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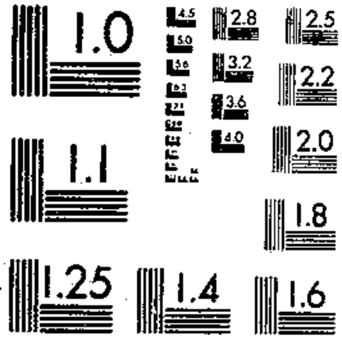

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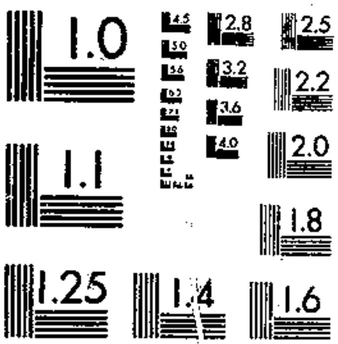

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NATIONAL BUREAU OF STANDARDS-1963-A

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Biology and Control of the American Dog Tick[1]

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SUMMARY

The American dog tick (*Dermacentor variabilis* (Say)) is an important pest of dogs and a dangerous carrier of disease. It is widely distributed east of the Rocky Mountains and also occurs in California.

The biological studies here reported were based on field observations and laboratory rearings at Martha's Vineyard, Mass. In the laboratory rearings a variety of caged mammals were used as experimental hosts, and the nonparasitic stages were maintained under conditions simulating those in nature.

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[2] Grateful acknowledgement is made of the helpful suggestions and criticisms of F. C. Bishopp, Assistant Chief of the Bureau of Entomology and Plant Quarantine, under whose direction, at the time when he was in charge of the Division of Insects Affecting Man and Animals, this study was conducted.

Under experimental conditions the adult ticks may live for more than 2 years without feeding. The maximum observed longevity was about 1,032 days. They feed only on the blood of mammals, and mate while on the host. The males feed and mate intermittently for an indefinite period, but the females become engorged in about 10 days, drop from the host, and seek a satisfactory hiding place, frequently in clumps of grass. Under normal conditions they begin to lay eggs in 6 to 58 days, depending upon the temperature.

The eggs are laid in masses of 4,000 to 6,500 over a period of 14 to 32 days, after which the female dies. The incubation period varies with the temperature, normal periods ranging from 36 to 57 days. An unusually extended incubation period of 303 days produced abnormally short-lived larvae.

Under experimental conditions larval ticks may live for more than a year without food. The maximum observed longevity was about 540 days. The larvae also feed on the blood of mammals, remaining attached to the host for about 4 days. When fully engorged they drop from the host and seek a protected place in which to undergo their transformation to nymphs. Observed periods from dropping to molting ranged from 10 to 247 days, according to the season.

Nymphs were observed to live for about 584 days without feeding. The observed engorging period for nymphs ranged from 3 to 11 days, and the period from dropping to molting ranged from 24 to 291 days.

Larval activity in the field began in March or April, reached a peak in March, April, or May, declined as the season progressed, but sometimes rose again to a peak in August or September, and ceased in September or October. Rearing records indicated that the individuals active before July had all hatched the previous year, whereas those causing the late peaks had hatched the same season.

Nymphal activity began in March or April and increased more or less steadily until July or August, then declined until it ceased in September or October. Rearing records indicated that activity before June was by nymphs emerging from hibernation, whereas many of the nymphs active after June had issued from larvae that molted the same season.

Adult activity began in April, increased until June or July, and then decreased until it ceased in August or September. Rearing records indicated that most of the activity was by adults that had hibernated.

A complete generation from a single infestation was traced through its development in a simulated meadow on a greenhouse-type table. Females that became engorged near the beginning and close of the season of 1939 produced an infestation of active larvae from August 3, 1939, to July 28, 1940, an infestation of active nymphs from August 25, 1939, to April 21, 1941, and an infestation of active adults from May 1, 1940, to September 1941.

Marked ticks persisted in an area throughout the greater part of one season, but only 0.24 to 0.57 percent of those marked one year reappeared the next.

Observations on the migration of marked ticks indicated that there was some movement in all directions, with a pronounced tendency to remain at the sides of roads or paths when reached, although roads were not a barrier to movement. Experiments with scented objects indicated that the attractiveness of roadsides was due to animal odors.

In the region of Martha's Vineyard meadow mice were the most important hosts of the larvae and nymphs. White-footed mice and cottontail rabbits were of secondary importance, and other small mammals were of minor importance. Dogs were the most important host of adults.

The time required for molting by larvae and nymphs, the preoviposition period, and the incubation period were closely correlated with the temperature, and unfavorable temperatures during these periods reduced the longevity of the ticks in the following stages. Unfed larvae and nymphs frequently survived temperature of −4° F., and adults frequently survived 0°. The activity of all stages ceased at a time of year when the temperature was still favorable for activity, but would have become unfavorable during the engorged condition.

Moisture is essential to the survival of all stages. Excessive rainfall is not detrimental, as all stages can survive submergence for 1 day and some for 5 or 6 days. Neither relative humidity nor precipitation shows any correlation with activity or length of developmental periods.

The photoperiod has been shown to affect the activity of the immature stages, long and increasing photoperiods being more favorable than short and decreasing ones.

A dip containing 1 ounce of neutral soap and 2 ounces of derris powder (4 percent rotenone) to 1 gallon of water was adopted as the standard treatment for the control of ticks on dogs. It was necessary to dip dogs every 3 or 4 days in order to maintain adequate control. When used on a large scale, the material cost about 5 cents per treatment. In laboratory tests certain wetting agents appeared superior to soap, but in practical application soap was as effective as the others. Dips containing sulfur-cube, pyrethrum, arsenic, and creosote were less satisfactory than the standard.

The tendency of the adult ticks to concentrate on roadsides makes it possible to kill many of the ticks in an area by spraying a relatively small portion of it. A spray containing 0.5 percent of DDT, 2.5 percent of soluble pine oil, and 97 percent of water was most promising, but other materials were effective.

The systematic treatment of all dogs in an area resulted in a substantial reduction of the numbers of ticks in the area, but required 3 years to reach its maximum effectiveness.

The control of meadow mice by poisoning reduced the abundance of ticks in the treated area. The reduction was apparent the year after treatment, but was not complete, the degree of tick control varying with the degree of mouse control.

The burning over of a portion of an area was followed by a reduction of the number of ticks in the burned portion.

Ixodiphagus texanus How., an indigenous tick parasite, does not appreciably reduce the numbers of this tick, and attempts to establish a colony of *Hunterellus hookeri* How. from Texas were unsuccessful.

INTRODUCTION

The American dog tick (*Dermacentor variabilis* (Say)) has attracted the attention of entomologists, parasitologists, and pathologists for many years, owing to its importance as a pest of man and domestic animals. A number of workers have contributed observations on its hosts, its distribution, its life history, and its relation to diseases. Since the discovery in 1931 of its role as a vector of Rocky Mountain spotted fever, it has commanded increasing attention. Because of the need of intensive field observations to determine accurately the seasonal cycles, persistence of infestations, relative importance of hosts, and other phases of its biology before possible methods for its control could be formulated, studies were conducted from 1938 through May 15, 1944, at Vineyard Haven, Mass., on the island of Martha's Vineyard. This bulletin gives a résumé of the results of these studies.

ECONOMIC IMPORTANCE

The American dog tick, often called the dog tick, the wood tick, or the Eastern Rocky Mountain spotted fever tick, has long been of importance as a pest of dogs and, to a lesser extent, of other domestic animals. In areas where the ticks are numerous dogs that are allowed to run at large sometimes pick up hundreds in a single day. Such severe infestations cause loss of condition and bad disposition in the animals, and impose on the owners the unpleasant burden of disinfesting them. Horses and cattle suffer some annoyance from the pests.

As early as 1911 Maver (*10*)[3] reported the experimental transmission of Rocky Mountain spotted fever by this tick, but as the disease was thought not to occur within the known range of *Dermacentor variabilis* this tick was not regarded as a vector of importance. After the discovery of the disease in the East in 1931 by Rumreich, Dyer, and Badger (*13*), the tick appeared at once as an important vector of disease. The number of reported cases attributable to this species now averages about 140 each year, with a mortality of about 25 percent, and the fear of the disease extends its economic effect far beyond the losses caused by its actual incidence.

The tick has also been shown to be an occasional vector of tularemia, and Parker et al (*11*) have summarized the relationship of this species to disease transmission.

DISTRIBUTION

In the United States the American dog tick is widely distributed east of the Rocky Mountains and in parts of California, and it also occurs in Mexico and Canada. The distribution in the United States, based on the records of the Bureau of Entomology and Plant Quarantine, is shown in figure 1. The records from Oregon were made a number of years ago, at which time Hooker, Bishopp, and Wood (*7*) reported the species to be common in that region. Cooley (*3*) reports that recent collections in southwestern Oregon failed to reveal the presence of the tick, indicating a possible reduction in its range. The species is most abundant along the east coast from Massachusetts to Florida and in parts of Texas, Iowa, Wisconsin, and Minnesota.

[3] Italic numbers in parentheses refer to Literature Cited, pp. 73-74.

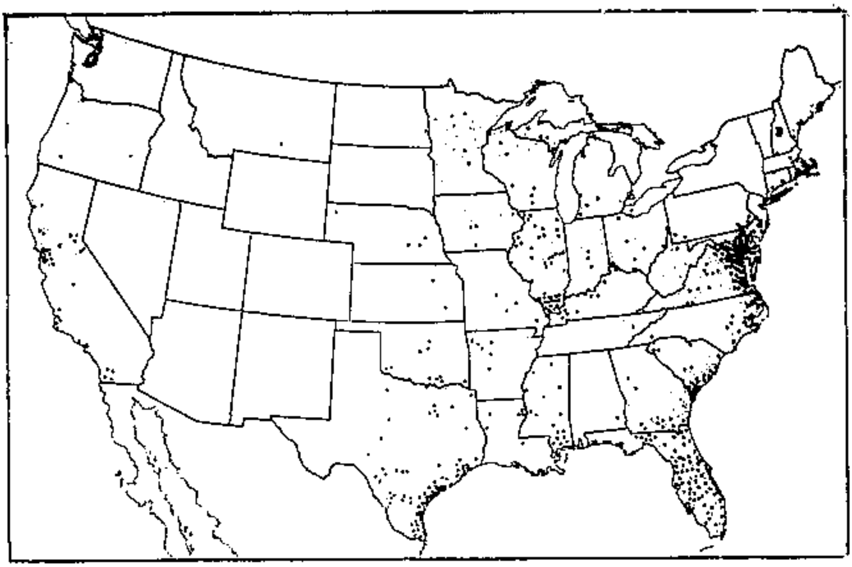

FIGURE 1.—Distribution of *Dermacentor variabilis* in the United States. Large dots indicate localities where collections were made by the Bureau of Entomology and Plant Quarantine; small dots indicate the probable range.

In New England the distribution is quite closely restricted to the coast line, ticks being literally unheard of only a few miles inland. The entire coast of Massachusetts south of Scituate is infested, the greatest density occurring on Cape Cod, Martha's Vineyard, Nantucket, and the Elizabeth Islands. In Rhode Island ticks are very rare on the eastern shore of Narragansett Bay but they are abundant on the western shore. They occur on the mainland shore of Block Island Sound, but not on the mainland shore of Long Island Sound, although Long Island is infested.

A small area of infestation occurs around Lake Winnipesaukee, N. H., with indications that in certain localities it has persisted there for at least several decades. In other localities the infestation is apparently recent, and may have been caused by the transportation of infested dogs by vacationists.

Even in the most heavily infested regions abundance is localized and sporadic, the infestations being usually associated with an abundance of grassy cover in which meadow mice can thrive. Beach grass and abandoned fields support large mouse populations, and if dogs are kept in such neighborhoods ticks are likely to be abundant. The increase and apparent spread of the species in the New England resort area may well be due to the decline of agriculture which accompanied the area's increased appeal to vacationists, with the consequent abandonment of numerous fields and pastures.

METHODS OF STUDY

The biological studies here reported were based on data of two general types, (1) observations on seasonal abundance and activity made in the course of collections in nature, and (2) data bearing on the developmental potentialities determined by laboratory rearings.

Small host animals were infested with ticks while confined in wire cylinders of the appropriate size, a modification of the method described by Hooker, Bishopp, and Wood (7) being used. Figure 2 illustrates a step in preparing a meadow mouse for infestation by this method. The mouse was placed in a cylinder of 4-mesh hardware cloth with a diameter so small that the mouse was not able to bite or scratch the ticks off while they were attaching. The cylinder was then wrapped in copper-wire screening and placed on a piece of white cloth. The ticks were placed on or inside the screen and the cloth rolled around the cylinder and sealed with adhesive tape to prevent the escape of ticks. Without the hardware cloth the mouse would be able to tear the screening, and without the screening it would be able to pull the cloth between the meshes of the hardware cloth and tear it. A piece of apple or carrot was sometimes put in the cylinder, and the mouse was confined for 24 hours or confined without food for 6 hours. Ordinarily the shorter period was satisfactory, as all ticks that would ever attach usually do so in that length of time. The same method was used for cottontail rabbits, squirrels, and muskrats by increasing the size of the cylinder.

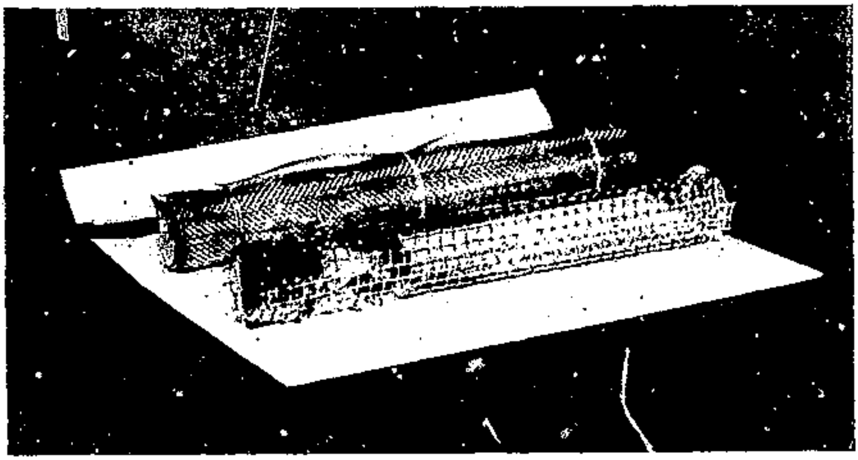

FIGURE 2.—Preparing a meadow mouse for infestation with ticks.

After the animals had been infested they were kept in cages made of hardware cloth, set over a pan of water while the ticks completed engorgement and dropped. A mouse held in this manner is illustrated in figure 3. When the ticks became engorged they dropped through the hardware cloth cage into the moat below. Once or twice each day the cage was moved to a clean pan and the ticks that had dropped were collected from the water. They were unable to escape from the water, and were not injured by submersion for 24 hours. Apple and carrot placed in the cages provided both food and water for mice, cottontail rabbits, muskrats, rats, and squirrels. Dogs were kept in larger

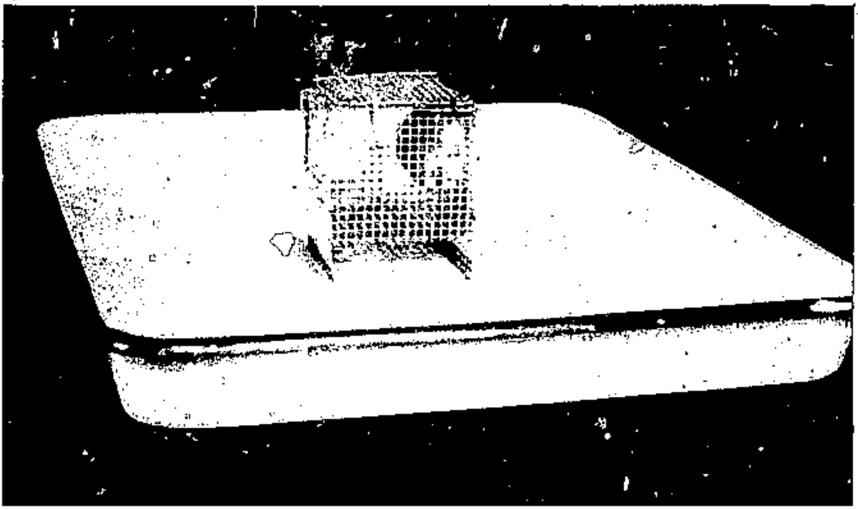

FIGURE 3.—Cage for holding meadow mouse over moat while ticks engorge and drop.

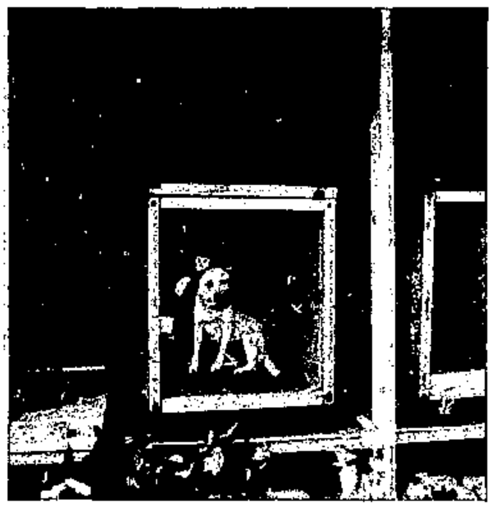

FIGURE 4.—Cage for holding dog over a moat while ticks engorge and drop.

cages over a moat in the manner shown in figure 4. In this case, however, the cage was provided with a removable floor to permit cleaning. Occasionally ticks were fed on domestic rabbits, using the engorging cell described by Jellison and Philip (*8*).

For observation of the movements of the different stages in natural surroundings an experimental meadow plot was laid out on a table in the laboratory yard.

This plot, shown in figure 5, was 30 inches wide by 59 inches long. It was built up on a greenhouse-type table constructed for the purpose. To prevent the escape of ticks, the table was surrounded by a 2-inch moat which was kept filled with creosote dip. Before being

FIGURE 5.—Table "meadow" with wire mouse run and nest and with moat for confining ticks.

placed in the table, the meadow sods were fumigated to kill all ticks present. A meadow mouse run and nest, constructed of hardware cloth, permitted the maintenance of mice in fixed areas on the surface of the ground. As the meadow was entirely in the open, the ticks were exposed to the same conditions they encounter in nature, with the possible exception of the relative availability of hosts.

Records on the molting of engorged larvae and nymphs, on preoviposition and oviposition, and on the incubation of eggs from engorged females were obtained under outdoor conditions from ticks kept in rearing tubes, and under incubator or room conditions from ticks kept in rearing tubes or in pill boxes set on moist sand. Records on the longevity of all stages under all conditions were obtained from ticks kept in rearing tubes.

The rearing tubes were prepared from test tubes of soft glass 6 inches long and ¾ inch in diameter. The glass bottoms were removed, and new bottoms were made by tamping in a moist mixture of sand, loam, and clay. This mixture conducts water readily, is firm, and will not draw away from the sides of the tubes if drying occurs. The tubes were kept in pans of moist sand indoors and in the soil outdoors. Light cloth tops confined the ticks in the tubes, but gave good ventilation and permitted rapid evaporation of excess moisture after rains.

In obtaining the outdoor records the tubes were kept under two different conditions to reduce the possibility of using abnormal records. In one lot the tubes were simply set in 1-inch screen cylinders inserted into the soil to a depth of 2 inches, so that the tubes were exposed to direct sunlight and rainfall as well as to all variations of temperature, humidity, and air circulation. These are referred to in subsequent tables as "outdoors-unsheltered." The tubes of the other lot were set in similar screen cylinders in the soil, but under crates with roofing-paper tops and sides of wood strips and hardware cloth, so that they were sheltered from direct rainfall and sunlight but exposed to all variations in temperature, humidity, and air circulation. These are referred to in the tables as being "outdoors-sheltered." The method of maintaining the tubes under the two conditions is illus-

FIGURE 6.—Maintenance of ticks in nonparasitic stages. When the box or crate is turned forward over the tubes in the foreground they will be sheltered from direct sunlight and rainfall; those in the background are not protected.

trated in figure 6. As will be shown later, no very great differences were noted between records from the two types of locations, indicating that those from both were about normal.

Studies on the seasonal abundance and activity of the adults were made by collecting them in nature with a drag. The drag used was of white flannel, 1 yard wide and 1½ yards long. A stick inserted in a hem in the front end kept the cloth spread out as it was dragged at normal walking speed over grass and other vegetation. The adult ticks which were waiting for a host caught onto the cloth as it passed. A rope fastened to the stick permitted the operator to remain erect while dragging low vegetation. Once each minute the ticks were removed and counted to obtain the record on abundance.

The larvae and nymphs cannot be collected with a drag, so in studies of their seasonal abundance it was necessary to collect their natural hosts, principally meadow mice and white-footed mice. As ticks begin to leave the host shortly after its death, it was necessary to capture the animals alive in order to obtain the complete infestation. Box-type traps were used successfully. At the first the mice were etherized and the ticks removed, but later all hosts were kept in cages over trays of water while the ticks on them completed engorgement and dropped into the water.

Records on the temperature and relative humidity were taken by means of a hygrothermograph kept in a standard weather instrument shelter set over grass-covered ground in an exposed location. The average daily temperature and relative humidity were obtained by averaging the readings at every other hour. Monthly averages were derived from the daily averages. Rainfall and snowfall were measured by means of the standard cylindrical rain gauge. The weather records, summarized by months, are shown in table 1.

TABLE 1.—*Monthly summaries of weather records at Vineyard Haven, Mass.*

Month	Average temperature	Average relative humidity	Precipitation	Rain or snow	Month	Average temperature	Average relative humidity	Precipitation	Rain or snow
1938	°F.	*Percent*	*Inches*	*Days*	1940	°F.	*Percent*	*Inches*	*Days*
Jan.	30.8	74.8	3.40	10	Jan.	23.0	70.2	2.20	7
Feb.	32.5	74.4	3.87	17	Feb.	20.6	71.5	5.35	13
March	37.0	65.7	2.93	11	March	31.5	71.4	4.91	8
April	47.5	69.9	4.27	12	April	40.4	78.2	6.23	12
May	53.7	70.4	4.03	10	May	52.1	80.6	2.43	12
June	63.6	72.2	5.50	11	June	60.2	78.8	2.03	7
July	70.9	74.7	5.51	11	July	68.8	84.9	5.82	7
Aug.	71.7	71.0	2.09	7	Aug.	66.9	80.1	.89	5
Sept.	62.2	67.8	8.35	14	Sept.	62.4	80.9	4.50	10
Oct.	56.1	82.9	4.30	9	Oct.	49.7	75.6	2.07	7
Nov.	48.7	80.4	4.76	9	Nov.	43.2	75.5	5.02	13
Dec.	36.6	70.8	3.08	12	Dec.	35.9	75.3	4.15	10
1939					1941				
Jan.	28.1	74.0	4.20	10	Jan.	28.2	69.9	4.67	9
Feb.	31.8	75.2	5.01	13	Feb.	29.0	71.3	1.46	6
March	31.7	72.6	6.90	11	Mar.	32.6	67.2	3.44	9
April	41.4	74.8	4.71	9	April	46.2	73.2	2.07	7
May	51.2	77.9	1.10	8	May	55.5	70.2	.99	8
June	62.5	81.2	3.56	8	June	62.4	77.9	6.13	9
July	68.5	82.3	1.97	8	July	66.8	84.7	4.76	12
Aug.	72.1	82.3	4.01	8	Aug.	65.3	81.0	3.49	10
Sept.	62.5	77.6	2.30	10	Sept.	62.3	75.2	1.05	3
Oct.	54.1	68.8	3.16	6	Oct.	51.6	71.3	2.48	10
Nov.	41.6	51.3	2.37	5	Nov.	46.9	69.5	2.80	6
Dec.	34.0	66.8	2.43	11	Dec.	36.2	71.4	3.31	7

LIFE HISTORY

The American dog tick was described by Say in 1821 (*14*), and since that time a number of entomologists have contributed to our knowledge of its life history and economic importance. The life history was worked out in detail by Hooker, Bishopp, and Wood (*7*) in 1912, and a few observations were made by Hadwen in 1913 (*5*). In 1925 Zebrowski (*21*) published a report on the morphology of the species, and Cooley briefly summarized the life history in 1932 (*2*) and the hosts and distribution in 1938 (*3*). Larrousse, King, and Wolbach (*9*) in 1928 reported meadow mice as hosts for the immature stages. The report of the Chief of the Bureau of Entomology for 1933 (*20*) discussed the host relationships, reporting meadow mice, pine mice, and white-footed mice as the principal hosts of the immature stages in the "vicinity of Washington, D. C." In 1938 Bishopp and Smith (*1*) published a detailed account of the distribution, hosts, and life history, based on the collections of the Bureau of Entomology and Plant Quarantine and on experimental rearings.

The Adult

The adult male (fig. 7) is about 4.5 mm. long by 2.5 mm. wide. The hard dorsal shield is dark brown, marked with a variable pattern of white. The unfed female (fig. 8) is slightly larger than the

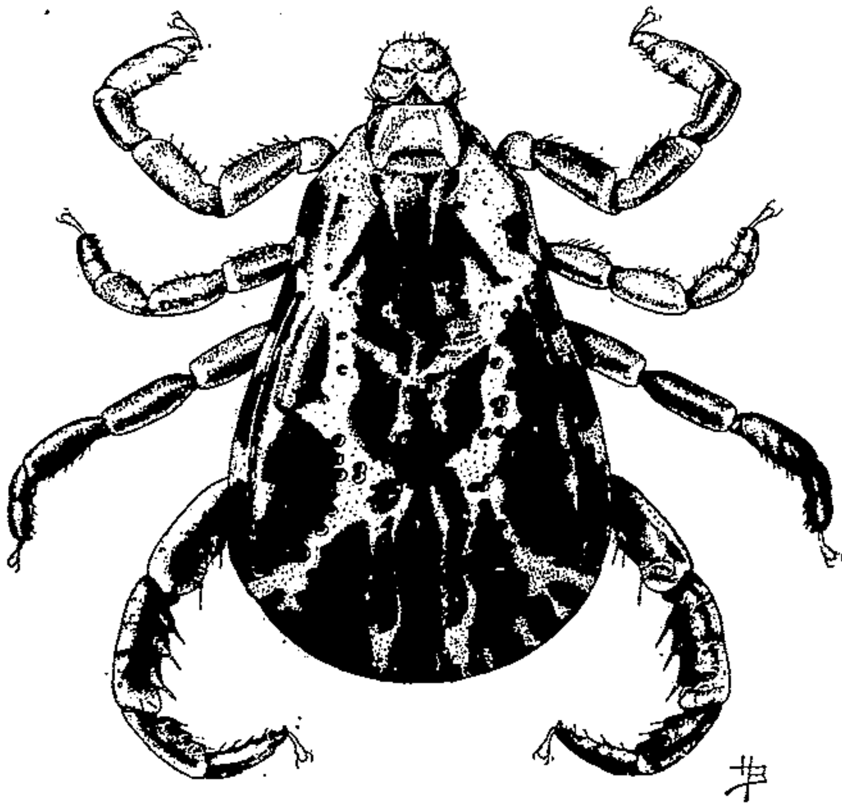

FIGURE 7.—*Dermacentor variabilis:* Dorsal aspect of a male.

male, and its shield, much more extensively marked with white than in the male, is restricted to the anterior portion of the dorsum. Feeding does not alter the size of the male, but as the female feeds it increases greatly in size, becoming about 13 mm. long by 10 mm. wide. An engorged female is shown in figure 9. The size of the shield does not change.

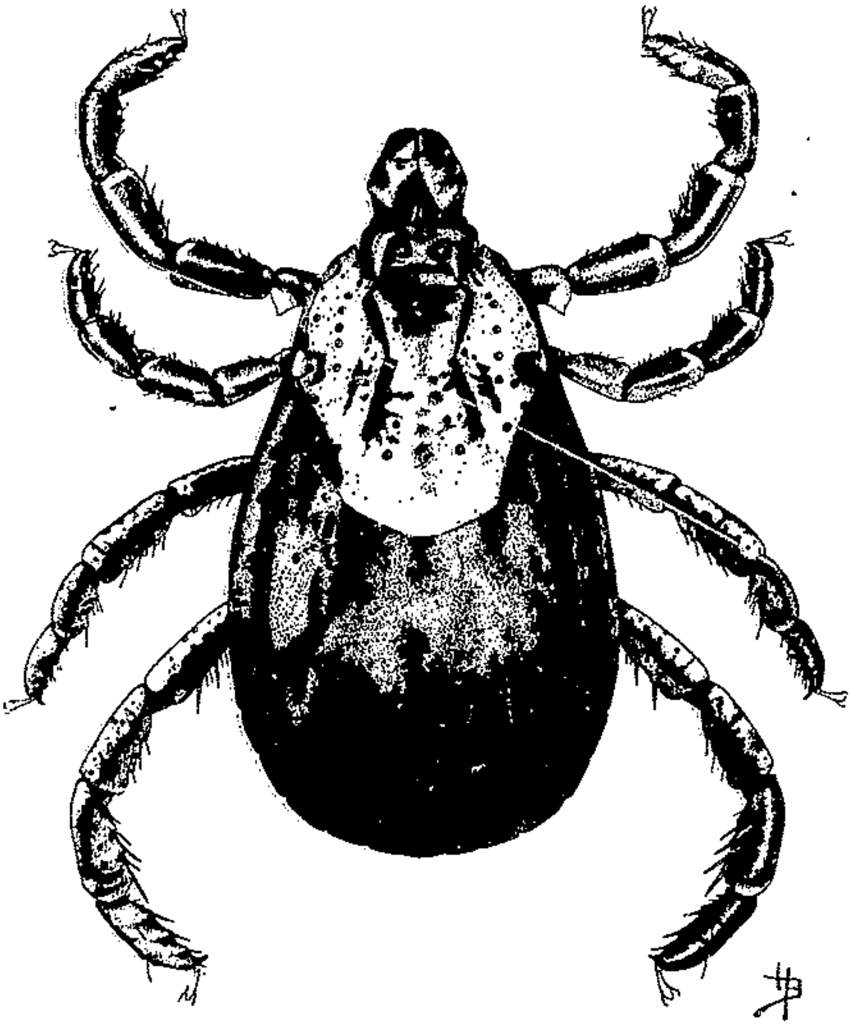

FIGURE 8.—*Dermacentor variabilis:* Dorsal aspect of unengorged female.

ADULT LONGEVITY

The American dog tick feeds only on the blood of mammals, but under favorable conditions of temperature and humidity the adults

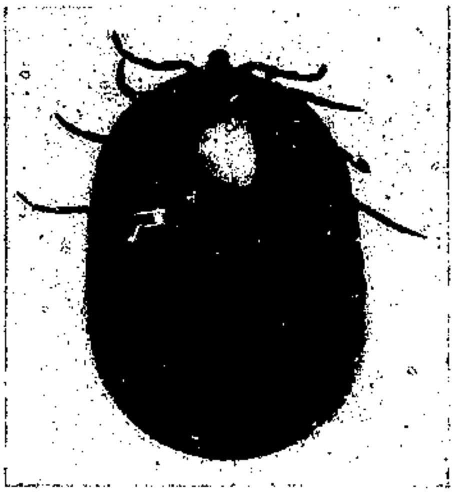

FIGURE 9.—*Dermacentor variabilis:* Dorsal aspect of engorged female.

may live for long periods before feeding. Records on the longevity of unfed adults in various environments are presented in table 2.

TABLE 2.—*Longevity*[1] *of unfed adults of Dermacentor variabilis, at Vineyard Haven, Mass.*

Environment of molting nymphs and adults	Lots	Season of molting nymphs	Greatest longevity in each lot	
			Average	Range
	Number		*Days*	*Days*
Outdoors-sheltered	3	May-June	645.7	321–864
Do	20	July	635.0	294–1,032
Do	9	August	704.1	386–913
Do	3	Sept.-Oct.	622.3	449–922
Outdoors-unsheltered	3	May-June	367.0	261–444
Do	13	July	522.4	14–814
Do	7	August	567.0	314–769
Do	2	Sept.-Oct.	642.0	463–921
Heated room	5		768.0	723–911

[1] In each lot a group of molting nymphs was used, all of which had dropped on the same day, and adult longevity was calculated from the date the nymphs began to molt to the last date on which any adults were noted alive.

The maximum longevity, 1,032 days, was attained by ticks kept under outdoor conditions, whereas the maximum longevity attained by ticks in a room heated in winter was 911 days. These are very slightly less than the maximum longevity of between 988 and 1,053 days recorded at Washington, D. C., by Bishopp and Smith (*1*). The records are based on the date of molting of the first nymph only in each lot, so the extreme longevity of any individual was possibly a few days less than the number of days shown. Including some records not listed in table 2, 4 lots lived less than 100 days, 4 lots lived about 200 days, 8 lots lived about 300 days, 17 lots about 400 days, 9 lots about 500 days, 9 lots about 600 days, 16 lots about 700 days, 8 lots about 800 days, 7 lots about 900 days, and 1 lot about 1,000 days.

ADULT ENGORGEMENT

When the adults are ready to feed they climb up on grass or other vegetation, and when approached by a possible host they become agitated, clinging to the foliage with the third pair of legs and waving the others about, ready to grasp any passing object. If they find themselves on a favorable host they attach and begin feeding. After both sexes have fed for several days, mating occurs on the host. The males continue to feed and mate for an indefinite period, whereas the females complete engorgement and drop. Records of female engorgement are presented in table 3. The ticks engorged on the rabbits were confined in engorging cells (see section Methods of Study), whereas those on the dogs were free to attach anywhere. The average engorging period for all the females was 10.5 days.

TABLE 3.—*Engorgement of females of Dermacentor variabilis*

Host	Females	Season of engorgement	Engorging period	
			Average	Range
	Number		*Days*	*Days*
Rabbit	87	Feb., Mar.	10.1	8–15
Do	70	Aug., Sept., Oct.	10.9	7–27
Dog	12	Mar.	11.8	9–14
Do	29	Aug., Sept., Oct.	10.3	7–16

On several occasions partly engorged females were picked up by dragging. It is of interest to note, in the case of ticks infected with the rickettsia of Rocky Mountain spotted fever, that if either partially engorged females or males that have ingested blood, but will feed again, become detached from their hosts and should reattach to man, they can transmit the infectious agent of spotted fever in a much shorter time than could the same ticks if unfed. This is particularly true during the early part of the season during which adult ticks are active.

PREOVIPOSITION AND OVIPOSITION

When the engorged females drop from the host they seek a protected location in which to lay their eggs. In view of the possibility that they might be seeking environments also favorable to their larvae (e.g., mouse nests and runs) as do the females of many insects, the movements of 14 engorged females were traced. Eight females were released in the table meadow (fig. 5) and their locations noted on the first, second, third, fifth, and fourteenth succeeding days. Two were not found, but the six that were found had crawled 23, 16, 15, 14, 14, and 8 inches, respectively. There was no indication of a tendency to crawl in any one direction, and individual females were observed to travel in circles or to double back on their paths. To trace their movements more accurately, a very small cylinder (3 mm. by 7 mm.) containing 72 inches of silk thread which paid out easily was fastened to the posterior end of each of six females. Experience had shown that ticks were not handicapped by such a "pack," and that they readily pushed through tangled grass, leaving a trail of thread to show the exact path they had taken. Of three "strung" females released in the table meadow within 7 inches of an occupied meadow mouse run, only one crawled directly to the nearest run, the others changing course at random. Three strung females also were released on a grassy bank near a road, where mouse runs were numerous. After 7 days they were picked up and their paths charted as shown in figure 10. All three still had avail-

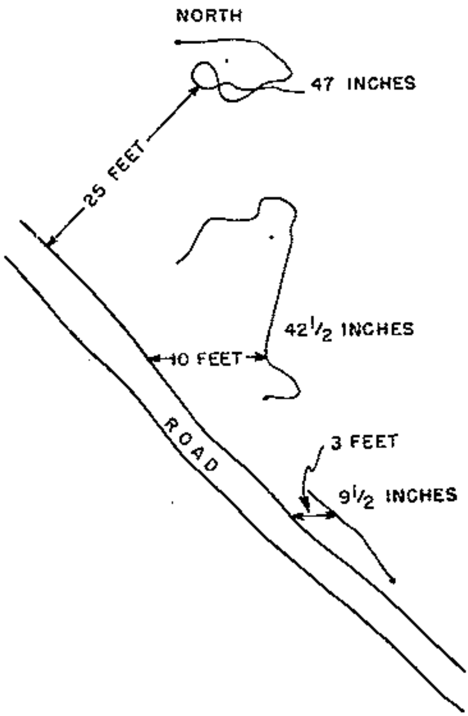

FIGURE 10.—Movement of engorged females of *Dermacentor variabilis* through tangled grass.

able thread not paid out. One had crawled only 9½ inches and had stopped under poor cover. The other two had crawled 42½ and 47 inches, respectively, changing their courses many times without reference to the mouse runs, and crawling through clumps of grass exactly like the ones in which they finally hid.

The interval between dropping from the host and the first oviposition varies with the temperature, and hence with the season. Preoviposition periods under various environmental conditions are summarized in table 4.

The shortest preoviposition period observed was 4 days, but the eggs in this case did not hatch. Preoviposition periods of 6 days were noted in an incubator at a constant temperature of 80° F.,

TABLE 4.—*Preoviposition period of Dermacentor variabilis at Vineyard Haven, Mass.*

Environment	Females	Season of engorgement	Preoviposition period	
			Average	Range
	Number		*Days*	*Days*
Incubator (80° F.)	2	Spring	6.5	6–7
Heated room	9	do	16.8	11–27
Do	10	Summer	6.7	4–10
Outdoors-sheltered	3	Spring	37.7	26–58
Do	19	Summer	10.9	6–25
Outdoors-unsheltered	6	do	11.0	8–15

indoors at an average temperature of 77.5°, and outdoors at an average temperature of 73.1°, all resulting in the production of viable eggs. This is somewhat longer than the minimum reported at Washington by Bishopp and Smith (*1*). Other normal preoviposition periods outdoors ranged up to 58 days. A single female survived the winter before ovipositing, giving a preoviposition period of 189 to 221 days, but the eggs did not hatch.

THE EGG

The slightly ellipsoidal, yellowish-brown eggs are laid in masses, coated with a viscous secretion to prevent desiccation. No oviposition records were made during this study, but at Washington, D. C., Bishopp and Smith (*1*) indicated the normal egg production of a female to be from 4,000 to 6,500 eggs, laid over a period of 14 to 32 days, as many as 800 eggs being laid in a single day. The female usually dies within a few days after oviposition is completed, but may live for several weeks.

INCUBATION

The incubation period varies with the temperature and season. Table 5 lists the minimum incubation periods (i.e., from first oviposition to first hatch) of lots of eggs kept under various conditions.

TABLE 5.—*Minimum incubation periods of eggs of Dermacentor variabilis, counted from the first egg laid in any mass to the first one to hatch, Vineyard Haven, Mass.*

Environment	Egg masses	Season of oviposition	Incubation period	
			Average	Range
	Number		*Days*	*Days*
Incubator (80° F.)	2	May	27.0	27–27
Heated room	10	Before Aug. 10	55.1	43–65
Do	8	After Aug. 10	51.0	39–67
Outdoors-unsheltered	4	Before Aug. 10	47.7	40–55
Outdoors-sheltered	5	do	48.0	36–57
Do	4	After Aug. 10	232.8	51–303

The shortest incubation period observed was 27 days, this being in two lots kept at a constant temperature of 80° F. The shortest period under outdoor conditions was 36 days, at an average temperature of 71.1°. The longest period under outdoor conditions was 303 days, in the case of eggs which survived the winter, but larvae from these eggs were abnormally short-lived. The longest outdoor incubation period of eggs producing normal larvae was 57 days at an average temperature of 65.2°.

The complete incubation records of six lots of eggs laid at intervals during the oviposition period are given in table 6. Each lot includes all the eggs laid by a female on a given day. The eggs were kept in a room at almost constant temperature, the average ranging from 63.6° to 66.9° F. Hatching in one lot (female No. 906) spread over 11 days. There was some tendency for eggs deposited late in the oviposition period to show shortened incubation periods.

TABLE 6.—*Incubation of eggs of Dermacentor variabilis at Vineyard Haven, Mass.*

Female No.	Date eggs deposited 1940	Eggs	Eggs hatched on specified day following oviposition													
			54	55	56	57	58	59	60	61	62	63	64	65	66	Total
		Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
906	Apr. 24	330			55	135	109	23	4							326
906	May 1	191			0	26	44	75	2	3	5	12	9	1	1	178
906	May 6	502	5	12	76	143	70	21	0	1						328
909	Apr. 24	313					10	39	200	35	20	5	3	0	1	313
909	May 1	189				8	36	121	20	4						189
909	May 6	617			46	167	72	114	16	2	2					419

THE LARVA

The larva (fig. 11) differs from the other stages in the absence

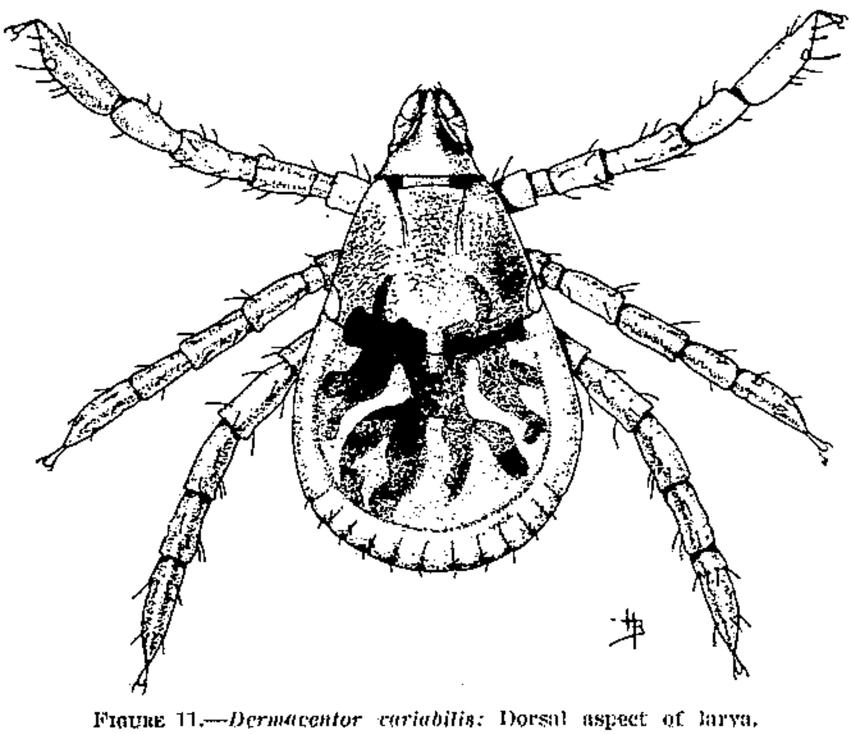

FIGURE 11.—*Dermacentor variabilis:* Dorsal aspect of larva.

of spiracles and in having only three pairs of legs, and from the adults in lacking white markings on the shield. Unfed specimens are yellow, with red markings near the eyes, and are about 0.6 mm. long. Engorged specimens are slate gray or black and about 1.5 mm. long.

LARVAL LONGEVITY WITHOUT FOOD

In the absence of hosts but under favorable environmental conditions, larvae may live for considerable periods without feeding, although not so long as can the adults. Records of such survival under various conditions are presented in table 7. The period shown is that from the time the first eggs in a clutch hatched until the late date when any larvae were observed alive, but since incubation covers from 20 to 30 days, the actual life of the last larvae might have been a few days shorter than the period given.

TABLE 7.—*Longevity of larvae of Dermacentor variabilis without feeding*

Environment	Lots [1]	Season of hatching	Longevity in each lot	
			Average	Range
	Number		*Days*	*Days*
Heated room	7	Before July 1	403.6	333–483
Do	6	After July 1	366.5	230–528
Outdoors-unsheltered	8	do	383.5	315–434
Outdoors-sheltered	5	Before July 1	82.0	14–130
Do	21	After July 1	410.7	95–540

[1] Each lot included all the larvae produced by one female.

The greatest longevities observed were 540 days under outdoor conditions and 528 days in a heated room—considerably greater than the maximum longevity recorded at Washington by Bishopp and Smith (*1*). Five other lots showed longevities of about 500 days, 20 lots about 400 days, 14 lots 300 days, 2 lots about 200 days, and 7 lots lived for about 100 days. Five of these last 7 lots were abnormal in that the eggs had been exposed to winter conditions.

LARVAL ENGORGEMENT

When the larvae are ready to feed they crawl about seeking their hosts. In the table meadow they were very rarely observed in the waiting position assumed by the adults, but were seen in numbers crawling along the wire enclosing the mouse run and along blades of grass. When any object approached them they ceased movement and stretched out their legs in the manner of the adults, grasping whatever was brought within reach. They were obviously concentrated along the mouse run, apparently attracted by the odor. They probably remain low in the vegetation, as they are never taken on drags.

Records on the experimental engorgement of 66,770 larvae on meadow mice are presented in table 8. The time required to complete engorgement ranged from 3 to 13 days, with the greatest number dropping on the fourth day. The average engorging period was 4.4 days. As many as 2,644 larvae were able to engorge on a single mouse at one time, but other mice died in the cages with much lighter infestations. Only the records from mice that survived for the entire period of observation are included in the table.

TABLE 8.—*Engorgement of larvae of Dermacentor variabilis on meadow mice at Vineyard Haven, Mass., 1937-39*

Season of engorgement	Larvae observed	Engorging period	
		Average	Range
	Number	*Days*	*Days*
Spring	31,792	4.30	3-11
Summer	16,153	5.13	3-11
Autumn	11,992	4.07	3-13
Winter	6,833	4.19	3-12

LARVAL MOLTING

After the larvae have completed engorgement and dropped from the host they seek a protected place in which to molt. The interval between dropping and molting varies with the temperature and season. Table 9 presents the molting records of larvae kept under various conditions. In each case only the minimum record for each lot is given, i.e., the period from dropping to the time the first larvae molted.

TABLE 9.—*Period from dropping from the host to molting of larvae and nymphs of Dermacentor variabilis at Vineyard Haven, Mass., 1938-40*

PERIOD FOR LARVAE

Environment	Lots	Season of engorgement	Period to molting in each lot	
			Average	Range
	Number		*Days*	*Days*
Outdoors-sheltered	16	May-Sept.	20.7	10-49
Do	4	Oct.-April	163.5	64-247
Outdoors-unsheltered	18	May-Sept.	21.6	10-47
Do	6	Oct.-April	185.5	76-247
Incubator (80° F.)	4	May-Sept.	6.5	6-7
Heated room	5	Oct.-April	13.8	8-17

PERIOD FOR NYMPHS

Outdoors-sheltered	9	Spring	97.4	52-142
Do	16	Summer	34.4	25-49
Do	10	Fall	267.8	241-291
Do	2	Winter	213.0	170-256
Outdoors-unsheltered	7	Spring	97.6	56-131
Do	16	Summer	35.5	24-54
Do	2	Fall	251.0	245-257
Do	5	Winter	198.4	172-240

The shortest observed period from dropping to molting was 6 days among ticks kept at a constant temperature of 80° F. Among ticks kept under outdoor conditions the molting period ranged from 10 days for larvae dropped in July and August to 247 days for larvae dropped in October. Records showing the molting periods of all individuals in a single lot were not taken, as an enormous number of records of this type had been made at Washington, D. C., and summarized by Bishopp and Smith (1). At moderate temperatures molting in a single lot spread over 18 days or less, and at low temperatures it spread over 26 days or less. However, in the case of some lots of larvae which dropped late in September and were kept under outdoor conditions, molting began the same fall after 32, 38, 49, and 47 days, was interrupted by winter, and began again in the spring after 209, 221, 245, and 220 days, respectively.

The Nymph

The nymph differs from the adult in the absence of a genital opening on the venter and of white markings on the shield; it differs from the larva in the possession of stigmal plates and four pairs of legs. The unfed nymph (fig. 12) is light yellowish brown, with

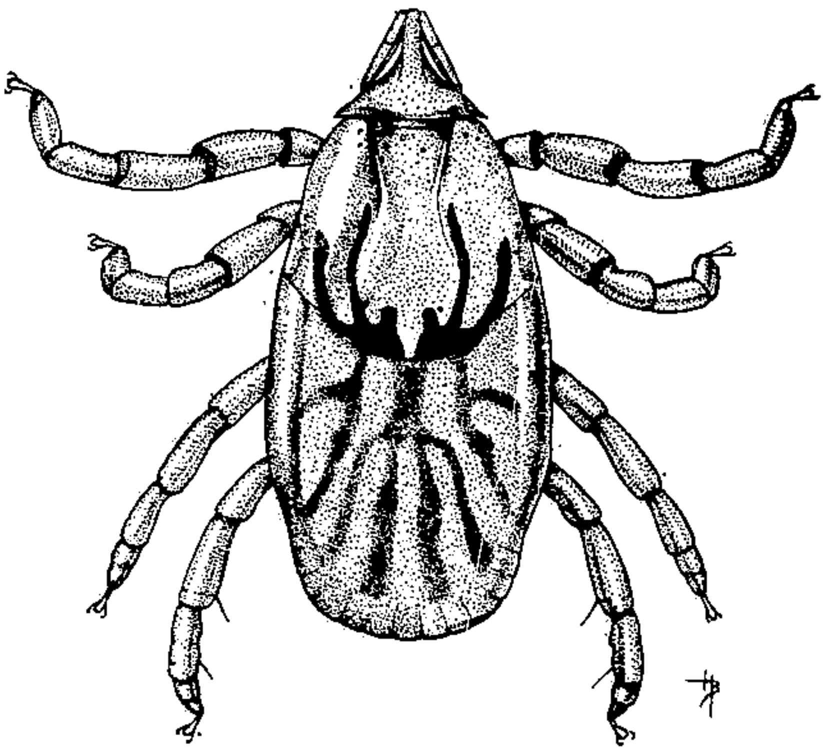

FIGURE 12.—*Dermacentor variabilis:* Dorsal aspect of nymph.

red markings near the eyes, and is about 1.5 mm. long. Engorged specimens are slate gray and about 4 mm. long.

NYMPHAL LONGEVITY WITHOUT FOOD

Like the larvae, nymphs feed only on the blood of small mammals, but in the absence of hosts they may live for long periods without feeding—for a longer time than larvae but for a much shorter time than adults. Longevity records of nymphs kept under various conditions are shown in table 10.

TABLE 10.—*Nymphal longevity of Dermacentor variabilis, without food, Vineyard Haven, Mass.*

Environment of molting larvae and nymphs	Lots of larvae	Season of molting	Longevity in each lot	
			Average	Range
	Number		*Days*	*Days*
Outdoors-sheltered [1]	11	July-Aug.	446.9	362–564
Do. [1]	13	Sept.-Jan.	304.1	149–478
Do. [1]	35	Apr.-June	205.1	29–584
Do. [2]	3		444.0	423–483
Outdoors-unsheltered [1]	11	July-Aug.	362.1	74–451
Do. [1]	13	Sept.-Jan.	315.4	151–519
Do. [1]	25	Apr.-June	223.1	29–458
Do. [2]	3		430.7	247–547
Heated room [2]	9		341.7	275–426

[1] In these lots a group of molting larvae, all of which had dropped on the same day, was used, and nymphal longevity was calculated from the date the first nymph molted to the last date on which any nymphs were seen alive.
[2] In these lots the longevity was calculated from the date the last nymph molted.

As molting in a single lot might spread over 2 weeks to a month, the actual life of the last nymph might have been shorter or longer than the periods shown. The greatest longevity attained, 584 days, was greater than that recorded at Washington by Bishopp and Smith (*1*).

NYMPHAL ENGORGEMENT

When the nymphs are ready to feed they crawl about seeking hosts in the same manner as do the larvae. In the table meadow they were observed concentrated along the mouse run, and, like the larvae, they are not picked up on drags.

Records on the experimental engorgement of 4,013 nymphs are presented in table 11. The engorging period ranged from 3 to 11 days, with the greatest number dropping on the sixth day.

TABLE 11.—*Engorgement of nymphs of Dermacentor variabilis at Vineyard Haven, Mass., 1938-41*

Host	Nymphs	Season of engorgement	Engorging period	
			Average	Range
	Number		*Days*	*Days*
Meadow mouse	382	Spring	5.17	3–8
Do.	159	Summer	5.81	4–8
Do.	471	Autumn	6.29	4–11
Do.	178	Winter	5.33	4–9
Rabbit	1,666	Spring	5.82	3–11
Do.	1,135	Summer	6.46	4–11
Do.	10	Autumn	6.10	5–7
Muskrat	12	Spring	7.75	7–9

The rabbits used were wild cottontails, with the nymphs free to attach anywhere on the body. Nymphs were also engorged in cells on domestic rabbits, but the records on these are not included in the table. The majority of the nymphs that dropped from rabbits were normal, but a sizeable minority were abnormally bloated and died a few days after dropping. Trager (*19*) has shown that rabbits and other animals may acquire immunity to tick engorgement, but the ticks that engorged on resistant animals were undersized rather than bloated. The nymphs were free on the muskrat and engorged normally.

NYMPHAL MOLTING

When the nymphs have completed engorgement and have dropped from the host they seek, as did the larvae, a protected place in which to molt. In one instance an engorged nymph was found in a mouse nest, but engorged ticks are rarely encountered in nature. Table 9 presents records on the periods between dropping and molting of nymphs kept under various outdoor conditions. In each case only the minimum period for each lot is shown. The shortest period observed under outdoor conditions was 24 days, the average temperature for the period being 72.3° F., but nymphs kept indoors molted in 20 to 22 days after leaving the host. Under outdoor conditions the periods vary with the temperature and season, the longest period recorded being 291 days for nymphs dropped in October, and the average temperature for the period being 42.9°.

No records on the molting of all individuals in a lot were made, as a large number of such records had been made in Washington and summarized by Bishopp and Smith (*7*). At high temperatures molting in a single lot spread over about 7 days, and at low temperatures it spread over about 50 days, with occasional records spreading it over as much as 70 days. In these experiments molting was completed the same season it began, no lots being divided by winter as in the case of the larvae. When the onset of winter found molting in a lot partly completed, the unmolted nymphs died, but in many lots which had not begun to molt the nymphs survived the winter readily. Therefore the spread of molting in a single lot presumably fell within the limits reported at Washington.

SEASONAL CYCLES

In spite of the numerous papers concerning this species, there were still many points about its biology that were obscure, and in the present study it was planned to investigate some of them.

Two main types of data were collected, following the methods described in the section on technique. Ticks were reared experimentally and all stages exposed out of doors in glass tubes, to determine just how long each of the nonparasitic periods lasted under natural conditions when started in any month of the year. Records on seasonal abundance were made by dragging for adults and trapping mice for larvae and nymphs. Seasonal-abundance records were made in several areas, but in this discussion only those from the most heavily infested area, Gay Head, will be presented, as this area was typical of all and was untouched by control experiments.

Considerable thought was given to the question of the best manner of comparing the seasonal abundance of the immature stages, as determined by trapping mice, in different areas and in different seasons in the same area. At first glance it would seem that a fair method of comparison would be to make a graph of the seasonal abundance, plotting on the abscissa the months and on the ordinate the average number of ticks for each mouse caught (dotted line, fig. 13). Mice that died before examination would have to be excluded from consideration, as many of the ticks would have detached soon after death, and no fair comparison could be made between the infestations from these and from living mice.

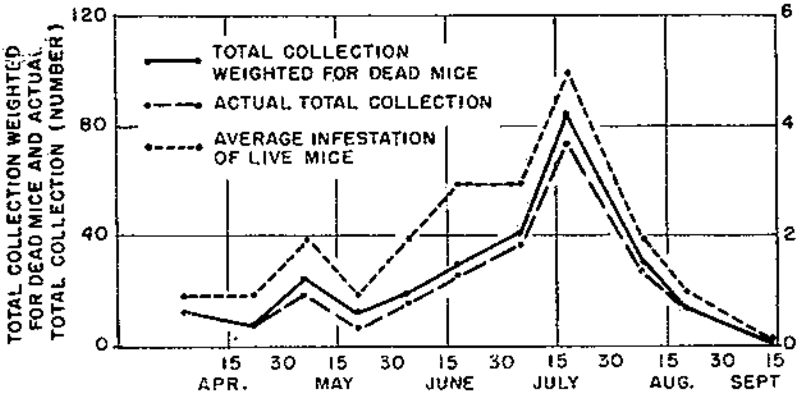

FIGURE 13.—Nymphal abundance of *Dermacentor variabilis* plotted by different methods.

The number of mice varies considerably in different areas, however, and at different times in the same area, and it seems reasonable to assume that an infestation of 50 mice to the acre, each carrying 20 ticks, would represent a greater abundance of ticks than an infestation of only 10 mice to the acre, each carrying 20 ticks. This aspect is particularly important, as we wish to consider the effect of the number of larvae that engorge at any one time on the nymphs present at definite

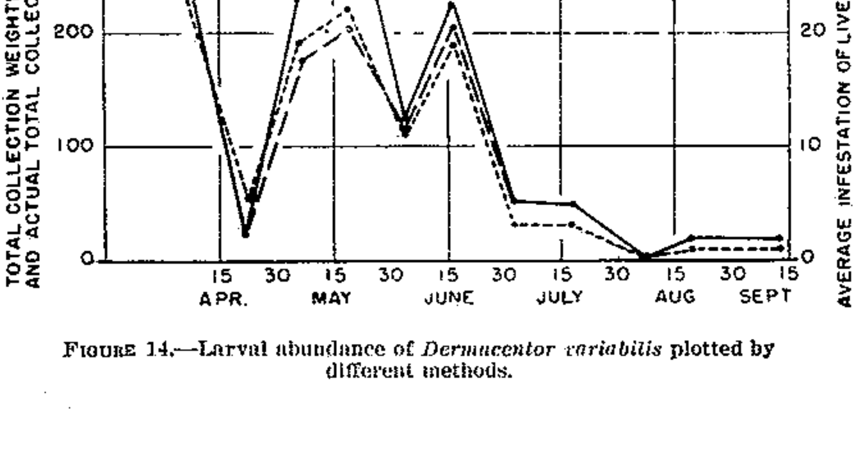

FIGURE 14.—Larval abundance of *Dermacentor variabilis* plotted by different methods.

later times, and the effect of nymphal engorgement on the subsequent seasonal abundance of adults. The proportion of white-footed mice to meadow mice also varies, and these species are not comparable as hosts.

A method that would give weight to these factors would use a constant number of traps at each collection and plot on the ordinate of the graph the total number of ticks collected as represented by the broken line in figure 13. As the mice that die would not be carrying their full infestation, it would be necessary to eliminate the collections from dead mice altogether, and increase the total collection by the proportion of dead mice to live mice. A plotting by this method is represented by the solid line in figure 13.

In the example plotted by these methods in figure 13, all three lines corresponded very well, but as the seasonal fluctuation was fairly regular this might not be considered a fair example. For this reason the same methods were applied to the most abnormal graph of larval abundance available, shown by the broken line in figure 14. Once more, plotting curves by all three methods revealed the same trends. It was therefore decided to use the complete collection from a fixed number of traps, weighted for dead mice.

The Larval Cycle

The seasonal abundance of larvae at Gay Head, Mass., during 1938, 1939, 1940, and 1941 is shown in figure 15. In the first year, 1938,

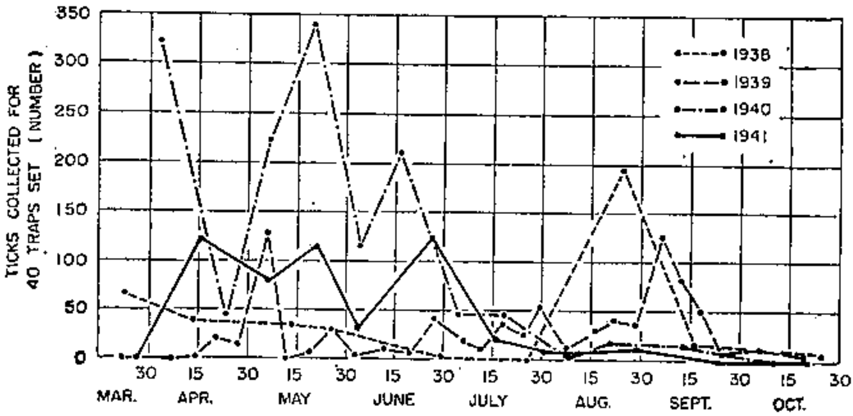

FIGURE 15.—Seasonal abundance of larvae of *Dermacentor variabilis* at Gay Head, Mass.

there was a moderate peak at the very beginning of the season, declining slowly to the point of complete disappearance in July. In August the abundance rose again to a high peak, from which the decline was much more abrupt.

The interpretation of this graph, made from conditions where no control was attempted, is of considerable importance in determining just what can be expected where control measures are applied. Since it is known that larvae can live for more than a year, and that lack of moisture is the most detrimental of all climatic factors, it would be logical to assume that the ticks estivate in the hot, dry summer, being active in the moist spring and fall. But weather records (table 1) show that the humidity was higher in July than in either August or September, and there was more rain in July than in August or the first half of September, by which time the peak of activity was past. Also, the abundance of nymphs (fig. 16) was rising while that of larvae was falling, and both respond to climatic conditions in the same way. The abundance of meadow mice, although low in July, was as high in June as in August and higher than in any other month.

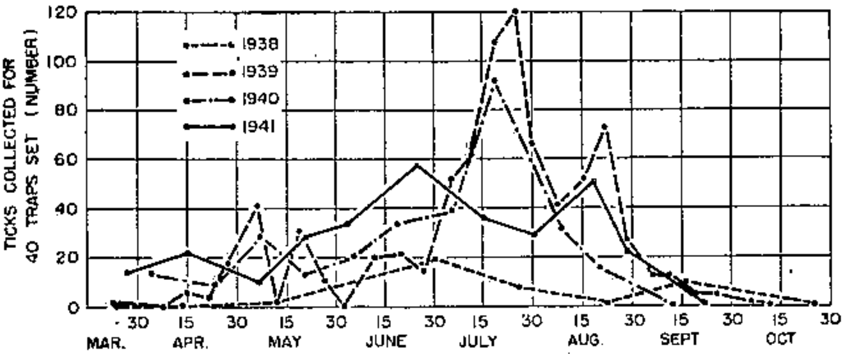

FIGURE 16.—Seasonal abundance of nymphs of *Dermacentor variabilis*, at Gay Head, Mass.

Typical outdoor records on oviposition and incubation, presented in table 12, show that the eggs of the first females to engorge in the spring of 1939 did not hatch until July 24, whereas the eggs from all females dropping between the end of March and the first of July began hatching during the period from August 1 to 24. This period of first hatching immediately preceded the summer peak of abundance as shown on the graph. It now becomes apparent that the fluctuations represent actual differences in the number of larvae present in the area, and the correct interpretation appears to be that the spring peak is due to hibernating larvae from eggs hatched the previous fall, since in most instances eggs did not survive the winter in breeding tubes. Since there can be no addition to their numbers until eggs from spring-fed females begin to hatch, their abundance constantly declines as more and more become engorged or die, until by July practically all are fed or killed. Then hatching begins, and the numbers rapidly increase as eggs from the numerous females dropped in April, May, and June all begin to hatch at once. Females fed after the middle of July produce eggs that will not hatch until the end of August or later, when larval activity is declining, and the larvae from these eggs carry over until spring.

From the close correlation between these collections and experimental rearing records, it appears that in the presence of an adequate number of hosts the potential longevity is never realized, and there is no estivation, practically all larvae engorging soon after hatching, or after becoming active in spring. Control measures directed against

TABLE 12.—*Preoviposition, incubation, and larval longevity of Dermacentor variabilis at Vineyard Haven, Mass.*

Date female dropped	Date oviposition began	Date hatching began	Last larva died sometime during period—
1938	*1939*	*1939*	
Nov. 4	(1)		
Do	May 12–June 13	(2)	
Nov. 17	(1)		
Do	(1)		
1939			
Mar. 22	May 12–June 13	(2)	
Do	do	July 24	Aug. 12–Sept. 13, 1940.
Apr. 5	do	Aug. 10	Nov. 13, 1939–Feb. 6, 1940.
Apr. 30	do	Aug. 1	June 11–July 13, 1940.
May 22	May 22–June 13	do	Jan. 16–Feb. 12, 1941.
May 29	June 13–June 27	Aug. 8	Do.
June 1	do	Aug. 7	Oct. 14–Nov. 12, 1940.
June 7	do	Aug. 11	Nov. 12, 1940–Jan. 16, 1941.
Do	do	Aug. 7	Oct. 14–Nov. 12, 1940.
July 6	July 10	Aug. 24	Do.
July 26	Aug. 4	Sept. 13	Nov. 12, 1940–Jan. 16, 1941.
July 27	do	do	Jan. 16–Feb. 12, 1941.
Aug. 2	Aug. 10	Sept. 20	Aug. 12–Sept. 13, 1940.
Aug. 8	Aug. 17	Oct. 7	Oct. 14–Nov. 12, 1940.
		1940	
Aug. 24	Sept. 2	June 17	Do.
Do	Sept. 7	(2)	
Sept. 16	Sept. 30	(2)	
Sept. 20	do	(2)	
Oct. 20	(1)		
Oct. 21	(1)		

[1] Female died without ovipositing.
[2] Eggs did not hatch.

adult ticks should therefore produce an effect on larval abundance by the end of the same season.

The abundance of larvae in 1939, as shown in figure 15, varied in some respects from that in 1938. Collections were made each week instead of each month, and the mice captured were held at the laboratory for 8 days to permit all ticks to drop, then released at the site of capture. Thus 1 week's catch was absent from the area at each trapping, and early in the spring, when mice were scarce, this might have affected the number captured. The greater frequency of collections made more irregularities in the graph, but in general the trends were the same. This year, as in 1938, there was a high spring peak representing activity by overwintered flat larvae, diminishing as the numbers of such larvae were diminished by engorgement or death. The peak occurred in May rather than March, probably because the weather was much colder (table 1). In 1939, however, there was also a peak in late June and early July, following directly the period of hatching of overwintered eggs in the breeding tubes (table 12). Such a peak was not present in 1938, when there had been no survival of eggs in the rearing tubes. The late-summer and early-fall increase in abundance, present both years, once more follows the hatching of eggs from females dropped in the spring.

The spring abundance of larvae in 1940 was enormous in comparison with other years, becoming apparent early in April, even though this month was as cold as in 1939. Once again this spring abundance can be attributed only to hibernating larvae, as hatching of overwintered eggs did not begin until the middle of June, and hatching of spring-laid eggs did not begin before August. Held up by the tremendous numbers of larvae that carried over from 1939, when adult abundance and hence oviposition were at their height (fig. 17), and perhaps assisted by hatching of overwintered eggs in June and July, larval abundance did not reach a real low until August. The late-summer and fall abundance was much lower than in either previous year, although there were more adult ticks than in 1938, and mice were abundant.

In 1941 the abundance of overwintered larvae was greater than in any year except 1940. Activity began early, April being warmer than in any year except 1938, and larvae continued to be numerous until the end of June, as in 1940. The fall population was lower than in any other year.

The reason for a late summer peak of larval abundance in 1938 and 1939 and its absence in 1940 and 1941 is obscure. Apparently it is not correlated with abundance of mice or rainfall. The average temperature for August (table 1), the hatching period of the eggs, was about 6 degrees lower in 1940 and 1941 than in 1938 and 1939. This does not, however, necessarily explain the difference in abundance of tick larvae in these two periods.

The Nymphal Cycle

Table 13 presents typical outdoor breeding records on larval molting that help explain the fluctuations in nymphal abundance shown in figure 16. Considering first the graph for 1940, the year corresponding to the records in table 13, we find moderate nymphal

TABLE 13.—*Molting of larvae and longevity of nymphs of Dermacentor variabilis at Vineyard Haven, Mass.*

Date larvae dropped	Date first nymph molted	Last nymph died during period between—
1939	*1939*	
June 10	June 30	Oct. 14–Nov. 12, 1940.
June 20	July 10	Sept. 13–Oct. 14, 1940.
June 27	July 10	Oct. 14–Oct. 30, 1940.
July 11	July 29	Feb. 12–Mar. 13, 1941.
July 18	Aug. 1	Sept. 13–Oct. 14, 1940.
July 24	Aug. 4	Jan. 16–Feb. 12, 1941.
July 31	Aug. 10	Sept. 13–Oct. 14, 1940.
Aug. 8	Aug. 18	Jan. 16–Feb. 12, 1941.
Aug. 15	Aug. 27	Nov. 12, 1940–Jan. 16, 1941.
Aug. 29	Sept. 10	Sept. 13–Oct. 14, 1940.
Sept. 5	Sept. 30	Jan. 16–Feb. 12, 1941.
Sept. 12	Oct. 8	Sept. 13–Oct. 14, 1940.
Sept. 19	Oct. 27	Oct. 14–Nov. 12, 1940.
Sept. 25	Nov. 13	Aug. 12–Sept. 13, 1940.
Oct. 3	(1)	
	1940	
Oct. 3	Apr. 15	July 13–Aug. 12, 1940.
Oct. 10	June 13	Aug. 12–Sept. 13, 1940.
Oct. 20	June 18	Aug. 12–Sept. 13, 1940.
Oct. 28	July 1	Sept. 13–Oct. 14, 1940.
Nov. 13	(1)	
1940		
Jan. 20	(1)	
Feb. 12	June 10	July 13–Aug. 12, 1940.
Mar. 2	June 11	Jan. 16–Feb. 12, 1941.
Mar. 26	June 10	Apr. 11–May 13, 1941.
Apr. 8	June 11	Nov. 12, 1940–Jan. 16, 1941.
May 1	June 11	(2)
May 11	June 13	June 12–July 16, 1941.
June 3	June 22	Jan. 17–Feb. 17, 1942.
June 21	July 13	Sept. 12–Oct. 13, 1941.

[1] Died without molting.
[2] Engorged.

abundance in April and May. This early activity was presumably by nymphs emerging from hibernation, as the records in table 13 indicate that the only larval molting during this period would be from larvae that engorged the previous October, a month when very few larvae were feeding. Large numbers of larvae engorged in April, May, and June 1940; table 13 shows that these would be molting to nymphs in June or early in July. The abundance of nymphs rose through June and reached its peak about July 15, indicating that the majority of nymphs attach soon after molting. In 1940 the abundance of nymphs then declined steadily, probably owing to reduction in numbers through engorging and molting. In 1938 there was an increase in nymphal abundance in September, following a peak of larval engorgement in August. In 1939 and 1941 nymphal abundance increased in August, presumably as a result of the increased larval engorgement in late June and July of these years.

The Adult Cycle

Figure 17 shows the seasonal abundance of adults in the area about Gay Head during 1938, 1939, 1940, 1941, and 1942 as determined by collecting with a drag. The rise and fall for all years is fairly steady, with the greatest abundance in June, although in 1940 the numbers remained almost constant from the end of May until the end of July. There is no apparent correlation between the seasonal abundance of

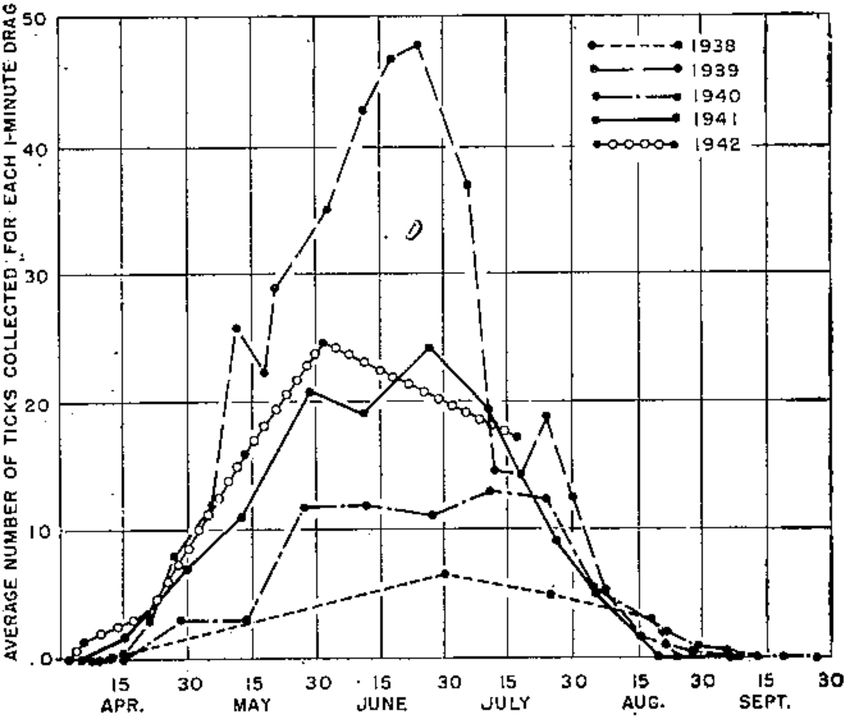

Figure 17.—Seasonal abundance of adults of *Dermacentor variabilis* at Gay Head, Mass.

nymphs and that of adults, as none of the fluctuations of the former are reflected in the latter. This seems to indicate that the adults are delayed longer in finding a host—a conclusion strengthened by their greater potential longevity, almost 3 years compared with a little over 1 year for larvae and nymphs.

From the typical breeding records on molting of nymphs listed in table 14 it will be seen that there is no molting before July from nymphs engorged the same season, and by this time the abundance of adults has already begun to decline. Nymphs that had engorged in September, however, sometimes passed the winter in the engorged condition and molted sufficiently early in the following year to assist in forming the season's peak. As only a few nymphs engorge in September it seems probable that the greatest number of nymphs molt to adults in the same summer they engorge, but that only a few of these adults become active that summer, most of them not becoming active until the next spring.

Bishopp and Smith (*1*) reported that in experimental rearing 54 percent of all nymphs molted to females. In the 1938, 1939, and 1941 collections the proportion of males to females agreed closely with this observation, 55 percent of the ticks taken in 1938, 53 per cent of those

TABLE 14.—*Molting of nymphs and longevity of adults of Dermacentor variabilis at Vineyard Haven, Mass.*

Date nymphs dropped	Date first adult molted	Last adult died during period from—
1938	*1939*	
Sept. 21	May 12–June 13	July 13–August 12, 1940.
Oct. 21	July 20	May 13–June 11, 1940.
Oct. 26	July 10	Sept. 13–Oct. 14, 1940.
Nov. 3	(1)	
Nov. 16	July 31	Nov. 12, 1940–Jan. 16, 1941.
Nov. 23	July 22	Sept. 13–Oct. 14, 1940.
Dec. 1	Aug. 14	Sept. 13–Oct. 14, 1940.
Dec. 17	(1)	
1939		
Jan. 1	Aug. 2	July 11–July 13, 1940.
Jan. 29	(1)	
Feb. 12	Aug. 7	Nov. 12, 1940–Jan. 16, 1941.
Feb. 25	(1)	
Mar. 11	July 16	Nov. 12, 1940–Jan. 16, 1941.
Mar. 25	July 15	Aug. 12–Sept. 12, 1941.
Apr. 9	July 17	Mar. 13–Apr. 11, 1941.
Apr. 24	Aug. 4	Feb. 12–Mar. 13, 1941.
May 7	July 18	Nov. 12, 1940–Jan. 16, 1941.
May 23	July 18	Sept. 12–Oct. 13, 1941.
June 4–5	July 18	Mar. 17–Apr. 15, 1942.
June 11	July 18	(2)
June 17	July 22	Oct. 13–Nov. 17, 1941.
June 24	July 27	Jan. 17–Feb. 17, 1942.
June 28	July 31	Feb. 17–Mar. 17, 1942.
July 4	Aug. 3	Nov. 17–Dec. 15, 1941.
July 14	Aug. 12	Sept. 12–Oct. 13, 1941.
July 22	Aug. 19	Feb. 17–Mar. 17, 1942.
July 29	Aug. 23	Nov. 17–Dec. 15, 1941.
Aug. 5	Aug. 30	June 12–July 16, 1941.
Aug. 12	Sept. 7	Mar. 17–Apr 15, 1942.
Aug. 24	Sept. 30	June 12–July 16, 1941.
Sept. 1	Oct. 11	Jan. 16–Feb. 12, 1941.
Sept. 24	(1)	
	1940	
Sept. 28	July 6	July 16–Aug. 12, 1941.
Oct. 1	(1)	
Oct. 11	July 28	Feb. 17–Mar. 17, 1942.
Oct. 14	(1)	
Oct. 17	July 22	Mar. 17–Apr. 17, 1942.

[1] Died without molting.
[2] Alive at close of study, May 15, 1942.

taken in 1939, and 54 per cent of those taken in 1941 being females, but it 1940 females made up only 51 percent of the total number. Males predominated early in the season, until some time in May, whereas females predominated thereafter.

Adults collected late in the season were apparently of lower vitality than those collected early in the season, as a much larger proportion died under confinement in pill boxes on moist sand than of those collected earlier. A greater proportion of the adults collected by dragging in May were still alive by the middle of August than of those collected only a few days previous to August 15, indicating that activity in the field reduced the tick's vitality much more than mere existence in close confinement, and that the longevities attained by ticks in the rearing tubes would probably not be attained by free ticks.

A Complete G neration from a Single Infestation

A third approach to the study of seasonal activity was carried out in the experimental "meadow" plot in the laboratory yard. The meadow was infested with tick eggs, and a mouse was exposed in the run once each week for 1 to 3 days, and then brought into the laboratory and held in an engorging cage so that the number of ticks that engorged and dropped could be recorded. The engorged ticks were returned to the meadow. Figure 18 shows the plan of the meadow, mouse nest and run, and sites where eggs, engorged larvae, and engorged nymphs were placed. By this method a complete and isolated tick generation was followed, and accurate information as to how soon each stage follows the next was obtained.

Two females which had completed engorgement on July 19, 1939, were released in the meadow, to provide the late hatching that would occur in nature from females engorged in late summer (table 12).

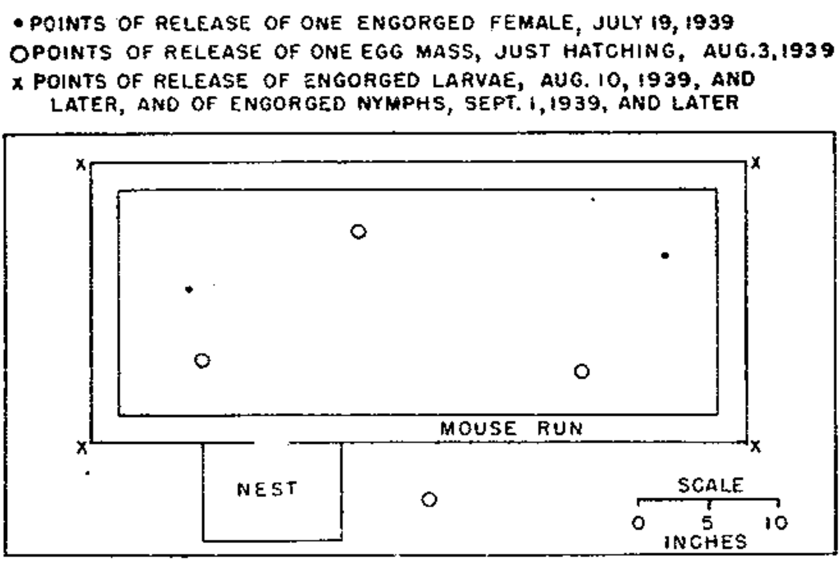

Figure 18.—Diagram of table "meadow."

To provide the hatching that would occur in nature from females engorged early in the season, four egg masses that began to hatch July 29, 5 days after the earliest record for eggs from a female fed that spring (table 12), were placed on August 3 in the meadow 3 and 4 inches from the run. Within 24 hours from that date a mouse had picked up 40 larvae, none over 5 days old. Between August 4 and 7 a mouse became infested with 556 larvae, and between August 17 and 20 a mouse picked up 1,717 larvae. The first engorged larvae were returned to the meadow August 7, and the first nymphs were picked up by a mouse between August 25 and 28, when 223 attached to 1 individual. Close inspection of the grass and mouse run did not reveal at any time any clumps of larvae, such as have been found in the case of the cattle tick or lone star tick. Few larvae or nymphs were seen waiting for hosts in the position taken by adults, but both stages were consistently observed crawling about in all parts of the meadow. These ticks readily grasped a finger when approached. They were more numerous along the mouse run than elsewhere.

The infestation of larvae and nymphs picked up by mice exposed in the "meadow" are graphically presented in figure 19. It will be noted that activity of both stages corresponded closely to that indicated for natural conditions by trapping, except that there was not the faintest suggestion of an increase of larval abundance in the fall of 1940, as no engorged females had been placed in the meadow that summer.

In the discussion in the foregoing pages, based on a comparison of rearing and collection records, it was concluded that the major fluctuations shown in the graphs of larval and nymphal abundance were

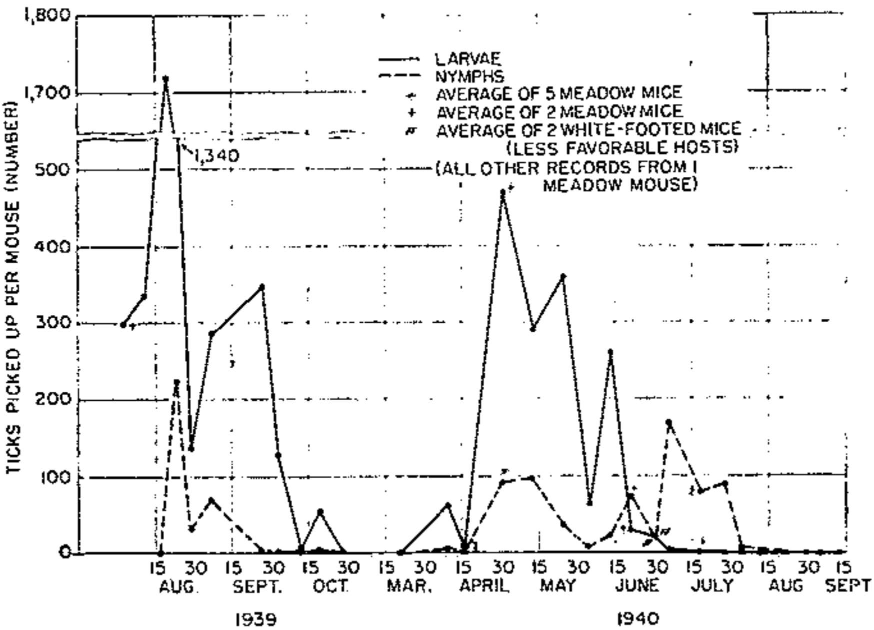

TABLE 19.—Activity of larvae and nymphs of *Dermacentor variabilis* in the table "meadow."

due to variations in the actual numbers present, and not to variations in activity caused by estivation, unfavorable weather conditions, etc. Rearing under the controlled conditions of the table meadow offers still further confirmation.

Larval activity conformed exactly to the pattern predicted. Immediately after their hatching, in August 1939, large numbers of larvae were found on mice in the meadow, corresponding to the late-summer peak in nature attributed to fresh hatching. Larvae were dormant in winter, and as soon as temperature conditions became favorable in spring they once more became active in great numbers, corresponding to the spring peak in nature attributed to hibernating larvae. With declining larval abundance in nature through June and July, attributed to exhaustion of the supply of larvae, there was a decline in

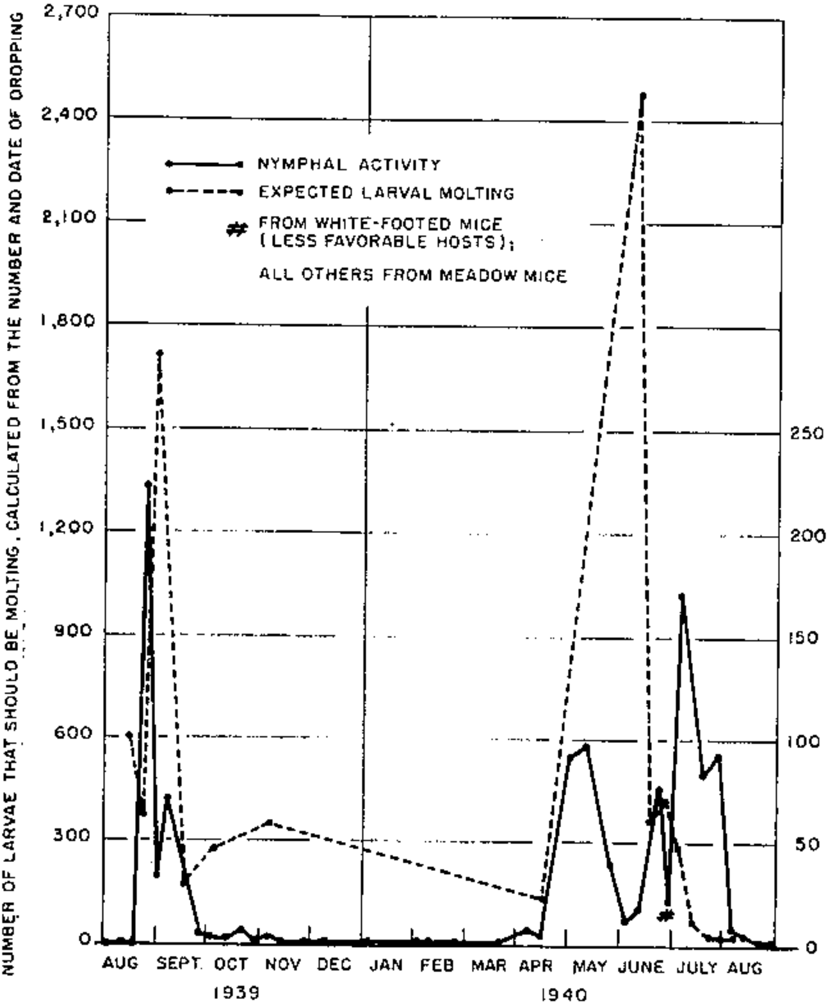

FIGURE 20.—Calculated larval molting and observed nymphal activity of *Dermacentor variabilis* in table meadow.

the table; but when abundance again increased in nature late in the summer it did not increase in the table meadow, as no new engorged females had been added.

Nymphal activity also conformed to the pattern predicted, as shown in figure 20: In this figure the broken line represents the expected larval molting, as calculated from the date on which the engorged larvae were returned to the meadow, the molting period for each lot being determined from out-door rearing records of engorged larvae dropped at the same time. The solid line represents the number of nymphs that attached to mice. It will be noted that fluctuations in nymphal attachments followed closely fluctuations in larval molting, confirming the assumption that the holdover of unfed nymphs was short, and low points in the graph are due to absence of nymphs rather than to inactivity.

A study of the average daily temperature and humidity during the 1940 season of activity indicated that the fluctuations of larval and nymphal activity do not correspond to variations in weather conditions.

Meadow mice were exposed in the "meadow," approximately at weekly intervals, from March 29 to August 25, 1941. One nymph attached to the mouse exposed April 21. There was no other nymphal activity.

The relationship between nymphal molting and adult activity is brought out in table 15.

TABLE 15.—*Calculated molting of nymphs and collections of unmarked adults of Dermacentor variabilis in the table meadow, Vineyard Haven, Mass.*

Date of observation	Nymphs molting	Unmarked adults collected	Date of observation	Nymphs molting	Unmarked adults collected
	Number	*Number*		*Number*	*Number*
1939			*1940*		
Oct. 9	32	...	Aug. 28	401	0
Oct. 31	71	...	Sept. 6	90	14
1940			Sept. 13	8	0
May 1	0	2	Sept. 20	59	2
May 13	0	0	Sept. 23	2	...
July 6	5	0	*1941*		
July 12	475		Apr. 14	0	49
July 17	100	13	Apr. 15	0	307
July 19	38	31	Apr. 29	0	59
July 23	31		May 19	0	15
July 28	11	95	June 13	0	0
Aug. 1	56		June 30	0	0
Aug. 12	30	29	July 12	1	0
Aug. 19	169	12			

The dates on which the various lots of nymphs would begin to molt were calculated from the dates on which they were returned to the meadow, the molting period for each lot being determined from outdoor rearing records of engorged nymphs dropped at the same time. The active adults were collected from the grass, marked with enamel, and returned to the meadow. In table 15 collections of marked adults, representing repeat collections of the same individuals, are not included. It will be seen that two adults were taken in May 1940, presumably from the nymphs dropped the previous fall and due to molt in October 1939. There should have been a peak of nymphal molting about July 12, 1940, and 201 adults were taken between July 17 and August 12. The next peak of nymphal molting should have been August 20 to 28, but only 28 adults were taken between August 19 and September 20, indicating that these adults would not become active until 1941. All but one nymph should have molted by September 23, 1940. Between April 14 and May 19, 1941, 430 adults were taken, all evidently having been hibernating in that stage. Also, 36 adults that had been marked in July and August 1940 were taken again in April and May 1941. No unmarked adults were found after May 1941, and no marked adults after June 1941.

Because the table was heavily scented by meadow mice, and larvae and nymphs were observed to congregate on the wire mouse run and nest, and because hosts for larvae and nymphs were present at frequent intervals, ticks in these stages should have had little incentive to attempt to escape from the table, and few were found in the surrounding moat. Therefore, their persistence in the table should represent conditions in nature in the presence of abundant hosts. On the contrary, no hosts for adults were present, and the table was very lightly scented by hosts for adults, whereas in the surrounding territory dogs had free run so that the adults had a strong incentive to attempt to escape from the table, and over 400 were found in the surrounding moat. Therefore, while the finding of unmarked (newly active) adults in the table should represent conditions in nature, marked adults would probably have persisted in numbers throughout the 1941 season under natural conditions, as was the case with ticks marked in April and May at Gay Head, to be discussed in the next section, instead of being trapped in the moat while trying to escape.

To summarize, it may be stated that females dropping near the beginning and close of the season of 1939 produced an infestation of active larvae from August 3, 1939, to July 28, 1940, an infestation of active nymphs from August 25, 1939, to April 21, 1941, and an infestation of active adults from May 1, 1940, to September 1941.

MOVEMENTS OF TICKS

Persistence of Unfed, Marked Adults under Natural Conditions

Although it was known that unfed adult ticks could live for almost 3 years under experimental conditions, it was not certain how long they would remain active in nature. An investigation of this question was begun in 1939, utilizing the weekly dragging collections at Gay Head. Dragging was carried out along 42 definite 1-minute courses, laid out along a highway and across adjacent fields. A map of these courses, or blocks, is shown in figure 21. The collection from each block was kept separate, and all ticks were taken to the laboratory, marked with enamel, and left in individual pill boxes for the enamel to dry. The following day they were released in the center of the same block in which they had been captured. Each tick was marked with a spot of colored enamel on the back the first time it was captured in each month, using a different color for each month. Thus a tick captured the first week in May would get a spot of blue, but would not get another spot until June, when orange would be used, even though it might be taken each intervening week. In this manner it was possible to tell how many ticks were captured month after month, and what proportion disappeared. This method of marking was suggested by the work of Philip (*12*) on the Rocky Mountain spotted fever tick (*Dermacentor andersoni* Stiles).

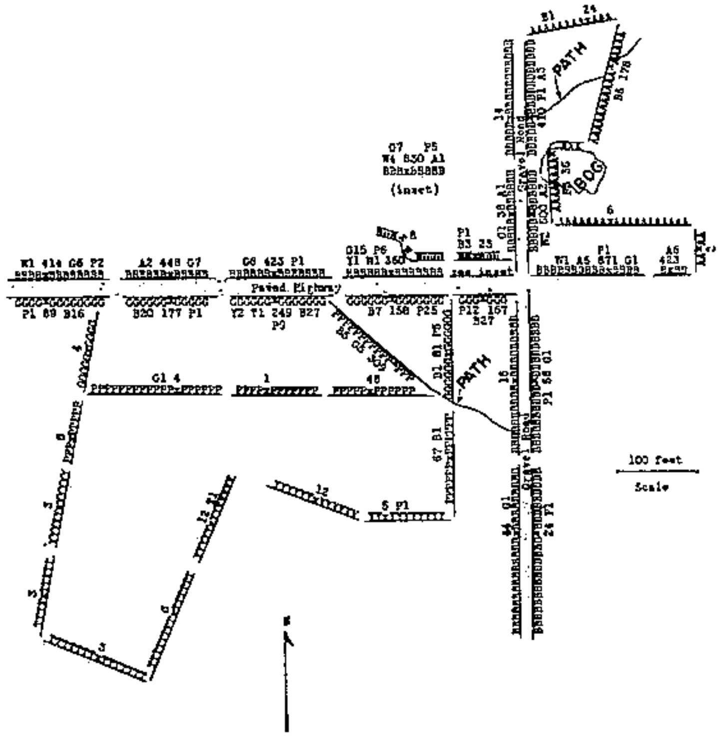

FIGURE 21.—Migration of adults of *Dermacentor variabilis* as determined by capture, marking, release, and recapture at Gay Head, Mass. Each black line indicates the exact course of one drag. Rows of letters indicate marking given to ticks collected in the respective drag courses. X indicates point of release of all ticks captured and marked in the drag course. Figures preceded by letters indicate the number of marked ticks recaptured in the respective drag courses originating in the drag course marked by those letters. Figures not preceded by letters indicate the number of unmarked ticks originally captured, marked, and released in the respective drag courses.

That the marking did not injure the ticks is shown by the fact that, of 2 lots of 20 ticks each, collected at the same time and kept together in the outdoor breeding cage, the lot that had been marked outlived the unmarked lot, living from June 1940 to August 1941.

The total number of individual ticks marked in 1939 was 6,348, but, as many of these were captured again and again, the total number collected rose to 14,049.

The weekly collections made in the area are summarized in table 16. The numbers of males and females bearing the different color combinations indicating the month of first capture are shown. Of the 400 ticks marked in April, 333 were recaptured at least once, 292 were

Table 16.—*Persistence of marked adults of Dermacentor variabilis as indicated by dragging collections at Gay Head, Mass., 1939*

Number of ticks collected bearing markings showing they had been previously captured in the months specified

Date	Unmarked ticks captured		April		April May		April June		April July		April May June		April May July	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Apr. 15	14	5												
Apr. 20	65	37	5	2										
Apr. 27	166	113	12	3										
May 5	188	156	61	37										
May 11	338	392	39	31	27	16								
May 18	214	218	21	6	29	17								
May 25	280	308	15	6	30	20								
June 2	275	353	28	30	42	21								
June 12	299	387	3	3	12	8	5	2			16	11		
June 19	291	338	6	6	9	6	3	2			23	11		
June 26	254	315	6	4	8	1	7	3			20	7		
July 5	169	177	2	2	1	2	3	2			17	8		
July 11	74	80	1	0	1	2	3	2	0	0	3	1	0	0
July 17	112	141	2	0	0	0	6	0	0	1	1	0	0	1
July 24	147	188	1	0	0	1	3	1	0	0			1	0
July 31	79	82	0	1			0	1	0	0			0	2
Aug. 7	23	29							1	0				
Aug. 16	11	8												
Aug. 21	2	11												
Aug. 28	2	4												
Sept. 6	0	0												
Sept. 11	2	1												
Sept. 18	0	0												
Total	3,005	3,343	202	131	159	94	24	13	1	1	80	38	1	3

Date	April June July		April May June July		May		May June		May July		May June July		May June July August	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Apr. 15														
Apr. 20														
Apr. 27														
May 5														
May 11					55	48								
May 18					161	148								
May 25					194	186								
June 2					263	246								
June 12					161	133	158	116						
June 19					75	72	200	172						
June 26					43	58	196	147						
July 5					23	29	149	123						
July 11	1	0	1	0	15	13	19	11	3	4	14	13		
July 17	0	1	1	1	11	6	14	13	7	7	15	14		
July 24	1	0	2	1	11	16	10	16	6	7	14	11		
July 31	0	1	1	0	3	7	6	8	5	5	6	11		
Aug. 7			1	0	1	1	1	1	1	5	5	7		
Aug. 16									1	1	1	1	0	1
Aug. 21									0	1	1	1	0	1
Aug. 28														
Sept. 6														
Sept. 11														
Sept. 18														
Total	2	2	6	2	1,016	963	753	607	23	30	56	58	0	2

Date	June		June July		June August		June July August		July		July August		August		Total	
	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females	Males	Females
Apr. 15															14	5
Apr. 20															70	39
Apr. 27															178	116
May 5															249	193
May 11															459	487
May 18															425	389
May 25															519	520
June 2															608	650
June 12	114	124													768	784
June 19	218	268													825	875
June 26	318	337													852	872
July 5	305	317													669	660
July 11	56	66	37	33					22	32					250	257
July 17	36	68	37	44					30	45					267	342
July 24	31	68	48	58					72	90					346	457
July 31	11	24	39	48					92	93					242	283
Aug. 7	5	5	8	27					48	58					94	133
Aug. 16	0	2	1	6	1	1	0	1	8	15	3	10	3	2	29	48
Aug. 21	0	1	0	1			0	4	1	6	1	10	3	5	8	41
Aug. 28							0	1	1	0	4	5	1	4	8	14
Sept. 6											1	0			1	0
Sept. 11															2	1
Sept. 18															0	0
Total	1,094	1,280	170	217	1	1	0	6	274	339	9	25	7	11	6,883	7,166

recaptured at least twice, 126 were recaptured at least three times, and 8 were recaptured at least 4 times; 67 were taken again as late as July and 2 in August. One individual, a male, was recaptured at least once each month from April to August. Ticks marked for the first time in April persisted until August 7; ticks marked for the first time in May persisted until August 21. Ticks marked for the first time in June persisted until August 28, and ticks marked for the first time in July persisted until September 6.

In 1940 the work was repeated following the same methods, except that collections were made biweekly and that only one spot of color was placed on any one tick, representing the first month in which it was taken. Although 2,461 individual ticks were collected, marked, and released, only 934 captures of marked ticks were made, whereas in the previous year 6,348 individual ticks were marked and 7,701 recaptures were made. Part of the difference in the proportion of recapture may be due to the fact that collections were made each week in 1939 and every other week in 1940, in consequence of which a tick remaining in one area would have been counted twice as often in 1939. Even if the number of recaptures in 1940 were doubled they would still represent a smaller part of the original number than in 1939. On the other hand, in 1940, ticks marked in April, May, and June persisted in the area until September, whereas the previous year they had disappeared in August. In other respects, persistence was similar to that in 1939.

Only 15 of the 6,348 ticks marked in 1939, or 0.24 percent, were recovered in 1940. None of the 5,006 ticks marked first in April, May, or June were recovered; 14 of the 1,249 ticks marked first in July, or 1.12 percent, were recoverd; and 1 of the 93 marked first in August and September, or 1.08 percent, was recovered. None of these 15 ticks from 1939 were collected more than once in 1940. Apparently, notwithstanding their great potential longevity, very few adults are active for more than 1 season under normal conditions.

In 1941 the study was repeated for the third year with collections made biweekly as in 1940. The proportion of marked ticks recaptured (47.0 percent) was greater than in 1940 (37.9 percent) but less than in 1939 (121.3 percent), when collections were made every week. In 1941 no marked ticks were found in the area after August 25, whereas in 1940 marked ticks were taken as late as September 17, and in 1939 as late as September 6. In other respects presistence was much the same as in previous years.

The proportion of marked ticks that survived the winter of 1940-41 was noticeably greater than in the previous year. Fourteen of the 2,461 ticks marked in 1940, or 0.57 percent, were recovered in 1941, whereas only 0.24 percent of those of 1939 were recovered in 1940. When this is considered in connection with the fact that persistence of marked ticks in the area was 3 times as great during the active season of 1939 as in the active season of 1940, the difference in overwinter survival appears even more significant. Also, no ticks marked before July 1939 survived the winter, whereas 1 tick marked in June 1940 and one marked in April or May 1940 were recovered the following year. However, the survival of ticks marked in July was practically the same for both years, 14 of 1,249 (1.12 percent) surviving from

1939 to 1940 and 8 of 728 (1.10 percent) surviving from 1940 to 1941. Some of the difference was caused by slightly greater survival of ticks marked first in August or September, 1 of 93 (1.08 percent) surviving from 1939 to 1940 and 4 of 276 (1.45 percent) surviving from 1940 to 1941.

The real explanation for the greater part of the difference, however, is to be found in the fact that the adult population during a season actually consists of two distinct groups, viz, adults that molted the previous fall but did not then become active, and adults that molted during the current season and immediately became active. The former group will include all ticks first encountered and marked in April, May, and June, and some of those marked later; the latter group will make up part of the ticks first marked in July, August, and September. There is extremely little winter survival of the former group, as shown by the fact that none of 5,006 ticks survived from 1939 to 1940 and only 2 of 1,457 survived from 1940 to 1941. Since practically all winter survival occurs in the group molting and becoming active the same season, and since all ticks of this group are first marked in July, August, and September, the ratio of ticks marked during this period to those marked earlier will be in direct correlation with the proportion of the total ticks active in one season which survive to the next. In 1939 this ratio was 1 to 4 and survival was 0.24 percent; in 1940 the ratio was 1 to 1.4 and survival was 0.57 percent.

Migration and Roadside Concentration of Adults

It has often been observed that ticks are most numerous along the sides of roads and paths, and in most localities on Martha's Vineyard this is the case. Why such a concentration along roads and paths should occur has never been determined, but two explanations suggest themselves. The simplest explanation would be that adult ticks from the adjacent fields had moved up to the points of concentration and remained there, either because the scent of dogs and persons was more concentrated or because the bare ground formed a barrier.

Another explanation would be that dogs, the principal hosts of adult females, spend more time at roadsides than along any single comparable line in the fields, and consequently drop more engorged females there. There would be more eggs and more larvae along roadsides, producing more nymphs and more adults in that location. This would work out only if neither the ticks nor the mice serving as their hosts moved very far, in which case mice near the road should be most heavily infested.

This theory was tested in two areas where adults were concentrated along roadsides. In one area it was found that mice captured at the very edge of the road were three times as heavily infested as those captured 100 feet back, and eight times as heavily infested as those 200 feet back, the numbers of mice being the same along all three lines. This, of course, supports the second theory. In another area there were far fewer mice at the edge of the road, and these few were less heavily infested than those in the center of the fields. One or two oxen had been pastured in these fields, which might account for this difference in distribution of immature ticks, as only dogs were adult hosts in the first area. As adults were concentrated on the roadsides in both areas, the ticks in the fields were marked, to determine whether they migrated to the road. This was done in connection with the marking plan described in the preceding section.

In addition to the dorsal mark representing the month, each tick was marked on a certain leg with the appropriate monthly color the first time it was captured, to indicate the group of blocks in which it was taken. The different letters on the map in figure 21 indicate the different leg markings. Most roadside blocks were given the same mark, one set being different, however, so that it could be determined whether a paved highway would constitute a barrier to tick movement. Blocks back in the fields were given different marks so that the direction and extent of tick migration from them could be determined. No new leg mark was given unless a tick was captured in a new block, when the mark of that block was added to the first. As leg marks corresponded to month marks in color, when a tick appeared in a third block its original source could be determined. Thus some ticks were first taken and marked in the blocks indicated by P, later in those indicated by G, and finally in those indicated by B. In both G and B blocks they would be recorded as originating in P, these repeat collections being indicated on the map by figures preceded by the letter corresponding to the point of origin.

It will be noted in figure 21 that there was some movement in all directions, but that the tendency was to move up to the roads. Particularly was it so in the case of ticks released back from the roads. A fair percentage of these moved up to the road 400 feet distant, but none from the road moved back that far into the field. The road was not a barrier, as ticks crossed it readily, but after crossing they remained near the roadside instead of continuing on into the field. Movement had no relation to the points of the compass, and the majority of the ticks stayed near the point of original capture.

Tarsal marking for migration studies was repeated in 1940 and 1941. In 1940 55 ticks were found at drag sites where they had not been released, representing 5.9 percent of the total number of recaptures and 2.2 precent of the number of ticks originally marked. In 1941, 120 migrants were collected, representing 7.4 percent of the number of recaptures and 3.5 percent of the number originally marked. In 1939, 274 migrants were collected, representing only 3.6 percent of the number of recaptures, but 4.3 percent of the number originally marked. In other respects migration agreed with that observed in 1939, with some movement in all directions, a marked tendency to move up to the roadside and remain there, and considerable movement from one side of the road to the other.

From these observations it is evident that, in this area at least, roadside concentrations of ticks are due to movements of ticks from the adjacent fields to the roads, where they remain. That the roads do not constitute an important barrier is evidenced by the fact that a greater proportion were recovered across the road than back from the road. Therefore it seems apparent that the ticks find the roadsides attractive, probably from the concentrated scent of their hosts, possibly from the greater reflected heat of the bare surface.

A few tests conducted in an area lightly infested with ticks indicated that adults were attracted by the scent of man and dogs rather than by warmth. Thirty-seven ticks were taken from stakes and towels handled by persons, rubbed against dogs, or sprayed with dog urine, while none were found on unscented stakes or towels. On the other hand, unheated cans exposed in the table meadow attracted as many ticks as cans heated by light bulbs.

Tarsal markings were employed in studying the migration of ticks in an area beside a pond to determine whether there was a tendency to move toward wet places during the hot, dry weather of midsummer. To supplement the ticks collected in the area, 298 laboratory-reared ticks were distinctively marked and released. During the season, 810 ticks were collected in this area, marked and released, and 96 recaptures of marked ticks were made, of which 25 were migrants. There was no tendency to move toward the pond.

HOSTS

The dog is the preferred host of the adult ticks, although they engorge readily on many other large mammals. The larvae and nymphs, on the contrary, engorge on meadow mice and other small mammals, principally rodents.

The records in the accession catalog of the Division of Insects Affecting Man and Animals, Bureau of Entomology and Plant Quarantine, include collections of adults from the following hosts: Dog, man, cattle, coyote, opossum, hog, horse, raccoon, wildcat, squirrel, sheep, badger, wolf, skunk, deer, fox, cat, peccary, weasel, ass, leopard cat, mountain lion, Mexican lion, mule, rabbit, and Norway rat. Cooley (*3*) lists the following additional hosts: "Eland," ground squirrel, woodchuck, and civet cat.

The Bureau's accession catalog lists collections of the immature stages from the following hosts: Larvae and nymphs from white-footed mouse, meadow mouse, pine mouse, jumping mouse (*Zapus* sp.), cottontail rabbit, swamp rabbit, muskrat, cotton rat, Norway rat, squirrel, cat, and short-tailed shrew; larvae alone from jack rabbit, house mouse, and mole; nymphs alone from wood rat, sheep, cattle, and dog.

Host Relationships of Larvae and Nymphs

In the region where this study was conducted, Martha's Vineyard, Nantucket, and the Elizabeth Islands, Mass., most of the hosts reported for larvae and nymphs are abundant, affording an opportunity for a comparison of their relative importance. As far as possible, all hosts were captured alive, and the ticks on them were permitted to complete engorgement and drop. In every case the ticks, after attachment, satisfactorily completed engorgement, even on relatively unfavorable hosts.

Meadow mice (*Microtus pennsylvanicus pennsylvanicus* (Ord.)) were by far the most important hosts for both larvae and nymphs. Mice were captured alive in box-type traps baited with a mixture of apple, oatmeal, and peanut butter. This bait was attractive to all species of mice, wild and domestic, and young rats and shrews were also taken occasionally.

From July 1937 to January 1942 a total of 3,077 meadow mice and 842 white-footed mice (*Peromyscus leucopus* ssp.) were captured and examined. In the following discussion only the live mice and the infestations on them will be considered. The 2,763 live meadow mice were infested with 8,600 larvae and 5,015 nymphs, while the 835 live white-footed mice were infested with 1,543 larvae and 258 nymphs.

The relative importance of the two species of mice in each of the five most heavily infested areas is indicated in table 17.

TABLE 17.—*Collections of Dermacentor variabilis on mice in 4 heavily infested areas on Martha's Vineyard Island and 1 on the Elizabeth Islands, Mass.*

Locality and years of collections	Meadow mouse collections					White-footed mouse collections				
	Mice	Larvae		Nymphs		Mice	Larvae		Nymphs	
		Total	Average	Total	Average		Total	Average	Total	Average
	Number	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*	*Number*
West Chop, 1937, 1938, 1940, 1941	253	490	1.9	499	2.0	157	153	1.0	10	0.1
Edgartown, 1937, 1938, 1940, 1941	366	187	.5	123	.3	116	61	.5	13	.1
Squibnocket, 1937, 1938, 1940, 1941	515	773	1.5	414	.8	141	43	.3	4	.03
Gay Head, 1937, 1938, 1940, 1941	446	1,384	3.1	492	1.1	213	650	3.0	85	.4
The Elizabeth Islands, 1941	367	3,978	10.8	1,999	5.4	64	529	8.3	144	2.3
Total or average	1,947	6,812	3.5	3,527	1.8	691	1,436	2.1	256	.4

The collections for 1939 are not included because during that season peanut butter was omitted from the bait, which was consequently much less attractive to white-footed mice than to meadow mice. The number of meadow mice exceeded the number of white-footed mice in every area, and consequently the number of larvae and nymphs collected from them exceeded the number collected from white-footed mice in each locality, but the difference between the two species in the average number of ticks for each mouse was not pronounced, particularly in the case of the larvae. Meadow mice were five times as heavily infested as white-footed mice at Squibnocket, but at Edgartown the two species showed identical average infestations. In the case of nymphs the average infestation of meadow mice was always greater, ranging from about twice as great on the Elizabeth Islands to 26 times as great at Squibnocket. The greater abundance of meadow mice and their heavier average infestation combine to make them the most important hosts for larvae and nymphs.

The heaviest natural infestations of single mice of both species with each stage were observed in the collections from the Elizabeth Islands. One meadow mouse was infested with 303 larvae and 30 nymphs, another with 48 larvae and 61 nymphs. One white-footed mouse was infested with 63 larvae and 1 nymph, another with 37 larvae and 12 nymphs.

Pine mice (*Pitymys* sp.), known to be good hosts for the immature stages, do not occur in this region. Jumping mice (*Zapus hudsonius* ssp.) are rare, only three having been captured, and these uninfested. House mice (*Mus musculus musculus* L.) are seldom found in tick habitats, and these are very lightly infested or uninfested.

Cottontail rabbits (*Sylvilagus floridanus* sspp.) are of some importance in these localities as hosts for larvae and nymphs, although apparently less so than in some other regions. Rabbits were captured in the same area as the mice, 77 being taken during the season of tick activity, of which 55 were uninfested and 22 infested with 101 larvae, 19 nymphs, and 1 male. This gives an average infestation of 1.3 larvae and 0.2 nymph per rabbit, making the rabbits slightly inferior to white-footed mice as hosts. As many as 26 larvae were found on a single rabbit, and as many as 6 nymphs on another.

Of three black-tailed jack rabbits (*Lepus californicus* ssp.) collected on Nantucket, 2 were uninfested and 1 was infested with 3 larvae. Of 37 Norway rats (*Rattus norvegicus* (Erx.)) captured in infested areas during the season of tick activity, 27 were uninfested, and 10 were infested with 24 larvae, 22 nymphs, and 2 males.

Occasionally muskrats (*Ondatra zibethica zibethica* (L.)) occur in tick habitats. In one such locality 5 muskrats were captured during the season of tick activity. Two were infested with 38 larvae and 2 nymphs.

Squirrels (*Sciurus carolinensis* ssp.) were rarely encountered in tick habitats, and of the five that were captured only one was infested, carrying a single larva.

Short-tailed shrews (*Blarina brevicauda aloga* Bangs) were frequently captured, one being infested with two larvae. Long-tailed shrews (*Sorex cinereus* ssp.) were encountered less often, and were not infested. On six occasions a single nymph, fully engorged, was taken from a dog, and a single nymph was found on a cat on two occasions, and a third cat repeatedly became infested with larvae.

Host Relationships of Adults

In the regions of these studies almost the sole host of adults is the dog. The wild animals which would be satisfactory hosts are not present. Domestic animals such as horses and cattle are occasionally infested if they are allowed to graze in brushy pastures where mice can exist. Sheep are also attacked under such conditions, but most of the ticks which attach to sheep are killed by the wool grease, although occasionally females attached in the short hair of the face became engorged. Three deer shot in a locality where ticks were active were uninfested, and circumstantial evidence indicates that they are not important hosts. Very infrequently adults are found on rabbits and rats, and squirrels may sometimes serve as hosts. Cats in good health are rarely satisfactory hosts, but ticks occasionally engorge in numbers on sick or crippled cats.

PHENOLOGY

The climatic factors known to affect the development of the American dog tick are the temperature, the relative humidity and precipitation, and the photoperiod. The temperature dominates the entire life cycle, affecting activity, the length of the developmental periods, and survival. The relative humidity and precipitation affect survival, but have little or no influence on the activity or duration of developmental periods. The photoperiod influences the activity of the immature stages.

Temperature

INFLUENCE OF TEMPERATURE ON RATE OF DEVELOPMENT

The influence of temperature on the molting of larvae is illustrated in figure 22. The individual records fit closely to the curve, which was plotted as follows: Using the average daily mean temperature as one variable (x) and the rate of development (1,000/number of days) as the second variable (y) the method of least squares was used to plot the position of a straight line. The values of y at various temperatures on this straight line were then used to determine the position of points at the same temperatures on the curve in figure 22 by the formula $1{,}000/y =$ number of days. The curve was passed through the points so determined. The correlation coefficient (determined by using x and y as above in the formula $r = Sxy/\sqrt{(Sx^2)\ (Sy^2)})$ was highly significant, 0.92, confirming the observations of Bishopp and Smith at Washington. In the case of lots kept outdoors, the temperature given is that recorded in the weather shelter, which undoubtedly varied from that to which the ticks in the outdoor breeding cage and uncovered vials outdoors were exposed. Keeping the tubes sheltered or exposed had little effect on the period from dropping to molting, as shown by the fact that many of the lots placed under the two conditions on the same day molted after the same period, while among others those uncovered sometimes molted earlier and sometimes later.

Figure 23 illustrates the effect of the temperature on the molting of nymphs. Here again the correlation is close, the correlation coefficient being also 0.92, with high temperature reducing the time required for molting.

The influence of temperature on the duration of the preoviposition period is illustrated in figure 24. The correlation is not so close as in the case of molting, but is still highly significant, the correlation coefficient being 0.77. Among the females kept outdoors uncovered, one that dropped September 20, 1939, oviposited after 10 days at an average temperature of 61.1° F. and an average relative humidity of 81.7 percent, whereas another female dropped July 22, 1940, also oviposited after 10 days although the average temperature was 12 degrees higher and the average relative humidity was 6 percent higher. Among the females kept in the tick room, one that dropped April 15, 1938, oviposited after 27 days at an average temperature of 72.1° F. and an average relative humidity of 47.3 percent, whereas another that dropped April 2, 1940, oviposited after only 11 days although the average temperature was 7 degrees lower, and the average relative humidity was 7 percent lower.

The influence of temperature on incubation is illustrated in figure 25. The correlation, again, is not so close as in the case of molting, but is highly significant, the correlation coefficient being 0.89. An example of the variation encountered is seen in the case of two lots of eggs kept outdoors uncovered. A female that dropped August 2,

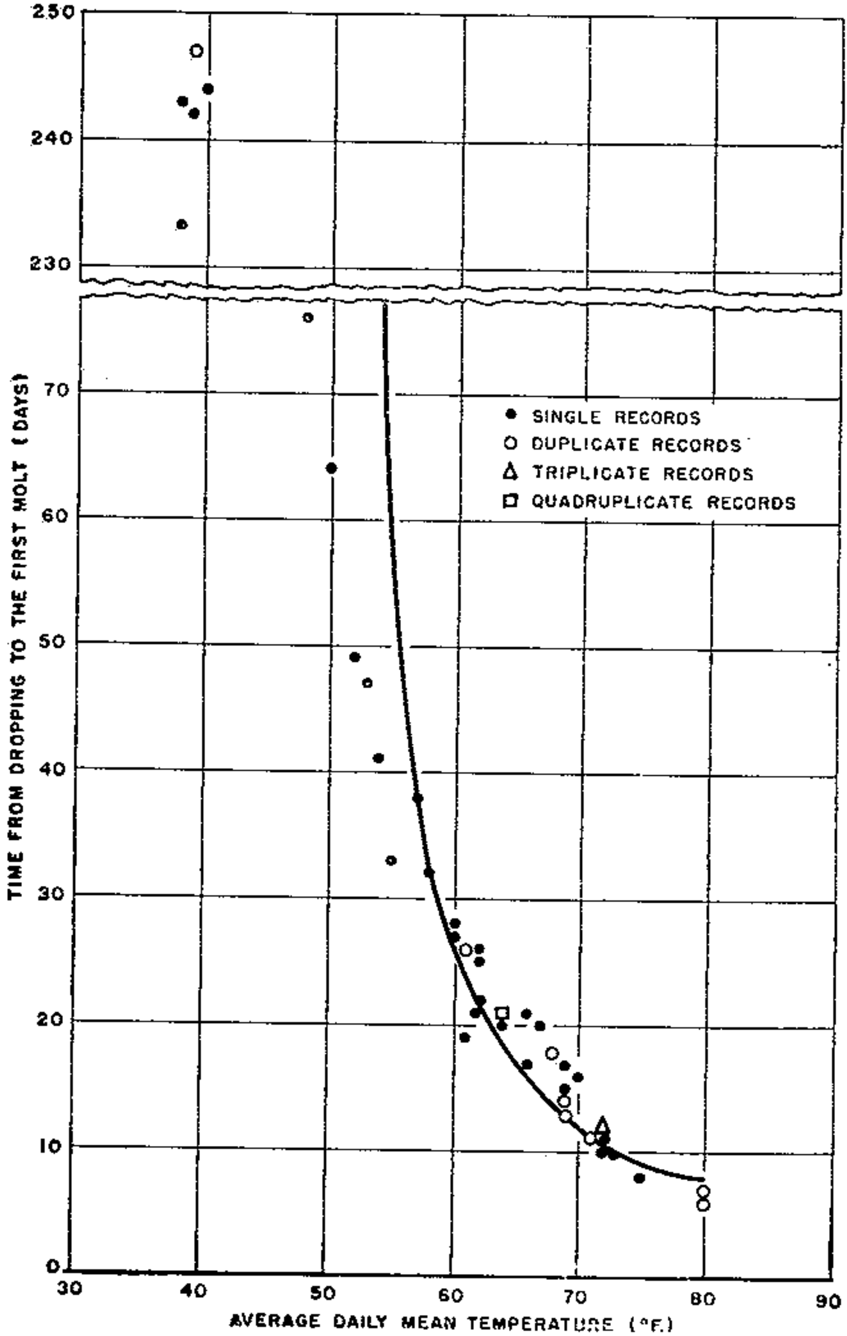

FIGURE 22.—Effect of temperature on larval molting of *Dermacentor variabilis*.

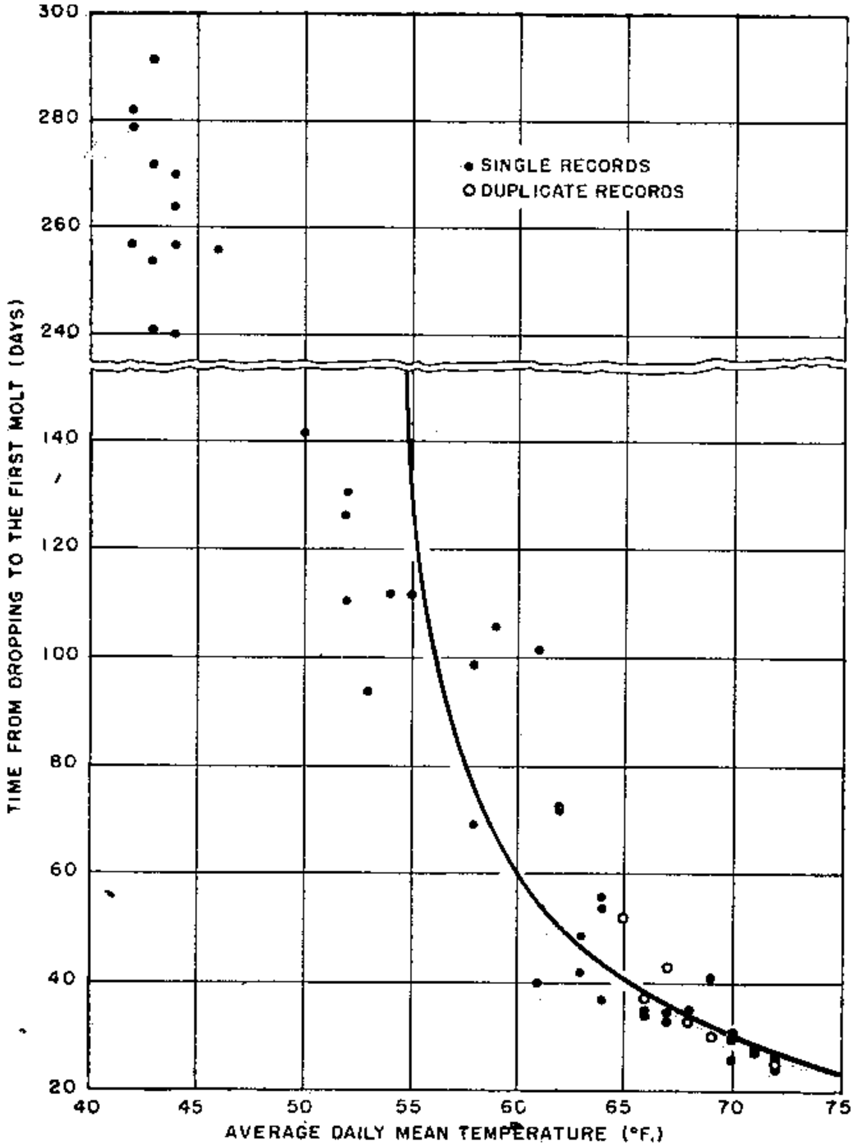

FIGURE 23.—Effect of the temperature on nymphal molting of *Dermacentor variabilis*.

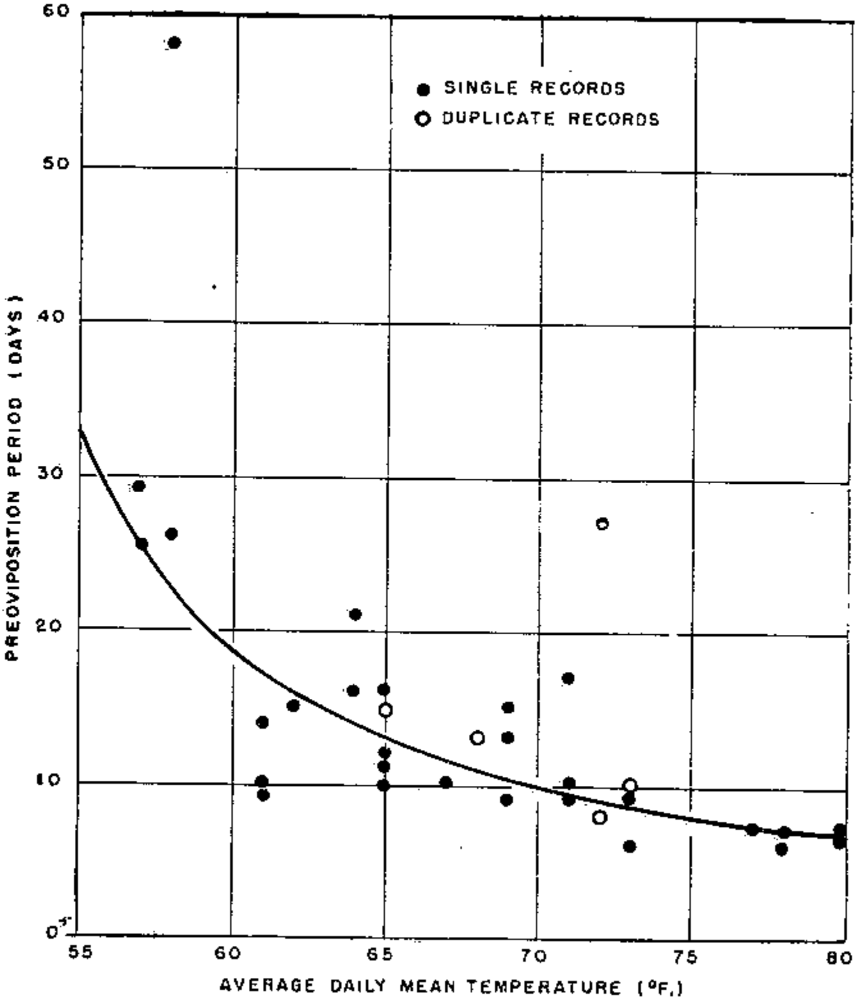

FIGURE 24.—Effect of temperature on preoviposition period of *Dermacentor variabilis*.

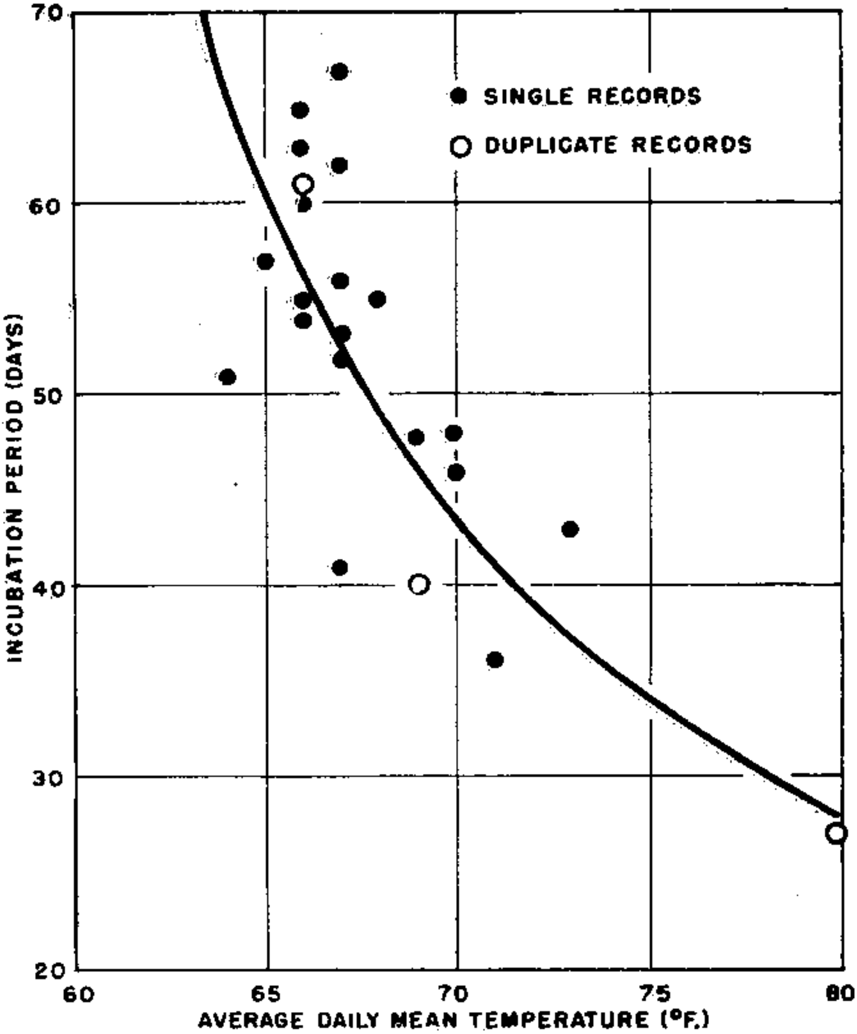

FIGURE 25.—Effect of temperature on incubation of eggs of *Dermacentor variabilis.*

1939, began oviposition August 10, and the eggs began hatching after 41 days, the average temperature for the period being 67.4° F. and the relative humidity 82.8 percent. A female that dropped May 24, 1940, began ovipositing June 19, and the eggs began hatching after 55 days, the average temperature being 68.2° and the relative humidity 82.7 percent.

INFLUENCE OF TEMPERATURE ON SURVIVAL

Under natural conditions temperatures in this region never become high enough to affect the survival adversely in any stage of development. Low temperatures, on the other hand, are of considerable importance in this respect. Unfed ticks in the early part of all stages are resistant to low temperatures and are able to survive the winter readily, and engorged larvae and nymphs are resistant under some conditions, but eggs and engorged females are very susceptible.

The effect of exposure to winter temperatures on the survival of engorged females and eggs has been indicated in table 12. From these and additional records taken over several years, it can be stated that the great majority of females exposed to winter died without ovipositing, and eggs exposed did not hatch. Only one female survived the winter and oviposited the following spring. It dropped November 4, 1938, was kept outdoors uncovered, and laid eggs, but these did not hatch. Only four lots of eggs survived the winter and hatched

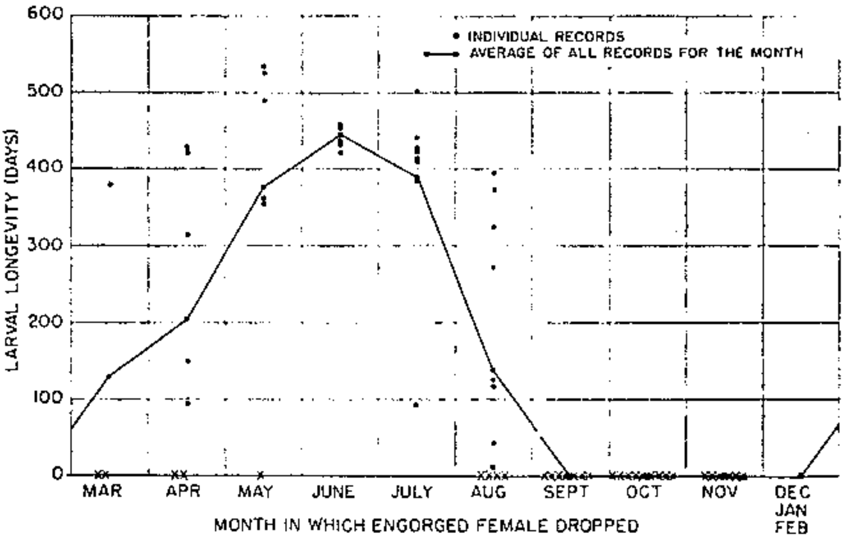

FIGURE 26.—Correlation between the month of female engorgement and longevity of larvae of *Dermacentor variabilis*. Crosses on base line indicate cases in which females failed to oviposit or eggs failed to hatch.

the following year, and the larvae from these were abnormally short-lived, living approximately 139, 119, 46, and 14 days, respectively.

Low temperatures during the period of preoviposition and incubation also occasionally affected the longevity of the resulting larvae in the case of females that dropped early in the spring, as shown by the females dropped in April (fig. 26). This figure illustrates the correlation between the month during which the female dropped, and hence the temperature, and the longevity of her larvae. The greatest individual and average longevities were attained by larvae from females that dropped during May, June, and July, and consequently were subjected to the highest average temperature during oviposition and incubation. The females dropped in August were subjected to high temperatures during oviposition, but incubation either extended into September and October, when the temperature was unfavorably low, or was delayed until the following year.

The influence of winter temperatures on the survival of engorged larvae and the longevity of the ensuing nymphs is shown by the data in table 13 which are supported by the trend of additional records taken over several years. In most cases engorged larvae survived the winter and molted the following year, although in a few instances they were killed. Four lots of larvae that dropped September 19 and 25, 1939, began to molt the same fall, producing nymphs of the fairly high longevity shown in the table. The unmolted larvae were separated from the nymphs during the winter and began to molt the following April, but the nymphs produced had extremely short lives, all less than 108 days. All the lots which dropped in October and molted the following year produced nymphs having very short lives,

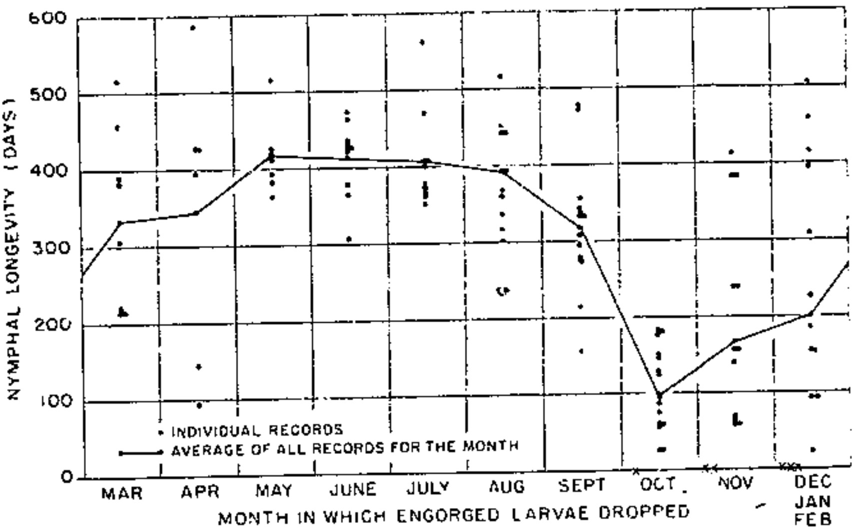

FIGURE 27.—Correlation between month of larval engorgement and longevity of nymphs of *Dermacentor variabilis*. Crosses on base line represent larvae which failed to molt.

whereas some of the lots that dropped in November and later and passed the winter before molting produced nymphs with normal life spans. In general, it appears that if engorged larvae hibernate before any progress toward molting has taken place, the resulting nymphs will be normal, but if engorged larvae which have partially completed development hibernate, the resulting nymphs will be abnormally short-lived. This is well illustrated in figure 27, which shows the correlation between the month in which engorged larvae dropped, and consequently the temperature during the molting period, and the longevity of the ensuing nymphs. Larvae dropped in May, June, July, and August produced the most uniformly long-lived nymphs, all living over 300 days.

The influence of the low temperatures of winter on the survival of engorged nymphs and on the adults they produce is shown by the data in table 14 and by additional records acquired over several years. In about one-third of the lots all nymphs were killed by winter, and in many of the others they developed to adults which were relatively short-lived. Figure 28 shows the correlation between the month of dropping, and hence the temperature during nymphal molting, and the longevity of the adults produced. Nymphs that dropped from April through August produced adults with significantly greater longevities than those dropped during the other months.

As previously mentioned, recently hatched or molted, unfed ticks are quite resistant to low temperatures, all stages surviving the winter readily in out-door rearing tubes. The survival of unfed ticks of different ages at controlled low temperatures is shown in table 18. Each lot of ticks to be tested was divided into four sublots, each sublot placed in a cloth-covered vial, and the four vials placed

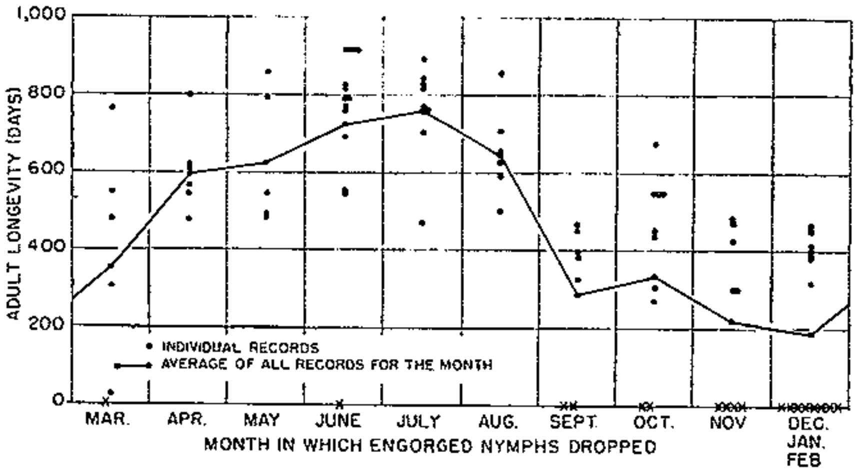

FIGURE 28.—Correlation between the month of nymphal engorgement and longevity of adults of *Dermacentor variabilis*. Crosses on base line represent nymphs that failed to molt.

in a thermos bottle. The thermos bottle was placed in an ice-cream cabinet at 4° F., and after 24 hours it was opened and the vials removed to the floor of the cabinet. On successive days the temperature was lowered to 2°, 0°, and —4°, respectively. Each day a vial was placed in a thermos bottle at refrigerator temperature and removed from the cabinet. After 24 hours the vial was removed from the bottle and the surviving ticks counted. Four adults, 10 nymphs, or 100 larvae were used in each sublot tested.

The tests were conducted principally to determine whether an increasing hardiness developed in the ticks with the gradually dropping temperatures of fall and winter, as has been observed in the study of a number of insects. Table 18 shows that this is not the case. It will be noted that there were seven groups representing seven different ages or environments. If the survival of the adults or nymphs in any group be followed through each of the tests, it

TABLE 18.—*Survival of all stages of Dermacentor variabilis at low temperatures.*

Group No.	Date first exposed	Exposed 24 hours at temperature indicated by x				Survival of—		
		4° F.	2° F.	0° F.	−4° F.	Larvae	Nymphs	Adults
						Percent	*Percent*	*Percent*
1	Oct. 28, 1940	x				42		50
		x	x			4		75
		x	x	x		0		0
		x	x	x	x	0		0
2	do	x				100	60	100
		x	x			79	50	100
		x	x	x		43	10	100
		x	x	x	x	1	10	0
3	do	x				86	100	100
		x	x			88	100	100
		x	x	x		84	70	25
		x	x	x	x	36	10	0
4	do	x						0
		x	x					0
		x	x	x				0
		x	x	x	x			0
5	do	x					70	0
		x	x				0	0
		x	x	x			0	0
		x	x	x	x		0	0
6	do	x				96	100	25
		x	x			96	80	25
		x	x	x		69	100	50
		x	x	x	x	27	90	0
1	Nov. 22, 1940	x						100
		x	x					0
		x	x	x				0
		x	x	x	x			0
2	do	x				99	80	
		x	x			97	60	
		x	x	x		60	10	
		x	x	x	x	0	0	
3	do	x				96	100	75
		x	x			87	100	50
		x	x	x		85	100	25
		x	x	x	x	2	70	0
4	do	x						0
		x	x					0
		x	x	x				0
		x	x	x	x			0
5	do	x					20	50
		x	x				0	0
		x	x	x			0	0
		x	x	x	x		0	0
6	do	x				100	100	0
		x	x			94	80	25
		x	x	x		50	70	0
		x	x	x	x	0	0	0
7	do	x				99		
		x	x			94		
		x	x	x		49		
		x	x	x	x	0		
2	Dec. 17, 1940	x				89	80	
		x	x			100	30	
		x	x	x		74	40	
		x	x	x	x	89	20	
3	do	x				100	100	
		x	x			100	100	
		x	x	x		98	70	
		x	x	x	x	76	90	
4	do	x						0
		x	x					0
		x	x	x				0
		x	x	x	x			0
6	do	x				90	100	0
		x	x			99	100	100
		x	x	x		82	90	0
		x	x	x	x	29	50	50
7	do	x				100		
		x	x			100		
		x	x	x		75		
		x	x	x	x	30		

TABLE 18.—*Survival of all stages of Dermacentor variabilis at low temperatures*—Continued.

Group No.[1]	Date first exposed	Exposed 24 hours at temperature indicated by x				Survival of—		
		4° F.	2° F.	0° F.	−4° F.	Larvae	Nymphs	Adults
						Percent	*Percent*	*Percent*
3	Feb. 12, 1941	x				94	100	
		x	x			97	90	
		x	x	x		70	100	
		x	x	x	x	31	60	
6	do	x				98	100	
		x	x			87	80	
		x	x	x		69	90	
		x	x	x	x	64	90	
7	do	x				99		
		x	x			95		
		x	x	x		92		
		x	x	x	x	75		

[1] Treatment:
Group 1: Kept outdoors, larvae hatched August 1939, adults issued from preceding stage August 1939.
Group 2: Kept outdoors, larvae hatched August 12, 1940, nymphs issued June 11, 1940, adults issued July 23, 1940.
Group 3: Kept outdoors, larvae hatched September 27, 1940, nymphs issued October 7, 1940, adults issued September 10, 1940.
Group 4: Kept outdoors, adults collected by dragging June 17, 1940.
Group 5: Kept indoors, nymphs issued September 20, 1939, adults issued September 20, 1939.
Group 6: Kept indoors, larvae hatched August 5, 1940, nymphs issued September 10, 1940, adults issued July 9, 1940.
Group 7: Kept indoors, larvae hatched November 1940.

will be seen that there was no greater resistance in the later tests than in the earlier ones. This also applies to the larvae in groups 3 and 6. The larvae in group 7 were progressively more resistant, but they were from indoors where the temperature was relatively constant, and they had just completed hatching at the time of the first test. The larvae in group 2, which had been kept outdoors and were over 60 days old at the time of the first test, showed a progressively increasing resistance except at the highest temperature in the last test. The increase was most marked at the lowest temperature.

Old ticks were less resistant than young ticks of the same stage from the same environment. Thus, in each test of adults from outdoor rearing tubes, dragged adults (1 year old or older) were least resistant, reared adults 1 year old were intermediate, and reared adults less than 1 year old were most resistant. The same observation applied to larvae and nymphs from outdoors and to nymphs from indoors, but in the case of larvae and adults from indoors the difference in resistance was not consistent.

In many cases larvae and nymphs survived the lowest temperature to which they were exposed, −4° F. In only one case did the adults survive −4°, but several lots survived 0°. Bishopp and Smith (*1*) reported that larvae and nymphs survived temperatures as low as −9°.

INFLUENCE OF TEMPERATURE ON ACTIVITY

In general, reasonably high temperatures are more conducive to tick activity than low ones, although temperature alone will not invariably cause ticks to become active. The correlation between emergence of hibernating ticks in the spring and temperature is not so close as might be expected. Figure 17 showed that adult activity increased as the season became warmer, and the proportion of ticks active in April was higher in 1941 than under the lower temperatures of 1939 or 1940 (table 1). Figure 15 showed that larvae became active in March or early in April in 1938, 1940, and 1941, but not until May in 1939. April and May were colder in 1939 than in 1938 or 1941, but warmer than in 1940. As the proportion of hibernating nymphs is more variable than that of larvae or adults, their spring abundance is not indicative of the influence of temperature on activity.

The activity of all stages ceases in the fall when temperatures are much higher than those which support activity in the spring. There is no activity of adults during winter, but larvae and nymphs are occasionally encountered on mice during the winter months.

The temperature may exert an indirect influence on activity greater than its direct influence. Figures 26, 27, and 28 indicate that adults dropped between August and April, larvae dropped between October and February, and nymphs dropped between September and March produce short-lived ticks in the succeeding stages, apparently because of the low temperatures to which the engorged ticks were subjected. Maximum longevities were attained in the ticks produced by females dropped from May through July, larvae dropped from March through September, and nymphs dropped from April through August. These periods correspond exactly with the periods of normal activity of the respective stages, creating a strong presumption that the species has become adapted to activity in months when the temperature will be favorable to subsequent development.

Relative Humidity and Precipitation

Moisture is essential to the survival of the American dog tick. Kept in dry containers, unfed ticks die within a few days, eggs fail to hatch, and many engorged individuals fail to molt. Some engorged ticks apparently derive enough moisture from the ingested blood to maintain development. In containers with paper or earth bottoms set on moist sand all stages lived normally. Rearing tubes set in the soil maintain sufficient moisture even after weeks without rainfall.

Ticks may be adversely affected by precipitation only if they are flooded and submerged. Unfed adults will survive submergence for 6 days or longer in fresh water and for 5 days in sea water; unfed larvae will survive submergence for 1 day in either fresh or sea water, and engorged larvae will survive 1 day in sea water and 5 days in fresh water; unfed nymphs will survive 1 day in fresh or sea water; and engorged nymphs will survive 5 days in fresh water and 3 days in sea water.

The relative humidity does not affect the molting periods of larvae or nymphs. Engorged specimens were left to molt at a constant temperature of 78° F. in containers where relative humidities of 31, 51, 71, and 79 percent were maintained. All lots exhibited similar molting periods and survival, except that few larvae kept at 31 percent completed molting.

Rearing data show that the average relative humidities during the preoviposition, incubation, larval molting, and nymphal molting periods are not correlated with the length of the periods.

Neither relative humidity nor precipitation shows any corrrelation with the activity of any stage.

Photoperiod

It was previously mentioned that ticks in all stages cease activity late in the summer or in the fall when the temperature is still higher than that at which activity began in the spring, and it has been suggested that this may be an adaptation to prevent the succeeding susceptible engorged ticks from being exposed to low temperatures. Some factor, however, must act upon the flat ticks themselves, and this is apparently neither temperature nor relative humidity. In the case of larvae and nymphs, the season of activity ceases when the length of daylight is about equal to that of the season at which it begins, suggesting that the photoperiod may influence activity. Smith and Cole (*15*) reported that by experimentally engorging larvae and nymphs on mice it was found that exposure to a gradually increasing photoperiod made ticks more active, i. e., more willing to engorge, than a gradually decreasing one, and that long photoperiods were more favorable than shorter ones. No effect on the activity of adults was obtained by artificial manipulation of the photoperiod.

CONTROL OF TICKS ON ANIMALS

Dusts or dips are effective in killing ticks on domestic animals, and to some extent in reducing reinfestation. None of the materials investigated was completely effective in preventing ticks from attaching, but derris greatly reduced the number of attachments and killed the majority of ticks that did attach for several days after treatment.

Wherever possible the use of a dip is preferable to the use of a dust. It is more difficult to secure complete coverage of the animal with a dust, which penetrates the hair less readily and does not adhere to the skin and hair.

Derris[4]

The materials most widely used for application to animals to control external parasites are derris, pyrethrum, sulfur, creosote, and arsenic. Derris has been preferred in the control of the American dog tick because it is effective against the ticks, harmless to the host, relatively inexpensive, and may be used either as a dip or as a dust. The purpose of these investigations was to make a more detailed study of the value of derris, to compare derris and the other insecticides mentioned, to determine the value of various wetting agents in derris dips, and to ascertain the necessary frequency of dipping to prevent any ticks from completing engorgement. The derris dip used as a standard was that recommended by Bishopp and Smith (*7*), viz, 1 ounce of neutral soap and 2 ounces of derris powder (4 percent rotenone) to 1 gallon of water.

General observations on the value of derris dip were made on dogs brought by their owners to experimental stations for treatment.

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[4] The war has reduced importations of derris, and the material is not generally available as this goes to press.

Owners were requested to bring their dogs for treatment twice a week. Few dogs were dipped as often as suggested, but many were treated at intervals sufficiently frequent to provide a basis for definite conclusions on the effectiveness of the treatment under various conditions. The dogs were of all types and from a wide variety of environments.

During the season of 1938, 192 dogs were brought in and 446 treatments were made. At 180 dippings dogs were uninfested, at 170 dippings lightly infested, at 60 dippings moderately infested, and at 36 dippings heavily infested. Six of the 192 dogs that were treated were made sick by the dip, 1 consistently.

Of the records on 58 dogs brought in as often as once a week for 2 or more weeks, only 25 were considered as giving any definite information, as many of the repeaters were from areas where the dogs picked up only 1 or 2 ticks a week in any event. These 25 records show, in general, that dippings every 3 or 4 days will keep dogs tick-free only in cases where the animals are lightly infested before the first treatment. Where dogs were heavily infested at the beginning of dipping, the numbers of ticks were materially reduced, but almost always some ticks were present after 3 days. In a few cases there was no visible evidence of improvement after dipping. As against this may be cited the case showing the most outstanding improvement. A cocker spaniel had actually been made sick by large numbers of ticks, and the owner had been on the verge of disposing of him. After the beginning of the semiweekly treatments few ticks were noticed, and the dog regained his full vigor. Several other dogs that had been heavily infested were kept almost free of ticks by the semiweekly dippings.

Records on 10 lightly infested dogs from different sections of the island showed that when dipping was done twice a week, the animals were either tick-free or carried very few ticks at each subsequent dipping. Only two dogs that were originally lightly infested, showed no improvement at subsequent semiweekly dippings.

Ticks on four dogs originally moderately infested and brought in at irregular intervals, were reduced or eliminated by dippings every 3 or 4 days, whereas dippings every 7 or 10 days were ineffective.

A difficulty encountered in certain long-haired breeds was the action of matted hair in protecting ticks from the dip. An outstanding instance was that of a female tick caught in a mat of hair. This tick had detached and laid eggs on the animal without being killed by the dip. With dogs having long hair about the face, as Scotties and Sealyhams, special care had to be given to prevent the engorgement of ticks in the beard. On certain dogs the ticks attached almost exclusively inside the ears; this is particularly true of beagles. Derris in vaseline applied to the ears proved helpful in such cases.

The cost of dipping varied with the number of dogs treated in one lot of dip. In one instance, in which a single 45-gallon lot of dip was used to treat 65 dogs over a period of 3 days, the cost was 4 cents per dog for materials. During the entire season of 1938, in the foregoing and in additional studies, 712 dogs were treated, requiring 636 gallons of dip at a total cost of $35.67, or an average of 5 cents per treatment.

In a more detailed test of weekly dipping, 5 dogs were dipped once each week for 13 weeks. All the dogs had been heavily infested before the dipping was begun, and the ticks were not picked by the owners. Throughout the test the dogs continued to carry many flat ticks, but in many cases no engorged females were present at the time dippings were repeated. In 54 such repeat dippings and observations, 31 times the dogs carried no engorged females and 23 times they carried some engorged females, the number ranging from 1 to 21 per dog. From these results it may be concluded that weekly dippings will prevent complete engorgement about half the time, and will greatly reduce the number engorging at all times. Based on the number of engorged females found on the dogs before dipping was begun, it is estimated that the weekly treatments reduced the number of females completing engorgement on these 5 animals by 90 percent.

WETTING AGENTS

The efficiency of various wetting agents in the preparation of derris dip was investigated under the supposition that an agent superior to soap might be found. In a preliminary laboratory test four synthetic commercial wetting agents and a mild soap were used to prepare dips in the proportion of 1 ounce of wetting agent and 2 ounces of derris to 1 gallon of water. These dips were tested against ticks of the following classes: (1) Males that had been confined in test tubes since molting, never having had an opportunity to become very active; (2) females of the same type; (3) males and (4) females collected from vegetation by dragging, which were active but unfed; (5) fed males picked from dogs; (6) flat to slightly engorged females picked from dogs; (7) females one-eighth to one-third engorged; (8) females one-half engorged; and (9) females fully engorged. All specimens were held in the solution with forceps, being submerged momentarily. The unfed ticks from vegetation and the fed ones from dogs were collected immediately before dipping so that they would not become inactive.

Considerable difference in the effectiveness of the dips on the various classes of ticks was apparent, their efficiency generally increasing as the metabolism of the ticks had advanced. Not one of the inactive ticks from test tubes was killed by any dip, 16 percent of the unfed females from vegetation were killed, 33 percent of the unfed males, 92 percent of the fed males, 92 percent of the slightly fed females (class 6), 44 percent of the females one-eighth to one-third engorged, 50 percent of the females one-half engorged, and 92 percent of the females fully engorged.

One of the synthetic wetting agents (sodium lauryl sulfate) gave better results than soap, and the others were about equal to soap in respect to the number of ticks killed by the dips. However, the soap held the derris in suspension longer than the synthetic wetting agents, a factor of some importance.

Other tests with 3 of the synthetic wetting agents and mild soap were made, the dips being applied to tick-infested dogs, which were afterward confined for 5 days. Whereas 130 ticks were picked from an untreated dog, only 3 to 6 live ticks were found after 5 days on dogs dipped in any of the solutions—numbers so small as to make it impossible to draw any distinctions between them.

Where the dogs were dipped before they were allowed to run in order to test the repellent and protective value of the dips, there was a wider variation in the results obtained. One of the dogs on which a synthetic wetting agent was used picked up a smaller number of ticks than the others, and fewer ticks survived for a week than on the other dogs. The other four dogs picked up approximately equal numbers of ticks, but on the three dipped dogs most of the ticks were killed by the derris remaining in the hair. In this manner the period of protection is seen to extend well beyond the time when ticks freshly attached are found on animals.

A comparison of mild soap with the synthetic wetting agent (sodium lauryl sulfate) that had given the best results in laboratory tests was made under normal conditions of use on 8 dogs belonging to private owners. The dogs were selected because they were habitually infested and because they ran in the same general areas. All dogs were dipped twice each week for a month. Two Irish setters belonging to the same man were dipped, 1 in each solution, and offered a particularly close comparison. The dog dipped in derris with soap had a few live flat ticks at each treatment from the second to the sixth, and no ticks at the seventh and eighth treatments. One fully engorged female was found. The dog dipped in derris with the synthetic wetting agent had a few live, flat ticks at each treatment from the second to the fifth and none at the sixth, seventh, or eighth. No engorged females were found. On the other 3 dogs dipped in derris with soap there were 11 occasions when no live ticks were found and 7 occasions when a few were found, while with the other 3 dipped in derris with the synthetic wetting agent there were 4 inspections when no live ticks were found and 14 when a few were found. From these comparisons it appears that the synthetic soap was as effective as any wetting agent with derris when used on dogs as often as twice each week.

The following season the two dips were compared on six privately owned dogs dipped at intervals of 5, 6, and 7 days, to determine whether the interval between dippings could be extended by the use of the synthetic wetting agent, without seriously lowering the effectiveness. No difference between the effectiveness of the two dips was noticed, and very little between dippings at the longer and shorter intervals, very good results being obtained even with dogs dipped every 7 days, as far as prevention of complete engorgement was concerned, although heavier infestations of partially engorged ticks were built up at the longer period. The synthetic material showed its superiority as a wetting agent, however, in that the dogs became thoroughly wet with the dip more easily and quickly. In the comparisons between the two wetting agents, enough attention was given to make certain that all animals were thoroughly wet, thus reducing the importance of this factor. It appears, then, that when thorough treatments are given, soap is as satisfactory as the synthetic agent, but in hurried or careless dipping, the latter might be superior, as heavy coats of hair become wet through with less effort. The synthetic wetting agent dissolves much more readily than soap in cold water, but the derris remains in suspension longer in the soap solution.

PERSISTENCE OF DERRIS IN THE HAIR

To test the protection afforded by the derris remaining in a dog's coat after dipping, a different dog was dipped on each of 3 successive days, and permitted to run in a tick-free yard until the fourth day, when all were permitted to run in a tick-infested area. Each was subsequently kept in a cage over a moat for 2 weeks to permit the ticks to develop and drop as they normally would. The dog that had been dipped 1 day before infestation picked up the fewest ticks, and all were killed while still flat. The dog dipped 2 days before exposure had the second lightest infestation, and a few females completed engorgement. The dog dipped 3 days before exposure picked up the most ticks, and some of the females engorged normally. Thus there was absolute protection for 24 hours and a fair degree of protection for 72 hours.

EXTRACT OF DERRIS

A hot-water extract of derris containing 3.08 mg. of rotenone per cubic centimeter was tested in comparison with the previously mentioned standard derris dip, which was calculated to contain only 0.6 mg. of rotenone per cubic centimeter, being made with 2 ounces of derris (4 percent rotenone) and 1 ounce of Dreft to 1 gallon of water. The water extract was expected to be 5 times as strong as the dip, and was tested in dilutions of 1:1, 1:2, 1:3, 1:4, and 1:5 as well as full strength. All were tested against fed males, flat to slightly engorged females, one-thrid- to one-half-engorged females, and fully engorged females. Only the full-strength extract was equal to the standard derris dip, both killing all ticks in 7 days. All dilutions killed all males and fully engorged females, but only the 1:1 dilution prevented the half-engorged females from ovipositing.

DERRIS DUST

The use of derris as a dust gives satisfactory control in light infestations. The dust used should be finely ground derris root containing 3 or 4 percent of rotenone. Application should be thorough, and the powder must penetrate to the skin. Treatments should be repeated every 2 or 3 days. As dipping is more effective than dusting, it should be used in preference whenever possible.

DERRIS WASH ON CATTLE

To test the effectiveness of the standard derris dip on cattle, an experiment was set up using milk cows at two small dairies and on a farm. There was considerable variation in individual host susceptibility, the infestations of individual cows in the same herd ranging from 1 to 80 ticks. Only the heads and the brushes of the tails were infested as a rule, and only these parts were washed with the dip. Treatments were given every other day at first, then every fourth day, and the final observation was made 1 week after the last treatment. The derris gave satisfactory kills and was as effective as when used on dogs. On most cows treatment at intervals of 4 days to a week gave excellent control, and even on especially susceptible cows treatments every other day gave almost complete freedom from ticks.

SULFUR-CUBE

The sulfur-cube dip customarily recommended for the control of cattle lice (100 pounds of wettable sulfur and 10 pounds of cube per 1,000 gallons of water) was compared with the standard derris dip on dogs infested with ticks in all degrees of engorgement. Sulfur-cube was ineffective, killing only a few of the ticks, whereas the derris dip permitted no engorgement.

In a second test the sulfur-cube dip was fortified by the substitution of 25 pounds of derris for 10 pounds of cube in the formula for 1,000 gallons. Because the dip had shown very poor wetting ability on dogs, soap was added to the formula at the rate of 50 pounds per 1,000 gallons. It was tested in comparison with the standard derris dip as in the preceding experiment. The fortified sulfur-cube dip was more effective than formerly but remained less effective than the standard derris dip.

PYRETHRUM

Emulsions of kerosene extract of pyrethrum of the type customarily used as mosquito larvicides were unsatisfactory as dips against ticks on dogs. The principal disadvantage was the difficulty in thoroughly wetting the dog's skin with the material, as it did not wet or penetrate the hair readily. Although the emulsion was a satisfactory killing agent in laboratory tests using partially fed ticks picked from dogs, it caused low mortalities (0 to 50 percent) on dogs dipped in a mixture of 4 ounces of New Jersey Larvicide to 3 gallons of water.

ARSENIC

The standard arsenical stock dip in the strength recommended for control of cattle ticks was slightly superior to derris in one test and inferior in two. The arsenic killed a high proportion of the females that were fully engorged at the time of dipping but a lower proportion of flat and slightly engorged ticks. Its inferiority was probably due in part to its inability to wet and penetrate the hair as well as did the derris dip. Although no injury to the skin was observed on the animals treated, the arsenic has been known to cause burns under certain conditions and is a dangerous stomach poison as well.

CREOSOTE

Coal-tar creosote was ineffective at the maximum strength at which it could safely be applied to animals. The dips tested contained 2 ounces of creosote (phenol coefficient 5 to 6) per gallon of water. At this strength there was a negligible mortality among female ticks, but moderate numbers of the males were killed. In one instance the creosote injured the skin on the ears of a dog, causing bleeding for several minutes after treatment.

CONTROL OF TICKS ON VEGETATION

The tendency of the adults of the American dog tick to concentrate on the grass at the sides of roads and paths provides an opportunity to kill a high proportion of the ticks active in an area by spraying a relatively small portion of that area. For example, in an area where ticks were collected once each week during an entire tick season, 5,628 ticks were collected by dragging along roadsides and paths, whereas only 535 ticks were collected in the adjacent field, even though the total distance dragged in the field was slightly the larger. Sprays could also be used to advantage to free the vegetation from ticks around camps, beaches, and other small resort areas, particularly where Rocky Mountain spotted fever is known to occur.

Smith and Gouck (*17*) reported that a spray containing 0.5 percent of nicotine sulfate (40 percent nicotine) and about 0.3 percent of soap reduced the abundance of ticks on vegetation by about 90 percent for 2 or 3 days. The addition of 1.5 percent sodium fluoride or 1 percent dinitro-orthocyclohexylphenol produced a reduction of longer duration, but made the spray injurious to foliage. Kerosene extract of pyrethrum, derris, pine oil, and diphenylamine were less satisfactory materials.

Later experiments indicated that an emulsion of DDT (2,2-bis (*p*-chlorophenyl)-1,1,1-trichloroethane) dissolved in soluble pine oil was as effective as any of the foregoing materials, produced more lasting control, and was not injurious to foliage as used. A spray containing 0.5 per cent of DDT, 2.5 percent of soluble pine oil, and 97 percent of water, applied to roadside vegetation at the rate of 7 pounds of DDT per acre, reduced tick abundance to less than 1 percent of the original infestation for 10 days, whereas abundance in an untreated area ranged from 82 to 106 per cent during the same period. The application of 2½ pounds of DDT and 12½ pints of soluble pine oil in 100 gallons of water per acre reduced tick abundance to less than 5 percent of the original for 21 days, whereas abundance in an untreated area rose to more than 200 percent of the original during the same period. The application of 2 pounds or less of DDT per acre was sometimes effective but not in every case. Emulsions prepared by using 2½ pints of xylene and ½ pint of synthetic wetting agent per pound of DDT were about as effective as those using soluble pine oil. Smith and Gouck (*18*) have reported DDT to be effective against other species of ticks for much longer periods, and it is probable that this will be found true in the case of *Dermacentor variabilis*.

CONTROL BY TREATMENT OF DOMESTIC ANIMALS

Over the greater part of its range the American dog tick is able to utilize both wild and domestic animals as hosts in the adult stage, but in restricted localities the only hosts available to the adult ticks are domestic animals. Under the latter conditions it should be possible to reduce tick abundance in the area by systematically dipping the infested animals, as this would prevent female ticks from engorging and ovipositing. The island of Martha's Vineyard provided an especially favorable locality for investigating this method of control, as no wild animals suitable as hosts of adult ticks were present. An area was selected as the site of the experiment on the outskirts of a town where ticks were reported to have been consistently numerous for many years. The area, approximately 1 mile long by ½ mile wide, was situated on the shore of a bay. Tick infestations were heaviest in the beach grass along the shore; on the adjacent bluff, which was covered with a tangle of fine grass, wild roses, and blackberries; and in a salt marsh at one end of the area. Many of the houses in the area were occupied only in summer, and very little of the land was in cultivation. Meadow mice were abundant in the uncut grass, providing an abundance of hosts for the larvae and nymphs. A view typical of the area is shown in figure 29.

Dogs were almost the only hosts of adult ticks in the area. A few cattle and horses were present, but they were kept in a closely grazed pasture and remained free of ticks. Several cats were present. but ticks were found on only one, which was treated as often as necessary. All the dogs were treated with derris twice each week during the tick season. In April, when the weather was too cold to permit dipping, the animals were dusted with derris powder. but from May to September they were dipped in the standard derris dip (2 ounces of derris and 1 ounce of neutral soap to 1 gallon of water). A dipping

FIGURE 29.—Typical habitat of the American dog tick. The thick grass mixed with blackberry, rose, bayberry, and beach plum provides excellent cover for meadow mice.

vat was mounted on a ¾-ton truck so that it could be taken to each house where dipping was necessary. Figures 30 and 31 illustrate the method of dipping and the equipment. The dog's entire body and neck were immersed in the dip, but the head was not immersed, as the dip would enter and irritate the eyes. Dip was scooped up by the handful, poured over the dog's head, and rubbed thoroughly into the hair. The systematic treatment of dogs was begun in April 1938 and conducted during the entire tick seasons of 1938, 1939, 1940, and 1941.

The cooperation obtained from the dog owners in the area was very good from the first, and grew even better as the benefits obtained from dipping became apparent. A few persons would not permit their dogs to be dipped, but they either substituted treatments of their own choice or resorted to hand picking of the ticks, so that their dogs did not drop engorged females to destroy the value of the experimental operations.

During the season of 1938, 13 dogs belonging to 11 persons were

FIGURE 30.—Using derris dip to control the American dog tick.

dipped 153 times, and one or more engorged female ticks were found attached in 6 instances. In one of these 6 cases the dog had been in the neighborhood a week before its presence was discovered by the worker, in 3 cases they were on dogs that had missed one or more treatments, and in 2 cases they were in the long hair around the mouths of Scotch terriers where they had not been washed with the dip.

FIGURE 31.—Portable dipping vat installed on truck by easily removable mountings.

As most of the persons in the area were much concerned over dog ticks, many ticks were picked from the dogs between dippings, so no very definite information as to the repellent value of the dip was obtained from the inspections at the semiweekly treatments. All the owners, however, reported a considerable reduction in the number of flat ticks attaching, and such observations as the authors were able to make confirmed this.

It is almost certain that a few tick-infested stray dogs had access to the area, but in general the operations were as successful and satisfactory as would be possible while voluntary cooperation of dog owners was depended on, and they should have provided an informative test of the value of such work for tick control.

During the season of 1939 a total of 200 dippings were given to 15 dogs. On 2 occasions a single engorged female was present at the time of dipping, but at the 198 other dippings the dogs were either free of ticks or carried only flat or partially fed ticks. In 1940 a total of 210 dippings were given to 12 dogs. On only one occasion were any engorged females present, when 4 were found on a dog the first time it was dipped after having been brought into the area. In 1941 very few ticks were active in the area, and in some instances dogs that remained free of ticks were examined at semiweekly intervals but not dipped. A total of 127 dippings were given to 14 dogs, and in no case were any engorged females found on the dogs at the time of treatment.

The abundance of adult ticks in the area was measured by collecting them with a drag, as described in the section on methods of study. Dragging was done along the sides of the roads, in the beach grass, on the bluff adjacent to the beach, and across a field at a greater distance from the water. The abundance throughout the experiment is shown in figure 32.

The abundance of adult ticks in 1938 may be considered to represent about the normal, as the effects of the systematic dipping were not apparent, as was to be expected, before 1939. Abundance normally varies greatly from year to year, as is shown in figure 17. A comparison of the abundance in various years in a normal area (shown in fig. 17) with that shown in figure 32 indicates what proportion of the fluctuation must be attributed to the control operations.

In 1939 there was a slight decline in abundance in the controlled

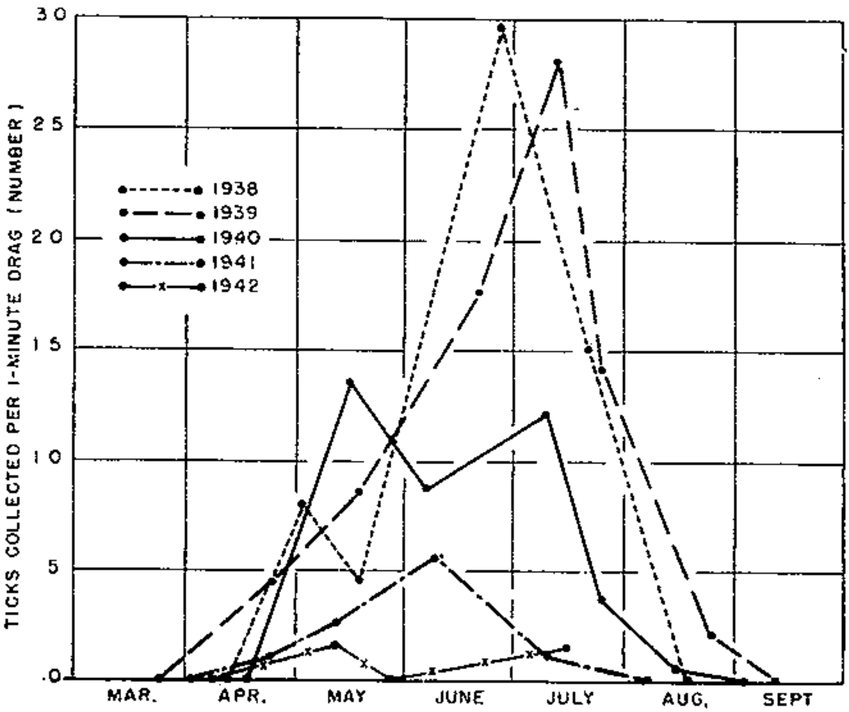

FIGURE 32.—Seasonal abundance of adults in an area where all dogs were dipped regularly.

area, whereas the abundance in the normal area increased greatly, ticks being more numerous than in any other year. As noted in the section on seasonal cycles the oviposition in any 1 year results in ticks molting to adults during the following 2 years (table 15). Thus, as shown in table 15, 35 percent of the adults produced by females engorged in 1939 became active in 1940 and the remaining 65 percent became active in 1941. This would mean that in the area of systematic dipping 35 percent of the value of the operations in 1938 should be apparent in 1939, and 100 percent in 1940. The slight decline in adult abundance in 1939, rendered more significant by the simultaneous increase in a normal area, may therefore be attributed to the dipping.

There was a further decline in adult abundance in 1940, but as the normal area showed a similar decrease, this may not necessarily have been produced by the dipping. However, the abundance in the controlled area continued to decline in 1941, and by 1942 very few ticks were to be found, whereas in the normal area adult abundance rose to a high level in both years. Considering the entire picture, a steady decline during 5 years in the controlled area in contrast to fluctuating abundance in a normal area, it becomes apparent that a substantial degree of control resulted from the systematic treatment of hosts.

An additional factor in the extremely low abundance in 1942 was that meadow mice were destroyed by poisoning in 1941 in a portion of the area.

Abundance in the area increased after 1942, in the absence of further control operations. A survey near the peak of adult activity in 1943 indicated that the ticks were about one-third as abundant as in 1938, before control measures began. In 1944 abundance had risen to about two-thirds of that in 1938.

Control by dipping of all dogs in an area is rather expensive. Although the cost of materials was small, less than $10 a year, the operations required about 17 days' labor. On a basis of 50 cents per hour for labor, the total cost for one season would be $78, exclusive of the cost of the truck and vat, for the control of an area of ½ square mile. The proportionate cost would vary in different areas with the number of animals per square mile requiring treatment.

CONTROL BY ERADICATION OF MEADOW MICE [5]

In the discussion of the relative importance of the various animals serving as hosts for immature ticks, it was pointed out that the meadow mouse was the principal species concerned. This was especially true on the island of Martha's Vineyard, where no pine mice were present. Although white-footed mice were sometimes heavily infested with larvae, they were rarely found to carry many nymphs. These facts indicate that if the meadow mice in an area could be eradicated, the majority of nymphal ticks would die without engorging, resulting in a high degree of control.

The Fish and Wildlife Service of the United States Department of the Interior has developed efficient methods for the eradication of meadow mice in orchards, where they frequently cause considerable injury to fruit trees (Garlough and Spencer *4*). With slight

[5] This study was conducted in cooperation with the Fish and Wildlife Service, U. S. Department of the Interior. The mouse-control operations were under the direction of Donald A. Spencer, to whom the authors are additionally indebted for assistance in the preparation of this part of the bulletin.

adaptations, these methods may be applied in the areas where the meadow mice are supporting severe tick infestations.

The method of mouse control used in this study was the exposure of poisoned baits under such conditions that they would be eaten only by mice. The bait used was either apple or oats or a combination of the two. The oats were of a rolled type prepared by the Fish and Wildlife Service for this particular purpose, and the apples were prepared by cutting them into ½-inch cubes. The oats were poisoned with strychnine or zinc phosphide, the apple with zinc phosphide. The bait was placed in established mouse runs, sometimes in small cylinders of roofing paper and sometimes directly on the ground. Baits were covered with grass or other material so that birds and mammals other than mice would not find and eat them. Both types of bait with either poison were readily accepted by meadow mice throughout the 4 years of observation, even when an abundance of other food was present.

The abundance of meadow mice declines through the winter, but increases very rapidly in spring and summer. As the nymphal ticks are most active and abundant during the months when mouse abundance is increasing, the problem of mouse control in relation to ticks is more difficult than the control practiced in orchards in the winter months. A single application of poison in the spring usually sufficed to reduce mouse abundance to a satisfactorily low level, but the numbers of mice again rose rapidly as breeding occurred in the area and migrating mice were forced into the area by the pressure of increasing populations in adjacent territory.

The study of mouse eradication as a method of tick control was conducted in two areas. The site of the first experiment was in the West Chop area, a narrow strip of grassland lying between a wood and a beach. Meadow mice and white-footed mice were found in the grassy portion, but only white-footed mice were taken in the wood. It was assumed that the wood constituted a barrier to migrating mice, but such was apparently not the case. This area had been poisoned for mouse control in the fall of 1936 and the spring of 1937 as a part of the Martha's Vineyard Woodtick Project, as described by Hertig and Smiley (*6*). Their report indicates a reduction in the number of mice in the area following their operations. In the present experiments poison was applied in October, November, and December 1937, June, October, November, and December 1938, and May, June, and August 1939.

The quarterly average abundance of meadow mice in the poisoned area, compared with that in a normal area, is shown in figure 33. Although the trends of abundance in the two areas correspond closely, the relative numbers are of some significance. At the beginning of their operations the authors found mice to be more abundant in the poisoned area than in the normal area. Following the first application of poison, mouse abundance fell below that in the normal area, and remained so throughout the period that poison was applied. The last application of poison was made in August 1939, and by the first quarter of 1940 mouse abundance in the poisoned area was above that in the normal area, and it remained so, with the exception of a single quarter, through the remainder of the period of observation.

The abundance of adult ticks was measured by collecting them with a drag, the majority being collected along paths. A graph of the abundance as measured by this method is presented in figure 34. No measurements of abundance prior to 1938 are available, but by this time the poisoning operations of the Martha's Vineyard Woodtick Project in 1936 and 1937 might have produced their effect. Nymphs engorged early in the season may produce active adults in the same

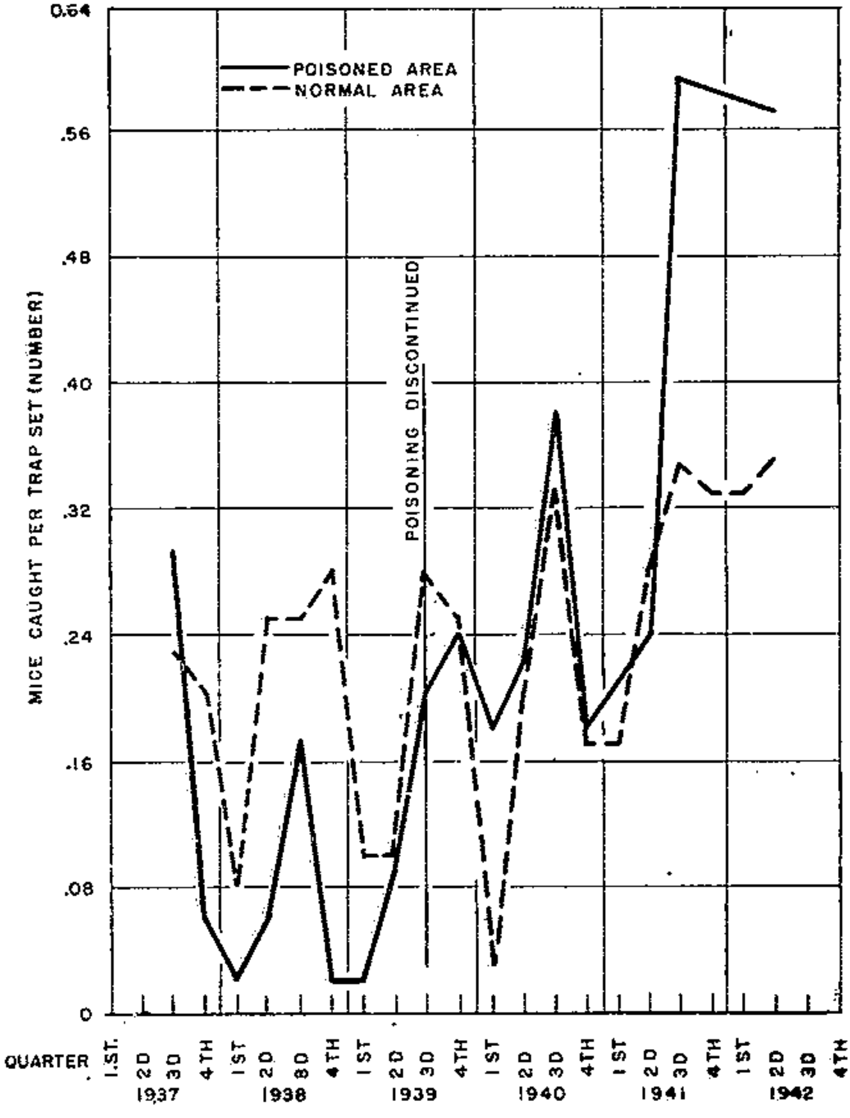

FIGURE 33.—Quarterly average abundance of meadow mice in the West Chop poisoned area and a normal area.

season, but the majority produce adults that do not become active until the following year. Reduction of adults should therefore have been apparent from 1938 through 1940 or beyond. Figure 34 shows that in each year from 1938 through 1941 abundance reached its peak in April or early in May, and was declining in June. This is abnormal,

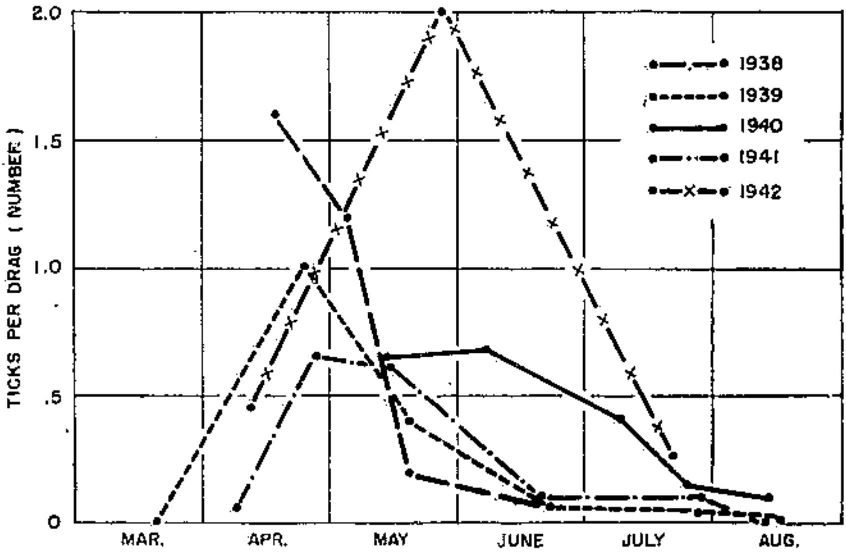

FIGURE 34.—Abundance of adult ticks in West Chop poisoned area.

as tick populations usually build up through June and reach a peak late in June or early in July. In 1942 the peak of abundance was considerably later than in previous years and twice as high as in any year except 1938. Single collections made in July 1943 and June 1944 showed the abundance to be low in both years.

In general it appears that some reduction in the number of meadow mice was obtained, although never in a completely satisfactory degree, and that tick populations were low and abnormal during the period of operations and for several years afterward.

The site of the second experiment was on Cedar Neck, a small peninsula exposed to reinfestation by migrating mice only at the point where it joined the mainland. The entire peninsula, 0.6 mile long by 0.1 mile wide, was treated at each operation. The basal portion was covered with a thick growth of uncut grass, the apical portion was wooded, with occasional small pockets of grass and vines, and there was a narrow strip of beach grass along most of the shore. Meadow mice were abundant in all the grassy areas, and ticks were numerous.

The baits used were rolled oats and apple, poisoned with zinc phosphide. They were placed directly in the mouse runs, without the use of tubes or feeding stations, and were covered with grass or other materials. Applications of poisoned bait were made in April and August 1939; March, May, August, and October 1940; and April and August 1941. Following the first application of poisoned bait, mouse abundance remained at a fairly low level. In 1939 the catches rose as high as 10 mice per 100 traps, in 1940 as high as 28, and in 1941 as high as 23, whereas in 1942, when no poison was applied, they rose to 43 per 100 traps.

The abundance of adult ticks in the area is shown in figure 35. The graph of abundance in 1939 must be considered normal, since no control measures were conducted in the area prior to 1939. Abundance in 1940, 1941, and 1942, however, should have been affected by the mouse-poisoning operations. The abundance in 1940 was only 10 percent of that in 1939, whereas in a normal area (fig. 17) abundance was 27 percent of that in 1939. In 1941 and 1942 the abundance in the poisoned area was 35 and 47 percent, respectively, of the abundance in 1939, whereas in a normal area it was 50 percent in each year.

The fact that 1939 was the year of greatest tick abundance in all

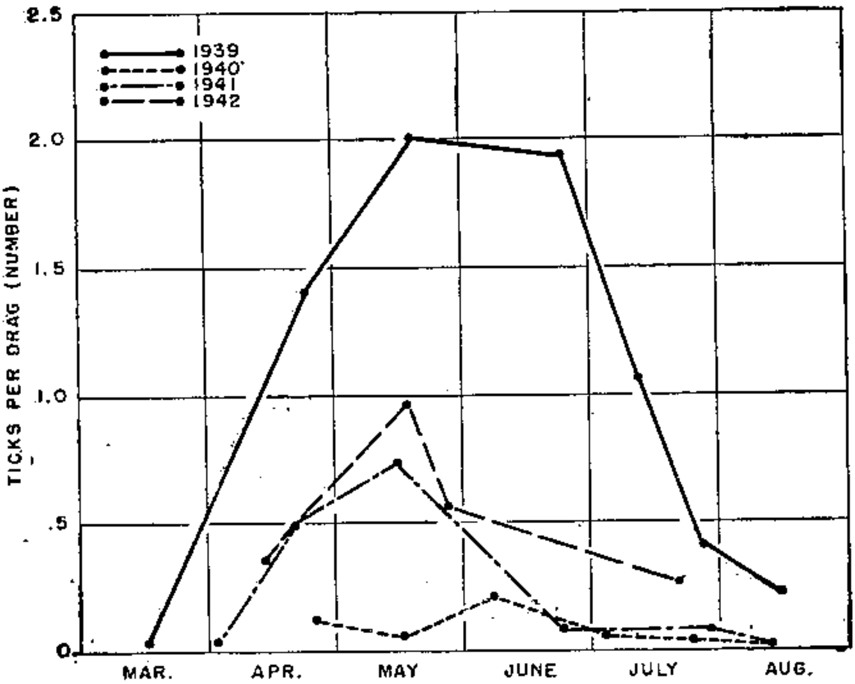

FIGURE 35.—Abundance of adult ticks in Cedar Neck poisoned area.

areas increases the difficulty of evaluating the control method. However, the difference between the abundance in 1939 and that in other years was consistently greater in the poisoned area, indicating that at least a portion of it was due to meadow mouse control. A survey near the peak of tick activity in 1943 showed tick abundance in the poisoned area to be about 140 percent of that in 1939. In 1944 tick abundance was about 170 percent of that in 1939.

On the basis of these two experiments, it may be concluded that a substantial reduction in the abundance of meadow mice in an area by the use of poison will be followed by a reduction in the abundance of adult ticks, that the first effects will be apparent in the year following treatment, that poison should be applied once each month during the breeding season of mice to obtain satisfactory control, and that the degree of tick control will not exceed the degree of mouse control. The benefits derived from this method will be greatly increased by the simultaneous treatment of domestic animals to prevent ticks from engorging and ovipositing.

CONTROL OF TICKS BY BURNING THE GRASS

Observations in several areas where accidental fires occurred when adult ticks were becoming active revealed marked reductions in tick abundance. In some cases, however, the wild fires were much hotter than controlled fires would have been.

Fires should reduce tick abundance in two ways (1) by destroying the ticks active at the time of the fire and (2) by removing the cover for meadow mice, the principal hosts of the immature stages.

The degree to which the cover for meadow mice was removed by fire is shown by figure 36, and the rapidity with which it returned by figure 37. The two photographs are of the same spot, but the one taken April 29, 1941, shows a well established mouse run completely exposed by the burning of the grassy cover. Mice would have no protection from their enemies, and could not survive. By the time the second picture was taken, June 12, the green vegetation had covered the run, but the protection to the mice was not so great as in the heavy growth preceding the fire.

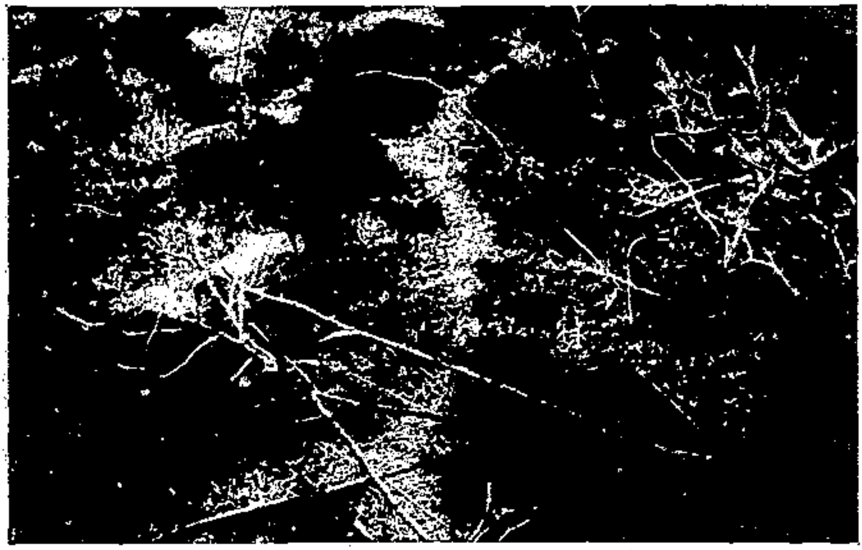

FIGURE 36.—Tick habitat after a fire, April 29, 1941. The small path in the foreground is a well established meadow mouse run exposed by burning off the cover.

Collections of mice and immature ticks were made in the burned and unburned portions of the area by trapping. Both meadow mice and white-footed mice were scarce in the burned area the night after the fire. Meadow mice were entirely absent from the burned portion during May and June, but white-footed mice were numerous. By the

FIGURE 37.—Identical spot shown in figure 36, 6 weeks later, June 12, 1941. The green vegetation conceals the meadow mouse run.

first of August meadow mice had become moderately numerous, and remained so in September, but white-footed mice were absent. In the unburned portion meadow mice increased steadily in numbers from May to September, as is normally the case, but white-footed mice were scarce.

No very heavy infestations of larvae or nymphs were found on mice in either area at any time, although adult ticks were numerous every year, including 1941. While meadow mice were absent from the burned area, white-footed mice from that area carried more larvae, but fewer nymphs, than meadow mice from the unburned, which were in turn more heavily infested than white-footed mice from the same locality. This confirms the observations in areas where mice have been poisoned that, when meadow mice are not available, white-footed mice are increasingly utilized as hosts by larvae, but not by nymphs.

There was a strong indication that the fire in April caused a considerable reduction in the abundance of adult ticks throughout the remainder of the season. The abundance in the unburned portion of the area was about 300 percent greater than that in the burned portion at the peak of adult activity, and remained greater until all activity ceased.

Collections of adult ticks had been made in the area in August 1940, providing a basis for evaluating the effect of the fire on adult abundance in August 1941. Abundance in places which remained unburned was the same in 1940 and 1941, whereas abundance in burned places was only about one-tenth as great in 1941 as it had been in 1940.

TICK PARASITES

Only two species of insects, *Ixodiphagus texanus* How. and *Hunterellus hookeri* How., are known to parasitize ticks. Both belong to the hymenopterous family Encyrtidae. *I. texanus*, which is widely distributed in the United States, is normally parasitic on the rabbit tick (*Haemaphysalis leporis-palustris* Pack.) but has been found parasitizing larvae and nymphs of the American dog tick in Massachusetts. It occurs in the latter species so infrequently that it is of no importance as a natural enemy, and, in fact, only attacks dog ticks in the localities where they are extremely numerous.

Hunterellus hookeri, which is indigenous to the warmer portions of the world, is normally a parasite of the brown dog tick (*Rhipicephalus sanguineus* (Latr.)), but readily parasitizes nymphs of the American dog tick in the laboratory. An attempt by Larrousse, King, and Wolbach (*9*) to utilize the parasite for the control of ticks in Massachusetts resulted in the establishment of a small colony which has persisted for years without causing a reduction in the abundance of the American dog tick. The strain was imported from France, and may be dependent on the black-legged tick (*Ixodes scapularis* Say) for its survival in Massachusetts. An attempt to establish a colony of a Texas strain of the parasite in Massachusetts was unsuccessful. In the course of the experiment, which has been reported by Smith and Cole (*16*), 90,000 females were released. None were recovered in ticks collected in the area of release, and no reduction in tick abundance was apparent.

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