THE REGULATION OF ADULT AMERICAN DOG TICK, *DERMACENTOR VARIABILIS* SAY, SEASONAL ACTIVITY AND BREEDING POTENTIAL (IXODIDAE : ACARINA)

BY

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ABSTRACT.

The conditions within the soil level microclimate regulate the initiation of activity, and the ambient water stress condition regulates the termination of activity. Both these factors combine to regulate the decline in seasonal activity by limiting tick survival.

Two cohorts of adults determine the distribution of activity within a season. Diapause adults, emerging from overwintering, enter seasonal activity in April. Diapause nymphs, after overwintering, feed in the spring and molt to active adults in July. The sum of seasonal activity represents the breeding potential of the population. The factors which limit seasonal activity regulate the population size by limiting the reproductive potential of the tick population.

The variation in seasonal adult tick activity found across south-eastern Massachusetts was related to the climatological gradient over this area.

RÉSUMÉ.

Les conditions microclimatiques au niveau du sol déterminent le début de l'activité de la tique *Dermacentor variabilis* Say et les conditions contraignantes de l'hygrométrie réglent l'arrêt de l'activité. La combinaison de ces deux facteurs détermine le déclin dans l'activité saisonnière en limitant la survivance des tiques.

Deux cohortes d'adultes sont responsables de l'activité dans une saison. Les adultes en diapause pendant l'hivernage entrent en activité en avril. Les nymphes en diapause pendant l'hivernage se nourrissent au printemps et se transforment en adultes actifs en juillet. La somme de l'activité saisonnière représente le potentiel reproducteur de la population. Les facteurs qui limitent l'activité saisonnière règlent la taille de la population en limitant le potentiel reproducteur de la population de tiques.

La variation dans l'activité saisonnière des tiques adultes constatée à travers le sud-est du Massachusetts est en relation avec le gradient climatologique relevé dans cette région.

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Introduction.

From April until September, the adult American dog tick, *Dermacentor variabilis* Say, engages in host seeking activity (questing) in southeastern Massachusetts. This activity is characterized by variation of the activity pattern both from year to year and location to location. As mating occurs on the adult host (Smith *et al*, 1946), the questing ticks, rather than the total adult population, make up the potential breeding population. Therefore the sum of seasonal questing activity plays a major role for the regulation of population size. The amount of seasonal questing also determines the pest infestation level and the importance of this tick as a disease vector.

The active adult tick population is believed to be essentially composed of only overwintered adults emerging from diapause for the following reasons : *1*/ Smith *et al* (1946) reported little adult activity expected from within season nymphal molting, *2*/ Sonenshine (1972) found low overwintering nymphal survival, and *3*/ Wilkinson (1968) found that newly molted adults of *D. andersoni* Stiles did not quest and proposed overwintering as a requirement for seasonal activity. However both Smith *et al* (1946) and Sonenshine *et al* (1966) postulated some late season adult activity from nymphal molting. A small late July peak in adult activity was ascribed to nymphal molting (McEnroe and McEnroe, 1973).

In general, the start of adult seasonal activity occurs with increasing spring temperature but it is not directly related to the daily temperature (Smith *et al* 1946, Becquaert 1945, Sonenshine *et al* 1966). Atwood and Sonenshine (1967) related the start and increase of seasonal activity to the increase of solar energy found in the spring. The distribution of activity within a season varies not only between locations but also from year to year in the same location. The highest seasonal level of activity is found as early as May or as late as August. The seasonal duration of high activity levels can be as short as two weeks or as long as two months (Smith *et al* 1946, Sonenshine *et al* 1966, Dodds *et al* 1969, Sonenshine 1972, McEnroe 1971 a, 1973 a). Questing behavior was shown to be regulated by the stage of the tick's water economy. As water loss approached 5 % of tick's initial weight, established under 20° saturated conditions, 50 % of the ticks were switched from the questing into the non-questing behavioral state. On the basis of net water exchange. it is estimated that diapause ticks, after overwintering, can go through about 25 cycles of questing to non-questing behavior prior to their 50 % mortality (McEnroe & McEnroe, 1973). The work associated with activity results in an ageing effect which reduces the tick's resistance to water stress. In the terminal stage, the tick can only maintain its water balance and survive under continuous saturated conditions (Lees 1969).

This study of seasonal activity was carried out to determine the factors regulating the adult seasonal questing activity in Southeastern Massachusetts.

Study areas and methods.

Adult seasonal activity was followed from 1969 to 1973 in a series of study areas extending across Southeastern Massachusetts. This transect of 160 km includes a climatological gradient, present during the tick season from April to August, which is caused by the modifying influence of the ocean (Fig. 1). The climate changes from cool and damp near the ocean to warm and dry inland. The records for Nantucket (U.S. Weather Bureau Station), an island, 40 km off the coast of Cape are similar to those for the adjacent island of Martha's Vineyard and Eastham on outer Cape Cod. These locations, with cool, damp conditions, have traditionally been areas of high tick infestation levels. Hatchville and Mashpee, near the base of Cape Cod, have intermediate weather conditions. These areas have medium levels of tick infestation and are near the original limit of the species range. The weather records from the bordering Otis Air Force Base were used for these areas. Lincoln, 22 km inland, has shown tick infestation since 1953 and Bolton 40 km inland has been infested since 1962. Bolton is near the present day limit of the species range. Both these are as characterized by a low level of tick infestation (McEnroe, 1973 a). The records for Hanscom Air Force Base, adjacent to Lincoln are representative for these inland areas and show the warmest and driest conditions during the tick season.

Seasonal tick activity was followed in all the areas, except Lincoln, by the standard method of pulling a cloth flag over a fixed course immediately adjacent to the roadside. Ticks not only accumulate in these areas, but also show enforced questing behavior (McEnroe, 1971 a). The maximum number of ticks per drag collected at the peak of 1973 seasonal activity ranged between 119 ticks for Bolton to 550 ticks at Nantucket. The seasonal tick activity in Lincoln was followed by the daily count of ticks removed from a dog. In 1973, 1196 ticks were collected during the season. The dog, an English setter, spent 8 hours a day (1100 to 1900 hrs.) in the open, and roamed a fixed territory of ca 1.5 km^2 made up of old pasture land around a small pond. The dog was groomed every evening and the ticks removed. Except on days of heavy rain, when the dog reduced its time in the field, the dog had a " more or less " consistent activity pattern. Check counts on a second English setter showed agreement both with days of high and low tick activity and the start of initial activity. During May 1973, the month of maximum tick activity, the dog recovered 4.8 % of 600 marked ticks released in the area. This recapture ratio gave an estimated May tick density of ca 80 ticks/ha. This density is much lower than that found in Virginia where several thousand tick/ha were usually present, although in one year only 140 ticks/ha were found (Sonenshine *et al* 1966, Sonenshine 1972).

In Lincoln, the soil temperature 1 cm below the surface and the dew point at the soil surface below the vegetative mat were recorded on an open, level, sunny location (Atkins temperature and LiCl dew point recorder ; United Eletric Control temperature recorder). In 1973 the ambient air temperature and humidity were recorded in Lincoln (Rustrack temperature and relative humidity recorder).

The mortality and equilibrium studies were held over saturated salt solutions (Winston and Bates 1960). The mortality studies were carried out with 30 adult males from their equilibrium weight at 20° and saturation, and the equilibrium studies with groups of ca 80 mg of females. The new adults were provided as engorged nymphs by D. E. Sonenshine. The other ticks were collected in the field as noted in the text.

Initial seasonal activity.

No adult tick activity has been found in March when the average mean temperatures are 2° + 0.25° and the average maximum temperatures are below 7° (Fig. 1). The start of activity occurs in April when the average maximum temperatures rise above 10°. The inland tick season is characterized by an earlier start and more rapid increase of activity than the season on Cape Cod. This difference in initial activity is associated with the rapid increase of maximum temperatures for April and May found inland (Fig. 1). The past five seasons in Hatchville showed initial tick activity as early as the first week in April and as late as the second week in May. The indirect relationship of activity to air temperature was shown by the start of activity in April when the average maximum temperature was above the monthly normal of 11.5° and the absence of activity when the average maximum temperature was below 11.5°. The lack of a direct relationship between air temperature and activity was shown by the overlap of average weekly maximum temperatures between the week prior to activity and the first week of activity. The average

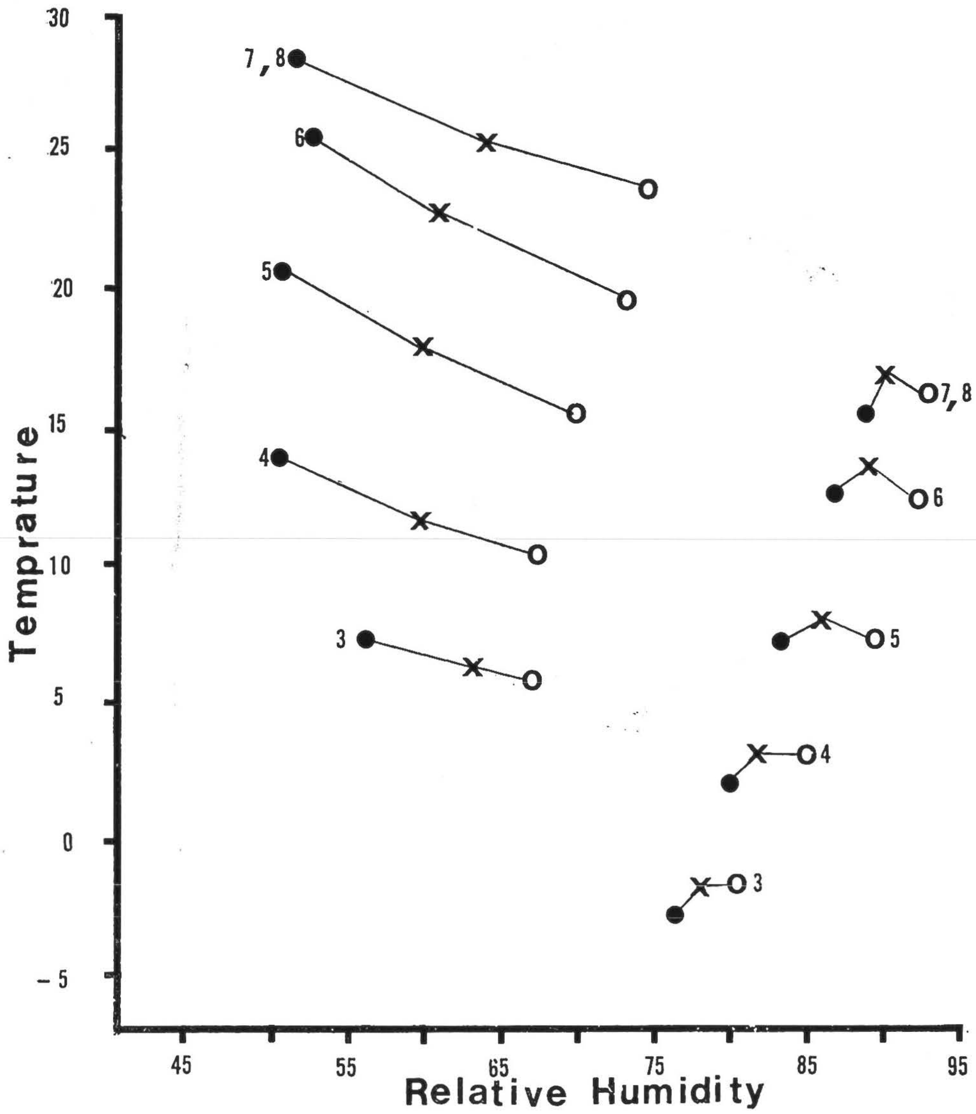

FIG. 1 : Average monthly maximum temperature versus monthly average relative humidity at 1300 hours and average monthly minimum temperature versus monthly average relative humidity at 0400 hours. Values shown for March through August, 3-8. Months of July and August have almost indentical values. Solid circles, Hanscom Air Force Base, values for Lincoln and Bolton ; X, Otis Air Force Base, values for Hatchville and Mashpee ; open circles, Nantucket Weather Station, values for Nantucket, Martha's Vineyard, and Eastham.

maximum temperature for the weeks immediately prior to activity were from 9° to 13° and for the first weeks of activity they were from 11.5° to 15.5°. Short term periods of high temperature will not induce activity. In Lincoln, days with maximum temperature up to 26° failed to produce activity. It would appear that air temperature has a slow cumulate effect on the initiation of activity. MILNE (1950) pointed out the importance of the soil level microclimate on tick behavior. As the ticks are in this microclimate, the temperature at soil level, rather than the ambient temperature, will influence behavior. The temperature at soil level, below the vegetative mat, will lag behind ambient air temperatures due to the thermal capacity of the soil and insulating properties of the vegetative mat. The soil level microclimate will also be strongly influenced by radiant heat exchange (GEIGER 1965). In effect, the soil temperature will follow the average change rather than daily fluctuation of ambient air temperature. Ticks are subject to desiccation during overwintering because of the low temperature characteristic of their water uptake (MCENROE 1971 b). Even at saturation below 15°, the tick's equilibrium water balance is below the threshold for questing (MCENROE 1973 b, MCENROE and MCENROE 1973). The soil level microclimate therefore must be suitable for water uptake before activity can start. During the initial period of tick activity, the dew point above the soil level remained at or above the soil temperature except for a few hours around mid-day on sunny windy days. Because of this saturated condition, the tick's water economy was a sole function of soil temperature. Both the tick's saturated equilibrium balance and the rate of water exchange approach minimum values below 10° and maximum values above 15° (MCENROE 1971b, 1973b). The stage of the tick water balance is the resultant of the previous net exchange. Short periods of high soil temperature were not sufficient to produce activity. A relationship of soil temperature and time was empirically developed to signal initial tick activity. The value of net temperature hours equal to the five-day sum of hours $> 15°$, minus hours $< 10°/4$ was negative prior to activity and became positive on the first day of activity. This relationship, developed on the basis of the 1971-73 seasons, also held for 1974 initial activity. In general, tick activity followed the change in net temperature hours. Two periods of inactivity occurred during the initial season when the net temperature hours became negative. In 1971, a year with a slow rise in soil temperature, a month after the start of the season the net temperature hours were between + 10 to + 16, and the tick counts were between 2 to 10 ticks per day. Within ten days in 1973, the net temperature hours rose to + 87, and the tick count went from 1 to 54 ticks per day. A rapid fall and rise of soil temperature through a minimum value of +2 net hours produced the following sharp dip in activity (Fig. 2). Soil temperature also has an immediate, as well as a delayed, effect on activity. During the period of positive net hours, all days of activity had maximum soil temperatures above 17°, but three days with maximum soil temperatures below 17° failed to show tick activity. Activity occurred on days with maximum air temperatures as low as 10°. Radiant heating was responsible for soil temperature above air temperature. The threshold for activity is the temperature in the soil level microclimate, not the ambient air temperature.

Initiation of activity requires *1*/ a temperature regime in the soil level microclimate suitable for water uptake in order to switch the ticks into the questing behavioral state, and *2*/ maximum soil temperatures above ca 17°.

Daily variation of tick activity in Lincoln.

The five day averages of daily tick counts for the Lincoln seasons and the flagging records for Bolton seasons have, in general, shown the same changes in level of activity (Fig. 2). The daily tick counts however showed a variation not present in Bolton (Fig. 3). Roadside populations, as in Bolton, showed a different behavioral pattern of enforced questing postulated to be the result of high CO^2 concentrations (MCENROE 1971 a). Over three seasons, tick activity both on the five highest activity days for each season and the five lowest activity days during the same period appeared to be independent of the ambient conditions of sunshine, rain, air temperature and humidity. The seasonal peak activity days did however have a common set of conditions when the soil level microclimate was included. The five days of peak activity (Fig. 3) must be associated with optimum conditions for questing activity. All these days had the following set of factors in common *1*/ both the soil and air temperatures remained above 20° for a minimum of 5 hours ; *2*/ the soil level microclimate, due to rain and/or heavy dew fall had previously remained at or

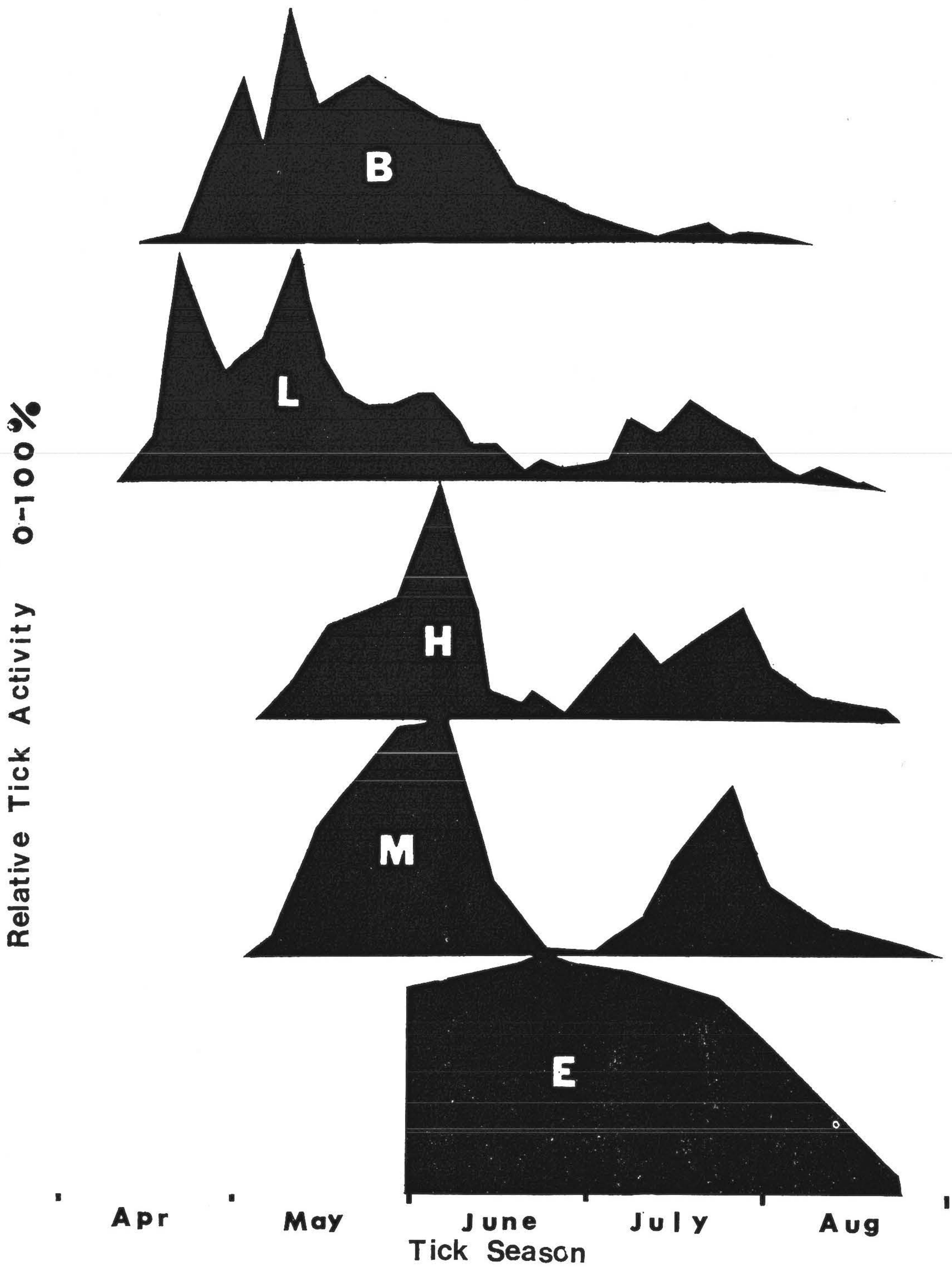

FIG. 2 : Tick seasonal activity versus months for 1973 — B, Bolton ; L, Lincoln ; H, Hatchville ; M, Mashpee ; E, Eastham. Activity scale adjusted to 100 % activity for maximum seasonal level present in each area.

near saturation for at least two days ; and 3/ during this period of saturation, the soil temperature had remained for more than 50 % of the time within the temperature range of 15° to 25°. Of the 15 highest activity days over three seasons, one occurred on a day with maximum air temperature of 14°, three with maximum air temperatures between 14° and 18°, and the remaining 11 on day with maximum air temperatures above 18°. The peak days all had air temperatures of 22°. All 15 days of high activity occurred on days with maximum soil temperature at or above 19°, and days with soil temperature below 16° were in the lowest activity class. The peak days of activity all had soil temperatures at or above 23°. Although adult *D. variabilis* activity has been

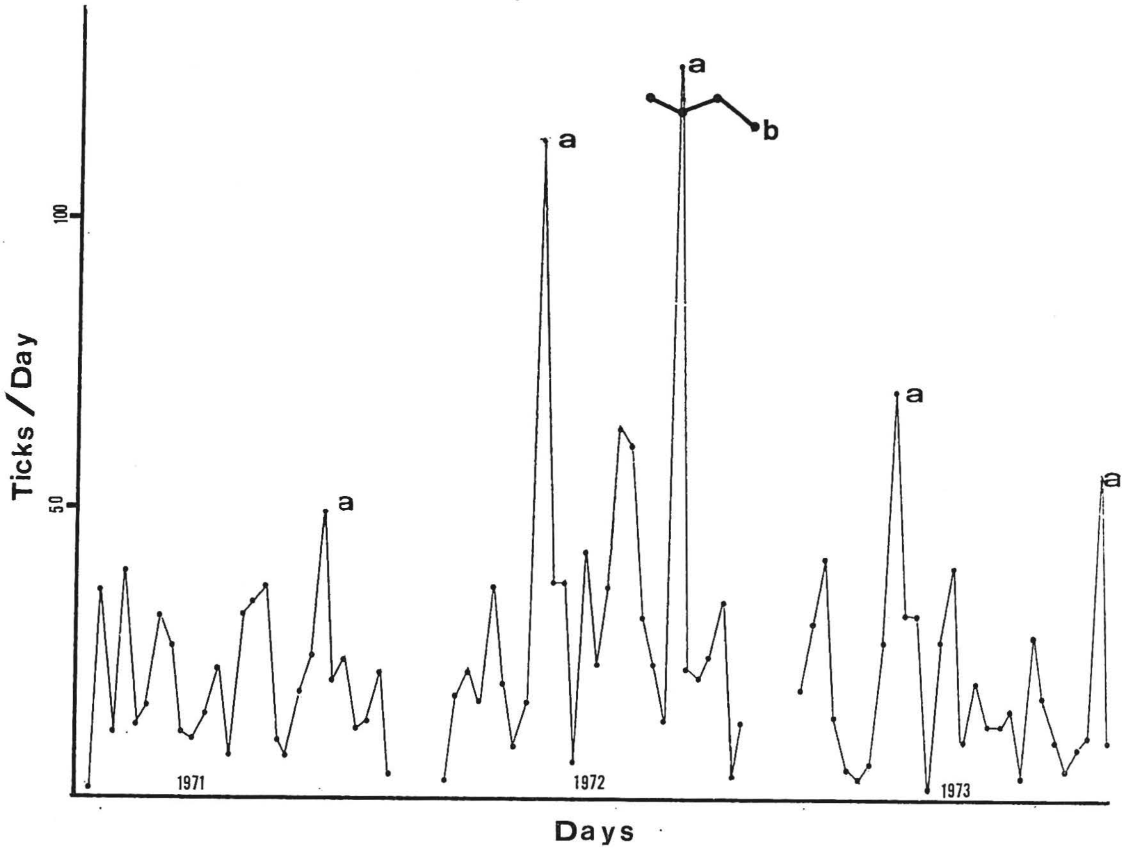

FIG. 3 : Day to day variation in Lincoln of tick collected from the dog at the height of the tick season 1971-73. a, five days of peak tick activity referred to in text ; b, variation of activity in Bolton in 1972. Tick scale for Bolton 3X scale shown for Lincoln.

reported with air temperature as low as 5°, (HALL and MCKIEL 1961), the record low temperature for activity in Lincoln was 7°. This activity day had a maximum soil temperature of 11.5° which was also the lowest temperature recorded on an activity day. Increasing soil temperature up to the twenties, like air temperature, appears to be optimum for questing activity. The temperature of the soil microclimate, rather than the ambient air temperature, however is the essential immediate condition which not only determines the threshold of response but also the level of response. Even with optimum temperatures however, a high level of activity did not occur unless the ticks were in the questing behavioral state as a result of positive water balance. The peak days followed a period in which the soil level microclimate remained saturated with optimum temperatures for water uptake. This previous regime provided ticks in the questing behavioral state to become active under the optimum temperature conditions.

Under the conditions in Lincoln, the variation in daily activity can be accounted for as follows. As the season progressed, the soil warmed up and dried out leaving the soil level microclimate no longer continuously saturated. This sub-optimum condition in the microclimate held the desiccated ticks at ground level as they returned from questing. A following optimum period of temperature and saturation for water uptake switched this group of ticks into the questing behavioral state, and optimum temperatures for activity produced a day of high activity. The initiation of questing activity is associated with a positive photoresponse and the termination of activity with desiccation (McEnroe and McEnroe 1973). These stimuli, under dry conditions, combine to produce a diurnal cycle of activity (McEnroe 1971 a). In the absence of desiccation ticks will remain questing. During a period of continuous fog, marked ticks were found to remain up on the grass during the night and questing the following day (McEnroe unpub.) The high temperatures and low humidities present during the season in Lincoln (Fig. 1) will, by desiccating questing ticks, account for their absence the following day. In areas where the soil level microclimate approaches uniform optimum conditions and the ambient water stress is lowered, as on Nantucket (Fig. 1), the ticks will spend less time in the soil microclimate and a longer time questing. As a result, random rather than group activity will occur and a larger fraction of the population will be questing for longer periods. On the islands, ticks activity appears to be more uniform. Smith *et al* (1946) reported that at the height of the season on Martha's Vineyard dogs would pick up hundreds of tick per day. Dogs on Nantucket also appear to show constant tick infestation levels during the height of the season (communication from Nantucket SPCA animal hospital).

Seasonal activity distribution.

Within the tick season the duration of a high level of activity, although more or less characteristic for an area, shows year-to-year variation in length. The time and rate of decrease of seasonal activity has been postulated to be the result of different rates of mortality occurring within a single cohort of adults (McEnroe 1973 a). However the studies in Lincoln indicated a second cohort of adults entered the active population in late July. Therefore adults were sampled during the 1973 season for resistance to water stress as an indication of their age. Lees (1969) has shown that the duration of previous activity reduces the tick resistance to water stress which he called an aging effect. This effect was used to determine if only a single cohort of active adults were present within a season. The 1973 seasonal activity records, converted to a percentage value for comparison, are shown in Fig. 2. Bolton shows the decline in activity from June typical of this area. Over three seasons the relative amount of activity in July has been very low (Fig. 4). Lincoln showed a small second peak of activity in the late July found over the past three seasons (Fig. 2, 4). The seasonal activities in both Hatchville and Mashpee showed their characteristic declines during June. However, unlike previous years, in 1973 activity did not continue to decline but a large distinct second peak of activity was present in July (Fig. 2, 4). In both Eastham and Nantucket the activity continued to increase up to the end of June, remained high throughout July, and declined during August (Fig. 2). This type of seasonal activity was also found on Martha's Vineyard (Smith *et al* 1946) where high levels of activity were maintained from June into August (Fig. 4).

The rate of mortality for ticks collected during the season changed in response to water stress (Fig. 5). As would be expected, the new adults showed the longest survival with 50 % mortality

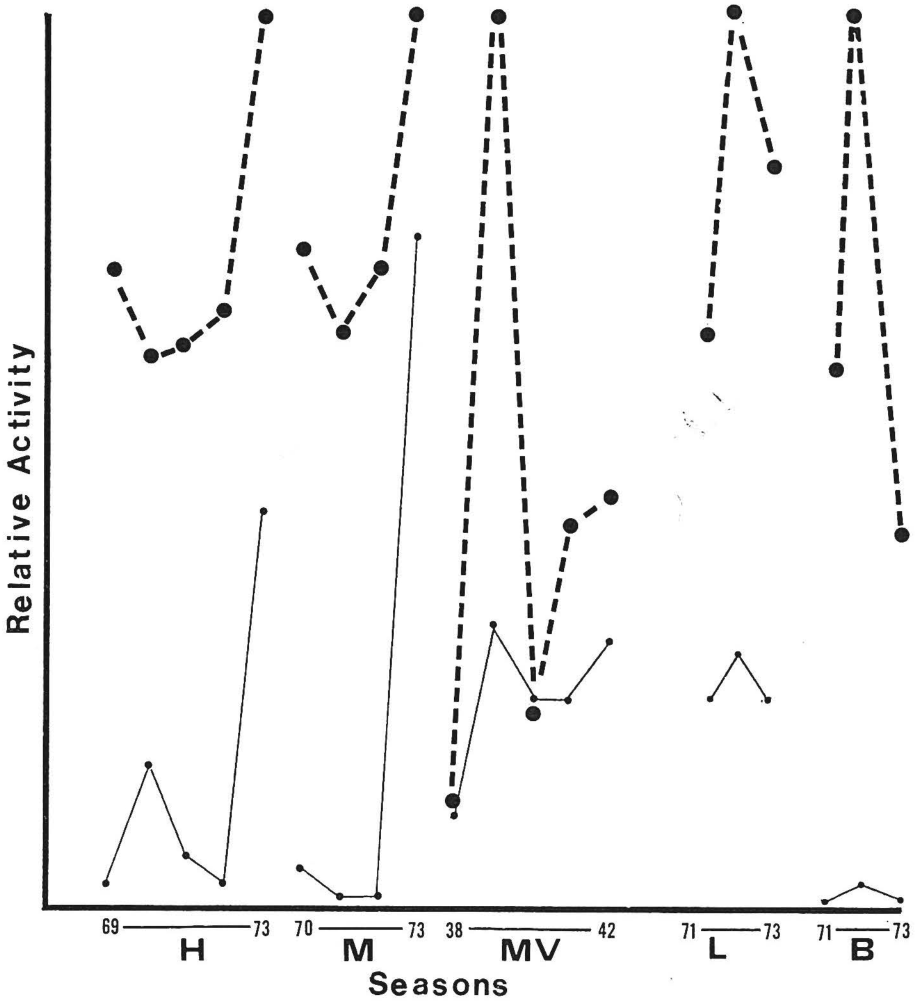

FIG. 4 : Yearly changes in seasonal activity distribution
The highest level of activity found in the series of seasons from each area has a relative value of one. The size of cohort I is based on the maximum level of activity prior to july and the size of cohort II is based on the maximum level of activity after mid-July. The relative size of each cohort is the equivalent fraction of activity compared to the maximum of I. Broken I line cohort solid line cohort II. H, Hatchville ; M, Mashpee ; M. V., Martha's Vineyard (Smith *et al* 1946) ; L, Lincoln ; B, Bolton. Years indicated for each series.

on day 38. The ticks collected in Bolton, Lincoln, Hatchville and Mashpee during initial activity all showed a decrease in survival. Their mortality response fell within a narrow range with a 50 % survival around 8 days. This decline in average survival of 30 days is the result of the over-wintering activity from the previous year. The survival of ticks from all the areas showed a further decline at the end of June with a 50 % mortality of less than one day. This average decrease in survivals of 8 days was the result of seasonal activity. In late July however, the ticks showed an increase in survival. The Nantucket ticks showed a 50 % mortality on day 5 and the Hatchville ticks on day 13. In addition 30-40 % of these ticks survived into the activity period of new ticks. The mortality response of ticks at the end of the season in August returned to that found in late June.

The 20° equilibrium humidity of female ticks in Lincoln showed an increase from 85 % at the

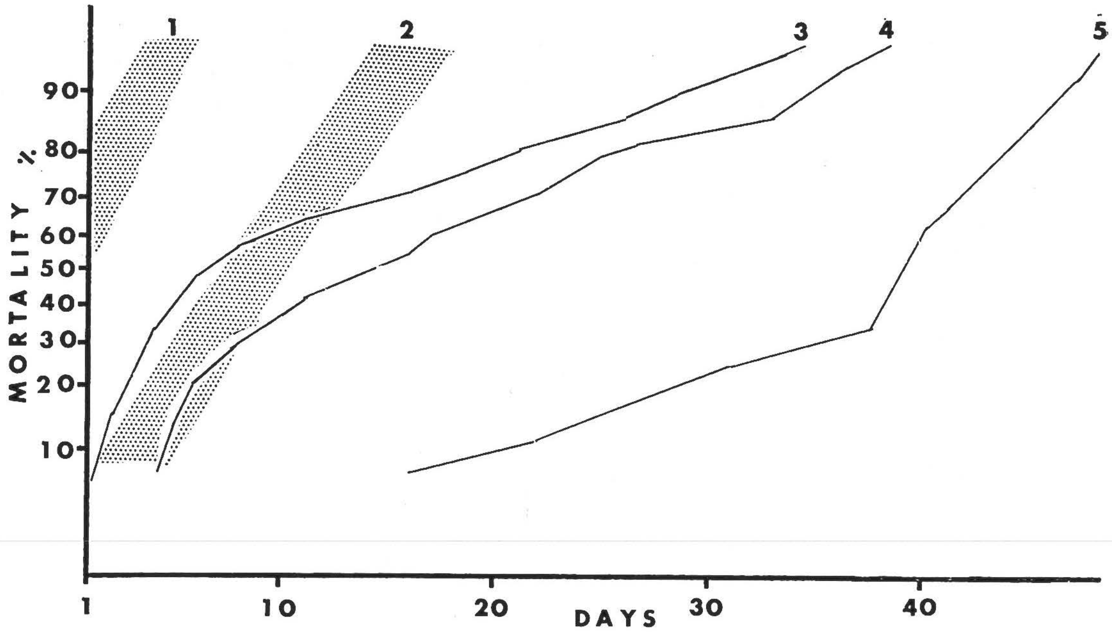

Fig. 5: Mortality of adult males versus water stress at 25° and 85 % RH. 1, late June response from all areas. 2, initial season response from Bolton, Lincoln, Hatchville and Mashpee. 3, late July response from Nantucket. 4, late July response from Hatchville. 5, response of new adults.

start of the season to 93 % in late June and again declined to 85 % in July. The increase in activity, survival, and decrease in equilibrium humidity found in late July, the period of highest ambient water stress, indicated that a new cohort of adults had entered the activity season. This cohort must be the result of a nymphal molt. Spring conditions permit the first appearance of new adults in July. Smith *et al* (1946) showed that overwintering nymphal feeding started in March and that under average spring temperatures, nymphs fed before June 15 would molt to adults in July. This was the group that produced July activity. Nymphs fed after June produced diapause adults. This adult diapause, during favorable questing conditions, prevents the production of late season eggs which Smith *et al* (1946) showed were unable to survive overwintering. The molting to active or diapause adults may be triggered by the change in daylength around the solstice as nymphs fed under increasing daylength molted to active adults and nymphs fed under decreasing daylength molted to diapause adults. The distribution of activity within a season will depend upon the proportion of diapause adults active from early in the season (cohort I adults) relative to the proportion of new adults active from July onwards (cohort II adults). This distribution will be further modified by the length of adult survival during the season. The conditions of the ticks in late June showed that they were limited in their ability to survive. The interaction of cohort I mortality rate and the size of cohort II was illustrated by the 1973 series of activity distributions. These distributions varied as follows : *1*/ a skewed type with cohort II producing a tail of activity through July and August, *2*/ a bimodal type with a minimum in June and a cohort II maxima of avariable size in late July, and *3*/ a unimodal distribution with a June maxima produced by overlapping cohort I and II activity (Fig. 2).

Declining seasonal activity.

The decline of seasonal tick activity is the result of the ageing effect on both reducing the ticks ability to quest and on the mortality of the tick population. The increase tick activity in July is due to the activity of new ticks, not changes in questing conditions. Optimum conditions for questing are present from June through August indicated by the similarities of minimum temperatures and maximum humidities (Fig. 1). The water stress, bassed on average maximum temperatures, average humidities (Fig. 1) and average weight losses under these conditions (McEnroe 1971 b), for Nantucket in July and August is ca 3/4 of that present in May in Lincoln and ca 1/2 of that present in Hatchville in June. This difference in water stress accounts for the difference in cohort I longevity and the different periods of seasonal decline.

Discussion.

The probability of the tick's reproductive success is directly proportional to the amount of seasonal activity and the density of the adult hosts. This relationship determines the tick's chance of attaching to a host, a requirement for mating and egg production. The maintenance of a fixed tick population size will depend first upon a constant value of the product of host density times the amount of seasonal activity. Reciprocal changes of the amount of seasonal activity and level of host density will maintain a constant value for an equal chance of reproductive success. The time during which cohort I is active will regulate the size of cohort II as it will determine the size of the nymphal group entering diapause at the end of the season. On the basis of interstage development times, the rapid attachment of sub-adult to their hosts, and the effect of day length on their termination of activity (Smith *et al* 1946, Smith and Cole 1941), eggs produced up to the end of May will develop into diapause nymphs and eggs produced after May will produce diapause larvae. The diapause nymphs will overwinter, feed the following spring and molt to cohort II adults in a one-year cycle. The eggs produced by both cohort I and II after May will enter the two-year cycle for cohort I by overwintering the first year as larvae and the second year as adults. Cohort I adults enter seasonal activity during the period of lowest water stress but with the aging effect from overwintering. Cohort II adults enter seasonal activity without an aging effect but in the period of highest water stress. A second stage in the regulation of cohort size must occur during overwintering. On Martha's Vineyard, where only 1/4 of the activity occurs prior to the end of Mays the season is characterized by a large cohort II. In contrast, in Lincoln where 3/4 of the activity occurs prior to the end of May, the season is characterized by a small cohort II. The early season activity on Martha's Vineyard represents significant breeding potential because of the survival of cohort II. In Lincoln however the early season activity fails to produce the expected cohort II size and the effective breeding potential is largely limited to the remaining 1/4 of adults active after May. The limited cohort II survival is however important for the maintenance of the population as it makes up 1/2 of the post-May season. Restriction of the size of cohort II regulates the overall population size by limiting the effective size of the breeding population.

The water stress both in the soil level microclimate, and in the ambient air regulates the potential breeding population. The day to day variations in activity are a record of the non-questing part of the tick population. The reproductive potential of this inactive group is lost. When cohort I and II activity overlaps, as a result of low water stress, the high mid-season activity present represents the major amount of seasonal breeding potential. Under high water stress, when cohort I dies off before the appearance of cohort II, this mid-season breeding potential is lost.

As the size of the adult population was found to be independant of the previous year's nymphal population size (Smith *et al* 1946), overwintering mortality must be regulating factor for adult population size. The relationship between the relative sizes of the cohorts shows both a constant difference in size for an area, and also a high year-to-year variation between cohort sizes. The small cohort II areas have average mean winter temperature below 0°, and the large cohort II areas have average mean winter temperature above 0°. The variable cohort II areas have an average mean winter temperature of ca 0°. Shifts of mean winter temperature around 0° are correlated with the size of the tick population the following seasons. The variation between cohort sizes appear to be the result of differences in threshold levels for overwintering adult and nymphal survival (McEnroe in press).

Lincoln and Bolton, areas where the seasonal activity pattern indicated the largest reduction in effective breeding potential, were outside the original range of this species. The large increase in host density, ie. dogs, which occurred as farmland was converted to suburban residential use has been postulated as the factor responsible for the extension of the species range. These inland ticks have developed an increased resistance to water stress (McEnroe 1973 a).

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NOTE (added in proof)

The soil temperature relationship was valid for the start of the Lincoln tick season in 1975.

GLADNEY and WRIGHT (Ann. Entomol. Soc. Amer., **63** : 1036-1039, 1971) showed the effect of changing photoperiod around the nymphal molt on subsequent adult activity for *Amblyomma americanum*.
