WINTER SURVIVAL AND SPRING BREEDING BY THE FALL TICK, *IXODES DAMMINI*, IN MASSACHUSETTS (ACARINA : IXODIDAE)

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OVERWINTERING IN TICKS

ABSTRACT : In Massachusetts, the *Ixodes dammini* fall breeding period is ineffective because of the limited survival of engorged females. Adult overwinter survival allows a spring breeding period to maintain the population.

HIVERNAGE DES TIQUES

RÉSUMÉ : Dans le Massachusetts, *Ixodes dammini* commence son activité de faire naître en automne. Le régime de température qui suit est fatal aux femelles gravides et l'effort reproductif d'automne est perdu.

Quand les adultes peuvent survivre l'hiver, une période de reproduction au printemps redonne une population.

The optimum life cycle strategy for a 3 host tick is to have its development stages in the favorable part of the year, and diapause stages during the unfavorable part of the year.

In the south, a fall and winter breeding period allows the eggs to avoid lethal summer temperature. The subsequent development can continue to diapause summer adults. These adults become active in the fall for a one year cycle. This system is illustrated by *Ixodes scapularis* in Florida (ROGERS, 1953).

In the north, a spring and summer breeding period has the subsequent development in the warmest part of the year with diapause stages during the winter. This system is illustrated by *Dermacentor variabilis* in Massachusetts (SMITH *et al*, 1946). A fall and winter breeding period is not suitable in Massachusetts. Although fall conditions are as favorable as those in the spring for adult activity, nymphal molting of *D. variabilis*, at this time, produces diapause adults which enter activity the following spring. Fall breeding was not successful for production of viable spring larvae. The survival of active adults into the following spring was extremely rare (SMITH *et al*, 1946).

In Massachusetts *I. dammini*, however, with an unsuitable fall breeding period, and with the absence of winter diapause stages, maintains an infestation level on the islands, a marginal infestation on adjacent Cape Cod and a disjunct low level infestation in the coastal area of Essex County *ca* 60 km north of Cape Cod (COOLEY and KOHLS, 1945, McENROE, 1977, unpublished) [1].

I. dammini is a member of the *I. scapularis* complex and it has been separated from the southern *I. scapularis* with a postulated boundary in the mid-Atlantic states (SPIELMAN *et al*, 1979).

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I. dammini has, in addition to a fall breeding season, an early spring season which is not present for *I. scapularis*. The spring adults are not from diapause as adult activity is continuous during warm winter periods. The mortality from the age effect (LEES, 1964) of fall activity would apparently prevent overwinter survival of active fall adults.

This study was conducted at Hatchville on upper Cape Cod adjacent to the mainland, where a continuous but only a marginal infestation of *I. dammini* is present. Although the study of a marginal population does limit the collection of ticks in the field, it can expose the factors which limit the species range.

METHODS [1] :

The relationship between fall adult activity and temperature was followed by tick burdens on dogs rather than by the standard dragging collection technique because of the low infestation level present in the survey area. In 1979 to 1982, from October 15 through November, adult activity was followed at the state Crane Game Management area at Hatchville on Cape Cod, Massachusetts, during the bird hunting season, the period of maximum adult *I. dammini* activity.

The survey was conducted on Friday, Saturday, and Monday, the days of maximum hunting activity, and also on cold days at the start of the season and warm days at the end of the season. The tick counts were restricted to spaniel and setter type dogs, as these carried the heaviest tick burdens. Most dogs were brought to the Cape about once a week from outside the tick infested area and were routinely groomed after returning from the field. Attached ticks were found only on dogs whose owners were unaware of the tick infestation and which had been in the field the previous week. With this exception, dogs appeared tick-free before entering the field.

The dogs were examined for ticks as they returned to the parking lots after actively coursing 2-3 hours in the field. Due to fatigue, the time in the field was shortened when the temperature was *ca* 15°C. One group of dogs, starting in the field at sunrise, had their tick burdens related to the 6 AM temperature at the adjacent Otis Airfield. A second group of dogs, starting around noon, had their tick burdens related to the 12 N temperature.

During this period, dogs were also examined at the Miles Standish state forest inland *ca* 29 km north of Hatchville. Ticks were rare on these dogs, and the hunters reported that this area had an infestation level constantly below that present in Hatchville.

For the survival studies, the ticks were collected from the upper Cape Cod area. The spring ticks were collected on Martha's Vineyard Island. The engorged females had either dropped off dogs or were easily removed after they had finished engorgement. The flat ticks were held in soil level cages. The cages were made from the small vials used for casting the blocks for the ultramicrotome and were perforated for ventilation. The engorged females were held in 5 cm plastic petri dishes placed under the vegetative mat which was exposed to full sun. Survival of female *I. dammini*, collected in the field at the times noted, was determined at 20°C and 85 % RH over a saturated KC1 solution (WINSTON and BATES, 1960). The lethal low temperature for engorged females and eggs was determined after 24 hours.

RESULTS :

The relationship between morning and afternoon average tick burdens and temperature for the 4 years is shown in Fig. 1. The low threshold for consistent activity was around 2.5°C, though ticks were occasionally found below this temperature following a sharp temperature drop. The tick burdens increased at around 10°C and maximum activity occurred around 15°C. The decline of activity which occurs in November, was not related to temperature inactivation. During last

1. A survey of tick burdens on dogs in the fall of 1983 showed that *I. dammini* was still absent in the coastal area *ca* 70 km north of Cape Cod. This tick reapeared on the north shore within an area bounded by Danvers, Gorgetown, and Amesbury. Here, ticks were rare or absent in 1975-1976 (MCENROE, 1977). The tick burdens indicated a low level of infestation.

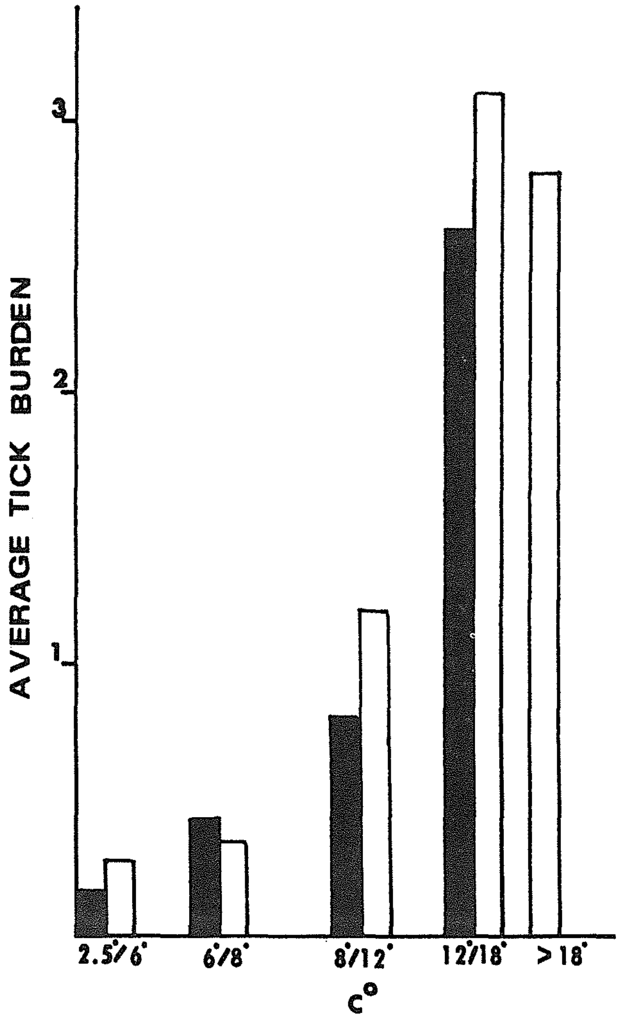

FIG. 1 : Average tick burdens on dogs. Black bars versus 6 AM temperature. Open bars versus 12 N temperature.

week of November, 1979, a high level of activity was found during a 5-day period with daily maxima ≥ 15°C. The level of tick activity was directly related to the immediate temperature and thus activity was determined by the daily maximum temperature [2].

From 1979 to 1981, of a total of 125 flat adults only 5 survived the winters in the field. Over the winter of 1981-82 only 1 of 8 engorged females laid eggs and produced larvae by June. This tick was engorged by October 2. The other ticks were engorged in late October and November. Four ticks, engorged in late March-April of 1981, all produced larvae by August. Of 5 ticks engorged in April and May of 1982, 4 produced larvae in August and September.

The 24-hour lethal low temperature exposure for newly engorged females (4) was between —3°C and —5°C. At the start of oviposition, after 24 hours at —10°C, 2 of 4 females failed to resume egg laying when returned to 25°C. Fresh eggs, held at —10°C for 24 hours, failed to hatch when returned to 25°C.

The survival of ticks at 20°C and 85° RH versus time is shown in Fig. 2. The ticks collected at both the start of fall and spring activity showed the longest survival times. The survival of ticks collected at the end of October had *ca* 70 % with short survival and 30 % with extended survival. The ticks collected at the end of the fall showed, with the exception of one tick, the shortest survival time.

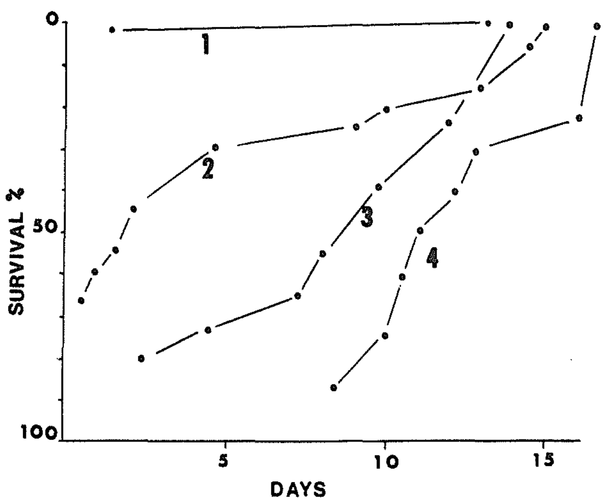

FIG. 2 : Adult survival at 20°C and 85 % RH. Line 1, late November — early December ticks (31). Line 2, late October ticks (30). Line 3, early spring ticks (20). Line 4, early October ticks (8).

2. On Martha's Vineyard island, during October and November, a golden retriever dog picked up as many as 3 dozen ticks after 1/2 hour in the field (P. JOSEPHS, personal communication). This shows the relative difference of infestation level between Cape Cod and the islands.

DISCUSSION :

It was previously postulated (MCENROE, 1977) that the higher fall mean temperature along the coast extended the fall breeding, and the lower mean inland was a factor in control of the species range. Adult activity is related to the maximum temperature, rather than the mean temperature. The average maximum temperature, in contrast to the mean temperature, runs the same during October (15°-16°C) and November (10°-11°C) both on the islands and inland. It is not until December, at the end of the tick season, that the maximum temperature inland declines below that on the islands (Anon.). As the maximum temperature means for October and November are the same over the area, the difference of the infestation level present is not caused by a difference of the fall temperature control of the breeding period.

Successful fall breeding is limited by the following lethal winter temperature. The newly engorged female is the most temperature sensitive stage. The most successful breeding would occur early in the fall period.

Both the low survival in the field and the limited resistance to water stress of active fall adults indicates that few fall adults survive over the winter. These ticks would be the summer diapause adults which first enter fall activity. The age effect of previous activity reduces the ability to resist water stress (LEES, 1964). The extended survival of the spring ticks, similar to that shown by early fall adults, shows that these ticks have had a limited amount of activity. The bimodal survival of adults from mid-season shows that they are a mix of new and old adults. A similar type of response was shown by *D. variabilis* for a mix of old spring adults and new summer adults at mid-season (MCENROE, 1974). Fall nymphal molting produces active adults rather than diapause adults. Late fall nymphal molting will produce active adults but their following activity will be repressed by low winter temperature. These adults will become active the following spring (Fig. 3). The intermittent activity present during warm winter periods shows that these are not diapause adults. On upper Cape Cod, adult *I. dammini* are usually rare in the spring. In contrast, a level of spring activity *ca* 1/2 of that present in the fall is found on the islands (MCENROE, 1977, 1978a, b, PIESMAN *et al*, 1979). Heavy fall infestations of *I. dammini* are present on Long Island, New York (GOOD, 1973) and spring infestations are significant but below the fall level (COLLINS *et al*, 1949). Both fall and spring activity is also present in southeastern Connecticut (ANDERSON and MAGNARELLI, 1980).

In Florida, *I. scapularis* had a unimodal fall adult activity pattern. However, a low level of activity was maintained until March (ROGERS, 1953). The age effect from 6 months of activity eliminates the summer diapause adults as the active late season adults. Nymphs engorged in the fall had an extended premolt period (ROGERS, 1953) and their molting provided the late season adults. The adult activity period indicates that spring and summer nymphal molting produces diapause adults, which become active in the fall, and fall and winter molting produces active adults (Fig. 3).

The immature *I. dammini* have a bimodal activity pattern. The level of spring larval activity is below that present in the summer. The level of spring nymphal activity is above that present in the summer (PIESMAN and SPIELMAN, 1979, MAIN *et al*, 1982). This indicates that although most breeding occurs in the fall it results in fewer larvae than those produced from spring breeding. The spring breeding is more successful as it is not restricted by low temperature. The spring nymphs produce the summer diapause adults which become active at the start of the fall season. The summer nymphs molt to active adults in the fall. The life cycle proposed for *I. dammini* is shown in Fig. 3. The cool summer on the islands will retard the fall nymphal molt. The following mild winter, with an average mean of 0.8°C (Anon.) is below the threshold for adult activity and will limit an accumulated age effect. It will also limit the exposure of ticks to the extreme desiccation of frozen bare ground (GEIGER, 1964). The warm December, with an average minimum temperature of —1.3°C and maximum of 5.5°C will extend the period of successful

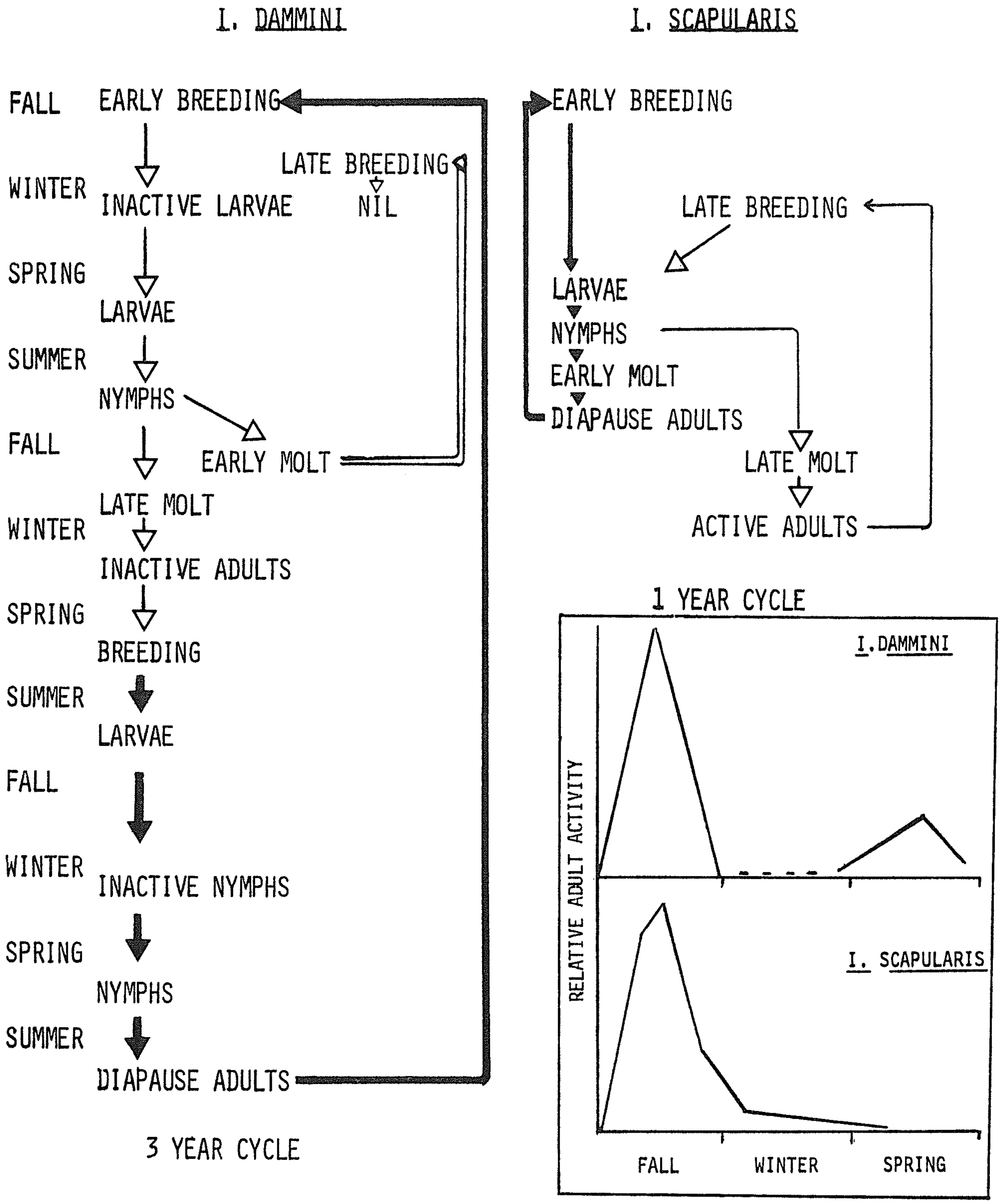

FIG. 3 : Schematic of *Ixodes dammini* life cycle in Massachusetts and *Ixodes scapularis* in Florida. Thick lines show major pathway of development. However, on Nantucket Island where the highest level of larval activity occurs in the summer in the dominant pathway, one season had most larval activity in the spring (PILSMAN and SPIELMAN, 1979). This relationship between spring and summer larvae reflects the relative success of fall and spring breeding.

fall breeding on the islands. The level of spring breeding will have a positive feedback on the population size, as the following adults enter the initial fall activity season when breeding has the best chance of success.

Departures from the average fall and winter mean temperature will have a strong influence on the population. This was shown by the unusually high level of infestation on upper Cape Cod in 1975 following 2 years with above normal fall and winter temperatures (McENROE, 1978). These seasonal temperatures were similar to those usually present only on the islands. The microclimate appears to be involved in the small areas of infestation, referred to as 'hot spots' by hunters. An area, *ca* 4 ha, around a kettle hole pond in Hatchville, but not the surrounding area, has consistently yielded adults by dragging, both in the fall and spring, since 1980. On Martha's Vineyard Island, a consistent area of heavy infestation is present around the Stone pond area (P. JOSEPHS personal communication, personal observation). There appears to be a requirement for a minimum level of spring breeding in order to maintain a population.

The north to south separation in the distribution of *I. scapularis* and *I. dammini*, which occurs in the mid-Atlantic states, is maintained in spite of the transport on birds of these ticks along a the Atlantic flyway (ROGERS, 1953, MAIN and ANDERSON, 1971, MAIN *et al*, 1982). *I. scapularis* does not extend its range into the area with sub-optimal condition for a fall and winter breeding period. *I. dammini* is not established in an area favorable to its fall and winter breeding period. Under the restriction of a fall and winter breeding period, these ticks would be expected to be sympatric not allopatric species. Their peculiar distribution suggests that they are geographical sub-species. Northern and southern subspecies are present in the winter tick, *Dermacenter albipictus*, complex (ERNST and GLADNEY, 1975), and the fall tick, *I. cookie*, is present all along the Atlantic seaboard (COOLEY and KOHLS, 1945).

The selection pressure on *I. dammini* at the northern edge of its range and the reproductive isolation of its alternate spring breeding would allow morphological divergence from *I. scapularis*. *D. variabilis*, under the selection pressure outside its original range, has adapted by changes in its morphology and physiology (McENROE, 1981, SPECHT & McENROE, 1984), but has maintained an unsuitable spring and summer breeding period in Florida (ROGERS, 1953). The response to the signal for diapause is maintained under negative selection pressure.

I. dammini requires a spring breeding period to complete its life cycle. The substitution of temperature control for a winter diapause requires a narrow climatic window for the production of spring adults.

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