WINTER SURVIVAL MICROHABITAT AND CONSTANT DENSITY REGULATION OF *DERMACENTOR VARIABILIS*, SAY (ACARINA : IXODIDAE)

BY

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ABSTRACT

The winter temperature regulates the area of the winter survival microenvironment for *Dermacentor variabilis*, Say. These microenvironments, as they vary from small isolated areas to large contiguous areas, controls the apparent average density of adult *D. variabilis* populations.

RÉSUMÉ

Pendant l'hiver, la température détermine la surface des microhabitats de survie hivernale de *Dermacentor variabilis*, Say. Ces microhabitats qui varient de petites surfaces isolées à de grandes surfaces contiguës, contrôlent la densité moyenne apparente des populations adultes de *D. variabilis*.

Both the level of adult seasonal activity of *Dermacentor variabilis*, Say, and the distribution of *D. variabilis* infestation in Massachusetts were determined by the previous winter temperature regime. As the average mean winter temperature (December, January, February) on Cape Cod rose through a 0° threshold, not only did the following adult *D. variabilis* population increase, but also the infestation shifted from a localized to a more or less continuous distribution. This increase of *D. variabilis*, which followed as means increased above 0° was attributed to decreased overwintering mortality. The immediate response of increased population size, following the relaxation of climate limitation, indicated that the maximum potential population was initially present and the winter climate acted as a gate to release only a certain proportion of this initial population (McENROE, 1975). Regulation of the initial size appears to be a function of the carrying capacity of the hosts of the immature ticks (McENROE, in preparation). The inland areas, which were outside the species range prior to 1945 (McEnroe 1974*a*), had the following characteristics, 1) winter means always below 0° with three average monthly means below 0°, 2) seasonal activity was at a constant low level of infestation independent of variation of winter means, 3) increased duration of snow cover, usually not continuous in this area, was followed by an increase in adult ticks, and 4) infestations were associated with large dog populations in exurban [2] areas. In general, the infestation levels of *D. variabilis* over eastern Massachusetts appeared to decline in

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average density from a maximum level in the warmest winter areas on Cape Cod to a minimum in the cold inland areas. The following discussion will show that this apparent density gradient resulted from the increasing restriction of overwintering habitat associated with a decline of winter means. In order to avoid mortality from desiccation during overwintering, the temperature characteristics of the tick's water vapor pump imposes a requirement of increasing relative humidity from 83 % at 15° to saturation at 2°, the lower limit for active uptake (McEnroe, 1971*a*, 1975). Adult survival under near saturated conditions shows significant differences around 0° (Fig. 1). At 5° and 98,5 % RH newly molted adults had a 50 % survival on day 90 and 10 %

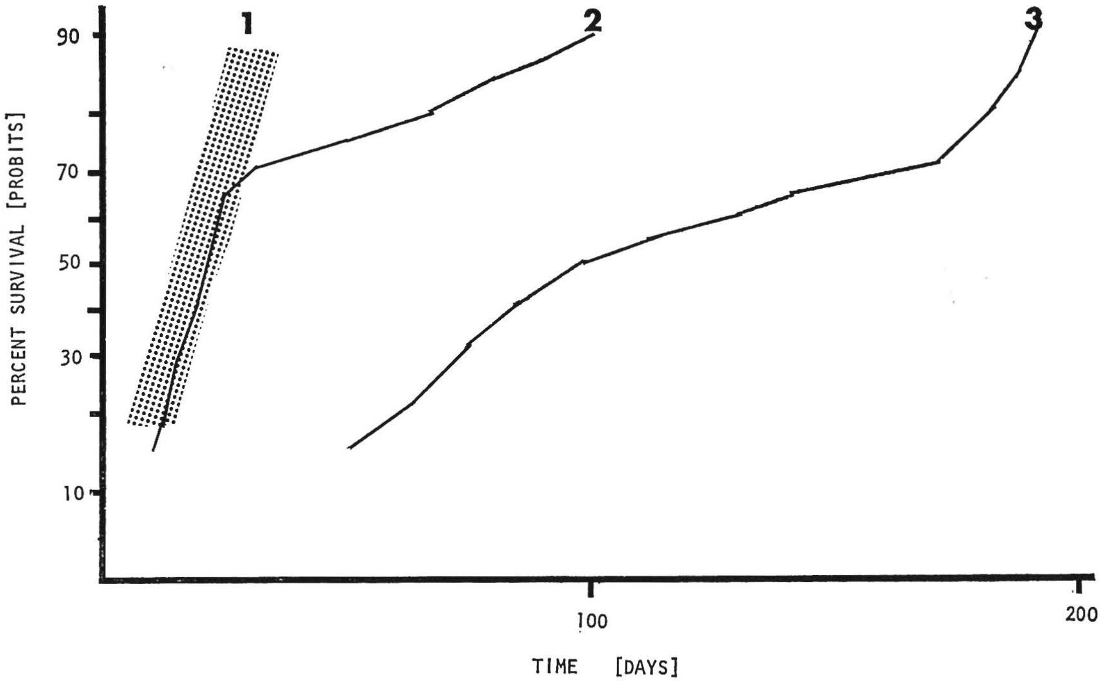

Fig. 1 : Probit plot of percent survival of adult female sticks versus time in days. 1) survival of newly molted and field collected ticks at 0° and 79.5 % RH ; 2) survival of field collected tick at 5° and 98.5 % RH ; 3) survival of newly molted at 5° and 98.5 % RH. New adults from Rocky Mountain Laboratory colony supplied by J. E. Keirans, overwintered tick collected in Hatchville at start of seasonal activity in 1975. Twenty animals per test. Relative humidity maintained over saturated salt solutions (P. W. Winston, D. H. Bates, 1960. Ecology 41 : 232).

survival on day 190. Overwintered adults, collected in the field at the start of the activity season, had 50 % survival on day 30 and 10 % survival on day 100. This difference between new and overwintered adults results from the ageing effect of overwintering stress. The utilization of the tick's metabolic reserves decreases the efficiency of the tick's water uptake (Lees, 1964). The change in the slope of the survival curve shows the variable stress in the different microhabitats of the overwintering ticks. At 0° and 97.5 % RH, both new and overwintered adults showed *ca* the same 20 day 50 % survival and 35 day 10 % survival. As the water vapor pump is shut off at 0° the previous stress does not affect survival. As shown by Smith *et al.* (1946) low temperatures, in themselves, are not lethal. At 0° and saturation, overwintered adults showed 50 % survival on day 80. The 50 % survival time at 0° for overwintered adults was reduced to 18 days 88 % RH and 12 days at 75 % RH. The inverse relationship of increasing relative humidity and decreasing temperature for survival will reduce the size of an area suitable for overwintering until at 0° or below, only a microclimate at saturation will permit overwintering. Even new adults at 5° require near saturated conditions for maintenance of their water balance. As shown in Fig. 2, at 96.5 % RH adult females are on the borderline for net water loss. At 88 % RH water loss resulted in intial mortality on day 10.

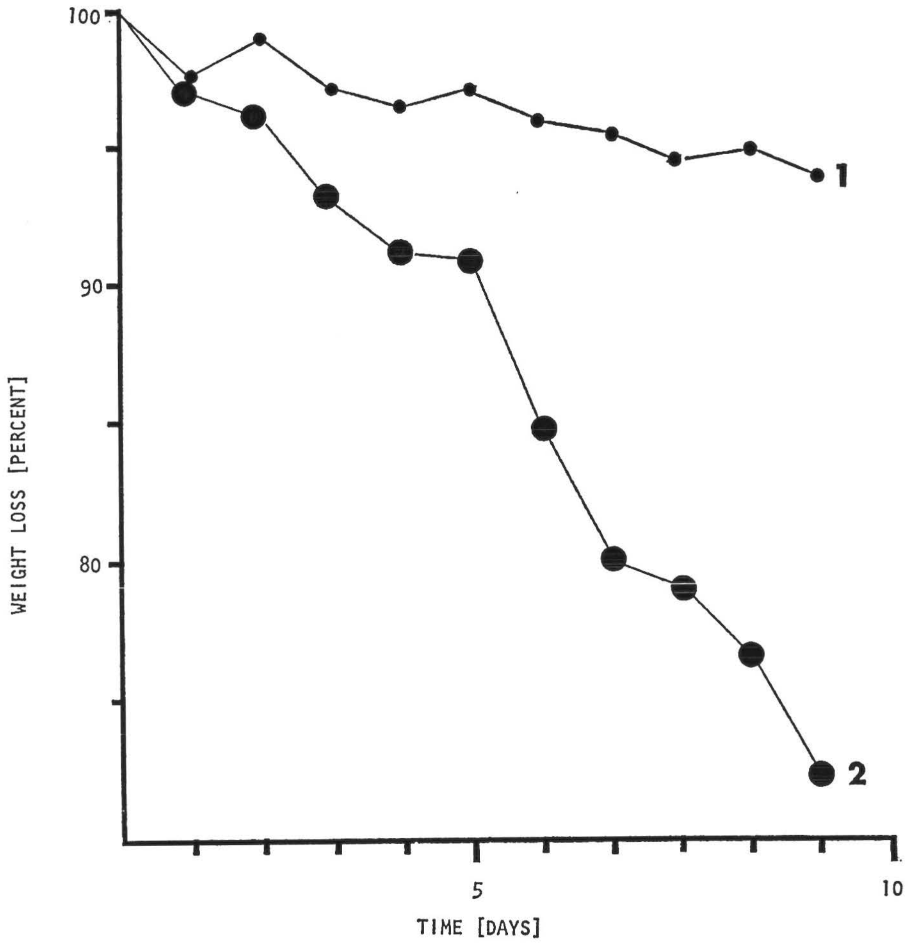

FIG. 2 : Percent weight loss of 10 new adult females from their 20° saturated weight. Relative humidity maintained over saturated salt solutions. 1) 96.5 % RH ; 2) 88 % RH, initial mortality on day 10. Ten animals per test.

Three widely separated *D. variabilis* infestations were studied in eastern Massachusetts. These areas showed different degrees of localization in tick infestation. The average winter mean for this division is — 3.0° with three months with means below 0°. This area, where monthly means below 0° vary yearly from two to four, was outside the species range of *D. variabilis* prior to 1945 (McENROE, 1974*a*, *b*, 1975, unpublished).

LUNENBURG

This area was an isolated exurban housing development in an old field ecosystem along a road 1/2 km in length. A high water table was indicated by bog areas along the road. In 1976 the tick season was investigated by interviewing the residents, all of whom had dogs which were allowed to run free. Dog owners reported that only dogs in this restricted area along the road picked up several dozen ticks per day. In the immediate surrounding area dogs picked up only several ticks during the entire season and in the surrounding rural area ticks were apparently absent. This unique infestation appeared to be completely isolated with a small central high density population and a restricted low density peripheral population. Previous to 1970, prior to the housing development with its dog population, ticks were not present in the area.

Bolton

The Bolton area was selected in 1970 following a survey along route 117 inland from the coast. This site was the only one found which, by dragging, provided a sufficient number of ticks to follow seasonal activity. The seasonal activity was followed from 1971 to 1975 over a fixed roadside drag course. This infestation was centered around a brook and small pond in an old field ecosystem. This area contained exurban housing with the typical large dog population. The tick infestation was noted after 1962. This area had a localized infestation like Lunenburg except the low density peripheral population was more extensive. Little year to year variation of the tick population occurred from 1971 to 1975 except for 1972 when the maximum population size was recorded. In this year two localized infestations were reported from the adjacent towns of Harvard and Lancaster. This followed a winter with above average continuous snow cover for the area.

Lincoln

This was an exurban housing area with an associated large dog population located in an old field ecosystem surrounding a small pond. Seasonal activity was followed from 1971 to 1976 by the daily removal of ticks from a free-running dog. The technique of having the dog collect ticks was used beacuse the standard dragging method of tick collection failed to yield enough ticks to follow seasonal activity. This dog consistently picked up more than 1000 ticks per season, with a record capture for one day of 126 ticks. Little year to year variation was noted in this area. This area, near the coast, has a shorter period of snow cover and in 1972, unlike Bolton, did not have continuous snow cover. The Lincoln infestation did not appear to be as isolated as that present in either Lunenburg or Bolton. The entire exurban perimeter of metropolitan Boston, which includes Lincoln, has a constant low level of tick infestation.

The adult tick density in 1973, was, with the assumption of constant density, estimated at 80 adult/ha over the dog's range of 1.5 km^2. The area was restudied by intensive dragging and the tick infestation was found to be restricted to the immediate vicinity of the small pond in an area only of *ca* 10 ha or less. The dog's house was within the area of infestation. That is, the apparent general low density population was actually a small localized high density population of *ca* 12000 ticks/ha. At the same time a survey of dog owners showed a pattern of high tick burdens (several dozen ticks per day) only on dogs immediately adjacent to the infested area with few ticks per season on dogs further away. However, unlike Lunenburg and Bolton, other centers of infestation were present in this region and were separated by either limited tick-free areas or areas with few ticks present. In 1974, an unrestrained dog 1/2 km.. away from Lincoln had a seasonal total of 74 ticks and a dog 1 km. away was tick-free versus 1229 ticks for the Lincoln dog. This pattern of small local high density tick populations, in areas with winter means below 0^{o}, will appear as a generalized low density infestation. It will also account for the anomalous report of one adult tick/m² [10,000/ha] in local areas along the lake shore resort communities around Lake Winnipesaukee, New Hampshire (BLICKLE and CONKLIN, 1957). This value, equal to the maximum reported from Virginia (SONENSHINE, *et al.*, 1966) the traditional area of maximum infestation, was unexpected from New Hampshire where *D. variabilis* is generally uncommon.

These local infestations in inland Massachusetts have three common environmental requirements, 1) old field habitats to provide the rodent host for the immature ticks, 2) the large dog population, associated with exurban housing, to insure the presence of an adult host within a small area, and 3) a high water table.

During the 1969-70 period of below normal winter means on Cape Cod, this traditional area of tick infestation was surveyed for collection sites with high tick yields suitable for long term population studies. In this period of depressed tick infestations, two of the sites selected were Hatchville and Barnstable. The Cape has an average winter mean of 0.5° with one or two normal monthly means of 0° or below depending upon the location. This area varies, year to year, from zero to two monthly means below 0° (MCENROE, 1974*a*, *b*, 1975, unpublished).

HATCHVILLE

In the Hatchville study area (average winter mean — 0.3°) adult seasonal populations were followed from 1969 to 1976. The method of collection by roadside dragging, sampled the population attracted by a CO_2 gradient from the area 100 m adjacent to the road (MCENROE, 1971*b*). The spring adult populationremained essentially stable from 1969 through 1973, a period when winter means were $< 0°$. The population increased 5 1/2X in 1974 following a mean of 1.1° and increased 13X (over 1969-1973) in 1975 following a mean of 1.4°. In 1976 the population returned to its 1969-70 level following a winter mean of — 0.1°. The average adult spring population during the period, following a mean below 0°, was estimated to be 300 adults/ha, and thus, a comparable value for 1975 of 4 000 adults/ha. By correlation with inland populations, what actually occurred was not a 13X increase in an average uniform density but a 13X increase of survival area or a 13X increase of the size of the isolated high density populations. The geology of this area is a typical terminal moraine with gently rolling well-drained sandy soil interspersed with small kettle holes. These kettle holes are small semicircular depressions 4 to 6 m deep and 10 to 15 m in diameter. The bottom, which lies near the average water table, is covered with *ca* 1/3 m of organic silt and a thick covering of vegetative duff. This produces a fine grained environmental difference most obvious in late summer. At this time, the general vegetation, mostly annual grasses, is dead and brown whereas the base of the kettle holes is still lush and green with a covering of hydrophytic plant growth. The native red cedar, *Juniperus virginiana*, which thrives best in moderately moist sandy loam (BAILEY, 1963) is found mainly around the walls and rims of the kettle holes. Twelve soil samples, from each location, taken during a dry spell in late July showed the following values of W/W % soil moisture after drying ; upper sandy soil 4.8 ± 1.5 %, walls of kettle holes 15.2 ± 6.5 %, and organic soil at base of kettle holes 24.2 ± 3.6 %. These kettle holes provides a natural point source gradient or relative humidity where the survival area will vary with a shift in winter means, the net effect of which is to produce an apparent shift in average density.

In the spring of 1975, the year of maximum tick activity, solid CO^2 traps (release rate 5 kg/day) were used prior to and during the initial period of spring activity. The traps were set back from the road to avoid the roadside CO^2 gradient. Twenty trap days in three locations on the level surface yielded only three ticks. Ten trap days at the base of a kettle produced 141 ticks. With similar CO_2 trapping for *Amblyomma americanum*, the effective sample area was 25 m^2. This type of trapping collects from only a restricted area (Wilson, *et al.*, 1972). As ticks do not migrate to damp areas (Smith, *et al.*, 1946) and remain *in situ* in open fields (Sonenshine, *et al.*, 1966), the difference in local tick density can only be the result of differential overwintering survival of ticks dropped at random from their nymphal hosts.

Within the emigrant area that supplied the roadside population are several kettle holes which occupy 1/3 of the entire area. As this restricted area essentially was the source of the 1975 roadside population, the density of the overwinter survival area can be estimated at *cv* 12 000 adults/ha, and this was also the order of magnitude of the initial adult diapause density. The initial regulatory step in setting this density value is the feeding success of the post diapause larvae which was estimated by Sonenshine (1972) to be 0.5 % of the eggs produced by 22.7 fed (= mated)adult females/ha. His work indicates an excess egg production of 99.95 % to maintain the population at an adult density of 1500 adult/ha. This indicates that even with a low average density population, the reproductive potential of the ticks can saturate the carrying capacity of the immature host complex as long as the adult density can supply both males and females on the same adult host.

Barnstable

In the Barnstable area (average winter mean 0.5°) the tick population was followed from 1970 to 1976. The population cycled, as in Hatchville, except the initial increase occurred one year earlier in 1973 following a mean of 0.9°. Like Hatchville, this area is on the Cape Cod moraine, but here the sandy soil overlies a bed of clay. Where the clay is exposed in the area, water accumulates throughout the year and supports growth of aquatic plants such as the common cattail, *Typha latifolia*. A cellar hole dug in the immediate survey site showed the clay about 1 m below the top layer of sand. Water runs in the layer of sand at the top of the layer of clay. Because of the drainage problem in the immediate area, new house construction has been stopped. This geological condition maintains more or less uniform soil moisture in the area. Carbon dioxide trapping, unlike Hatchville, in the spring of 1975 indicated a uniform overwintering soil level microclimate. Three traps, placed at random, had catches of 48, 62, and 81 adults during the same five-day period. No density estimates were made in this area, but the 1975 tick season was at such an extreme level of infestation that dogs in the area were not allowed to run free because of the tick burdens.

By contrast, dogs in adjacent areas picked up only one or two ticks per week. This variation between less than one tick per day to hundreds of ticks per day on a dog was first noted by Smith, *et al.* (1946) for different areas on the island of Martha's Vineyard, a traditional area of high tick infestation in Massachusetts.

Around the perimeter of an infestation, the low density adult population indicates that it is maintained by immigration of nymphs on their hosts rather than maintenance of a continuous local population. In effect, the total *D. variabilis* population for a region will be limited by the area of suitable overwintering soil level microclimate. Below winter means of 0°, this area will tend to remain constant except as influenced by duration of snow cover. Above 0°, the survival area will expand and contract with year to year variation of winter temperature. The requirement for the host complex in such areas is self evident. The presence of the high water table is not so obvious. The soil temperature is buffered against both seasonal and daily changes of ambient temperature. For exemple, at the Kingston Road Island Station, the ambient 1975 January temperature was 1.2°. The mean January soil temperature 10 cm below bare ground was 10.5° and 3.7° below sod (Annon). With this temperature gradient, water will distill from the moist soil and condense at the soil surface maintaining saturation in the soil level microclimate (GEIGER, 1965) It is postulated that the absolute tick density is a relatively constant value. The apparent density is the function of the number and area of localized high density infestations.

Adult host density does not appear to be a regulating factor as long as hosts are present in the overwintering survival area.

In areas with winter means above 0°, and widespread survival microenvironments, wild hosts with their extensive territories will provide mated pairs to maintain the tick population. The requirement for high dog density, correlated with the extension of the range of *D. variabilis* in Massachusetts, is not a high average host density requirement. Instead it is a requirement for the constant presence of an adult host within a restricted overwintering survival microhabitat fulfilled by the local dog population.

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1. Paper No. 0000 Massachusetts Agricultural Experiment Station, University of Massachussets at Amherst. This research supported in part from Experiment Station Hatch Project No. 341.

2. " Exurban " Housing at the suburban and rural interface characterized by housing within large areas of undeveloped land, usually abandoned farm land.

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Added Note on Hatchville.

The overwintering survival of 50 individually caged new adults on the soil surface was followed through the winter of 1977-78, mean — 2.0° at both the base of a kettel hole and on the upper sandy surface (McEnroe in preparation). The mortality from mid-October through December was 84 % on the upper surface and 16 % in the kettel hole. Even under the December mean of 0.5° there was a high stress on the ticks at the upper surface. All the ticks on the upper surface were dead by mid-March, whereas the ticks in the kettel hole showed 40 % survival at mid-April prior to the activity season. The dead ticks from the upper surface, but not the kettel hole, appeared desiccated. These results confirm the distribution found by CO_2 trapping. The discontinuity of survival area accounts for the traditional terms of " pests " or " hot spots " used on Cape Cod to describe small area of high tick infestation.

Paru en Juin 1978

ERRATUM : For 12,000 ticks/ha read 1,200 ticks/ha. — McEnroe, W.D. (1977) Acarologia **19** : p. 409.