THE ROLE OF THE SUMMER COHORT IN THE POPULATION REGULATION OF THE TWO COHORT CYCLE OF DERMACENTOR VARIABILIS (SAY)

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Abstract. In the two cohort per season life cycle of Dermacentor variabilis (Say) in Massachusetts, the primary regulation of the population occurs in the development of the summer adult cohort. In the passage from the parental spring adults, a density dependent factor limits summer larval host attachment. Summer larval tick burdens appear to be independent of the amount of spring breeding and are maintained at a constant low level. This regulates the number of diapause nymphs. Overwintering survival of nymphs is the most sensitive period for density independent climatic regulation. The net effect of this regulation is to reduce the level of summer adult activity below the level of spring adult activity. As the spring adults depend upon the summer adult reproductive potential, each passage through the summer adult cohort renews the population size.

The adult Dermacentor variabilis period of seasonal host seeking activity has been followed from 1969 to 1981 at Hatchville, Massachusetts (McEnroe 1979, unpublished). For 8 seasons, the maximum level of adult activity remained as constant, following winters having a mean temperature $\leq 0^\circ C$ and bare ground. The level of activity increased in 2 years following winter means $> 1^\circ C$ and in 3 years following winters with continuous snow cover. It was postulated that under average winter conditions, having short periods of frozen bare ground when the soil surface becomes desiccated (Geiger 1965), adult survival was limited to microenvironments with near saturated conditions. With winter means above $1^\circ C$, the ticks were able to maintain their water balance and increase the probability of winter survival. Snow cover improved the conditions for survival by protecting the ticks against desiccation. The postulated explanation for this change in seasonal activity is that the population, prior to overwintering, is regulated at a near constant level, and that only a fraction of this population will enter the following activity season as a result of climatic regulation. Smith et al. (1946) in their studies at Gay Head, Massachusetts, found no relationship between the abundance of adults and immature ticks, presumably because of climatic regulation.

The temperature regime in Massachusetts, interacting with the temperature regulation of the D. variabilis development cycle, produces in each period of seasonal activity a spring and summer cohort of adult and immature ticks. Spring adults, prior to mid-July, produce summer fed larvae, overwinter nymphs, spring fed nymphs, and the summer adults. Summer adults, after mid-July produce overwinter larvae, spring fed larvae, summer fed nymphs, overwinter adults, and active spring adults. The spring larvae are active from the start of seasonal activity until July, and the summer larvae are active from July until the end of the season (Smith et al. 1946, McEnroe 1974). The amount of adult activity (=$\text{cactability}$) is a measure of reproductive potential. The first step in the breeding cycle requires host attachment and feeding prior to egg laying (Pappas and Oliver 1971).

The study of Smith et al. (1946) demonstrated that although most of adult activity occurred prior to mid-July, the resulting number of larvae found on hosts was well
below the number found prior to July. That is, the residual adult activity after mid-July produced most of the adult females that contributed to the residual adult density the following spring. The significant relationship between the larval population and attached larvae was also found in other studies (Sonnehulse et al. 1966; Sonnehulse et al. 1972, Jackson and DeFoliart 1975, Anderson and Magnarol 1980).

The levels of summer adult activity, compared to spring activity, show a sharp decline from the coastal area (Gay Head on the island of Martha’s Vineyard) to inland Massachusetts. This difference is constant from year to year (Smith et al. 1946; McEnroe 1974, 1979, unpublished). The reduction of adult activity after mid-July limits the production of diapause larvae. The formation of the summer adult cohort requires nymphal overwintering. Smith et al. (1946) recognized the low success of nymphal overwintering. Nymphs, even under mild Virginia winters, were found to be the least successful overwinter stage (Sonnehulse et al. 1972). The depression of summer adult activity was related to the increased hardness of winter conditions inland.

Current population biology theory (for review see Emmel 1976) proposes 2 types of regulating factors: 1. density independent factors which exert the same control on the population regardless of the number of individuals present, i.e. climatic, and 2. density dependent factors which exert effects that vary in proportion to the size of the population, and serve to regulate the population by a homeostatic or feedback process. These factors, intrinsic to the population, are responsible for the steady state conditions seen when the carrying capacity of the limiting resource is approached.

The carrying capacity of larval tick burdens in the summer appears to be a density dependent factor which regulates the size of the summer adult cohort. In Hatchville this factor was investigated by following the level of larval tick burdens on the host in adjacent areas where high and low adult tick densities were present in the spring.

The levels of summer adult activity appear to be most susceptible to the density independent regulation by climatic control of nymphal overwintering. This factor was investigated by following the adult tick season at Bolton, an inland study area. The investigation period included a winter with 3 months means below 0 °C but bare ground was present through the winter (once per ca 50 year event). The period of frozen bare ground was about 3 times as long as that usually present in the Hatchville coastal area.

METHODS

The data of Smith et al. (1946), from their tick study at Gay Head for the period from 1938 to 1941, was analyzed to show the relationship between the larval tick burdens and the amount of the parental adult activity.

The two adjacent sample areas in Hatchville used for the larval study were near where the D. variabilis adult season has been followed since 1969. These areas, from previous observation, were known to be lightly and heavily infested with ticks. The first site was in an overgrown airfield and the second site was in a beach dune (D. variabilis). The second site was a large swamp ca 3 m below the outwash plain of the Cape Cod terminal moraines. The soil at the airfield remained dry, and that in the swamp remained damp. A moist soil microenvironment has been shown to increase adult overwinter survival (Mc Enroe 1976).

An estimate of adult density was made over 3 consecutive days in early June when tick activity was at a high level. In each area, 100 marked ticks were introduced into 2 km 2 samples taken prior to the days on which the tick density was estimated. The estimate of the tick density was calculated. The captured ticks on the sample dates was determined by the % recapture of marked ticks from recapture release sites. These check sites were sampled and the recapture ratio was used as the recapture ratio for the entire sample area. These ticks were marked with fluorescent paint and their location determined in the evening with a U.V. lantern (Mc Enroe 1971). In this open field area, marked ticks remained within the check area. Each study site was crossed with a total drag area of 1500 m x 0.5 m with the pattern rotated daily. The estimate of adult density for the airfield was 705 ticks/ha (560, 623, 531), and for the swamp it was 284 ticks/ha (1246, 7391, 13860).

Traps were located within both areas in active runways of Microtus pennsylvanicus. Potential trap sites were kept baited with a mixture of peanut butter and grass seed. The traps were moved to new locations for each trapping period. Trap were baited with the same mixture of peanut butter and grass seed. Thirty traps were set out in the late afternoon in each area, and the trap line was continuously checked until about midnight. The maximum time for an animal in a trap was one hour. The animals were then sealed in plastic bags until checked for larvae. Animals were trapped between the first and fifth of June and once each week between July 6 and September 20.

The adult tick season in Bolton has been followed since 1971. This is a small isolated infestation (McEnroe 1978). Here activity was sampled a long a fixed roadside drag course of ca 500 m where adults are concentrated at the roadsides by CO₂ (McEnroe 1971).

RESULTS AND DISCUSSION

Larval host tick burden

The relationship between adult activity and larval tick burdens at Gay Head, for the period of 1938—1941 is shown in Fig. 1 (data replotted from Smith et al. 1946). Adult activity after July 15 was directly proportional to the number of spring attached larvae up to July of the following year. In contrast, the number of larvae found from July on was independent of the amount of adult activity up to July 15 of the same year, and remained at a low level. As the larval value used was based on larvae per trap, it represented the tick burden on the host population. In a concurrent study of the larval host population in an adjacent area, the summer host population remained equal to or larger than that present in the spring. The average value of host per trap for the spring and summer were between 0.26 and 0.34 hosts per trap. The depression of the larval value in the summer was due to a change in host availability but due to a change in the tick burdens on the hosts. The average spring and summer larval tick burdens can be estimated with the average number of hosts and larvae caught per trap for the spring and summer quarters. The estimated average larval tick burden in the spring was between 9.9 and 20 larvae per host and, in the summer, between 0.4 and 2.2 larvae per host.

The dominant larval host at Hatchville was the meadow vole, Microtus pennsylvanicus, with the white footed mouse, Peromyscus leucopus, the secondary host. This host relationship was also found on Martha’s Vineyard (Smith et al. 1946). In early June, the larval burdens were 18 larvae/animal (12) in the swale, and 2.5 larvae/animal (16) at the airfield site. The average summer larval tick burden found at the airfield was 1.4 ticks per host (54 animals), and 1.6 ticks per host at the swale (39 animals). The difference in the
average summer tick burdens does not relate to the 16 x difference in the estimated spring adult densities, Woodchucks (Marmota monax) were common in both areas and serve as host for adults (Cooney and Burgdorfer 1974). These animals are heavily infested with adult D. variabilis in the spring (McEnroe, unpublished). In the spring, their territorial behavior, when the females have their pups, would ensure that larvae are produced within a restricted area. The unattached larval density can be expected to be directly related to the adult density.

Overwintering survival

The change in the level of adult seasonal activity at Bolton for the period of 1977 to 1981 is shown in Fig. 2. The passage from spring to summer activity in 1978 and 1979 shows the normal increase. The normal increase for the passage from summer activity to spring activity occurred in 1979. The extreme stress present during the open winter of 1979-1980 sharply reduced the maximum spring count to 3 ticks. In comparison, the maximum spring count in 1972 was 173 ticks. The 1972 season followed a winter with an above average snow depth and continuous snowpack. The presence of spring ticks in Bolton in 1980 indicated some overwinter adult survival, however the amount of summer activity fell below measurable limits and indicated a failure of nymphal overwintering. In 1981, the level of spring activity approached normal levels showing larval survival over the winter of 1979-1980. Summer activity again failed to appear. This reflected the limited reproductive potential of the small 1980 spring season.

Conclusions

The level of larval tick burdens in summer both sets and maintains the level of nymphs for overwintering in the passage to summer adults. A factor involved in this regulation is the inhibition of host attachment of larvae under a decreasing photoperiod (Smith and Cole 1941). This factor would reduce the tick burden but would not maintain a stable level. It has been shown that previous host exposure to tick bite will limit the amount of larval D. variabilis attachment (Trager 1939a, b). This would provide a stable level of host burdens. Climatic regulation is most effective, in the passage from spring adults to the summer adults, on nymphal overwintering. In summary, with a two-adult cohort cycle, the passage from spring adults to summer adults, with its density dependent regulation of summer larval host attachment, and its density independent regulation of nymphal winter survival, resets the population size each year. The reproductive potential for the increase of the spring adult cohort will be determined by the amount of summer adult activity. The stability of the potential population will only be expressed under stable winter conditions. Variations of climate will produce wide swings in the level of infestation. There will be a lower limit for winter survival of the summer cohort, and the summer activity level for the maintenance of a continuous infestation. Above this minimum level there will be an increase in the reproductive potential during summer activity for the production of the spring adult cohort.

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хозяев жизнью ограниченно зависящим от плотности фактором. Летнее количество паразитирующих личинок, видимо, не зависит от количества мест обитания размножаются и удерживаются на постоянном уровне. Это обстоятельство регулирует числа имаго в диапазоне зимой. Выживание имаго в зимний период является самым чувствительным периодом для климатической регуляции независимо от плотности. Конечным результатом этой регуляции является повышение уровня личинок имаго зимы. Так как осенние имаго зависят от летнего репродуктивного потенциала имаго, каждый проход через личинку которого имаго восстанавливает исходный уровень популяции.

REFERENCES


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