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THE LIFE HISTORY AND DEVELOPMENT OF THE SHEEP TICK IXODES RICINUS LINNAEUS IN SCOTLAND, UNDER NATURAL AND CONTROLLED CONDITIONS.

by

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INTRODUCTION

It has long been recognised that infestation of domestic stock with ticks (Ixodes ricinus L.) is a seasonal phenomenon in Great Britain. Wheler (1899) recognised two well-defined seasons of infestation, spring and autumn, in Northumberland, and proposed the theory that ticks engorge on their hosts in spring and autumn and undergo metamorphosis on the ground during the intervening seasons. This hypothesis, which has been referred to as the two-brood theory by Macleod (1939) and Milne (1945) offers an explanation for the seasonal appearance of ticks on the assumption that the whole population undergoes cyclical changes in its composition. In winter and summer it consists of engorged individuals in a passive state undergoing development, while in spring and autumn the emergence of the succeeding instars transforms it into an active population seeking food, and hence infestation of stock animals in those seasons.

Macleod (1932, 1939) confirmed Wheler's observations, and concluded from his experiences in Northumberland, Southern Scotland, and the Western Highlands of Scotland that the activity curves for all parts of Britain were probably diphasic in character, with the peak periods of infestation of the host occurring in spring and autumn. He drew attention to the fact, however, that the decline in activity at the end of spring could not be a simple consequence of the engorgement of all available unfed ticks, since the decrease in infestation level took place concurrently in all districts without regard to the

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density of stocking of the host animals. For example, infestation of sheep diminishes in comparable degree simultaneously whether on farms with one sheep per acre, or on farms with one sheep to five or more acres. He concluded, therefore, that the seasonal variations in tick activity were not to be explained on the basis of the two-brood theory, but rather that tick activity and host infestation are directly controlled by climatic factors. Thus, Macleod (1932, 1936, 1939) suggested a hypothesis of temperature control, and he claimed (1935a) that the host-seeking activities of unfed ticks are confined to a limited range of temperature conditions (40°F-60°F) through the operation of a negative geotropisim within that range. Above the upper temperature limit, the tropistic movements undergo a reversal, and the tick recedes from the herbage tips, and its chances of acquiring a host are thereby reduced. Below the lower limit of temperature, cold torpor supervenes and the tick becomes inactivated. In Macleod's opinion, seasonal activity is merely the result of the influence of temperature on behaviour.

Totze (1933) working in North Germany advanced evidence for the view that there is inherent in the tick a seasonal physiological rhythm which is independent of environmental conditions, and Falke (1931) recorded a phenomenon of the nature of a diapause which intervened to retard development in winter indoors, even when temperatures were maintained at levels considerably above winter temperatures in nature out of doors. Macleod (1934, 1935b) was unable to confirm the findings of

/Totze

Totze and Falke regarding ticks in Great Britain.

More recent observations on the seasonal behaviour of tick-populations in Great Britain raise doubts regarding the adequacy of Macleod's temperature hypothesis. Fleming (1940 unpublished) reported that infestation of sheep in Ettrick Valley was confined to the spring months, and throughout the rest of the year the stock remained relatively tick-free (Macleod (1932) mentions that "the autumn recrudescence of activity was common to both districts but was more pronounced in Argyll than in Selkirkshire"). Fleming's observations were confirmed by the author in 1943-47 in Ettrick Valley, and similar conclusions were obtained from surveys of tick infestations during the same years in Yarrow Valley and Tweeddale. It was concluded that from 1939-1947 tick activity in the counties of Roxburgh, Selkirk, and Peebles was exclusively a spring phenomenon. Milne (1945, 1947) records a restriction of tick activity to the spring months during the years 1940-1947 in the College Valley, Northumberland. On the other hand in other Northumbrian Valleys, and in Cumberland, Milne observed a diphasic activity cycle such as Macleod assumed to be the general pattern for Britain. Other areas where the diphasic cycle has been observed include South Wales (Edwards and Arthur, 1946); Dumfries-shire (Foggie, personal communication); Sutherland (Carrick, personal communication); Argyllshire, Inverness-shire, Perthshire, Ross-shire, Devonshire, Denbighshire (Campbell - unpublished) and South West Ireland (Crowley - personal communication).

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In North East Scotland, the activity of the sheep tick differs widely from that reported in other parts of Britain according to Hendrick, Moore, and Morison (1938), in that midsummer is the season of maximum activity. Macleod (1939) refers to this observation, and suggests that the conditions on the hill in question were atypical, but Moore (1938, 1939, 1943) records a similar state of affairs on other hills in the area. Macleod (1939) suggested the further possibility, that the ticks in North East Scotland may comprise a physiologically modified race.

Milne (1945) reviewed all the hypotheses that have been put forward (two-brood, temperature control, diapause and seasonal rhythm, and physiological races) and arrived at the non-committal conclusion "that all four theories may contribute something to the truth", but he considers that "temperature-cum-humidity in the microclimate deserves further investigation."

In spite of the considerable body of work devoted to the study of ticks in the field, there is no direct evidence available regarding the developmental processes in nature. Apart from a single observation by Macleod (1932) and some unpublished evidence by Fleming, information on the time-relations of the developing tick has been derived almost entirely from experiments confined to the laboratory, and ideas on the course of development in nature have been based on theoretical deductions from such work. Consequently, the speculative nature of hypotheses advanced towards the explanation of seasonal behaviour is clearly due to inadequate information on the life-history of the species in its natural

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environment, a fact realised by Dr. A. E. Cameron who in 1942 suggested to the author the desirability of an investigation planned to gain a fuller understanding of the course of the tick life-cycle in the field in Scotland.

Observations were made on the development of engorged ticks, and their habits subsequent to emergence, at selected stations in the field between 1943 and 1947. Records of rainfall, air temperatures, and of the temperature and relative humidity beneath two types of vegetative cover, were kept continuously throughout the course of the work. Parallel studies were carried out, at all stages of the investigation, on the development of engorged ticks under controlled conditions in the laboratory.

Following Macleod it is proposed to regard the life cycle of the tick as a succession of alternating phases active and passive. After completion of engorgement there follows a stage of existence on the ground when the tick remains inconspicuous, and undergoes metamorphosis towards the next instar (or in the case of adults at the time of oviposition and incubation of eggs). The termination of the passive phase is regarded as the time of emergence of the new instar, and the events leading up to acquiring a host and completion of engorgement are here regarded collectively as comprising the active phase, although it is recognised that tick-activity is a term usually confined to the host-seeking behaviour. The description is thus divided for convenience into two parts dealing separately with the two phases of existence under the headings

1. The engorged tick and its development

and 2. The unengorged tick and activity.

Fig. 1.

Apparatus for collecting and
washing ticks engorged on hedgehogs.

METHODS AND TECHNIQUE

Engorged adults and nymphs were readily obtained during the active seasons by collection from cattle and sheep. (Large numbers of replete females were often gathered from the ground in pens where sheep had been gathered.) Some larvae were included in these collections, but they were supplemented by larvae collected from infested ground by captive hedgehogs. On fine days the hedgehogs were allowed to run over the ground for periods of about one hour, and then confined to cages over recovery trays filled with water, from which the engorged larvae were later removed.

At the seasons when ticks were not readily obtainable in the field, engorged ticks were obtained by feeding stock ticks (stored at field, or known constant temperatures) on hedgehogs and sheep. When sheep were used as hosts, the ticks (usually adults) were confined in muslin bags attached to the ears by a beeswax-resin mixture, and recovered at appropriate intervals. Hedgehogs were used (Langeron, 1934, and Macleod, 1932) chiefly for feeding nymphs and larvae. On account of the contamination of the water in the recovery trays with hedgehog food and faeces it was necessary to devise a method of washing the ticks fed by this method. The water-trays were removed twice daily and the ticks counted as they were removed through a nozzle connected through a collecting flask to a suction pump (Fig.1). The ticks were collected in lots (usually 50 nymphs or 500 larvae) and transferred to Petri dishes. Loose debris was removed through a finer nozzle of which the aperture was too small to permit the passage of engorged larvae (hypodermic syringe needles after

/removal

removal of their points were found most suitable for this purpose). Badly contaminated samples necessitated repeated washings with water. After all debris was removed a solution of 0.1% brilliant green, or gentian violet was then added and the ticks were left for 5 - 10 minutes, after which the dye solution was removed and the ticks washed into a Büchner filter funnel, and finally dried by spreading over clean filter paper. This treatment reduced the subsequent development of moulds during incubation, and made it possible to deal with as many as 10,000 larvae a day if necessary.

For routine observations in the laboratory ticks were incubated in shell glass tubes ($1\frac{1}{2}$" by $\frac{1}{2}$") closed with non-absorbent cotton wool. They were confined at the rate of one female, ten nymphs, or one hundred larvae per tube. Rapid recognition of the different series of tubes was facilitated by the use of coloured wools. Some difficulty was experienced in labelling individual tubes. Incubation of ticks required fairly long periods at high relative humidities and these conditions are apt to encourage the growth of moulds, with consequent destruction of the labels. Various materials were tried in order to overcome this difficulty including waxed paper and even celluloid, but were not wholly satisfactory, and the method ultimately adopted was to enclose a numbered paper-slip in each tube, and with a fairly large surplus of tubes for each experiment it was found convenient merely to discard those in which contamination with moulds became excessive.

Most of the laboratory observations were carried out at relative humidities at or near saturation. The tubes were stored in 1 quart screw-topped glass jars containing a basal

layer of approximately ½" of plaster of Paris kept damp with a saturated solution of calcium sulphate. When experiments were conducted at lower controlled relative humidities, the tubes were stored in dessicators over saturated salt solutions (Buxton (1931), Buxton & Mellanby (1934)) such as Ammonium chloride, Ammonium hydrogen phosphate etc.

desiccators.

Incubation was studied at a range of temperatures including 5°, 8°, 10°, 14°, 18.5°, 21°, 25° and 30°C., and in some cases the ticks were subjected to diurnal alternations of temperature by transferring them at intervals from one incubator to another. Temperatures below room-temperature were maintained in ice-cooled incubators.

During the course of development the ticks were disturbed as little as possible until the approach of the time of emergence. When moulting of nymphs and larvae was due to occur, daily inspections were made, and the moulted individuals were recorded and removed to fresh tubes. The exuviae were also removed to prevent possible misinterpretations. In this way an accurate record of the period of development was obtained for every individual of a sample population. In the case of developing eggs an attempt was made to utilise the method of enumeration described by Nuttall (1913) but manipulation invariably resulted in damage to the eggs, and consequently it was obligatory to confine observations on the duration of embryonic development to the time of onset of hatching of egg clusters. (Cf. Macleod (1935b) who encountered the same difficulty.) To obtain more precise information on the duration of oviposition, and the distribution of variations in the embryonic developmental period, a method was adopted which

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involved the removal of the female to a new clean tube daily during the course of oviposition. Thus a daily egg quota was obtained and observations were made on the duration of egg development for several egg quotas from a single female.

For observations on development under field conditions, 2" x 1" diameter corked phosphor-bronze, or brass wire-gauze tubes were employed (40 mesh per linear inch). A loose plug of grass was included in each tube, and the ticks were confined at the same rate as in the laboratory experiments. The tubes were placed at ground level at various sites on a hill-sheep farm, embracing several kinds of vegetational cover. Parallel series of ticks were enclosed in short lengths (2") of $\frac{3}{4}$" diameter glass tubing closed at both ends with glass-wool plugs. These permitted of more rapid examinations and made it possible to follow the course of development without disturbing the interned ticks until the time of emergence, when examinations of the wire-gauze containers were begun. There was a free ventilation in both types of tube and it was assumed that the atmosphere inside the tubes was probably not widely different from that of the microclimate within the vegetation in which they were placed. Since there were no significant differences between development or survival rates in the two types of tube, it was considered justifiable to dispense with the wire-gauze tubes in the later stages of the investigation on account of the greater convenience of the glass type. In all experiments controls were maintained in the field in the standard plaster-base storage jars.

At two of the field stations, one a heather site, and the other a grass (Agrostis-Festuca) site, both at 650 feet O.D., continuous records of temperature and humidity were taken by

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recording Edney thermohygrographs. These instruments were constructed with the recording elements situated in arms which projected horizontally twelve inches from the side, and the instruments were so placed that the records applied to the microclimate just above the ground level beneath the vegetation cover. The results obtained under open field conditions and those obtained under controlled field conditions could thus be compared and related.

To serve as a check on conclusions based upon these methods, and to complete the investigations on the history of ticks subsequent to their emergence from the preceding developmental condition a further series of field experiments was undertaken. A number of dispersed plots approximately 10 yards by 10 yards was fenced off and rabbit proofed. Engorged ticks were introduced and planted at the base of numbered pegs and left unconfined to undergo development. There was practically no lateral spread of ticks from these artificially infested sites, and with careful observation naked-eye examinations of planted ticks were always possible at each visit to the enclosures. Infestations were made at the rate of 1,000 engorged larvae or 100 nymphs, or 10 females per site, and at least 10 sites were infested on each occasion. At intervals after introduction of the ticks turfs of one square foot were removed and the ticks extracted by a modification of the magnesium sulphate flotation technique as used for estimating wireworm populations (Salt and Hollick 1944). The examinations were considerably facilitated by the use of a power-washing machine designed and loaned by Dr. F. S. J. Hollick, Department of Zoology, Cambridge University.

Throughout the duration of the investigation, the course of

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events in the natural tick populations in the areas under study was surveyed (1) by the use of the Techniques of counts on sheep and cattle, (2) by the blanket-dragging method described by Macleod (1932) and Milne (1943), and (3) by a method of static blanketing developed during this work (Campbell 1944. Agricultural Research Council report unpublished). These survey-methods are mentioned here merely by way of reference, but it is not proposed to enter into a detailed discussion of the results achieved by their use.

SECTION I

The Engorged Tick : Development

SECTION IA

Duration of Developmental Stages in the Field

Apart from a single reference to the development of tick eggs out of doors by Macleod (1932), the only other work devoted to the study of development of Ixodes ricinus L in the field in Great Britain was undertaken by Mr. I. Fleming, Research Scholar, Department of Entomology, University of Edinburgh in 1938, at the suggestion of Dr. A. E. Cameron, Reader in Entomology, who had in mind the desirability of completing the account of the life-history of the Sheep-Tick in the field. Despite the accumulation of a considerable literature on the habits and host-relationships of the tick, the question of its life-cycle under natural conditions had been neglected. Fleming was further instructed to enquire into the question of so called "broodedness" of the tick and to variable distribution in the Border counties of Scotland. By way of introduction to the investigation of the life-cycle, Fleming by confining engorged ticks in muslin covered tubes among herbage on a hill pasture in Ettrick, Selkirkshire was able to demonstrate that in a sample of ticks fed in spring (March-May) the earliest did not complete their development until mid-August, when larvae, nymphs and adults began to emerge simultaneously.

Fleming's work was interrupted in 1940, and still with the intention of completing the life-cycle, Dr. Cameron in 1942 recommended to the present author to continue the investigation where Fleming left off. The present paper records the results of this investigation.

There is one other record on the time-relations of development of a tick in the field by Smith (1945) who studied

/Ixodes

Ixodes dentatus Neum. in Massachusetts and Georgia, and it will be of interest to compare his results with those obtained on Ixodes ricinus L. in Scotland.

The observations described in the present paper were made on ticks from several districts of Scotland and Northern England. The ticks were placed in tubes and transferred to a variety of stations on the hill at Traquair, Peeblesshire, and for three years the work was confined to this area. At the two principal stations a temperature-humidity record was kept within the vegetation at 600 feet O.D. In addition to these two, there were twelve subsidiary stations, in which ticks were kept for comparative purposes, but it was not possible to record the temperatures or humidities in these sites except on the occasions when they were visited. Between them the following types of habitat were represented:-

Callunetum associations

1. Climax heather, over 1' tall. 600' O.D. - Principal site.
2. Climax heather, c. 8" tall. 600' O.D.
3. Seral heather 3 years (1944)
   including Vaccinium & Empetrum 700'
4. Seral heather 2 years (1944)
   mossy floor (Hylocomium sp.) 700'
5. Seral heather.
   Bare ground, 1st year (1944) 600'

Graminaceous associations

6. Climax Agrostis-Festuca 600' O.D. - Principal site.
7. Seral Agrostis-Festuca
   (return from cultivation) 650'
8. Sheep-lair facies
   Festuca + Poa trivialis 1200'

9. Agrostis-Festuca. Bracken invaded 600'

10. Agrostis - Juncus articulatus 600'

(Flush facies)

11. Nardetum strictae Association 1500'

12. Molinietum coeruleae Association 900'

Other associations

13. Pteridietum aquilinae 800'

14. Juncetum communis (agg) 500'

These stations together afford a representative sample of the range of conditions occurring on hill pastures in the Southern Uplands of Scotland.

Observations were most detailed at sites 1 and 6 where the results could be related directly to the record of temperature and relative humidity in the microclimate, while at the other sites they were just sufficiently extensive to determine how far conclusions based on results obtained at the principal sites were applicable to other habitats. Some differences were recorded in the survival rates at the different stations, but, except in the cases of stations 8 and 11 which were situated on exposed hill-tops, where the population density of ticks in nature was extremely low, there was no significant difference noted between the time relations of development at any of the sites. From the three years experience at Traquair, it was concluded that variations in environmental vicissitudes due to vegetational differences were not sufficiently marked to produce significant differences in the course of the life-cycle, and that the course of events observed at the principal stations was representative of the major part of the tick-infested land

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in the area. (While it is not the present intention to deal with the surveys made on the distribution of ticks on infested hills, it is of interest to add at this point that the influence of vegetation on the differential survival rate of ticks was much less pronounced than had been anticipated in view of Milne's (1944, 1946) conclusions derived from blanket-sample surveys in Northumberland).

In 1946 the experiments were continued on a reduced scale at Traquair, and were extended to a limited number of sites at Benderloch, Argyllshire, and Glensaugh, Kincardineshire, as representing areas where the cycle of tick-activity showed, or had been reported to show differences from that found in the Border area. On account of the long distances from Edinburgh, however, these sites could only be visited at fairly long intervals, and consequently the observations were limited. The results are sufficiently complete however to be taken as a good true indication of the course of events in these areas, and they provide sufficient information to serve as a comparative check on the deductions drawn from the Border studies.

A summary of the temperature data for site 1 is given in Table 1, and represented graphically in fig. 2. For convenience, the months are divided into periods I, II & III representing the 1st - 10th, 11th - 20th, and 21st to end of month respectively. The month to month differences in period III are ignored, and the period is regarded as a ten day interval for all months. We have been unsuccessful in reducing the data on relative humidity to convenient dimensions. (It is obviously meaningless to quote the mean values for a period.) From November to March the relative humidity of the microclimate within both heather and

/grass

grass remained almost continuously at saturation level throughout the whole period of investigation. In the warmer months, there was a diurnal fluctuation during dry periods, between saturation for at least six hours during the hours of darkness, and lower levels down to 60% during the daytime. The driest conditions encountered were a 10 millibar saturation deficiency in the heather site, and a 12 mb saturation deficiency in the grass site. There were very few occasions, however, when the saturation deficiency at either site exceeded 8 mb (60% RH at 18.5°C) and dessication was never sufficiently severe to become a limiting factor. Although no success was obtained in attempts to correlate events in development with the humidity conditions, Table 2 indicating the number of hours during which the relative humidity fell below 90%, 80% and 70% is included for completeness.

The results obtained for the various developmental processes are dealt with seriatim and the data for site 1 are summarised in Tables 3 - 15.

1. Observations on Tubed Ticks at Traquair: Peeblesshire

In the protocols of the experiments which are summarised below, the ticks which were maintained as field stock before being fed on experimental animals are marked with an asterisk, all other ticks were obtained directly from their hosts in the field and the source of origin is indicated in each case.

(a) Preoviposition period

Table 3 gives a summary of the duration of the preoviposition period in a series of over one thousand females fed during the years 1943 - 1946.

TABLE 1

Summary of Temperature Record under Heather at 600' O.D.

Traquair, Peeblesshire °C

Month	1943			1944			1945			1946			1947		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Jan I				2.0	3.0	2.5	1.0	1.5	1.5	5.0	6.5	6.0	3.0	3.5	3.5
II				2.0	5.0	3.5	0.5	1.5	1.0	4.5	5.0	5.0	3.5	4.5	4.0
III				3.5	5.0	4.0	-1.0	0.0	-0.5	4.0	5.5	5.0	0.0	0.0	0.0
Feb I				2.0	3.5	2.5	1.5	2.5	2.0	5.0	7.0	6.0	-1.5	-0.5	-1.0
II				0.5	2.0	1.5	2.5	5.0	3.0	0.0	3.5	1.5	-0.5	1.0	0.5
III				1.0	2.0	1.5	5.5	7.5	7.0	0.5	3.5	2.0	0.0	0.5	0.5
Mar I				0.0	2.0	1.0	6.5	8.0	7.0	2.0	4.0	3.0	0.0	0.0	0.0
II				1.5	5.5	3.5	8.0	11.5	10.0	4.5	6.0	5.0	0.5	1.0	0.5
III				2.5	7.5	5.0	8.0	12.5	10.0	8.5	10.0	8.0	0.0	1.0	0.5
Apr I	4.0	8.0	5.5	2.5	7.5	4.5	8.0	12.0	9.5	6.0	11.5	8.5	0.5	4.0	2.0
II	6.5	10.0	8.0	4.5	6.0	5.0	9.5	14.5	12.0	6.0	11.0	8.5	3.0	8.0	5.5
III	4.5	9.0	6.5	5.0	11.0	7.5	8.0	12.5	9.0	5.5	9.5	7.5	3.0	6.0	4.0
May I	3.0	8.5	5.5	4.5	9.5	7.0	8.0	13.0	10.5	5.0	14.0	9.0	3.5	8.0	5.5
II	6.0	12.0	9.0	5.0	9.0	7.0	1.0	15.5	13.0	5.0	12.0	8.5	5.0	11.0	8.5
III	7.0	13.0	10.0	7.0	13.0	10.0	9.5	14.0	12.0	8.5	14.5	10.5	6.0	12.0	9.0

Jun/

TABLE 1 (cont.)

Month		1943			1944			1945			1946			1947		
		Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Jun	I	9.0	13.0	10.5	8.0	12.0	9.5	11.0	15.0	13.0	8.5	13.5	11.0	11.5	13.5	12.5
	II	9.0	13.0	10.5	7.5	13.5	10.5	10.5	15.5	14.5	8.5	13.0	10.5	11.5	14.5	13.0
	III	9.5	14.5	12.0	9.5	15.5	11.5	10.5	16.0	14.5	10.0	16.0	12.5	13.5	17.0	15.0
Jul	I	9.0	14.5	11.0	10.5	15.0	12.5	12.0	18.0	15.0	10.5	18.0	13.0	12.0	15.5	14.0
	II	9.0	14.0	12.0	10.0	14.5	12.0	10.5	17.5	15.0	11.0	15.5	12.5	12.5	18.0	15.5
	III	10.0	17.5	13.5	10.5	15.5	12.5	10.5	16.5	13.5	10.5	13.5	12.0	13.5	16.5	15.0
Aug	I	11.5	13.0	12.0	10.5	17.5	14.0	10.5	17.0	14.0	11.5	16.0	13.5	10.0	16.0	13.0
	II	10.0	13.0	11.0	11.0	15.0	12.5	12.5	17.5	14.5	11.5	15.5	13.5	11.5	19.0	15.0
	III	9.5	12.5	11.0	10.0	13.5	11.5	10.0	15.5	14.0	10.5	14.5	12.5	11.0	18.5	14.5
Sept	I	9.0	12.0	10.5	7.0	9.0	8.0	10.0	17.0	13.5	11.0	13.5	12.5	10.0	14.5	12.0
	II	9.5	12.5	11.0	7.5	11.5	9.5	13.5	16.5	14.0	10.0	11.5	11.0	9.5	13.5	11.5
	III	5.5	9.5	7.5	7.0	9.5	8.0	10.0	12.5	12.0	10.5	12.5	11.5	7.0	10.5	9.0
Oct	I	7.0	9.5	8.5	5.5	8.0	6.5	10.5	14.0	12.0	9.5	11.5	10.5	8.0	11.0	9.0
	II	6.0	8.5	7.0	6.0	7.0	6.5	7.5	12.0	9.5	8.5	9.5	9.0	7.0	10.0	8.5
	III	6.5	9.0	7.5	5.0	6.5	5.5	8.5	11.0	10.0	5.5	7.5	7.0	6.5	8.5	7.5

Nov/

TABLE 1 (cont.)

Month	1943			1944			1945			1946			1947		
	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean	Max.	Min.	Mean
Nov I	6.0	8.0	7.0	3.5	4.5	4.0	8.0	10.0	9.0	7.5	9.0	8.5	7.0	9.0	8.0
II	2.0	4.0	3.0	2.5	4.0	3.0	5.5	9.5	7.5	5.5	6.5	6.0	2.5	4.5	3.0
III	2.5	4.0	3.0	2.0	3.0	2.5	6.5	10.0	8.0	6.5	7.5	7.0	3.0	7.0	5.5
Dec I	3.0	4.5	3.5	1.5	2.5	3.0	6.5	7.5	7.0	4.0	4.5	4.5			
II	0.5	1.5	1.0	1.5	2.5	2.0	6.0	8.5	7.5	3.0	4.0	3.5			
III	1.5	3.5	2.5	1.0	2.0	1.5	6.5	7.5	7.0	4.0	5.0	4.5			

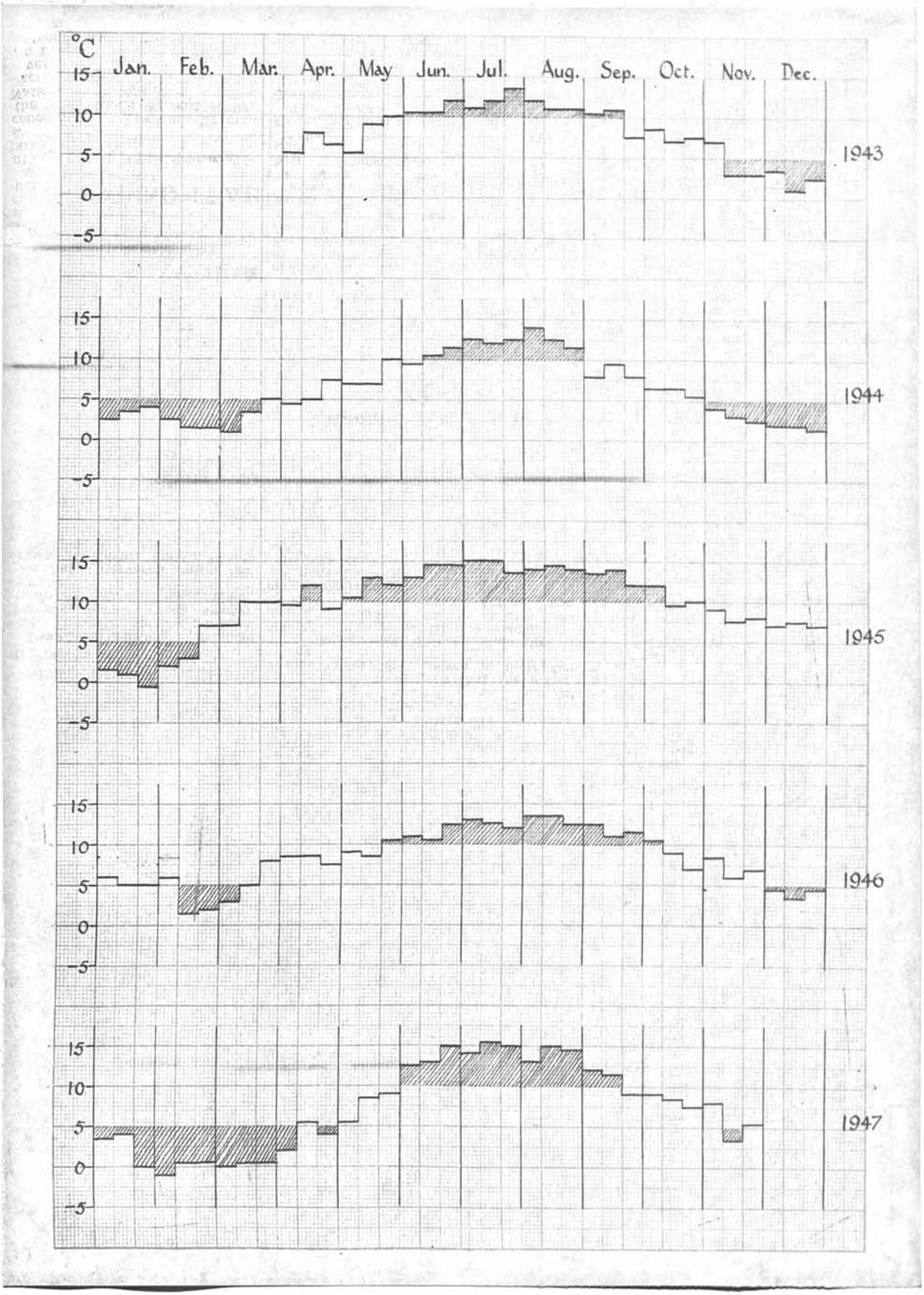

Fig. 2. Mean Temperatures in Heather Site.
Traquair.

TABLE 2

Summary of Record on Relative Humidity under Heather at 600' O.D.

Hours per day with Relative Humidity less than saturation

Month	1943			1944			1945			1946			1947		
	90%	80%	70%	90%	80%	70%	90%	80%	70%	90%	80%	70%	90%	80%	70%
Jan I	-			0			0			0			0		
II	-			0			1	0		0			0		
III	-			0			0			0			0		
Feb I	-			0			0			0			0		
II	-			0			0			0			0		
III	-			0			0			0			0		
Mar I	-			1	0		7	1	0	1	0		0		
II	-			10	3	0	6	1	0	1	0		0		
III	-			9	3	0	2	1	1	4	2	1	0		
Apr I	7	1	0	2	1	0	3	1	0	13	7	5	3	2	0
II	5	2	0	1	0		6	2	1	11	6	3	0		
III	5	2	0	9	5	1	13	7	4	13	7	3	0		
May I	6	4	1	6	3	1	6	3	2	16	13	10	4	1	0
II	8	4	2	8	5	2	7	4	1	10	7	5	0		
III	7	4	2	11	7	3	6	3	0	8	6	4	9	6	1
Jun I	1	0		1	0		2	0		3	1	1	3	1	0
II	2	0		8	2	1	7	4	1	5	2	1	4	0	
III	6	3	1	7	5	3	1	1	0	7	5	2	2	1	0
Jul I	6	2	0	1	0		7	1	1	9	5	2	3	0	
II	5	0		6	3	0	1	0		4	3	2	0		
III	8	2	1	7	2	0	5	1	0	1	0		0		
Aug I	0			5	3	1	5	1	1	5	1	0	8	3	1
II	0			3	1	0	0			3	0		10	6	1
III	0			7	2	1	3	0		1	0		11	7	2
Sept I	0			0			7	2	0	0			6	2	1
II	0			0			0			0			1	0	
III	3	0		0			0			0			1	0	
Oct I	0			0			0			1	0		3	0	
II	1	0		0			0			5	0		1	0	
III	0			0			0			4	0		1	0	
Nov I	1	0		0			0			1	0		0		
II	4	0		0			0			1	0		1	0	
III	0			0			0			0			0		
Dec I	0			0			0			0			-		
II	0			0			0			0			-		
III	0			0			0			0			-		

TABLE 3

Preoviposition period in the field

Group	Source	No.	Engorgement completed	Laying began		Minimum duration
				Earliest	Latest	
1	Peeblesshire	20	17.iii.43	14.v.43	10.vi.43	58 days
2	Peeblesshire	24	25.iii.	17.v.	5.vi.	53
3	Peeblesshire	30	6.iv.	20.v.	18.vi.	44
4	Peeblesshire	36	15.iv.	25.v.	12.vi.	38
5	Perthshire	15	12.v.	9.vi.	15.vi.	27
6	Peeblesshire	10	8.vi.	30.vi.	10.vii.	22
7	Peeblesshire	5	16.vi.	8.vii.	15.vii.	22
8	Peeblesshire	5	21.vi.	12.vii.	15.vii.	21
9	Selkirkshire	12	22.iii.44	15.v.44	8.vi.44	54
10	Peeblesshire	30	1.iv.	20.v.	8.vi.	49
11	Peeblesshire	20	8.iv.	21.v.	8.vi.	43
12	Selkirkshire	100	17.iv.44	25.v.	12.vi.	38
13	Peeblesshire	10	5.v.	4.vi.	12.vi.	30
14	Cumberland	20	29.v.	23.vi.	3.vii.	25
16	Peeblesshire	5	8.vi.	29.vii.	5.viii.	21
17	Aberdeenshire	15	25.vii.	14.viii.	21.viii.	20
18	Perthshire	12	10.viii	9.ix.	20.ix.	30
19	Perthshire	8	17.viii.	22.ix.	28.ix.	36
20	Cumberland	16	29.viii.	4.x.	15.x.	36
21	Perthshire	15	12.ix.	9.x.	19.x.	27
22	Cumberland	30	22.ix.	25.x.	1.xi.	33
23	Cumberland	30	24.ix.	25.x.	29.x.	31
24	Perthshire	30	2.x.	30.x.	6.xi.	28
25	*	10	18.xi.	6.i.45	14.iii.45	49
26	*	10	15.xii.	14.iv.	11.v.	117

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TABLE 3 (Cont.)

Group	Source	No.	Engorgement completed	Laying began		Minimum duration
				Earliest	Latest	
27	*	10	12.i.45	20.iv.45	21.v.45	88 days
28	*	8	18.ii.	9.v.	21.v.	60
29	*	9	12.iii.	8.v.	18.v.	57
30	Peeblesshire	7	19.iii.	11.v.	26.v.	53
31	Cumberland	6	21.iii.	11.v.	20.v.	51
32	Cumberland	23	22.iii.	15.v.	20.v.	54
33	Selkirkshire	6	28.iii.	18.v.	24.v.	51
34	Selkirkshire	14	30.iii.	16.v.	23.v.	47
35	Peeblesshire	20	31.iii.	15.v.	28.v.	45
36	Selkirkshire	12	6.iv.	15.v.	21.v.	39
37	Peeblesshire	71	9.iv.	18.v.	24.v.	39
38	Selkirkshire	35	9.iv.	18.v.	24.v.	39
39	Peeblesshire	47	10.iv.	19.v.	26.v.	39
40	Peeblesshire	101	12.iv.	15.v.	25.v.	33
41	Peeblesshire	35	13.iv.	18.v.	24.v.	35
42	Cumberland	42	16.iv.	21.v.	26.v.	35
43	Perthshire	31	17.iv.	22.v.	30.v.	35
44	Argyllshire	20	30.iv.	26.v.	31.v.	26
45	Selkirkshire	15	9.v.	6.vi.	21.vi.	27
46	Cumberland	14	25.v.	13.vi.	18.vi.	19
47	Cumberland	18	1.vi.	21.vi.	26.vi.	20
48	*	10	15.vi.	2.vii.	9.vii.	17
49	*	10	22.vi.	8.vii.	14.vii.	16
50	*	5	6.vii.	22.vii.	24.vii.	16
51	Aberdeenshire	12	12.vii.	31.vii.	7.viii.	19
52	Aberdeenshire	18	25.vii.	15.viii.	30.viii.	21

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TABLE 3 (Cont.)

Group	Source	No.	Engorgement completed	Laying began		Minimum duration
				Earliest	Latest	
53	Perthshire	12	3.viii.45	21.viii.45	29.viii.45	18 days
54	Perthshire	8	17.viii.	4.ix.	9.ix.	18
55	Perthshire	9	26.viii.	12.ix.	16.ix.	17
56	Aberdeenshire	8	30.viii.	16.ix.	21.ix.	17
58	Perthshire	18	14.ix.	4.x.	16.x.	20
59	Cumberland	20	14.ix.	4.x.	14.x.	20
60	Aberdeenshire	24	19.ix.	7.x.	13.x.	19
61	Cumberland	54	21.ix.	10.x.	21.x.	20
62	Perthshire	16	21.ix.	10.x.	16.x.	20
63	Perthshire	17	1.x.	21.x.	10.xi.	20
64	Perthshire	16	11.x.	29.x.	12.xi.	18
65	*	6	18.x.	15.xi.	2.xii.	28
66	Perthshire	20	22.x.	17.xi.	4.xii.	26
67	*	8	26.xi.	4.i.46	27.iv.46	39
68	*	6	17.xii.	20.iv.	20.v.	131

Table 3 reveals several striking features in the duration of the preoviposition period at different seasons of the year. When replete female ticks were collected during the normal period of spring activity, the duration of their preovipositional development was apparently related quantitatively to the environmental temperature. Thus between mid-March and late May in all three years, the ticks which engorged earliest required the longest interval before they began to lay eggs, while those which fed late in the season were enabled to complete their preovipositional phase in a much shorter time. A

/progressive

progressive decrease is observed as the season advances and temperatures become higher in groups 1-8, 9-14, and 30-47.

After the termination of the spring period, ticks are not readily obtainable in nature until mid-August. No evidence of a July peak of activity, such as has been reported by Moore in Aberdeen, was obtained during this investigation, although small numbers of engorged ticks were encountered in July in Aberdeenshire and Perthshire. The midsummer activity is, therefore, considered here as representing the earliest phase of the second or autumn period of tick activity. In contrast to the spring-active ticks, the autumn-active ticks do not reveal a direct relationship between the duration of the preoviposition period and the temperature. Although the temperatures undergo a progressive decline from the beginning of August there is no evidence of a progressive prolongation of the preoviposition period from then until mid-October. In 1944 (Series 17-24) the preoviposition varied only slightly around the 30 day mark. - Thus in group 18 fed on 10th August the minimum time was 30 days, while in group 24 fed on 2nd October the earliest individuals commenced oviposition after 28 days, and yet from the temperature summary (Fig. 2) it is seen that in August the mean temperature lay above 10°C while in October it had fallen to around 5°C. Similarly in 1945 there was little difference in the preoviposition period of individuals fed in August and those fed in October.

It will be noted that in 1945 the oviposition period in autumn-fed females (groups 51-66) was consistently shorter than in the autumn ticks of the previous year (groups 16-24). It may be added that in 1946 the time required (not recorded in Table 3)

/was

was about 28 days, and it may be observed that the summer and autumn temperatures of 1944 and 1946 were from 1°C to 2°C lower than in 1945. If this slight elevation of temperature can be regarded as the reason for the shorter preoviposition interval in 1945, it is difficult to understand how small annual seasonal temperature differences can influence the rate of development, while the very much more significant seasonal changes of temperature in a single year apparently produce no response. Discussion of this subject must, therefore, be postponed until the temperature responses of autumn ticks at controlled temperatures have been considered.

The laboratory fed groups 48-50 do not differ to any great extent from the late spring individuals on the one hand, and the early autumn ones on the other, and the groups may be regarded as a connecting link between the two series. In the other 'out-of-season' ticks, however, there is a very significant change which occurs around mid-December. Individuals whose engorgement is completed before then appear to be able to complete pre-ovipositional development in the manner of autumn ticks, but when engorgement is postponed until after mid-December the preoviposition period is considerably prolonged and egg-laying does not commence until the spring. Thus, the latter individuals behave like very early spring ticks (e.g. groups 26-29, Table 3).

From the column in which the dates of inception of oviposition are detailed, it is seen that there is a considerable range of variation in the duration of the preoviposition period, and this is particularly evident in those individuals which feed early in spring (vide groups 1-4, 9-11, 28-39) when the temperatures are lowest.

/If

If the results are considered from the point of view of tick populations, rather than individual ticks it is apparent that the spring-active population presents a more compact seasonal relationship than the autumn-active population. The active feeding season of females extends over approximately the same range of time (up to 12 weeks) in both spring and autumn, but while the onset of oviposition in spring occurs within the limits mid-May to mid-June, and the duration of oviposition occurs uniformly in the whole of the spring-fed female population, in the autumn period, the inception of oviposition is not so sharply defined but may occur any time between August and October according to the time of engorgement.

(b) Course of Oviposition

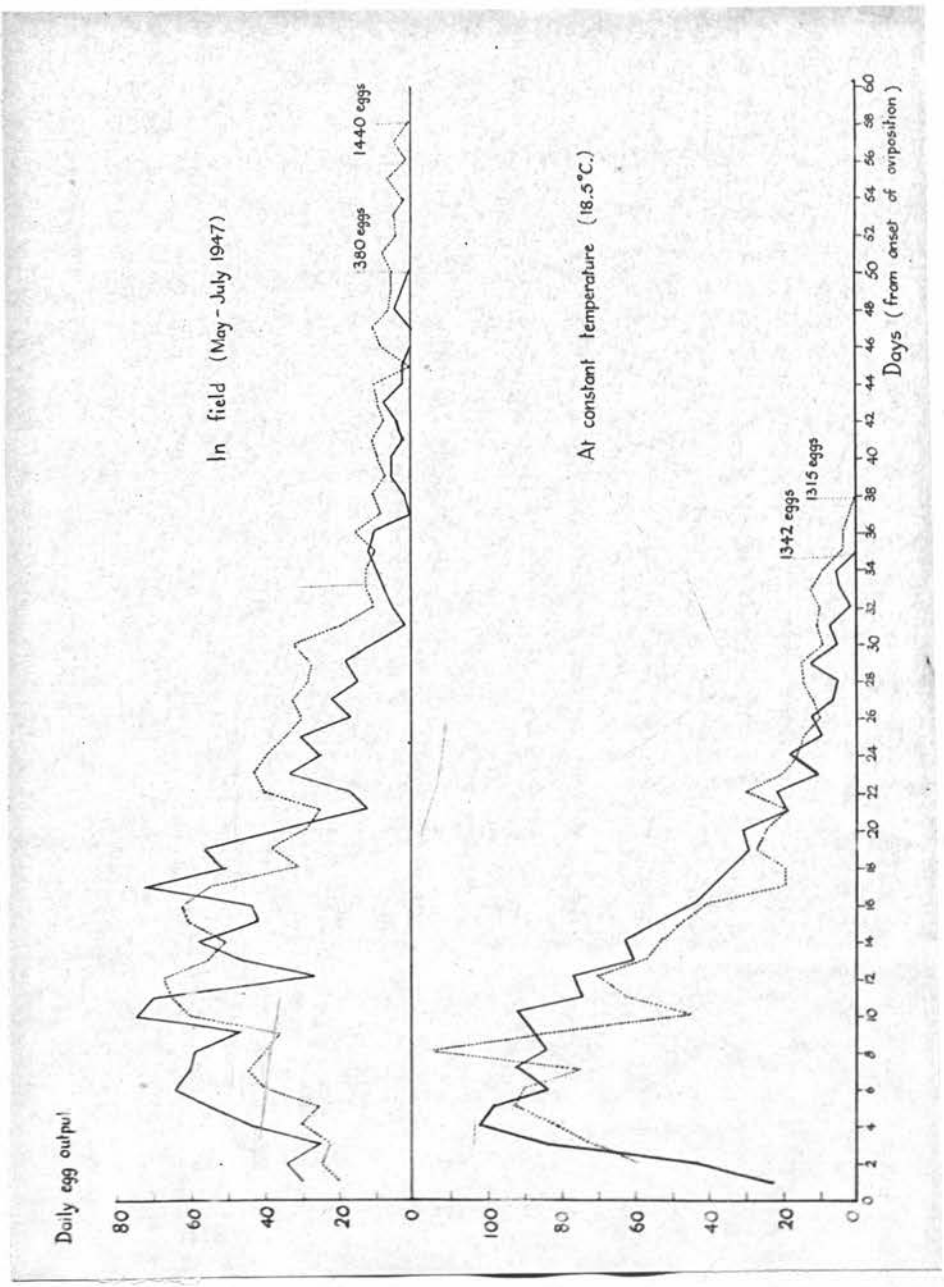
When preovipositional development has been completed, the female commences egg-laying. Oviposition is an uninterrupted process in the tick, and the female continues to lay eggs until the ovary is exhausted, after which death supervenes. There is no advantage to be gained by detailing the rate of egg-laying observed in ticks under field conditions, since there were no significant differences observed from the results obtained under conditions of constant temperature etc. in the laboratory. Examples of the rate and duration of oviposition are included in Figs. 3 and 10a. The greatest output of eggs was achieved during a period of about one week beginning some 5 days after the inception of egg laying. After this time eggs were laid at a steadily declining rate until the process was completed in from 8 to 10 weeks. Macleod (1935b) has shown how the rate of oviposition under laboratory conditions is influenced by temperature. A direct relationship with temperature was

/observed

Figs. 3 and 10a.
Course of oviposition in individual females. Daily egg output.

Figure 3.

Figure 10a.



observed in the present investigation in the rate of egg laying under field conditions. When the temperature fell below 2°C there was a temporary inhibition of oviposition.

(c) Embryonic development and Hatching of eggs (Incubation)

On account of the variation in the times of onset of hatching it is impossible conveniently to present the whole data for the duration of incubation in the egg batches of all females recorded in Table 3. An extract from the crude data on incubation for 1944 is given in Table 4, and in Table 5 the data for 1945 are summarised so that a group of egg clusters is referred to on each horizontal line irrespectively of the source of the parent ticks.

The range of times required for the completion of embryonic development, clearly indicates that the individuals fall into two well defined classes, spring and autumn. When the eggs are laid before the end of June (groups A-K, and AA-GG) they are capable of completing development, and are ready to hatch before the end of the same year. On the other hand, if engorgement of the parent female takes place in the autumn period, the winter intervenes before the embryonic development of the eggs is completed and hatching does not occur until the end of the following spring. The groups M-S and MM-YY exemplify the prolonged period of incubation of eggs of autumn-fed females.

From the aspect of the population, the extent of the hatching period is more clearly indicated in Tables 6 and 7 which show the limits of the period of hatching of spring-laid eggs, and Tables 8 and 9 which give the course of hatching of autumn-laid eggs.

TABLE 4

Onset of hatching in egg batches in the field (1944)

Source Group	Group Ref.	No.	Oviposition began	Hatching began in		Duration of incubation (minimum)
				earliest batch	latest batch	
10 & 11	A	10	23.v.44	28.viii.44	4.ix.44	97 days
	B	10	27.v.	28.viii.	7.ix.	93
	C	15	2.vi.	28.viii.	4.ix.	87
	D	10	8.vi.	28.viii.	15.ix.	81
12	E	10	27.v.	28.viii.	15.ix.	93
	F	30	6.vi.	28.viii.	18.ix.	83
	G	20	8.vi.	29.viii.	15.ix.	82
	H	10	14.vi.	6.ix.	8.x.	84
	I	5	21.vi.	21.ix.	14.x.	92
14	J	5	23.vi.	11.ix.	23.x.	80
	K	5	29.vi.	14.ix.	16.x.	77
16	L	2	29.vii.	18.xi.	2.iv.45	113
17	M	3	14.viii.	29.v.45	10.vi.	285
	N	2	21.viii.	26.v.	28.v.	275
18	O	2	9.ix.	15.v.	21.vi.	245
	P	5	22.ix.	12.vi.	18.vi.	262
22	Q	3	25.x.	8.vi.	20.vi.	226
22	R	10	29.x.	31.v.	23.vi.	214
22	S	4	6.xi.	5.vi.	12.vi.	211

TABLE 5

Onset of Hatching of Egg Batches laid in 1945 in field

Group	Number	Laying began before	Hatching Began		Minimum duration
			Earliest batch	Latest batch	
AA	20	15.v.45	19.viii.45	7.ix.45	95 days
BB	50	22.v.	19.viii.	18.ix.	89
CC	50	29.v.	23.viii.	20.ix.	86
DD	100	5.vi.	19.viii.	6.x.	75
EE	50	12.vi.	23.viii.	14.ix.	72
FF	50	19.vi.	29.viii.	11.x.	73
GG	20	26.vi.	7.ix.	14.x.	73
HH	10	3.vii.	18.ix.	7.xi.	77
JJ	10	10.vii.	12.x.	3.ii.46	94
KK	5	17.vii.	26.x.	6.iii.	101
LL	3	24.vii.	13.xi.	4.iii.	112
MM	2	31.vii.	15.vi.46	2.vii.46	319
NN	5	7.viii.	18.v.	10.vii.	284
OO	10	14.viii.	16.vi.	29.vi.	303
PP	10	21.viii.	12.vi.	3.vii.	292
QQ	10	28.viii.	30.vi.	3.vii.	303
RR	30	4.ix.	15.vi.	29.vi.	281
SS	30	11.ix.	17.vi.	14.vii.	276
TT	25	18.ix.	15.vi.	3.vii.	267
UU	20	25.ix.	21.vi.	29.vi.	268
VV	10	2.x.	28.vi.	8.vii.	268
WW	10	9.x.	12.vi.	29.vi.	247
XX	10	16.x.	12.vi.	7.vii.	240
YY	10	23.x.	12.vi.	25.vi.	233

TABLE 6

Incidence of inception of hatching in egg-batches laid in spring 1944

Week ending		Number of egg-batches hatching	% hatching to date
August	21	0	0
	28	9	4%
September	4	50	26%
	11	70	57%
	18	37	73%
	25	20	82%
October	2	15	89%
	9	10	93%
	16	4	95%
	23	3	96%
April	10	2	97%
Failed to hatch		6	3%
	Total	226	

Reference has been made hitherto solely to the inception of hatching in different egg batches. In an individual batch of eggs there was always an interval of from one to two months required to complete hatching. It is not possible to tabulate the results in detail. Of the egg batches recorded in Table 6, in 90% (208 batches) more than half the eggs were hatched by the end of the year, and of these 82 (30%) were completely hatched. By the beginning of the following April, approximately 80% of all the eggs had hatched, and the remainder ultimately died.

TABLE 7

Incidence of inception of hatching in egg-batches laid in spring 1945

Week ending		Number of batches hatching	% Hatching to date
August	15	0	
	22	42	9%
	29	214	50%
September	5	127	80%
	12	25	85%
	19	32	91%
	26	4	92%
October	3	6	95%
	10	9	95%
	17	8	97%
	24	5	98%
	31	0	98%
November	7	4	99%
Failed to hatch		4	1%
	Total	480	

By the end of the year hatching was more than half completed in 452 of the egg batches recorded in Table 7, (94%) and in 362 (75%) it was completed.

The peak period for the onset of hatching in 1945 occurred approximately a fortnight earlier than the 1944 peak.

TABLE 8

Incidence of inception of hatching (1945) in egg batches laid in autumn 1944

Week ending	Number of batches hatching	% Hatching to date
1945 May 10	0	0
17	4	3%
24	11	10%
31	9	17%
June 7	41	45%
14	52	81%
21	16	91%
28	3	94%
July 5	4	97%
Failed to hatch	5	3%
Total	145	

TABLE 9

Incidence of inception of hatching (1946) in egg batches laid in autumn 1945

Week ending	Number of batches hatching	% Hatching to date
1946 May 11	4	2%
18	3	3%
25	5	6%
June 1	5	9%
8	9	13%
15	12	19%
22	31	40%
29	47	58%
July 6	48	77%
13	9	81%
20	6	85%
Failed to hatch	23	15%
Total	202	

By the end of July, hatching was more than 75% completed in all the egg batches in 1945, and in 165 (92%) of the egg batches in 1946. The differences recorded in the time relations for embryonic development between these two years are comparatively slight. In 1946 the peak period of larval emergence was delayed until the end of June, whereas in 1945 it was some two to three weeks earlier, and occurred in mid-June (Tables 8 and 9). This difference is presumably related to temperature differences between the two years, but discussion of this question will be postponed until the problem of temperature relations under controlled conditions has been examined.

(c) Metamorphosis of Engorged Larvae and Nymphs

It is convenient to deal with the development in these two instars collectively since they present parallel features under field conditions. To avoid needless repetition of similar details it is proposed to omit the complete protocols of the experiments devoted to the study of engorged nymphs and larvae. The active feeding periods of the preimaginal instars as well as adults virtually occur within the same seasonal limits. Thus, in some areas (e.g. Tweeddale) preimaginal activity is confined almost exclusively to the spring months, while in others (e.g. Argyll) a second season of activity in another section of the population occurs in autumn. While slight differences have been observed in the onset of activity in different seasons, as between adults, nymphs, and larvae, the engorgement period for the major part of any population was practically identical for all three instars in all the active seasons from 1943 to 1947. Similar findings have been reported from other districts and for other years by Macleod (1932, 1939), Cameron (1938), Linton (1941)

/Milne

Milne (1945, 1947), Heath (1946), Edwards & Arthur (1947). In view of this fact there is good reason for the separate consideration of the developmental processes in spring and autumn populations.

The majority of immature ticks which engorge in spring succeed in completing their development during the summer, and moult in the following autumn. In the years 1943-1946 the period of moulting began slightly in advance of the egg hatching period, but in all years the emergence of larvae, nymphs and adults took place more or less simultaneously for all in the period August to October. The moulting period extended over this same interval in groups of individuals whether they had engorged in March or in June, and there was no correlation between the time of emergence of adults and nymphs, and the time of engorgement, within the normal limits of spring activity, of the preceding immature stages. Even in individuals which had been induced to engorge well in advance of the spring months (Dec.-Feb.) there was no advance in the inception of moulting, and emergence of the next instar occurred unfailingly during the normal moulting season (Aug.-Oct.). The relation between the time of engorgement and the limits of the moulting season are shown for a series of engorged nymphs in Table 10, and for a series of engorged larvae in Table 11.

These tables clearly indicate a lack of correlation between the times of engorgement and moulting. On the other hand, from a consideration of the survival rates in the different categories, early feeding appears to be a disadvantage rather than advantage

/to

TABLE 10

Times of engorgement of Nymphs and subsequent emergence of adults in field, 1944

Engorgement	Number engorged	Number survived	Adults emerged Earliest	Latest
Dec - Feb	200	18	14.viii.	4.ix.
Mar - Apr	200	31	28.viii.	9.x.
Apr - May	200	75	21.viii.	28.viii.
May - June	200	62	14.viii.	25.ix.

TABLE 11

Time of engorgement of Larvae, and subsequent emergence of nymphs in the field, 1944

Engorgement	Number engorged	Number survived	Adults emerged Earliest	Latest
Dec - Feb	500	50	28.viii.	9.x.
	500	102	28.viii.	13.xi.
	500	119	14.viii.	25.ix.
Mar - Apr	600	281	14.viii.	2.x.
	500	187	28.viii.	20.xi.
	500	293	28.viii.	25.ix.
May	500	391	4.ix.	25.ix.
	700	509	14.viii.	20.xi.
June	800	644	14.viii.	23.x.
	400	328	11.ix.	20.xi.

to the species. The mortalities in the above groups are:-

Fed in	Nymphs	Larvae
Dec - Feb	91%	82%
Mar - Apr	85%	43%
Early May	62%	25%
Late May - June	69%	19%

The mortalities are probably higher than would normally occur in nature, and are accounted for in part by the fact that confining tubes are liable to waterlogging during periods of heavy rain.

The course of moulting in groups of ticks fed in May is indicated in Tables 12 and 13.

TABLE 12

Chronological course of moulting in a group of 200 spring-engorged nymphs maintained in the field 1944

Week ending	No. of Adults Emerged	Males	Females
August 7	0		
14	6	4	2
21	19	11	8
28	21	4	17
September 4	9	3	6
11	1	0	1
18	4	1	3
25	2	0	2
	62	23	39
	2	developed the following spring	
	10	failed to develop	
	128	died early in season.	

/Table

TABLE 13

Chronological course of moulting in a group of 1200 spring-engorged larvae maintained in the field, 1944

Week ending		No. of Nymphs emerged	% moulted to date
August	7	0	
	14	58	8%
	21	151	28%
	28	183	52%
September	4	177	76%
	11	37	81%
	18	32	85%
	25	94	98%
October	2	5	
	9	6	99%
	16	0	
	23	2	
	30	0	
November	6	1	
	13	2	
	20	1	100%
	Total	749	
	plus	282 - which failed to complete development	
	plus	169 - which died early in the year.	

The peak period for moulting of both immature instars occurred at the beginning of September in 1944, in mid-late August in 1945, and in mid-September in 1946. The foregoing observations, therefore, clearly indicate that the completion of development in all stages of spring active ticks coincides with

/the

the beginning of autumn, and by winter almost the whole of the spring population has completed one or other developmental phase of the life cycle and passes the winter period in the unengorged state. Individual exceptions occur, however, and examples are indicated in Tables 12 and 13 where it is shown that 12 nymphs, and 282 larvae failed to complete development in the usual prescribed times. The 12 nymphs were retained in the field, and two of them emerged as adults at the end of the following April. The remainder died before completing development. The 282 undeveloped larvae in this series (Table 13) were returned to the laboratory and 142 completed development and moulted within 10 days of transference to 18.5°C. The remainder died. In several other experiments involving development of nymphs and larvae in the field, there remained about 10% engorged larvae and up to 5% engorged nymphs which failed to moult before the onset of winter. The mortality among such left-over individuals during the winter period was invariably very high, (90% and over), but a small number successfully survived the cold season and eventually emerged in the following April or May. Larvae and nymphs which failed to moult were clearly referable to 2 types. One presented the passive immobile features characteristic of preimaginal engorged ticks in the course of metamorphosis, while the other preserved the active mobile state characteristic of recently engorged ticks. The second type, thus represents the immature tick in which the inception of development has been delayed.

While the whole interval between engorgement and moulting has been treated so far as a single definitive phase of the life-cycle, and we have referred to it as the developmental

/period

period, it is, in fact, the sum of two intervals which we may term predevelopmental and developmental respectively. The true nature of the period between engorgement and moulting in preimaginal ticks was first recognised by Falke (1931) who designated the two intervals Vorruhestadium (mobile) and Ruhestadium (immobile) from the appearance of the ticks during these stages. (Since the passive tick is in the course of development to the next instar, it is somewhat confusing to name it the Resting Stage, and Falke's terms have been avoided.)

Spring-engorged larvae and nymphs remain active until mid-June when they begin to assume the rigid appearance, and enter into the dormant developing state. By the end of July the major part of the engorged preimaginal population has entered into this condition. The termination of the predevelopmental phase does not take place while the temperature remains low, and in spring ticks the lower limit for the inception of development appears to lie in the region of 10°C. Development, once it has been initiated, however, can continue below this temperature, and this is evidenced by the fact that moulting can occur in October and November when the prevailing temperature lies below this level. There is usually a minority of individuals, both larvae and nymphs, in which the transition from the active engorged, to dormant developing condition is either abnormally delayed, or completely inhibited. It is this minority which fails to complete moulting before the onset of winter. When the onset of development is delayed, completion of the process is prevented by the fall in temperature which occurs in October, and consequently moulting does not take place until the following spring. Among such individuals, the mortality is very high

/during

during the period of interrupted development. When transition to the developing state is delayed until winter, the fall in temperature obviates the possibility of development. Spring ticks which remain in the active engorged state when winter arrives invariably die during the cold weather. Out of several hundreds which have been observed in the present investigation, only one larva was recorded to survive the winter and subsequently develop.

Whereas the interval between engorgement and moulting in spring ticks is completed in from c. 120 days to 180 days, and moulting takes place before winter of the same year, it is prolonged to at least 240 days in the case of autumn ticks and may extend to over 300 days, so that moulting does not take place until the early summer of the following year. There is, thus, a close parallel existing between the course of incubation of eggs and the course of development of engorged preimaginal instars of autumn active tick populations. The moulting season is clearly defined, and with insignificant variations from year to year between 1944-1946 it occurred between mid-June and the end of July. Thus, although engorgement can be completed at any time between early August and mid-October, the termination of development is virtually simultaneous for all individuals of an autumn population.

The transition from the active engorged state to dormancy typical of development is delayed in nymphs and larvae which feed later than July, and does not supervene until the temperatures exceed c. 5°C in February or March of the following year. The autumn active nymph and larva, thus, present a very notable difference from the spring active immature instars, in that they

/overwinter

overwinter in an active engorged condition. Though the mortality among overwintering autumn ticks is invariably high (we have never succeeded in rearing more than 38% of autumn-fed larvae or more than 21% of autumn fed nymphs under field conditions) it is never so complete as we have remarked in connection with overwintering of active spring-engorged larvae and nymphs. Furthermore, after they have experienced the low-temperature conditions of winter, autumn-engorged larvae and nymphs are enabled to pass from the active to the developing state at temperatures considerably below the inferior temperature limit for transition of spring-fed larvae and nymphs.

Table 14 indicates the course of moulting in a sample population of larvae engorged in September 1944, and Table 15 refers to nymphs engorged at the same time.

TABLE 14

Course of moulting in larvae engorged in autumn 1944

Week ending		Larvae moulted	%
June	14	3	
	21	18	5%
	28	95	25%
July	5	114	50%
	12	162	85%
	19	21	90%
	26	33	97%
August	2	8	
	9	2	
	16	4	100%
	Total	460	
	Plus	31	failed to assume passive state
		8	failed to complete development
		701	died before spring.

/In

In 1944 and 1946, the moulting period began somewhat later than in 1945, the first nymphs emerging from autumn-engorged larvae of the previous years being noted on June 27th, 1944 and July 6th, 1946. This remark applies equally to the emergence of adults in those years.

TABLE 15

Course of moulting in the field of nymphs engorged in autumn 1944

Week ending		Nymphs moulted	Adults emerged		% Total moult to date
			Males	Females	
June	14	0			
	21	7	4	3	7%
	28	18	11	7	26%
July	5	21	2	19	48%
	12	34	16	18	83%
	19	7	2	5	90%
	26	2	0	2	92%
August	2	3	2	1	96%
	9	2	1	1	98%
	16	0	0	0	
	23	2	0	2	100%
	Total	96	38	58	
	Plus	26	failed to assume passive state		
		378	died before summer.		

2. Other Observations

In the years 1946 and 1947 experiments were extended to Benderloch, Argyllshire, and Glensaugh, Kincardineshire. The time-relations of developmental processes in ticks of all instars

/were

were virtually identical to those observed to occur concurrently in the Borders. These observations included ticks drawn from all localities, and it may safely be concluded that the climatic differences between Peeblesshire, Kincardineshire, and Argyllshire are not sufficiently marked to produce any recognisable differentiation in the duration of development, and consequently variations in seasonal activity are not to be explained as arising from modifications in the developmental cycle.

Evidence from the development of ticks in experimentally infested hill plots, and from random turf samples in naturally infested areas amply confirms the conclusions drawn from the observations on tube-confined ticks described above. It is convenient, however, to defer discussion of these experiments until the point where the succession of events in the complete life cycle in nature is considered.

Summary of Field Observations on Development

The salient deductions from observations on development of tubed ticks may be summarised as follows:-

1. The time relations of the developmental processes are readily divisible into two distinct types depending on the season when engorgement takes place. Development of ticks which engorge in the period of rising temperatures before midsummer takes place during the warm season and is comparatively rapid, so that the next instar emerges before winter. When engorgement takes place in the period of declining temperatures after midsummer, development is considerably retarded, and emergence of the next instar is delayed until the temperature begins to rise after winter. These two types of developmental cycle may be termed the spring cycle and autumn cycle respectively.

2. In each cycle, the time relationships of the interval between engorgement and emergence is of the same order for all instars, and in all instars it consists of two parts, namely the predevelopmental and developmental periods, in the case of the engorged preimaginal instars, and the preoviposition and embryonic developmental periods which succeed engorgement and impregnation of the adult female. In consequence the population which engorges in spring has a well-defined season of emergence in autumn, while the population which engorges in autumn has an equally well-defined season of emergence in early summer of the following year.

3. The winter period appears to operate as one of adjustment, during which the activities of individuals become synchronised, and the population becomes uniform in its physiological pattern.

4. The temperature relations of ticks in the autumn cycle appear to be of quite a different order from those of ticks in the spring cycle.

We have been concerned so far with a purely descriptive account of the time relations of tick-development in the field. The information gained, however, raises a number of problems, and it remains to be decided (a) whether the clear definition of the two cycles is a direct result of climate, or whether there is a physiological rhythm; (b) why two types of seasonal stock-infestation should occur; (c) whether in areas where diphasic activity is the rule the ticks representing the two types of developmental cycle are interchangeable and finally (d) in what manner the alternating passive and active phases are related.

/Quite

Quite clearly the most significant controlling factor from the aspect of duration of development is temperature, and it is proposed to review the effect of temperature on development under controlled conditions.

SECTION IB

1. Laboratory observations on development of spring ticks

Although much work has been published on the duration of development in many species of tick, the subject as a whole has not received systematic attention. The series of papers published by Macleod (1932 - 36) remains the only comprehensive study on development and reproduction in Ixodes ricinus L. under controlled conditions. Macleod's results and conclusions, however, do not provide a completely satisfactory basis for the interpretation of the results got from field observations and described in the previous section of this paper. The inadequacy of Macleod's conclusions may be explained partly by the fact that they are based upon inadequate data and also because of his failure to appreciate the distinction of spring-engorged and autumn-engorged ticks. The possibility that ticks of both spring and autumn cycles were included in the experiments described in his earlier paper is indicated from the data quoted in the summary (Macleod, 1932) (vide p.87). There are indications of a similar kind in the scattered records of earlier workers, including Kossel, Schütz, Weber and Meissner (1903), Ashworth (1909), Nuttall (1911, 1913) and Stockman (1911). It was not until Falke (1931) recognised a prolongation of the "vorruhestadium" in immature instars fed in autumn, that we find a clear indication recorded of a definite difference between spring and autumn ticks. In his later papers which deal more extensively with the actions and interactions of temperature and humidity on development, Macleod (1934) states "The ticks used in the experiments described below were bred for one or

/more

more generations in the laboratory". Consequently, it is probable that this, coupled with the fact that most of his observations refer to ticks maintained at temperatures above 20°C, has resulted together in obscuring the seasonal changes which are clearly evident in nature.

In order to understand more fully the seasonal changes in the response to climatic factors, therefore, it was considered essential to undertake a re-examination of the development of ticks under controlled conditions. In the following description of these experiments, observations on spring and autumn ticks are dealt with separately.

(a) Preoviposition period

From each spring collection of engorged females, a number was incubated in the laboratory under conditions of humidity near saturation and at various temperatures. The protocols for one series of observations on the duration of the preoviposition are given in Tables 16 - 19 and these are summarised in Table 20.

/Table

TABLE 16

Duration of preoviposition period of spring-engorged females maintained at constant temperatures 14° - 30°C

Duration of Preoviposition in days	Number of individuals at				
	14°C	18.5°C	21°C	25°C	30°C
6				5	2
7			15	41	27
8			66	57	41
9		3	112	31	15
10		148	77	18	14
11		190	52	10	4
12		178	33	3	6
13		89	18	6	3
14		34	10	1	3
15	3	21	4		0
16	5	14	2		2
17	24	8	1		
18	66	3			
19	79	1			
20	61	2			
21	33				
22	22				
23	15				
24	7				
25	3				
26	7				
27	2				
28	1				
29	2				
30	0				
31	1				
	n = 331	691	390	172	117
	$\bar{x}$ = 20.0	11.8	9.9	8.7	8.8

/Tables

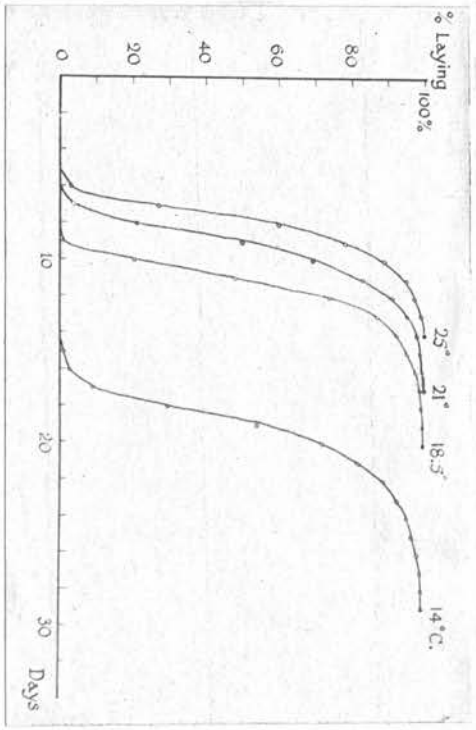


Figure 4.

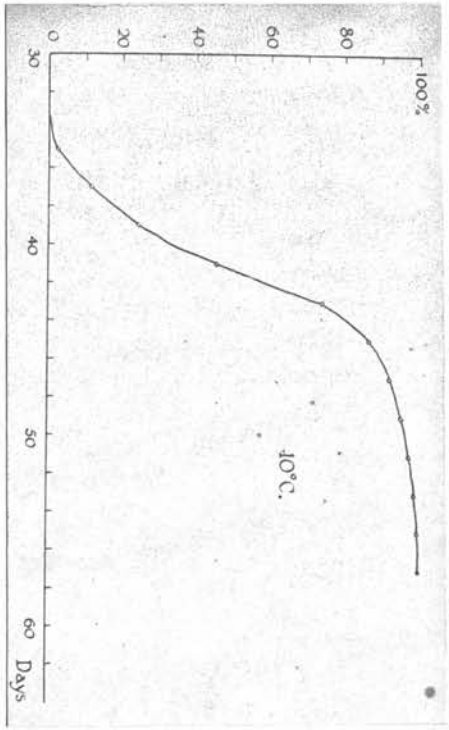


Figure 5.

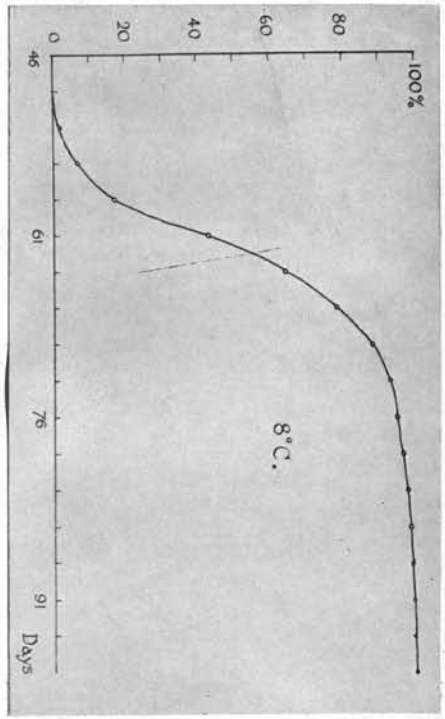


Figure 6.

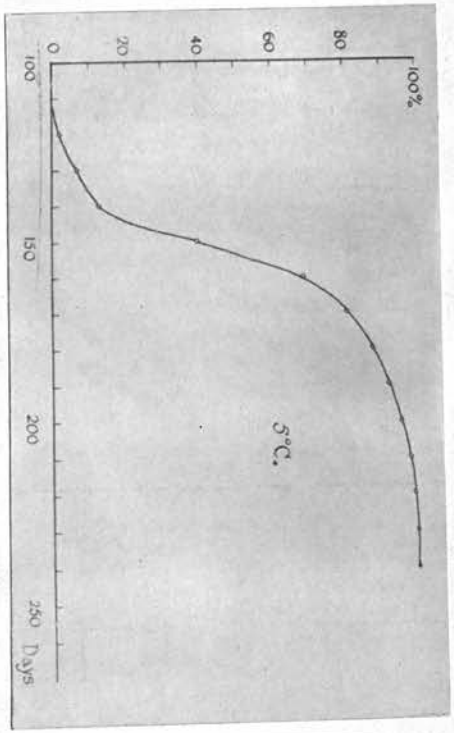


Figure 7.

Figs. 4 - 7.

Cumulative ogives indicating duration of preoviposition period in groups of spring-engorged females maintained at various temperatures.

TABLES 17 - 19

Duration of Preoviposition period at 10°C, 8°C and 5°

Table 17
at 10°C

Duration in days	Number of individuals
34	3
35	4
36	8
37	18
38	18
39	18
40	15
41	44
42	50
43	30
44	27
45	11
46	6
47	9
48	3
49	7
50	2
51	2
52	3
53	3
54	1
55	1

n = 283

$\bar{x}$ = 41.9

Table 18
at 8°C

Duration in days	Number of individuals
50 - 52	11
53 - 55	35
56 - 58	64
59 - 61	171
62 - 64	131
65 - 67	94
68 - 70	62
71 - 73	31
74 - 76	11
72 - 79	13
80 - 82	11
83 - 85	5
86 - 88	4
89 - 91	2
92 - 94	1

n = 646

$\bar{x}$ = 63.6

Table 19
at 5°C

Duration in days	Number of individuals
110-119	3
120-129	9
130-139	11
140-149	47
150-159	51
160-169	20
170-179	13
180-189	8
190-199	6
200-209	4
210-219	2
220-229	1

n = 175

$\bar{x}$ = 156.7

It is apparent from these Tables that there is a considerable variation in the preoviposition period between individuals maintained at each temperature. The distribution curves, however, indicate a very definite modal region, and their shape is the same for all temperatures. For convenient comparison, the data in Tables 16 - 19 are converted to percentages and represented graphically as cumulative ogives in

/figures

figures 4 to 7. From these figures there is no question that there is a clear quantitative relationship between temperature and the duration of preovipositional development, and MacLeod's (1935b) statement that "The apparent tendency for the period to be shorter at higher temperatures than at low is rendered insignificant by its irregularity" is partly due to the fact that his statistics were incomplete, and probably also to the fact that his table was constructed from data obtained at different times and included observations on ticks in "autumn condition" as well as spring ticks.

TABLE 20

Summary of observations on the preoviposition period in spring ticks maintained at different constant temperatures

Temperature C°	Number of individuals	Duration of preoviposition in days		
		Minimum	Maximum	Mean
5	175	119	226	156.7 ± 1.50
8	644	50	94	63.6 ± 0.26
10	283	34	55	41.9 ± 0.22
14	331	15	31	20.0 ± 0.13
18.5	691	9	20	11.8 ± 0.06
21	390	7	17	9.9 ± 0.09
25	172	6	14	8.7 ± 0.14
30	117	6	16	8.8 ± 0.19

Fig. 9 is the curve indicating the relationship between time and temperature, and the velocity (reciprocal of time) temperature relationship is shown in fig. 10. The velocity curves (maximum, minimum and mean) are sigmoidal in form and

/demonstrate

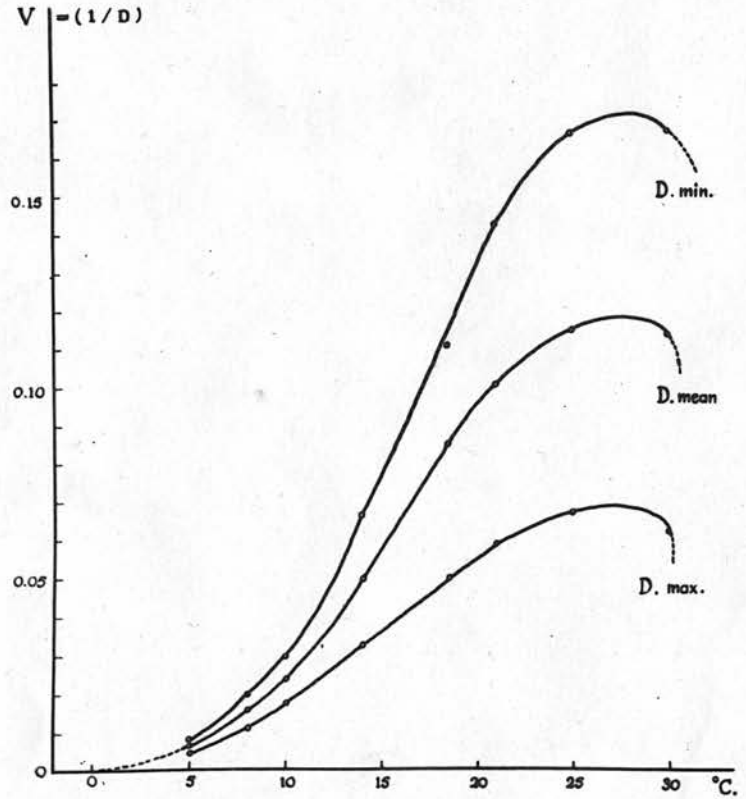


Figure 9.

Temperature-velocity curves for preovipositional development of spring-engorged females

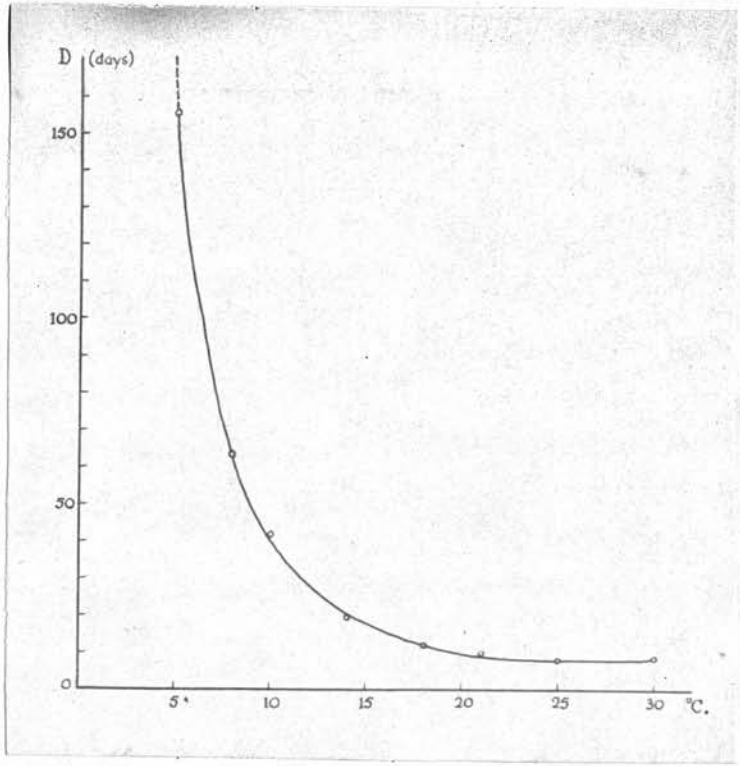


Figure 8.

Mean duration of preoviposition period of spring-engorged females maintained at various temperatures.

demonstrate that (in the mean case) the acceleration of developmental velocity with increase in temperature is greatest at temperatures below 14°C ($\frac{dV}{dT} > 1$), where V is velocity of development, and t is temperature, between 14°C and 21°C the relationship is rectilinear ($\frac{dV}{dt} = 1$), and above 21°C the rate of acceleration decreases with increasing temperatures ($\frac{dV}{dt} < 1$) until the region of 30°C when the inhibitory effect of high temperatures causes a retardation of development ($\frac{dV}{dt} < 0$). The inhibitory effect of high temperature becomes progressively more marked in passing in series from individuals with the greatest developmental velocity to those with the slowest rate of development. Thus, the inversion points of the three velocity curves in fig. 10 are seen to occur at successively higher temperatures respectively for the fastest, mean, and slowest developmental velocities.

Relative humidity plays a much less obvious rôle in determining the duration of the period of preoviposition. There is no significant difference between the rates of development at relative humidities between 80% and saturation. Below 80%, however, the preoviposition period becomes prolonged and individuals vary in an irregular manner, but at low relative humidities, since oviposition is often abortive, and eggs if laid are frequently non-viable, these abnormalities cannot be regarded as a physiological retardation of developmental velocity, but as a pathological consequence of exposure to an unfavourable environment.

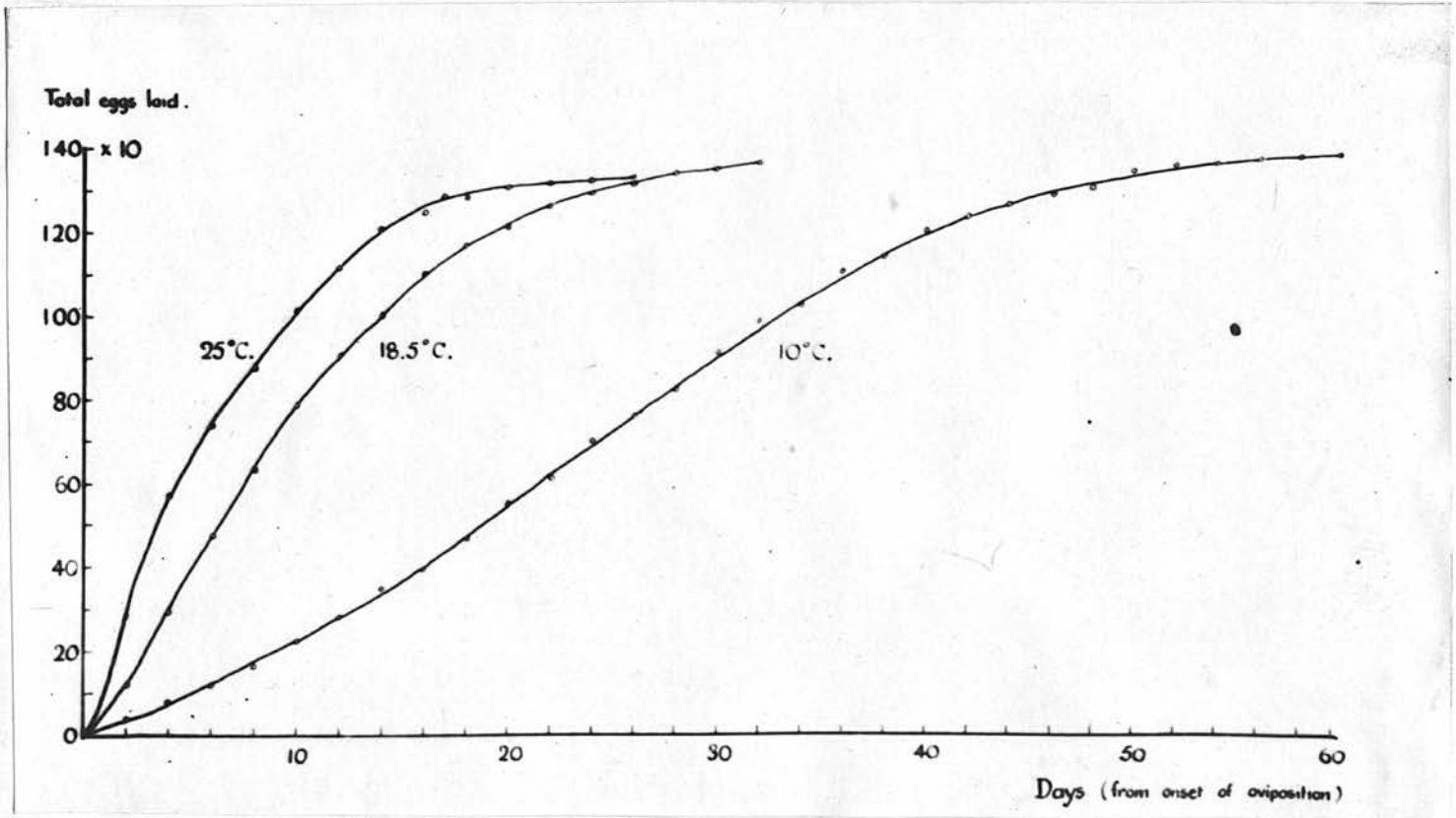
(b) Oviposition

Under conditions of optimal humidity the total output of eggs varies between individuals from about 1,000 to 2,000.

/The

Figure 10.

Mean rate of egg-laying in groups of 10 females at different temperatures.



The course of oviposition in groups of 10 females maintained at various temperatures is indicated in Fig. 10. This figure is self-explanatory and further comment is unneccessary.

(c) Embryonic development.

Since the manipulation involved in isolating individual eggs from their batches almost invariably interfered with their viability it was deemed necessary to confine observations on embryonic development to undisturbed egg-batches. The period of embryonic development was consequently taken to be the interval between the inception of oviposition, and the emergence of the first larva or larvae as we have described already in the field observations. There is no advantage in including the complete protocols of every series of observations, and it is proposed in discussing this and other developmental processes to present the data in condensed form (as was done for pre-oviposition p.51).

Table 21 gives the results of one series of eggs maintained at a relative humidity near saturation.

TABLE 21

Duration of embryonic period at different temperatures

Temperature C	Number of batches	Duration in days		
		Minimum	Maximum	Mean
10	119	220	302	249.1 ± 1.65
14	246	86	109	91.2 ± 0.20
18.5	355	47	63	53.2 ± 0.15
21	101	36	48	38.8 ± 0.26
25	102	28	39	29.9 ± 0.18
30	52	22	32	25.1 ± 0.32

/Here

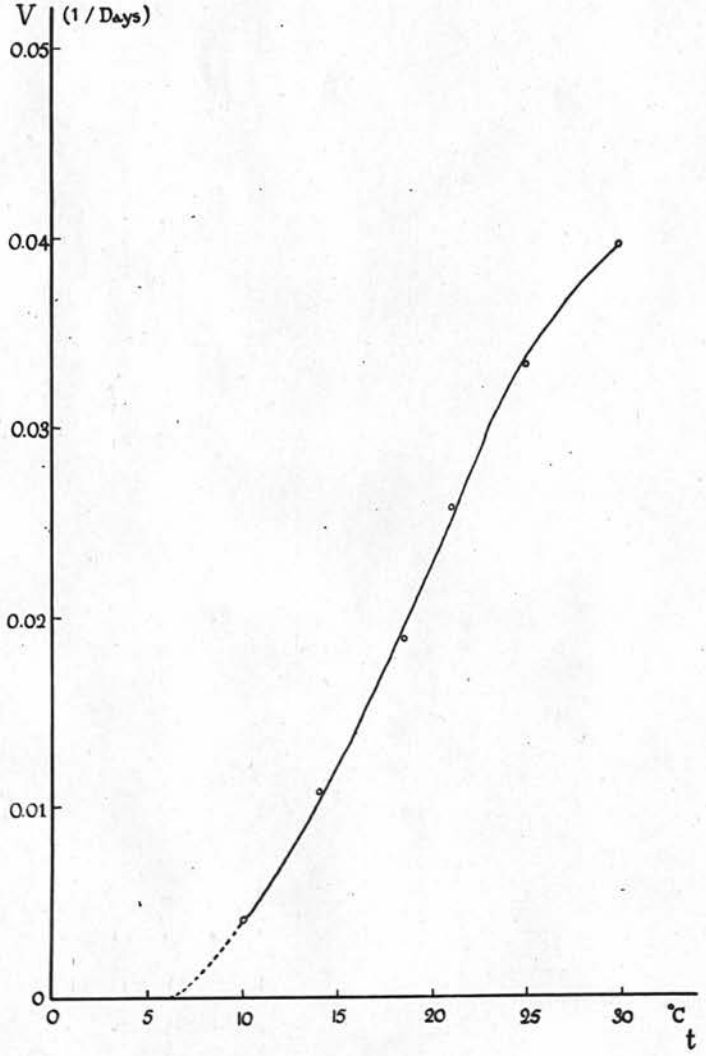


Figure 12.

Velocity-temperature curve for incubation of spring eggs.

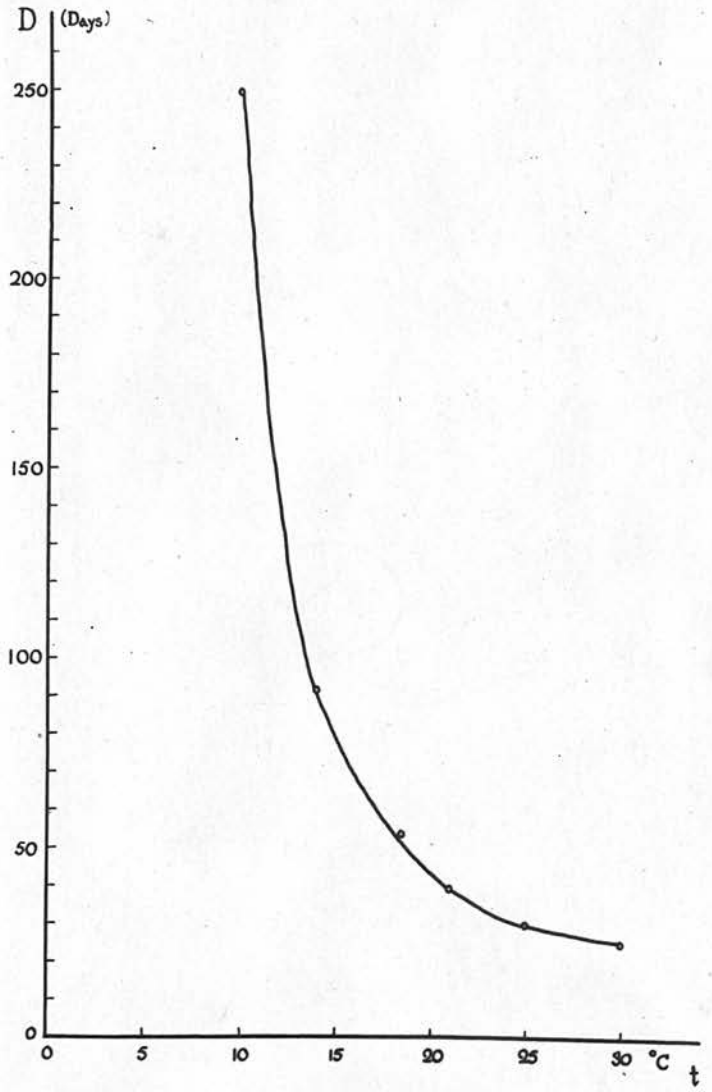


Figure 11.

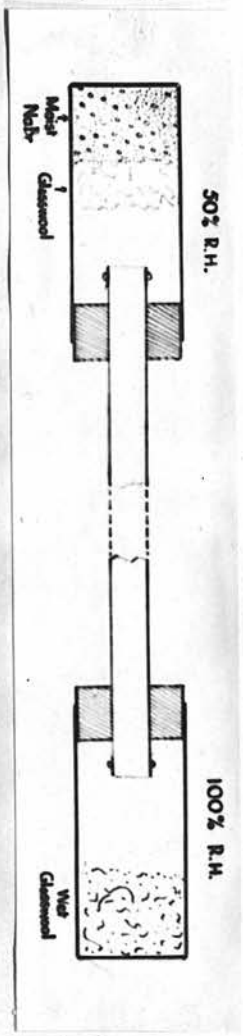
Time-temperature curve for incubation of spring-laid eggs.

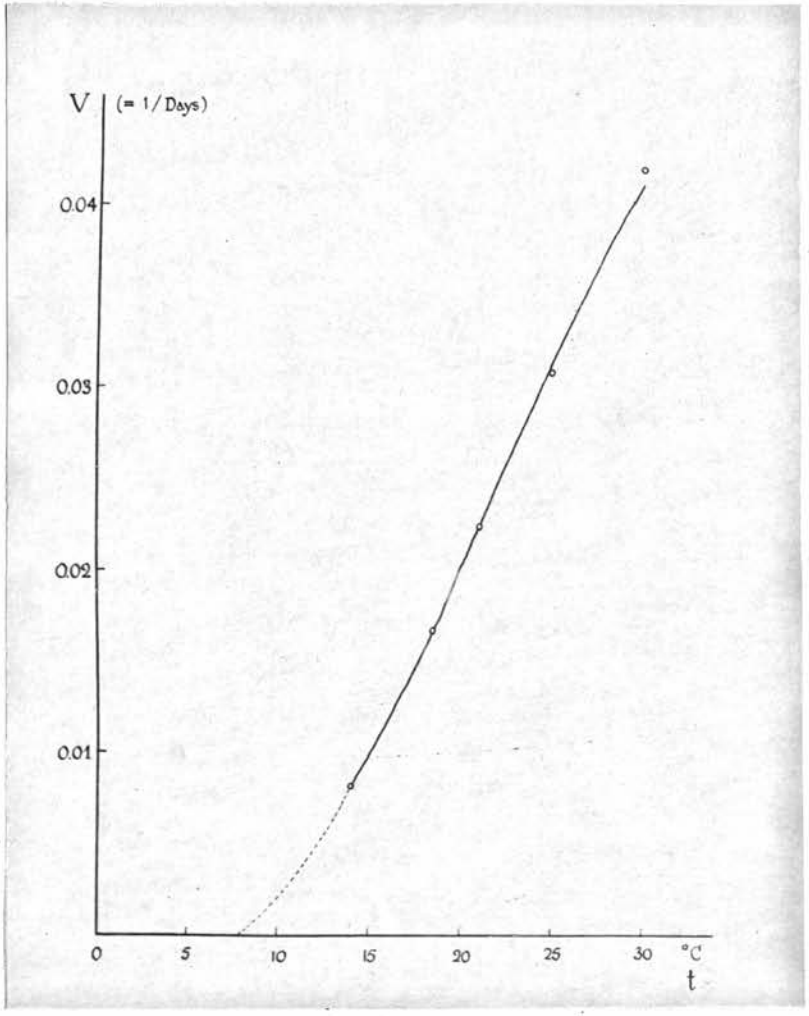
Here again we observe a quantitative effect of temperature on developmental velocity; in contrast to the preoviposition period however, it is apparent that embryonic development is a process which is adapted to a higher range of temperature. Below 10°C, there is strong evidence that embryonic development does continue very slowly, but we have not succeeded in hatching larvae from eggs incubated at this temperature (see p.40). These results are in marked disagreement with Macleod's (1935b) conclusion that 15.5°C is the threshold of development. This question will receive attention in a later section. The time-temperature, and velocity-temperature relationships are indicated in Figs. 11 and 12, which are based upon the data in Table 21.

(d) Development of Engorged Larvae.

It has already been remarked (p.40) that the interval between engorgement and ecdysis in larvae and nymphs includes two phases, which we have termed predevelopmental, and developmental. The lower limiting temperature for transition was found to be around 10°C. Below 10°C engorged larvae invariably failed to begin development, but larvae in which development had been initiated at a higher temperature were transferred to 10°C and below there was evidence of their capacity to continue development at these latter temperatures. Tables 22 and 23 indicate the duration of the overall period, and the developmental period sensu stricto, respectively. From the data included in these tables, the velocity, and time-temperature curves have been constructed in Figs. 13 and 14.

/Table





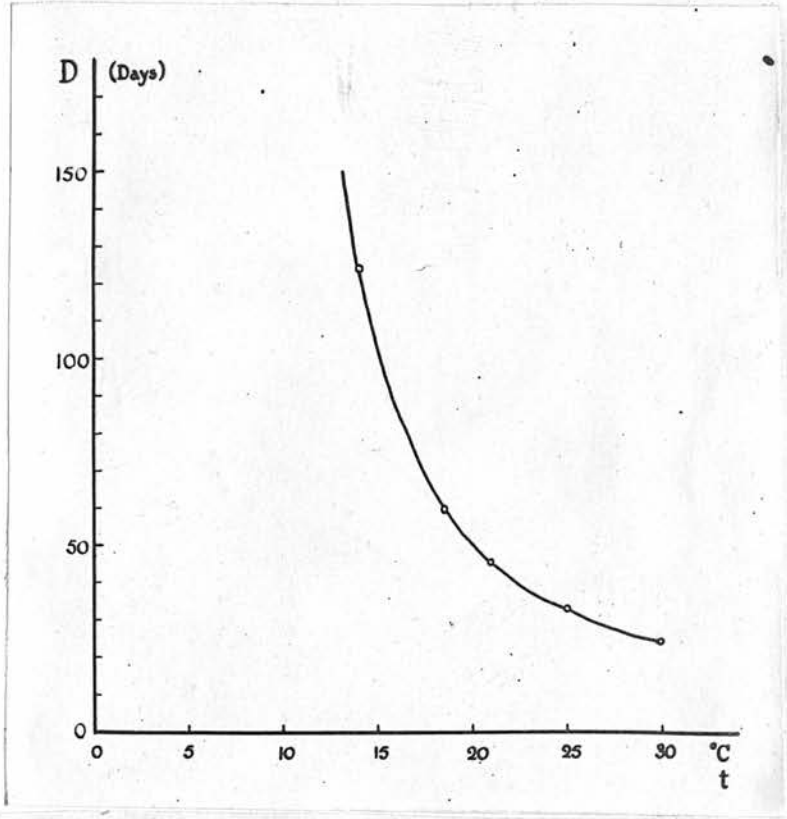


Figure 13.

Larval metamorphosis. Time-temperature curve.

Figure 14.

Larval metamorphosis. Temperature-velocity curve.

Figure 15.

Alternative humidity apparatus.

TABLE 22

Summary of data on the duration of the interval between engorgement and ecdysis in larvae at various constant temperatures, (including both predevelopmental and developmental periods)

Temperature °C	Number	Duration of Engorgement and Ecdysis interval in days		
		Minimum	Maximum	Mean
10		250+		
14	200	109	143	123.1 ± 0.54
18.5	593	52	75	59.3 ± 0.11
21	878	38	57	44.9 ± 0.13
25	754	27	41	32.9 ± 0.11
30	363	19	31	23.8 ± 0.16

TABLE 23

Duration of developmental period (sensu stricto) in engorged larvae at different temperatures

Temperature °C	Number	Developmental period in days		
		Minimum	Maximum	Mean
14	156	84	102	89.4 ± 0.38
18.5	175	44	53	47.2 ± 0.09
21	142	34	42	36.5 ± 0.09
25	124	25	33	27.0 ± 0.09
30	100	18	24	19.4 ± 0.13

A comparison of these tables reveals that the duration of the predevelopmental period is quantitatively related to temperature, and by subtraction we find that it is progressively

/reduced

reduced as the temperature increases, thus:-

14°C - 23.5 days

18.5°C - 12.1 days

21°C - 8.5 days

25°C - 5.9 days

30°C - 4.4 days

The developing larva exhibits a response to temperature of the same order as that which was observed in developing eggs.

The larvae used in these experiments were collected from a Peebles-shire hill-grazing by the hedgehog method in May 1945.

(e) Development of Engorged Nymphs.

The remarks which have been made regarding the process of development of engorged larvae apply equally to development of engorged nymphs. A comparison between the duration of the strictly developmental period with the overall period between engorgement and emergence of the adult may be obtained from the data summarised in Tables 24 and 25.

TABLE 24

Duration of the interval between engorgement and ecdysis in nymphs at different temperatures

Temperature °C	Number	Duration of overall period		
		Minimum	Maximum	Mean
14	126	112	169	132 ± 1.89
18.5	111	54	72	63.1 ± 0.39
21	110	37	55	45.5 ± 0.30
25	111	30	44	35.9 ± 0.29
30	107	25	38	29.6 ± 0.24

/Table

TABLE 25

Duration of developmental period in engorged nymphs

Temperature °C	Number	Duration of Development		
		Minimum	Maximum	Mean
14	68	100	126	110.4 ± 2.01
18.5	114	48	60	52.1 ± 0.74
21	101	35	45	38.9 ± 0.68
25	106	25	32	27.4 ± 0.37
30	94	20	26	21.6 ± 0.29

It will be noted from a comparison of Tables 22 and 24 that there is comparatively little difference between the intervals from engorgement to ecdysis in nymphs and larvae. These results are not in agreement with the findings of Macleod (1932, 1934) where differences of from 30 to 75% are recorded between the interval in nymphs and larvae at the same conditions. A comparison of some of the data from Macleod with the data presented here appears in Table 26.

/Table

TABLE 26

Comparison of intervals from engorgement to ecdysis in nymphs and larvae at different temperatures
Data from Macleod (1934), and Tables 22 and 24

Temperature °C	Data from Macleod				Data Table 22		Data Table 24	
	Larvae		Nymphs		Larvae		Nymphs	
	Min.	Mean	Min.	Mean	Min.	Mean	Min.	Mean
32.5	17	20	23	28				
30	19	23	25	30	19	24	25	30
26	25	38						
25			44	49	27	33	30	36
22.5	34	55	50	55				
21					38	45	37	46
18.5					52	59	54	63

The results from Tables 22 and 24 indicate that at certain temperatures development of nymphs appeared to be unduly prolonged in Macleod's observations but his times are based on very much smaller numbers of individuals and this accounts for some of the apparent irregularities in his data. It is of interest to note, however, that a difference of a very marked order between nymphs and larvae has been recorded by several earlier workers. For example, Kossel, Schütz, Weber & Meissuer (1903), Nuttall (1913) and Falke (1931) record a disparity which approached 100% (i.e. nymphs required twice the time taken by larvae). Some light on these discrepancies may be obtained by comparing the findings on Ixodes ricinus L. with some of the recorded observations on other species of Ixodidae from temperate regions.

/There

There are indications from the figures given for Haemaphysalis punctata Can. & Fanz. by Stockman (1911); Haemaphysalis concinna Koch by Nuttall (1915); Haemaphysalis leporis-palustris Packard and Ixodes scapularis Say by Hooker Bishopp & Wood (1912); Ixodes dentatus Neum. (in the field) by Smith (1945); and Dermacentor hunteri Bishopp by Bishopp & Wood (1913) that metamorphosis is completed in approximately the same time for the nymphs and larvae of all. When nymphs and larvae of the one-host ticks Dermacentor nigrolineatus Packard, and Dermacentor albipictus Packard were removed from their host Bishopp and Wood (1913) found that metamorphosis was more prolonged in nymphs than larvae. According to the observations of Cameron and Fulton (1924), however, there was no marked difference in the times of nymphs and larvae of Dermacentor albipictus in situ on the host. The records of Nuttall (1915) on Haemaphysalis cinnibarina Koch Dermacentor andersoni Stiles and Dermacentor reticulatus Neum. contain a very striking and interesting discrepancy. Nuttall found metamorphosis to occupy approximately the same time in nymphs and larvae at 24°C, while at 30°C the nymphs required more than twice as long as the larvae to complete development.

The possibility is suggested that the potentiality for development is more markedly depressed in nymphs than in larvae at high temperatures. (Cf. Overall period from engorgement to ecdysis for immature Ixodes ricinus L. at high temperatures in the present record (Tables 22 and 24), and in Macleod's (1934) data; and in H. cinnibarina etc. in Nuttall's (1915) record,

/to

to these may be added the records of Hooker, Bishopp and Wood (1913) on Amblyomma americanum L, Dermacentor occidentalis Neum. and Dermacentor variabilis Say)

Prolongation of the interval between engorgement and acdysis in nymphs probably operates through extension of the predevelopmental phase (Cf. Tables 23 and 25) and further evidence of this will be presented when development of autumn engorged ticks is discussed. (The diapause state, represented by the failure of engorged immature ticks to undergo transition to the passive rigid condition, is much more difficult to overcome in nymphs than larvae by exposing them to high temperatures. A further possible explanation lies in the fact that during continued maintenance under laboratory conditions, the temperature relations of the tick undergo modification (See p.81). Any one of these possibilities alone, or a combination of them, would tend to cause a more pronounced retardation in nymphs than in larvae. Finally, it may be noted that throughout our work, and in the experience of Macleod (1934) the mortality among nymphs under observation always exceeded the mortality among larvae.

It seems reasonable to conclude, therefore, that for many three-host ticks of temperate climates metamorphosis under field, or favourable laboratory conditions, requires the same time interval for both the preimaginal stadia.

From Table 12 which records the course of moulting in a sample population of engorged nymphs it may be observed that there was a tendency for male ticks to complete development and emerge slightly earlier than female ticks. This phenomenon was repeatedly observed both under field and laboratory conditions at all temperature levels. In his observations on Ixodes dentatus, /on

on the other hand Smith (1945) found no significant difference between the rate of development of male and female nymphs. In Ixodes ricinus the difference only occurred in those series for which the whole period from engorgement to ecdysis was recorded. When the times for the true development period were noted, there was no significant difference. It is therefore concluded that the longer interval required by females is due to a longer delay in the predevelopmental period in that sex. The sex differences in the series referred to in Table 24 are shown in Table 27.

There is probably no biological significance in the phenomenon of differential developmental velocities in the two sexes. In nature the differences which occur in the times of moulting are negligible in comparison to the long period which is spent on the ground after moulting, before the tick begins to exhibit host-seeking activity. When observations are carried out on comparatively small numbers, however, it is a point which much be considered when estimates of mean developmental times are made, since a preponderance of either sex in the sample populations would bias the population parameters.

TABLE 27

Interval between engorgement of nymphs and emergence of males and females

Temperature	Mean interval	
	Males	Females
14	126 ± 2.1	138 ± 1.9
18.5	60.5 ± 0.54	64.3 ± 0.47
21	44.4 ± 0.51	46.3 ± 0.41
25	35.0 ± 0.45	36.5 ± 0.41
30	29.1 ± 0.36	29.9 ± 0.40
Totals	211	354

/The

The sex ratio in all these experiments lay in the region of 50 - 60 males to 100 females. (Cf. Table 27. 57♂♂ : 100♀♀ while Macleod (1932) records 54♂♂ to 100♀♀).

In view of the marked disparity between the sexes, it is of interest to note, that mating takes place on the host, and males and females are found coupled while the female mouth-parts are inserted into the host tissues. The males usually disengage before the female completes engorgement. In collections including several hundred of replete females gathered from the floors of sheep-pens immediately after infested sheep had passed through, we have rarely found individuals in copula. In the absence of males the female frequently requires a considerably protracted period to complete engorgement. (We have observed females to remain attached to hedgehogs for as long as 30 days, and up to 24 days on sheep when there were no males present, whereas they normally engorge in 6 to 8 days.)

Under experimental conditions, multiple pairing occurs, one male impregnating two or three females in succession. It is probable that this occurs in nature, since males remain on the host until they die, and during this time they have opportunities for feeding and mating more than once.

There was a marked tendency for female nymphs to be larger than male nymphs, (♂♂ c 3.2 mm, ♀♀ 3.5 mm) and on the basis of size it was possible to estimate with up uo 70% accuracy the probable sex of developing nymphs. Nuttall (1913) records a difference in size between male and female nymphs of Ixodes putus.

but in this case males were larger than females.

In the course of his laboratory experiments, Macleod (1934) observed differences in the rate of development of nymphs maintained at different relative humidities. He states that development proceeded at a maximum rate at 100% RH at 27.5 °C and above. Below this temperature (22.5° and 25°C) the maximum velocity of development was realised at 90% RH. When these experiments were repeated in the course of the present investigation, Macleod's findings were not confirmed. No significant differences were observed between developmental velocities at 100% RH, 92% RH and 88% RH. At 80%, however, development was retarded, and the mortality was considerably increased. Two observations were made, however, which provide a possible explanation of the results obtained by Macleod. When nymphs were stored wet in the tubes after completion of engorgement, a considerable prolongation of the predevelopmental period often resulted. In view of this observation, an experiment was set up to examine the tropistic behaviour of newly engorged nymphs and larvae, in relation to moisture. Newly engorged ticks were placed in alternative humidity tubes, 18" long, projecting into two chambers containing glass wool soaked in water, at one end and at the other end containing a saturated solution of sodium bromide, (diagram in Fig. 15). The tube, thus presented a gradient from 100% RH to 50% RH. Soon after introduction to the tubes the ticks congregated at the 50% RH end, and remained there for a period of time which was longer at lower temperatures, (about 12 hours at 30°C and about 1 week at 14°C). After this period, they returned to the other end of the tube and in due

/course

course underwent transition to the passive developing state. None began metamorphosis at the dry end, but a small number of individuals remained there until they died from dessication. It may be noted here that in the field experiments, unconfined ticks were observed to remain in an active state for as long as one month after engorgement, and during this interval they were observed several times during rainy periods to climb the vegetation and remain in a more exposed situation for a few days at a time. (This may account for the odd cases of engorged nymphs and larvae which were collected in blanket samples.) It appears, therefore, that after engorgement the preimaginal instars are at first negatively hygrotropic, and this is probably due to a need to reduce their water content. The tropism later becomes reversed, and the developing state then supervenes.

It is possible that slight fluctuations in the temperature led to some degree of condensation from the saturated or nearly saturated atmospheres in Macleod's experiments. This would be more pronounced at low than at high temperatures, and there is a strong possibility that herein lies a reason for the observed differential rates of development at different relative humidities at the lower temperatures. A second possibility occurs from the fact that contact with liquid water (due to condensation) frequently delays moulting in fully developed nymphs.

We have already indicated the statistical incompleteness of Macleod's data, and consider that the observed differences in developmental velocities at different humidities upon which he based his views on the combined effects of temperature and

/humidity

humidity were simply random variations (probably due to causes such as have been indicated above). It is concluded that within the humidity range where the chances of survival are unimpaired (85% - 100%) there is no significant variation in developmental velocities of engorged nymphs in response to variations of relative humidity when the temperature is constant. Within the vital range, therefore, the relative humidity plays no part in determination of the velocity of development at any stage of the life cycle of Ixodes ricinus.

SECTION IB

2. The Quantitative Expression of Temperature Relations

There are few examples recorded of attempts to express the relationship between temperature and the kinetics of development in ticks. Hunter & Hooker (1907), Hunter (1908) Hooker, Bishopp & Wood (1912), Bishopp & Wood (1913) and others have expressed the temperature relations of various species of tick by the rule of thermal summation. The only recorded essay of a mathematical definition of the temperature to relations of development of Ixodes ricinus is that of Macleod (1934, 1935b). Macleod, however, reviewed his experimental data solely on the basis of the hypothesis that the time-temperature curve is a rectangular hyperbola, and after concluding that the hypothesis was inapplicable he did not submit the problem to any alternative mathematical treatment.

With the intention of relating the observations in the field to results obtained under controlled conditions the data in this investigation were analysed on the basis of several mathematical hypotheses, and these are reviewed briefly.

(a) Linear Hypothesis

This hypothesis (Cf. Sanderson (1908, 1910), Peairs (1914, 1927), Krogh (1914), Shelford (1927, 1929) et al.) proved quite inadequate on account of the very limited temperature range over which there was a linear relationship between developmental velocities at different temperatures. Estimates of the threshold (the alpha point of Shelford (1927)) from the equation $V = K(t - \alpha)$ were found to be quite useless, since development continued at temperatures below the alpha point derived from

/observations

observations at 14°C and above.

(b) Exponential Formulae

The temperature coeficcient Q_{10}, derived from van t'Hoff's equation, calculated from data on development of Ixodes ricinus, proved to vary according to the temperature, with values ranging from 20 at 5° to 8°C down to 1.4 at temperatures above 20°C. The thermal characteristic μ of the Van t'Hoff - Arrhenius equation was similarly found to vary with temperature when applied to this organism, and values ranging from μ = 46,850 to μ = 5,900 were obtained. We found no evidence for the view advanced by Crozier and his co-workers that the value of μ changes abruptly at critical temperatures, although it is admitted that the temperature intervals employed in the investigation were too great to permit of a critical examination of Crozier's views (Cf. Crozier (1924 - 6) Glaser (1925) Navez (1928, 1931). On the contrary μ appeared to vary in a continuous manner related directly to changes in temperature.

The corrected exponential formulae of Janisch (1925, 1932) and Stephens & Barrow (Krafka, 1920) were examined and found unsuitable for the present purpose.

None of the exponential equations available, therefore, provides a satisfactory instrument for the analysis of the temperature relations of tick-development.

(c) Empirical equation

A formula $V_2/V_1 = (T_2/T_1)^m$ was applied by Veley & Waller (1910) to define the relationship between temperature and the action of certain drugs on muscle tissues. In this formula, T is the temperature on the absolute scale, and m is a constant.

/In

In a slightly modified form, Porodko (1926) applied it to heat coagulation of proteins, and the killing of protoplasm at high temperatures, and independently it was applied by Bělehrádek (1926 a, b, c, 1927, 1939, 1930, 1931) to define the temperature relations of a wide range of biological phenomena. In the work of both these latter authors the temperature was measured on the centigrade scale.

The equation is most simply expressed in the form:-

$$D = a/t^b$$

where D is the time, t is the temperature in °C, a is the thermal constant, and b is the temperature index. (In the discussions relating to this equation, the symbols employed differ in some cases from those which occur in the original papers by Bělehrádek. The use of D to denote the duration, V (= $^1/_D$) velocity, and t the actual temperature helps to avoid confusion. Moreover, it is proposed to refer to b as the temperature index, rather than the temperature coefficient as Bělehrádek terms it, since it is not a coefficient in the sense that Q_{10} is a coefficient - albeit an inconstant one. Before this formula can be applied to the experimental data, however, account must be taken of the zero point, since this does not necessarily coincide with 0°C. Thus the temperature measure should be the effective and not the actual temperature, and Bělehrádek introduced the factor alpha to denote the threshold. (Since we have already referred to the hyperbolic zero in the thermal constant theory as the alpha point, it is proposed to employ theta for the zero point of the curve of the present equation. The use of yet another symbol

/is

is justified by the fact that in tick development, alpha and theta have materially different numerical values).

The equation now becomes

$$D = a/(t - \theta)^b \qquad (1)$$

In this form, the kinship with the algebraic expression of the thermal constant theory is readily recognised, the empirical equation simply being a more general form of an equation, of which the thermal constant equation is a special case. Thus when b = 1

$$D = K/(t - \alpha) = a/(t - \theta)^b$$

The great advantage of this formula is that it is readily applied, and while it is applicable to all phenomena which are in agreement with the thermal constant theory, it can also be made to fit the data, as in the present example of tick development, over the lower temperature range in those cases where the observations at low temperatures diverge from the rectilinear velocity curve. This point may be illustrated by reference to Fig. 16, where it is shown that the reciprocal ($V = (t-\theta)^b/a$) of the hyperbola $D = a/(t-\theta)^b$ is not rectilinear but parabolic. (Fig. 16).

We have seen from Figs. 9 and 12, however, that the actual velocity curve obtained from the observations is a sigmoid, while the curve $V = (t-\theta)^b/a$ is a simple parabola without an inversion point. Thus, it is apparent that the equation is not in accordance with the observations at high temperatures, and consequently does not define the whole of the temperature relations. The most convenient practical standpoint, therefore, is to regard the empirical velocity sigmoid as a combination of two parts,

/the

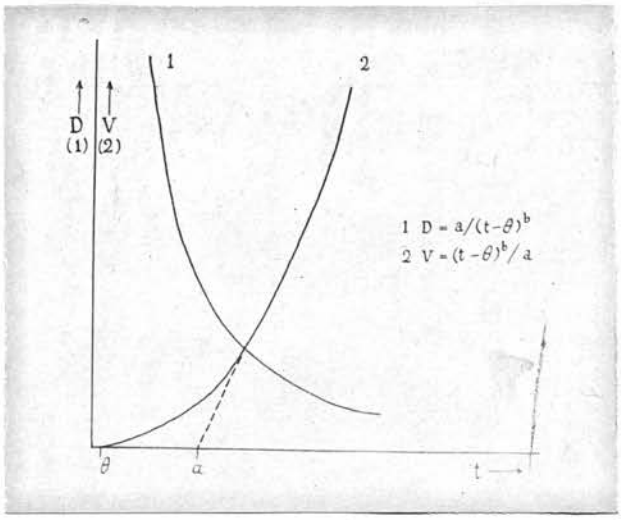


Figure 16.

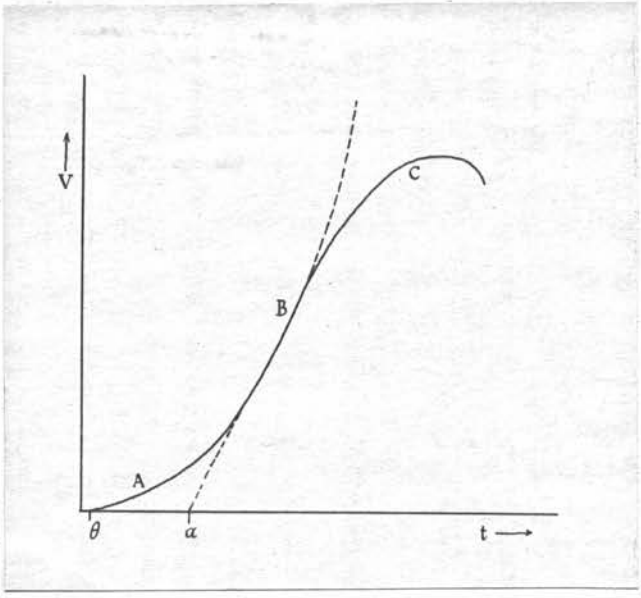


Figure 17.

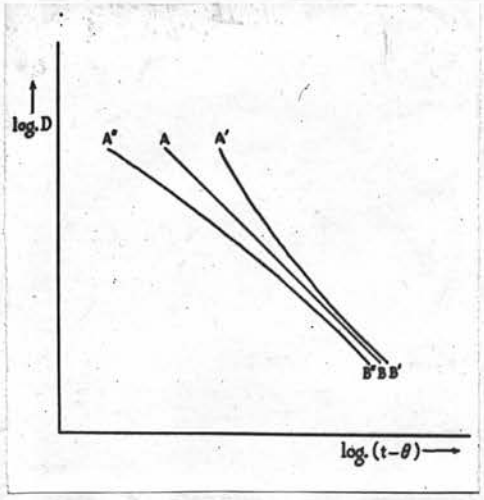


Figure 18.

the first a parabola which is in agreement with the equation of Bělehrádek, and the second a modification of this curve which only becomes apparent at temperatures above the inversion point. This may be regarded as the retarding effect of high temperatures, since the retardation becomes relatively more pronounced as the temperature becomes progressively higher, until at the thermal death point it becomes absolute. (Fig 17). We have mentioned in connection with Fig.10, that the sigmoid consists of three parts A - B, B where $dV/dt > 1$, B - C where $dV/dt = 1$ and C - D where $dV/dt < 1$. It is of interest to note that between A and B, $dV/dt = b$.

The fact that the equation is inapplicable to the results at high temperatures does not diminish its practical value, however, since the inversion point in the velocity curves of tick development occurs at a temperature level which is beyond the normal field range. On the other hand, its suitability for the analysis of the data obtained at low levels of the temperature scale makes it a valuable ecological instrument, and on this account is was adopted in the present study.

It may be emphasised at this point, that although Bělehrádek has developed a theoretical argument on the basis of his experience with this equation, there is no theoretical rationale for the equation, and it can be applied to observed data purely as a means of obtaining a quantitative definition, and it is on these grounds that it has been used in the present work. In this respect the equation has an advantage over the exponential equations referred to above. The theoretical implications of the results vis-à-vis Bělehrádek's theory are of interest, but

/they

they will not be discussed in the present paper.

The equation is most conveniently applied in the form of its logarithmic transcription

$$\log. a = \log. D + b.\log. (t - \theta) \qquad (2)$$

In the first instance, however, there are three unknown factors a, b, and θ, and the equation is algebraically insoluble. If θ is known, on the other hand, the solution is a simple matter, since

$$b = \frac{\log.D_1 - \log.D_2}{\log.(t_1-\theta) - \log.(t_2-\theta)}$$

Thus, by substituting trial estimates of θ, the values of b and a can be determined. When, however, there are several points to be considered (D_1 D_2 D_3 D_4 at t_1 t_2 t_3 t_4 etc.) this method is too laborious, and the equation is more conveniently solved by a graphical method.

From equation 2 above

$$\log. D = \log. a - b \log. (t-\theta)$$

and since a, and b, are constants, it is clear that there is an inverse linear relationship between log. D and log. $(t-\theta)$ (or a direct one between log.V and log. $(t-\theta)$). Thus by substituting trial values of theta and plotting the various points on the coordinates log.D and log.$(t-\theta)$, the value of θ for which the points are linearly disposed is the true value. For example in Fig. 18 the line AB indicates the correct estimate of θ while in A'B' θ is under-estimated, and in A"B" it is over-estimated. The gradient of AB equals the index b. After b and θ have been determined for any particular series of observations, a comparison of the numerical values of the thermal constant for the different data provides a valuable confirmation

/of

of the closeness of fit of the equation. The size of a thus indicates a significant departure of any observation from the expected result. If, for example, a second series of observations (on the same developmental process) were found to give a materially different set of a values calculated upon the same values of b and θ this would be regarded as evidence of a difference in the temperature response between the two sets of individuals, in which case the values of b and θ would require adjustment to obtain agreement between the a values for the two series. Thus, a significantly lower a than normal might be regarded as evidence of a lowered threshold. This subject will be discussed at a later stage when the phenomenon of temperature conditioning is reviewed.

There is a second problem involved, however, in the question of the significance of the numerical value of a. We have shown earlier, that there is a considerable individual variation in the developmental times of ticks of all instars. Thus, if b and θ are assumed to be the same for all individuals, the range of variation found in the developmental times will be reflected in the numerical estimates of a, and a will be smallest in the case of those individuals which develop most rapidly. Janisch (1932) considers that when individual variations become pronounced, it is an indication of a relatively unsuitable environment, since the variation range increases as conditions become further removed from the optimum. Individual variation thus measures individual resistance to adverse factors. This point of view, however, offers little assistance in the present circumstance. Although the significance of a is impossible of precise appreciation, it obviously represents the sum of two factors, namely

/the

the potentiality for rapid development, and the dynamic response to the temperature environment. Unfortunately, there appears to be no method by which these two factors may be separately assessed. It remains an open question as to whether the individuals which develop most rapidly at one temperature would be those which developed most rapidly at all other temperatures. If such were really the case, then the individual variations in developmental velocity (and in a) would simply be due to variations in the developmental potential, and would consequently remain independent of the temperature. In all probability, the variations are due to changes in both factors.

In treatment of the observed data from the standpoint of this equation, it has been assumed that for populations with the same temperature history the developmental potential varies as between individuals, while their temperature responses are of equal magnitude. When, however, population parameters are considered, and comparisons are made between populations, it is assumed that the mean developmental potentialities remain unchanged. Thus where differences obtain in the values of a as between two populations they are due to a change in the effect of temperature. While it is admitted that there is no evidence for the first of these assumptions, it is a useful working hypothesis. On the other hand, if the first assumption be admitted, the second is capable of experimental verification, since a change in the dynamic response to temperature if it occurs will produce a result which is proportionate to the temperature, and observations at different temperatures should provide a check.

/Consequently

Consequently, the thermal constant a is treated as a variable within constant limits, that is to say, that for the individuals which develop fastest a is constant at its minimum numerical value, while for the population mean it is constant at a higher value.

These points are illustrated in the example which follows.

Table 28 indicates the values of a calculated for the minimum and mean times of the series on preovipositional development for which the data are contained in Table 20. The points are plotted in Fig. 19 against the co-ordinates log.D and log.$(t - \theta)$. From this the value of θ is found to be 0°C and b = 2.00. (In Fig. 20 the curve $D = 4000/(t - \theta)^2$ is plotted and the mean data are added)

TABLE 28

Estimates of Thermal Constant a for preovipositional development
(Data from Table)
b = 2.00 θ = 0°C

T°C	log $(t-\theta)$	D Min	D Mean	log.D Min	log.D Mean	a	
						Minima	Means
5	0.699	119	156.7	2.076	2.195	3,000	3,900
8	0.903	50	63.6	1.699	1.804	3,200	4,050
10	1.000	34	41.9	1.532	1.622	3,400	4,200
14	1.146	15	20.0	1.176	1.301	3,000	3,900
18.5	1.267	9	11.8	0.959	1.072	3,100	4,050
21	1.322	7	9.9	0.845	0.996	3,100	4,375
25	1.398	6	8.7	0.778	0.940	3,750	5,450
30	1.477	6	8.8	0.778	0.945	5,400	6,300

/With

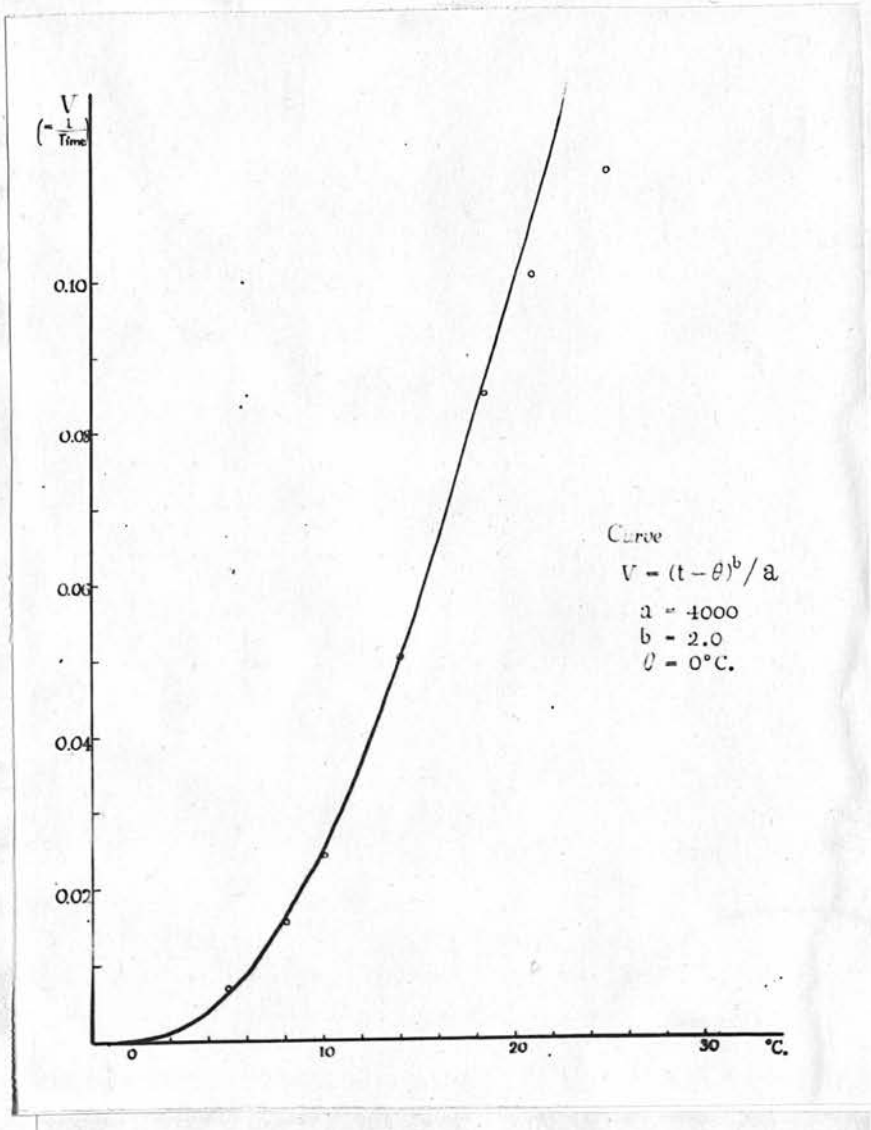


Figure 20.

Curve of empirical equation of Belehradek. Points added from observations on preoviposition period.

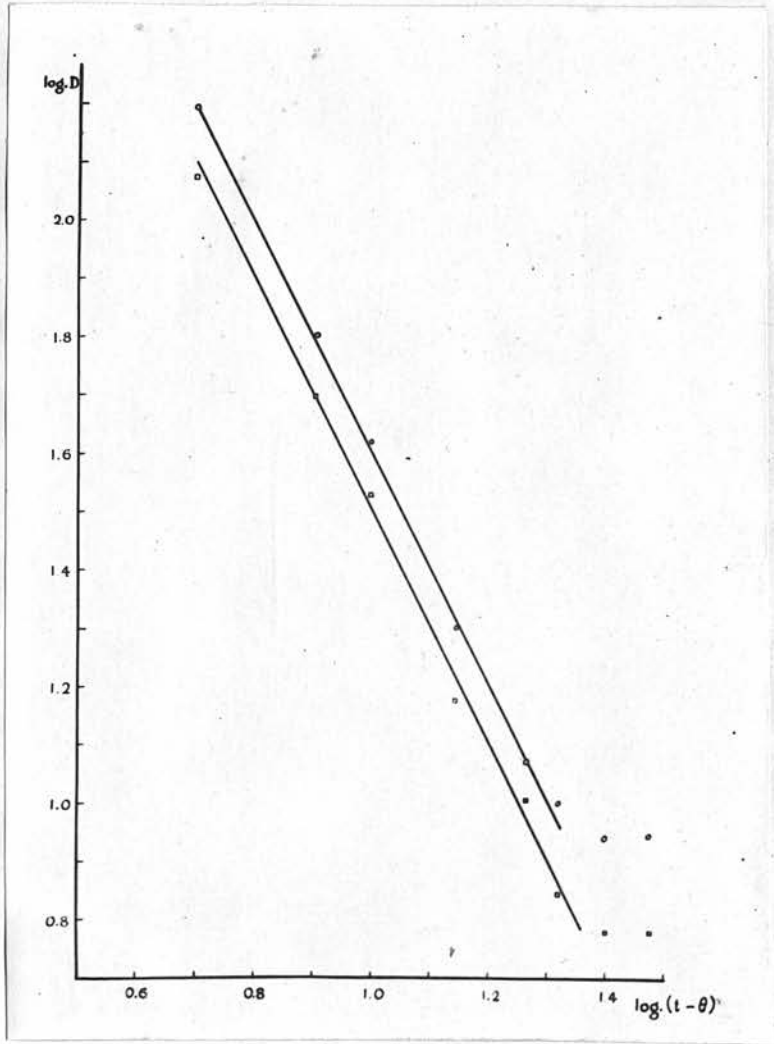


Figure 19.

Action of temperature on preoviposition. Time and temperature represented logarithmically.

With the exception of rather high values at 10°C the calculations of a in Table 28 indicate that the equation fits the data quite satisfactorily. In the case of the minima there is a good agreement between the a values up to 21°C and the a values for the means are quite uniform up to 18.5°. At high temperatures the values of a become progressively too high, and indicate the retarding effect of high temperatures. This effect is apparent at a lower temperature for the bulk of the individuals, than for those which develop most rapidly.

The equation $D = /(t-\theta)^b$ similarly affords a useful quantitative expression of the effects of temperature on the kinetics of development for the other stadia in the life-cycle of the tick. When it is applied separately to the different stages, however, it is found that there are slight differences in the values of the equation constants in the various developmental processes. Equation constants for the separate stages of development are summarised in Table 29.

TABLE 29

Summary of Thermal Constants for development of spring ticks under controlled conditions

Stage of Development	θ °C	b	a minimum	a mean
Egg-Larva	7°	1.25	1000	1050
Larva-Nymph	7°	1.30	1060	1140
Nymph-Adult	8°	1.35	1130	1240
Preoviposition	0°	2.00	3150	4000

/A

A change in temperature responses with increase in age has been recognised in other organisms. Bodine (1929) records that the metabolic response to temperature during embryonic development of certain Orthoptera becomes more pronounced as development proceeds. Ludwig (1928) records that development of the later instars of Popillia japonica Newm. is influenced by temperature to a greater extent than in the earlier instars, and Bělehrádek (1929, 1930) has drawn attention to a progressive increase in the thermal index b in the successive instars of Dytiscus semisulcatus Müll. as recalculated from the data of Blunck (1923) together with examples from the work of other authors.

Hitherto, we have been concerned with development under constant temperature conditions in the laboratory. The problem remains to ascertain whether the empirical formula is applicable to development under field conditions. Consider the case of preovipositional development. The shortest time at any given temperature can be obtained from the formula $D = 3,150/(t-0)^2$. For example, at 7°C we should not expect any females to begin egg-laying in less than $3,150 \div 49 = 64$ days, and yet from Table 3 we see that there were individuals which began to lay eggs as early as 54 days after completion of engorgement, during which time the mean temperature was below 7°C. Thus, it appears that the equation is not directly applicable to development in the field. Two alternative conclusions are possible: (a) that the true minimum times for any temperature were not realised under laboratory conditions; or (b) that additional factors intervene in the field which invalidate the theoretical definition derived from laboratory observations.

/The

The statistical distribution of the observations on populations in the laboratory is so regular as to preclude the possibility that the maximal developmental potentialities were not realised. It appears very probable, therefore, that there are factors which act in the field to cause a modification of the temperature responses. The possibility of two such factors has been studied, and they are:-

1. A modification of the temperature response due to temperature adaptation, and
2. fluctuating temperatures operate with a different result from constant ones.

SECTION IB

3. Temperature Conditioning or Adaptation

While the application of the empirical temperature equation ($D = a/(t-\theta)^b$) to developing eggs has not been discussed in detail, it may be noted that when eggs were developed in the ovary and laid at temperatures of 10°C and below, there was an apparent reduction in the subsequent incubation period relative to the periods observed in eggs laid at higher temperatures, since the values of the equation constant a were smaller. This observation indicates the possibility that the magnitude of the temperature responses is capable of modification in relation to the previous temperature history. In contrast to this, Macleod (1935b) denied that there was any effect produced on the rate of development of eggs at a particular temperature by the temperature at which they were laid. In an earlier paper, however, Macleod (1934) considered that there was evidence of a possible retardation of development of engorged tick larvae after 60 days exposure to 2 - 3°C. Hunter & Hooker (1907) record a similar example in the development of eggs of Boöphilus annulatus Say after subjection to a temperature close to 0°C.

Among insects, several observations have been recorded where modified rates of development followed after previous exposure to low temperatures. After a period of maintenance at subliminal temperatures Bodine (1925) and Parker (1929, 1930) obtained evidence of accelerated development in eggs of certain Orthoptera, while Janisch (1930) records a retardation of development in Prodenia littoralis F., and Hase (1927) found a similar

/retardation

retardation in eggs of Ephestia kühniella Zell. and (1930) Cimex lectularius L. and C. rotundatus Sign. Uvarov (1931) suggested that the apparent contradiction in these two sets of results may be due to the fact that the cotton-worm, flour moth and bed bug are insects which are susceptible to the injurious effects of exposure to low temperatures. It is possible, however, that subjection to low temperatures results in a modification of the temperature responses, so that the rate of development in a particular subject will alter to a different degree at different temperatures. Whether the change in developmental velocity is positive or negative, will depend upon the actual temperature at which development takes place. (Cf. Fig. 19).

Evidence of modification of the temperature relations of Ixodes ricinus is to be found in the seasonal differences observed between spring and autumn-fed ticks, and this phenomenon is discussed in detail in a later section. A striking example occured, however, in the altered time - reactions at different temperatures, of the preoviposition period in spring 1947 following the very cold conditions which prevailed for the first three months of that year. Comparison of the three previous years 1944-1946, revealed slight but insignificant differences in the velocity of development, and the constants of the temperature equation ($D = a/(t-\theta)^b$) were $b = 2.00$, $\theta = 0°C$ for all three years. In 1947, however, the velocity-temperature curve was quite different, showing a reduction in the degree of slope, and an origin at a lower temperature. The velocity-temperature

/curves

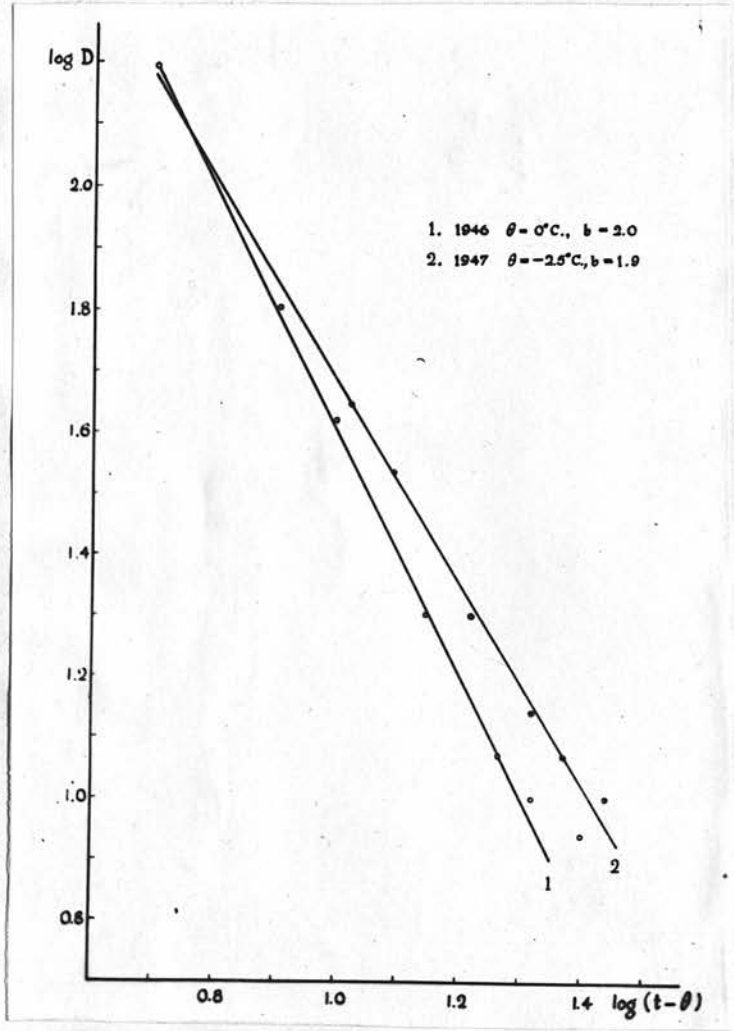


Figure 22.

Comparison of preoviposition periods in 1946 and 1947. Time and temperature plotted logarithmically.

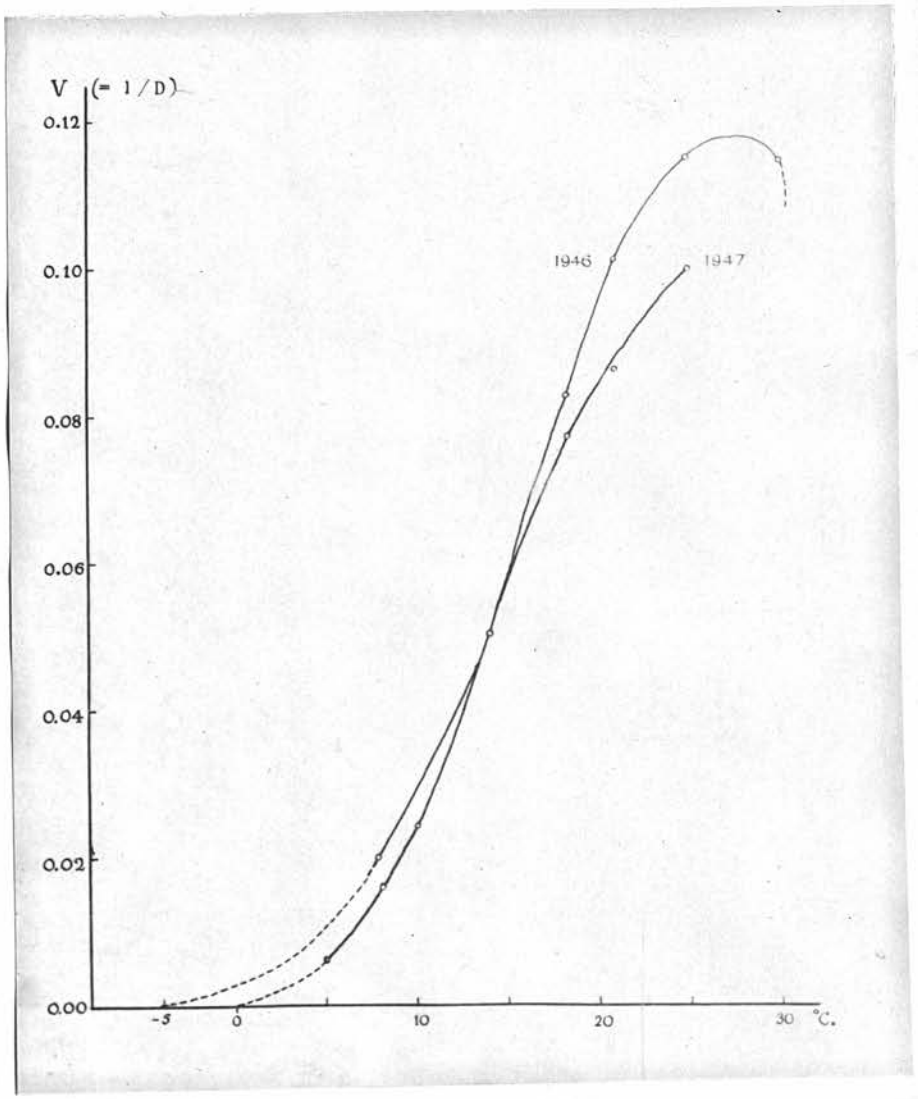


Figure 21.

Comparison of velocity curves of preovipositional development in 1946 and 1947.

curves for the years 1946 and 1947 are compared in Fig. 21, and the time-temperature points are plotted on bilogarithmic co-ordinates in Fig. 22.

TABLE 30

Duration of Preoviposition Period of Spring-fed females maintained at different constant temperatures 1947

Temperature °C	Number of Ticks	Duration of Minimum	Pre-oviposition Maximum	In Days Mean
8	148	39	80	50.0±0.58
10	88	27	46	34.4± 0.41
14	93	16	30	20.0±0.28
18.5	250	10	20	13.0± 0.11
21	92	8	18	11.8± 0.28
25	80	7	15	9.9± 0.21

In Table 31 the mean times for 1946 and 1947 are compared.

TABLE 31

Comparison of Mean Duration of Preoviposition Period of Spring-fed Ticks in 1946 and 1947

Temperature °C	1946 Mean	1947 Mean	Difference
8°C	63.6 ± 0.26	50.0 ± 0.58	Marked
10°C	41.9 ± 0.22	34.4 ± 0.41	Marked
14°C	20.0 ± 0.13	20.0 ± 0.28	Nil
18.5°C	11.8 ± 0.06	13.0 ± 0.11	Significant (t = 9.07. P 0.01)
21°C	9.9 ± 0.09	11.8 ± 0.28	Significant (t = 8.25. P 0.01)
25°C	8.7 ± 0.14	9.9 ± 0.21	Significant (t = 4.74 P 0.01)

/From

From these tables it is seen that in 1947 the rate of development was greater at temperatures below 14°C than in 1946, but the inversion point of the velocity curve occurred at a lower temperature (viz.c16°), and above 14°C development was slower than in 1944-46.

From Fig. 22 the equation constants obtained for the 1947 data are θ = -2.5°C and b = 1.90. The two years 1946 and 1947 are compared in relation to the equation in Table 32.

TABLE 32

Comparison of Values of constant for preovipositional development in 1946 and 1947

Temperature °C	1946 θ = 0°C			1947 θ = -2.5°C		
	t - θ	a		t - θ	a	
		min	mean		min	mean
5	5	3000	3900	-	-	-
8	8	3200	4050	10.5	3400	4000
10	10	3400	4200	12.5	3300	4200
14	14	3000	3900	16.5	3400	4100
18.5	18.5	3100	4050	21.0	3250	4200
21	21	3100	4375	23.5	3300	4650
25	25	3750	5450	27.5	3800	5400

This example affords very strong evidence for the view that the temperature relations of different individuals of the same species are conditioned by previous temperature experience. Adaptation to low temperature results in a lowering of the threshold together with a reduction in the magnitude of the temperature index. The modification of developmental velocity depends in consequence upon the actual temperature at which development takes place. Thus, low conditioned material

/develops

develops at an accelerated rate over the lower temperature range, but at higher temperatures it is retarded in comparison to development of high conditioned material. (This is of interest, and may afford a basis for explanation of the apparently conflicting evidence quoted above, of Bodine and Parker on the one hand, and Janisch and Hase on the other.

A large series of experiments was undertaken employing all stadia, to investigate the phenomenon of temperature conditioning under experimental conditions. Brief reference is made to one series of experiments designed to determine the relationship between temperature conditioning of ovarian eggs, and the resultant modification of their temperature responses during incubation. Engorged females were allowed to undergo preovipositional development and to continue oviposition at various constant temperatures, and their daily egg quotas were removed. Different egg quotas were subjected each to a particular constant temperature, so that observations were made on incubation at several temperatures of eggs with different temperature conditioning histories. An example of the effects on the rate of embryonic development at a particular temperature (18.5°C) brought about by different conditioning temperatures is summarised in Table 33.

/Table

TABLE 33

Incubation of eggs at 18·5°C with different conditioning histories

Conditioned and Laid at °C	Number of daily egg quotas	Duration of incubation in days		
		Minimum	Maximum	Mean
10	130	49	65	53.5 ± 0.36
14	272	47	64	52.8 ± 0.23
18.5	436	48	76	56.4 ± 0.22
21	179	48	80	58.8 ± 0.47
25	166	49	86	60.9 ± 0.54
30	37	53	84	64.5 ± 1.16

The results in Table 33 indicate a clear correlation between the temperature at which ovarian development took place, and the subsequent rate of development at 18.5°C. This result is contrary to the conclusion reached by Macleod (1935b). It is considered, however, that Macleod's experiment was too limited to permit of sound conclusions, since it was based upon no more than four egg batches at each conditioning temperature, and the experiment was restricted to two temperatures (20°C and 25°C). There is a feature in the present result which merits comment, namely, that the exposure of ovigerous females to low temperatures reduces the variability in the incubation time of their eggs.

The full significance of the result in Table 33 can only be appreciated in relation to the results obtained for incubation at other temperature levels. To avoid extensive tabulation, however, it is proposed merely to refer to the application to all series of the temperature equation ($D = a/(t - \theta)^b$). When all the results were plotted on the bilogarithmic scale, there was

/found

found a systematic change in the values of θ according to the temperature at which the eggs were conditioned, and when eggs were conditioned at 10° there appeared to be a slight reduction in the value of the index b as well. The values obtained are shown in Table 34.

TABLE 34

The equation constants for incubation of eggs with different temperature conditioning histories

Conditioning temperature °C	10°	14°	18.5°	21°	25°	30°
θ °C	6.0°	6.5°	7.2°	7.5°	8.0°	8.5°
b	1.23	1.25	1.25	1.25	1.25	1.25

The results obtained in this experiment were amply confirmed by further experiments on conditioned ticks of all instars. As in this example, modification of the constants of the empirical temperature equation provided a very useful indicator of changes in the temperature relations of ticks following conditioning by different temperatures. In some experiments, however, when developmental processes proceeded at temperatures near the extremes of the vital range, there were discrepancies attendant on application of the empirical equation, and it was realised that the relationship between temperature and kinetics was more complex than had been assumed. Not only is the temperature response at a particular stage capable of alteration from conditioning by (or adaptation to) various levels of temperature experience in the period prior to inception of the developmental process under review, but it is also susceptible to modification

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by adaptation to the actual temperature environment during the course of development. Where an organism exhibits a plasticity of this nature in its temperature relations, caution must accompany attempts to define velocity curves, of processes extending over long intervals of time, by mathematical equations. In reference to mathematical interpretation of curves expressing temperature relations Buxton (1933) has remarked: "In several cases the precision of the mathematical argument exceeds the precision of the technique with which the original facts were collected.". To avoid this charge it is to be noted that, at the outset, it was remarked that the equation employed in the present instance provided a convenient empirical quantitative measure of the temperature relations. From this point of view, and for comparative purposes, the equation is invaluable, although it is admitted that the numerical values of its constants are without significance in an absolute sense. Where the phenomenon of continuous temperature adaptation occurs, the equation is inapplicable without judicious manipulation of its terms. It is not to be expected that an expression of form so simple as $D = a/(t - \theta)$ could cover every instance, and indeed its shortcomings in the example of continuous adaptation supplied a key to recognition of the phenomenon. Furthermore, it is emphasised that while we have described the nature of temperature adaptation on the basis of a shift in the developmental threshold θ, this must be regarded simply as a convenience. The point θ is clearly not the developmental threshold in a standard sense, but an abstract algebraic concept, namely the point of origin of the parabola of the empirical equation.

In regard to interpretation of phenological observations

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the phenomenon of conditioning is of considerable importance, since the temperatures in nature undergo continuous changes, and moreover they do not depart to a great extent from the region of the thresholds we have calculated from laboratory observations.

SECTION IB

4. Development of Autumn-fed ticks under controlled conditions

It has been remarked above (p. 47) how various authors have recorded that development in Ixodes ricinus is more prolonged in autumn and winter than in spring and summer. We have referred, for example, to Macleod's (1932) observation that nymphs emerged after 6-7 weeks from larvae which engorged in summer, while from larvae engorged in September and October emergence of nymphs was delayed until 28-37 weeks had passed. These arguments were based on the result of experiments carried out under the normal fluctuating temperature conditions of the laboratory, and while it is presumed that there would be a fall in the mean temperature during the winter months, it is unlikely that this would be sufficiently great as to cause such a marked retardation of development. In spring ticks, which we have considered in Section I, prolongation of the developmental period of the same magnitude would take place only when the temperature was lowered from c. 19°C to c. 10°C. It is, therefore, improbable that the reduction in velocity recorded by Macleod was due solely to a reduction in the actual temperature.

This question is of interest in view of the observations of Falke (1931) on the slower rate of tick-development in autumn, which, he contends could not be accelerated even when the temperature was raised to 25°C. Macleod (1934) apparently overlooked his own earlier record when he denied that a delay occurred in ticks fed in autumn in Britain, and stated "...that humidity conditions being uniformly optimum, unit exposure to a fixed temperature has a fixed developmental effect, irrespective of the previous history of the organism in regard to temperature,

/except

except where this involves exposure to lethal high temperatures or to very low temperatures." Macleod further criticised Falke on what appears to have been a misunderstanding of an ambiguous statement by the German author. Falke stated: "Die während diese Zeit erfolgende Entwicklung weist keine wesentlichen Schwankungen mehr auf; sie dauert im Durchschnitt etwa 25 Tage." It would appear, however, that Falke carried out his observations at one temperature (20°C), and it is probable that he only refers in his statement to this temperature, and does not imply, as Macleod suggests, that after transition to the "Ruhestadium" has occurred, development proceeds at a uniform rate irrespective of the actual temperature. We have already indicated (p.47), however, that Macleod's conclusions regarding seasonal changes in the tick are invalidated by the fact that his material was bred in the laboratory, and so isolated from the normal temperature experience of its natural environment.

We have seen how under field conditions embryonic development and metamorphosis of the immature instars are reduced to a negligible rate of progress, or are completely inhibited by winter temperatures. In preovipositional development of females on the other hand, the temperature response presents distinctly anomalous features. Whereas, the preoviposition period was long in individuals which engorged earliest in spring, and became progressively shorter in individuals which engorged later as the temperatures rose, (thus indicating a direct temperature relationship) in autumn the reverse process was not observed. If the temperature relations of autumn ticks were of the same character as those of spring-fed ticks, a progressive prolongation of the preoviposition period would have been expected as

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the season advanced. In fact, there was no progressive change in the duration of the interval between engorgement and oviposition, and within limits, the developmental processes were completed as rapidly under the relatively cold conditions prevailing in October, as they were in the warmth of July. These observations suggest that the actual temperature conditions play no part in determining the length of preoviposition in autumn, and that preovipositional development proceeds at a fixed rate irrespectively of temperature changes. This conclusion, however, is not borne out when ticks engorged in autumn are studied under controlled conditions.

(a) Preoviposition Period

Collections of engorged females from cattle and sheep were made each year at frequent intervals between July and October. The data (1945) for preoviposition periods at different temperatures are summarised in Tables 35 - 38, and from the mean values, the velocity-curves have been constructed in Fig. 23.

TABLE 35

Preoviposition period at various temperatures of females engorged in July, 1945

Temperature °C	Number of Females	Duration of Preoviposition Period		
		Maximum	Minimum	Mean
10	19	44	65	55.0 ± 1.42
14	20	19	31	25.4 ± 1.09
18.5	20	17	35	23.9 ± 1.17
21	20	18	44	25.5 ± 1.85
25	13	20	58	37.0 ± 4.03

/Table

TABLE 36

Preoviposition period in females engorged in August 1945

Temperature °C	Number	Preoviposition Period		
		Min	Max	Mean
10	32	40	57	46.8 ± 0.76
14	33	17	29	23.1 ± 0.46
18.5	32	14	27	18.9 ± 0.62
21	33	14	41	24.0 ± 1.25
25	13	15	48	32.5 ± 3.23

TABLE 37

Preoviposition period in females engorged September 1945

Temperature °C	Number	Preoviposition Period		
		Min	Max	Mean
10	141	35	54	41.7 ± 0.32
14	82	16	32	20.0 ± 0.49
18.5	61	12	24	15.9 ± 0.39
21	64	10	23	16.3 ± 0.59
25	42	12	45	26.4 ± 1.35

TABLE 38

Preoviposition period in females engorged October 1945

Temperature °C	Number	Preoviposition Period		
		Min	Max	Mean
10	32	31	45	38.4 ± 0.54
14	20	15	25	20.1 ± 0.65
18.5	20	11	17	13.9 ± 0.38
21	20	11	21	13.6 ± 0.65
25	18	10	25	14.6 ± 1.03

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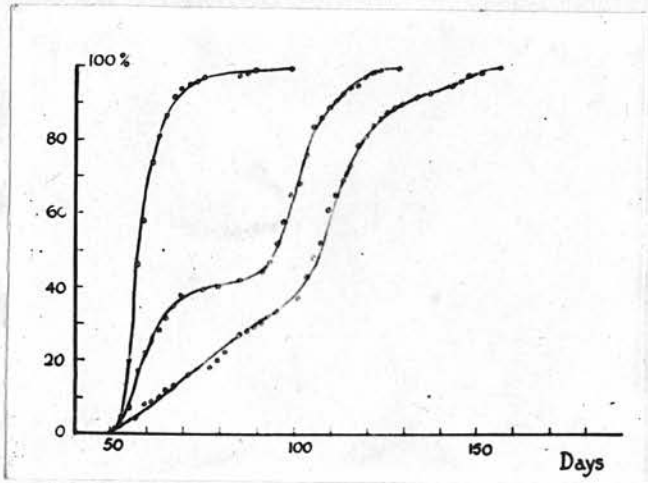


Figure 24.

Course of hatching at 18.5°C in series of autumn laid eggs, conditioned and laid at different temperatures.

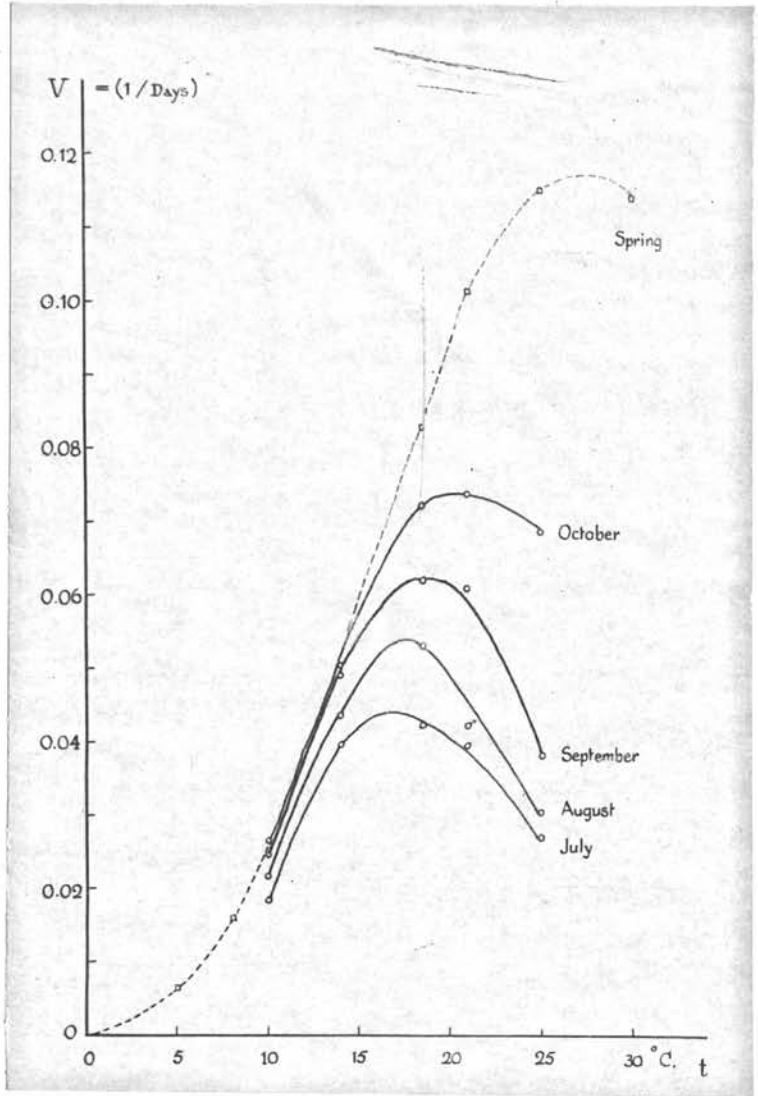


Figure 23.

Preovipositional development of autumn-engorged females. Temperature-velocity curves.

We have already indicated the duration of preovipositional development in spring-fed ticks (Table 20). For convenience of comparison, the mean times given in Tables 35 - 38 above are expressed as percentages of the spring periods at corresponding temperatures in Table 39.

TABLE 39

Duration of preoviposition period in autumn-fed ticks expressed as percentages of preoviposition period in spring ticks at corresponding temperatures (means)

Time of Engorgement	10°	14°	18.5°	21°	25°
July	131%	127%	206%	258%	425%
August	112%	113%	162%	242%	372%
September	100%	100%	137%	161%	303%
October	91%	100%	119%	137%	168%

The times required for preovipositional development in autumn-fed females are in very marked contrast to the times in which the process is completed in spring. There is clear evidence that developmental velocity is retarded under all conditions above the field temperature range in comparison to spring-ticks. At temperatures above 18.5°, the comparative retardation becomes absolute, since an increase in temperature produced an actual reduction in developmental velocity. It is very striking, that as the season advanced, retardation of development became progressively less marked until by October at 14° and below there was no marked difference from the velocity of preovipositional development of spring ticks, and the comparative retardation at higher temperatures was less pronounced.

/Below

Below 14° (e.g. in the field) by the end of September the phenomenon of retardation was completely eliminated, and ticks which engorged later than then completed development at a greater rate than spring-ticks under the same conditions.

This progressive change with the advance of autumn suggests very strongly that there is a continuous process of thermal adaptation in operation. When the field temperatures begin to fall, a marked tendency to become adapted to low temperatures develops. While the velocity curves have been presented in Fig. 23 it is quite apparent that they are not capable of a direct mathematical analysis in the manner that has been adopted in relation to the velocity curve for spring preovipositional development. It is doubtful whether the curves joining the points can be regarded as more than a convenient method of presenting the results as they obtain. The curve quite definitely does not represent a simple quantitative response to the actual temperature. The behaviour of these ticks submitted to high temperatures suggests that they are already in a state of high-temperature condition such that they respond to temperature in a manner indicative of a very high d evelopmental threshold. After exposure to low temperatures, however, the threshold rapidly falls and the material readily passes into a state of medium or low temperature condition. Autumn females, therefore, exhibit a considerably greater degree of plasticity in their temperature relations, and exhibit a marked degree of adaptibility to their temperature environment particularly when the levels are reduced.

/There

There is one point which deserves mention concerning the differences observed between ticks fed in spring and autumn, and that is that while spring samples were collected principally from sheep, in autumn a large proportion of the females studied were obtained engorged from cattle. The possibility that engorgement on different species of host might play a rôle in determining the duration of subsequent development was considered. Comparison of the course of events in ticks engorged on sheep, cattle and hedgehog blood revealed no significant differences between them. One example will suffice to illustrate this. Table 40 indicates the duration of preoviposition in two series at 10°C, which were collected on the same day in Cumberland from sheep and cattle and placed in the incubator about 8 hours after they were removed from their hosts.

TABLE 40

Comparison of preoviposition period at 10°C in two series of females engorged on sheep and cattle in Mid-September

Days	No. of Sheep series	No. of Cattle series
36	1	
37	3	2
38	5	2
39	7	1
40	5	5
41	4	7
42	11	4
43	10	4
44	4	3
45	2	-

TABLE 40 (Cont.)

Days	No. of Sheep series	No. of Cattle series
46	1	2
47	3	3
48	-	2
49	-	-
50	1	-
51	1	-
	n = 58	n = 35

In these two series the distribution is very similar and the mean times are identical:-

Engorged-sheep Mean preoviposition period 41.8 ± 0.41

Engorged-cattle Mean preoviposition period 42.2 ± 0.51

(b) Embryonic development

The duration of the embryonic period of eggs laid by females engorged in autumn is markedly prolonged in comparison to the same period in spring. Here, however, the pattern of the temperature responses is complicated by the conditioning effect of the previous temperature history during preoviposition and oviposition such as we have already demonstrated in spring eggs. If this phenomenon is disregarded for the present, we find that the retardation in development is greatest in eggs laid by females which engorge in the early part of the autumn active season, and least in eggs laid by females engorged at the end of autumn. Development of eggs in autumn 1945 at 14°, 18.5°and 21°is taken to illustrate this, and the results are

/summarised

summarised in Tables 41 - 43. In these examples, the engorged females completed preoviposition and oviposition at one temperature, and their eggs remained to undergo embryonic development at the same temperature.

TABLE 41

Embryonic development in autumn eggs at 14°C

Parent engorged in	No. of egg batches	Duration of embryonic development		
		Minimum	Maximum	Mean
July	27	121	196	164.1± 4.51
August	34	107	181	136.6± 4.14
September	87	103	162	115.8± 2.17
October	49	94	132	109.1± 1.57

TABLE 42

Embryonic development in autumn eggs at 18.5°C

Parent engorged in	No. of egg batches	Duration of embryonic development		
		Minimum	Maximum	Mean
July	78	77	156	114.0± 3.62
August	42	73	146	98.9± 3.83
September	116	55	132	89.9 ±2.31
October	215	55	115	79.7± 1.55

/Table

TABLE 43

Embryonic development in autumn eggs at 21°C

Parent engorged in	No. of egg batches	Duration of Embryonic Development		
		Minimum	Maximum	Mean
July	44	49	129	71.6 ± 2.66
August	23	52	117	67.0 ± 4.64
September	101	52	97	69.1 ± 2.85
October	124	42	95	65.4 ± 1.61

For convenient comparison, the mean times for the various series in Tables 41 - 43 are reproduced together in Table 44 and in Table 45 these figures are expressed as percentages of the times obtained under comparable conditions in spring (Table 21).

TABLE 44

Mean duration of embryonic development in autumn at different temperatures

Parent engorged in	At 14°C	At 18.5°C	At 21°C
July	164.1	114.0	71.6
August	136.6	98.9	67.0
September	115.8	89.9	69.1
October	109.1	79.7	65.4

/Table

TABLE 45

Mean duration of embryonic development in autumn at different temperatures, expressed as percentages of times under comparable conditions in spring

Parent engorged in	Mean Embryonic period x $\frac{100}{\text{Spring Times}}$		
	At 14°C	At 18.5°C	At 21°C
July	171%	204%	164%
August	142%	178%	153%
September	121%	160%	157%
October	113%	141%	147%

It will be noted that the retardation of developmental velocity was comparatively greater at 18.5° than at 14° throughout the autumn period and this may be compared with the trends indicated in the duration of preovipositional development during autumn. At 21°C, on the other hand, the retardation represented by the figures is comparatively less (in eggs laid in the early part of the season) than at 18.5°C. It is probable, however, that this result is spurious, and perhaps affected by the high mortality experienced in eggs laid above 18.5°C which tends to bias the means of the series. There was, indeed, a differential survival rate as between individuals which developed more rapidly, and those which developed more slowly, (compare the maxima in Table 43). Further evidence for this supposition was afforded by results obtained at 25°C. These have been omitted from the tables because, on account of very heavy mortalities, they present a completely wrong picture.

/It

It may be mentioned however that in eggs laid in August the mortality was over 80%, and the mean embryonic period of the survivors was about 50 days, while in October the mortality had fallen to less than 50%, and the mean embryonic period of the survivors was about 47 days.

The results at temperatures below 14°C are of great interest. There was no significant seasonal trend in the velocity of development in eggs laid and incubated at 10°C, and the mean times for all series lay between 265 and 285 days. That is, the prolongation never exceeded 12% of the incubation period of spring eggs laid and incubated at 10°C.

Taken together, these results give a very strong indication that the phenomenon which we have described as temperature-conditioning is operative with very marked effects in autumn eggs. When eggs are developed in the ovary and maintained at high temperatures, they remain in what may be termed the "autumn state". Submission to low temperatures has the effect of reducing the "autumn state" and brings about a more rapid course of development after a return to higher temperatures. When a sufficiently strong effect is obtained after exposure to low temperature, the autumn state is completely eliminated, and the temperature-relations of development assume characteristics obsely comparable to those of spring ticks (Table 21 and Fig.12). The "autumn state" is clearly acquired by the unengorged female during its history prior to engorgement.

As autumn advances, the pre-engorgement history of the female under conditions of falling temperatures has a progressively more marked effect in reducing the degree of autumn state, with the result that a progressively less intense

/exposure

exposure to cold is necessary to produce a 'normal' temperature response during the embryonic development of its progeny. This accounts for the seasonal trends noted in preovipositional development, and in the development at 14°C and 18.5°C of eggs derived from females which complete preovipositional development at these temperatures. At all times during autumn, however, a sufficiently marked effect results from preovipositional development at 10°C, such that there is but a slight seasonal change noted in the subsequent embryonic period. Periods of exposure to 0°C during the preoviposition period produce so marked a difference in the temperature responses during embryonic development, that the eggs become indistinguishable from spring eggs in their time relations. Table 46 indicates the development at different temperatures in eggs derived from females which had been exposed for 40 days to 0°C (Females engorged in September 1946).

TABLE 46

Embryonic development in autumn eggs laid by females which experienced 0° for 40 days during the preoviposition period

Temperature °C	No. of egg batches	Duration of Embryonic Development		
		Min	Max	Mean
14	38	74	101	84.1 ± 1.13
18.5	33	46	65	51.0 ± 0.76
21	29	36	50	40.0 ± 0.63
25	26	33	43	35.7 ± 0.48

These results are very similar to the results obtained with eggs laid in spring, and the empirical equation can be

/readily

readily applied. The equation constants are $\theta = 6^{\circ}C$, and b = 1.25, and the values of the temperature constant a are shown in Table 47.

TABLE 47

Values of constant for autumn eggs after conditioning by low temperature

Temperature °C	Values of constant a	
	Minima	Means
14	996	1132
18.5	1081	1199
21	1063	1181
25	1309	1417

(The values of a for the temperatures of 18.5° and above are rather higher than the values we have regarded as correct for spring eggs. It is possible that during development at 14° there has been a continuous adaptation so that the apparent threshold for eggs developing at this temperature is lower than in the other series (for which $\theta = 7^{\circ}C$ would be a better estimate.)

In view of the differences in state which have been assumed for the eggs referred to in Table 44, it follows that a unique equation for all temperatures in each horizontal series is not applicable. Confirmatory evidence for the assumption, that different preoviposition conditions result in a difference in the temperature relations in embryonic development, is given in Table 48, where the data are presented for development at 18.5°C of three series of eggs conditioned and laid at 14°C, 18.5°C and 21°C respecitvely. These eggs were laid by females

/collected

collected engorged towards the end of autumn (September 22, 1946). The interesting bimodal distribution of developmental times of eggs laid at 18.5°C warrants a presentation in extenso. (Cf. Fig.24).

TABLE 48

Duration of the embryonic period at 18.5°C in eggs condition and laid at different temperatures

Duration of Embryonic Period	No. of Egg batches laid at		
	14°C	18.5°C	21°C
51 - 55	34	16	3
56 - 60	83	31	5
61 - 65	36	15	5
66 - 70	15	12	4
71 - 75	1	2	0
76 - 80	2	2	4
81 - 85	1	4	7
86 - 90	3	5	2
91 - 95	0	20	4
96 - 100	1	27	2
101 - 105		31	13
106 - 110		14	14
111 - 115		6	10
116 - 120		8	8
121 - 125		4	7
126 - 130		1	2
130 +			8
	$n = 175$	$n = 198$	$n = 98$
	$\bar{x} = 59.9 \pm 0.53$	$\bar{x} = 86.4 \pm 1.59$	$\bar{x} = 100.6 \pm 2.14$

/The

The duration of development on these three series is significantly different. To examine the temperature responses of autumn eggs on the basis of the empirical equation [illegible] therefore, an attempt was made through adopting the expedient of comparing the development at different temperatures of daily egg quotas with the same temperature history. Although a large series of observations was undertaken, however, no measure of success resulted from attempts to fit a unique equation to the results at all temperatures. One example may be quoted. In a series of egg quotas laid at 18.5°C, the duration of the embryonic period was 115 days, 69 days, and 60 days at 14°C, 18.5°C and 21°C respectively. If various estimates of b are applied, the values of θ obtained by substitution are susceptible of great variation. Thus we find, when b = 1.25, the values obtained for θ are 7.5°C, 8.8°C and 10.0°C for development at 14°, 18.5° and 21°C, or when b = 1.33 the corresponding points of origin are θ = 8.3°C, 10.1°C and 13.7°C. From these results it is evident that the temperature responses are capable of great variation during the course of development, and do not remain constant throughout. Unfortunately there is no means by which either of the variables b or θ can be controlled, and a precise definition of the complex temperature relations of eggs developing in autumn is quite impossible. There is however a strong suggestion from the trends which occur that it is not unreasonable to regard the "autumn state" as a state in which the velocity-curves for development at high temperatures have points of origin (θ) situated at a higher temperature level than the points of origin obtained for the velocity-curves of development in spring. While the points are high they are

/very

very susceptible to modification during the course of development. During exposure to low temperatures, there occurs a fall in the θ points, and when they have been lowered to the region of 7°C, they become relatively stable, and the temperature responses subsequently become 'normal'. (Cf. Table 46).

While it is undesirable to continue this hypothesis beyond the point of implication justified by the data, it is of interest for the purpose of illustration to apply the equation to the data presented in Table 48. Assuming the index b to be 1.25 throughout, the values of θ which would correspond with the mean times indicated in Table 48, are shown in Table 49.

TABLE 49

Hypothetical values of θ for development of autumn eggs assuming b = 1.25 and a = 1100

Time of engorgement of parent	Values of θ for embryonic development of eggs conditioned, laid and incubated at		
	14°C	18.5°C	21°C
July	9.4	12.3	12.1
August	8.7	11.6	11.6
September	7.8	11.0	11.8
October	7.6	10.3	11.4

These values of θ are of interest, and although they are purely hypothetical, the trends observed suggest a possible basis for an understanding of the "autumn state". While this state has been referred to as the "autumn state" since it is characteristic of ticks which engorge during the so-called

/autumn

autumn active season, it is important to recognise that it is a condition which achieves its fullest expression during the warmest period of the year, July, after which it undergoes a gradual reduction with decreasing environmental temperatures, and is eliminated by the cold of winter.

It is of interest to record that the degree of "autumn state" exhibited slight differences from year to year, and during the period of study, 1943-1946, it was most marked in the autumn ticks of 1945. In Table 50 the incubation times are given for eggs conditioned, laid and incubated at 18.5°C in the years 1944, 1945 and 1946, and these results are compared with the mean field temperatures for the autumn periods of the same years.

TABLE 50

Comparison of incubation times at 18.5°C for autumn eggs laid by females fed in autumn 1945-1946, together with the mean field temperatures for the autumn months of the same years

Parent collected engorged in	Mean incubation period of egg batches at 18.5°			Mean field temperatures °C		
	1944	1945	1946	1944	1945	1946
July	112.1	114.5	104.8	12.3	14.5	12.5
August	96.6	98.9	94.6	12.6	14.2	13.2
September	77.3	89.9	83.6	8.5	13.2	11.7
October	74.8	79.7	70.8	6.2	10.5	8.8

/The

The phenomenon of retarded development during autumn in ticks maintained at constant temperatures presents a distinct contrast to the condition of asthenobiosis which has been described in a number of insects reared under constant temperature conditions in autumn. The examples of development in Anopheles plumbeus Hal. & Steph. studied by Roubaud & Colas-Belcour (1934), and in Phlebotomus papatasii Scopoli recorded by Theodor (1934) may be cited. In these cases a reduction of developmental velocity occurred in laboratory maintained stocks after a long history under controlled conditions. Cases of retarded development began to appear in September and development became progressively more prolonged as winter advanced. In Ixodes ricinus the retardation is a consequence of a direct adaptation to the environmental conditions during its immediate prehistory, and when individuals are reared under constant conditions they do not present seasonal variations such as those which occur when field-ticks are under observation. (Cf. also Macleod's failure to observe seasonal variations in laboratory-reared ticks). It is concluded that there is no evidence of an inherent physiological seasonal rhythm in the tick, but that the observed seasonal variations are directly related to its environmental history. These results thus appear to present a parallel to the observations of Cousin (1932) (cited by Bonnemaison, 1945) on Lucilia sericata Meig., Calliphora erythrocephala Meig., etc., which are normally regarded as heterodynamic insects. When these insects are continuously reared under carefully controlled conditions they develop uniformly without entering into a condition of diapause, and thus behave like homodynamic organisms.

/The

The evidence is strongly in favour of the view that the reaction of the tick to seasonal changes in the environment is determined principally by the temperature factor, and that this reaction is expressed through a modification of its temperature relations.

(c) Metamorphosis of Larvae and Nymphs

The considerable range of individual variation encountered in autumn-fed larvae and nymphs made the study of their development under controlled conditions an exceptionally difficult one, and the results obtained were too irregular to permit of a satisfactory tabular presentation of the data. It has been indicated above (p 41) that the predevelopment active phase persists for a considerable period after engorgement and it is not until the spring of the following year that the passive developmental phase supervenes in nymphs and larvae in the field. The protracted predevelopmental phase is not a simple corollary of reduction of the field temperatures, however, since a delay in inception of the passive metamorphic state is equally evident at temperatures up to 21°C (i.e, up to 10°C above the field range, within which inception of metamorphosis occurs readily in spring-fed ticks). Exposure to temperatures above 21°C, on the other hand, has the effect of promoting the initiation of development in a small proportion of individuals within a few weeks after engorgement. This proportion increases in sample populations which engorge later in autumn. Between 10° and 18.5° the typical autumn prolongation of the predevelopmental period invariably occurs in all individuals. Among these, transition to the passive state may happen at any time within a period from 3 - 12 months (3 - 6 months in the majority),

/after

after which metamorphosis proceeds normally. It is admitted that the definition of these limits lacks precision, but as we have already mentioned, the marked irregularity in the sample populations which it is practicable to maintain under observation precludes an exact definition of the modal range of the interval preceding the inception of metamorphosis.

In Tables 51 and 52 a broad summary is presented of the results obtained from observations on two series of 1000 engorged larvae. These were reared from eggs laid by females confined in tubes in the field in Autumn 1945. Incubation took place in the field and the larvae were fed on hedgehogs when required in early August (Table 51) and mid-October (Table 52) the following year (1946). The temperature experience of these larvae prior to engorgement was thus typical of the normal experience of autumn ticks in nature. The vertical columns in Tables 51 and 52 refer to the numbers of larvae which developed without an abnormally long delay (about 4 weeks) - Column A, the numbers in which the predevelopmental phase was considerably protracted - Column B, and the numbers which died before transition to the passive state - Column C.

TABLE 51

The effect of constant temperatures on the inception of metamorphosis in larvae engorged in August 1946

Temperature °C	No. of Larvae	A developed	B delayed	C died
25	200	19	22	159
21	200	0	38	162
18.5	200	0	53	147
14	200	0	87	113
10	200	0	74	126

/Table

TABLE 52

The effect of constant temperatures on the inception of metamorphosis in larvae engorged in October 1946

Temperature °C	No. of Larvae	A developed	B delayed	C died
25	200	32	74	94
21	200	26	59	115
18.5	200	2	82	116
14	200	0	121	79
10	200	0	97	103

We may regard the arrest of development which occurs in autumn-cycle nymphs and larvae as representing a condition analagous to diapause in heterodynamic insects. It presents some features, however, which are in contrast to the true diapause of insects. There is no evidence of depression of the basal metabolism and it is striking that the tick remains potentially mobile and responsive to external stimuli. Three significant features are embodied in the results presented in Tables 51 and 52 They are:-

1. In a small number of individuals, arrest in the pre-developmental phase can be overcome by subjection to very high temperatures.

2. Between 10° and 20°C a marked delayin transition to the passive developing condition is evident in all ticks engorged in autumn.

3. There is a progressive trend during the advance of the season, so that the phenomena become less marked in examples which engorge late in autumn.

/These

These features recall the findings described for pre-ovipositional development and incubation of eggs, and promote the conclusion that during summer there is probably a rise in the threshold for transition from the active to passive engorged state. Before development can be initiated in autumn, therefore, exposure to temperatures in excess of the threshold is required to promote development without delay and this can only take place at 21°C or above. At lower temperatures prolonged exposure is necessary to facilitate temperature conditioning, involving a reduction in threshold. This normally occurs in winter in the field, and consequently development begins whenever the field temperatures exceed the low threshold level acquired during the winter experience.

SECTION IC.

On the application of temperature equations to data on development in the field.

Before it is possible to apply the empirical equation ($D = a/(t - \theta)^b$) to examples of development of ticks under field conditions, it is necessary to take account, not only of the occurrence of the phenomenon of continuous adaptation to changing temperature levels during the extended course of the process (with contingent modification of the equation terms b and θ), but also of the fact that field temperatures undergo diurnal fluctuation. From a wide range of experiments in the laboratory under conditions of diurnal alternations of temperature within the range 5^o - $18.5^oC.$, it was found that the duration of a particular process was shorter at alternating temperatures than at a constant temperature equivalent to the mean of the alternations. Consequently the empirical equation is not directly applicable to development under conditions of alternating temperature by substitution of the arithmetic mean temperature for the term t. For such conditions, it is necessary to expand $(t - \theta)^b$ to the form $(t_\lambda - \theta)^b.\delta + (t_\nu - \theta)^b.(1 - \delta)$, where t_λ and t_ν are the lower and upper temperature levels, and δ is the fraction of each day spent at t_λ. Instead of t_μ (mean temperature), t_ω, which may be designated the "operative mean temperature" should be used for the estimate of the term t. (When $b > 1$, $t_\omega > t_\mu$, and hence the increase of developmental velocity at alternating temperatures in comparison to arithmetically equivalent constant temperatures.)

Under experimental conditions of simple diurnal alternation between two temperature levels, the calculation of t_ω is a relatively straightforward process. For example, in the case

/quoted

quoted above:-

$$t_\omega = \sqrt[b]{(t_\lambda - \theta)^b . \delta + (t_\upsilon - \theta)^b . (1-\delta)} + \theta$$

The calculation of t_ω for field conditions is a very laborious procedure, however, since the variations of temperature are so complex. In Table 1 the mean field temperatures were calculated from 2-hourly spot readings

$$\text{(Thus } t_\mu \text{ (daily)} = \frac{t_1 + t_2 + \ldots + t_{12}}{12} \text{)}$$

Using the same readings, t_ω would be calculated, for a particular process, from the equation

$$t_\omega = \sqrt[b]{\frac{(t_1 - \theta)^b + (t_2 - \theta)^b + \ldots + (t_{12} - \theta)^b}{12}} + \theta$$

Such a procedure is obviously impossible of practical application for processes lasting up to 100 days. Alternative methods of calculation were adopted and proved useful.

It is important to note that the numerical value of t_ω depends upon the magnitude of b and consequently t_ω varies for different processes under the same conditions of temperature. Moreover, where long time intervals are involved it is improbable that b remains constant throughout the whole course of development. Consequently, it is proposed to omit detailed discussion of the application of the temperature equation to data on development in the field, since, for the present purpose, the practical advantages derived would not be commensurate with the lengthy treatment required.

SECTION II

The Unengorged Tick: Activity

When development is completed, the new instar emerges as a "flat-tick". It is, however, not yet ready to feed and an interval whose duration varies according to the prevailing temperature must elapse before the tick enters upon its host-seeking activities. During the period, which extends from ecdysis to the assumption of active behaviour, the chitinous exoskeleton becomes hardened, the waste products of metabolism which accumulated during development are eliminated, and the food material remaining in the gut from the previous blood-meal (in larvae the yolk residue) is consumed. Until these processes are completed, the organism displays no propensity for feeding. If left undisturbed, the tick remains inactive, or if placed on a host animal, it merely wanders over the body surface without attempting to insert its mouth parts and engorge.

When newly-engorged ticks (of all stadia) are maintained in the laboratory at temperatures of 25°C, or above, the post-ecdysial period is reduced to a minimum. After 10 days increasing proportions of sample populations introduced to hedgehog hosts are able successfully to feed. When they are maintained at 14°C, on the other hand, the post-ecdysial period is prolonged to about 4 weeks, and at 10°C the elapse of 8 weeks or more is required before ticks exhibit any tendency to attach when placed upon host animals.

The relationship between the duration of the post-ecdysial period and temperature is not a simple direct one, but is susceptible to variations which are associated with the temperature history experienced during the developmental period.

/These

These variations are particularly evident in examples maintained at medial and low temperatures. When development has occurred at comparatively high temperatures the post-ecdysial changes are retarded at a particular temperature in comparison to the rate at which they are completed in individuals whose metamorphosis took place at a low temperature.

We have observed how moulting in the field occurs during two well marked seasons depending upon the season when engorgement takes place. Spring-fed ticks moult between mid-August and mid-September, and autumn-fed ticks moult in June and July. Thus, in the one series (spring-engorged) moulting occurs at the time of year when temperatures are falling, while in the other (autumn-engorged) the new instar emerges when temperatures are rising. It is to be expected, therefore, that in the spring-fed series a longer period would elapse after moulting before hunger supervened.

Experiments were undertaken to ascertain the temporal limits of the interval between moulting and the evident inception of readiness to feed under field conditions. It is proposed merely to indicate the broad outlines of the results obtained. At successive intervals ticks which had moulted at one of the stations in the field were transferred to the laboratory and immediately given an opportunity to feed by placing them on hedgehogs. Spring-engorged ticks which moulted during autumn of the same year were found to be unready to feed during the months of September and October. In November from 30% to 40% of individuals engorged normally and after the middle of this month, the proportion increased, until by mid-December the proportion of sample populations which engorged successfully

/was

was not significantly different from the proportion which fed in laboratory reared stocks maintained at relatively high temperatures. There were no significant differences noted between the three instars (larvae, nymphs and adults beginning concurrently to display a readiness to engorge).

From these observations it follows that a population of ticks which engorges during spring is unable to complete development and renew host-seeking activities before the onset of winter. Autumn-engorged ticks, on the other hand, after moulting in June and July were found to be capable of feeding successfully on hedgehogs to which they were introduced in late August.

Obviously, before a population becomes active (i.e. the individuals begin to climb the stems of grasses to assume the host-seeking attitude) it must contain individuals which have completed all the processes which precede the supervention of hunger. In populations which feed in March-May, a renewal of activity cannot take place before December of the same year, and those which feed in August-October do not become active again until August of the following year. Under the conditions of seasonal rise and fall in temperature levels which occur in Great Britain, it is quite clear that spring-fed ticks are unable to complete development and become active during the following autumn season, and autumn ticks cannot become active before the end of the following spring season.

These observations were amply confirmed by experiments on unconfined ticks which developed under field conditions. Ticks which engorged in spring became active the following spring, and ticks which engorged in autumn became active the following autumn. In all experiments with ticks planted out in enclosures,

/the

the limits of the season of activity correspond closely to the limits of the active season of the natural population in the area. Spring-engorged populations began to exhibit host-seeking behaviour when the temperature levels began to rise above 5°C. During the three months following the inception of activity there was a gradual increase in mortality among ticks which were deprived of access to hosts, and by mid-June less than 5% of the population remained alive. It is concluded, therefore, that ticks which engorge in spring do not become active until the following spring, and if they fail to acquire a host then they do not survive. Thus, three years are required to complete the evolution of a generation, and engorgement takes place in three successive spring seasons.

Apart from a small minority which appear to be able to survive the winter without feeding, it was found that ticks which engorged in the autumn period of one year became active in the same period of the following year, and if they failed to obtain a host before the onset of cold conditions, they died. The life cycle of autumn-feeding ticks, therefore, is completed in three years. With very few exceptions, the three year limits can neither be reduced nor extended, and there is practically no possibility of miscegenation of spring-feeding and autumn-feeding populations.

SECTION III

The Life-Cycle: Discussion

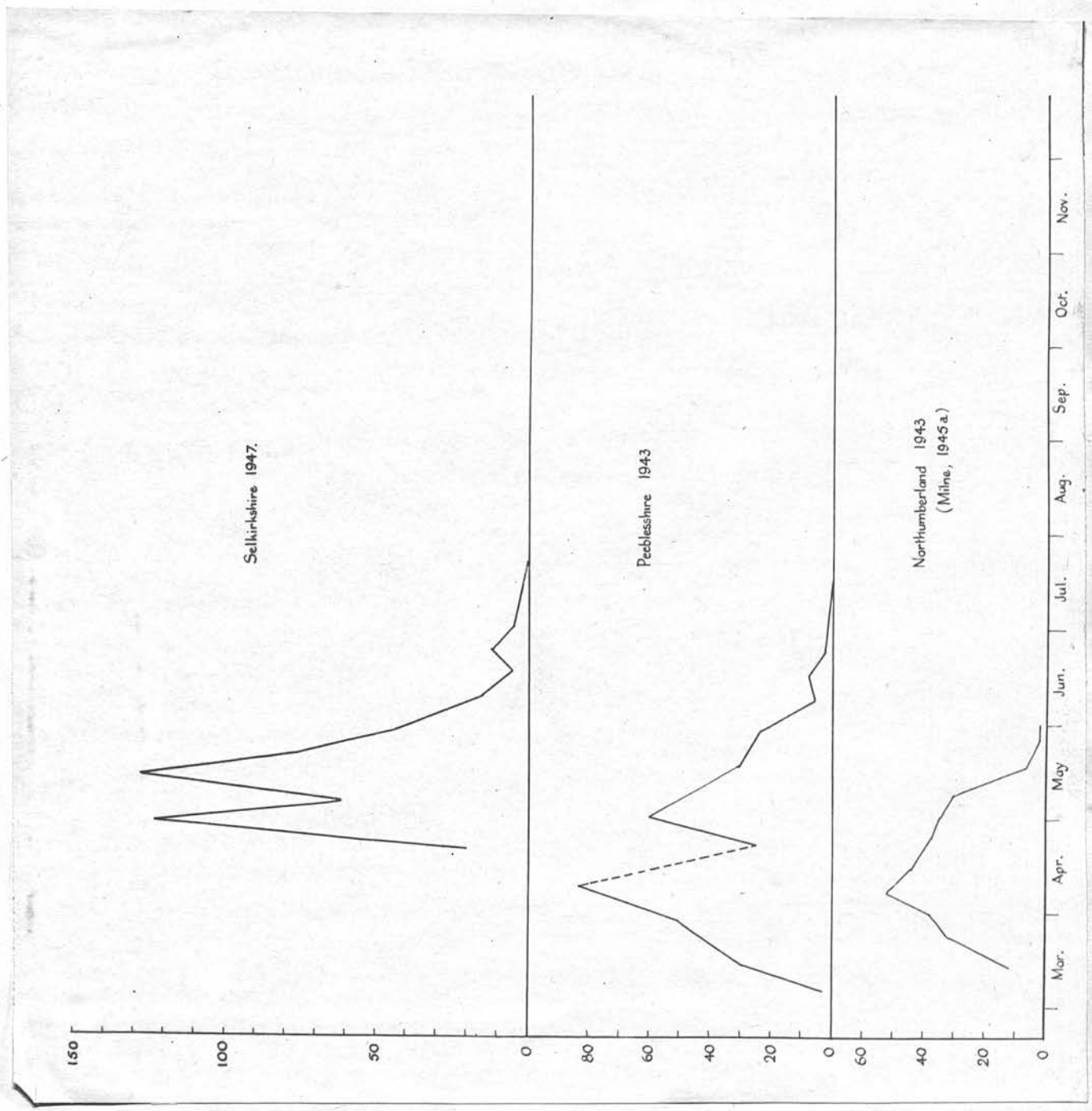
Curves describing seasonal variation in levels of tick-infestation of farm-stock in different districts of Britain are presented in Figs. 25 and 26. In some areas, for example South Wales (Edwards & Arthur, 1947), Cumberland (Milne 1945a), and Argyllshire (Macleod, 1939, and this investigation) ticks have been observed on host animals in large numbers in March-May, and August-October; while in other areas, for example College Valley, Northumberland (Milne 1945a), Ettrick Valley, Selkirk-shire (Fleming, unpublished, and this investigation), and Tweeddale (this investigation) infestation of stock is confined to the spring months. It has been shown in Sections I and II that two distinct series of ticks (which we have termed spring-active, and autumn active) are present in Great Britain. Where single seasonal periodicity occurs (Fig. 25), the tick population is composed entirely of individuals of the spring-active series, while in areas where the activity curve is bimodal, both spring-active and autumn-active series coexist. Thus, to describe the autumn phase of activity as a "recrudescence of activity" (Vide Macleod (1939), and Milne (1945)) is obviously incorrect, since autumn infestation of stock is due neither to a renewal of activity after moulting by the same population which engorged in the previous spring, nor to a resumption of activity after aestivation in the unengorged state by those individuals which failed to obtain a host in spring.

Although ticks have been found in small numbers on cattle and sheep in June and July, we have not encountered any example of a midsummer maximum of infestation such as Hendrick, Moore &

/Morison

Figure 25.

Seasonal variation in stock-infestation.
Examples of monomodal curves.



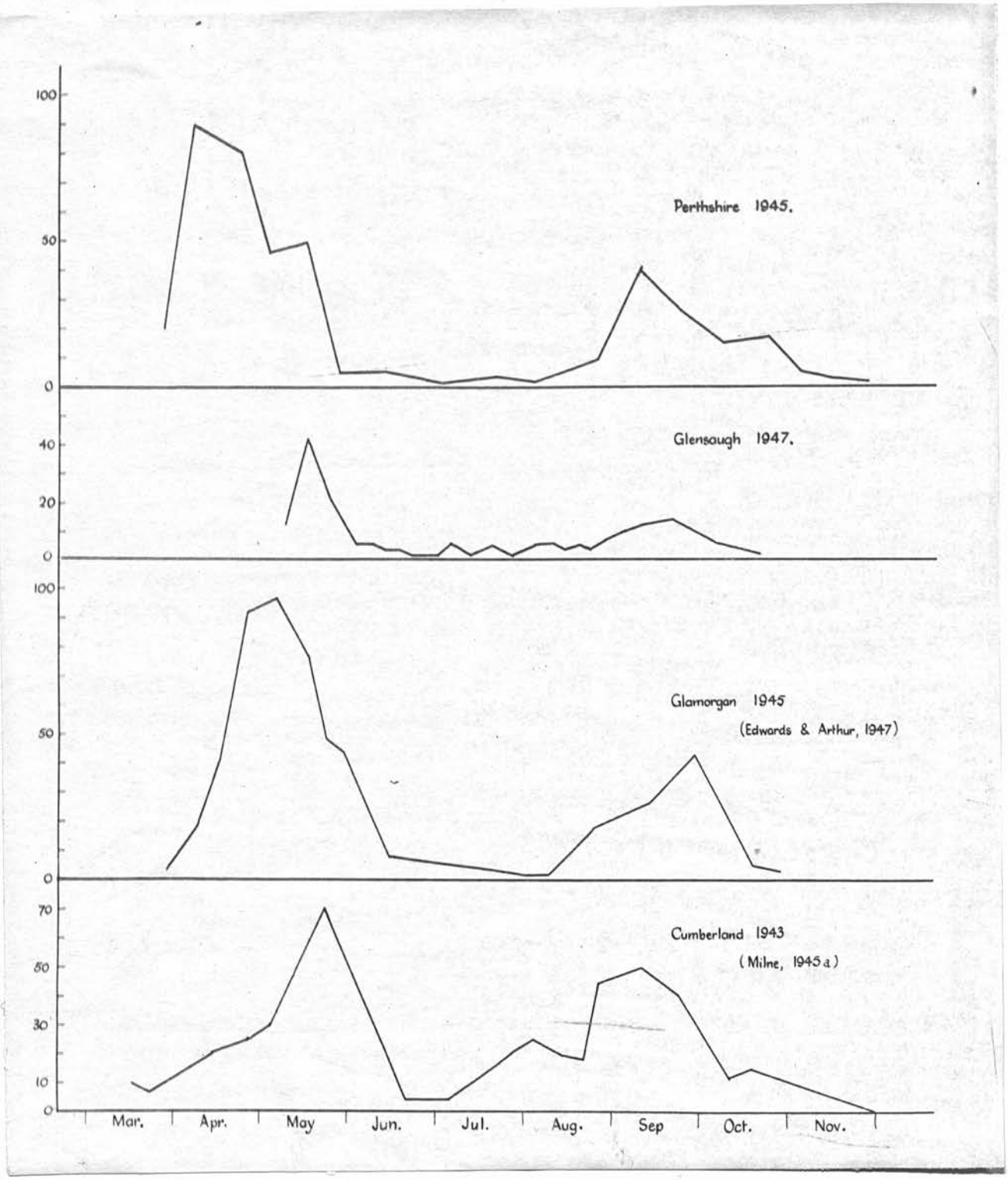


Figure 26.

Seasonal variation in stock-infestation.
Examples of bimodal curves.

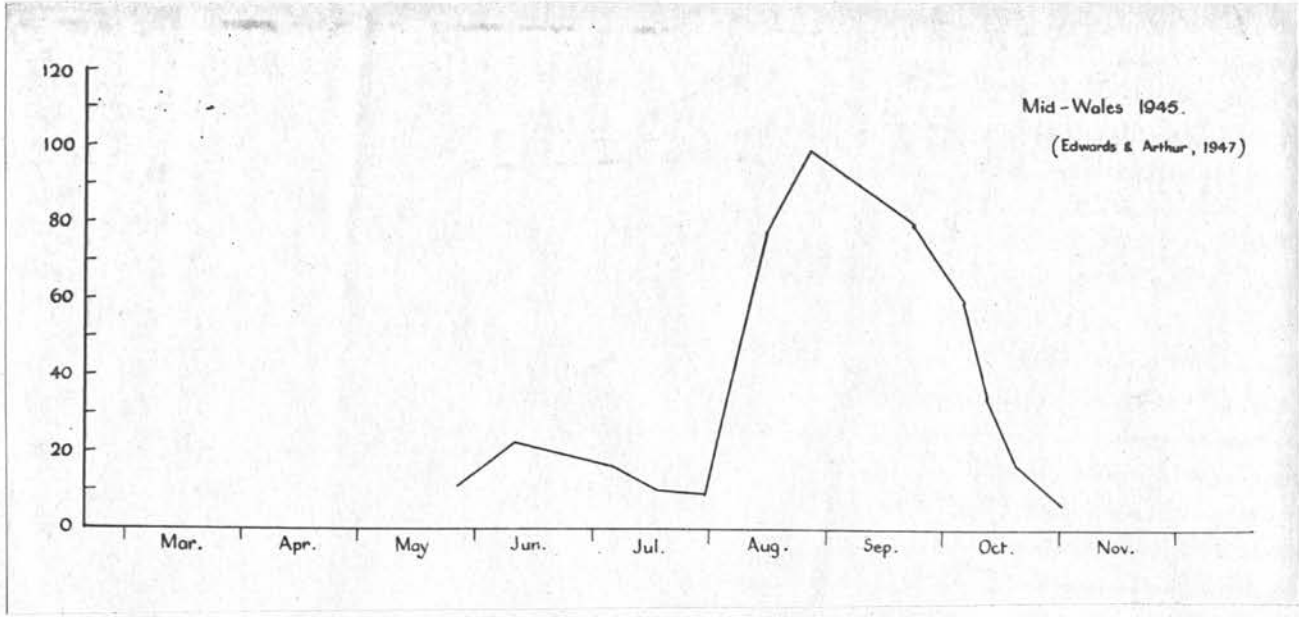


Figure 27.

Seasonal variation in stock-infestation.
Example from Central Wales.

Morison (1938) described. From examinations of sheep and cattle in North East Scotland in 1945-7 it was concluded that the tick populations in that district present no peculiar features. An example (Glensaugh) of the seasonal variation in infestation of stock in North East Scotland is included in Fig. 26. This is a typical bimodal curve. More recently, Edwards & Arthur (1947) have reported that the seasonal infestation curve in mid-Wales (Cahn Hill area) is peculiar, and the evidence, they state, "strongly suggests a single peak of activity, attaining its maximum about August and comparable with that in the Hill o' Fare in Aberdeenshire" (Hendrick et al.). A single case is quoted and figured (Hendre Eirian Farm), but this does not afford support for the suggestion that the activity curve is comparable to that described by Hendrick et al. for ticks on Hill o' Fare (Cf. Fig. 27). On the farm in question, Edwards & Arthur state that cattle do not gain access to tick-infested land until mid-May. From the figure it appears that they become infested as soon as they are introduced to the infested area. At this time the infestation is a comparatively light one, but it falls to a minimum in July and early August, and then rises to a maximum in late August and early September. The seasonal variation is therefore directly comparable to the bimodal kind which is typical of South Wales, and Western Scotland, but on account of the low host potential in spring, the spring active series is strongly reduced numerically.

To explain the bimodal activity curve, Wheler (1899) advanced the hypothesis that a tick population which feeds in spring, develops during summer, and after moulting, the newly emerged instars become active and feed in autumn. Spring and

/autumn

autumn infestations in this view would, therefore, represent the engorgement of two successive broods of one and the same population. This hypothesis is, however, not in agreement with the facts obtained in the present investigation regarding the course of the life-cycle under field conditions, and must in consequence be rejected. Milne (1945a), had already concluded that the two-brood theory was not an adequate basis for the explanation of "seasonal activity rhythms in Britain as a whole", on account of the absence of autumnal infestation of stock in College Valley and Ettrick. (It should be recognised that Wheler was aware of the fact that in some districts infestation of stock is confined to spring, but he assumed that the absence of autumn infestation would only occur in cold upland regions, where it would be due to a retardation of metamorphosis. His assumption is invalid, however, because presence and absence of autumn infestations cannot be correlated with differences in climatic conditions prevailing in the respective areas. For example, Tweeddale, where the autumn-active series is absent, is certainly no colder than Perthshire glens in which autumn infestation occurs.) As regards areas where a bimodal activity curve obtains, on the other hand, Milne considered that the two-brood theory might be applicable, and he developed an extended hypothesis to explain why autumn infestations are often smaller than spring ones. (He states, incorrectly, that autumn peaks (i.e. infestation levels) are invariably lower than spring ones.) Milne (1945a) argues: "Although development proceeds faster at summer than at winter <u>air</u> temperatures (Macleod, 1934), it must be remembered that the microclimate in which eggs and gorged ticks exist (i.e. the deeper layers of the vegetation) is

/cooler

cooler in summer and warmer in winter than the air. Again, the time from autumn peak to spring peak, (September-May, 8 months) is twice as long as from spring peak to autumn peak (May-September, 4 months). Winter-microclimate duration-temperature conditions may permit all the ticks fed in autumn to complete their development in time for the following spring season, while those conditions for summer may permit only a fraction of the ticks fed in spring (i.e. those fed in the first part of the season) to complete their development in time for the following autumn season. Thus where autumn activities are half the weight of spring: (a) each autumn activity would be composed of ticks developing from the first half of the previous spring activity; (b) each spring activity would be composed of ticks developing from the second half of the previous spring activity plus the whole of the previous autumn activity." There is no more evidence for this hypothesis, which is derived from unsupported speculation, than there is for the two-brood theory upon which it is based. Development is arrested at winter temperatures in the field, and in summer it does not proceed with sufficient rapidity to permit of moulting of spring-engorged ticks in time for them to become active in autumn. Again, ticks which feed early in spring do not moult any earlier than those which feed late in spring. Finally, it may be added that it is not a valid claim that autumn infestations are only half the weight of spring infestations (Vide Fig. 25 where the Cumberland example is extracted from Milne's own data, and Fig. 27 where the autumn infestation is considerably greater than the spring one). Milne's theory must, therefore, be rejected.

When he advanced his theory of temperature control of

/activity

activity, Macleod (1936, 1939) overlooked the unimodal activity curves of Ettrick and Tweeddale. This theory was based upon observations on infestations of stock, which were limited to the periods of the year when the weekly average of the maximum air temperatures lay between 45°F and 60°F, together with laboratory observations on geotropism of ticks at different temperatures. Macleod claimed that the relapse of the incidence curve at the end of spring was due to a change in behaviour of the host-seeking population (i.e. when the weekly maxima exceeded 60°F ticks became positively geotropic). He rejected the view that the diminished infestation of stock by early summer was due to engorgement of the available unengorged population, on the basis of the argument that "were this so, the termination of the spring period of high infestation would depend to a large extent on the density of stocking, heavily stocked ground becoming exhausted of its unfed population earlier than ground lightly stocked". Since the limits of the tick season were unrelated to the density of stocking Macleod concluded that the fall in stock infestation at the end of May must be due to a cessation of host-seeking behaviour by the remaining unfed ticks. Milne (1945b) pointed out that the rise and fall of infestations in spring could be due to "a varying number of ticks becoming active for the first time each week of the active season". Thus an increase in the sheep stock "could lower the level of individual infestation but could not cause the season to end before the last week in which ticks became active". According to this view "a prolongation of activity into the normal off-season" should take place when the host animals are withheld until the normal season of infestation is at an end (i.e. delayed stocking).

/Milne

Milne (1945b) found that delay in stocking an infested pasture resulted in higher than normal infestations of sheep after their introduction but did not extend appreciably the season of infestation beyond the normal limits. Milne's findings were confirmed in the present investigation by experiments based upon stocking of enclosures with hedgehogs, which were first introduced to the different plots at successive intervals during the spring season. Delay in stocking did not extend the season of infestation by more than 2 weeks. Delayed stocking experiments would therefore appear to support Macleod's view that the decline of infestation in early summer was due to factors other than the engorgement of all available unfed ticks.

We have shown, from observations on unconfined ticks in the field, that where ticks fail to obtain a host by the end of spring, they usually die. This result was repeated in all types of vegetation in South, West and North East Scotland, and provides the explanation for termination of stock-infestation in early summer irrespective of the stocking density, and of the time of introduction of stock.

It is important to observe that neither Macleod nor Milne in their discussions on spring infestation curves have taken cognisance of the fact that the host potential on sheep grazings increases during the season of infestation. On most hills, for every 100 ewes present at the beginning of spring, c. 100 lambs are born, during late April and early May, and about 25 hoggs are returned to the hill from winter grazings some time in May. Thus the host potential is more than doubled by the end of May. It is concluded, therefore, that the curve of incidence of ticks on stock declines because: (1) The number of unfed individuals

/progressively

progressively decreases; (2) In May the host potential increases and hastens the process of exhausting the available unfed population; (3) As the hosts increase the individual infestation levels become reduced, and (4) The mortality among hungry ticks gradually increases, until by June very few unengorged individuals survive.

The onset of activity in spring (and the final cessation of activity in autumn) is probably related to the prevailing temperature as Macleod (1932-39) has suggested. For example, it has been indicated that spring-engorged ticks become capable of feeding by December, but spontaneous activity does not occur until the following March or April. There is no evidence for the view that unengorged ticks enter a dormant condition of hibernation which is unaffected by weather conditions during the winter months (Diapause in the unengorged phase described by Totze (1933)), and Macleod and others have drawn attention to the appreciable but low infestations of stock which are sometimes observed in mild periods in winter.

There is no evidence for Macleod's (1939) suggestion that the tick population in North East Scotland might represent a separate, physiologically distinct race. Ticks from that area were identical in all respects to ticks from other parts of Britain when studied under the same conditions.

It is concluded that all the theories advanced hitherto, in explanation of seasonal variation of tick-activity, are deficient on account of incomplete understanding of the course of the life-cycle in nature. A diagrammatic representation of the life-cycle, and its seasonal relationships is presented in Fig. 28. Spring-active populations consist of individuals (of

/all

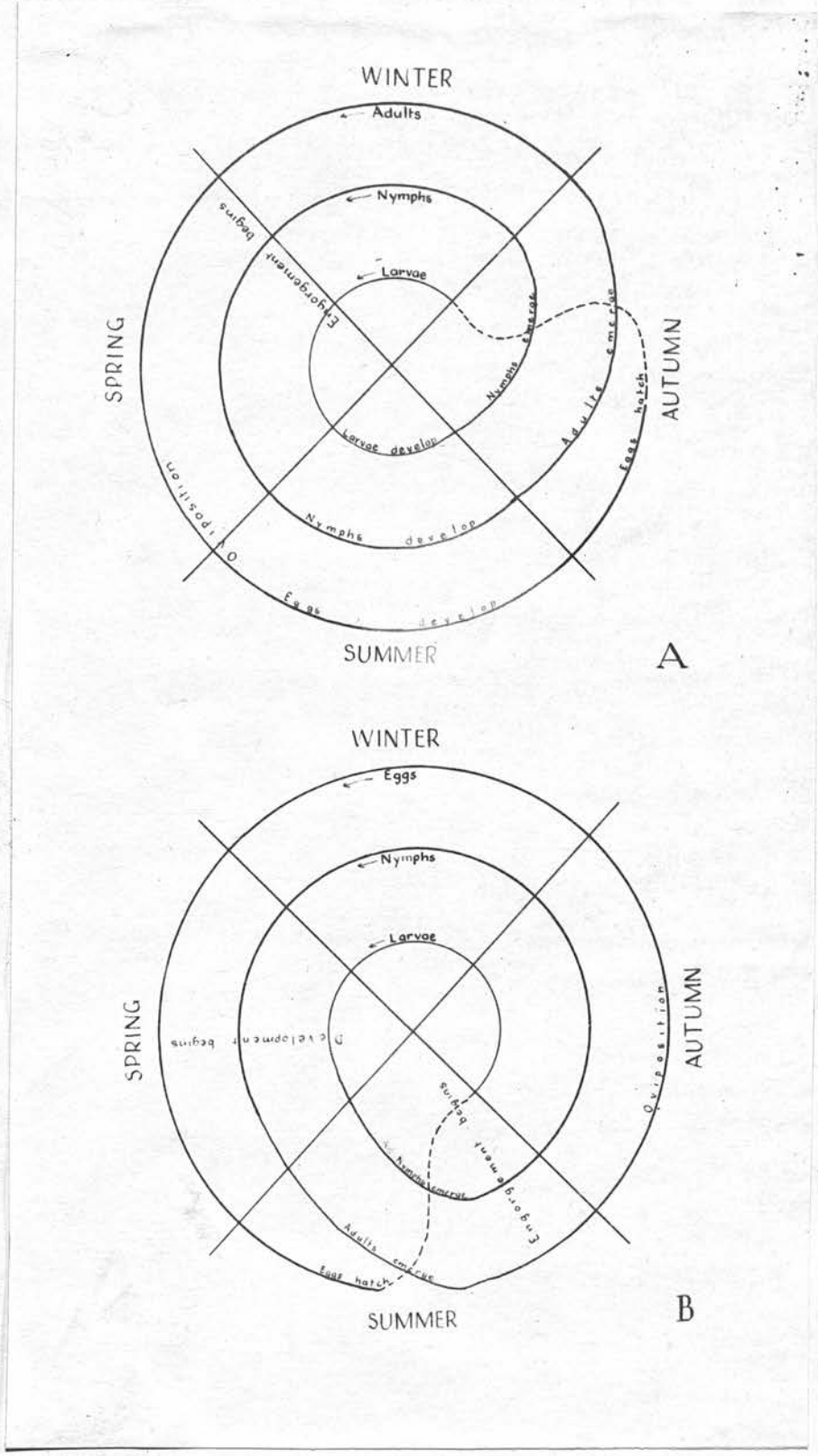


Figure 28.

Diagrammatic representation of the Life Cycle of Ixodes ricinus L.

all three stadia) which overwinter as "flat ticks". When the temperature rises in spring, the population becomes active and infestation of stock reaches a maximum about mid-April. As the proportion of engorged individuals increases, the degree of infestation diminishes since fewer "flat ticks" remain to be fed, (after prolonged activity the rate of mortality among unengorged ticks increases to nearly 100% by the end of June) and by the end of May the stock becomes virtually tick-free. During summer the tick-population undergoes metamorphosis until in late August-September moulting takes place and the new stadia emerge. Hunger does not supervene until about December, and by this time the temperature is usually too low to permit of host-seeking activity. The next phase of activity is thus delayed until the following spring.

Autumn-active populations overwinter as eggs, engorged larvae, and engorged nymphs. When the temperature rises in spring, metamorphosis is initiated, and the new instars emerge in late June-July. Within 2 months of moulting, the flat ticks become hungry and begin host-seeking. Thus infestation of stock begins in August, reaches a maximum in early September, and thereafter declines gradually until all individuals have engorged, or until the remaining unengorged ticks are inactivated by falling temperature. A state of diapause delays the inception of metamorphosis until the cold of winter has been experienced. In the evolution of a generation, therefore, the three instars feed once each in three successive seasons (spring or autumn according to series), and the life-cycle occupies 3 years.

There is evidence for the view that presence or absence of ticks of the autumn-active series is associated with different

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methods of sheep and cattle husbandry in different districts, but discussion of the subject is regarded as outside the scope of this thesis.

SUMMARY

1. Observations on the life-cycle of Ixodes ricinus L. under field conditions are recorded, and evidence is presented indicating that temperature is the principal factor determining the duration of the developmental phases.

2. The evolution of one generation occupies 3 years, one year for each instar.

3. Two series of ticks (designated spring-active and autumn-active) are present in Great Britain. Spring-active ticks overwinter in the unengorged state, and infest stock between March and May; autumn-active ticks overwinter in the engorged state, and infest stock between August and October.

4. The influence of temperature on the rate of development can be defined quantitatively by the empirical formula of Bělehrádek ($D = a/(t - \theta)^b$).

5. Under controlled conditions in the laboratory, the temperature relations of spring-engorged and autumn-engorged ticks are different. Development of autumn-engorged ticks is slower than development of spring-engorged ticks at the same temperatures.

6. The temperature relations of developing ticks vary

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according to the previous temperature history. The phenomenon is regarded as a process of preconditioning, and is characterised by altered numerical values of the terms b and θ in the temperature equation.

7. Seasonal variations in the temperature relations of developmental processes are regarded as the result of temperature conditioning under field conditions.

8. Development of autumn-engorged ticks is delayed or retarded by a condition of diapause which is overcome after a period of exposure to low temperature.

9. Theories regarding seasonal variations in infestation of stock are discussed.

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