# Vectorial Capacity of North American *Ixodes* Ticks

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*Ixodes dammini,* the vector of Lyme disease and babesiosis, is distributed in various locations in the northeastern quadrant of the United States and nearby Canada. The life cycle of this tick, which includes larval, nymphal, and adult stages, spans at least two years. The tick over-winters between larval and nymphal feeding. Horizontal transmission of pathogens is facilitated by a feeding pattern in which both the larval and nymphal stages feed on the white-footed mouse, *Peromyscus leucopus,* and by a seasonal pattern of activity in which nymphs precede larvae. The species range appears to have expanded from a single island location, and has invaded new sites since the 1940s, some as recently as 1980. This increased abundance appears to be related to the increased abundance of deer, the preferred host of the adult stage. *I. muris* predominated in coastal Massachusetts before *I. dammini* became abundant, but is probably now extinct. *I. scapularis,* which is present in the southern U.S., is a poor vector of mouse parasites because about 90 percent of these immature ticks feed on lizards. To the extent that horizontal transmission occurs, we suggest that mice serve as the principal reservoir for the Lyme spirochete as well as *Babesia microti.*

*Ixodes* ticks are "notorious" vectors of disease. European *I. ricinus* has been implicated as the vector of at least eight diverse veterinary infections, including viral, rickettsial, and protozoan agents [Hoogstraal: personal communication]. Eurasian *I. persulcatus* transmits four infections. Similarly, the newly described American species, *I. dammini,* transmits rodent babesiosis as well as the Lyme spirochete [1,2] and both seem to be recent agents of human disease, dating back only over the last two decades or so [3,4]. In both infections, the nymphal stage seems to be responsible for transmission; thus the chronology of introduction and mode of transmission of both infections would be similar, but the geographic distributions of these diseases differ. Lyme disease appears to occur wherever the vector is abundant, but babesiosis occurs solely along the New York-southern New England coast. The basis for this paradox has not been explained.

The term "vectorial capacity" has come to include all those vector-related variables affecting stability of pathogen transmission. Macdonald [5] originally described stability of malaria in terms of duration of infective life of the anopheline vector, narrowness of host range, and duration of the permissive season; Garrett-Jones [6] adapted these terms for convenient malariological use and coined the general term. Additional variables, such as biting interval and abundance of the vector relative to the human host, have been included in various attempts to evaluate transmission. The possibility of inherited or of venereal transmission of a pathogen

presents additional problems [7], and this mode is designated "vertical." In contrast, "horizontal" modes of transmission require that pathogens directly pass from reservoir to vector. When differential competence of a given vector as a host for various pathogens is ignored, vectorial capacity, as stated, describes the ability of a given vector to sustain transmission of any pathogen. In this manner, African *Anopheles gambiae* as well as Malaysian *A. campestris* capably maintain both malaria and lymphatic filariasis.

Present differences in North American geographic distribution of Lyme disease and of babesiosis may reflect recent changes in the distribution of vector species, each differing in vectorial capacity. Accordingly, the following discussion compares the bionomics of potential vectors, particularly focusing on factors that may determine effectiveness of transmission.

## BIONOMICS OF POTENTIAL VECTOR TICKS

Ixodes dammini:

The known distribution of *I. dammini* presently is limited to the northeastern quadrant of the United States [8], mainly along the southern New England coast (including eastern Long Island) and well inland around the state of Wisconsin. In Canada, the tick is present on Long Point in Lake Ontario. In addition, the tick is abundant in New Jersey and adjacent portions of mainland New York as well as parts of the state of Maryland. In New England, this tick is known mainly from islands and locations adjacent to the coast, notably around the moraine formed by the great piedmont glaciers. These include Cape Cod and the islands of Nantucket, Martha's Vineyard, Naushon, Prudence Island, Block Island, and Long Island. Mainland records include Ipswich and Onset in Massachusetts, Old Lyme (and environs) in Connecticut, Armonk in New York, Cape May and various locations in New Jersey, and Assateague and various locations in eastern Maryland.

The present distribution of *I. dammini* reflects recent expansion in range [8]. Before 1949, the tick was recorded only from Naushon Island in Massachusetts, where it was abundant in the early 1920s [9]. Anomalous records from the 1930s of adult *I. dammini* on mice in New Haven, Connecticut, and Brooklyn, New York, should be regarded as labeling errors because adults have never since been discovered on small rodents. But, by 1950, the tick was established in various locations on Cape Cod and eastern Long Island. Concurrent records from farther inland probably represent imported infestations on human and domestic canine hosts. By 1960, seemingly recent infestations were recognized in Rhode Island [10]. Northern Wisconsin records date to 1968. By the middle 1970s, southern New Jersey, Nantucket, and Martha's Vineyard were recognized as being infested, and other sites were added in the 1980s.

Although this chronology suggests that the range of the tick has expanded in recent years, locality records may merely represent accidental discovery. The Ipswich record, however, appears to demonstrate recent introduction. Beginning in 1979, deer collected on Hog Island (near Ipswich) were routinely examined for ectoparasites. Three or four deer were collected there during the winter of each year. Abundant *I. dammini* were collected beginning in the winter of 1981–82. This site represents the northernmost extension of the known range of *I. dammini* in New England and indicates recent introduction.

Martha's Vineyard island appears to have become infested by *I. dammini* during the two decades following 1945. A Harvard-based tick-control effort (conducted by

Marshall Hertig) was directed against *Dermacentor variabilis* in that location during the middle 1930s and a student from George Washington University (Carroll Smith) worked there on tick bionomics during the late 1930s and early 1940s. Although both efforts were intensive, neither resulted in collections of *I. dammini,* whereas both recorded incidental observations of that species on nearby Naushon Island. *I. dammini* appears to have been absent from Martha's Vineyard at least until the 1950s.

This progressive increase in the distribution of *I. dammini* correlates with apparent changes in abundance of deer. The deer herd has been rapidly expanding since the 1920s. This correlation is particularly evident on Nantucket Island, where deer were absent until the 1920s [11]. They were thereafter imported and proliferated, such that hunting was permitted by the late 1930s. Naushon Island is the main coastal location that has been studied in which deer were abundant before 1940, and this is the site in which the tick originally was recorded (in 1926). On the mainland, farmland has increasingly been replaced by forest. Indeed, 80 percent of present-day forest was clear of trees in 1900 [12], thereby promoting, by that increment, opportunity for deer. *I. dammini* is present solely where deer are abundant and deer are the sole natural hosts (at least on Nantucket) for the adult stage of the tick. In addition, forestation of grassland has resulted in replacement of voles by mice.

Climatic or physiographic factors may restrict the range of *I. dammini* in New England [13], but the presence of similar ticks in northern Wisconsin suggests otherwise. Although abundance of deer remains the most likely determinant [11,14], formal proof is lacking. Other mammals may serve as host to adult *I. dammini* in mainland locations.

*I. dammini* appears to complete its life cycle in two years. Adults feed during early winter, larvae during the following summer, and nymphs during the second spring and early summer. If, as seems likely, the larval-nymphal molt occurs during the fall, the nymphal stage would be that which hibernates and nymph-transmitted pathogens would overwinter in the nymph.

Horizontal transmission of pathogens by nymphal ixodid ticks is facilitated when the season of transmission is long and when the nymphal stage precedes the larval stage. Indeed, immature *I. dammini* span the entire warm season (Table 1). Of these, 90 percent are present throughout the five-month period from May through September, and nymphs precede larvae. In this manner, the two-year cycle optimizes transmission. Prevalence of infection in mice would be greatest when larvae are present on hosts.

Narrowness of host range inevitably provides a major contribution to stability of transmission because larval-nymphal transmission cannot occur unless both larva and nymph attach to reservoir-competent hosts. Diversion of either stage obviates the effects of feeding by the other stage. On Nantucket Island, most immature *I. dammini* attach to mice (Table 1). The ticks may be relatively more abundant on deer, but we estimate that about 400,000 mice are present there, greatly outnumbering the 2,000 estimated deer. Voles are seldom parasitized. Except for rabbits and birds, which may harbor a few immature *I. dammini,* no potential alternative hosts are abundant on this island. Domestic animals rarely intrude near the collecting sites. This restricted availability of potential hosts greatly enhances stability of transmission and provides an important feature promoting human disease. The term "host attachment ratio" specifies the distribution of ticks among available host species. Clustering of bites on a particular parasite-competent species of host favors

TABLE 1
Variables Potentially Affecting Transmission
of Pathogens by *Ixodes dammini*
on Nantucket Island (Ram Pasture)

1. Permissive period for 90 percent of ticks:
   Larvae—July through September (three months)
   Nymphs—May through July (three months)

2. Narrowness of host range:

| Host | | % on Host | |
| --- | --- | --- | --- |
| Species | Relative Abundance | Larvae | Nymphs |
| Mice | 200 | 91 | 91 |
| Voles | 100 | 4 | 5 |
| Deer | 1 | 5 | 4 |

3. Abundance of vector relative to primary host:
   Larvae per mouse, 5.4
   Nymphs per mouse, 1.6

4. Larva to nymph survival:
   3.4 larvae/nymph = 29 percent

*Note*
Prevalence of pathogen (*Babesia microti*):
   in mice, 51 percent
   in ticks, 5 percent

transmission. Zoonotic disease depends upon such restricted conditions, which "narrow the bridge" of infection between reservoir and human hosts. Greater diversity of non-reservoir host species would decrease stability of infection as well as reduce risk of human disease.

Risk of infection increases with increasing vector-host contact, but absolute tick abundance may be misleading [15]. Abundance of ticks relative to a reservoir host depends upon local abundance of that host, and transmission is determined by this relative value. Thus, in a counter-intuitive manner, prevalence of infection may be an inverse function of reservoir density. In the event that reservoir abundance does not affect vector density, reduction of that host will increase the abundance of ticks relative to the host and, hence, increase transmission. During the three-month season permissive to transmission in a Nantucket Island site, mean prevalence of nymphal *I. dammini* was 1.6 per mouse (Table 1). Perhaps 50 nymphs would have attached to each mouse in a three-month season. In another site, where mice were twice as abundant, only 25 would have attached. Because babesial infection was present in about one in 20 nymphs, two or three infectious ticks would have attached per mouse per year in the former site and only one in the latter. This may explain corresponding prevalence estimates for *Babesia* of 51 percent and 27 percent, respectively.

Successful development from larva to nymph is suggested by estimates of abundance of larvae relative to nymphs or mice. About 3.4 larvae were present per

TABLE 2
Variables Potentially Affecting Transmission
of Pathogens by *Ixodes muris*
on Martha's Vineyard (after [16])

1. Permissive period for 90 percent of ticks:
    Larvae—July through October (four months)
    Nymphs—April through September (seven months)

2. Narrowness of host range (total period):

| Host | | % on Host | |
| --- | --- | --- | --- |
| Species | Relative Abundance | Larvae | Nymphs |
| Voles | 4 | 94 | 93 |
| Mice | 1 | 6 | 7 |

3. Abundance relative to primary host:
    Larvae per vole, 0.3
    Nymph per vole, 0.1

4. Larva to nymph survival:
    4.7 larvae/nymph = 21 percent

nymph, which implies that 29 percent of larvae survived to the nymphal stage and attached to another host. This parameter is useful for two purposes: *(1)* in the event that the various populations are in stable equilibrium, the ratio can be used to describe the permissive nature of the environment; *(2)* alternatively, the larval/nymphal ratio could serve to monitor trends in tick abundance. For example, we have observed ratios as high as 25:1 in newly established sites. A successful tick-reduction program would be reflected first in a relative preponderance of nymphs.

Ixodes muris

*I. muris* was abundant on Nantucket Island and Martha's Vineyard during the 1930s [16]. But the species subsequently became rare. It now may be extinct. A relict population was present on Muskeget Island in 1979 [8] but three collecting trips to that location in 1980 through 1983 failed to reveal ticks of any species. This remote oceanic islet, located between Nantucket and Martha's Vineyard, contains at least one other indigenous species, the vole, *Microtus breweri.* The site has been devoid of deer. *I. muris,* presumably, was the vector of *B. microti* on Martha's Vineyard in the 1930s when three of four voles were parasitized [17].

Nymphal *I. muris* appear to have been effective vectors of parasites of voles. The nymphal period spanned seven months and generally preceded the four-month period of larval activity (Table 2). More than 90 percent of immatures fed on voles. Abundance relative to the primary host, however, was somewhat lower than in the case of *I. dammini.* Only about eight nymphs would have fed on a vole during the permissive period. Successful development of larvae to nymphs was somewhat less than that of *I. dammini,* suggesting that the environment may have been less permissive for *I. muris.*

TABLE 3
Variables Potentially Affecting Transmission
of Pathogens by *Ixodes scapularis*
(after [18])

1. Permissive period for 90 percent of ticks:
   Larvae—May through June (two months)
   Nymphs—May through August (four months)

2. Narrowness of host range:

| Host | | % on Host | |
| --- | --- | --- | --- |
| Species | Relative Abundance | Larvae | Nymphs |
| Skinks | 1 | 98 | 86 |
| Rodents | 1 | 2 | 14 |

3. Abundance relative to primary host:
   Larvae per skink, 2.7
   Nymphs per skink, 0.4

4. Larva to nymph survival:
   6.8 larvae/nymph = 15 percent

## Other Species

Until recently, *I. dammini* was confused with *I. scapularis,* a related tick that is most numerous in the southern quadrant of the eastern United States. Larvae seem to precede nymphs during their season of activity and about 90 percent of immatures feed on reptiles, at least in Florida (Table 3). Adults feed on deer, but no immatures have been recorded from that host. Skinks seem to be parasitized by about 13 nymphs per year and about 15 percent of larvae develop and attach as nymphs. If these interpretations of Rogers's data [18] can be generalized to the entire species, then *I. scapularis* would not serve as an efficient vector for parasites of mice.

We know of no data that permit similar analysis for *I. pacificus* of the western United States, or *I. ricinus* of Europe. Both ticks, however, appear to transmit Lyme disease, and perhaps babesiosis, to human hosts. Published reports suggest that immatures of both species may attach to a great variety of animals. *I. pacificus,* in particular, parasitizes an extraordinary variety of animals, including reptiles, birds, marsupials, rodents, rabbits, ungulates, and carnivores, as well as human hosts [19].

## CONCLUSION

Narrowness of host range seems to constitute a crucial element affecting the capacity of ixodid ticks to transmit pathogens between reservoir hosts. It follows, therefore, that one vector cannot maintain horizontal transmission of pathogens having diverse reservoir hosts. Conversely, two pathogens, transmitted by one vector, must share a common reservoir host to the extent that these pathogens are transmitted horizontally. In the case of vertical infection, reservoir hosts become relatively unimportant because the pathogen is inherited and hence maintained entirely by the vector.

The wide distribution of Lyme disease as compared to babesiosis suggests that the spirochete is transmitted transovarially, at least occasionally. Our reasoning suggests that the mouse *P. leucopus* is the most likely reservoir host for this pathogen, to the extent that horizontal transmission occurs.

## ACKNOWLEDGEMENTS

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