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## A Study of a Natural Population of *Phytodecta olivacea* (Forster) (Coleoptera, Chrysomeloidea)

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# A STUDY OF A NATURAL POPULATION OF *PHYTODECTA OLIVACEA* (FORSTER) (COLEOPTERA, CHRYSOMELOIDEA)

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[Plate 14]

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This is a study of the seasonal and annual changes in a self-contained natural population of the Chrysomelid beetle, *Phytodecta olivacea* (Forster) which lives on broom, *Sarothamnus scoparius* (L.) Wimm. The adult beetles emerge in the spring from hibernation in the soil and after laying their eggs on the food-plant re-enter the soil where between one-third and one-fifth of them survive to the next summer. Their offspring on the broom become adult in the late summer and after a short period of feeding join their parents in hibernation. The adults rarely fly and dispersal seems to take place mainly by walking. Regular estimates of the numbers of the insect were obtained by sampling the food-plant, the quantity of which was known in terms of standardized 'armfuls' and which could be related to weighed armfuls. Adult beetles were estimated by shaking armfuls over a tray and eggs and larvae by examining sprigs of broom of known weight. Some records of the numbers of adult beetles are available from 1948–59, but detailed estimates of all stages were kept only in 1954–58. The numbers of adult beetles in 100 armfuls tended to fall into a negative binomial

series, indicating some tendency to aggregation. The total number of adults which emerged in the spring is equivalent to the total sum of all the weekly samples divided by the effective adult life (i.e. the time spent by the beetles on broom) which was determined in the laboratory. This total emergence was independently estimated by counting the number of beetles which were found in forty special enclosures in the field. The number of eggs laid each week could be estimated by knowing the number of females present (from counts in armfuls) and by the use of a regression equation, calculated each year in the laboratory, relating the oviposition rate to the age of the population and the mean temperature. The total number of eggs laid in the season was the sum of the weekly figures. Assuming that the destruction of eggs was exponential, it was possible to deduce the mortality from the initial numbers (based on the regression equations) and the duration of the stage at the prevalent temperature. The relation of egg and larval stages to temperature had earlier been established experimentally (Waloff & Richards 1958). The mortality in the larvae was similarly deduced, treating the surviving eggs as the initial number of first-stage larvae.

Adult beetles were destroyed by a braconid parasite, *Perilitus dubius* (Wesm.), and by a fungus *Beauveria bassiana* (Bals.) Vuill. Destruction by the braconid was 5 to 13% of the spring and 5 to 26% of the autumn beetles. The fungus destroyed the beetle chiefly during hibernation. In dissections, 0 to 25% of the beetles were found to be infected in different years, but there are some grounds for thinking that much of the winter mortality was also due to this cause. Of the eggs laid in the field, 4 to 10% were found to be sterile and less than 1% were parasitized by Hymenoptera. Between 1 and 3% of the larvae were parasitized by the fly, *Meigenia mutabilis* (Fall.), and another small fraction by various other parasites. Most of the mortality of the eggs and larvae was due to predatory insects, especially Hemiptera Heteroptera (Miridae, Anthocoridae, Nabidae) and earwigs (Dermaptera). The losses due to these causes were confirmed quantitatively in 1958 and 1959 by using a serological method to detect the food of the predators (Dempster 1960). There was also an additional small mortality of the pupae in the soil due to carabid beetles and possibly other predators.

The effects of most of these causes of mortality were made more striking by concentrations of the populations which occurred in 1956 and 1958 after about half of all the broom had died in the preceding winters. Many of the plants had reached the end of their natural life (10 to 15 years) and had become susceptible to frost and unable to survive a heavy production of pods. On the reduced quantity of broom, the number of beetles per armful in 1956 was about twice as great as in the year before while the numbers of alternative prey, such as aphids and psyllids, were lower than in subsequent years. The calculated mortality of the eggs and larvae in 1956 was 99% compared with 79% in 1955. Similarly, the mortality of the early stages was 92% in 1958 compared with 78% in 1957. Although one or other species of predator is found throughout the season, the most abundant, the Miridae, hatch early and their numbers decline sharply at about the time their adults appear. Thus, *Phytodecta* suffers from much more predation in the early part of the season than later, after the middle of June. In 1955, eggs had been found in the field for 6 weeks before any larvae were found. In general, the early stages of *Phytodecta* whatever other disadvantages they may suffer have a better chance of avoiding predation in the second half of the summer.

Temperature and rainfall are the two climatic factors which most influence *Phytodecta*. Temperature has an important influence on the oviposition rate and the duration of the immature stages and seems also to alter the length of time spent above ground by the adults. It also has indirect effects through parasitism and predation. Rainfall during the period of larval development influences the size of adult population in the following year.

These observations on the changes in the population are summed up in life-tables for the years 1954–58. In short-lived species these would be best described as ‘budgets’, since they deal directly with the causes limiting the growth of the population and not with the age distribution within it. Each cause of mortality is expressed as a percentage of the stage on which it acts and as a percentage of the total mortality in the complete annual cycle. The second method of expression gives a better measure of the importance of any factor because a large apparent mortality late in the cycle may be only a small fraction of the initial numbers. By using this method, it is found that about 78 to 99% of all mortality occurs in the eggs and larvae on broom; 0.3 to nearly 19% occurs in the later stages in the soil in the early autumn, and 0.4 to 4.5% in the adults in the soil in the winter and spring. In the adult stage, deaths due to hymenopterous and fungal parasites if added to the

numbers of beetles known to survive until the following year, leave a certain proportion unaccounted for (5 to 42% according to the year). This discrepancy is probably largely due to additional deaths from fungal attack during the winter. In the eggs and larvae, while disappearance from the broom was recorded each year, only in 1957–58 was predation, the principal cause, measured; in these 2 years it apparently accounted for 71 and 88%, respectively, of the disappearance. In these stages, some of this discrepancy is due to parasitism and to sterility of the eggs.

Although all these estimates are subject to large sampling errors, we find some support for them when we compare the difference between actual mortality and that necessary for a stable population with the actual trends in the population from year to year. In four years the trend was in the right direction and only in 1957–58 did an increase of population follow an estimated excess mortality.

The life-cycle of *Phytodecta olivacea* has one feature which makes it partially independent of the mortality in any one year. A variable proportion of the adults survive to reproduce a second time and a high mortality or ineffective reproduction during one summer can be partly compensated if a high proportion of the parents survive. Further, both emergence of the adults in the spring and reproduction are relatively protracted, so that each stage has a chance of avoiding some of the seasonal hazards, such as predation or unsuitable weather.

#### INTRODUCTION

The present study is concerned with seasonal and annual changes in the population of a chrysomelid beetle, *Phytodecta olivacea* (Forst.), living on a small relatively enclosed area of broom (*Sarothamnus scoparius* (L.) Wimm.) at the Imperial College Field Station, Silwood Park, Berks. We have attempted to measure the changes, to assess and interpret multiplication and mortality quantitatively and finally to construct a life-table for the insect.

The population of *Phytodecta* is nearly self-contained. The beetle is almost monophagous on broom; although it has been recorded feeding on tree lupin, *Lupinus arboreus* Sims in Suffolk (G. E. Woodroffe, private communication) and there are a few other such records, there is no alternative food plant at Silwood Park. The area of broom studied was rather sharply delimited. The beetle normally has very low powers of dispersal and the populations studied seem to have had negligible emigration or immigration.

The life history and the general reproductive biology have been described by Waloff & Richards (1958). There is only one period of mating and oviposition in the year; though young beetles are seen again in the autumn before hibernation, they do not mate nor lay eggs. The adult beetles usually begin to emerge from the soil in late April and the first eggs are seen on broom about a fortnight after the beginning of emergence. The emergence of the over-wintered beetles is protracted and is continued into May and June. The result of this is that the eggs and the four larval instars occur on broom simultaneously for most of the time, between May and the end of August. The fully fed fourth-instar larvae descend to the ground where they pupate in the litter and in the grass roots under the bushes. The adults of the autumn generation ascend the broom, feed, develop large fat bodies, but remain immature until next spring. They hibernate beneath the broom bushes and up to 60% may survive the winter (see table 14). Not all the adults of the spring generation die in the current year, but a fifth to a third of them (table 14) hibernate for the second time and oviposit again in the following season. The oviposition rates of individual beetles are normally very similar in the 2 years; some data on this point have already been published and more have been obtained since. The beetles which emerge as the spring

generation are thus a mixed population, consisting of the young autumn adults of the previous year with an admixture of the older beetles which had lived and reproduced during the previous early summer.

#### DESCRIPTION OF THE HABITAT

The area studied at Silwood Park consists of about two acres (0.81 hectares) of broom (figure 1, plate 14) surrounded on three sides by tall trees and on the fourth by some huts and a relatively open abandoned parade ground. There is very little broom in the adjacent woods. The area is not covered with broom but has a number of dense patches, separated by grass (*Festuca rubra* L., *Agrostis tenuis* Sibth., *Holcus mollis* L., *Deschampsia flexuosa* (L.) Trin.), brambles, birch (*Betula*) and *Ulex europaeus* L. Under the older bushes all the other plants die and there is an accumulation of characteristic broom litter. The soil is sandy or gravelly.

Judging by the ring counts made by Mr J. Levy on sections of one of the larger plants, the broom started its growth about 1944 or 1945. From our own notes, only one plant was 6 ft. high (2 m) in 1947. In 1959 the broom was less extensive than it was in 1955; many of the older plants had died. According to Mr D. F. Fourt of the Forestry Commission (personal communication) the length of life of a broom plant is usually 10 to 15 years. For most of the period 1954–58, about half of the area was covered by broom. Over this period broom showed little signs of regeneration and only a few young plants were visible. Measurements of the actual amount of broom in different years are given later (table 1).

Broom is a perennial shrub found from Scandinavia to Spain and the Canary Islands, but it does not extend eastwards of Poland and Hungary in Central Europe. It is widely distributed in the British Isles (except Orkney and Shetland) and is found especially on disturbed soils. The leaves (at Silwood) may start falling as early as the middle of September and this determines when some forms of sampling have to finish. By the end of October few but the very youngest leaves will be left. Flowering occurs some time in May and varies much in amount from year to year. The flowers are attractive to a great variety of insects. Very heavy flowering often seems to lead to the death of old plants since pods are produced at the expense of leaves. The pods ripen and eventually dehisce to release the seeds, usually in July and after this, young shoots of broom grow rapidly and many leaves are produced. It is this late growth which is especially sought by the autumn generation of adult *Phytodecta*.

A Stevenson screen and a rain-gauge were maintained by Mr J. W. Siddorn in the open grass areas amongst the broom and all meteorological data, unless otherwise stated, are from this site. Wind, however, is measured about 300 m away. A special mercury in steel recording thermometer was used to measure the temperature just below the litter under a broom bush.

In 1958, Mr Siddorn measured temperatures for us with sixteen thermocouples in a number of points on the leaves and stems of two broom bushes. The sites were chosen to represent the different aspects of the bushes and were at different heights from the ground. On dull days the average temperature read from the thermocouples did not differ from the screen measurements. On three bright days, 12 to 14 September, (figure 3) the

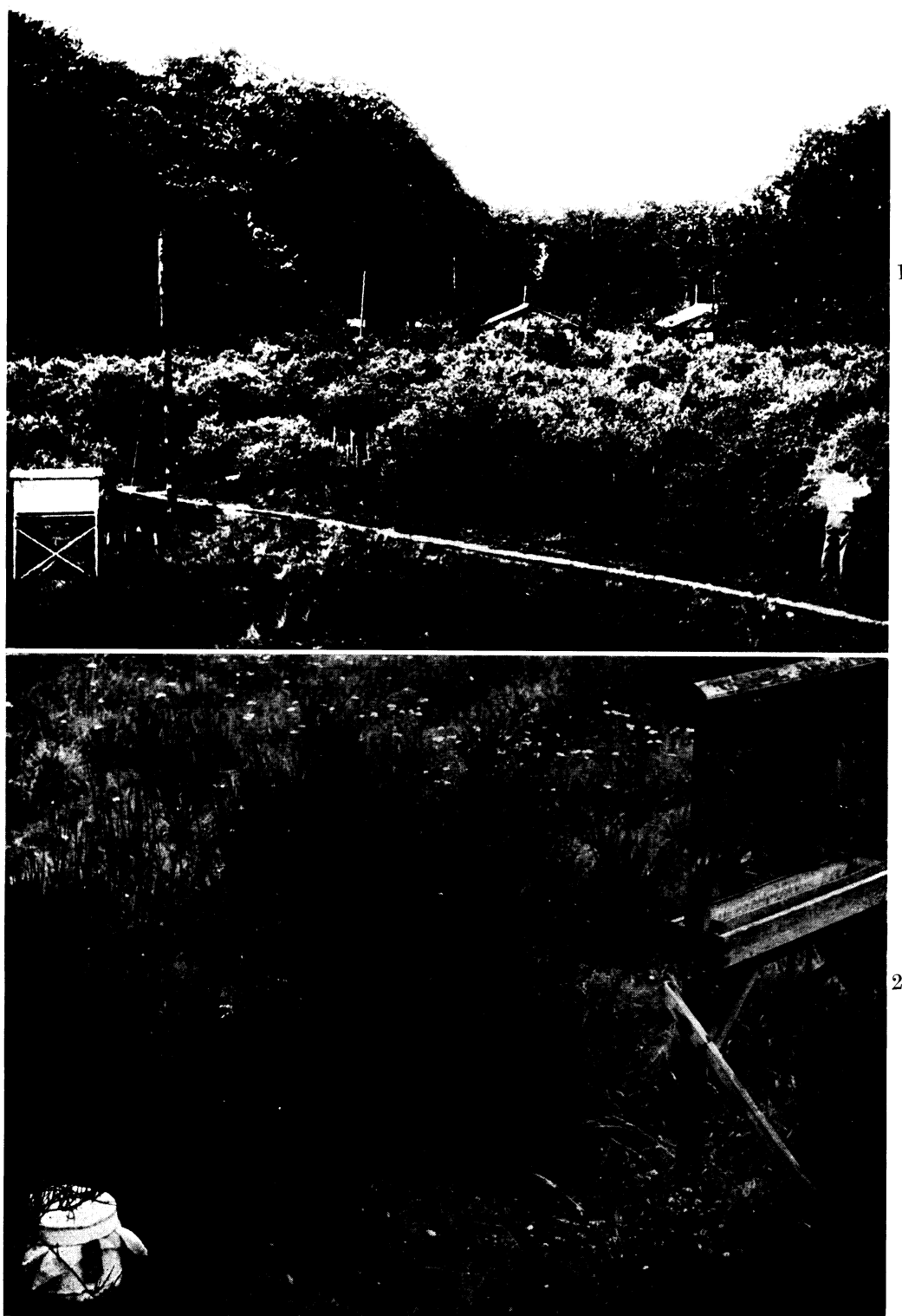


FIGURE 1. Northern half of the area of broom, Silwood, May 1955. Stevenson screen on the left.

FIGURE 2. One of the tubs used for measuring the emergence of beetles from the ground in the spring and a 'window-trap' used to try and catch flying adults.

(Facing p. 208)

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temperature was still almost the same as regards daily averages (screen 14.3 °C, thermocouples 14.45 °C) though they might differ at certain times of the day. We are therefore using the screen temperatures to represent the average temperature of the habitat of the egg and feeding stages of *Phytodecta*.

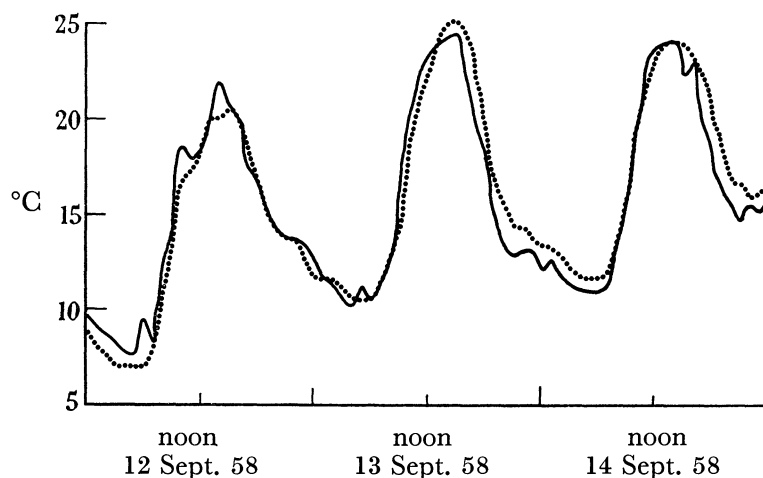


FIGURE 3. Comparison of screen temperatures (continuous line) with the mean of 4-min thermocouple readings at sixteen points on two broom bushes on 12 to 14 September 1958 (J. W. Siddorn).

MEASUREMENT OF THE QUANTITY OF BROOM AND THE METHODS OF SAMPLING  
THE POPULATION OF *PHYTODECTA*

The method of obtaining the adult beetles was to shake broom over a square tray with sides of 1 m made of cotton sheeting spread over a frame of light aluminium tubing. The quantity of broom which can be conveniently shaken at a time, using one hand, is called an 'armful' and with a little practice can be standardized so that the number of armfuls on the area of broom can be counted in a repeatable manner. To make this easier the broom on the area was divided into 105 irregular clumps by paths and each clump was numbered and labelled; this also made it possible to keep a record of the parts of the area sampled on any day.

TABLE 1. NUMBER OF ARMFULS OF BROOM AND THE AREA COVERED BY  
BROOM IN THE FIELD IN DIFFERENT YEARS

year	spring		autumn		figure used	area beneath broom in autumn, ft. <sup>2</sup> (× by 0.093 for m <sup>2</sup> )
1953	—	—	24. ix.		4769	
1954	—	—	—	—	4769	18968
1955	2. v. 55	4615	—	—	4615	18356
1956	1. v. 56	2619	x. 56	2103	monthly estimates	9393
1957	2. v. 57	2991	ix. 57	2161	2576	10248
1958	2. v. 58	1386	ix. 58	1471	1429	5685

In 1949–52 rough counts by students suggest that there were 4000 to 5000 armfuls. During the first years 1954–55 the numbers of armfuls remained nearly the same though many of the plants were nearing the end of their natural life. The hard frosts of winter of

1955–56 killed many plants and not much more than half of the broom survived to 1956. There were further deaths during the year and on this occasion monthly estimates were calculated based on the May and October counts. In 1957 in which much growth occurred early, the estimate in May was considerably higher than in the previous October. Both in 1957 and 1958 the estimate used was the mean between the May and September figures.

To find eggs and larvae of *Phytodecta* it is necessary to search the broom carefully with a hand lens. To sample these stages, 100 cuttings of broom were taken from points distributed widely over the area and put into a covered tin. The cuttings were weighed and then searched. If they were wet, they were searched, then dried and then weighed. Each season 10 to 30 armfuls were cut in different months and weighed so that the cuttings of known weight could be converted to a standard armful. In order not to deplete the area the armfuls were cut on other nearby habitats. On the average, an armful weighs 394.8 g.

To estimate the length of broom stems which is of interest in relation to the searching behaviour of predators, the lengths of all the shoots was measured in 190 samples weighing 512.0 g. From these measurements a regression equation was calculated and it can be said that the average armful includes 198.7 m of broom stems.

The fourth-instar larva of the beetle enters the litter under the broom bushes to pupate just below the surface. The adult beetles hibernate in the same site. As far as we could discover pupation and hibernation always take place beneath the broom. This conclusion is based first on taking 47 out of 200 samples in 1954 between the bushes and finding no beetles (ten beetles beneath the broom) and secondly, failure to find the beetle in over 1600 samples taken between the bushes in 1947–51, when we were sampling for eggs of grasshoppers. Soil samples which were taken in October to November and in one year (1955) also in July were obtained with a wire-worm sampler cutting a cylindrical core 4 in. (10.2 cm) in diameter (area  $12.57 \text{ in.}^2 = 82.05 \text{ cm}^2$ ). The emergence of the adult beetles from hibernation in the spring was estimated by placing forty white-painted, open ended 'tubs' (figure 2, plate 14) with the upper end covered with muslin, each enclosing an area of  $0.9939 \text{ ft.}^2$  ( $40 \text{ tubs} = 39.72 \text{ ft.}^2$ ) under the broom in the spring before the beetles had started to emerge from the soil. The interior of the tub had much of the vegetation removed and replaced by clean sand. This made it easier to find the beetles when the tubs were examined once a week.

The area of the 4 in. core and the tubs had to be related to the area covered by broom. This area was calculated as follows. The areas of sixty clumps of broom of more or less regular outline were measured and a regression equation was calculated for area upon the number of armfuls in the clump. This is equivalent to  $9.17 \text{ ft.}^2$  ( $0.85 \text{ m}^2$ ) an armful. The total area under broom was then calculated from the equation by using the figure for the total number of armfuls on the area. The samples, whether armfuls of broom, tubs measuring spring emergence, or soil samples of hibernating beetles, were taken systematically so as to cover the whole area in accordance with the distribution of broom bushes. This, though not a centric-systematic area sample in the sense of Milne (1959), probably approximates sufficiently to it to allow the samples to be treated as random.



ROUTINE SAMPLING OF *PHYTODECTA* AND OF ITS ENEMIES

Every week 100 armfuls of broom were shaken over a tray and the adult beetles collected. The armfuls were chosen so as to cover the whole area and were classified as high, medium or low according to the part of the plant sampled. A record was kept of the clump of broom from which each sample came.

The beetles from the samples were taken into the laboratory, sexed, classified into colour forms and weighed individually, at least in part. Half were then kept alive in muslin-covered 7 lb. jam jars containing sprigs of broom standing in about 2.5 in. of a mixture of builder's sand and bulb fibre. The sand was watered once or twice a week. On some occasions a number of pairs were also isolated in 3 in.  $\times$  1 in. tubes for oviposition records. The rest of the beetles were preserved in alcohol for later dissection to detect parasites. The adult stage of the hymenopterous parasites emerged in the following year from the jars which had contained the beetles.

TABLE 2. STANDARD ERRORS OF SEASONAL MEANS OF THE NUMBERS OF THE IMMATURE STAGES ON BROOM CUTTINGS

year	stage	no. of sets of 100 cuttings involved	total no. of cuttings	uncorrected totals of each stage actually encountered in samples	standard error of the seasonal mean as a $\pm$ percentage
1955	egg	36	3187	372	11.9
	instar I	27	2462	88	11.7
	II	29	2662	57	13.9
	III	29	2662	57	13.8
	IV	30	2782	39	16.1
1956	egg	58	5025	426	5.1
	instar I	44	3925	149	8.6
	II	42	3875	80	11.1
	III	37	3375	54	13.2
	IV	37	3375	37	16.2

The eggs and larvae of *Phytodecta* were obtained from cuttings, as described previously (p. 210). Eggs were kept for hatching to measure parasitism and sterility. Larvae were either bred or dissected to obtain parasites and for this purpose additional larvae were also removed from the beating trays when the adults were being sampled. Thus a fraction of the population was removed from the field every week and in the adults this is allowed for in the life-tables (see tables 14, 37 and 38).

An approximate estimate of the sampling errors of our counts of eggs and larvae may be obtained as follows:

In 1955 and 1956 we recorded separately the numbers of these stages found on each cutting of the 100 that made up a sample. The cuttings are not in fact all of the same size but if they are treated as the sampling units a standard error of the mean can be calculated. As the only figure we have used in detailed calculations is the accumulated total for the whole season, all the sets of samples in which any particular stage occurred can be added together. The standard error is expressed as a percentage of the mean so that it would apply equally to the calculated total of the stage in the field (see table 2).

The principal predators of the early stages of *Phytodecta* are the mirid (Waloff & Southwood 1960) and anthocorid bugs and earwigs (*Forficula auricularia* L.) (Dempster 1960). This was only fully realized in 1956 and the numbers of these predators (apart from sporadic records in 1954–55) were estimated in 1956–58. This was done by counts on the beating tray and on the cuttings of broom in the course of ordinary sampling for *Phytodecta*. Dempster also made independent counts on beating trays on different days in 1957–58. Carabid beetles appeared also to play some part as predators of the pupae. This was studied in a small way in 1958 (Dempster, Richards & Waloff 1959). The method of detecting predation was in all cases to use a rabbit serum sensitive to *Phytodecta* tissues to detect whether the gut contents of the predators contained any *Phytodecta* material.

#### DISTRIBUTION OF ADULT *PHYTODECTA* IN THE FIELD

The primary data in the period April to October were the number of adult beetles shaken from 100 armfuls of broom. The numbers of armfuls with 0, 1, 2, ... beetles on any day seem to form a negative binomial series and an example of their distribution is given in table 3. Such figures are partly determined by the amount of broom in the field. The numbers of beetles per armful are particularly high in 1956 because a great deal of broom had died during the previous winter and the emerging beetles were concentrated on a reduced volume of the food-plant.

TABLE 3. FREQUENCY OF BEETLES IN 100 ARMFULS (FIGURES FOR 29 MAY 1956)

no. beetles in the armful	frequency	no. beetles in the armful	frequency
0	16	9	0
1	13	10	0
2	11	11	4
3	16	12	1
4	9	13	0
5	7	14	1
6	10	15	0
7	5	16	1
8	5	17	1

total 392 beetles in 100 armfuls

Such a distribution is far from random, i.e. the numbers do not form a Poisson series, for both the low numbers and the high ones are too common. It is necessary to determine the type of distribution in order to calculate the fiducial limits of the total. We gave all our data for the year 1954 to Dr R. E. Blackith and he was able to show that they could be satisfactorily fitted to a negative binomial distribution (Bliss & Fisher 1953). In the data for 32 days, the distribution of seven of them was consistent with the Poisson and on twenty-five with a negative binomial distribution, the values of  $K$  in the latter lying between 0.317 and 2.803. The size of the 'aggregation' of beetles was calculated as predicted by the negative binomial distribution, and since the calculated number was generally less than one it seems likely that the 'aggregation' was due to heterogeneity of the environment rather than to an active process (cf. Waters 1959).

Only a partial explanation can be given for the amount of aggregation recorded (see also p. 231). It is not due to a tendency to lay eggs in groups. Observations showed that

young, green, rather than woody plants often had more beetles on them, especially in the autumn generation. Plants on the periphery of the area often have more beetles than those in the centre of large clumps of broom. However, quite often a plant which was apparently unsuitable produced a number of beetles and vice versa. Adults are neither attracted nor repelled by the flowering of broom.

We also used to record whether the armful of broom being shaken was from a high, medium or low position on the plant. Examination of these records shows that at the start of the season the beetles are somewhat commoner in low positions but later they become evenly distributed. The autumn generation when it first appears usually spends some time on the tips of shoots, especially on the young ones.

#### METHODS OF ESTIMATING THE NUMBERS OF *PHYTODECTA* FROM THE SAMPLING DATA

From the numbers of beetles found in the field each week it is possible to deduce the number of beetles produced, if it is known how long on the average they stay on broom. An estimate of this period was obtained from the sample of beetles which was put each week into large jars and examined three times a week. The 'time above ground' of the beetles in the jars was obtained by dividing the number of 'beetle days', i.e. the sum of the regular censuses of the jars by the number of beetles known to have been added to the jars. This laboratory figure for 'time above ground' was then applied to the field data, that is, it was divided into the total of beetles in all the weekly samples to estimate the number of adults which had emerged in the field. It is admittedly surprising that the laboratory figures for the 'time above ground' should be applicable to field conditions but all our data suggest that they are (see p. 218). There is some evidence that the adult period above ground is in some way related to day-length but the various experiments tried so far have not suggested any simple relation.

The number of eggs in the field was estimated by examining cuttings. Three or four samples (each of a 100 cuttings) were taken a week. The weight of these samples was between 800 and 1200 g. The total number of eggs found on the cuttings throughout the season was corrected to that number which would have been obtained had the samples been taken daily. The accumulated total of eggs in the field was denoted by  $N$ . The quantity  $N$  does not include the eggs lost by extensive and often rapid predation and the total number of eggs laid in the season, or  $n$ , was estimated in the following way.

It has been shown (Waloff & Richards 1958, p. 113) that the number of eggs  $y$  laid per female per day can be estimated as  $y = b_1x + b_2t + c$ , where  $t$  = mean temperature in degrees Fahrenheit and  $x$  is the mean age of the population. The temperature was taken from the record in the Stevenson screen and it was found that the number of days since the first female beetle was seen\* in the field could be substituted for the mean age of the population. The calculated oviposition rate multiplied by the number of females in the field (estimated by weekly beats) gives the number of eggs added each week (see appendix 1). The total number of eggs laid in the season is the sum of all these weekly figures, or  $n$ .

\* In 1957, a very early season, the date the first female oviposited in the laboratory was used as 'day 1'. It makes little difference in practice from which day the age of the population is measured.

If  $a$  is the duration of the incubation period at the prevailing temperature\* and  $k$  is the fraction surviving per unit time, and if  $N$ ,  $n$  and  $a$  are known,  $k$  can be calculated. The duration of incubation and the intervals between the samples have to be expressed in the same units of time and it has to be assumed that the mortality throughout the egg stage is approximately uniform, then  $N$  can be expressed in the terms of  $n$ , or

$$N = n \int_0^a k^t dt = n \frac{k^a - 1}{\ln k}.$$

The calculation for the value of  $k$  is simplified by substituting the term  $u$  for  $k^a$  as then

$$N = an \frac{u-1}{\ln u} \quad \text{or} \quad \frac{N}{an} = \frac{u-1}{\ln u}.$$

A table for the value of  $(u-1)/\ln u$  was constructed for the values of  $u$  from 0.01 to 0.99. Intermediate values were found by interpolation. From this table the value of  $u$  corresponding to  $N/an$  can be read off and the mortality is  $100(1-u)\%$ .

Owing to sampling errors and irregularity in mortality it was often necessary (p. 232) to group the immature stages and to obtain the total mortality in several instars combined.

When the egg mortality is calculated, the number recruited into the first-larval instar is then known. This gives the starting point  $n$  for the calculation of mortality within that instar, since the values of  $N$  and  $a$  have been obtained in the same way as for the egg stage. The same process can be repeated for the successive instars, but in the fourth-stage larvae there is a feeding period and a period spent underground. Only the feeding period was used in these calculations.

The application of this method of estimating mortality to an artificial population of locusts is described by Richards, Waloff & Spradbery (1960).

The number of beetles which hibernated was also estimated by taking about 200 samples from the litter beneath the broom each October or November. The samples were broken up on a tray and searched for adult beetles. Only living ones were counted since parts of dead beetles were recognized in the litter after more than one season. In 1955 samples were taken in July to obtain an estimate of the previous year's beetles which were entering the soil for a second hibernation. In the spring, the number of beetles emerging from hibernation was estimated by examining forty 'tubs' once a week and removing the beetles. The numbers of the pupal stage were not separately estimated.

The accumulated total of beetles, i.e. the number in all the weekly samples added together, is equal to the product of the number of beetles which actually emerge with the average length of life above ground. Thus an independent estimate of the period spent by the beetles above ground was obtained by dividing the total of beetles emerged (based on counts from tubs) into the total of beetles in all the weekly samples. The reasonably close agreement (table 4) between the period calculated in this way and one based on beetles kept in jars in the laboratory is a reason for treating the latter figures as reliable. The first figure gives a somewhat higher estimate.

The estimates of the 'time spent above ground' included both sexes; if these are considered separately, the females are then seen to spend a longer time above ground than the males. Thus, in 1956 the average for both sexes in jars was 3.05 weeks, whereas that

\* The incubation periods are given in Waloff & Richards (1958).

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for females alone was 3.39 and that for males 2.59, Similarly in 1958, the average was 2.44 weeks, that for females 2.63 and for males 2.25 weeks. The sex ratios did not greatly deviate from 1:1 and are summarized in table 15.

TABLE 4. 'TIME SPENT ABOVE GROUND' IN WEEKS IN SPRING GENERATION ADULTS, ESTIMATED IN TWO WAYS IN 5 YEARS

(a) By observation of beetles in jars in the laboratory. (b) By dividing the sum of all beetles in the weekly field samples by the number of beetles which emerged, deduced from counts in the 'tubs'. (c) The 'time above ground' for the autumn adults, based on observations in jars only.

year	time spent above ground		
	(a)	(b)	(c)
1954	4.69	6.15*	1.35
1955	3.67	3.80	1.26
1956	3.05	3.65	1.11
1957	3.05	4.88	1.18
1958	2.44	2.80	0.71

\* This discrepancy is partly due to difficulties in estimating the number of beetles which emerged in the first year of work.

The estimations of the natural enemies of the immature stages have already been discussed. The dissections of half the weekly samples of adult beetles gave estimates of the percentage parasitism by *Perilitus dubius* (Wesm.) (Hymenoptera, Braconidae) and *Beauveria bassiana* (Bals.) Vuill. (Fungi, Moniliales). Well-developed *Beauveria* infections are easily recognized in dissections, even of beetles which have been preserved in alcohol, by the occurrence of white granulations in some or all of the fat body, muscles and gut. In the beetle cultures the braconid emerged in the following year and initially it was not easy to overwinter chiefly perhaps because no bulb fibre was added to the sand. The percentage survival of beetles in jars, overwintered in an unheated outdoor shed gave figures that agreed surprisingly well with the figures based on the difference between the number of beetles entering hibernation in autumn and leaving it in spring (table 8).

## THE NUMBERS OF ADULT BEETLES

Figure 4 shows the curve of numbers of the adults of the two generations in the field in 1955. Where they overlap they are assigned to the correct generation by their colour. It should be noted that the numbers actually obtained in samples as opposed to the numbers emerged depends to a large extent on the time the beetles spend above ground which is very different in the spring and autumn generations. In the five years 1954-58, the ratio between the number of beetles emerged and the peak number in the weekly samples of the spring generation is 1.14 to 2.67 mean 1.73. We have records of the numbers at or very near the maximum of the spring generation for 12 years (1948-59) obtained by students in the course of class work (figure 5). The peak numbers vary between 33500 in 1950 and about 1000 in 1959, so that the numbers emerged may have been about 1.73 times these figures.

The students also estimated the numbers of the beetles on the same day by marking, release and recapture; the agreements are not very good but the figures based on the two methods tend to support one another. In table 5 we give the 95% fiducial limits of the beating and marking data for the 5 years 1954-58.

The weekly figures of number of beetles have been used only in the first generation for estimating the amount of oviposition (Appendix 1). Otherwise, the figure used is the accumulated total (table 5), i.e. the sum of all the weekly estimates, and it may be hoped

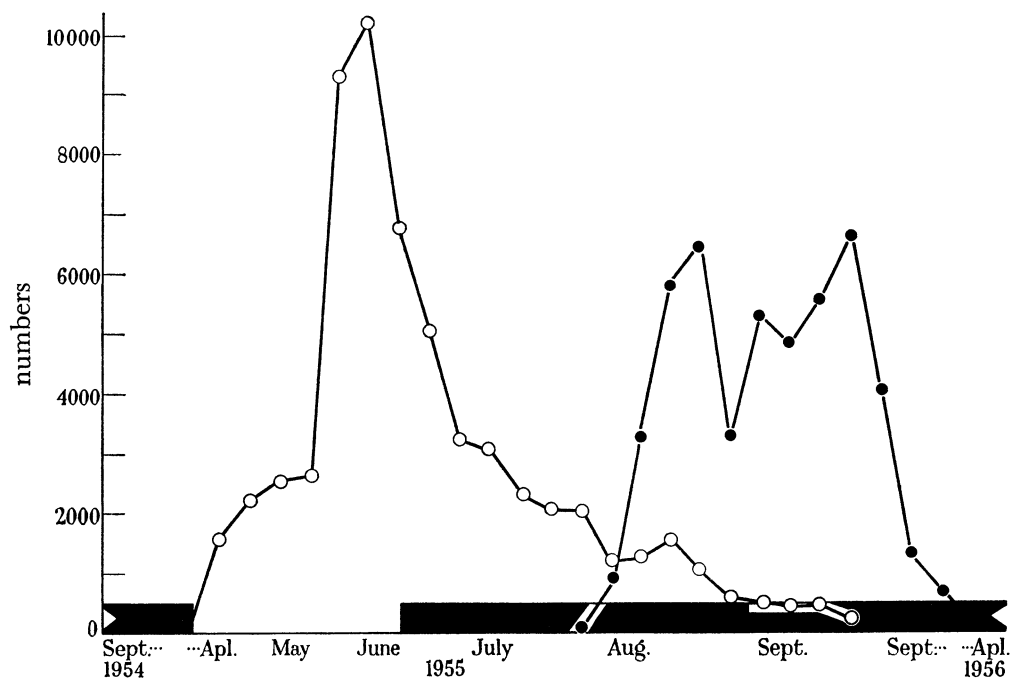


FIGURE 4. Seasonal occurrence of adult *Phytodecta* on broom in 1955. Open circles, spring generation. Black circles, autumn generation. Black area indicates period when some or all the adults are underground.

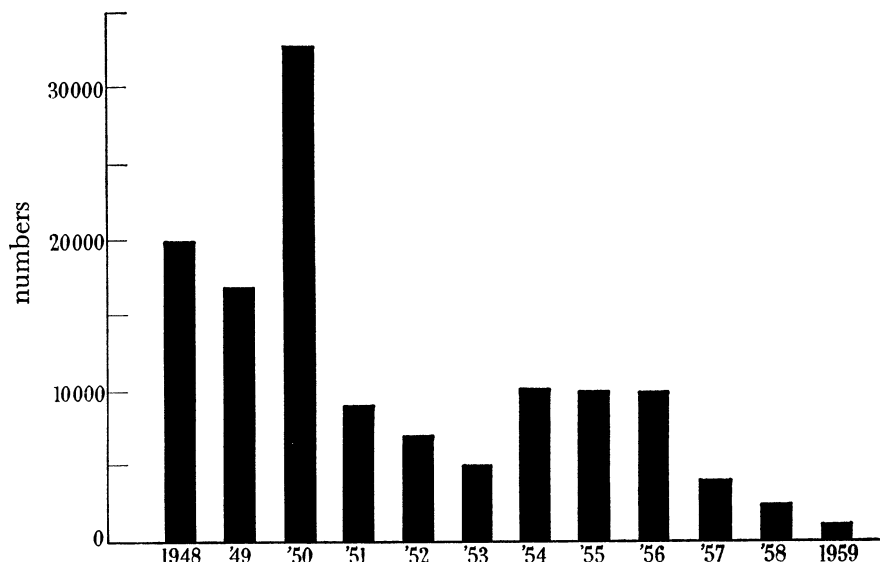


FIGURE 5. Histograms of the maximum numbers of the adults of the spring generation for 12 years.

that in this figure some of the errors tend to cancel out. The accumulated totals were divided by the average time spent by each generation on broom (see p. 214) and this gave an estimate of the total number of beetles which had emerged in that season (see table 7).

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The second method used in estimating the total numbers of beetles of the spring generation was derived from the numbers found in the 'emergence tubs'. Each year these tubs were shifted to new positions and were distributed throughout the growth of broom, so as to sample the area in accordance with the distribution of the bushes. It was assumed that hibernation took place only under living broom and thus the areas covered by the bushes in the previous season were used in these calculations.

TABLE 5. ESTIMATES OF THE NUMBER OF SPRING GENERATION BEETLES IN THE FIELD ON OR NEAR THE DAY WHEN THEY ARE AT A MAXIMUM, TOGETHER WITH THEIR 95% FIDUCIAL LIMITS, 1954-8

[S] = data obtained by students.

year	occasion	estimate by beating	estimate by marking
1954	24-25. v.	5200 ± 1620*	5115 ± 1680†
	8. vi. (maximum)	10400 ± 1875	—
1955	3. vi. (maximum)	10150 ± 2130	—
	8-9. vi.	—	10600 ± 12300 [S]
1956	29. v. (maximum)	10010 ± 1880	—
	5-8. vi.	4420 ± 880 [S]	4510 ± 280 [S]
1957	28. v. (maximum)	4100 ± 970	—
	5-8. vi.	3410 ± 950 [S]	2600 ± 1690 [S]
1958	4-5. vi. (maximum)	2460 ± 630 [S]	3400 ± 60 [S]

\* Fiducial limits based on treating the figures in the 100 beats as a negative binomial series.

† Fiducial limits calculated as described by Bailey (1952).

TABLE 6. THE ACCUMULATED TOTALS (I.E. THE SUMS OF WEEKLY ESTIMATES) AND THE MAXIMUM WEEKLY NUMBERS OF ADULTS IN EACH YEAR, 1954-58

The numbers are given to the nearest 100. (For sex ratios see table 15.)

year	spring generation		autumn generation	
	accumulated total	maximum weekly no.	accumulated total	maximum weekly no.
1954	55400	10400	45900	6500
1955	59400	10200	47600	6400
1956	51900	10000	5900	1000
1957	19500	4100	8700	1300
1958	16500	2500	3800	600

TABLE 7. COMPARISONS OF ESTIMATES OF NUMBER OF SPRING BEETLES

year	no. of beetles emerged in 40 tubs	95% fiducial limits of beetles in 40 tubs*	estimated emergence in spring in whole area†	estimate based on beating armfuls‡
1954	19	11.44-29.67	9010	11820
1955	33	22.72-46.34	15649	16184
1956	31	21.07-44.00	14226	17027
1957	17	9.90-27.22	3992	6393
1958	28	14.58-34.51	5893	6757
1959	27	17.79-39.28	3838	—

\* Treating the number of beetles emerging per tub as a Poisson distribution; 95% fiducial limits of total number of beetles from Pearson & Hartley (1954), table 40.

† Estimate = area beneath broom (see table 1) divided by area of tubs (p. 210) multiplied by figure in col. 2.

‡ Accumulated total divided by the time spent above ground.

It also appears that the survival of beetles in the jars can be used as an index of survival in the field. If the fraction which survives the winter in jars is taken also as the fraction which survives in the soil in the field, the number expected to emerge in the spring turns out to be very close to the number expected from an independent calculation of the same figure (accumulated total divided by mean time spent above ground, the following year, table 7, col. 5). The mortality seen in table 8 is a sum of all the mortalities the adults experience from one spring to the next, though the causes of mortality are not here distinguished.

TABLE 8. THE USE OF THE FRACTION OF ADULT BEETLES WHICH SURVIVE IN JARS TO PREDICT THE FRACTION WHICH WILL SURVIVE IN THE FIELD

current year	total* which emerged the previous year		fraction surviving in jars		estimated nos. surviving		estimated nos. emerging next spring (col. 6 + col. 7)	second estimate of nos. emerging in spring*
	spring gen.	autumn gen.	spring gen.	autumn gen.	(col. 2 × col. 4) spring gen.	(col. 3 × col. 5) autumn gen.		
1955	11 820	36 055	0.261	0.459	3085	15 631	18 716	16 184
1956	16 184	37 844	0.349	0.361	5 648	13 662	19 310	17 027
1957	17 027	5 297	0.206	0.529	3 508	2 802	6 310	6 393
1958	6 393	7 344	0.276	0.623	1 764	4 569	6 333	6 757

\* Calculated by dividing the accumulated total of beetles in the 100 beats by the mean time which the sample spent above ground in jars.

#### CAUSES OF MORTALITY IN ADULT BEETLES

The two certain causes of mortality in the adults of *Phytodecta olivacea* are the braconid parasite *Perilitus dubius* (Wesmael) and the fungal parasite *Beauveria bassiana* (Balsamo) Vuillemin. *Perilitus dubius* has not previously been recorded from the British Isles and has recently been redescribed by Richards (1960). The most extensive accounts of the biology of *Perilitus* are those of *P. coccinellae* (Schrank) (Oglobin 1913; Balduf 1926) and of *P. rutilus* Nees (Jackson 1928) and the available data on the genus are summarized by Clausen (1940).

*Beauveria bassiana* belongs to the Deuteromycetes Moniliales and is the fungus causing the muscardine disease of the silkworm (see Steinhaus 1947, 1949). Sussman (1952) lists sixty-three species, including the Colorado beetle, *Leptinotarsa decemlineata*, parasitised by *Beauveria bassiana*, while the most recent investigations on the genus *Beauveria* Vuill. are those of MacLeod (1954).

*Perilitus dubius* (Wesmael) (Hymenoptera, Braconidae) is parasitic in its larval stages on the adults of *Phytodecta olivacea*. In the 5 years of this study the wasp has been captured in the field on only five occasions (see Richards 1960). The rarity of the capture in the field must be due to the elusive behaviour of the parasite, as its larvae occurred in considerable numbers in the beetles and the wasps have been bred out of the host-beetles in four successive years. We have also bred two wasps from larvae collected in the field on 6 August 1957. A fuller account of the biology of *Perilitus dubius* is given elsewhere (Waloff 1961) and only a brief summary follows. The braconids insert the ovipositor in the membrane between the head and the thorax of the host. The eggs and the recently hatched



larvae are usually found in the thorax, while the older larvae lie in the abdominal haemocoel. From one to seven larvae have been found in one host beetle, but the usual number is two or three. As described by Ogloblin (1925) and by Jackson (1928, 1935), the embryonic membrane encloses the larva after hatching but the cells dissociate, absorb nutrients, enlarge and proliferate and form the main food of the growing larvae. The larvae hibernate within the hibernating host and the adult braconids emerge in the following spring and summer. The adult wasps are short-lived and in captivity the majority survived for under a fortnight. Only one or two wasps per host emerged from the beetles isolated in the laboratory. The beetles died after the emergence of the parasite and never came up from hibernation in the soil. The emergence of *Perilitus* adults in the laboratory jars fell into two distinct periods, the first in early May and the second a month or 5 weeks later, in June. The early emergence was entirely from the hosts of the previous year's spring generation and the later one from the later members of the spring generation, but mainly from the beetles of the autumn generation (see table 9). An August or September emergence was never obtained in the laboratory though it must occur in the field.

TABLE 9. DATES OF EMERGENCE OF *PERILITUS DUBIUS* IN THE LABORATORY FROM ADULT *PHYTODECTA OLIVACEA* COLLECTED IN THE FIELD THE PREVIOUS YEAR

field collections of <i>Phytodecta</i>	emergence of <i>P. dubius</i> in the laboratory	field collections of <i>Phytodecta</i>	emergence of <i>P. dubius</i> in the laboratory
24. vi.—22. vii. 55	7–9. v. 56	29. vii.—11. viii. 55	18. vi.—2. vii. 56
5. vi.—24. vii. 56	8–22. v. 57	7 viii.—25. ix. 56	17–25. vi. 57
6. vi.—2. vii. 57	12–16. v. 58	—	—
17. vi.—1. vii. 58	6–7. v. 59	23. viii. 58	4–5. vi. 59
		5. viii.—9. ix. 58	10–29. vi. 59

It thus appears that the date of the emergence of the parasite is in some way controlled by the host as, for instance, is that of *Diplazon* by its syrphid hosts (Schneider 1951). Although there may be only one generation a year, its emergence is so spread out in time as to coincide with the periods spent by the two generations of the host on broom. It is considered that the times of the laboratory emergences are well in advance of the field ones, as the parasitized field beetles have been found between 21. vi. and 11. x. 54; 24. vi. and 13. x. 55; 5. vi. and 16. x. 56; 12. vi. and 10. ix. 57; and 17. vi. and 9. ix. 58.

*P. dubius* must be considered as essentially adapted to the autumn generation of *Phytodecta*, as no parasitic larvae were found in the host beetles at the time of their greatest abundance in the field in the spring. In the years 1954–57 the maxima of the spring generation of *Phytodecta* and the highest percentage of parasitism by the braconid are as much as 4 to 5 weeks apart, and as much as 10 in 1958. In other words, the greatest incidence of parasitism in the spring generation occurs when the numbers of the hosts are rapidly declining. On the other hand, the greatest degree of parasitism synchronizes perfectly with the maxima of host numbers of the autumn host generation in 1954, 1956 and 1957. In 1955, the maximum of parasitism occurred in 2 of the 7 possible weeks of the greatest host abundance, while in 1958 the autumn peak numbers of the beetles, which were late and occurred in the first half of September, were missed by the parasites. Table 10 summarizes the data of the times of the greatest numbers of the spring and autumn

generations of *P. olivacea* and the dates of the greatest incidence of parasitism. The percentages were obtained from dissections of weekly samples of beetles. The high level of parasitism in the late members of the spring generation is due to the lingering on broom of the parasitized beetles.

TABLE 10. DATES OF THE PEAK NUMBERS OF THE SPRING AND AUTUMN ADULTS OF *PHYTODECTA OLIVACEA* AND OF THE MAXIMUM PARASITISM BY *PERILITUS DUBIUS*

year	1954	1955	1956	1957	1958
generation: spring					
date when beetles most abundant	8. vi.	3. vi.	29. v.	28. v.	4. vi.
no. beetles on this date	10400	10200	10000	4100	2500
date max. % parasitism	12-19. vii.	8. vii.	10-17. vii.	25. vi.	12. viii.
parasitism in this period (%)	32	27	25	40	65
average no. beetles in this period	2100	2300	1900	1400	500
generation: autumn					
date max. no. field beetles	6-20. ix.	11. viii.-22. ix.	28. viii.-18. ix.	23. vii.-10. ix.	2-30. ix.
date max. % parasitism	6-20. ix.	18-25. viii.	28. viii.-4. ix.	7-20. viii.	12-26. viii.
parasitism in this period (%)	27	30	55	31	20

TABLE 11. PERCENTAGE OF PARASITISM OF *PHYTODECTA* ADULTS BY *PERILITUS DUBIUS* BASED ON DISSECTIONS OF WEEKLY SAMPLES

year	no. dissected	parasitism (%)	no. hosts emerged in field*	calculated no. of parasitized hosts
spring generation				
1954	409	5.6	11300	661
1955	522	5.5	16184	890
1956	565	4.8	17027	817
1957	304	13.1	6393	837
1958	510	6.5	6757	439
autumn generation				
1954	376	11.5	34055	3916
1955	404	9.9	37844	3747
1956	119	26.4	5297	1398
1957	194	17.6	7344	1293
1959	112	5.0	5356	263

\* Sum of weekly estimates divided by 'time spent on broom'.

With the exception of 1958, not only the percentage of parasitism but also the actual numbers of parasitized beetles were always higher in the autumn than in the spring generation (table 11). As may be seen, in 1954 and in 1955 the sizes of the population of *Phytodecta* and the degree of parasitism were very similar, but a conspicuous change occurred in the autumn generation of 1956. It may be recalled that much of the broom died in the winter of 1955-56 and that the area covered by the living bushes was reduced. This shrinkage of the habitat led to the great destruction of the eggs and larvae of *Phytodecta* by the predators (see p. 239).

The resultant autumn generation of beetles was only a seventh of that in the previous years, and this small number of hosts was more heavily attacked by *Perilitus* than in any other year. Although the absolute number of parasitized beetles was lower than in the preceding seasons, the proportion of the population attacked was the highest recorded (26.4%). The high percentage of parasitism was maintained in the two generations of 1957, but fell to 5.0% in the autumn of 1958. It is considered that this low level of parasitism may be connected with the unfavourable weather throughout the summer of 1958. The month of August was characterized by the lowest numbers of hours of sunshine in the years 1954–58 (121.1, i.e. 63 h below the Kew average) with 25 days below the daily average for this month, whereas the highest rainfall for the 5 years in September again occurred in that year (see Table 32). Unfavourable weather may have interfered with the searching behaviour of *Perilitus* and this may partly explain the low degree of parasitism of the autumn beetles.

TABLE 12. PERCENTAGES OF THE SPRING AND THE AUTUMN GENERATIONS OF *PHYTODECTA* INFECTED WITH THE FUNGUS *BEAUVERIA BASSIANA* CALCULATED FROM WEEKLY SAMPLES OF THE HOST

The numbers dissected are the same as in table 10.

year	generation of host	percentage found to be infected with fungus
1954	spring	24.7
	autumn	11.5
1955	spring	20.9
	autumn	19.0
1956	spring	2.3
	autumn	0
1957	spring	0
	autumn	0
1958	spring	3.5
	autumn	3.6

*Phytodecta* adults are killed by the parasitism of *Perilitus*. Even when the parasitic larvae are quite small the host ovaries begin to atrophy, though oviposition continues for a short period; by the time the larvae are fully grown, the internal organs of the host are exhausted and shrunken and even the abdominal and thoracic muscles are reduced to thin threads. The effect of the fungus *Beauveria bassiana*, the second prevalent parasite of the adult beetles, is also to kill the host. Dead beetles in tubes and jars may be completely ensheathed by a soft white mycelium which becomes chalky and dry after the insect has been dead some time. In dissections of weekly samples of beetles preserved in 70% alcohol, the fungus could be seen to form white, chalky growths in the fat body, the muscles and sometimes in the gut of the host. The percentages of dissected beetles indentified with certainty as infected with *Beauveria* are given in table 12. There is little doubt that these estimates are too low, as the early stages of infection and the fungal spores were not looked for. Thus, *Beauveria* probably did not entirely disappear from the autumn generation in 1956 or throughout 1957, as some beetles died of the fungal attack in tubes and in jars, but it was sufficiently scarce to escape detection in dissections.

There is some evidence that death of the beetles in the soil due to *Beauveria* and to other causes occurred throughout the summer and the autumn months, as the numbers of live *Phytodecta* calculated from the soil samples taken at the end of October and in November tend to approximate to the numbers emerging in the following spring and are much more close to them than to the numbers calculated to have lived on broom in the current year. It may be seen from table 13 that in spite of the great standard errors in the estimates of the numbers of beetles in the soil, they indicate that the bulk of the mortality occurs before the onset of winter.

TABLE 13. NUMBERS OF *PHYTODECTA* IN SOIL IN LATE OCTOBER AND NOVEMBER (ESTIMATED FROM SOIL SAMPLES) AND THE NUMBERS EMERGING IN THE FOLLOWING SPRING (ESTIMATED BY DIVIDING THE SUM OF WEEKLY TOTALS BY 'THE TIME SPENT ON BROOM')

year	area under broom (ft. <sup>2</sup> )	no. soil samples	total no. beetles in samples	95 % fiducial limits of no. beetles in col. 4*	no. beetles in soil	no. beetles emerging in the following spring
1954	18968	153	10	4.80-18.39	14095	16184
1955	18356	201	12	6.20-20.96	12470	17027
1956	9393	200	6	2.20-13.66	3208	6393
1957	10248	201	5	1.62-11.67	2892	6757

\* Treating the number of beetles in soil samples as a Poisson distribution; 95 % fiducial limits of the number of beetles in the samples from Pearson & Hartley (1954), table 40.

It should be recalled (table 8) that the mortality of the beetles in jars approximates to the mortality in the field much more closely than to that apparently due to the combined effects of *Perilitus* and *Beauveria*. This is due to several causes, the greatest being the underestimate of death due to *Beauveria*, when early infections are unrecognized. It is noteworthy that in the three successive generations of *Phytodecta*, when *Beauveria* was not detected in dissections, the percentage of deaths attributed to unknown causes dropped considerably (see table 14). Predators may also contribute to mortality of the beetles in the soil. A certain, though probably a small number of beetles also disappear from the field each year as the result of dispersion (see p. 224).

Another cause of death of the spring generation can be called 'old age'. Whereas each autumn generation consists of the progeny of the current year, each spring generation is composed of the survivors of the autumn and spring beetles of the preceding year. Beetles emerging in the autumn of year 1 may emerge and reproduce in the spring of the years 2 and 3. Only extremely rarely will they survive and reproduce in year 4, although in the 6 years of these observations, one female out of the total of over 500 beetles kept as pairs in tubes did emerge and oviposit in the fourth season.

It is safe to assume that the beetles which survive from the spring generation of the preceding year will die out after reproducing in the current year. Some idea of the proportions of the generations surviving to the following year has been obtained by keeping weekly samples of *Phytodecta* in large jars and estimating their mortality. These data have been summarized in table 8, where column 8, which represents the 'estimated numbers emerging next year', consists of the spring and the autumn generations in the following proportions: 1:5.07 in 1955; 1:2.42 in 1956; 1:0.79 in 1957 and 1:2.59 in 1958. The old beetles can be assumed to die of 'old age' in the current season. A set of 105 soil samples

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TABLE 14. SURVIVAL OF *PHYTODECTA OLIVACEA* ADULTS

1 year	2 genera- tion	3 no. emerged (sum of weekly totals divided by time spent on broom)	4 proportions of spring and autumn generations in col. 3	5 with <i>Perilitus</i> no. % with <i>Beauveria</i> no. % with <i>Perilitus</i> and <i>Beauveria</i> % no.	6 no. dying of 'old age' i.e. survivors of previous year's spring genera- tion, minus those para- sitized (see cols. 4, 5)	7 no. removed from field laboratory, minus those parasitized, * or para- sitized and dying of old age (see cols. 5, 6)	8 accounted for in previous columns no. % those emerged of col. 3	9 autumn deaths on broom and in soil and possible emigration, i.e. no. not previously accounted for
1954	spring	11 820	—	5.6 663 24.7 2 924 30.3	—	943—(30.3%) = 657	6 912 58.5	4 908 41.5
	autumn	34 055	—	14.2 4 849 11.5 3 923 25.8	—	500—(25.8%) = 371	22 659 66.5	11 396 33.5
1955	spring	16 184	1:5.07 2 668:13 516	5.5 882 20.9 3 391 26.4	(2 668—26.4%) = 1 964 = 12.1%	1 180—(26.4%+12.1%) = 726	11 943 73.8	4 241 26.2
	autumn	37 844	—	9.9 3 749 19.0 7 202 28.9	—	969—(28.9%) = 689	23 278 61.5	14 566 38.5
1956	spring	17 027	1:2.42 4 980:12 047	4.8 815 2.3 3 95 7.1	(4 980—7.1%) = 4 626 = 27.2%	1 100—(27.2%+7.1%) = 723	10 113 59.4	6 914 40.6
	autumn	5 297	—	26.4 1 400	—	239—(26.4%) = 176	4 302 81.2	995 18.8
1957	spring	6 393	1:0.79 3 554:2 839	13.1 839	(3 554—13.1%) = 3 088 = 48.3%	728—(13.1%+48.3%) = 281	6 090 95.3	311 4.7
	autumn	7 344	—	17.6 1 291	—	370—(17.6%) = 305	6 471 88.1	873 11.9
1958	spring	6 757	1:2.59 1 882:4 875	6.5 436 3.5 235 10.0	(1 882—10%) = 1 694 = 25.1%	1 033—(10.0%+25.1%) = 670	4 293 63.5	2 464 36.5
	autumn	5 356	—	5.0 270 3.6 192 8.6	—	237—(8.6%) = 217	3 421 63.9	1 935 36.1
1959	spring	4 000 (approx.)	1:2.18 1 258:2 742	—	—	—	—	—

\* The number parasitized is subtracted from those taken into the laboratory because the percentage parasitism has been calculated on the whole population on each date (including those removed).

was taken and examined in July 1955, before the autumn generation began to descend into the soil and it was estimated that only 5953 of the 16184 which had emerged in that season, were still alive.

These data are summarized in table 14, and the arguments which were used in its construction are given below for 1 year, namely, for 1955.

First, it was calculated from the sum of weekly estimates of the population in the field divided by the time spent by beetles above ground that 16184 *Phytodecta* emerged as the spring generation.

Secondly, from the survival of the 1954 beetles of the spring and of the autumn generations kept at out of door temperatures through the winter, it was estimated that the 1955 spring generation was composed of these two groups of beetles in the proportion of 1:5.07. Thus there were 2668 old and 13516 young beetles. The older group of 2668 died of 'old age' after reproducing in 1955. However, 26.4% of this group were parasitized and the reduction of the population due to 'old age' alone was equal to (2668-704), i.e. 1964 or 12.1%.

Thirdly, the mortality due to parasitism was estimated by dissection of weekly samples and it was found that 5.5% of the population, or 882 beetles, were infected with *Perilitus* and 20.9%, or 3391 with *Beauveria*.

Fourthly, 1180 or 7.3% of the population was removed to the laboratory for dissections, etc. Since some would have died of 'old age' and of parasitism (i.e. 12.1+26.4%, see table 14, col. 7), 454 beetles can be subtracted from this total and the removal is equivalent to 726. In tables 37 and 38 the removal is treated as one of the causes of mortality.

Fifthly, the 1956 spring generation of 17027 consisted of spring and autumn beetles in the proportions of 1:2.42 or of 4980:12047.

Thus the total number of beetles accounted for is:

4960—surviving to next spring;

4273—or 26.4% killed by parasites;

2668—dying of 'old age'; 26.4% or 704 of these were also parasitized;

1180—removed to the laboratory, but 26.4% of them would have died of parasitism and 12.1% of 'old age', i.e. 454 beetles should be subtracted from this total.

Thus the total is 13101 - (704 + 454) or 11943 beetles. This leaves 4241 or 26.2% of the estimated 16184 not accounted for, but it is considered that mortality due to *Beauveria* is underestimated in dissections. The fall in the numbers of beetles may also be due to other factors, for instance to predation, which has not been considered and also to dispersal and emigration from the area of old broom.

#### DISPERSAL OF ADULT *PHYTODECTA*

One would expect a beetle with specialized feeding habits to have good means of dispersal. The wings of *Phytodecta olivacea* are large and no reduction of the wing muscles has been noticed in dissections. Yet the beetle has very rarely been seen to fly during the 5 years it was intensively studied or indeed over the last 13 years. Nevertheless, the beetle is found at Silwood on several small groups of broom bushes widely separated from the main area. Specimens suspended from the thorax will fly in the laboratory but only when

warmed up and only for 1 to 7 seconds. One was once seen to fly in the field when on a beating tray (30 July 1957, temperature 65 to 70 °F).

It was thought that there might be a dispersal flight soon after emergence from hibernation as recorded by Gradojević (1953; pp. 28–9) in *P. fornicata* Brüggm. In this species, after the maturation of the eggs no long flights were recorded. We attempted to detect flight by means of traps of two kinds. The first were two ‘window-traps’ (figure 2, plate 14) as described by Chapman & Kinghorn (1955). The beetles fly into a pane of glass (3 ft. 3 in. × 2 ft. 3 in.) and drop into a trough of water. In 2 years 1955–56 only one female was found in the trough of water. It was caught on 31 May 1956 and on dissection was found to be quite immature. As well as the ‘window-traps’, eight groups, each consisting of five potted plants, were distributed within, or near to the colony of broom. The potted plants were 1½ years old and up to 3 ft. in height. Six groups each of five pots were placed in the gaps between the broom, from 5 to 20 ft. away from the nearest bushes, while two of the groups were placed outside the broom area; one about 50 ft. and the farthest 100 ft. away from the main broom colony. All the forty plants were shaken on to a white beating tray three times a week, between 4 May and 1 June 1956 and any insects were recorded and removed. Altogether twenty-five *Phytodecta* (11♀, 14♂) were found in these plants between 11 May and 1 June, twenty-three of them on the groups of plants within the broom colony and two males (both on 31 May 1956) on the potted plants 100 ft. away. It may be of interest that as compared with the 25 *Phytodecta*, 409 *Sitona regensteiniensis* (Herbst), a beetle which is restricted to broom and gorse (*Ulex europaeus* L.), were shaken off these plants at the same time. Most of the females of *Phytodecta* were immature, but they were feeding actively, as their intestines were full of food. It is considered that much of the dispersal of *Phytodecta* is by walking rather than by flight, although it is unlikely that the two males on the potted plants 100 ft. away from the main broom colony found the food-plant by walking alone. Similarly, it is much more likely that the female in the ‘window-trap’ was caught on wing. Yet another example of a female *Phytodecta* caught in flight was provided by Dr Trevor Lewis who found the beetle in a suction-trap at crop level in the middle of a wheat field 400 yards away from the broom plantation on 8 June 1958, between 6 and 7 G.M.T. when the air temperature varied between 10 and 12 °C.

There are four areas with concentrations of *Sarothamnus scoparius* at Silwood Park, but a number of scattered bushes, up to 200 yards away from these areas occur throughout the field station. *Phytodecta* is found on most of the scattered bushes, in other words the species has sufficient powers of dispersal. One of the areas of concentration of broom is a new plantation of 1600 bushes in twenty-four rows, which were planted out as seedlings in March 1957. Between 3 June and 4 July 1957, every eleventh seedling was infected with five first-instar larvae of *P. olivacea*. By 20–21 August 1958 the beetle appeared to be evenly distributed throughout the plantation, as when the plants were shaken on to a beating tray, it occurred in every 3·7 uninfected and 3·5 infected bush. A suction-trap was set on 3 June 1959 in the middle of this broom plantation, but no *Phytodecta* were caught in it throughout the summer. As has been suggested, it is likely that dispersal to neighbouring bushes is by walking, especially at the times of descents and ascents of the spring and autumn generations to and from the soil. It also seems that on rare occasions the

beetles will take to wing, although flight may be confined to a short part of their lives, when they are still immature. The magnitude of the loss from the field due to dispersion is not known, nor is it known whether many of the beetles survive after leaving the concentrations of the broom bushes. In some species of insects a very high degree of mortality occurs during dispersal. It has recently been shown by Dethier (1959) mortality of the larvae of the butterfly, *Melitaea harrisii* Scud. may be as great as 80% during dispersal, owing to failure to find new host plants. On the other hand analysis of the random dispersal in theoretical populations (Skellam 1951) suggests that dispersal by walking would be a very slow process and that rare accidental displacements due to external agencies are of great importance in the spread of a species. Probably, the spread of *Phytodecta* is a combination of 'random' walking and accidental displacements (flight, etc.), which might together explain all our observations.

THE DATES OF EMERGENCE OF ADULT BEETLES AND THE LENGTH OF TIME  
SPENT ON BROOM

There are two emergences of adults a year. The spring generation is composed of survivors of the previous year's spring generation and of the 'autumn' generation. These have all overwintered as diapausing adults. The second, i.e. the summer-autumn emergence is of new beetles which emerge from the pupal stage in the soil, without an intervening diapause. The physiological process underlying these two emergences, in the three different sets of beetles are thus dissimilar.

TABLE 15. THE SEX-RATIO OF THE SPRING AND AUTUMN BEETLES IN 1954-58

The numbers examined (beetles from 100 beats each week) are given in brackets

	spring generation	autumn generation
1954	1 ♂:0.9 ♀ (1213)	1 ♂:1.7 ♀ (828)
1955	1 ♂:1.3 ♀ (1256)	1 ♂:1.1 ♀ (1020)
1956	1 ♂:1.0 ♀ (1971)	1 ♂:1.2 ♀ (250)
1957	1 ♂:1.4 ♀ (781)	1 ♂:1.3 ♀ (328)
1958	1 ♂:1.3 ♀ (1070)	1 ♂:1.2 ♀ (244)

TABLE 16. DATES OF THE FIRST AND LAST ADULTS OF THE SPRING GENERATION

year	1954	1955	1956	1957	1958	1959
beginning of emergence	27. iv.	20. iv.	24. iv.	26. iii.	29. iv.	20. iv.
last seen	25. x.	22. ix.	18. ix.	10. ix.	23. ix.	—

In the spring the males begin to emerge 2 or 3 weeks before the females and then, after the peak number in the field has been reached, they gradually descend back to the soil to hibernate for the second time, or to die. The females linger on in the field and overlap with the autumn generation. In the autumn generation the sexes occur in equal numbers throughout the time which they spend on broom.

The totals of the males and females which emerge throughout the whole season are approximately equal and are given in table 15.

The beginning of the spring emergence was usually towards the end of April, except in the warm spring of 1957, when the first beetles were seen a month earlier i.e. at the end of March (see table 16).



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From 1955 to 1959 continuous records of temperatures under a broom bush, at an inch below the soil covered by litter, i.e. in the hibernating sites of *Phytodecta* were taken with a mercury-in-steel thermograph. Some of these temperatures are summarized in table 17 and suggest that average soil temperatures above 5 °C lasting for 3 to 4 weeks stimulate the beetles to emerge. However, in the early months of 1957 the temperatures were sufficiently high for emergence to occur in January, or in February and since it did not take place, other requisites, such as the time factor in the breaking of the diapause may also have been operating. It is also possible that maximum temperatures might be more efficacious than averages.

The average daily maxima preceding emergence were above 8.1 °C (4 weeks) or 8.5 °C (3 weeks), but these averages again failed to explain why the beetles did not emerge in January and in February of 1957.

TABLE 17. AVERAGE MONTHLY SOIL TEMPERATURES (IN °C) RECORDED WITH A MERCURY-IN-STEEL THERMOGRAPH, 1 IN. BELOW THE SOIL AND LITTER UNDER A BROOM BUSH

year	Jan.	Feb.	Mar.	Apr.
1955	2.9	2.1	2.0	6.4
1956	3.5	0.5	3.1	5.3
1957	6.5	7.5	8.8	9.9
1958	3.6	5.0	3.2	5.5
1959	2.3	0.8	—	7.6

TABLE 18. DATES OF EMERGENCE OF THE SURVIVORS OF THE SPRING GENERATION OF *PHYTODECTA* IN THE FOLLOWING YEAR. BEETLES KEPT IN JARS (1955–59) (DURING WINTER OUT OF DOORS)

month beetles collected in previous year	no. emerged	dates and percentage emergence in the following year				
		20–30. iv.	1–10. v.	11–20 v.	21–31. v.	1–10. vi.
April	12	100	—	—	—	—
May	27	74	26	—	—	—
June	123	39	46	11	2	1
July	148	15	55	24	6	—
August	62	16	39	45	—	—
September	8	75	—	25	—	—

In the field, the spring emergence is gradual and continues for 6 to 8 weeks before the peak numbers for the season are reached. The wave of greater emergence, which includes both sexes, begins when the weekly soil temperatures reach the averages of 9.5 to 11 °C.

The influence of the time factor on the duration of the imaginal diapause, and subsequently on the time of emergence is also suggested in the distribution of the emergence dates of the spring beetles, which had been kept at out of doors temperatures. It appears that the survivors of the beetles collected late in season 1, tend to emerge later in the spring of season 2 (see table 18). This is not true of the survivors from the September collections, but their number is very low.

No suggestion of this relationship was detected in the spring emergence of the previous year's autumn beetles. The length of time that the spring population of beetles can be found on broom varies with each year (see table 16), but the majority of them descended into the soil when the day length was still increasing, i.e. before 21 June. The percentage

of the total population which was in the soil before this date was 56·1, 69·1, 71·2, 75·0 and 79·3 in 1954–58, respectively. The percentage of the total spring population which persists on broom in the conditions of decreasing day length is composed almost entirely of females and corresponds to about 50 to 70 % of the total female population. These beetles, together with the autumn generation of adults thus live in conditions of decreasing day length.

It is possible that the duration of the period spent on broom is to some extent determined by temperature, as the greater part of the spring generation beetles disappeared from the field most rapidly in the warm summers of 1955 and 1959. Moreover, the beetles transferred to a constant temperature of 25 °C entered hibernation more rapidly than those kept at room temperature. Whereas the females generally continue to oviposit until the middle of September, the last eggs to be seen in the field in the warm summer of 1955 were in the middle of August.

Each year, the first appearance of the autumn generation is largely determined by the time of emergence of the spring females and by the duration of the developmental period of the immature stages, which are dependent on temperature. Table 19 gives the dates of the first and the last appearances of the autumn adults.

TABLE 19. DURATION OF DEVELOPMENTAL PERIODS OF IMMATURE STAGES OF *PHYTODECTA* ON BROOM AND THE FIRST AND LAST DATES OF THE ADULTS OF THE AUTUMN GENERATION

year	1954	1955	1956	1957	1958	1959
duration of immature stages on broom (weeks)	5·82	4·75	5·97	4·57	5·69	—
first date of autumn adults	3. viii.	22. vii.	7. viii.	16. vii.	29. vii.	8. vii.
last date of autumn adults	1. xi.	13. x.	23. x.	8. x.	14. x.	—

The presence in the field of the autumn generation for a period of approximately 3 months is not due to the time which any individual spends on broom, which is short (see table 5) but to the protracted emergence of the spring beetles and the long oviposition and developmental periods.

It may be concluded that the spring generation leave the soil when it begins to warm up but probably a minimum time of diapause is also necessary at least at ordinary outdoor temperatures. This generation tends to re-enter the soil when the hours of daylight are no longer increasing much, or are decreasing, and does so more rapidly at high temperatures. The autumn generation leave the soil as soon as the pupal period is ended and re-enter the soil after a short period of feeding and accumulating reserves. The long period spent by this generation on the broom is not due to the time spent on it by any one individual, but to the spread in date of emergence (and ultimately of oviposition by their parents).

#### OVIPOSITION IN *PHYTODECTA*

Although the average time spent by a female on broom is short, the oviposition period of the population as a whole is a long one. The dates between which eggs occur in the field (table 20) is an underestimate of this period, as most of the early eggs are destroyed by predators and hence do not appear in the samples. Again, the last date cannot be considered to be precise, as by that time the ovipositing females and the eggs are very scarce and may fail to appear in the samples.

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For records of oviposition, pairs of beetles were kept in 3 in. × 1 in. tubes containing  $\frac{1}{2}$  in. of sand at the bottom and a sprig of broom which was regularly renewed. The tubes were closed with a bored cork and a piece of muslin and were kept in the laboratory with a thermograph nearby. In the laboratory tubes the beetles stayed up on broom longer than in the field and in the big jars. The extended oviposition period in the field is explained partly by the protracted emergence period of the beetles and also by the extreme length of time which a relatively small number of females spends on broom.

As has been described on p. 213, regression equations relating the number of eggs laid by a female a day can be calculated experimentally. The equations based on the daily oviposition rate in the laboratory can be transferred to the field, where temperatures were recorded in the Stevenson screen in the broom area, and the 'age in days' was that of the female population as a whole. The application of the method to the data in 1955 is shown in appendix 1.

TABLE 20. DATES BETWEEN WHICH EGGS HAVE BEEN SEEN IN THE FIELD

year	1954	1955	1956	1957	1958
dates	1. vi.–25. viii.	12. v.–12. viii.	28. v.–12. ix.	15. v.–12. ix.	20. v.–8. ix.
no. days	86	93	108	111	112

TABLE 21. MEAN DAILY OVIPOSITION RATE AND AVERAGE FECUNDITY OF *PHYTODECTA* IN THE FIELD

year	1954	1955	1956	1957	1958
mean daily oviposition rate/♀	2.35	2.78	3.67	2.80	1.92
mean fecundity/♀	77.3	71.4	78.3	58.7	32.9

The average fecundity of *P. olivacea* given by Waloff & Richards (1958) is the potential fecundity under laboratory conditions. In the years 1954–56 it averaged between 250 and 320 eggs per female. These egg numbers are much higher than the estimated averages in the field (see table 21), but in the laboratory experiments, the females which died of *Beauveria* and *Perilitus* were not included in the calculations. Moreover, the time which the females spent on broom in tubes was greater than that in the jars and in the field. In the calculations of the regression equations, however, all the field females were included automatically, whether they laid eggs or not and whether they were attacked by parasites or remained healthy.

The annual variations in fecundity shown in table 21 are not due to the changes in the mean weights of females which varied very slightly from year to year (p. 230) and probably independently. If the figures are compared with those in table 4 giving the length of time which the females spent on broom there is again not a good correlation though both sets of figures are higher in the first 2 or 3 years. There is a marked discrepancy, however, in 1957 when there is a reduction in fecundity, but not in the time spent on broom. It seems possible that a deterioration of the nutritive quality of the ageing broom plants may have contributed to reduced fecundity in the last 2 years.

The regression equations used in estimating the oviposition rate were calculated from new data each year, as it was not known whether the differences between them would be

significant from season to season. There are several assumptions which are implicit in the use of these equations. The first is in assigning a single mean age to a population of females which emerges over a period of several weeks. However, the laboratory data were also derived from a heterogeneous age group, as the early sets of females were supplemented by field beetles at successive later dates in the season. Secondly, factors other than age and temperature may influence fecundity. For example, it is known that a relationship exists between the weight of the mature females and the total number of eggs laid. Donia (1958) by using a multiple regression analysis of the effects of temperature, age and weight of the female on the oviposition rate, has shown that 16% of the total variation was induced by the effects of weight. The variations in the weights of the females selected by him for the experiment, were considerably greater than those encountered in the field populations, in which the means lay between 11.5 and 12.4 mg in the 5 years of this study. It is thus probable that in the field conditions, the weights of the females contributed to less than the 16% variation, quoted above. In Donia's analysis, temperature contributed to 21%, and the age of the females to 44% of the total variation in the oviposition rate, whereas the remaining 19% was due to unknown causes. Amongst the latter is the influence of the state of the food plant. In a set of preliminary experiments we found that fecundity was higher when the beetles were feeding on the young broom shoots, than when they were given older shoots, with old leaves (Waloff & Richards 1958). These observations were extended and confirmed by Donia. Much of the broom was dying of old age throughout this study and some of the variations in fecundity were probably due to the altering state of the food plant.

TABLE 22. REGRESSION EQUATIONS FOR THE OVIPOSITION RATE PER FEMALE PER DAY

$y$  = number of eggs;  $b_1$  = regression due to age of population in days;  
 $b_2$  = regression due to temperature ( $^{\circ}$ F).

year	regression equations	significance		standard error	
		$b_1$	$b_2$	$b_1$	$b_2$
1954	$y = -0.02974b_1 + 0.14568b_2 - 4.62983$	***	***	$\pm 0.00276$	$\pm 0.03082$
1955	$y = -0.02603b_1 + 0.14235b_2 - 3.80829$	***	*	$\pm 0.00598$	$\pm 0.05374$
1956	$y = -0.03170b_1 + 0.21770b_2 - 7.3859$	***	*	$\pm 0.00576$	$\pm 0.08564$
1957	$y = -0.02081b_1 + 0.12553b_2 - 3.63288$	*	***	$\pm 0.12553$	$\pm 0.02861$
1958	$y = -0.04519b_1 + 0.43910b_2 - 21.0296$	***	***	$\pm 0.43910$	$\pm 0.06991$

Meaning of asterisks: \*\*\*  $P < 0.001$ ; \*  $P < 0.05$ .

The calculated regression equations for the daily oviposition rate per female are given in table 22. To see whether the regression coefficients  $b_1$  (due to age in days) and  $b_2$  (due to temperature), differed significantly from year to year, a simple test was applied on the suggestion of Dr R. E. Blackith. When the difference between  $b_1$  of year 1 and  $b_1$  of year 2 exceeded the sum of their standard errors, it was considered to be probably significant at the 5% level. The regression coefficients for 1958 differ from those of the preceding years, while those of the other 4 years appear to be homogeneous.

As this divergence was encountered in the five regression equations, it was considered that the use of yearly equations was preferable to that of a single generalized one.

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## THE DISTRIBUTION OF EGGS AND LARVAE ON BROOM

The eggs are mainly laid on the upper surfaces of the leaves, occasionally on the sides of the young growing shoots and also amongst the dense hairs which fringe the young broom pods. In July 1955 an attempt was made to see whether the larvae occur on certain parts of broom in preference to others. The broom shoots were subdivided into three categories: the 'new', which were the young shoots of the current year's growth and which bore no pods; the 'medium-aged' shoots, which had pods but also bore some new side shoots and leaves, and lastly the 'old', which had pods and bore only the first leaves of the season, i.e. which did not show any current year's stem growth. A number of 60 ft. lengths of tape were stretched across the bushes in different parts of the area, and any shoot which touched the tape was examined and classified. Altogether 1207 ft. were thus sampled, and they included 1358 shoots, 324 or 24% of which were 'new', 315 or 23.2% 'medium' and 717 or 52.8% 'old'. This shows the proportions of the three types of shoots and makes possible an analysis of the distribution of early stages on the shoots in the routine samples.

Between 12 July and 14 September 1955 the standard samples (broom cuttings) were subdivided into the three types of shoot. There was little rain in 1955, high temperatures prevailed in July and August and the larvae developed rapidly and none was seen after 2 September. Very few eggs were seen on the samples, as the peak of the oviposition period was already over, but in making the estimate of the distribution of the early stages of *Phytodecta*, the hatched eggs adhering to broom are here included with the intact ones, as they also serve to indicate the sites of oviposition. Between 25 July and 30 August 1120 cuttings of broom were examined and the immature stages of *Phytodecta* were found on 261 of them. There was no difference in the frequency of occurrence of the egg and larval stages on the 'new' and the 'medium' shoots and hence they are treated together in table 23.

TABLE 23. DISTRIBUTION OF IMMATURE STAGES, i.e. THE FREQUENCY OF OCCURRENCE OF *PHYTODECTA* ON BROOM SHOOTS OF DIFFERENT AGES (1120 cuttings taken between 25 July and 30 August 1955.)

dates	...	...	25. vii.–12. viii.		16–30. viii.	
			'new' and 'medium' shoots	'old' shoots	'new' and 'medium' shoots	'old' shoots
shoots with eggs and hatched eggs (%)			19.4 (0.9 on pods)	11.1 (5.3 on pods)	8.7	3.6
shoots with I and II larvae (%)			5.7	0.3	1.4	0.5
shoots with III and IV larvae (%)			4.3	0.6	2.9	1.1

It can be seen that more eggs were laid on the 'new' and the 'medium' shoots than on the 'old' and when they were laid on the 'old' they were frequently laid on pods. Again, most of the larvae between 25 July and 12 August occurred on the younger parts of broom and frequently the first-instar larvae were found near the tips of the growing shoots. By 16 to 30 August the distribution became more uniform, indicating that the older larvae move more and wander on to the older parts of the plant.

## ESTIMATION OF MORTALITY IN THE IMMATURE STAGES

The numerical method of estimating the mortality of the early stages is described on p. 214 and the data from which the mortality in the egg stage can be calculated are given in table 24. It is probable that the field records of numbers of eggs are liable to considerable sampling errors. It is also certain that the mortality is not the same from week to week as is assumed by the formula. In a population of caged locusts it is possible to measure the error introduced by irregular mortality (Richards *et al.* 1960) but this cannot be done in the field. As a result of the errors from these two sources, it is not always possible to apply the formula to the records of a single instar, but by grouping two or more of the immature stages, the total mortality in this part of the life-cycle can be calculated.

The durations of the development in days of the eggs, larvae and pupae of *P. olivacea*, at six constant temperatures of 15, 18, 20, 25, 27 and 30 °C were determined experimentally and fitted to Davidson's formula (1944) where  $y$  is equal to  $100(1 + e^{a-bx})K$ ,  $x$  being temperature in °C. The calculated values of the constants  $K$ ,  $a$ ,  $b$  can be found in Waloff & Richards (1958).

TABLE 24. THE DATA USED IN CALCULATIONS OF MORTALITY IN THE EGG STAGE

year	1954	1955	1956	1957	1958
no. eggs calculated by regression equations = $n$	460169	659554	701563	201760	125039
accumulated total of eggs in the field, corrected to daily sampling intervals = $N$	2803388	6304018	3161151	2332428	1513253
average temperature (°C)	13.97	14.05	14.16	15.05	13.79
incubation period (days) = $a$	14.35	14.07	13.65	11.05	15.13
mortality in egg stage (%)	87.2	56.4	94.2	39.0*	37.2
greatest number of empty egg shells in the field	132580	258800	233290	105270	60100

\* In 1957 mortality of 39.0% includes deaths in the egg stage and in the first-larval instar.

The mean temperature at which an instar had developed was calculated as follows. The screen temperature in any sampling interval was multiplied by the number of the instar found in that interval and the sum of all these products was divided by the total number of that instar found throughout its period of occurrence. Having obtained the mean developmental temperature, the duration of the instar was determined from the experimental values of  $K$ ,  $a$  and  $b$ . The duration of the immature stages and the mean temperatures at which they developed are included in tables 24 and 25.

Hatched eggs, or eggs sucked by predatory bugs remain for some time on the broom. The time is variable depending on the weather, but the number present per week tends in each year to rise to a maximum and then remain constant for 2 to 3 weeks. The maximum figure for empty shells is given in the last row of table 23 and gives some confirmation of the magnitude of the counts of eggs.

Table 25 gives the data from which the percentage mortality in the larvae was calculated. Mortality within the fourth-instar larvae included in table 25, applies to the feeding stage on broom only. In 1956 and in 1957 it was impossible to detect mortality in the late

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larvae on broom by this method. It was known, however, that in 1956—2.06% and in 1957—3.03% were parasitized, hence the numbers corresponding with the percentages are subtracted from the figures used in estimation of mortalities in soil (see table 26). The fully fed fourth-instar larvae descend into the soil where they pupate and later emerge as

TABLE 25. DATA USED IN THE CALCULATION OF MORTALITY IN THE LARVAL INSTARS ON BROOM

year	instar	accumulated total, corrected to daily sampling = $N$	mean developmental temperature in °C	duration in days = $a$	calculated mortality on broom
1954	I	1248590	15.4	7.35	eggs and larvae, instars I-IV, 86.1%*
	II	1074276	14.6	5.53	
	III	1764973	14.7	7.28	
	IV	1291514	14.4	6.28	
1955	I	1320967	16.8	6.02	Larval instars I-IV, 52.1%
	II	911078	18.1	3.92	
	III	939407	17.7	4.83	
	IV	729267	16.9	4.41	
1956	I	925057	14.3	7.42	larval instars I-III, 81.9%
	II	477309	14.3	5.67	
	III	321202	13.9	8.26	
	IV	203441	13.9	5.39	
1957	I	451731	16.3	6.44	not detectable in instar IV†
	II	351526	16.7	4.48	
	III	333935	16.7	5.67	
	IV	182707	17.1	4.34	
1958	I	309589	15.9	7.26	eggs and larval instar I, 39.0% larval instar II, 62.4% mortality in instars III and IV not detectable†
	II	225176	15.5	5.06	
	III	170086	14.4	6.74	
	IV	130487	15.1	5.67	

\* This figure is smaller, though not significantly so than the mortality in the egg stage alone. It is probable that much of the predation this year was on the egg stage.

† Mortalities not detectable by the method of integration, but loss due to parasitism estimated by other means.

TABLE 26. PERCENTAGE MORTALITY OF LARVAE AND PUPAE IN THE SOIL

year	calculated no. IV larvae and pupae in the soil	no. emerging as autumn adults	mortality in soil (%)
1954	63939	34055	46.7
1955	137610	37844	72.5
1956	7100	5297	25.8
1957	44826	7344	83.6
1958	10454	5356	48.8

the autumn generation of beetles. The calculated numbers of larvae going down into the soil are those remaining alive, after the total mortality on broom has been estimated, while the death in the soil is equivalent to the difference between this estimate and the total number of beetles emerging as the autumn generation (see table 26). This includes also death in the pupal stage.

## PARASITISM OF EARLY STAGES AND STERILITY OF EGGS

To estimate the extent of parasitism and the degree of sterility, most of the eggs found in the field samples were kept in tubes and examined at later dates, when the numbers hatched or parasitized were recorded. Sterile eggs remained unhatched and rapidly shrivelled up. The estimated percentages of sterile and parasitized eggs are given in table 27. In 1954 a further 1071 eggs laid in the laboratory were examined and their hatching was recorded and the percentage of sterility in them was estimated as 10·1, which is almost identical to that recorded in the field eggs.

TABLE 27. THE PERCENTAGE OF STERILE AND PARASITIZED FIELD EGGS

year	no. field eggs examined	sterile (%)	parasitized (%)	total not hatched (%)
1954	98	10·20	0	10·20
1955	283	6·00	0·35	6·35
1956	337	3·56	0·29	3·85
1957	368	4·89	0·54	5·43
1958	350	8·00	0·57	8·57

As can be seen in table 27 the percentage of sterile eggs was never high and that of parasitized ones almost negligible. The egg parasites which emerged were identified as *Trichogramma* sp. (Hym., Trichogrammatidae) and *Tetrastichus* sp. (Hym., Eulophidae). The greater, remaining part of mortality is considered to be due to predation, mainly by the Heteroptera which live on broom. This important cause of death, together with the evidence for it, is discussed later together with the mortality of the larvae. The effects of the feeding of Heteroptera on the eggs, were frequently seen in the samples. For instance, in 1956 428 intact eggs were found throughout the season and a further 94 damaged and obviously recently half-sucked eggs were also seen in the early part of the season. The fully sucked eggs cannot be distinguished from the hatched ones, nor are the partially sucked ones long identifiable.

The degree of parasitism in the larvae was low, ranging between 2 and 3%. The commonest dipterous parasite was *Meigenia mutabilis* (Fallén) (Tachinidae), although a single specimen of *Macquartia brevicornis* (Macq.) [= *occlusa* Rond.] (det. L. P. Mesnil), was also bred out of a larva. Jolivet (1950) lists *Macquartia occlusa* Rondani amongst the parasites of *Phytodecta olivacea*, but as has been reported elsewhere (Richards & Waloff 1960) this was the first time that this *Macquartia* has been bred in this country.

*Meigenia mutabilis* lays one or two eggs externally, on the beetle larvae, to which they are very firmly fixed. Generally, the eggs are laid on the third- or fourth-instar larvae but rarely also on the second instar. At times, the host escapes parasitism by moulting and casting off the eggs, before the parasitic larvae have had time to hatch. This has been seen to occur four times in the course of the present observations. Normally, the dipterous larvae bore into the beetle larvae where they develop and eventually pupate in the soil inside the skin of the host. The extremely low percentage of larvae with *Meigenia* (see table 28) may have been conditioned by some unfavourable factors in the immediate environment. This was suggested by contrasting the 1·27% parasitism in 1956 with 41·4% infection with *Meigenia* in another broom area, half a mile away from the experimental



plot. It is true that 1.27% is the seasonal mean, whereas 41.4% infection applies to a short period of time between 19 and 23 September 1956 but on no one occasion has this degree of parasitism been seen in the experimental broom area.

*Meigenia* is known to parasitize other chrysomelids and also tenthredinid larvae. The larvae of *Phytodecta* usually became infected with this dipterous parasite throughout July, and the adult flies emerged out of the parasitized larvae throughout the month of August.

The other parasites were hymenopterous. One specimen of *Nepiesta* sp. (Ichneumonidae, det. J. F. Perkins) and two of *Perilitus dubius* (Wesmael), i.e. of the braconid parasite of the adult *Phytodecta*, were bred out of the host larvae. Hymenopterous larvae (?*Nepiesta*) have also been encountered in dissections, but again the level of parasitism was extremely low. The percentages of parasitism given in table 28 are the means for the season. The host larvae were collected on beating trays throughout the season; some were dissected but most were reared in tubes and in jars.

A very small percentage of *Phytodecta* larvae were also infected with the fungus *Beauveria bassiana*.

TABLE 28. SEASONAL MEANS OF PARASITISM OF *PHYTODECTA* LARVAE  
EXPRESSED AS PERCENTAGES OF THE NUMBERS EXAMINED

year	1954	1955	1956	1957	1958
no. of larvae reared in tubes and jars	230	87	505	463	575
no. of larvae dissected	—	277	126	—	164
parasitism by <i>Meigenia mutabilis</i> (%)	0.87	2.75	1.27	2.38	0.80
parasitism by Hymenoptera (%)	—	0	0.79	0.65	1.22
total parasitism (%)	0.87	2.75	2.06	3.03	2.02

#### PREDATION ON THE EARLY STAGES OF THE BEETLE ON BROOM

By far the greatest single cause of mortality in the eggs and larvae of *Phytodecta* on broom is due to predatory insects. Almost at the beginning of this study, i.e. in 1954 and in the early part of the season of 1955, it became clear that the dates of the appearance of the first eggs in the field and of the first-instar larvae, were too widely separated to be accounted for by the length of the incubation period alone, which generally lasts about a fortnight. For instance, in 1955 the first eggs were seen on broom on 12 May and the first-instar larvae on 21 June, i.e. 41 days later. Moreover, the numbers of larvae on broom in the first half of the oviposition period were low compared with those of the eggs, while the calculated numbers of eggs were much higher than the number detected in the field samples. Also, when the total numbers of *Phytodecta* offspring are plotted against time, the graphs show bimodality, the second peak and the building up of the population of the progeny occurring late in the season, when the numbers of ovipositing females in the field have already greatly declined (see figures 5, 6). Since it was apparent that parasitism in the immature stages was extremely low and that the larvae were not prone to any obvious disease, predators appeared to be implicated, and their seasonal occurrence on broom was then investigated.

The fauna on broom is a large one, comprising numerous predatory Hemiptera, (mirids,

anthocorids, nabids) coccinellids, earwigs, phalangids, spiders and mites. Birds, which certainly feed on the aphids, may also take a few *Phytodecta*. Initially we carried out some tests to see which of the arthropod predators would feed on the eggs and larvae of *Phytodecta*, but the work has been amplified and placed on a quantitative basis by Dempster (1960) in 1957 and 1958. Dempster has published a full account of his work, but briefly, it is based on the precipitin test, i.e. on the interaction of *Phytodecta* material in the gut of the predator with the antibodies in the blood serum of the rabbits which have been

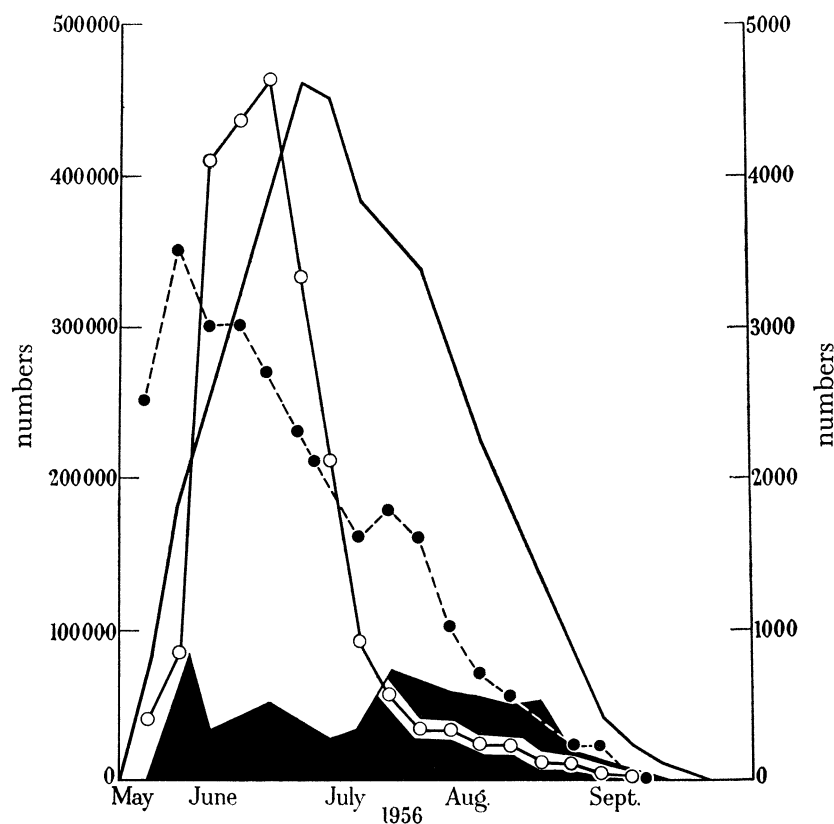


FIGURE 6. Reproduction of *Phytodecta* in 1956 and the predation on the early stages. Black area = actual number of eggs and larvae of *Phytodecta*. Area under unbroken line = estimated numbers of eggs and larvae in the absence of mortality.  $\circ$  = numbers of insect predators (instars I and II of Heteroptera omitted).  $\bullet$  = numbers of *Phytodecta* females on broom—to a different scale (shown on right).

innoculated with an extract of the beetle. By this means the chief predators of *Phytodecta* have been identified as *Asciodema obsoletum* (Fieber), *Heterocordylus tibialis* (Hahn), *Orthotylus adenocarpus* (Perris), *O. virescens* (Douglas & Scott), *Heterotoma merioptera* (Scopoli) (Heteroptera, Miridae), *Anthocoris nemorum* (L.), *A. sarothamni* Douglas & Scott (Heteroptera, Anthocoridae), *Nabis apterus* (Fabricius) (Heteroptera, Nabidae), *Forficula auricularia* L. (Dermaptera) and red mites, of which nearly all identified were *Anystis agilis* Banks.

Amongst the Heteroptera, the first-named species lives on gorse (*Ulex europaeus* L.) as well as on broom, whereas *Heterocordylus tibialis*, the two species of *Orthotylus* and *Anthocoris sarothamni* are found on broom only. The remaining predators are not confined to any one host-plant. None of the predators feeds specifically on the immature stages of *Phytodecta*

and numerous other sources of animal protein are available to them, but the eggs of *Phytodecta* are easily pierced and sucked, common, large and fully exposed to predation. The alternate prey available to the predators were the far more abundant aphids (*Aphis sarothamni* Frannsen and *Acyrtosiphon spartii* (Koch)), the psyllids (*Arytaina genistae* (Latreille) and *Psylla spartiicola* Sulc.), in some years the extremely abundant nymphs of the coccid *Eulecanium corni* (Bouché) and various caterpillars. It has also been shown by Dempster (1960) by the precipitin test, that most of the heteropteran predators also feed on the broom itself.

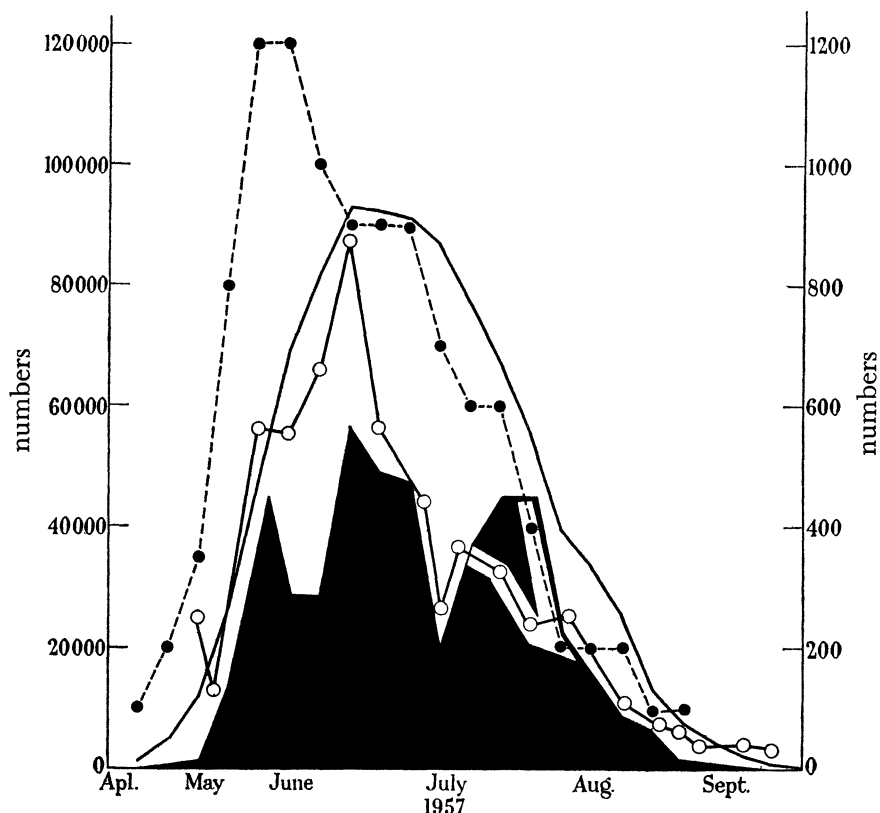


FIGURE 7. Reproduction of *Phytodecta* in 1957 and the predation on early stages. Symbols as in figure 6, but different scales.

The commonest alternative prey, i.e. aphids and psyllids, outnumbered the available immature stages of *Phytodecta* in 1957 and 1958. In 1956, however, the building up of the aphid population was very slow and at the time the heteropteran predators were in their maximum abundance, the combined numbers of aphids and psyllids only slightly exceeded those of *Phytodecta* (see table 30). After conducting over 11 000 precipitin tests Dempster (1960) has shown that with rare exceptions, only the larger nymphs and adults of Heteroptera, i.e. the third instar and onwards, will feed on *Phytodecta*, consequently, in general the counts of predators omit instars I and II of the Heteroptera. Observations showed that the beetle is attacked by Heteroptera in its egg stage and in the first two larval instars. Similar selective feeding of the broom Heteroptera has been demonstrated by Smith (1957), who found that the anthocorids preferred to feed on the aphids whilst the latter were still in their early instars. The total mortality of the immature stages on broom estimated by us, and mortality due to predation estimated by Dr Dempster for the years 1957 and 1958 are

given in table 29. It is inferred that predation was equally important in the three preceding years. Dempster (1960) detected the greatest number of meals of *Phytodecta* in the guts of *Asciodema obsoletum*, *Orthotylus adenocarpus* and in *Anthocoris nemorum*. The period of the greatest abundance of the first two predators coincides in time with that of the young stages of *Phytodecta*, but in varying degrees the effects of predation are spread throughout the season. This arises from the distribution in time of the emergence dates of broom Heteroptera (Waloff & Southwood 1960) and is also connected with the selective behaviour of the predators, i.e. their preference for the prey of smaller size. Predators such as earwigs and nabids, however, which occur throughout the season, will destroy larger larvae as well.

TABLE 29. TOTAL MORTALITY OF IMMATURE STAGES OF *PHYTODECTA* ON BROOM

year	1957	1958
total mortality of immature stages on broom (%)	77.78	91.63
percentage (maximum)* accounted for by egg sterility and parasitism of eggs and larvae	8.46	10.59
percentage accounted for by predation (J. P. Dempster)	55.31	81.01

\* The figure for parasitism and sterility would be smaller if possible predation on affected eggs and larvae were allowed for.

By the serological method Dempster estimated that the loss of 111 600 eggs and larvae could be accounted for by predation in 1957 and 101 300 in 1958. Simultaneously the loss estimated by us which could not be accounted for by sterility of the eggs or by parasitism of the immature stages was equal to 140 848 to 149 744 in 1957 and to 102 312 to 112 255 in 1958 (tables 37, 38). The difference of 29 248 to 38 144 between the two estimates in 1957, may well be due to causes other than predation and also to sampling errors. The greater agreement in 1958 may be considered fortuitous, as no doubt similar sampling errors existed in the 2 years.

We attempted to estimate the numbers of predators systematically in three successive years, 1956–58, but only sporadically in the two preceding ones. In the light of our later work on Heteroptera on broom in 1959, we now know that counts of Heteroptera on broom cuttings tend to be too high, as the insects are not uniformly distributed through the bushes; on the other hand counts on the beating trays (such as Dempster's) of the third and younger instars are too low. We thus consider that the figures which we obtained, although subject to errors, do provide us with a comparison of the relative abundance of the predators in the three successive years and they are summarized in table 30, which also gives the abundance of psyllids and aphids, the chief alternative prey.

Predators, particularly *Orthotylus adenocarpus* and *Asciodema* were much more numerous in 1956 than in 1957. Again, in our estimates (based on numbers found on cuttings) the predators were more abundant in 1958 than in 1957, although far fewer than in 1956. The density of predators as gauged by the number per metre was the greatest in 1956 and fairly high in 1958. The high density in 1958 was not due to the great abundance of predators, but resulted from the death of many broom bushes throughout the winter of 1957–58, so that the number of metres of broom was reduced.

Figures 5 and 6 depict the changes in the numbers of the immature stages of *Phytodecta* on broom in 1956 and 1957. The actual weekly estimates are compared with the numbers

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which would have been present with the observed oviposition rates and numbers of females, had there been no mortality whatsoever. The figures illustrate not only the effect of predation, which was conclusively demonstrated in 1957 and 1958 and which is inferred in 1956, but also the paradoxical fact that the progeny of *Phytodecta* begins to increase when the number of ovipositing females is already rapidly declining. The increase in the progeny coincides in time with the fall in the numbers of predators when the commonest mirids are entering the adult stage. We have found that the nymphal stages of the Miridae on broom are often much parasitized. The parasitic larvae rarely (Leston 1959) persist into the adults; never apparently in our species. Thus the emergence of the parasitic larvae from the late nymphs would contribute to the heavy fall in the numbers of predatory mirids. An example of this is illustrated in table 31.

TABLE 30. DENSITY AND RELATIVE ABUNDANCE OF PREDATORS OF IMMATURE STAGES OF *PHYTODECTA* AND OF PSYLLIDS AND APHIDS BETWEEN 3–23 JUNE 1956, 5–20 JULY 1957 and 2–20 JUNE 1958, THE TIME OF THE MAXIMUM ABUNDANCE OF THE HETEROPTEROUS PREDATORS

year	1956	1957	1958
no. of metres of broom in field	444 131	415 098	283 722
no. of predators per m	0.951	0.163	0.513
no. of eggs, I and II larvae <i>Phytodecta</i> per m	0.096	0.086	0.107
no. of psyllids and aphids (alternative prey) per m	0.135	1.087	0.774

TABLE 31. NUMBERS OF *ASCIODEMA OBSOLETUM* AND *ORTHOTYLUS ADENOCARPI* ON BROOM IN 1956 (INSTARS I AND II INCLUDED)

date	<i>Asciodema obsoletum</i>		<i>Orthotylus adenocarpi</i>	
	nymphs	adults	nymphs	adults
4–8. vi.	144 614	0	307 303	0
18–22. vi.	142 242	0	352 601	0
25–29. vi.	154 843	0	181 625	0
2–5. vii.	59 055	0	137 796	0
9–13. vii.	12 698	14 404	6 349	29 333
16–19. vii.	0	6 257	6 574	27 435
24. vii.	2 152	4 811	0	20 710
30. vii.–3. viii.	0	2 336	0	21 170
6–10. viii.	0	0	0	10 218
13–17. viii.	—	—	—	9 755
20–24. viii.	—	—	—	7 389
27–31. viii.	—	—	—	2 432

CHANGES IN THE HABITAT CONTRIBUTING INDIRECTLY TO THE MORTALITY OF THE IMMATURE STAGES OF *PHYTODECTA*

The life of a broom bush is some 10 to 15 years and the bushes were reaching this age in 1955 (see p. 208). At this age they seem to become especially susceptible to stress such as that due to excessive flowering and ripening of seeds, unusually severe winters, and possibly insect attack. The fauna on broom is a large one and though we have not seen anything that looked like dangerous defoliation we do not know the effect of root feeders. Of these, at least the larvae of the weevil *Sitona regensteinensis* (Herbst) must be abundant as the numbers of the adult equal or exceed those of *Phytodecta*.

The heavy mortality of the immature stages of *Phytodecta* on broom in 1956 (see tables 24, 25) was not due to the great abundance of predators alone. In 1956, many broom bushes were dying and the rate of regeneration in the area was very slow. After a heavy flowering season in 1955, the broom was covered with pods and there was very little vegetative growth. During the severe frosts of the 1955–56 winter, many of the bushes died and the area occupied by the living shrub was reduced to almost a half (see table 1). Dead bushes were dispersed throughout the area and even more frequently parts of the bushes would be dead with a few living armfuls still surviving. As the result the insect fauna was concentrated. As has already been mentioned, the numbers of mirid predators were large as compared with those in the subsequent years, while the total number of *Phytodecta* adults which had emerged as the spring generation, was almost the same as in 1955. The adult beetles were, however, less sparsely distributed, there being one to every

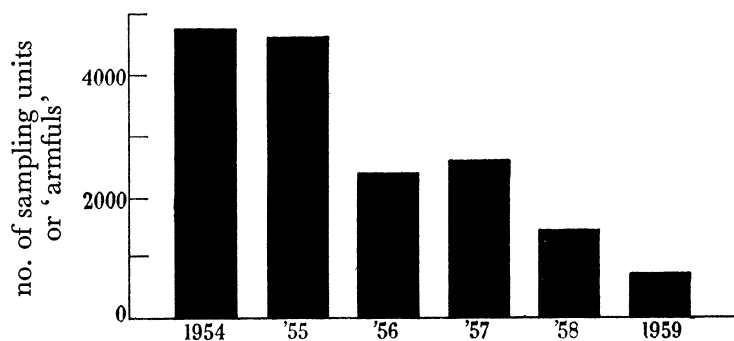


FIGURE 8. Histograms of the numbers of armfuls of broom on the area for 6 years.

4·31 m of living broom stem, compared with one to 11·08 m at their maximum in 1955. The mean daily oviposition rate was the highest recorded in the 5 years (see table 21) and the numerous progeny of *Phytodecta* were concentrated on a reduced volume of the food-plant. At no time, however, was there competition for food. There was always an immense volume of broom available to the numerous insect species.

The increased density of the prey and the high numbers of predators were, no doubt, responsible for the extremely heavy mortality of *Phytodecta* on broom in 1956. The quantity of broom remained almost the same in 1957, although the bushes did recover slightly, but the total number of eggs laid by the depleted population was low, while the predators (at their maximum) were 6·2 times less abundant than in 1956. Mortality on broom in 1957 fell to 77·78% as compared with 98·98% in 1956. Yet another striking alteration in the size of the habitat occurred in the winter of 1957–58, when the area occupied by the living broom was yet again halved. However, the population of *Phytodecta* which had not recovered from the devastation in 1956, was at a very low level, while the fecundity of the beetles was the lowest recorded in the 5 years (see table 21). At the same time, while the numbers of predators were greater than in 1957, they did not exercise as big an effect on the *Phytodecta* population as in 1956, possibly as the result of the unfavourable weather conditions throughout the summer (see table 32), which may have reduced their activity. Alternate prey, particularly psyllids and aphids, were more abundant than in 1956. Even so, the percentage of mortality of the immature stages of *Phytodecta* on broom was the second highest in the 5 years of this study.

The density dependent effects described here are not of the conventional type, for the increased mortality did not follow a rise in the population of prey. This remained at a relatively steady level in the first 3 years of this study, but in 1956 the abundance of predators was coupled with a concentration of all the insect populations into a smaller area. This 'induced rise in density' must be a very common phenomenon in the lives of monophagous insects, especially in those which live on annual plants, the densities and the patterns of distribution of which may vary independently of the insect fauna on them. Watt (1947) described the gradual changes which occur in the pattern of plant communities and further evidence has been forthcoming from other plant ecologists (e.g. Kershaw 1958, 1959). There is little doubt that the cyclical changes which occur in the distribution and abundance of vegetation will result in the local alterations of the insect fauna, and the changes which occurred as the broom aged are an instance of this.

#### MORTALITY OF THE LARVAE, PUPAE AND THE NEWLY EMERGED BEETLES OF THE AUTUMN GENERATION IN THE SOIL

Mortality in the soil, inferred from the difference between the estimated number of fully fed fourth-instar larvae entering the soil and the total number emerging as young adults in autumn was equal to 46.7% in 1954, 72.5% in 1955, 27.3% in 1956, 57.1% in 1957 and 48.8% in 1958. At least one cause of this mortality, namely predation, has been identified and analysed by the serological method in 1958. A full account of this analysis has already been published (Dempster *et al.* 1959) and only the salient points are recapitulated here. It was thought that the carabid beetles were the most likely predators and some hundreds of these, belonging to thirteen species, were trapped in pitfall traps. Serological tests were made on 265 specimens and three were positive for *Phytodecta*, namely, two *Feronia madidus* (Fab.) and one *Abax parallelopedus* (Pill. & Mitt.). Making various simplifying assumptions, it was estimated that carabids might have destroyed 1505 *Phytodecta* in the soil. The actual number which disappeared is now estimated at 5098, which is higher than the total of 2241 quoted in Dempster *et al.* (1959). Other predators such as Formicidae, Staphylinidae and *Forficula* which are known under some circumstances to feed on *Phytodecta* pupae were also present in the habitat and probably increased mortality due to predation. Small mammals might also feed on the pupae and are known to occur in the habitat.

#### THE EFFECTS OF TEMPERATURE AND RAINFALL ON *PHYTODECTA*

*Phytodecta olivacea* is a species which in Great Britain is near to the middle of its geographical and climatic range, and hence it is not as rigorously affected by climatic variations as are the species at the edge of their distribution. The effects of weather on the life cycle of *P. olivacea* are masked and complicated by the heavy attacks of predators on the immature stages. Some of these effects have been partly discussed before, but they are brought together and summarized below.

The time of emergence of the hibernating adults in the spring is to some extent related to the rise of soil temperature and the averages of 5 °C and above for 3 to 4 weeks stimulate the beetles to emerge. Similarly, the averages of maxima of 8.1 °C for 4 weeks and of 8.5 °C for 3 weeks precede emergence. In 1957, however, the beetles failed to emerge in

January and February when these temperatures were reached and it thus seems that other factors, as well as temperature are responsible for the breaking of the diapause.

With the exception of 1955, the spring-summer temperatures throughout this study tended to fall below and the rainfall above the Kew averages for the last 30 years (see table 32). Usually the spring generation beetles disappeared from the broom bushes by the second or third week in September, but they lingered on until the third week in October in 1954.

TABLE 32. AVERAGE MONTHLY VALUES OF CLIMATIC FACTORS IN THE BROOM AREA AT SILWOOD PARK, BERKS

	J.	F.	M.	A.	M.	J.	J.	A.	S.	O.	N.	D.
temperature (°F)												
1954	37	37	44	44	52	57	58	58	56	54	45	44
1955	35	35	37	48	49	58	63	63	56	46	42	40
1956	36	31	43	44	54	55	60	55	57	49	41	43
1957	42	41	48	48	50	61	62	60	54	51	43	38
1958	38	42	40	46	53	57	60	60	59	51	43	43*
total precipitation (mm)												
1954	30.7	56.4	53.2	8.0	70.8	110.3	61.3	69.6	55.9	62.8	102.7	50.3
1955	56.6	41.9	24.4	8.5	109.8	72.7	42.3	28.5	43.7	97.8	47.6	56.1
1956	98.3	2.5	12.8	39.2	4.9	45.3	112.3	99.3	61.1	87.7	11.8	72.6
1957	38.8	80.9	30.8	5.8	29.0	42.3	80.4	72.7	77.3	44.7	70.6	52.2
1958	69.3	57.7	40.4	32.8	55.3	92.9	116.9	85.5	93.7	56.6	57.1	75.5*
total no. of days of rain (with snow in brackets)												
1954	8 (3)	16 (1)	14 (2)	5	17	17	20	17	22	16	21	12
1955	8 (4)	7 (7)	4 (3)	8	21	12	2	8	15	13	13	17
1956	17 (1)	8 (2)	8	11	5	18	14	23	15	15	9	14 (2)
1957	20	17 (2)	14	9	12	10	23	19	20	12	11	14
1958	12 (2)	15 (2)	12 (5)	11	16	18	17	20	16	14	15	24*
total no. hours of sunshine												
1954	—	—	—	178.5	151.2	150.0	156.8	145.2	170.9	—	—	—
1955	—	—	—	171.1	214.0	160.4	239.7	183.9	146.8	—	—	—
1956	—	—	—	140.1	244.6	131.7	163.0	154.1	96.8	—	—	—
1957	—	—	—	164.8	193.6	259.1	167.6	165.3	96.4	—	—	—
1958	—	—	—	93.6†	185.1	150.2	198.4	121.1	131.9	—	—	—
Kew averages (30 years, 1921–51)												
temperature (°F)	40.1	40.4	43.8	48.3	54.3	60.2	63.8	62.8	58.4	51.2	44.5	40.8
total precipit. (mm)	54.4	39.4	37.1	45.9	45.9	43.7	61.9	56.9	50.3	57.1	63.2	52.3
hours of sunshine	—	—	—	147	192	206	195	184	137	—	—	—

\* Kew figure used for this month.

† 7 days this month not recorded.

The prolonged occurrence of the beetles on broom may have been linked with the cool, relatively sunless months of June, July and August. The most recent summer of comparable coldness was in 1920 and for a similar combination of low temperatures, low sunshine and high rainfall one has to go back to 1903 (Anon 1955). Although no detailed observations were made in 1959, it was noted that in this exceptionally fine summer, very few of the first generation of beetles remained on broom after July. Similarly, in the fine summer of 1955, the last eggs to be seen on broom were found on 12 August, whereas in



the other years they occurred to the end of August and even in the first 2 weeks of September. The latest eggs were found in the field in 1956, i.e. after an August which was characterized by the lowest temperature and the greatest number of days of rainfall for this period in the years of this study.

Temperature has a direct effect on *Phytodecta* by influencing oviposition rate and by determining the length of the immature stages but it also has indirect effects through its influence on parasitism and predation. This effect was particularly striking in 1958 and it is possible that the low level of parasitism in the autumn generation of beetles that year was related to the low numbers of hours of sunshine and to high precipitation throughout August and September (see table 32). In 1956 the ratio of predator days to *Phytodecta* days (i.e. days  $\times$  no. of eggs or larvae) was 1:1.88, in 1958 1:1.05. But in 1956 there were fewer alternate prey and the prey were spread over more broom (see table 30). It is difficult to speak very positively, but probably a further factor such as the weather is needed to explain the greater mortality (table 35) on broom in 1956.

No obvious effects of the soil temperature and of rainfall could be detected on the mortality of beetles throughout autumn and winter, but it was noted that the decline in fungal parasitism by *Beauveria bassiana* in 1956 and 1957 occurred after the exceptionally dry summer of 1955.

TABLE 33. CORRELATIONS RELATING THE MAXIMA OF *PHYTODECTA* ADULTS (1) WITH THE WEATHER OF THE PREVIOUS YEAR; (2) = MEAN °F AND (3) = MM PRECIPITATION, BOTH FOR JUNE TO AUGUST. DATA FOR 12 YEARS

	correlation coefficient	significance
$r_{12}$	+0.5479	not significant
$r_{13}$	-0.7064	0.02 > $P$ > 0.01
$r_{12.3}$	+0.1200	not significant
$r_{13.2}$	-0.5426	

In figure 4 (p. 216) the maximum number of adults of the spring generation in the last twelve years was 33500 in 1950 after the exceptionally dry and warm summer of 1949. The maxima in the field are themselves related to the totals of beetles which emerge throughout the season and in the 5 years of this study, the greatest number emerged in 1956 after the warm summer of 1955. These observations prompted a further analysis of the effects of weather during the main periods of oviposition and of development of the immature stages (i.e. in June, July and August) on the numbers of adults in the following year. Figure 9 depicts a climograph combining the average temperature and the total precipitation for June to August in the years 1947-58. A second figure superimposed on the climograph was produced by plotting the maxima of adult beetles against the average temperature in June to August of the year before when their immature stages were developing. The climograph and the second figure are surprisingly alike suggesting a relationship between the amount of precipitation and the survival of the immature stages. The correlation coefficients between the maximum numbers of beetles in the current year and the precipitation and temperature during the developmental period in the preceding year are given in table 33. The correlation between the maxima of adults and the amount of precipitation throughout the developmental period in the preceding year is negative

and significant. When the effect of temperature is eliminated from this correlation ( $r$  13·2) its value falls below the level of significance, indicating that an interaction between the climatic factors is partly responsible for this effect. The effect of temperature by itself is not significant, nor is the partial correlation ( $r$  12·3) when the influence of precipitation is eliminated from it. It seems in a general way that the amount of precipitation and the interacting effects of temperature and rainfall throughout the oviposition and the developmental period influence the size of the adult population of *Phytodecta* in the following year.

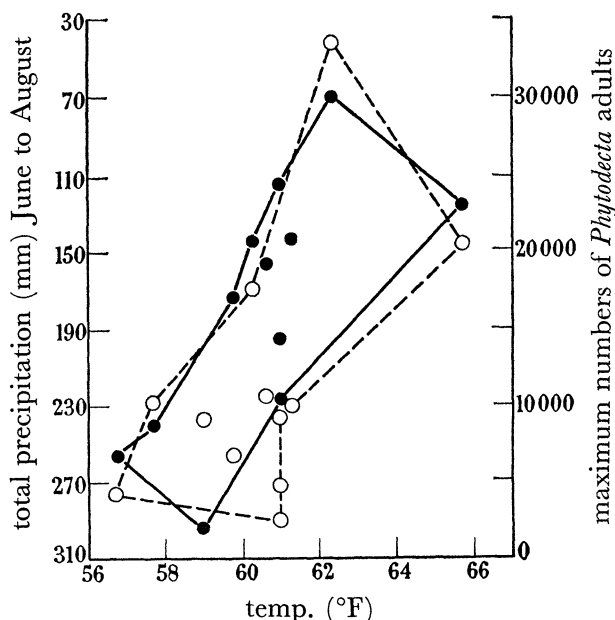


FIGURE 9. Maximum numbers of adult *Phytodecta* of the spring generation plotted against the weather of the period when their early stages developed in the previous year (1948–59). Solid line: mean temperature for June–July–August (scale on abscissa) plotted against total precipitation for the same months (scale on left). Broken line: maximum numbers of adults of the spring generation plotted against the mean June–August temperatures of the previous year.

Some of the most important effects of weather were exercised through the host plant itself. We were able to see in a new plantation of broom in 1957–59 that the growth of the young plants is greatly increased when the rainfall is high. The effects of severity of winter months on old broom were seen in the experimental area where three-quarters of the bushes were killed in the winters of 1955–56 and 1957–58. It may be recalled that the month of February 1956 was the second coldest for a century and that January and February 1958 were characterized by successive cold spells and snowfalls. The consequences of the destruction of the broom have already been discussed (p. 239).

Finally, it should again be stressed that it is difficult to isolate and evaluate the influence of weather on a population such as *Phytodecta* which is greatly affected by predators and by the continuous alteration of the size of its habitat.

#### THE LIFE-TABLES FOR 5 YEARS

The life-tables presented in this section might better be called ‘budgets’ since the population changes are not mainly due to changes in age distribution (see p. 247). The causes of the population changes are discussed in detail on p. 250 for 1957–58. Mortalities

1954–58 are expressed as percentages of the total number of eggs laid and also whenever possible as percentages of the number entering the stage.

In the next section an attempt is made to relate the changes in the population with the magnitudes of the known causes of mortalities.

Before discussing the causes of mortality, their incidence is examined in table 35, which shows that the severest death rate occurs in the immature stages, while they are still on broom; the total mortality is given in the last line. It may be recalled that if the sexes occur in equal numbers (which is approximately true of *Phytodecta*) then a species laying a 100 eggs would have a mortality equal to 98% for the population to remain stable. The average fecundity of the beetles was below a 100 in 1954–58 (see table 21) and mortalities equivalent to 97·41%, 97·19%, 97·44%, 96·60% and 93·92% would have resulted in stability of the population. Percentages above these would have led to a decrease and those below to an increase in the population. Before considering the reliability of the estimated mortalities one has to exclude the survivors of the spring generation of the preceding year whose numbers are shown in the penultimate row of each year's figures in table 34. The changes in population level are examined in table 36 in relation to the estimated mortalities of table 35 and those which would give stability with each year's fecundity.

The age composition of the 1954 spring generation was unknown, since this was the first year of the study, and thus the increase from 1954 to 1955 indicated by +0·37% is a minimum figure which is supported by the increase in the spring generation of 1955. In 1955 the percentage of mortality (98·16%) was above that which theoretically would have produced stability in the following year, and this is reflected in the slight fall in the number of survivors of the autumn generation beetles (i.e. from 13 516 in 1955 to 12 047 in 1956). In 1956 mortality was considerably greater than that which would have resulted in stability, i.e. it was 99·59%, instead of the requisite 97·44% and this is borne out by the great fall in the numbers of *Phytodecta*. In 1957 the estimated mortality is 0·59% above that which is required for stability and does not correspond with the observed increase in the relevant section of the population. The average fecundity was low in 1958 and stability would have been maintained had the total mortality been equal to 93·92%. The estimated mortality of 97·80% therefore suggests a decrease in the population in 1959, which did actually occur (2742 adults, see table 14). Thus, with the exception of 1957, the differences in the two sets of mortalities are reasonable indices of the trends.

A factor which complicates the consideration of the fluctuations in the numbers of *Phytodecta* adults is the survival of some of the members of the spring generation from one year to the next. This survival was of particular value to the species in 1956, when its progeny was drastically reduced by predation and the resulting autumn adults were more heavily parasitized than in any other year. It is possible that this survival of the adults for two or more reproductive seasons has evolved as a safeguard against extinction in abnormally rigorous conditions. A number of other insects (Lepidoptera, Hymenoptera, Diptera) achieve the same end by having a prolonged diapause in some individuals, so that part of the population emerges after two or more winters instead of after one (Lees 1955, pp. 58–60).

TABLE 34. LIFE-TABLES 1954-58

stage	no. entering stage	no. of that stage which died	% of that stage which died	mortality of that stage of % of initial egg no.	accumulated mortalities % of egg no.
year—1954					
eggs	460169	—	—	—	—
eggs and larval instars I-IV (i.e. total mortality on broom)	—	396230	86.10	86.10	86.10
IV larvae and pupae in soil	63939	29884	46.73	6.49	92.59
adults in autumn 1954	34055	20439	60.32	4.45	97.04
survivors of preceding adults to spring 1955	13516	—	—	—	—
survivors of spring adults of 1954 to spring 1955	2688	—	—	—	—
total adults spring 1955	16184	—	—	—	—
year—1955					
eggs	659554	372054	56.41	56.41	56.41
larval instars I-IV	287500	149890	52.13	22.72	79.13
total mortality on broom	—	521944	—	—	79.13
IV larvae and pupae in soil	137610	99766	72.49	15.12	94.25
adults in autumn 1955	37844	25837	68.17	3.91	98.16
survivors of preceding adults to spring 1956	12047	—	—	—	—
survivors of spring adults of 1955 to spring 1956	4980	—	—	—	—
total adults spring 1956	17027	—	—	—	—
year—1956					
eggs	701563	661163	94.24	94.24	94.24
eggs and larval instars I-III	—	694273	98.96	—	98.96
IV instar	7290	150	2.06	0.02	98.98
total mortality on broom	—	694423	—	—	98.98
IV larvae and pupae in soil	7140	1843	25.81	0.26	99.24
adults in autumn 1956	5297	2458	46.41	0.35	99.59
survivors of preceding adults to spring 1957	2839	—	—	—	—
survivors of spring adults 1956 to spring 1957	3554	—	—	—	—
total adults spring 1957	6393	—	—	—	—
year—1957					
eggs	201760	—	—	—	—
eggs and larval instar I	—	78686	39.0	39.0	39.0
larval instar II	123074	76847	62.44	38.09	77.09
larval instars III and IV	46227	1401	3.03	0.69	77.78
total mortality on broom	—	156934	—	—	77.78
IV larvae and pupae in soil	44826	37482	83.61	18.58	96.36
adults in autumn 1957	7344	2469	33.62	1.22	97.58
survivors of preceding adults to spring 1958	4875	—	—	—	—
survivors of spring adults of 1957 to spring 1958	1882	—	—	—	—
total adults spring 1958	6759	—	—	—	—
year—1958					
eggs	125039	46499	37.18	37.18	37.18
larval instars I-IV	78086	68086	86.68	54.45	91.63
total mortality on broom	—	114585	—	—	91.63
IV larvae and pupae in soil	10454	5098	48.76	4.08	95.71
adults in autumn 1958	5356	2614	48.81	2.09	97.80
survivors of preceding adults to spring 1959	2742	—	—	—	—
survivors of spring adults of 1958 to spring 1959	1258	—	—	—	—
total adults spring 1959	4000	—	—	—	—

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TABLE 35. DISTRIBUTION OF MORTALITY THROUGHOUT THE LIFE-CYCLE OF *PHYTODECTA*.  
MORTALITIES ARE EXPRESSED AS PERCENTAGES OF THE INITIAL EGG NUMBERS

year	1954	1955	1956	1957	1958
mortality of the immature stages on broom	86.10	79.13	98.98	77.78	91.63
mortality of larvae, pupae, adults in soil (autumn)	6.49	15.12	0.26	18.58	4.08
mortality of adults in soil (winter)	4.45	3.91	0.35	1.22	2.09
total mortality	97.04	98.16	99.59	97.58	97.80

TABLE 36. ANNUAL DEVIATIONS OF MORTALITY FROM THOSE NECESSARY FOR STABILITY

year	1954	1955	1956	1957	1958
survivors of previous autumn generation	(11 820)	13 516	12 047	2 839	4 875
mortality necessary for stability (%)	97.41	97.19	97.44	96.60	93.92
'actual' mortality (%)	97.04	98.16	99.59	97.19	97.80
difference (%)	+0.37	-0.97	-2.15	-0.59	-3.88

THE CAUSES OF THE POPULATION CHANGES SHOWN IN THE LIFE-TABLES FOR 1957-58

The causes of the changes in the size of the population of *Phytodecta* from year to year include the variability in fecundity, predation on its immature stages and parasitism of its immature and adult stages. It is also possible that to a small degree emigration contributes to the changes in numbers. Climatic factors which interact with all of these are not here considered. The causes of mortality have been more fully analysed for the 2 years 1957 and 1958 and they are summarized in tables 37 and 38. The full data on which these summaries are based can be found in tables 14, 24, 25, 26 and 28. Although all the known causes of mortality are included, some of them overlap. For example, some of the adults destined to die of 'old age' were also parasitized and thus to obtain the loss due to old age alone a proportion of parasitized beetles was subtracted from the total estimate. Similarly, some of the adults which were removed into the laboratory would have died of 'old age' or of parasitism, and hence the true loss due to removal was obtained by subtracting the percentages of mortality from the original figures.

Similar adjustments had to be made in evaluating the causes of mortality of the immature stages. For instance, in 1958 it was estimated by serological methods that the destruction of the immature stages by predators on broom was equivalent to 81.01%. Simultaneously it was also estimated that 8.0% of the total eggs laid were sterile and 0.57% were parasitized. The figure of 8.57% is equivalent to 10716 eggs in the field, but the predators probably destroyed an unknown fraction of this number, which at its maximum would have been equal to 81.01%. Thus the minimum reduction which can be attributed to sterility and parasitism in the egg stage becomes equal to 18.99% of 10716 or 2035 and the loss due to these causes lies between 2035 and 10716. In considering the mortalities in the reproductive stage, it will be seen in tables 7 and 14 that the spring generation is composed of beetles of mixed ages and that the survivors from the preceding spring die of 'old age' after their second period of multiplication. The other known causes of mortality are due to the parasites *Perilitus dubius* and *Beauveria bassiana*. The degree of

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TABLE 37. THE KNOWN CAUSES OF MORTALITY OF *PHYTODECTA OLIVACEA* AND THEIR DISTRIBUTION THROUGHOUT THE LIFE-CYCLE 1957

stage	no. entering stage	causes of mortality	no. and percentage of population affected by causes in col. 3	remarks	items in budget (some modified by overlapping mortalities)	percentage of stage
adults of spring generation	6393	parasitism by <i>Perilitus</i> survivors from spring of old age removed to laboratory	831 3554	13.1% parasitized, hence death due to old age reduced	-831 -3088	13.1 48.3
immature stages on broom eggs	201760	predation of all immature stages on broom estimated serologically	111600	13.1% parasitized, 48.3% dying of old age not accounted for (? emigration or deaths in soil due to <i>Beauveria</i> ) survivors to next spring	-281 -311	4.4 4.9
larvae instar II	123074	sterility	9866		+1882	29.4
larval instars III, IV	46277	parasitism	1090		-111600	55.3
		parasitism	3729	up to 55.3% may have been destroyed by predators	-4897	2.4
		parasitism	1401	total of immature stages disappearing on broom here (col. 4) 127686, minimum (col. 7) 118790 not accounted for (? underestimated predation, deaths during moults, weather)	-2293 29248-	1.1 14.5-
IV larvae entering soil	44826	predation of larvae and pupae in soil	37482		38144	18.9
adults of autumn generation	7344	parasitism by <i>Perilitus</i> removed to laboratory	1291 370	17.6% of these parasitized not accounted for (? emigration or deaths in soil due to <i>Beauveria</i> ) survivors to next spring	-37482 -1291 -305 -873	83.6 17.6 4.2 11.9
					+4875	66.4

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TABLE 38. THE KNOWN CAUSES OF MORTALITY OF *PHYTODECTA OLIVACEA* AND THEIR DISTRIBUTION THROUGHOUT THE LIFE-CYCLE 1958

stage	no. entering stage	causes of mortality	no. and percentage of population affected by causes in col. 3	remarks	items in budget (some overlapping mortalities)	percentage of stage
adults of spring generation	6757	parasitism by <i>Perilitus</i> parasitism by <i>Beauveria</i> survivors of spring 1957 dying of old age removed to laboratory	436 6.5 235 3.5 1882 27.9 1033 15.3	— — 10% parasitized, hence death due to old age reduced 10% parasitized, 25.1% dying of old age not accounted for (? emigration or deaths in soil due to <i>Beauveria</i> ) survivors to next spring	-436 -235 -1694 -670 -2464	6.5 3.5 25.1 9.9 36.5
immature stages on broom eggs	125039	predation of all immature stages on broom estimated serologically	101300 81.01	—	+1258 -101300	18.6 81.01
larvae I-IV	78086	sterility parasitism parasitism	10003 8.0 713 0.57 1558 2.02	up to 81.1% may have been destroyed by predators	-2035 — -296 1012	1.6 — 0.4 0.8
IV larvae entering soil	10454	predation of larvae and pupae in soil	5098 48.8	total immature stages disappearing on broom 114586 (see table 34) : maximum accounted for here (col. 4) 113574, minimum (col. 7) 103631 not accounted for (? underestimated predation, deaths during moults, weather) 1505 eaten by carabids (estimated serologically)	10955 -1505	8.8 14.4
adults of autumn generation	5356	parasitism by <i>Perilitus</i> parasitism by <i>Beauveria</i> removed to laboratory	270 5.0 192 3.6 237 4.4	not accounted for, but probably destroyed by other predators — — 8.6% parasitized not accounted for (? emigration or deaths in soil due to <i>Beauveria</i> ) survivors to next spring	-3593 -270 -192 -217 -1935 +2742	34.4 5.0 3.6 4.1 36.1 51.2

parasitism varied from year to year ranging between 5.0 and 26.0% in the former and from 0 to 24.7% in the latter.

As far as the immature stages on broom are concerned, by far the greatest destruction is due to predators. Only in 1957 and 1958 was an independent estimate made of predation. The mortality due to this cause was apparently 14.5 to 18.9% less than the total percentage disappearance of the larvae in 1957 and 0.8 to 8.8% less in 1958. No doubt sampling errors contribute to these discrepancies as well as the approximations involved in the formula used to estimate disappearance of early stages.

#### DISCUSSION

The essential results of the present work are contained in tables 34, 37 and 38. These have been described as constituting a 'budget' rather than a life-table, chiefly because in a short-lived animal the age distribution of the population is relatively unimportant. In a true life-table age distribution is one of the main considerations whereas it is rarely of much importance in any one insect instar. Whichever type of summary is prepared the ultimate purpose is the same. Without some understanding of all the main factors influencing the growth of the population it is impossible to assess the importance of any of them. In particular, a factor which acts near the peak of the annual cycle of numbers has quite a different significance (particularly if expressed as a percentage) from one which acts later. Any real understanding of the dynamics of environmental changes depends on assessing all the factors at their true values.

Unfortunately, it is as yet possible to draw only the elementary outlines of an ideal budget. Adequate sampling methods are only gradually being evolved and also methods for the full analysis of the sampling data have not yet been devised. An essential feature of a budget should be as many independent checks on numbers as possible. This will help to remove the uncertainties which are necessarily associated with all sampling methods. These uncertainties are not only of the usual type which can be confined within fiducial limits but may take the form of a permanent bias. In many forms of field sampling it is always easier to overlook organisms than to find too many and a bias of this type cannot be removed by statistical analysis. In some respects the work on fish (Beverton & Holt 1957; Graham 1956) is far in advance of anything done on insects because in a long-lived animal it is possible to analyse and forecast population changes from the life-table even where there is little information on natural mortality of the sort which we try to provide in the annual budget. We have not so far discussed population theory and we do not now wish to examine at length a topic which has recently led to a great deal of controversy amongst entomologists. It is necessary, however, to make some reference to the current ideas before stating what we think is the relative importance of the various factors which act on the population of *Phytodecta*. The word 'control' is often ambiguous but we shall use it here for those forces which ultimately determine the level of the population. Large annual changes may well be due to causes which could not by themselves control the population over a somewhat longer period. Briefly, the potentially exponential increase of any living population can only be controlled by an agency which at some point adjusts itself to the density of the population. How soon and how frequently the adjustment occurs may well be variable. Many factors, such as parasites for instance, which could in



theory be density-dependent in the required way may not be so in particular cases; not, for instance, if there is too great a disparity in reproductive rates. In fact intraspecific competition for food or living space is the only controlling factor which must ultimately act on all species if other controls break down.

Although detailed records of the *Phytodecta* population are available only for the 5 years 1954–8, some information on the size of the population has been recorded for 12 years (1948–59). This covers a period when the food-plant, broom, spread over the experimental area and then receded as many of the plants died of old age. The greatest number recorded of spring beetles was 33 500 and the least 1000. Thus in 12 years the population fluctuated by a factor of 35·5 which is considerable, but much less than in those insects such as some lepidopterous forest pests which assume plague proportions (Schwerdtfeger 1941; Lack 1954, pp. 8–20). During the 12 years of observation there were two points at which the population was drastically reduced—in 1950–51 and 1955–56. The second reduction fell within our period of detailed study and was mainly due to a decrease in the quantity of broom and to the consequent concentration of the population and of its enemies into a smaller space. The earlier reduction, whatever were its causes, was not associated with a decrease in the quantity of broom.

The factors likely to be involved in population changes fall into four groups which are rarely independent of one another—climatic factors, factors of the habitat (in this case the food-plant), intraspecific factors and the effects of other kinds of organisms.

Climate or its local expression in the weather can never be a controlling factor because it does not adjust itself to the density of the insect population. Nevertheless, it is commonly the major factor in determining annual or short-lived fluctuations in numbers and by its effects on the other controlling agencies has an all-pervasive influence. Moreover, although not exercising control, climate may well cause outbreaks by favouring a high rate of reproduction and survival. In all insects, both in vegetarians such as *Phytodecta* and in its parasites and predators, the rates of oviposition and of larval development are greatly influenced by temperature. This determines not only the reproductive rates but the period over which the vulnerable stages are exposed to predation. The number of eggs laid by *Phytodecta* seems also partly to depend on the time which the adult spends above ground which is also in some complicated way determined by the weather. Finally, there is evidence that the rainfall during the period when the early stages are developing has a marked influence on the number of adults which will be found in the following spring.

The habitat of a monophagous vegetarian such as *Phytodecta* is relatively simple. Apart from the pupal stage and the hibernating adult in the litter beneath the broom the whole life of the insect is spent on the plant. Unfortunately, we have insufficient biochemical information to show in any detail how the plant affects the insect. We know that it tends to feed selectively on the younger shoots, but the proportion which these make up of the whole plant varies from plant to plant and in different seasons and years. It seems possible that as plants get older they provide a less suitable diet which reduces the fecundity of the beetle. There is no evidence that *Phytodecta* was ever able to reduce appreciably the quantity of broom but, conversely, changes in the amount of broom were a major factor during our 5-year study in determining the size of the insect population. The broom was

dying partly of old age, partly of drought or frost after excessive flowering (which may be partly the same thing expressed in other words); possibly the total insect fauna was contributing to a weakening of the broom. Huffaker (1957, 1959) has collected evidence which shows that in a new country in the absence of the usual insect fauna, many plants may flourish in a surprising way and may be checked when the fauna is intentionally introduced. As far as *Phytodecta* on broom is concerned, the situation appears to be that with the normal English set of predators, a given amount of broom can only maintain a certain density of *Phytodecta*. If the quantity of broom is reduced, *Phytodecta* and its predators become more concentrated and predation becomes more intense. As a result of interactions with climate and parasites this relation is not strictly linear but it would appear to be nearly so. The predators are particularly effective because they are only facultative and can feed on the broom or on other insects if *Phytodecta* is not available. Many of the species are also confined to broom and rapidly find their way to new plants; thus the whole assemblage is generally present on a new group of plants after only a year or two.

The type of intraspecific competition which ultimately sets an upper limit to all populations is competition for food but this has never occurred at Silwood during the last 12 years. There seems no reason why on occasions *Phytodecta* should not defoliate the broom but we have no record of it. Shortage of food well below the level of starvation might affect the fecundity of the species. Changes in fecundity tend to be relatively less important when the potential egg-number is high and in most insects fecundity is highly correlated with mean weight. The mean weight of the *Phytodecta* populations was relatively constant, lying between 11.5 and 12.4 mg. The fecundity over the 5 years varied by a factor of two. This is much less than the variation in the fecundity which we found in grasshoppers in an earlier 5-year period. The fecundity of *Chorthippus brunneus* (Thunb.), for instance, varied by a factor of eleven (Richards & Waloff 1954, p. 165).

There are also in some species more subtle changes induced by changes in population density. Familiar examples are the phase changes in locusts (Kennedy 1956; Uvarov 1928) or the physiological changes in rodents (Chitty 1960) exposed to increasing population densities. Similar effects of density are known in Lepidoptera (Long 1953) and Wellington (1960) has recently described in the moth *Malacosoma* two different types of individual which occur in different proportions according to the density. *Phytodecta* is certainly polymorphic in colour pattern and probably in the detailed determination of its diapause (see p. 227) but whether this is influenced by population density we do not know.

It is other species of insects which seem to exercise the main control over the *Phytodecta* population at Silwood. The parasites, of which there were six insects and one fungus, seem to have a buffering rather than a controlling effect. Most of them were rare and the commonest insect parasite, *Perilitus*, seems to exist in a relatively stable absolute population, so that its effects were apparently greatest when its host was rare. It is possible, however, that the marked reduction in the numbers of *Phytodecta* which took place in 1950–51 when we were not making a detailed study of the species was due to parasites.

Predators, on the other hand, especially the common mirid bugs which are mostly confined to broom, clearly exercise an important control. There is little evidence if any that they increase in abundance with *Phytodecta* and control it in the way in which a parasite is usually supposed to do. It is rather that there is a relatively steady population of these

predators, perhaps able to subsist on broom alone and certainly able to find alternate food amongst the aphids and psyllids. This predator population destroys a large number of the early stages of *Phytodecta* which it happens to meet. There will thus tend to be an upper limit to the possible density of *Phytodecta*; if it increases beyond this point more will be eaten. No doubt this relation does not always work perfectly smoothly but our observations on the results of two natural reductions in the quantity of broom allow us to draw this general conclusion. The population of mirids is probably in no way dependent on *Phytodecta* and is controlled by its own complex of parasites and by fractricidal predation. The importance of the Heteroptera as predators of *Phytodecta* finds a close parallel in the earlier work of Collyer (1953 *a, b*) and Masee (1955) on the predacious enemies of *Metatetranychus ulmi* (C.L.K.) the fruit tree red spider mite.

The complex interrelations amongst the large insect fauna living on broom prompt some reflexions on the concept of animal communities. It is easy to use the term community for the assemblage of species found in some habitat. But beyond the fact of concurrence it is usually very uncertain what effects if any the species have on one another; whether in fact they are at all interdependent. Species which live on one food-plant such as broom must be on closer terms than those which inhabit some more diffuse habitat, and in this case we have good evidence that many of them have significant effects on one another's abundance. Some actually feed on one another; others by acting as alternate sources of food for predators act as protective agencies. It may well be that the broom itself often dies prematurely from the attack of the whole complex. The dying broom is immediately attractive to two species of scolytid bark-beetles and this starts up a whole new complex of parasites and predators (M. R. Smith 1958).

We may discuss last how far *Phytodecta olivacea* seems to be adapted to the conditions in which it has to live. The species is effectively monophagous and the whole life history is spent on or beneath the food-plant. The plant is perennial though with a somewhat limited life so that a colony of the beetle need not be highly mobile. But it is perhaps surprising that the beetle so rarely uses its wings. We conclude from our observations that it has rather poor but nevertheless adequate powers of dispersal.

It is difficult for a poikilotherm to be closely adapted to a variable environment. The weather of Great Britain poses many problems for an insect. It seems possible that polymorphism may be a device by which at least part of the population may find itself on even terms with its environment. *Phytodecta* is certainly polymorphic in colour (Waloff & Richards 1958, p. 106) but the significance of this is not yet clear. It is also probable that there is genetic variation in the control of length of diapause (p. 227) so that the life history of the population is much more prolonged than that of the individuals. This allows the species to sample the full range of the weather of an English summer. It may be at least as important that only part of the population is exposed to the full force of predation and parasitism. Diapause is usually thought of as a mechanism by which the barren part of the year is avoided by the feeding stages, but in a number of insect species it may act equally as a device by which the peak incidence of predation or parasitism is avoided. Whether there are other types of polymorphism such as Wellington (p. 252) found in *Malacosoma* we do not know and it would be interesting to study *Phytodecta* over a wider geographical area.

Another feature of the life history which is surely adaptive is the ability of a substantial proportion of the females to survive and breed a second year. In other insects this is done by a prolongation for an additional year of the normal diapause. However this spread of the population over more than 1 year is accomplished the effect is the same. There is always a chance that unusually severe weather (as in 1958) or heavy predation (as in 1956) will be avoided by a part of the population. The risks will be spread though they cannot be altogether avoided.

We conclude then that on the whole *Phytodecta olivacea* is well adapted to its milieu though we should not expect too much from an insect with so high a reproductive rate.

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## APPENDIX I. OVIPOSITION IN 1955

To show how the number of eggs laid by *Phytodecta* during a season was estimated, the data for 1955 are given below. The daily oviposition rate was calculated from the regression equation for the year,  $y = b_1 x_1 + b_2 x_2 + c$ , where  $x_1$  is the age of the female population in days (day 1 being the beginning of the oviposition period for females brought into the laboratory) and  $x_2$  is the mean field temperature ( $^{\circ}$ F) for the week. The constants of the equation were calculated from a series of females brought into the laboratory at intervals throughout the season and kept under regular observation. In this year  $b_1 = -0.02603$ ,  $b_2 = +0.14235$ ,  $c = -3.80829$ . In the table, the stages of the calculations for the 20 weeks of the laying season are shown in successive columns and the sum of all the figures in the last column gives the total laid in the whole season.

week	age (days)	product $x_1 \times b_1$	mean weekly field temp. ( $^{\circ}$ F)	product $x_2 \times b_2$	daily oviposition rate col. 3 + col. 5 —3.80829	mean daily no. ♀♀ in field (mean of two estimates a week apart)	total eggs laid in field = col. 6 $\times$ col. 7 $\times$ 7
1	3.5	-0.09111	51	7.25985	3.36045	162	3810
2	10.5	-0.27332	48	6.83280	2.75119	552	10631
3	17.0	-0.44251	51	7.25985	3.00905	923	19441
4	24.0	-0.62472	43	6.12105	1.68804	2884	34078
5	30.0	-0.78090	50	7.11750	2.52831	4776	84526
6	36.5	-0.95009	55	7.82925	3.07087	4500	96732
7	44.0	-1.14532	55	7.82925	2.87564	3530	71057
8	51.0	-1.32753	58	8.25630	3.12048	2492	54434
9	59.0	-1.53577	60	8.54100	3.19694	2377	53194
10	65.0	-1.69195	60	8.54100	3.04076	2492	53043
11	72.0	-1.87416	59	8.39865	2.71620	2031	38616
12	79.0	-2.05637	67	9.53745	3.67279	1732	44529
13	86.0	-2.23858	64	9.11040	3.06353	1292	27706
14	93.0	-2.42079	63	8.96805	2.73897	992	19019
15	99.0	-2.57697	64	9.11040	2.72514	1065	20316
16	106.0	-2.75918	58	8.25630	1.68883	923	10911
17	113.0	-2.94139	64	9.11040	2.36072	392	6478
18	120.0	-3.12360	69	9.82205	2.89016	308	6290
19	127.0	-3.30581	61	8.68335	1.56925	254	2790
20	134.0	-3.48802	60	8.54100	1.24469	231	2012

In 1955 the average fecundity of *Phytodecta* in the field was estimated as 71.4 eggs (see table 21). At the laboratory temperatures the mean fecundity of the same set of females was 103.9. The mean fecundity of thirty-two females in the laboratory, which laid and did not die of *Beauveria* and *Perilitus* was 269 (see Waloff & Richards 1958), five of them laying between 415 and 603 eggs. Thus, the chief difference between the egg numbers published in 1958 and the field data recorded here is due to the elimination of parasitized specimens from the 1955 series; there is a further slight effect due to the laboratory temperatures being higher than field ones.

1



2



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FIGURE 1. Northern half of the area of broom, Silwood, May 1955. Stevenson screen on the left.

FIGURE 2. One of the tubs used for measuring the emergence of beetles from the ground in the spring and a 'window-trap' used to try and catch flying adults.