-south distribution of vegetation types.

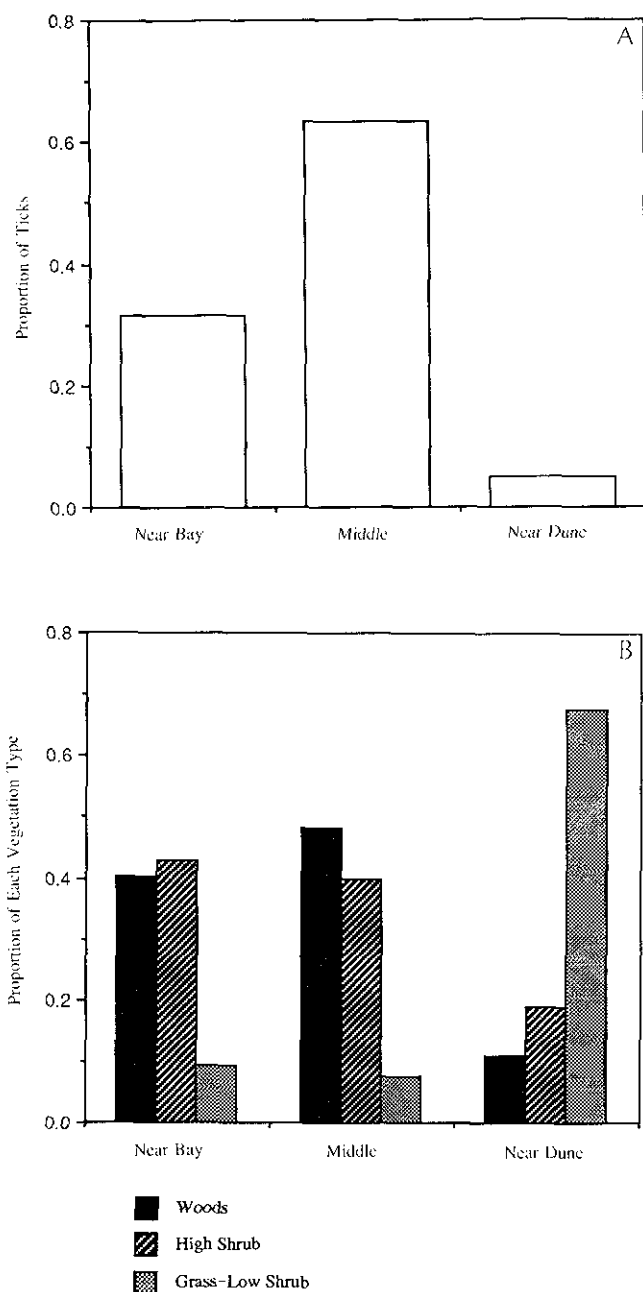


Fig. 9. Relation of adult tick abundance to habitat types along north-south transects on Fire Island. Fall samples, 1986. A. North-south distribution of fall adults; B. north-south distribution of vegetation types.

Table 1. *Percentage of samples with more than one tick.*

Species	Stage	Sample type	Percentage with >1 tick	N
<i>Ixodes dammini</i>	adult	transects	26.8	82 ^a
	adult	drags (both)	20.0	10 ^a
	nymph	drags (both)	72.2	97 ^a
	larva	drags (small)	64.3	28 ^a
<i>Amblyomma americanum</i>	adult	drags (both)	0.0	10 ^b
	nymph	drags (both)	61.9	42 ^b
<i>Dermacentor variabilis</i>	adult	path-no path	24.2	66 ^b
	adult	drags (both)	40.0	55 ^b

^a Data from Ginsberg and Ewing 1989a.^b Data from this study.

Ixodes dammini Immatures

Habitat Distribution

Habitat distributions of immature ticks in drag samples are given in Table 2. The numbers of both nymphal and larval *Ixodes dammini* captured per minute during drag samples were significantly greater in the woods than in beach grass-low shrub and high shrub habitats (Ginsberg and Ewing 1989a). Nymphs and larvae were most commonly collected in forest litter, but some were found in all habitats sampled. Tick abundance varied considerably within each habitat type from site to site.

Samples of nymphs taken by myself did not differ significantly from samples taken by Ewing (Ginsberg and Ewing 1989a), so data from both investigators were combined in the analysis. Figure 10 gives the densities of

Table 2. *Habitat distribution of immature Ixodes dammini in drag samples on Fire Island. Nymphal samples with large and small drags, larval samples with small drag only. Data from Ginsberg and Ewing (1989a).*

Tick densities ($\pm 95\%$ confidence limits)			
Stage	Sample unit	Woods	Grass-shrub
Nymphs	ticks per min	0.51 (± 0.43)	0.04 (± 0.05)
Larvae	ticks per 5-min drag	2.88 (± 2.54)	—

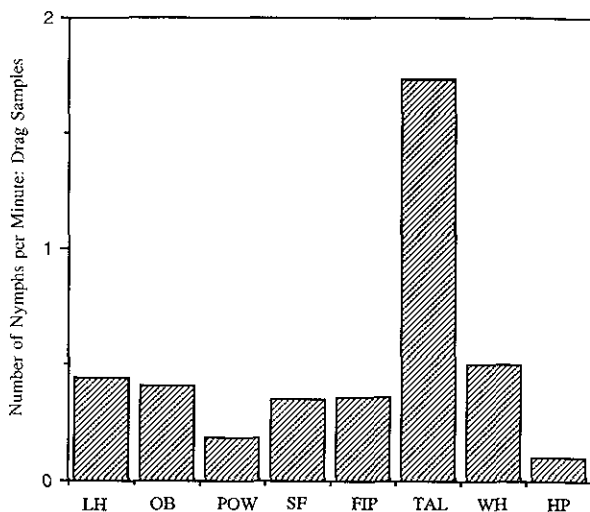


Fig. 10. Average numbers of nymphal *Ixodes dammini* per minute in drag samples at sites along Fire Island. LH = Lighthouse; OB = Ocean Beach; POW = Point O' Woods; SF = Sunken Forest; FIP = Fire Island Pines; TAL = Talisman; WH = Watch Hill; HP = Hospital Point.

nymphal ticks at the eight sample sites along Fire Island. To allow between-site comparisons, only samples taken in forest litter at each site are plotted. Tick densities were relatively low at Hospital Point and high at Talisman but were fairly uniform at most sites. Unfortunately, the samples were not randomly taken, so they could have been biased by the field workers' abilities to find favorable tick habitat at each site. Furthermore, the samples differed in variance among sites (Bartlett's test, chi-square = 25.233, $df = 3$, $P < 0.001$) and were not normally distributed. Various transformations failed to stabilize the variance or normalize the distributions. A nonparametric Friedman two-way analysis of variance by ranks found no significant differences among sites (Ginsberg and Ewing 1989a).

The distribution of habitat types among sites on Fire Island (based on spring transects) is shown in Fig. 11. Woods were most extensive in central Fire Island (from Point O' Woods to Talisman in these samples) but were more limited at the east and west ends of the island. A multiple regression of nymph density (number of ticks per minute in drag samples in forest litter) was performed on the proportion of each habitat type (four independent variables) along transects at each site. No significant relationships were detected between tick density in forest litter and the relative frequency of any combination of habitat types ($F = 1.625$, $df1 = 4$, $df2 = 3$, $P > 0.25$). Similarly, nymph density (all habitats) showed no relation to habitat frequencies ($F = 1.245$, $df1 = 4$, $df2 = 3$, $P > 0.25$).

These results must be interpreted with care because some of the violations of statistical assumptions noted previously also apply to this analysis,

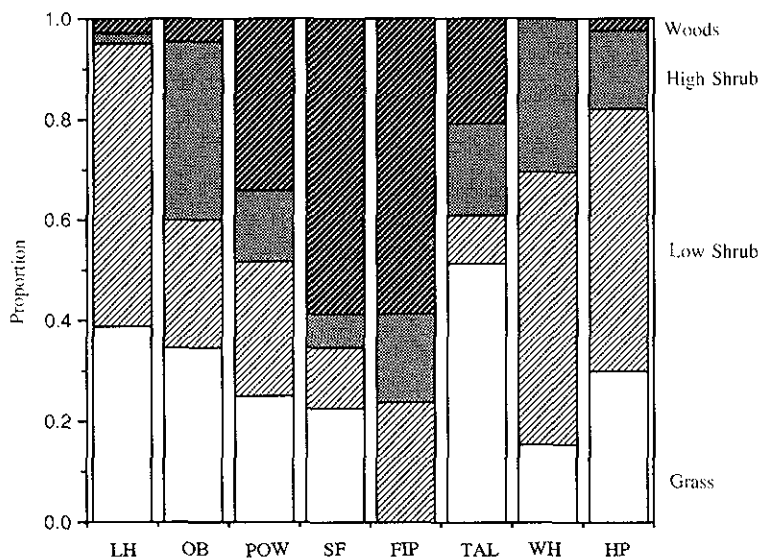


Fig. 11. Distribution of habitat types at different sites on Fire Island. Proportion of distance along north-south transect covered by each habitat type is plotted. *LH* = Lighthouse; *OB* = Ocean Beach; *POW* = Point O' Woods; *SF* = Sunken Forest; *FIP* = Fire Island Pines; *TAL* = Talisman; *WH* = Watch Hill; *HP* = Hospital Point.

and because only eight data points (sample sites) were used with four independent variables. However, the data suggest that no strong relationship occurs between the abundance of any habitat type and the tick density in a given area (but note also the multiple coefficient of determination = 0.684). Additional samples would be needed to determine whether the extent of any given habitat type influences tick density in an area. A tentative interpretation is that more favorable nymph habitat (woods) exists in central Fire Island than at the east or west end, but that the density of ticks in the woods did not differ greatly among wooded sites along Fire Island.

Spatial Distribution

The distribution of the number of immature ticks found on the drags (large and small combined) showed significant clumping for both nymphs and larvae (Ginsberg and Ewing 1989a). Of the drags with nymphal ticks, about 72% had more than one tick (Table 1). Similarly, most drag samples that had at least one larva (small drag only) had more than one individual.

The number of nymphs captured by carbon dioxide-baited traps on trails did not differ significantly from matched traps placed 3 m away, off the trails. Therefore, nymphal ticks can attack both on and off trails. The number of ticks in trail traps was not significantly correlated with the number of ticks in

the nearby nontrail traps, suggesting that the 3 m between traps was far enough so that the traps sampled different clusters of ticks. Therefore, during the trapping period nymphs moved only short distances (if at all) in search of hosts (Ginsberg and Ewing 1989a).

Tick Distribution in Residential Areas of Fire Island

The eight sample sites along Fire Island can be loosely grouped on the basis of density and permanence of human residents. Ocean Beach, Point O'Woods, and Fire Island Pines have relatively dense human populations for the summer (Ocean Beach also has numerous year-round residents). The Lighthouse, Sailors Haven, Talisman, and Watch Hill have small numbers of summer residents with numerous summer transients. Hospital Point has only transient visitors. Tick densities near human residential areas were comparable to those in other areas of Fire Island (Figs. 6 and 10).

On 24 July, larval *I. dammini* were collected in 5-min drag samples in the yards of 10 randomly selected houses in Ocean Beach. These yards had mostly natural vegetation, not manicured lawns. Eight of the 10 yards had leaf litter habitats (mostly pine needles). Larval tick distribution in the yards was statistically equivalent to that in woods habitats on Fire Island (Kolmogorov-Smirnov test, $n_1 = 20$, $n_2 = 48$, $D = 0.079$, $P > 0.90$). As in the woods, the larvae were clumped in distribution (variance-to-mean = 23.083, chi-square = 438.571, $df = 19$, $P < 0.001$). Larvae were found on the small drag in 6 of the 20 samples, with more than 1 larva in 5 of these samples (about 83% of the time, compared to 64% in the woods). Samples ranged from 0 to 30 ticks per drag (the range was 0–31 in the woods). Larval tick distribution in residential areas of Ocean Beach was, therefore, quite similar to that in wooded areas of Fire Island. Although tick distribution is similar in residential areas to that found in natural areas, overall densities appear to be higher in natural than in densely residential areas (see Chapter 4 and Tables 8 and 9 in Chapter 4).

Host Relations of Ixodes dammini

Ixodes dammini on Mice

A total of 49 white-footed mice (*Peromyscus leucopus*) were captured in 225 trap-nights in 1986. This species predominated among trap captures, with only five meadow jumping mice (*Zapus hudsonius*) and one meadow vole (*Microtus pennsylvanicus*) captured. Similarly, in a recent survey of small mammals on Fire Island (Northup 1985), *P. leucopus* composed 91% of the captures.

The capture frequencies (number of white-footed mice per trap-night) averaged 0.173 at Watch Hill, 0.173 at Sailors Haven–Sunken Forest and 0.307 in the natural area between Ocean Beach and Robbins Rest. The

number of mice captured did not differ significantly among sites (Friedman two-way analysis of variance by ranks, chi-square = 4.626, $P > 0.19$).

Nymphal *I. dammini* predominated in early summer, and larvae predominated in mid- to late summer, 1986 (Ginsberg and Ewing 1989a, 1989b), as in samples of questing ticks. Densities of nymphs on mice peaked earlier in the season than larvae in 1988 as well, when average numbers of nymphs per mouse were as high as 6.75 at Watch Hill and 11.5 in Point O'Woods in late May (see Chapter 4 and Fig. 20 in Chapter 4). During the larval activity peak that year, mice averaged 25.3 larvae at Watch Hill and 24.0 at Point O'Woods in early August.

The number of ticks per mouse did not differ significantly in different habitats for either larvae or nymphs (Ginsberg and Ewing 1989a). The comparable densities of ticks on mice in various habitats contrasts with the case of questing ticks in which clear differences in densities existed in different habitats. Thus immature ticks may disperse from high density areas on mice. On the other hand, mice may simply encounter more ticks in open habitats than do muslin drags. The mice are active in areas near the ground surface where drags do not reach effectively (because of interference from low shrubs, etc.).

Ixodes dammini on Deer

Ticks were not sampled from deer as part of this study. However, a simultaneous study of the deer herd (O'Connell and Sayre 1989) examined the interactions between *I. dammini* and *Odocoileus virginianus* on Fire Island. O'Connell and Sayre collected *I. dammini*, *A. americanum*, and *D. variabilis* from deer, with *I. dammini* composing 92% of the ticks collected. A total of 26% of the ticks on deer had spirochetes (determined by dark-field microscopy) including both *I. dammini* and *A. americanum* (O'Connell et al. 1988). Antibodies to *B. burgdorferi* were detected (IFA titers $\geq 1:64$) in 68% of the deer sampled ($n = 42$). Some individual deer had fluctuating antibody titers over time, suggesting either fluctuating levels of antibody production or intermittent deer reinfection.

Distribution of *Amblyomma americanum*

Nymphal lone star ticks (*Amblyomma americanum*) captured in drag samples were most abundant in the woods. A total of 59 *A. americanum* nymphs were captured in forest habitats. An additional 19 ticks were captured in mixed habitat samples (including pine woods, shrub, and salt marsh), 16 along trails at Talisman, and 5 in the campground at Watch Hill. Ecotonal areas were not specifically sampled in this study. However, these results are compatible, at least, with previous reports that this species is abundant in wooded ecotonal habitats (Hair and Bowman 1986).

Lone star ticks were most common at the east end of Fire Island

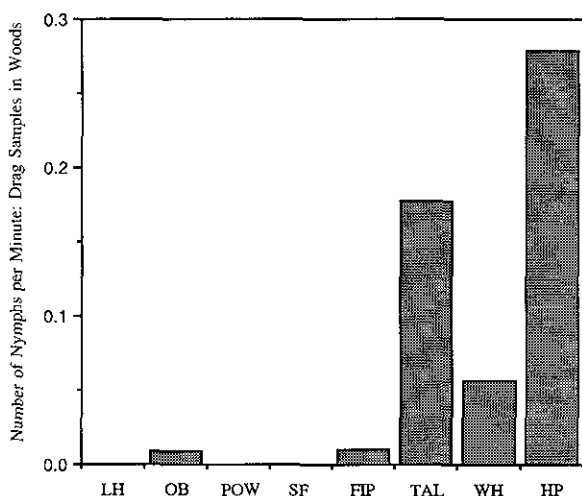


Fig. 12. Number of *Amblyomma americanum* nymphs collected per minute in drag samples at various sites on Fire Island, 1986. Sample sites are arranged on a horizontal axis from west (Lighthouse) to east (Hospital Point). Abbreviations refer to natural areas in and near the sites: *LH* = Lighthouse; *OB* = Ocean Beach; *POW* = Point O' Woods; *SF* = Sunken Forest; *FIP* = Fire Island Pines; *TAL* = Talisman; *WH* = Watch Hill; *HP* = Hospital Point.

(Fig. 12), with only one nymph collected west of Fire Island Pines. The number of ticks captured per minute (in forest habitats) was negatively correlated with distance from the east end of Fire Island (Ginsberg et al. 1991). This distribution differs considerably from that of *I. dammini* nymphs, which were common all along Fire Island. Thus, the density of *A. americanum* nymphs was not correlated with that of *I. dammini* nymphs at sites along Fire Island ($r_s = 0.174$, $n = 8$, not significant at $\alpha = 0.05$). *Amblyomma americanum* nymphs were most common at Hospital Point, where *I. dammini* nymphs were least common.

Only 13 adult lone star ticks were captured in the 1986 samples. Adults were found at all sites except Point O' Woods and the Lighthouse (at the west end of Fire Island).

The numbers of lone star ticks per drag sample were not Poisson distributed ($G = 121.786$, $df = 4$, $P < 0.001$), and the ticks were clumped in distribution (variance-to-mean ratio = 2.601, chi-square = 504.501, $df = 194$, $P < 0.001$). More than one tick was found on the drags in about 62% of the collections (Table 1) taken in 1986.

Tick traps on trails at Talisman caught an average of 3.5 *A. americanum* nymphs (range 0–33), compared to only 0.7 in traps off trails (range 0–4). However, the variability was so great that the difference was not statistically significant ($t = 0.856$, $df = 9$, $P > 0.30$).

Distribution of *Dermacentor variabilis*

The habitat distribution of adult American dog ticks (*Dermacentor variabilis*) among habitat types on Fire Island is shown in Figs. 13 and 14. Unlike *I. dammini* or *A. americanum*, American dog ticks were common in grass-low shrub habitats and in high shrubs and woods. The proportion of *D. variabilis* in grass-low shrub was significantly greater than that of *I. dammini* in this habitat type (chi-square = 6.007, df = 1, $P < 0.02$). These results agree with those of previous investigators who have found *D. variabilis* to be common in open habitats and in ecotonal areas (Sonenshine et al. 1966; Sonenshine and Stout 1968; Dodds et al. 1969; Sonenshine and Levy 1972; Campbell and MacKay 1979).

Figure 15 shows the densities of *D. variabilis* in sites along Fire Island. Like *A. americanum*, the greatest density was at Hospital Point, but densities did not decline smoothly with distance from the east end of Fire Island (Spearman rank correlation coefficient, $r_s = 0$) as did those of lone star ticks. Therefore, densities of *D. variabilis* were not correlated with those of either *I. dammini* ($r_s = -0.310$, $n = 8$, not significant at $\alpha = 0.05$) or *A. americanum* ($r_s = 0.195$, $n = 8$, not significant at $\alpha = 0.05$) at sites along Fire Island.

The number of American dog ticks found on the investigator during path-no path samples varied from 0 to 8. On tick drags (large and small combined), the sample size varied from 0 to 24. The ticks were not Poisson distributed in the drag samples ($G = 186.534$, $P < 0.001$). The variance-to-mean ratio was 6.492, indicating significant clumping (chi-square = 811.462,

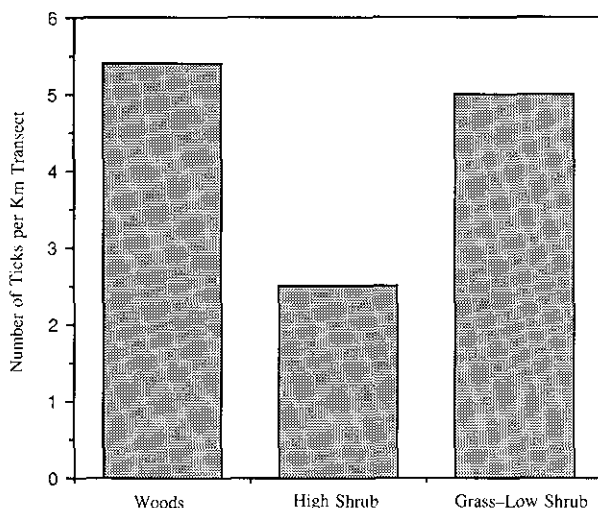


Fig. 13. Distribution of adult *Dermacentor variabilis* among habitats on Fire Island, 1986: transect samples.

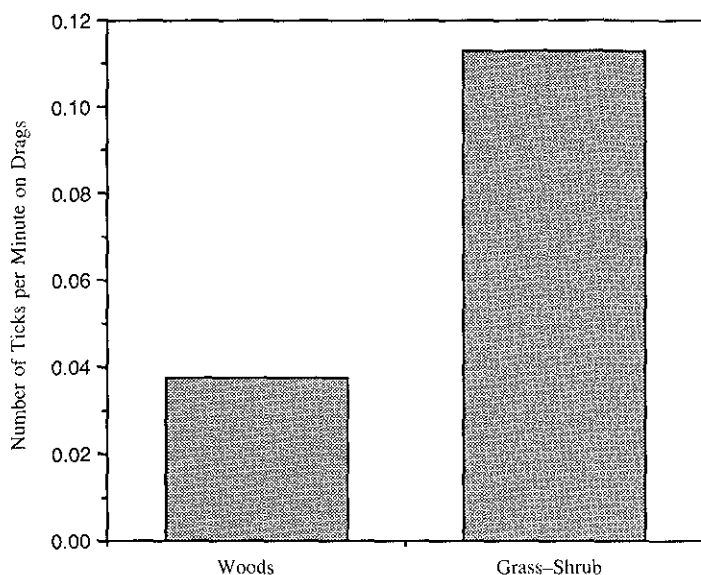


Fig. 14. Distribution of adult *Dermacentor variabilis* between habitats on Fire Island, 1986: drag samples.

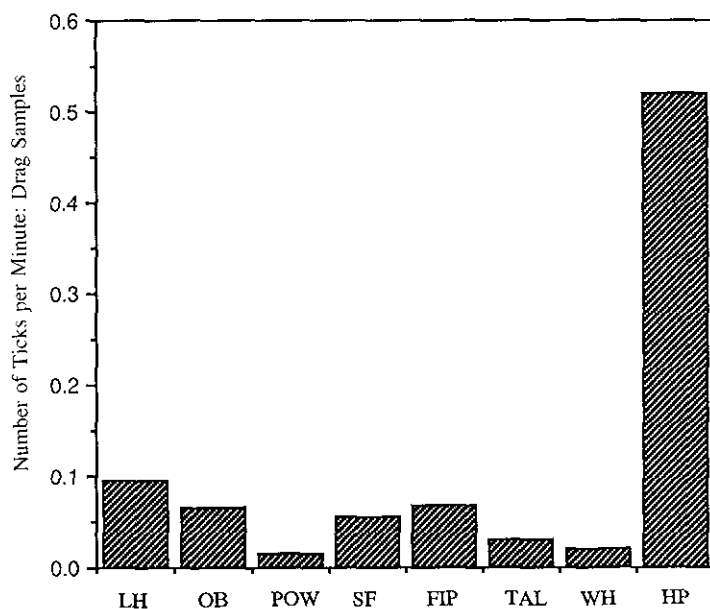


Fig. 15. Number of *Dermacentor variabilis* adults captured per minute in drag samples at various sites on Fire Island, 1986. LH = Lighthouse; OB = Ocean Beach; POW = Point O' Woods; SF = Sunken Forest; FIP = Fire Island Pines; TAL = Talisman; WH = Watch Hill; HP = Hospital Point.

df = 125, $P < 0.001$). In the path-no path samples, 24% of the collections had more than one tick (Table 1). In drag samples, 40% of the collections had more than one tick.

The well recognized tendency of *D. variabilis* to be more abundant at the sides of roads or trails than in uninterrupted vegetation was documented by Smith and coworkers (1946). On Fire Island, *D. variabilis* adults were far more commonly encountered clinging to the investigator's clothing on trails than off (Wilcoxon matched-pairs signed-ranks test, $n = 9$, $T = 0$, $P < 0.005$).

Spirochete Prevalence in Ticks

Of the *Ixodes dammini* adults examined for spirochete infection, 50.0% were infected in the spring ($n = 32$) and 38.0% in the fall ($n = 121$) of 1986. The nymphal infection rate was 32.1% ($n = 184$), and none of the 15 larvae examined were infected (Ginsberg and Ewing 1989a). These estimates are probably slightly lower than the true values because they were obtained by looking for spirochetes using dark-field microscopy. We examined 100 fields of view before calling a tick negative, but even so, we probably missed the spirochetes in some ticks that had low spirochete loads. The spirochete prevalences in nymphal and adult *I. dammini* did not differ in different habitats (Ginsberg and Ewing 1989a).

A total of 57 *Amblyomma americanum* (3 adult males, 2 females, and 52 nymphs) were dissected and the guts examined for spirochetes under dark-field. No spirochetes were found in free-living lone star ticks on Fire Island.

Sampling Biases

Immature ticks were not commonly collected in either high or low shrub habitats during drag samples. Unfortunately, the samples of immatures may have been biased because the nymphs and larvae were common in leaf litter in the woods, where the drags could easily be placed down in the litter. In shrubby habitats, on the other hand, low branches interfered with drag movement, so the leaf litter was difficult to sample. Therefore, the samples may have missed immature ticks that were present in the litter layer of shrub habitats. The actual difference between the habitat distributions of adult and immature *I. dammini* may be less of a difference in gross habitat distribution than in microhabitat distribution: adults quest up in the vegetation while immatures stay down in the leaf litter. Of course, leaf litter was probably not as thick in shrub areas as in the woods. In any case, samples of the leaf litter from each habitat type (e.g., using tick traps or Berlese funnel samples) can determine whether there is a true difference in tick distribution among gross habitat types or only among microhabitats.

As might be expected, different sampling techniques differ in efficiency at sampling different tick species. For example, tick traps generally captured

more *A. americanum* than *I. dammini*, even where *I. dammini* predominated in drag samples from the same general areas (Ginsberg and Ewing 1989b). *Amblyomma americanum* actively seeks hosts (Waladde and Rice 1982), while some other tick species wait in ambush. Therefore, *A. americanum* might be more active than *I. dammini* and more likely to encounter stationary traps. In laboratory trials, *A. americanum* nymphs displayed greater mobility than *I. dammini* nymphs (Ginsberg and Ewing 1989b). Similarly, Schreck and coworkers (1986) commented that *A. americanum* is more aggressive than *I. dammini*. This difference in activity levels could contribute to the sampling bias observed between carbon dioxide-baited traps and muslin drags.

Another potential source of sampling bias is the influence of weather on tick activity. Samples were taken on clear days with moderate weather, whenever possible, to minimize any effects of weather. No significant correlations were found between tick abundance and either temperature or relative humidity (Table 3), suggesting that weather did not introduce any important bias into the results. However, because the samples were taken during calm weather, no conclusions can be drawn on the influence of weather on tick activity. Samples would be needed under a wide variety of weather conditions to make such a judgment.

Conclusions

Northern Deer Tick (Ixodes dammini)

1. Adults were most common in high shrub habitats (1 m and taller) in both spring and fall, and in the woods in fall. They were found singly on the investigator in most of the collections. Adult deer ticks were more common on trails than in nearby areas off trails.
2. Nymphs were most common in leaf litter in the woods in early summer. No significant differences were found in nymph densities among sample sites along Fire Island. Nymphs were clustered in distribution; most of the collections on muslin drags had more than one nymph. The density on and off trails was statistically equivalent.
3. Larvae were most common in woods leaf litter in the late summer. They were clustered in distribution; most of the collections on small muslin drags had more than one larva.
4. *Ixodes dammini* larvae were found in residential yards in Ocean Beach on Fire Island. The spatial distribution of larvae in residential areas was not significantly different from that in natural areas on Fire Island.
5. An average of 3.00 nymphs per white-footed mouse (*Peromyscus leucopus*) were found during early summer and 8.18 larvae per mouse in late summer 1986. In 1988, densities as high as 11.5 nymphs per mouse were recorded during the peak of nymphal activity (at Point O'Woods) and 25.3 larvae per mouse during the larval peak (at Watch Hill). The number of immatures per mouse did not differ significantly in different habitats.

Table 3. *Relation of tick densities to temperature and relative humidity (RH).*

Tick stage	Time of year	Sample Type	N	Correlation ^a with	
				Average temperature	Average RH
Adult	spring	transect	4	0.302	-0.325
Adult	fall	transect	8	0.084	-0.236
Adult	fall	drag	8	0.293	0.251
Nymph	early summer	drag	6	0.611	-0.614
Larva	late summer	drag	8	0.298	0.034

^a Product moment correlation coefficients—none of these correlations are significant at the 0.05 level (Rohlf and Sokal 1981).

6. Approximately one-half of the adults were infected with spirochetes in the spring, and two-fifths in the fall of 1986 on Fire Island. About one-third of the nymphs were infected in early summer. Spirochete prevalence in nymphs and adults did not differ significantly in different habitats.
7. The likelihood of being bitten by infected ticks was greatest in early summer (May–July) when nymphs were active and numerous visitors were on Fire Island. The nymphs are small and hard to see, are spatially clustered, and are often infected with spirochetes. Activities that involve direct contact with leaf litter (e.g., children playing in leaves, campers gathering leaves for bedding, families picnicking on leaf litter in the woods) bring a relatively high risk of being bitten by infected ticks. The likelihood of exposure to infected ticks also increased in shrub habitats in the spring (March–May) and fall (October–November) when adult ticks were most active. Activities such as landscaping, brush and trail clearing, and trail patrolling at these times of year entail a relatively high risk of exposure to infected adults.

Lone Star Tick (Amblyomma americanum)

1. Nymphs were most common at the east end of Fire Island.
2. No spirochetes were found in questing lone star ticks on Fire Island.

American Dog Tick (Dermacentor variabilis)

Adults were common in grass and low shrub habitats as well as high shrub and woods habitats. Adult dog ticks were more common on trails than off.

Recommended Precautions

Ticks were found in all habitats sampled, including bare sand, beach grass meadows, low shrub, high shrub, pine and broadleaf woodlands, salt marshes, and residential yards. Therefore, precautions to avoid tick bites should be taken in all natural areas on Fire Island. However, special care should be taken in high shrub habitats and woods in the spring and fall and in leaf litter in early summer.

General Precautions to Avoid Tick Bites

Several precautions can minimize the likelihood of being bitten by deer ticks, and if bitten, can minimize the probability of disease transmission:

1. When in natural areas, tuck pant legs into socks and shirts into pants. This precaution will keep ticks on the outside of clothing where they can be spotted and picked off.

2. Wear light-colored clothing. Dark ticks can be most easily spotted against a light background.
3. Inspect yourself frequently for ticks while in natural areas. Have a companion inspect your back. Remove ticks before they have a chance to attach. If a tick is attached, remove it as soon as possible. The tick can be saved in a sealed vial for future identification.
4. Repellents should be used according to label instructions. Applying repellents to shoes, socks, and pants will probably be most effective against deer ticks, which quest low in vegetation.
5. Upon returning from the field, inspect your entire body (including your head and back) carefully for ticks. Remove any attached ticks immediately. The best method is to grasp the tick anteriorly (near the mouth parts) with fine forceps and to steadily pull the tick straight out. If part of the tick breaks off in the wound, seek medical attention to have it removed. See Needham (1985) for details.

Special Precautions in Spring and Fall (Adult Ticks)

In the spring and fall, rangers patrolling trails and maintenance workers involved in landscaping and brush or trail clearing are especially likely to encounter infected adult ticks. Note that during drag samples in the fall of 1986, an average of about three ticks were collected per 5-min sample in woods and high shrub. Therefore, workers in these habitats should take special precautions to avoid tick bites. Recommendations include the following:

1. Workers should wear light-colored coveralls, with the pant legs tucked into their socks, or coveralls with feet. High rubber boots should be worn when possible. The work clothes should be treated with repellent, especially the legs of the coveralls. These work clothes should not be worn home but should be stored in a cabinet or closet at the workplace that is reserved for this purpose.
2. Workers should inspect themselves and one another frequently (every few minutes) for ticks while in tick habitat. One approach is to establish a buddy system, where companions can inspect one another's backs when in the field.

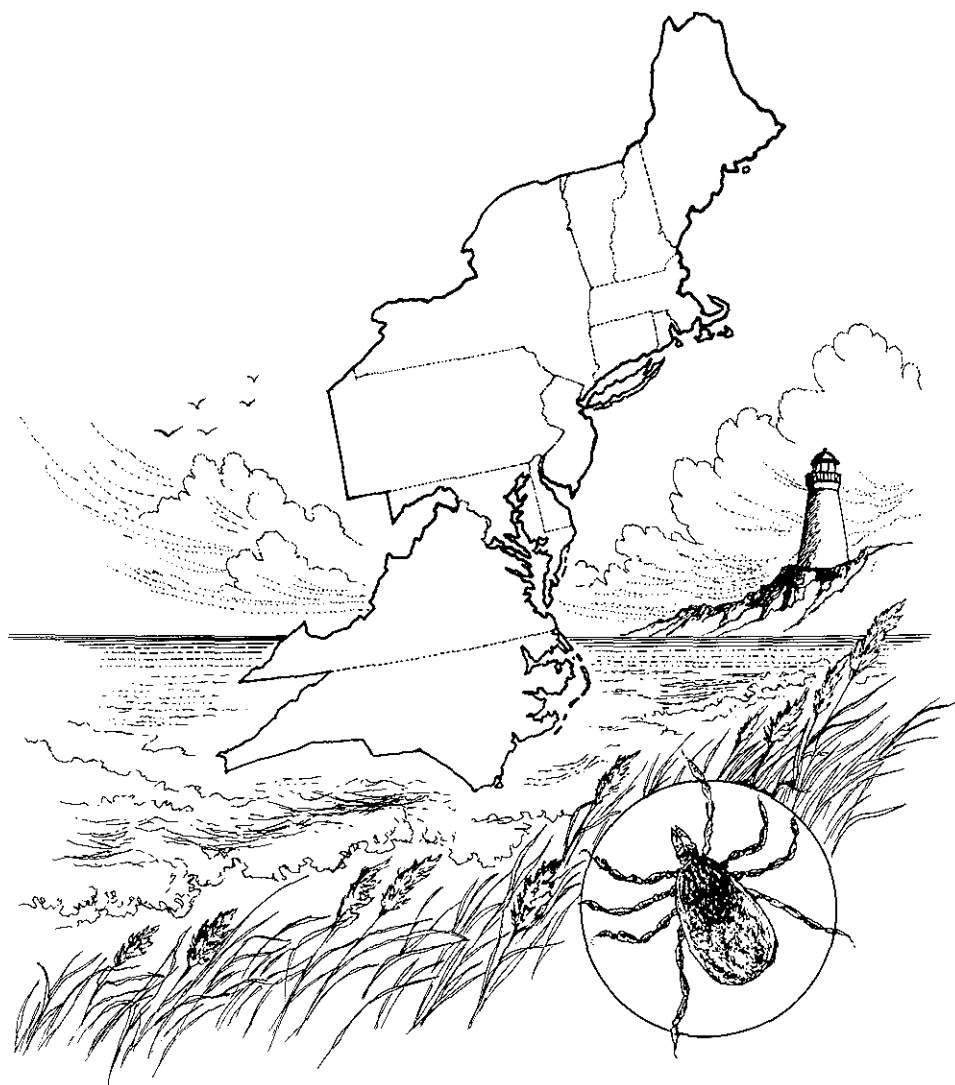
Special Precautions in Spring Through Midsummer (Nymphal Ticks)

In early summer, direct contact with leaf litter entails an especially high risk of exposure to infected nymphs, which are difficult to see and remove. This type of exposure is likely to be a problem for children playing in the leaves, campers (especially wilderness campers) who gather leaves for bedding, and any individuals who sit, lie down, or move about in the leaf litter. The following actions are recommended:

1. Tick information should be made available to all visitors to Fire Island. The information should be included in interpretive talks and displays at the visitor centers and should be posted throughout Fire Island. Informational brochures on ticks and Lyme disease and preserved specimens of the ticks (larvae, nymphs, and adults) should be available for inspection at all checkpoints and visitor centers.
2. Woods in high-use visitor areas should be posted with specific warnings about ticks in leaf litter. Examples of high-priority areas for such posting include the secondary dune area and woods at Hospital Point, the woods at Watch Hill (especially near the campground), the Carrington tract (between Fire Island Pines and Cherry Grove), and Sailors Haven (especially in the Sunken Forest).
3. Wilderness campers should be shown specimens of deer ticks (all stages) before setting forth, and campers should be specifically instructed not to use leaf litter for bedding. Campers should use a ground cloth or tent with a floor and should exercise great caution when packing away the tent or ground cloth.
4. Finally, preserved specimens of ticks (all stages) should be provided to physicians and medical clinics all along Fire Island, with concise explanatory information sheets on the ticks and on Lyme disease. Many health care workers, though familiar with Lyme disease, are apparently unaware of the diminutive size of nymphal deer ticks.

Tick monitoring should continue on Fire Island so that changes in the epidemiological status of Lyme disease can be detected early. Specifically, data should be gathered on the distributions and abundances of deer ticks and lone star ticks on Fire Island and on the prevalence of spirochetes in each of these tick species.

CHAPTER 2. Geographical Distribution of *Ixodes dammini* and *Borrelia burgdorferi* in North Atlantic and Mid-Atlantic National Parks



Lyme disease is commonly believed to be increasing its range in the eastern United States. One source of evidence for geographical spread comes from the discovery of human cases of Lyme disease in areas where the disease was not previously known. Cases were reported to the Centers for Disease Control from 11 states in 1980, 18 states in 1983, and 28 states in 1986 (Ciesielski et al. 1988). The second major line of evidence for geographical spread is the discovery of *Ixodes dammini* in areas where it had not been previously reported (Spielman et al. 1985).

Unfortunately, these approaches both depend on comparisons of present with past distributions. Lyme disease was first recognized in 1975 (Steere et al. 1977b), the tick was first described in 1979 (Spielman et al. 1979), and the spirochete was recognized and described in the 1980's (Burgdorfer et al. 1982; Benach et al. 1983; Steere et al. 1983c; Johnson et al. 1984). Lyme disease mimics many other ailments (Pachner 1988) and is often misdiagnosed. Therefore, previous records may be sparse largely because the disease, tick, and spirochete were not recognized, rather than because they were absent. The actual rates of spread of northern deer ticks and Lyme disease are not known.

A more direct way to measure geographical spread is to sample ticks quantitatively in several areas both within and outside the current range, to determine the percentage of ticks infected with spirochetes, and to repeat the sample in subsequent years for comparison. Unfortunately, the baseline survey data needed for such a comparison are lacking. An initial survey of ticks and Lyme spirochetes in national parks of the eastern United States was taken in 1987 and 1988. The data from this survey can be used to gauge the current extent of the problem in eastern national parks (e.g., to compare the risk of acquiring Lyme disease in various parks), and as baseline data for studying subsequent spread of *I. dammini* and *B. burgdorferi* in eastern North America.

Methods

Sixteen National Park System units were included in this survey (Fig. 16; Table 4). At each site, potential tick habitats (as described by Ginsberg and Ewing (1989a)) were delineated using vegetation maps, consulting with local staff, and performing preliminary habitat surveys of the park. Where possible, samples were concentrated in forests with leaf litter on the ground and signs of mammal activity. Tick habitat was divided into roughly equal-sized sections (e.g., patches of forest separated by roads, bodies of water, or other habitat types). Five sections from each park were selected with a random number table and sampled for ticks. This random sample generally produced only small sample sizes because of the highly clustered distributions of *I. dammini*. Therefore, after the initial survey, any areas with dense tick populations or promising-looking sites outside of the random sections were sampled to

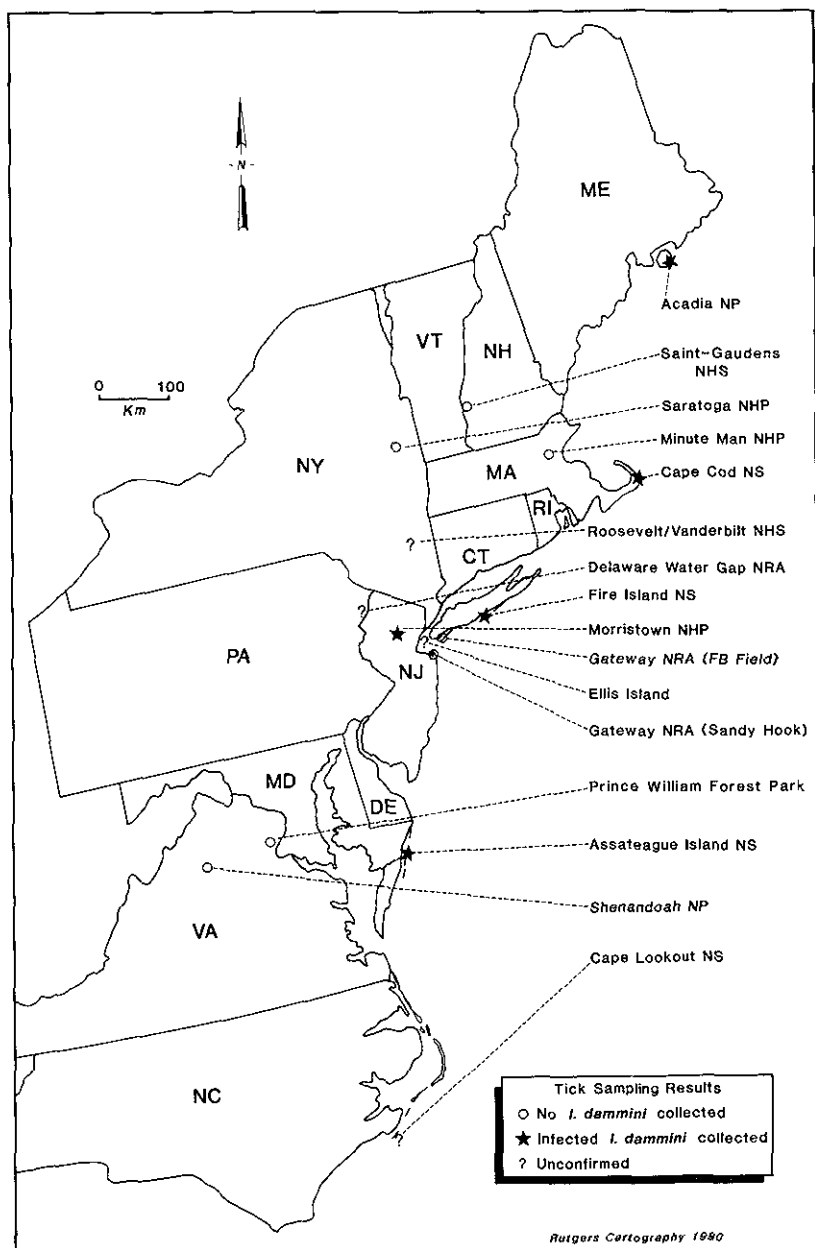


Fig. 16. Parks sampled in geographical survey. *NP* = National Park; *NHS* = National Historic Site; *NHP* = National Historical Park; *NS* = National Seashore; *NRA* = National Recreation Area.

Table 4. *National park sites included in survey.*

Site	Dates sampled	Minutes flagging (f) or walking (w)	Description
Acadia National Park, Maine	23, 24, 27 July 1987	223 (f)	coastal, mountainous
Minute Man National Historical Park, Mass.	11 June 1987	33 (f)	inland, developed
Saratoga National Historical Park, N.Y.	16 July 1987	25 (f)	inland, hills
St. Gaudens National Historic Site, N.H.	17 July 1987	35 (f)	inland, hills
Cape Cod National Seashore, Mass.	18-19 June 1987	323 (f)	coastal, cape
Roosevelt-Vanderbilt national historic sites, N.Y.	22 June 1988	100 (f)	inland, hills
Delaware Water Gap National Recreation Area, N.J. and Pa.	24 November 1987	100 (w)	inland, mountainous
Fire Island National Seashore, N.Y.	24-25 June, 1, 3, 6, 10-12 July 1987; 28 June, 1, 6-8, 14 July 1988	350 (f); 300 (f)	coastal, barrier island, developed and natural areas
Gateway National Recreation Area-Floyd Bennett Field, N.Y.	1 June 1987	15 (f)	coastal, developed
Gateway National Recreation Area-Sandy Hook, N.J.	5 June 1987	35 (f)	coastal, developed
Ellis Island, N.Y.	14 August 1987	80 (f)	coastal island, developed
Morristown National Historical Park, N.J.	9 June, 1 December 1987	98 (f) 120 (w)	inland, hills
Assateague Island National Seashore, Md.	20 October 1987; 8, 10-11 June 1988	189 (w); 336 (f)	coastal, barrier island
Shenandoah National Park, Vt.	17 October 1987	120 (w)	inland, mountainous
Prince William Forest Park, Va.	18 October 1987	120 (w)	inland, hills
Cape Lookout National Seashore, N.C.	12-13 May 1987	30 (f)	coastal, barrier island

increase the number of specimens for determining spirochete prevalence in questing ticks.

Free-living nymphs were sampled by the flagging and dragging method of Ginsberg and Ewing (1989a, 1989b), and spirochetes were detected and identified with the methods described in Chapter 1.

Results

Ixodes dammini was collected at 5 of the 16 national park sites sampled (Fig. 16; Table 5), including Acadia National Park, Cape Cod National Seashore, Fire Island National Seashore, Morristown National Historical Park, and Assateague Island National Seashore. In addition, specimens of *Ixodes* (not determined to species) were found by workers at Eleanor Roosevelt National Historic Site, Delaware Water Gap National Recreation Area, and on Ellis Island (part of the Statue of Liberty National Monument). In each case, however, the worker involved had recently been in an area offsite where he or she could have picked up the tick. Flagging samples at these three parks failed to collect *I. dammini*. A single male *Ixodes* sp. was collected on the Shackleford Bank at Cape Lookout National Seashore. The tick was inadvertently destroyed during dissection before being identified to species (no spirochetes were detected).

Overall tick densities differed significantly among parks (Kruskal-Wallis test, $df = 4$, $H = 52.717$, $P < 0.001$), with highest densities on Fire Island, New York. Data from the random samples alone showed a similar trend (Table 5), but the sample sizes were far smaller and the differences were not statistically significant (Kruskal-Wallis test, $df = 4$, $H = 8.837$, $0.10 > P > 0.05$).

The percentage of nymphs infected with spirochetes (Table 5) differed significantly among parks (Morristown National Historical Park was excluded from chi-square test because of small sample size, chi-square = 29.23, $df = 3$, $P < 0.001$), with an average of 28.0% of the nymphs infected. An average among parks of 51.5% of the adults were infected (Acadia National Park was excluded because of small sample size). Piesman and coworkers (1987a) used the number of infected ticks encountered per person per hour (= number of ticks collected per person per hour times proportion of ticks infected) to quantify transmission risk for Lyme disease on Nantucket Island. Using this index (calculated from the overall data), transmission risk was greatest on Fire Island (11.1 infected nymphs per person per hour), with considerably lower risk at Assateague Island National Seashore (5.6), Cape Cod National Seashore (1.5), and at Acadia National Park (0.1).

Discussion

The distributions of *I. dammini* and *B. burgdorferi* reported in this study agree with previously published reports from eastern North America. *Ixodes*

Table 5. *National park sites with Ixodes dammini, 1987-1988.*

Park ^a	Dates	Stage	Nymphs per sample (N) ^b		Percent with spirochetes (N)	
			Random samples	All samples		
Acadia National Park	7/87	nymphs	0.2 (5)	0.1 (10)	11.8 ^{c,d}	(17)
Cape Cod National Seashore	6/87	nymphs adults	0.6 (5)	0.6 (5)	21.3 ^d 71.4	(47) (7)
Fire Island National Seashore	6-7/87 6-7/88 10/88	nymphs nymphs adults	3.44 (5)	3.25 (69)	28.4 ^d 26.7 47.2	(102) (30) (36)
Morristown National Historical Park	6/87 12/87	nymphs adult	0.6 (5)	0.5 (6)	0.0 33.3	(7) (12)
Assateague Island National Seashore	10/87 6/88	adults nymphs			54.2 ^e 78.3 ^f	(24) (23)

^a Other parks that may have *Ixodes dammini*: Roosevelt-Vanderbilt national historic sites, Delaware Water Gap National Recreation Area, Ellis Island, Cape Lookout National Seashore.

^b Five-minute flagging samples (see Methods section in Chapter 1).

^c Data from Ginsberg and Ewing (1988).

^d Spirochetes identified on selected slides using monoclonal antibody 11G1 (see Methods section in Chapter 1).

^e Spirochetes identified on selected slides using polyclonal antibody (initial attempts using the monoclonal antibody were not successful; see Methods section in Chapter 1).

^f Twenty-one of these 23 nymphs were collected at just one spot, so sample cannot be considered representative of infection rates over all of Assateague Island.

dammini has previously been recorded from Maine (Anderson et al. 1987) to Maryland (Coan and Stiller 1986), and ticks infected with *B. burgdorferi* have been reported from Maine (Ginsberg and Ewing 1988) to New Jersey (Schulze et al. 1986). The comparative samples in this study suggest that of the parks sampled, the greatest risk of acquiring Lyme disease is at Fire Island National Seashore in New York.

This distribution correlates well with human case reports. In 1986, New York State had the most case reports of any of the states covered in this study (Ciesielski et al. 1988). Within New York State, the majority of reported cases have come from Suffolk County on Long Island (which includes Fire Island; Hanrahan et al. 1984a). Numerous cases have also been reported in Westchester County (just north of New York City), with a declining number of cases in the counties north of Westchester, up the Hudson River as far as Dutchess County (site of Roosevelt-Vanderbilt national historic sites). Human cases north of this point all had travel histories to southern endemic areas or out of state (White 1988). I did not find ticks at Saratoga National Historical Park, which is located along the Hudson River far north of the known endemic areas. However, Anderson and coworkers (1987) reported that *I. dammini* were collected from a deer shot in Washington County, across the Hudson River from Saratoga.

Several features of the hosts of immature ticks, such as infectiousness to uninfected ticks, efficiency of vertical transmission, and phenology of reproduction, can apparently influence the prevalence of Lyme spirochetes in nymphal ticks (Ginsberg 1988). Different mammal species differ considerably in transmission efficiency to uninfected ticks (Donahue et al. 1987; Telford et al. 1988a, 1988b). Therefore, the prevalence of *B. burgdorferi* at a site depends, in part, on the relative abundances of efficient reservoir species, such as white-footed mice, *Peromyscus leucopus* (Levine et al. 1985), compared to the abundances of less efficient reservoirs or reservoir-incompetent species in the area (Mather et al. 1989a, 1989b). Given the environmental differences among the parks sampled (Table 4), it is not surprising that infection rates of questing nymphs varied significantly among parks. Interestingly, the average among parks of spirochete prevalence in *I. dammini* was about one-third of the nymphs and half the adults infected. This average prevalence matches well with infection rates in free-living ticks previously reported from several endemic areas, which display considerable site-to-site variation, but with average values of about one-fifth to one-third of the nymphs and one-half of the adults infected (Anderson 1988; Falco and Fish 1988; Ginsberg and Ewing 1989a).

The parks surveyed for this study include areas that have long been recognized as endemic areas for Lyme disease. However, several well known foci of Lyme disease in the Northeast (e.g., coastal Connecticut, Rhode Island, and parts of coastal Massachusetts) were not sampled because no national park sites are located in these areas. Unfortunately, samples from these areas taken by other investigators cannot be compared with the data

reported herein unless the field techniques were the same. For example, Piesman and coworkers (1987a) sampled nymphal *I. dammini* on Nantucket Island with corduroy flags of unspecified colors and dimensions. I used unbleached muslin flags with specific shapes. The differences in texture and possibly color and surface area of the flags used in these two studies compromise the value of any comparisons between them. Therefore, the results reported here are most valuable as baseline data on the current distribution of *I. dammini* infected with *B. burgdorferi* in North Atlantic and Mid-Atlantic national parks.

Fortunately, *I. dammini* was not detected in most of the parks sampled. Of course, given the spotty distribution of nymphal *I. dammini*, focal hotspots of this species could have been missed in some of these parks. Therefore, ticks may be present at some of the parks at which I failed to detect them. These samples were designed for statistical comparability, and not to detect ticks at all sites where they might be present. Resource managers, staff, and visitors should maintain vigilance at all parks in the eastern United States. The major value of the results reported here is their role as a baseline for comparison with future surveys using identical techniques with comparable sampling effort. Such comparisons can provide relatively objective data on the rate of spread of these species (and of Lyme disease) in national park sites in eastern North America.

Conclusions

Ixodes dammini was sampled by flagging at 16 national park sites in the North Atlantic, Mid-Atlantic, National Capital, and Southeast regions in 1987 and 1988, and infection rates with *Borrelia burgdorferi* were estimated. Overall tick densities differed significantly among parks, ranging from 0.1 nymphs per 5-min flagging sample in Acadia National Park to 3.24 nymphs per sample on Fire Island. Spirochete prevalence in ticks also differed significantly among parks. Average values for all parks with infected ticks were 28.0% of nymphs and 51.5% of adults infected. In parks where *I. dammini* was collected, transmission risk (number of infected ticks encountered per person per hour) varied from 0.1 at Acadia National Park to 11.1 on Fire Island National Seashore. Therefore, of the parks sampled, the risk of acquiring Lyme disease is greatest at Fire Island in New York State. These baseline data can be compared to results from future surveys (that use the same field techniques) to quantify the rate of spread of *I. dammini* and *B. burgdorferi* in eastern North America.

CHAPTER 3. Epizootiology of Lyme Disease



Theoretical aspects of the epizootiology of Lyme disease have, to the present time, received only limited attention. Ginsberg (1988) used a simple model to examine the influence of infectivity, efficiency of vertical transmission, and timing of vertebrate host reproduction on the spread of spirochetes through natural populations. Mather and coworkers (1989b) used a slightly different model and field data to estimate the proportion of infected nymphal ticks that had picked up spirochetes from various host species.

This paucity of theoretical studies results partly from the fact that the population dynamics of *Ixodes dammini*, the major vector of Lyme disease in North America, are not yet well understood. Most studies to date have dealt with the basic life cycle and natural history of this species (Piesman and Spielman 1979; Carey et al. 1980; Main et al. 1982; Spielman et al. 1985; Schulze et al. 1986; Ginsberg and Ewing 1989a); only a few have examined population dynamics (Wilson et al. 1984, 1985, 1988; Daniels et al. 1989). In contrast, a considerable amount of information has been collected on the vertebrate hosts of *I. dammini*, the vector potential of various arthropod species, and reservoir competence of various vertebrate species (reviewed by Anderson 1988, 1989; Spielman 1988a).

This chapter's approach to Lyme disease ecology differs in several respects from that of most theoretical studies of the epidemiology of infectious diseases (Bailey 1975). Since the nymphal stage of *Ixodes dammini* is responsible for most human cases of Lyme disease (Spielman et al. 1985), the epidemiology of this disease is approached by examining the factors influencing spirochete prevalence in nymphal ticks. Humans are assumed to play only a negligible role in Lyme disease epizootiology in most areas (that is, of all nymphs in an area, only a small percentage have picked up spirochetes by feeding on humans as larvae). Second, epizootiology is modeled as a discrete rather than a continuous process because in northeastern North America, *I. dammini* goes through three feeding periods that are substantially separate in phenology (larvae feed in mid- to late summer, nymphs in late spring to midsummer, and adults in the fall to early spring). Therefore, each feeding period is treated as a discrete event, and factors influencing changes in spirochete prevalence during that feeding period are emphasized.

Specifically, the model of Ginsberg (1988) is expanded in this chapter to examine the factors that influence spirochete prevalence in questing ticks and vertebrate hosts. The model is applied to data collected on Fire Island and to published data from other areas to examine the influences of various factors on spirochete prevalence. A preliminary analysis of the interactions of these factors in endemic areas is presented, including the effect on spirochete prevalence of alternative host species and of tick immigration.

Factors that Influence Spirochete Prevalence in Ticks

Northern deer ticks, *Ixodes dammini*, feed three times during their lifetime: once as larvae, once as nymphs, and once as adults. The proportion of ticks of

a given stage infected with Lyme spirochetes after a season of feeding (k_t') depends on the proportion that was infected before feeding (k_t), and the proportion of those that were not infected before feeding ($1 - k_t$) that pick up spirochetes during the season. This last proportion depends on the proportion of individuals of each host species (h) that are infected with spirochetes (k_h), the infectivity of each host species (i_h = of the uninfected ticks that feed on infected individuals of host species (h), the proportion that become infected with spirochetes), and the proportion of ticks that feed on each host species (p_h). Ginsberg (1988) used the following equation to model changes in spirochete prevalence in nymphal *I. dammini*:

$$k_t' = k_t + (\sum_h k_h i_h p_h) (1 - k_t). \quad (1)$$

This equation assumes that infected ticks remain infected throughout the feeding season and that no difference exists in mortality rates between infected and uninfected ticks. Of course, tick migration into an area during the feeding season could influence k_t' if spirochete prevalence in immigrants differed from that of resident ticks. This could occur if the hosts of immigrants (s) differed in spirochete prevalence or infectivity from the hosts of residents (h). Emigration, on the other hand, would not influence k_t' unless the likelihood to emigrate is influenced by whether or not a tick is infected. For the present, therefore, I will consider only the effects of immigration. If P_r is the proportion of ticks after a feeding season that were resident in the area before feeding, P_i is the proportion of ticks that immigrated during the season ($P_r + P_i = 1$), and k_i is the proportion of immigrants that were infected before feeding, then

$$k_t' = [k_t + (\sum_h k_h i_h p_h) (1 - k_t)] P_r + [k_i + (\sum_s k_s i_s p_s) (1 - k_i)] P_i. \quad (2)$$

The factors in this equation that influence k_t' are considered individually in the following sections.

Proportion of Ticks Infected Before Feeding (k_t and k_i)

The proportion of questing ticks that are infected differs in different stages. *Ixodes dammini* are rarely infected with spirochetes transovarially, so infection rates in questing larvae are low. Spirochete prevalences in field-collected larvae were 0% in Connecticut (Steere et al. 1983a) and 0.7% in Massachusetts (Piesman et al. 1986). Magnarelli and coworkers (1987) reported that 1.9% of the larvae reared from the eggs of engorged females in Connecticut were infected (the females had been removed from deer). In a survey of questing ticks in northeastern and Mid-Atlantic national parks, I recorded an average of 28% of questing nymphs and 52% of questing adults infected with spirochetes (see Chapter 2). For the purposes of this discussion, I will use k_t values of 0.01 for larvae, 0.28 for nymphs, and 0.52 for adults.

Proportion of Hosts Infected (k_h and k_s)

The prevalence of spirochetes in a given host species depends, in part, on the prevalence of spirochetes in ticks (k_t) and on the number of ticks per host individual (n). Even when k_t is small, if numerous ticks bite each host individual, the probability that the host individual will be bitten by at least one infected tick can be high. The probability that a host is bitten by at least one infected tick (P_I), given n ticks per host and an overall proportion of k_t of the ticks infected, can be calculated from the binomial distribution as follows:

$$P_I = 1 - (1 - k_t)^n. \quad (3)$$

This probability is plotted at different spirochete prevalence levels (in ticks) and from 0 to 50 ticks per host in Fig. 17. At a typical prevalence level (in an endemic area) of spirochetes in nymphal ticks ($k_t = 0.28 = 28\%$ of the questing ticks infected), the probability of being bitten by at least one infected tick is high, given multiple tick bites per host. For example, at just 3 ticks per host, the probability is 63%; at 10 ticks per host, the probability is 96%.

Hosts are bitten by ticks throughout the season, so the number of ticks per host at any one time composes only a small fraction of the total number of tick bites per host individual over the season. Data from Fire Island on the number of attached nymphal *I. dammini* per white-footed mouse over the season in 1987 were used to estimate the mean total number of nymphs per mouse over the season. This is done by fitting a curve to the data points ($r^2 = 1$; Fig. 18), assuming an attachment period of one week (longer than a typical attachment period), estimating the number of ticks per mouse each week, and summing over the season. These calculations underestimate the actual mean number of ticks per mouse because nymphs usually attach for less than one week (Mather and Spielman 1986) and because attachment is continuous. Nevertheless, the probability that the average mouse was bitten by at least one infected tick was estimated at near 100% (Table 6). This analysis was extended to data from other host species by assuming the same seasonal distributions of nymphs on hosts as at Fire Island, and by using the seasonal maximum of the average number of ticks per host individual (as reported in the literature) to estimate P_I at each site. Even in species with relatively low tick loads, the probability of being bitten by at least one infected nymph is high (Table 6). If this analysis is valid, then most host individuals in endemic areas are exposed to Lyme spirochetes during a typical season. The high probability of infective tick bites may explain the high spirochete prevalence in hosts in endemic areas noted by Anderson (1988, 1989).

Ginsberg (1988) modeled infection rates in a host species h after a season of tick feeding (k_h'), given an infection rate of k_h before the season, a spirochete prevalence in ticks of k_t , and n ticks per host, as follows:

$$k_h' = k_h + (1 - (1 - k_t)^n) (1 - k_h). \quad (4)$$

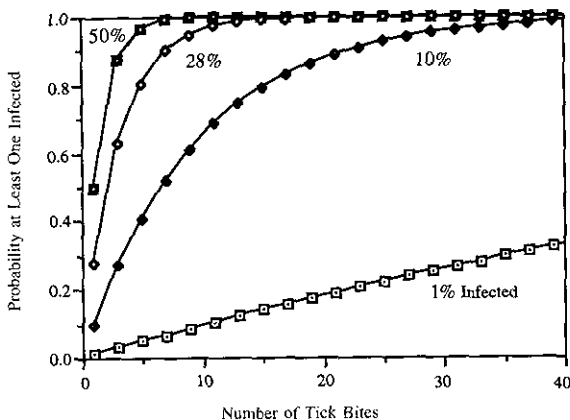


Fig. 17. Probability of being bitten by at least one infected tick. Different curves are shown for different percentages of ticks infected.

Simulations with this equation predict high prevalences in wild animal populations due to multiple tick bites per host (Table 6) and building k_h values over the years. However, several factors can lower expected spirochete prevalence levels in tick hosts. For example, host reproduction would result in numerous uninfected juveniles (unless vertical transmission was very efficient), lowering spirochete prevalence. Some tick host species might not be susceptible or might recover from spirochetal infections, or infected individuals might die (lowering the percentage of living hosts that are infected). Under some

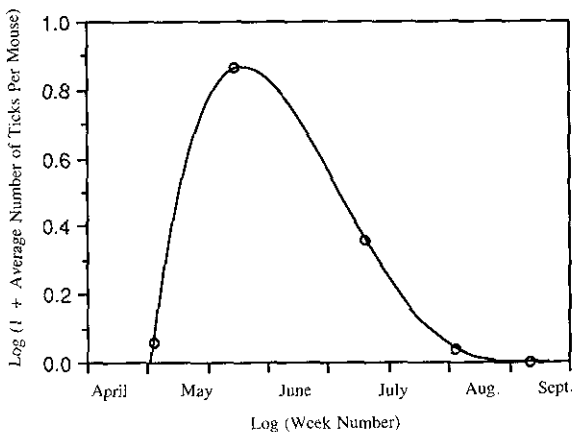


Fig. 18. Number of nymphs per mouse, Fire Island, 1988. Data fitted to a curve for estimate of total number of nymphs per mouse over season.

Table 6. *Estimated proportion of hosts that are bitten by at least one infected nymphal Ixodes dammini. Estimates based on data from Fire Island, New York.*

Host species	Locality	Year	Maximum mean nymphs per host	Source ^a	Estimated total ticks per host	Probability of at least one infected nymph ^b
Mammals						
White-footed mouse (<i>Peromyscus leucopus</i>)	Fire Island, N.Y.	1988	6.3	HSG	36.8	1.00
White-footed mouse	Naushon Island, Mass.	1988	10.1	TNM	59.4	1.00
White-footed mouse	East Haddam, Conn.	1983	3.4	A & M	20.2	1.00
White-footed mouse	East Haddam, Conn.	1979	2.9	CCMKS	17.5	1.00
Gray squirrel (<i>Sciurus carolinensis</i>)	East Haddam, Conn.	1979	34.7	CCMKS	209.2	1.00
Eastern chipmunk (<i>Tamias striatus</i>)	East Haddam, Conn.	1979	6.7	CCMKS	39.4	1.00

Table 6. *Continued.*

Host species	Locality	Year	Maximum mean nymphs per host	Source ^a	Estimated total ticks per host	Probability of at least one infected nymph ^b
Birds						
Common yellowthroat (<i>Geothlypis trichas</i>)	Naushon Island, Mass.	1988	0.8	TNM	5.0	0.81
Carolina wren (<i>Thryothorus ludovicianus</i>)	Naushon Island, Mass.	1988	4.5	TNM	26.4	1.00
Gray catbird (<i>Dumetella carolinensis</i>)	Naushon Island, Mass.	1988	0.9	TNM	5.5	0.84
Birds (27 spp.)	East Haddam, Conn.	1983	1.7	A & M	10.2	0.96

^a HSG = data collected for this study by authors; TNM = Mather et al. (1989a); A & M = Anderson and Magnarelli (1984); CCMKS = Carey et al. (1981) and Main et al. (1982).

^b Assumes 28.0% of the nymphs are infected with spirochetes (see Chapter 2).

conditions, therefore, k_h will decline from year to year and an epizootic will not be maintained. However, Lyme disease apparently has little effect on most wild animals that have been studied (Burgess 1991), which should minimize any possible effect of host mortality. Furthermore, Lyme disease endemic areas typically have high tick densities relative to population densities of reservoir hosts (Table 6), providing conditions that theoretically should allow persistence of the epizootic (May and Anderson 1979).

Infectivity of Vertebrate Hosts (i_h and i_s)

Spirochetes have been isolated from several species of mammals and one bird species (Anderson et al. 1986; Anderson 1989). However, the infectivity of infected vertebrates to uninfected ticks has been studied in only a few species. Infected white-footed mice (*Peromyscus leucopus*) have been demonstrated in the laboratory to be highly infectious to ticks (Donahue et al. 1987). The data suggest an infectivity peak about two weeks after a single infection period ($i_h \approx 0.75$), with subsequent decline in infectivity (to about $i_h \approx 0.5$ after nine weeks). Uninfected nymphal *I. dammini* fed on field-collected *P. leucopus* (from Naushon Island, Massachusetts) picked up spirochetes from 91% of the mice in August, 82% in September, and 90% in May. Spirochete prevalence in the ticks from infective mice varied from 83.3% in May to 89.3% in September (Mather et al. 1989a). Similar data from Ipswich, Massachusetts, showed 90% of mice infecting ticks, and an average of 46.3% of the ticks picking up spirochetes from mice (Mather et al. 1989b). Data on other species are less definitive because they are based on ticks with unknown histories that are removed from field-collected vertebrates. Nevertheless, the available data strongly suggest that white-tailed deer, *Odocoileus virginianus*, and gray catbirds, *Dumetella carolinensis*, are not competent reservoirs (Telford et al. 1988a, 1988b; Mather et al. 1989a), while infected individuals of other mammal and bird species vary in infectiousness to ticks (Fish and Daniels 1989; Weisbrod and Johnson 1989; Telford et al. 1990).

Proportion of Ticks Feeding on Each Host Species (p_h and p_s)

Ixodes dammini has a broad host range. Immatures have been collected from 29 mammal species and 49 bird species, and adults have been collected from 13 mammal species (Anderson 1988, 1989). *Peromyscus leucopus* is often common in areas endemic for Lyme disease and has been reported to be the primary host of larval *I. dammini* (Levine et al. 1985; Schulze et al. 1986). These studies provided data on the number of ticks per host individual, but they did not estimate the population densities of the various host species, so the overall proportion of ticks that fed on each host species cannot be determined. Furthermore, spirochete prevalence levels reported for questing *I. dammini* cast doubt on the notion that *P. leucopus* is the primary larval host. Infectivity of *P. leucopus* is high, based on laboratory studies and

infection rates in ticks from field-collected mice. If we assume that $i_h = 0.75$ (infectivity of *P. leucopus*), $k_i' = 0.28$ (proportion of nymphs infected), $k_t = 0.01$ (proportion of larvae infected), and $k_h = 0.95$ (proportion of *P. leucopus* infected), equation (1) predicts that at most, 38% of the larvae in this hypothetical endemic area feed on *P. leucopus*. This result suggests that the claim that *P. leucopus* is the major host of larval ticks needs to be studied more quantitatively.

The proportion of larvae that feed on *P. leucopus* apparently differs among sites. In East Haddam, Connecticut, field studies have suggested that gray squirrels (*Sciurus carolinensis*), eastern chipmunks (*Tamias striatus*), raccoons (*Procyon lotor*), and birds can be major larval hosts, comparable in importance to *P. leucopus* (Carey et al. 1980; Main et al. 1982; Anderson and Magnarelli 1984). Data collected from Fire Island in 1986 gave an average infection rate of 25.4% of nymphs and (using equation (1)) an estimated maximum of 34.6% of the larvae having fed on *P. leucopus*, suggesting that other vertebrate species were important larval hosts. In the only study to date that quantified host population levels, Mather and coworkers (1989b) found that 58% of nymphs were infected at a site in coastal Massachusetts (giving an estimated maximum of 80.8% of the larvae on *P. leucopus*) and estimated that the vast majority of infected nymphal ticks had fed as larvae and picked up spirochetes from *P. leucopus*. However, at sites with lower spirochete prevalence in questing nymphs, such as Fire Island, the percentage of ticks feeding as larvae on *P. leucopus* is probably lower.

Expected Prevalence of Lyme Spirochetes in Nymphal *Ixodes dammini*

The analysis in the previous sections considers the influence of relative densities and reservoir competences of the various vertebrate host species in an area, as well as the intensity of tick immigration into an area, on spirochete prevalence in questing ticks. These factors would be expected to vary geographically, and indeed, spirochete prevalence in questing ticks differs in different areas (see Chapter 2). The interplay of these factors can be subtle, making prediction of spirochete prevalence in any one area difficult at our present level of knowledge. However, several general predictions can be made about expected spirochete prevalences in endemic areas with specified characteristics.

Interacting factors that contribute to spirochete prevalence in questing ticks are depicted in Fig. 19. This simulation uses the same parameter values as used previously ($k_t = 0.01$, $k_h = 0.95$, $i_h = 0.75$). Here PH and PHI denote the overall infectivity of the hosts of resident ticks and immigrant ticks, respectively. PH and PHI can be defined from equation (2) as: $PH = \sum_h k_h i_h p_h$ and $PHI = \sum_s k_s i_s p_s$. The case of an endemic area with no tick

immigration is illustrated by the points along the vertical axis ($P_i = 0$). An overall infectivity of $PH = 0.5$ produces a spirochete prevalence, after larval feeding, of $k_i' = 0.51$. This PH value would result if 70% of the larvae fed on *P. leucopus* and the other 30% fed on hosts that were not reservoir competent (e.g., white-tailed deer). If only 14% of the larvae attached to mice, and the rest attached to reservoir incompetent hosts, then $PH = 0.1$ and $k_i' = 0.11$. If any of the hosts other than *P. leucopus* were reservoir competent (which is probably true in most areas), then the percentage of larvae feeding on *P. leucopus* would have to be lower to give the same values of k_i' .

The effect of immigration on spirochete prevalence in endemic areas probably depends on how much of the immigration is from neighboring areas and how much is long distance. When immigration is from nearby areas that are also endemic, the mix of hosts and prevalence values should be comparable to the target area, so $PH \approx PHI$ and this immigration does not influence k_i' . However, long-distance immigration could have a strong influence on spirochete prevalence. Long-distance larval transport on birds probably occurs primarily in the fall when birds are migrating south along the East Coast of North America. Only once has *Borrelia burgdorferi* been isolated from a bird (spirochetes isolated from a veery, *Catharus fuscescens*; Anderson et al. 1986). Catbirds are not reservoir competent (Mather et al. 1989a). Therefore, birds may, in general, be poor reservoirs for Lyme disease. If birds are generally poor reservoirs, the values of i_s and PHI will be low, and long-distance immigration will lower spirochete prevalence in endemic areas. The greater the immigration intensity, the lower the ultimate value of k_i' . The possible role of long-distance immigration is depicted by the line for $PH = 0.5$ and

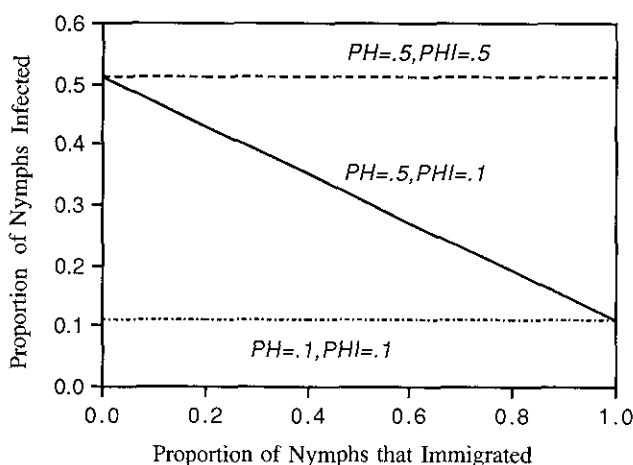


Fig. 19. Effect of tick immigration and alternative host species on expected proportion of questing nymphs infected with spirochetes. PH = average infectivity of hosts of resident larvae = $\sum_h k_h i_h p_h$. PHI = average infectivity of hosts of immigrant larvae = $\sum_s k_s i_s p_s$.

$PHI = 0.1$ in Fig. 19. Unfortunately, data that can be used to assess the importance of migrants in actual populations of *I. dammini* are lacking. The role of migration in the population dynamics of *I. dammini* clearly warrants further study.

The ultimate prevalence of Lyme spirochetes in ticks and vertebrates in an area cannot be predicted at our current level of knowledge. Ginsberg's original model (1988) predicted that under a variety of conditions, spirochete prevalence in questing nymphs in an area where infected nymphs were newly introduced would stay low for several years (or decades), and then suddenly rise to a stable level. Unfortunately, the simulations performed with this model used some simplifying assumptions that compromise their predictive value. To accurately model the prevalence of Lyme spirochetes in an endemic area or the spread of Lyme disease into new areas, a great deal of research remains to be done. Most importantly, more detailed information is needed on the reservoir competence of various vertebrate species (including squirrels, chipmunks, raccoons, and birds) and on the host ranges, seasonal cycles, and population dynamics of *I. dammini*, *I. scapularis*, and *I. pacificus* in areas where Lyme disease is currently rare or absent (Piesman 1988).

Conclusions

The epizootiology of Lyme disease was examined by using models to assess the potential influence of various ecological factors on spirochete prevalence in ticks and vertebrates.

1. In areas endemic for Lyme disease, the vast majority of vertebrate host individuals should be exposed to the spirochete because of multiple tick feedings per individual host over the season.
2. The infectivity of a host species to uninfected ticks and the frequency of tick feeding on the host species are predicted to influence the effect of that host species on spirochete prevalence in questing ticks.
3. The relative abundance of immigrant ticks (compared to resident ticks) and the reservoir competence of the host species on which the ticks immigrated are predicted to influence spirochete prevalence in questing ticks. Immigration from nearby areas is expected to maintain spirochete prevalence at local levels. Long-distance immigration could lower spirochete prevalence if most immigrants arrive on bird species that are not competent reservoirs.

CHAPTER 4. Managing Ticks and Lyme Spirochetes: Efficacy and Potential Environmental Impact of Permethrin-treated Cotton Balls



Investigators have tried several methods to manage the northern deer tick, *Ixodes dammini* Spielman, Clifford, Piesman, and Corwin, which is the primary vector of Lyme disease in the northeastern and north-central United States (Spielman et al. 1985). These methods include burning or mowing vegetation (Wilson 1986), applying pesticides in sprays or granular formulations (Schulze et al. 1987, 1988, 1991), and eliminating deer from an area (Wilson et al. 1984, 1988). Unfortunately, each of these techniques has substantial drawbacks. Spraying, mowing, and burning reduce tick populations temporarily, requiring repeated applications. All of these techniques have impacts on nontarget species, and deer removal in particular requires decimating a local vertebrate population.

A recent approach, which avoids some of these problems, uses cotton balls treated with permethrin, a broad-spectrum synthetic pyrethroid with low mammalian toxicity (Elliot et al. 1973; Mather et al. 1987). The cotton balls are offered in cardboard tubes (to keep them dry) and placed in a grid pattern with 9.1 m (10 yards) between tubes. White-footed mice, *Peromyscus leucopus* (Rafinesque), the primary reservoir of Lyme disease in North America (Levine et al. 1985; Donahue et al. 1987; Mather et al. 1989b), use the cotton balls for nest material, targeting the chemical at the vector on the primary reservoir host. This approach allows small dosages (about 0.04 kg permethrin per ha, applied twice a year) and minimizes effects on nontarget organisms (only parasites and nest associates of *P. leucopus* should be substantially affected). Since the tick is killed on a major reservoir host, this technique should not only reduce tick numbers, but should also lower infection rates in those ticks that remain, because the surviving ticks would come mostly from alternate host species that may be less efficient reservoirs than white-footed mice (Mather et al. 1988; Spielman 1988b). Results from initial trials in Massachusetts were encouraging (Mather et al. 1987, 1988), but this technique has not yet been tested under a range of environmental conditions.

In this chapter, I report field trials of permethrin-treated cotton balls on an East Coast barrier island. Efficacy is examined when full coverage of a substantial area is achieved, as well as when treatment is on a house-by-house basis. I also examine possible environmental impacts of this method, including the potential for soil contamination with permethrin.

Methods

Study Site

The vegetation of Fire Island was described in detail by Art (1976) and Stalter et al. (1986). Treated and untreated (control) plots were set up in Fire Island National Seashore (the treatment plot was in Talisman, the untreated plot in Watch Hill) and in the Fire Island communities of Point O'Woods and Ocean Beach. Treatment plots received tubes of permethrin-treated cotton

balls as described in the next subsection; untreated plots received no treatment. Treated and untreated plots were matched as closely as possible as to vegetation type and density of man-made structures. Each plot was 130×130 m (except the Fire Island National Seashore plots, which were 90×190 m because the island was too narrow at Talisman to fit a square plot). Fire Island National Seashore and Point O'Woods are developed at low densities with extensive natural areas. In contrast, Ocean Beach is densely developed with most lots about 15×25 m, nearly all with houses (the untreated area in Ocean Beach included one unused lot with $1,394 \text{ m}^2$ of natural vegetation).

Treatment

Damminix (permethrin-treated cotton balls) was obtained from the manufacturer (Ecohealth, Boston, Massachusetts) and applied according to label instructions. Treatment tubes were placed in all wooded and shrubby areas in the treatment plots; only open areas of sparse beach grass were not treated. The tubes were placed in square grids with 9.1 m (10 yards) between tubes on 10–17 May and again on 14–17 July 1988. The tubes placed in May had been purchased in summer 1987 and stored in the original boxes until used. They were retested by the manufacturer in early April 1988 and were still potent, with 6.88% permethrin (the label value is 7.4% permethrin by weight). The tubes placed in July were newly purchased. Coverage by Damminix was complete in the Fire Island National Seashore treatment plots (Talisman; 196 tubes in May, 190 in July) and in the Point O'Woods plots (196 tubes in May, 190 in July). At Ocean Beach, however, permission could not be secured from all of the landowners to treat their property, so roughly half of the yards in the treatment plot were treated in May (100 tubes) and only the five properties used for tick sampling were treated in July (28 tubes). Each property was treated according to label instructions.

Tick Samples

Ticks were removed from white-footed mice that were captured on 26 April–5 May 1988 (pretreatment) and monthly posttreatment (24 May–2 June, 30 June–8 July, 4–11 August, and 16–18 September). In each sample, 25 Sherman traps were placed in a 5×5 grid with 10 m between traps, at the center of the treatment and control plots (total of 50 traps). The traps were baited with a 3:1 mixture (by volume) of rolled oats and peanut butter, set in the afternoon and collected the following morning. Mice were taken to the field lab at Talisman, where they were anesthetized with methoxyflurane, their ticks removed, and small hair samples taken (from the rump). The mice were measured, weighed, and marked by toe-clipping. After recovery from the anesthesia, each mouse was released in the capture plot.

Free-living immature ticks were sampled by dragging (see Chapter 1). A small cotton flag on a wooden dowel was used to stir up the leaf litter and a

large cotton flag was dragged behind. At least 10 drag samples, 5 min each, were taken in each plot. Nymphs were sampled pretreatment on 28 June and on 1, 6, 7, and 14 July 1988. These samples were considered pretreatment because the Damminix applied in May would not have had an effect on questing ticks in the first season of application but would only affect those that encountered mouse hosts. Larvae were sampled pretreatment on 7, 8, and 14 July, 17, 18, and 31 August, and 2 September 1988. Adults were sampled posttreatment by walking through thickets for 5-min periods and collecting ticks from the investigator's tan clothing (pants tucked into socks). Walking samples were taken on 20, 21, and 27 October and on 3 and 8 November 1988. Posttreatment samples of nymphs were taken by flagging on 12, 23, 26, and 27 June and 3 and 4 July 1989. Ticks were returned alive to the lab where they were dissected and examined for spirochetes by dark-field microscopy (see Chapter 1, *Determining Spirochete Prevalence*).

Permethrin Samples

Samples of mouse hair and soil were analyzed for permethrin using gas chromatography-electron capture detection by CAL Technologies (Somerville, New Jersey). Permethrin movement in the soil was assessed by placing cotton balls from Damminix tubes in 10-cm-deep holes in the ground (one tubeful in each hole) near the Lighthouse on Fire Island, and by analyzing soil cores for permethrin. The site was in the secondary dune area and had thick vegetative cover, mostly of bayberry and poison ivy. Treatment holes were 10 m apart in a 3 × 4 grid, and sample holes were selected at random on each sample day. Three pretreatment samples were taken on 27 July 1989. Posttreatment samples were taken on 28 July and on 9 and 22 August 1989. Each posttreatment sample consisted of soil cores directly beneath three of the holes with cotton balls. Soil (mostly sand) from directly beneath and from 25.5 cm beneath the cotton balls was tested for permethrin. Three additional cores were taken around one of the sample cores on each sample day. These additional cores were taken 3 cm from the central core at 0° (north), 120°, and 240° to test for possible laterally moving permethrin in the soil. These samples were tested for permethrin at 10 cm from the surface (the level of the cotton balls) and from 25.5 cm beneath the surface. The soil corer was a 30.5-cm (12-inch) zero-contamination corer (JMC Soil Investigation Equipment, Clements Associates, Inc., Newton, Iowa). New inner sleeves were used for each sample and the corer was washed with tap water and dried between samples.

Statistics

Mann-Whitney U tests were used to compare tick densities in treatment versus control plots. Proportions of ticks infected with spirochetes were compared between treatment and control sites using Fisher exact probability tests on 2 × 2 contingency tables.

Treatment effectiveness was assessed by comparing the probability, from 0 to 50 tick bites, that at least one of the ticks was infected. This probability (P_I) was calculated (from the binomial distribution) using equation (3) from Chapter 3:

$$P_I = 1 - (1 - k_t)^n,$$

where k_t = proportion of ticks infected and n = number of tick bites.

Results

Effectiveness

The average numbers of ticks per white-footed mouse in treated and untreated areas are plotted in Fig. 20. Untreated plots averaged 6.75 ticks (all species) per mouse in Fire Island National Seashore and 11.5 in Point O' Woods during the peak of nymphal activity in May-June. During the peak of larval activity in August, mice in untreated plots averaged 25.3 ticks in Fire Island National Seashore and 24.0 in Point O' Woods (Figs. 20A and B). In areas of Fire Island National Seashore and Point O' Woods that received full coverage with permethrin-treated cotton balls, however, the mice were completely free of ticks. The partial treatment at Ocean Beach gave inconsistent results (probably due, in part, to small sample sizes), with numbers of ticks per mouse at times apparently higher in treated than in untreated areas (Fig. 20C). Overall, after the initial treatment, an average of 1.6 ticks were found per mouse in the untreated area of Ocean Beach ($n = 10$ mice), and 1.5 ticks were found per mouse in the treated area ($n = 8$ mice).

Table 7 gives concentrations of permethrin in hair samples from mice in treated and untreated areas. All mice from the Fire Island National Seashore and Point O' Woods treated areas (which received full coverage) had permethrin on their hairs, with average concentrations of 218.5 mg/kg at Fire Island National Seashore and 413.0 mg/kg at Point O' Woods. In contrast, only one of seven mice in the partially treated Ocean Beach plot had permethrin on its hair. Permethrin on mice from untreated plots could have resulted from mice moving between treated and untreated plots, residents using permethrin or permethrin-treated cotton balls in areas that were not treated for this study, and so on. Precautions were taken to avoid sample contamination, but this contamination cannot be completely ruled out. Nevertheless, the positive results from all mice in completely treated areas indicate that the permethrin was effectively disseminated among mice in these plots. The generally negative results from Ocean Beach indicate that the material was not effectively disseminated at that site.

Pre- and posttreatment tick densities and spirochete prevalence levels are given for the spring treatment in Table 8. Before treatment, densities of

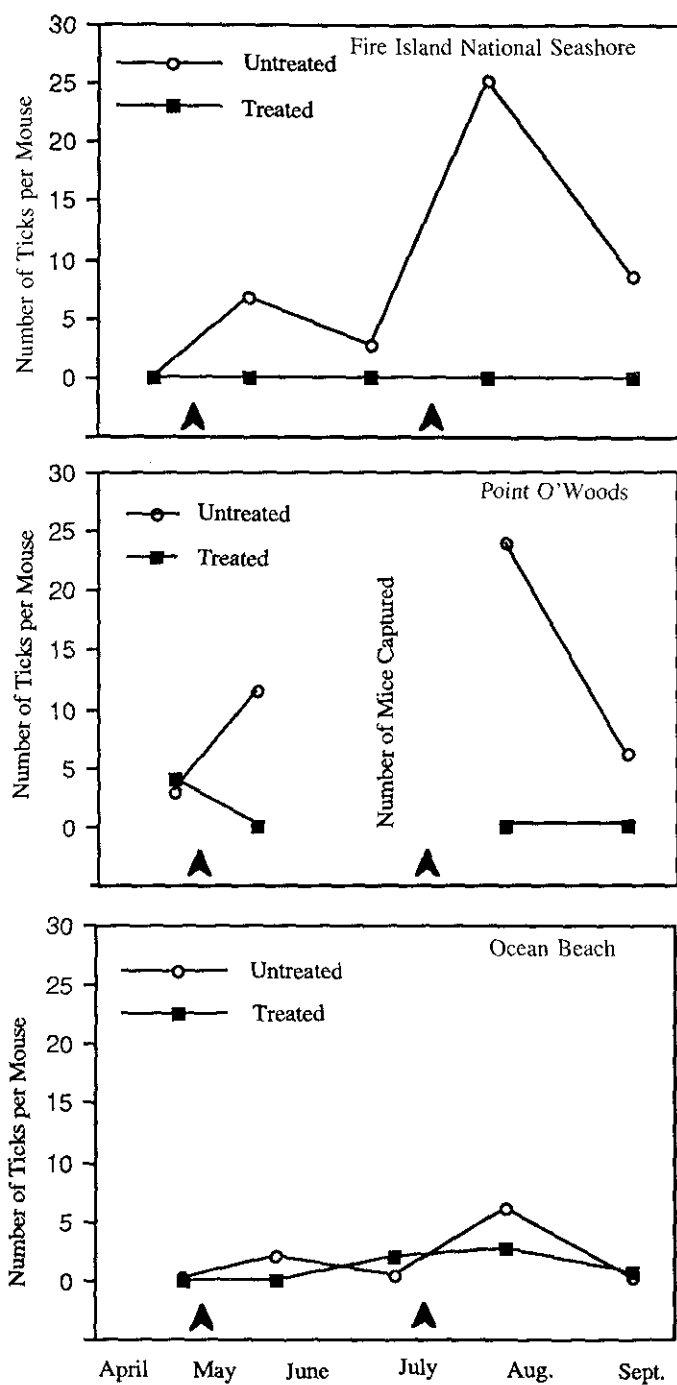


Fig. 20. Average numbers of ticks per white-footed mouse in treated and untreated plots on Fire Island, 1988. Arrows indicate date of treatment.

Table 7. *Permethrin on mouse hairs, Fire Island, 1988.*

Site	Treated or untreated	Mice tested	With permethrin	Average mg/kg on mice with permethrin $\pm$ S.E.
Fire Island	treated	16	16	218.5 $\pm$ 28.6
National Seashore	untreated	14	6	128.8 $\pm$ 46.9
Point O'Woods	treated	3	3	413.0 $\pm$ 152.6
	untreated	11	3	289.3 $\pm$ 156.9
Ocean Beach	treated	7	1	334
	untreated	9	1	59

free-living nymphs did not differ significantly between treatment and control plots at any of the sample sites (Mann-Whitney U tests; Fire Island National Seashore, $U = 44.5$; Point O'Woods, $U = 44$; Ocean Beach, $U = 30$; $n_1 = n_2 = 10$, $P > 0.1$ in all cases). Similarly, pretreatment infection rates with *B. burgdorferi* did not differ significantly between treatment and control sites (Fisher exact probability tests; Fire Island National Seashore, $n = 51$, $P = 0.74$; Point O'Woods, $n = 15$, $P = 0.47$). Posttreatment, both the adult tick density and the infection rate were significantly lower in the treated than in the untreated plot at Fire Island National Seashore (density, Mann-Whitney $U = 28.5$, $P < 0.001$; infection rate, Fisher exact probability test, $n = 45$, $P = 0.009$). In contrast, neither tick density nor infection rate were significantly lower in the treated plot at Point O'Woods (density, Mann-Whitney $U = 102$, $P > 0.05$; infection rate, Fisher exact probability test, $n = 29$, $P = 0.33$). However, the absolute infection rate was lower in the treated plot at Point O'Woods, and the sample size was small, so the result regarding spirochete prevalence is inconclusive.

Results from the midsummer treatment are given in Table 9. Pretreatment larval densities were greater in the untreated than in the treated plot at Fire Island National Seashore (Mann-Whitney $U = 15.5$, $P < 0.02$), but were higher in the treated than the untreated plot at Point O'Woods ($U = 21.5$, $P < 0.05$). Nevertheless, posttreatment nymph densities did not differ significantly between treated and untreated plots at either Fire Island National Seashore or Point O'Woods (Fire Island National Seashore, $U = 104$; Point O'Woods, $U = 93$; $n_1 = n_2 = 15$, $P > 0.1$ in both cases). Posttreatment spirochete prevalence was significantly lower in the treated than in the untreated plot at Fire Island National Seashore (Fisher exact probability test, $n = 64$, $P = 0.029$), but not elsewhere (Point O'Woods, Fisher exact probability test, $n = 88$, $P = 0.78$).

Treatment effectiveness can be evaluated by calculating the probability of being bitten by at least one infected tick, given the posttreatment tick

Table 8. Tick densities and spirochete prevalence in pretreatment nymphs and posttreatment adults, spring treatment, 1988.

Sample site	Treated or untreated	Ticks per sample $\pm$ S.E. ^a		Percent of ticks infected (N)	
		Pretreatment	Posttreatment	Pretreatment	Posttreatment
Fire Island	treated	2.4 $\pm$ 0.69	0.67 $\pm$ 0.21 ^b	19.0 (21)	0.0 (9) ^c
National Seashore	untreated	3.2 $\pm$ 0.99	2.47 $\pm$ 0.34 ^b	26.7 (30)	47.2 (36) ^c
Point O'Woods	treated	3.8 $\pm$ 0.73	1.07 $\pm$ 0.28	14.3 (7)	7.1 (14)
	untreated	3.5 $\pm$ 1.07	1.13 $\pm$ 0.22	0.0 (8)	26.7 (15)
Ocean Beach	treated	0.0	0.07 $\pm$ 0.07	—	0.0 (1)
	untreated	0.8 $\pm$ 0.36	0.14 $\pm$ 0.10	0.0 (2)	0.0 (3)

^a Pretreatment nymphs, $N = 10$ samples (5-min flagging samples). Posttreatment adults, $N = 15$ samples (5-min walking samples).

^b $P < 0.05$ for comparison of treated versus untreated site.

^c $P < 0.05$ for comparison of treated versus untreated site.

Table 9. Pretreatment larval densities and posttreatment nymphal densities and spirochete prevalence, summer treatment, 1988.

Site	Treated or untreated	Number ticks per sample $\pm$ S.E. ^a		Percent of nymphs infected after treatment (N)
		Pretreatment	Posttreatment	
Fire Island	treated	2.3 ± 1.15^b	2.2 ± 0.51	3.1 (32) ^c
National Seashore	untreated	7.7 ± 2.01^b	2.3 ± 0.43	21.9 (32) ^c
Point O' Woods	treated	24.5 ± 6.83^d	2.8 ± 0.61	14.6 (41)
	untreated	9.9 ± 2.87^d	3.3 ± 0.49	17.0 (47)
Ocean Beach	treated	1.4 ± 0.75	0.2 ± 0.11	100.0 (2)
	untreated	2.8 ± 2.8	0.9 ± 0.41	0.0 (12)

^a Pretreatment larvae, $N = 10$ samples (5-min flagging samples, small flag). Posttreatment nymphs, $N = 15$ samples (5-min flagging samples, small and large flags).

^b $P < 0.01$.

^c $P < 0.05$ for comparison of treated versus untreated site.

^d $P < 0.01$.

densities and infection rates in treated versus untreated plots. These probabilities are plotted for 0 to 50 tick bites in Fig. 21. The differences in tick densities were included by plotting projections from the treated and untreated plots on separate, appropriately scaled, horizontal axes. For a person bitten by 5 nymphs over the season in the Fire Island National Seashore untreated area, for example, the probability that at least 1 of those ticks is infected is 71%. In the treated area, the expected number of tick bites is 4.9, with a probability of only 14% of being bitten by at least 1 infected tick. At Point O'Woods, however, the comparable probabilities are 61% for 5 tick bites in the untreated area and 49% for 4.3 tick bites in the treated area.

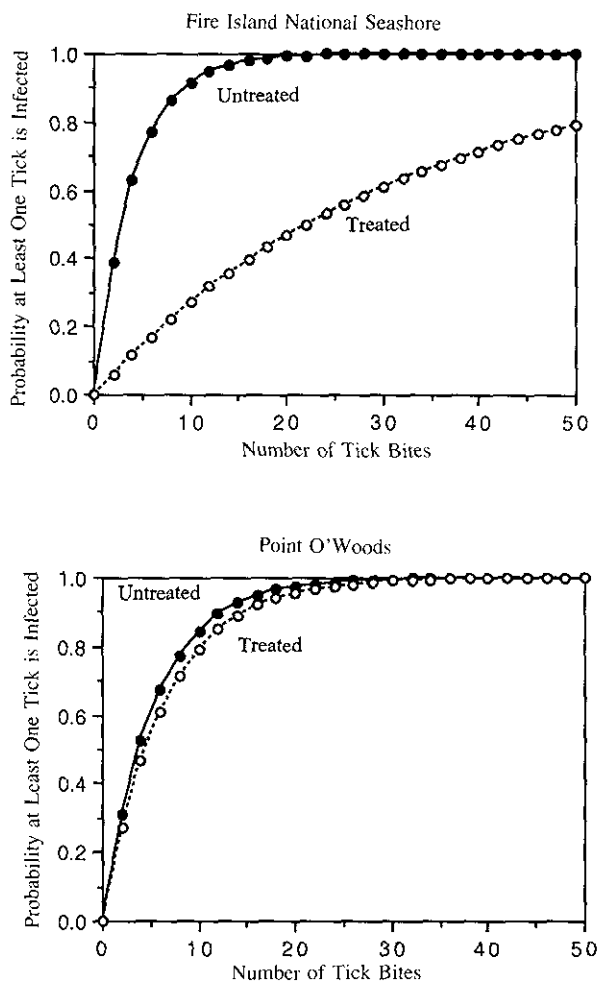


Fig. 21. Probability of being bitten by at least one infected nymphal tick in treated versus untreated sites on Fire Island, 1989.

Permethrin Movement in Soil

Concentrations of permethrin in soil samples are given in Table 10. Soil samples directly beneath the cotton balls averaged 15.49 mg/kg permethrin the day after treatment. Average concentrations changed little over the following 25 days. Concentrations in soil samples from 25.5 cm directly below the cotton balls and lateral samples (3 cm away) from the same depth and from 15.5 cm deeper than the cotton balls differed slightly or not at all from background levels (Table 10). The highest concentrations in individual samples directly beneath cotton balls were 22.95 mg/kg from just beneath (day 13) and 1.58 mg/kg from 25.5 cm beneath the cotton balls (day 1). Among lateral samples, the highest concentrations were 2.85 mg/kg in soil level with the cotton balls (day 13), and 5.32 mg/kg at 15.5 cm deeper than the cotton balls (day 1). Thus, some movement occurred in the sandy soil, although overall concentrations were low even a few centimeters from the cotton balls.

Discussion

Treatment with permethrin-treated cotton balls gave inconsistent control of ticks infected with *spirochetes* in these trials. Nevertheless, the technique shows promise for further development and for integration with other techniques to manage ticks and Lyme disease.

The complete elimination of ticks from white-footed mice captured in areas that received full treatment was impressive, considering the substantial tick burdens on mice in untreated areas (Fig. 20). The inconsistent results in the partially treated area (Fig. 20) indicate that treatment of an individual yard on a small lot does not guarantee effective reduction of the risk of acquiring Lyme disease. The lack of permethrin on the hairs of most mice at Ocean Beach, the partially treated site (Table 7), suggests that the mice gathered nesting material from outside treated yards. Spring renovations of houses at this site left abundant waste material (e.g., discarded fragments of insulation and furniture padding) that may have competed with the treated cotton balls as alternative mouse nesting material. Unfortunately, it is not clear which of these factors was responsible for the lack of permethrin on the hairs of most mice captured at Ocean Beach. Therefore, it seems prudent to treat as large a continuous area as possible and to remove possible alternative nesting material to get best results in treated areas.

Despite removing ticks from mice in fully treated areas, the effect on tick populations in subsequent stages varied among sites and treatments. Spring treatment apparently lowered numbers of fall adults at Fire Island National Seashore, but not at Point O'Woods (Table 8). Midsummer treatment did not significantly lower nymphal densities the following spring at either site (Table 9). Thus, permethrin-treated cotton balls did not dependably lower densities of subsequent stages of ticks. Interestingly, posttreatment nymphal densities were the same in treated and untreated sites, even though

Table 10. *Concentrations of permethrin in soil samples. Average concentration (of three readings) in ppm, range (high minus low values) in parentheses. Pretreatment readings: average = 0.58 ppm (range = 0.48).*

Samples taken	Days after treatment		
	1	13	26
Directly beneath cotton balls	15.49 (4.09)	9.41 (20.72)	10.89 (19.15)
25.5 cm beneath cotton balls	1.26 (0.63)	0.46 (0.58)	0.75 (0.58)
10 cm beneath soil surface, 3 cm laterally from cotton balls	0.41 (0.40)	1.12 (2.75)	0.28 (0.36)
25.5 cm below soil surface, 3 cm laterally from cotton balls	1.88 (5.32)	0.35 (0.95)	0.22 (0.25)

pretreatment larval densities were higher in the treated than the untreated site at Point O'Woods, but higher in the untreated than the treated site at Fire Island National Seashore. These data suggest that some factor other than survivorship on white-footed mice (and thus some factor other than treatment with permethrin-treated cotton balls) regulated nymphal population densities at these sites.

Spirochete prevalence, however, was lower in treated than untreated plots in both trials at Fire Island National Seashore. Unfortunately, infection rates were not significantly lowered in either trial at Point O'Woods (although the differences were in the right direction). Therefore, the expected reduction in human cases of Lyme disease differed markedly between the Fire Island National Seashore and Point O'Woods treatments. The probability of being bitten by at least one infected nymph in treated and untreated areas, given various numbers of tick bites, is plotted in Fig. 21. This figure gives projections from results with nymphal ticks because nymphs are responsible for most human cases of Lyme disease (Spielman et al. 1985). The probability that a person is bitten by at least one infected nymph during the season was greatly reduced by the treatment at Fire Island National Seashore, but any reduction at Point O'Woods was so small as to be of little practical consequence.

These results provoke two related questions. First, why, when treatment completely eliminated ticks from mice, were the numbers of free-living ticks in subsequent stages not always significantly lowered? Second, why was spirochete prevalence significantly lowered at the Fire Island National Seashore treatment site, but not at Point O'Woods? The immature ticks' survival from the previous year (Yuval and Spielman 1990) could partly answer the first question (but not completely; populations in treated areas should still be lower than in untreated areas). However, tick survivorship would not be expected to differ between the Fire Island National Seashore and Point O'Woods plots. Two factors that could potentially explain both of these apparent problems are the presence of alternative hosts and the immigration of ticks into the sample areas. For example, squirrels (*Sciurus carolinensis*) and domestic dogs were present at Point O'Woods but not in the treated plot at Fire Island National Seashore. Neither squirrels nor dogs would be likely to pick up the cotton balls, so ticks on these animals would not be affected by this treatment. If squirrels or dogs are effective reservoirs of Lyme spirochetes, their presence could account for the relatively high infection rates in the Point O'Woods treated area. Interestingly, squirrels were absent from the site where Mather et al. (1987) initially obtained effective control with this method (T.N. Mather, personal communication).

Immigration of mice infested with immature ticks probably also differed between sites. Fire Island is narrow at Talisman, so coverage with treatment tubes was complete from primary dune to bay. The only access to the treated area for mice was along the western 90-m end (the eastern end of the treated area abutted on Barrett Beach, a developed sandy area with little opportunity for mouse immigration). In contrast, at Point O'Woods, mice had access to

the treatment plot from three sides (total of 390 m of edge). Mice probably serve as important dispersal agents for *I. dammini* on Fire Island (Ginsberg and Ewing 1989a). Sonenshine (1973) found that radioisotope-labeled immature American dog ticks (*Dermacentor variabilis*) moved up to 302 m on white-footed mice. Immigration of infected ticks on *P. leucopus* could have played a role on Fire Island. If immigration was greater at Point O'Woods than at Talisman, the result could have been higher infection rates (relative to untreated plots) in the treated area at Point O'Woods.

The high concentrations of permethrin on the hair of mice in treated areas (Table 7) suggest that predators will ingest this material from mice. The potential importance of such an effect is mitigated, somewhat, by the low mammalian toxicity of permethrin (Elliot et al. 1973; Glickman and Lech 1981, 1982). Furthermore, the high concentrations were on mouse hairs that were presumably in direct contact with cotton balls in the nest. Concentrations in mouse tissues may have been far lower. However, the potential for biomagnification has not been studied for permethrin applied on cotton balls.

Permethrin movement in sandy soil was limited during the 26 days of the soil study (Table 10). However, selected individual samples showed evidence of some degree of chemical movement. Concentrations in soil directly under the cotton balls declined little during this experiment and remained at concentrations sufficient to induce considerable mortality in crickets in moist sandy soil (Harris and Turnbull 1978). Permethrin has broad-spectrum toxicity to invertebrates (Muirhead-Thomson 1978; Anderson 1982) and fish (Mulla et al. 1978; Glickman et al. 1981; Glickman and Lech 1981, 1982). Therefore, treatment should be restricted to avoid areas directly adjacent to standing water where permethrin could potentially come into contact with fish and aquatic invertebrates.

The presence of permethrin on the hairs of some mice in untreated areas suggests another means of chemical dissemination: mice carrying cotton balls out of the treated area. The primary impact of treated cotton balls, both inside and outside the treated area, would probably be on nest associates of white-footed mice. Therefore, permethrin-treated cotton balls would probably affect some nontarget organisms, but the extent of impact would probably be far less than that of a spray or other broadcast pesticide application.

The fact that permethrin-treated cotton balls did not consistently lower densities of questing ticks and prevalence levels of spirochetes suggests that alone, this technique cannot be depended upon to provide adequate control. Recent field trials by independent investigators have had variable results, ranging from effective control (Deblinger and Rimmer 1991) to effective tick removal from mice but ineffective questing tick control (Stafford 1991) to failure even to remove ticks from mice (Daniels et al. 1991). The variability of these results agrees well with the variability in the Fire Island trials. Large-scale application of this technique would probably lower the incidence of human Lyme disease because the technique works well in some situations.

Unfortunately, the effectiveness at any one site would not be predictable. People in treated areas should still use personal protection techniques and should check themselves carefully for ticks after leaving tick habitats.

Integrated Pest Management for Ticks and Lyme Disease

Numerous techniques are available to manage ticks and Lyme disease (Schulze et al. 1988; Spielman 1988b; Jaenson et al. 1991). Public education and personal protection techniques are probably the most widely applicable measures and the most effective long-term strategies. Also, a variety of control techniques can be integrated to manage ticks. The efficacies of some techniques, such as habitat modification and some chemical approaches, have been established (Wilson 1986; Schulze et al. 1987, 1991). Other techniques, including releasing parasitoid wasps, manipulating host populations, and applying targeted pesticides, remain controversial (Jaenson et al. 1991).

Permethrin-treated cotton balls can play a role in some management programs for *I. dammini* and Lyme disease because of this technique's effectiveness at eliminating ticks from white-footed mice in many areas. Practical problems limit the usefulness of this technique for very large areas. However, if eliminating ticks from mice at small and moderate-sized sites (by permethrin-treated cotton balls) is supplemented by eliminating other sources of infected ticks, control could be excellent. The approach to eliminating other sources of infected ticks depends on the source of the infected ticks. If the source is a reservoir host (e.g., squirrels, rabbits, raccoons, rats), then applying treated nesting material or systemic acaricide in an appropriate bait (or in the case of rats, lowering reservoir populations by rat management techniques) could result in effective control (unfortunately, it is not known how efficient most of these species are as reservoirs of Lyme disease). However, if the source of infected ticks is immigration from outside the treated area, then a barrier around the treated area that prevents tick host immigration, if feasible, should improve control.

The overall approach to tick management should be tailored to the specific requirements and constraints of the target site. For example, at a park with a conservation mandate, high-impact techniques such as broadcast pesticide applications or host mammal population manipulation may not be appropriate. Such techniques might be more applicable at smaller, developed sites. At some sites, manipulation of human activities to avoid high-risk habitats (e.g., clearly posted sand paths from parking lot to beach) might be sufficient. More research on the epizootiology of Lyme disease in various environments is needed to fine-tune the integrated pest management approach. At present, personal protection remains the most effective means to avoid Lyme disease.

Conclusions

Permethrin-treated cotton balls were applied to three treatment plots on Fire Island National Seashore, New York. Control was inconsistent, with tick densities or infection rates significantly lowered in some trials, but not others. When coverage with treatment tubes was complete, all white-footed mice examined from treated areas had permethrin on their hair and were completely free of ticks. In contrast, mice from matched untreated plots had substantial tick loads. When coverage was partial (some residential yards were treated, others not) and alternative nesting material was available (scattered insulation and torn cushions), most mice had no permethrin on their hairs, and several mice had ticks.

After spring treatment, the density and spirochete prevalence in questing fall adults were significantly lower than the control at one of the plots with full coverage, but not the other. Midsummer treatment did not reduce densities of free-living nymphs the following spring, but spirochete prevalence in nymphs was markedly lower than the control at one of the two fully treated sites. Permethrin-treated cotton balls can play a role in an integrated management program for ticks and Lyme disease because the treatment effectively removed ticks from white-footed mice. However, the inconsistent effect on free-living tick populations (even when mice were rendered tick-free) suggests that other sources of ticks, such as alternate host species or immigration, can influence tick population levels. The technique apparently works best when full coverage of a large area is attained and when alternative mouse nesting material (such as discarded insulation and furniture padding) is removed. However, since full treatment lowered tick densities and spirochete prevalence only part of the time, people should continue to use self-protection techniques to avoid tick bites, even in fully treated areas.

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As the nation's principal conservation agency, the Department of the Interior has responsibility for most of our nationally owned public lands and natural and cultural resources. This includes fostering wise use of our land and water resources, protecting our fish and wildlife, preserving the environmental and cultural values of our national parks and historical places, and providing for enjoyment of life through outdoor recreation. The department assesses our energy and mineral resources and works to ensure that their development is in the best interests of all our people. The department also promotes the goals of the Take Pride in America campaign by encouraging stewardship and citizen responsibility for the public lands and promoting citizen participation in their care. The department also has a major responsibility for American Indian reservation communities and for people who live in island territories under U.S. administration.