POPULATION ECOLOGY OF *CICADELLA VIRIDIS* (L.) AND BIONOMICS OF *GRAPHOCEPHALA COCCINEA* (FORSTER) (HOMOPTERA : CICADELLIDAE).

By

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ABSTRACT

The biology and population ecology of Cicadella viridis (L.) were studied in conjunction with the bionomics of Graphocephala coccinea (Forst.) in Silwood Park, Berkshire, Southern England.

Both species are univoltine and overwinter in the egg stage. Study of undercooling point indicated that eggs of both species are extremely cold-hardy. Most eggs of both species could hatch without having to pass through a period at low temperature, but the proportion capable of doing this is greater in C. viridis than in G. coccinea.

Larvae of both species hatched during the second half of May, and adults emerged in July. Oviposition in C. viridis commenced towards the end of August, but was slightly later and during the second week of September in G. coccinea.

It was found through rearing experiments that although C. viridis laid its eggs in Juncus effusus L., the larvae required Holcus mollis L. for growth and development.

The number of C. viridis eggs produced each season was estimated by sampling the egg-bearing Juncus stems. The larvae and adult numbers were estimated by sampling at regular intervals with a Dietrick vacuum suction sampler, as well as by direct counting.

During the egg stage, mortality is caused mainly by fungal attack, parasite and predators being the other main contributory factors. Predation by spiders and Nabidae

appeared to be the main cause of mortality in larvae and in the adult stage. Adults were also attacked by a fungus Entomophthora sp. but its effect during 1969 to 1971 was slight. Population budgets for 1969, 1970 and 1971 are presented.

A brief study of the flight activity and dispersal of C. viridis and G. coccinea was made. Their movements are essentially trivial and largely confined to the immediate vicinity of their habitats, but adequate power for dispersal is shown in occasional individuals caught in traps far away from their breeding grounds.

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GENERAL INTRODUCTION

The subfamily Cicadellinae is represented in Britain by two species, Cicadella viridis (L.) and Graphocephala coccinea (Forst.). In Europe and East Asia, C. viridis is known to be a pest of young fruit trees, and has often been recorded from agricultural crops, but it is of no economic importance in Britain. The British strain of C. viridis also differs from the European one in voltinism. G. coccinea is a relatively recently introduced species from North America. In Britain this insect is generally associated with 'bud blast' disease of Rhododendron and is therefore a pest of minor importance.

The thesis is mainly concerned with a population study of C. viridis, but its biology is also studied in order to get a better understanding of the species. Because of the time factor, only bionomics of G. coccinea were studied.

The thesis is divided into two sections, the first section dealing with C. viridis. The undercooling point and diapause of the eggs, the oviposition of the adults, and the food plants of immature stages were investigated. As the insect has not previously been studied in any detail in Britain, an account of its life history and description of the immature and adult stages is also given.

The population study includes a comparison of current methods of estimating the numbers of recruits entering a stage in a population with widely overlapping

stages. Population budgets for the years 1969, 1970 and 1971 are presented. Investigations were carried out to acertain the cause of mortality occurring in all stages. Predators were studied by means of serological techniques and laboratory feeding trials. Varley and Gradwell's (1960) graphical key factor analysis was employed to identify the principal mortality in the egg stage and the stage where mortality was most likely to have a regulating effect on the population as a whole.

Flight activity and dispersal were studied, but not in great details.

In Section II, the bionomics of G. coccinea are described, and compared with those of C. viridis. A brief study was also made of flight and dispersal of this insect.

SECTION I

Cicadella viridis (L.)

I DESCRIPTION OF THE STUDY AREA

Imperial College Field Station, Silwood Park is situated in southern England at 51° 24' N and 0° 39' W. It consists of some 230 acres of parkland, including marsh, farmland, experimental plots and a lake. The work was carried out in an area known as the Rush Meadow by the northern shore of Silwood Lake. The study site is located at the Eastern end of Rush Meadow where *Juncus effusus* L. the host plant of *Cicadella viridis* (L.) is abundant. The total area of the study site covers roughly 1,785 square metres, and its location in the Field Station is shown in Fig. 1. The area is divided longitudinally by a ditch about one metre wide and one and a half metres deep, into two unequal areas of 711 and 1,074 square metres. For ease of reference, the larger area referred to as B is situated near to the lake and the smaller area designated A being at the bottom of the slope of a gently rising hill. Towards the western end of the study area *Juncus* was quite patchy and the area was mainly occupied by *Holcus* spp. and *Cirsium* spp. The ground inspite of the draining ditch was damp throughout the year, and in part of area A, surface water was always present.

According to Luff (1964), Rush Meadow had been cultivated with Barley in 1952 and 1953, then *Lolium perene* L.

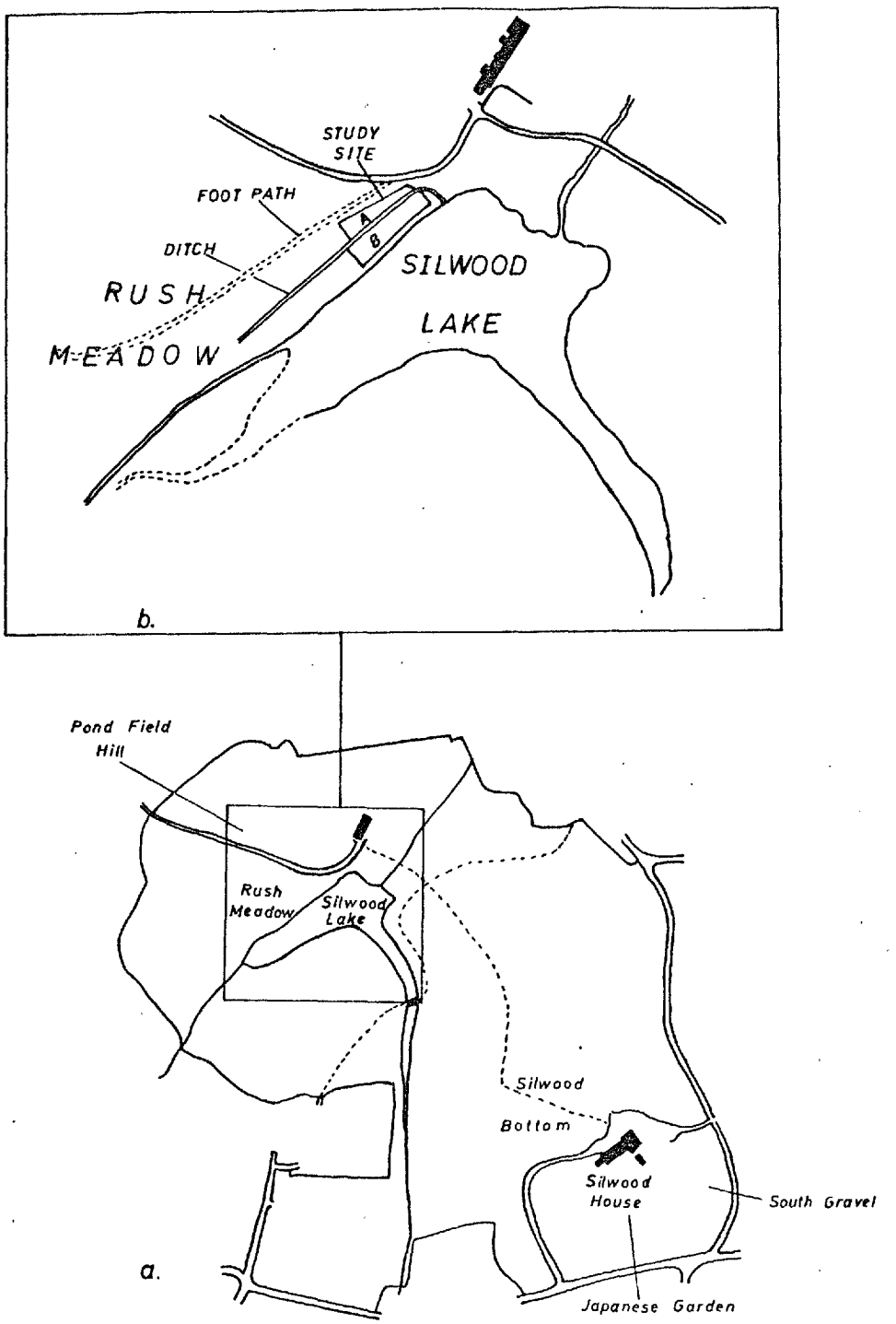


FIG. 1 Sketch of Silwood Park (a) with an enlargement of the area surrounding the study site (b).

was sown in 1954, and it was grazed by cattle from 1955 to 1963. The area since then was laid fallow. At present the vegetation consists mainly of a pure stand of Juncus effusus L., Holcus spp., buttercups Ranunculus repens L., Urtica dioica L. and various species of Rumex. Distribution of Juncus within the area is fairly even, with Holcus and Ranunculus interspersed among the rushes (see plate 1). Both Holcus lanatus L. and Holcus mollis L. are present, with H. mollis being the predominant species. Among the Rumex spp., R. obtusifolius L. is the most abundant. Cirsuim arvense (L) Scop. is also present in reasonably large numbers, but mainly in area B. Salix atrocinerea Brot. was present only in very small numbers when the work started in the winter of 1968, but its number had increased over the years. Other plant species present are:-

Cirsium palustre (L.) Scop.

C. vulgare (Savi) Ten.

Rumex crispus L.

R. acetosa L.

R. acetosella L.

Polygonum hydropiper L.

P. persicaria L.

Epilobium palustre L.

E. hirsutum L.

Stalleria graminea L.

Lysimachia vulgaris L.

Lycopus europaeus L.

Galium aparine L.

Sarothamnus scoparius (L.) Wimmer

Glyceria fluitans (L.) R. Br.

Carex ovalis Good.

Deschampsia caespitosa (L.) Beauv.

Agrostis tenuis Sibth.

Dactylus glomeratus L.

Lotus uliginosus Schkuhr.

The numbers of Juncus stalks in both areas of the field were counted during the winter of 1968, 1969 and 1970 for estimation of the C. viridis egg population. These counts have shown that over the three year periods, the number of Juncus stalks in area A dropped slightly each year. This might be caused by tramping during sampling and other activities in the field. Together with this decrease, there was a visible increase in the number of Rumex spp. and Urtica dioica. In early 1968 the ground along the ditch in area B was disturbed by digging and soil was piled onto the plants. This resulted in a low Juncus stalk count in 1968; the plant recovered in 1969, but its number again decreased slightly in 1970. The number of Juncus stalks estimated for both

areas together are shown in Table 1. This shows that the total number of Juncus stems available for egg laying remains fairly constant over the three years studied.

Table 1. The estimated number of Juncus effusus stems in 1968, 1969 and 1970.

Year	Estimated number of Juncus stems	95% confidence limit
1968	1956217	1753123 - 2159311
1969	2206688	1974858 - 2438579
1970	2000200	1745709 - 2254670

II BIOLOGY OF C.VIRIDIS

1. Methods of rearing

1.1 Eggs

Juncus stems with eggs of *C. viridis* were brought in from the field. As the oviposition sites are visible externally, the stems were cut into short pieces with the eggs and placed inside seven and a half by two and a half centimetres glass tubes covered with cork. Des iccation of the egg was prevented by placing a moistened disc of filter paper at the bottom of the glass tubes. Hatching in these containers was good, provided that fungal attack either on the *Juncus* stem or eggs did not take place. If the embryo inside the egg was already well advanced in development, hatching could take place inspite of attack by fungus. Both the eggs and the *Juncus* stems were very susceptible to fungal attack, and treatment with one percent Nipogen failed to prevent establishment of fungus.

1.2 Larvae and adults

Cicadella viridis is extremely difficult to rear in the laboratory. Attempts to rear it in large numbers was unsuccessful. Two methods were used in rearing immature stages in small numbers. The first method consisted of using glass tubes of the size of 10 cm tall and 2.2 cm in diameter. These tubes were filled to one third with 1:1 moistened sand and peat mixture into which

a young Holcus was planted. The open end of the tube was covered with muslin. Young larvae hatched out in the laboratory were reared individually in each tube.

In the second method food plants of Holcus, Ranunculus or Juncus were planted in a conical shaped flower pot of 12.5 cm in height, and 13 cm in diameter. A cylindrical cage made of cellulose acetate 35 cm in height was inserted round the pot. Two windows of seven square centimetres were cut on opposite sides of the cage but at different levels, and covered with muslin to allow for ventilation. This is to prevent condensation of water on the sides, also cellulose acetate is known to emit fumes which may be lethal to some insects. Introduction of insects into the cage was carried out, after the plants have established themselves. Up to ten larvae were kept in each cage.

The first method of rearing was unsuccessful, in spite of frequent change of food plants at the rate of once every two days. Larvae survived up to the second instar, then died.

The second method proved to be more successful and it was possible to rear some larvae up to the adult stage, provided the food plants were kept in good condition. However, the rate of successful rearing was still low.

For experiments on egg laying, the second method and an enlarged version of it were used. The enlarged version consisted of using Watkins and Doncaster cages of diameter of 22 cm and a height of 39 cm (see plate 2 for the two types of cages used).

2. Life history

C. viridis has only one generation a year in Britain. The overwintering eggs hatch in the early part of May. For the three years of 1969, 1970 and 1971, hatching in the field commenced on the 20th, 18th and 11th of May respectively. There are five larval instars, each instar occuring over a period of five to six weeks. Thus there is considerable overlapping of stages. By the end of June, all five larval instars could be found in the field. The chart in Fig. 2 summarises the period during which each instar appears. As is common in most insects, male C. viridis generally emerged about a week earlier than the females. The males lived for about two months, by the end of August, most died off. Sexual maturity in male was probably reached in about three to four weeks after emergence. No mating has been observed in the field, but in captivity at 20°C constant temperature, this took place about three weeks after emergence of females. The preoviposition period of the female is a long one. Field observations made in 1971 show that the period from the

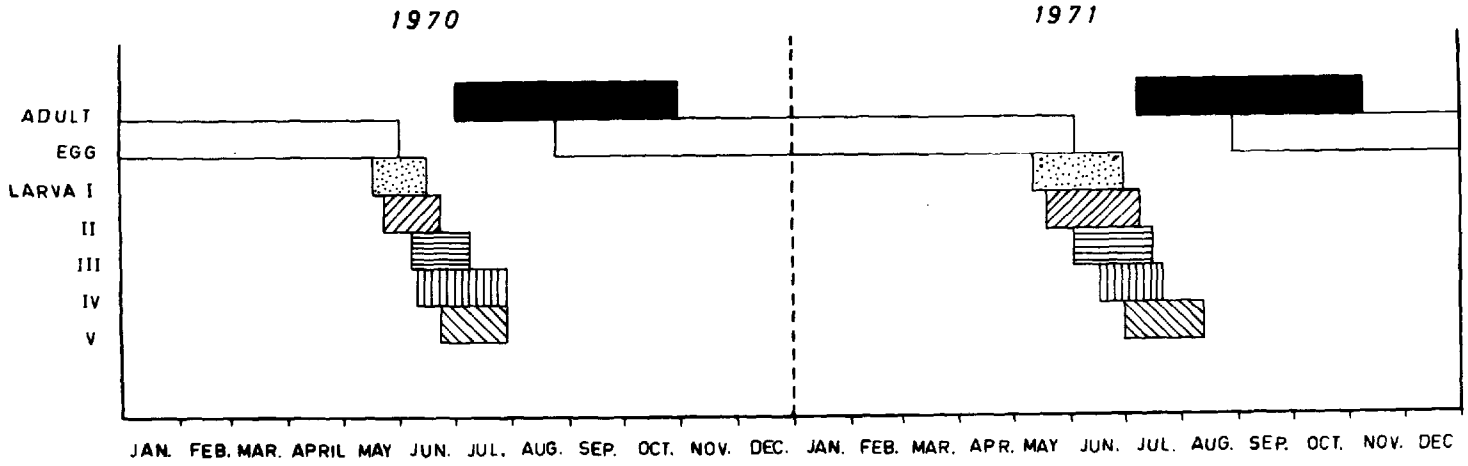


FIG. 2 LIFE HISTORY OF *C. viridis*.

first appearance of the female to the first observed oviposition was 51 days. Observation at 20°C constant temperature on 20 females reared on Holcus showed a variation from 50 to 69 days with a mean of 59.35 ± 1.23 days. As C. viridis generally does not survive well under captivity, it could be assumed that conditions for its development under such circumstances were not ideal. Thus the figure might be slightly lower than would be expected in the field, and as such could only be taken as an indication of the approximate length of preoviposition period. Comparing this to the other known preoviposition periods of other leaf hoppers, this period in C. viridis was extremely long, e.g. in Empoasca fabae (Harris) this was 6.4-23.3 days, 12.8 days in Endria inimica (Say) and 7 to 13 days in Colladonus geminatus (Van.D.) (DeLong 1971). Adults commenced laying eggs as from the last week of August and continued till the end of November; by then most individuals had died. Dissections of females showed that egg production is continued until the end of the female's life. The eggs entered into diapause and resumed development in the following spring.

3. Food plants

C. viridis is polyphagous in habit. It had been reported to feed on a number of species of plants with a preference for grasses and rushes and short herbaceous plants. Balachowsky (1941) observed that larvae migrate from trees on which they hatch to fields of long grasses where they feed in moist sheltered positions at the bases of the plants. These 'long grasses' consisted of Phragmites, Cyperus, Arundo and Juncus. On agricultural crops, it has been recorded on Sorghum (Sorghum valgare var. saccaratum) (Goidanich 1938), wheat, maize. groundnut and Sorghum in addition to such wild hosts as Polygonum fagopyrum L. and Potentilla sp. (Chu and Teng 1950). Servadei (1948) recorded an attack of both cultivated and wild graminae (species not specified) and Frediani (1955) has observed feeding on Agropyron repens Beauv. In Britain there are no records of C. viridis feeding on agricultural crops. Whalley (1958) reared C. viridis larvae to adults successfully on Potentilla anserina L., but found that on Juncus effusus they would not survive beyond the third instar. In the present study site, Potentilla was absent. As Juncus effusus, Holcus mollis and Ranunculus repens are the three dominant plants in the study area, these three species were used for rearing.

On both Juncus and Holcus feeding was on the stems,

whereas on Ranunculus, the first two instars tend to feed on the veins on the underside of leaves, but in later instars they migrate to feed on the leaf stalks. In all cases, if the food plant is suitable, once feeding commenced there was very little movement. Individuals have been observed to stay on the same spot for days.

The suitability of the three species of plants as food for C. viridis was compared. The plants were grown in a sand peat mixture in flower pots of height 12.5 cm and 13 cm in diameter. Each pot was then enclosed with a cylindrical cellulose acetate cage 38 cm in height. Rearing was carried out at 20°C constant temperature rooms. All plants were planted as rhizomes and produced new shoots. Ten newly hatched larvae were confined to each cage, and there were eight replicates for each species of host plants.

Chemical analysis for nitrogen content was carried out on the three plant species collected in the field in the beginning of June and then at fortnightly intervals to mid August.

The number of survivors in each instar is given in Table 2. Irrespective of the type of food plant supplied the highest mortality occurred during the first instar. Of the 80 first instars, only 39, 42 and 33 surviv ed and moulted to second instar on Holcus, Juncus and Ranunculus respectively. Mortality during the

Table 2. The relationship of food plants on the survival of C. viridis and the sex ratio of adults.

Food	initial number of first instar larvae	Number surviving in each instar at 20°C					
		I	II	III	IV	V	Adult
Holcus mollis	10	3	3	2	2	2	2
	10	4	2	1	1	1	0
	10	3	3	3	3	3	2
	10	8 (39)	8 (35)	8 (27)	7 (22)	7 (21)	7 (10 ♂♂)
	10	5	4	3	0	0	2 (9 ♀♀)
	10	2	2	2	2	1	1
	10	6	5	3	2	2	1
	10	8	8	5	5	5	4
Ranunculus repens	10	8	8	7	6	6	4
	10	3	3	3	3	2	2
	10	4	4	4	3	3	0
	10	7	6	5	2	2	2
	10	7 (42)	7 (39)	6 (36)	6 (29)	6 (27)	5 (12 ♂♂)
	10	4	2	2	2	1	0 (2 ♀♀)
	10	6	6	6	6	5	0
	10	3	3	3	2	2	1
Juncus effusus	10	6	1	1	0	0	0
	10	7	0	0	0	0	0
	10	5	5	2	1	0	0
	10	1 (33)	1 (13)	0 (7)	0 (5)	0 (3)	0 (2 ♂♂)
	10	7	1	0	0	0	0
	10	3	1	1	1	1	0 (0 ♀♀)
	10	2	2	1	1	1	1
	10	2	2	2	2	1	1

subsequent stages was lower, this is illustrated graphically in Fig 3. Variance analysis (see table 4) indicated that in the first instar, there was no significant difference on the mortality between larvae on different plants. From second instar onwards to the fifth instar the numbers surviving on the Holcus and Ranunculus were significantly higher than the numbers on Juncus, whereas there were no significant differences between the numbers that survived on Holcus and Ranunculus. For the number which survived to adult stage, there was a significant difference between larvae reared on Holcus and Juncus, and Holcus and Ranunculus at 5% level but not between those on Ranunculus and Juncus. The reason for the lack of statistical significance in the latter pair might be due to low number of survivors in each case and probably also due to insufficient replicates. However biologically it is interesting to note that:

(a) The numbers that survived on Ranunculus were consistently higher than those on Juncus and Holcus in all stages except the adult.

(b) Except with Holcus, the other two species of food plants produced more males than females. On Juncus only two out of the total survived to adults and both were males. On Ranunculus there were 12 males to two females out of the 27 that survived to fifth instars.

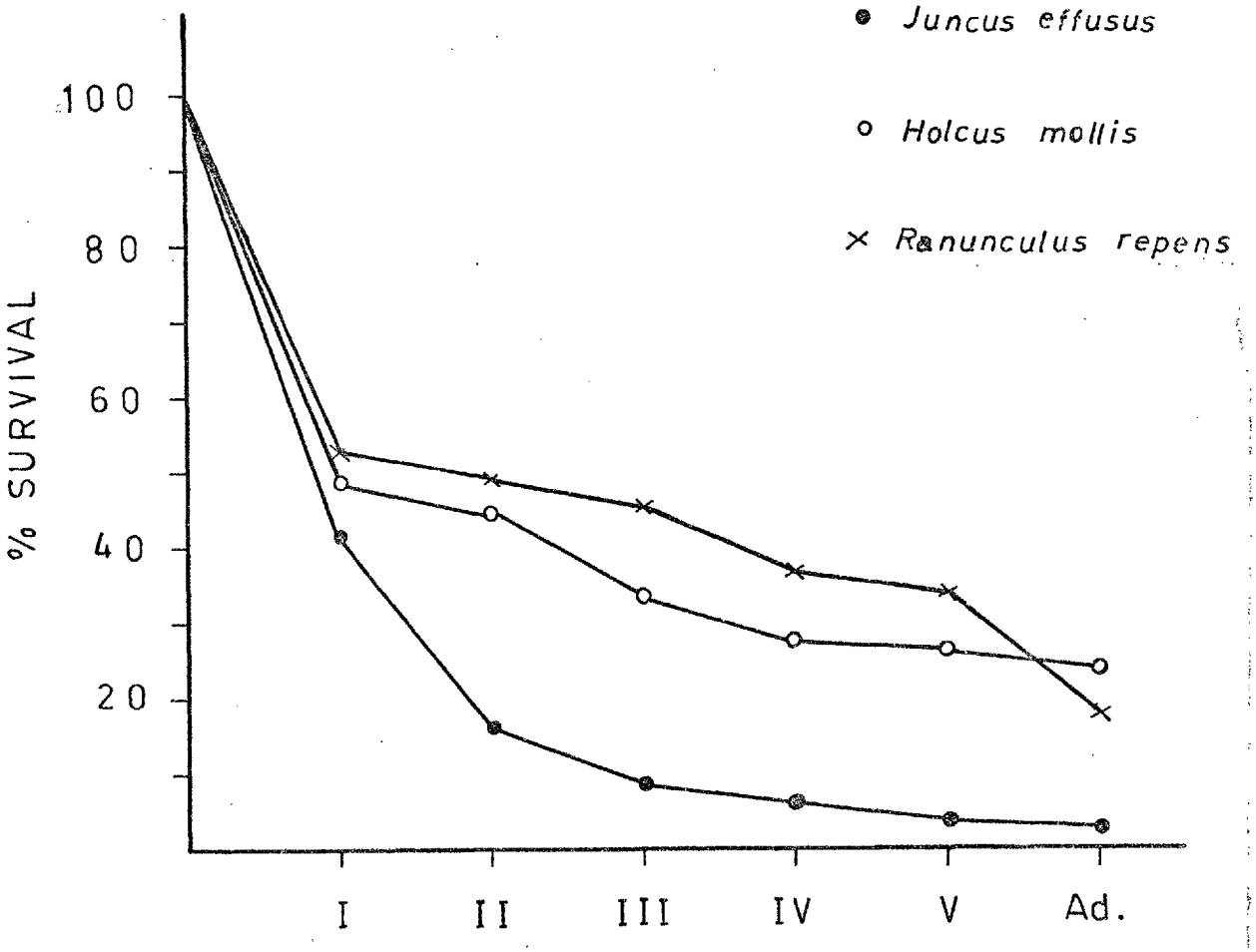


FIG. 3 The relationship of food plants and the percentage of survival of *C. viridis* in each instar.

Examination of the dead fifth instars showed that 10 were females and three were males, which indicates that when they feed on Ranunculus alone, certain nutrients were lacking for the growth of females resulting in their greater mortality.

The mean duration of each instar reared on the three food plants are shown in Table 3. With the exception of the third and fourth instars, the duration of instars were not significantly different on different food plants. In the third instars individual reared on Ranunculus have a significantly longer instar duration than those reared on Holcus (F=6.019 significant at 1% level), and Juncus (F= 4.8170 significant at 5% level). In the fourth instar, the instar duration of those reared on Ranunculus was significantly longer at 1% level than of those reared on Holcus. The differences in durations on Holcus and Juncus or Juncus and Ranunculus in the fifth instar were not significant (see Table 5). Thus individuals reared on Ranunculus have a longer larval period.

Theseresults agreed with Whalley's (1958) finding that Juncus is not suitable for rearing of C. viridis. But for those that survived instar durations were not affected. Ranunculus gave the highest number of survivors upto the fifth instar but it seems to lack in certain nutrients; this results in greater mortality in the female insects, and a longer larval period.

Table 3. Food plants and the duration of instar.

Food plant	Mean duration of instar (day) with standard error at 20°C							
	I	II	III	IV	V		Total duration	
					Male	Female	Male	Female
Holcus mollis	8.24±0.50	8.33±0.48	9.05±0.85	9.95±0.50	13.80±0.33	14.11±0.37	47.60±1.15	51.80±1.15
Juncus effusus	10.46±0.27	9.00±1.76	9.20±1.16	10.67±1.22	17.00±3.00		51.0±3.0	
Ranunculus repens	10.20±0.55	8.19±0.43	12.14±0.46	11.76±0.44	16.25±1.35	23.00±1.00	51.58±2.10	66.50±3.46

Table 4. Analysis of variance on the number of individual survived to various instar on different food plants.

First instar

Source of variation	Sum of Squares (S.S.)	Degrees of freedom (df.)	Mean Square (M.S.)	Variance ratio (F)
Between food plants	5	2	2.5	0.50 Not significant
Residual	105	21	5.0	
Total	110	23		

Second instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plants	49	2	24.5	6.4473**
Residual	80	21	3.8	
Total	156	23		

Detailed Comparisons

Holcus v Juncus	30.25	1	30.25	7.9606**
Ranunculus v Juncus	64.00	1	64.00	16.8421***
Holcus v Ranunculus	1	1	1	0.2631 Not significant

Third instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plant	55	2	27.5	9.48275**
Residual	61	21	2.90	
Total	116	23		

Table 4 contd.

		Detailed comparisons		
Holcus v. Juncus	25.00	1	25.00	8.6200**
Ranunculus v. Juncus	52.56	1	52.56	18.1250***
Holcus v. Ranunculus	5.0625	1	5.0625	1.7456 Not significant

Fourth instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plant	38	2	19	5.9561**
Residual	67	21	3.19	
Total	105	23		
		Detailed comparisons		
Holcus v. Juncus	18.0625	1	18.0625	5.6622*
Ranunculus v. Juncus	36.0000	1	36.0000	11.2853**
Holcus v. Juncus	3.0625	1	3.0625	0.9600 Not significant

Fifth instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plant	38	2	19	5.9561*
Residual	67	21	3.19	
Total	105	23		
		Detailed comparisons		
Holcus v. Juncus	20.25	1	20.25	6.3480*
Ranunculus v. Juncus	36.00	1	36.00	11.2953**
Holcus v. Ranunculus	2.25	1	2.25	0.7053 Not significant

Table 4 contd.

Adult

Source of variation	S.S.	d.f.	M.S.	F.	
Between food plant	24	2	12	4.4618*	
Residual	58	21	2.7619		
Total	82	23			
		Detailed comparisons			
Holcus v. Juncus	18.0625	1	18.0625	6.5173*	
Ranunculus v. Juncus	9.0000	1	9.0000	3.2586	Not significant
Holcus v. Ranunculus	23.1500	1	23.1500	7.7166*	

*, **, ***, indicates the level of significant at 5%, 1% and 0.1%.

Table 5. Analysis of variance on the relationship of food plant and duration of instar.

First instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plants	55	2	27.5	2.9433 Not significant
Residual	785	84	9.3452	
Total	840	86		

Second instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plants	3	2	1.5	0.2027 Not significant
Residual	496	67	7.40	
Total	499	69		

Third instar

Source of variation	S.S.	d.f.	M.S.	F.
Between food plants	63	2	31.5	4.6247*
Residual	361	53	6.8113	
Total	424	55		

Detailed comparisons

Holcus v. Juncus	5.0909	1	5.0909	0.7474 Not significant
Ranunculus v. Juncus	32.8100	1	32.8100	4.8170*
Holcus v. Ranunculus	41.4260	1	41.4260	6.0819**

Table 5 contd.

Fourth instar

Source of variation	S.S.	d.f.	M.S.	F.	
Between food plants	38	2	19	3.6627*	
Residual	249	48	5.1875		
Total	287	50			
		Detailed comparisons			
Holcus v. Juncus	1.3393	1	1.3393	0.2582	Not significant
Ranunculus v. Juncus	3.1148	1	3.1148	0.6000	Not significant
Holcus v. Ranunculus	37.7828	1	37.7828	7.2729**	

Fifth instar

Male

Source of variation	S.S.	d.f.	M.S.	F.	
Between food plants	39	2	19.5	1.5282	Not significant
Residual	268	21	12.76		
Total	307	23			

Fifth instar

Female

Source of variation	S.S.	d.f.	M.S.	F.	
Between food plants	11	1	11	0.7676	Not significant
Redsidual	129	9			
Total	140	10			

McNeill(in press) has shown that if individual Leptopterna dolabrata L. (Heteroptera) were confined on low nitrogen food after the third instar, they would show a higher mortality rate than those that were given food with high nitrogen content. Also those that survived to adults on low nitrogen diet were very weak and showed little sexual development. It was therefore decided to analyse for the nitrogen content of Holcus, Juncus and Ranunculus. As the total duration of larval instars were approximately similar both in the field and in the laboratory, it was decided to collect plant materials for analysis during the period which corresponded to the presence of third, fourth and fifth instars in the field. Analysis for nitrogen was carried out on freeze dried material collected fortnightly. The actual determination was by the Kjeldah method and nitrogen was determined by colourimetric method expressed in one part per million.

Fig. 4 illustrates the variation in nitrogen content in the three species of food plants from early June to mid August. At the beginning of June nitrogen content of Juncus was the highest, but fell sharply and by mid August it was the lowest of the three species of plants. Ranunculus shows two peaks of high nitrogen. It is high in early June falls off sharply towards the end of June, rises again to a peak towards the end of July and falls off by mid-August. During early June, nitrogen content in Holcus is the lowest

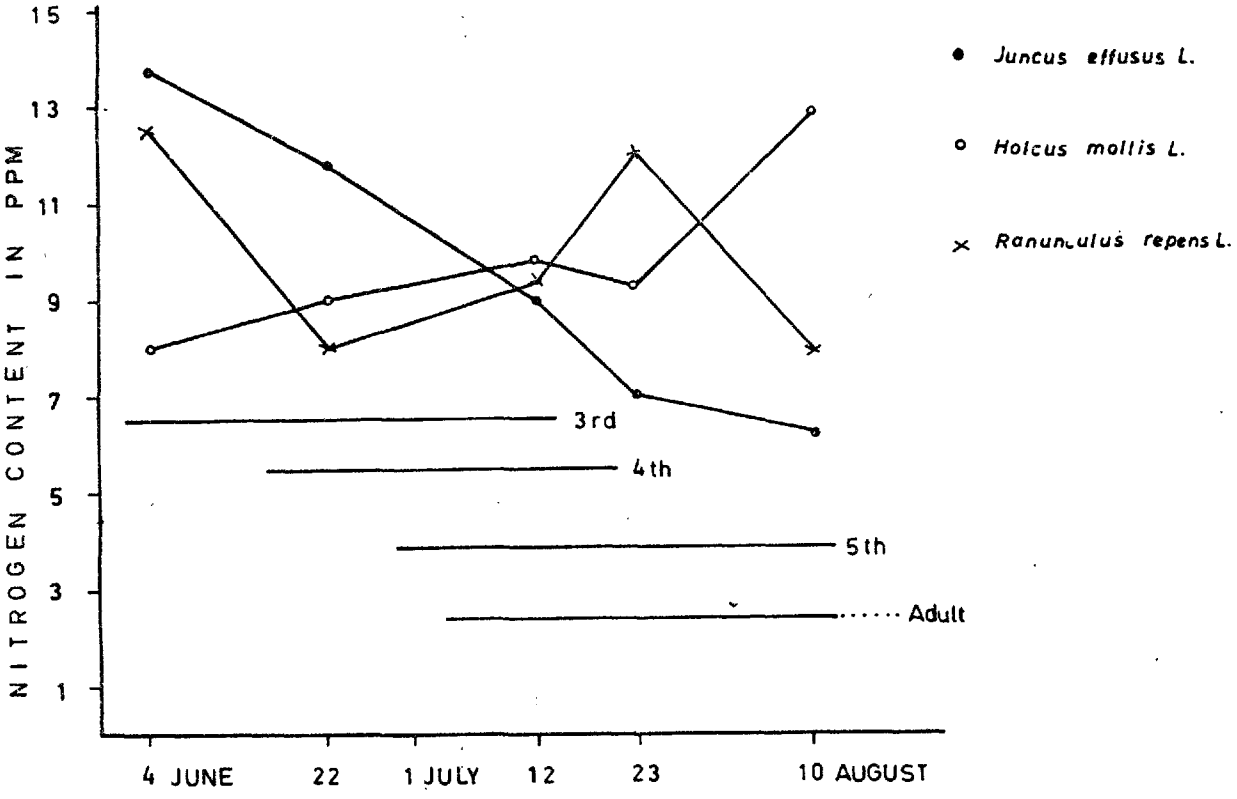


Fig. 4 Variation in N_2 content in *Juncus effusus*, *Holcus mollis* and *Ranunculus repens* from June to August. The straight lines indicat the period during which the relevant stages of *C. viridis* occured.

of the three food plant species, but rises steadily to a peak by mid August. The importance of nitrogen in food plants in nutrition of insects has been shown by McNeill(In Press) in Leptopterna dolabrata and by Feeny (1970) in the winter moth Operophtera brumata L. and other species of Lepidoptera on oak trees. Feeny found that spring peak of insects feeding on oak is associated with the peak of nitrogen in young leaves, and that lack of insects later in the year on oak is associated with both the decrease of nitrogen and the increase of tannin in the older leaves. McNeill(In Press) also demonstrated that the number of leaf hoppers (Cicadellidae (Jassidae) and Delphacidae) obtained from weekly suction samples were highest at times of relatively high nitrogen.

It is possible to explain the pattern of survival of C. viridis on Holcus and Ranunculus in terms of nitrogen content. The higher nitrogen content in Ranunculus during the early spring (thus younger plant) may account for the higher number of survivors in the early instars. The drop in N_2 content occured at the beginning of the third, throughout the whole of fourth and the first half of fifth instars. This probably accounts for the longer duration of instar three and four. The low N_2 content during the beginning of the fifth instar might have affected the survival of female insects more than the males and resulted in the

greater mortality of the former. As the N_2 increases again, the females that survive might continue to develop and moult into adults. This is indicated in Table 3 where the total mean larval duration of females on Ranunculus was 66.50 ± 3.46 days as compared with 51.8 ± 1.15 days in individuals fed on Holcus. In the case of Juncus, it is however more difficult to explain in terms of Nitrogen content alone. As nitrogen content of Juncus was higher than in both Ranunculus and Holcus in the early part of its life, and yet the numbers that survived on it were significantly lower than on the other two species of plants. Two possible explanations are that:

(a) the epidermis of Juncus may be too tough for the young larval to feed properly

(b) As Juncus is a less succulent plant than either Holcus or Ranunculus, the amount of sap flow may not be as high and there is insufficient sap flow to the requirements of the insect. As shown by Kennedy and Mittler (1953) that in aphid the force responsible for moving the sap out of the plant into the normally feeding insect is provided almost entirely by the pressure in phloem sieve-tubes, the same may be true in the case of C. viridis. Andrzejewska (1967) working on the energetics of C. viridis showed that the amount of plant sap sucked by a single individual adult varies from 1.14 ml to 1.37 ml daily according to the density of the insects. The average mean weight for newly

emerged adult female is 19.00 ± 0.8 mg. (0.019 gm.) and weight of male is 9.96 ± 0.05 mg. (0.00966 gm.), which means that on the average a single individual would remove about a hundred times its own weight of fluid per day. No experimental evidence was available to support either of these postulations but it would appear that the second reason was more plausible. It would be interesting to compare the sap flow of these three species of plants.

In conclusion, it could be said that Holcus was the most suitable food plant for C. viridis. (Inspite of very high mortality of the first instar on all the three plants.) This species thus has a different requirement for food and oviposition. A similar situation was found by Pitre (1967) in Dalbulus maidis (DeLong and Wolcott), the adult of which could feed on 33 different kinds of plants, but only 20 species of Graminaceae were found suitable for oviposition; eggs hatched on 16 hosts, but larvae developed successfully only on maize.

4. Description of the egg

The egg of Cicadella viridis (L.) is translucent white in colour with shiny chorion. It is elongated oval in shape broader at the posterior pole and tapering towards the anterior. The size is rather large for a Cicadellid, the length measured between 1.57 mm to 1.80 mm with a mean of 1.67 mm, and its greatest width ranged between 0.35 mm to 0.47 mm with a mean of 0.38 mm. The measurement was based on ten batches of egg masses with a total of eighty-one eggs. There is some variation in the size of eggs within a single mass and this is usually more pronounced in length than in width.

The figure shown by Morcos (1953), was that of a mass of eggs with well formed embryos. In eggs when the embryo is still not visible through the chorion, there is a large yolk body towards the anterior pole. A description of the development of the egg with illustrations was given by Müller (1951). The first visible sign of egg development commenced with the egg turning opaque, a white patch appearing at both poles; this was followed by the appearance of the eye spots round the middle of the egg. Over-wintering eggs have embryos developed to the stage when segmentation commences and it is at this stage that they enter diapause.

5 Oviposition

5.1 Host plants and the numbers of eggs per egg site

In Continental Europe and in Asia Cicadella viridis (L.) has been recorded to lay its eggs on woody trees, and frequently causing damage to trees of economic importance. In Germany Betram and Mannheins (1939) reported that fruit trees especially pear, apple and plum of the Rhine-land were injured by oviposition of C. viridis in the stems, branches and twigs, this resulting in the weakening of the trees and rendering them more susceptible to attack by other pests. Schindler (1960) described damage by oviposition of C. viridis on deciduous forest trees in Southern Germany, Ash being the most affected. Balachowsky (1936) found that in France C. viridis preferred woody trees and low branches of one to three year old ones. The resulting wound could lead to desiccation and death of young shoots and grafts. In a later paper Balachowsky (1941) reported feeding of C. viridis on Phragmites, Cyperus, Arundo and Juncus. He also gave a list of plants where eggs were found, which included Fraxinus excelsior, Alnus glutinosa, Salix caprea, Populus sp. Prunus spinosa, Prunus armeniaca, Prunus domestica, Prunus persica, Rosa sp. Crataegus, Rubus, Pirus communis, Pyrus malus, Mespilus germanica, Cydonis vulgaris, Rubus idaeus, Ribes rubrum, Syringa vulgaris, Ligustrum vulgare and Sambucus nigra. He also speculated that oviposition of eggs on trees probably resulted from a lack of suitable plants with a hard haulm (Phragmites or Juncus) in marshy localities where C. viridis was abundant.

In Italy Frediani (1955) found that the eggs of the summer generations were deposited on the stalks of graminaceous plants, particularly Agropyrum repens and Erigeron canadensis, while those of the third generation were exclusively deposited on twigs of rose. Oviposition on raspberry and vine and other herbaceous plants was recorded by Dirimanov and Kharizanov (1964) in Bulgaria, while oviposition on twenty different species of woody trees were recorded by Chu and Teng (1950) in China. Populus spp., Prunus persica, Robinia pseudoacacia, apple pears, Salix spp. and Begonia were found to be most frequently oviposited on. Most eggs were laid at heights between three to eight feet.

In Britain no oviposition on woody trees has been recorded. Whalley (1958) examined thirty-two different species of plants including Populus sp. and Salix sp. but found no oviposition sites. He had found eggs laid on two species of Juncus, Juncus effusus and J. inflexus. J. effusus was most frequently laid on and J. inflexus less frequently. He also noted that eggs laid in J. inflexus tends to be deformed. In the present study only one species of Juncus i.e. J. effusus is present on the site.

Examination of plant species within the study area, which included Salix atrocinerea confirmed Whalley's finding that eggs were laid only in Juncus. In the laboratory gravid females when confined with Holcus mollis will

occasionally lay a few batches of eggs on the matured and hardened stem.

Oviposition sites on Juncus have been described by Morcos (1953) and by Whalley (1958) and they have been re-examined here. Briefly, the female inserts its ovipositor into the Juncus stem and makes long slits down-wards as the eggs are being laid. A pale white waxy substance generally appears round the egg site, and the wound caused shows up in a day or two as a brown line on the epidermis of the stem. The length of the slit varies between 3.8 mm to 12 mm It is generally true that the larger the egg slit, the more eggs will be found within the slit, however exceptions do occur where a long slit will contain only a few eggs. Usually eggs are inserted right into the pith of the Juncus stem at right angles to its axis and show no external sign of their presence. Occasionally eggs are deposited just beneath the epidermis and form a distinct swelling. Inside the slit the eggs are arranged in almost a straight row curving slightly outwards at the lower end. Individual eggs are arranged in a slanting fashion with the apical end pointing upwards. In most cases where C. viridis laid its eggs on woody plant the eggs were described as arranged in a crescent.

The number of eggs per egg site varies from one to nineteen with a mean of around ten. The mean number of eggs per site appears to be constant over the three

Table 6. Mean number of eggs per egg mass over three seasons

Year	No. of egg masses examined	Mean no. of eggs per mass with standard error
1968	169	10.54 ± 0.21
1969	358	10.67 ± 0.16
1970	426	10.48 ± 0.14

seasons studied, as shown in Table 6. A frequency distribution of number of eggs per egg site based on 428 sites and 4483 eggs is shown in Fig. 5. Empty egg sites are occasionally present. Rothschild (1962) had observed similar unoccupied sites in Conomelus anceps (Germ.) which also laid its eggs in Juncus. In C. viridis empty egg sites do not appear to be attempts by the female to select suitable oviposition site. During study on fecundity in an outdoor insectary it was found that some females towards the end of their egg laying period, would make an egg slit, but fail to deposit any eggs. When dissected it was found that small number of eggs were still present in the oviducts.

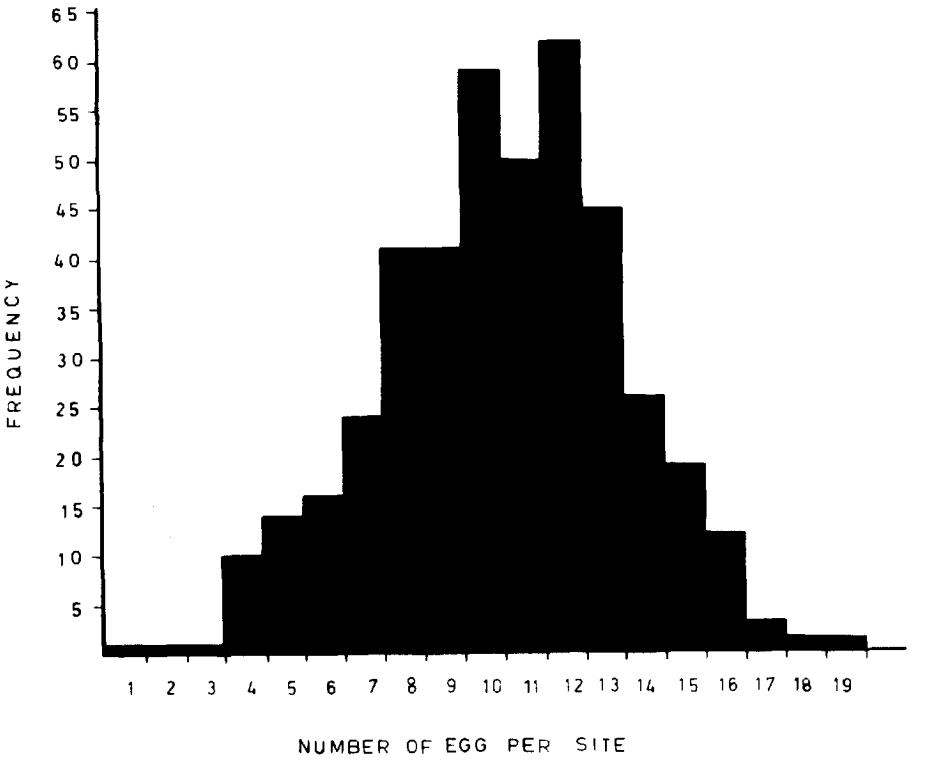


FIG.5 FREQUENCY DISTRIBUTION OF NUMBER OF *C viridis* EGG PER SITE.

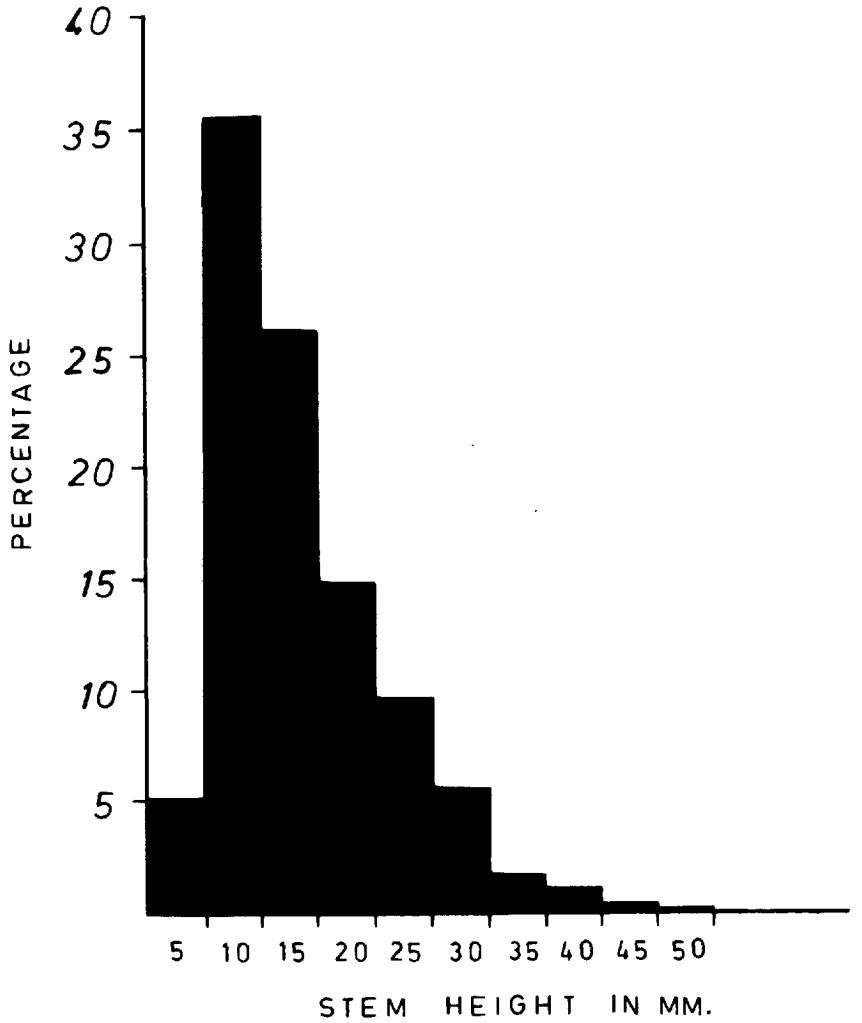


FIG. 6 DISTRIBUTION OF *C. viridis* EGG SITE ON *Juncus* STEM.

5.2 Distribution of oviposition site and its relationship to the diameter of Juncus stem.

The distribution of oviposition site on Juncus stem was examined. Juncus stems were collected at random in bundles of ten or more per sample in the course of sampling for populations of eggs during the winter months. Stems were cut as close to the ground as possible, and measurements were made from the base of the stem to the lower end of an egg slit. Fig. 6 shows the percentage of total oviposition sites plotted against stem height. Eighty-five percent of the total eggs were deposited at the height between 6 to 25 mm , with 5.05% between 0 to 5 mm. and 8.86% between 25 to 50 mm In fact very few eggs were found above 41 mm (0.47% of the total), and no eggs were found above 50 mm Altogether 3798 stems with a total of 1286 egg sites were examined. A similar pattern of oviposition behaviour was also found in the Delphacid Conomelus anceps (Germ.) by Rothschild (1962); Conomelus also laid its eggs on the basal 6 inches of Juncus stem. Apart from the obvious advantages of better shelter and more favourable microclimate at the base of a Juncus clump, in C. viridis females may have preference to lay eggs in stems of large diameter. In Juncus stems, the first 20 mm or so are generally the largest and of uniform diameter, then they taper towards the tip.

The diameters of 1426 stems were measured by a pair of vernier calipers, and the number of egg sites and number of eggs per site counted. The results are shown in table 7.

No oviposition had been recorded on stems of diameter of 1.5 mm and less. A graphical representation of a comparison between the distribution of Juncus stem diameter and the distribution of oviposition sites on the stems is given in Fig. 7. Although stems of diameters between 2.1 - 2.5 were the most common the majority of the egg sites were found on stems of diameter of 2.5 - 3.0 mm The mean number of egg sites per stem calculated as a fraction of the number of egg sites over the number of stems examined, shows that with the increase in the stem diameter, there is a corresponding increase in mean number of egg sites per stem. The percentage of stems with eggs laid in each size interval also shows an increase with increase in stem diameter as is indicated in Table 7. This is particularly pronounced in stems of diameter of 4.1 - 4.5 mm. In terms of stem population, this constituted only about 0.9% of total, but 84.6% of these were oviposited on. All the evidence therefore suggests that oviposition by C. viridis is not random and that the female clearly choses stems of large diameter for oviposition, whenever these are available.

Table 7. Diameter of stems in relation to incidence of oviposition sites and the number of eggs per site.

Stem diameter in mm	Frequency of stems	% of total stem	No. of egg sites	% of total sites	Total no. of eggs	Mean no. of eggs/site	Mean no. of egg sites/stem	% of stem with eggs
1.0 - 1.5	33	2.31	0	0	0	0	0	0
1.6 - 2.0	310	21.73	21	2.67	196	8.04	0.07	4.51
2.1 - 2.5	525	36.82	112	14.24	1014	9.05	0.21	13.14
2.6 - 3.0	392	27.49	329	41.85	3217	9.77	0.84	30.10
3.1 - 3.5	118	8.27	210	26.71	2104	10.01	1.78	49.15
3.6 - 4.0	35	2.45	67	8.52	721	10.76	1.91	48.57
4.1 - 4.5	13	0.91	47	5.97	478	10.17	3.61	84.61

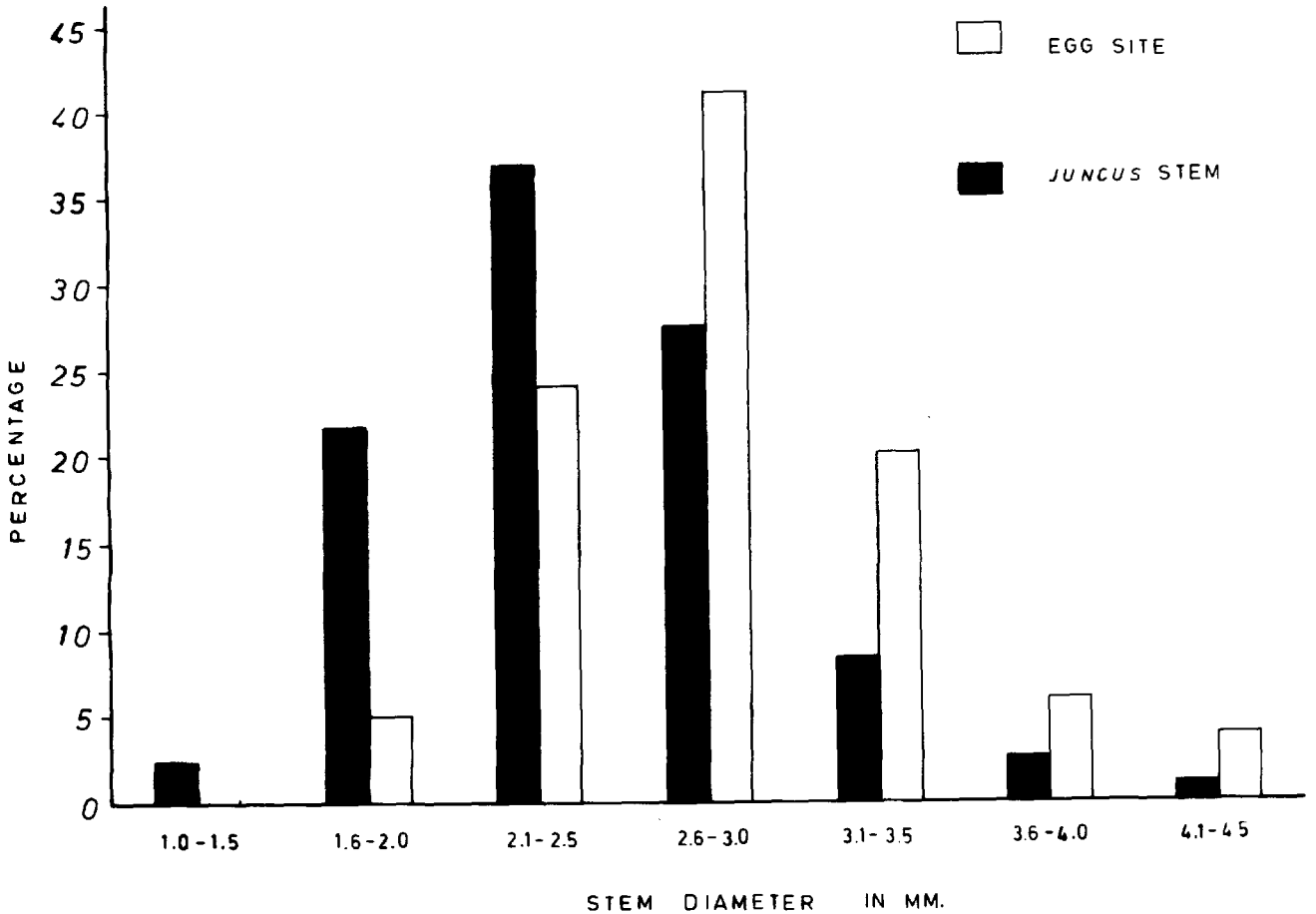


FIG. 7 RELATIONSHIP OF *Juncus* STEM SIZE AND THE DISTRIBUTION OF *C. viridis* EGG SITE.

The size of stem also seems to affect the number of eggs per egg site. Analysis of variance carried out on the above data (see Table 8) indicated that there were fewer eggs per oviposition site on stem of 3.5 mm diameter and below than in those of 3.5 mm and above. The mean number of eggs per site of 3.5 mm and below, range from 8.05 to 9.78 as compared with 10.02 to 10.76 in stems of 3.5 mm to 4.5 mm in diameter. The significance level was at 0.1%.

Table 8. Variance analysis on stem diameter in relation to number of eggs per egg site.

Source of variation	Sum of Squares (S.S)	Degrees of Freedom (d.f)	Mean Square (M.S.)	Variance ratio (F)
Between level	205	5	41	4.2589***
Residual	7509	780	9.6269	
Total	7714	785		

Detailed comparison

Stem diameter (in mm.)

2.0 V. 2.5	17.8954	1	17.8954	1.8589 N.S.
2.5 V. 3.0	43.8637	1	43.8647	4.5564 *
3.0 V. 3.5	597.7534	1	597.7534	62.0920***
3.5 V. 4.0	27.9765	1	27.9765	2.9060 N.S.
4.0 V. 4.5	9.6475	1	9.6475	1.0021 N.S.

N.S. = not significant

The number of * indicate level of significance at 5%, 1% and 0.1%.

5.3 Effect of direction on oviposition

Balachowsky (1936) found that in Europe C. viridis would lay its eggs in the subcortical tissue of most of the woody trees, including a number of species of economical importance. He mentioned that low branches of one to three years old, on the southern and south-western sides of the trees were most frequently selected for oviposition. A survey was carried out during the present study to investigate whether C. viridis when oviposited close to ground level on Juncus would exhibit such preference.

During the course of sampling for egg populations, each Juncus clump was divided into four parts according to the compass direction. About ten or more Juncus stems were collected from each direction in every sample collected, by cutting the stems at ground level. The stems were then examined in the laboratory for egg clusters.

The result of this analysis is shown in Table 9. The mean number of egg clusters per stem for the direction of North, East, South and West were 0.3012, 0.3927, 0.4303 and 0.3418 respectively. These figures appear to suggest that Juncus stems facing South were preferred for oviposition, with a second preference for East and West, the North being least preferred. However

variance analysis carried out suggests that there is no significant differences between these data ($P > 20\%$).

Table 9. Number of egg clusters and the direction the stems were facing

Direction	Number of stems examined	Number of egg clusters	Mean number of cluster/ stem
N	976	294	0.3012
E	955	375	0.3927
S	990	426	0.4303
W	1027	351	0.3418

Analysis of variance

Source of variation	Sum of Squares	d.f.	Mean Sqaure	F.
Between level	9.3	3	3.1	1.5271 not significan
Residual	7999.4	3944	2.03	
Total	8008.7	3947		

6. Egg development

6.1 Humidity and egg development

Eggs of C. viridis are extremely sensitive to dehydration. When dissected out from the Juncus stems they would dry up within two hours. Whalley(1958) incubated eggs over a range of humidities, he found that, below 98% relative humidity eggs would not hatch, and although development did take place at 92.4% R.H., hatching did not occur. As eggs are normally deposited inside Juncus stems, they are undoubtedly under conditions of saturated humidity. All experiments on incubation mentioned in experiments that follow were all carried out under conditions of saturation.

6.2 Effect of low temperature on egg survival

6.2a Determination of undercooling point of eggs of C. viridis

The eggs of C. viridis are laid between mid-August and the end of October, and hatched in the following May. Thus between laying and hatching is a period of seven to nine months in which the eggs may be subjected to low temperatures below the freezing point. An investigation was carried out to find out whether low temperature which occur from time to time throughout the Winter and in early Spring have any effect in causing mortality to eggs at

different stages of development. One of the common means of measuring cold-hardiness in insects is to determine their supercooling points. In the freezing of a cold blooded organism, the body temperature falls to a point below zero from which it suddenly rises as the latent heat of freezing is released, the point at which the body temperature suddently rises is the 'supercooling point or the 'undercooling point' (Salt, 1936). Although the undercooling point is the lowest temperature that an organism can survive, cold death can also take place on freezing at any temperature between this lower limit and the time of freezing of the body fluid (Salt, 1950, 1961). Thus measurement of undercooling point will only give an indication of the ability of an insect to withstand cold conditions, but need not necessarily be the actual temperature that it can withstand. Apart from intrinsic physiological factors, in immature and adult insects cold - hardiness could be altered by various factors, such as the presence of food in the gut (Salt, 1953), and the insects' moisture content (Salt, 1956), both of which raise the undercooling point. The undercooling point also depends on several parameters, notably on the rate of cooling (Salt, 1966a, 1966b). On the other hand, cooling rates varying from $1^{\circ}C$ to $18^{\circ}C$ per minute were tested by Sullivan (1965), but in the range feasible for laboratory testing, no major differences in the undercooling point was observed.

Timber and Danks (1970) described an apparatus with rate of cooling control, but such a device is relatively expensive. Other methods which have little control of cooling usually involved using a cooling coil immersed in alcohol (Salt, 1936) or by adding solid carbon dioxide to alcohol (Way, 1960; Sullivan and Green, 1964). Luff (1964) devised a method whereby insects are inserted individually in a holder cooled thermoelectrically by a device called 'frigistor'. With this device he was able to reach a temperature of down to -35°C. A similar system to ~~as~~ Luff's was first used in the present study, but because the 'frigistor' used were not of the same quality, it was not possible to produce temperatures below -21°C. An adaptation of Goodwin and Thiel's (1967) portable cooling device was used instead. This in principle is similar to the apparatus used by Sullivan (1965) for the study of eggs of the European pine sawfly Neodiprion sertifer (Geof.) The construction of the apparatus is shown in Fig. 8. Basically it consists of a block of aluminium insulated with expanded polystyrene and was connected with a detachable aluminium heat transfer rod at its base. The block was drilled with holes to receive 4.5 X 1 mm plastic ampules. When in use, the aluminium rod is immersed into

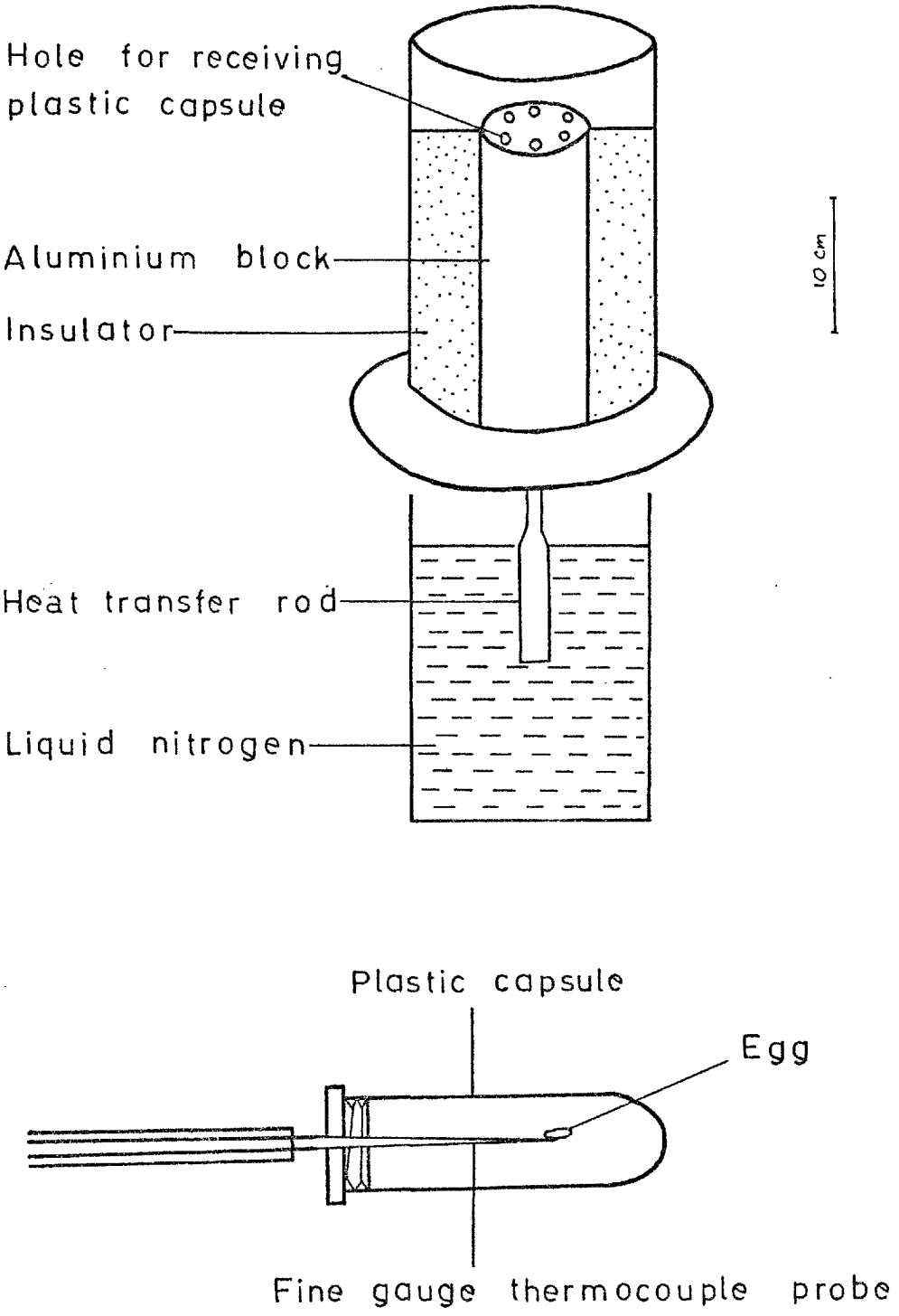


FIG. 8 Apparatus used for the determination undercooling point of egg.

liquid nitrogen, resulting in cooling down of the entire block. With this device very low temperatures can be reached. The rate of cooling is about 0.48°C per minute. Once cooled down, the temperature is maintained by the insulation for up to two hours. For convenience, in the present study, the block was pre-cooled to -40°C. The thermo-couple used for measuring temperature was made up of copper constantin wire, one end of which is twisted together, and immersed in a flask of melting ice to give a constant zero reference, the other end being an extension of fine 40 gauge copper-constantin wire was used to give a fine end probe. The thermocuples were then connected to an amplifier and in turn to a Rustrak recorder calibrated for direct reading of temperature. The egg to be tested was attached to the end of the probe with vaseline and put inside a plastic ampoule, which was then placed in the hole of the cooling block for determination of undercooling point (See Fig. 8). The plastic ampoule acts as a form of insulator to prevent too rapid cooling down of the egg. The rate of cooling was around 10°C per minute.

Eggs at different stages of development were tested to see whether any differences in cold-hardiness exist. For ease of recognition, eggs were classified arbitrarily into five stages. Those classified as stage I were diapausing eggs brought in directly from the field, and which show no visible sign of development. Examination on a slide under

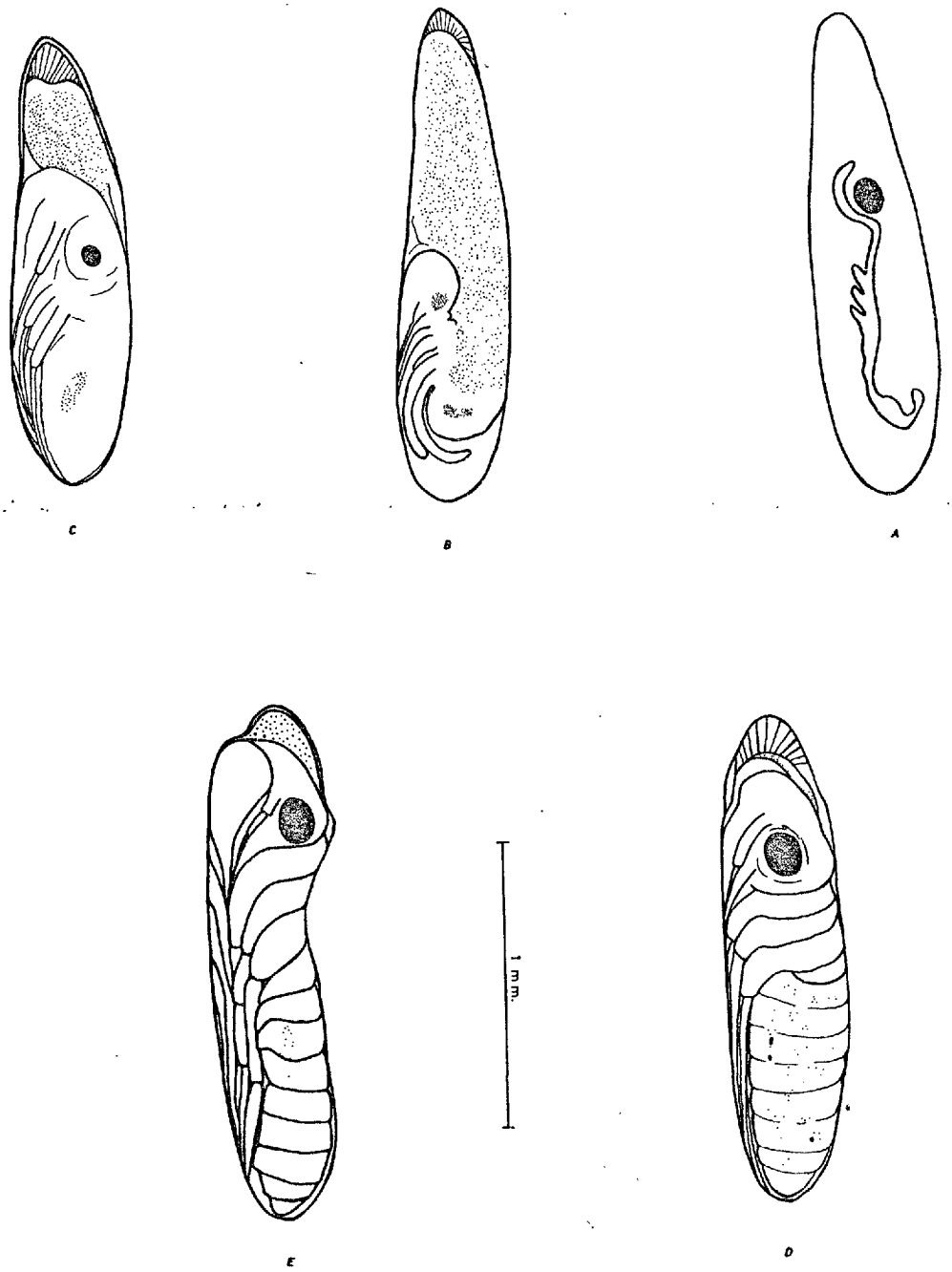


FIG. 9 Different stages in the development of C. viridis egg.

the miscroscope shows the embryo at the beginning of segmentation (Fig. 9A). Stage II were eggs with embryos which have completed segmentation, and with eye spots appeared at the posterior pole, visible as red dots externally (Fig. 9B). Stage III eggs have their embryo well formed in with the head pointing towards the anterior pole. The embryo travelled half way up the eggs and the eye spots appeared in a midway position (Fig. 9C). In stage IV the embryo was well formed occupying the whole eggs, the eye spots now appearing at the anterior pole (Fig. 9D). In Stage V (Fig. 9E) the embryo is on the verge of hatching, and the chorion is slightly ruptured. For determination of undercooling point, a minimum of twenty eggs at each stage of development were used.

Results

The results are summarised in Table 10, and graphically represented in Fig 10 . The mean undercooling point for diapausing eggs (stage I) is -28.67°C with a minimum of -30.5 and maximum of -27.0°C. The variation between eggs was very small with a range of only 3.5°C. The same small range of variations was found in eggs on the verge of hatching (stage V), where the mean was -22.64 °C with a minimum of -24.0 and a maximum of -21.0 °C. It appears that it is not uncommon that variations in cold-hardiness in eggs is generally small. A similar picture was found in the eggs of Leptohylemyia coarctata Fall. (Diptera) (Way, 1960) where there was a range of less than 3°C, and a mean of 1°C difference between two consequetive years. Greater range was obtained in eggs at stage II, III and IV of development. However, this might have been due to experimental error, as each stage was selected arbitrarily on morphological grounds, mainly on the positioning of eye spots, error might have occured in placing the right stage of development in the right category. Thus it would be expected that the variation of physiological conditions within these three stages would be greater.

The overall picture shows a trend towards raising of undercooling point as the embryo proceeds in its development, and lowering again at the stage approaching hatching. Analysis of variance shows the significant level

at 0.1% (see table 11). A detailed comparison between each stage was also carried out. Comparing stages I and II, the level of significance was at 0.1%, II and III at 5%. III and IV at 5% and IV and V at 0.1%.

From the result it could be concluded that eggs of C. viridis are extremely cold hardy at all stages of development. The Winter temperature at Silwood Park seldom drops below -10°C and with a grass [illegible] of about -14°C. Luff (1965) had conducted an extensive comparative study on microclimate of Dactylis tussocks and Holcus. He found that temperature within clumps of Holcus is generally a few degrees higher than the grass mean at soil level. Eggs of C. viridis being embedded inside the Juncus stem and generally surrounded by thick Holcus growth, they would never be subjected to temperatures of such a low level as to cause any mortality. The mechanism of cold-hardiness of the egg was not investigated. In eggs of phytophagous mite Panonyclus ulmi (Koch) it was related to the glycerol and sorbitol content (Sømme, 1965), and with eggs of Neodiprion sertifer (Geof.) cold-hardiness was related with glycerol.

Table 10. The undercooling point of eggs at different stages of embryonic development. The last column shows the variance ratio F when in a comparison between stages. * indicates the level of significance

Stage	No. of egg tested	under cooling point °C			F
		Min-imum	Max-imum	Mean	
I	25	-30.5	-27.0	-28.67 ± 0.17	115.97***
II	20	-27.5	-18.5	-22.93 ± 0.53	5.77*
III	20	-25.5	-17.0	-21.55 ± 0.58	5.77*
IV	20	-23.0	-17.0	-20.23 ± 0.37	19.10***
V	22	-24.0	-21.0	-22.64 ± 0.17	

Table 11. Analysis of variance on the under cooling-points of eggs of C. viridis at different stages of embryonic development.

Source of variation	Sum of Squares	Degree of freedom	Mean Square	Variance ratio
Between stages	979.09	4	244.77	77.45***
Residual	322.64	102	3.16	
Total	1301.73	106		
		Detailed comparison		
I v. II	366.4672	1	366.4672	115.97***
II v. III	18.2250	1	18 .2250	5.77*
III v. IV	18.2750	1	18.2250	5.77*
IV v. V	60.9156	1	60.9156	19.10***
II v. V	0.8728	1	0.8728	0.28 N.S.

*, **, *** = levels of significant at 5%, 1% and 0.1% level.

N.S. = Not Significant.

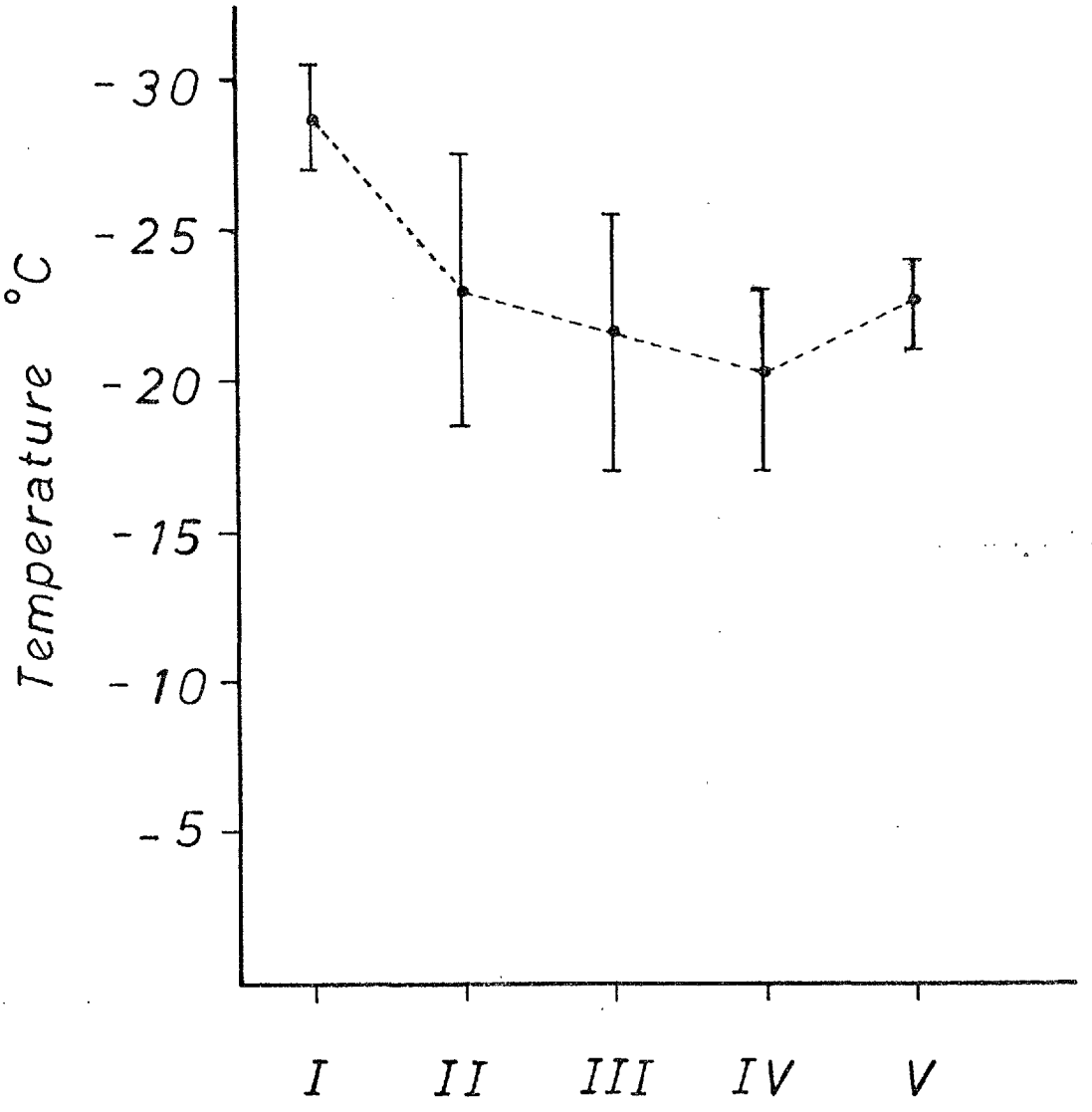


FIG.10 UNDER COOLING POINTS OF *C. viridis* EGGS AT DIFFERENT STAGES OF DEVELOPMENT.

6.2b Incubation at sub-zero temperature

A further experiment was set up to test the result obtained in the determination of the undercooling point in experiments of Cicadella viridis eggs. Juncus stems with C. viridis eggs were collected in September. Stems with the eggs were then cut into sections of about 8 cm. and placed in a petri dish lined with moistened filter paper. The one section per dish was then placed at the bottom of a deep freeze. The eggs were subjected to this treatment for the duration of 2,4,8,16 and 32 days. Six replicates were carried out for each duration, however one replicate of the 2 day and 32 day period was spoiled by fungal infection. The temperature of the deep freeze was measured with a copper constantin thermocouple and read with a potentiometer. Readings were taken at weekly intervals ten on each of the five occasions. The temperatures were found to fluctuate between $-16.9^{\circ}C$ and $-25.5^{\circ}C$ with a mean of $-19.92 \pm 0.43^{\circ}C$. After the eggs were subjected to the set number of days of cold treatment, they were transfered to a $20^{\circ}C$ constant environment room with 16 light hours for incubation.

The results of incubation at $20^{\circ}C$ are summarised in table 12 , and the percentages of hatch in each set were compared. The data were tranformed into degrees and a variance analysis was carried out. No significant difference between the percentage of hatch of eggs

Table 12. Percentage of hatch of C. viridis eggs after exposure to -20°C for various durations (days).

	Number of days at -20°C														
	2 days			4 days			8 days			16 days			32 days		
	No. of eggs	No. hatched	% hatched	No. of eggs	No. hatched	% hatched	No. of eggs	No. hatched	% hatched	No. of eggs	No. hatched	% hatched	No. of eggs	No. hatched	% hatched
	56	53	94.64	42	19	45.24	13	11	84.62	78	61	78.21	99	45	45.45
	24	6	25.00	23	14	60.87	45	37	82.22	13	4	30.17	45	32	71.11
	10	9	90.00	21	17	80.95	21	16	76.19	12	9	75.00	99	73	73.74
	53	49	92.45	12	8	66.67	19	15	78.95	18	14	77.78	7	2	28.57
	38	13	34.21	15	11	73.33	14	10	71.43	10	4	40.00	30	18	60.00
	-	-	-	47	43	91.49	25	20	80.00	22	8	36.36	-	-	-
Total	181	130	71.82	160	112	70.00	137	109	79.56	153	100	65.36	280	170	60.71

exposed for 2 days at -20°C and those exposed for 4,8,16 and 32 days was detected. Assuming that the percentage of hatch was a criterion of eggs survival at low temperature, seemed reasonable. Results of this experiment confirm the finding that C. viridis eggs are capable of withstanding low temperatures as was indicated by the determination of undercooling point. Prolonged exposure to low temperature does not seem to affect the viability of the eggs. The percentage of total eggs hatched varied from 60.71% to 79.56%; and this compares favourably with 70.88% hatch of eggs not exposed to cold treatment. It is therefore safe to conclude that in Southern England the temperature attained during the Winter is unlikely to cause any mortality in C. viridis eggs.

Table 13. Analysis of variance of proportion of eggs hatched after exposure to low temperature for different periods of time.

Analysis of variance

Source of variation	Sum Square	Degree of freedom	Mean Square	F	
Between day of exposure to -20°C	871.7104	4	217.9276	1.2132	Not significant
Residual	4131.4721	23	179.6292		
Total	4706.5341	27			

6.3 Diapause in the eggs of C. viridis

6.3a Introduction

Diapause is a physiological adaptation which frequently helps a species to survive unfavourable environmental conditions by the temporary cessation of growth or reproduction, reduced metabolism and often by the enhanced resistance to adverse climatic factors such as cold, heat and drought. Also it is frequently 'triggered off ' by changes in day length (photoperiodism). In insects, diapause may occur in any of the major stages of life history i.e. in the egg, larval, pupal or adult stage. In many species diapause occurs in the eggs at one of the following stages of embryonic development:- before segmentation is completed, near the close of anatrapsis, or when the embryo is fully formed (Andrewartha 1952).

Reviews on the known embryonic diapausing stages were given by both Andrewartha (1952) and Lees (1955). Examples of embryonic diapause occurring early in the developmental stage were found in Lepidoptera Bombyx mori (L.) (Umeya, 1950), Archips carasivorana (Fitch) (Andrewartha, 1952, Andrewartha and Birch 1954) and in Orthoptera Acheta (Gryllulus)commodus walker (Browning, 1952). Some examples of those developed to the stage near the close of anatrapsis were found in Diptera Aedes triseriatus Say (Baker, 1935), Orthoptera Melanoplus differentialis Uhl.

(Bodine, 1929), Gomphocerus sibiricus L. (Bei-Benko, 1928) and Camnulla pellucida Scudder (Moore, 1948). Whereas in some Orthoptera e.g. Melanoplus bivitatus (Say) (Salt, 1949), M. femur-rubrum DeG. (Salt, 1949), M. mexicanus Saussure (Parker, 1930) and Coleoptera Timarcha tenebricosa Fab. (Abeloos, 1935) the egg enters diapause with a fully developed embryo.

Not much information is available on the egg diapause in Homoptera. From the present observations, the eggs of both Cicadella viridis (L.) and Graphocephala coccinea (Forst.) entered diapause just before the completion of segmentation (see Fig. 9A). In C. viridis, examination of eggs from the field shows that when Autumn temperatures were high as in 1970, there were a few individual eggs with fully developed embryo before Winter conditions set in. According to Lees (1955) the point of occurence of diapause within the life cycle is normally a very constant specific feature, but larval arrest are sometimes influenced by temperature. Readio (1931) reported that high temperatures, could cause the stage of arrest to be postponed to a later instar in the bug Reduvius personatus (L.). It appears that this is also true of the eggs of C. viridis. In experiments on cold-hardiness of eggs, it was seen that the fully developed embryos appeared to be equally capable of withstanding the low temperatures and that the survival of the eggs does not seem to be affected by embryonic

development. In literature, C. viridis is generally described as having more than one generation a year (Balachowsky, 1936; Sch indler 1960; Dirimanov and Kharizanov 1964; Frediani 1955; and Chu and Teng 1950). Frediani (1955) had in fact recorded three full generations plus an incomplete fourth generation in central Italy, the eggs of the third generation females hatched, but the larvae did not survive the Winter. This means that in Southern Europe and East Asia, one or more generations of C. viridis eggs could develop and hatch without having to pass through a diapausing stage. In Britain C. viridis is however a strictly univoltine species. Although eggs are laid from mid-August and may experience relatively high temperatures until November (as in 1970), no hatching occurs until the following Spring.

Three experiments were carried out to find out whether the British strain of C. viridis produces eggs that must go through a diapausing stage before further development is possible.

6.3b. Experiment 1. Hatching of eggs that have not been exposed to low temperatures.

Newly laid eggs which had not been subjected to cold temperature were collected from the field early in September. The eggs were brought in embedded within the Juncus stems. These stems were then cut into section of 5 cm in length, each section containing one egg mass.

The epidermis of the stems was then stripped off to expose the eggs to ease observations. Egg bearing stems were put into a 7.5 x 2.5 cm glass tube topped with cork and lined with a disc of moistened filter paper and the eggs were incubated at 25°C.

Results

First observable development occured after 66 days of incubation with the appearance of the red eye spot, and the first hatching was observed six days later.

Development of the embryo proceeds rapidly after the appearance of eye spot. In the section on the determination of the undercooling point of eggs (p.49) five arbitrary stages of embryonic development are described (see Fig. 9). Observation on 20 eggs showed that Stage I takes about a day to complete, Stage II about 0.5 day, Stage III 1.5 days and Stage IV and V together about 3.75 days. On the average at 25°C hatching usually occured about a week after the first appearance of eye spot.

The number of eggs hatching was small initially, but increased gradually and the majority of the eggs hatched between 75 to 84 days at 25°C.

The main hatch was followed by sporadic hatching spreading over a further two weeks. The pattern of hatching is illustrated in Fig. 11b. The entire hatching period spread over a total of 25 days and 70.88% of the total incubated eggs hatched. The experiment was terminated by

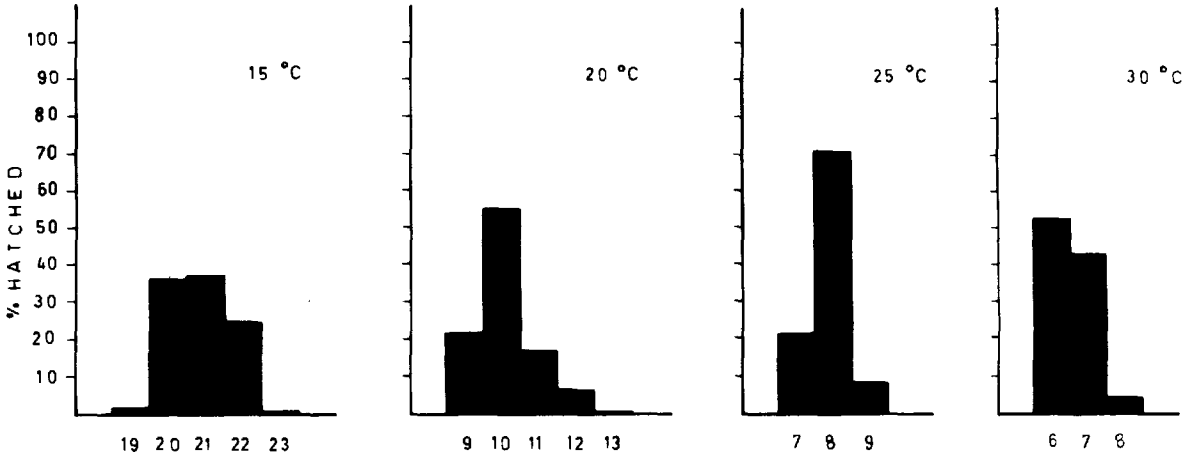


FIG. 11a Hatching of *C. viridis* at various constant temperature *(post diapause eggs)*.

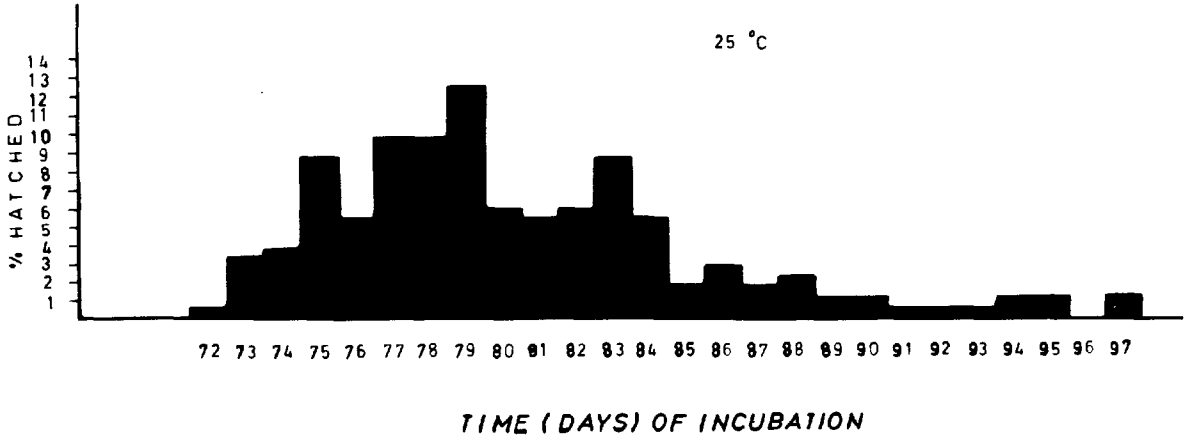


FIG. 11b Spread of hatching of preddiapause eggs at 25 °C.

fungal infection of the remaining unhatched eggs, no doubt otherwise the hatching period would have spread over a much longer period. The larvae that hatched were successfully reared to the adult stage.

6.3c. Experiment 2. Hatching of eggs after a period at low temperatures.

An experiment similar to the last one was set up, with the eggs collected in early February and thus had been exposed to temperatures below the freezing point during December and January. Twelve batches of egg masses containing a total of 150 to 200 eggs were incubated at the temperatures of 15°C, 20°C, 25°C and 30°C in constant environment rooms with 16 light hours and at 20°C with eight light hours.

Results

First hatching at 15°C, 20°C, 25°C and 30°C were observed on days 19, 9, 7 and 6 after exposure to these temperatures. Hatching spread over five days at 15°C and 20°C and over three days at 25°C and 30°C. These results are summarised as histograms in Fig. 11a. Eggs incubated at 20°C and eight hours of light have the same hatching pattern as those incubated at this temperature but at sixteen light hours. Thus Figs. 11a and 11b provide a good comparison of hatching patterns between eggs that have been subjected to low temperature and those that were not.

The mean of incubation days was 20.50±0.07 days at 15°C, 10.09±0.06 (16 light hours) and 10.52±0.07 (8 light hours) at 20°C, 7.87±0.05 days at 25°C and 6.52±0.05 days at 30°C. The decrease in the mean number of incubation days was sharp between 15°C and 20°C and evened out between 25°C and 30°C. Thus high temperatures have both the effect of shortening the incubation period and at the same time synchronising the hatching of all the eggs as is seen from the spread of hatching of the post diapause eggs of C. viridis. The hatching percentages of total incubated eggs were 97.0% at 15°C, 86.4% (16 light hours) and 92.7% (8 light hours) at 20°C, 93.8% at 25°C and 75% at 30°C. It appears that 25°C is probably the optimum hatching temperature, since above it the percentage of hatchability decreased. Numbers of light hours do not appear to affect either the hatching pattern or the percentage of hatchability.

6.3d. Experiment 3. The effect of lengths of exposure to low temperature on hatching.

Eggs collected from the field in the beginning of September were exposed to -20°C in a deep freeze for the periods of 2, 4, 8, 16 and 32 days and then restored to 20°C for incubation. The details of the experiment were as described in the section on the survival of eggs under low temperature.

Results

The results are summarised in the histogram in Fig.12 plotted with the number of days of incubation at 20°C against

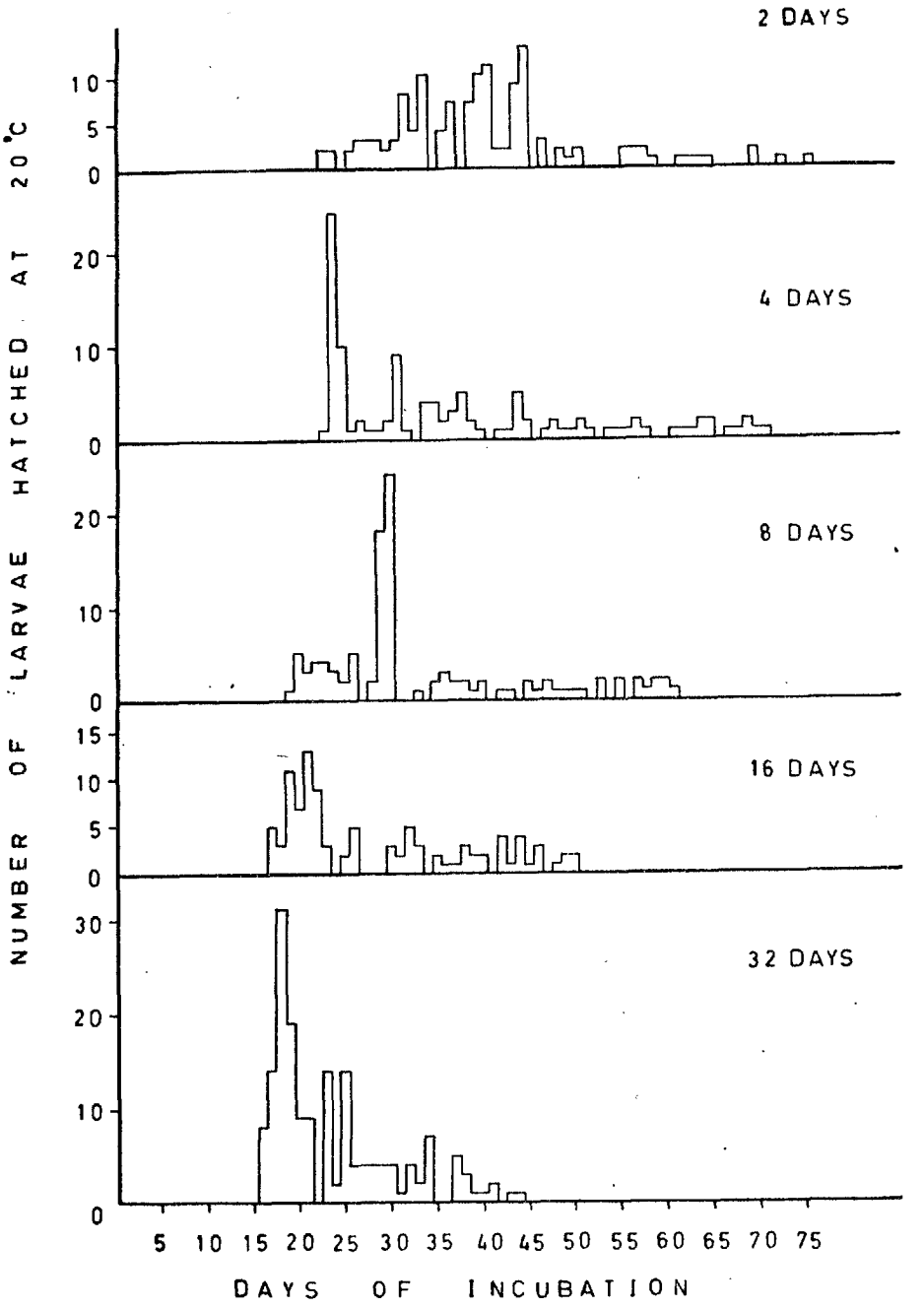


FIG. 12 The number of larvae hatched at 20 °C after cold treatment for different periods.

the number of larvae hatched after the different period of cold treatment. It is clear from Fig. 12, that as the length of exposure to low temperature increases, there is a corresponding decrease in the incubation period and a shortening of the spread in the hatch of all the eggs. This agreed with the results obtained in the two experiments described in the last section. With longer exposure to cold temperature there is also a tendency for the majority of the eggs to hatch at the begining of the hatching period. The mean incubation periods were 40.71, 37.72, 33.80, 28.50 and 23.48 days for 2, 4, 8, 16 and 32 days of exposure to $-20^{\circ}C$ respectively. A graphical representation of this result is presented in Fig. 13, which indicates that cold treatment at the beginning of embryonic development produces a greater response in the shortening of the incubation time than at a later stage. The percentage of hatching varies from 60.71% to 79.56% (see table 12), but the analysis of variance shows that this difference was not significant.

6.3e. Discussion

From the results of the three experiments, the following conclusion can be drawn:

(a) eggs of C. viridis could hatch without actually going through a period of dormancy when exposed to high temperature shortly after being laid, but hatching under these conditions tends to spread over a long period of time.

(b) Exposure to low temperature has the effect of shortening the subsequent incubation period required for hatching when eggs are returned to high temperature. It appears that up to a limit, the longer the duration of exposure to low temperature, the shorter is the duration of subsequent incubation period as is indicated in Fig. 13.

(c) Cold temperature seems to have a synchronising effect on the egg development, resulting in the majority of the eggs hatching within a very short interval.

(d) Eggs collected in February from the field have a higher percentage of hatch than those collected in September and incubated directly at high temperature.

No significant difference was detected in the percentage of hatch between eggs exposed for two days to -20°C and those up to thirty-two days. It is possible that the period of thirty-two days of cold treatment was not of a sufficient duration to produce a difference.

The ability of eggs which normally undergo diapause during Winter to develop and hatch when exposed to high temperature was also found in other insects such as Orthoptera Acheta commodus Walk.(Browning 1952; and Hogan 1960), and the leaf hopper Colladonus geminatus (Van. D.)

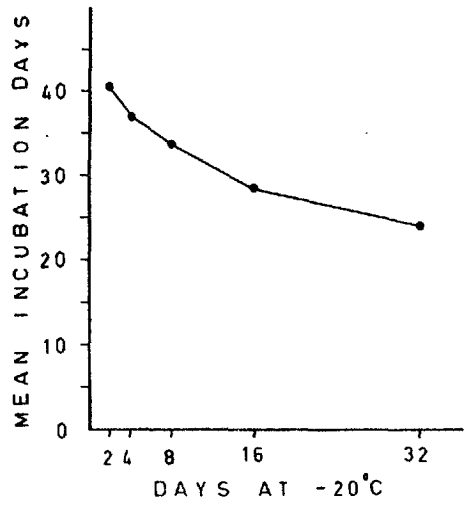


FIG.13 The relationship between the length of exposure to -20°C and the mean incubation days require to hatch at 20°C by *C. viridis* eggs.

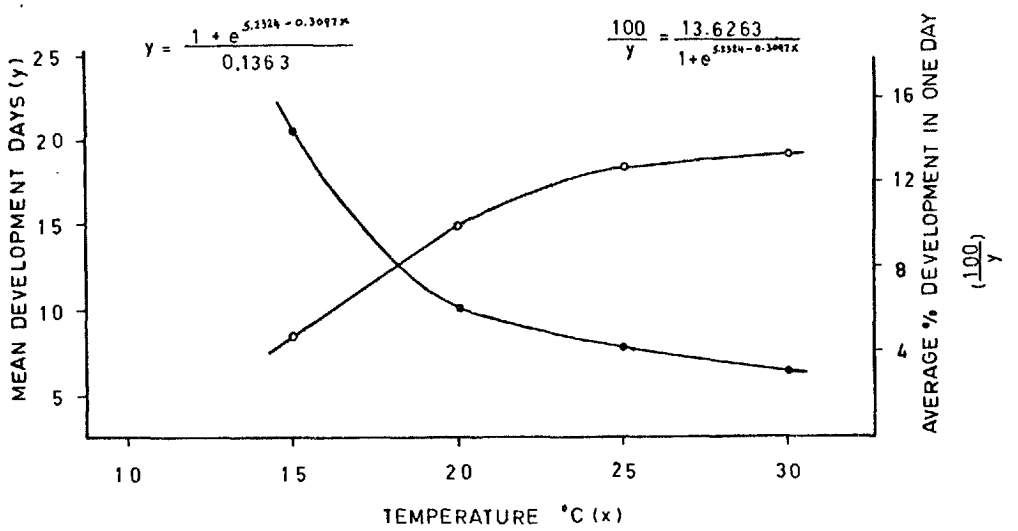


FIG. 14 Observed points on the temperature - time curve (closed circles) and the temperature velocity curve (open circles) for development of *C. viridis* eggs.

(Kaloostian, 1956). In Acheta commodus high temperature permits the completion of diapause, although under these conditions 'diapause development' proceeds slowly and uncertainly. With Collandonus ge minatus Kaloostian (1956) found that in Utah, the leaf-hopper overwinters in the egg stage, there was no dormancy period required for hatching and temperature merely delayed development, and the leafhopper could be reared continusously in the green-house.

Andrewartha (1952) proposed that diapause should be considered in two aspects:

(a) in terms of its morphological aspect or morph ogenesis and

(b) its physiological aspect of physiogenesis.

Completion of physiogenesis was necessary before morphogenesis could commence. He put forward the term 'Diapause development' to mean physiological development or physiogenesis which goes on during the diapause stage in preparation for the active resumption of morphogenesis. In turn the resumption of morphogenesis could be taken as an indication of completion of diapause.

With the eggs of C. viridis the different patterns of hatching between those that were exposed to cold temperature and those that have not might be explained by Andrewartha's theory. It appears that there is a specific period in which 'diapause development' would be completed, and after completion of 'diapause development', morphological development could commence if the temperature is suitable.

'Diapause development' could proceed and be completed at high temperature; however at high temperature the rate of development was slow and varied between eggs, resulting in sporadic and long spread of hatching. Low temperatures have the effect of accelerating 'diapause development'. From Fig. 13 it could be seen that the speeding up was more rapid on the first sixteen days of cold treatment, thereafter the rate began to slow down. When 'diapause development' was completed, morphogenesis could not commence until the temperature was sufficiently high, this would allow eggs with slower rate of 'diapause development' to catch up. Thus when returned to high temperature most eggs would have completed 'diapause development' and morphogenesis could commence altogether resulting in synchronisation of hatch and a very short spread of hatching period. This would also account for the pattern of hatching as shown in Fig. 12 which indicates that a longer exposure to cold temperature results in shorter subsequent incubation period.

The phenomenon of acceleration of 'diapause development' in eggs when exposed to cold temperature has been observed in Lepidoptera Lymantria dispar L. (Masaki, 1956) and particularly in Orthoptera (Parker, 1930, Browning, 1952, Hogan 1960 and Rakshpal, 1962). The exact nature of 'diapause development' is still not known. Working on Gryllus pennsylvanicus Burm. Rakshpal (1962) observed that

the consistency of yolk changed and became more or less semi-fluid. He postulated that this change in consistency possibly allows for easier assimulation by the embryo and so speeds up growth. A similar observation was recorded by Tuleschkov (1935) on eggs of Lymantrid moth and Andrewartha (1952) considered these changes as a visible process of 'diapause development' and elaborated his food 'mobilisation hypothesis of diapause'. A similar mechanism may be working in C. viridis eggs, though no visible changes in yolk consistency was noticed.

According to Lees' (1955) definition, when insects that have obligatory diapause are reared under varied conditions, virtually every individual enters diapause each generation regardless of its environment. In this context, eggs of C. viridis may be described as having a facultative diapause. Facultative diapause generally produces more than one generation a year, but at the limit of a species' geographical distribution facultative diapause may result in virtually univoltine life cycle (Andrewartha, 1952). This would fit the description of the life cycle of C. viridis in Southern Europe (multivoltine) and in Britain where it is univoltine.

6.4 The effect of temperature on the rate of development of the eggs.

The importance of temperature changes on many aspects of the biology of insects has been reviewed by Bursell (1964), and Howe (1967) has discussed the studies that have been made into the effect of temperature on the development rate of insect eggs.

Generally the reciprocal of developmental period estimated as a mean, medium or shortest period is regarded as rate of development. This involves the assumption that the change from fertilisation to hatching is a process that always takes the same course and that any environmental change affects it equally at all stages of embryonic development. As C. viridis eggs have a facultative diapause, this is obviously untrue, as an individual egg may complete the 'diapause development' stage without delay while others may remain inactive for a long period. In order to obtain some form of uniformity, only postdiapause eggs were used for incubation and its mean in days was used for estimation of rate of development. The results as summarised in Table 14 refer to eggs collected in early February and incubated at different temperatures (as was described in paragraph 6.3c). The analysis was carried out by the method described by Davidson (1944) and a curve constructed to indicate the relationship between temperature and the rate of development. The mean developmental periods in days (y) and their reciprocals multiplied by 100 to give the percentage of

development are plotted against temperatures (x), and a logistic curve of the form of $\frac{100}{y} = \frac{K}{1+e^{a-bx}}$ is fitted to the data. $\frac{100}{y}$ represent the average percentage development made by the embryo per day at the given temperature. The constant K is calculated from the formula $K = \frac{2P_1P_2P_3 - P_2^2(P_1 + P_3)}{P_1P_3 - P_2^2}$ where P_1, P_2 and P_3 are values for $\frac{100}{y}$ on the curve at three equally spread temperatures, a and b are the constants given by the equation $\log_e \frac{K - P}{P} = a - bx$.

The derived equations for the average percentage development in one day at known constant temperature is $\frac{100}{y} = \frac{13.63}{1 + e^{5.2324-0.3097x}}$ where x is the constant temperature in degrees centigrade. The mean development per day is expressed as $y = \frac{1 + e^{5.2324-0.3097x}}{0.1363}$ (See Fig. 14).

Watt (1968) does not consider it justified to apply logistic curve to data on temperature versus rate of development either on theoretical reasons or as giving a good fit to such data. The equation tends to leave off points from one or both ends of the empirically obtained curve, and thus does not present a true picture of cases where individuals might survive to temperature at which temperature-rate curve is decending. In case of eggs of C. viridis, Whalley (1958) had shown that at 33°C embryos develops but fails to hatch, and at 37°C and 45°C no

Table 14 . The effect of temperature on rate of development of eggs of C. viridis.

Temperature °C	No. of eggs	Mean development day (y)	$\frac{100}{y}$ percentage of development in one day cold method	
			Observed	Calculated
15	130	20.5	4.78	4.87
20	191	10.1	9.90	9.97
25	137	7.9	12.66	12.60
30	114	6.5	13.39	13.41

development took place. At the lower end of the temperature scale he found that at 12.5°C the egg showed no sign of development after 60 days, and no development after 80 days at lower temperature. By comparing the observed and calculated value obtained from Davidson's logistic equation (see Table 14), between 15°C to 30°C, it gives an accurate description of the rate of development of C. viridis eggs.

7. Hatching in the field

Hatching in the field generally commenced as from the second or the third week of May, and continued for a period of about three weeks. The hatching curve as shown in Fig. 15 was that of the 1971 season and was estimated by two different methods.

Method I involved direct observation. Juncus stems with eggs were enclosed within cylindrical cages made of cellulose acetate. The cage was essentially a cylindrical tube of 20 cm long, 7.5 cm in diameter with muslin sleeves attached at both ends and a muslin covered window of 5 square cm in size on the side for ventilation. Juncus stems were put into the cage and the muslin at both ends tied round the stems with pieces of string to form an enclosure cage. The larvae that emerged were counted

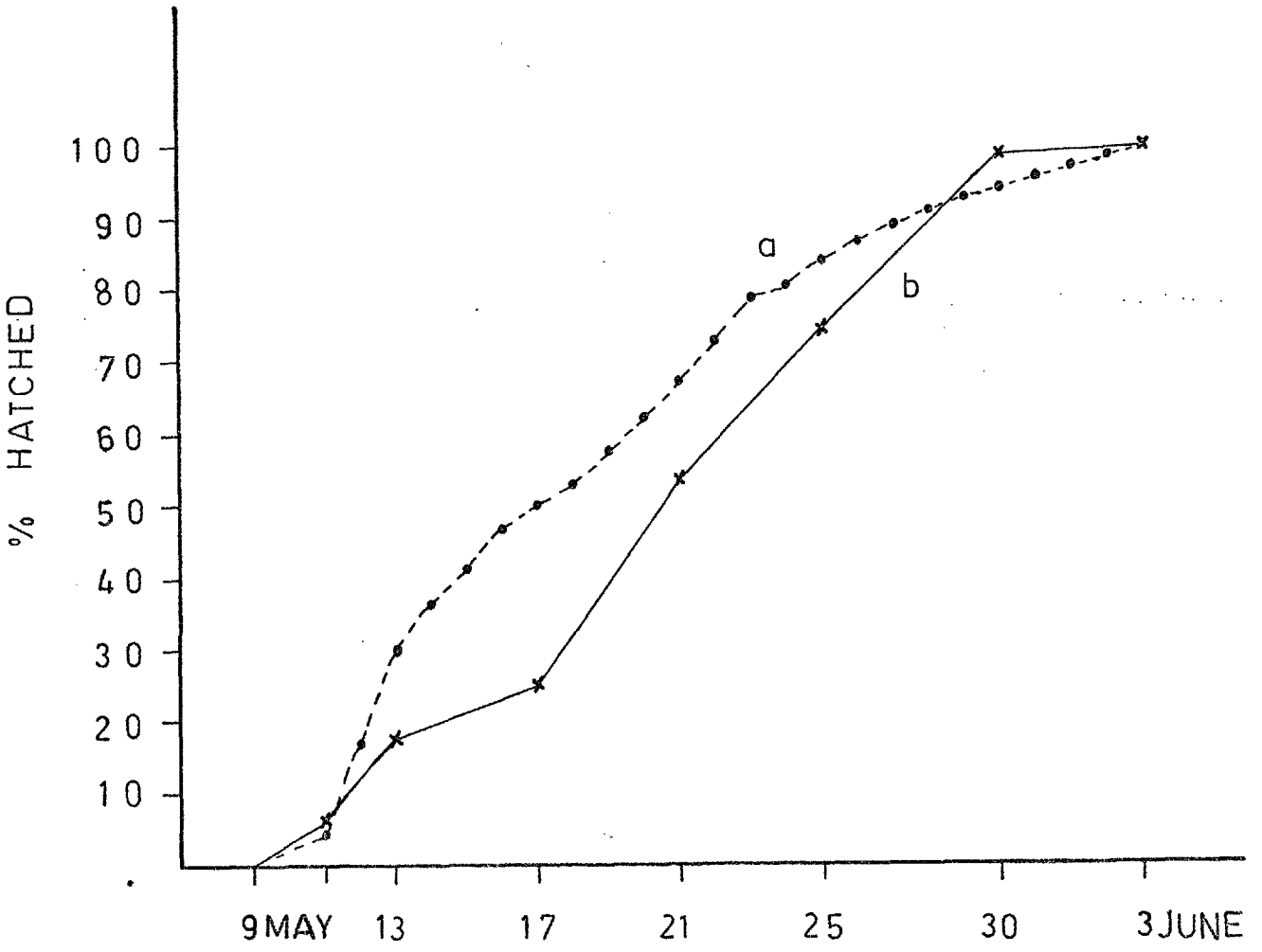


FIG.15 HATCHING CURVE OF *C. viridis (L.)*. a. ESTIMATED FROM DIRECT OBSERVATION ON CAGED EGGS. b. ESTIMATED FROM REGULAR EXAMINATION OF THE PROPORTION OF EGGS HATCHED IN THE FIELD.

at the end of each day. In all 25 such cages were used. Two to four Juncus stems with eggs of C. viridis were enclosed in each cage, depending on their proximity to each other. A total of about 1,819 eggs were enclosed and 365 larvae hatched.

Method II. About one hundred Juncus stems were collected randomly at four to five days intervals. Eggs that hatched leave the empty egg shells and the embryonic cast skin of the young larvae. By examination of these remains it was possible to estimate the percentage of eggs that have hatched to date. Sometimes, for reasons not known, young larvae emerged from the eggs but failed to cast off the embryonic skin that enclosed them, and died. For the purpose of the emergence curve, those that failed to hatch properly were included as hatched. In 1971, this failure to hatch completely amounted to about 10.33% of total viable eggs.

The two curves agree reasonably well. The differences between the two might be due to the smaller sample examined in the caging experiment.

Hatching took place slowly during the first week, and the majority emerged over the next ten days and a few hatched throughout yet another week. This pattern of hatching was different from that in the post diapause eggs incubated under constant temperature (see Fig. 11a)

when all hatching occurred within a very short period of time. This long spread of hatching may be due to the early Spring of 1971. In 1969 and 1970 hatching began on the 20th and 18th of May respectively. In 1971 hatching began on the 11th of May which was a week earlier than the previous two years. Richards and Waloff (1954) found that a warm Spring would promote earlier hatching in the British grasshoppers, but would result in prolonged hatching period. Fig. 16 illustrates graphically the average monthly maximum and minimum temperatures for the months of February to that part of May before hatching commenced. It was obvious that the maximum and minimum temperature for February and March in 1971 were higher than those of 1969 or 1970. Unfortunately data were not available on the spread of hatching in 1969 and 1970. But there was an indication that warm Spring did in fact prolong the spread of hatch in C. viridis, for in 1970 the peak of the first instar larvae was reached only ten days after hatching began, while in 1971 the peak was not reached until twenty-two days later. The result could probably be explained if morphogenic development of individual eggs was assumed to proceed at a different but a constant rate, and that the rate of development increases with temperature. At lower temperature development of all individuals proceeds at a slower pace, and this

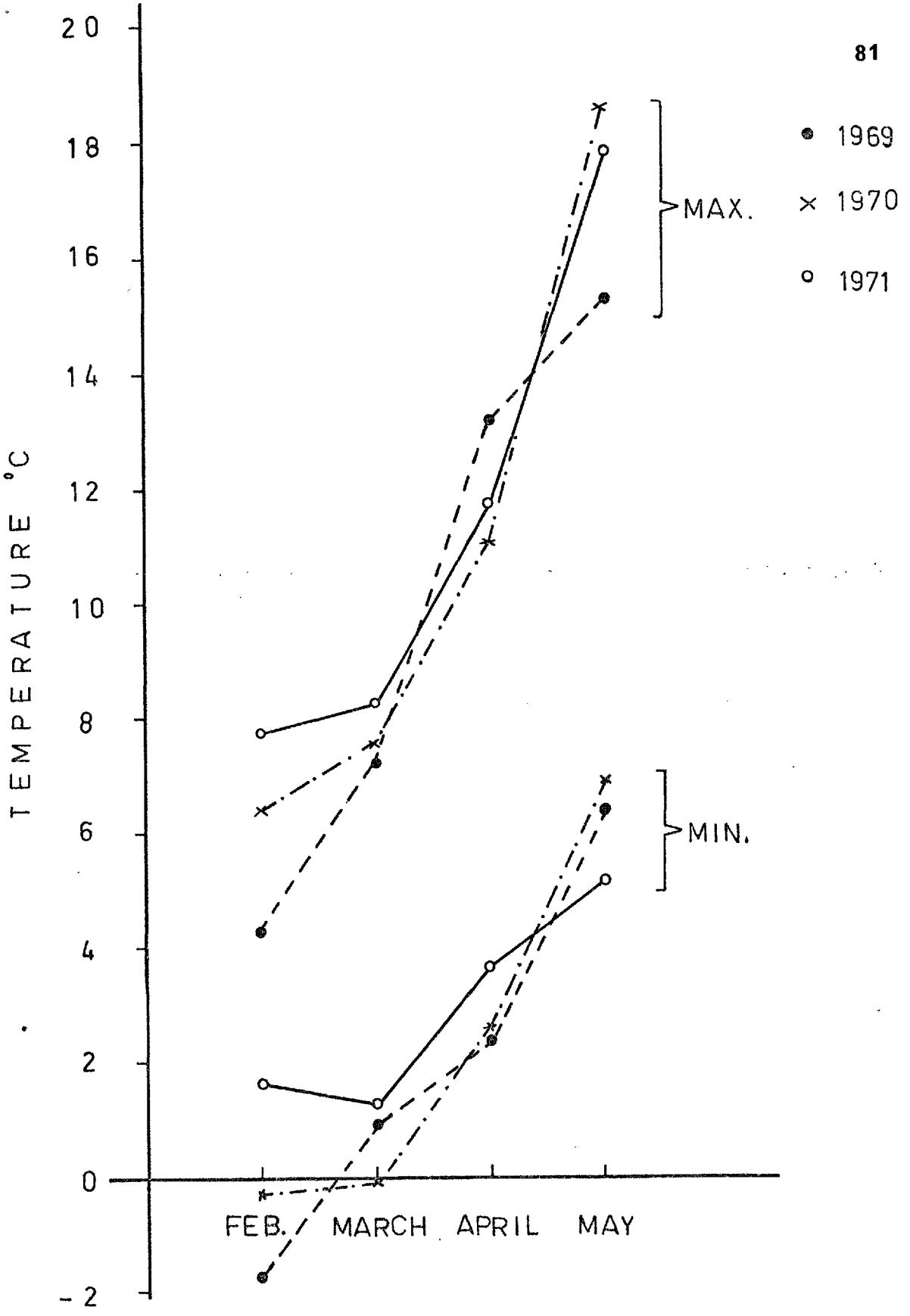


FIG. 16 Mean monthly maximium and minimium temperatures from Febuary to May in 1969, 1970 and 1971.

could result in a bigger gap between those that were capable of quick development and those that developed at a slower pace . While at higher temperature development of all individuals was speeded up resulting in a narrower gap, and thus a shorter spread. This was evident in Fig. 11a which showed that eggs incubated at 15°C have a spread of five days as compared to those incubated at 25°C and 30°C where the spread was only three days. The mean monthly air temperature in May for the years 1969, 1970 and 1971 was 11.48, 13.0 and 11.78°C respectively. In the field apart from normal fluctuation, the differences in temperature caused by topographical differences and the location of the egg carrying Juncus clump would no doubt accentuate the fluctuation and prolong the spread of hatching. Thus the effect of temperature on egg developments appear to be two fold, during the process of 'diapause development' low temperature would accelerate development, while during 'morphogenesis' low temperature would slow down development.

8. Duration of larval instars

8.1 Rearing in the outdoor insectary

The method of rearing had been described previously, Holcus mollis was used as food plant. The temperature in the outdoor insectary fluctuates with the outdoor air temperature. During the period of rearing in May, June and early July, the temperature in the insectary varied between 16 to 36°C. This was on the average about two degrees higher than the outdoor temperature. The higher temperature in the insectary was caused by provision of artificial lighting and insulating effect of the building. C. viridis is a difficult insect to rear under captivity, and very high mortality was experienced. The results shown in Table 15 were the pooled results of many individuals of the same stage, as very few survived through to adult stage. Thus no attempts were made to calculate the standard error of total larval duration.

A rough estimate of the total larval duration in the field was obtained by observation on the first appearance of first instar larva and the first adult. In 1969, the total larval duration was 57 days, 45 days in 1970 and 58 days in 1971. The differences in the duration between these three years might be explained by the temperature differences in May and June during which most individuals pass through the major part of larval development (see Table 16).

Table 15. Duration of larval period in days of C. viridis reared in outdoor insectary.

	Duration of instars in days						Total duration	
	I	II	III	IV	V			
					♂	♀	♂	♀
Max.	14	25	22	25	15	23		
Min.	8	6	6	6	12	12		
Mean with standard error	10.53 ±0.39	9.75 ±0.69	11.33 ±0.62	12.95 ±0.40	14.18 ±0.33	17.70 ±0.67	58.74	62.26

Table 16. The effect of temperature on the length of larval period in the field.

Month / Year	Mean temperature in °C		Duration of larval period in the field in days
	May	June	
1969	11.4	13.9	57
1970	13.0	16.8	45
1971	11.7	12.8	58

8.2 Duration of instars under different constant temperatures.

Rearing was also carried out at 15°, 20°, 25° and 30°C constant temperatures, using Holcus as the food plant. The mean duration of instars from moult to moult to the nearest days for the different temperatures were as shown in Table 17. Fig. 17 shows the inverse of developmental time plotted against temperature. The data did not fit a logistic curve, and a linear regression of the form of $Y = 0.0014x - 0.0094$ was fitted, and it could be seen that the developmental zero was approximately eight degrees centigrade. At 30°C both C. viridis and Holcus did very poorly and few C. viridis managed to survive over the whole duration of an instar inspite of regular changes of Holcus twice a week. However those that survived had shorter larval duration.

9. Description of larvae and adults

9.1 The larval stages

Description of immature stages of C. viridis had been given by Pierre (1906), Frediani (1955), and Chu and Teng (1950). Whalley (1958) working on British specimens gave a short account and a brief description of the different instars. The following is a short description of the immature stages with references to characters used for distinguishing the different stages. More detailed diagrams than those given by Whalley of all the immature stages are also presented in Fig. 18. Measurements were made on the head length, head width, hind femur length, tibial length

Table 17. Relation between duration of instars in days to the nearest days and different constant temperature. Figure in bracket indicate the number of individuals reared.

Temperature °C	Mean duration of instar in days					Total duration in days	Inverse of total duration
	I	II	III	IV	V		
15	16(33)	16(20)	17(10)	19(10)	27(8)	95	0.0105
20	8(35)	8(27)	9(22)	10(21)	14(19)	49	0.0204
25	7(30)	7(22)	7(17)	8(10)	11(10)	40	0.0250
30	5(26)	5(15)	6(10)	6(5)	9(2)	31	0.0323

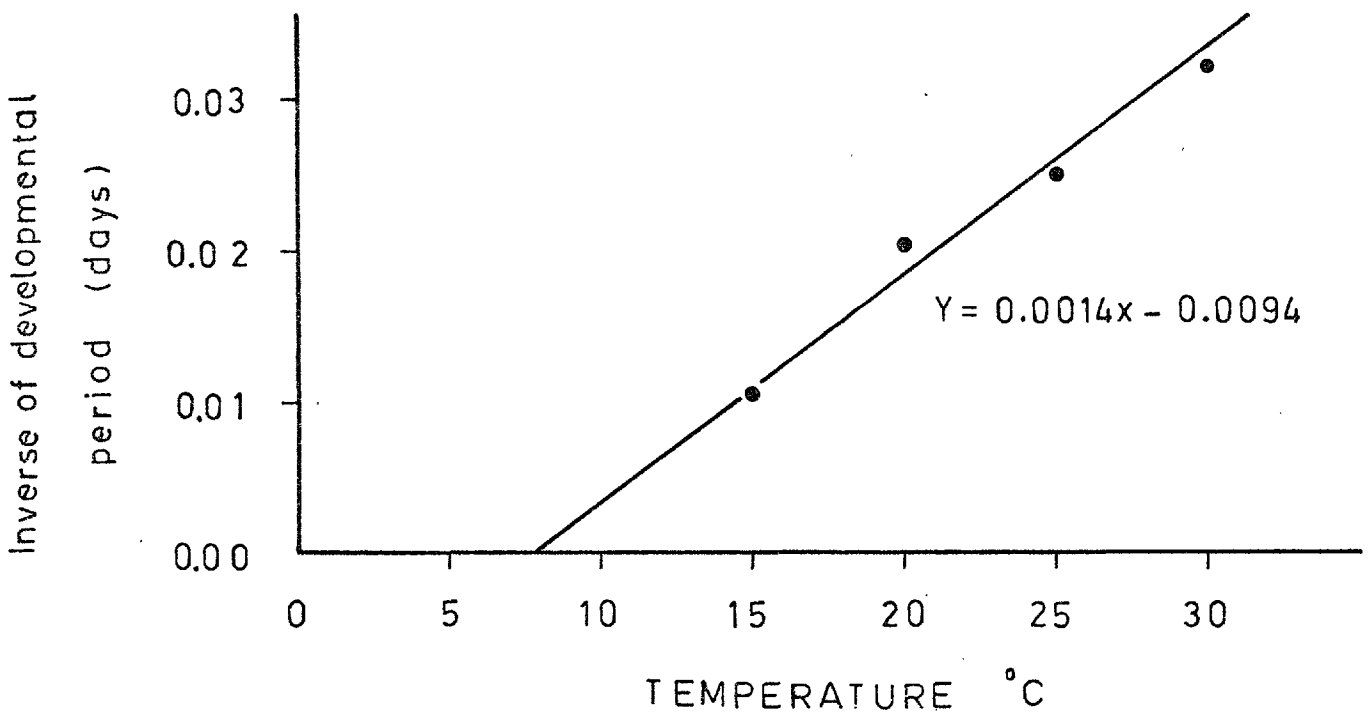


FIG. 17 Relationship between inverse of developmental time (days) to the final moult and temperatures.

and body length of successive instars using fresh insects. These measurements are presented in Table 18.

Instar I (Fig. 18 I)

Body length measured from vertex to tip of pygophore varies from 1.75 to 2.19 mm with a mean and standard error of 2.01 $\pm$ 0.04 mm. Newly emerged larva is yellowish in colour, which turns into the normal bluish grey colour in about one and a half hours after emergence. There is a distinctive pale medium dorsal stripe extending throughout the whole length of the body.

Head - Bulbous shape, with compound eyes situated on the sides, Ocelli absent in all the immature stages. On the posterior end of the vertex, is a pair of elongated dark spots situated on either side of the pale medium stripe. The ecdysial cleavage line runs along the medium stripe and at the anterior end of the vertex branches off into two arms, the ecdysial cleavage line thus assuming the shape of the letter T. The horizontal arm can be seen as a pale transverse stripe separating the vertex from the crown. The multiple segmented antennae are situated on the sides of the head in front of the compound eyes near the frontal genal sulci. There is also a dark spot on both genae.

Thorax - Dorsally the anterior margin of the pronotum is narrower than that of the posterior margin. Wing pad absent in both the meso - and meta-thorax. The metathorax being the most prominent and equal in length

to both the pro- and mesothorax together.

Legs - Femur with two terminal dorsal spines, these are present in all immature stages. Tibia cylindrical in shape with two rows of ventral and two rows of dorsal spines. The exact number of spines do not seem to provide any pattern for differentiation of instars. Tarsi two segmented.

Abdomen - There are nine visible abdominal segments. Some fine hairs are present on the dorsal surface of the first eight segments and bristles are present on the ninth. Genital appendages not yet differentiated.

Instar II (Fig. 18 II)

Body length measured between 2.17 to 2.88 mm with a mean of 2.48 $\pm$ 0.07 mm. General colouration similar to instar I.

Head - Anterior margin of vertex broadens out and loses the characteristic bulbous shape of the first instar. The two dark spots on the vertex become rounded and patches of light colour also appear.

Thorax - As in instar I. Wing pads beginning to show as slight projections at the posterior corners of the mesothorax, but are less noticeable in the metathorax.

Legs - Tibia became slightly rectangular in this stage, otherwise as in instar I.

Abdomen - Similar to instar I, still no visible external genitalia.

Instar III (Fig. 18 III)

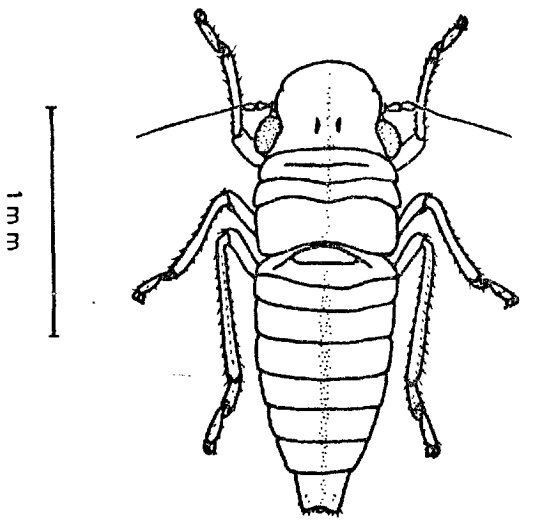
Body length measures between 2.87 to 3.70 mm with a mean of 3.21 ± 0.08 mm. Body colour as in instars I and II, but in addition to the medium dorsal stripe, two lateral stripes have developed extending from mesonotum to the sixth abdominal tergum. Patches of lighter colour developed between the compound eyes on the vertex and on the anterior margin of the pronotum. Triangular shaped wing pads prominently developed on mesothorax, on metathorax these wing pads showed up as protrusions at the corners of the posterior margin. Tibia clearly rectangular in shape and rudiments of external genitalia appear.

Instar IV (Fig. 18 IV)

Body length varies between 4.86 to 5.87 mm, with means of 5.02 ± 0.16 mm. General body colouration as in instar III, with the two dorsal lateral stripes much more clearly developed than in III. Forewing pads on mesothorax well developed, greatly elongated, and extending about $^{2}/_{3}$ way down towards the tips of metathorax. The hindwing pads assume triangular shapes. External genitalia well differentiated and it is possible to distinguish between males and females.

Instar V (Fig. 18 V)

Male insect measured between 6.31 to 7.81 mm in length with a mean of 6.98 ± 0.31 mm. Female is larger and measured between 6.92 to 8.00 mm with a mean of 7.33 ± 0.15 mm. The two dorsal lateral stripes extending



I

FIG. 18 I First instar C. viridis

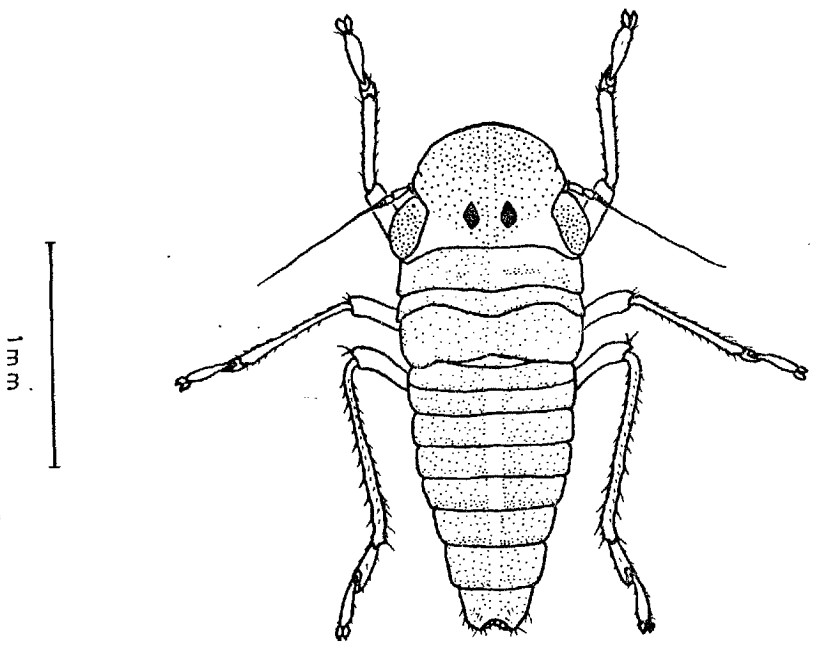
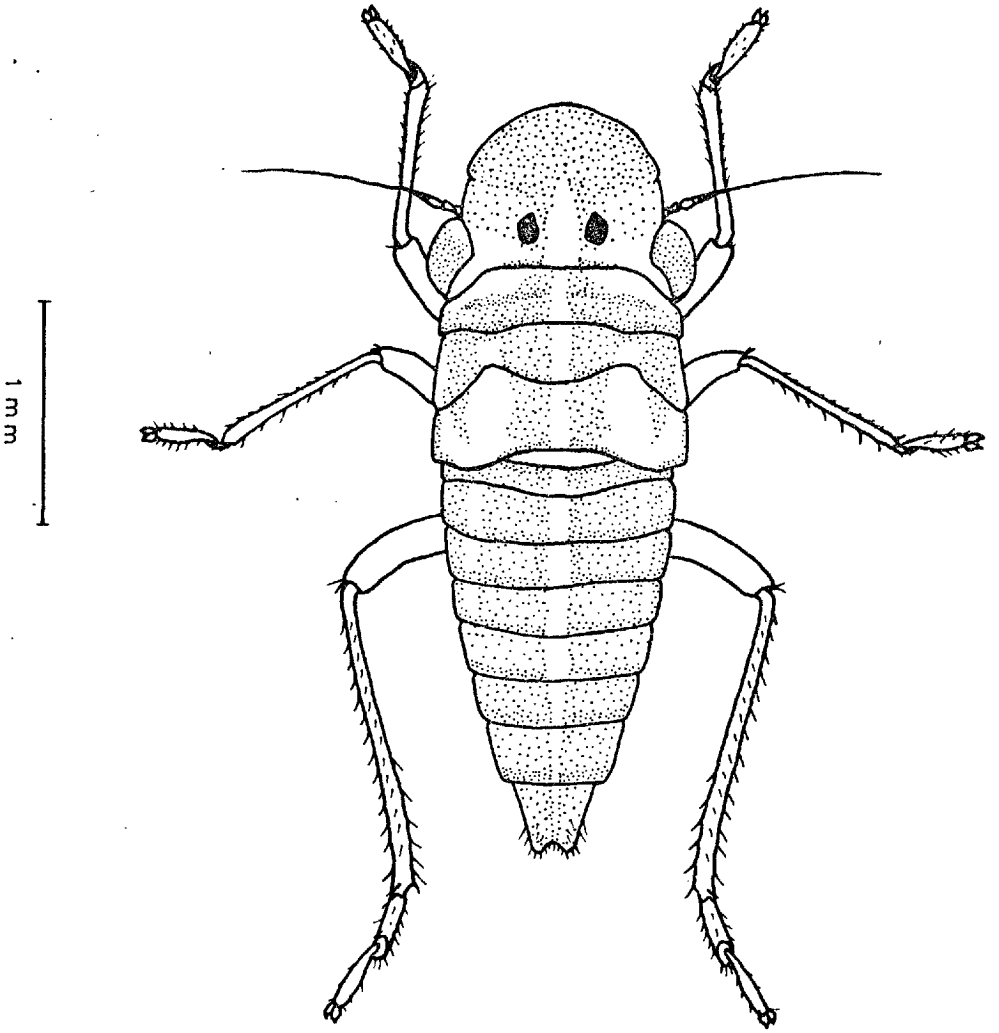


FIG. 18II Second instar C. viridis



III

FIG. 18 III Third instar C. viridis

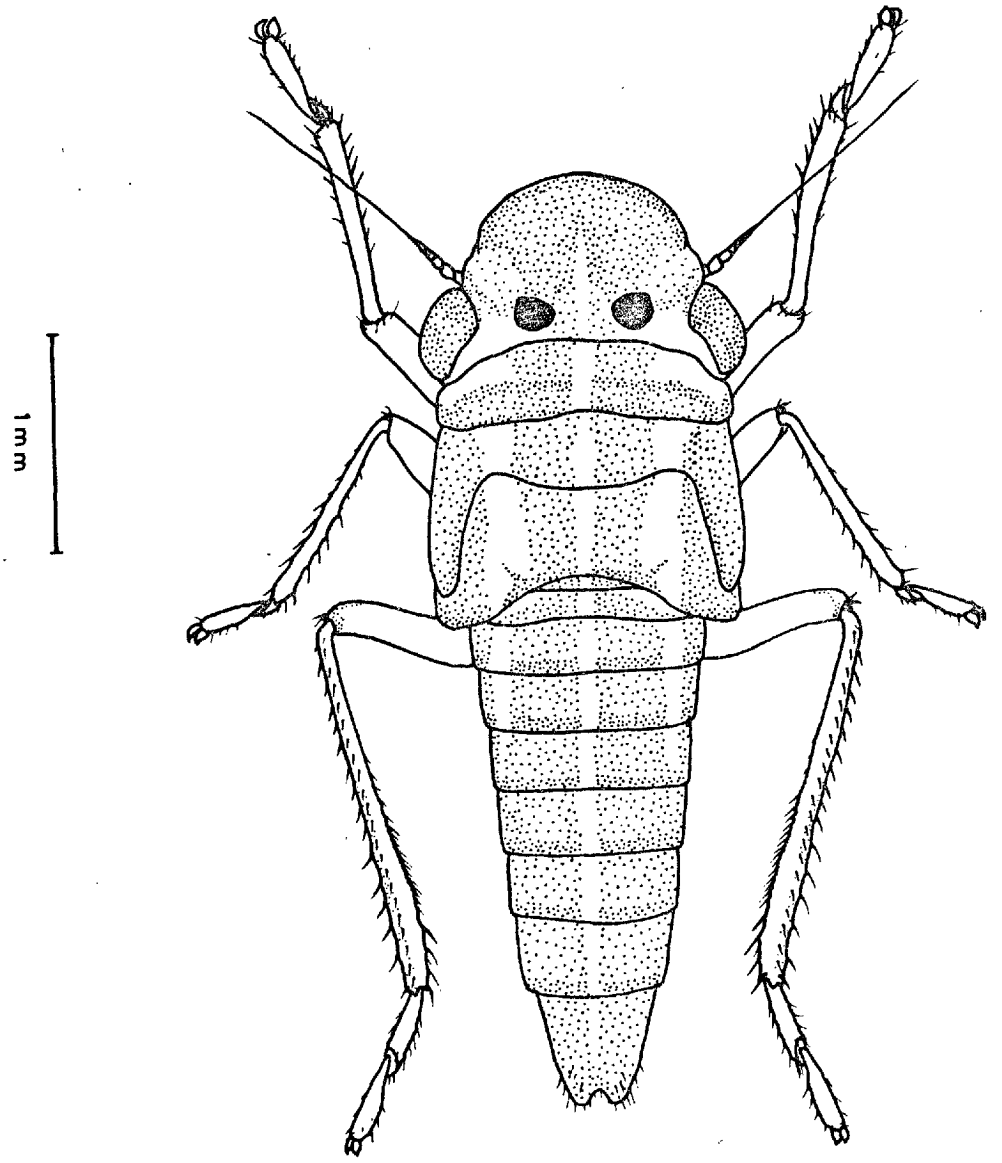
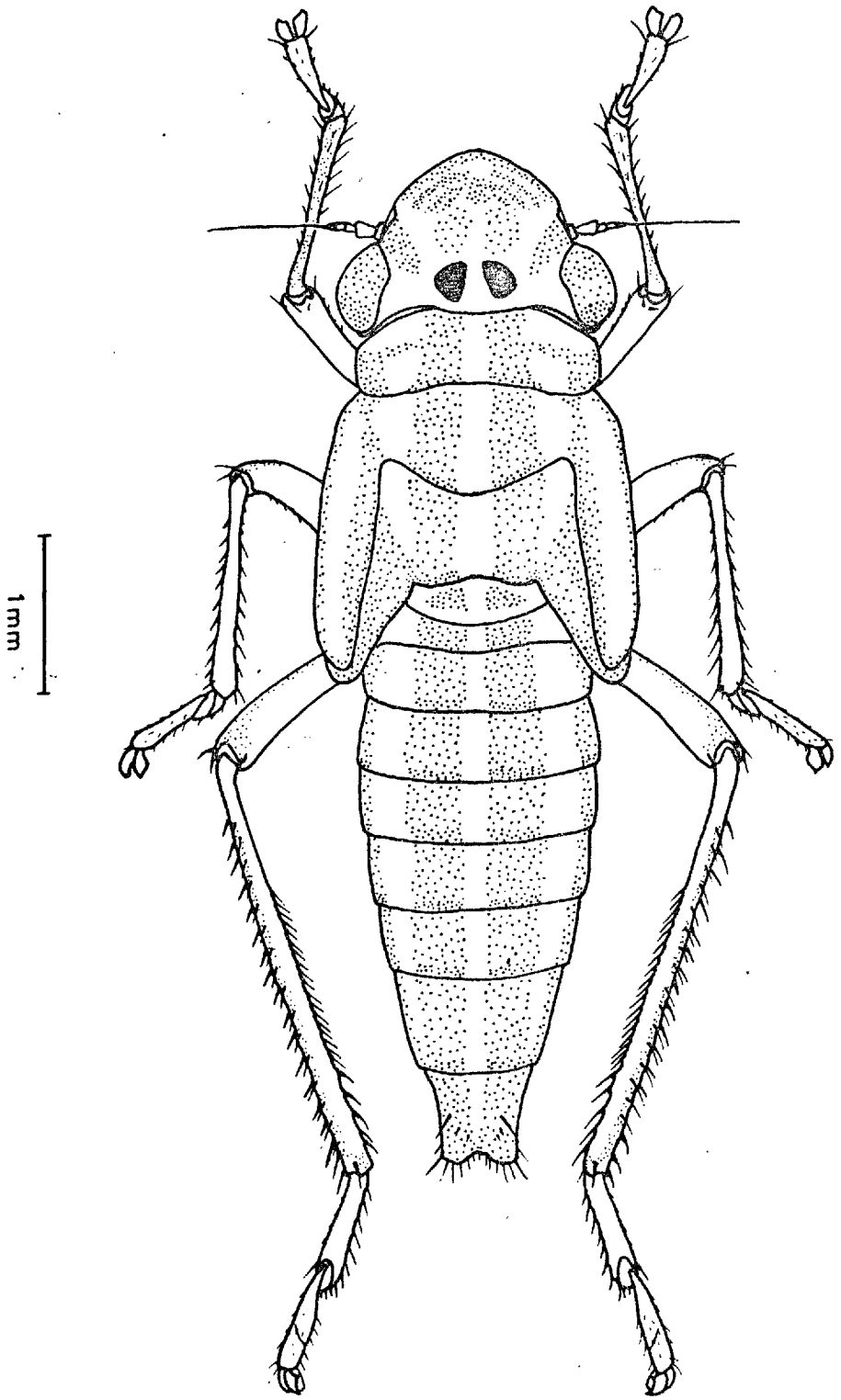


FIG. 18 IV Fourth instar C. viridis



V

FIG 18V Fifth instar C.viridis

from pronotum to the whole length of the body. In addition pale stripes also appear on the forewing pads.

Head - with very distinctive pale and darker patches which give it a mottled appearance. Anterior margin of vertex slightly pointed instead of rounded as in the previous four instars. Forewing greatly elongated the tip of which almost reaches the tip of the hindwing pad. Although the hind tarsi remain two segented, in the last segment a faint cleavage line can be seen which marks the beginning of development into the three segmented tarsi of the adult stage. External genitalia very well developed and assumed the form of that in the adult.

Sex ratio

Chu and Teng (1950) recorded a sex ratio of of 1 : 1.02, 1 : 1.04 and 1.44 : 1 for three generations in the same year. The numbers examined were 4,786, 9,237 and 7,320 for the first, second and third generations respectively. A χ^2 test was carried out using this data, which showed that the ratio was not significantly different from a 1 : 1 ratio for the first two generations ($\chi^2 = 0.4814$, $P > 40\%$; $\chi^2 = 3.547$, $P > 5\%$. respectively), but was significant in the third generation ($\chi^2 = 238.0328$, $P < 0.1\%$). Whalley (1958) recorded a sex ratio of ♂ : ♀ of 0.67 : 1.0 and 1.0 : 0.75 for two generations in two successive years. As he did not state the number of insects examined, it was not possible to see whether the ratio was a departure from the

1 : 1. As it has been said, the adult males generally emerged before the females and disappeared by the end of August. Also, the males tend to be more agile than the females. Thus it is obvious that the time of collection and method of collection will affect the estimated sex ratio. For example, when a De-Vac vacuum suction sampler was used, a greater proportion of males was caught. On the other hand, with a pooter the more sedentary females tend to be caught in greater proportion than the males. Hence in the present study, the sex ratio of fifth instar larvae were used to give an indication of sex composition. In each year about 150 fifth instar larvae collected with a pooter during the last week of June when numbers of fifth instar larvae tend to reach their peak. The sex ratios of 1969, 1970 and 1971 were ♂:♀, 1 : 1.24, 1 : 1.13, 1 : 0.94 with χ^2 = 1.7067, P > 10%; 0.6, P > 30%; and 0.4267, P > 40% respectively. On the basis of fifth instar larvae, it appears that sex ratio in C. viridis is close to 1 : 1.

9.3. The Adults

Description of adult was adequately given by Le Quesne (1965). Forewings of male usually purplish and less commonly green in colour; female all greenish (see plate 3). Apart from colouration difference the male is also smaller in size. Body size of males measured between 6.75 to 8.83 mm with a mean of 7.80 $\pm$ 0.21 mm. Female measured between 8.91 to 10.42 mm with a mean of 9.51 mm. Ten specimens of each sex were measured.

In both instances fresh material was used. This can be compared with Le Quesnes' measurements of 6.0 - 6.7 mm for the male and 7.5 - 8.4 mm for the female. It is interesting to note that head length in the adult is the same as in the Fifth instar although it has grown in width. In other Homoptera that migrate e.g. Stenocranus minutus (Delphacidae) (Yin Yin May,1970) and Cicadullina spp. (Cicadellidae) (Rose,1971) there are forms with different wing lengths, the migratory forms having longer wings. No such distinction exists in C. viridis. This may be related to the fact that under conditions of this study C. viridis had no true migratory phase and any dispersal resulted from strictly trivial movements.

9.4. Relationship between measurements of successive instars

Dyar (1890) observed that in Lepidoptera the head capsule and other linear measurements of cuticular structures increases in a regular geometrical progression in successive instars. Dyar's 'law' has been successfully used to determine the number of instars in the life cycle of an insect. But there are many exceptions to this rule and the growth factors change with instars. Richards (1949) found that in his examples the progression is regular only if account is taken of the fact that the different instars differ in duration. Growth apparently proceeds at a uniform rate so that the longer the stadium the greater the amount of growth. He also concluded that the relationship between

linear measurements and time is not affected by ordinary temperature fluctuations provided each instar is subjected to the same mean temperatures. Yin Yin May (1970) had applied this to the measurements of Stenocranus minutus and found this to hold true. The mean head length, head width, and the log. of hind femur length and tibia lengths of C. viridis were plotted against the accumulated days of instar durations (Fig. 19). The measurements were taken from insects collected from the field, and duration of instars were then estimated from the mean duration of each staduim under outdoor insectary condition. It is clear from Fig. 19 (i) that head width bears a linear relationship with accumulated days, which confirms the suggestion of Richards that growth proceeds uniformly with time whereas in head length, no growth took place between fifth instar and the adult stage. When adult stage is excluded the regression equation is $Y = 0.0145x + 0.4289$ with r the coefficient of correlation being equal to 0.9838. The fit is less good when the adult is included the equation being $Y = 0.0083X + 0.4768$ with $r = 0.9245$. With femur and tibia length, the growth appears to be exponential, with proportionately greater growth taking place during the third, fourth and fifth instars (Fig. 19 iii & iv). The mean weekly temperatures in 1970 starting from the week when first instar larvae appeared in the second week of May to the appearance of adults were 11.6, 14.3, 16.0, 19.5, 15.9, 16.5 and 14.0°C.

Table 18. Measurements of C. viridis from instar I to Adult stage with mean duration of each stage and accumulated days.

		I	II	III	IV	V	Adult		
							♂	♀	♂ + ♀
Head Length (mm)	Max.	0.51	0.57	0.76	0.88	1.12	1.00	1.17	
	Min.	0.39	0.45	0.59	0.71	0.76	0.67	0.83	
	Mean	0.41± 0.001	0.49± 0.01	0.67± 0.02	0.79± 0.02	0.95± 0.04	0.68± 0.03	0.98± 0.02	0.87± 0.03
Head width (mm)	Max.	0.69	0.92	1.24	1.68	2.15	2.29	2.75	
	Min.	0.65	0.84	1.12	1.44	1.85	2.08	2.50	
	Mean	0.68± 0.004	0.89± 0.01	1.19± 0.01	1.54± 0.03	2.03± 0.04	2.22± 0.02	2.59± 0.001	2.45± 0.05
Hind Femur length (mm)	Max.	0.39	0.59	0.80	1.18	1.71	2.08	2.42	
	Min.	0.31	0.47	0.67	0.88	1.41	1.75	2.00	
	Mean	0.37± 0.01	0.51± 0.01	0.72± 0.01	1.05± 0.03	1.56± 0.03	1.94± 0.04	2.30± 0.04	2.12± 0.05
Hind Tibia length (mm)	Max.	0.71	1.02	1.51	2.15	3.24	3.75	4.50	
	Min.	0.59	0.82	1.22	1.71	2.65	3.33	4.08	
	Mean	0.66± 0.001	0.93± 0.02	1.33± 0.03	1.88± 0.05	2.94± 0.06	3.58± 0.05	4.27± 0.03	3.92± 0.08
Body length (mm)	Max.	2.19	2.88	3.70	5.87	8.00	8.83	10.42	
	Min.	1.75	2.17	3.02	3.94	6.31	6.75	8.91	
	Mean	2.01± 0.04	2.48± 0.07	3.21± 0.08	5.02± 0.16	7.21± 0.50	7.79± 0.20	9.51± 0.16	8.65± 0.23
Mean duration of stage (days)	-	10.5	9.8	11.3	12.9	15.9	-		
Accumulated days	-	0	10.5	20.3	31.6	44.5	60.4		

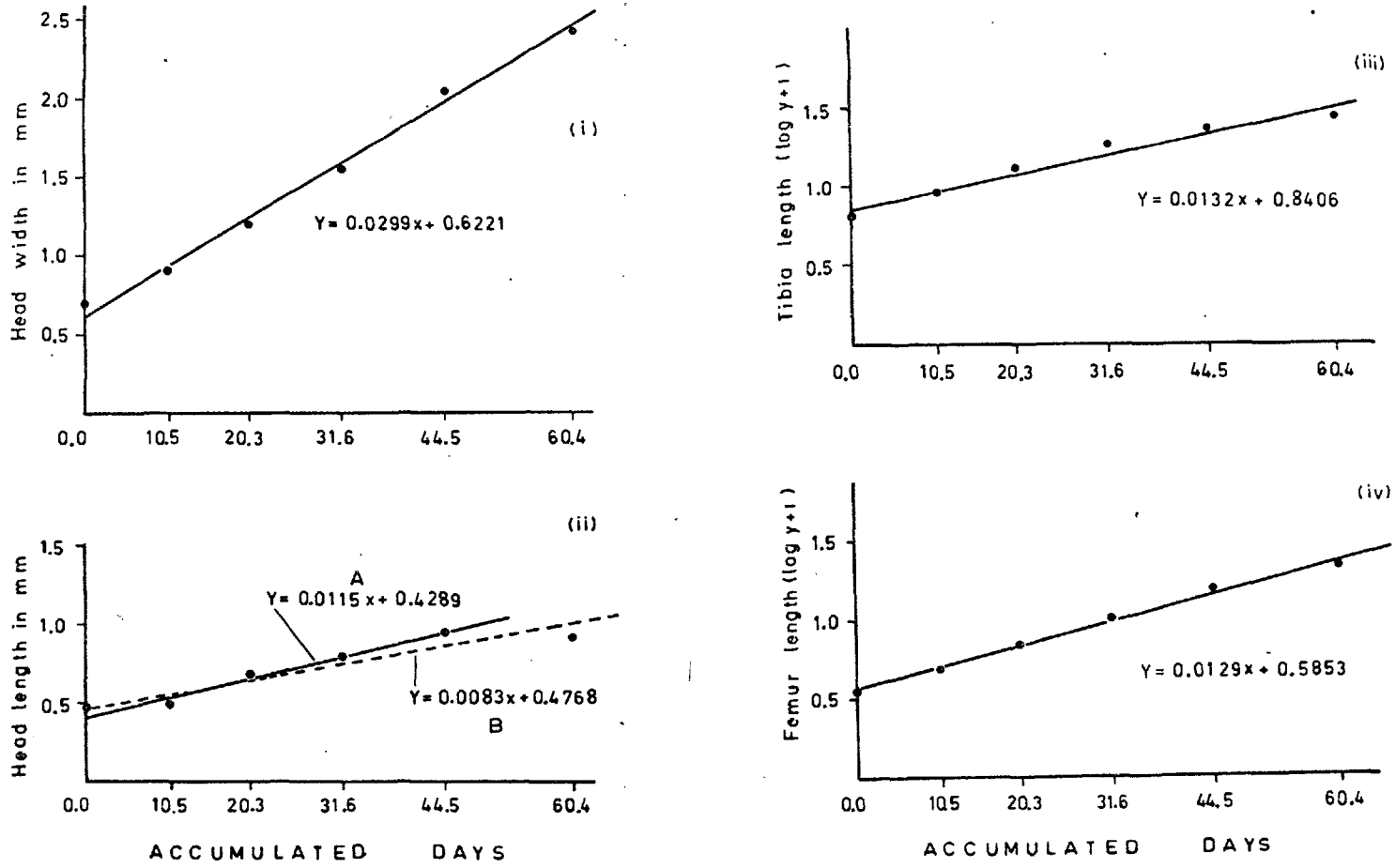


FIG. 19 Relation of measurements of different parts of the body of *C. viridis* to accumulated development days. (ii) A, excluding adult stage; B, including adult stage.

The three weeks with the highest temperature of 16.0, 19.5 and 15.9°C coincided with the occurence of second, third and fourth instars. While during the second week of fifth instar the temperatures dropped to 14.0°C. Therefore it appears unlikely that the greater growth of femur and tibia in the last three larval instars was caused by temperature. C. viridis thus seems to be another exception to Dyar's and also Richard's observations, in that different parts of the body progress at different rates between instars even though consideration has been taken of the length of instars.

10. Internal reproductive organs and sexual maturation

10.1 Male (Fig. 20)

The paired testes are each made up of six white, pear shaped follicles. The follicles are not enclosed in a common testicular sheath. The vasa deferentia are very fine when leaving the testes, but enlarged midway down into an elongated muscular vesicula seminalis. The vesicula seminalis from each testis approximate closely to each other forming almost a single structure. Just posterior to the vesicula seminalis, a pair of convoluted accessory glands joined the now narrowed vasa deferentia. The pair of vasa deferentia ultimately open into a bulbous sac-like structure, the bulbus ejaculatorius. The internal reproductive organs are well formed by the fifth instar. Sexual maturation is associated with some increase in size of

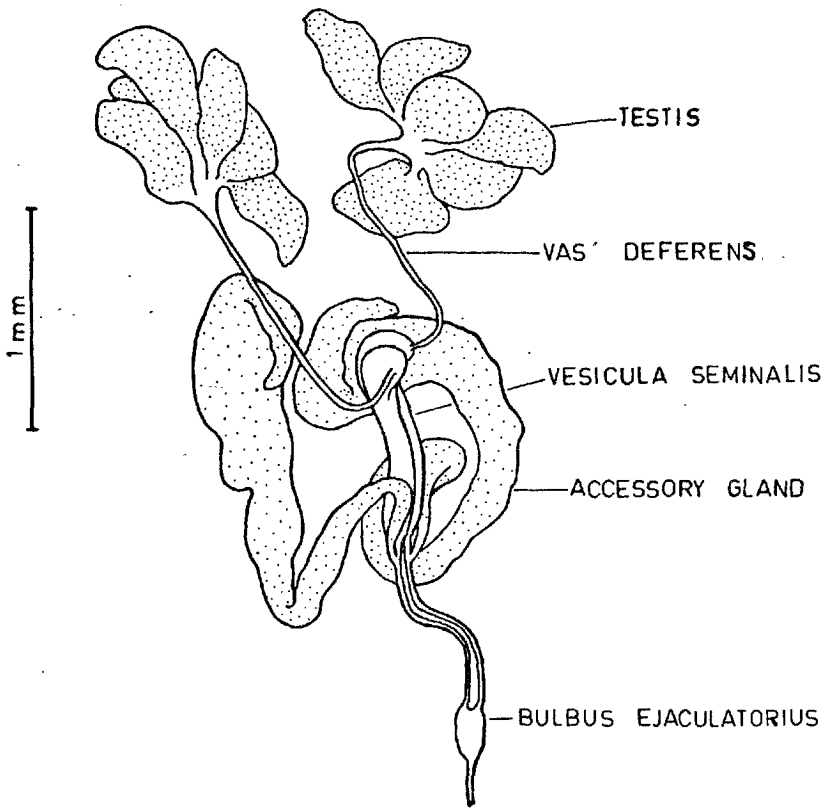


FIG. 20 INTERNAL REPRODUCTIVE ORGANS OF *C. viridis*.

testes and accesory glands, this is reflected in the slight increase in mean weight of male insects by the third week after emergence. Thereafter the weight remains reasonably constant. In the field male insects began to die off from mid August and by the beginning of September few males were left. Dissections of male insects caught at the end of August show no sign of degeneration of the internal reproductive organs as had been obversed in other Homoptera such as Conomelus anceps (Delphacidae) (Rothschild, 1962).

10.2 Female

The female reproductive organs consist of a pair of meroistic ovaries, each with six ovarioles. Dissection of a hundred females showed that the numbers of ovarioles per ovary remain constant. In the immature form each ovariole consists of a single germarium (Fig. 21A), which later form strings of eggs (Fig. 21 B). Matured eggs can be distinguished by their shiny chorions and are yellowish in colour. From the ovaries, the two lateral oviducts join up into a common vagina. Two ducts enter the vagina the anterior one ends in the spherical shaped spermatheca, and the posterior one is from the long tubular accessory gland. This latter increases in both length and diameter as the ovaries mature. Maturation in the females takes longer than in the male.

The preoviposition period in females is in the region of 59 days, but copulation occurs before the eggs are fully developed. The numbers of fully formed eggs per

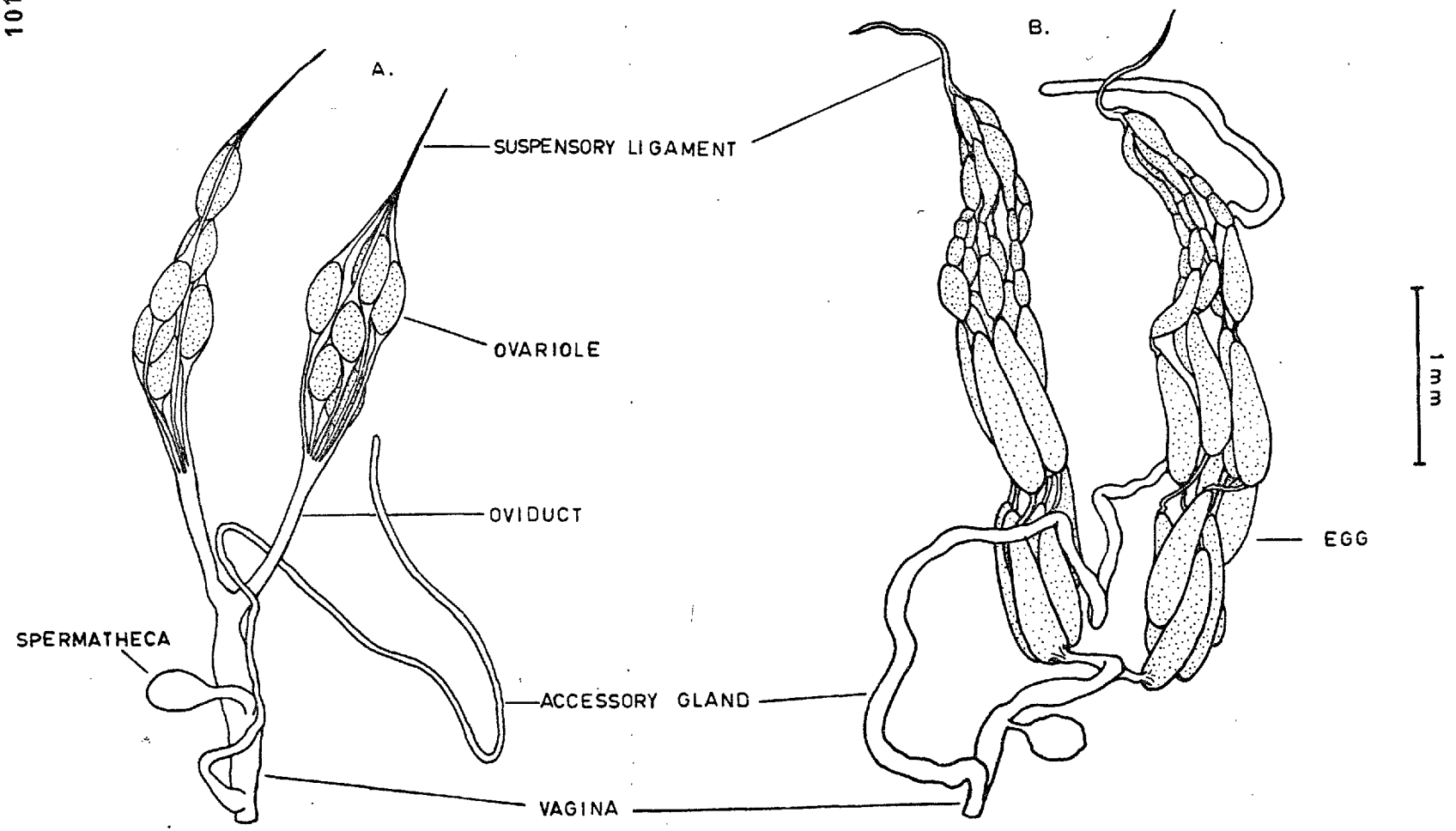


FIG. 21 Female reproductive organs of *C.viridis*. A. immature form; B mature form.

ovary is not equal most of the time, in general one ovary tends to have one egg more than the other. The total number of eggs in the ovaries varies with maturity of the insects. Weekly dissection of 20 females for nine weeks commencing from the first week of September to the last week of October have mean numbers of 21.8 $\pm$ 1.4, 18.6 $\pm$ 0.7, 20.6 $\pm$ 1.1, 20.4 $\pm$ 1.5, 21.0 $\pm$ 1.4, 16.1 $\pm$ 1.8, 13.5 $\pm$ 1.6, 14.6 $\pm$ 1.5 and 11.9 $\pm$ 1.9. The maximum number of eggs encountered was 32. It could be seen that for the initial five weeks, the mean numbers of full grown eggs remain reasonably constant, but decreases over the next four weeks. By the end of October, most females died off. Although the mean number of eggs were low towards the end of October, the maximum number could still be as high as 28 in an individual. There was no obvious degeneration of ovary with old age, but from observation on egg laying in the outdoor insectary, it was found that towards the end of the season some females failed to lay eggs inspite of their gravid condition. This phenomenon has been observed in other Hemiptera by Johansson (1958) in the Milk weed bug Oncopeltus fasciatus and by Rothschild (1962) in Conomelus anceps.

11. Weight changes in adults and its relationship to oviposition cycle in the females

In 1971 20 males and 20 females C. viridis were collected from the field each week and weighed. Fig. 22 illustrated the weekly changes in weight of male and female insects throughout their adult life.

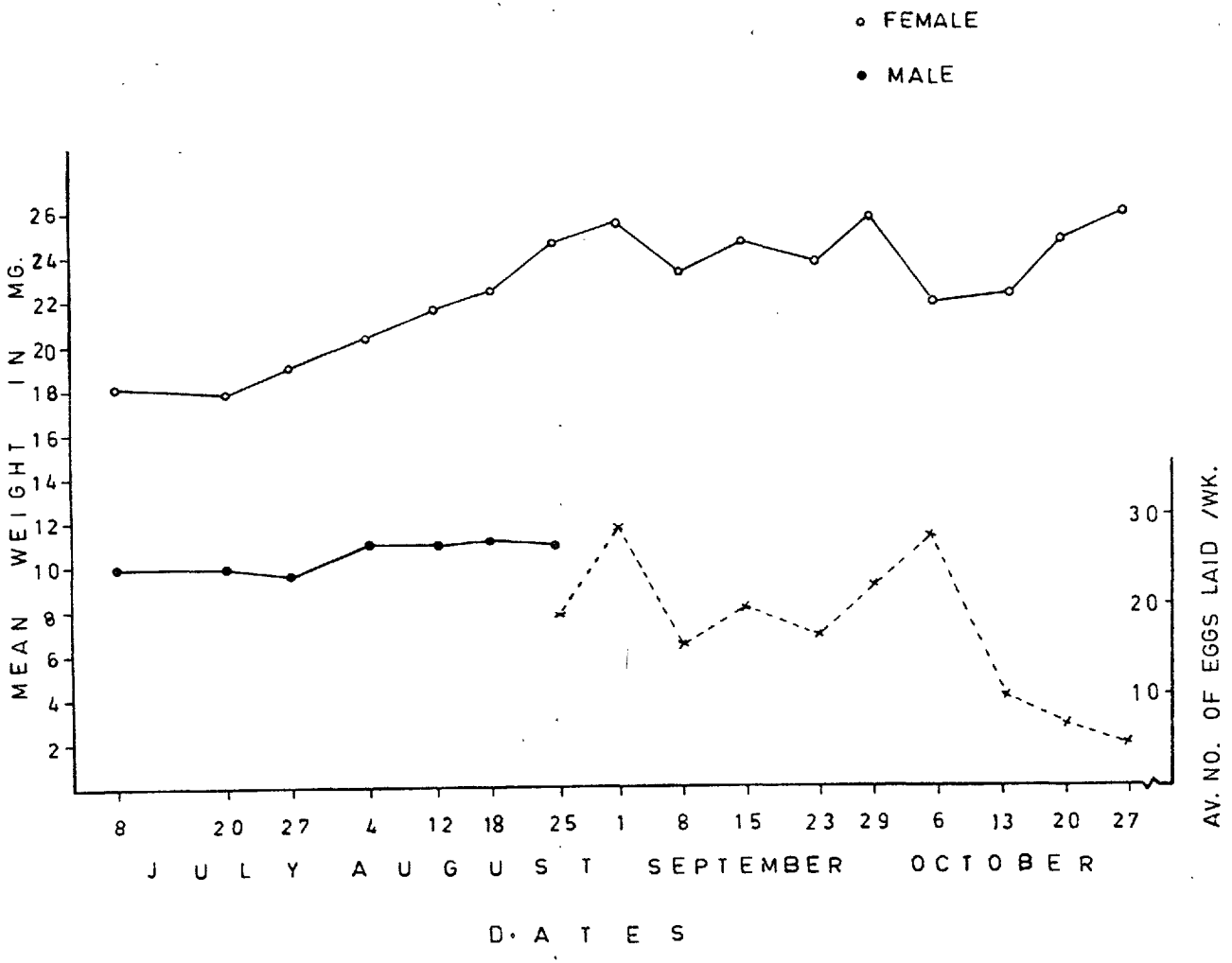


FIG.22 WEIGHT CHANGES IN *C. viridis* AND ITS RELATIONSHIP TO OVIPOSITION CYCLE.

Newly emerged males weigh about 9.5 to 11.3 mg with a mean with standard error of 10.4 $\pm$ 0.01 mg. Sexual maturation was accompanied by a slight increase in weight. On maturation (about third week after emergence), the weight had increased to a mean of 11.08 $\pm$ 0.28 mg. Thereafter the mean weight remained in the region of 11 mg. The heaviest male encountered weighed 12.85 mg.

The female insect is almost twice as heavy as the male, and the increase in weight after maturation was also more marked than in the male. Newly emerged females weighed between 14.9 to 19.3 mg with a mean of 18.18 $\pm$ 0.87 mg. Egg laying occurs round about the seventh week after emergence, by then the mean weight increases to 24.56 $\pm$ 0.49 mg. some females weighing up to 28.9 mg. The increase in weight was associated with the maturation of eggs in the ovaries, and also to a lesser extent possibly with the enlargement of the accessory gland. Study of fecundity of female per week in cages under outdoor insectary conditions indicated that for the first five weeks of oviposition the mean numbers of eggs produced per week were related to the mean weight of female during that week (Fig. 22). After a large batch of eggs was laid there was a drop in the mean weight during the following week together with a corresponding drop in the number of eggs laid that week. The weight would then rise again until a further large batch of eggs was laid. On the sixth week there was a decrease in weight,

but a high number of eggs was laid. The reason for this discrepency was not known, and was most likely due to some experimental error. From the seventh week onwards till the disappearance of all the females, the numbers of eggs laid were actually dropping inspite of an increase in weight. The lower number of eggs laid was partly due to failure of some gravid females to lay, and to the drop in the mean number of mature eggs in the ovaries. The reason for the increase in weight during this late stage was not obvious possibly it may be connected with senescence and alterations in physiology of the females.

12. Longevity of adult C. viridis

No accurate estimation of longevity of adult C. viridis is available. This is because the insect does not do well under cultural conditions. Cageing of thirty pairs of newly emerged adults in an outdoor insectary gave an average life span of 20.7 days, and a range between ten and sixty days (one female only). An indication of adult longevity in the field was obtained through the mark and recapture experiment, when in 1970, one female was recovered fifty seven days after release.

Another rough estimation of longevity was obtained by noting the period between the last appearance of fifth instar larvae in the course of regular sampling and the last appearance of adults. This method showed that longevity was at least eighty five days in 1969, eighty three days in 1970 and seventy nine days in 1971.

The mean longevity was calculated by multiplying the number of adults estimated in the field in regular samples by the number of days since emergence of the adults. The sum product of these was then divided by the sum total of adults taken in all samples. With this method, the mean longevity is estimated to be 36.78 days in 1970 and 38.38 days in 1971. It is probable that the estimation based on the dates of the last larvae and last adults denotes the potential longevity of survivors whereas the above method is a better index of "ecological longevity" in the field, which takes into account early deaths caused by predators and disappearance of adults caused by dispersal.

13. Fecundity

Because of the rearing problems, attempts to obtain an absolute estimate of fecundity of C. viridis in 1969 and 1970 had failed. In 1971 twenty females collected from the field were caged singly each week. Juncus and

Holcus were provided for egg laying and food. At the end of the week, the number of eggs laid were counted and the insects dissected to examine the state of the ovaries. The experiment was carried out for ten weeks commencing on the 21st of August to the end of October and this covered the entire egg laying period of C. viridis in the field. The average numbers of eggs laid per female per week were 19.4, 29.3, 18.8, 20.2, 17.3, 22.9, 28.3, 10.0, 6.9 and 5.0 for weeks one to ten. This gave a mean number of eighteen eggs per female per week. The number of eggs laid per female ranged from 0 to 51. By multiplying the mean number of eggs per week by the number of females as obtained in the regular population census, the number of eggs in the field was estimated to be 1,023,723 with an average of 63.2 per female in 1969; and 1,591,704 with an average of 52.9 per female in 1970. These figures are far below those estimated by the direct egg count; the basis for these estimations were derived from the 1971 data only.

Using the data collected in the direct egg counts and regular population sampling of adults, a rough estimate of fecundity is obtained as follows:-

$$\text{Fecundity} = \frac{\text{Total number of eggs estimated in the egg count}}{\text{Initial number of females available for egg laying}}$$

In 1969 the total number of eggs estimated in the field was 8,826,758 and the number of females was estimated as

16,196, which gives the fecundity of 54.5 eggs per female. In 1970 the eggs were estimated to be 10,281,028 and the number of females 30,100 which gives a fecundity of 34 2 eggs per female.

Because of the size of samples taken, there is reason to believe that the figure for the egg count is reasonably accurate. But it is probable that the number of females, was underestimated in 1969 and thus has resulted in an overestimation in fecundity for that year. Otherwise the large discrepancies between experimental results and field observations are thought to be caused by (a) the difficulty of keeping the insects in good conditions under captivity. When dissected at the end of the week of experiment, the ovaries of the caged females were mostly empty of eggs except towards the end of the laying season. This condition was seldom found in females collected from the field. This indicates that for some reason females under captivity were unable to continously produce new eggs, possibly because of nutritional factors and stress. (b) In view of (a), a more accurate figure might be arrived at, if the interval of changing of the caged females were reduced to two or three days instead of a week. (c) Ideally the fecundity estimate should be based on the cageing experiment carried out for each season's

population. As this was not done, the results obtained in 1971 population have to be used for the 1969 and 1970 populations. In conclusion, the fecundity as derived from field observation appears to be nearer to the truth, but with the lack of conclusive experimental evidence, the figures arrived at can only be taken as a guide.

14. Some observations on the biology of egg parasite Anagrus atomus (L.) (Mymaridae : Hymenoptera).

The eggs of C. viridis are parasitised by a Mymarid (Hymenoptera) parasite Anagrus atomus(L.) Identification was based on a key given by Whalley (1956). The characters used to distinguish the two morphologically very similar species A. atomus and A. incarnatus Hal. were: in the case of the female, the presence or absence of antennal groove on the fifth segment, and again the presence or absence of a glabrous space in the distal part of the forewings. In the male, the presence or absence of the hooks or of elongation of the parameres were used in addition to the forewing character. Whalley (1956) found that the presence or absence of a glabrous space on the forewings provides a constant feature in separating the two species. The glabrous space in the forewing A. atomus is illustrated in Fig. 23C. Based on Whalley's key, Anagrus bred from

C. viridis were mainly A. atomus with only occasional individuals of A. incarnatus.

Life History

The life history of A. atomus and its larval stages have been described by Pierre (1906), Whalley (1956, 1970) and Maillet (1960). It is not proposed to describe these again, except to fill in some details which have not been mentioned previously.

Eggs of Anagus atomus were laid singly. The egg is pear shaped, with a long stalk at the posterior end (see Fig. 23a.) The main body of the egg measured about 0.1mm in length and the stalk about 0.06mm, thus giving an overall length of 0.16mm. The maximum width of the egg is about 0.02mm. At 20°C the eggs hatched in two to three days after being laid. The newly hatched larva is pale in colour, but becomes orange as it matures. A mature larva measures about 0.35mm in length, and its mouth hooks and lateral palps are greatly reduced. Segmentation in both young and mature larvae is indistinct. The drawing of Anagrus larva as presented by Whalley (1970) is too diagrammatic. Fig. 23b illustrates a mature larva. Whalley (1970) had described a pair of 'ear' organs of unknown function on the sides of the mature larva. However, careful examination of mature larvae in the present study had failed to find these 'ear' organs. In the drawing given by Maillet (1960) 'ear' organs were not depicted

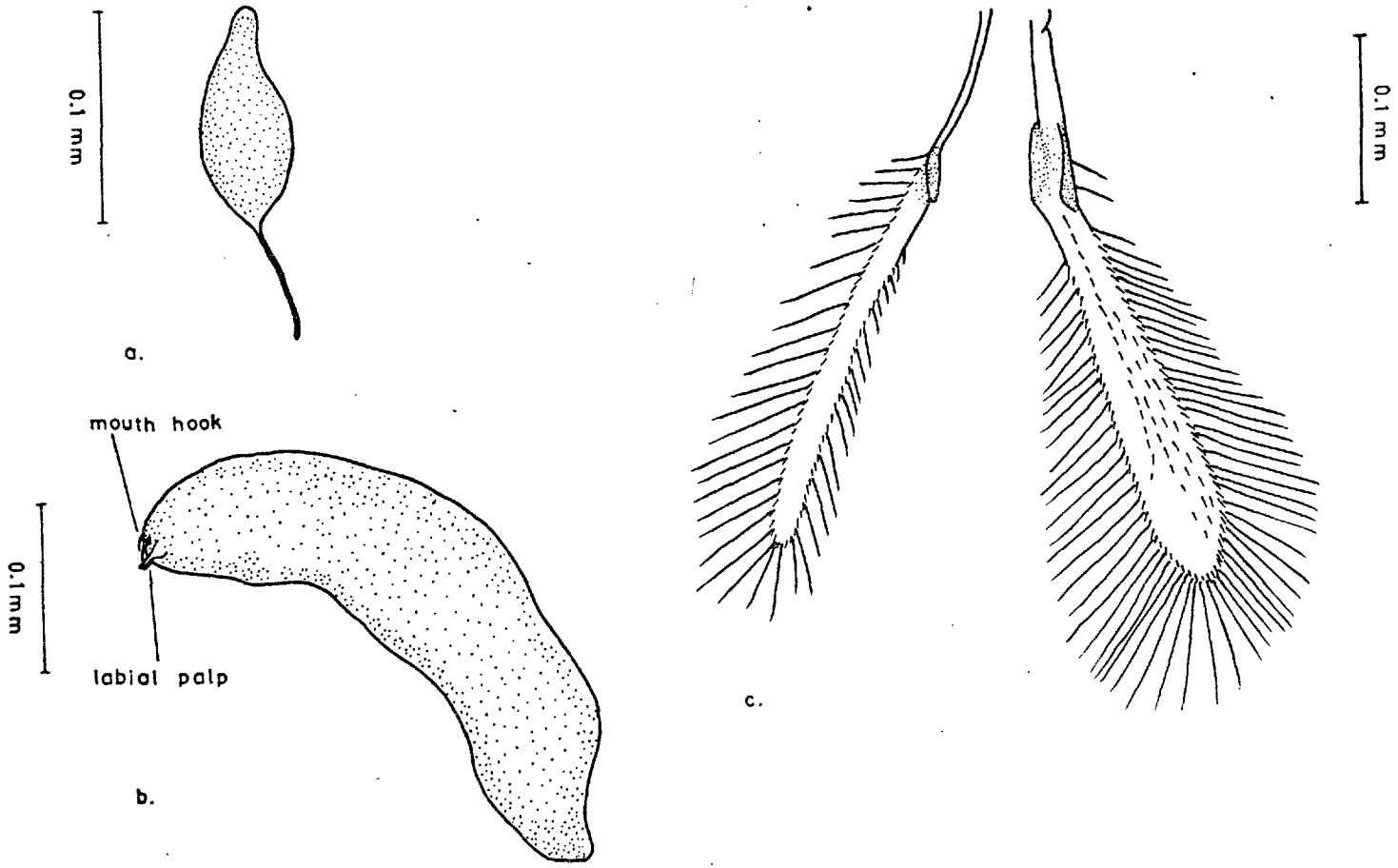


FIG. 23 a. Egg, b. Mature larva, c. Fore and hind wings of *Anagrus atomus L.*

either. The larval stages lasted for about six days, and the pupal stage for six to seven days. The adult emerged by biting its way through the host chorion and the Juncus stem. It is not unusual to find individuals which failed to bite their way through and died. The whole life cycle from egg to egg is completed between twelve to fourteen days. The adult females are capable of reproducing pathenogenetically although mating has been observed frequently.

.Number of parasites per C. viridis egg - the number of Anagrus per host egg varies from one to five with a mean of 3.56 ± 0.13; this estimate is based on forty -five parasitised C. viridis eggs and a total of 160 Anagrus that emerged under laboratory rearing, up to eight Anagrus per egg have been obtained, while Whalley (1970) came across twelve parasites per egg. Maillet (1960) had recorded ten parasites per egg from a field population in France. There were no signs of larval cannibalism when large numbers of larvae were present in a single host egg.

Overwintering - A. atomus overwintered as larvae, and resumed development in the following spring. For Winter the larvae go into a quiescent stage rather than diapause, since they resume development when they are brought into high temperature. In the field, adults begin to emerge towards the end of April and early May,

and are about two weeks ahead of the hatching time of the host.

The number of annual generations in C. viridis eggs - The ability of A. atomus to parasitise C. viridis eggs with well developed embryos observed by Whalley (1970) was confirmed. The adults that emerged in Spring parasitise the developing C. viridis eggs and thus produce a second generation on the single generation of the host. Developing C. viridis eggs show the black puncture marks made by the ovipositors of A. atomus. There was evidence that when conditions are favourable, three generations of the Mymarid could pass through in one generation of C. viridis eggs. This was evident in 1970, when some C. viridis eggs collected in November had empty egg shells with signs of parasites that had already emerged; simultaneously some eggs had well developed pupae of A. atomus. Thus at least two and possibly three generations of parasites could develop in one generation of C. viridis eggs. In spite of this, the increase in percentage of parasitism in the Spring was small or negligible (see Table 31 , p.155), and the overall role played by A. atomus as a population regulator appears to be insignificant.

Sex ratio - Male and female Anagrus are frequently found together within a single host egg, though it is not uncommon to find only individuals of the same sex. Observations on 160 individuals produced 94 females and

66 males, which gave a ratio of 1.42 : 1, female to male. χ^2 being 4.9, which is significant at 5% level. This is consistant with Whalley's (1970) finding of the presence of more females than males, though the ratio he found was as high as 3 : 1, females to males.

Fecundity - An absolute fecundity estimate was carried out by confining a pair of newly emerged A. atomus in a 4.5 x 2.5mm glass tube with twenty eggs of C. viridis and topped with a cork. The experiment was set up in a 20°C constant temperature room and there were thirty six replicates. The host eggs were dissected after a week and the number of A. atomus larvae counted. The number of eggs laid by twenty females varied from fourteen to thirty six with a mean of 22.95 $\pm$ 1.24 per female.

III POPULATION OF C. VIRIDIS

1. Method of sampling eggs

1.1 Estimates of oviposition sites

The study area was divided up into several rectangles and the approximate area of the total study site calculated. The area estimated was 711 square metres for area A and 1,074 square metres for area B. As the eggs of Cicadella viridis (L.) were laid inside the stems of Juncus, the first step towards egg estimation was therefore to estimate the number of available Juncus stems in the field for oviposition. A quadrat was used for counting Juncus stems. A preliminary count was made with quadrats of the size of 0.25 square metres and of 0.0625 square metres. Fifty samples of each were taken at random and the results obtained compared in order to decide upon the final quadrat size to be used. During this preliminary count only area A was used, and the quadrat was laid down at ten pace intervals. The number of Juncus stems within the quadrat was counted, where no Juncus was present a zero count was registered. The estimates of Juncus stems obtained with quadrat size of 0.25 m^2 was 984,020 stems with a 95% confidence limit of between 824,760 to 1,115,986. This compared with the estimate obtained with 0.0625 m^2 quadrat of 1,042,000 stems with a confidence limit of between 873,677 and 1,208,130. As the two estimates appeared to be

reasonably close, it was decided to use the smaller quadrat for the estimation of Juncus stems, since this involved a considerable saving of time in counting. Beall(1931) and Finney(1946)have found that the smaller sampling unit is more efficient than a larger one particularly when the dispersion of a population is a contagious one. When the appropriate quadrat size had been decided upon, fifty counts were taken from each of area A and area B, i.e. one hundred counts were made for the whole study area. Two such counts were carried out each winter and the resulting counts of Juncus stems were as shown in Table 1. (Page 7).

1.2 Methods of estimating eggs

After an estimate for the numbers of Juncus stems had been established, ten Juncus clumps were selected at random from area A and ten from area B. Each clump was then divided into four parts according to the direction it faced. From each direction a minimum of ten stems were cut at ground level. From the whole study area a total of not less than eight hundred stems was collected during each sampling occasion. The stems were then brought back for examination of eggs. The reason for the division of each clump into four parts according to the direction it faces was to discover whether there was any directional effect on the oviposition of the female. A discussion on

this was presented earlier on (P. 43). The mean number of eggs per stem was then established and this was multiplied by the estimated number of Juncus stems to give a total estimate of eggs present in the study area. When eggs were examined, records were made of the number of eggs per egg mass and the condition of the eggs - whether they were healthy, infected by fungi, or attacked by predators or parasites, in order to obtain an estimate of mortality and of its causal agents. The position of eggs on the stems was also noted. The diameter of some 1,400 eggs bearing stems was also measured to see whether there was any relation between stem diameter and preference for oviposition. The result of this was discussed in an earlier section (see p. 38).

2. Methods of sampling larvae and adults

The difficulties encountered in sampling insects, in a Juncus field was mainly caused by the dense mat of collapsed Juncus stems on the ground from the previous year, the tall and stiff growth of the new stems and the water-logged condition of the ground. Both Whalley (1958) and Rothschild (1966) used a corer to collect samples and used floatation methods to extract the insects studied. Coring method was not considered here because of the difficulties in pushing a corer through dense Juncus mat and the laborious process involved in extraction.

2.1 Methods tried

Methods tried, but found to be unsuitable were

(i) sweeping with a net

(ii) marking and recapture method and

(iii) an adapted version of the electrical powered vacuum suction sampler devised by Johnson, Southwood and Entwistle (1957).

(i) Sweep Net. Trials carried out in 1969 by making several one hundred sweeps per fifty steps over Juncus caughtfew C. viridis. This was due to the height of Juncus stems and the fact that C. viridis, particularly during the larval stages, tends to stay fairly low down near the base of the clump.

(ii). Marking and recapture method. Larvae were placed in a conical flask and were marked with Rota Red R dye. Two glass tubes passed through the rubber cork of the flask. Underneath one glass tube there was a minute glass container with a small quantity of the dye. By blowing gently onto the dye powder through the glass tube, the larvae were dusted. Adult insects were marked with cellulose paint on the wings or prontum. The method was discarded because recoveries of marked insects were too few.

(iii) Electric vacuum suction sampler. The machine was described in detail by Johnson, Southwood and Entwistle (1957). The collecting bag inside the machine was replaced by a 3 X 1 inch hollow glass or plastic tube inserted into

the 1 inch diameter hose inlet. The tube has an opening at one end and is covered with muslin at the other end to retain the collected plants and insect material. The area sampled was delimited by a bottomless bucket of diameter 0.21 metre (8 inches) pushed firmly into the ground. Low numbers collected were probably due to the tall and dense vegetation in the Juncus field, which made thorough coverage with the suction hose difficult. For a comparison with the Dietrick/(De-Vac) suction sampler, 26 samples were taken at one minute of suction per sample and covering a total area of 0.9 square metres; all together nineteen C. viridis larvae were collected giving an equivalent of about 18.0 insects per square metre. This was compared with 160 insects collected with a Dietrick sampler in ten samples covering a total of 0.9 square metres, and giving a figure of 177.8 per square metre.

2.2 Methods chosen for population estimate of larvae and adults.

Population estimates were obtained by both direct counting and by using a Dietrick vacuum suction sampler (Dietrick 1961). The machine consists of a two stroke petrol engine driving a squirrel-cage type of fan. Connected to the fan is an eight inches (0.21 metre) diameter hose, fitted with a one square foot (0.09 square metre) suction head. Insects and plant materials were sucked up and collected in a bag contained in the head.

During sampling, the head was first pressed firmly into the area to be sampled, and was then followed by moving the head up and down in order to stir up any insects that might cling on to the vegetation. For each sample a count of sixty was made which approximated to about one minute sampling time. Each sample collected was kept in a polythene bag for examination in the laboratory. Sorting was carried out by emptying the contents of the bag inside an insect screen. This is a rectangular box made up of muslin on top and two sides, a hard board bottom and a cellulose acetate screen which from the transparent vertical side. Hoppers are attracted to the screen with the help of a light.

The Dietrick sampler was mainly used during the larval stages. In adults it was found that the females particularly during oviposition periods tend to gather lower down in the vegetation, and tend to cling tightly to grass or Juncus stems, this resulting in very low catches. As C. viridis is a large but not particularly agile insect, it is possible to carry out direct search and counts. In direct counting the one square foot head of the Dietrick sampler was used as a quadrat to define the area to be sampled.

In 1969, the Dietrick sampler only was used for sampling both larvae and adults. In 1970 in addition to this sampler, direct counting was also carried out for

the adult stage. In 1971 the Dietrick sampler was used for larval stage and direct counting for the adult stage as experience in 1970 showed that the latter is a more efficient method.

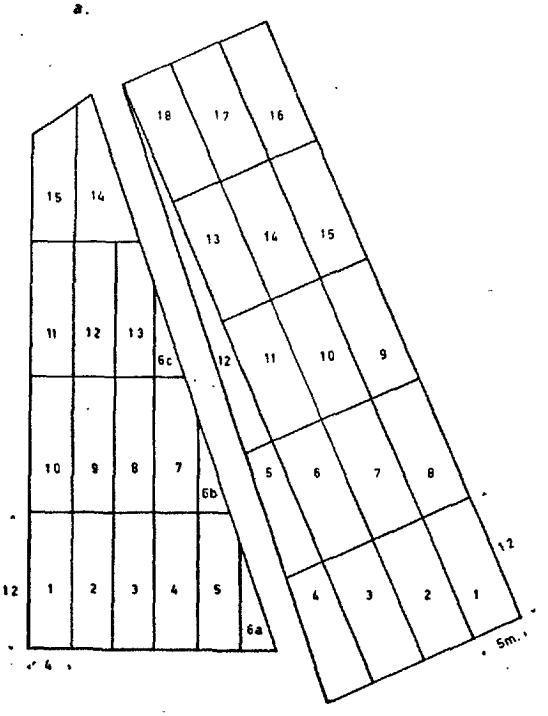
In 1969 and 1970, thirty-three samples were collected on each sampling occasion. The field was divided into thirty-three squares. Area A was divided into fifteen roughly equal areas of forty-eight square metres each, and area B was divided into eighteen squares each of about sixty square metres (Fig. 24a). Sampling was carried out at weekly intervals.

One sample was taken from each square, and the sampling point was taken at random. During 1971, because of the time factor, the total number of samples taken per occasion was cut down to twenty-five for the whole area, and the samples were taken at weekly intervals. The field was divided as in Fig. 24b. Area A was divided into ten squares each of about seventy square metres, and area B was divided into fifteen squares each of about seventy-two square metres.

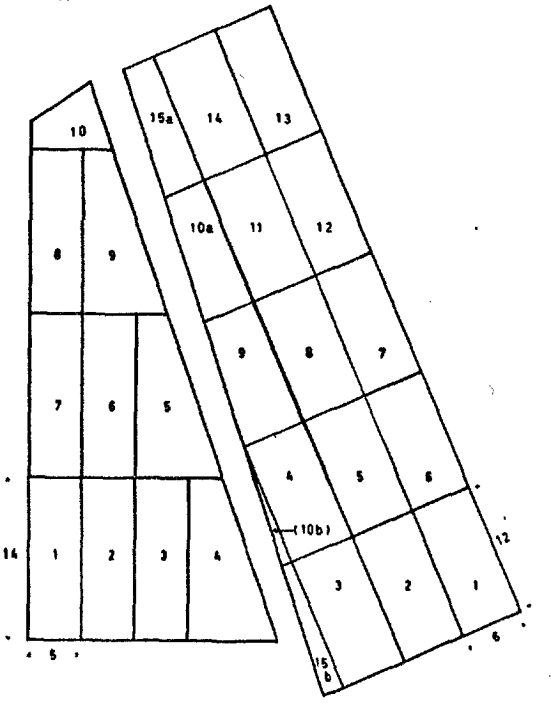
The time interval between sampling was kept as constant as possible, weather permitting, and sampling commenced after 10 a.m. when dew on vegetation begins to disappear and air temperatures were rising.

FIG. 24 SUB DIVISION OF STUDY AREA FOR POPULATION SAMPLING IN (a) 1969, 1970 AND (b) 1971.

a.



b.



2.3 Effieiency of the Dietrick Machine

Callan et al (1966) had compared the Dietrick machine with sweep nets and found it to be more efficient, but more laborious for sampling Cicadellidae on an alfafa field. An attempt was made to estimate the rate of extraction of larvae of C. viridis among Juncus and Holcus spp. Five hundred first instars hatched in the laboratory were released in ten batches of fifty individuals each in ten marked localities. Five batches were released among Holcus and five among Juncus. Releasing took place in early May when the field population was not yet around. Temperature at the time of release was 11°C. The insects were allowed one hour to settle down before recapture with 'Dietrick' was carried out. The machine went through each releasing point for about one minute, and the number recaptured was counted. In Holcus the percentage of recovery for the five releasing points were 80, 68, 90, 86 and 82 with a mean of 81.2. In Juncus the recoveries were 86, 82, 78, 84 and 94% with a mean of 84.8%. The overall recovery rate was 83%.

2.4 Comparison between direct count method and the Dietrick Machine for the estimation of adults.

Comparison between the Dietrick machine with direct count was made on four occasions during the adult stage. In the direct count the head of Dietrick was used as a quadrat. On each occasion, eighteen samples were taken, and the results are as shown in Table 19.

Table 19. Comparison between numbers of adults caught with the Dietrick machine, and the number counted directly. Note the differences in sex ratio.

Date	No. caught with Dietrick	Sex ratio ♂ ♀	No. counted directly	Sex ratio ♂ ♀	% caught with Dietrick
4.VIII.70	38	1:0.19	47	1:0.42	80.85
11.VIII.70	31	1:0.19	46	1:0.80	67.39
18.VIII.70	11	1:1.80	41	1:2.14	26.83
25.VIII.70	7	0:1	38	1:3.22	18.4

Table 20. Estimated number of eggs in the field for the seasons 1968-71.

Year	No. of stems in the field	No. of eggs per stem	No. of eggs estimated	95% confidence limit
1968-69	1,956,217	2.6	5,105,726 (2,860/m^2)	4,575,651-5,635,802
1969-70	2,206,688	4.0	8,826,752 (4,896/m^2)	7,820,438-9,656,535
1970-71	2,000,200	5.1	10,281,028 (5,704/m^2)	8,972,944-11,589,003

A greater number was accounted for by direct counting. With the Dietrick sampler a greater proportion of males were caught. This is because the males are much lighter in weight, more agile and less likely to cling on to vegetation tightly, particularly during the oviposition period as from the last week of August, the females tend to go deep down into the Juncus clump for egg laying. The reverse of the sex ratio in the later half of August is due to the gradual dying out of the male population.

3. Estimated number of eggs in the field

To obtain an estimate of eggs in the field, Juncus stems were collected and examined and the mean number of eggs per stem calculated. The mean number of eggs per Juncus stem was them multiplied by the total estimated Juncus stems in the field to give the estimated total number of eggs. In the seasons of 1968-1969, 1969-1970 and 1970 - 1971, 1,860, 3,090 and 3,333 Juncus stems were examined respectively, and the mean number of eggs per stem was estimated as 2.6, 4.0 and 5.1. Table 20 shows the estimated number of eggs in the whole study area of 1,785 square metres for the three seasons.

As can be seen in Table 20 there was an increase in the number of eggs in each successive year. The increase may be due to:-

(i) the exceptionally high rainfall during the oviposition period in 1968. The total rainfall from the

beginning of egg laying in the second week of August to the end of October was 217.4mm in 1968, as compared with 31.3mm in 1969 and 97.8mm in 1970.

(ii) Also there was an increase in the number of Juncus stems in 1969 and 1970. Early in 1968 a ditch was dug across the study area, and some of the soil so removed covered up a considerable area of Juncus, which subsequently had recovered.

(iii) There was a higher number of adult females in 1970, and hence a higher number of eggs in the season of 1970-71 than in 1969-70.

4. Number of larvae and adults

The number of first instars hatched in the field was obtained by subtracting from the total eggs estimated in the field from the number of eggs that were not viable. Details of factors causing egg mortality will be discussed later. The survival rate of the eggs for the three seasons were o,3821, 0.2006 and 0.1828 for 1969, 1970 and 1971. The estimated numbers of first instars hatching in the field for the three seasons are shown in Table 21 .

Inspite of the variation in the number of eggs laid, the numbers of first instars hatched remain reasonably constant.

The relative number of individual instars present throughout the season for the three years are shown in

Table 21 Estimated number of first instars in 1969, 1970 and 1971. Figures in bracket expressed the number of individuals in terms of per square metre.

Year	1969	1970	1971
Estimated No. of 1st instars	1950898 (1093/m^2)	1770646 (992/m^2)	1878334 (1053/m^2)
95% confidence limit	1748356 - 2153440 (979 - 1206/m^2	1568780 - 1937100 (870 - 1085/m^2	1640254- 2118470 (919 - 1187/m^2

Table 22 , 23 , and 24 ; and are illustrated graphically in Fig. 25, 26, and 27. The numbers of larvae were estimated directly from the Dietrick suction sampler. Those of the adults, apart from 1969 which were derived from the Dietrick machine, were derived from direct counting. As regular sampling in 1969 was not carried out until the peak of first instars was over, and with the general inexperience in using the Dietrick machine, the figure arrived at in that year can-not be very accurate. Thus no attempt was made to correct the adult figures which were estimated by direct counting in 1970 and 1971. The overall patterns of decrease in the population throughout a season for the three seasons appears very similar. The analysis and causes of mortality are discussed later.

5. Pattern of distribution of larvae and adult C. viridis in the field.

The pattern of distribution of animals in its habitat is of considerable ecological significance, as it may give a description of the condition of a population. Changes in dispersion patterns together with changes in the size of a population often give an indication of a mortality factor related to density, or the intensity of competition. Various methods have been used to describe the randomness or aggregation of insects in the field. Southwood (1966) and Reyna-Robles (1969) have reviewed most of the commonly used methods.

Table 22. Estimated population of larvae and adults of C. viridis in the field in 1969. Above each accumulated peak value, a line is drawn.

Date		Population						Accumulated population = y						y = log Y					
		I	II	III	IV	V	Adult	I+	II+	III+	IV+	V+	Adult	I+	II+	III+	IV+	V+	Adult
June	4	10,200						10,200											
	10	13,713	7,614					21,327	7,614										
	17	9,114	4,563	3,437	1,145			18,259	9,145	4,582	1,145								
	18	19,220	39,161	43,805	3,468			125,704	106,434	47,273	3,468			5.0993					
	25	11,974	14,971	63,492	28,033	671		119,141	107,167	92,196	3,474	671		5.0761					
July	2		2,270	27,640	77,396	9,768		117,074	117,074	114,804	87,164	9,768		5.0654	5.0654	5.0599			
	9		507	7,209	54,151	34,781		96,648	96,648	96,141	88,932	34,781		4.9852	4.9852	4.9829	4.9491		
	15			507	20,884	39,997	2,153	65,541	63,541	63,541	63,034	42,150	2,153	4.8030	4.8030	4.8030	4.7996		
	23				2,816	7,902	23,822	34,540	34,540	34,540	34,540	31,738	23,822	4.5383	4.5383	4.5383	4.5383		
	30					3,674	44,907	48,581	48,581	48,581	48,581	48,581	44,907	4.6865	4.6865	4.6865	4.6865	4.6865	
August	6					2,403	45,685	48,088	48,088	48,088	48,088	48,088	45,685	4.6820	4.6820	4.6820	4.6820	4.6820	4.6598
	13						16,578	16,578	16,578	16,578	16,578	16,578	16,578	4.2195	4.2195	4.2195	4.2195	4.2195	4.2195
	18						26,058	26,058	26,058	26,058	26,058	26,058	26,058	4.4159	4.4159	4.4159	4.4159	4.4159	4.4159
	21						16,196	16,196	16,196	16,196	16,196	16,196	16,196	4.2094	4.2094	4.2094	4.2094	4.2094	4.2094
	28						10,376	10,376	10,376	10,376	10,376	10,376	10,376	4.0160	4.0160	4.0160	4.0160	4.0160	4.0160
Sept.	3						10,758	10,758	10,758	10,758	10,758	10,758	10,758	4.0318	4.0318	4.0318	4.0318	4.0318	4.0318
	9						9,237	9,237	9,237	9,237	9,237	9,237	9,237	3.9655	3.9655	3.9655	3.9655	3.9655	3.9655
	24						6,634	6,634	6,634	6,634	6,634	6,634	6,634	3.8218	3.8218	3.8218	3.8218	3.8218	3.8218
Oct.	1						1,777	1,777	1,777	1,777	1,777	1,777	1,777	3.2497	3.2497	3.2497	3.2497	3.2497	3.2497
	8						1,264	1,264	1,264	1,264	1,264	1,264	1,264	3.1017	3.1017	3.1017	3.1017	3.1017	3.1017
	16						632	632	632	632	632	632	632	2.8007	2.8007	2.8007	2.8007	2.8007	2.8007

Table 23. Estimated population of larvae and adults C.viridisin the field in 1970. Above each accumulated peak value, a line is drawn.

Date		Population						Accumulated population = y						y = log Y					
		I	II	III	IV	V	Adult	I+	II+	III+	IV+	V+	Adult	I+	II+	III+	IV+	V+	Adult
May	19	156,052						156,052											
	23	136,842	632					137,474	632										
	28	294,471	45,528					339,945	45,528					5.5314					
June	7	96,259	146,361	41,997				284,617	188,358	41,997				5.4543					
	10	10,369	66,092	97,113	10,883			184,451	174,088	107,996	10,883			5.2659					
	16	507	17,585	115,191	73,618			206,901	206,394	188,809	73,618			5.3158	5.3147	5.2760			
	23		1,646	59,561	102,572	23,787		187,566	187,566	185,920	126,359	23,787		5.2732	5.2732	5.2693			
	27			7,216	62,742	42,629		112,587	112,587	112,587	105,371	42,629		5.0515	5.0515	5.0515			
July	2			1,521	49,213	89,043	1,264	141,041	141,041	141,041	139,520	90,307	1,264	5.1493	5.1493	5.1493	5.1446		
	9			632	6,070	26,808	28,805	62,315	62,315	62,315	61,683	52,613	28,805	4.7946	4.7946	4.7946	4.7902		
	17				1,896	27,940	65,360	95,196	95,196	95,196	95,196	93,300	65,360	4.9786	4.9786	4.9786	4.9786	4.9699	4.8153
	22				1,646	21,537	35,302	58,485	58,485	58,485	58,485	56,839	35,302	4.7670	4.7670	4.7670	4.7670	4.7546	4.5478
	29				632	1,014	48,721	50,367	50,367	50,367	50,367	49,735	48,721	4.7021	4.7021	4.7021	4.7021	4.6967	4.6777
August	4						42,389	42,389	42,389	42,389	42,389	42,389	42,389	4.6273	4.6273	4.6273	4.6273	4.6273	4.6273
	11						39,719	39,719	39,719	39,719	39,719	39,719	39,719	4.5990	4.5990	4.5990	4.5990	4.5990	4.5990
	18						40,108	40,108	40,108	40,108	40,108	40,108	40,108	4.6040	4.6040	4.6040	4.6040	4.6040	4.6040
	25						30,100	30,100	30,100	30,100	30,100	30,100	30,100	4.4786	4.4786	4.4786	4.4786	4.4786	4.4786
Sept.	1						22,016	22,016	22,016	22,016	22,016	22,016	22,016	4.3427	4.3427	4.3427	4.3427	4.3427	4.3427
	8						10,376	10,376	10,376	10,376	10,376	10,376	10,376	4.0160	4.0160	4.0160	4.0160	4.0160	4.0160
	15						8,730	8,730	8,730	8,730	8,730	8,730	8,730	3.9410	3.9410	3.9410	3.9410	3.9410	3.9410
	23						7,084	7,084	7,084	7,084	7,084	7,084	7,084	3.8503	3.8503	3.8503	3.8503	3.8503	3.8503
	27						5,924	5,924	5,924	5,924	5,924	5,924	5,924	3.7937	3.7937	3.7937	3.7937	3.7937	3.7937
Oct.	6						2,785	2,785	2,785	2,785	2,785	2,785	2,785	3.4448	3.4448	3.4448	3.4448	3.4448	3.4448
	13						2,273	2,273	2,273	2,273	2,273	2,273	2,273	3.3576	3.3576	3.3576	3.3576	3.3576	3.3576
	20						1,139	1,139	1,139	1,139	1,139	1,139	1,139	3.0565	3.0565	3.0565	3.0565	3.0565	3.0565

Table 24. Estimated population of larvae and adults of C. viridis in the field in 1971. Above each accumulated peak value, a line is drawn.

Date		Population						Accumulated population = y						y = log Y					
		I	II	III	IV	V	Adult	I+	II+	III+	IV+	V+	Adult	I+	II+	III+	IV+	V+	Adult
May	13	54,303						54,303											
	18	181,776	6,168					187,944	6,168										
	25	298,184	31,462					329,646	31,462										
June	2	308,733	89,168	6,927				404,228	96,095	6,927				5.6066					
	8	70,630	156,137	38,402				265,169	194,539	38,402				5.4235					
	16	18,413	109,208	123,104	8,447			259,172	240,759	131,551	8,447			5.4136	5.3816				
	22	13,849	90,733	133,144	16,168			253,894	240,045	149,312	16,168			5.4047	5.3803	5.1741			
	29	3,084	16,140	79,219	33,867	771		133,081	129,997	113,857	34,638	771		5.1241	5.1139	5.0564			
July	1		2,302	39,978	49,230	3,072		94,582	94,582	92,280	52,302	3,072		4.9758	4.9758	4.9651			
	8		1,536	3,078	49,955	49,230	1,531	105,330	105,330	103,794	100,716	50,761	1,531	5.0226	5.0226	5.0162	5.0031		
	15			771	4,615	76,192	8,442	90,020	90,020	90,020	89,249	84,634	8,442	4.9543	4.9543	4.9543	4.9506		
	21				771	33,068	33,056	66,895	66,895	66,895	66,895	66,124	33,056	4.8254	4.8254	4.8254	4.8254		
	27					30,744	63,885	94,629	94,629	94,629	94,629	94,629	63,885	4.9760	4.9760	4.9760	4.9760	4.9760	
August	4					5,386	79,214	84,600	84,600	84,600	84,600	84,600	79,214	4.9274	4.9274	4.9274	4.9274	4.9274	4.8988
	11					771	69,968	70,739	70,739	70,739	70,739	70,739	69,968	4.8497	4.8497	4.8497	4.8497	4.8497	4.8449
	18						56,886	56,886	56,886	56,886	56,886	56,886	56,886	4.7550	4.7550	4.7550	4.7550	4.7550	4.7550
	25						36,117	36,117	36,117	36,117	36,117	36,117	36,117	4.5577	4.5577	4.5577	4.5577	4.5577	4.5577
Sept.	1						21,514	21,514	21,514	21,514	21,514	21,514	21,514	4.3327	4.3327	4.3327	4.3327	4.3327	4.3327
	8						15,369	15,369	15,369	15,369	15,369	15,369	15,369	4.1866	4.1866	4.1866	4.1866	4.1866	4.1866
	15						17,705	17,705	17,705	17,705	17,705	17,705	17,705	4.2481	4.2481	4.2481	4.2481	4.2481	4.2481
	22						15,356	15,356	15,356	15,356	15,356	15,356	15,356	4.1863	4.1863	4.1863	4.1863	4.1863	4.1863
	29						10,771	10,771	10,771	10,771	10,771	10,771	10,771	4.0323	4.0323	4.0323	4.0323	4.0323	4.0323
Oct.	6						3,844	3,844	3,844	3,844	3,844	3,844	3,844	3.5847	3.5847	3.5847	3.5847	3.5847	3.5847
	12						1,536	1,536	1,536	1,536	1,536	1,536	1,536	3.1864	3.1864	3.1864	3.1864	3.1864	3.1864

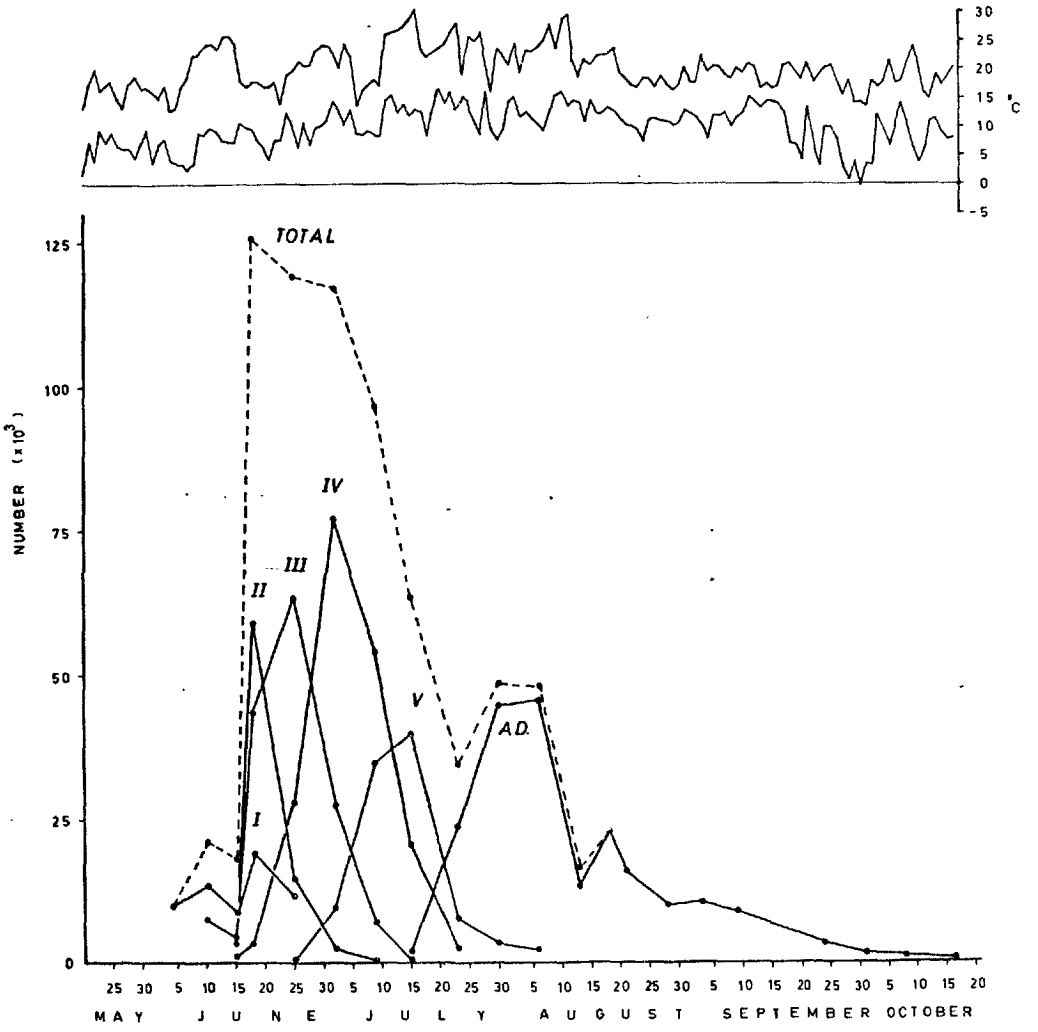


FIG. 25 Seasonal changes in the population of the immature stages and adult *C viridis* in 1969. Daily maximum and minimum temperatures are shown.

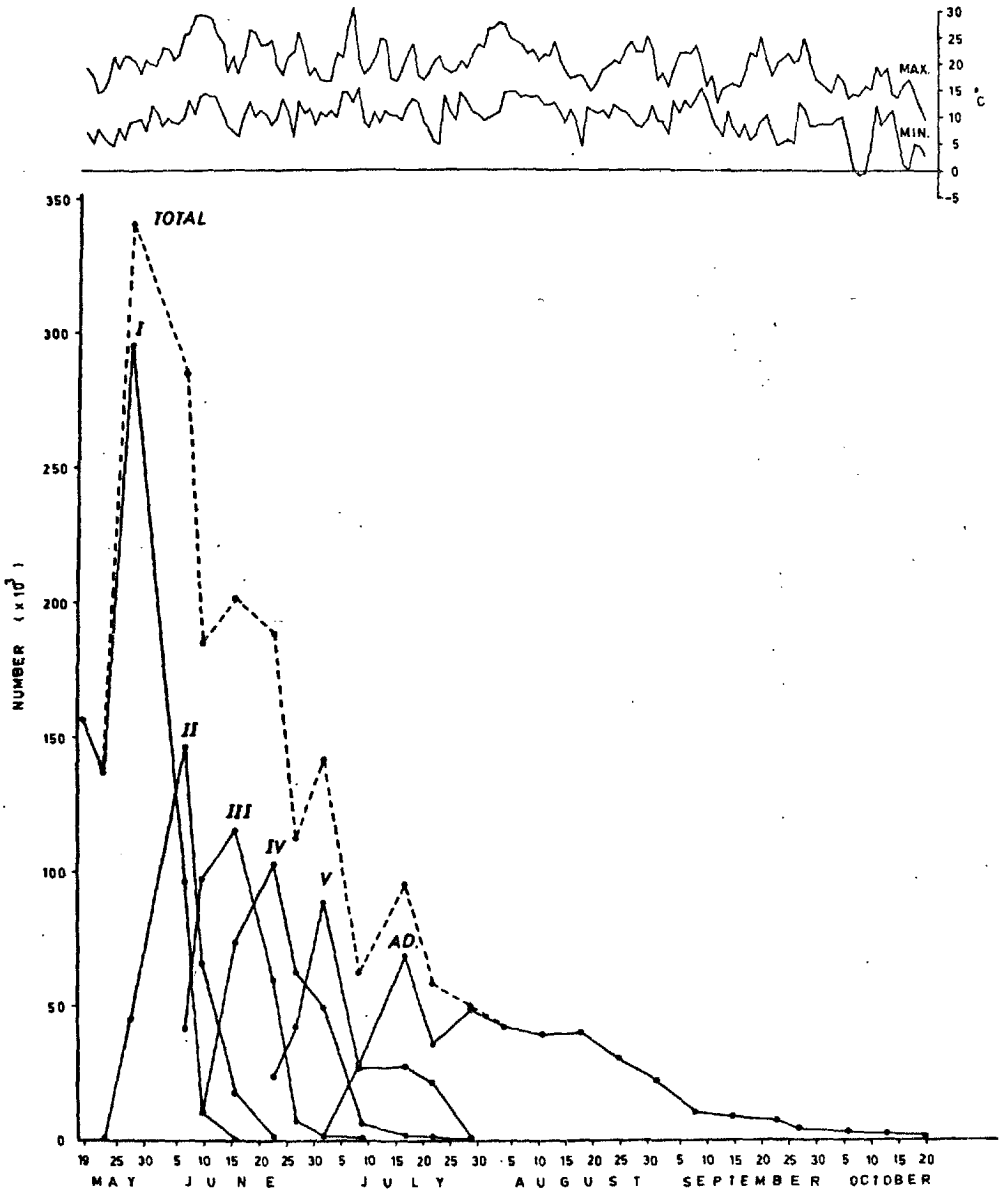


FIG. 26 Seasonal changes in the population of the immature stages and adult *C. viridis* in 1970. Daily maximum and minimum temperatures are shown.

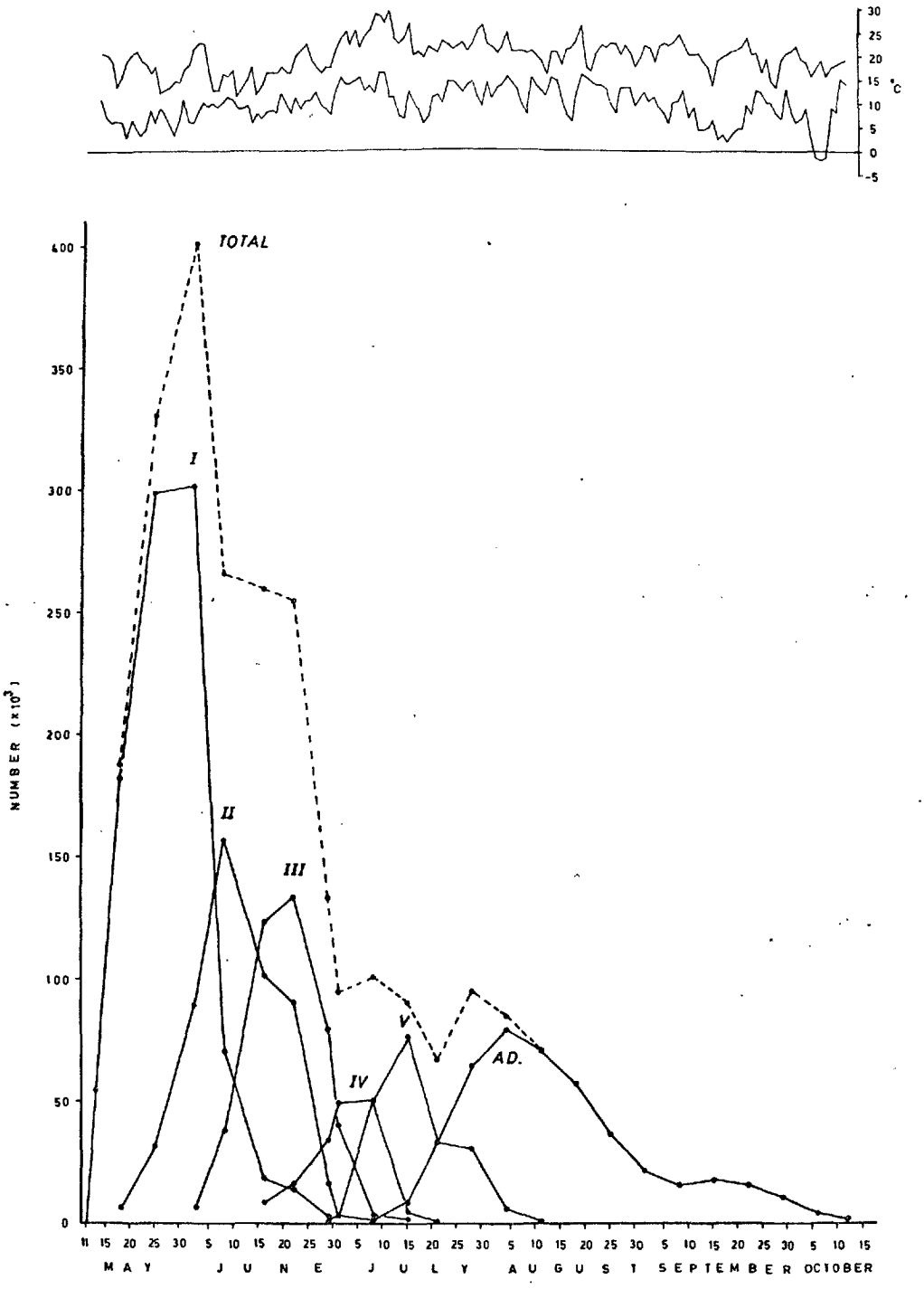


FIG. 27 Seasonal changes in the population of the immature stages and adult *C. viridis* in 1971. Daily maximum and minimum temperatures are shown.

The patterns of distribution of C. viridis in each instar for the years 1970 and 1971 were studied. The data used for analysis were collected during regular Dietrick sampling. In each instar, samples collected during their peak numbers were used for this analysis in order to ensure the true state of the distribution. The number of sampling units taken were thirty-three in 1970 and twenty-five in 1971, and the size of each unit was 0.09 square metres.

Analysis were carried out using Morisita's Index of dispersion Iδ (Morisita, 1959), comparison of the variance with the mean and the negative binominal distribution.

(i) Morisita's Index Iδ

Morisita's Index Iδ is calculated as

$$I\delta = n \frac{\Sigma x^2 - \Sigma x}{(\Sigma x)^2 - \Sigma x}$$

The index is independent of sample mean ($\bar{x}$), and total number in the sample (Σx), but is a strong function of the number of sampling units (n) at both ends of its range. Iδ equals one for random distribution, is greater than one for contagious distribution and is less than one for a regular distribution. Departures from randomness are judged significant ($P < 0.005$) when $I\delta\ (\Sigma x - 1) + n - \Sigma x$ is outside the appropriate 5% significance level of χ^2 for n - 1 degrees of freedom. Reyna-Robles (1969) in his

extensive study on insect dispersion found that Morisita's I_δ to be the most reliable index for most of the 'aggregate' range.

(ii) The ratio of variance upon mean. Comparison of variance with mean can be used to indicate the dispersed pattern of an insect in the field. If the ratio is equal to the mean, the population is dispersed randomly (Bliss and Owen, 1958; Bliss and Fisher, 1953). If the ratio is significantly above or below unity, this indicates aggregation or under dispersion (Hutchinson, 1962).

(ii) Negative binominal distribution. Many contagious populations can be adequately described with the negative binominal distribution. Briefly, the distribution is described by two parameters, the mean and the exponent k . The value of exponent k can vary from zero, when aggregation is maximal to infinity which will indicate random distribution. Methods of calculating k have been given by various authors e.g. Anscombe (1949 and 1950), Bliss and Fisher (1953) and Debauche (1962). In this work, the value of k was calculated by a computer with program written by Reyna-Robles (1969). Fisher's (1950) 'alternative' χ^2 was used to test the goodness of fit instead of the standard χ^2.

The results of the analysis are summarised and presented in Table 25 . A graph of sample mean and Morisita's Index (I_δ) is plotted against the instars (Fig 28),

Table 25. The values of k of negative binominal distribution; Morisita's Index (IS) and the ratio of variance on mean in the description of the distribution pattern of larvae to adult stage of C. viridis.

Stage	Year	k of negative binominal	χ^2	P	Morisita's Index (IS)	* χ	P	Variance / Mean
I	1970	0.4597	χ^2_{18} 13.7173	0.10>P>0.05	2.5576	817.0	0.001	25.54
	1971	0.3853	χ^2_{10} 16.6412	P = 0.10	4.5073	1392.5	0.001	58.14
II	1970	0.4503	χ^2_{13} 4.8978	0.98>P>0.95	3.2668	592.9	0.001	18.53
	1971	0.4965	χ^2_{11} 3.6050	P = 0.98	3.1258	589.5	0.001	24.56
III	1970	0.5025	χ^2_{10} 6.6879	0.80>P>0.70	3.3490	266.6	0.001	14.73
	1971	0.5912	χ^2_{12} 3.8062	0.99>P>0.98	2.8104	335.4	0.001	14.05
IV	1970	0.8762	χ^2_{10} 7.3969	0.70>P>0.50	2.4906	285.4	0.001	8.97
	1971	0.5787	χ^2_{6} 5.9660	0.50>P>0.30	2.0852	95.94	0.001	4.16
V	1970	0.5181	χ^2_{10} 2.3349	P>0.99	2.7655	293.3	0.001	9.17
	1971	0.7450	χ^2_{8} 4.5600	0.90>P>0.80	2.7000	190.6	0.001	7.94
Adult	1970	0.5311	χ^2_{7} 6.7347	0.50>P>0.30	3.4390	285.7	0.001	9.01
	1971	1.0901	χ^2_{7} 9.5802	0.30>P>0.20	2.0916	769.0	0.001	4.51

* The degree of freedom of χ^2 is 32 for 1970 and 24 for 1971.

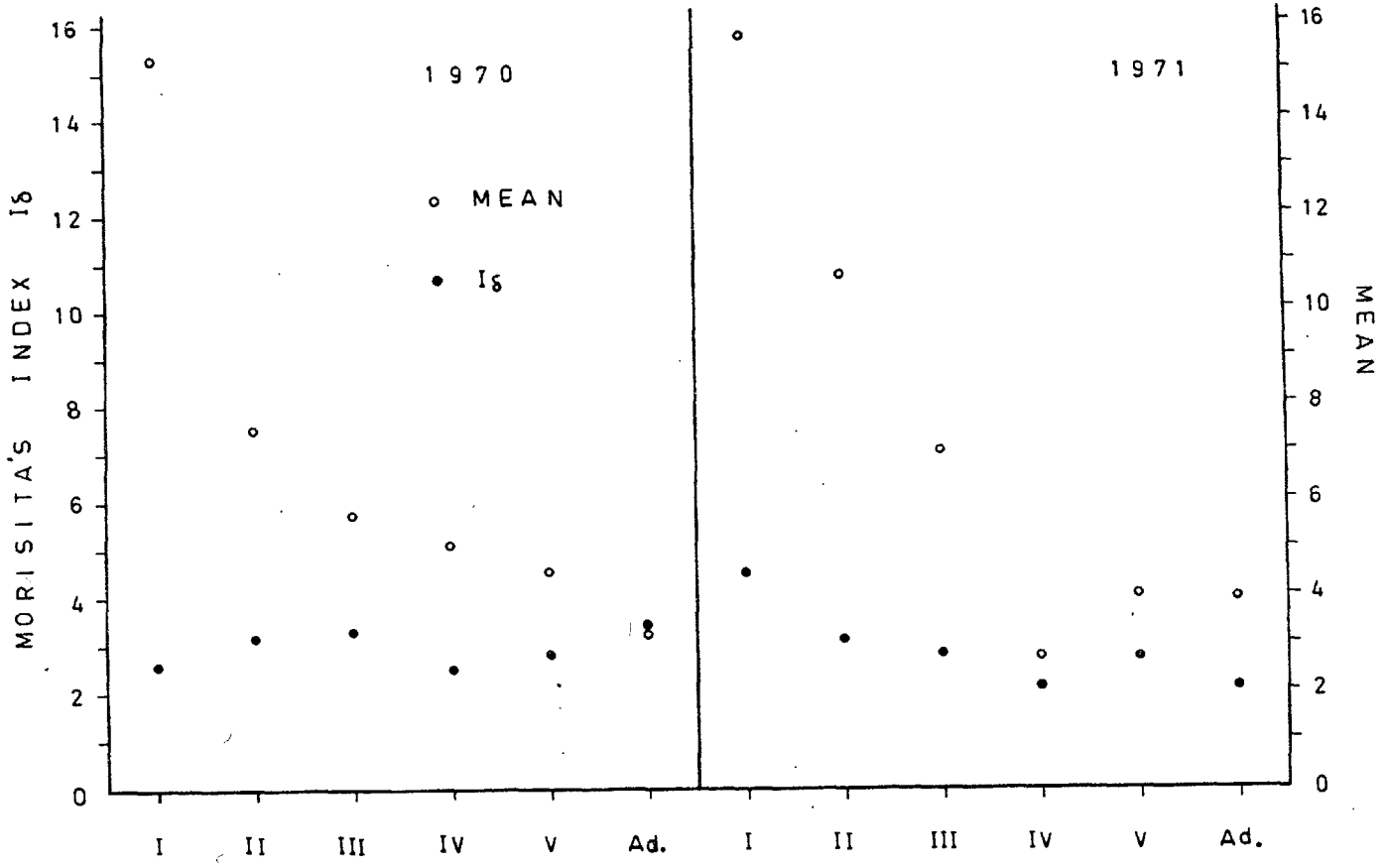


FIG. 28 Relation of Morisita's Index (Iδ) to sample mean for all stages of *C. viridis*.

which indicate clearly the independence of IS from the mean.

As shown in Table 25, the ratios of variance upon mean are all above one, and the value of IS fluctuates between 2.0916 and 4.5073, which indicates strong aggregation in all stages of C. viridis. The value of k of the negative binominal, are all very small and vary between 0.4503 to 0.8762 in 1970 and 0.3853 to 1.090. in 1971, which again indicates strong aggregation in C. viridis distribution. With the exception of first instars, the goodness of fit for the negative binominal distribution is very good. Reyna - Robles (1969) in his detailed studies of the models describing insect dispersal found that the negative binominal is usually considered 'robust', when small values of k are obtained though the fit of this distribution is generally poor. The poor fit in the distribution of the first instar is yet another instance.

The three tests agreed in that there is a tendency to aggregate in all the larvae and in the adult stages of C. viridis. Aggregation in the first instars may be explained by the fact that eggs are laid in clusters and on Juncus clumps, and in adult females by the virtue of their oviposition behaviour on Juncus stems. However no plausible explanation can be given to the aggregation in the other instars. Thus the tendency to aggregate in C. viridis may be a characteristic of its behaviour without the direct influence of environmental factors.

6. Estimation of recruits and mortality in the larval and adult stages

6.1 Methods of estimation of recruits entering a stage.

To estimate the mortality and the initial number of individuals entering successive stages in an insect population with stages overlapping has always proved to be difficult. There are at present various methods developed for this purpose. They are developed by Richards and Waloff (1954); Richards, Waloff and Spradberry (1960); Southwood and Jepson (1962); and Kiritani and Nakasuji (1967). All these methods assume that there is a constant steady mortality rate throughout the stages.

The method of Southwood and Jepson (1962) consists of plotting successive estimates on graph paper. The points are then joined up and the area under the line counted. This total is then divided by the mean developmental time under field conditions.

The method of Richards and Waloff (1954) can only be applied to populations in which successive stages show a definite peak. A regression line is then plotted on the fall off of numbers after the peak with time. The line is then extended back to the time t_o when the stage was first found, the corresponding value of the interception point of the regression line and y axis at t_o will give the estimate of number of recruits. The regression line has the form of $\log Y_t = \log P_o + t \log S$ where Y_t = population on day t, P_o is the peak population and S = the fraction

of the population which survive to the end of a unit time. In practice Y_t was taken as accumulated population. That is, Y_t is the total of that instar after the peak plus all individuals that have passed through that instar and are in subsequent ones. Dempster (1956) found that if Y_t was based on the number of that particular instar only, the estimates of the population were too high, the slope of the line being too steep because of the confusion of moulting with mortality. The use of accumulated totals avoids this.

Where the populations do not have a definite peak, and recruitment and mortality overlap widely the methods of Richards et al (1960) is more suitable. The total number of any stage taken in all the samples (N) will be given by

$$N = P_o \int_o^a S^t \, dt = P_o \left(\frac{S^a - 1}{\log_e S}\right)$$

where a = duration of instar, P_o = total number entering the stage, S = fraction of population survive per unit of time. Calculation is more conveniently carried out by substituting U for S^a, and the equation becomes

$$N = aP_o \frac{U - 1}{\log_e U} \quad \text{or} \quad \frac{N}{aP_o} = \frac{U - 1}{\log_e U}$$

A table for the value of $\frac{U - 1}{\log_e U}$ can be calculated by substituting the values U from 0.01 to 0.99. As the value of $\frac{N}{aP_o}$ is known the corresponding value of U can be read off the table. The mortality is 100 (1 - U) %.

In Kiritani and Nakasuji's method (1967), the survival rate of each developmental stage is calculated as $K^{\alpha i} = 1 - \frac{F\alpha i}{F}$ where $K^{\alpha i}$ is the survival rate at ith instar, $F\alpha i$ is the total number of ith instar taken in all the samples and F the total number taken of ith and subsequent instars. The initial number of (i + 1)th instar (N_{i+1}) is estimated by $N_{i+1} = N_i K^{\alpha i}$. In cases where there is differential mortality rate between larvae and adults, a further approximation of the survival rate is recommended to reduce error. The corrected survival rate is calculated with the formula

$$S'_{\alpha} = \frac{(1+K^{\alpha})\ (1-\frac{F_{\alpha}}{F})\alpha}{(L_{max} - \alpha)\ \frac{F_{\alpha}}{F}}$$

where S'_{α} is the revised survival rate of the larvae, and L_{max} is the maximum larvae plus adult duration. $\frac{F_{\alpha}}{F}$ being the mortality rate of larvae as obtained by the first calculation and K^{α} being the survival rate. α is the total larval duration. The value of S'_{α} being the new estimated total survival rate of the larvae, from which the daily survival rate of each instar is calculated according to its duration.

6.2 Estimates of larvae and adults.

Estimates of recruits of C. viridis entering into each stage is carried out with all the methods mentioned, except that of Southwood and Jepson (1962). As the latter method tends to underestimate the population, because

individuals that are destroyed, for example by predators, are present for less than the full developmental time (Southwood 1966). When using Richards and Waloff's regression method, the estimates are based on accumulated population. The larval durations for Richards et al and Kiritani and Nakasuji's methods are based on insects reared in the outdoor insectary in 1970. The maximum longevity of adults is taken as the period between the last appearance of 5th instar larvae to the last appearance of the adult which is eight-three days in 1970 and seventy-nine days in 1971.

The regression equation for each instar as calculated with Richards and Waloff's method for the three seasons are as in Table 26. Estimations of recruits entering the successive stages calculated with different methods are summarised in Table 27 . The estimate of instar I in all cases was derived from the direct egg count, which because of intensity of egg sampling is taken to be nearer the truth.

The method of Richards et al is the only one which is found to be applicable to the data of all the three seasons of study. The estimated recruits entering each stage obtained by this method agreed reasonably well with the estimates obtained by the method of Kiritani and Nakasuji, when the survival rate is not adjusted to take differential mortality.

Kiritani and Nakasiji's method cannot be applied to data of 1969, because of insufficient sampling carried

out during that year. The method works well for the years of 1970 and 1971, and the results approximate to those obtained with the Richards et al's method. When the survival rate is adjusted for possible differential mortality rate, the recruits for the fourth, fifth and adult stages tend to be underestimated.

With Richards and Waloff's regression method, the estimated recruits for second and third instars agree well with those obtained with the method of Richards et al and the uncorrected form of Kiritani and Nakasuji. However, anomalous results are obtained for the fourth and fifth instars in 1969, fourth instars in 1970 and fifth and adult in 1971, as the recruits estimated in these stages are higher than their respective preceeding stage. The cause of this anomaly is not known. It may probably be due to the more gradual decrease in numbers throughout the adult stage, and as the method is based on a regression line after a peak, the height of the peak and the rate of decrease after that would obviously affect the gradient of the slope and thus the number of recruits. Comparing the three methods used, Kiritani and Nakasuji's method is the easiest to use mathematically and it is also independent of the duration of the instars. But to be applicable, regular sampling at short intervals is required. If the survival rate is to be adjusted for differential mortality, the method suffer from the same deficiency as that of Richards et al, in that

Table 26. The regression equation which gives the number of recruits entering the various stages with Richards and Waloff's method.

Equation of log Y = bx + a

Year	I	II	III	IV	V	Adult
1969	-0.0181x+5.8323	-0.0196x+5.5842	-0.0196x+5.4908	-0.0199x+5.5133	-0.0277x+5.5501	-0.0231x+5.1186
1970	-0.0158x+5.8015	-0.0165x=5.7911	-0.0165x+5.5455	-0.0175x+5.5875	-0.0188x+5.4794	-0.0176x+5.2043
1971	-0.0145x+5.9315	-0.0148x+5.8871	-0.0142x+5.6126	-0.0164x+5.6035	-0.0207x+5.7332	-0.0217x+5.6260

Table 27. Estimated number of recruits entering each stage calculated with Richards and Waloff's regression method; the method of Richards, Waloff and Spradbery and the method of Kiritani and Nakasuji. The number of first instars are estimated from direct egg count.

Year	I	Method	II	III	IV	V	Adult
1969	1950898	Richards and Waloff	383990	309610	357520	354890	131400
		Richards et al	419443	163960	106213	91715	60668
		Kiritani and Nakasuji	Not applicable because of insufficient sampling.				
1970	1770646	Richards and Waloff	618160	351150	386810	301580	160070
		Richards et al	846723	396605	312921	202710	128437
		Kiritani and Nakasuji	519330	439657	267294	178108	111863
		Kiritani and Nakasuji after correction	760138	352400	151285	55688	16278
1971	1878334	Richards and Waloff	771080	409830	401360	541000	422670
		Richards et al	1062386	592280	362356	169727	112309
		Kiritani and Nakasuji	575522	407808	266095	211679	145211
		Kiritani and Nakasuji after correction	836114	400331	178067	68360	21040

duration of larval instars has to be considered, it has also an added disadvantage in that L_{max} also include the maximum possible longevity of adult, which is another potential source of error. In calculating the recruits of C. viridis, under estimation for the last three stages is probably due to the lack of accuracy in the maximum longevity of adults rather than the absence of differential mortality rate. For the data of C. viridis, Richards el al's method appears to be most suitable, as P_o - the number of first instar can be determined accurately by egg sampling, and the duration of larvae can be established reasonably accurately by laboratory rearing.

The availability of all these methods for estimation of recruits into the population studied is of obvious advantage. The applicability of any methods clearly depends on the nature of the population studied. In the case of C. viridis population, the method of Kiritani and Nakasuji and the method of Richards et al, are applicable on the ground of the close approximation of the results and their consistency. In the absence of an alternative check, it is impossible to decide which method is more accurate than the other.

6.3 Population budget of C. viridis

Apart from the egg stage and the first instar, the budget is based on recruits estimated by the methods of Richards et al for the population of 1969, and for the population of 1970 and 1971 by both Richards et al and Kintani and Nakasuji. Estimates obtained with Richards and Waloff's

regression method are not used because of the inconsistency of the results. The estimates obtained by Kiritani and Nakasuji's method after adjustment for differential survival rate is considered inaccurate, as the number of recruits obtained for the last three stages are consistently lower than field sample estimates. The budgets are presented in Table 28 ,29 and 30.

In 1969 (Table28), the mortality of eggs is 61.79% and that of first instar larvae is 29.99%. Together these two stages account for 91.98% of the overall mortality. Mortality in the second instar is the next highest at 5.0%. From third to fifth instars the mortality remains low at 1.97% of the total. The percentage of survival in terms of the original recruits i.e. egg is 1.25%. In 1970 (Table29), the general trend is similar to that of 1969, with heaviest mortality occuring in the egg stage (79.94%); this is followed by the first and second instars. The mortality arrived at by the method of Richards et al is 10.46% and 5.10% for the first and second instar respectively, and by the method of Kiritani and Nakasuji the rate is 14.18 and 0.90 respectively. Comparing stage by stage, there is considerable discrepancy between the estimates by different methods. However, if first and second instars are to be grouped together, the mortality becomes 15.56% for Richards et al's method and 15.08 for the method of Kiritani and Nakasuji. Together the first three stages i.e. eggs, first

and second instars account for 95% of the total mortality. From third to fifth instars, the mortality remains constantly low. The percentage of survival estimated by the method of Richards et al is 2.29% and by Kiritani and Nakosuji 2.11%.

The pattern for 1971 (Table30) is similar to the previous two years. Egg mortality being 81.73%. Mortality as estimated with the method of Richards et al for first and second instars combined is 12.51% and that by Kiritani and Nakasuji 14.30%. The mortality for third and fifth instars combined and the overal survival rate as estimated by the method of Richards et al is 4.67% and 1.09% respectively, while estimates obtained with Kiritani and Nakasuji's method is 2.48% and 1.41% respectively.

From the point of view of method, although estimates obtained with the two methods agreed in general, the detailed mortality from stage to stage tends to differ occasionally. In particular, the method of Kiritani and Nakasuji consistently give a higher mortality rate in the first instars and a lower rate in the second when compared with that derived from the method of Richards et al. As shown in previous paragraphs, however, the estimates agreed when the mortality of the two stages are combined. Together, the two methods appear to present a reasonably clear picture of the behaviour of the population of C. viridis. There is no doubt that the factors controlling the population of C. viridis rest in the egg stage and possibly the first two larval instars. The general

Table 28. Estimates of recruits entering a stage in 1969 and mortality based on calculation with method developed by Richards, Waloff and Spradbery (1960)

Stage	Number entering stage	Number died within stage	Survival rate	% died within stage	% mortality of recruit (egg no.)
Egg	5105726	3154828	0.3821	61.79	61.79
I	1950898	1531455	0.2150	78.50	29.99
II	419443	255473	0.3909	60.91	5.00
III	163960	157747	0.6478	35.22	1.08
IV	106213	14498	0.8635	13.65	0.28
V	91715	31037	0.4882	51.18	0.61
Adult	60668				

Accumulated mortality % of recruits (egg number) = 98.75

Table 29. Estimates of recruits entering a stage and mortality based on calculation with methods of Richards, Waloff and Spradbery (1960) and Kiritani and Nakasuji (1967) in 1970.

Stage	Number entering stage		Number died within stage		Survival rate		% died within stage		% mortality of recruit (egg No.)	
	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji
Egg	8826752	8826752	7056106	7056106	0.2006	0.2006	79.94	79.94	79.94	79.94
I	1770646	1770646	923923	1251316	0.4782	0.2933	52.18	70.67	10.46	14.18
II	846723	519330	450118	79673	0.4684	0.8466	53.16	15.34	5.10	0.90
III	396605	439657	83684	172363	0.7890	0.6080	21.10	39.92	0.95	0.95
IV	312921	267294	110211	89189	0.6478	0.6682	35.22	33.18	1.25	1.01
V	202710	178108	74273	66245	0.6336	0.6263	36.64	37.37	0.84	0.75
Adult	128437	111863								
							Accumulated mortality % of recruit(egg no.)		97.71	97.99

Table 30. Estimates of recruits entering a stage and mortality based on calculation with methods of Richards, Waloff and Spradbery (1960) and Kiritani and Nakasuji (1967) in 1971.

Stage	Number entering stage		Number died within stage		Survival rate		% died within stage		% mortality of recruit (egg no.)	
	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji	Richards et al	Kiritani & Nakasuji
Egg	10281028	10281028	8406696	8406696	0.1818	0.1818	81.72	81.72	81.73	81.73
I	1878334	1878334	815948	1302812	0.5656	0.3063	43.44	69.37	7.94	12.67
II	1062386	575522	470106	167714	0.5575	0.7086	44.25	29.14	4.57	1.63
III	592280	407808	229924	141713	0.6118	0.6525	38.82	36.75	2.24	1.30
IV	362356	266095	192629	54416	0.4684	0.7955	53.18	20.45	1.87	0.53
V	169727	211679	57418	66478	0.6617	0.6860	33.83	31.40	0.56	0.65
Adult	112309	145211								
							Accumulated mortality % of recruits (egg No.)		98.91	98.59

pattern of decline in the population remains similar for the three generations studied. The number of recruits entering adult stage is smaller in 1969, which may be explained by the correspondingly smaller egg number for the 1968-1969 season. But inspite of an increase in egg number in the 1970-1971 seasons the adult recruits for 1970 and 1971 remains rather constant. This probably suggests that the numbers attained in these two years may be the optimum number that is possible in this habitat.

7. Mortality factors

7.1 Mortality in the egg stage

Factors causing egg mortality can be classified into five groups as follows:-

(1) Fungal infection.

(2) Egg parasite.

(3) Predation.

(4) Egg sterility.

(5) Other factors.

In numerical terms, the heaviest mortality is caused by fungal infection, followed by egg parasite and miscellaneous mortalities of minor importance together with those whose exact causal agents cannot be pinpointed. Egg predation and sterility remain constantly at a low level. Apart from sterility which will be the first to

cause mortality, the rest of the factors appears to act simultaneously. The percentage of mortality caused by each factor in the three seasons are summarised in Table 31 a, b, and c. The relative importance of each factor will be discussed later.

7.1a Fungal infection

The fungus infecting C. viridis eggs was identified by Dr. B.J. Wheeler and the Commonwealth Institute of Mycology as Tritirachium sp. (Moniliaceae). Apart from Tritirachium sp. egg mortality could also be caused indirectly by other fungi that attack Juncus stems. Eggs attacked by Tritirachium sp. became whitish or greyish white in colour. In an advanced stage of infection, white mycelium can be seen covering up the whole egg mass.

Tritirachium spp. are described in literature as similar in appearance to Beauvaria sp. (Limber,1940, Langeron 1947, MacLeod 1954). A species Tritrachium brumpti Langeron was reported to have been obtained from a case of Keratoconjunctivites in a girl (Langeron 1947). MacLeod (1954) believed that in some Tritirachium spp. there were a varying degree of pathenogenicity, although for the most part these fungi appeared to be saprophytic in nature. Maran (1948) conducted pathogenicity tests with Tritirachium brumpti against several species of

Table 31. Mortality of C. viridis eggs for the season of 1968-69, 1969-70 and 1970-71.

a.

1969	Item	Fungus	Parasite	Predators	Sterility	Other factors	Survivors	Total eggs
May	No.of eggs	1150	276	32	46	364	1155	3023
	percent of total	38.04	9.13	1.06	1.52	12.04	38.21	100

b.

1970	Item	Fungus	Parasite	Predators	Sterility	Other factors	Survivors	Total eggs
March	No.of eggs	2611	629	106	41	456	2672	6515
	percent of total	40.08	9.65	1.63	0.63	7.00	41.01	100
May	No.of eggs	2978	263	23	31	156	866	4317
	percent of total	68.98	6.09	0.50	0.70	3.61	20.12	100

c.

1971	Item	Fungus	Parasite	Predators	Sterility	Other factors	Survivors	Total eggs
Feb.	No.of eggs	3607	318	143	47	359	3212	7686
	percent of total	46.93	4.14	1.86	0.61	4.67	41.79	100
March	No.of eggs	2478	190	111	40	156	2556	5531
	percent of total	44.80	3.44	2.00	0.72	2.82	46.21	100
May	No.of eggs	2795	195	125	21	256	758	4150
	percent of total	67.35	4.70	3.01	0.51	6.16	18.28	100

insects and mites. He found that Tenebrio molitor L. Sitophilus (Calandra) granaria (L.) and Ephestia kühniella Zell. were susceptible to infection, while Phagiodera versicolora Laich (Chrysomelidae: Coleoptera), Melasoma aenea L. (Chrysomelidae .), Forficula auricularia L. (Dermaptera) and the flour or meal mite Tyroglyphus (Aleurobrius) farinae DeG. appeared to be unaffected.

The total mortality caused by fungi is estimated as 38.04% in 1969. In 1970 a comparison was made of the infection rate of eggs collected in March and those collected in May when the eggs were about to hatch. It was found that infection was around 40.08% in March but increased to 68.98% in May. In 1971, samples were collected in February, March and May. The result showed that the level of infection remained similar for February and March 46.33% and 44.8% respectively, but increased to 67.35% in May. This increase is thought to have been caused by the gradual spreading of infection from one or more infected eggs to entire batches, and also to the increases in activity of the fungi with the rise of air temperature in April and May. Whalley (1958) working in North Wales also found that fungi were the major cause of mortality, but the level of infestation that he recorded was lower i.e. 31.4%.

7.1b. Egg Parasites

Anagrus atomus was the only species of egg parasite found in eggs of C. viridis at Silwood Park.

Table 32. Relationship between height of egg site and the incidence of parasitism by Anagrus atomus.

Stem height in cm	Number of eggs	Number of eggs with parasites	Percentage of eggs parasitised
1-5	1308	0	0
6-10	3102	32	1.06
11-15	1483	57	3.84
16-20	846	55	6.50
21-25	351	80	22.79
26-30	203	36	15.65
31-35	86	5	4.72
36-40	29	2	6.82
41-45	30	1	3.33

The degree of parasitism amounts to approximately 9.13% in 1970, 6.09 to 9.65% in 1970 and 3.44 to 4.70% in 1971.

The relationship between the degree of parasitism and stem height was studied. In 1971, 1,428 Juncus stems with 7,438 eggs were examined. The results as presented in Table 32 showed that C. viridis eggs laid at the height between 21 to 30 cm were most liable to be attacked by A. atomus, although the majority of C. viridis eggs were laid below 15 cm. No eggs laid below 5 cm had been attacked by A. atomus. This suggests that A. atomus tend to concentrate most of its searching activity on the upper

part of the Juncus stem. The low level of parasitism of the eggs laid above 31 cm is probably due to scarcity of host's eggs (see Table 32).

7.1c Egg Predation

This contributed only a very small percentage to the total egg mortality. Two species of Mirids known to be predators of Homoptera were present, i.e. Cytorhinus caricis (Fallén) and Tytthus pygmaeus (Zetterstedt). Larvae of Tetrastichus sp. (Hymenoptera) are also commonly found in Juncus stems. In the eggs destroyed by Mirids the chorion remains intact, while those attacked by Tetrastichus sp. the chorion is generally mutilated. The low level of egg predation by Mirids could be explained by the short period when C. viridis eggs were available to them. The adults of both of these non-specific predators occured from July to October, but the eggs of C. viridis were not laid until towards the end of August. The larvae of Tetrastichus sp. in the course of tunneling through Juncus stem would attack any eggs that were on its path. But it does not seem to be capable of actively searching for eggs. The percentage of egg mortality caused by predation is estimated as 1.06, 0.5 to 1.63 and 1.86 to 3.01 for the season of 1968-69, 1969-70 and 1970-71.

7.1d. Sterility of eggs

The number of sterile eggs laid by C. viridis for the three seasons studied were consistently low. These

eggs can be distinguished by absence of yolk. The percentage of sterile eggs was estimated as 1.52% in 1968-69; 0.63 to 0.70 in 1969-70; and 0.51 to 0.72 in 1970-71.

7.1e Mortality caused by other factors

This category includes eggs destroyed by the ovipositing activities of other Homoptera; those that fail to hatch and egg mortality the causal agents of which cannot be identified.

Two species of Delphacids, Conomelus anceps and Delphacodes fairmairei (Perris) also laid their eggs inside the Juncus stems. Occasionally, these two species of Delphacids were found to oviposit their eggs into a batch of C. viridis eggs and to puncture it. The number of eggs destroyed in this way is very small. None were recorded for the season of 1968-69, while the percentage was 0.30 for 1969-70 and 0.27 for 1970-71.

Failure to hatch was observed in the season of 1970-71 by sampling eggs once a week during hatching period in May. This was found to be about 2.11% of the total eggs laid. The embryo was well developed, but for some unknown reason it failed to emerge i.e. to break through the embryonic sheath that envelops it; this resulted in death. No figures are available for the season of 1968-69 and 1969-70.

In some eggs the exact cause of mortality could not be identified; death under this category amounts to 12.04%

of the total eggs in 1968-69; 3.61% in 1969-70 and 6.16% in 1970-71.

7.1f. Relative importance of various mortality factors

The term key factor was introduced by Morris (1959) for mortality factors which cause a variable mortality and appear to be largely responsible for the observed changes in population density in successive generations. Of the different methods available, the one developed by Varley and Gradwell (1960, 1963a and b, 1965, and Varley 1963), is easier to use than either Morris' key factor (1959, 1963) or Watts' survival analysis (1961, 1963,1964). In a comparison between the methods of Morris and Varley and Gradwell carried out by Luck (1971), he found that Varley and Gradwell's method was superior in detecting density relationship of a mortality factor.

The relative importance of each mortality factor in the egg of C. viridis is analysed with the method of Varley and Gradwell. The actual working of the method was described in the original papers of the authors, and clearly summarised by Southwood (1966).

Briefly, it involved the transforming into logarithms the original egg population and the number of eggs that experienced different mortalities. The value of log. mortality is then substracted from the value of log. population successively to give the various k values. Preferably, the mortality factors should be arranged according to the sequences

of their action on the eggs, since a different order of arrangement would give a different value to each k . In C. viridis eggs, sterility is the only factor which can be recognised as the first to act on the eggs, the rest of the factors appear to act simultaneously. The order is thus arranged arbitrarily, in the following sequence:- Sterility, effects of fungus, effects of parasite, of predators and of other factors.

The total mortality K is equal to the sum of k's obtained for each of the mortality factors. The values of K and of k's for the three seasons are presented graphically in Fig. 29 and also in Table 33 a, b, and c.

In Fig. 29, K_1 is the total mortality of eggs, k_{11} represents mortality due to sterility, k_{12} mortality due to fungus, k_{13} mortality due to egg parasite, k_{14} mortality due to predators and k_{15} due to other mortality factors. By means of visual correlation it is clear that k_{12} i.e. mortality due to fungus, is the key factor of egg mortality, i.e. it produces the greatest effect on egg numbers.

As only three years of data were available, it was not possible to carry out density dependence analysis as suggested by Varley and Gradwell (1963a). Instead, the densities of the egg populations for the three years were plotted against the estimated numbers of eggs that died from various causes. These graphs are given in Fig. 30. A straight line relationship was obtained when the initial

density was plotted against numbers that died of fungus. Egg sterility appears to be constant inspite of variations in egg density (see Fig. 30). With regards to other mortalities, no definite conclusion can be arrived from the present data.

7.2 Mortality in the larvae and adults

7.2a Parasitism

Homoptera are commonly parasitised by internal parasites such as Strepsiptera, Pipunculidae (Diptera) and Dryinidae (Hymenoptera). However, C. viridis in Southern England, with the exception of a single instance when a Dryinid sac was found on a first instar larva, virtually has no internal parasites on larvae and adults. Externally, two species of mites are commonly found attached to various parts of the body of both larvae and adults. These mites were identified by Dr. D. Macfarlane of the Commonwealth Institute of Entomology as Charletonia singularis (Ouds). (Trombidiidae) and Leptus ignotus (Ouds.) (Erythracidae). The sites where the mites are attached to the host appear to be random; they were found on the vertex, on the less sclerotised regions of the meso-and meta-thorax, legs and on the intersegmental membranes of the abdomen. The number of mites per host varied from one to four. The family Trombidiidae consists of ectoparasitic species, parasitic only during the larval stages. The species C. singularis has also been recorded on the Delphacid, Stenocranus minutus

Table 33. The values of k's in the egg stage of C. viridis in 1968-69, 1969-70 and 1970-71.

a. 1968-69

Mortality factor	Number died	Number surviving	Log number surviving	k
-	-	5105726	6.7081	-
Sterility	77607	5028119	6.7014	0.0067 k_{11}
fungus	1942218	3085901	6.4894	0.2120 k_{12}
Parasite	466153	2619748	6.4183	0.0711 K_{13}
Predators	54121	2565627	6.4092	0.0091 k_{14}
Other factors	614729	1950898	6.2902	0.1190 k_{15}

K_1 total = 0.4179

b. 1969-70

Mortality factor	Number died	Number surviving	Log number surviving	k
-	-	8826752	6.9458	-
Sterility	61787	8763965	6.9428	0.0030 k_{11}
fungus	6088693	2676272	6.4275	0.5153 k_{12}
Parasite	537549	2138723	6.3302	0.0973 k_{13}
Predator	44133	2095590	6.3211	0.0091 k_{14}
Other factors	318646	1775944	6.2494	0.0717 k_{15}

K_1 total = 0.6964

c. 1970-71

Mortality factor	Number died	Number surviving	log number surviving	k
-	-	10281028	7.0120	-
Sterility	52433	10228595	7.0098	0.0022 k_{11}
Fungus	6924272	3304323	6.5191	0.4907 k_{12}
Parasite	483208	2821115	6.4504	0.0687 k_{13}
Predator	309459	2511656	6.4000	0.0504 k_{14}
Other factors	633311	1878334	6.2738	0.1262 k_{15}

K_1 total = 0.7382

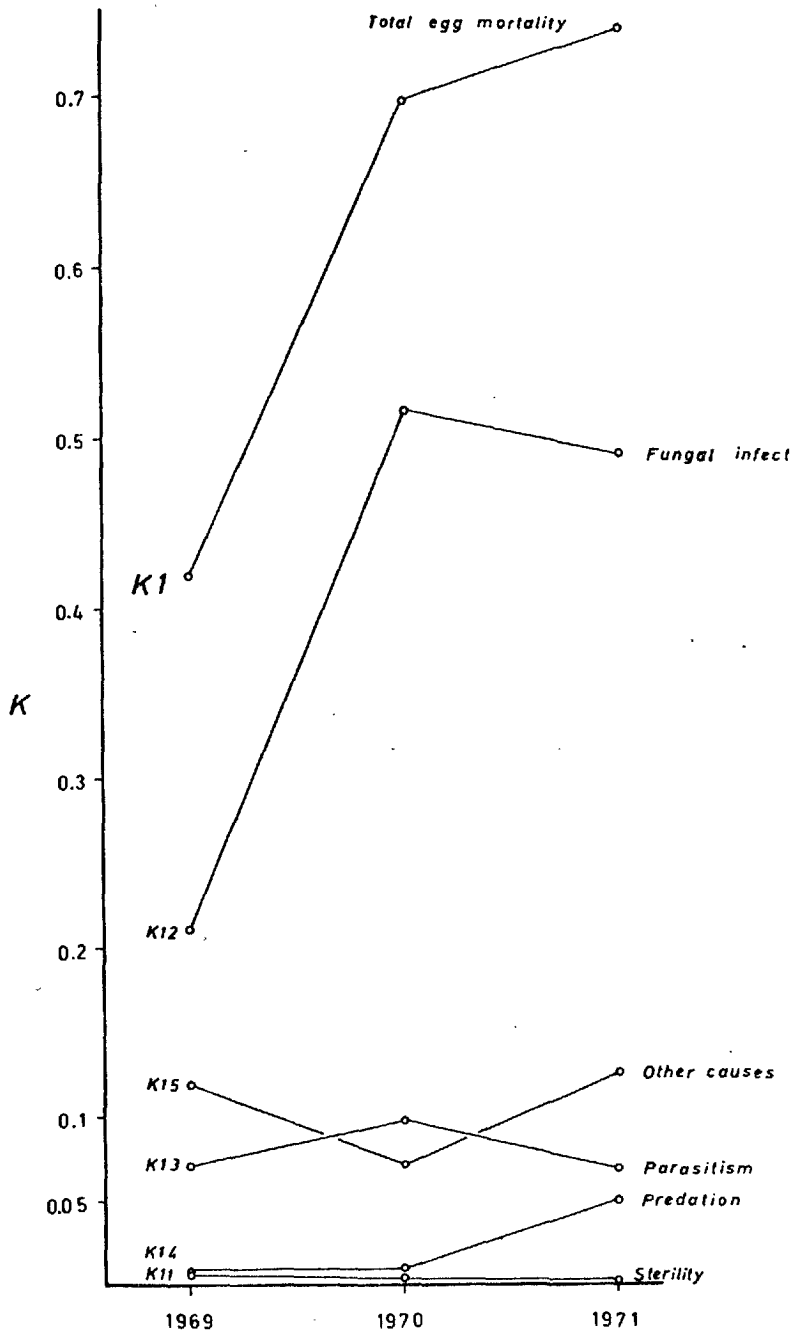


FIG. 29 Graphical key factor analysis of the various mortality factors in the eggs of C. viridis.

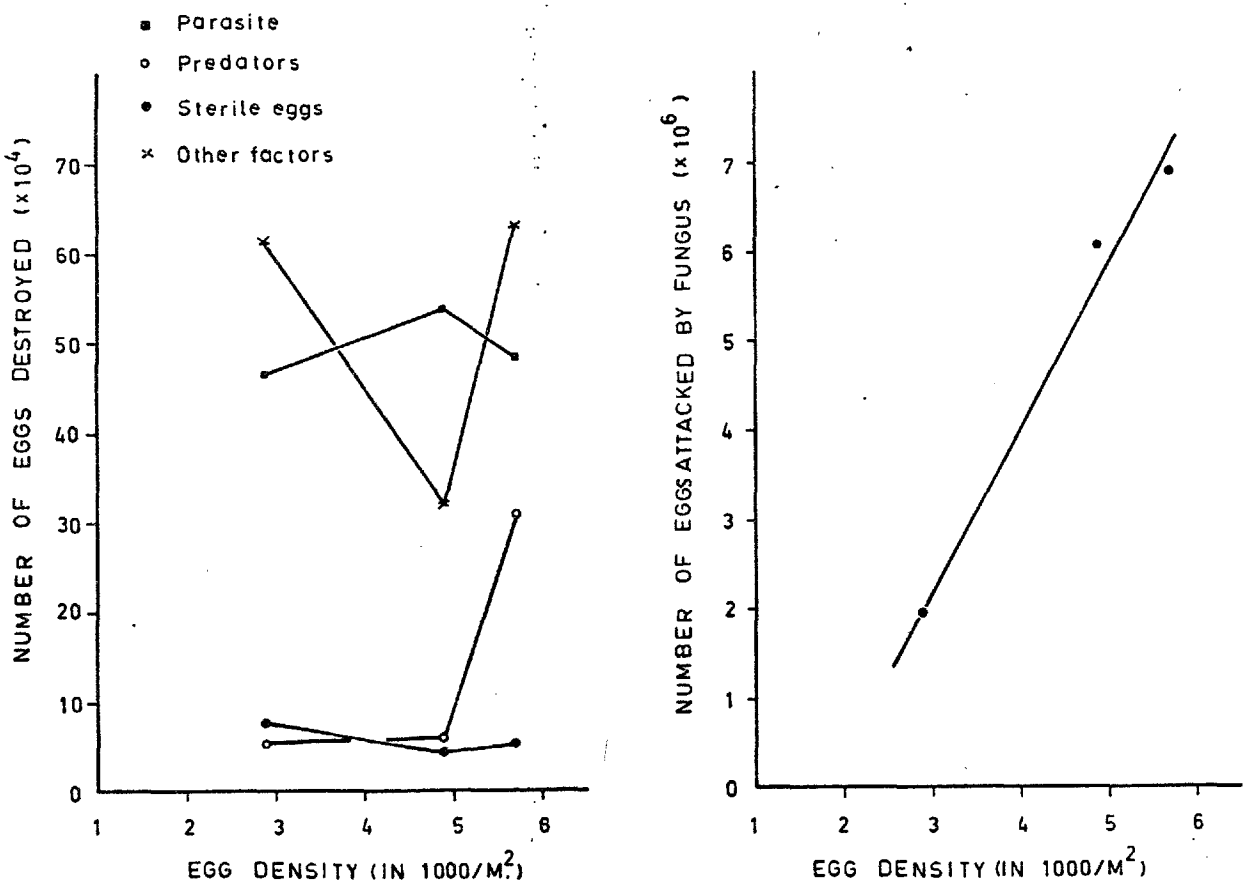


FIG. 30 Relationship between the density of *C. viridis* egg and the different mortality factors.

(Yin Yin May 1970). In S. minutus, moderate infections of mites do not seem to have any detrimental effect on the growth and reproduction of the host. However, heavy infestations could lead to some damage or even death. Laboratory rearing of larvae and adults of C. viridis infected with mites showed no deleterious effect on the growth and survival of the hosts. In the larval stages, the mites were always dislodged when the host moulted. When the host was reared singly, after having been dislodged, the mite did not seem capable of finding the host again.

Leptus ignotus has been collected from a wide range of insects including earwigs, grasshoppers, Membracids, Cercopids, Aphids, Tabanids, elaterid beetles, Lagria sp. and Phytodecta sp. (Macfarlane personal communication). Parasitism thus appears to play little or no part at all in the mortality of the larvae and adults of C. viridis.

7.2b. Fungal infection (Plate 4.)

A species of fungus was occasionally found to attack adult C. viridis, but infection of the larval stages has not been found. The fungus was identified by Dr. M. Madlin of Bristol University as Entomophthora sp. Species belong to this genus, E. aphrophorae had previously been recorded on other Cicadellidae, Euscelis grisescens (Zett.) by Leatherdale (1958). In the three seasons of this study, individuals infected by the fungus were never encountered in any appreciable numbers, and fungal infection did not

contribute appreciably to the mortality of C. viridis. Although it is probable that under favourable weather conditions increased mortality due to this cause may occur.

7.2c Predation

Predation probably accounts for the bulk of the mortality in the larval and adult stages of C. viridis. Present in the study site are large numbers of potential predators which include various species of harvestman Opiliones, Spiders, Miridae, Nabidae, Carabid beetles, Cantharid beetles and small mammals. All these predators appear to be non-specific in the choice of their prey and would feed on other Homoptera, as well as on other insects and on spiders. It is therefore difficult to obtain an estimate of the contribution made by each of these predator species to the mortality of C. viridis. An attempt was made to identify the main predators of C. viridis and feeding tests were carried out in the laboratory. Serological technique i.e. the precipitin tests on predators collected in the field were also made.

(i) Laboratory Feeding tests

The main object was to find out some of the potential predators of C. viridis. No measurement was taken of the weight of the predators and the weight of the prey consumed. The tests with invertebrate predators was carried out in a circular transparent plastic box 10.5 cm in diameter and 40 cm high. The lid was perforated

for ventilation, and the atmosphere inside the box kept moist by lining the bottom of the container with moistened filter paper. One predator and up to four C. viridis were placed inside the box. Fresh Holcus plants were also placed inside the box for C. viridis to feed on. Altogether 21 species of potential predators, comprising insects, spiders, harvestman and small mammals were used in each experiment. Ten replicates were set up except with the small mammals, when only one bank vole (Clethrionomys glareolus (Schr.) and one common shrew Sorex araneus (L.) were tested. The predators so tested were :-

Insecta

Hemiptera

Nabidae

Dolichonabis limbatus (Dahlbon)

Nabis rugosus (L.)

N. flavomarginatus Scholtz

Stalia major (Costa)

Miridae

Tytthus pygmaeus (Zetterstedt)

Cyrtorhinus caricis (Fallén)

Coleoptera

Carabidae

Lestus terminatus (Hellwig)

L. ferruginus (L.)

Cantharidae

Rhagonycha fulva (Scop.)

Arachnida

Araneae

Thomisidae

Xysticus cristatus (Clerck)

Clubionidae

Clubiona reclusa O.P. Cambridge

C. subtilis L. Koch

Theridiidae

Theridion ovatum (Clerck)

T. bimaculatum (L.)

Linyphiidae

Linyphia clathrata Sunderall

L. triangularis (Clerck)

Lycosidae

Lycosa spp.

Opiliones

Phalangidae

Phalangium opilio L.

Oligolophus agrestis (Meade)

Mammalia

Soricidae

Sorex araneus (L.)

Cricetidae

Clethrionomys glareolus (Schr.)

No feeding was observed by Tytthus pygmaeus, Cyrtorhinus caricis, Lestus terminatus, L. ferrugineus, Lycosa spp. and Sorex araneus. Rhagonycha fulva were seen feeding on C. viridis only once, while Phalangium Opilio and Oligolophus agrestis would feed on C. viridis reluctantly and only when starved. The rest of the predators listed took C. viridis readily. The bank vole although it would take C. viridis readily when fed by hand, did not appear capable of catching the prey on its own.

(ii) The Precipitin test

The technique is based on the interaction between the specific proteins of the prey with the serum of a mammal sensitised with the proteins. The technique has been used extensively for the detection of predator/prey relation (e.g. Leone 1947; Dempster, Richards and Waloff 1959, Dempster 1960, Loughton and West 1962, Loughton et al 1963, Rothschild 1966, 1970 and 1971). It is essentially a qualitative method, although it is possible to give it a quantitative interpretation (Dempster 1960).

The method used here is essentially the same as that used by Dempster (1960), with some slight modification. The antigen is prepared by crushing 5 g of dry weight of C. viridis into fine powder with a pestle and mortar. One hundred ml of distilled water is then added to the powder and the mixture is kept overnight in a refrigerator. This mixture is constantly agitated with a mechanical stirrer.

The solution is then centrifuged and the supernatant fluid collected. This is then transferred to 10 ml sterilised ampoules each ampoule containing an equivalent of 0.25 gm of the original insect material, and the liquid is then removed by freeze drying. The remaining solid is the antigen used for injection into the rabbit. The antigen is stored for future use by sealing the ampoule in air-free condition. The antigen is reconstituted with distilled water and added with Freund's Bacto-adjuvant to form an emulsion, it is then injected into the lymph nodes of a rabbit. Injection into the lymph nodes has an advantage over intra-muscular injection as used by Dempster (1960), in that it induced a quicker reaction, and smaller quantity of antigen is needed to stimulate the antibody production. Injection is carried out at 10 day intervals, and two weeks after the second injection the rabbit serum is extracted and tested against the antigen for sensitivity through serial dilution. Further injection is then carried out to increase sensitivity. The production of antibodies varies between rabbits, but usually reaches a peak after the fourth injection. Fifty ml of rabbit blood is then collected and the serum extracted. The fat content in the serum is removed with ether to give a clear liquid. This is done so that the precipitin reaction will not be confused by the cloudiness of the fats in the antisera.

Antisera of both C. viridis and Grapho cephala

'coccinea' (Forst.) were prepared. The final sensitivity of the antisera was $\frac{1}{800}$ for C. viridis and $\frac{1}{1200}$ for G.'coccinea'.

The tests for cross reaction with the antigen of other insects and spiders were carried out and the results from them are presented in Table 34 . The results indicated that the antisera of C. viridis and G. coccinea are very similar and cross react with each other's antigen strongly. This to a certain extent is expected as the two species belong to the same sub-family. Cross reaction with Cicadellidae in general is reasonably strong, and indicates the non-specificity of the antisera. But it is of interest to find that the antisera would react with Schistocerca gregaria which belongs to an altogether different Order. As the antisera of C. viridis and G. 'coccinea' are indistinguishable in their reactions, the two antisera are pooled together for subsequent tests for predators.

The predators were collected with a sweep net and a "pooter", and the specimens killed by squashing them between strips of filter paper and then dried over silica gel. The vole and the shrew were trapped with Longworth traps. Whole animals were kept in a deep freeze at -20°C until ready for testing.

With insects and spiders the test was carried out by soaking the smear in 0.2 ml of distilled water overnight and then centrifuging. The supernatant fluid was extracted

Table 34. Results of tests for specificity of C. viridis antisera.

Species tested	Result and sensitivity
C. viridis	positive at $\frac{1}{800}$
Eggs of C. viridis	positive at $\frac{1}{4000}$
G. 'coccinea'	positive at $\frac{1}{1200}$
Cicadellidae (general)	positive at $\frac{1}{400}$
Schistocerca gregaria (Forsk.) (Orthoptera)	positive at $\frac{1}{200}$
Pieris brassica (L.) (Lepidoptera)	No reaction
Diptera (general)	" "
Drosophila melanogaster Mg.	" "
Dysdercus sp. (Heteroptera)	" "
Nabidae	" "
Carabidae	" "
Spiders (general)	" "
Collembola	" "

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and used for testing. In test of the shrew and the vole, the entire alimentary canal was dissected out, and the gut contents washed with distilled water. These mixtures of water and gut contents were then allowed to stand overnight, and then centrifuged. The supernatant fluid was extracted and freeze dried. The resultant solid was then reconstituted with 0.2 ml of distilled water for testing.

All predators were collected in the summers of 1970 and 1971 between June and September. The predators tested and the results are shown in Tables 35 and 36.

Because of the cross reaction between the general Cicadellid antigen with C. viridis antisera, a positive reaction could only indicate that the predator concerned had preyed upon C. viridis or a member of the family Cicadellidae. Nevertheless, the results of feeding tests and of the precipitin test together suggest that the major predators of C. viridis are most likely to be the four species of Nabid bugs i.e. Dolichonabis limbatus, Nabis rugosus, N. flavomarginatus, and Stalia major; five species of spiders, Clubiona reclusa, Xysticus cristatus, Theridion ovatum, T. bimaculatum, and Linyphia clathrata. Other possible predators, which had been found either feeding on C. viridis under laboratory conditions or through a positive precipitin test were the carabid beetle Leistus terminatus; Opiliones Phalaguim opilio, Oligolophus agrestis; spiders Lycosid spp. Lepthyphantes ericaeus and Linyphia triangularis.

Small mammals such as the bank vole and the common shrew although present in reasonable numbers in the habitat, do not appear to prey on C. viridis. However, the bank vole is known to be omnivorous in habit and the common shrew is an insectivore. Whalley (1956) had reported feeding by

Table 35. Results of the precipitin test on the predators of C. viridis in 1970.

Predator	No. tested	No. positive	% positive
Insecta			
Hemiptera			
Nabidae			
Dolichonabis limbatus (Dahlbom)	38	8	21.05
Nabis rugosus (L.)	24	2	8.33
N. flavomarginatus Scholtz	30	2	6.67
Stalia major (Costa)	16	2	12.50
Coleoptera			
Cantharidae			
Rhagonycha fulva (Scop.)	33	0	0
Carabidae			
Leistus terminatus (Hellwig)	5	1	25.0
Arachnida			
Aranaea (spiders)			
Thomisidae			
Xysticus cristatus (Clerck)	31	4	12.90
Tibellus oblongus (Clerck)	4	0	0
Clubionidae			
Clubiona reclusa O.P. Cambridge	17	1	5.88
Theridiidae			
Theridion ovatum (Clerck)	19	3	15.80
T. bimaculatum (L.)	7	2	28.57
Tetragnathidae			
Tetragnatha extensa (L.)	9	0	0

Table 35. cont.

Linyphiidae			
Hypomma bituberculatum (Wider)	6	0	0
Oedothorax gibbosus (Blackwell)	15	0	0
Bathyphantes approximatus (O.P. Cambridge)	7	0	0
B. pullatus (O.P. Cambridge)	16	0	0
Pocadicnemis pumila (Blackwell)	9	0	0
Linyphia clathratha Sundeval	18	1	5.56
L. triangularis (Clerck)	12	0	0
Opiliones			
Phalangidae			
Phalangium opilio L.	40	0	0
Oligolophus agrestis (Meade)	13	0	0

Table 36. Results of precipitin test on the predators of C. viridis in 1971.

Predator	No. tested	No. positive	% positive
Insecta			
Hemiptera			
Nabidae			
Dolichonabis limbatus	25	3	12.01
Nabis rugosus	33	8	24.30
N. flavomarginatus	17	3	17.69
Stalia major	19	1	5.26
Miridae			
Tytthus pygmaeus	13	0	0
Cyrtorhinus caricis	15	0	0
Coleoptera			
Carabidae			
Leistus terminatus	2	0	0
L. ferrugineus (L.)	5	0	0
Brachycellus sp.	3	0	0
Staphylinidae			
Tachyporus sp.	2	0	0
Stenus sp.	1	0	0
Cantharidae			
Rhagonycha fulva	7	0	0
R. testacea L.	3	0	0
Arachnida			
Araneae			
Thomisidae			
Xysticus cristatus	21	1	4.76
Tibellus oblongus	8	0	0
Clubionidae			
Clubiona reclusa	12	1	8.33
Cheiracanthium erraticum (Walkenaer)	7	0	0
Theridiidae			
Theridion ovatum	23	2	8.70
T. bimaculatum	6	1	16.67

Tetragnathidae			
Tetragnatha extensa	11	0	0
Pachygnatha degeeri Sundevall	5	0	0
Linyphiidae			
Linyphia clathratha	3	1	33.13
L. triangularis	5	0	0
Lepthyphantes ericaeus (Blackwall)	7	1	14.29
Pocadicnemis pumila	3	0	0
Oedothorax gibbosus	7	0	0
Lycosidae			
Lycosa sp.	8	1	12.50
Opiliones			
Phalangium opilio	6	1	16.67
Oligolophus agrestis	2	0	0
Mammalia			
Soricidae			
Sorex araneus (L.)	7	0	0
Cricetidae			
Clethrionomys glareolus (Schr.)	2	0	0

frogs and by the grasshopper warbler, in the present study site, these animals are rather uncommon.

(iii) Populations of spiders

Forty-two species of spiders comprising ten families were collected from the habitat during regular sampling with the Dietrick suction sampler. A list of the spiders collected is presented in Table 37 . The fluctuation of the total spider population[1] expressed as numbers per square metre in 1970 and 1971 are shown in Table 38 and 39 and, illustrated in Fig 31 . Although the Dietrick machine is highly selective e.g. large spiders particularly Lycosids are not picked up readily, however an overall, picture of the relative abundance of the spiders in the area throughout the season has been obtained. In both 1970 and 1971, two peaks can be recognised, one in May to June, and the other towards August and September. The May to June peak probably indicates both a higher number and also higher acitivity which resulted in greater catch by the Dietrick machine. In May to June the immature and the sub-adult spiders maturing, become more active, partly as a result of the rising temperature and partly because the males are wandering around searching for mates. In many species males died after mating and females retired to egg laying which may account for the drop in the catch in July. By August, the hatching of young spiders resulted in the rise in numbers to a second peak. This annual cycle with spring

and autumn peaks has also been noted in other spider population studies (Duffy, 1962). The number of spiders caught in 1970 was higher than that in 1971. The peak also occurred earlier in 1971 and coincided with the early hatching of C. viridis. Although there was a difference in the populations between the two years, the species composition remained similar. Table 40shows the percentages of the total catch of the most likely predators of C. viridis caught in 1970 and 1971.

In terms of predatory behaviour, the essential characteristics of a spider as a predator are its size, its hunting methods and the position of the microstructure of the habitat it occupies. The medium sized or larger spiders (2.5mm to 8.5mm) living on the litter surface or aerial vegetation either building three dimensional webs or lying in wait are probably the most important predators of an insect like C. viridis which either rests on Juncus or on Holcus stems or is hopping about within the vegetation. The most numerous spiders in this category are Clubiona reclusa, Xysticus cristatus, Theridion ovatum, T.bimaculatum, and Linyphia clathrata. All these species are voracious feeders. This characteristic together with the results of laboratory feeding tests and the positive precipitin tests suggest that these species are the most important spider predators of C. viridis.

Table37. Spiders from Rush Meadow

Family DICTYNIDAE

Dictyna arundinacea (L.)

Family CLUBIONIDAE

Clubiona reclusa O.P.-Cambridge

C. terrestris Westring

C. subtilis L. Koch

Cheiracanthium erraticum (Walkenaer)

Zora spinimena (Sundevall)

Family THOMISIDAE

Xysticus cristatus (Clerck)

Philodromus aureolus (Clerck)

Tibellus oblongus (Walkenaer)

Family LYCOSIDAE

Lycosa amentata (Clerck)

L. prativaga L. Koch

Pirata hygrophilus (Clerck)

Family PISAURIDAE

Pisaura mirabilis (Clerck)

Family MIMETIDAE

Ero cambridgei Kulczynski

Family THERIDIIDAE

Theridion denticulatum (Walkenaer)

T. ovatum (Clerck)

T. instabile O.P.-Cambridge

T. bimaculatum (Linnaeus)

Family TETRAGNATHIDAE

Tetragnatha extensa (Linnaeus)

Pachygnatha degeeri Sundevall

Family ARGIOPIDAE

Meta segmentata (Clerck)

Araneus redii (Scopoli)

Family LINYPHIIDAE

Dismodicus bifrons (Blackwall)

Hypomma bituberculatum (Wider)

Gonatium rubens (Blackwall)

Pocadicnemis pumila (Blackwall)

Oedothorax gibbosus (Blackwall)

Cnephalocotes obscurus (Blackwall)

Agyneta subtilis (O.P.-Cambridge)

Meioneta saxatilis (Blackwall)

Oreoetides abnormis (Blackwall)

Bathyphantes approximatus (O.P.-Cambridge)

B. pullatus (O.P.-Cambridge)

B. parvulus (Westring)

Poeciloneta globosa (Wider)

Floronia bucculenta (Clerck)

Taranucnus setosus (O.P.-Cambridge)

Lepthyphantes zimmermanni Bertkau

L. ericaeus (Blackwall)

L. pallidus (O.P.-Cambridge)

Linyphia triangularis (Clerck)

L. clathrata Sundevall

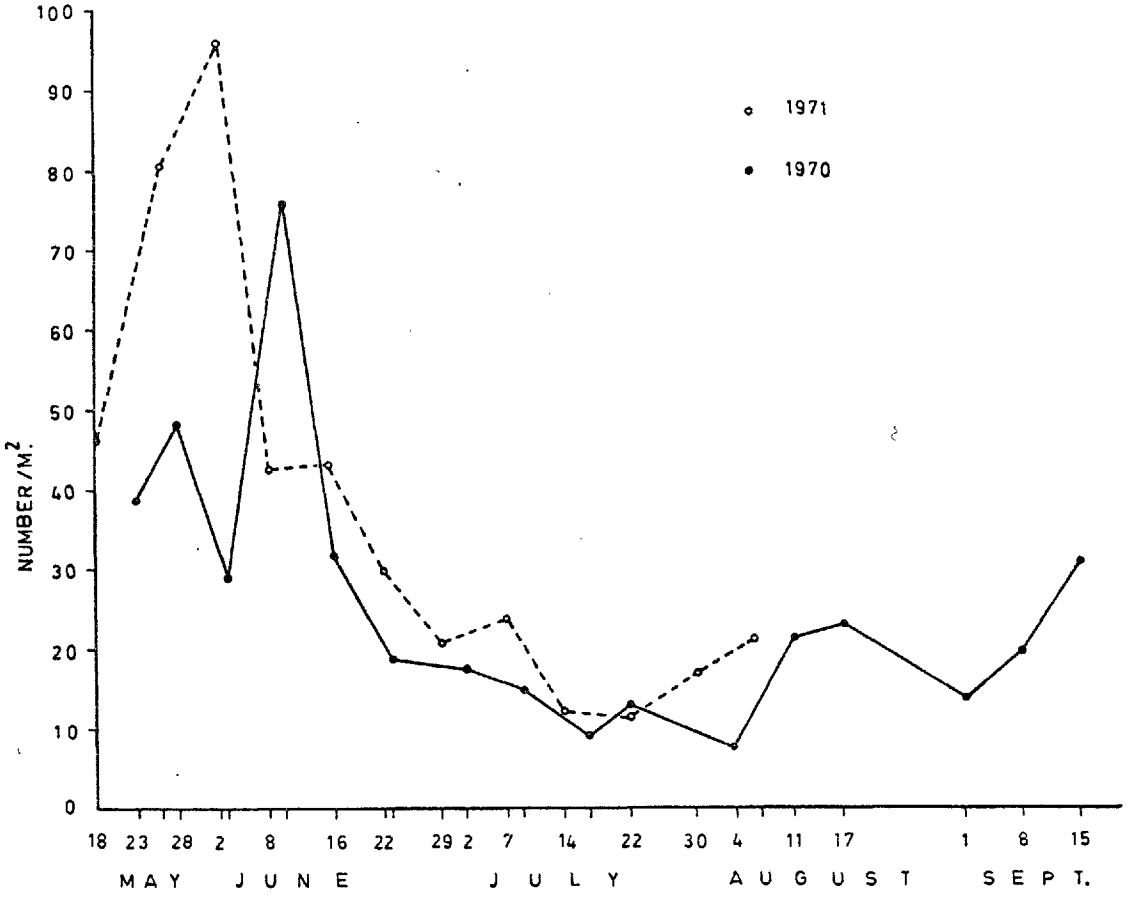


FIG. 31 Seasonal fluctuation of spider populations in the Rush Meadow in 1970 and 1971.

Table 38. Estimated total spider population in the study area in 1970

Date	Estimated Number	Number/m^2
May 23	69115	38.72
28	85943	48.15
June 3	51686	28.96
10	134624	75.42
16	56494	31.65
23	33656	18.85
July 2	31252	17.51
9	26444	14.81
17	16227	9.09
22	22838	12.79
August 4	13823	7.74
11	37863	21.21
17	40858	22.90
September 1	24641	13.80
8	34858	19.53
15	55292	30.98

Table 39. Estimated total spider population in the study area in 1971.

Date	Estimated Number	Number/m^2
May 17	87230	46.36
26	144326	80.85
June 2	171288	95.95
8	76128	42.65
16	76921	43.09
22	53121	29.77
29	37271	20.88
July 7	42822	23.99
14	22204	12.44
22	20618	11.55
30	30927	17.33
August 7	38064	21.32

Table 4Q Species composition of some predatory spiders in 1970 and 1971.

Species	Percentage of total catch (Total number caught in 1970 = 1,682 1971 = 1,278	
	1970	1971
Clubiona reclusa	6.96	4.85
Xysticus cristatus	1.72	1.17
Theridion ovatum	5.95	10.41
T. bimaculatum	3.27	7.36
Linyphia clathrata	1.90	2.66
Other spiders	80.2	73.55

(iv) Populations of Nabidae

Four species of Nabids have been collected regularly during sampling with the Dietrick suction sampler. They were Dolichonabis limbatus, Stalia major, Nabis rugosus and N. flavomarginatus. Another species Nabis ferus (L.) was collected occasionally, but this species most likely had come in from a nearby habitat and did not breed in the study area.

All the four main species have been observed to feed on C. viridis in the field. The total number of Nabidae as estimated with the Dietrick machine is presented in Table 42a and b. Of the four species, Dolichonabis limbatus, is the most abundant, followed by Stalia major, whereas Nabis rugosus and N. flavomarginatus were present in smaller numbers. The proportion of numbers of each species caught in 1970 and 1971 are as in Table 41.

According to Southwood and Leston (1959), Dolichonabis limbatus, Stalia major and Nabis flavomarginatus all overwinter as eggs, their larvae hatching in the second week of May, and adults appearing from June to July. These three species thus have almost similar life cycles as C. viridis and appear in the field at the same time. N. rugosus on the other hand over-winters as an adult and lays eggs in mid May, the larvae hatching in the second week of June and the first adult appearing in early August.

The seasonal fluctuation in numbers for

the total number of all Nabids including D. limbatus is presented in Fig. 32. The species are not presented separately, because the number collected on each sampling occasion was erratic and did not give a clear picture. When the total Nabid population was considered, the peak of the population appeared between May and June. After that, the numbers dropped gradually. In 1970 the population was much higher than 1971. The peak number for 1970 was 77.4 per square metre compared with only 40.0 per square metre in 1971. Fewkes (1958) found that over fifty percent of the prey of Nabids consists of leaf hoppers, they tend to eat a fairly constant weight of food in each instar, and there was little species variation in the weight of the food taken per individual per day (i.e. predation value). Taken all factors into consideration, undoubtedly, Dolichonabis limbatus is the most important Nabid predator of C.viridis in the area of study.

7.3 Analysis of mortality in the egg,larval and adult stages.

While it is not possible to attribute the exact contribution of each species of predator to the mortality of C. viridis in the present data, nevertheless, it is clear that the combined spring peaks of the spiders and Nabids must have caused the heavy mortality in the first and in the second instars of C. viridis. It is interesting to note that the spider population of 1970 is lower than in 1971, while, the reverse is true in the Nabids, which means that

Table 42 a and b. Estimated total populations of Nabidae in 1970 and 1971.

a. 1970

Date		Estimated number	Number/m^2
May	23	24040	13.47
	28	109983	61.62
June	3	132821	74.41
	10	138230	77.44
	16	121402	68.01
	23	45075	25.25
	28	46277	25.93
July	2	35459	19.86
	17	30050	16.83
	22	22838	12.79
	27	20434	11.45
August	4	14424	8.08
	11	12621	7.07
	17	7212	4.04
	25	8414	4.71
Sept.	8	2404	1.35
	15	1803	1.01
	19	1202	0.67

b. 1971

Date		Estimated number	Number/m^2
May	26	34892	19.55
June	2	71370	39.98
	8	64233	35.98
	16	42822	23.99
	22	32513	18.21
	29	22997	12.88
July	7	24583	13.77
	14	19825	11.10
	22	17446	9.77
	30	22204	12.44
August	2	13481	7.55
	11	12688	6.77

Table 41. The proportion of Nabids caught in 1970 and 1971.

Species	Proportion of each Species (Total number caught in 1970 = 1,289 1971 = 480	
	1970	1971
Dolichonabis limbatus	81.15	59.58
Stalia major	10.94	21.04
Nabis rugosus	3.65	18.13
Nabis flavomarginatus	4.90	1.25

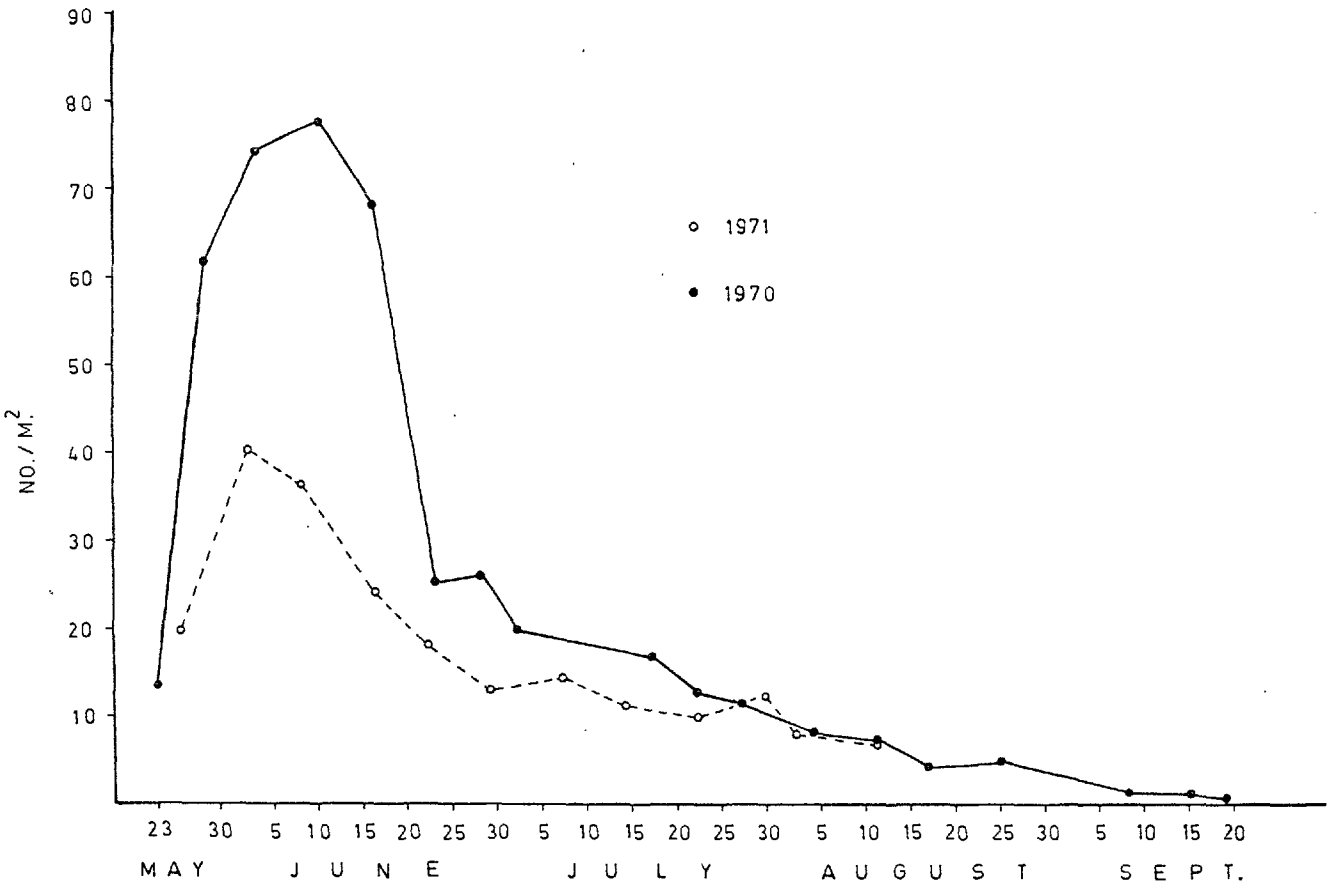


FIG. 32 Seasonal fluctuation of populations of Nabidae in the Rush Meadow during 1970 and 1971.

the total number of predators remained roughly similar in the two years. Varley and Gradwell's method (1960) of key factor analysis was tried for all stages of C. viridis. Except for the egg stage, the numbers entering each stage was estimated with the methods of Richards et al (1960). Table 43 a,b and c give the values for mortality in each stage, and these are plotted against generations in Fig. 33. K is the total mortality, k_1 being mortality in the egg stages, k_2, k_3, k_4, k_5 and k_6 are mortalities of the first to fifth instars. Bearing in mind the limitation of the present data - since only three generations were studied, a visual correlation suggests that the mortality within the egg stage k_1 produced the greatest effect on the population numbers. Although heavy mortality occurred in the first and second instar larvae, there is no suggestion that these mortalities have any major effect on the level of the population as a whole. Also the mortality of first instar larvae k_2 appears to have an inverse effect in relation to K the total mortality and the egg mortality. In conclusion, it can be said that the key factor causing mortality in the population of C. viridis occurred in the egg stage, and that death caused by the fungus can be identified as the key factor concerned.

Table 43. The value of k's for all stages of C. viridis in 1969, 1970 and 1971.

a. 1969

Stage	No. surviving	Log. no. surviving	k	
Egg	5105726	6,7081		
			0.4179	k_1
I	1950898	6.2902		
			0.6675	k_2
II	469443	5.6227		
			0.4080	k_3
III	163960	5.2147		
			0.1885	k_4
IV	106213	5.0262		
			0.0638	k_4
V	91715	4.9624		
			0.1794	k_5
Adult	60668	4.7830		
		K total =	1.5072	

b. 1970

Stage	No. surviving	Log. No. surviving	k	
Egg	8826752	6.9458		
			0.6964	k_1
I	1775942	6.2494		
			0.3217	k_2
II	846723	5.9277		
			0.3293	k_3
III	396605	5.5984		
			0.1390	k_4
IV	312921	5.4954		
			0.1525	k_5
V	202710	5.3069		
			0.1982	k_6
Adult	128437	5.1087		
		K total =	1.8371	

c. 1971

Stage	No. surviving	Log. No. surviving	k	
Egg	10281028	7.0120		
			0.7383	k_1
I	1878334	6.2738		
			0.2475	k_2
II	1062386	6.0263		
			0.2538	k_3
III	592280	5.7725		
			0.2166	k_4
IV	362356	5.5559		
			0.3261	k_5
V	169727	5.2298		
			0.1794	k_6
Adult	112309	5.0504		
		K total =	1.9617	

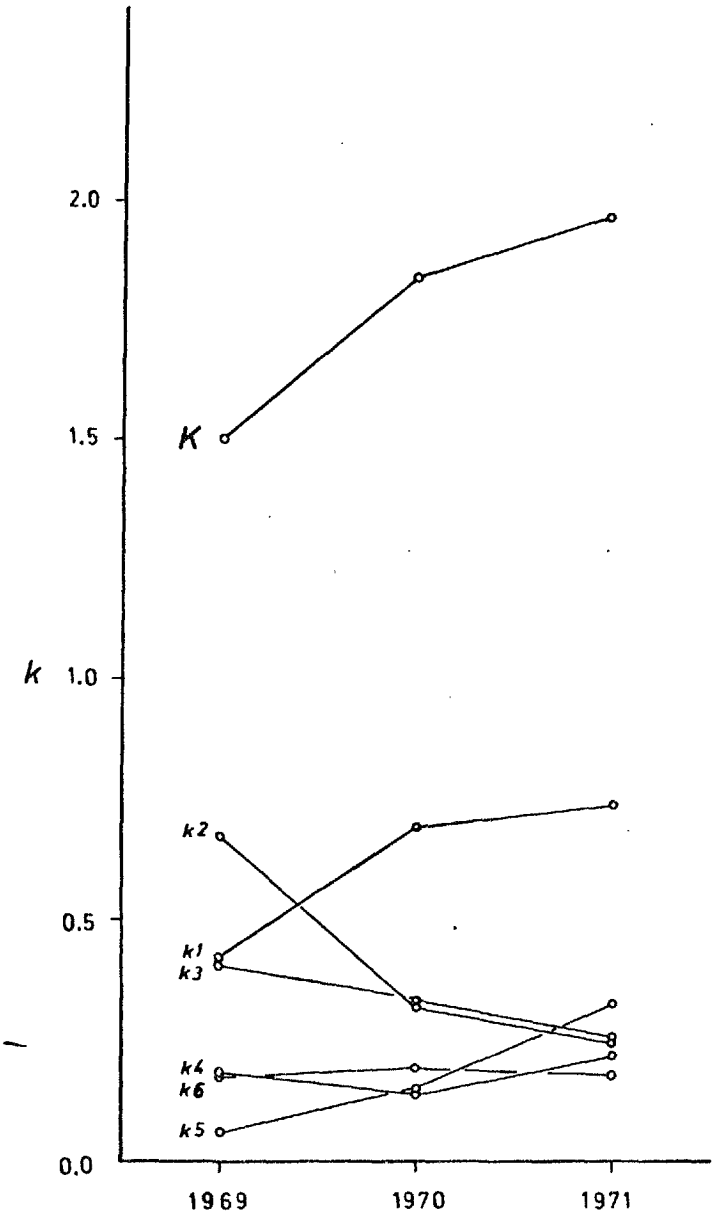


FIG. 33 Graphical key factor analysis of the mortalities in all stages of C. viridis. K = total mortality; k_1 = egg mortality; k_2, k_3, k_4, k_5, k_6 = mortality in 1st, 2nd, 3rd, 4th, 5th instar respectively.

IV DISPERSAL AND FLIGHT ACTIVITY

1. Dispersal

All insects at some stage of their life cycle would move from or within their breeding place in search of food, mate or suitable place to oviposit. Movements may be over long distances or simply to neighbouring plants. Southwood (1962) has classified insect movements into two categories: (a) Migratory, where the animal leaves the population territory or habitat in which it has previously lived and whilst engaged in such movement does not respond normally to any vegetative stimuli such as food, mate or shelter;

(b) trivial, when movements are concerned with searching for food or mate in response to visual or olfactory stimuli, and movements normally confined to the habitat of the population to which the animals belong. Movements of C. viridis appear to be primarily of the trivial type. From the study of food preferences and during regular samplings, it has been observed that young larvae when hatched would move away from the Juncus plants onto Holcus and surrounding vegetation. This is achieved by short hops from plant to plant. The adults move around by jumping and short flights. The movement of adults had been studied with the use of mark and recapture method, water traps and sticky traps.

1.1 Mark and recapture method.

The experiment was conducted in 1970. Two hundred and thirty one individuals, consisting of one hundred and one males and one hundred and thirty females were marked on the pronotum with red cellulose paint during the first week of August. Ten marked individuals were kept in the laboratory as a check for the effect of marking, and two hundred and twenty one were released in the field. Eighteen individuals - seven males and eleven females were recovered after searching the following day, all within one metre from the original point of release. Three females were recovered one week after being released; two from within two metres from the point of release and the third one at 4.5 metres. The distances covered by these twenty one individuals could all be achieved by hopping from plant to plant without involving flight. Insects kept in the laboratory showed that marking had no effect on their survival. As only twenty one individuals were recovered out of a total of two hundred and twenty one released, there was a possibility that some individuals might have travelled to a greater distance but were not recovered.

1.2 Water traps.

Two water traps with baffle of the type designed by Coon and Rinicks (1962) were set at one metre above ground level in the study area. The height of one metre was chosen, as this was the approximate average height of

vegetation in the area. Throughout the season, only three females were caught. Two were caught on the 3rd of August and the other on the 14th of August. The females were all immature, but the ovaries had some well formed eggs. The numbers caught were too low for analysis, however, they suggest that the acitivity of C. viridis probably seldom extends above the top of vegetation.

Outside the study area, one female was caught in a similar water trap in South Gravel, (for location of South Gravel, see Fig. 1) on the 12th of August 1969. The nearest Juncus clump was about sixty metres away from the trap. This female was still immature, but with twenty fully formed eggs in its ovaries.

1.3 Sticky traps.

Sixteen sets of cylindrical sticky traps were set up in 1970. The traps were made of cellulose acetate sheet, each with a surface area of 0.09m^2 (i.e. 1 sq. ft.). Each set of traps consisted of two traps situated at 1 metre and 1.5 metre above ground level.

Altogether five males and six females were caught between the first week of July and the last week of August on 1 metre high traps, none was caught at 1.5 metre.

In 1971, the height of the traps was reduced to 0.5 metres, which set them among the vegetation. Ten traps were set up. The catch was far greater and a total of 383 C. viridis (140 males and 243 females) were caught on

the traps. The first insect was caught on the 26th of July and the last on the 27th of August. The ovaries of the females caught were at different stages of maturation. The number caught per day varied from 0 to 29, Fig. 34 gave the fluctuation of daily catches for the 1971 season.

The relationship between the number of C. viridis caught on the trap and weather factors such as maximum and mean temperatures, percentage of relative humidity, sunshine and rainfall were looked into. The raw data is presented in Table 44 . Results of the analysis show that there was no correlation between the number caught with temperature or rainfall; but the catch is positively correlated with hours of sunshine and negatively correlated with relative humidity. The coefficient of correlation (r) between number and the hours of sunshine was 0.5448, t_{32} = 3.6175 which was significant at 1% level; that between the number caught and relative humidity r = - 0.3824, t_{32} = 2.3042 and was significant at 5% level.

A multiple correlation analysis was carried out taking into consideration all the weather factors at the same time. The coefficient of this multiple regression r = 0.5564, the variance ratio F = 3.1391. With the degrees of freedom n_1/ n_2 being 4/28 , it was significant at 5% level. The beta weight which indicates the relative contribution of corresponding variables were; 0.0601, 0.1857, 0.6618 and - 0.0765 for mean temperature, relative

humidity, sunshine and rainfall respectively. Sunshine appears to be the main influence in the activity of C. viridis, followed by relative humidity. The contribution of temperature and rainfall being about the same.

Thus increase in the number of hours of sunshine and a corresponding decrease in relative humidity induces an increase in activity in C. viridis. The temperature over the period when C. viridis were being caught on the trap remained relatively stable with a mean varying between 14.2 to 19.3°C. This may account for the lack of correlation with the number of insects caught. Rainfall, unless very heavy, does not seem to impair the activity of C. viridis, except that it exerts some influence on the relative humidity.

Table 44. Relation of number of C. viridis caught on sticky traps to weather condition.

Date	No. of insects caught	Max. temp °C	Mean temp °C	% R.H.	Sunshine hour	Rainfall in mm
July 26	6	22.00	18.50	76	0	1.6
	0	20.25	15.70	84	0	7.0
	5	22.00	17.10	74	5.3	0.3
	4	24.75	17.90	70	7.6	0
	17	25.75	18.70	63	11.7	1.5
	18	21.75	17.40	70	9.3	1.6
Aug. 1	6	21.25	16.40	70	7.5	3.4
	3	20.00	16.50	72	4.6	0.7
	10	21.25	16.40	82	3.6	16.7
	12	19.25	17.10	75	4.6	0.5
	16	20.25	16.60	77	8.9	26.7
	15	20.50	16.65	73	7.5	0
	17	20.50	14.50	73	9.0	0.8
	16	20.00	15.30	73	4.8	0
	16	21.25	17.50	80	1.4	0
	11	19.00	16.00	83	3.3	1.6
	6	18.25	15.40	64	3.7	0
	2	15.50	14.20	86	0.5	0.7
	15	20.25	16.50	78	2.5	0.6
	17	20.25	17.10	74	7.2	8.4
	9	17.50	14.30	79	1.9	0.2
	29	20.75	14.50	72	10.7	0
	28	21.25	14.70	63	11	0
	19	22.75	17.70	70	5.4	0.2
	11	25.75	19.30	77	4.2	0.2
	0	17.00	15.40	85	0	5.1
	10	16.20	14.90	87	0	7.0
	7	20.00	16.20	84	1.3	0.4
	15	21.75	17.10	76	4.8	0
	13	21.25	16.50	79	1.0	0
	18	22.25	15.80	70	9.5	0
	9	22.00	15.70	77	8.1	0
Aug.27	3	19.75	15.80	65	10.9	0.7

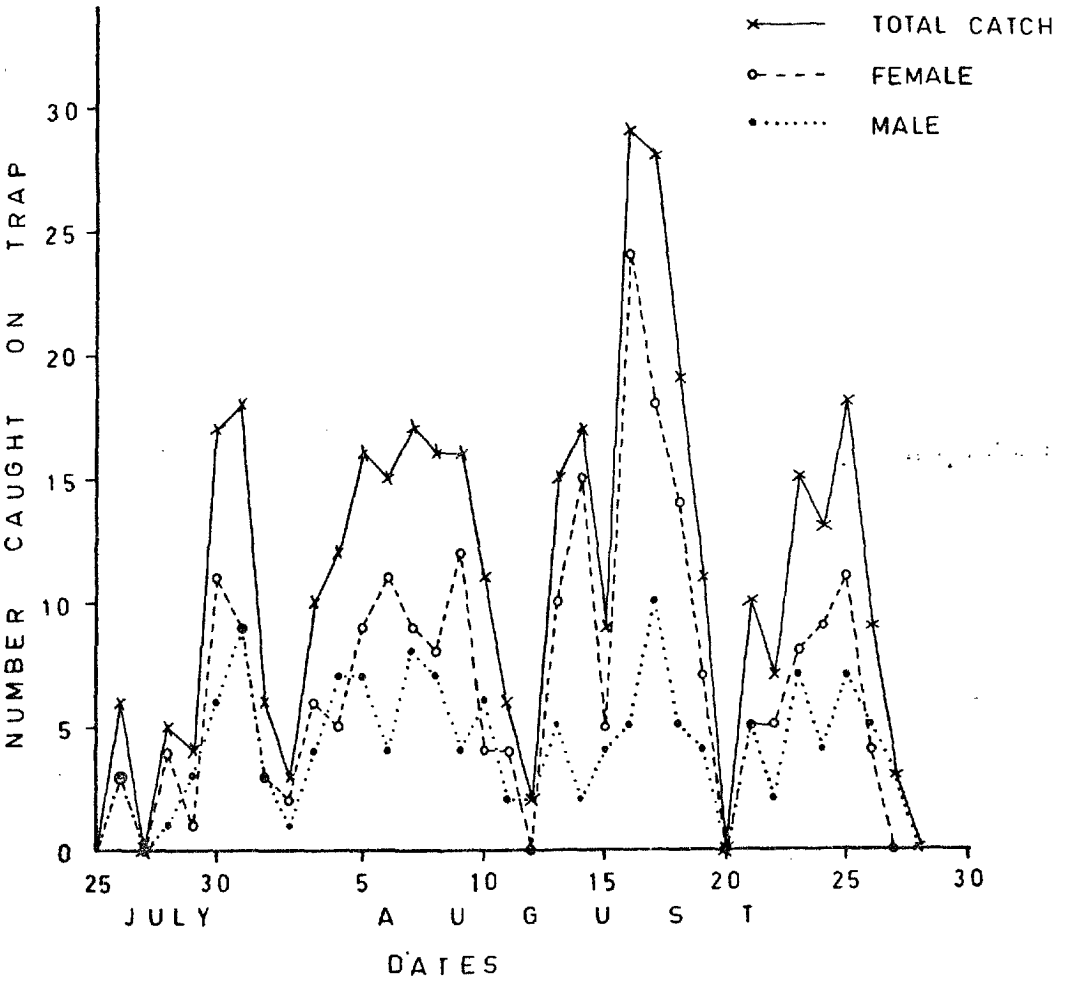


FIG. 34 DAILY CATCHES OF *C. viridis* ON STICKY TRAP.

2. Flight ability of C. viridis

Duration of flight of C. viridis was studied by flying the insects while attached onto a pin. Individuals of C. viridis were attached by the pronotum to the head of an entomological pin with a wax mixture. The mixture is made up of three parts beeswax to one part of colophonium resin (rosin), it was first used by Wooltan and Sawyer (1954) for studying locust flight.

The insect to be studied is first anaesthetized with carbon dioxide. The head of the entomological pin is slightly heated over a Bunsen burner in order to pick up the wax mixture; it is then applied to the pronotum of the insect. The wax mixture on the pin head cooled down and solidified rapidly and secured the insect on to the pin.

Flight was carried out on two occasions, once before females oviposited and once during the oviposition period. On the first occasion which was during the second week of August, fifteen females and ten males were flown. The experiment was conducted in the laboratory where the room temperature was 21^{o}C and relative humidity was 74.6%. The insect was induced to fly by lifting it sharply off the bench on which it rested. Each insect was flown in such a way ten times, and the duration of each flight was recorded with a stop watch from which the mean duration of flight was worked out. Of the fifteen females,

one individual sustained a mean flight duration of 4 minutes and 55.65 seconds, with a range of 13 seconds to 21 minutes and 25 seconds. One individual flew for an average of 57.72 seconds, one for 38.51 seconds and one for 30.19 seconds. The rest all flew for less than 4 seconds. The females were then dissected to examine the condition of their ovaries. The numbers of well formed eggs in the ovaries varied from three to twenty two, with a mean of 12.53 ± 1.18 eggs per female. There was a weak negative correlation between the length of flight and the number of fully formed eggs in the ovaries ($r = -0.3549$, $t_{14} = -1.3687$, $0.2>P>0.1$). The male insects all flew for less than four seconds. The second experiment was conducted during the second week of August, when egg laying was already in progress in the field. On this occasion only female insects were flown, as males had almost disappeared from the field. The temperature during the flight experiment was $24^{o}C$ and the relative humidity 66.5%. Out of the fifteen individuals flown, one achieved a sustained mean flight duration of one minute and 32.33 seconds, with a range of 27 seconds to 5 minutes and 49 seconds. The rest all flew for less than 4 seconds. The mean numbers of eggs per female had increased to 15.47 ± 1.69.

It can be seen that females are stronger flyers than the males. There is a vast difference in the ability

of a strong flyer and that of a poor flyer to sustain prolonged flight. The number of such strong flyers appears to be small. As the females matured, there was also a corresponding decrease in their ability to fly. In the field long distance flight has been observed occasionally by catches in water traps, suction traps and on sticky traps. Apart from the female caught in a water trap at South Gravel (p.197), one female was caught in a suction trap situated at Silwood Bottom on the 16th August in 1971, and one male and one female caught on sticky traps in the Japanese Garden behind Silwood Main House (for location see Fig. 1). The male was caught on a trap one metre above the ground, and the female at 1.5 metres. In the Japanese Garden there is a small patch of Juncus, however in the case of the suction trap at Silwood Bottom, the nearest Juncus clumps were about 100 metres away.

3. General discussion

As a whole the movements of C. viridis are essentially of trivial nature, confined within the habitat. In the three seasons of study, no noticeable dispersal into or out of the habitat had been observed. There are however, individuals that are capable of long distance flight as was indicated by the catches in the water, sticky, suction traps and by laboratory flying of insects. These experiments also indicated that, the male C. viridis in spite of their apparent agility in the field are more restricted

in their movements than the females.

It is worth noting that most catches in the various traps took place before the end of August, i.e. before the commencement of oviposition, which means that at least in the females, any dispersal activity must occur before full maturation of the ovary. Johnson (1969) put forward the term 'oogenesis - flight syndrome' to describe the relationship between development of flight apparatus and ovarial development. He postulated that if flight apparatus becomes fully mature while the ovaries remain immature, the insect may become a migrant; and if the ovaries become mature and the flight apparatus does not, eggs are laid in or near the old habitat. If this is true, C. viridis appears to be a potential migrant. This perhaps explains the wide distribution of the species within Silwood Park and elsewhere in Britain, as it occurs wherever Juncus is present, and such Juncus habitats are usually of a discontinuous nature. Johnson (1969) wrote that many species with quasi permament breeding places obviously need to migrate less intensely or less frequently than those whose breeding places last for a season only. A Juncus habitat is rather permament, and under normal conditions dispersal out of the habitat would not be necessary. However in times of extreme adverse conditions such as drought, dispersal might take place, as in the case of some British grasshoppers, where dispersal was observed in one year out of five years when drought had modified the habitat (Richards and Waloff 1954).

SECTION II. BIONOMICS OF GRAPHOCEPHALA COCCINEA (Forst.)

1. Introduction

The so called Graphocephala coccinea (Forst.) is a common North American Cicadellid. The insect is known to have been introduced into Britain around 1931-32. It was first noticed on Rhododendron round Chobham and Woking, Surrey in Southern England (China, 1935; Wilson, 1937). The insect has since then become widespread throughout Southern and Central England, and extends as far north as Cheshire (Le Quesne, 1965). In Britain this insect is solely associated with various Rhododendron spp. during its egg and larval stages. The adult being an active insect has been seen feeding on other shrubs, but no oviposition has ever been observed on plants other than Rhododendron. In its native North America, G. coccinea has been collected on a great variety of plants, including 50 spp. of weeds, on many ornamental plants, shrubs and various trees and it was the only species found to feed on the leaves of the American holly (Gibson 1915). Other plant species from which G. coccinea has been collected include:-
Aster (Kunkel, 1926), Narcissus (Blanton, 1938), Rubus sp. and Forsythia sp. (DeLong, 1948), blue berry (Tomlinson et al, 1950), Prunus sp. (Phillip, 1955) and on Rhododendron and Azalea (Fattig, 1955).

With the exception of Gibson's (1915) record of nymphal castskins on the underside of leaves of magnolia

tree, and DeLong's (1948) record of all stages found on Forsythia sp., the rest of the records did not suggest breeding on the plants on which the insect was collected. Also Fattig's record (1955) appears to be the only one where the insect was collected from Rhododendron and Azalea.

Because of its vast variety of food plants in America, and the rather restricted association with Rhododendron in Britain, it was suspected that the so called G. coccinea in Britain may not be the same species as the insect of that name in America. This is now confirmed by Dr. D.A. Young (Personal Communication) who says the British species is not true coccinea, but that this Graphocephala species is however, common in America, but it has a more restricted distribution than coccinea.

In the present study, the name 'coccinea' is retained with inverted commas since it is still used for the Graphocephala species in Britain. Dr. Young's publication on this subject is expected in the future.

Since its introduction G. 'coccinea' has always been associated with the spreading of the 'bud blast' disease of Rhododendron buds. The disease itself is caused by the fungus Pycnostysanus (Sporocybe) azaleae (Peck). As such it could be regarded as a pest of minor importance.

The biology of G. 'coccinea' in Britain has been briefly investigated by Baillie (1950) and Morcos (1953). Baillie had studied the hatching of eggs, the choice of Rhododendron variety for feeding and oviposition and its

status as a pest of this ornamental plant. In Morcos's (1953) paper he gave a brief account of the hibernation, host plants and a short description of some stages of the larvae. No details of the life history and or description of the immature stages were given by either author. The following is an attempt to provide some of this information and to compare it with the biology of C. viridis, the only other British species within the subfamily Cicadellinae.

2. Methods of rearing

2.1 Eggs

The eggs of G. 'coccinea' are laid exclusively on the scales of leaves or flower buds of Rhododendron. The eggs are inserted just underneath the outer epidermis of the scale, and are visible externally. Buds were collected from the field, and the scales containing eggs were cut out, placed in a petri dish lined with moistened filter paper and incubated for hatching. The humidity inside the dish was kept near to saturation by the addition of a few drops of water when required. Eggs incubated in this way gave a very good hatching result. At 20°C constant temperature a 90% hatch had been achieved.

2.2 Larvae and adults.

The method used is essentially the same as that used for the rearing of C. viridis. Young Rhododendron seedings were planted in the usual 12.5 cm high by 13 cm diameter flower pots. One to one ratio of sand and peat

mixture was used with one seedling to each pot. The cellulose acetate cage used was as described for C. viridis (see p.9).

3. Life history of G. 'coccinea'

Like C. viridis, Graphocephala 'coccinea' is univoltine. The eggs were laid between September to the end of October, and entered into diapause for the Winter. Development resumed in the following Spring, with hatching taking place in the second or the third week of May. Larvae were first observed in the field in Silwood Park on the 22nd, 21st and 18th of May in 1969, 1970 and 1971 respectively. Morcos (1953) had recorded larvae as early as on the 7th of May in 1948.

In 1971 hatching of larvae in the field was studied by enclosing egg bearing Rhododendron buds in muslin sleeves, of 25 cm in diameter and 60 cm in length. The buds were enclosed in the sleeve individually, and altogether 35 sleeves were used. The sleeves were examined daily and the number of larvae that had emerged were counted. A total of 181 larvae emerged, the hatch commencing on the 18th of May and spreading over a period of sixteen days. The pattern of hatching is as illustrated in Fig. 35, with 51.4% of the total hatching in the first four days. The overall spread of hatching appears to be shorter than that of C. viridis. In the laboratory under constant temperature the spread of hatch was much shorter, being 9 days, 7 days, 6 days and 5 days at 15°C, 20°C, 25°C and 30°C respectively.

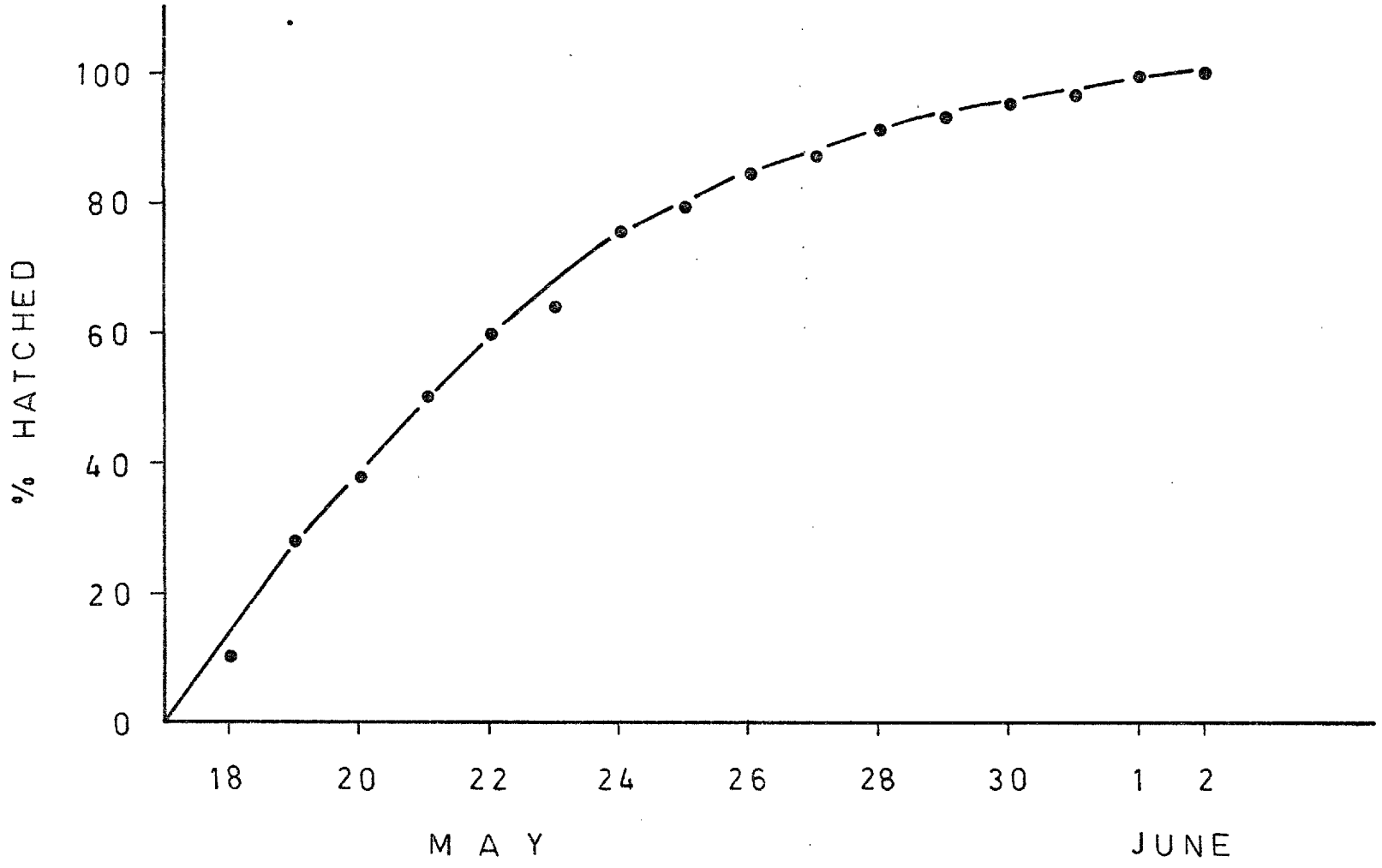


FIG. 35 Hatching curve of *G.'coccinea'*.

There are five larval instars, with considerable overlapping of stages. The larvae feed mainly on the underside of Rhododendron leaves, concentrating mainly along the veins. This feeding behaviour changed when they reached the adult stage and when feeding was mainly on the upper surface of the leaves. Commonly the adult insects line themselves up along the mid ribs of the leaves feeding, with their head pointing towards the petioles of the leaves. Both larvae and adults appear to be gregarious in habit.

Adults usually appear in the field during the second half of July and continue to be present until the first week of November. As in C. viridis, males preceded females in emergence, but the males of G. 'coccinea' are long lived, and persisted until the end of October. But by then, there were usually more females than males.

The sex ratio was looked into during 1970. By mid August out of 310 insects collected with a sweep net, 156 were males and 154 were females, which gave a good 1:1 ratio of males to females. While by mid October, out of 550 insects only 116 were males and 434 were females, giving the sex ratio of 1:3.74 ($\chi^2 = 183.86$, $P < 0.001$). This indicated that the males were long lived but died earlier than the females. Mating commenced during the first week of August. At that time, the females are still immature and the oocyts are at an early stage of differentiation. Courting involves the male approaching the female from the side,

flapping its wings and at the same time bending its abdomen towards the female. If the female was not receptive it would kick its hind legs to ward off the male. Pairing lasted from 30 minutes to an hour, and occurred more frequently in the afternoon than in the morning. Oviposition does not begin until the first/or the second week of September. Observation in 1970 showed that females first appeared on the 21st of July; mating was observed on the 8th of August and oviposition was first observed on the 10th of September. This means that there was a preoviposition period of about 51 days, and this is comparable to that of C. viridis.

Eggs are laid singly into the outer epidermis of the bud scale; oviposition either of single eggs or eggs in clusters of two to nine which spread out like a fan (plate 5). The scales of the Rhododdendron bud are arranged in spiral whorls. The outer-most ones are small, and are arranged round the base of the bud. Eggs are seldom laid in these scales, but mostly in the third to fourth whorls. Only a rudimentary embryo was formed when the egg entered diapause for the Winter.

4. Egg stage

4.1 Description of the Egg

The eggs of G. 'coccinea' are yellowish in colour and with a very soft chorion. Newly laid eggs are pear shaped, laterally compressed, pointed at the anterior pole, broad and round at the posterior pole (Fig. 36A). The odd shape of the egg is most certainly due to the pressure

exerted on it by the epidermis of the bud scale. As the embryo developed, the egg gradually assumed a cylindrical shape, breaking through the host's epidermis. The measurements based on 20 underdeveloped eggs have a length ranging from 1.68 mm to 2.12 mm, with a mean of 1.97 ± 0.03 mm; its maximum width being between 0.65 to 0.88 mm with a mean of 0.80 ± 0.03 mm.

4.2 Determination of the undercooling point of the eggs

The undercooling point of the eggs was determined with the same method as that used for eggs of C. viridis. The egg is again divided up arbitrary into five stages of development. Stage I being the diapausing egg, where only a rudimentary embryo was formed, but externally showing no visible signs of development (see Fig. 36A). In stage II, the eye spots have developed and are clearly visible at the posterior pole of the egg. The reversion of the position of the embryo then commences (see Fig. 36B). In stage III, segmentation and reversion of the embryo have been completed. Externally the eye spots appear at the middle of the egg (Fig. 36C). In stage IV, the embryo is well formed, and the eye spots appear at the anterior pole. The embryo at this stage is visible externally and the egg begins to assume a cylindrical shape (Fig. 36D). In stage V, the embryo is fully developed, with its head bulging out through the chorion, the egg becomes cylindrical in shape (Fig. 36 E).

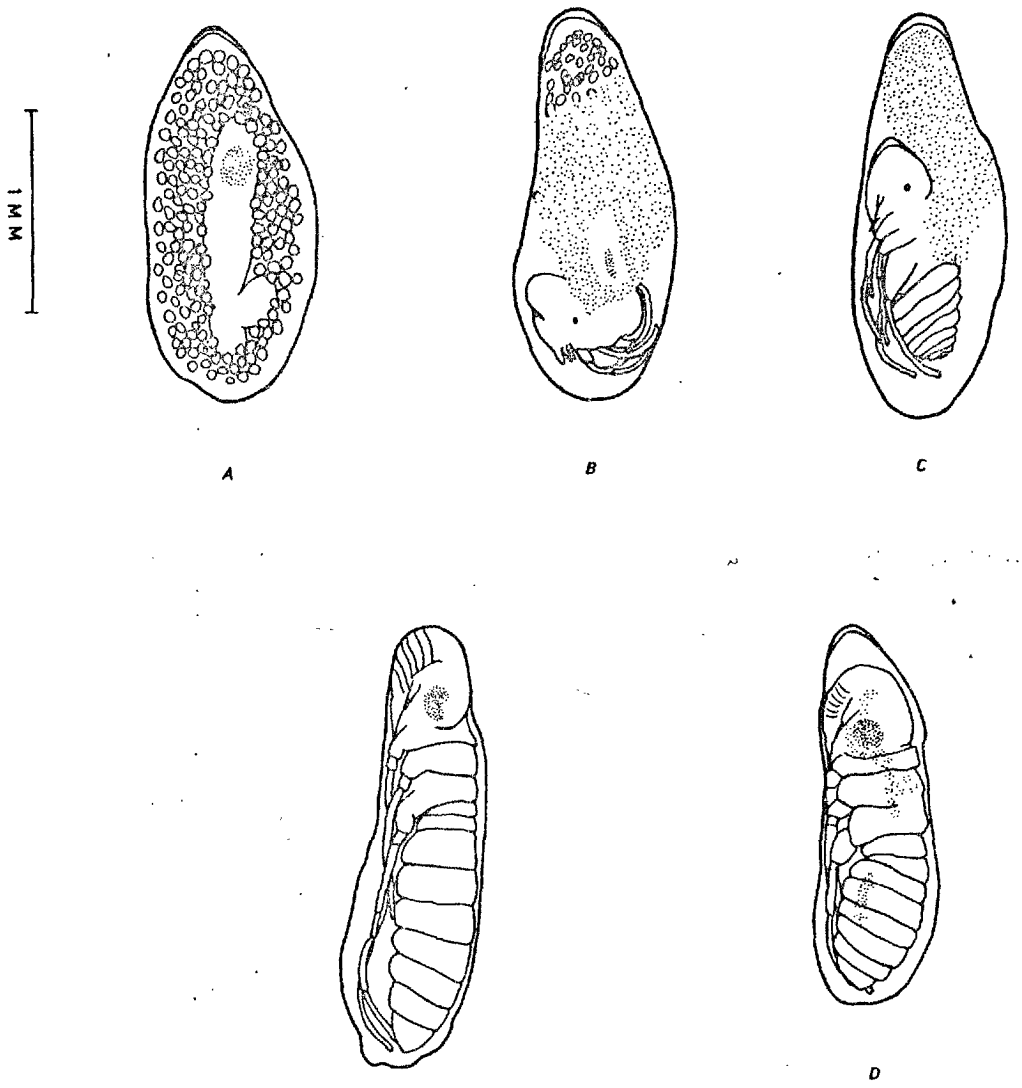


FIG. 36 Different stages in the development of *G. coccinea* egg.

The results are presented in Table 45, and illustrated in Fig. 37. The mean undercooling point for stage I, II, III, IV, V are -28.06, -22.96,-25.14, -23.48 and -22.17°C respectively. Variance analysis indicates that the differences in the undercooling points between the stages is significant at 0.01% level ($F = 18.44$, $P < 0.001$). In a series of detailed comparisons, it was found that no significant differences exist between stage II, IV and V, but that the differences between I and II ($F = 15.80$, $P < 0.001$) and between III and IV ($F = 4.68$, $0.05 > P > 0.01$) are significant. The details of analysis of variance is presented in Table 45. The overall result is similar to that obtained for C. viridis eggs. There are considerable variations in the under cooling points throughout the development of the egg. As is to be expected, the most cold hardy stage occurs when the egg is diapausing. The range of under cooling points varies from 3°C in stage III to 16.5°C in stage I, this is considerably greater than that found in C. viridis, where the ranges are from 2.5°C in stage I to 8.5°C in stage III. Inspite of this variation, even in the least cold resistant stages, the mean undercooling is in the region of -22°C. Thus both C. viridis and G. coccinea share the same degree of cold heardiness in their egg stage. This characteristic may be common to insects where the egg is the overwintering stage. It follows that in Southern

Table 45. Under-cooling points of the eggs of Graphocyhala 'coccinea' at different stages of development.

Stage	No. of eggs tested	Under-cooling point °C		
		Minimum	Maximum	Mean
I	25	-32.5	-16.0	-28.06± 0.71
II	14	-24.5	-18.0	-21.96± 0.57
III	22	-26.0	-23.0	-25.14± 0.19
IV	21	-25.5	-18.0	-23.48± 0.47
V	12	-24.0	-17.0	-22.17± 0.67

Variance analysis on the under cooling points of different stages of eggs of G. 'coccinea'.

Source of Variation	Sum of Squares	Degree of Freedom	Mean Square	Variance ratio
Between stages	467	4	116.75	18.44***
Residue	563.5	89	6.33	
	1030.5	93		
		Detailed Comparison		
I V. III	100.03	1	100.03	15.80*
III V. IV	29.61	1	29.61	4.68*
IV V. V	13.09	1	13.09	2.07 N.S.
V V. II	0.19	1	0.19	0.03 N.S.
II V. IV	18.30	1	18.30	2.89 N.S.

N.S. = Not Significant

The number of * indicates the level of significant at 5%, 1% and 0.1%.

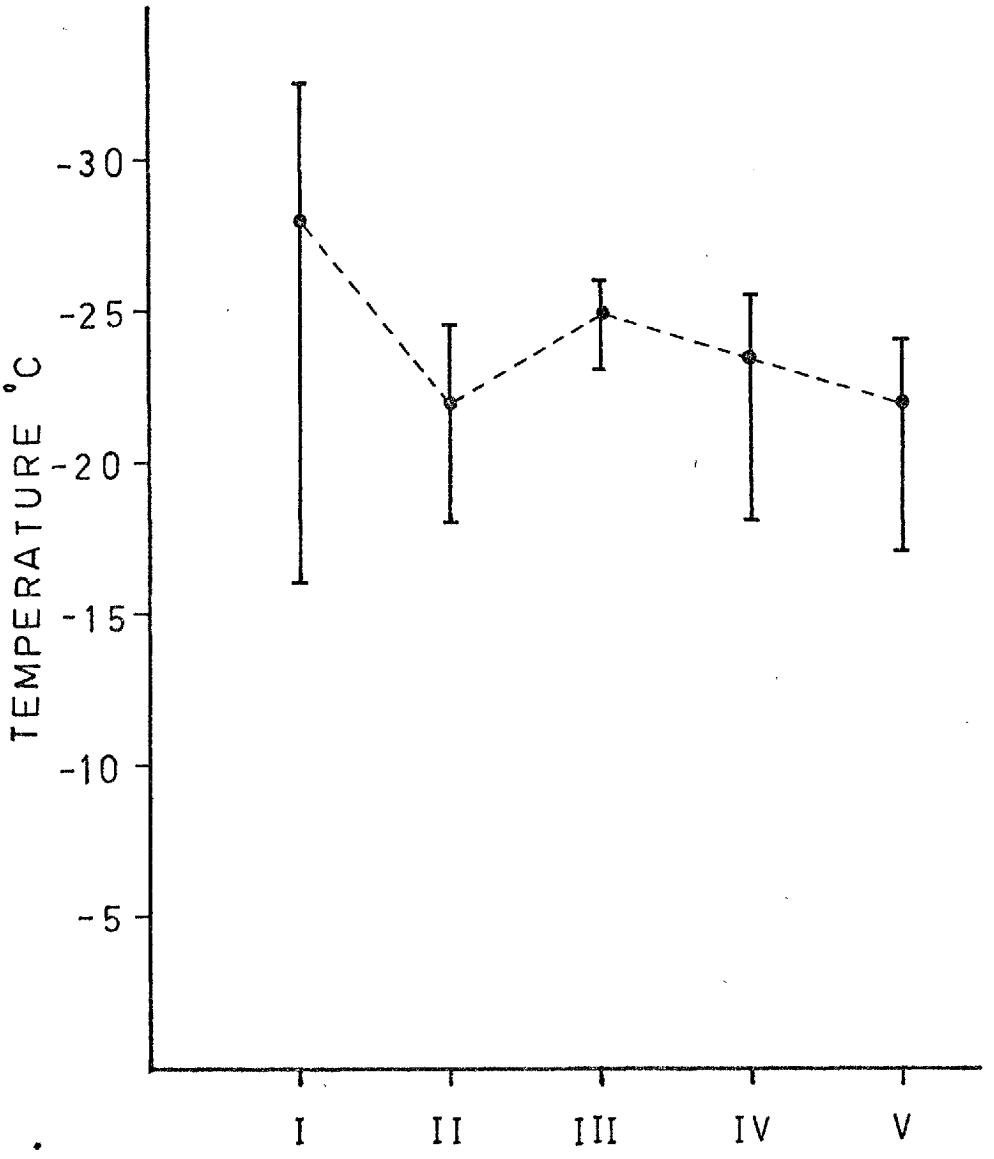


FIG. 37 UNDERCOOLING POINTS OF EGG OF *G. coccinea* AT DIFFERENT STAGES OF DEVELOPMENT.

England these two species of Cicadellidae are unlikely to suffer any mortality through low temperature.

4.3 The effect of temperature on the rate of development of the eggs.

The diapausing eggs of G. 'coccinea' to a certain extent behave as those of C. viridis. Some eggs could hatch without having to pass through a period of low temperature, but the proportion of eggs capable of doing so is much smaller than in C. viridis.

Three hundred and sixty eggs collected early in November 1970 were incubated at 20°C constant temperature. Only 20.56% (i.e. 75 eggs) of the incubated eggs hatched, this is compared with a 70.88% hatched in C.viridis. The spread of hatching was 45 days. The lower percentage of hatch probably indicates that diapause in G. 'coccinea' is of the obligatory type, but nevertheless, diapuse development could be accomplished at high temperature by some eggs.

To study the effect of temperature on the rate of development, eggs were collected in February when most could have completed the diapause stage. The eggs were incubated at constant temperatures of 15, 20, 25 and 30°C. The results are given in Table 46.

Davidson's (1944) logistic equation of the form of $\frac{100}{y} = \frac{K}{1+e^{a-bx}}$ was fitted to the data, where $\frac{100}{y}$ is the

percentage of development at the given temperature x. K, a and b are constants. The method of calculation has been described on page 75 . The derived equation has the form of $\frac{100}{y} = \frac{10.0091}{1 + e^{2.5537-0.1643x}}$, where x is the temperature in degree centigrade, and the mean developmental day is designated as $y + \frac{1 + e^{2.5537 - 0.1643x}}{0.1001}$.

Temperature also appears to affect the hatchability of the eggs. At 15 and 30°C, 54.91 and 46.50% hatched, compared with a hatch of 90.53 and 80.17% at 20 and 25°C.

Comparing Fig 14 and 38, it is evident that the rate of egg development in G. 'coccinea' differs from that of C. viridis in two aspects: (i) the mean developmental time of G. 'coccinea' is considerably longer than that of C. viridis at all temperatures. (ii) a rise in temperature produces a smaller developmental response in G. 'coccinea'; e.g. when temperature is raised from 25 to 30°C, the mean developmental day in C. viridis is shorten by 1.4 days, whereas in G. 'coccinea' the mean developmental day remains virtually the same as at 25°C (the shortening was only by 0.07 days). The small developmental response to temperature is also reflected in spring emergence of first instar larvae. During the warm Spring of 1971, hatching of C. viridis occurred about a week earlier than in the previous two years, while in G. 'coccinea' the difference was only by three days.

Table 46. The effect of temperature on the rate of development of eggs of G. 'coccinea'.

Temperature °C	No. of eggs	Mean development day (y)	$\frac{100}{y}$ percentage of development in one day	
			Observed	Calculated
15	275	23.76	4.2088	4.7483
20	190	14.38	6.9541	6.7202
25	116	11.39	8.7796	8.2299
30	143	11.32	8.8339	9.1366

Table 47. Duration of larval stages of G.'coccinea' reared in the outdoor insectary.

Instar	Duration of instar in days		
	Maximum	Minimum	Mean with standard error
I	12	6	8.95 ± 0.35
II	20	6	10.89 ± 0.77
III	18	9	14.00 ± 0.53
IV	18	7	12.84 ± 0.65
V	21	14	16.83 ± 0.43

Total duration = 63.53

5. Larval stages and the adult

5.1 Duration of the larval instars

The methods of rearing have already been discussed. Newly emerged larvae were reared five to a cage in the outdoor insectary, the temperature in the insectary varied between 16 to 36°C during the period of rearing, this was on the average about two degrees higher than the outdoor temperature. No attempt was made to separate the male and female larvae during rearing. The results given in Table 47 are the mean durat ion of both sexes reared together. The duration of the fifth instar was longer than that of any other instar. The total mean duration of the whole larval stage was 63.53 days which is longer than that of C. viridis by about three days reared under the same conditions.

5.2 Description of the larval stages

Immature stages of G. 'coccinea' have not been described previously. The following is a general description of the larval stages and the characteristics which can be used to distinguish them. The measurements on various parts of the body were made from 10 insects of each instar collected from the field.

The larvae appear dorso-ventrally compressed. All larval stages are uniformly yellowish-white in colour, glabrous and without any markings. Head is longer than broad, shaped like an inverted U, with a pointed vertex. The pair of red compound eyes are situated close to the

posterior margin of the vertex on both sides of the head. Ocelli are absent in all the immature stages. The multi-segmented antennae are located in front of the eyes, next to the frontal genal sulci.

Femora with two fine terminal spines dorsally, these are present in all stages, but become more prominent in the later instars. Tibia cylindrical in shape in the first three instars, and later become rectangular. There are two rows of ventral and two rows of dorsal spines. As in the case of C. viridis, the number of spines cannot be used to differentiate the instars. Tarsi two segmented, in the fifth instar, the last tarsal segment has a fine cleavage line, which will eventually develop into the three segmented tarsal condition in the adult.

There is a steady increase in the size with each larval instar, with the minimum size always larger than the maximum size of the previous instar.

First instar (Fig. 43I). Body length ranges from 1.71 to 1.84 mm with a mean and standard error of 1.83± 0.02 mm Antennae about 0.83 mm. Apart from size, the thorax provides the most easily distinguishable character from the other instars. Thorax 0.47 mm in length and 0.67 mm at its maximum width. In the prothorax, the anterior margin being narrower than the posterior, and the meta-thorax is the largest in terms of length and width. Wing pads very rudimentary, the fore wing pads can be seen as a small triangular projection

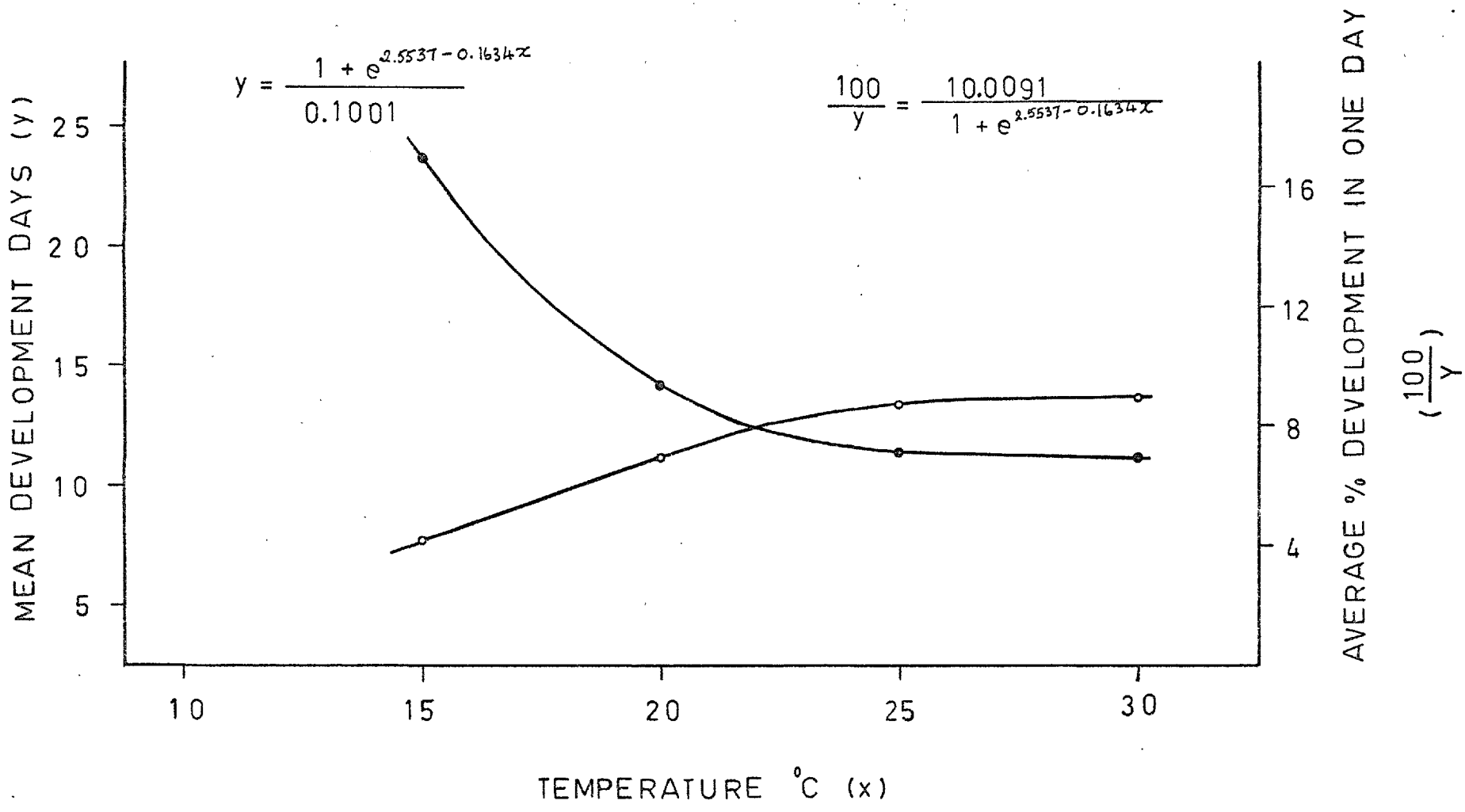


FIG. 38 Observed points on the temperature time curve (closed circles) and the temperature velocity curve (open cicles) for development of *G. coccinea* eggs.

at the lateral posterior margin of the meso-thorax. Meta-thorax almost rectangular in shape, wing pads not visible, and there is a fine bristle at each posterior corner. Abdomen with nine visible sements, with some bristles present on the lateral margins of the last three segments. External genitalia not yet differentiated.

Second instar (Fig.43 II). Body length ranges from 2.96 to 3.45 mm with a mean of 3.16 $\pm$ 0.06 mm; antennae 0.99 mm. Most characters are essentially the same as in the first instar. Wing pads on the thorax are more developed than in the first instar, they appear as distinct triangular projections at the corners of meso-thorax, but are less noticeable in the meta-thorax. Rudiments of external genitalia beginning to appear.

Third instar (Fig. 43 III). Generally similar to previous instar. Body length ranges from 3.5 to 4.28 mm with a mean of 4.06 $\pm$ 0.05 mm. Antennae 1.07 mm long. Wing pads on the thorax developed further with the tips of the forewing pad almost reaching halfway towards the tips of hind wing pads. The latter are elongated further and show up as protrusions at the corners of the posterior margin of the meta-thorax. External genitalia visible, but it is still difficult to differentiate between the sexes.

Fourth instar (Fig. 43 IV). Essentially the same as the previous instar. Body length measures between 4.82 to 5.61 mm with a mean of 5.10 $\pm$ 0.09 mm. Antennal length

1.19 mm. Wing pads on thorax by now are well developed, with the forewing pads greatly elongated, their tips reaching two thirds of the way towards the tips of the hind wing pads. Tibia assume a rectangular shape in contrast to the cylindrical shape of the previous instar. External genitalia well differentiated, and it is now possible to distinguish the sexes apart.

Fifth instar (Fig. 43 V). Male insects generally smaller than the females, but there is a considerable overlap in size between the sexes. The body length ranges from 6.71 to 7.93 mm with a mean of 6.90 $\pm$ 0.11 mm. Antennae 1.4 mm. Wing pads very well developed, with the tips of forewing pads almost reaching those of the hind wing. External genitalia essentially similar to these of the adult. Tarsi although still two semented, the last tarsal segment show signs of impending division into the three semented condition in the adult.

5.3 The adults

China (1935) and Le Quesne (1965) have both given a good description of the adults of G. 'coccinea'. Comparing it to C. viridis, it is a much more slender insect. The overall length of the males measured between 7.26 mm to 8.67 mm, with a mean of 7.89 $\pm$ 10.17 mm, with a mean of 8.98 $\pm$ 0.23 mm. As in C. viridis, the length of the head remained almost the same as in the fifth instar, but there is an increase in the head width. While most insects are

bright green with orange and red markings, there are some dark coloured individuals, which have their green colour replaced by dark purple. The two colour forms are shown in plate 6. The cause or significance of these colour forms is not known. Female external genitalia have been described by Morcos (1948), and the male genitalia illustrated by Le Quesne (1965). The male aedeagus is almost scythe shaped and arising from the horizontal base are two elongated projections. These two projections are broad at the base and pointed towards their tips, and are arranged in tandem.

5.4 The relation between measurements of successive instars.

The measurements of head length, head width, hind femur and hind tibial length of successive instars were taken from ten insects of each instar. The range and means of these measurements are given in Table 48. Richards (1949) suggested that irregularities in the growth factors of successive instars in some insects can be explained if the durations of the stadia are considered. The mean measurements of the four parts measured are plotted against the accumulated instar durations. As is shown in Fig. 39 linear relationships were obtained in all cases. However, with head length a better fit of the regression line is obtained if the adult stage is excluded. This is because there is no growth in head length between the fifth instar and the adult stage.

The linear relationships obtained suggested that Richard's supposition is applicable to growth in G. 'coccinea'

Table 48. Measurements of head length, head width, hind femur and hind tibia length of G. 'coccinea'

		I	II	III	IV	V	Adult
Head length (mm)	Max.	0.51	0.69	0.82	1.03	1.32	1.17
	Min.	0.47	0.61	0.73	0.88	1.09	0.92
	Mean	$0.49^{\pm}_{0.01}$	$0.66^{\pm}_{0.01}$	$0.78^{\pm}_{0.01}$	$0.96^{\pm}_{0.02}$	$1.15^{\pm}_{0.02}$	$1.05^{\pm}_{0.02}$
Head width (mm)	Max.	0.73	0.92	1.22	1.44	1.76	2.00
	Min.	0.65	0.88	1.04	1.29	1.62	1.66
	Mean	$0.68^{\pm}_{0.01}$	$0.91^{\pm}_{0.01}$	$1.11^{\pm}_{0.02}$	$1.38^{\pm}_{0.01}$	$1.67^{\pm}_{0.01}$	$1.85^{\pm}_{0.03}$
Hind Femur (mm)	Max.	0.49	0.71	0.94	1.26	1.71	2.25
	Min.	0.39	0.65	0.82	1.12	1.59	2.00
	Mean	$0.44^{\pm}_{0.01}$	$0.68^{\pm}_{0.01}$	$0.88^{\pm}_{0.01}$	$1.19^{\pm}_{0.01}$	$1.64^{\pm}_{0.01}$	$2.07^{\pm}_{0.02}$
Hind tibia (mm)	Max.	0.84	1.24	1.53	2.29	3.03	4.25
	Min.	0.73	1.16	1.65	2.00	2.79	3.58
	Mean	$0.78^{\pm}_{0.01}$	$1.21^{\pm}_{0.01}$	$1.60^{\pm}_{0.13}$	$2.15^{\pm}_{0.01}$	$2.91^{\pm}_{0.02}$	$3.88^{\pm}_{0.05}$
Mean duration of stage (days)		9	11	14	13	17	-
Accumulated days		0	9	20	34	47	64

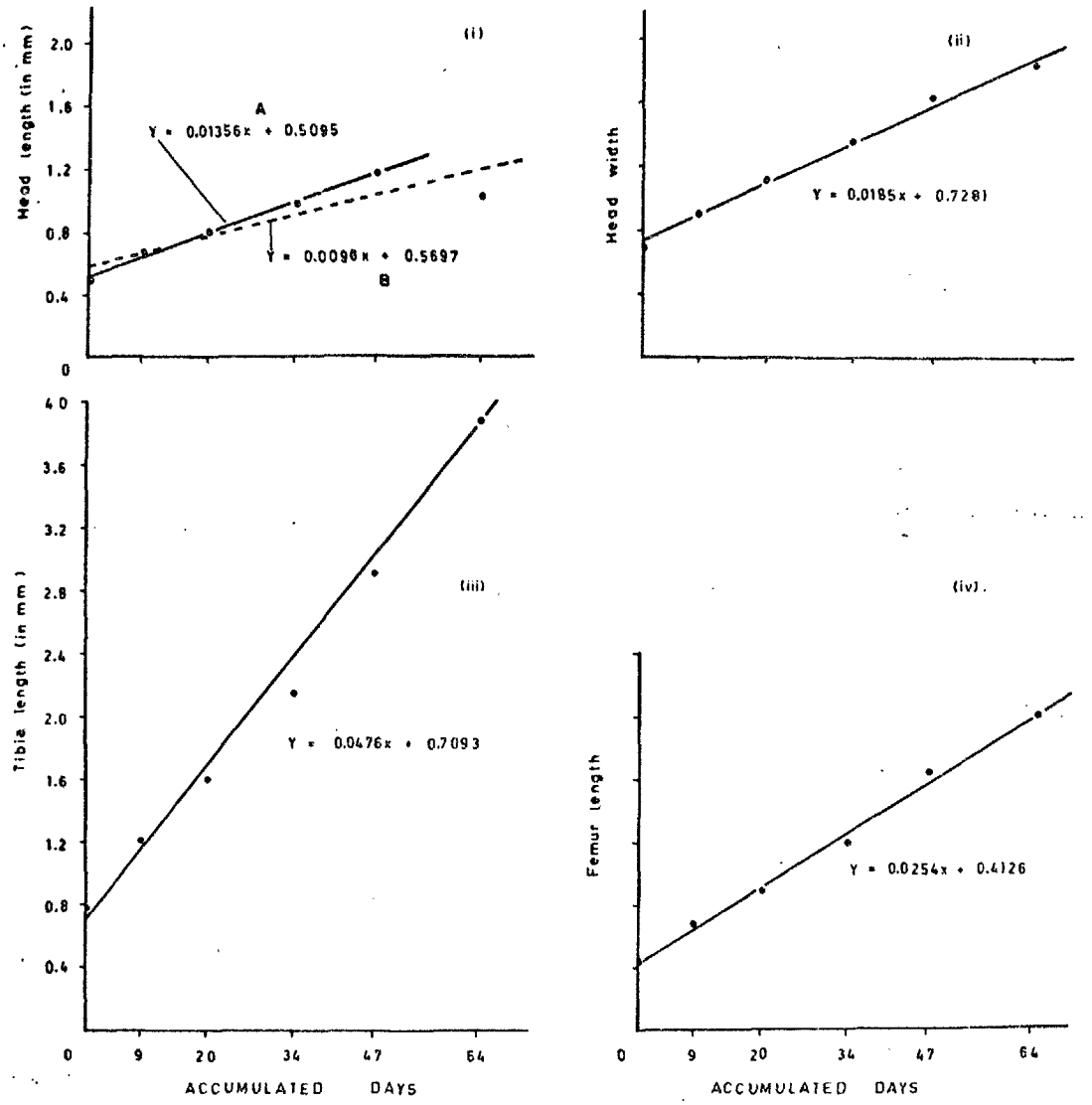


FIG. 39 Growth of different parts of the body of *G. crassinea* in relation time. (i)A, excluding adult stage; (i)B, including adult stage.

and with the exception of head length between fifth instar and adult, the growth increment per day is constant. The result also provides a counter check on the accuracy of the estimated duration of each instar.

5.5 Internal reproductive organs

5.5a Male (Fig. 40)

The male internal reproductive organs are basically similar to those of C. viridis. The paired testes are each made up of four individual, white, fleshy and pear shaped follicles. The vasa deferentia in G. 'coccinea' are fine and long, but enlarged along their course to form the elongated but short muscular vesiculae siminalis. As in C. viridis, the pair of vesiculae seminalis closely approximate each other to give the appearance of a single structure.

The pair of accessory glands are long and highly convoluted, each opens into the vas deferans just posterior to the vesicula seminalis. Ultimately the vasa deferentia lead into the common bulbus ejaculatorius.

Apart from the difference in the number of testicular follicles, the reproductive organs of G. 'coccinea' and C. viridis also differ in terms of size. The vasa deferentia anterior to the vesiculae seminales are longer in G. 'coccinea', but the vesiculae seminales are shorter. The accessory glands are also longer and the bulbus ejaculatorius larger in G. 'coccinea' than in C. viridis.

5.5b Female (Fig. 41)

The paired ovaries of G. 'coccinea' each consist of

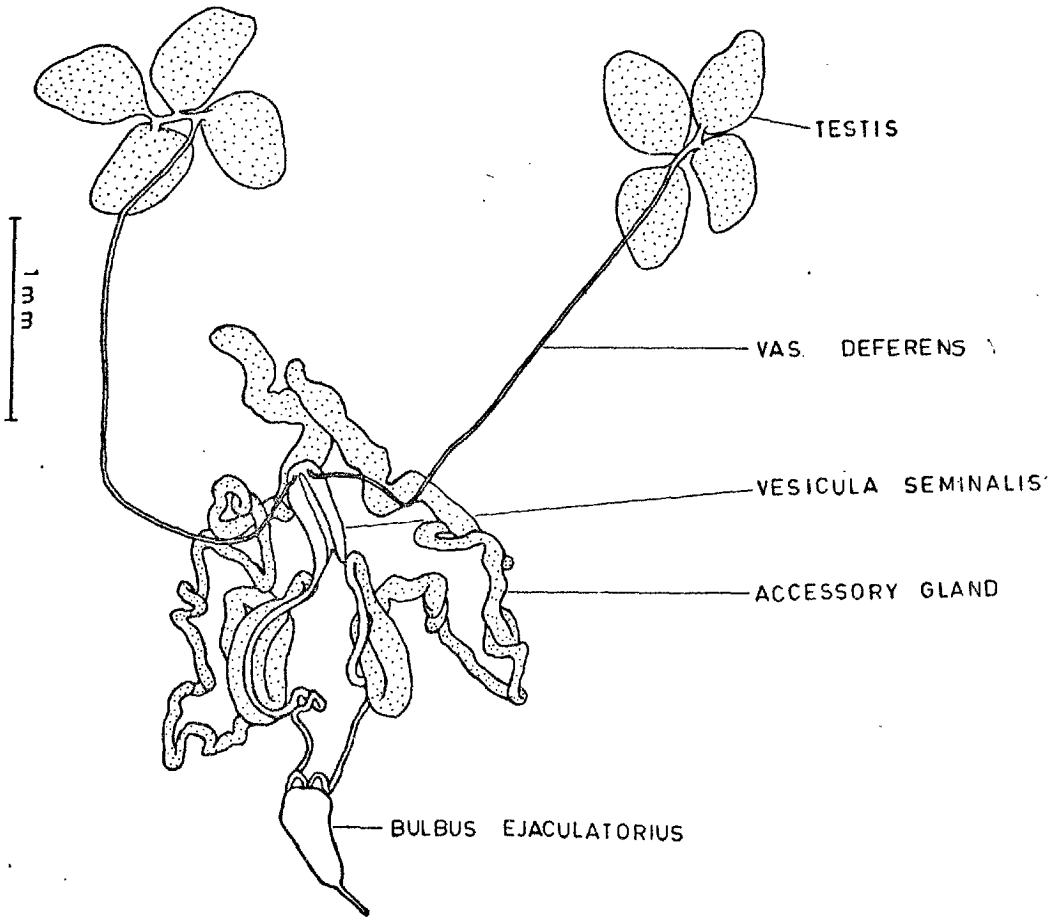


FIG. 40 MALE REPRODUCTIVE ORGAN OF *G. 'coccinea'*

four ovarioles. In the immature form (Fig. 41A), each ovariole possesses a single germarium, which later differentiates and forms a string of eggs (Fig. 41B). Fully grown eggs are cylindrical in shape and yellowish in colour with a shiny chorion. The maximum number of fully grown eggs present in the ovaries is ten, but eight is the usual number. The two lateral oviducts leading from the ovaries ultimately join to form the common oviduct. Posteriorly, this is enlarged into the muscular vaginal pouch. Such a pouch is absent in C. viridis. The oval shaped spermathea with its slightly convoluted duct opens into the vagina just posterior to the vaginal pouch, while the long tubular accessory gland joins the vagina a little further back. The accessary gland enlarges as the insect becomes mature.

5.6 Weight changes in the adults and fecundity of the females.

Seasonal weight changes were studied by weighing twenty males and twenty females collected from the field each week. Fig. 42 illustrates the weekly changes in weight of males and females throughout the adult life in 1971.

The difference in weight between males and females is not as marked as in C. viridis. Newly emerged males have a mean weight of 9.3 $\pm$ 0.02 mg, which ranges between 7.8 to 10.6 mg. The mean females weight is 11.0 $\pm$ 0.03 mg and ranges between 9.8 to 12.4 mg. The difference in weight between males and females is only in the region of 1.7 mg as compared with about 7.8 mg in C. viridis. Throughout the season, the weight of males remained fairly constant, whereas

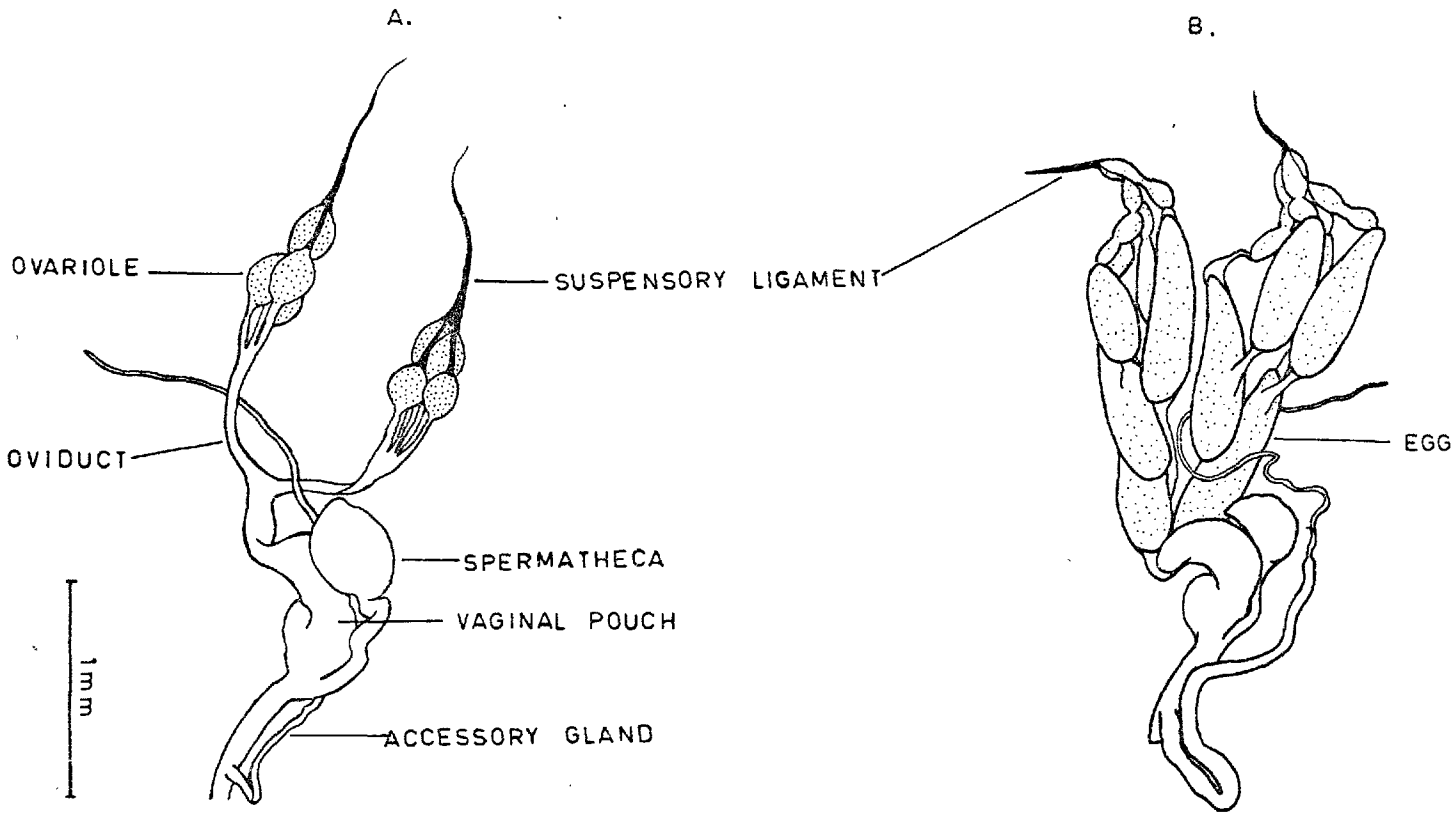


FIG 41 Female reproductive organs. A. immature form; B. mature form.

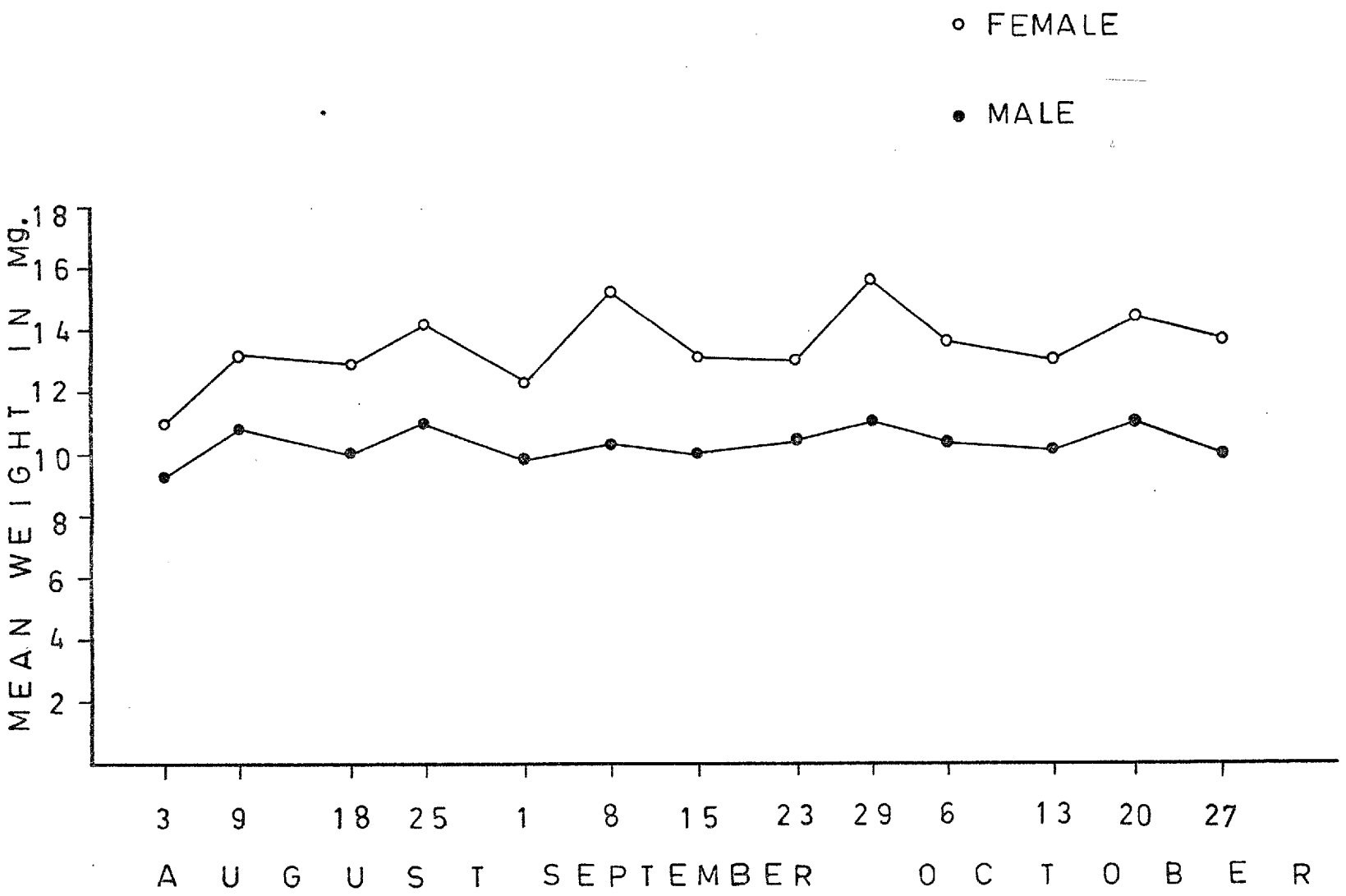


FIG. 42 Seasonal weight changes in *G. 'coccinea'*.

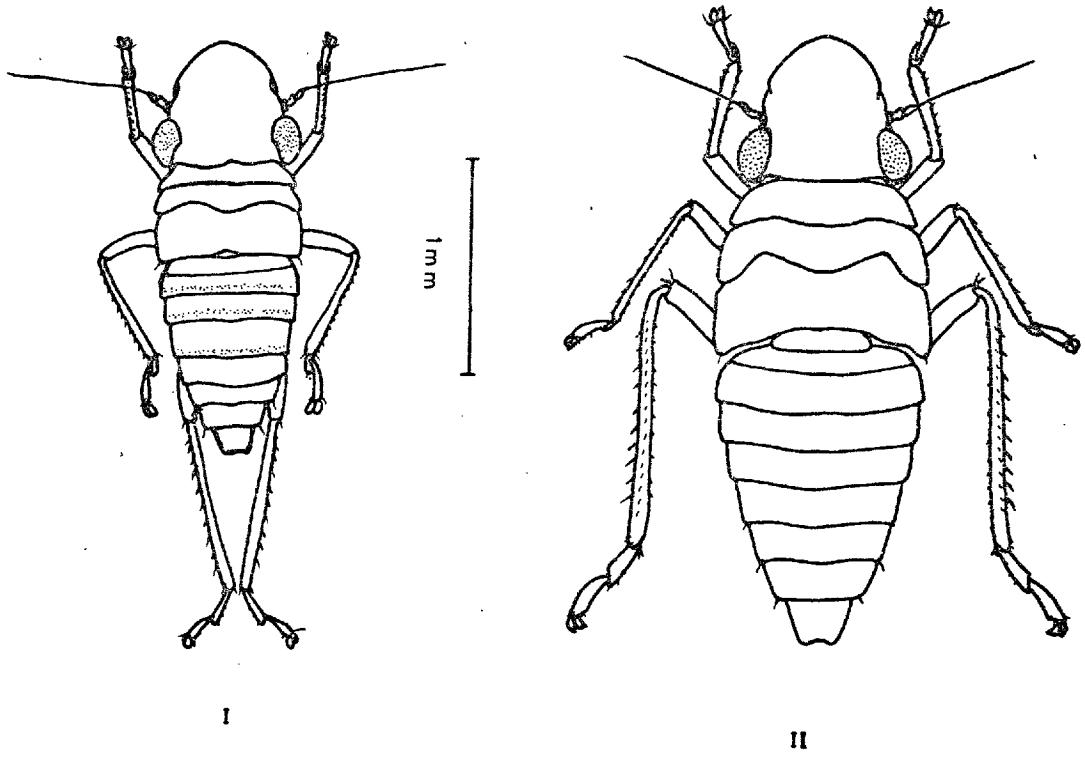
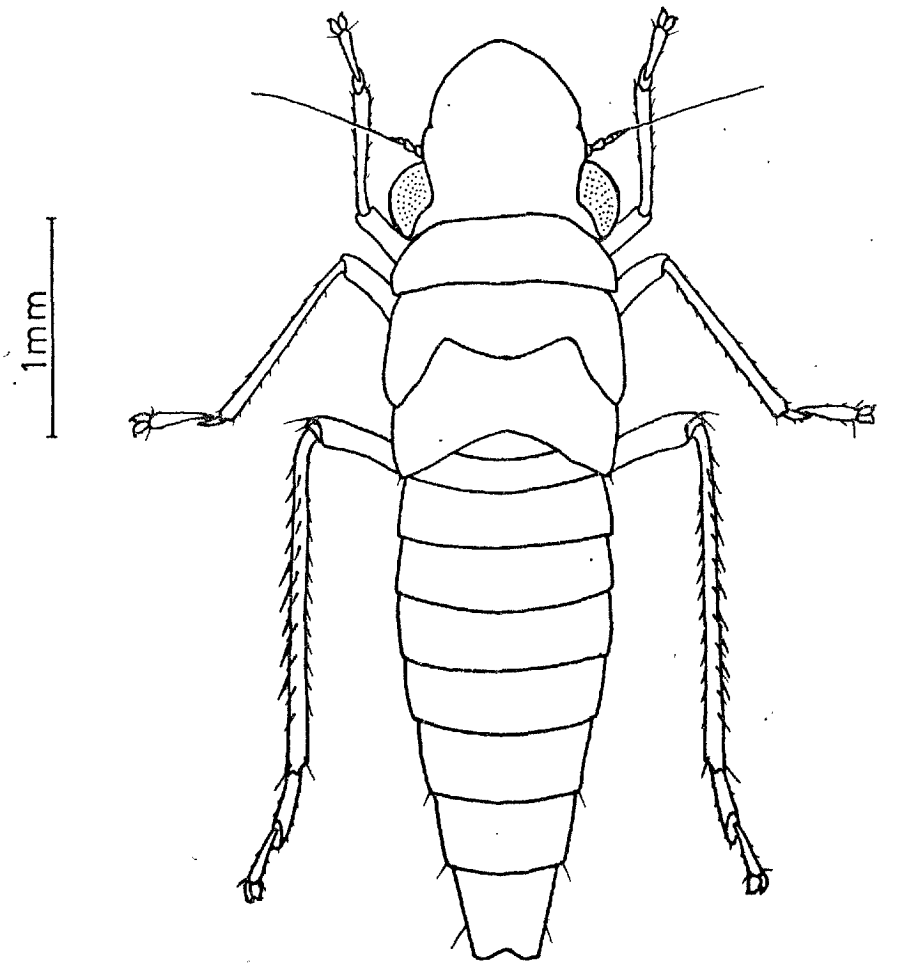


FIG. 43 I&II First and second instar G. 'coccinea'



III

FIG. 43 III Third instar G.'coccinea'

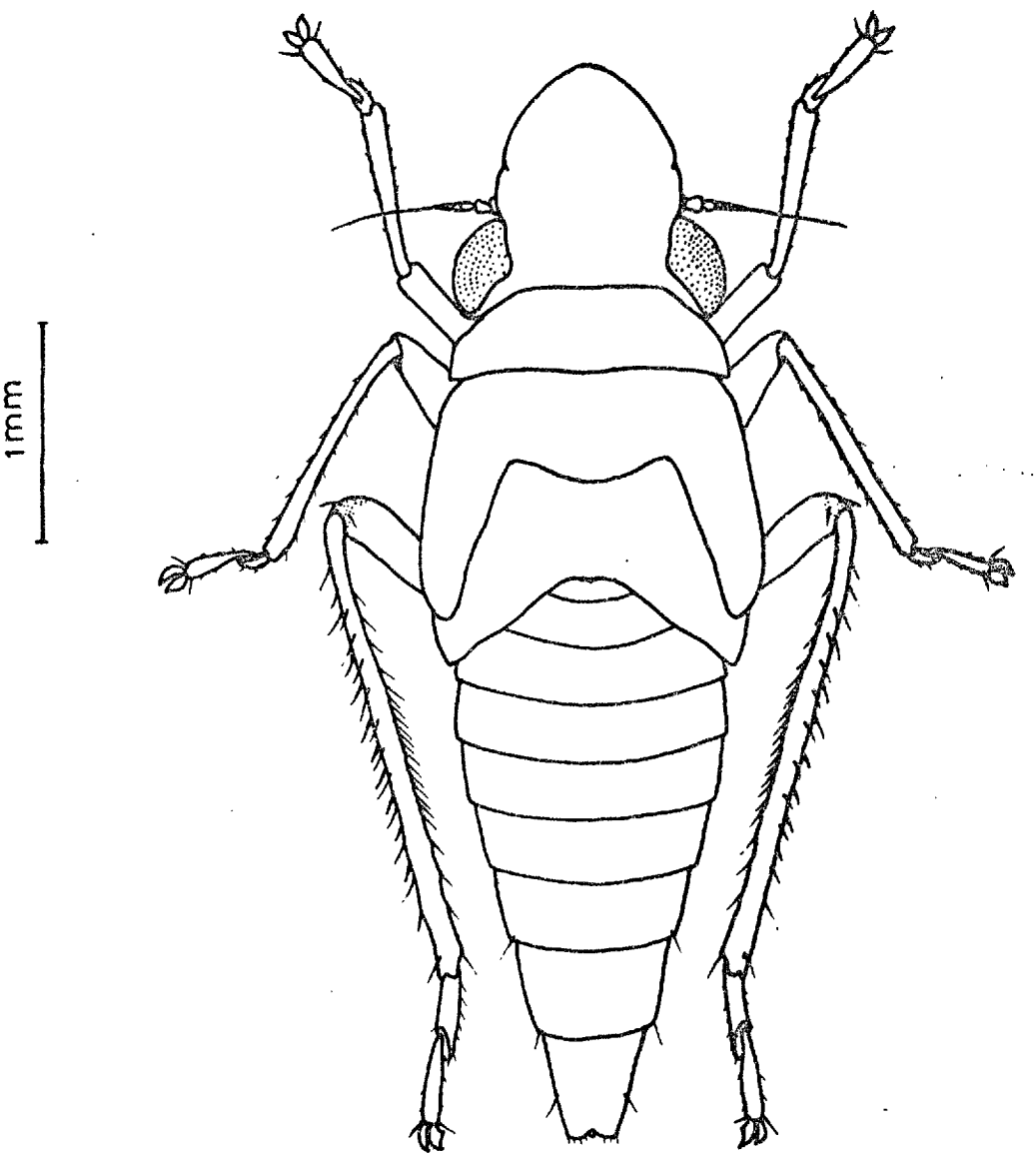
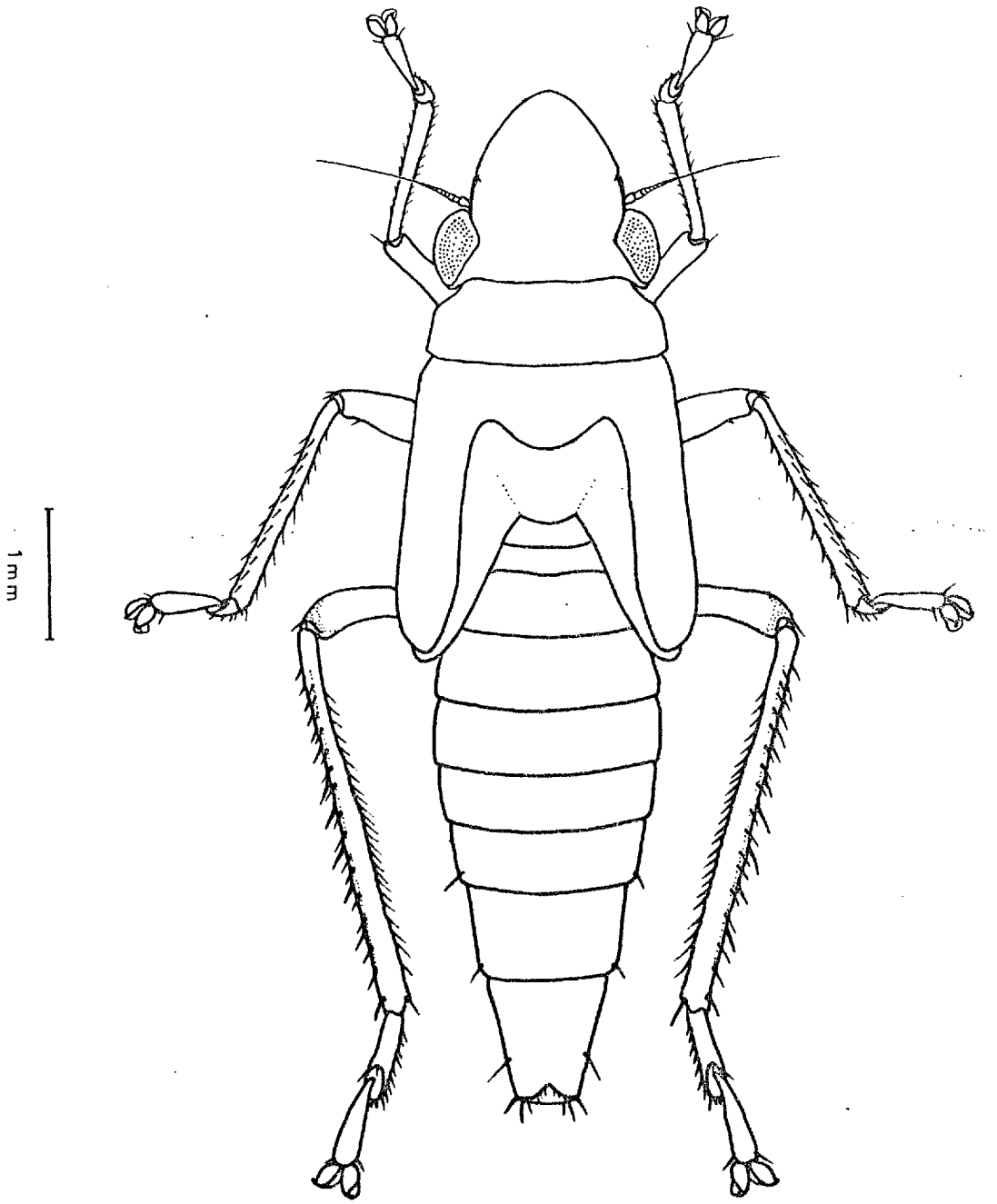


FIG. 43IV Fourth instar G.coccinea



V

FIG. 43V Fifth instar G. coccinea

the gravid females showed a slight increase in weight, the magnitude of this increase is much smaller than in C. viridis. This smaller increment is no doubt linked with the lower egg number present in the ovaries of G. 'coccinea'.

Absolute fecundity of the females was studied by enclosing mating pairs on Rhododendron flower buds with muslin sleeves. Description of the sleeve has been given on page 209. A pair of insects was enclosed in each sleeve with two flower buds, and the buds were then examined for eggs at the end of the season. Thirty sleeves were used. The number of eggs laid per female varied between 13 to 56 with a mean of 28.17 ± 1.79, about 70% of the females laying between 21 to 40 eggs. The fecundity of G. 'coccinea' is thus lower than that of C. viridis.

6. Mortality of the eggs, larvae and adults of G. 'coccinea'

6.1 Egg

No egg parasites or predators have been observed in the present studies. It would seem that when G. 'coccinea' was introduced into Britain, none of its parasites or predators were introduced simultaneously. Apart from birds it is not known what natural enemies exist in its native North America, as no record of parasites or insect predators were found in the existing literature.

In the laboratory, eggs of G. 'coccinea' were presented to the Mymarid egg parasite of C. viridis, Anagrus atomus. The eggs were presented in two ways: (i) The Rhododendron buds were cut up into single scales so that the embedded eggs

were fully exposed; (ii) The bud was presented as a whole, so that most eggs were concealed by the outer layer of the bud scale. A pair of Anagrus atomus were presented with one egg-bearing bud or one egg-bearing bud scale in a petri dish, with ten replicate for each. The eggs were examined for signs of parasitism after one week.

In both experiments, oviposition by A. atomus took place in two of the replicates. In eggs fully exposed on bud scales, three eggs were parasitisied, while in the case of the whole bud, five eggs were parasitisied.

The results showed that eggs whether concealed or exposed presented no problem to A. atomus, and the parasite larvae proceeded to develop normally in the eggs of G. 'coccinea'. In both cases the incidence of parasitisim is very much lower than when eggs of C. viridis are exposed to a similar experiment. This may be caused by the hairs on the Rhododendron bud scales which may hamper efficient search by the parasite; also when a bud scale is presented singly, the parasite often gets caught up in the sticky substances on the scale surface and dies.

The lack of parasitism by A. atomus could be explained by the behaviour of the parasite. Most natural hosts of A. atomus are grass feeding Homoptera, with their eggs laid in vegetation comparatively close to the ground; while eggs of G. 'coccinea' being oviposited on Rhododendron buds are comparatively high above the ground.

In the field it has been observed that flower buds heavily oviposited by G. 'coccinea' appear to be more susceptible to fungus disease, which in turn would destroy the eggs, Examination of thirty diseased and thirty healthy buds showed that the average number of eggs per bud was higher in the diseased buds. The mean number of eggs per healthy bud in 1970 was 28.97 $\pm$ 3.14, and the number on di seased buds was 37.20 $\pm$ 2.4; t = 2.0812 which is significant at 5% level.

Another cause of mortality was due to the characteristics of the host plants. In the spring when Rhododendron commenced flowering, all the bud scales tended to drop off and dehydrated. Any eggs remaining on these scales would die. Certain variety of Rhododendron e.g. 'Pink Pear', would bloom in late April, and thus any eggs oviposited on the buds would perish. The situation rather resembles that in newly hatched winter moth larvae, whose mortality depends on whether or not the hatching coincides with the bursting of Oak buds (Varley and Gradwell, 1968).

Mortality caused by fungus indirectly and the early blooming of Rhododendron, thus appear to be the major mortality factors in the egg stage.

6.2 Mortality in larvae and adults.

The main cause of mortality in the larvae and adults is probably predation. The main predators found on Rhododendron bushes in Silwood Park are the spider Linyphia triangularis, the earwig Forficula auricularia, Opiliones Oligiophus agrestis, Liobunum rotundum and a Mirid Dicyphus sp.

Of these species, L. triangularis and F. auricularia are always present in large number. Both larvae and adults are commonly seen caught in the webs of L. triangularis. Prec-ipitin tests were carried out to detect the predatory species. Predators were collected in the summer of 1971. The species tested and results of the tests are presented in Table 49.

The results indicate that Linyphia triangularis is probably the main predator of G. 'coccinea'. Although no positive reaction has been obtained with the earwig, laboratory rearing showed that the insect would readily take both larvae and adults of G. 'coccinea'.

North American G. 'coccinea' has been preyed upon by two species of vireos (Chapin, 1925). The two species mentioned were the blue headed vireo (Lanivireo solitarius) and the white eyed vireo (Vireo griseus). In Silwood Park, the house sparrow, the British great tit and the British blue tit are found among the Rhododendron bushes. All these species would feed on both vegetative materials such as fruits and seeds and as well as on insects. Feeding on G. 'coccinea' cannot be ruled out.

7. Flight and dispersal

7.1 Flight ability of G. 'coccinea'

The flight ability of G. 'coccinea' was studied by suspending the insect by the prothorax fixed to a pin with beeswax-rosin mixture. The procedure used is the same as for C. viridis. Flight on pin was carried out on three

Table.49. Predatory species tested for the presence of G. 'coccinea' antigen.

Species	No.tested	No.of positive	Percentage positive
Forficula auricularia	15	0	0
Oligiophus agrestis	25	1	4.0
Leiobunum rotundum(Lat.)	14	0	0
Linyphia triangularis	28	10	35.7
Theridion denticulatum	9	0	0
Dicyphus sp.	21	0	0

occasions: first, during early August when the insects were sexually immature; then in early September, when the females were just about to commence oviposition; and thirdly in early October, when the females were ovipositing and some of the males were beginning to die off. On each occasion, ten males and ten females were flown. The average of ten flight was taken as the flight duration of which an insect is capable. Flight was induced by firstly letting the insect rest on the bench, then sharply lifting it into the air. The temperatures during the experiments were between 21.5°C to 22°C, and the relative humidity between 59.4 to 61%.

The results are presented in Table 50. All individuals flew readily, with the exception of one male in its sexually immature stage. Average flight durations for the three occasions were between 3.04 to 5.13 seconds. Analysis of variance showed that there was no significant difference in the mean flight durations between individuals on the three occasions. This would suggest that in G. 'coccinea' ability to fly does not change with maturation or age. Flight ability of G. 'coccinea' thus differs from that of C. viridis in two aspects: (i) The flight durations between individuals are more uniform, with a suspended flight duration varying between 0 and 11.67 seconds. In C. viridis this varied from 0 after oviposition has commenced to 21 minutes 25 seconds in one immature female tested. (ii) In C. viridis, sexual maturation is accompanied by a reduction in the ability to fly, which is

Table 50. Mean suspended flight duration of G. 'coccinea' in seconds.

7th August		6th September		8th October	
Male	Female	Male	Female	Male	Female
1.80	4.88	2.15	3.60	5.07	3.66
3.30	3.24	3.26	4.09	3.38	3.94
6.40	7.10	2.19	3.35	4.08	7.80
6.70	7.98	2.69	5.57	4.37	3.77
6.14	3.71	3.78	5.39	5.45	3.21
4.25	6.40	4.52	3.67	5.20	5.12
6.43	6.05	5.95	4.45	4.99	2.83
11.67	3.13	5.01	2.77	2.99	5.43
4.63	3.23	4.78	5.06	4.00	5.06
0	2.68	2.38	4.82	2.82	2.79
Mean duration $5.13^{\pm}_{1.0}$	$4.84^{\pm}_{0.6}$	$3.04^{\pm}_{0.4}$	$4.28^{\pm}_{0.3}$	$4.24^{\pm}_{0.3}$	$4.36^{\pm}_{0.5}$

Variance analysis.

Source	Sum of square	Degree of freedom	Mean square	F.	
Between flight duration	13.0305	5	2.6061	0.8045	N.S.
Residual	174.9320	54	3.2395		
	187.9625	59			

N.S. = Not significant.

not the case in G. 'coccinea'. Nevertheless, when immature some C. viridis appear to be much stronger fliers than G. 'coccinea'.

7.2 Periodicity of flight

Flight periodicity was observed briefly in October 1971, over a period of six days with the aid of a cylindrical sticky trap. The surface area of the trap was 0.09 m^2 and it was hung over a low Rhododendron bush at a height of 1.4 metres above the ground. A day was divided into four periods, i.e. between 6 to 9 a.m., 9 a.m. to 12 noon, 12 noon to 3 p.m. and 3 p.m. to 6 p.m. The trap was examined five times a day at 6 a.m., 9 a.m., 12 noon, 3 p.m. and 6 p.m. and the number of insects caught on the trap collected. Temperature, relative humidity and light intensity were measured during the middle of each period. Light intensity was measured with a 'Launasix 3' photographic light meter, and the scale reading was then converted into lux units with the conversion table provided with the meter.

The total number caught between 6 to 9 a.m. was nil, between 9 -12 noon 9, between 12 noon to 3 p.m. 80, and between 3 to 6 p.m. 40. The males to females caught were 30 : 99, giving a ratio of 1 : 3.3. Coefficients of correlation between the numbers caught on trap and temperature, relative humidity and light intensity were calculated. There is a positive correlation between the number of insects caught and temperature; $r = 0.5859$, $t_{24} = 3.3911$,

which is significant at 1% level. A weak negative, but not significant correlation was found with relative humditiy ($r = -0.2316$, $t_{24} = 1.1167$, at 5% level, $t = 2.064$). No correlation was found with light intensity as well ($r = 0.0086$, $t = 0.0403$).

The result indicated that G. 'coccinea' is most active in a period between 12 noon to 3 p.m. and less so between 3 p.m. to 6 p.m. (British Summer time) This is probably mainly caused by the rise in temperature in the later half of the day. A similar result was obtained by Lewis and Taylor (1964) using a suction trap located in the Rothamsted Experimental Station. Lewis and Taylor have also detected some activity during the night. Light intensity, although it bears no correlation with the numbers caught on the sticky trap, appears to play an important part in the flight activity of G. 'coccinea'. A set of sticky traps located in the shade close to a Rhododendron bush seldom produced any catches.

7.3 Dispersal

Sticky traps and suction traps were used to study the dispersal of G. 'coccinea'.

a. Sticky trap

Cylindrical sticky traps with a surface area of $0.09m^2$ were used. The traps were arranged in two tiers, at 1 metre and 1.5 metres above the ground level. Traps were set up in the Japanese Garden within Silwood Park (see Fig.1 for location). Four sets of traps were arranged at a

distance of 2, 4, 8 and 16 metres from the Rhododendron bushes and placed in an exposed position; another set of four traps were similarly arranged, but were located inside woodland and therefore shaded. Trapping was carried out between mid July and mid October of 1971.

During the three months of trapping, a total of 36 insects were caught on the traps set in the open. Majority of the insects were caught between September and mid October. In terms of height, 22 insects were caught on traps 1.5 metre and 14 at 1 metre above ground level. The number caught at 2, 4, 8 and 16 metres from the Rhododendron bushes were 26, 7, 2 and 1 respectively.

Only two insects both females were caught on traps set up under the shade of wood. One was caught at 2 metres and one at 4 metres away from Rhododendron bushes, but both were at the height of 1.5 metre.

During 1970, similarly designed sticky traps were set up to study the dispersal of C. viridis in the Rush Meadow. G. 'coccinea' was caught on these traps on three occasions. One male was caught at 1 metre height on 1st September; one male and one female were caught at 1.5 metre on the 3rd, and one male caught at 1.5 metre on the 5th of September. The nearest Rhododendron bushes were well over two hundred metres to the West of the traps. On the day the insects were caught the wind speed taken at 30.5 metres (100 feet) high on the nearby Pond Field Hill averaged 11,

6, and 9 knots per hour on the 1st, 3rd and 5th of September respectively, with the wind direction being West, West-North-West and South-South-West; and the maximum temperature being 16.75, 15.5 and 22.0°C. It is therefore highly probable that the insects were carried or were assisted by the wind.

b. Suction trap

Two suction traps of the Johnson and Taylor (1955) 18 in. propeller type are located at Silwood Bottom. One trap is 1.22 metre (4 ft) high and the other 12.2 metre (40 ft) above the ground. The nearest Rhododendron bushes are about 95 metres South of the traps. Some G. 'coccinea' were caught in these traps occasionally. The number caught in 1970, 1971 and the weather condition when caught are summarised in Table 51.

7.4 Discussion

The absence of catch on traps set in the shade shows that G. 'coccinea' prefers to fly in localities with plenty of sunshine. In terms of vertical distribution, more insects were caught on traps 1.5 metres high than at 1 metre, but few were caught in the suction trap 12.2 metres high.

The very sharp drop in the number of insects caught between 2 metres and 4 metres away from the Rhododendron bushes suggested that movements of most G. 'coccinea' are generally confined to the immediate vicinity of the food and breeding site, with occasional individuals venturing

Table 51. The number of G. 'coccinea' caught in suction traps in 1970 and 1971.

Date	No. caught	Trap height in metre		Average wind speed in knots/hr.	Wind direction	Max. temp. ^{0}C
		1.22	12.2			
1970 Sept.18-21	1		x	3-4	mainly N.N.W.	21.5to 25.0
	1	x				
22	1	x		7	E	17.75
24-25	1	x		3	S	20.75 to 21.75
27	1	x		5	S	20.75
1971 August 24	1		x	4	E	21.25
Sept. 10.-12	1	x		3 - 5	E	20.0 to 20.25
23	1	x		7	W.S.W.	20.0
30	1	x		6	N.S.W.	20.25

further afield.

Although suspended flight experiments showed that the flight ability of G. 'coccinea' remains constant throughout its adult life, catches in traps at distances away from Rhododendron all occurred in late August and September, which suggests a definite increase in flight activity during that period. Nearer to Rhododendron bushes, this increase in activity appeared to continue into October. Female insects caught and dissected all had matured eggs, and from the life history study, it is known that oviposition commenced in the second week of September. In the females this increase in activity may be associated with searching for oviposition sites, but it is difficult to explain it in the males. Johnson (1969) discussing insect take off in general, suggested that the strength of stimuli needed to induce take off vary with the state of balance between internal inhibition and excitation, and this varies with age, sexual maturation and other internal factors. It seems that this readiness to take off may account for increased activity in September.

Because of the low number of catches in traps, it was not possible to carry out a meaningful correlation analysis to determine the association of dispersal with weather factors. Temperature light and wind speed undoubtedly played a major role. In long distance displacement, the wind speed may be of particular significance, since all individuals trapped at a distance away from Rhododendron

bushes were caught on warm days with temperatures between 16.5 to 25°C and an average wind speed between 3 to 11 knots. In conclusion, it can be said that G. 'coccinea' are most active in the early part of the afternoon. While flight activity remains the same throughout adult life, it appeared that readiness to take off varied with age. Although the insect is by no means a strong flying species, long distances can be covered in suitable weather conditions. There are no signs of mass movements away from the habitat, dispersal seems to depend on random flying of individuals and landing on the right habitat by chance.

GENERAL DISCUSSION

This discussion is divided into two parts, the first is concerned with the biology of the two species of Cicadellinae, and the second considers the population of *Cicadella viridis*.

1. *Biology of the two species.* *Cicadella viridis* and *Graphocephala* '*coccinea*' are the only two British species within the subfamily Cicadellinae. In the present study only the bionomics of *G.* '*coccinea*' were examined, whereas the population ecology of *C. viridis* was studied for three successive seasons.

There is a great deal of similarity in the biology of the two species and the close relationship of the two genera is also indicated by the strong cross-reaction between their antisera with each other's antigen in the serological tests. Further, Kathirithamby (1971) who worked on the morphological characters of the Cicadellidae again demonstrated close relationship between these hopper species by the method of single cluster analysis.

In Britain, both species are univoltine, and overwinter in the egg stage. The diapausing eggs are characterised by their extreme cold-hardiness, their undercooling point being in the region of $-29^{\circ}C$. Temperature appears to be the main factor leading to the breaking of diapause and photoperiod probably plays little part. With the eggs of *C. viridis*, a period at low temperature has the effect of accelerating subsequent development at high temperature.

However, most eggs of both species are capable of development without having to pass through a period at low temperature. Under these conditions, the incubation period is long and the spread of the hatching period is prolonged. In G. 'coccinea' the proportion of eggs capable of such development is smaller than in C. viridis, indicating a more intense form of diapause. Incubation at different temperatures also produces a smaller response in the developmental rates of the eggs of G. 'coccinea' than of C. viridis.

Andrewartha (1952) coined the term 'diapause development' to cover physiological development which goes on during diapause in preparation for resumption of morphological development, and it is equivalent to 'reactivation' of Danilevskii (1965). Ability to complete diapause development at high temperature has also been observed in other insects such as Lymantria dispar (Masaki, 1956) and Acheta commodus (Browning, 1952; Hogan, 1960). In another species of Cicadellidae, namely Colladonus geminatus, there was no obligatory dormancy in the overwintering egg stage and low temperature merely delayed development (Kaloostian, 1956). Clearly, the ability to complete diapause development at high temperature would enable a temperate species to spread into warmer regions of the world. As the taxonomical position of British G. 'coccinea' is still not clear, its distribution is at present unknown. However, judging from its more intense form of diapause and its smaller response in its developmental

rate to temperature, its North to South distribution should be more restricted than that of C. viridis. The fecundity of C. viridis is higher than that of G. 'coccinea' and this is reflected in its smaller ovaries and a lower number of eggs per ovariole. Also, the seasonal changes in body weight of females are smaller in G. 'coccinea' than in C. viridis. Although no numerical estimations were carried out of the eggs of G. 'coccinea', no predators, parasites or attacks by pathogens have been encountered. It is probable that egg mortality in G. 'coccinea' is lower than in C. viridis and this in temperate climates would compensate for its lower fecundity. Durations of the larval stages and the preoviposition periods of the adult females are somewhat longer in G. 'coccinea' than in C. viridis.

Throughout this period of study, no mass migrations in or out of the habitat have been observed, and all movements were generally confined to the immediate vicinity of the habitat. Flight ability of the two species was studied in the laboratory by suspending the insects by the thorax on to a pin with a beeswax rosin mixture. The results indicated that, flight activity of G. 'coccinea' was more uniform among individuals and throughout the adult life, and there were no differences between the sexes, although the readiness to take off varied with age. The females of C. viridis are stronger flyers than the males, but they ceased to fly after oviposition had commenced. There was

a great variation in the ability to sustain continuous flight between individuals which could be called strong and weak flyers. On the whole C. viridis showed greater ability to sustain longer continuous flight than G. 'coccinea'. But more G. 'coccinea' than C. viridis were caught on suction traps and sticky traps set up at various distances from their breeding grounds. This is probably related to behaviour and body build rather than to flight ability. C. viridis is not a very active insect, and lives among grasses and rushes close to the ground, while G. 'coccinea' is active and is commonly found flying among the Rhododendron bushes. G. 'coccinea' also has the advantage of having a greater wing area and lighter body weight which may enable it to be more efficiently carried by air currents. A rough calculation showed that the wing area to body weight ratio in G. 'coccinea' is about 0.5 kg/m^2 in comparison to 0.8 kg/m^2 in C. viridis. Glick (1939) while collecting from an aeroplane had recorded catches of North American G. 'coccinea' at the height of up to 610 m (2,000 ft).

Active flight in C. viridis is limited to the preoviposition period, which may suggest that it is linked with colonisation of new suitable breeding sites. On the few occasions where long distance displacements were observed by catches in suction traps or on sticky traps, the nearest breeding ground was invariably 'poor' with only a few isolated clumps of Juncus. It is probable that C. viridis is stimulated to fly out of declining habitats.

Catches of G. 'coccinea' in traps at distances away from Rhododendron bushes all occurred in late August and in September, which suggests a definite increase in flight activity during that period. This could be explained by Johnson's (1969) postulation that readiness to take off varies with age. Another possible reason is probably linked with competition for oviposition sites. Examination of Rhododendron buds around Silwood Park during 1969 and 1970 showed that 69 to 100% of the buds had been oviposited upon. If this tentative suggestion is true, it is possible that the migratory habits of the two species are linked with the availability of breeding sites.

In literature, no distinguishable morphological differences between the British, European and East Asiatic specimens of C. viridis are given, yet biologically they differ in voltinism and in the type of host plants used for oviposition. On the Continent of Europe, the number of generations per year varied from one in Germany (Schindler, 1960), two in Bulgaria (Dirimanov and Kharizanov, 1964), and three with an occasional incomplete fourth generation during autumn in Central Italy (Frediani, 1955). The increase in the number of generations appears to be correlated with a corresponding increase in the temperature of the locality concerned. Germany is to the North of both Italy and Bulgaria, but the latter two countries occupied almost the same latitude. According to Thran and Broekhuizen (1965) the

mean monthly temperature of Bulgaria is generally two or three degrees lower than in Italy.

When there is more than one generation a year, it is essential for some generations to go through without diapause. This plasticity is still retained in the British C. viridis as was indicated by the ability of eggs to hatch without having to pass through a period at low temperature. Rearing of British C. viridis at different temperatures however, showed that at 25°C the time taken to complete larval development and the duration of the preoviposition period were still much longer than in the multivoltine species on the Continent of Europe, also at 30°C the insect did not do well and few survived. This indicates that there may be a more fundamental difference in the genetical structure of the Continental and the British strains of C. viridis and even in the most favourable environmental conditions it would be difficult for the British strain to complete two generations a year.

There are many species in which the number of annual generations varies regularly in different parts of their geographical range. Among the insects, the European cornborer Ostrinia (Pyrausta) nubilalis (HB.) is a familiar example. This species is widely distributed in Europe with well defined one-generation and two-generation areas. The species is univoltine in Northern France, Germany, Hungary and Northern Yugoslavia and bivoltine in Southern France, Italy,

Greece and Southern Yugoslavia (Badcock, 1927; Badcock and Vance, 1929).

The mechanism of diapause in C. viridis has not been fully investigated in the present study. However, all detailed studies on diapause and hence of voltinism in the present days have to be considered in conjunction with photoperiodism as has been both discussed and demonstrated by Lees (1955) and Danilevskii (1965). The effect of photoperiod on egg diapause had been demonstrated in the silkworm Bombyx mori by Kogure (1933), where he showed that continuous illumination of eggs incubated at 19°C produced 97% of moths that would lay diapause eggs. A further significant feature is that the egg becomes reponsive only quite late in its embryogenesis, when all the organ systems have been differentiated. Danilevskii (1965) also provides other examples e.g. in the Noctuid moth Acronycta rumicis, where the response to the day-length which induces diapause was different in insects from different latitudes. Whether C. viridis would exhibit similar responses to photoperiod is not known. The fact that Bulgaria and Italy are situated in about the same latitude and yet C. viridis from each of these countries have different voltinism probably suggests that photoperiod plays little part.

It would be of interest to see whether British C. viridis could mate with those from the Continent of Europe. But, undoubtedly C. viridis is a species with a complex

group of many races each capable of adapting itself to different environments to the best advantage. This adaptability is probably a characteristic of most widely distributed species, as is evident in another Cicadellid, Macrostelis fascifrons. Studies on its ecology, and economics have revealed isolated populations of this species which were biologically, ecologically, or physiologically specific, but could not be separated morphologically (DeLong, 1971).

2. Population ecology of C. viridis Numerical estimations of all the stages of life history throughout the three years of study have already been described. The following is an account of the methods used in analysing the field data, and an attempt to evaluate the importance of the recognised mortality factors and to gauge their impact on the population of C. viridis.

In the studies of the population of C. viridis, three methods of estimating the number of recruits entering a stage were used. These are Richards and Waloff's (1954) regression method; Richards, Waloff and Spradbery's (1960) method, and the method of Kiritani and Nakasuji (1967). In general it is impossible to judge which method is the best, as the requirements for an accurate estimation by each method are different. The prerequisite for the method of Richards and Waloff (1954) is a distinct peak number in each of the developmental stages. The method of Kiritani and Nakasuji (1967) requires frequent sampling at relatively short inter-

vals of time; and in populations with differential mortality rates, an accurate estimate of larval durations and of the adult life span. The method of Richards et al (1960) also requires an accurate estimation of the duration of larval stages. Any set of requirements depend on the nature of the population studied, sampling technique and the response of the insect concerned to artificial rearing in laboratory conditions. Kiritani and Nakasuji's (1967) claim that their method is superior to that of Richards and Waloff's regression method is therefore hard to justify, though their method does have the advantage of ease of calculation. In the present studies the method of Richards et al (1960) is considered the most suitable because of the consistency of results obtained.

Richards (1961) considered that in a climate like that of Britain where all years are in some respect exceptional, a minimum of five years period is required to get a useful idea about population dynamics of a species. While no definite conclusion can be drawn from data based on three seasons about the regulatory processes in the population of C. viridis, there is sufficient evidence to give an indication as to which are the major factors that may influence the abundance or otherwise of the population.

The essential results of the population work are presented as a budget contained in Tables 28, 29 and 30. During the seasons studied, there was little visible change within the habitat which could have influenced the population

of C. viridis.

From the study of the undercooling point of eggs, it is clear that low temperature is unlikely to result in any egg mortality. The main causes of mortality in the egg stage can be recognised as fungal infection, parasitism, predation, sterility and other undetermined causes.

Numerically, fungal infection causes the greatest mortality. In 1969 death due to this cause amounted to 38%, in 1970 69% and 67% in 1971. The fungus Tritirachium sp. has been identified as the main pathogen. Death may also occur when the rush stems are attacked by other fungi such as Melanospora sp. Tritirachium sp, though it has been recorded to attack other insects (Maran, 1948; Macleod, 1954), has never assumed such importance as a mortality factor as in the case of C. viridis eggs. A linear relationship was obtained when the initial density of eggs was plotted against the number that died of fungus attack (Fig. 30), which seems to indicate that death from fungal attack is a density related process.

Parasitism has contributed less than 10% of the total egg mortality. Anagrus atomus is the only egg parasite encountered. The species is also known to attack eggs of other Homoptera. This non-specificity of choice of hosts may be one of the reasons for the low level of parasitism in eggs of C. viridis. The behaviour of the parasite could be another reason. It was found that C. viridis eggs laid

between the height of 21 to 30 cm on the Juncus stems are most liable to attack by A. atomus, but the majority of the eggs, are laid below 15 cm and thus escape the attack by the parasite. As illustrated in Fig.29 the level of parasitism remains constant for the three seasons. The theoretical possibility of regarding the effect of parasite to be density dependent may not apply in the present case. The effect of predation on the egg population is also slight. This again is probably due to the non-specificity of such predator as Cyrtorhinus caricis and Tytthus pygmeus, which could feed on the eggs of a vast number of other Homoptera present in the same habitat.

A small proportion of eggs laid each yearare infertile. The level of infertility seems to be constant for the seasons studied. The actual number varied from 78,000 (1.52%) in 1969 to 62,500 (0.70%) in 1970 and 52,000 (0.51%) in 1971. The cause of this infertility is not know, but at such low level it is unlikely to have any impact on the population as a whole.

Included in the category of other mortality factors are those eggs destroyed by the oviposition activity of other Homoptera, notably Conomelus anceps and Delphacodes fairmairai; as well as the eggs destroyed by agents not identified. C. anceps and D. fairmairai also lay their eggs in Juncus stems, and occasionally they will oviposit into a batch of C. viridis eggs and destroy it. The number of eggs destroyed

in this way is small, but it is likely to increase if there is a great increase in the population of these two species of Homoptera.

When oviposition behaviour was examined, it was found that there was a distinct preference for C. viridis to lay eggs in Juncus stem of a large diameter; also the females appear to avoid laying on stems that had already been oviposited upon. This latter tendency is indicated by the fact that the number of Juncus stems containing more than one egg mass decreases as the number of egg masses per stem increases. Thus out of a batch of 391 egg-bearing Juncus stems, 144 stems had one egg mass, 95 were with two, 49 with three, 33 with four, 59 with five to ten and only eight with more than eleven egg masses. The maximum number encountered was 24 egg masses on a single stem. In spite of this, there is no shortage of plant hosts for oviposition, as not more than 20% of the total avilable Juncus stems were laid in. There is therefore no evidence of intraspecific competition for egg laying sites, but interspecific competition with other Homoptera cannot be ruled out, particularly if there is a great upsurge in the numbers of C. anceps and D. fairmairei.

The relative importance of various known mortality factors was analysed with Varley and Gradwell's(1960) graphical method. By means of visual correlation it is clear that k_{12} i.e. mortality due to fungus, is the factor

that produces the greatest effect on egg numbers (Fig. 29).

Inspite of the fluctuation in egg numbers, the larval and adult population during the three seasons studied seem to remain relatively constant. Two species of mites Charletonia singularis and Leptus ignotus are commonly found attached to both larvae and adults C. viridis. But insects infested with these mites showed no apparant deleterious effects on their growth or survival.

Precipitin test and feeding trials carried out in the laboratory show that spiders and 4 species of Nabidae are the main predators of larvae and adult C. viridis. With the absence of any internal parasites, predators are undoubtedly the main contributors to the mortality of C. viridis. The species of predators involved are five spiders: Clubiona reclusa, Xysticus cristatus, Theridion ovatum, T. bimaculatum. Linyphia clathrata and four species of Nabidae: Dolichonabis limbatus, Stalia major, Nabis rugosus and Nabis flavomarginatus.

Not sufficient work has been done to assess the contribution of each individual species to the mortality of C. viridis. But, as a whole, the two groups of predators i.e. spiders and Nabidae are probably complementary to each other in their effect on the population of C. viridis, and the level of predation seems to be constant in 1970 and 1971. This is illustrated by the fact that the spider population in the Rush Meadow during 1970 is higher than in 1971 and

the reverse is the case for the population of Nabidae (Fig. 31 & 32). Inspite of the fluctuation in the numbers in each group of predators, the final population of C. viridis remained constant. The estimated initial numbers of the first instar C. viridis larvae in 1970 are 1,775,944 and the initial number of adults are 128,437, while in 1971 the figures are 1,828,344 for the first instars and 112,309 for the adults. None of the predators mentioned feed specifically on C. viridis. In fact, all would feed on the vast number of other species of Homoptera and other insect species present in the habitat. Although it is difficult to arrive at any definite conclusion based on two or three years' results, it may be speculated that the stable state of larvae and adults of C. viridis population is the result of the non-specificity of the predators. With the presence of abundant alternative prey species in the habitat, the population of spiders and Nabidae are probably in no way dependent on the population of C. viridis, which in turn may provide a constant level of predation on C. viridis.

Experiments on food plant preferences showed that C. viridis survived very well on Holcus mollis. But if it was fed on Ranunculus repens alone, the fifth instars had difficulty in developing into adults, because of a shortage of Nitrogen in Ranunculus during that time of development. However, in the field, feeding on both species of plants is most likely to take place, and the two species of plants were abundantly present during the period of study. The

usual type of intraspecific competition which ultimately sets an upper limit to all populations is competition for food (Nicholson, 1933, 1958; Milne, 1961; Solomon, 1964). Within the conditions of Rush Meadow, competition for food was unlikely to have taken place during the last three years.

The weather conditions over the period of study were, on the whole, rather similar. Apart from the influence of temperature on development, there were no major observable changes in population which could be attributed to climatic factors. But the potential effects of climate in causing annual fluctuation is certainly there. The adult C. viridis has been occasionally attacked by an Entomophthora sp. of fungus. In general fungal pathogens infect insect hosts not so much through ingestion as by penetration into the body cavity through the cuticle. This requires conditions of adequate moisture and humidity. It is quite possible that the low number of eggs found in the 1968-69 season could be the result of the exceptional amount of rainfall during the autumn of 1968. High humidity and rain probably promote fungal infection of the adults and at the same time may interfere with oviposition activity. There is no evidence to support this as the present work did not start until spring of 1969.

Varley and Gradwell's (1960) graphical key factor analysis was carried out to determine at which stage mortality is most likely to affect the population. As shown in Fig. 33,

mortality occurred in k_1 i.e. mortality in the egg stage appears to be the most influencial factor in deciding the size of subsequent populations. As has already been discussed earlier, the factor that produces the greatest effect on egg numbers is fungal infection. From information available up to date, it can be suggested that the main regulatory factor of the size of C. viridis population, is egg mortality caused by fungal attack. Mortality in the larval and adult stages is influenced by predators, but since they are non-specific, it is possible that their effects are stabilising rather than disturbing or regulatory. Dispersal and migratory flight had little influence on altering population size throughout the period of study, but its potential effect in years of drought and drying up of the habitat is realised, though it remains unknown.

SUMMARY

1. The life cycle of Cicadella viridis and Graphocephala 'coccinea' in Britain are rather similar. Both are univoltine with eggs as the overwintering stage. Larvae emerged in the following spring during mid May and continued into the first week of June. Adults emerged in July, and egg laying in C. viridis commenced at the end of August, while G. 'coccinea' did not commence laying until the second week of September. Male C. viridis are short lived and die off by mid August, while male G. 'coccinea' live almost as long as the females.

2. According to Dr. D.A. Young (Private Communication, 1971), the British species of Graphocephala 'coccinea' is not the same as the species bearing that name in North America.

3. Overwintered eggs of both species could hatch without having to pass through a period at low temperature. In G. 'coccinea' the proportion of eggs capable of immediate development is smaller than in C. viridis. With the eggs of C. viridis, a period at low temperature has the effect of accelerating subsequent development at high temperature and synchronisation of hatching. Overwintered eggs of both species have a very low undercooling point which is in the region of $-29^{\circ}C$.

4. Eggs of G. 'coccinea' are laid in the bud scales of Rhododendron buds. C. viridis laid its eggs in Juncus stems, and had a preference for stems of large diameter.

There are also signs that the females of C. viridis avoid laying in stems which have already been laid upon.

5. The larval and adult stages of both species are described, and measurements of head width, head length, hind femoral and tibial lengths were made. In both species, the head length of the fifth instar and the adult remains the same. In G. 'coccinea' the rate of growth in successive instars of the body parts measured, on the whole, confirmed Richard's (1949) extension of Dyar's law. However, the femora and tibia of C. viridis grow at a faster rate in the third, fourth and fifth instars than in the earlier stages.

6. The internal reproductive organs of both species are described. The size of the ovaries is larger in C. viridis than in G. 'coccinea', and also have a higher number of eggs per ovariole.

7. Anagrus atomus (Mymaridae) is the only egg parasite of C. viridis. Eggs of C. viridis laid between the height of 21 to 30 cm on the Juncus stems are most liable to be attacked by the egg parasite. Under laboratory conditions A. atomus could parasitise and develop in the eggs of G. 'coccinea'.

8. Results of rearing experiments showed that although C. viridis laid its eggs in Juncus stems, the hatched larvae could not survive on it. In the environment studied Holcus mollis is probably the best food plant during the larval stage. Nitrogen content of the food plants appears to be the

main factor affecting the survival of larvae.

9. Both species are not strong flyers, but appear to have adequate powers of dispersal. Most movements observed were confined to the immediate vicinity of the habitat.

10. Population ecology of C. viridis was studied for three successive seasons. Egg sampling was carried out in the winter months by collecting and examining the egg-bearing Juncus stems. Larvae and adults were sampled at regular intervals with a Dietrick suction sampler and also by direct counts.

11. The egg population in 1969 was estimated as 5,105,726 and was lower than in 1970 and 1971 when the numbers were 8,826,752 and 10,281,028 respectively. The method developed by Richards, Waloff and Spradbery (1960) was used successfully to estimate the initial number of recruits entering a stage. Population budgets for 1969, 1970 and 1971 are presented.

12. The greatest losses in population numbers occurred during the egg stage and during the first and second instars.

13. Mortality in the egg stage is caused by fungal infection, the egg parasite, predators, egg sterility and other miscellaneous causes such as the oviposition activity of other Homoptera. Fungal infection causes the greatest loss of eggs, it was also identified by the Varley and Gradwell's (1960) graphical key factor analysis as the key factor affecting the egg population.

14. Larvae and adults are free of internal parasites. Adults are occasionally attacked by Entomophthora sp. Two species of ectoparasitic mites Leptus ignotus and Charletonia singularis are commonly found on both larvae and adults, but do not cause any ill effects to the host.

15. Predators appear to be the main contributors to mortality of the larvae and adults. Precipitin tests and feeding tests show that the major predators are five species of spiders and four species of Nabidae.

16. Weather, dispersal and migratory flight had little influence on altering the size of the population.

17. Graphical key factor analysis shows that fungus induced mortality in the egg stage is the most influential factor in determining the size of C. viridis populations.



Plate 1. Close up view of Juncus, Holcus and Ranunculus growth in the Rush Meadow.



a.

b.

Plate 2. Cages used for rearing C. viridis and G. 'coccinea'.

a. Cylindrical cellulose cage with flower pot; b. Watkins and Doncaster cage.

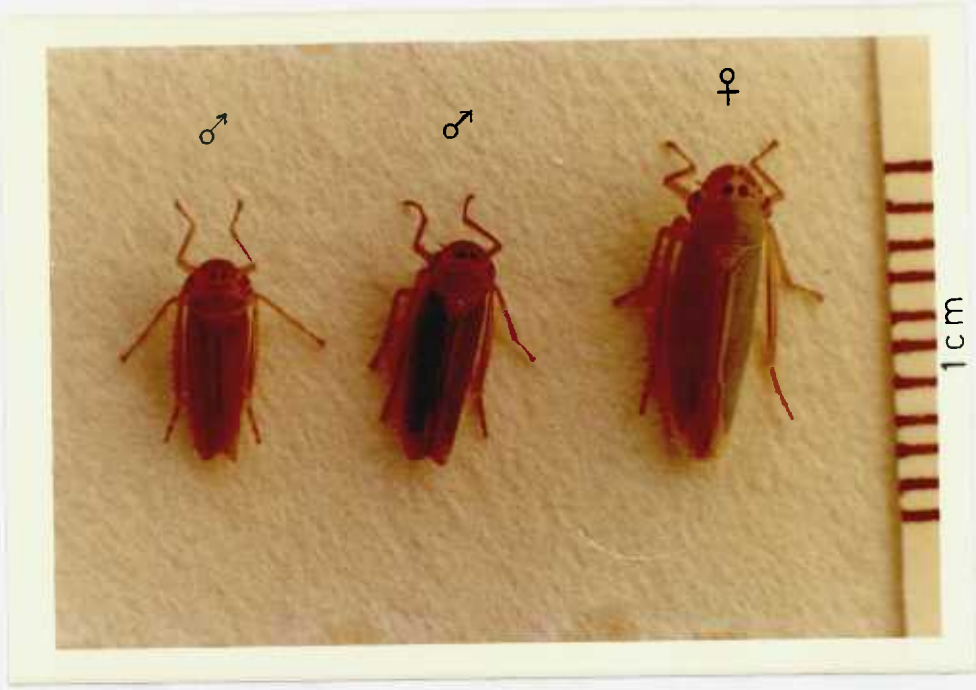


Plate 3. Male and female C. viridis. Note the colour variation in the male.

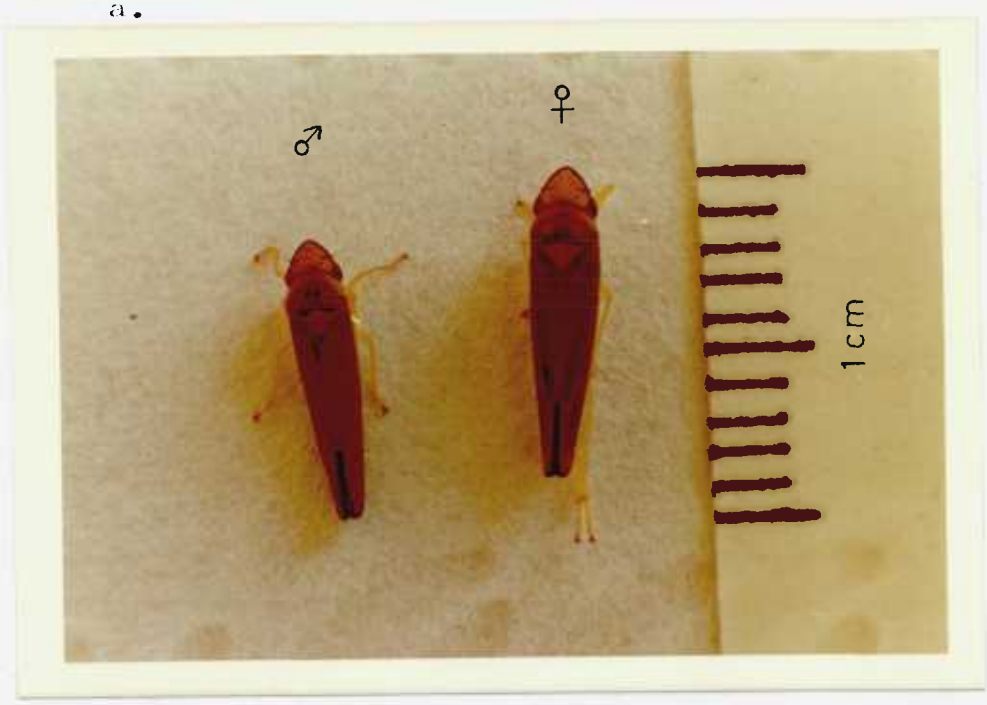


Plate 4. Female C. viridis infected with Entomophthora sp.



Plate 5. Eggs of G. 'coccinea' embedded in the scale of Rhododendron bud. (X 3.5)

a.



b.

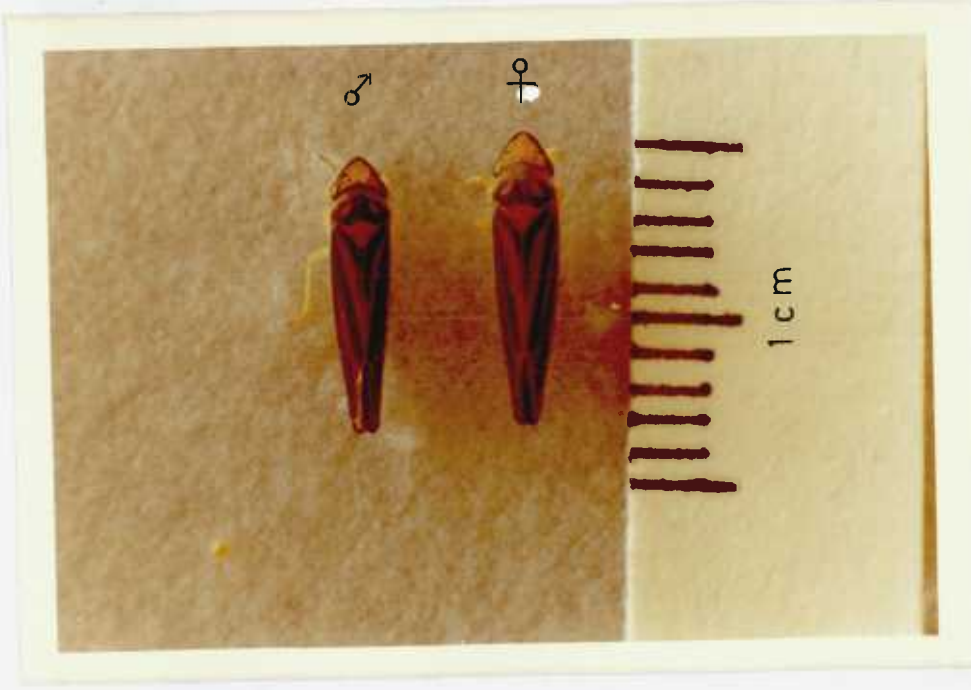


Plate 6. Adult Grapocephala 'coccinea'. a. the normal green form; b. the less common dark colour form.

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