THE RESTRICTION OF THE SPECIES RANGE OF *IXODES SCAPULARIS*, SAY, IN MASSACHUSETTS BY FALL AND WINTER TEMPERATURE

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ABSTRACT

The species range of *Ixodes scapularis* (Say) in Massachusetts is restricted to a small coastal area of Southeast Massachusetts by a minor climatological gradient present during the fall and winter. Heat from seawater keeps the fall and winter temperatures above those inland such that *I. scapularis* can just maintain enough adult seasonal activity and a one year generation to establish a population. Minor shifts around the average mean temperature produce population crashes and explosions. Under these marginal climatic conditions, this species requires a high adult host density to maintain an infestation level.

RÉSUMÉ

La répartition d'*Ixodes scapularis* (Say) est limitée à une faible surface près de la côte du Massachusetts du Sud Est par un petit changement du climat pendant l'automne et l'hiver. La chaleur de la mer produit des températures plus hautes que celles de l'intérieur, de telle sorte que *I. scapularis* peut maintenir une activité adulte suffisante et une première génération pour produire une population. De petits changements dans les températures moyennes provoquent de fortes différences dans cette population. A cause des conditions climatiques marginales cette espèce exige une forte densité d'hôtes adultes pour maintenir son niveau d'infestation.

On Cape Cod Massachusetts the common name " Deer tick " traditionally has been used for tick infestations which occur in the fall and sporadically during the winter. These infestations, although variable from year to year, have " always " been present on the Cape. The " Deer tick " problem was brought to my attention by O. JOHNSON of the Cape Cod Extension Service. This " Deer tick " was identified as adult *Ixodes scapularis* Say. The adult sexual dimorphism of this species had confused the issue of whether one or two species or stages made

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up the " Deer tick " season. Adult *I. scapularis* had only been previously reported as common on the Elizabeth Islands off Cape Cod (COBB, 1942), and a single record from inland Massachusetts (PARSONS, 1962). A survey of Southeastern Massachusetts, by tick collections from dogs, showed that *I. scapularis* was restricted to Cape Cod and the Islands of Martha's Vineyard and Nantucket. These islands are off the south side of Cape Cod. A few *I. scapularis* were collected in the New Bedford, Westport coastal area on the mainland adjacent to the south coast of Cape Cod and opposite the Elizabeth Islands. (MCENROE, unpublished).

Immature *I. scapularis* are common on birds off Cape Cod (MAIN and ANDERSON, 1971) and must be continuously introduced in to the inland areas. The dwell time of immature stages on migratory birds along the Atlantic flyway would permit the transportation of immature *I. scapularis*, during the period of host attachment, of at least 1 500 km. (R. FORSTER, Personal communication). *I. scapularis* is not restricted by lack of a suitable host complex as it utilizes the same hosts as *Dermacentor variabilis* (Cooley and Kohls, 1945). Some unknown factor restricts their species range. It will be shown that a minor difference in the fall and winter temperatures limits the species range.

During the period from 1969 to 1973, following winters with below normal temperatures, the *I. scapularis* population was apparently depressed as no reports of infestations were noted. Only a few ticks were collected either from dogs or by dragging. In the fall of 1974 infestation levels of " Deer tick " were reported. In late October a heavy infestation was reported from North

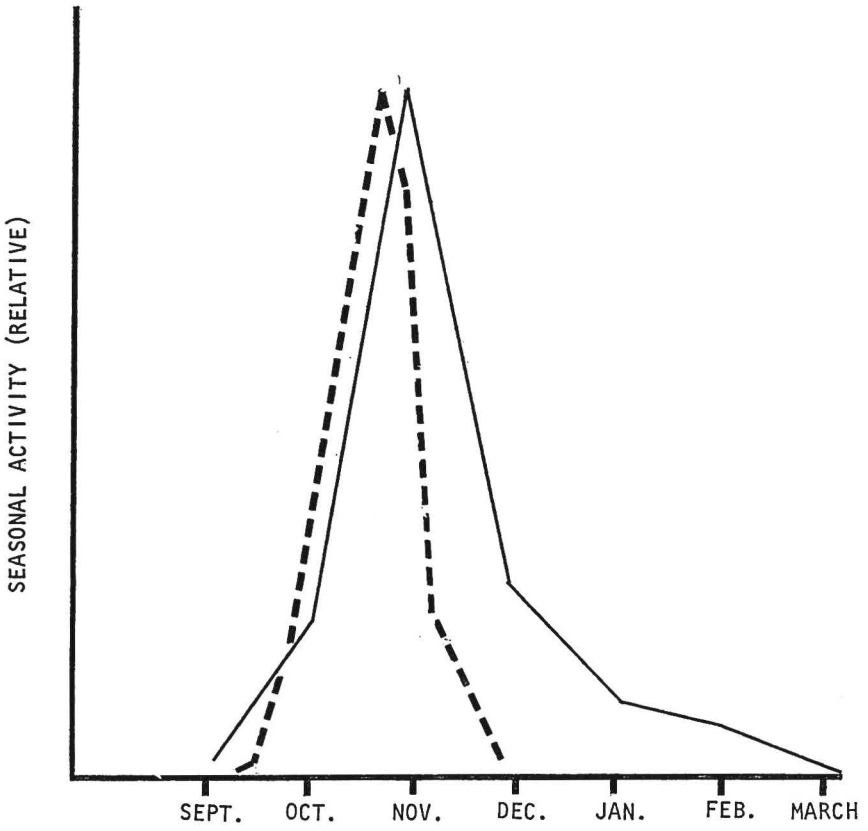

FIG. 1. — Solid line) *I. scapularis* season from Rogers (1953) ; Broken line) 1975 *I. scapularis* season in North Falmouth. Maximum number of tick collected in single collection, 108 over 0.5 km roadside drag course.

Falmouth where a dog picked up several dozen ticks in a few hours (R. BURK, Personal communication). This area was surveyed for ticks and, for the first time, *I. scapularis* was consistently picked up by dragging. Dogs were reported to be continuously infested by ticks into December. The previous winter had above normal temperatures and it was postulated that this factor was responsible for the increased *I. scapularis* population (MCENROE, 1975).

In the fall of 1975, again following a winter with above normal temperatures, the seasonal activity of *I. scapularis* was followed in this North Falmouth area. Ticks were collected by dragging over fixed roadside drag courses with a total length of ca 0.5 km. The seasonal activity of *I. scapularis* in North Falmouth differs from that found in Northern Florida (ROGERS, 1953) as shown in Fig. 1. Despite a mean monthly temperature difference of ca 8°C (Fig. 2) the seasonal activity starts in late September in both areas. This period is also the start of activity for adult *I. scapularis* on Long Island, New York. (GOOD, 1973). This is unlike the start *D. variabilis* activity which is temperature dependent (MCENROE, 1974a). This difference indicates a photoperiod control of *I. scapularis* activity with initial activity correlated with the fall equinox on September 22. Although adult *I. scapularis* are active during the summer, they do not enter questing activity but remain in a behavioral diapause (ROGERS, 1953). In North Florida, where the average minimum mean is 12° during the winter, *I. scapularis* remains active throughout the winter into March. In contrast, activity in North Falmouth ceased in mid-December. Tick activity also ceased at this time in the adjacent area of Martha's Vineyard Island, when there was a sharp decline in temperature. In the latter half of February, tick activity resumed on Martha's Vineyard during a period with a mean temperature 3° above normal. Activity continued into the first week of March when it ceased following a fall in the mean temperature (P. JOSEPH, Personal communication). It would thus appear that a temperature threshold for *I. scapularis* activity is present during the winter in Massachusetts but not in Florida. That is, the decline in temperature causes a temporary suspension of activity but not a diapause. *I. scapularis* again becomes active in March and April. This spring level of activity is minor compared to that of the previous fall level. Only a few ticks have been collected from dogs in the spring and in 1975 only a few ticks were collected in the North Falmouth area by dragging. A similar difference in the level of fall and spring activity was found on Long Island (GOOD, 1973). *I. scapularis* is rare in May and June. Seasonal activity ceases earlier in Florida than in Massachusetts and New York. This type of seasonal decline indicates that it is the result of seasonal mortality. ROGERS (1953) stated that adults did not survive for more than one season.

In North Falmouth, the 1975 December 1 to 15 mean temperature was 5.5° during the period of tick activity. The December 16 to 31 mean was — 0.8° during the period of inactivity. During the latter half of February 1976 when the resumption of activity was noted on Martha's Vineyard, the temperature mean rose from — 1.1° (Feb. 1-15) to 4.4° (Feb. 16-28). Activity continued into the first week of March when it was terminated by below normal temperatures. Isolated warm days in a period of cold weather apparently will not allow activity. This is also the case for the start of *D. variabilis* activity which does not respond to single days but to the previous 5 day period (MCENROE, 1974a). The residual seasonal activity starts in late March when the average mean temperatures remain above 4°. This indicates that the threshold for *I. scapularis* activity is a period of several days with a mean of 4° or above. A decline in temperature to this threshold level apparently will repress activity. In North Florida, the seasonal increases of activity continued through mid-November, a period of means, 14° or above. In North Falmouth, activity declined from the end of October to mid-November, when the weekly mean declined to 8.5° from the October mean of 15°. This early decline of activity cannot be due to mortality, as the activity is resumed in following warm periods, rather it is a temperature limitation on acti-

vity. The period of fall and winter temperatures above 4° in Massachusetts sharply decreases inland because of the localized effect of warm seawater around the Cape and Islands. This moderating effect is most pronounced south of Cape Cod and over the islands because the seawater temperature in Massachusetts Bay, north of the Cape, is colder than on the south side of the Cape. During the fall, mean temperature on the Cape and Islands remains ca 3° above those present inland and this temperature gradient occurs inland, just off Cape Cod. This difference in mean temperature limits the allowable period of inland activity to only the month of October during the start of the season. In contrast, on the Cape and Islands, the fall period above 4° normally lasts through November and can extend through January (Fig. 2) allowing continuous adult activity. The fall temperature gradient inland from the coast is a factor in the limit of the species range *I. scapularis*. In inland areas, there is not sufficient time for egg production to maintain

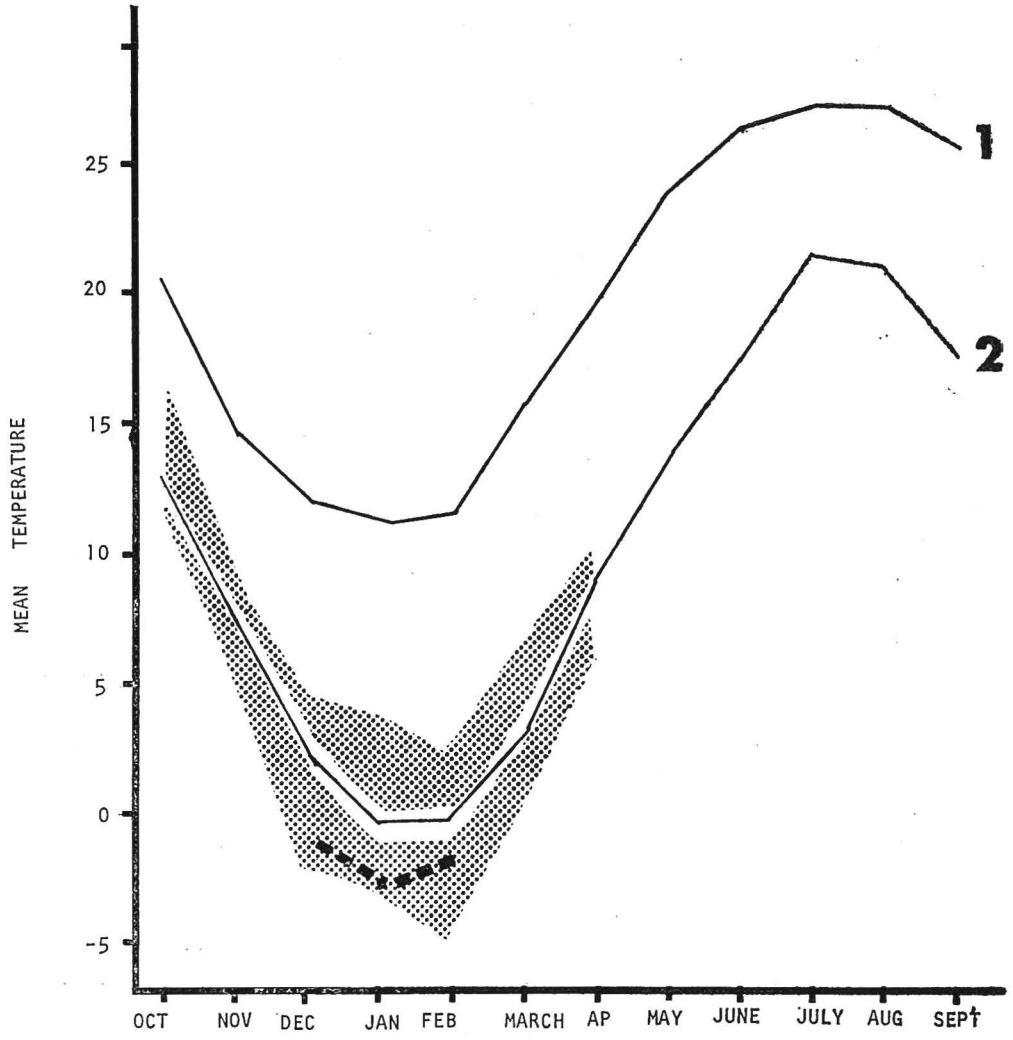

FIG. 2. — Line 1) Average mean monthly temperatures for North Florida division ; Line 2) Average of mean monthly temperatures from New Bedford and Edgartown, stations located across the area of *I. scapularis* infestation. Shaded area extremes of mean temperature ; Broken line) winter monthly means for East Wareham at the head of Buzzards Bay outside the area of *I. scapularis* infestations.

a population. On the Cape and the Islands the increase of allowable seasonal activity to normally two months is sufficient to produce enough eggs to maintain a continuous population.

The effect of winter temperature on the *I. scapularis* population size will be most important during the month of December, as above normal monthly means will rise above the threshold for activity and extends the season to three months of continuous activity. During the period of below normal winters, the December means are below 4°. The December previous to the infestation levels in North Falmouth, had a 1973 mean of 5.5° and in 1974 the December mean was 4.8°. The duration of seasonal activity is thus dependent upon variations of temperature in late November and December (Fig. 2). During this period, above normal temperatures will extend the season of breeding activity and in turn increase the population size the following fall. Below normal temperatures in like manner will restrict seasonal activity and the potential size of the following generation. Warm periods during the winter will also increase the size of the following generation when temperatures around 5° permit questing activity.

In North Florida, the temperature regime (Fig. 2) permits continuous development of the generation following the breeding season, for a one year generation time. Diapause adults emerge throughout the summer and enter activity in the fall (ROGERS, 1953). In Massachusetts the temperature regime (Fig. 2) will primarily retard the preoviposition period of the fall females and to a lesser extent egg hatching and nymphal molting. Low temperatures will essentially stop metabolism but active movement of adults was observed at 1.5° (ROGERS, 1953). Growth, although slow, continues to just above 0°. Assuming the usual Q10 logarmithmic relationship between growth and temperature, the Florida time periods for interstage development can be extrapolated to the Massachusetts temperature regime. With above normal temperatures, eggs would be laid in January-February, and with the average rise in spring temperature, larvae would hatch in June. June larvae could, in the following three summer months, enter fall adult activity as the nymphal molting period would be 2 ½ months with the average summer mean. As the preceding temperature rises above normal, an increasing proportion of the previous fall generation would enter the larval stage prior to the summer and enter fall adult activity in the one year cycle. Below normal fall and winter temperatures would retard or stop preoviposition. As a result eggs would not be laid until the spring rise in temperature, and larval activity would be delayed until summer. The following nymphal stage in turn would not have sufficient time to enter the one year cycle into adult activity. The decline in fall temperature would terminate nymphal molting until the following spring. The proportion of engorged nymphs in the nymphal stage, however, is a significant factor in the two year cycle as field survival of engorged nymphs is greater than four months versus survival of nymphs of only several weeks (ROGERS, 1953). Therefore, the lower the preceding fall and winter temperatures the fewer nymphs can become engorged because of time limitation. Three observations suggest that the Southeastern Massachusetts climate is marginal for a one year cycle. 1) The winter activity of immatures found on the Elizabeth Islands (COOLEY and KOHLS, 1945) cannot result from fall eggs because of temperature restrictions on development. This activity therefore must represent the fraction of the population in a two year cycle. The limiting stages in a two year cycle is the short survival of unengorged nymphs and active adults found under field conditions. This suggests that the depressed fall populations, following below normal winter mean temperatures, are emerging from a two year cycle. 2) The increase of fall activity, which followed the above normal winter means in both 1974 and 1975, suggest that high winter temperatues accelerate development producing a one year cycle for a significant proportion of the adult population. Above normal winter means would thus have the additive effect of not only extending seasonal egg production but also of increasing the proportion of the active adults emerging from a one year cycle. 3) *I. scapularis*

infestations are localized in areas with the highest December temperatures. The overall temperature effect will account for the peculiar distribution found around Buzzards Bay. This species is present on the Elizabeth Islands and along the adjacent coast of Cape Cod (North Falmouth area). *I. scapularis* is rare or absent around the head of the bay and again appears in the Dartmouth-Westport shore opposite the Elizabeth Islands. The temperature on both sides of the bay entrance runs considerably above those at the head of the bay. In 1973, the December means were 5.6° and 5.5° (New Bedford, Woods Hole) at the entrance to the bay and 2.6° at the head of the bay (East Wareham). The winter monthly means in East Wareham, about 24 km. from both Woods Hole and New Bedford, run *ca* 3° below these adjacent stations (Fig. 2). Hatchville has been a study area for *D. variabilis* from 1969 to 1975 (McENROE, 1975). Although only 10 km. inland from the North Falmouth coastal area, it has never produced a specimen of *I. scapularis*. In 1973, the December mean for Hatch ville was 3.9°. This area has winter means *ca* 2° below Woods Hole. In 1973 the December means were at near record highs over this area. The winter temperature gradient over Southeastern Massachusetts limits the infestation areas of both *D. variabilis* and *I. scapularis* to the Cape and Islands. *D. variabilis* however has been able to extend its range inland because limited winter survival is possible in the diapause stages. The low inland temperature however, essentially prevents fall and winter activity of *I. scapularis*. This limits the inland extension of its species range. The fall and winter temperature variations, rather than those in the spring, are significant for *I. scapularis* development because of the change in the relationship between average ambient and seawater temperatures. During the fall and winter seawater temperature remains above ambient, and during the spring it remains below ambient. This relationship interacts with warm air masses to increase fall and winter temperature but to decrease spring temperature. The higher spring temperature found inland however do not allow the establishment of *I. scapularis*. An additional factor in the present inland population of *D. variabilis*, outside its original range, was postulated to be the increase of the dog population. This increase of adult hosts insured the reproductive success of the limited number of overwintering adult survivors under marginal climatic conditions (McENROE, 1974b). *I. scapularis*, although first identified from the Elizabeth Islands in 1926 (LARROUSE *et al*, 1928) it was not reported from Martha's Vineyard during a five year study of *D. variabilis* from 1938 to 1942 and in this study, where deer were found uninfested with ticks, it was concluted that the dog was « almost the sole host of adults. » (SMITH and COLE, 1943, SMITH *et al*, 1946). According to P. JOSEPH (Personal communication) there is no history of a " Deer tick " season from that period. During the first deer hunting seasons in the early fifties, " Deer tick " was not noted on the deer collected (E. DUARTE, Personnal communication). During the following twenty years, *I. scapularis* has increased from a rare to infestation level on Martha's Vineyard. That is an additional factor other than climate was regulating the *I. scapularis* population. This intrinsic factor is believed to be an increase of adult host density. This effect operates under the marginal climatic conditions for *I. scapularis* in the same manner found with *D. variabilis* in inland Massachusetts. Prior to 1945, Martha's Vineyard was largely a seasonal resort area. The dogs that were essentially the sole adult hosts for *D. variabilis* were present during the *D. variabilis* season but not during the *I. scapularis* season. Since 1965 Martha's Vineyard has had a large increase in the permanent population and an extension of the seasonal population into the fall. This increase, combined with the present day popularity of dogs as pets, has resulted in a high dog density during the *I. scapularis* season. In 1930, there were only two White Tail deer on Martha's Vineyard. In 1931, English Fallow and White Tail deer were introduced and the deer herd slowly increased for the next 20 years and rapidly since 1950 (C. HOYLE, Personal communication). From 1960 to 1966 skunks and raccoons were introduced and rapidly built up large populations

in the absence of natural enemies. (P. JOSEPH, Personal communication). Neither of these animals were collected by SMITH *et al* (1946). The increase of these animals, especially dog, can supply the high host density to account for the increase of *I. scapularis* in an area of only marginal climatic suitability as it has for *D. variabilis* in inland Massachusetts [2]. The dog is believed to play a major role as an adult hots for *I. scapularis*. Even in Georgia, where *I. scapularis* is common, it was rare on all wild hosts except for fox and lynx (MORLAN, 1952, WILSON and BAKER, 1972). In Florida, *I. scapularis* is a major pest of dogs, and it is also reported to be common on dogs on Long Island (GOOD, 1973). Even during periods of low infestation levels, it is consistently present on dogs (R. SILVA, Personal communication). The territorial behavior of wild hosts also limits their density, a factor that does not regulate dog density. The unnatural concentration of favorable adult hosts which results from dog populations is believed to play a major role in maintaining *I. scapularis* populations under marginal conditions.

In the coastal area between New Bedford and Westport, where the climatic conditions are similar to Cape Cod, there is no tradition of a " Deer tick " season and *I. scapularis* is rare. This area unlike Cape Cod has maintained its rural character as a farming area with a low dog density. During the period when *I. scapularis* was reported as common on the Elizabeth Islands (COBB, 1942), the adult hosts could not have been dogs as these islands were uninhabited during the fall and winter. Three possible hosts, however were present. During the extreme cold winters of the early thirities, the formation of sea ice was reported to have allowed foxes to migrate from Cape Cod and subsequently build up an unusually large population (A. LANE, Personal communication). Foxes were exterminated on Martha's Vineyard during the nineteen twenties (P. JOSEPH, Personal communication). In contrast to Martha's Vineyard, deer were so plentiful on the Elizabeth Islands that they looked like a " herd of cows " (A. SULLIVAN, Personal communication). During this period sheep were kept on the Elizabeth Islands. *I. scapularis* was initially suspected to be the European sheep tick *I. rincus* introduced by a parasite control program around 1920. *I. scapularis* was originally listed as *I. rincus* var. scapularis until raised to specific rank. The presence of these hosts are suspect for the requirement of high host density.

High adult host density, by insuring reproductive success of surviving adults, would appear to be a requirement for maintaining a tick population under marginal climatic conditions for survival. The various reports of its distribution indicates that *I. scapularis* is not abundant except in the extreme southern United States especially in Florida where it becomes the dominant tick pest (ROGERS, 1953).

The increasing number of cases of Rocky Mountain spotted fever, south along the Atlantic coastal states, following the *D. variabilis* season (Annon, 1970-74), makes *I. scapularis* a prime suspect for the tick vector during this period as suggested for Massachusetts (1976).

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2. The lack of adult hosts on Martha's Vineyard was due in part to an attempt to protect the last surviving Heath hens, a relic population which became extinct.

around 1950 ; Mr. R. SILVA of the Barnstable Animal shelter for recent information of the " Deer tick " season on Cape Cod ; the Veterinarians and dog owners who submitted ticks for the localization of the species range ; Mrs. R. BURK, and her dog, for their information on the tick infestation in North Falmouth ; C. HOYLE, president emeritus of the Martha's Vineyard Rod and Cun Club (1918) for his information on the deer herd ; A. SULLIVAN for her information on the deer herd on Elizabeth Islands while she was working there during the summer ; Ms. M. A. MCENROE for collecting ticks in the Westport area ; my wife, Ms. M. P. MCENROE, for help in following the tick season in North Falmouth ; and numerous individuals for information on fall and winter tick activity. Special thanks are due to P. JOSEPHS and his dog for following the *I. scapularis* season on Martha's Vineyard. Mr. JOSEPHS was also of great help in developing information on the " Deer tick " season and the possible changes in host density.

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