THESIS

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by

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I. — Smynthurus Viridis L.
PART I.

"Nature must be considered as a whole if she is to be understood in detail." - Bunge.

I. INTRODUCTION.

The Collembola are a group of insects which have usually been regarded with a certain degree of scepticism so far as the economic entomologist is concerned. Recently, however, the activities of certain species, particularly those belonging to the genera Bourletiella and Smynthurus, have resulted in an increasing amount of publicity for this order of primitive insects. The subject of the present investigation is Smynthurus viridis, Linn., which, from its jumping habits and the depredations it causes to lucern (alfalfa), has come to be commonly known as the "Lucerne Flea", although the damage it causes to clovers is equally serious.
On the establishment of Farnham House Laboratory (1927), under the scheme of the Empire Marketing Board, for the biological control of insect and plant pests, one of the first demands for parasites was that from Australia for the "Lucerne Flea". Accordingly, Dr. J.G. Myers commenced investigations with a view to obtaining an effective biological factor of control, and while several predatory species were obtained, the dissection of numerous specimens, in the hope of discovering parasites, was without avail. It was evident, however, that a thorough investigation into the natural controlling factors of this species, was an essential preliminary to assessing the significance of those predators as natural agents of control, and their consequent utilisation on a rational economic basis. This task was assigned to me by Dr. W.R. Thompson on my arrival at the Laboratory, working under a Research Scholarship from the Ministry of Agriculture.

Previous to the commencement of this investigation, Smynthurus viridis had been described, and various anatomical structures figured, in the works of several authorities on the taxonomy of Collembola, but all that was known concerning the biology of the species was contained in two papers, one by Davies, working at Rothamsted in this country, and another by Holdaway, working at Adelaide University in South Australia, and while both those workers concentrated
on the life-history of the "flea", practically no information, of a quantitative ecological character, was available. Hence this paper, while embodying considerable additions to a knowledge of the life-history and bionomics in sensu stricto, is largely devoted to a determination of the role of environmental factors in limiting the normal increase of the _Smynthurus_ population in nature, while the data obtained therefrom has been utilised in the construction of a theoretical distribution map for the species. In concluding, an attempt has been made to elaborate some general principles on the decidedly intricate and difficult problem of natural control, the writer being of opinion with Woodger that "we are in danger of being overwhelmed by our data and of being unable to deal with the simpler problems first, and understanding their connection. The continual heaping up of data is worse than useless, if interpretation does not keep pace with it."

**HISTORICAL.**

The species was originally described by Linnaeus, in 1746, under the name _Podura viridis_, being subsequently described by several others, a fairly complete description being given by Lubbock, so that it will be unnecessary to repeat the description here. However, it should be
mentioned that the original genus Podura was split up by Latreille in 1802, separating the globular from the elongate forms, under the name Smythurus, while the latter has been subjected to further devastating subdivision until the species viridis is now the only British one included in the genus Smythurus.

**GEOGRAPHICAL DISTRIBUTION.**

S. viridis has got a widespread but also a rather peculiar distribution being restricted to two bands of territory running approximately parallel to the equator, one in the Southern, and the other in the Northern Hemisphere. In his monograph on the Collembola, Lubbock (1873) states it occurs in Sweden, Switzerland, France, England, and Germany. The known distribution has of course considerably increased since then, while it seems almost certain that the insect has been introduced from Europe to those countries in which it is now found in the Southern Hemisphere. By referring to a variety of literature I have been able to augment Lubbock's known distribution of the species (by countries) as follows:— Russia (Arctic Ural), Rumania, Spitzbergen, Italy, Finland, Hungary, Algeria, Morocco, Iraq, Denmark, and almost the whole of the British Isles, while in the Southern Hemisphere, there are Argentina, Australia,
and Tasmania. The distribution in Australia is at present restricted to South Australia and the South-West of Western Australia, while it is only within the last few years that it has been recorded from Tasmania. There seems no reason why the "flea" should not extend to certain other parts of Australia, as well as a few other countries in the Southern Hemisphere, unless definite measures are taken to prevent its spread, but this subject will be treated in greater detail in a subsequent section.

**NATURE OF THE DAMAGE.**

The depredations of this Springtail have undoubtedly been overlooked; due in part to the confusion of damage with that of other species, such as Apion, Sitona, and probably Slugs, while the elusive habits, small size, and colouration, tend to make this species very inconspicuous to the eye of an untrained observer. Even when one has gained some familiarity with the insect, and then attempts to observe specimens in their natural environment, the population may appear to be very sparse compared with its true density. The actual damage consists of a skeletonisation of the leaf surface in severe cases, brought about through the chiselling and rasping action of the insect's mandibles and maxillae in the course of feeding, while partially eaten leaves are soiled by the excrement and
rendered distasteful to stock where the "flea" is present in very large numbers, as in Western Australia. Sometimes the attack commences from the upper surface of the leaf, sometimes from the lower surface, or indiscriminately from either, depending on the plant attacked and the protective armament on its leaf surface, such as hairs, wax, etc. In either case the epidermis is stripped off, the underlying mesophyll eaten, and the adjacent epidermis left as a mere skeleton which serves as a support for the insect in the furtherance of its depredations.

**HOST PLANTS.**

*Smyththurus* has a tremendous variety of host plants, including such diverse families as Urticaceae, Cruciferae, Polygonaceae, Compositae, Graminaceae, and Leguminosae. Indeed the only factor which inhibits attack by the "flea" is morphological structure, the physiological characteristics of most plants being quite incapable of affording protection, although they affect to some extent the growth rate and general well being of the insect, which seems to thrive best on species belonging to Leguminosae, together with a few members of the Compositae. Cape Weed (*Cryptostemma calendulaecem*) seems to be a favourite host plant in Australia, while the writer has observed *Centaurea nigra* and *Achillea millefolium* as favoured Compositae in this country, but *Leguminosae*
have pride of place in this connection and *Smynthurus* has been observed flourishing on so many members that it would appear capable of thriving on any species in this family. Plants having a broad leaf expanse with few 'veins' make good subjects for *Smynthurus* attack, whereas narrow leafed species, with close set 'veins', such as are found among grasses, are much less liable to injury, although by no means immune. In the latter instances the "flea" has to proceed in a longitudinal direction between the vascular strands, being held up by the tougher nature of the bundles if it attempts to cross them.

During the summer of 1929 a trial was conducted with the object of obtaining a variety of Lucerne which was less susceptible to injury than the others, since it was thought that perhaps a very hairy-leaved variety might resist attack to some extent. However, out of the nine varieties tested, only one, namely "Hairy Peruvian" (from Arizona) seemed to exhibit fewer signs of injury than the others, and the difference was not sufficient to warrant the replacement of another variety, which, from its general characteristics, the agriculturist finds highly suitable to his particular conditions.

From field observations and experiments conducted in the laboratory *Smynthurus* is undoubtedly selective in its
feeding habits, preferring legumes if these are available, and thriving best, in this country at least, on members of the genus *Trifolium*, especially *repens*, including all its varieties. It should be mentioned here that although *Smynthurus viridis* and one or two others are exceptions, the phytophagous habit of feeding is not characteristic of the order Collembola, the vast majority of species being saprophytic with a few carnivores, such as *Anurida maritima*, *Isotoma sepulchralis*, and *I. macnamarai*.

**ECONOMIC SIGNIFICANCE.**

The first authentic record of *S. viridis* being of economic significance is that of Froggatt who mentions that in 1896 a species allied to the European *S. viridis* appeared in countless millions in lucern paddocks in South Australia. Although there has been some doubt as to the identification of the insect in South Australia, it seems to be fairly well settled now that the species there is none other than the common European, *S. viridis*, exhibiting a variation in the different environment, and which varies very considerably with the season, even in the South of England.

After several experiments designed to determine the cause of their seasonal colour variation, the writer found
that it was not due to light or humidity, but seemed to be a temperature effect, brought about through its influence either on the distribution or composition of the green pigment, to which the insect owes its colour. As the nymph which hatches from the egg is pale yellow and remains so if green food is withhold, there seems no doubt that the green colour of the insect is due to chlorophyll or one of its derivatives.

In 1920, Lea reported that "the lucerne flea is troublesome in some years in S. Australia" and subsequent reports from the same author, and Newman in Western Australia, have served to emphasize the serious nature of the damage caused by this pest in Australia. In England, a few outbreaks have been recorded in the 'Monthly Reports of the Ministry of Agriculture' but to the average agriculturist Smynthurus is unknown. From observations conducted in several counties in Scotland the writer was able to ascertain that Smynthurus is of greater economic importance there than in England, some pastures being so heavily infested that one could not find a single clover leaf which did not exhibit traces of Smynthurus damage.

LIFE HISTORY AND BIONOMICS.

For the order Collembola as a whole very little is known concerning the biology of its members. S. viridis
seems to have received more attention in this respect than any other species, and the life-history has been worked out in Australia by Holdaway, who has also described the egg, nymph, and adult stages in considerable detail, so that it will be unnecessary to repeat those descriptions here. However, no one has described the course of events occurring under the very different climatic conditions of this country, and to which Smynthurus is peculiarly susceptible, so this will be presented in some detail.

**Seasonal History:**

Observations were commenced at the end of September, 1928, and continued till July, 1930. Three separate fields in the neighbourhood of the Laboratory were utilised for the purpose of making general observations on Smynthurus, and deriving quantitative estimates of the population, together with sweepings of lucerne and soil samples obtained in the South of France; also, from sweepings of the permanent hay plots at Rothamsted Experiment Station.

A gradual decrease in the Smynthurus population took place from October 10th (the time at which a census was first made) till December 21st, after which not a single specimen could be found in the fields until April 10th, when nymphs were obtained for the first time since the previous September. From April 10th there was a gradual rise in numbers till June 26th, and subsequent to this the level of the population underwent a series of violent
fluctuations, correlated with the rainfall.

Since Smynthurus could not be found in the fields for three months of the year, namely January, February, and March, it seemed evident, that the life-cycle must be carried over the winter in the egg stage. This was proved conclusively as follows — A piece of clover turf was cut from the outdoor insectary, where the insects had been numerous the previous autumn, and brought into the laboratory, where a thorough examination for Smynthurus was made in order to make certain that there were no adult survivors. Not a single specimen could be seen. The turf was then placed under a bell-jar and left in a room where the temperature varied between 7° and 15° C. (approx.), and in three weeks' time numerous nymphs were observed crawling up the side of the glass jar. The gradual reduction of the Smynthurus population with the advance of winter is thus due to the non-replacement of a generation which gradually dies out, on account of the inhibiting influence of low temperatures upon the development of the egg stage. This affords an interesting illustration of how an insect may carry over its life-cycle during the unfavourable period under vastly different climatic conditions. Here, the unfavourable period is the winter, where development is inhibited on account of low temperature, while in South and Western Australia, the unfavourable period is the summer, where
development is inhibited on account of low relative humidity. In both cases the life-cycle is carried over in the egg-stage, which, when undeveloped, is extraordinarily resistant to high temperatures accompanied by low relative humidities, as shown by Holdaway in Australia, and is equally resistant to low temperatures, which was demonstrated by the writer as follows:—

A batch of 60 eggs, laid by one female, were allowed to develop in a saturated atmosphere, at a temperature ranging between 17° and 22°C, for 7 days. On the seventh day, development had proceeded to an extent which enabled one to see distinctly the eyes of the embryonic nymphs shining through the chorion. The eggs were then placed in cold storage at a temperature varying between 0° and 4°C, on December 5th, 1928, and allowed to remain there until February 15th, 1929, when they were brought into the laboratory. The temperature to which they were now subjected varied between 10° and 15°C. (obtained from a continuous chart record), and they were left there till hatching took place. Nymphs began to emerge on the morning of March 2nd, and continued to emerge until the end of the next day. One hundred per cent emergence occurrence. The experiment demonstrates conclusively that partially developed eggs are quite unharmed by low or, what is of more importance in this country, fluctuating temperatures (at
least those whose amplitude falls within the range 0°-20°C.) since the eggs were taken directly from 20°C. to 0°C., and from 0° to 15°C., without any gradations. All that occurs, evidently, is the temporary arrest of development, which again proceeds whenever the temperature rises above the developmental zero. The practical significance of the experiment is that it demonstrates -

(1) The extraordinary vitality of the eggs - resistance of undeveloped eggs to dry conditions, as shown by Holdaway, and of partially developed eggs to freezing and fluctuating temperatures between 0° to 20°C., as shown above.

(2) That eggs would be quite unharmed during winter or spring despite the alternation of cold and fairly warm spells such as is commonly experienced in this country.

Seldom do we come across examples, in the animal kingdom of an egg stage which is equally capable of immediate development or of resisting both freezing and dessication, according as the conditions presented are favourable or otherwise, such exigencies usually resulting in elimination or being met by the production of eggs of a different type, when the life-cycle is carried over the unfavourable period in the egg-stage. e.g., the 'Immediate' and 'Resting' eggs of
Rotifers; also the 'winter' and 'summer' eggs of freshwater Cladocerans and Copepods.

Following the emergence of the first generation in springs, sometime in the middle of April, varying in either direction with environmental conditions, there are five subsequent generations. The second generation appears about the end of the first week in June, the third generation about the beginning of the second week in July, the fourth about the end of the second week in August, the fifth about the beginning of the second week in September, and the sixth about the middle of October. A point of interest with regard to the seasonal cycle of events is the gradual shortening of the time required for the appearance of the successive generations throughout the summer and early autumn, due to the rapid speeding up of metabolism by increasing temperature as the season advances. It should also be mentioned that there is very great diversity in the maximum size attained by the generations, this being largely dependent on rainfall, as will be shown in a subsequent section. The cycle of events in Nature as outlined above has been described from observations conducted during a somewhat abnormal year, namely 1928-1929, so that during years characterised by wet summers, or mild winters, one would expect that while the general course of events would be the same there would be
considerable differences in the time of appearance and size of the respective generations, and this has been confirmed by observations carried on in 1929-30. For example, in 50 strokes in Field A on November 26th, 1928, 29 Smynthurus were taken, whereas in the same field subjected to the same treatment, 115 Smynthurus were obtained in 50 strokes on November 28th, 1929; again, in 1929 the first generation appeared about the beginning of the second week in April, while in 1930 it did not appear until the end of the third week. During the exceptionally cold months of January and February, 1929, no Smynthurus were obtained in the sweepings, but were obtained in the same months of 1930, although in very small numbers. Such examples serve to illustrate the variability in numbers of Smynthurus and in the timing of events in the life-cycle, over different years. So much, therefore, for the cycle of events in the life-history of Smynthurus, as occurring in Nature. For a more detailed account of the various stadia, time spent therein, number of eggs laid etc., we must now turn to an examination of certain experiments carried out in the laboratory, since this would be an extremely laborious task to attempt under natural conditions with a relatively small insect like Smynthurus.
Method of Rearing.

Observations were made on 50 isolated nymphs reared to maturity in small glass vials. A considerable amount of thought and time was devoted to the development of a suitable technique for the expeditious manipulation and satisfactory rearing of a somewhat delicate and small insect, Smynthurus having special requirements, including abundant moisture, a limited range of temperature, soil, etc., for its normal existence. It was eventually, found however, that the successful rearing of the insect under laboratory conditions was relatively easy of attainment, provided certain precaution were taken. When specimens had to be dealt with individually e.g., for growth measurements, it was found most satisfactory to rear each individual separately in a small glass vial, 1 c.m. x 4 c.m., stoppered with a tight fitting cork upon which finely sifted soil, moistened with distilled water, was placed. A clover leaf was inserted into the vial and the stalk pressed firmly between the cork and glass, the object of this being to keep the leaf in position while it also helped to maintain a state of turgidity in the leaf so that it served longer as food for the insect. The tube was placed with the cork downwards, and the soil was kept very moist so that the atmosphere in the vial was almost continually in a state of saturation or very near it, a very humid atmosphere being one of the essential requirements
for Smynthurus. Fresh soil and food were supplied as required, which was usually about every fifth day, sometimes every third day, when growth was proceeding rapidly.

**Number of Instars:**

One of the first things which obviously required investigation was the determination of the number of instars and the approximate times spent in the various stadia, as this, so far, was unknown. In the early stages, however, the moulted skins could never be found, or at least, only occasionally, due to the facts, which were subsequently ascertained from observations, that

(a) the moulted skins are very minute and almost transparent;

(b) after moulting, the insect turns round and proceeds to eat the nymphal exuviae.

Recourse was therefore had to the application of Dyar's Law, which proved an invaluable asset. Accordingly, measurements were made of the width of the head capsule of 50 nymphs, throughout the various stadia from the first instar to the imago, and the results presented below represent the average of these measurements:
<table>
<thead>
<tr>
<th>Observed Width</th>
<th>Ratio of Increase</th>
<th>Theoretical Width (as calculated from Dyar's factor)</th>
<th>Instar</th>
</tr>
</thead>
<tbody>
<tr>
<td>1.0</td>
<td>-</td>
<td>-</td>
<td>1st</td>
</tr>
<tr>
<td>1.2</td>
<td>1.20</td>
<td>1.0 x 1.2 - 1.20</td>
<td>2nd</td>
</tr>
<tr>
<td>1.5</td>
<td>1.25</td>
<td>1.2 x 1.2 - 1.44</td>
<td>3rd</td>
</tr>
<tr>
<td>1.8</td>
<td>1.20</td>
<td>1.44 x 1.2 - 1.73</td>
<td>4th</td>
</tr>
<tr>
<td>2.1</td>
<td>1.17</td>
<td>1.73 x 1.2 - 2.08</td>
<td>5th</td>
</tr>
<tr>
<td>2.5</td>
<td>1.19</td>
<td>2.08 x 1.2 - 2.50</td>
<td>6th</td>
</tr>
<tr>
<td>3.0</td>
<td>1.20</td>
<td>2.50 x 1.2 - 3.00</td>
<td>7th</td>
</tr>
<tr>
<td>3.5</td>
<td>1.17</td>
<td>3.00 x 1.2 - 3.60</td>
<td>Imago</td>
</tr>
</tbody>
</table>

Average Ratio of Increase $= 1.197 \times 1.2$ (approx.)

It will be noted that:

(1) There is an extraordinary close agreement between the observed and the calculated widths, confirming the applicability of Dyar's Law to a primitive order of insects such as the Collembola (to which order the law has never been applied so far as the writer is aware) as well as some of the more highly organised orders.

(2) The approximation of the observed to the calculated measurements is sufficiently close to dispose of
any doubt as to the possibility of an ecdysis having been overlooked. Hence *S. viridis* undergoes seven moults, there being seven nymphal instars and an imago.

(3) The only marked discrepancy between the actual and theoretical width of the head capsule is that of the fourth instar, where there is a difference of .07 microscopic units or .01 mm. actually 4 per cent, which is of no significance when making allowance for the experimental error involved in the measurement of such small dimensions in a live insect.

(4) Each unit in the previous table represents .19 mm. so that when converted to actual morphological measurements, the width of the head capsule in the various instars is as follows:

<table>
<thead>
<tr>
<th>Instar</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
</tr>
</thead>
<tbody>
<tr>
<td>Head Width</td>
<td>.19mm.</td>
<td>.23mm.</td>
<td>.28mm.</td>
<td>.34mm.</td>
<td>.39mm.</td>
<td>.47mm.</td>
<td>.57mm.</td>
</tr>
</tbody>
</table>

In describing the first instar nymph, Holdaway remarks that the width of the head is .21mm., so it seems that he has overlooked the first instar, and what he actually described was a second instar
nymph, the two being very similar except in size.

(5) In the measurement of the early instars it was found that a considerable variation exists in the width of the head capsule, depending upon the time during the interval between successive moults, at which the measurement is made. This is on account of the expansion of the chitin while it is still thin and elastic; in the latter instars it becomes thick and more rigid, so that although the measurements be made at various intervals of time during a stadium, the value for the head-width remains practically constant.

Duration of Stadia:

The interval of time necessary for the completion of a stadium depends upon the number of the instar and the influence of environmental factors. At an average temperature of 13°C. (obtained from a continuous chart record) and with optimum conditions of humidity and soil type, the duration of the respective instars is approximately as follows:

<table>
<thead>
<tr>
<th>Instar -</th>
<th>1st</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
<th>Imago</th>
</tr>
</thead>
<tbody>
<tr>
<td>Time</td>
<td>2</td>
<td>3</td>
<td>3</td>
<td>5</td>
<td>5</td>
<td>10</td>
<td>20</td>
<td>15 days</td>
</tr>
</tbody>
</table>
That is, the duration of the life-cycle from the time of hatching to the mature adult is 48 days and the length of the life of the imago 15 days, when the individual is subjected to the above stated environmental conditions. The developmental period in the egg-stage under the same conditions is about 26 days, making the total duration of the life-cycle, from ovum to imago, approximately two and a half months. There are several points of interest in connection with the above, and firstly, the length of the life-cycle is much longer than one would anticipate from general observations, taking into consideration also the comparatively small size of the insect, while secondly, the protracted period spent in the seventh instar is worthy of comment. This, however, seems to be due to the fact that sexual maturity is attained in this instar, as numerous individuals oviposited during this stadium, and, as will be observed from the growth curves (q.v. subsequent section), the process of oviposition acts as a severe check upon growth. The result is a prolongation in the duration of the seventh instar, and the occurrence of the remarkable and exceptional phenomenon of an ecdysis taking place after the attainment of sexual maturity.

**Length of Life-Cycle.**

At higher temperatures there is a rapid speeding up of metabolism, resulting in a much shorter duration of the life-
cycle, which, at a mean temperature of 17°C., is completed in approximately 51 days, whereas at 13°C., it took 74 days, i.e. an increase of 4°C., produces a decrease in life-cycle duration of 31 per cent. Temperatures over 17°C., however, are not favourable to *Smynthusurus*, individuals subjected to such temperature assuming a pale colouration with a pinched appearance and produce fewer eggs, in marked contrast to the dark-green and rotund forms of those maintained at lower temperatures. This effect would appear to be due to over-rapid growth, with consequent weakened constitution, resulting in alimentary troubles and the improper functioning of the physiological processes of reproduction. (See subsequent section for Effect of Temperature on Growth and Reproduction).

**Growth of Nymphs:**

The normal growth curve of *Smynthusurus* from first instar to imago is presented in Graph I. The point of attainment of the various instars and the amount of food eaten throughout the growth period are also indicated in this graph, so that the relationship of those factors to the complete developmental cycle and to each other, is visible at a glance. The problem of growth has been studied from various aspects, and a large amount of data concerning the growth of mammals has been accumulated, but very little is known concerning
Average Length of Individuals (in mms)

- Growth Curve
- Food Curve

Food Eaten (in sq. \( \frac{1}{100} \) in.)

- No. of Instar
  - 1

- 2

- 3

- 4

- 5

- 6

- 7

- 10 days
- 20 days
- 30 days
- 40 days
- 50 days
- 60 days

Period of Gonad Maturation

Oviposition of 1st Egg Batch.
growth phenomena in the lower organisms, particularly insects. Hence the graph illustrates several features of considerable interest, as follows:

(1) The growth of Smynthurus nymphs is, on the whole, a reasonably smooth and uninterrupted process, but throughout the course of the normal growth curve there can be recognised a series of distinct cyclic variations, each cyclic effect being manifested in the assumption of a sigmoid form by different portions of the complete growth curve. Each cycle consists of three phases, namely a period of slow growth, followed by a period of rapid growth, and finally a falling off in the growth rate, and since there are three distinct cycles the total number of phases is nine. Actually, however, the last and the first phases of the first and second and of the second and third cycles, respectively, overlap making the normal growth curve of the Smynthurus nymph a seven phase curve. Provided the growth measurements had been made at longer intervals then the growth of Smynthurus would appear to conform to a single sigmoid curve, but measurements were made at intervals sufficiently frequent to avoid this pit-fall, as the graph adequately illustrates. Hence the problem
now before us is the interpretation to be given to the form of growth curve exhibited by this primitive insect.

(2) It will be observed that the first cycle commences immediately after emergence from the egg, the second cycle commences soon after attainment of the fifth instar, and the third cycle approximately mid-way between attainment of the seventh instar and the imago. Now although these recurrent cycles are conveniently indicated with reference to the various stadia, since there is evidently a synchronisation between the initiation of the cycles and the attainment of certain stages in the life-cycle, the primary cause would appear to be the release of certain substances, of a growth promoting nature, at fairly definite intervals throughout the course of development. The graph adequately illustrates the second rapid growth phase which occurs synchronously with the period of gonad maturation, so that we have here, something at least analogous to the pre-puberal acceleration of growth which takes place in the human. The oviposition of the first batch of eggs marks
the initiation of the third and last cycle, but the rate of growth acceleration in this cycle is the least of all three, being most pronounced in the second cycle. The process of oviposition imposes, therefore, a considerable check on growth, the first batch of eggs being deposited by *Smyrthus* before the adult stage is reached, and once this has been accomplished the growth process evidently receives an added stimulus.

At temperatures much above $13^\circ C$, the cyclic variations in growth are not so apparent, so that although the slope of the curve is steeper, such temperatures have the effect of smoothing out the growth curve on account of their abnormally stimulating effect.

(3) In higher organisms, especially mammals, variations in growth rate have been fairly conclusively associated with the rise and fall in amount of secretions produced by certain ductless glands, such as thymus, etc., but this explanation cannot be applied to insects, for nothing analogous in function to those glands, (with the possible exception of the corpora allata) have as yet been identified in this order. However, further
investigation will doubtless reveal in the insect body, cells with the capacity to secrete substances associated with growth and various physiological processes (other than digestion) and it has already been shown by Burge that there is a positive correlation between metabolic rate and catalase content. Meanwhile, we must be content with describing the relationship which exists between growth velocity and period of development, and in recognising that whatever the fundamental cause may be, there is a characteristic physiological rhythm underlying the growth process even in such lowly creatures as the Collembola.

(4) As regards the food curve it should first be mentioned that the amount eaten was measured by placing a piece of tracing paper over the clover leaf and marking in the leaf area eaten, the tracing paper being then transferred and placed above squared paper and the shaded areas totalled up. Since the depth of tissue eaten is always approximately the same, namely from one epidermis through to the beginning of the other, it was possible, by supplying leaves of fairly uniform size, to obtain a pretty good
idea of the relative amount of food eaten at various stages throughout the growth period. After attainment of the sixth instar there is a very marked rise in the amount of food eaten, corresponding with the rapid acceleration of growth in the second cycle, after which there is a slight falling off followed by a second maximum, corresponding with the middle of the last growth-cycle, and the attainment of the imago. Subsequent to this there is a gradual reduction in the amount of food eaten, corresponding with the onset of senescence. From the point of view of damage done, while this will, of course, depend primarily upon the density of population, the injury caused by the individual up to the end of the fifth instar is comparatively insignificant with that of the three last stages.

In the previous graph there was demonstrated the absolute growth rate and the total amount of food eaten at various intervals throughout development but this gives no indication of the relative growth rate, i.e., the increment of growth in proportion to the size already attained, or the amount of food eaten in relation to bodily size. Graph II has, therefore, been constructed to illustrate these relations. The data used in the construction of both
Average Increase in Length
(as per cent per day).

Amount of Food Consumed
per 1% Increase in Length.
The growth curve presented in Graph II represents the average increase in length per day expressed as a percentage of the size already attained. The graph illustrates the very rapid falling off in relative growth rate which occurs after the attainment of the third instar, followed by a more gradual decrease with increasing age, but punctuated as it were by spurts of growth corresponding with the mid-point in each growth-cycle. This means that the rate of tissue formation is greatest during a period which represents approximately the initial ten per cent of the total growth phase. On the other hand the amount of food consumed for every one per cent increase in length, increases rapidly with age, the relationship being roughly rectilinear in character, with the exception of the periods of most rapid growth in each cycle, during which the insect is either capable of deriving a greater energy value from its food or of utilising that energy in the process of tissue formation, more efficiently, such as might be provided by the periodic stimulation of enzyme secretion.

Oviposition:

During the seventh instar the nymphs become sexually mature and the first batch of eggs laid. Macnamara states that an English writer who had studied Collembola for 50
years had never succeeded in observing oviposition, but a
detailed account of the process in *Smynthurus viridis* has
been given both by Holdaway and Davies, and indeed may be
observed without difficulty in Smynthurus throughout the
egg-laying period. On account of its somewhat unusual
nature the oviposition process will be briefly described
here to enable the reader to obtain a connected account of
the present investigation. The female, having chosen a
suitable spot for oviposition (and, as will be shown later,
the female does exhibit a selective action in this respect)
depresses her head and raises the end of the abdomen. Soon
after this a yellow mass exudes from the reproductive opening
and gradually assumes a spherical form. The insect re-
 mains in this position for a few moments and a mixture of
earth and excrement from the anal opening gradually
envelopes the egg, which is worked round by a circular move-
ment of the end of the abdomen and pressed firmly on to the
soil thereby. The whole process requires about three
minutes. Oviposition in this insect is therefore a somewhat
lengthy process, on account of the necessity of consuming
sufficient soil to act as a coating for each egg, and
judging from its effect upon growth is also of a very
exhausting character.

The eggs are arranged in the form of a dome-shaped
mass, and as the result of numerous observations the writer
Eggs of *Smynthurus* Deposited on a Soils of Different Type; Partially-Covered Ones Just Visible (Nat. Size).
found the average number of eggs in each batch to be about 30.35, but varying by as much as 3-100, according as conditions are favourable or otherwise. The maximum number of eggs laid per individual, under optimum conditions, is about 120. Egg-laying commences in the seventh instar, and at a mean temperature of 13°C., and relative humidity almost 100 per cent; this usually takes place 30-35 days after emergence. As will be shown later, however, these conditions are not optimum for the oviposition process in Smyththurus. A second batch of eggs may be laid at an interval of about 10 days after the first, but this interval may vary from 8-14 days, and in some instances a third batch of eggs are laid. Out of 20 females which deposited a first batch of eggs, 10 deposited a second batch, and 3 a third; the number of eggs in each batch, however, was very different. Generally, the second egg-batch contains nearly 50 per cent more eggs than the first batch, a fact which is doubtless due to the smaller size and relative immaturity of the individuals, when the first egg-batch is deposited, as compared with the full-grown adults which deposit the second batch. The third egg-batch varies very considerably in size, but usually contains about 33 per cent of the number of eggs in the first batch, and is deposited (by about 15 per cent of ovipositing females) after the second batch at an interval which varies widely, but averages about
In order that oviposition by Smyntharus may proceed normally there must be present in the environment a certain combination of factors, otherwise there results a profound reduction in the number of eggs laid. The essential factors are:

(a) low temperatures,
(b) high relative humidity, and
(c) soil of a suitable chemical and mechanical constitution.

These factors will be treated in detail in a subsequent section. Suffice it to say for the present that the demands of this physiological process upon the environment, in order that it may function with maximum efficiency, are greater than those of any other life-process and hence the period of oviposition may be aptly termed the "critical phase" in the life-cycle.

Hatching:

The egg is spherical, smooth, and pale yellow in colour, being 0.25 mm., in diameter when oviposited. The eggs are deposited at the base of herbage, and on the soil surface, and on account of the coating of soil are extremely difficult to discover in the field. Holdaway suggested that the coating of soil round the egg assisted hatching by distributing moisture over the egg surface, and while this is highly
probable, it certainly would appear that the coating of soil affords a considerable measure of protection against other animals, (including insect larvae and adults) whose mode of living consists of scavenging along the soil surface amongst the layer of decaying vegetable matter and organic debris, which tend to accumulate there.

Just before hatching a slight elongation in a direction corresponding to the longitudinal axis of the embryonic nymph, takes place, followed by a circular splitting of the chorion slightly towards the anterior end. There being nothing in the nature of hatching spines or any other device for the specific purpose of facilitating eclosion, the latter takes place by means of body movements of the embryonic nymph, presumably assisted by the purely mechanical effects resulting from fluctuations in the physical factors of the environment. When development of the embryonic nymph has proceeded to about 80 per cent of completion, the eyes and antennae become clearly visible through the chorion, and so afford a valuable criterion as to degree of development. Hence in the course of laboratory experimentation, such as the effect or temperature upon speed of development of the egg, the appearance of the eyes in the form of two black dots shining through the chorion, acts as a warning of the approach of developmental completion, so that from the
time of their appearance, the careful investigator will increase the frequency of his observations, if it is desired to determine the time of eclosion with any degree of accuracy.

The time required for hatching to occur varies tremendously, depending upon environmental conditions, of which by far the most important are temperature and humidity. No matter what the temperature may be, unless the substratum upon which the eggs are placed is kept continually saturated with moisture, or the eggs be maintained in an atmosphere of 100 per cent R.H., when this is the only source of moisture, hatching will not take place. On the other hand, if excessive moisture is supplied so that a film of liquid water is continually maintained on the surface of the egg (and on account of capillarity there is a tendency for this to occur on a moisture laden substratum), the result is delayed or totally inhibited development, due to deprivation of oxygen. Given suitable conditions of temperature and moisture, i.e., about 14°-16° C., and a saturated atmosphere, hatching occurs in 19 days. Development still proceeds normally, and with increasing speed, up to 21°C., while below 9°C., development proceeds exceedingly slowly, and is almost inhibited below 7°C.
Sex Ratio:

The disparity in the numerical relative proportion of the sexes is very marked, and seems worthy of comment before bringing this study of the life-history to a close. Out of 30 third instar nymphs taken from the insectary at random, and reared singly in small glass vials under laboratory conditions, 25 attained to sexual maturity and 20 laid eggs. Again, out of 70 last instar nymphs and adults taken at random from the field and kept isolated in the laboratory, no less than 58 laid eggs, the remainder dying off without laying any eggs, and hence being, presumably, males. The latter appear to be more abundant in late autumn than during the summer, when higher temperatures prevail, so that the production of males appears to be associated with certain environmental conditions. In any case the sex-ratio (tertiary) is remarkably low, being 22 : 1.0 (approximately) when expressed as the number of males per 100 females, and this inequality in numerical proportions is not due (at least entirely) to a differential sex mortality.

THE SIGNIFICANCE OF LIFE-HISTORY STUDIES.

(1) At one time it was thought that a knowledge of the life-cycle of an insect pest was sufficient to en-
sure its speedy elimination, the object being to break the weakest link in the biological chain. Entomologists, however, are beginning to realise that a greater breadth of outlook is required on the whole problem of insect abundance, and that a knowledge of the life-history is merely a preliminary to a proper understanding of the species in relation to its surroundings, both animate and inanimate.

(2) This idea of the relationship between the organism and its environment assumes greater significance in the study of insect control, the more it is realised that the life as lived in Nature is an expression of the reaction of the organism to its environment, and that different factors in the environmental complex call forth different responses on the part of the organism. Man, being a mammal, is provided with a regulating mechanism which tends to stabilise his internal environment, and render him, to a certain extent, indifferent to external changes, whereas in the case of the invertebrate changes in temperature, humidity, barometric pressure, acidity, electrical state, etc., may have a profound significance.
(3) It is this instability of environmental factors
(resulting in many cases from a deliberate altera-
tion of the environment by man in his attempt
to accommodate the growth of crops) which is in
large measure responsible for the abnormal
variation in the numbers of animals, known as
"plagues". Accordingly, an attempt has been
made (presented in Parts II and III) to
analyse quantitatively the effect of the various
environmental factors, biotic and physical, which
contribute towards checking the normal increase
in the numbers of Smynthurus, under conditions
existing in this country. By this means it has
been possible to determine the factors which are
effective in stabilising the Smynthurus population,
and so to account for the fact that in one en-
vIRONMENT the insect may be present in numbers
of negligible economic significance while in
another the population may attain sufficient propor-
tions to assume the characteristics of a
"plague" and become a menace to man's welfare.


LINNAEUS, C. (1746) ...... "Fauna Suecica".


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BIBLIOGRAPHY.
PART II.

"If arithmetic, mensuration and weighing be taken away from any art, that which remains will not be much." - Plato.

1. THE POINT OF VIEW.

(A) THE METHOD ADOPTED.

The previous section of this paper concluded with a reference to the fact that an attempt had been made to analyse quantitatively the effect of the various environmental factors in checking the potential increase of the S. ynthurus population. This task, however, is by no means a simple one, and it seems worth while to state briefly the difficulties involved and the guiding principles adopted by the writer in the pursuit of the present investigation, since it is hoped that apart from the results obtained in this specific instance, the method adopted may serve to some extent as an example of the
lines along which an "outbreak", whether plant or animal, should be attacked.

In regard to the difficulties involved in an investigation of this kind, one of the most serious is due to the fact that there are few methods for obtaining quickly and easily, an accurate quantitative sample of the numbers and kind of organisms; secondly, on account of a multiplicity of factors acting simultaneously in Nature, the effective action of any single factor is rendered very difficult of assessment. In regard to the method adopted, the writer has attempted to steer a middle course between two extremes, or rather, to effect a judicious combination of those, in recognition of the fact that there are two distinct methods available in studying the factors of insect control, as follows:

(a) By means of accurately controlled experimentation in the laboratory, involving the use of sensitive apparatus, to create a known environment, and observe the effect it produces.

(b) By means of field observations, involving the use of quantitative estimates of the population to attempt an analysis of the environment by the correlation of fluctuations in the population with meteorological phenomena.
Both methods have their disadvantages, the most serious to the first being the high cost of apparatus sufficiently sensitive to obtain accurate control of the environmental factors which it is desired to vary; secondly, despite the obvious advantages of controlled experimentation in the laboratory, when their object is to explain the population variations in a natural environment, the results will only hold good in so far as they approach the conditions obtaining in Nature. The second method is an empirical one, and it is frequently hard to distinguish between primary and secondary effects. An additional complication results from the interrelationship of external factors such as temperature and humidity, so that the effect produced may not be entirely a function of a single factor, but dependent, to a certain extent, on the intensity of action of some other factor in the environment. This, of course, also constitutes an additional complication in the first method. In studying the factors of insect control, therefore, the writer is of opinion that

(i) the two methods are complementary and that the first must act as a reinforcement to the second;
(ii) in order to get a proper understanding of the fundamental principles governing insect abundance,
distribution, and control, that the correct method of procedure is to correlate the results of quantitative field observations with those obtained from critically planned and controlled experimentation in the laboratory, i.e., by a judicious combination of the methods of the experimental entomologist and the animal ecologist.

(B) EXPERIMENTAL PROCEDURE.

Having obtained a fairly complete account of the life-history of the "flea", including a detailed examination of the various stadia, number of instars, growth rate, etc., under controlled conditions of temperature, humidity, and soil type, the next appropriate step in the investigation (following the method outlined above) appeared to be the collection of quantitative field observations. These included a fortnightly record of the seasonal distribution of Smythurus on pastures of different type, and in the outdoor insectary, where conditions of temperature and humidity were somewhat different from outside, but were accurately recorded on instruments for the purpose; also a monthly census of the entire insect population in those fields where records of
the fluctuations in the Smythurus population were being made, the object of the latter being to determine whether there was any evidence of a correlation between the variation in level of the Smythurus population and the fluctuations of biotic factors in the environment.

The necessary field data having been obtained, the next advance in the investigation consisted in the accumulation of accurate quantitative evidence as to the effect of various environmental factors, which, as ascertained by an analysis of the field data, were obviously influencing the natural activities of the insect, but could only be correlated with them in a semi-empirical manner. For instance, the fact of a high negative correlation between the size of the Smythurus population and the atmometric index can only be explained scientifically by a careful analysis of the effect of the several factors influencing the atmometric index upon those vital activities which contribute towards the physiological make-up of the individual in all its phases, from the formation of the ovum till death. Hence this section of the paper contains an account of the activities of the investigator as transferred from the field to the laboratory, with a view to substantiating the evidence obtained from field data, by means of quantitative results derived from controlled
experimentation in the laboratory. The reader must bear in mind that, although the account of the laboratory experiments is presented before the field data, they were actually undertaken as the result of suggestions derived from an analysis of the latter, the object being to facilitate the explanation of the fluctuations in the Smynthurus population, since the latter are due to the simultaneous action of several factors, and will be more readily appreciated by the reader with some previous knowledge of the effect of environmental factors upon the physiological processes of Smynthurus.

(C) MODE OF ACTION OF ENVIRONMENTAL FACTORS.

Now it is the belief of the writer, that the effective action of any environmental factor in limiting the size of a natural population may come into operation in two different ways, although, of course, this does not preclude the simultaneous action of that factor in either manner; firstly the effect of that factor upon the actual number of individuals, and secondly, the effect of that factor upon the potential number. The former is obvious, e.g., the action of parasites and predators as biotic factors of control, and the effects of physical factors such as abnormal heat or cold, dessication, etc., upon the various
stages in the life-cycle of insects and other animals, as well as plants. The latter is less obvious and has thus, perhaps, not received the attention it merits, although increasing examples of this effect are gradually becoming known, e.g., "twinning" in sheep has been correlated with the absence of rainy days during the rutting period, (Nichols); the number of eggs shed at each heat period in the rabbit is dependent on climatic conditions during the breeding season (Hammond); the effect of temperature and humidity on the reproductive processes in Sminthurus is profound. The effect of an environmental factor upon the potential number of individuals also includes the action of biotic factors, e.g., the "parasitic castration" of certain bees of the genus Andrena by Stylops, Typhlocyba by Chalarus, the nematode Sphaerularia in queen bees of Bombus, etc., while the more subtle and, as yet, hardly examined effect of the presence of one individual upon another of the same species, and which in the present imperfect state of our knowledge must be termed "psychological", is also referable to this category (see later in this paper).

Since (1) the action of an environmental factor upon the potential number of individuals is brought about through its effect upon the adult of the
preceding generation (and perhaps in some cases upon the grandparent) and

(ii) the size of a population at any time represents the difference between the birth rate and the death rate, - it follows that experiments conducted with the object of explaining the size of a population in terms of the inhibiting and decimating effect of environment upon the potential and actual numbers of individuals, respectively, must be largely concentrated on the effect of environmental factors upon

(A) Growth

(B) Fecundity

(C) Longevity. Accordingly, there follows the results of a series of laboratory experiments dealing largely with various environmental effects upon these three vital characteristics. In addition to the above there must also be taken into consideration -

(D) Survival (in the presence of enemies) i.e., the influence of biotic factors. The latter will be taken up for consideration first.
II - EFFECT OF BIOTIC ENVIRONMENTAL FACTORS UPON SURVIVAL.

From time to time, throughout the progress of the work, insects and arachnids appeared in the sweepings from France and the collections at Farnham Royal, which suggested the probability of their being predators upon Smynthurus. In order to test out the probability of any insect or arachnid, which appeared as being a likely predator, a series of laboratory feeding tests were conducted. These simply consisted of transferring the supposed predator to a clean glass vial of suitable size, and feeding Smynthurus adults. A note was made of the locality in which the likely predator was taken, the number of days it remained alive in captivity, and the total number of Smynthuri consumed during that period. Having accumulated information of this type for a considerable number of insects and spiders, a problem arose in regard to the correct basis for calculating predatory efficiency. Obviously, the average number of Smynthuri eaten per day does not alone convey an accurate idea of the predatory value of a species, since it gives no idea of the total number consumed during the life-cycle. However, when taken in conjunction with the number of days over which the average consumption was obtained it acts as a valuable criterion of predatory efficiency. The total number of Smynthuri
eaten is undoubtedly the best single index for assessing the value of a predator. Eventually it was decided to use two criteria as follows:

**No. 1. Criterion of Predatory Efficiency.**

(i) Average number of not less than 1.4 Smyththurus eaten per day, and no fewer than 35 days in captivity = "Good Predator".

(ii) Average number of not less than 1.4 Smyththurus eaten per day, and no fewer than 21 days in captivity = "Fairly Good Predator".

**No. 2. Criterion of Predatory Efficiency.**

(i) Total consumption during captivity of not less than 90 Smythuri = "Good Predator".

(ii) Total consumption of not less than 60 Smythuri during captivity = "Fairly Good Predators".

The list of insect and spider predators, with data pertaining thereto, is presented in tabular form (See Tables III and IV respectively), from which it will be observed that those two criteria of predatory efficiency are in complete agreement in all important respects, the most important differences being in the fact that in No. 2, *Stenus cincindeloides* and *Evophrys* sp. drop out of the "Good Predators" and *Cyrtocus cyanipennis* moves into them.

According to No. 1 there are thirteen different species of
"Good Predators" and six "Fairly Good Predators", whereas according to No. 2 there are twelve different species of "Good Predators" and six "Fairly Good Predators", both spiders and insects being judged on the same standards of efficiency. From an examination of the data in Tables III and IV it is fairly evident that all species listed as "Good" or "Fairly Good Predators" must, when considered collectively, exert at least a significant degree of control, just exactly what degree of significance in population control of Smythurus is to be attributed to those predators, in comparison with other agencies, must be postponed until those other agencies have been considered in more detail. Meanwhile we can proceed to an examination in greater detail of the individual predators, with the object of attempting to throw further light on their predatory significance by a consideration of their geographical distribution, habits, life-history, etc. In this way it becomes possible to focus attention upon the similarities or discrepancies existing in the ecological peculiarities of the different species, and thus obtain a view of the relationship between prey and predator in its proper environmental perspective.
<table>
<thead>
<tr>
<th>Family</th>
<th>Name</th>
<th>Locality</th>
<th>Period of Captivity</th>
<th>Days in Captivity</th>
<th>No. Smynthurus eaten</th>
<th>Av. No. Smynth. eaten per day</th>
<th>Grade of Predatory Efficiency</th>
<th>No. 1 Criterion</th>
<th>No. 2 Criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Coccinella sp.</td>
<td>Avery - Robinson</td>
<td>Sept. 25th-Oct. 17th</td>
<td>22</td>
<td>40</td>
<td>1.8</td>
<td>Fairly Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. Undecimpunctata L.</td>
<td>Lotto.</td>
<td>Sept. 26th-Oct. 19th</td>
<td>29</td>
<td>50</td>
<td>1.7</td>
<td>Fairly Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. septempunctata L.</td>
<td>Avrute Alais.</td>
<td>Oct. 23rd-Dec. 16th</td>
<td>48</td>
<td>70</td>
<td>1.5</td>
<td>Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>Staphylinidae</td>
<td>Hyeres</td>
<td>Apr. 8th-June 10th</td>
<td>63</td>
<td>170</td>
<td>2.7</td>
<td>Good Predator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Larva of C. 7 punctata</td>
<td>France.</td>
<td>Sept. 25th-Oct. 17th</td>
<td>21</td>
<td>60</td>
<td>1.0</td>
<td>Fairly Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Philonthus politus, F.</td>
<td>Farnham Royal.</td>
<td>May 27th-June 5th</td>
<td>9</td>
<td>70</td>
<td>7.7</td>
<td>Fairly Good Predator</td>
<td></td>
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<td></td>
</tr>
<tr>
<td>P. laminatus, Creutz.</td>
<td>Farnham Royal.</td>
<td>Sept. 29th-Nov. 13th</td>
<td>45</td>
<td>62</td>
<td>1.4</td>
<td>Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Stenus cicindeloides Sch.</td>
<td>Farnham Royal.</td>
<td>May 10th-May 20th</td>
<td>10</td>
<td>30</td>
<td>3.0</td>
<td>Good Predator</td>
<td></td>
<td></td>
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<tr>
<td>Lathrobium brunipes F.</td>
<td>St.Pierre-sur-Dives.</td>
<td>May 10th-May 27th</td>
<td>17</td>
<td>60</td>
<td>3.5</td>
<td>Fairly Good Predator</td>
<td></td>
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</tr>
<tr>
<td>F. littoralis (2) Grav.</td>
<td>Farnham Royal.</td>
<td>June 1st-Aug. 15th</td>
<td>75</td>
<td>419</td>
<td>2.8</td>
<td>Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Xantholinus linearis Ol.</td>
<td>Farnham Royal.</td>
<td>Oct. 11th-Oct. 22nd</td>
<td>11</td>
<td>40</td>
<td>3.6</td>
<td>Good Predator</td>
<td></td>
<td></td>
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</tr>
<tr>
<td>Dendibium littoralis Ol.</td>
<td>Corseilles.</td>
<td>Oct. 27th-Nov. 7th</td>
<td>11</td>
<td>20</td>
<td>1.8</td>
<td>Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Carabidae</td>
<td>Cyrtus cyanipennis Er.</td>
<td>Hyeres</td>
<td>May 2nd-June 1st</td>
<td>30</td>
<td>100</td>
<td>3.3</td>
<td>Fairly Good Predator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Anthocoridae</td>
<td>Anthocoris nemorum Linn.</td>
<td>Farnham Royal</td>
<td>Oct. 5th-Oct. 9th</td>
<td>4</td>
<td>10</td>
<td>2.5</td>
<td>Good Predator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Lygaeidae</td>
<td>Lygus pratensis, Linn.</td>
<td>Farnham Royal</td>
<td>Oct. 11th-Oct. 15th</td>
<td>4</td>
<td>20</td>
<td>5.0</td>
<td>Good Predator</td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. auricularia Linn.,(2)(o.s)</td>
<td>Farnham Royal.</td>
<td>Sept. 24th-Dec. 12th</td>
<td>79</td>
<td>958</td>
<td>6.0</td>
<td>Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>F. auricularia Linn.,(o)</td>
<td>Farnham Royal.</td>
<td>Nov. 1st-Dec. 5th</td>
<td>34</td>
<td>195</td>
<td>5.7</td>
<td>Fairly Good Predator</td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
(A) INSECT PREDATORS.

Cocinella septempunctata, L.

This common species of Ladybird, well known as a devourer of Aphides and Cocids, proved itself capable of taking to a Smynthurus diet with considerable avidity, and of living on nothing but Smynthurus adults for as long as nine weeks, in one particular instance. That C. septempunctata would take Smynthurus as a source of diet was not altogether unexpected, since this species exhibits considerable catholicity of taste, in that it is predaceous upon larvae of the vine moths, Clydia ambiguella, Hb., and Polychrosis botrana, Schiff., in France, upon the Psyllid Trioza viridula in Latvia, upon Cocids in Palestine, and has been shown to take the eggs and larvae of Pyrausta nubilelis, Hb., in Germany. Snee found that the adults ate small frog-hopper nymphs as well as aphides when kept in captivity. Whether those different species contribute towards a variation of the daily menu or simply act as stop-gaps in times of aphide scarcity is not exactly known, but in the case of Smynthurus viridis at least, there exists a potential source of food supply which is presumably utilised, when other sources run short or when Smynthurus numbers become large and this source of food supply more readily available in comparison with that from other sources. Since S. septempunctata is
common throughout Britain and the Continent, and the adults (of different generations) active from the end of April till the beginning of October, the seasonal and geographical range of activity in Europe of \(C. \) septempunctata and Smynthurus viridis, exhibit a considerable degree of similarity.

Coccinella undecimpunctata, L.

This species of Ladybird also proved its capacity to take Smynthurus, but not with the same avidity as its 7-spotted relative. It is also a great devourer of aphides, and has been reported predaceous on Aphis sorghi in the Anglo-Egyptian Sudan. The variation in the menu would appear to be somewhat more restricted than that of \(C. \) septempunctata.

Coccinellid larvae (\(C. \) septempunctata) were much less inclined to accept Smynthurus as food than the adults, but this may have been partly due to the fact that the larvae used in the feeding tests were fairly well grown, and commenced to pupate after 10-20 days in captivity.

Philonthus politus, F.

This beetle attacked and devoured Smynthurus without any hesitation when the latter were placed in the experimental feeding vial, and although it lived for only three weeks in captivity the average number of Smynthurus eaten per day was fairly high. F. politus is found in vegetable
debris, moss, etc., and has a wide distribution, being found over the Palaearctic and Neartic regions, Tasmania, and New Zealand, according to the Coleopterorum Catalogus of Junk and Schenkling. Here again we have areas which are at least climatically favourable for a considerable portion of the year to both species, as will be shown subsequently in this paper.

Philonthus grammatus, Creutz.

This species of Philonthus proved to be a slightly more efficient predator than the previous one. It, also, is common and widely distributed throughout Britain and the Continent, particularly in the Mediterranean region.

Stenus cicindeloides, Grav.

It soon became evident that this species required fairly moist conditions for survival, so sterilised soil was added to the feeding vial and maintained in a moist condition. The beetle was observed on several occasions in the act of catching and devouring its prey, which it sought with considerable agility. According to Fowler, S. cicindeloides is common and generally distributed in the London, South, and Midland districts of England, being rarer further North, and in Scotland confined to the Solway.
district. On the continent, it is found over Europe, in Siberia, and in Madeira, always preferring moist, shady situations such as obtain among the roots of tall grass and among mosses.

**Stenus similis**, Herbst.

This species was not supplied with moist soil, which perhaps contributed to its relatively short life in captivity, as it was observed that most species of *Stenus* lived much longer when maintained on a soil substratum kept well moistened with water, although, according to Fowler, *S. similis* is usually found in comparatively dry places, in marked contrast to the previous species. Both *S. cicindeloides* and *S. similis* belong, however, to the group of the genus *Stenus* which is characterised by having a bilobed penultimate tarsal joint, which is supposed to facilitate their clinging to plant stems. *Stenus similis* is quite common throughout Britain and the Continent of Europe particularly in the Mediterranean region.

**Lathrobium brunipes**, F.

This Staphylinid proved itself a great devourer of *Smyththurus*, "cleaning up" the victims almost entirely, so that nothing but a few scattered pieces of chitinous integument remained after the completion of a meal. According
to Fowler, the genus Lathrobium is a large one, but is chiefly confined to the temperature and cold regions of the Earth, again coinciding very well with the approximate distribution of Smynthurus. *Lathrobium brunnipes* is common throughout Britain, northern and middle Europe, and Siberia, always preferring comparatively shady situations.

**Paederus littoralis**, Grav.

This brightly coloured Staphylinid is easily placed amongst the best predators of *Smynthurus viridis*. Chasing its prey with great agility and seizing the unfortunate victim in its power jaws, *Paederus littoralis* soon disposes of the Smynthuri, whether nymphs or adults, although the former would appear to be preferred, presumably because they are younger and more palatable. It is not improbable that the noxious agent which appears to be present in the body fluids of Smynthurus, judging from the conduct of certain ants and other species is present in the nymphs in a less highly concentrated form, rendering them less distasteful, so that some species which will not countenance an adult will sample nymphs without much reluctance. Specimens of *Paederus littoralis* used in these feeding tests were all taken from different localities in France, although the species is well known in England from the midland counties southwards, being exceedingly common, according to Fowler, in the South of England. The genus is best represented in
the Tropics, but a dozen species are found in Europe, inhabiting the roots of grass in damp, marshy situations — a very favourable habitat for Smynturus viridus.

Xantholinus linearis Ol.

This species is undoubtedly a slightly better predator than the data would appear to make it on account of its short period in captivity. Several other species of Xantholinus are very good predators, e.g. X. cephalus on Ipspini in America and X. hamatus on Chortophila brassicae in Canada. According to Junk and Schenkling, Xantholinus linearis is known throughout the Palaeartic region.

Bembidium littorale Ol.

In the list of Smynturus predators this is the only representative of the Carabidae, and it is a more efficient predator than the data would appear to make out, and for a similar reason to that of the previous species. The Smynthuri were devoured almost entirely, there being nothing left in the feeding vial but a few chewed up fragments of chitinous integument. The species of Bembidium are largely confined to the temperate regions of the Northern Hemisphere, and are typically inhabitants of damp, marshy places. In his 'Genera des Coleopteres d'Europe', Jacquelin du Val remarks "les Bembidium sont des insectes generalement petits et extrement agiles; ils aiment pour la
plupart les lieux humides, le bord des eaux courantes, et se cachent sous les pierres, les detritus etc." The reader will observe that the morphological characteristics and ecological relationships contribute much towards the likelihood of this species being a fairly constant predator of Smynthurus. Other species are known to be good predators, e.g., B. lampros on gravid females of Longitarsus parvulus, Payk., and B. mutatum on Chortophila brassicae. *Cyrtosus cyanipennis*, Er.

This voracious devourer of Smynthurus was maintained in captivity for 30 days, after which it escaped from the vial while being fed and could not be recovered, despite an exhaustive search. It is the only member of the Cantharidae (a large family with numerous carnivorous species) represented in the list of Smynthurus predators. Specimens were taken from Hyeres, in the South of France, this species being apparently more or less confined to the Mediterranean regions of Spain, Italy, and France, although extending farther North in the case of the latter country.

*Anthocoris nemorum*, Lin.

The bug was observed with its victims impaled on its 2 proboscis. Butler, quoting Bold, says it is a great devourer of Aphides, and doubtless the latter will normally
fall a much easier victim than the saltatory Smynthuri, although there is little chance of escape when confined in a small glass vial. However, this species is undoubtedly carnivorous, and being very common and widely distributed, will doubtless include Smynthurus occasionally in the menu. According to Oshanin, the distribution of *A. nemorum* includes the whole of Europe, Algeria, Egypt, Asia Minor, Caucasus, and Siberia, so that it not only occupies the geographical territory of Smynthurus but extends somewhat beyond it. The bug is found on numerous shrubs and low plants.

*Lygus pratensis*, Lin.

This Capsid sucked the juices of its Smynthurus victims fairly well, but the remarks made in regard to the previous species, in its relationship to Smynthurus, also apply to a large extent in this instance. The remarks of Butler may be quoted in this respect; "this is one of the most widely distributed species in the whole of the Capsidae, occurring over the entire Palaeartic region, and over the American Continent as far South as Mexico and Guatemala. It is a species which is evidently possessed of great plasticity as is shown by its great variability, its wide geographical range, and its great variety of host plants. If, as appears probable, it is a carnivore as well
as a vegetarian in diet, this would be further evidence of its adaptability and a guarantee of its survival."

Forficula auricularia, Lin.

The common European Earwig proved to be one of the most voracious of all the Smynthurus predators, the females having a greater appetite than the males. Two females ate no less than 958 Smynthuri in 79 days, after which no food was supplied, and both individuals died on the 59th and 60th day, respectively. The average food requirement per day per female earwig is about six Smynthuri, that of the male being about 5.7. Much has been written about the food of the European Earwig, and it is now recognised as an omnivorous species, sometimes wreaking havoc amongst the gardener's ornamental plants and vegetables, and sometimes eating up his insect enemies. Although it is generally recognised among entomologists that the evil reputation of the Earwig is only partially merited, never before have Collembola been listed in the menu. After some time in captivity the Earwigs became extremely fond of the Smynthurus diet and darted about the container in pursuit of their prey with the utmost agility.
<table>
<thead>
<tr>
<th>Family</th>
<th>Name</th>
<th>Locality</th>
<th>Period in Captivity</th>
<th>Days in Captivity</th>
<th>No. Symnthurus Eaten</th>
<th>Average No. of Symnthurus eaten per day</th>
<th>Grade of Efficiency</th>
<th>No. 1 Criterion</th>
<th>No. 2 Criterion</th>
</tr>
</thead>
<tbody>
<tr>
<td>Philodromus sp. (immature)</td>
<td>Farnham Royal</td>
<td>(Symnthurus Insectary)</td>
<td>Oct. 5th - Nov. 26th</td>
<td>52</td>
<td>100</td>
<td>1.9</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td>Thomisidae</td>
<td>Xysticus sp. (immature)</td>
<td>Confians St. Honorine</td>
<td>Sept. 14th - Nov. 23rd</td>
<td>70</td>
<td>120</td>
<td>1.7</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Tibellus oblongus, Wal.</td>
<td>Farnham Royal</td>
<td>Sept. 26th - Dec. 17th</td>
<td>82</td>
<td>140</td>
<td>1.7</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Ericone sp.</td>
<td>Farnham Royal (Field B)</td>
<td>May 10th - June 21st</td>
<td>42</td>
<td>100</td>
<td>2.4</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td>Mayphidae</td>
<td>Trachygnatha dentata, Wid.</td>
<td>Confians St. Honorine</td>
<td>Sept. 14th - Sept. 25th</td>
<td>11</td>
<td>5</td>
<td>0.5</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Lepthyphantes zimmermannii, Bertk.</td>
<td>Farnham Royal</td>
<td>(Symnthurus Insectary)</td>
<td>Oct. 5th - Dec. 17th</td>
<td>73</td>
<td>110</td>
<td>1.5</td>
<td>Good Predator</td>
<td>Good Predator</td>
</tr>
<tr>
<td>Heteropoda segmentata, Clerck (immature)</td>
<td>Farnham Royal</td>
<td>(Symnthurus Insectary)</td>
<td>Oct. 5th - Dec. 27th</td>
<td>22</td>
<td>50</td>
<td>2.3</td>
<td>Fairly Good Predator</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Ptenopidae</td>
<td>Meta segmentata, Clerck</td>
<td>Les Clayes</td>
<td>Oct. 5th - Nov. 27th</td>
<td>53</td>
<td>90</td>
<td>1.7</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Neprius umbra, Clerk.</td>
<td>Les Clayes</td>
<td>Oct. 11th - Nov. 13th</td>
<td>33</td>
<td>40</td>
<td>1.3</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>Salticidae</td>
<td>Pachygnatha degeerii, Sund.</td>
<td>Les Clayes</td>
<td>Oct. 11th - Dec. 7th</td>
<td>37</td>
<td>90</td>
<td>1.6</td>
<td>Good Predator</td>
<td>Good Predator</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Singa hamata</td>
<td>Uzijn</td>
<td>Nov. 22nd - Dec. 3rd</td>
<td>11</td>
<td>10</td>
<td>0.9</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Syrphus sp. (Immature)</td>
<td>Hyeres</td>
<td>Apr. 8th - May 26th</td>
<td>50</td>
<td>70</td>
<td>1.4</td>
<td>Good Predator</td>
<td>Fairly Good Predator</td>
<td></td>
</tr>
</tbody>
</table>

**NOTE:**

No. 1. Criterion of Predatory Efficiency -

1. Average number of not less than 1.4 Symnthurus eaten per day and no fewer than 35 days in captivity - **"Good Predator"**

2. Average number of not less than 1.4 Symnthurus eaten per day, and no fewer than 21 days in captivity - **"Fairly Good Predator"**

No. 2. Criterion of Predatory Efficiency -

1. Total consumption during captivity of not less than 90 Symnthurus - **"Good Predator"**

2. Total consumption during captivity of not less than 60 Symnthurus - **"Fairly Good Predator"**
(B) **SPIDER PREDATORS.**

Since it was not possible to determine the species of some of the spider predators on account of their immaturity, these cannot be treated in such detail as the individuals which have been determined specifically. However, in the case of spiders this is not of very much significance since the food habits of spiders are, as a rule, not peculiar to any single species, the class exhibits such catholicity of taste. Further, in regard to general ecological relationships whole genera, and even families, exhibit a considerable homogeneity, so that it is often quite unnecessary to treat of a particular species.

*Philodromus* sp. (immature).

This spider was taken amongst the Smynthuri on the clover in the outdoor insectary, and, like the other two Thomisid spiders (all of different genera) proved a great devourer of the Collembola. Thomisidae exhibit the familiar phenomenon of protective resemblance, *Xysticus* (the following genus) lurking among fallen leaves, while *Philodromus*, on account of its more elongated form, is better designed to obtain invisibility along grass-stems, whence it pounces upon the unsuspecting prey.
*Xysticus* sp. (immature).

This is a large genus of crab spiders which live under stones or loose bark and at the roots of plants. They are of a brownish-fawn colour with a characteristic pattern on the cephalothorax so that these spiders are easily recognised, the species cristatus being very common and widely distributed. During 70 days in captivity this individual ate no less than 120 *Smynthuri*, of which nothing was left but the dried-out and shrivelled exoskeletons.

*Tibellus oblongus*, Wal.

Of all the Thomisids predatory upon *Smynthurus viridis* this species was perhaps the best. It is an exceedingly active creature, with a long and slender body upon which are three long and tapering brown stripes, making it a difficult object to perceive amongst semi-decayed grass stems. The species is a very common one and is particularly abundant in marshy localities in the South of England. Besides Europe and Asia, it is found throughout the United States of America and in Alaska.

*Erigone* sp.

This specimen was taken in the vicinity of the laboratory on May 10th from a field in which *Smynthurus* was very abundant, and despite its small size this individual devoured no less than 100 *Smynthuri* within 42 days. The
disembowelled corpses were placed in a neat pile in a corner of the vial. The characteristic habitat of the genus is among grass roots and low herbage, and on account of the small size and secluded lives led by the members they seldom attract attention. Nevertheless, they are very abundant in Britain during the early summer and late autumn. In a private communication, Mr. Bristowe informs the writer that on calm, sunny days in October and November they represent, as a rule, at least 50 per cent of the small black spiders which migrate at that time of the year. Numerous specimens of the two Erigonid species, *atra* and *dentipalpis*, were observed in the same field during the month of November. Dr. Myers also observed that species of *Erigone* were predaceous upon these *Collembola*,

**Trachygnatha dentata**, Wid.

Although a poor predator, judging from the data presented, this species is, perhaps, considerably better than it would appear to be, as it did not remain alive in captivity long enough to subject it to a proper test. It is largely restricted to marshy ground or damp herbage.

**Lepthyphantes zimmermannii**, Bertk.

This Linyphiid was taken in the outdoor insectary at Farnham Royal where the *Smy nthuri* were being reared on
white clover, and it proved to be extremely fond of this form of food, devouring 110 Smynthuri within 73 days.
The species belongs to the section Linyphiaceae of the family Linyphiidae, that is to say, their activities are pursued on a slightly higher level than the ground-loving Erigones. L. zimmermannii builds a flimsy sheet-web at the roots of grasses and other herbage.

Meta segmentata, Clerck. (immature).

This genus, together with the three following ones, are included in the family Epeiridae, the mostly highly specialised of all spiders. According to Savory, Meta segmentata is the most numerous of British spiders, and from spring to autumn may be found on almost every bush. Moreover, it is one of the few spiders that produce two broods in one year. Specimens were taken in Smynthurus sweepings from both France and England, and when fed in captivity accepted the Smynthuri with great avidity.

Epeira umbratica, Clerck.

The spider was taken in the Smynthurus insectary at Farnham Royal. It may almost be described as a nocturnal species, preferring the shade, and never building its orb-web in sunny situations. Blackwall remarks that it is "more abundant in England and Wales than generally
supposed to be, its apparent scarcity being attributable to its nocturnal habits and the care with which it conceals itself during the day; preys chiefly on moths."

_Pachygnatha degeerii_, Sund.

This is a common species in Britain and the Continent. It is fairly easy to recognise with its black cephalothorax and the black and white pattern on the abdomen. It proved to be a good _Smynthurus_ predator. Spiders of the genus _Pachygnatha_ do not build webs of any kind, although they belong to a family characterised by the orb-weaving habits of the majority of its members. Their habitat is on the ground under leaves, etc., particularly in damp or marshy situations.

_Singa hamata_, Clerck.

Experiments on this species were not carried to completion due to the difficulty in obtaining sufficient food supply at the time of year (beginning of December). In any case its value as a predator is somewhat doubtful. The genus includes small species with short legs, which live among low herbage in damp situations. Although not a very common species, Blackwall remarks that _S. hamata_ is "sometimes found in great abundance locally."
Evophrys sp. (immature).

This is the only member of the Salticidae or 'Jumping Spiders' represented in the arachnid predators of Smynthurus viridis. These spiders do not construct a web but carefully stalk and spring upon their prey. The quadrangular cephalothorax which supports the enormous eyes (necessary for their mode of living) renders the Salticidae fairly easy to recognise.

This concludes the list of insect and spider predators tested out in the laboratory; however, lest the reader be under a misapprehension it should be mentioned that this list represents but a small proportion of the total number of insects and arachnids to which Smynthurus was fed, in the hope of discovering and putting to quantitative trial, an efficient predator of the Collembolan. There now remains to be considered, the general characteristics of the different groups of predators, the characters common to the most efficient predators, and finally to contrast and compare the insect and arachnid groups, all with a view to eliciting, if possible, further information which might reinforce existing knowledge as to the predatorial significance of the different species.
(C) COMPARISON OF INSECT WITH ARACHNID PREDATORS.

In regard to the insect group of predators, it is obvious that the family Staphylinidae contains the greatest number of predators as well as a large majority of the more efficient ones, and thus collectively may be regarded as exerting a greater check upon the increase of the Smynthurus population in Nature than any other single family of insects. Further the two most efficient predators of the group belong to the same sub-family (Paederinae) and the same tribe (Paederini).

The next best Staphylinid predator is *Stenus cindeloides*, belonging to the sub-family Steninae. These are all small insects, but with a very distinctive appearance, so that it is impossible to mistake them, and although they present considerable diversity in some respects, yet in others they have much in common. For example, they are found in greatest number and variety in the temperate regions of the globe (but not exclusively so), prefer damp situations as a general rule, and are probably all carnivorous. These features all reinforce existing information as to the probability of *Smynthurus viridis* being a common item in the food supply of certain species of Stenus. Here it should be mentioned that Dr. Myers has found two other species of *Stenus* which are predatory
upon Smyntthusus, namely, S. paganus and S. speculator. By far the majority of the insect predators regarded as 'Good' or 'Fairly Good' were taken during the months of September - October, May - June, and it is noteworthy that the Smyntthusus population during either of these two-monthly periods is larger than in any other two consecutive monthly periods throughout the year, despite the fact that the insect population as a whole is highest during July - August.

As regards the spider group of predators, the family Thomisidae (Crab Spiders) contains a greater number of efficient predators than any other family of spiders, and it is interesting to investigate why this should be so, although it must be borne in mind that the Epeiridae and Linyphiidae are not greatly inferior in this respect. The first and most obvious feature lies in the mode of obtaining the prey. *Smyntthusus viridis* by no means affords an easy victim to predators, due to its tremendous leaping power which it duly exercises on the slightest provocation, e.g., the touching of the sensory hairs on the abdomen. Hence a would be predator must proceed circumspectly. Thomisidae, being spiders which do not build webs, either ambush their prey or chase and stalk it, pouncing
when opportunity offers. They conceal themselves under fallen leaves, herbage, under stones, etc., and are widely distributed over the globe. On the other hand, the Epeiridae and Linyphiidae are web-spinners, of sedentary habit, seldom travelling far from the snare set for their victims. Course grass and other herbage seems to be the typical haunt of these families. Hence it happens that the best spider predators are typically ground loving forms, making occasional excursions up the coarse stems of grass, but living generally within six inches of the ground stratum. This is what one would naturally expect, provided the so-called efficient predators had been judiciously and carefully selected, because six inches within ground level represents the vertical range of activity of Smynthurus. The species in question are as follows: three Thomisids, the Erigonid, Lepthyphantes zimmermanii, and Pachynatha degnerii (the Epeirid with non-characteristic habits).

On account of the relatively small thorax and large rotund abdomen with definite pattern thereon, some of the Epeiridae and Linyphiids above mentioned present a striking resemblance to an adult Smynthurus viridis, when viewed from the dorsal surface, but whether this has any significance or is purely an accident it is perhaps wiser not to hazard a definite opinion.

Coming to a comparison of the insects and spiders
as to their relative predatorial efficiency, we broach a difficult subject, which must be postponed for fuller consideration until after we have examined the effect of biotic factors upon the Smynthurus population in Nature, as derived from quantitative field data. However, judging from the preceding information obtained from laboratory experiments we may draw up a list of predators and place them in their order of efficiency. Taking into consideration only those regarded as "Good" or "Fairly Good" predators, and using No. 2 Criterion of Efficiency, the list is as follows:

1. Forficula auricularia, L.,
2. Paederus littoralis, Grav.,
3. Coccinella septempunctata, L.
4. Tibellus oblongus, Wal.,
5. Xysticus sp.,
6. Lepthyphantes zimmermanni, Berth.,
7. (Equal) - Philodromus sp.,
8. Pachygynatha degeerii, Sund., and Meta segmentata, Clerck.,
9. (Equal) - Lathrothrips brunnipes, F.,
10. (Equal) - Pachynathus maculatus, Creutz.,
11. Stenus cicindeloides, Sch.,
12. Philanthus politus, F.

Lest the reader be under a misapprehension, it may be stated that the above list of predators is not intended
to be all inclusive; and that while it contains the majority of the most efficient predators of *Smynthurus viridis* others doubtless exist, especially amongst the Linyphiidae, Staphylinidae, and perhaps Carabidae. Nor does the list make any pretensions as to representing the order of utilisation for purposes of biological control, since it takes no account of ecological relationships between prey and predator, seasonal periodicity, numerical abundance, economic significance, or feasibility of collection or rearing in adequate numbers. All these must receive a critical and dispassionate analysis, in making a judicious selection of predators, if their utilisation as natural agents of control is to proceed on a rational economic basis. The final choice of predators, their significance in checking the increase of the *Smynthurus* population, and feasibility of economic utilisation, will be taken up for consideration in Part III in conjunction with the field data. Meanwhile, we must proceed to examine the laboratory experiments dealing with the effect of various physical environmental factors upon different phases in the life-history of *Smynthurus*, after which we shall be better able to give a correct interpretation of the field data, and to attribute to the various natural controlling factors their true significance.
I

TABLE

Temperature,

average Length

3.0°c.

5.80 6.00 6.66 7.00 7-25 7-50

V.

of Smynthurus nymphs throughout Growth

7-66

7.83

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hrs. at

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(in days)

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9-21

9-42

9-58

6

5

3.25 5.68 6.71 8-75 9-1
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III - EFFECT OF PHYSICAL ENVIRONMENTAL FACTORS.

(A) GROWTH.

(1) Effect of Temperature upon Growth Rate and Total Growth.

It soon became evident after a few preliminary experiments with Smynthurus nymphs that slight differences in temperature produced very profound differences in the rate of growth and even total growth of nymphs, while it was evident from the field data that the length of time required for the attainment of sexual maturity varied considerably in the successive generations, becoming gradually shorter as summer advanced and gradually longer with the approach of winter. Accordingly, several experiments were carried out to determine the effect of different temperatures upon the growth of nymphs, and these are presented in Graph III. The graph has been so constructed as to be almost self-explanatory, and the tracing out of the various curves should convey to the mind a more accurate representation of the facts than can be expressed in words. However, the following notes will facilitate its interpretation.

(1) With the exception of 21°C, the curves represent the absolute growth rate under conditions of
slightly fluctuating temperatures, so that $16.7^\circ C$, $13.0^\circ C$, and $7.93^\circ C$, represent mean temperatures, as calculated from 6-hourly intervals on a continuous chart record. The temperatures of $21^\circ C$, and $25^\circ C$, are constant within $\pm 0.5^\circ C$.

(ii) In order to convey some idea of the relationship of these temperatures to outdoor conditions, it may be stated that the curve for $7.93^\circ C$, was plotted from nymphs placed outside from October 11th to December 20th, the daily mean temperature from May 15th to July 10th (1929) at Farnham Royal (in a Stevenson screen) was $12.4^\circ C$, and the daily mean temperature from July 11th to September 19th (1929) was $16.4^\circ C$.

(iii) It will be observed that in the case of $13.0^\circ C$, growth curve, the typical sigmoid form is very closely approximated, as has already been described together with its several cycles, in Part I. However, the characteristic cycles in the Smynthurus growth curve are still distinctly indicated above and below $13.0^\circ C$, namely, at $16.7^\circ C$, and $7.93^\circ C$, respectively, although not to such a marked degree. This suggests that at temperatures significantly removed from $13.0^\circ C$, growth proceeds abnormally in this species, i.e., being over-accelerated or unduly retarded. The ultimate effects of the abnormal
growth rate will be observed later, when we come to consider fecundity and longevity.

(iv) The higher the temperature (up to a certain limit) the steeper the curve, i.e., the more rapid is the growth rate - as one would expect; also, the higher the temperature (up to a certain point) the greater is the total amount of growth - which one would not necessarily expect. The total growth, being the length of the body from the anterior end of the head to the tip of the abdomen, expressed as a percentage of the total at 16.7°C., is as follows:

<table>
<thead>
<tr>
<th>Temperature</th>
<th>16.7°C</th>
<th>13.0°C</th>
<th>7.93°C</th>
<th>3.0°C</th>
<th>21.0°C</th>
<th>25.0°C</th>
</tr>
</thead>
<tbody>
<tr>
<td>Percentage</td>
<td>100</td>
<td>91.0</td>
<td>82.2</td>
<td>68.0</td>
<td>42.5</td>
<td>38.3</td>
</tr>
</tbody>
</table>

When the data in this table is plotted in the form of a curve, with percentage of total growth as ordinate and temperature as abscissa, the points on the graph corresponding to the four lower temperatures are found to lie almost exactly on a straight line, indicating that total growth in Smynthurus is directly proportional to the temperature, up to 16.7°C., at which maximum growth occurs. Thereafter a sudden and very rapid falling off takes place up to 25°C., beyond which Smynthurus nymphs (even under optimum humidity conditions)
cannot exist for any length of time.

(v) The growth rate also increases up to 17.0°C (approx.), and after a certain temperature (somewhere between 17.0°C and 21.0°C) is exceeded, decreases rapidly. Since growth continues, although very slowly, at 3.0°C, proceeding at a maximum pace about 17.0°C, and then rapidly falling off, it is evident that the range of activity of Smynthurus, even where humidity conditions are at an optimum (those experiments being carried out in an almost saturated atmosphere) is situated low down on the temperature scale, in comparison with other insects.

(vi) An extremely interesting feature in this graph is indicated by the double circles and the arrows. The former indicate the period during growth at which 75 per cent of the nymphs are in the seventh instar, sexual maturity being attained in this stadium. It will be observed how remarkably constant is the attainment of sexual maturity, with reference to the growth cycles, despite differences in temperature, this phase being located with great definitly on the "crest" of the second "growth wave". Further, the attainment of sexual maturity is always followed by a period of decreased growth rate, during which, presumably, food is directed towards accumulation of yolk material in the ova, indicating an antagonism between growth and re-
production. These growth curves are dominated by the course of growth in the females, since the sex ratio is, at the highest 25 : 100, when expressed as number of males per hundred females.

(vii). It will also be observed that the higher the temperature (up to $17^\circ$C. approx.) the smaller the individuals and the shorter the time interval, when sexual maturity is reached, the time required at $16.7^\circ$C, being almost exactly half that required at $7.9^\circ$C. At $21.0^\circ$C., and $3.0^\circ$C., the nymphs never attain to the seventh instar, dying off before this is reached on account of the very adverse temperature effects, such temperatures being too far removed from the normal growth temperature for Smynthurus. Again, it will be observed that oviposition of the first egg batch initiates the third and last growth cycle, but the latter does not appear in those nymphs reared at $7.9^\circ$C. This seems due to the fact that the nymphs gradually died off on account of a general reduction in metabolic vigour at this somewhat low temperature, so that adverse secondary factors, such as fungus and bacterial attacks, gained ascendancy, resulting in the death of the nymphs. The gradual falling off in body length at the close of the growth period is a definite characteristic of those
--- 13.0°C (slight variation)
--- 3.0° and 23.0°C (12 hrs at each)
--- = 13.0°C (slight variation)
--- = 3.0° and 2.3.0°C (12 hrs at each).
insects, there being a general shrinkage in body size just prior to, and during, the onset of conditions resulting in the death of the individual.

Graph IV illustrates the effect of violent fluctuations in temperature upon the growth of Smynthurus nymphs. A batch of these (10 in all) were subjected to temperatures of 3.0° and 23.0°C, for 12 hours alternately, giving a mean temperature of 13.0°C. In comparison with the slightly fluctuating temperature of 13.0°C, it is apparent that these violent fluctuations in temperature have a marked initial stimulating effect, but eventually prove harmful, and result in a rapid decrease of growth rate. Thus varying temperatures stimulate growth provided the variation be not too violent.

(2) **Effect of Humidity upon Growth Rate and Total Growth.**

Under natural conditions, humidity tends to vary inversely with temperature; it was obviously desirable, therefore, to isolate the effects of temperature and humidity upon the several phases in the life history of Smynthurus, in order to demonstrate how much of the effective action was attributable to the respective factors constituting the combined effect, as high temperatures and low humidity usually act simultaneously
in Nature, with the exception of certain tropical areas, in which Smynthurus cannot exist, as will be shown later. Previous experiments had shown that as one proceeds from developing egg, to early nymph, late nymph, and adult stage of Smynthurus, one encounters successive stages in the life-history, which become decreasingly sensitive to the adverse effects of low humidities. Hence to demonstrate the effect of low humidities upon growth one had to effect a compromise between choosing an early nymphal stage, which would demonstrate growth but could not survive long at the low humidities, and a later stage which could resist the adverse effect of low humidity for a longer period, but was incapable of any considerable amount of further growth. Eventually it was decided to use fifth and sixth instar nymphs, these being distributed equally in the respective humidities, namely, 50 per cent R.H., 70 per cent. R.H., 90 per cent R.H., and 100 per cent R.H., using 10 individuals for each humidity and making measurements every third day. Each individual was subjected to three different measurements (as in all experiments involving the effect of environmental factors, upon growth),

(i) width of head capsule - in order to ascertain whether a moult had taken place or not;
(ii) width of abdomen, and
(iii) length of body from anterior end of the head to tip of the abdomen.

Two experimental difficulties encountered should be mentioned; firstly, the fact that the individuals had to be removed from the experimental humidity chamber for a few moments in order to be measured, and secondly, the food was always supplied fresh and thus several hours elapsed before it came into humidity equilibrium with the experimental atmospheric humidity. It was deemed wiser, however, to do so rather than to supply food of the same moisture content as the atmosphere in the container, the former being regarded as a closer approximation to natural conditions, since the plant can maintain its moisture content (if the humidity is not excessively low) by drawing upon the reserve of moisture in the deeper layers of the soil, the latter being unavailable to Smynthurus.

The growth curves of Smynthurus nymphs under the above stated conditions are presented in Graph V (for data see Table VI), and an account of the experimental difficulties mentioned, should perhaps be regarded as indications of the relative effect of the different humidities, rather than the absolute effect. The actual figures have been transformed into a per centage of the
original size, and then converted into the natural logarithm, the transformation having the effect of eliminating small fluctuations without obscuring the main features, which the curves are meant to demonstrate; and further, the natural logarithms of the successive growth measurements represent the average relative growth rates for each successive period, i.e., the increase per unit of time per unit of growth attained.

**Table VI.**

<table>
<thead>
<tr>
<th>Relative Humidity</th>
<th>Average Length of Smynthurus Nymphs (in micro. units - a unit = .19 mm.)</th>
<th>Actual Body Length in Micro-units.</th>
<th>Same as Above Reduced to Percentage of Original Size.</th>
</tr>
</thead>
<tbody>
<tr>
<td>100% saturated</td>
<td>7.05 7.60 8.00 7.83** 8.25 -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>90% saturated</td>
<td>6.70 6.90 7.31 7.37 7.25 6.83</td>
<td></td>
<td></td>
</tr>
<tr>
<td>70% saturated</td>
<td>6.80 6.85 7.44 7.35 7.25 7.00</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50% saturated</td>
<td>7.05 6.75 6.92 - - -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>100% saturated</td>
<td>100 107.8 113.5 110.0 117.0 -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>90% saturated</td>
<td>100 103.0 109.1 110.0 108.2 102.0</td>
<td></td>
<td></td>
</tr>
<tr>
<td>70% saturated</td>
<td>100 100.7 109.4 108.9 106.6 102.9</td>
<td></td>
<td></td>
</tr>
<tr>
<td>50% saturated</td>
<td>100 96.0 98.2 - - -</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 3 3 3 3 3</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Effect of Relative Humidity upon Growth of Smythurus Nymphs - Graph V
It will be observed that -

(i) one hundred per cent relative humidity is decidedly the optimum, resulting in both greater growth rate and maximum growth. While the difference in growth rate and maximum growth between 70 per cent R.H. and 90 per cent R.H. must be regarded as almost insignificant, the difference produced by 100 per cent R.H. as compared with 90 per cent R.H. is considerable. This is apparently due to the fact that although a decreasingly low relative humidity increases the rate of loss of moisture, Synthurus can only counteract this loss when access to liquid moisture, either via the food or a liquid film, is available. In the lower humidities, therefore, the only source of moisture is the food, while in the 100 per cent R.H., both food and environment act as sources of supply, the slightest variation in temperature producing condensation of liquid moisture in the 100 per cent saturated atmosphere.

(ii) In those individuals subjected to 50 per cent R.H., there actually takes place a considerable decrease in size during the first three days at this humidity, followed by a definite recovery during the next three days, the recovery, however, never being complete. It should
be noted that this recovery which takes place is not due to the elimination by death of a certain number of individuals less tolerant to adverse humidity conditions than their fellows, and thereby raising the average size of the remainder, but is an actual increase in size of the individuals, resulting undoubtedly from a certain degree of acclimation. (One does not require to experiment long with Smynthurus to realise the capacity for acclimation, and varying degrees of tolerance to adverse circumstances, exhibited by these primitive insects, even by individuals hitherto subjected to identical conditions - this physiological variation rendering laboratory work a very dangerous source from which to attempt broad generalisations, when unaccompanied by field data).

(iii) The gradual reduction in size after attaining their maximum, in the 70 per cent and 90 per cent saturated atmospheres, can be explained as the result of a gradual reduction in vitality in the struggle against adverse circumstances, so that the resistance is gradually lowered, and the individual eventually succumbs.

(iv) If the growth curves be plotted from width of the abdomen, instead of body length, similar results are obtained to the above, but the differences tend to be
exaggerated on account of the collapsible nature of the abdomen in Smythurus, so that more reliable results accrue by using body length as a growth criterion.

(v) By examining the data on the width of the head capsule during the period at which maximum growth is attained in the respective humidities it is found that there is not a great divergence in the four humidities, as to the instar reached, despite the difference in growth, showing that the latter factor is not the only one determining whether a moult will or will not take place.

(3) **Effect of Soil p.K. Value upon Growth Rate and Total Growth.**

Very few laboratory studies in regard to the role of hydrogen ion concentration in insect development have been undertaken, despite the known importance of hydrogen and hydroxyl ions in catalysing many biochemical reactions especially those involving enzymes. Resulting from the neglect of this important phase of investigation we know very little concerning the role of these ions in such a common and universal phenomenon as insect metamorphosis, although a valuable beginning has been made by Fink who has shown that

(i) the reaction of the body fluids of insect species
is different in species belonging to different orders, and that

(ii) in *Leptinotarsa decemlineata*, Say., at least, there are marked changes in p.H. value throughout the course of development from egg to adult. The relation of soil p.H. value to insect distribution has received more appreciation, although by no means the attention it merits, and this will be briefly referred to when we proceed to consider the relation of soil type to the geographical distribution of *Smythurus*. (See Part III).

In order to determine whether soil reaction would produce a differential effect upon growth of *Smythurus* nymphs an experiment was conducted in which 40 early-instar nymphs were reared to maturity on soils of different type: (each nymph being isolated in a small glass vial) and utilising ten for each of the four soils. Fresh food and soil were supplied as required, about every fifth day, the soil being kept continually moist with distilled water, and the food consisting of white clover leaves. The soils employed in this experiment were *natural soils*, it being deemed inadvisable to alter the hydrogen ion concentration artificially, since a considerable interval of
Some must elapse before the various reactions involved in such a procedure would resume the normal equilibrium; soils extending over a sufficiently wide range on the pH notation were obtained whilst on vacation in Scotland, and the pH value determined by the potentiometer method in order to check up the values with my own colorimetric standards.

**TABLE VII.**

<table>
<thead>
<tr>
<th>Soil pH Value</th>
<th>Average Body Length of Smynthuri Reared on Soils of Same pH Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>H. 4.1</td>
<td>4.0 4.3 4.9 5.3 5.6 6.75 7.8 8.9 9.1 9.6 9.7 10.0 10.1 10.2 10.3</td>
</tr>
<tr>
<td>H. 5.5</td>
<td>4.0 4.35 5.05 5.70 6.50 7.90 9.00 9.60 10.1 10.1 11.0 11.1 11.2 11.3</td>
</tr>
<tr>
<td>H. 6.5</td>
<td>4.0 4.35 4.90 5.90 6.20 8.20 9.10 9.50 10.1 10.1 11.0 11.1 11.2 11.3</td>
</tr>
<tr>
<td>H. 7.8</td>
<td>4.0 4.25 4.70 5.60 6.20 7.60 8.60 9.30 9.60 9.60 9.70 10.0 10.1 10.2</td>
</tr>
</tbody>
</table>

The four different soils in the experiment had the respective pH values of 4.1, 5.5, 6.5, and 7.8.
first and last types are somewhat uncommon, although soils more acid than 4.1 and more alkaline than 7.8 are by no means unknown. The majority of agricultural soils, however, have a value ranging somewhere between 5.0 and 7.0 on the p.H. scale. In view of the economic relationship of Smynthurus to the production of leguminous crops it may be mentioned here that lucerne is very intolerant of acid conditions, preferring a slightly alkaline soil, i.e., over p.H. 7.0, and that clovers also grow best under slightly alkaline conditions, but exhibit a greater degree of tolerance to acid conditions than lucerne. The results of the experiment have been presented graphically (see Graph VI), the chief points of interest being as follows:

(i) The experiment clearly demonstrates that soil p.H. value produces a differential effect upon growth of Smynthurus nymphs. Although there is not a great deal of difference in the growth curves of the nymphs reared on soils of p.H. 5.5 and 6.5 respectively, yet from the fact that the growth curve for p.H. 6.5 more closely approximates the normal growth curve for Smynthurus, and from other considerations in relation to sexual maturity and fecundity, the optimum soil p.H. value in these experiments is undoubtedly 6.5. Actually, the optimum
p.H. would appear to lie somewhere between 5.5 and 6.5, and much nearer to the latter than the former.

(ii) The differential effect upon growth produced by soils of p.H. 7.8 and 4.1 is quite considerable, being a decrease from the optimum of 8.4 per cent and 12.1 per cent, respectively, when growth is practically complete, while the effect upon fecundity and time required for the attainment of sexual maturity is greatly intensified. The double circles on the respective growth curves indicate, as before, when 75 per cent of the nymphs have reached the seventh instar, the stadium in which sexual maturity is reached. It will be observed that the time required to reach this stage on soil of p.H. 4.1 is slightly more than double that required on soil of p.H. 6.5, and the time required on soil of p.H. 7.8 is slightly over 150 per cent of that required on the optimum soil.

(iii) Now if the degree of departure from the optimum p.H. (taking this to be 6.3, since these experiments suggested that the actual optimum lay slightly on the acid side of 6.5) be plotted against the time required for the attainment of sexual maturity by 75 per cent of the nymphs, then it is found that those two variables have a linear relationship, i.e., the time required for sexual maturity is a linear function of the deviation from
optimum soil reaction, when expressed in terms of the p.H. notation. This has been presented diagrammatically in Graph VII, and although only four points on the p.H. scale have been considered, their approximation to a straight line is so close that the above linear relationship can hardly be doubted.

(iv) The characteristic physiological rhythm underlying the growth process in Smynthurus is again clearly demonstrated by these curves of growth on different soil types, the maximum growth rate again being evidenced in the second cycle. The three recurrent cycles are convincingly demonstrated and also the analogous effect of low temperature and a deviation from optimum p.H., in that both produce a slowing up in the growth rate, a retardation in the time of attainment of sexual maturity, and an increase in size when the latter stage is reached. This slowing up of the growth rate, as in the case of low temperatures, results in a lateral displacement of the respective growth curves to the right.

(v) The mode of action by which soil p.H. value brings about its effect upon the growth process in Smynthurus is not altogether easy of interpretation, but would appear to be associated with the question of ionic balance, adverse effects resulting from a disharmony be-
tween the ionic equilibrium obtaining in the insect's body fluids and the soil complex, the latter being an important feature of the diet.

(B) FECUNDITY.

(1) Effect of Various Combinations of Temperature and Humidity.

This environmental effect was determined by a series of experiments in which the adults were taken direct from the field, supplied with abundance of clover leaves for food as well as soil of optimum p.H. value, and subjected in each experiment (using 10 individuals in each) to a different combination of temperature with humidity, making use of 25 different combinations. Each experiment was allowed to run for a week, enough food being added at the beginning to supply the requirements for that period, so that the experimental difficulty of having to open the humidity chamber (encountered in the growth experiments) was thereby avoided. At the end of a week's time each experiment was examined and the number of eggs deposited were counted. The results of the experiments are presented in tabular form in Table VIII, where there are presented

(i) the actual number of eggs laid,

(ii) the same calculated as a percentage of the
<table>
<thead>
<tr>
<th>Temperature</th>
<th>0</th>
<th>4</th>
<th>7</th>
<th>0</th>
<th>No. of Eggs</th>
<th>Percentage of Maximum</th>
<th>Saturation Deficiency</th>
</tr>
</thead>
<tbody>
<tr>
<td>30°C</td>
<td>0</td>
<td>1.8</td>
<td>3.2</td>
<td>0</td>
<td>14.4</td>
<td>11.2</td>
<td>7.3</td>
</tr>
<tr>
<td>25°C</td>
<td>0</td>
<td>18.2</td>
<td>31.8</td>
<td>32.7</td>
<td>30.9</td>
<td>10.7</td>
<td>8.1</td>
</tr>
<tr>
<td>12.6°C</td>
<td>0</td>
<td>136</td>
<td>195</td>
<td>175</td>
<td>131</td>
<td>4.3</td>
<td>3.2</td>
</tr>
<tr>
<td>7.0°C</td>
<td>0</td>
<td>168</td>
<td>220</td>
<td>200</td>
<td>198</td>
<td>3.0</td>
<td>2.2</td>
</tr>
<tr>
<td>3.0°C</td>
<td>0</td>
<td>8</td>
<td>X</td>
<td>24</td>
<td>No. of Eggs</td>
<td>Percentage of Maximum</td>
<td>Saturation Deficiency</td>
</tr>
<tr>
<td>60% R.H.</td>
<td>2.4</td>
<td>18</td>
<td>1.2</td>
<td>0.6</td>
<td>0</td>
<td>30% R.H.</td>
<td>70% R.H.</td>
</tr>
</tbody>
</table>
Effect of Temperature upon Reproduction - Graph VIII
maximum (which was obtained at 7.0°C., and 80 per cent R.H.),

(iii) the saturation deficiency at each of the 25 temperature-humidity combinations. Several interesting points are brought out by these figures, the most important of which are presented in Graphs VIII, IX, and X, as follows:

(i) Both temperature and humidity have evidently a profound effect on the physiological process of reproduction, and therefore on the potential number of individuals. As regards temperature, perhaps the most striking fact is the very low optimum, the latter not being far from that at which reproduction ceases, and much below the temperature optimum for growth rate and maximum growth.

(ii) In Graph VIII, the effect of temperature at 80 per cent R.H. (the optimum from those figures, although actually it probably lies between 80 per cent R.H. and 90 per cent R.H.) has been plotted, and is indicated by the curve of the solid line, from which it will be observed that the rate of reproduction gradually rises from 30°C. (at which it is practically nil) with decreasing temperature, passing through an optimum slightly above 7°C., and then falling off very rapidly to 3.0°C., at which reproduction is again practically nil.
Effect of Humidity upon Reproduction - Graph IX
In order to ascertain the effects of temperature under a variety of humidity conditions, the columns in Table VIII have been summed horizontally, and the results presented by means of the broken line, from which it is evident that the effects in both cases are very similar. As the latter is based on 50 individuals instead of 10 the dotted curve probably gives a more accurate representation of the effect of temperature upon the reproductive processes of Smythurus.

(iii) Graph IX presents the effect of humidity on rate of reproduction, the solid line indicating the effect of humidity at the temperature corresponding to the temperature-humidity optimum for reproduction in Smythurus, namely, 7.0°C. The dotted line indicates the effect of humidity under a variety of temperature conditions, as obtained by summing the columns in Table VIII vertically. The two curves are again fairly similar, while the latter, for the same reasons as stated in connection with the temperature effect, is probably a more accurate indication of the effect of humidity upon rate of reproduction in Smythurus. Graph IX clearly demonstrates the very limited range of humidity conditions in which normal reproduction is possible, the reduction in
the number of eggs deposited falling off very rapidly as the humidity falls from 80 per cent to 70 per cent. At the latter degree of saturation, reproduction is only 75 per cent of that under optimum humidity conditions, falling off at an increased rate to nil at 60 per cent R.H.

(iv) In looking over Table VIII, the interesting point arose as to the relative proportion in which the constituent factors of a temperature-humidity effect might become influenced as one proceeded in a direction away from that particular combination productive of the maximum response in reproduction. Since saturation deficiency combines temperature and humidity in a single unit, being a function of both, it can be utilised as an index of the change in response to changes in any one variable, when the other variable is kept constant. Hence Graph X illustrates the differences in rate of response to similar changes of temperature under different conditions of constant humidity. The graph clearly demonstrates that if temperature be altered in either direction away from the optimum, the rate at which unfavourable temperatures can exert their adverse effect on the reproductive process of Smynthurus, decreases as the departure from saturation increases, irrespective of the humidity optimum, or in other words, there is a
differential rate of response to temperature with different conditions of humidity, becoming greater as the humidity conditions approach saturation, and reaching a maximum when the saturation deficiency is nil. This probably holds good for most, if not all, physiological processes, and the writer believes a similar phenomenon in relation to dilution and rate of enzyme reaction has been proved. Hence to demonstrate the rate of response to temperature, a saturated atmosphere would appear to be the optimum, since under any other conditions of humidity, the saturation deficiency acts in a 'limiting' capacity, with which temperature is indissolubly associated, the vapour pressure of water being a function of temperature.

(v) From the data in Table VIII, it can also be shown that there is a differential rate of response to humidity with different conditions of temperature, being a maximum at the temperature corresponding to the temperature-humidity optimum. This would also appear to hold good for other vital processes as well as reproduction in Smynthurus. It is also evident that any attempt to utilise saturation deficiency as an index of the combined temperature-humidity effect must be restricted to constant conditions of relative humidity, since the response to changes in temperature becomes a
different function of the latter with different relative humidities.

(vi) The results as a whole illustrate the very restricted temperature-humidity range under which anything approaching to normal reproduction can take place, so much so, that even in Britain, where the conditions are climatically favourable to Smynthurus in comparison with most other geographical areas, (there being a few other more favourable areas, q.v., Part III), the maximum rate of reproduction can only be obtained during a very limited period of the year, namely, April and October.

(2) Effect of Soil p.H. Value upon Fecundity.

Continuing the analysis of various environmental effects upon the life processes of Smynthurus, there remains to be considered the influence of soil type upon reproduction. An ever increasing number of instances are being recorded in which soil type has an important bearing upon intensity of infestation in connection with insect pests. The effect may be purely a physical one depending upon the water holding capacity of the soil, as determined by its texture and structure; on the other hand, there are undoubtedly influences of a chemical nature in soil, which determine its favourability or otherwise for a particular species. For instance, the factors influencing
the choice by gravid females of particular sites for purposes of oviposition, are often extremely obscure, but nevertheless of great determining significance. Indeed it would appear that the facilities involved in the 'placing of the egg' are very highly developed in their sensitivity to environment, although it is not always easy to locate the particular factor, or combination of factors, to which the organism responds. In regard to chemical conditions in the soil complex perhaps the most useful all-round general index is the hydrogen ion concentration, since it expresses in one unit, a greater amount of information than any other index of soil type, with the doubtful exception of exchangeable base content, and the latter involves a somewhat laborious process for determination.

With the object of determining in quantitative terms this influence of soil upon the reproductive process in Smynthurus, an experiment was undertaken in which early instar nymphs were reared to maturity on soils of different p.H. value, and maintained there till death (to determine the effect on longevity). Since the same experiment was employed to ascertain the effect of soil upon growth, and this was previously reported, it will be
unnecessary to repeat the details. The results of the experiment are as follows:

(i) Soil type does not only influence appreciably the period over which oviposition takes place, by lengthening or shortening the normal reproductive phase in the life-cycle of Smynthurus, but its effect upon the total number of eggs deposited is profound. The former effect is brought about as a result of the influence upon time of attainment of sexual maturity, but is outstripped in significance by the latter.

(ii) The number of eggs deposited on the four different soils is presented in tabular form below:

<table>
<thead>
<tr>
<th>Soil p.H. Value</th>
<th>4.1</th>
<th>5.5</th>
<th>6.5</th>
<th>7.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Total No. of Eggs</td>
<td>116</td>
<td>137</td>
<td>360</td>
<td>219</td>
</tr>
<tr>
<td>Percentage of Maximum</td>
<td>32.2</td>
<td>38.1</td>
<td>100.0</td>
<td>60.8</td>
</tr>
</tbody>
</table>

From these results it is clear that the optimum p.H. value for reproduction is 6.5, or perhaps slightly on the acid side of this figure, and it will be recalled that this was also the optimum for growth. Any significant departure from 6.5 produces a profound reduction in the number of eggs deposited, the detrimental effect of a soil on the
acid side of the optimum being greater than one with a p.H. value equally removed from the optimum in the alkaline direction. An interesting fact in connection with the above is that the soils in Southern Australia, where Smynhurus is very abundant, have a p.H. value ranging between 6.0 and 7.0, i.e., the optimum for Smynhurus, and hence contributing in a considerable degree, doubtless, to the intensity of infestation by the "flea".

(iii) The mode of operation by which soil brings about its effect upon the physiological processes of reproduction in Smynhurus is not fully comprehensible but would appear to be through its effect upon the nutrition of the adult, since soil forms an important part of the diet, especially during the reproductive phase. Briefly stated, p.H. value may be of little significance in itself, but what it may and would appear to do, is to act as an index of the balance of ions in the soil complex, so that at the optimum p.H. the relative proportion of the various ions are such that they most closely approximate a state of equilibrium with the physiological conditions obtaining in the insect's body fluids. After all it is only reasonable to conclude that large quantities of acid or alkaline soil
(i.e., relative to the normal p.H. of the insect's digestive tract) passing through the intestine, would result in a perturbation of the physico-chemical equilibrium of the cells lining the tract, and hence product an adverse effect on metabolism, and eventually affect the general well-being of the individual.

(3) **Effect of Soil Type upon Choice of Site for Oviposition.**

One further experiment in connection with soil reaction remains to be considered, of which the object was to determine whether Smynthurus, if given the opportunity, could select certain types of soil for purposes of oviposition. With this object in view, four soils of p.H. 4.1, 5.5, 6.5, and 7.8 respectively (the same four as above) were placed in small uniform patches upon damp filter paper in a glass container, and about 50 Smynthuri added, being supplied with clover leaves for food. At the end of three days the number of eggs which had been deposited on the respective soils, was totalled and found to be as follows:-

- p.H. 4.1 - 11
- p.H. 5.5 - 39
- p.H. 6.5 - 136
- p.H. 7.8 - 11

The experiment was repeated, using the same four soils as above, and so arranged that each soil occupied the
quadrant of a circle. The eggs were removed and counted each day this time, the total results for the three days being as follows:


The results of these two experiments, taken together or singly, seemed so suggestive that it was determined to undertake a third experiment in order to obtain convincing proof of their significance. The same conditions were observed as previously, with the exception that the eggs were allowed to remain till the elapse of four days, when they were removed and counted as before, with the following results:


The results of all three experiments are presented in tabular form herewith:

<table>
<thead>
<tr>
<th>Soil p.H. Value</th>
<th>4.1</th>
<th>5.5</th>
<th>6.5</th>
<th>7.8</th>
</tr>
</thead>
<tbody>
<tr>
<td>Experiment No. 1</td>
<td>11</td>
<td>39</td>
<td>136</td>
<td>11</td>
</tr>
<tr>
<td>Experiment No. 2</td>
<td>40</td>
<td>66</td>
<td>78</td>
<td>24</td>
</tr>
<tr>
<td>Experiment No. 3</td>
<td>38</td>
<td>48</td>
<td>80</td>
<td>48</td>
</tr>
<tr>
<td>Total No. of Eggs</td>
<td>89</td>
<td>153</td>
<td>294</td>
<td>83</td>
</tr>
<tr>
<td>No. of Eggs as %</td>
<td>14.4</td>
<td>24.7</td>
<td>47.5</td>
<td>13.4</td>
</tr>
<tr>
<td>Preference (very approx.)</td>
<td>1</td>
<td>2</td>
<td>4</td>
<td>1</td>
</tr>
</tbody>
</table>
Out of a total of 619 eggs, therefore, 47.5 per cent were oviposited upon the soil of p.H. 6.5, 24.7 per cent on the soil of p.H. 5.5, and 13.4 per cent and 14.4 per cent on soils of p.H. 7.8 and 4.1 respectively. The difference between the last two cannot be regarded as significant, and thus rank equally desirable, or rather undesirable, for oviposition purposes. In round numbers, soil of p.H. 5.5 is twice as attractive for oviposition as soil of p.H. 4.1 or p.H. 7.8, while the soil of p.H. 6.5 is four times as attractive as the latter types. The above experiment again emphasises the significance of soil type in relation to numbers of individuals, and serves to reinforce the conclusions previously arrived at, as a result of the experiments in which Smynthurus was reared on a particular soil type, and thus could not exert a preference.

The experiment demonstrates conclusively that

(i) Smynthurus can and does exhibit a selective action in the choice of soil for purposes of oviposition.
(ii) the particular sense which renders the insect capable of this discrimination is very likely taste;
(iii) p.H. may not be the ultimate determining factor, although it may be acting as an index of certain factors, or combination of factors, which render the soil complex physiologically desirable for the oviposition pro-
cess, each egg being coated with an exudate of soil passed via the anus.

(C) - LONGEVITY.

(1) **Effect of Temperature on Longevity.**

The rapid response of the growth and reproductive processes of Smynthurus to relatively slight environmental changes has now been demonstrated, and there still remains to be considered the influence of environment upon longevity. The effect of temperature under natural conditions is very evident from an examination of the field data, which seemed to indicate, in an empirical way, that with increasing temperature there was a gradual shortening of the total life-span. This effect is presented quantitatively in Graph XI, where the survival curves have been plotted for the same temperatures and the same individuals, as those employed to demonstrate the effect of temperature upon growth, so that by referring to Graph III the relation between growth and survival at different temperatures can be considered. The percentage number of survivors is converted to a common logarithm and plotted against age, equal gradients on such 'survival curves' representing equal death rates.
<table>
<thead>
<tr>
<th>Temperature</th>
<th>Percentage survival of Nymphs throughout total Life-Span.</th>
</tr>
</thead>
<tbody>
<tr>
<td>3.0°C.</td>
<td>100 100 90 80 60 60 60 40 40 20 0 - -</td>
</tr>
<tr>
<td>3.0°C. and 23.0°C. (12 hrs. at each)</td>
<td>100 90 90 50 10 0 - - - - - -</td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 6 6 6 6 6 6 6 6 6 6 -</td>
</tr>
<tr>
<td>7.93°C.</td>
<td>100 100 100 80 80 70 70 60 60 30 10 10 0 -</td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 6 6 6 6 6 6 6 6 6 6 6 6</td>
</tr>
<tr>
<td>13.0°C.</td>
<td>100 100 90 90 90 90 80 70 70 50 50 40 20 0 -</td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 3 5 5 5 5 10 5 5 5 5 5 5 5</td>
</tr>
<tr>
<td>16.7°C.</td>
<td>100 80 70 50 50 40 20 20 10 0 - - - -</td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 5 5 6 5 5 5 5 5 5 - - -</td>
</tr>
<tr>
<td>21.0°C.</td>
<td>100 100 60 10 0 - - - - - - - -</td>
</tr>
<tr>
<td>25.0°C.</td>
<td>100 90 20 10 0 - - - - - - - -</td>
</tr>
<tr>
<td>Time (in days)</td>
<td>0 3 3 3 3 3 - - - - - - -</td>
</tr>
</tbody>
</table>
The main features illustrated by Graph XI are:

(i) Temperatures over 13°C. cause a rapid rise in the death rate of Smynthurus; an increase in temperature of 4°C. (from 13°C. to 17°C.) reducing the normal life-span by 34 per cent, and an increase from 17°C. to 21°C., causing a similar reduction.

(ii) Temperatures below 13°C. cause a slight increase in the total life-span provided the temperature does not fall below 3°C. (approx.) when secondary effects come into operation, on account of severe depression of metabolism, resulting in general lowering of vitality with decreased resistance to disease, to which the individual eventually succumbs.

(iii) The optimum temperature for survival would appear to be 8°C. (approx.) - the temperature which depresses metabolism to a minimum without decreasing general vitality, and thereby inducing adverse secondary effects. It will be remembered that this was just about the optimum for reproduction, and also that it is only about 2.5°C. above the development zero of the egg stage. Further, experiments have shown that in a saturated atmosphere there is 100 per cent mortality in 75 hours (approx.) at 30°C., in 12 hours (approx.) at 35°C., and in 3.5 hours at 40°C.
Effect of Relative Humidity upon Survival of Smythurus Nymphs. - Graph XII
TABLE X.

<table>
<thead>
<tr>
<th>Relative Humidity</th>
<th>Common Logarithms of Percentage Survival.</th>
</tr>
</thead>
<tbody>
<tr>
<td>50% R.H.</td>
<td>2.0 1.9031 1.8451 1.0000 0 - - -</td>
</tr>
<tr>
<td>70% R.H.</td>
<td>2.0 2.0 1.9542 1.8451 1.7782 1.3010 0 -</td>
</tr>
<tr>
<td>90% R.H.</td>
<td>2.0 2.0 1.9031 1.9031 1.9031 1.4771 1.0 0</td>
</tr>
<tr>
<td>100% R.H.</td>
<td>2.0 2.0 1.8451 1.7782 1.3010 1.0000 0 -</td>
</tr>
</tbody>
</table>

(2) Effect of Humidity on Longevity.

It is evident from Graph XII and numerous other experiments conducted by the writer, that 100 per cent R.H. is the optimum for the survival of Smythurus, provided secondary effects do not enter, as they tend to do when Smythurus (especially the nymphal stages) is maintained continually in a saturated atmosphere. This effect is clearly brought out in Graph XII, where, although maximum growth took place in the saturated atmosphere, the nymphs lived slightly longer in the 70 per cent, and considerably longer in the 90 per cent saturated atmosphere. The adverse effects of a continually saturated atmosphere are therefore secondary, the nymphs
especially assuming a "blown-out" appearance and 100 per cent R.H. remains the optimum, provided other conditions, such as food, temperature, etc., are conducive to maximum vitality and resistance to disease. This is confirmed by further experiments which have shown that the higher the relative humidity the greater the resistance of Smynthurus to the adverse effects of high temperature, e.g., at 30°C., there is 100 per cent mortality in 4 hours (approx.), at 0 per cent R.H., in 6 hours (approx.) at 20 per cent R.H., in 7 hours (approx.) at 40 per cent R.H., in 51 hours (approx.) at 60 per cent R.H., and in 75 hours (approx.) at 100 per cent R.H.

(3) **Effect of Soil p.H. Value upon Longevity.**

As previously mentioned, the effect of soil p.H. value would appear to be a nutritional one, so that marked departures from the optimum have the effect of reducing the speed of metabolism (as seen in the retarding effect upon growth) and thereby prolonging the total life-span. The difference, however, is not very marked and cannot be regarded as one of any practical significance.

**IV. EFFECT OF DENSITY UPON RATE OF POPULATION INCREASE.**

There now falls to be considered, briefly, and somewhat tentatively, the little known influence of one organism
upon another of the same or a different species; in short, the effect of **density** upon rate of population increase. In order to obtain some idea of the action of this factor upon reproduction a series of experimental populations were set up, in which the only difference as regards environmental factors was space per individual. The experimental universes consisted of 7 glass jars of equal volume, in which the numbers of Smynthurus were placed in the following geometrical proportions - $2^1, 2^2, 2^3, 2^4, 2^5, 2^6, 2^7$ - it being deemed advisable to adopt this ratio in view of the fact that populations tend to increase in the form of a geometrical progression, provided there are no inhibiting influences. The space available per individual, therefore, decreased in the ratio -

$$\frac{1}{2}, \frac{1}{4}, \frac{1}{8}, \frac{1}{16}, \frac{1}{32}, \frac{1}{64}, \frac{1}{128}$$

When all the individuals died off the number of eggs which had been deposited in each experimental container were counted. The experiment was repeated and the results of both experiments are presented below:

<table>
<thead>
<tr>
<th>Space per Individual</th>
<th>$\frac{1}{2}$</th>
<th>$\frac{1}{4}$</th>
<th>$\frac{1}{8}$</th>
<th>$\frac{1}{16}$</th>
<th>$\frac{1}{32}$</th>
<th>$\frac{1}{64}$</th>
<th>$\frac{1}{128}$</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. of Eggs (Exp. 1)</td>
<td>0</td>
<td>0</td>
<td>36</td>
<td>25</td>
<td>86</td>
<td>90</td>
<td>60</td>
</tr>
</tbody>
</table>
Taking into consideration only the higher densities (since perhaps the lower ones do not include a sufficient number of individuals to eliminate the possibility of there being many more males than females) it is clear that the number of eggs per individual decreases approximately in the form of an arithmetical progression from $2^5$ upwards. Now the density existing in the case of the container with 32 individuals amounted to one Smynthurus per 2 ccs, a concentration which was not approached in the field (in this climate, where the population is well controlled) even when the Smynthurus population reached its maximum. However, if the effect obtained above is not specific and can be induced by the presence of other species or organisms, which is not likely, then it would come into operation very much sooner, probably before "plague" dimensions were attained. The manner in which the above effect operates is probably in part due to continual disturbance and interruption of females in their attempts to oviposit, and partly due to "psychological" influences.
That Smynthurus is very sensitive to 'contact' influences can be readily demonstrated by placing a large number inside a glass jar, when they will be seen to distribute themselves almost uniformly over the interior area, as a result of each individual attempting to avoid its neighbour.

This density factor has only been investigated in a very few instances, so that very little is known about it, and I only put forward the above remarks in a somewhat tentative fashion. If the above example holds good for other species, it would appear that populations automatically check their own increase in virtue of the density effect, and that the organism itself imposes the ultimate limit to its own increase, although this effect will doubtless only come into operation when all other factors inhibiting population increase, are at, or near, their optimum.

V. INTER-RELATIONSHIP OF DIFFERENT PHASES OF THE LIFE-CYCLE.

Having now considered the effect of various environmental factors upon the three vital processes, growth reproduction, and longevity, there still remains to be briefly treated the relationship of those phases in the life-cycle of Smynthurus, to each other.
Frequency Curve to Illustrate Distribution of Death Rate. - Graph XIII
(i) Distribution of Death Rate with Age (No. of individuals % of the original population).

(ii) Distribution of Oviposition Rate with Age (No. of eggs per ovipositing female).

<table>
<thead>
<tr>
<th></th>
<th>0</th>
<th>6</th>
<th>10</th>
<th>2</th>
<th>8</th>
<th>22</th>
<th>24</th>
<th>14</th>
<th>8</th>
<th>6</th>
<th>The time interval</th>
</tr>
</thead>
<tbody>
<tr>
<td>(i)</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>0</td>
<td>16.75</td>
<td>25.3</td>
<td>21.3</td>
<td>22.8</td>
<td>15.2</td>
<td>0 is 10</td>
</tr>
</tbody>
</table>

This is presented in Graph XIII (based on 50 individuals). The solid black line indicates the distribution of death-rate with age, at intervals of 10 days, and the broken line indicates the distribution of reproduction and the position of the reproductive phase, in relation to the total lifespan. The scale for the solid line is on the left-hand side of the graph, and that for the broken line on the right. The frequency curve for death-rate with age is bimodal, the first mode coinciding with the period of greatest growth, when 10 per cent of the nymphs die off. Evidently the rapid growth phase has the effect of eliminating most of the individuals with an inherited constitutional defect or those which are physiologically unstable, since at this period metabolism is proceeding at a maximum pace and is most liable
to aberration or injury. The second mode occurs about the 50-60 day interval (depending on the environment) when approximately 46 per cent of the original population succumb, and it will be observed that the coincidence of this second mode with maximum rate of reproduction is very close. Sexual maturity is attained during the last nymphal instar, i.e. before the adult stage is reached, while the reproductive phase extends over approximately 50 per cent of the total life-span.

VI GENERAL SURVEY OF ENVIRONMENTAL EFFECTS UPON SMYNTHERUS.

These experiments substantiate in quantitative terms the main arguments to be subsequently put forward to account for the natural control of Smynthurus viridis. Looking back over the results of these experiments as a whole, perhaps the most striking conception derived, is the tremendous impress of environment upon population, operating through the actual and potential numbers of individuals. Secondly, one gains the impression of the individual as consisting of a heterogeneous assemblage of diverse physiological processes, each with its own optimum, rather than as a single harmonious physiological unit. Evidently, an organism with a physiological 'make-up' like that of Smynthurus, having different optima for growth,
reproduction, and the development of the egg, is endowed with a serious handicap from the start in the race for increase in numbers, and doubtless this is the case with most other organisms. Hence the optimum environment is one which presents the most effective compromise between a variety of conflicting physiological requirements on the part of the organism concerned. Thirdly, one is inclined to ask the question, to what extent does the so-called adaptation of the organism to its environment exist in actual fact? Doubtless evolution could not have taken place without adaptation, but it seems that the former has not proceeded to the extent often imagined, and fortunately so for the human race. The actual facts appear to be that population increase in a natural environment is seriously handicapped on account of the diverse physiological ensemble of the individual, and the fact that organisms flourish to the extent they do, is not due so much to their adaptation to the environment as to their increase in spite of it, on account of the enormous reproductive potential with which every creature is endowed.
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PART III.

"In dealing with any natural phenomenon - especially one of a vital nature, with all the complexity of living organisms in type and habitat - the mathematician has to simplify the conditions until they reach the attenuated character which lies within the power of his analysis." - Karl Pearson.

I. SEASONAL VARIATION IN ABUNDANCE OF SMYNTHURUS.

A. PRINCIPLES AND TECHNIQUE INVOLVED IN THE STUDY OF POPULATION VARIATIONS IN A NATURAL ENVIRONMENT.

(1) Guiding Principles in Selection of Area for Population Census.

Following the method of procedure already outlined, the life history of the "flea", bionomics in sensu stricto, and influence of environmental factors under controlled laboratory conditions have now been investigated, so that the next appropriate step in this study of Smynthurus consisted of a complete examination of the seasonal cycle of
events as occurring in Nature. Part III is, therefore, devoted largely to an analysis of the field data, coupled with an interpretation thereof as substantiated by critically planned and controlled laboratory experimentation; this reinforcement being rendered necessary on account of a multiplicity of factors acting simultaneously in Nature. The chief difficulty in an investigation of this kind (as with all problems concerned with fluctuations in the numbers of organisms) lies in the fact that there are few methods for obtaining quickly and easily an accurate quantitative sample of the numbers and kind of organisms; and, secondly, there is the difficulty of finding (in a long inhabited country like Britain) a normal environment, i.e. one in which purely natural agencies have been allowed free play over a sufficient interval of time to allow a state of equilibrium to have become established between the various members of the 'community' to which Smynthurus belongs, in their relationship to the physical factors of the environment and to each other.

The reason for carrying out the investigation in a 'normal' environment as distinct from merely an environment in which the Smynthurus population was 'controlled', was in order to eliminate the effect of cultural practice - a double-edged tool - which may favour the increase of
certain species and at the same time eliminate others, so that actually in the original home of an insect its non-appearance in destructive numbers may be due as much to the unconscious efforts of man, in his attempts to accommodate the growth of crops, as to purely natural factors of control. Further, it is only in such a 'normal' environment that one can be sure of the reproductive potential of the species being in equilibrium with the environment, so that one can validly interpret the variations in level of the population as due to the pulsation of environmental factors. Not until this equilibrium has been attained can the variations in level of the population be regarded as a true index of the magnitude of the fluctuations in the environmental resistance, although previous to this the fluctuations would doubtless be indicated. The above precautions have been amply justified from subsequent experience, and the difficulty of obtaining a representative sample of the population at any time, quickly and easily, in a 'normal' environment, has been satisfactorily overcome, due mainly to the suitability of Smynthurus for the purposes of an investigation of this kind.

(2) The Method Adopted in Making the Census of Insect Population.

The method adopted was to make a definite number of
strokes of the net over a small area (approximately 3 yards x 50 yards), at fortnightly intervals, care being taken to execute the strokes in the same manner, and at the same time of day. It was sometimes necessary to postpone the sweepings for a day or two on account of wet or very windy weather. The plots chosen for the purpose lie in three different fields, known as A, B, and C, and consist of permanent pasture, which has been undisturbed by cultivation for at least 40 years in the case of B and C, and for at least five years in A. While the pasture in C is grazed for the greater part of the year by cattle and horses, B is only grazed during late autumn and early winter by cattle and sheep, and A is ungrazed, so that in A and B we have a very good approximation to a 'normal' environment, and thus represent almost ideal conditions for the purpose of investigating the seasonal variations, etc., of Smynthurus, or any other insect belonging to the grassland 'community'.

The reason for adopting fourteen days as the interval of time between two consecutive sweepings was due to the fact that it was feared any shorter interval, such as a week, might interfere with the normal course of events by actually removing too many members of the population, and that this would influence the numbers of the succeeding
generation. However, as the sweepings were made fortnightly and the net actually traversed the same piece of ground (within the plot) monthly, the effect on the subsequent generation must be negligible, as any marked local lowering of the population would soon be levelled up again by influx from surrounding areas. After several trials, it was ascertained that 50 strokes of the net secured more than sufficient numbers to reduce the percentage of error involved in the method to a minimum. As a result of the above method of investigation there is now available a complete yearly record of the seasonal variation in the Smynthurus population, as occurring in each of the three fields A, B, and C, and in addition, almost three-fourths of a second year's record, made until the time of the writer's departure for America. The second year's record serves as a check upon the first one, and is valuable for purposes of comparison, since the climatic conditions in each of the two years were very different.

(3) Recording of Fluctuations of Environmental Factors.

In order to determine whether there existed any correlation between the variations in level of the Smynthurus population and the fluctuations of environmental factors, both biotic and physical, the monthly census of
the entire insect fauna in the respective fields, together with the records of temperature, rainfall, etc., kept at the Laboratory, have been utilised, as the plots are all less than half a mile distant. In addition, a Livingston atmometer was set up in the field, and weekly measurements made of the evaporation which had taken place. The mean temperature is calculated from measurements made twice daily at 9 a.m. and 9 p.m. (sun-time) for the fourteen days interval previous to the day on which the sweeping was made; while the mean maximum is taken from daily measurements at 9 a.m. (representing the maximum temperature for the previous 24 hours) and calculated for the corresponding fortnightly interval. All measurements represent shade temperature, the instruments being enclosed in a Stevenson screen. The rainfall for the interval between two consecutive sweepings represents the total rainfall for that period, as calculated from daily measurements, and similarly the atmometric index represents the total evaporation in cubic centimetres of water for the same period, as calculated from weekly measurements.

B. **SEASONAL VARIATIONS OF SMYNTHRUS POPULATION IN FIELD B.**

(1) **General Trend of Events.**

The results obtained for field B are represented in Graph XIV, and the following observations will facilitate
Seasonal Variation of Smynthurus Population.
its interpretation. The data will be found in Table 12. The Smynthurus population is represented in actual numbers per 50 strokes of the net. It will be observed that there is a gradual decrease from the time at which a census was first made, namely, on October 10th, till December 21st, after which not a single specimen could be found in the fields until April 10th (the first time they actually appeared in a fortnightly census was April 17th, as they did not occur in the previous census on April 3rd) when nymphs were obtained for the first time since the previous October. After April 17th there is a gradual rise in numbers till June 13th, and subsequent to this the level of the population undergoes a series of violent fluctuations. It now remains to account for the above fluctuations, and in this connection both the biotic and physical environmental factors have to be considered. The latter will be taken up first.

A glance at the Smynthurus population curve in Graph XIV shows immediately that there are two distinct periods in the seasonal cycle of events; one in which the course of the population curve is at first gradually falling and then gradually rising, and extending from October 1st (approx. 10th of May) and one in which the curve undergoes a series of violent fluctuations, extending from June 1st (approx.)
to the end of September or thereabout. This suggests, of course, that there are two distinct and fundamental influences at work, which are responsible for the above conditions, and this is so. Again looking at Graph XIV, it will be observed that the mean temperature curve may also be divided into two distinct periods, which correspond roughly in extent to one in which the temperature falls below $45^\circ F.$, and another in which it exceeds this temperature. The graph also demonstrates conclusively a high degree of correlation between the level of the Smynthurus population and the mean temperature, for the first period, and an equally extraordinarily high degree of correlation between the Smynthurus population and the rainfall, for the second period, with a time-lag effect in the Smynthurus curve of 14 days (approx.), which will be accounted for later. It will now be evident that temperature and rainfall are the two fundamental effective factors governing the fluctuations in the Smynthurus population, and that temperature is the 'limiting' factor for the first period, while rainfall becomes the 'limiting factor' in the second and short period from approximately June to September (inclusive). How, then, do these two 'limiting' factors bring about their respective effects, and so govern the numbers of Smynthurus? In order to understand this it will be necessary to follow in greater
detail the actual course of events occurring in the life-cycle in Nature, together with the sequence of generations which appear throughout a complete year. The first point to be determined, in order to understand the temperature effect is the developmental zero of the egg-stage.

(2) Developmental Zero and the Concept of Temperature Summation.

As demonstrated by Krogh, Peairs, Shelford, and a few others, the time-temperature curve of development conforms in part to an equilateral hyperbola, so that the reciprocal (for this portion) is a straight line. Hence within the straight line limits of development one may legitimately apply the original phenological conception of temperature-summation, because within this range of so-called medial temperatures (Shelford) the rate of development is directly proportional to the temperature, i.e., the number of effective degrees of temperature (degrees above the developmental zero) x time = K. The range of temperatures characterised by this hyperbolic rate is usually about a third of the total, and commences about a fifth of the range above the developmental threshold. Hence in attempting to apply this biological phenomenon to the problems of climatology one
<table>
<thead>
<tr>
<th>Date</th>
<th>Rainfall (ins.)</th>
<th>Mean Temp. (°F)</th>
<th>No. of strokes</th>
<th>Date</th>
<th>Normal Atmos. Temp.</th>
<th>No. of strokes</th>
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<td>1</td>
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<td>0.16</td>
<td>48.7</td>
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<td>2:10:28</td>
<td>53.4</td>
</tr>
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<td>10:10:28</td>
<td>0.66</td>
<td>48.9</td>
<td>16:10:28</td>
<td>50.2</td>
<td>335</td>
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<tr>
<td>3</td>
<td>24:10:28</td>
<td>2.31</td>
<td>49.1</td>
<td>30:10:28</td>
<td>46.3</td>
<td>104</td>
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<td>7:11:28</td>
<td>1.20</td>
<td>43.2</td>
<td>14:11:28</td>
<td>44.2</td>
<td>48</td>
</tr>
<tr>
<td>5</td>
<td>26:11:28</td>
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<td>30:11:28</td>
<td>40.8</td>
<td>5</td>
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<tr>
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<td>42.0</td>
<td>13:12:28</td>
<td>39.3</td>
<td>1</td>
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<tr>
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<td>36.6</td>
<td>14:2:29</td>
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<td>20:2:29</td>
<td>0.18</td>
<td>27.8</td>
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<td>1:3:29</td>
<td>39.1</td>
</tr>
<tr>
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<td>6:3:29</td>
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<td>13</td>
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<tr>
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<td>8:5:29</td>
<td>49.6</td>
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<tr>
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<td>57.1</td>
<td>7:6:29</td>
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<td>243</td>
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<tr>
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<td>61.8</td>
<td>11:9:29</td>
<td>57.7</td>
<td>283</td>
</tr>
<tr>
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<td>19:9:29</td>
<td>0.00</td>
<td>62.4</td>
<td>25:9:29</td>
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<td>150</td>
</tr>
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<td>55.1</td>
<td>10:10:29</td>
<td>50.5</td>
<td>122</td>
</tr>
<tr>
<td>28</td>
<td>16:10:29</td>
<td>1.40</td>
<td>52.3</td>
<td>23:10:29</td>
<td>48.4</td>
<td>91</td>
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<tr>
<th>Interval Number</th>
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<th>5</th>
<th>6</th>
<th>7</th>
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<th>15</th>
<th>16</th>
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<td>Accum. Temp.°F</td>
<td>68.5</td>
<td>76.4</td>
<td>72.4</td>
<td>49</td>
<td>12.0</td>
<td>0.0</td>
<td>6.5</td>
<td>0.0</td>
<td>6.0</td>
<td>0.0</td>
<td>0.0</td>
<td>0.0</td>
<td>20.0</td>
<td>10.0</td>
<td>33.0</td>
<td></td>
</tr>
</tbody>
</table>
must remember that the method will only hold good provided the conditions already postulated do actually obtain, or at least, are closely approximated. This may partially account for the aspersions frequently cast on the conception of temperature-summation, together with the fact that the idea is not a new one. As in the field of statistics, where results are sometimes obtained which appear to conflict with common sense, the inaccuracy is not usually due to an inherent defect in the statistical formula, but to the inapplicability of the method in that particular field.

The straight line limits of development for the egg of Smyththurus have been determined approximately, and would appear to extend over the temperature range 9°- 21°C; this being situated low down on the temperature scale in comparison with most developmental stages which have been investigated, but, as has already been pointed out, all the metabolic activities of Smyththurus have this characteristic in relation to temperature. It now remains to be observed whether the temperatures experienced out-of-doors during the developmental period of the overwintering egg-stage, namely from October to March in Britain, ordinarily fall within the limits 9°- 21°C., in order to enable one to predict with reasonable accuracy the appearance of Smyththurus nymphs in spring. In so far as temperatures
above 21 °C., are concerned those are easily disposed of, since they do not obtain in Britain during the period under consideration. Now, by projecting the straight line portion of the temperature-velocity curve it is found that the temperature axis is cut at 7.2°C., which means that one can utilise this temperature as the basis for purposes of summation, although it does not represent the developmental zero of the egg-stage. However, for purposes of practicability and simplicity (the latter being the essence of the former) 7.2°C. has been assumed as the developmental zero, although development in the egg of Smynthurus would appear to continue at a perceptible rate down to 5°C.

Hence, if outdoor temperatures do not fall between 7.2°C and 9°C. one can make a fairly good approximation to the probable date of emergence of the Smynthurus nymphs in spring, because when below 7.2°C. development is almost inhibited, and when above 9°C it is proceeding at the hyperbolic rate. Now, using mean daily temperatures for purposes of summation, it is found that slightly under 25 per cent of the observations fall within the prohibited range, 7.2°C - 9.0°C.; but this does not mean that they are on that account valueless, although it does mean that our prediction is going to be out somewhat, and the larger the number of observations falling within this "non-hyperbolic" range, the greater the probable error of our prediction. Putting the
above principle into operation, we shall observe by referring to Table XII (where the total number of day-degrees of effective temperature, i.e. over 45°F., for each interval between two consecutive sweepings is indicated) that from September 26th onwards the total heat energy available falls far below the requirements for complete development of the egg-stage, which necessitates 263 day-degrees (F.) of 'medial' temperature, whereas the total accumulated effective temperature from September 26th to December 21st is only 228.9 (day-degrees F.). The gradual decrease in the Smynthurus population from September 26th to December 21st is undoubtedly due, therefore, to the gradual dying out of a generation and its non-replacement by a subsequent generation, on account of an insufficient heat-energy to allow of the complete development of the egg-stage. Any eggs which were oviposited after September 26th were, therefore, unable to develop until the following spring. Now the total accumulated effective temperature from the above date to the 20th March is still below the requirements for complete development of the egg, being only 241.4 (day-degrees F.), but by April 10th this had increased to 261.4, and nymphs emerged on this date. Making allowances for the known short-comings of the method employed, it will be admitted that the agreement between
the calculated and the actual time of emergence is extraordinarily close, the difference being only 1.6 day-degrees Fahrenheit. The writer is fully aware that the conception of a constant sum of effective temperatures has been subjected to much adverse criticism, due to the different effects of constant and fluctuating temperatures, as well as the fact that the action of one degree of temperature for a known period of time, varies slightly at different temperatures. It must be remembered, also, that the principle only holds good provided there is no other 'limiting factor', or if such is present, that it acts with equal intensity throughout the developmental stage, and that the constant sum of temperatures is calculated with reference to this factor. Since the optimum humidity for the various stages in the development of insects is now known to vary tremendously, it seems highly reasonable to suspect that those instances in which the principle gave very inaccurate results, may have arisen from neglect of the minimum effective humidity requirements, let alone excessive humidity conditions, which may also slow up metabolism. In any case, the principle is highly adaptable for all practical purposes in this instance.

Before making use of the idea involved in a constant sum of effective temperatures, it was attempted to utilise ordinary, and effective temperatures (i.e. taking into
consideration only those days in which the temperature exceeded 45°F.) in correlating disappearance and reappearance of nymphs with the reasonable variations in temperature. The results are tabulated below and from these it will be noticed that in each instance the temperature at which hatching commenced is somewhat lower than the corresponding temperature at which hatching ceased, which is, of course, due to the cumulative temperature effect over the long intervening period.

<table>
<thead>
<tr>
<th></th>
<th></th>
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<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Hatching Ceased</td>
<td>42.4°F.</td>
<td>62.6°F.</td>
<td>48.9°F.</td>
<td>51.1°F.</td>
</tr>
<tr>
<td>Hatching Commenced</td>
<td>33.0°F.</td>
<td>59.5°F.</td>
<td>44.0°F.</td>
<td>47.7°F.</td>
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<tr>
<td>Difference in Temp.</td>
<td>9.4°F.</td>
<td>3.1°F.</td>
<td>4.9°F.</td>
<td>3.4°F.</td>
</tr>
</tbody>
</table>

The mean maximum and mean effective temperatures apparently act as the best indices to the actual temperature conditions affecting the development of the egg, and one may say, that in the neighbourhood of the station in which the above temperature records were made, Smynthurus nymphs will cease to emerge in autumn when the mean maximum temperature falls below 62.6°F., or the mean effective temperature falls below 51.1°F., while nymphs may be expected in
the fields in spring, whenever the mean maximum temperature reaches 59.5°F., or the mean effective temperature reaches 47.7°F. As the above temperatures do not represent the actual temperatures obtaining in the micro-climate of the developing egg they are only of relatively local significance, but once determined for any locality, act as a reasonably accurate index to the emergence time of Smynhurus nymphs, and avoid the more laborious process of temperature-summation. To eliminate, as far as possible, fluctuations in temperature, it is better to take fortnightly, (or better monthly) rather than weekly means, the above representing the mean temperatures for the preceding fortnight. The mean temperature for the whole climatic area known as 'England E.,' under the scheme of the Meteorological Office, was 42.8°F. for the two weeks previous to the emergence of Smynhurus nymphs at Farnham Royal in April, 1929, while for the corresponding period in April, 1930, it was 45.6°F. a difference of only 2.8°F., despite two very abnormal seasons, namely the winter and spring of 1928-29 and 1929-30. The deviation from the mean value at Farnham Royal is almost negligible, so it seems reasonable to conclude that the latter method possesses a very considerable degree of practical utility.

(3). Temperature and Rainfall as 'Limiting' Factors to Population Increase.

Emergence of the nymphs in spring marks the commence-
ment of the second part of the first period, during which the Smynthurus population steadily rises under the stimulating influence of a gradually rising temperature, a schematic illustration of the course of events being presented in Diagram A. where the solid columns represent rainfall, and cross-hatched, the numbers of Smynthurus, both drawn to the same scale as in Graph XIV. A steady rise in numbers occurs till May 15th due to the gradual emergence of nymphs throughout the period, since temperature is still acting in a highly 'limiting' capacity (q.v. Graph XIV), while the rapid rise of temperature during the fortnightly interval ending May 29th causes the appearance of numbers of early nymphs, on account of delayed development on the part of a small proportion of the overwintering eggs. By May 15th, many of the nymphs have reached the seventh instar, during which sexual maturity is attained, and the period of oviposition by nymphs of the first generation has commenced. In all cases throughout the season, this period of oviposition has not been defined as the result of direct observation in the field, which is extremely laborious in this instance, but by knowing (i) that oviposition will occur after the attainment of the seventh instar, provided conditions of temperature, humidity, etc., are suitable, and (ii) the
period of emergence of the young nymphs - it is easy to calculate back, by means of the developmental constant, to the exact period during which oviposition must have taken place.

For instance on June 13th, numerous nymphs of the second generation appeared in the sweepings for the first time, and between May 29th and this date the heat energy available for development of the egg-stage amounted to only 104 day-degrees F., so that oviposition must have taken place prior to May 29th, and since the nymphs had not reached sexual maturity before 15th, oviposition must have taken place between May 15th and May 29th. The heat energy for this period is 167 day-degrees F., i.e., just more than enough to allow complete development of the eggs, and the appearance of nymphs on June 13th. Nymphs of this generation continued to emerge, of course, up till June 26th, since oviposition was continued over the interval, May 15th to May 29th (approx.) This marks the close of the first and the commencement of the second period in the seasonal cycle of events, during which the population of Smynthurus undergoes a series of rapid and violent fluctuations correlated with the rainfall, temperature being no longer the 'limiting' factor to population increase.

It may be advisable to state here that by the term
'limiting factor' as applied to natural populations, the writer implies that factor which is of preponderating significance in comparison with any other single factor inhibiting the rate of population increase. This definition involves the conception, that although there are numerous factors acting simultaneously to reduce the rate of population increase in Nature, there is usually one factor of outstanding significance in comparison with any other, and sometimes many or all other factors combined. The writer believes this to be so, the reasons for which will be treated in a subsequent paper. Hence the labours of the economic entomologist, or biologist, must be largely concentrated, to begin with, in determining the 'limiting factor', as above defined.

In this instance, temperature still checks the rate of population increase, through the adverse effect of high temperatures upon survival of the early nymphs, and upon the developing embryo in the egg (see later); also to a certain extent indirectly through its effect upon the evaporating power of the air, but temperature is no longer the 'limiting factor' to population increase. In the discussion of this second period it will be unnecessary to describe at length the course of events in each successive generation, since these are presented, in more or less detail in Diagram A. All that will be attempted, therefore, is a consideration of the successive generations
in their relation to each other, and as a combined expression of the inevitable reaction of numerous individual organisms to a complex of environmental stimuli, the most important of which (on account of its 'limiting' amount) is atmospheric and soil moisture. Looking at Graph XIV, in this second phase, that which immediately strikes the eye is the extraordinarily high correlation between rainfall and numbers of Smynthurus, bearing in mind that there is a time-lag effect of approximately 14 days, so that the total rainfall for any fortnight is correlated with the Smynthurus population at the end of the following fortnight. This extraordinary close correlation is not mere chance coincidence, but is the logical and necessary result of the synchronisation between life-cycle and the 'limiting factor' in the environmental complex. How, then, does this 'limiting factor' - rainfall - regulate the "timing of events" during the second period of the seasonal cycle, as well as the magnitude of the Smynthurus population?

C. QUANTITATIVE ANALYSIS OF ENVIRONMENTAL COMPLEX.

(1) The Method Adopted and the Criteria of Significant Factors.

In order to determine the above it is necessary to analyse a maze of interlocking and interdependent environ-
mental factors, which operate simultaneously, and on different phases of the life-cycle, with different intensities. Since the method adopted in unravelling what, at first sight, appears to be a bewilderingly tangled skein, may be of some interest, it will be described in detail. The procedure consisted of an analysis of the effects of temperature, rainfall, and evaporating power of the air, over the respective generations in the second (and by far the most important) period of the seasonal cycle of events. This was done by breaking up the life-history into its component phases and plotting the response of the phase (e.g. oviposition) in each generation, against each of the respective environmental factors, so that in this way the degree of correlation could be assessed by the form of the curve obtained. The best correlation, in the above instance, between any phase and a particular environmental factor will be obtained when the factor in question is acting in a highly 'limiting' capacity, every increment of that factor producing a relatively greater response than the corresponding increment of any other factor during that same period of time. The ecological significance of this is simply that the environment is more deficient in the supply of this factor than any other factor, relative to the physiological process in question, on account of its peculiar intrinsic requirements.
To carry out the above analysis demands an intimate knowledge of the actual course of events taking place in the field, so that one can determine with accuracy the particular periods of time in which the respective phases are located. Another essential is diversity of environmental conditions throughout the different generations, in order to have a wide range of observations, and in this the writer was fortunate, due to the abnormal weather conditions of 1929, which presented a variety of temperature and rainfall during the several phases of the respective generations. Proceeding in the manner just indicated, a total of nine different graphs were constructed, plotting the response of the phase on the ordinate against the environmental factor on the abscissa. It is important to note that the measure of response was not the actual population resulting from the operation of a particular factorial intensity, but the ratio of increase or decrease on the already existing population. In assessing the relative significance of the different factors as ascertained from an examination of the graphs above described, these are the main points which require careful consideration, (i) the form of the curve which produces the best possible fit to our observations, (ii) the degree of adherence of our observations to the curve so obtained, (iii) the relative position of our observations to the total range of response.
### Table XIII

Effect of Certain Combinations of Temperature and Rainfall upon Oviposition by Smynthurus.

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<tr>
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<tr>
<td>29: 5:29</td>
<td>0 f 1st Genrn.</td>
<td>1.20</td>
<td>57.1</td>
<td>69.5</td>
<td>3915</td>
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<td>0.85</td>
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<td>69.0</td>
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<td>(1)</td>
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<td>1.02</td>
<td>55.1</td>
<td>66.2</td>
<td>172</td>
<td>60:172 (1: 2.8)</td>
<td>(3)</td>
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Effect of Certain Combinations of Temperature and Rainfall upon Emergence of Smynthurus Nymphs.

<table>
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</thead>
<tbody>
<tr>
<td>26: 6:29</td>
<td>0 f 2nd Genrn.</td>
<td>0.10</td>
<td>58.5</td>
<td>69.0</td>
<td>3915</td>
<td>716:3915 (1: 5.4)</td>
<td>(2)</td>
</tr>
<tr>
<td>24: 7:29</td>
<td>0 f 3rd Genrn.</td>
<td>0.07</td>
<td>65.6</td>
<td>80.4</td>
<td>1220</td>
<td>555:1220 (1: 2.2)</td>
<td>(3)</td>
</tr>
<tr>
<td>21: 8:29</td>
<td>0 f 4th Genrn.</td>
<td>0.42</td>
<td>58.2</td>
<td>72.8</td>
<td>3340</td>
<td>140:3340 (1: 24.0)</td>
<td>(1)</td>
</tr>
<tr>
<td>19: 9:29</td>
<td>0 f 5th Genrn.</td>
<td>0.00</td>
<td>62.4</td>
<td>75.6</td>
<td>511</td>
<td>1172:511 (1: 0.4)</td>
<td>(4)</td>
</tr>
</tbody>
</table>

Effect of Certain Combinations of Temperature and Rainfall upon Survival of Early Nymphs of Smynthurus.

<table>
<thead>
<tr>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>26: 6:29</td>
<td>0 f 2nd Genrn.</td>
<td>0.10</td>
<td>58.5</td>
<td>69.0</td>
<td>555</td>
<td>3915:555 (1:0.14)</td>
<td>(2)</td>
</tr>
<tr>
<td>24: 7:29</td>
<td>0 f 3rd Genrn.</td>
<td>0.07</td>
<td>65.6</td>
<td>80.4</td>
<td>140</td>
<td>1220:140 (1:0.11)</td>
<td>(4)</td>
</tr>
<tr>
<td>21: 8:29</td>
<td>0 f 4th Genrn.</td>
<td>0.42</td>
<td>58.2</td>
<td>72.8</td>
<td>1172</td>
<td>3340:1172 (1:0.35)</td>
<td>(1)</td>
</tr>
<tr>
<td>19: 9:29</td>
<td>0 f 5th Genrn.</td>
<td>0.00</td>
<td>62.4</td>
<td>75.6</td>
<td>60</td>
<td>511:60 (1:0.12)</td>
<td>(3)</td>
</tr>
</tbody>
</table>
Effect of Rainfall upon Oviposition  Graph XV (a)

- Actual Data.
- Value to Illustrate Complete Response.
Bearing the above in mind, out of the nine graphs constructed, two have been selected as representing the most important physical factors in the control of the Smynthurus population, and these are presented in Graph XV, the data being supplied in Table XIII. Examination of the data, facilitated by the graphical illustrations, indicates that the relative importance of the different factors, and their mode of operation, in checking the natural increase of the Smynthurus population is as follows:— (a) the effect of rainfall upon oviposition. (b) the effect of rainfall upon development and emergence of nymphs from the egg, (c) effect of temperature upon development and emergence of nymphs from the egg.

(2). Effect of Rainfall upon Oviposition.

The reasons for the above selection are briefly these. Firstly, in Graph XV (a) all the observations fall on the theoretically best fitting curve, and the latter assumes the typical sigmoid form of population increase curves; the first point indicating that we are, in this instance, dealing with a "dominating reaction" or "master effect" which cannot be subjugated by the preponderating influence of any other environmental factor, and the second point acting as a reinforcement to the conclusion that we have here a real effect and not merely an
artefact. Further, out of the five observations, four fall below the mid-point of inflexion of the curve, showing that conditions of rainfall during the oviposition period throughout the five generations, were, with one exception, far removed from conditions productive of the maximum response, more so indeed, than those for any other phase in the life-cycle. This is, of course, due to the intrinsic requirements of the oviposition process in Smyminthus, involving a very high rainfall during its progress, so that the demands of this vital process upon the environment (if the reproductive process is to give rise to its fullest expression) are such that the latter is least able, of all the vital processes in the life-cycle, to fulfill these requirements. The necessity of a high rainfall during the oviposition period is undoubtedly associated with the peculiar habit of the insect, in that it covers each egg with an exudate of soil passed via the anus. To this end, an enormous amount of soil has to pass through the alimentary tract, and unless the soil be in a very moist condition the insect is incapable of eating the necessary quantity. The following simple experiment was conducted to demonstrate this point. Forty adults were collected from the field and equally distributed to four glass petri dishes as follows:— (1) provided with dry filter paper; (ii) provided with filter paper kept
continuously moist, (iii) provided with powdered dry soil of pH 6.5 (i.e. almost optimum pH); (iv) provided with the same type of soil, but kept constantly saturated with distilled water. All four were supplied with fresh green clover leaves, and at the end of five days the number of eggs produced in each lot were counted and found to be as presented below:

<table>
<thead>
<tr>
<th>Without Soil</th>
<th>Without Moisture</th>
<th>With Moisture</th>
</tr>
</thead>
<tbody>
<tr>
<td>Without Soil</td>
<td>(i) - 0</td>
<td>(ii) - 11</td>
</tr>
<tr>
<td>With soil</td>
<td>(iii) - 0</td>
<td>(iv) - 99</td>
</tr>
</tbody>
</table>

This confirms the suggestion of Holdaway that the presence of soil has a stimulating effect upon oviposition in the case of females ready to lay eggs, and also demonstrates, that in addition, a certain moisture content of the soil is essential before oviposition will take place. The exact amount of moisture necessary will vary with different types of soil, depending upon its saturation capacity, as determined by the texture and structure of the soil-type. In any case, it is very high, and would appear to be almost 100 per cent saturation for maximum oviposition.
Graph XIV Effect of Rainfall upon Emergence of Nymphs

- Actual Data.
- O Value to Illustrate Complete Response.
(3) Effect of Rainfall upon Development and Emergence of Nymphs.

Continuing the analysis of the physical environment, the next most important controlling factor of the Smynthurus population is the effect of rainfall during the development and emergence of the nymphs from the eggs, as presented in Graph XVI, b. Here we must make allowance for a slight artefact as indicated by the emergence of a small population when the rainfall is nil. This is due to the fact that when the moisture requirements for maximum response are so small (as in this instance) the effects of dew assume very considerable significance, although unrecorded. The well-known dew-ponds of the chalk-Downs afford a good illustration of the amount of water vapour deposited in this form, even when the rainfall has been negligible over long periods. Three of the observations fall below the mid-point of inflexion of the curve, but these are not so far removed from the maximum response as indicated by the curve, i.e., if we consider a rainfall of nil as the zero, but if we take the point where the projected curve cuts the rainfall axis as the zero, then we obtain the true measure of departure of our observations from the maximum response. The mode of operation of rainfall upon the developing egg of Smynthurus is bound up with the question of atmospheric humidity in
in the micro-climate, the relative humidity as recorded in
the Stevenson screen being too far removed from the actual
conditions obtaining in the immediate environment of the
egg to have much value for comparative purposes, since the
relative humidity in proximity to the ground surface, de-
pends to such an extent upon the nature of the substratum.
However, experiments conducted with a view to determining
the actual effect of various relative humidities upon the
partially developed eggs will be considered later in this
section, together with the effect of temperature upon the
same stages.

(4). Effect of Temperature upon Development and Emergence

of Nymphs.

The third significant factor controlling the Smyn-
thurus population is the effect of temperature during the
development of the egg, and in this respect, the evidence
drawn from the field data indicates that up to a daily
mean temperature of 58.0°F., the destruction of partially
developed embryo nymphs, due to the adverse effects of
high temperatures, is negligible, but that above this
temperature there is a profound and rapid reduction in
the numbers of nymphs which emerge from the egg-stage.
The effect continues with increasing intensity up to 66°F.
(approx.), when the numbers escaping destruction become
practically nil. Experiments conducted in the laboratory
to determine the exact effect of temperature (and various combinations of temperature with different relative humidities) on the partially developed eggs of Smynthurus, gave the following significant results. The several associations of temperature, humidity, and time of exposure were so arranged as to approximate conditions actually obtaining in the field, since in order to throw some light on the mortality effects of these factors in Nature, it was obviously useless to subject the developing egg to artificial climatic conditions which were not approximated in the field, interesting though they might be from a purely scientific standpoint. The factor intensities and exposure periods were taken from a hygro-thermograph chart record and slightly modified to facilitate experimental procedure, the modification always being made in a direction favourable to increased survival, so that if anything, conditions in the field are occasionally more severe than those indicated. The conditions presented in Experiment No.3, however, are seldom approximated in Britain for any length of time.

Series of Experiments to Determine the Effect of Fluctuating Conditions of Temperature and Humidity upon the Percentage Hatch of Partially Developed Eggs of Smynthurus.

The eggs had completed 80 - 85 per cent of their total development and were subjected to the following conditions
for a period of 10 days, after which they were transferred to an environment highly favourable for the completion of their development, and the percentage which emerged was noted.

<table>
<thead>
<tr>
<th>Exp.</th>
<th>Time Interval</th>
<th>Environmental Conditions</th>
<th>Percentage Egence (highest ever obtained time indicated)</th>
</tr>
</thead>
<tbody>
<tr>
<td>No.1</td>
<td>9 p.m. - 9 a.m.</td>
<td>12 hrs. @ 16°C. and 100% R.H.</td>
<td>28% in 180 h, 48% in 204 h, 62% in 228 h, 66% in 276 h</td>
</tr>
<tr>
<td></td>
<td>9 a.m. - 9 p.m.</td>
<td>12 hrs. @ 21°C. and 85% R.H.</td>
<td></td>
</tr>
<tr>
<td>No.2</td>
<td>9 p.m. - 9 a.m.</td>
<td>12 hrs. @ 16°C. and 100% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9 a.m. - 11 a.m.</td>
<td>2 hrs. @ 21°C. and 85% R.H.</td>
<td>4% in 228 h</td>
</tr>
<tr>
<td></td>
<td>11 a.m. - 7 p.m.</td>
<td>8 hrs @ 25°C. and 60% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7 p.m. - 9 p.m.</td>
<td>2 hrs. @ 21°C. and 85% R.H.</td>
<td></td>
</tr>
<tr>
<td>No.3</td>
<td>9 p.m. - 9 a.m.</td>
<td>12 hrs. @ 16°C. and 100% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>9 a.m. - 11 a.m.</td>
<td>2 hrs. @ 21°C. and 85% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>11 a.m. - 12.30 p.m.</td>
<td>1½ hrs. @ 25°C. and 60% R.H.</td>
<td>Nil</td>
</tr>
<tr>
<td></td>
<td>12.30 p.m. - 5.30 p.m.</td>
<td>5 hrs. @ 29°C. and 50% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>5.30 p.m. - 7 p.m.</td>
<td>1½ hrs. @ 25°C. and 60% R.H.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>7 p.m. - 9 p.m.</td>
<td>2 hrs. @ 21°C. and 85% R.H.</td>
<td></td>
</tr>
</tbody>
</table>
The above experiments clearly demonstrate the adverse effects of high temperatures in conjunction with low humidities on the developing egg of Smynthurus. The conditions presented in Experiment No.1 are often exceeded in intensity in Britain during the summer and early autumn months, while those presented in Experiment No.2 are not uncommon in late summer and early autumn but do not exist for as long as 10 days in succession. An environment of 100 per cent R.H. and a temperature of 16°C is highly favourable for development of the egg. In connection with these adverse effects it must be borne in mind that the eggs are deposited on the soil surface or amongs the vegetable debris which tends to accumulate thereon, and it will therefore be necessary to consider briefly the ecological peculiarities of this habitat.

Studies by Buxton, Chapman, and Williams have shown that the sand surface in desert areas is characterised by violent diurnal fluctuations in temperature. The same holds good, however, for the soil surface in temperate regions, although the amplitude is not so great. Analysis of the records made under the meteorological scheme of the Ministry of Agriculture and Department of Agriculture for Scotland, shows that from May to August the mean daily air temperature is considerably lower than the mean daily soil temperature, even at a depth of four inches, by which
time the temperature effect has been much reduced in the course of penetrating the upper four inches of soil. During this same period the difference between the mean maximum and the mean minimum at four inches is at its highest, being about 20°F. Since it is known that the reduction in amplitude of the soil temperature wave with increase in depth approximates to a relationship such that the amplitude decreases in geometrical progression as the depth increases in arithmetical progression, it follows that the amplitude of soil surface temperatures, even in temperate regions, is very considerable, and awaits detailed investigation. Now the mean maximum temperature at Farnham Royal during the incubation period of the second, third, fourth, and fifth generations was 69°, 80.4°, 72.8° and 75.6°F. respectively. The significance of this in relation to Smyntthurus, since the eggs are deposited on the soil surface, is obvious, especially in view of the results obtained in the preceding laboratory experiments on the effect of fluctuating conditions of temperature and humidity upon the developing egg. The fact that the eggs are deposited on this physically unfavourable substratum is undoubtedly associated with the primitive nature of the insect, for even if they were deposited a few inches above the soil surface among the herbage they would be subject to less violent
temperature variations, while if deposited somewhat below the surface the eggs would also be in a less variable environment and have an increased supply of moisture. Ecologically, therefore, an exposed soil surface is the most primitive of terrestrial habitats, but as the covering of herbage increases in density conditions become more favourable for existence, largely due to the tendency of the former to damp down violent oscillations of physical environmental factors. The insect also illustrates 'the return to the primitive' during periods associated with reproduction (this being usually the last to yield to evolutionary change), since the actively growing nymphs spend most of their time up amongst the herbage, returning only occasionally to browse on the soil surface.

The fact that there is a pronounced temperature gradient of decreasing magnitude from the soil surface upwards during the warmest period of the year explains why the mortality amongst the embryo nymphs is heavier than amongst the newly emerged and early nymphal instars although their physiological requirements as regards temperature and humidity are much the same, the latter being able to escape the unfavourable conditions on the soil surface by climbing a few inches upwards amongst the herbage. On very hot days, the writer was surprised to find many Smynthuri poised on the very tip of grass stems (as if
they were attempting to climb upwards as far as they could) and was unable to account for this peculiar behaviour until the above explanation was discovered.

Since humidity might not be a serious mortality factor in Britain during a wet season, and in certain tropical areas of the world, it seemed desirable to determine the effect of high temperatures upon partially developed eggs in a saturated atmosphere, to which end the following experiments were performed. Eggs which had completed approximately 64 per cent of their development were subjected to temperatures of 25°C. and 29°C., and allowed to remain there until the nymphs emerged, with the following results. At 25°C., 76 per cent emerged in 108 hours, 80 per cent in 132 hours, and 84 per cent in 156 hours, and at 29°C., the emergence was 44 per cent in 108 hours and 52 per cent in 132 hours. A control at a mean temperature of 16°C. gave one hundred per cent emergence in 252 hours. Hence it is evident that soil surface temperatures exceeding 25°C. will have a considerable mortality effect on the partially developed eggs of Smynthurus, even in the presence of favourable (i.e. high) humidity conditions, and from the above considerations of air temperatures in relation to soil temperatures, will come into operation in Britain in all but very cool summers.
Effect of Temperature upon Survival of the Early Instar Nymphs and Adults.

The fourth factor, in order of significance, controlling the Smynthurus population, is the adverse effect of high temperature upon survival of the early instar nymphs, which are much more sensitive than the adults to these effects. Analysis of the field data in the manner already described shows that daily mean temperatures above 60°F. are very unfavourable for survival of the young nymphs, and that there is a very rapid reduction in the number of survivors as the temperature increases beyond this mean until the attainment of 70°F., when the survival is nil. This temperature effect upon the young nymphs takes place even in the presence of optimum humidity conditions, and is intensified when the humidity is lowered. It must be borne in mind that the above temperatures are mean temperatures recorded in a screen four feet above the ground, so that the actual temperatures experienced by the nymphs, for about six hours of the day, were considerably higher. To illustrate concretely the mortality effect of various temperature-humidity combinations, a series of experiments were conducted in which adults were used, being much more convenient for experimental purposes than the young nymphs, which are so small and not always easily
obtainable in the large numbers required for these experiments. Bearing in mind that the nymphs are more sensitive than the adults to adverse temperature-humidity conditions, the following results demonstrate the high mortality brought about by comparatively moderate temperatures and humidities such as 80 per cent R.H. and 30°C.

The results are presented below, while those for the 'Flea Beetle', *Longitarsus melanoccephalus*, have been added as an interesting comparison, being one of the dominant species occupying the same habitat as *Smynthurus*.

<table>
<thead>
<tr>
<th></th>
<th>10% R.H.</th>
<th>40% R.H.</th>
<th>80% R.H.</th>
<th>100% R.H.</th>
<th>Species</th>
</tr>
</thead>
<tbody>
<tr>
<td>30°C</td>
<td>20% in 1 hour</td>
<td>20% in 1½ hour</td>
<td>20% in 4 hrs.</td>
<td>20% in 6 hrs.</td>
<td><em>Smynthurus</em></td>
</tr>
<tr>
<td></td>
<td>60% in 3 hrs.</td>
<td>60% in 4 hrs.</td>
<td>60% in 30 hrs.</td>
<td>60% in 30 hrs.</td>
<td>viridis*</td>
</tr>
<tr>
<td></td>
<td>100% in 5 hrs.</td>
<td>100% in 7 hrs.</td>
<td>100% in 51 hrs.</td>
<td>100% in 75 hrs.</td>
<td></td>
</tr>
<tr>
<td>35°C</td>
<td>20% in ½ hr.</td>
<td>20% in 1 hr.</td>
<td>20% in 1½ hr.</td>
<td>20% in 2 hrs.</td>
<td></td>
</tr>
<tr>
<td></td>
<td>60% in 2 hrs.</td>
<td>60% in 3 hrs.</td>
<td>60% in 3 hrs.</td>
<td>60% in 6 hrs.</td>
<td><em>Smynthurus</em></td>
</tr>
<tr>
<td></td>
<td>100% in 4 hrs.</td>
<td>100% in 5 hrs.</td>
<td>100% in 9 hrs.</td>
<td>100% in 9 hrs.</td>
<td>viridis*</td>
</tr>
<tr>
<td>40°C</td>
<td>20% in 10 hrs.</td>
<td>20% in 20 min.</td>
<td>20% in 1½ hr.</td>
<td>20% in ½ hr.</td>
<td><em>Longitarsus</em></td>
</tr>
<tr>
<td></td>
<td>60% in 25 min.</td>
<td>60% in ½ hr.</td>
<td>60% in 45 min.</td>
<td>60% in ½ hr.</td>
<td><em>melanoccephalus</em></td>
</tr>
<tr>
<td></td>
<td>100% in 1½ hr.</td>
<td>100% in 2 hrs.</td>
<td>100% in 2 hrs.</td>
<td>100% in 3½ hrs.</td>
<td></td>
</tr>
<tr>
<td>40°C</td>
<td>20% in 2 hrs.</td>
<td>20% in 3 hrs.</td>
<td>20% in 3 hrs.</td>
<td>20% in 4½ hrs.</td>
<td><em>Longitarsus</em></td>
</tr>
<tr>
<td></td>
<td>60% in 2 hrs.</td>
<td>60% in 4 hrs.</td>
<td>60% in 5½ hrs.</td>
<td>60% in 6½ hrs.</td>
<td><em>melanoccephalus</em></td>
</tr>
<tr>
<td></td>
<td>100% in 3½ hrs.</td>
<td>100% in 6 hrs.</td>
<td>100% in 8 hrs.</td>
<td>100% in 9 hrs.</td>
<td></td>
</tr>
</tbody>
</table>
It is evident that the mortality effect of temperatures over 30°C. accelerates very rapidly with rise of temperature and decrease of relative humidity. A saturated atmosphere delayed the onset of death longer than any other humidity investigated, including 90 per cent R.H., so that if there is a humidity more favourable to the prolongation of life at those temperatures it must lie between 90 and 100 per cent saturation, but the writer is not inclined to the belief that there is such an 'optimum' (between 90% and 100%) for Smynthurus, when temperatures above 30°C. are involved, or for temperatures approaching the limit of tolerance in the case of other insects. The reasons for this are of somewhat theoretical interest and will not be discussed here. The above may appear contradictory when it is recalled that definite optima below 100 per cent saturation were obtained for growth and reproduction, but it may be worth while to emphasize that the resistance of protoplasm to adverse temperatures is a signally distinct phenomenon from normally proceeding physiological processes. As regards Longitarus melanocephalus, the resistance of this species to high temperatures is considerably greater than that of Smynthurus, although both species are among the predominating ones in a grassland 'community' investigated by means of a monthly census.
During the winter months, if temperatures below freezing point prevail for any length of time, the Smynthuri die off fairly rapidly, but this effect is apparently due as much to the gradual drying out of the atmosphere which takes place during long spells of frosty weather as to the adverse effect of the low temperature, since they move about and feed, although sparingly, at 0°C., provided the atmosphere remains very humid, as the following experiments show. Adults maintained at 0°C., and 10 per cent R.H. were all dead within 24 hours, while at 60 per cent R.H., at the end of two weeks, there was 20 per cent mortality, and at 80 per cent R.H. there was 10 per cent mortality during the same period. At 3°C. the insects move about and feed, provided the relative humidity remains above 80 per cent, but they eventually succumb to adverse secondary effects such as bacterial and fungal attack on account of the excessive lowering of metabolism and gradual reduction of general vitality. Oviposition occurs at 5°C. but the number of eggs produced is only about 10 per cent of the maximum, and no eggs were ever obtained at 0°C.

Whilst there is a high negative correlation between the size of the Smynthurus population and the atmometric index, the relation between the latter and any particular phase in the life-cycle, is not so apparent, since the
SUMMARY OF SMYNTHERUS LIFE HISTORY, ILLUSTRATING RELATION TO ENVIRONMENTAL FACTORS.

<table>
<thead>
<tr>
<th>Date</th>
<th>Generation</th>
<th>Description of Events</th>
<th>Moisture Condition</th>
<th>Accum. Effic. Temperature</th>
</tr>
</thead>
<tbody>
<tr>
<td>April 3</td>
<td>I</td>
<td>Mostly 2nd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of Nymphs of 1st Generation</td>
<td>Low: 2.0</td>
</tr>
<tr>
<td>April 17</td>
<td>I</td>
<td>Mostly 2nd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of Nymphs of 1st Generation</td>
<td>Low: 10</td>
</tr>
<tr>
<td>May 2</td>
<td>II</td>
<td>Mostly 3rd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 2nd Generation</td>
<td>Low: 3.3</td>
</tr>
<tr>
<td>May 15</td>
<td>III</td>
<td>Mostly 4th Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 104</td>
</tr>
<tr>
<td>May 29</td>
<td>III</td>
<td>Mostly 2nd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 2nd Generation</td>
<td>Low: 10</td>
</tr>
<tr>
<td>June 13</td>
<td>III</td>
<td>Mostly 2nd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 2nd Generation</td>
<td>Low: 10</td>
</tr>
<tr>
<td>June 26</td>
<td>III</td>
<td>Mostly 2nd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 2nd Generation</td>
<td>Low: 10</td>
</tr>
<tr>
<td>July 10</td>
<td>III</td>
<td>Mostly Adults</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>July 24</td>
<td>IV</td>
<td>Mostly Early Nymphs</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Aug 7</td>
<td>IV</td>
<td>Only Adults</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Aug 21</td>
<td>V</td>
<td>Mostly Late Nymphs</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Sept 5</td>
<td>V</td>
<td>Mostly Adults</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Sept 19</td>
<td>V</td>
<td>Mostly Adults</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Oct 4</td>
<td>VI</td>
<td>Mostly Adults</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 2.88</td>
</tr>
<tr>
<td>Oct 16</td>
<td>VI</td>
<td>Mostly 3rd Instar Nymphs</td>
<td>Period of Incubation &amp; Growth of 3rd Generation</td>
<td>Low: 8.3</td>
</tr>
</tbody>
</table>

DIAGRAM A
atmometric index is compounded of several factors which tend to mask any single factor effect. Hence to demonstrate a correlation between a particular phase and the atmometric index, the latter has to be analysed into its several components (i.e. the various factors affecting it) and then subjected to the procedure already indicated. Since the factors concerned are mainly those which we have been examining, it will be unnecessary to repeat the process. The pronounced negative correlation between the size of the Smynthurus population and the atmometric index is clearly demonstrated in Graph XVI, the effect being operative only during the second period in the seasonal cycle of events, with a time-lag effect of approximately fourteen days, similar to that for the rainfall curve.

(6) The 'Timing of Events' in the Life-Cycle.

Having now discussed in some detail the major physical factors controlling the Smynthurus population one can return to the problem of 'the timing of events' in the life-cycle. An examination of Diagram A shows that each fortnightly interval marked "Period of Oviposition" is usually accompanied by a plus sign in the following column, indicative of "high moisture" conditions throughout this period. The term "high moisture conditions" is purely relative and is taken from the position on the graph showing the oviposition response to
rainfall, at which the curve turns sharply upwards. Hence, although relative, the phrase is by no means arbitrary being indicative of certain minimum rainfall requirements which must obtain before any appreciable response, on the part of the oviposition process, can take place, and below which, the ratio of the actual to the maximum organic response is not more than $1:10$. This amount of rainfall is not a fixed quantity, since it will vary somewhat with different types of soil, depending upon its saturation capacity, but in the environment investigated it is approximately one inch of rainfall per 14 days, throughout the period of oviposition. Each interval marked by a minus sign indicates that less than a total of one inch of rain fell throughout the period, and it will be observed that each "Period of Incubation of the Eggs" almost invariably coincides with a period of "low moisture" conditions. This is not mere chance coincidence, and requires an explanation.

Now, it has already been shown, from laboratory experiments and field data, that sexually mature individuals of Sminthurus will only oviposit above certain minimum moisture requirements, and that for anything approaching to normal oviposition to take place these moisture requirements are relatively high, i.e., in comparison with any other phase in the life-cycle. Hence
the period of oviposition tends to become synchronous with a period of high moisture conditions, and this is apparently the most important way in which the environment exerts its "timing effect" upon the life-cycle during the second, and most important period, in the seasonal cycle of events. Should the necessary moisture be unavailable at the time of sexual maturity, oviposition is delayed, just as absence of soil brings about a delay in the process; the delay is not of long duration, however, and if oviposition has to take place under adverse conditions of soil moisture, the effect is seen in an enormous reduction in the number of eggs laid, e.g., the oviposition periods of the second and fourth generations, namely, the fortnightly intervals ending July 10th and September 5th, respectively.

Temperature is, of course, the most important "timing factor" during the first period in the seasonal cycle, because it not only determines when the first generation shall emerge in spring, but it also determines the time (as well as the amount) of oviposition by the last generation in late autumn, namely when (and by how much) soil surface temperatures rise above 3°C. Throughout the seasonal cycle of events, therefore, the life-cycle of Smynthurus becomes synchronised with the 'limiting factor' in the environmental complex, through the 'timing effect' of
of temperature upon oviposition during the first period, and of rainfall during the second period. That the 'timing' and 'limiting' factors are identical categorically in this instance is purely fortuitous; they differ widely in their implications, the former involving a threshold of organic response to an environmental factor, and the latter, degree of intensity of operation of a factor which may or may not be the same. The difference between the two is of fundamental ecological significance.

A stage has now been reached in this ecological study of Smynthurus in which it can be said, that so far as the evidence goes, the physical environmental factors appear to be the major ones concerned in checking the natural increase of the Smynthurus population; and as no significant correlation, positive or negative, has been obtained, between the numbers of Smynthurus and those of any other biotic factor in the natural environments investigated in the neighbourhood of the laboratory, one may say with certainty, that in those areas, at least, the physical factors are the only ones exerting significant control over the increase of the Smynthurus population. It would be foolish, however, to attempt broad generalisations and to conclude from the above that biotic factors are seldom of any consequence in controlling the increase of Smynthurus, since the areas investigated were undoubt-
edly small and we may have hit upon such, as a matter of pure chance, which were inimical for some peculiar reason, to the survival of a reasonably large predator population. Hence the question of biotic factors requires further investigation. Moreover, the effect of soil pH value was left out of the discussion, because the departure from the optimum pH of 6.2 was never more than .3, which is negligible for all practical purposes in this instance. There still remains to be analysed therefore, the rôle of biotic factors in the natural control of Smynthurus, as ascertained from an analysis of samples of the entire insect and arachnid fauna, taken from numerous different localities where Smynthurus was present, and similarly, the rôle of soil pH value in controlling the Smynthurus population in Nature has still to be investigated. The latter will be considered first.

II. GEOGRAPHICAL VARIATION IN ABUNDANCE OF SMYNTHERUS.

A. QUANTITATIVE ANALYSIS OF FIELD COLLECTIONS.

(1. Significance of Soil Reaction in the Distribution of Terrestrial Animals.

It is a matter of general agreement amongst ecologists and other workers concerned, that soil reaction is an important factor in the geographical distribution of
plants. In relation to the distribution of terrestrial animals, however, the subject has been comparatively neglected, and for the obvious reason that animals are not so intimately associated with the soil substratum in the struggle for a livelihood, as are plants. Nevertheless, for those species which spend a portion of their life history in or on the soil, or depend upon the organic matter contained therein as a source of food supply, the study of soil reaction in relation to distribution merits greater attention than it has received up to now.

Perhaps the first indication of the significance of soil reaction in relation to insects was suggested some years ago by Williams as the result of preliminary observations on the froghopper pest of sugar-cane in Trinidad. These suggestions have been followed up by recent workers in collaboration with soil chemists, resulting in a most striking demonstration of the influence of soil reaction on the distribution of this serious pest. In regard to other terrestrial animals, it was found by Arrhenius that earthworms could not live in very acid soils, and that pH 6 - 7 appeared to be the optimum range, while Atkins and Lebour have shown that there is a definite relation between the soil reaction and abundance of snails, being most numerous in soils of pH 7 - 8, and those with calcareous shells being limited to the alkaline end of the pH scale.
As a result of controlled experimentation in the laboratory, it had been determined (see Part II) that soil p.H. value has a definite effect on Smynturus, both in regard to growth and reproduction, especially the latter. It thus became desirable to determine whether the effect was of sufficient significance to make itself observable in the size of the Smynturus population under natural conditions, or whether, in the latter instance, the other natural factors of control were capable of operating with an intensity sufficient to dwarf into insignificance any effect of soil p.H. value, so that the latter would only be observable in significant degree when other conditions were at or near their optimum, such as obtained in the laboratory experiments. Now, with all field data the chief difficulty lies in its correct interpretation, due to the fact, that usually numerous variables are simultaneously involved. Hence to reduce the complexity (we cannot eliminate it in Nature) to a minimum, the careful investigator must so choose his experimental areas that they approach as nearly as possible to the ideal (laboratory) experiment, in which there is only one variable and a control.

On account of the above difficulties, the variables including such factors as temperature and rainfall, the
effect of different cultural measures, rotations, intensity of grazing, etc., the writer had almost despaired of demonstrating by means of field data the role of soil pH value in determining the size of the Smynthurus population in Nature. However, the idea of sweeping the 'Park Grass Plots' at Rothamsted ultimately presented itself, and it will be admitted that the conditions obtaining there are probably as near an approach to the ideal laboratory experiment with a control and one variable, as is possible to obtain under natural conditions. These plots have carried hay each year since 1856; hence the effects of different rotations, grazing intensities, and cultural measures, are eliminated, and as the plots are adjoining one another the effect of different climatic conditions is also eliminated. The plots, however, have been subjected to different manurial treatments, with the exception of two untreated plots which were left as a control. This has produced a differential effect on the bulk and composition of the herbage in the respective plots, which will have to be taken into consideration, but those variables have been rendered capable of quantitative treatment, as careful records of the yield and composition of the herbage are made annually, and were obtained from the monograph of W. E. Brenchley. The different manures
have also produced considerable changes in the soil reaction, so that a fairly wide range of p.H. values are obtainable, and it is these which have to be utilised for the purpose of the present investigation. The p.H. values utilised were those determined by E. M. Crowther from surface samples taken on June 27th and 28th, 1923, in the 78th year of the plot experiments. Although the Smythurus sweepings were made on May 15th, 1930, it is highly improbable that the soil reaction (p.H. values) will have changed to any significant extent, since laboratory experiments suggested that Smythurus was not sensibly affected by a change of less than .2 on the p.H. scale. As it was not permissible to tread on the plots the sweepings had to be made along the edges, but this was satisfactorily accomplished. Strokes to the number of 50 were made in each instance. The data is presented below in tabular form:-
TABLE XIV.

<table>
<thead>
<tr>
<th>Manurial Treatment</th>
<th>Soil p.H.</th>
<th>Per Cent Yield of Hay Per Cent Value Legumin-</th>
<th>(Surface sample)</th>
<th>(over the period 1912-21)</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>No Nitrogen Group.</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Unmanured.</td>
<td>5.63</td>
<td>5.2</td>
<td>12</td>
<td>60%</td>
</tr>
<tr>
<td>Unmanured (after dung 1856-63)</td>
<td>5.72</td>
<td>4.5</td>
<td>10</td>
<td>13%</td>
</tr>
<tr>
<td>Complete minerals (Group with Manurial Changes)</td>
<td>5.86</td>
<td>4.3</td>
<td>-</td>
<td>1%</td>
</tr>
<tr>
<td>Minerals, without potash</td>
<td>5.43</td>
<td>8.7</td>
<td>26</td>
<td>27.5%</td>
</tr>
<tr>
<td>Superphosphate</td>
<td>6.69</td>
<td>2.7</td>
<td>17</td>
<td>28%</td>
</tr>
</tbody>
</table>

| Ammonia Group. | | | | |
| -43 lbs. N. (after dung 1856-63) | 4.84 | 0.0 | 14 | 2.0% |
| -86 lbs. N. & complete minerals | 4.04 | 0.0 | 32 | 0 |
| -86 lbs. N. & minerals without potash | 3.90 | 0.0 | 22 | 6.0% |
| -86 lbs. N. and superphosphate | 3.93 | 0.0 | 17 | 1.0% |
| -129 lbs. N. & complete minerals | 3.79 | 0.0 | 43 | 1.0% |

| Nitrate of Soda Group. | | | | |
| -43 lbs. N. | 6.30 | 0.4 | 23 | 34% |
| -43 lbs. N. & complete minerals | 5.94 | 1.2 | 40 | 1% |

| Group with Manurial Changes. | | | | |
| Complete minerals after nitrate of soda (-86 lbs. N.) 1858-75. | 5.54 | 5.4 | - | 7.0% |
| Complete minerals after ammon. salts (-86 lbs. N.) 1866-68 | 5.31 | 11.3 | - | 35.0% |
| Unmanured, after ammon. salts (-86 lbs. N.) 1856-97 | 4.82 | 0.4 | - | 17.0% |

| Plots which have received Lime. | | | | |
| L (for Manurial Treatment see 'Amm. Group') | 4.83 | 0.0 | 26 | 10.0% |
| 10 L (for Manurial Treatment see 'Amm. Group') | 4.71 | 0.0 | 34 | 10.0% |
| 7 L (for Manurial Treatment see 'No Nitrogen Group') | 6.68 | 19.6 | 32 | 85.0% |
| 5 L (for Manurial Treatment see 'Group with Manurial Changes') | 6.13 | - | - | 100.0% |

@) The complete mineral manure consists of 3½ cwt. Super; 500 lbs. S/POT; 100 lbs. S/SODA; 100 lbs. S/MAG (all per acre).

@) The maximum number of Smyththurus was obtained in Plot 15 L, the actual number per 50 strokes of the net being 240.
As previously explained, the numerous variables usually involved in field data have been largely eliminated in this instance, so that we are only concerned with the effect of the different manurial treatments upon the Smynthurus population brought about through their differential effects upon

(1) the soil reaction;
(2) the yield, and
(3) composition of the herbage.

It is therefore necessary to consider separately, each of these factors in their relationship to the Smynthurus population.

(2) Relation between the Smynthurus Population and the Soil Reaction (p.H. value).

This has been presented graphically by means of a dot diagram (No. 1), which is a valuable method of rendering visible at a glance, the range and associations of our observations, especially if the latter are not very numerous. The plots at Rothamsted are nearly all on the acid side of p.H. 6.2, so that, in order to complete the observations, a composite diagram has been constructed by utilising data obtained from the South of France, where the soils examined were all fairly alkaline. It has therefore been possible to obtain a range of observations
Dot Diagram No. 1.

- Data from Rothamsted.
- Data from South of France.

Population of Smythurus.

Soil p.H. Value.

extending from 3.8 to 7.9 on the p.H. scale, and since the majority of soil types have a p.H. value somewhere within these limits, the diagram is a fairly inclusive one.

It will be observed that:

(i) There is a short but distinct optimum p.H. range, extending approximately from p.H. 6.1 to 6.3, and it is interesting to note in this connection that the optimum both at Rothamsted and in the South of France falls within this range, and, as previously pointed out, the soil p.H. value regarded as the optimum from laboratory experiments was considered to be slightly on the acid side of 6.5.

(ii) Any departure from this optimum range, either on the acid or the alkaline side, produces a marked decrease in the Smyththurus population, the decrease being slightly more rapid on the alkaline side. Soil p.H. values outside the range 4.5 - 7.5 are very unfavourable to Smyththurus, although by no means inhibitive.

(iii) There are a few exceptions to an otherwise reasonably close correlation and these are enclosed by the broken line. Five observations are here included, being plots 2, 3, 15, 16, 17; the first two are unmanured plots, and the remainder are all plots which have
received nitrate of soda. In all five plots the Smynthurus population is lower than one might expect from the soil p.H. value, but it would appear that different causes are operating, in the first two and last three plots respectively, to bring about a similar effect. It seems that in both of plots 2 and 3 the low Smynthurus population follows from a remarkably low yield of herbage, so that the soil surface is exposed to the direct rays of the sun, marked fluctuations in temperature obtaining, with consequent adverse effect upon Smynthurus in all stages. On the other hand, in plots 15, 16, and 17, the nitrate of soda has produced a type of herbage, both as regards composition and bulk, which acts as a "blanket" as far as temperature is concerned, but which results in rapid and extensive loss of soil moisture, it being a well known fact that land under heavy crop tends to "dry out" much more rapidly than land sparsely covered or under bare fallow. It also affords greater cover for predators. The end result is that in these exceptions we have failed to eliminate the climatic variable, due to the differential effect of the manures upon the type of herbage, and the microclimate (especially during the hottest months) is very different
received nitrate of soda. In all five plots the Smynthurus population is lower than one might expect from the soil p.H. value, but it would appear that different causes are operating, in the first two and last three plots respectively, to bring about a similar effect. It seems that in both of plots 2 and 3 the low Smynthurus population follows from a remarkably low yield of herbage, so that the soil surface is exposed to the direct rays of the sun, marked fluctuations in temperature obtaining, with consequent adverse effect upon Smynthurus in all stages. On the other hand, in plots 15, 16, and 17, the nitrate of soda has produced a type of herbage, both as regards composition and bulk, which acts as a "blanket" as far as temperature is concerned, but which results in rapid and extensive loss of soil moisture, it being a well known fact that land under heavy crop tends to "dry out" much more rapidly than land sparsely covered or under bare fallow. It also affords greater cover for predators. The end result is that in these exceptions we have failed to eliminate the climatic variable, due to the differential effect of the manures upon the type of herbage, and the microclimate (especially during the hottest months) is very different
in these instances.

(iv) The subject under consideration in the last paragraph illustrates clearly the "master effect" of climate, so that the effect of soil p.H. value is always dominated by climatic effects. Hence the greater the departure from the climatic optimum the less significant does the effect of soil reaction become, while the nearer the climatic factors of the environment approach to the optimum, the greater the significance of differences in soil reaction. In the laboratory experiments, where temperature and humidity conditions were almost at the optimum for Smynthurus, the effect of soil reaction obtained for growth and reproduction probably represents the maximum for this effect.

(3) Relation between the Smynthurus Population and the Yield of Herbage.

(i) This is presented graphically in dot diagram No. 2. It will be observed that there is evidence of a negative correlation between the yield of herbage and the Smynthurus population. This is not due to any relation between soil p.H. value and bulk of herbage, or between yield of hay and percentage Leguminosae, as one might be inclined to suspect, there being no correlation, positive or negative,
between these variables, in this instance, and the writer can only explain this correlation as due to the introduction of another variable, namely, the climatic factor. The increased amount of herbage results in more rapid and extensive "drying out" of the soil, while there is also the possibility of the denser herbage affording greater cover for predators and thereby introducing still another variable.

(ii) Plot 7 L forms a marked exception to this general correlation, and consequently calls for some comment. If we compare this plot with another which has a similar yield and does conform to the above relationship, we can probably arrive at an explanation for the discrepancy. For this purpose we may take plot 10 L. On examining the botanical composition of these two plots we find that there are very great differences; e.g., in plot 10 L. the herbage is of a very "open" nature, consisting of Meadow Foxtail (Allopecurus pratensis) to the extent of 76.8 per cent, False Oat Grass (Arrhenatherum avenaceum) 8.1 per cent, and only one species outside Graminaceae, namely Rumex acetosa, .4 per cent, Leguminosae being unrepresented. The remainder is made up of a few grass species, of which Poa pratensis and Festuca ovina contribute 11.2 per cent. On the other hand the herbage on plot 7 L is of a much "closer"
type, the predominant species being Field Vetch
\textit{(Lathyrus pratensis)} which is present to the extent of 19.5 per cent of the herbage. The predominant grasses are Cocksfoot \textit{(Dactylis glomerata)} 18.6 per cent, and Meadow Foxtail \textit{(Alopecurus pratensis)} 15.2 per cent, with a variety of other grasses, and miscellaneous species other than grasses, in lesser amount, thus presenting a herbage type characterised by the presence of thick bottom grasses completely covering the soil surface. Hence the effects of meteorological factors are modified to a different degree in the two instances, and are apparently responsible for the difference in the population; on the other hand it might be argued that the larger Smyntthurus population in plot 7 L is simply due to an increased food supply as represented by \textit{Lathyrus pratensis}, but the writer does not consider this to hold in fact, since Smyntthurus is by no means entirely dependent upon Legumes as a source of food, being able to utilise a large variety of other plants, including Mosses and Algae, for this purpose.

(4) Relation between the Smyntthurus Population and the \textbf{Leguminosae} in the Herbage.

As regards the food supply of Smyntthurus the family \textbf{Leguminosae} is undoubtedly the most important, hence it
is interesting to see if there is any relation between the Smynthurus population and the food supply, or whether the latter is never a really significant factor as far as its effect upon population increase is concerned. It will be observed from an inspection of dot diagram No. 3, that there is a fairly good positive correlation between the percentage of Leguminosae in the herbage and the Smynthurus population, but the relationship is not a very close one, and would appear to be due to the fact that there exists some relation between the percentage of Legumes and the soil reaction. This latter relationship is, however, not a simple one, different species coming in, and others dropping out, at different points on the p.H. Scale, while as an additional complicating factor there is the suppression of certain Legumes, brought about as the result of intense competition with other species especially favoured by a particular soil reaction. It seems, therefore, that food supply seldom acts as a 'limiting factor' to the increase of Smynthurus in a natural environment, except in certain abnormal and peculiar instances, where the other factors in the environment are operating at, or near, their optimum for the species, and the struggle for existence then becomes largely a struggle for food.
(5) **Influence of Biotic Factors upon the Smynthurus Population.**

The only definite result concerning the effect of predators on the Smynthurus population in nature, which could be ascertained from an analysis of the field data obtained in the neighbourhood of the laboratory, was to the effect that when the Smynthurus population was high the predator population also tended to be high, and that at no time was there any significant deviation from what one might expect as the result of a good correlation between the Smynthurus population and the physical environmental factors already described. In order to obtain corroborative evidence for this result, which might not be of universal application, a number of Lucerne sweepings from the South of France were subjected to a rough quantitative analysis, separating out and counting the chief recurring insects and arachnids. The main conclusions are as follows, and these serve to reinforce from a different aspect, the principal results already derived from the ecological studies on Smynthurus in the South of England.

There is no evidence of a correlation, either positive or negative, between the Smynthurus population and the total number of other insects or any single family of insects, but there are indications of a fairly
Dot Diagram No. 4.

Smynthurus Population

Spider Population.
good positive correlation between the Smynthurus population and the Spider population. The data (q.v. Table XV) has been depicted graphically by means of a dot diagram (No. 4)

**TABLE XV.**

<table>
<thead>
<tr>
<th>Date from South of France to Show Relationship between Soil p.H. Value, Spider Population, and Population of Smynthurus.</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Smyn. Pop. (1%)</strong></td>
</tr>
<tr>
<td><strong>Soil p.H. Value</strong></td>
</tr>
<tr>
<td><strong>Spider Pop. (1%)</strong></td>
</tr>
<tr>
<td><strong>Smyn. Pop. (1%)</strong></td>
</tr>
</tbody>
</table>

The diagram indicates, that with some exceptions, there is a reasonably good positive correlation between the Smynthurus and Spider populations. This may be interpreted in two ways: either that a similar type of habitat is favourable to both insect and arachnid, or the spiders are attracted to the Smynthuri as a source of food, but are unable to bring about a significant
depletion of their numbers. While the former explanation is to a certain extent true, the latter appears to be the important point and the correct interpretation. In samples No. 3 and 4 the soil was strongly alkaline, thus accounting for the relatively small number of Smynthuri in proportion to the number of spiders present, which were evidently finding some other satisfactory source of food. On the other hand, in samples Nos. 6 and 8, the soil conditions were peculiarly favourable to Smynthurus. Incidentally, it seems worth while mentioning the fact that where Smynthurus was very abundant it was found that Phytonomus larvae (the pest of Lucerne known in America as the 'Alfalfa Weevil') were also present in large numbers.

From general observations in the Smynthurus insectary, and elsewhere, it occurred to the writer that another biotic factor of control, under certain circumstances, was the eating of the eggs (since the latter are scattered about on the soil surface) by animals whose mode of feeding consists of scavenging along the surface of the soil amongst the layer of decaying vegetable matter and organic débris, which tend to accumulate there. This suggestion was supported by the fact that Smynthurus
failed to become abundant in the greenhouse, although humidity conditions were very favourable, and though the temperature was somewhat high it did not nearly approach the limits of temperature tolerance by the insect. Examination of the soil surface in the clover plots revealed numerous small Dipterous larvae of the genus Sciara (Mycetophilidae), and Arthropleon Collembola belonging to the genus Isotoma. By feeding Smynthurus eggs to both these forms, it has been found that they devour the eggs readily. Now it has been shown, as a result of comparatively recent quantitative studies on the fauna of the soil, by workers in Britain, Denmark and Japan, that the Arthropleon group of Collembola are amongst the most abundant (and often by far the most abundant) of the macro-inhabitants of the soil. However, both Sciara and Isotoma contain species which are peculiarly sensitive to low humidity conditions, and are consequently inhabitants of damp, moist situations. Experimental studies by Davies on the sensitivity of Collembola to various relative humidities have shown that the Arthropleon forms are less tolerant of low humidities than the Symphypleon group, and that of all the species investigated Isotoma viridis was the most intolerant. The writer has ample reason to confirm
this, so that although these saprophagous Collembola must undoubtedly exert a considerable controlling influence, in virtue of their numbers, when climatic conditions are favourable, their action period is extremely limited in Nature, on account of their incapacity to withstand relatively slight dessication, whence they are forced to avoid the soil surface and retreat to the cooler and moister conditions obtaining in the superficial layers of the soil.

When put to quantitative trial, the scavenging capacity of these saprophagous Collembola was astounding, organic débris being 'cleaned up' with extraordinary rapidity, and leaving nothing but the bare soil and living roots of the herbage. The scavenging action of soil Collembola is undoubtedly one of the important factors in the transformation of organic matter in soil; and has been overlooked or attributed to other agencies. Their rôle in the formation of soil would appear to rank next in importance to the classical rôle of the earthworm, first propounded by Darwin.

Still another biotic factor of control, is the attack of the eggs by fungi, which, however, is of very little significance, and only comes into operation under
peculiar and exceptional circumstances, in which highly favourable conditions of temperature and moisture for these lowly organisms are involved. No entomophagous parasites of Smyntthrus having been discovered, these are easily disposed of.

(6) **Relative Significance of Factors in the Controlling Complex in the South of England.**

Having discussed in some detail all the major factors, both biotic and physical, which contribute towards checking the potential increase of the Smyntthrus population in Nature, we have now reached a stage when we may briefly recapitulate the evidence, present a variety of facts as an ordered and comprehensive unity, and so visualize a general scheme of events, taking place in time and space, to produce a pattern of nature characterised by the delicious harmonisation of materials, striking in its complexity, and woven with infinite subtlety. The main features of this pattern, in which we may regard the factors and phases as the warp and woof, respectively, are presented below in their order of decreasing significance. (These obtain for the second period in the seasonal cycle of events, temperature being, as already explained, the major controlling factor during the first
period from October to May (approx.), on account of its inhibiting effect upon the growth of nymphs and development of the eggs. —

(i) Effect of rainfall upon oviposition.

(ii) Effect of rainfall upon development and emergence of nymphs from the egg.

(iii) Effect of temperature upon development and emergence of nymphs from the egg.

(iv) Effect of temperature upon survival of the early instar nymphs.

(v) Effect of temperature upon reproduction.

(vi) Effect of physical and chemical conditions of the soil type upon reproduction.

(vii) Effect of predators upon nymphs and adults.

An interesting phenomenon in regard to the above factors of control is that all the major ones are associated with reproduction or the embryonic stages. This is not altogether unexpected, in view of the fact that characteristics associated with reproduction are usually the last to succumb to evolutionary change, are least adaptable, and, therefore, most susceptible to adverse environmental agencies; whereas with increasing departure from the reproductive phases we encounter stages which become progressively more adapted to withstand 'the bludgeonings of chance', and consequently, have a lower mortality. Further, we have here an interesting
actual example of natural control by a number of 'independent' factors operating in a sequence, and it has been mathematically demonstrated by Dr. W.R. Thompson that in a controlling complex of this type the ultimate effect of the disappearance of factors is a minimum, those which disappear being largely replaced, automatically, by the succeeding factors. This means that a natural controlling complex of the type here involved is comparatively stabilized or 'buffered', if one may borrow a more apt term from chemistry, and that the amplitude of the environmental fluctuations has to be very considerable before any appreciable change is produced in the size of the population. However, it cannot be too strongly emphasized that relatively large environmental fluctuations do occur in Nature and that the stability above indicated, is merely relative to that produced by other types of natural controlling complexes. That is to say, although the system is to some extent self-regulating, the mechanism is far from perfect, and can be readily thrown out of gear if the more sensitive elements in the structure are interfered with, namely, the factors affecting reproduction and the early stages.

Such is the natural controlling complex of
**Smynthurus viridis** Lin., in the South of England. It must be emphasized, however, that although the end result tends towards a mean on account of the composition (type of factors) and mechanism (mode of operation of factors) of the complex, the relative significance of the respective factors is continually varying in time and space, and even in one small area the relative significance of the less important factors may be occasionally reversed. What we mean, therefore, by placing a series of natural controlling factors in order of significance is, that at a particular place the control is of that type, at a particular time, or on the average. Now the writer is somewhat sceptical of the employment of averages in biology, because they are often mere fictions which lead to false assumptions, no matter how satisfying they may be to the aesthetic appeals of the investigator who delights in the production of 'smooth curves'. Nevertheless, they are sometimes very useful for practical purposes, and it is to this end we must now proceed to utilise them, as exemplified in a bioclimatic study of the insect.

**B. BIOCLIMATIC STUDY OF SMYNTHURUS.**

(1) **Prediction of Complete Geographical Range of Existence.**

The practical utility of all scientific efforts which involve considerable expenditure of time and energy is
dependent, to a large extent upon the general applicability of the results. Since the climatological study of Smynthurus, about to be described, involves the prediction of the geographical range of the insect, it may be asked by critical and cautious observers, to what extent is such bold generalisation scientifically legitimate? An important part therefore, of this aspect of the ecology of Smynthurus, will be the justification for the various steps, and, as far as possible, confirmation of the results. Apart from all consideration of economic significance which may accrue from carefully conducted climatological studies, the one about to be considered is of particular interest from an academic standpoint, because it is based not only upon data obtained under natural conditions, but upon critically planned laboratory experiments bearing upon the 'field physiology' of the insect, so that the degree of confirmation of the actual with the theoretical distribution of the insect, acts as a good check-up on the accuracy of the many observations and conclusions made up till now.

Prior to the commencement of this bioclimatic study of Smynthurus, few satisfactory efforts of this type, in relation to animal abundance and distribution, had been attempted, being based on information of a somewhat empirical nature. For example, contrasting the climate
of "controlled" and "outbreak" areas by means of the shape and position of their respective climographs or hythergraphs, often with little or no exact quantitative evidence of climatic effects upon the various phases of the life-cycle, to reinforce results obtained from a method with an essentially empirical basis. Further, while the climograph method is very useful for comparing or contrasting particular climates in connection with insects or other animals, whose life-history extends over the whole year (and hence the deviations of any one of the twelve points may be of significance) the utility of this method is greatly diminished with a species which may have as many as five generations in six months. By far the best work of this type, of which the writer is aware, is that of Cook (9) on the Pale Western Outworm (Porosagrotis orthogonia), although very valuable work, of a more general nature, has been conducted by Bodenheimer (9) in connection with several insect species.

The bioclimatic study of Smynthurus was conducted, primarily, with a view to determining, if possible, the following three relations -

(i) the various parts of the world in which Smynthurus could exist;

(ii) the localities in which Smynthurus, if present,
would be likely to cause damage of economic significance every year, at some period of the year;

(iii) those parts of the world in which Smynthurus would not usually be of economic importance, but might become so occasionally, namely whenever the climate of the particular locality deviated from the normal, or average, in a direction favourable to the "flea".

Having already determined the natural factors of control in the South of England, together with numerous observations on the effect of rainfall, temperature, and soil type, almost covering the total range of effective action of those factors, as far as their influence upon Smynthurus is concerned, the task of elucidating the three relations above indicated was greatly facilitated thereby. The latter information is, of course, essential for the accomplishment of the task in hand.

Altogether, three sets of data have been utilised, namely,

(i) the results derived from the field data in England;

(ii) the results derived from controlled experimentation in the laboratory; and

(iii) the information available from meteorological records together with a knowledge of the approximate distribution of the pest in Western Australia.
The first step was to determine the limits of heat and moisture under which Smynthurus could exist, and then translate these limits into convenient meteorological terms of temperature and rainfall. After investigation into the available meteorological records throughout the world it was decided to utilise the mean monthly temperature and the total monthly rainfall, more detailed information, such as weekly means and records of humidity, being not always obtainable. Now from what has been said in connection with the natural factors of control, it will be evident that the minimum rainfall under which oviposition can take place. This has been determined as 0.12 inches per month. By referring to Graph XV (a), however, in which the rainfall is represented as the total per fourteen-day interval, it will be observed that 0.6 inches of rainfall would allow the existence of a very small population, but at tropical and sub-tropical temperatures the effective action of this small rainfall would be very greatly reduced on account of the increased saturation capacity of the air. Since it is only being attempted to represent conditions on the average, the selection of 0.12 inches of rainfall per month as the minimum rainfall for existence of Smynthurus seems justified. The
other rainfall limit is ultimately continual submergence, but adverse secondary effects, due to fungal and bacterial attacks on the eggs and young nymphs, come into operation before this stage is reached, making the upper rainfall limit approximately 7.0 inches.

In regard to temperature, the maximum for the species is the maximum which can be tolerated by the stage least tolerant of high temperatures, and those are the embryonic nymphs, which cannot survive mean temperatures exceeding 66.0°F. The other temperature extreme is determined by the stage whose activity ceases first when the temperature is lowered, namely, the developing egg. In this connection, it will be recalled that the egg of Smythurus continues developing at a perceptible rate, down to 5.0°C. However, since mean monthly temperatures have been utilised, the lower temperature limit has been determined as 6.6°C or 44°F, development below this temperature being so slow as to require several years for completion, even assuming that the very low temperatures experienced during the colder months, where such conditions obtain, are harmless. The northern and southern geographical limits of existence of the insect are, therefore, determined by a line drawn through these points on the surface of the Earth whose mean temperature, for the warmest month of the year, does not
exceed 44°R. Rainfall never acts as a 'limiting' factor in such areas. On the other hand, the southern and northern limits of existence in the northern and southern Hemispheres, respectively, are determined, sometimes by rainfall and sometimes by temperature, depending on whether the particular place has a mean monthly temperature exceeding 66°F. or a total monthly rainfall of less than 0.12 inches. In either instance the continued existence of Smynthurus is impossible, irrespective of the favourability of all other factors.

Once the necessary meteorological data had been obtained, the geographical limits of existence of the insect were thus relatively easy to determine, and have been charted in the outline map of the World presented herewith. The stippled areas indicate the regions of the World in which continued existence of Smynthurus is, theoretically at least, impossible, and it remains for others to prove by the discovery of the Collembolan living permanently in those areas that the writer's prediction is incorrect. There may be certain favourable areas in the semitropical parts of the world which support a meagre population in exceptionally favourable years, by influx from surrounding areas, but they have been excluded
from the map, since the latter is intended to represent conditions which obtain on the average. In this connection, it must be emphasized that the limits of existence are by no means immutable, but oscillate about the mean limits indicated on the map on account of continually fluctuating environmental factors. The large double circles, within the stippled regions, in Peru, Southern India, and Ceylon, indicate isolated areas which are climatically favourable to the "flea" on account of high altitude, and there may be similar isolated areas in the highlands of Abyssinia and Kenya, but meteorological records were not available.

(2) Prediction of Areas of Economic Significance (Permanent and Occasional).

The next step in this bioclimatic study of Smynthurus was to determine the optimum conditions for existence of the insect. This is not so easy, since at best it is essentially a compromise between a variety of conflicting physiological requirements on the part of the organism concerned for reasons already discussed in Part II of this paper, and hence the optimum natural environment is that which presents the most effective compromise to those conflicting requirements. The initial procedure consisted in determining what the writer has called the "critical points", these being the amount of rainfall and degree of
temperature, respectively, any departure from which (in an upward direction for rainfall, and downward for temperature) did not evoke any further appreciable response on the part of the organism, as indicated by an increase in population, but from which a deviation in the opposite direction resulted in a profound reduction of the population. Since the typical response of organisms to successive increments of a particular factor (in so far as its effect upon population increase is concerned) assumes the form of a sigmoid curve, it will be understood that the "critical point" is located at the crest of the curve beyond the mid-point of flexion.

By referring to Graph XV (a) in which the effect of factorial increment upon population increase is well illustrated, it will be observed that the "critical point" on the rainfall curve is 1.55 inches per 14-day interval. As regards temperature, the "critical point" is 57°F.

Having thus ascertained the critical rainfall and temperature, respectively, it is relatively easy to fix the limits of these two environmental factors, such that Smynthurus may be expected to increase very rapidly and maintain a high population. The other rainfall limit would appear to be 5.5 inches per month, when adverse secondary factors come into operation; while the other temperature limit is 52°F, due to the rapid slowing up
of the growth rate at temperatures below this point, with consequent delay in the arrival of sexual maturity, one of the most important factors for the maintenance of a high population level in Nature. The reason for locating the "critical points" on the crest of the sigmoid curve beyond the mid-point of flexion, and not where the curve reaches the asymptote, is that the latter would represent the theoretical maximum of the factor, which seldom exists under natural conditions; and further, their relation to the organic response of the insect is such that when these conditions obtain, Smynthurus is very favourably conditioned for the production and maintenance of a high population. Hence we are now in a position to state that from our knowledge of the dominating rôle of rainfall and temperature in the natural control of the insect in Europe, the Smynthurus population will attain to almost its maximum natural level, in those areas of the World where there is a rainfall of 3.1 - 5.5 inches per month, together with a mean monthly temperature ranging between 52.0° and 57.0°F, provided there does not exist a significant biotic factor of control which is not present in the insect's original home. Further, from considerations relative to the economic status of the "flea" in Europe and Western Australia, the damage it causes to Lucerne and Clovers
will be of economic significance, whenever and wherever such conditions of temperature and rainfall obtain for two consecutive months. The non-conformance of the environment to any one of these climatic requirements offsets the favourability of the other, and thereby renders impossible the attainment of a population density sufficient to bring about damage of economic importance.

One further point concerning the climatology of Smynthurus remains to be considered, namely, the determination of those parts of the world in which the "flea" is not normally of economic significance, but may become so whenever the climate deviates from the mean in a direction favourable to the insect. This involves warmer conditions for those areas in which the normal mean monthly temperature is lower than 52°F., cooler conditions for those areas in which it is higher than 57°F., and a heavier rainfall for those areas in which the monthly total is normally less than 3.1 inches. To determine such areas, with mathematical accuracy, would involve fairly advanced statistical treatment together with the compounding of probabilities, and it is not intended to pursue this avenue of approach meantime. All that is intended, for the present, is to indicate the areas in which Smynthurus may become of economic
significance occasionally, irrespective of the actual probability of occurrence. In general, such areas are characterised by a total monthly rainfall of not less than 2.5 inches, combined with a mean monthly temperature within the range 51°-58°F., exclusive of those areas which conformed to both the temperature and rainfall requirements of the 'optimum' environment. As in the latter instance, the climatic conditions indicated must obtain for two consecutive months.

The areas of occasional economic significance (relative to the damage done to clovers and lucerne) have been represented in the outline map of the world by means of a solid circle, whereas the areas in which the pest is normally of economic significance (i.e., almost every year) have been represented by means of a double circle. It will be observed from the map that the circles are grouped with a fair degree of precision into three main regions, namely,

(a) the western, southern, and eastern portions of Australia and the whole of New Zealand;

(b) the northern and southern parts of Argentine and Uruguay, respectively, and the coastal regions of Chile;

(c) the countries immediately surrounding the
Mediterranean Sea and the north-western parts of the British Isles. However, Smynthurus does not flourish abundantly in all these favourable areas at the same time or even the same season, of the year, being found in greatest numbers in Western Australia, for example, from May to August; in countries bordering the Mediterranean, from February to April; and in Britain during June and late August, the intervening period being too hot and dry. Thus Smynthurus finds conditions most favourable in Australia during the winter season, during spring in the regions bordering the Mediterranean, and during summer and early autumn in Britain.

In order to demonstrate that the theoretically possible distribution in no way conflicts with the actual distribution, so far as known from all available records, and also that there are several highly favourable areas, climatically at least, to which Smynthurus has not yet penetrated, a list of the meteorological stations recorded in the outline map of the world, together with the known distribution of the insect, by countries, has been prepared and presented in Table XVI.
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From the latter it is evident that there are several countries to which Smynthurus is potentially a serious economic menace, the most important being New Zealand, the south-west corner of Cape Province, Natal, Chile, New South Wales, and the United States of America, (northern California, South Carolina, southern Alabama, and Georgia). The question of soil type has not been taken into consideration in the prediction of the favourable areas for Smynthurus, because on the average (the conditions for which the theoretical distribution map has been constructed) the controlling effect of soil type is of very minor significance in comparison with climate. However, in certain instances where the hydrogen ion concentration lies outside the range 5.5 to 7.0 on the p.H. scale or the soil is of a remarkably porous nature, then our predictions as to the probable abundance of the insect, cannot be expected and are not intended to hold good. Under such circumstances, or if it is intended to predict the average abundance of Smynthurus in a relatively small area, soil type enters as an additional complicating factor which must receive due consideration in our calculations. Hence until the soil chemists have prepared accurate survey maps, the prediction of the geographical distribution and abundance
of many terrestrial arthropods will be seriously handicapped.

(3) **Known Distribution and Areas of Possible Colonisation in Australia.**

As the economic significance of *Smynthurus*, at the present time, is of greatest moment in Australia, it has been attempted to portray the distribution of the insect in that part of the World with somewhat greater detail than was done for the World as a whole. The accompanying map illustrates, by means of stippling, the known distribution of the "flea" in Australia and Tasmania, while the broken line indicates the approximate limits of economic significance, and the solid line, the limits of existence.

The distribution in South Australia is taken from Dr. Holdaway's paper, and for the approximate distribution in Western Australia the writer is indebted to Mr. L.J. Newman (Chief Entomologist for W. Australia). For the accuracy or inaccuracy of the areas delimited by the broken and the solid lines the writer is entirely responsible.

It will be observed that in South Australia, from which the "flea" was first reported in that continent, *Smynthurus* has spread beyond the limits of economic significance, whereas in Western Australia it has not yet reached these limits. In neither instance has the insect attained to the limits of existence, although it is much nearer to them.
In South than Western Australia, and consequently the rate of dispersal inwards will be much more rapid in the latter than the former. The map also indicates that there is a large tract of country in New South Wales and southern Victoria, from which the "flea" has not yet been recorded, but to which, (in the event of its introduction), it would undoubtedly prove to be a serious economic problem. Also, there exists a fairly large band of territory in the North and Western parts of Tasmania which is highly favourable for the production and maintenance of a large Smynthurus population, although the insect has been introduced into the island only within the last few years, and therefore has not yet had time to demonstrate its full potentialities as regards numerical increase.

(4) **Areas of Economic Significance in Great Britain and Ireland (detailed).**

On account of the greater number of meteorological stations in the British Isles, it has been possible to map out the areas which are favourable to Smynthurus in much greater detail than was done for the World as a whole. When we come to consider the climate of the British Isles in some detail, we find that there are very considerable differences in different areas. To
illustrate this, four hythergraphs have been constructed (Diagram B) each point of which represents the total monthly rainfall (abscissa) and mean monthly temperature (ordinate), the number of the month being indicated by a Roman numeral. The four 'Meteorological Divisions' selected to illustrate the different climatic types encountered in the British Isles are

(i) Scotland,
(ii) Ireland N., with six stations;
(iii) England N.W., with eight stations;
(iv) England E., with nine stations.

The rectangular area delimited on each hythergraph indicates a climatic type having a rainfall of not less than 2.5 ins. and not more than 7 ins. per month, together with a mean monthly temperature falling within the limits 51°-58° F. Any point of the hythergraph which falls within the stippled rectangle indicates, therefore, climatic conditions which are favourable (not equally favourable) to the Collembolan. It is quite apparent from the hythergraphs that as we proceed from Scotland N. to Ireland N., England N.W. and England E., we encounter climates types which become progressively hotter and drier during the five months of the year from May to September, and on that account the areas indicated become more and more unfavourable to the insect. The climatic conditions
AREAS IN BRITISH ISLES CLIMATICALLY FAVOURABLE TO SMYNTHERUS.
of those 'Meteorological Divisions', however, represent the average conditions obtaining over considerable areas, and for many purposes are quite sufficient, but if it be desired to define the areas favourable to Smynthurus with still greater accuracy, then it is essential to consider individual stations. The localities in which Smynthurus may be expected to cause damage of economic importance to clovers almost every year, have been indicated in the outline map of the British Isles by means of a double circle, and the localities in which the pest may cause serious damage to clovers occasionally, by means of a black dot.

Now it will be observed that by far the majority of the favourable localities lie north-west of a line drawn between Newcastle and Torquay, and that they are somewhat localised in their distribution, being confined for the most part to the coastal districts or river valleys. In some instances the favourable localities are so close to each other as to render possible a grouping into a favourable area, as shown by means of the stippling. The counties in Great Britain, from which Smynthurus has been recorded, have been outlined on the map, being as follows:— in Scotland - Elgin, Fife, West Lothian, Mid Lothian, East Lothian, Perthshire, Forfarshire, Lanarkshire, Ayrshire;
in England - Yorkshire, Cheshire, Derbyshire, Hertfordshire, Nottinghamshire, Buckingham, Kent, Devon, Cornwall, Isle of Wight; In Wales - Flint, Carnarvon, Cardigan. There is reason to believe, however, that the insect exists at present, to a greater or lesser extent, throughout the British Isles.

An interesting feature in regard to the geographical distribution of the favourable areas in Britain is that they coincide to a remarkable degree with the areas of incidence of a disease of horses, known as "grass-disease", which causes serious loss to horse-owners every summer, particularly in Scotland and the North of England. The seasonal incidence of the disease also shows a marked correlation with the seasonal abundance of Smynththurus. Whether the insect will be eventually incriminated as the direct cause, or the "carrier" of the disease producing agent, remains to be seen, but it at least points to the economic possibilities of bio-climatic studies. Prof. Russell Greig, Director of the Animal Diseases Research Association, has shown great interest in the theory propounded by the writer as to the relation between the insect and the disease, and extensive researches are to be prosecuted this summer with a view to testing out the writer's suggestions.

The great value of a bioclimatic study, such as the one just presented, lies in the fact that it renders
possible, the prediction of animal abundance and distribution, both seasonal and geographical. For some unknown reason, properly conducted scientific studies of this type have been comparatively neglected. Within the last few years, however, the subject has been receiving increasing attention, and the writer is convinced that, as a field of scientific endeavour, bioclimatics offer results of great promise from the viewpoints of both economic and purely academic research; and further, that in future the results of such studies will be one of the most important tools employed by the economic biologist, particularly those engaged in combating the ubiquitous insect.

III. APPLIED CONTROL AND REMEDIAL MEASURES.

A. APPLIED BIOLOGICAL CONTROL.

(1) Utilisation of Insect Predators.

Having now discussed in considerable detail the life history and bionomics of Smynthurus, together with the influence of environmental factors, biotic and physical, upon the seasonal and geographical abundance of the insect, all that remains in order to bring this sequence of discussion to its logical conclusion is a consideration of the applied controls and remedial measures which may be adopted in any attempts to maintain the population of the insect.
below the level of economic significance. This immediately recalls to our attention the question of economic utilisation of the predators listed and discussed in Part II of this paper.

It will be recalled that a list of predators was drawn up, in order of efficiency, based entirely on laboratory feeding tests. This, of course, (as then stated) was of little value as an aid to the final choice of predators with a view to their utilisation as biological agents of control, because it left out of consideration such factors as density of predator population, seasonal abundance, ecological relationship between prey and predator, and the feasibility of collecting or rearing an adequate number of them. However, since each species was briefly analysed from an ecological viewpoint in Part II, and the action en masse of the insect and arachnid predators has been discussed in Part III, we are now in a position to make a dispassionate analysis of the feasibility of biological control as regards this species, bearing in mind always that such attempts are intended to be economically justifiable, and not merely interesting biological experiments. This immediately rules out of consideration all but those bracketed as 'Good Predators', and even this list must be
subjected to some culling.

Number one on the list, namely, Forficula auricularia, is obviously out of the question as a possible biological agent of control, since it has proved itself a serious pest on introduction into countries outside Europe, particularly in the Pacific North-West of America and in New Zealand. The next species on the list, Paederus littoralis, Grav., is in almost every respect a suitable species for introduction to Australia, where Smynthurus is of greatest economic importance at the present time, as it is found in considerable abundance in Nature, is easy to maintain alive for long periods under laboratory conditions, and occupies a similar habitat to Smynthurus. The writer succeeded in obtaining eggs of this Staphylinid, which were oviposited in the laboratory, and from which larvae eventually emerged. However, another species belonging to the genus Paederus, namely, P. cingulatus, Macl., has been recorded as an enemy of Smynthurus viridiss in South Australia by Holdaway, so that the chances of the European species bringing about significant control where the native one is apparently unable to do so, are very small indeed. In fact Paederus littoralis, Grav., is in all probability already present in the Australian environment, although it has not been recorded, and in this connection
the writer takes the opportunity of stating that one of
the essential preliminaries to the introduction of biol¬
ogical agents of control is a survey of the main biotic
factors already present in the country of introduction,
before launching out on the large scale shipment of
parasites or predators.

The third species on the list is the common Ladybird
(C. septempunctata), well known as a devourer of Aphides
and with a wide geographical distribution, having been re¬
corded from almost every country in Europe, as well as
from North Africa, Siberia, and India. However, despite
great climatic adaptability together with a great
catholicity of taste (q.v., Part II) it is highly
questionable whether the introduction of this species to
Australia would have any significant effect on the
Smynthurus population, as the Collembolan is not its
primary source of food but apparently acts as a stop-gap
in times of Apide scarcity, or when the Smynthuri are un¬
usually abundant and thus more readily obtainable. Be¬
sides, it was evident from an analysis of the field data
that the effect of all Coccinellids on the Smynthurus
population in England and the South of France was
negligible, except under the above circumstances. We are
thus left with only two good insect predators as
possibilities for economic utilisation, these being
Lathrobium brunnipes, F., and Cyrtosus cyanipennis, Er.
A small preliminary introduction of both species to South and Western Australia would appear to be a rational, economically justifiable procedure, and for the following reasons. The former is a member of the same sub-family (Paederinae) and the same tribe (Paederini) as the two good predators of Smynthurus, Paederus cingulatus, Macl. and P. littoralis, Grav.; moreover, it prefers damp situations as Smynthurus does, and since it is found commonly throughout England in moss and vegetable debris, at the roots of grasses, etc., it could be collected without much difficulty in sufficient numbers for such a shipment. The Cantharid, Cyrtosus cyanipennis, Er. flourishes under the climatic conditions of the Mediterranean littoral, while similar climatic conditions obtain in Western Australia where Smynthurus causes such serious damage. Both species proved themselves to be voracious devourers of the Smynthuri, concerning the details of which the reader is referred to Part II.

(2) Utilisation of Arachnid Predators.

Coming to the spider predators it will be recalled that the field data indicated a closer correlation between the Smynthurus population and the Spider population than any other constituent of the biotic environment. Based
on laboratory feeding tests and ecological relationships, it was also shown that members of the families Thomisidae, or Crab-spiders, and Linyphiidae, or Dwarf-spiders, were amongst the most efficient Smynthurus predators. However, having examined, quantitatively, the rôle of Spiders in checking the Smynthurus population in Nature, we can now proceed further and state that, of all the natural biotic agents of control, Spiders appear to exert a greater effect on the Smynthurus population than any other group of Arthropods, or other biotic factor of control. Hence the possibility of their economic utilisation demands careful consideration.

The most important species, in this connection, are

(i) *Tibellus oblongus*, Wal.;
(ii) *Xysticus sp.* (cristatus ?);
(iii) *Philodromus sp.* (dispar ?);
(iv) *Lepthyphantes zimmermannii*, Bertk.;
(v) the two *Erigonid species, E. atra*
    and *E. dentipalpis*, and
(vi) *Pachygnatha degeeri*, Sund.

The chief points of interest concerning the above spiders, in so far as they have some bearing on the ecological relationships of Smynthurus, have already received attention in Part II, so that it will be unnecessary to
The first three species are all Thomisids and quite common throughout England; indeed the Crab-spiders were the most numerous of the Smynthurus predators taken in the field sweepings. Their collection in sufficient numbers for shipment would not present, therefore, a very serious problem, the months of greatest abundance being August, September, and October. As these species possess considerable climatic adaptability, being found over a wide range of territory, the question of survival in sufficient numbers to exert a controlling influence is of little moment, so far as their introduction to Western Australia is concerned. The Linyphiid species (iv and v) present greater difficulties in regard to prediction of their survival under the climatic conditions obtaining in Australia where Smynthurus causes such damage. Hull states that the family is the predominant one in temperate and arctic regions. "Even within the limits of Great Britain", he says, "The proportion of spiders belonging to the family Linyphiidae, increases as one proceeds northwards." Also, it is known that very few species have been recorded from the Australian continent, the reason for this being probably climatic, as the species are relatively small, and judging from laboratory observations, somewhat susceptible to low humidities. However, since they make up in numbers for what they lack in size, and they undoubtedly
exert some controlling influence on the Smynthurus population in Britain, a small preliminary shipment to determine their survival capacity in the Western Australian environment, would appear to be an economically justifiable procedure. The species mature in early summer and gradually disappear from the middle of May onwards, the tiny young appearing in numbers by September, and becoming very abundant in October and November. During these months, the collection of the above mentioned Linyphiid spiders, in adequate numbers for shipment, would be a relatively simple matter.

The idea of utilizing spiders in the applied biological control of insects may be regarded by some as being rather unorthodox, due in large measure to the generally prevailing exaggerated opinion concerning the rôle of entomophagous parasites in the control of natural populations. A word in support of the arachnids may, therefore, not be out of place. Regarding the part played by entomophagous parasites in Nature, several valuable papers by Dr. W.R. Thompson, published within the last few years, have done much to dispel many illusions attached thereto, and to place the subject of biological control in its proper perspective. In one of those, Dr. Thompson calls attention to the almost
universally underestimated value attached to insect predators, on account of their supposedly inferior specificity; and states that they "are at least relatively restricted in their choice of food, and since this is the most we can say of parasitic insects, of which many are extremely polyphagous, the average predator cannot on the score of specificity be considered as markedly inferior to the average parasite." The same argument as to specificity is invariably adduced against the employment of arachnid predators, and which the writer believes to be equally unjustified, in so far as it has any real significance in the control of population increase in Nature. Long before the present renewed impetus given to the study of natural agents of control, as the result of attempts to place applied biological control on a sound scientific basis, several famous naturalists had remarked on the voracity of many spiders, and their important rôle in the economy of Nature. In the introduction to his monograph on the "Spiders of Great Britain and Ireland", Blackwall says, "By contributing to check the too rapid multiplication of insects, from which they chiefly derive their sustenance, spiders perform an important part in the economy of nature." Again, the well known American arachnologist, McCook, in
his voluminous work on the "American Spiders and their Spinning Work", says, "The number of insects which a healthy spider is able to devour during a day, without apparent inconvenience, has often been a great surprise to me." Perhaps the best known arachnologist of all, the Rev. O. Pickard-Cambridge, in his introduction to the "Spiders of Dorset" goes so far as to state that, "The spider is doubtless Nature's chief check against the undue increase of insects. Despised Arachne is entitled by her services to occupy the chief place among invertebrate philanthropists." This seems to be overstating the case, but at least serves to draw attention to a group of Arthropods whose predatory activities appear to have been underestimated in recent researches (mostly by entomologists) into the decidedly intricate phenomena associated with natural control. In view of the numerous attempts being made at present to utilise biological agents of control in the struggle against insects, the elusive Arachne seems not unworthy of more serious consideration.

B. MECHANICAL AND CULTURAL METHODS OF CONTROL.

As the purpose of the present paper is to provide a rational scientific basis for the choice and putting into operation of control measures, rather than with the
actual measures themselves (other than biological), it is not intended to discuss in any detail the subjects indicated in this sub-heading. The details of such artificial controls vary to such an extent, depending upon the soil type, rotations adopted, local agricultural practices etc., that the writer believes such an attempt would be essentially futile, and should be left to the judgment of those immediately concerned with the supervision of control measures in their particular locality. However, there are certain obvious measures which immediately suggest themselves as a result of this scientific analysis of the situation, and which may serve as guides to those whose duty it is to elaborate the necessary details before putting such artificial controls into effective operation.

Since soil moisture plays an all-important part in the propagation of the species, anything which tends to reduce the moisture content of the surface layers of soil will help to minimise infestation by the "flea". This can, of course, be best obtained by "mulching" the top two inches of soil. Alternately harrowing and rolling the soil surface would not only help the production of a fine tilth, but would result in the crushing of many eggs, nymphs, and adults. The introduction of a bare fallow into the rotation, where this is not the
custom, would expedite the above measures, and render possible deep ploughing, with a view to burying all stages. In order to secure complete inversion of the furrow, a plough of the American type is the most desirable. Bare fallowing is also advantageous from the point of view of starving the insect, provided it is accompanied by the above mechanical measures, and all weeds are eliminated.

The application of lime to the soil to render it more alkaline has been suggested by Holdaway, and this would appear to be a feasible remedial measure where the cost is not too great. Once the p.H. value, or "lime requirement", had been determined, the economics of the situation may be gauged, but in any case the soil p.H. value should be raised to not less than 7.0, otherwise it is doubtful whether the increased control would repay the expense involved. The question of chemical control is outside the province of this paper and will therefore not be considered, except to state that from our knowledge of the effects of environmental factors upon the "flea", lime compounds have certain obvious advantages on account of their adverse alkalinity effect and capacity to absorb moisture.
Seasonal Variation of Population of Smythurus—Field C

Graph XVI

Developmental Zero (approx.)

Population of Smythurus

Mean Temperature

Altimetric Index

[Graph showing seasonal variation with months on the x-axis and population, temperature, and altimetric index on the y-axis.]
From general observations in England and Scotland it was apparent that man's disturbance of the natural environment in the husbandry of stock and crop had very different effects upon the Snyththurus population, sometimes rendering conditions more favourable and sometimes more adverse, depending upon the prevailing agricultural practice. Intensive grazing, for example, was found to exert a profound influence in lowering the level of the Snyththurus population, as will be seen from referring to Graph XVI. This field (namely, Field C) is adjacent to Field B, and is almost identical with the latter as regards texture, structure, and reaction of the soil type, insect and arachnid fauna, cultural treatment, etc., but differs from it in that cattle and horses are grazed therein for the greater part of the year. The population density is markedly less than in B. One is therefore forced to the conclusion that intensive grazing exerts a powerful check upon the increase in numbers of Snyththurus, by means of the trampling action of the stock in crushing eggs, nymphs, and adults, while many must be swallowed with the herbage. Heavy stocking of pastures with cattle and sheep should therefore be practised wherever the agricultural economics of the situation render this at
IV. GENERAL CONCLUSIONS OF ECONOMIC, ECOLOGICAL, AND EVOLUTIONARY SIGNIFICANCE.

As a result of this investigation, originally prompted by economic motives, there have been developed several conceptions of general biological and ecological significance from a purely scientific standpoint, apart from all considerations of economic value attached to the results. In the introduction it was stated that the intention throughout the paper was not simply accumulation of data but also interpretation of the latter, in so far as this was scientifically justifiable. This primary objective has been continually borne in mind. Moreover, throughout the course of the investigation the writer has stressed the fundamental principles involved and the logical method of procedure, with a view to placing the entire study on a sound scientific basis. In reading through many of the present day "research papers" such considerations are apparently regarded as superfluous, but are none the less necessary, especially in a young science like ecology, which has not even attained to adolescence, and consequently still requires much guidance if a normal
healthy adult is to be produced. On account of the complex nature of the investigation, its presentation has by no means been an easy task, but it is hoped that as far as possible each of the many components has been placed in proper perspective and that the variety of facts have been presented as a balanced and comprehensive unity.

(1) Economic Considerations.

As regards the economic aspect, a mass of evidence has been produced to show that the major factor, or combination of factors, responsible for the abnormally high Smythurus population in Western and South Australia are abnormally favourable conditions of rainfall and temperature - much more so than those obtaining in the original home of the insect - not only in regard to actual climatic conditions but also in that they prevail uninterruptedly for a longer period and thus allow the rate of increase to gather momentum. Since populations tend to increase in a geometrical progression wherever environmental conditions are favourable, it is evident that under such circumstances, a doubling of the rate of increase, or even one more generation, may make all the difference between a population density of no economic significance and one sufficient to produce a 'plague'.
The maximum density of the Smynthurus population was obtained on June 26th in Field B and since it was found by trial that the numbers obtained by the stroke method represent approximately 75 per cent of the actual population, it follows that the true number per stroke was 104, making a true density of almost 14 per square foot. The writer is unaware of the density obtaining in Australia, but judging from climatic considerations alone it must be considerably higher than in England, and a density of twice the above would certainly mean that Smynthurus assumed the economic status of a serious pest in this country, as far as damage to clover pastures is concerned.

The problem of controlling the pest by biological methods has been treated in considerable detail and serves to demonstrate that a dispassionate analysis of the facts relative to the environmental controlling complex is an essential preliminary to placing the biological method of control on a rational economic basis and to its furtherance as a logical, scientific procedure. This involves not merely a consideration of biotic factors of control but the whole complex of biotic and physical factors, since the latter have a profound influence on parasite, predator, and host, resulting in
a maze of often unsuspected inter-relationships. The physical environmental factors undoubtedly assume the major role in the natural control of insect populations, but this does not mean that the biotic factors are on that account negligible and can be immediately disposed of. On the contrary, the assessment of their true significance as natural agents of control is thereby rendered more difficult, and requires an investigator with a broad academic background and penetrative intelligence, if the true rôle of biotic factors in each particular instance is to be analysed, and the chances of success in their economic utilisation is to be gauged with a reasonable measure of certainty. Pending the analysis of the environmental complex, inexpensive tentative measures should, of course, be put into operation.

As regards artificial remedial measures (other than chemical), the investigation has shown that these must centre round a judicious manipulation of the micro-climate, with the object (in this instance) of thereby lowering the humidity and raising the temperature to an extent compatible with the prevailing type of agriculture; also, the nature of the pest renders feasible direct mechanical treatment with a view to crushing eggs, nymphs, and adults, the latter being arranged to fit in, as far as possible, with the routine cultural measures in the
husbandry of stock and crop, in order to minimise expense.

(2) Ecological Considerations.

Coming to the more direct ecological relationships, especially the bioclimatic aspect, the writer realises the danger of entering the realms of prophecy, but at the same time believes that the prediction of abundance, outbreaks, and distribution of insect populations is full of promise for the future, and will yet prove to be the most efficient weapon in the hands of the economic entomologist. To draw a parallel from medicine, a stage has been attained in the science in which it can be said that prophylactic measures are in every respect superior to therapeutic treatment. The rapidity of the advance in this direction will depend to some extent upon the meteorologist, but as the latter scientist has shown his willingness to co-operate with the biologist, and in view of the advances being made along the lines of long range weather forecasts, it seems reasonable to conclude that bioclimatics have every prospect of providing a fruitful field of scientific endeavour and should yield results of great interest and value in the near future.

The analysis of the environmental controlling complex of Smynthurus affords a good concrete illustration of how such complexes continually vary in their composition and
structure, both spatially and chronologically; the variation, although continuous, is by no means uniform, and the fluctuations, although often sudden, take place with some degree of regularity when viewed over a period of time, thereby rendering prediction of the organic response a statistically feasible proposition.

(3) **Evolutionary Considerations.**

Critically planned laboratory experiments bearing upon the 'field physiology' of the insect have served to demonstrate that the living organism is by no means the beautifully co-ordinated and harmonious physiological unit that it is so often represented to be. Doubtless, this fact is more pronounced in Smynthurus, on account of its lowly position in the evolutionary scale, than in many other more highly evolved organisms in which the various co-ordinating and regulating mechanisms are better developed, e.g. hormones are known to be deficient in the invertebrates. Nevertheless, although we may a priori expect to find a greater degree of harmony between the various physiological systems of the individual as we progress up the evolutionary scale, it seems that in many instances this diverse physiological ensemble sets a severe handicap upon environmental adaptation. Further, the deeper one delves into the quantitative study of
organism and environment the more critical one becomes concerning their harmonious relationships. What actually appears to take place in Nature is that the organism is continually mustering its forces to the attack of a hostile environment, which it proceeds to conquer with varying degrees of success, by occupying situations in which it is less prone to adverse agencies, by the elaboration of mechanisms which buffer external changes of an unfavourable character, and in the highest stages, by the creation of an immediate environment of its own, which thereby renders the organism to some extent independent of the adverse circumstances presented by the external environment. The writer does not mean to imply that actual modification of morphological structure and physiological function in response to environmental changes no longer occurs as an integral evolutionary function, but simply that it does not and never has proceeded to the extent often imagined; those so-called 'hand-to-glove' adaptations, in particular, being mere fictions of the imagination resulting from over-prolific biological philosophising.

As a quantitative study in the modern outgrowth of the older science of natural history, known as ecology, it is hoped that the present investigation will contribute towards the consolidation and reinforcement of
the latter as the fundamental basis of all applied biology.

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"Depuis qu'ils ont appris à lire et à écrire la bêtise latente se dégage" - Maupassant.