AN ECOLOGICAL STUDY OF COCCINELLIDAE (COL.) ASSOCIATED WITH *APHIS FABAE* SCOP. ON *VICIA FABA*.[1]

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Contents.

Some insect populations are kept in check by the action of their natural enemies which may operate as density-dependent mortality factors of the concurrent type (Solomon, 1949, p. 13). Other insect species are often very abundant in spite of natural enemies which are apparently not able to control the population in question, especially if they are able to find much of their food elsewhere. Furthermore, an insect enemy may be ineffective in reducing the numbers of a particular species if its life-cycle is not synchronised with that of the prey.

Coccinellid predators of the Black Bean Aphid, *Aphis fabae* Scop., are polyphagous and attack Aphid species on many types of plants (Smith, 1931). *A. fabae* itself is polyphagous, having a complex life-cycle involving several different host plants, and on one of its summer hosts, *Vicia faba*, enormous populations of the pest often develop. To be effective against the Aphid on

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any one of its host plants, the natural enemies would have to synchronise their attack with the arrival of the Aphids.

This paper describes fluctuations in numbers of Coccinellids during the spring and summer of 1952 at Rothamsted, and how they are related in time and place to populations of *A. fabae* on three experimental bean plots, and of *Microlophium evansi* (Theo.) * on stinging nettles (*Urtica dioica*), for the availability of an alternative aphid prey on nettles near the plots might influence not only the time of arrival but also the numbers of all stages of Coccinellids on the beans.

The most important species of Coccinellids, Aphid-eaters of the tribe COCCINELLINI, found on the nettles and bean plots were as follows:

Adalia bipunctata (L.) was the most abundant species, *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.) were common species but were not abundant, *C. undecimpunctata* L. and *A. decempunctata* (L.) were uncommon.

Methods.

The period during 1952 when field observations were made has been divided into 26 weekly intervals (Table IV), extending from 9th April until 8th October. The area studied and places mentioned in the text are shown in fig. 1.

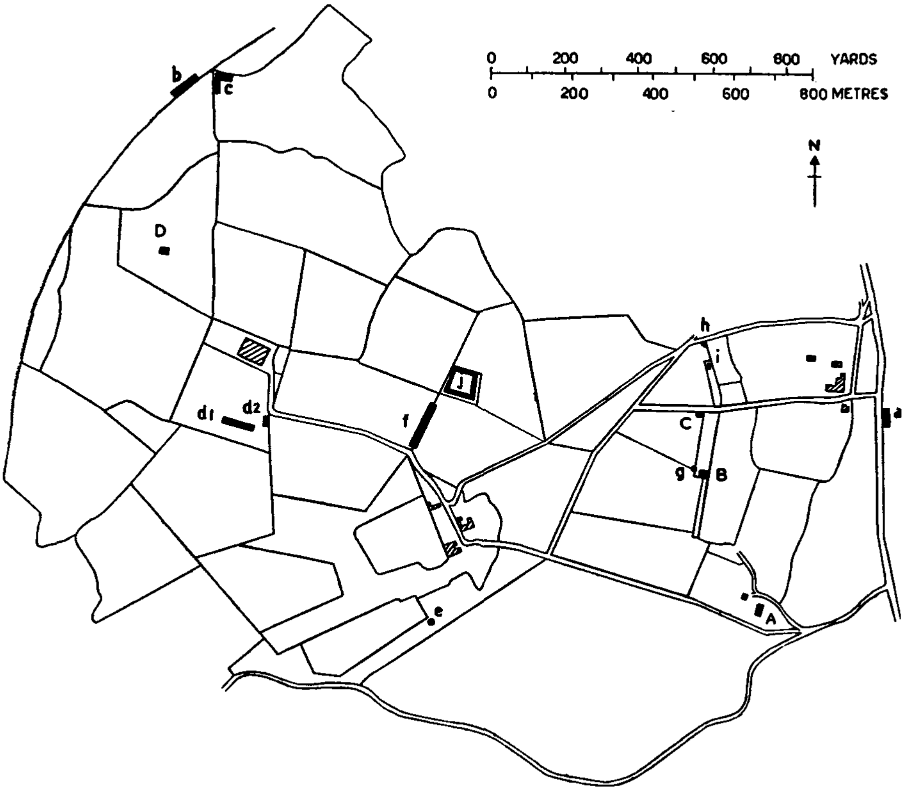

Fig. 1.—Plan of Rothamsted showing locations of bean plots A, B, C and D and places where concentrations of ladybirds were found in 1952.

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* = *Macrosiphum urticae* (Schr.).

Nettles.

Numbers of adult Coccinellids were estimated at three selected clumps of nettles supporting large populations of ladybirds and Aphids; these were at Broadbalk (site f), Great Field II (site g), and Great Field III (site h). Each week, two observers collected all the ladybird beetles visible on the nettles during 30 minutes; after identification, the insects were liberated where found.

Bean plots.

Four experimental plots each of 12 rows, 35 ft. long and 30 in. apart, were sown with beans (*Vicia faba*) of one variety during March. The field bean used was a cross between a tick bean and broad bean.

Plot A, in Rothamsted Lodge garden, was surrounded by tall trees and buildings, and on one side was a high brick wall.

Plots B and C, about 150 yd. apart, were on Great Field II, 400–500 yd. from Plot A. They were exposed to the wind. Plot B was used only for a suction trap. Plot C was situated between two nettle sites, Great Field II and Great Field III, being only 100 yd. from each, while a large plot of beans and barley lay 300 yd. away.

Plot D, about one mile distant from the other plots, was very exposed. Surrounding crops were wheat and lucerne and some small experimental plots of potatoes and beetroot. The nearest bean field was 500 yd. away.

Towards the end of May, the numbers of stems on each plot were estimated as Plot A, 2,099 (S.E. ± 62), Plot C, 2,988 (S.E. ± 79), Plot D, 2,604 (S.E. ± 56). The plots were examined weekly for the duration of the infestations by *A. fabae* (weeks 7–15), Plot A on Tuesday, Plot C on Wednesday, and Plot D on Thursday.

The unit of sampling adopted was the bean stem, because stems rather than plants become infested with Aphids. On each plot, 13–14 per cent. of the stems were sampled by examining a fixed number of stems in each row, Plot A, 288; Plot C, 384; Plot D, 336.

Sampling was systematic in that rows were always traversed in the same order and approximately every seventh stem was examined; but sampling was started from a randomly chosen stem at the end of a row and stems were selected at ground level to avoid bias in choosing aphid-infested stems. Every leaf was scrutinised and predators counted and recorded at once but not removed from the plants.

Bean stems were classified arbitrarily according to their degree of infestation by *A. fabae*; *zero* (0), *very light* (V), *light* (L), *medium* (M) and *heavy* (H); descriptions of these classes and estimates of their numbers of Aphids for each plot have been published (Banks, 1954*c*).

Suction traps.

Two traps, with fans of 9 in. diameter, were used to supplement the data from field counts (Johnson, 1950).

Trap (a) in the centre of Plot A, ran continuously from 17th April (week 1) to 17th September (week 23); trap (b) in Plot B, ran from 4th June (week 8) to 7th October (week 26).

The traps, whose mouths were level with the tops of the beans, were emptied once each day except in the early and late weeks of the trapping periods when they were emptied every two or three days. Insects of special interest caught in the traps were Coccinellids, Syrphids, Chrysopids, Hemerobiids and Anthocorids. The daily catches were totalled each week ending on Wednesday, for comparison with the populations of Coccinellids counted on nettles and beans.

Marking of Coccinellids.

Before week 11, all captured ladybirds were marked with a spot of coloured paint on an elytron to denote the place of capture; thereafter a large proportion was labelled. The insects were always liberated within 24 hours at the places where they were found.

A variety of paints and adhesives was tested but it was difficult to find one which would adhere satisfactorily to the glabrous elytra. A cellulose paint was adopted, despite the fact that it chipped off or came off completely, sometimes leaving a dark mark on the elytron. The secretion from the thoracic glands was held partly responsible for the loss of the paint, which could not be applied if the secretion had crept on to the elytra.

Changes in Populations of Aphids on Nettles and Beans.

Large populations of Nettle Aphids (*Microlophium evansi*) were well established in week 3 on the nettle sites, Broadbalk, Great Field II and Great Field III, maximum numbers occurring approximately in weeks 7–8; by weeks 10 and 11, the numbers had fallen almost to zero.

Primary migrants of *A. fabae* arrived on all bean plots during week 6 and the infestations lasted until weeks 14 or 15.

The numbers of Aphids per stem, estimated by the method already described and published elsewhere (Banks, 1954*c*, where weeks of sampling were numbered 1–9), are plotted against weeks on arithmetic (fig. 5) and logarithmic (fig. 2) scales respectively; the former emphasises the arithmetical differences between aphid numbers of the plots while the latter shows the proportional differences and the close similarity in shape of the curves.

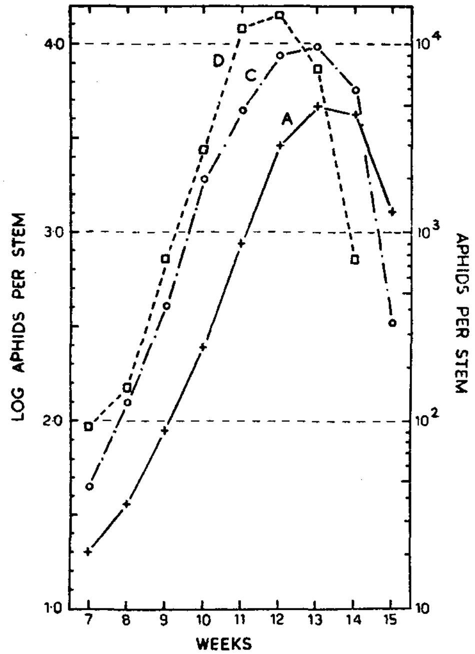

Fig. 2.—Changes in numbers of *Aphis fabae* on the bean plots A, C and D on a logarithmic scale.

The initial levels of infestation of the plots recorded in week 7 differed considerably, the percentages of infested stems being 54 per cent. on Plot D, 37 per cent. on Plot C, and 23 per cent. on Plot A, while the mean number of Aphids per stem of Plot D was more than four times that of Plot A and more than double that of Plot C.

For the first few weeks, the Aphids were confined mostly to the colonies in the crowns of small leaves (class V) but during weeks 9 and 10 the Aphids increased very rapidly and spread over the plants. The stems most heavily infested (classes M and H) formed only 1–3 per cent. of all stems at week 9 (Plots C and D) and week 10 (Plot A) but increased to 17–19 per cent. in weeks 9–10 (Plots C and D) and 10–11 (Plot A).

Aphid populations of Plots D and C multiplied enormously during weeks 8–9 and 9–10 respectively; the maximum rate of increase of population of Plot A occurred in week 10–11 and was considerably lower than that of the other plots.

Maximum densities were recorded in week 12 (Plot D) and week 13 (Plots C and A) in the ratio D:C:A::3:2:1; the areas of the curves were approximately in the same ratios.

There followed a decline in aphid numbers, very rapid on Plot D, less rapid on Plots C and A, due mainly to the departure of alatae and the loss of reproductive capacity of the apterae. The effect of parasites and predators in this decline was considered negligible in comparison with these two causes.

In week 13 at Plot D, nymphs and apterae were seen crawling off the beans on to the ground and on to nearby potatoes and beetroot and by week 14 the infestation had almost completely destroyed the plants and, as most of the leaves had fallen to the ground, no count could be made in week 15.

This investigation shows that the Aphids on nettles had become well established before *A. fabae* arrived on the beans and that bean plots of identical size within a small area, planted with the same variety of beans, may differ in several important respects as regards their populations of *A. fabae*.

The sizes of the bean-aphid populations in successive weeks and the conspicuously different maxima attained were associated with the different initial levels of infestation of the plots. The three curves in fig. 2 show that populations which were initially higher reached higher maxima, at an earlier date, and then declined correspondingly earlier, than those which were initially lower in density.

Sequence of Changes in Numbers of adult Coccinellids on Nettles and Beans.

The sequence of changes in populations of adult Coccinellids during the surveys was as follows.

Overwintered Coccinellids emerged from hibernation quarters in the spring of 1952, mated and dispersed to other habitats (Banks, 1954*a*). Many accumulated at clumps of nettles infested with *M. evansi*, and there laid large numbers of eggs which subsequently developed into a " nettle brood ". Some of the overwintered beetles then died off but most re-dispersed to other habitats, accumulating especially on bean plots after the arrival of *A. fabae*. Here they laid more eggs which developed into a " bean brood ". Before the insects of the bean brood reached the adult stage, those of the nettle brood reached maturity, mated and dispersed rapidly from nettles, many of them appearing on the bean plots, thereby augmenting the numbers of the overwintered generation already there. The bean brood reached the adult stage when the aphid infestations of the beans had finished. On the bean plots, then, three phases in changes in numbers of adult Coccinellids were apparent; (1) overwintered insects, dispersing from nettles and other places, accumulated on the beans; (2) insects of the nettle brood (progeny of overwintered Coccinellids) emigrated from nettles to beans; (3) a bean brood (also progeny of the overwintered Coccinellids) appeared at the end of the aphid infestations.

Changes of numbers of adult Coccinellids at nettle sites.

At the end of April and early in May, a search was made for Coccinellids newly-emerged from hibernation. Many clumps of stinging nettles (*Urtica dioica*) were searched and although individual insects were occasionally found,

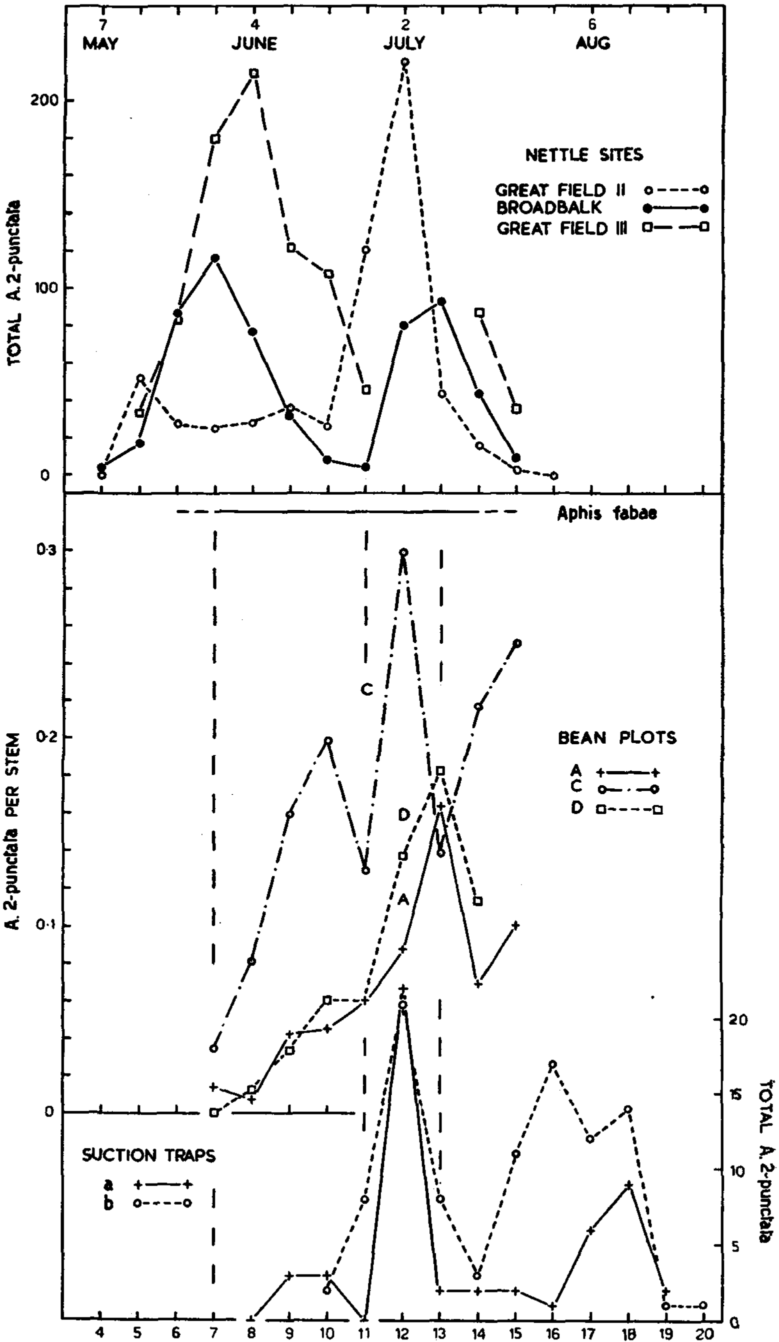

Fig. 3.—Changes in numbers of adult *Adalia 2-punctata* at nettle sites, bean plots and in suction traps, 1952.

concentrations occurred only at the places listed in Table I. Coccinellids were most abundant at the nettle sites at Broadbalk, Great Field II and Great Field III which were heavily infested with *M. evansi*, while at all other nettles Aphids were scarce or absent. There were probably many other places where Aphids and Coccinellids occurred but those examined had the largest numbers of ladybirds and probably formed a large part of the total ladybird population of the neighbourhood.

TABLE I.

Concentrations of overwintered ladybirds at Rothamsted; maximum numbers counted during April and May 1952.

	Site	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*C. 11-punctata*
Harpenden Common (grass)	a	111	0	0	12
West Barnfield (grass) ..	b	40	0	0	0
Sawyers (nettles)	c	7	0	0	0
Little Knott (beans) ..	d1	11	0	0	0
Little Knott (nettles) ..	d2	6	0	0	0
Highfield (nettles) ..	e	7	0	3	0
Broadbalk (nettles) ..	f	108	137	47	0
Great Field II (nettles) ..	g	27	60	9	0
Great Field III (nettles) ..	h	37	218	13	0
Bee enclosure (nettles) ..	i	*ca.*10	0	0	0
Kitchen Garden (nettles) ..	j	0	*ca.* 6	0	0

The most abundant species of Coccinellid at the nettle sites was *Adalia 2-punctata* whose numerical changes are shown in fig. 3. For comparison with the weekly counts on bean plots, the records at nettle sites (Table II) have been adjusted by interpolation to give an estimate of numbers of ladybirds on Wednesday of each week (fig. 3). The records for *C. 7-punctata* and *P. 14-punctata*, which were less abundant, are discussed below (p. 572).

The numbers of overwintered *A. 2-punctata* rose to a maximum in weeks 7 and 8 and then declined as the insects re-dispersed, although some died at this time. Numbers of all species of Coccinellids on nettles were lowest during weeks 9–11 but populations of larvae and pupae had already risen during weeks 5–11, developed from eggs laid earlier by the overwintered generation.

In weeks 11 and 12 there were rapid increases to second maxima at the nettle sites as the new brood emerged from the pupae. This change was especially noticeable in *A. 2-punctata* but similar changes occurred in *C. 7-punctata* and *P. 14-punctata* whose numbers were much lower. The new maxima were followed by rapid declines as the newly-emerged adults dispersed; Aphid populations of the nettles at this time had almost completely disappeared and the ladybirds were without food.

Each of the three common species of Coccinellids, therefore, developed one brood on the nettles from the overwintered insects.

TABLE II.

Records of adult Coccinellids counted at three nettle sites, 1952.

	Broadbalk (site f)				Great Field II (site g)				Great Field III (site h)			
	C. 7-punctata	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*
May 5	108	2	0	0								
7					31	1	0	0				
9									37	4	6	1
12	78	8	1	0								
13	53	8	6	1	45	60	3	1				
16					14	33	1	0	14	45	10	0
17	74	0	0	0								
20	51	67	21	0								
21					9	27	7	0				
23	50	131	47	0								
24									7	106	13	1
26	38	137	30	0								
27					1	25	0	2				
29	16	106	13	0								
30									3	218	6	4
June 1	22	87	4	0								
3					0	26	0	1				
6	4	71	4	1					3	212	0	4
9					4	37	1	0				
13	3	17	4	0					6	101	2	0
16					5	29	0	0				
20	3	5	0	1					2	109	0	9
22					5	19	1	4				
27	21	4	0	0					31	18	0	0
30					25	300	4	9				
July 5	19	126	1	0								
6					6	58	4	1				
11	5	76	1	1								
13					0	23	0	3	17	109	0	3
18	1	29	0	1								
20					0	6	0	0	3	57	1	3
25	0	0	0	0								
26					0	0	0	0				
27									2	6	0	0

Changes of numbers of adult Coccinellids on the bean plots.

A. fabae arrived on the beans during week 6; maximum densities of Aphids were reached in weeks 12 or 13 and the infestations lasted until weeks 14 or 15.

Some Coccinellids were present on the bean plots before the arrival of the Aphids and, on Plot D in week 6, batches of coccinellid eggs and even well-developed larvae of *C. 7-punctata* were found, indicating that oviposition must have occurred at this plot several weeks before but had escaped notice. These larvae had probably fed as cannibals.

The total numbers of all stages of Coccinellids counted on the bean plots are given in Table III. The most abundant species was *A. 2-punctata* which formed 67–76 per cent. of all Coccinellids found on the plots and the following description of events refers to this species (fig. 3).

Plot C was noted for its comparatively high density of ladybirds at all times; populations of Plots A and D were lower. On each plot, three phases in the changes in populations of *A. 2-punctata* were distinguished.

Phase 1 (weeks 7–11) was a period when numbers were comparatively low on all plots, but the maximum population of adult Coccinellids at Plot C was

TABLE III.

Total numbers of Coccinellids of all species counted on the bean plots A, C and D.

Week	Adults					Eggs	Larvae			Pupae
	A. 2-punctata	*P 14-punctata*	*C. 7-punctata*	*Others*	*Total*		just hatched	older larvae	all larvae	
Plot A										
7	4	5	0	0	9	154	0	0	0	0
8	2	10	0	0	12	327	13	0	13	0
9	12	4	0	0	16	232	18	8	26	0
10	13	3	0	0	16	571	34	17	51	0
11	17	0	0	0	17	270	52	40	92	0
12	25	4	3	0	32	1,293	14	148	162	26
13	47	10	3	5	65	979	45	231	276	70
14	20	9	0	2	31	538	52	229	281	31
15	29	4	10	1	44	21	8	138	146	32
Totals	169	49	16	8	242	4,385	236	811	1,047	159
Plot C										
7	13	13	1	0	27	456	0	0	0	0
8	31	17	3	0	51	537	25	4	29	0
9	61	12	3	0	76	1,392	4	24	28	0
10	76	6	11	0	93	2,444	139	122	261	0
11	49	2	4	4	59	1,883	108	222	330	4
12	115	23	34	1	173	3,527	28	659	687	85
13	53	31	15	3	102	1,193	15	430	445	328
14	83	28	6	2	119	215	12	390	402	130
15	96	2	32	2	132	6	0	103	103	63
Totals	577	134	109	12	832	11,653	331	1,954	2,285	610
Plot D										
7	0	4	2	0	6	249	13	0	13	0
8	4	1	0	0	5	180	11	4	15	0
9	11	8	0	0	19	324	47	4	51	0
10	20	3	0	1	24	616	17	22	39	0
11	20	3	3	1	27	527	31	68	99	1
12	46	16	7	2	71	2,922	34	236	270	58
13	61	10	12	5	88	1,794	16	233	249	112
14	38	27	1	2	68	323	30	318	348	105
Totals	200	72	25	11	308	6,935	199	885	1,084	276

considerably higher than those of Plots A and D. The insects of this phase were overwintered Coccinellids which arrived on the beans before and during the early stages of the aphid infestation; as the ladybird numbers on nettles declined during these weeks, those of bean plots increased.

Phase 2 (weeks 12–13 Plot C; 12–14 Plots A and D) was characterised by a sudden rise in numbers in week 12, the cause of which was an immigration to the bean plots of ladybirds, mostly *A. 2-punctata*, developed from eggs laid earlier on the nettles by the overwintered beetles (nettle brood). Aphid populations on beans had now reached their highest densities.

On Plot C, a maximum density of ladybirds was quickly attained, for this plot was situated close to the two nettle sites Great Field II and Great Field III, both of which had high populations of ladybirds. On the other hand, Plots A and D reached their maxima a week later (week 13); they were remote from nettle sites and Plot A was sheltered by tall trees and buildings. The maximum of Plot C was again high in comparison with the maxima of Plots A and D which were almost identical in this phase. The end of the phase was characterised by a sharp fall in numbers as the insects died off and dispersed.

Phase 3 (weeks 14–15) was a second rise in numbers after the decline at the end of the second phase, and resulted from the emergence of Coccinellids

TABLE IV.

Weekly totals of adult Coccinellids captured in suction traps a and b.

Week ending	Week No.	Trap a						Trap b						
		A. 2-punctata	*P. 14-punctata*	*A. 10-punctata*	♂♂	♀♀	Total	*C. 7-punctata*	*A. 2-punctata*	*P. 14-punctata*	*A. 10-punctata*	♂♂	♀♀	Total
April 16 ..	1	0	0	0	0	0	0							
23 ..	2	0	0	0	0	0	0							
30 ..	3	0	0	0	0	0	0							
May 7 ..	4	0	0	0	0	0	0							
14 ..	5	0	0	0	0	0	0							
21 ..	6	0	2	0	1	1	2							
28 ..	7	0	0	0	0	0	0							
June 4 ..	8	0	0	0	0	0	0	0	0	0	0	0	0	0
11 ..	9	3	0	0	2	1	3	0	0	0	0	0	0	0
18 ..	10	3	3	0	2	4	6	0	2	0	0	2	0	2
25 ..	11	0	0	0	0	0	0	0	8	0	0	8	0	8
July 2 ..	12	22	1	0	18	5	23	0	21	0	1	17	5	22
9 ..	13	2	0	0	1	1	2	2	8	1	1	9	3	12
16 ..	14	2	1	1	4	0	4	0	3	1	1	4	1	5
23 ..	15	2	1	0	2	1	3	1	11	3	0	7	8	15
30 ..	16	1	1	0	2	0	2	0	17	0	1	7	11	18
Aug. 6 ..	17	6	0	0	4	2	6	0	12	1	0	4	9	13
13 ..	18	9	0	0	4	5	9	2	14	1	0	3	14	17
20 ..	19	2	1	0	1	2	3	0	1	0	0	0	1	1
27 ..	20	0	0	0	0	0	0	0	1	0	0	0	1	1
Sept. 3 ..	21	0	0	0	0	0	0	0	0	0	0	0	0	0
10 ..	22	0	0	0	0	0	0	0	0	0	0	0	0	0
17 ..	23	0	0	0	0	0	0	0	0	0	0	0	0	0
24 ..	24							0	0	0	0	0	0	0
Oct. 1 ..	25							0	0	0	0	0	0	0
8 ..	26							0	1	0	0	0	1	1
Total		52	10	1	41	22	63	5	99	7	4	61	54	115

developed from eggs laid on the beans also by the overwintered beetles (bean brood). Aphid populations of the plots had fallen rapidly. No results could be obtained for Plot D in this phase as counts had to be discontinued after week 14, the infestation being finished and the plants nearly completely defoliated. Many Coccinellids and other predators of the Aphids were found in the accumulated litter on the ground at Plot D at this time (see p. 579).

The three phases were shown also by the population changes of *C. 7-punctata*, especially on Plot C, the numbers of this species being much smaller than, and the phases not so distinct as, those of *A. 2-punctata*. The numbers for *P. 14-punctata* were too small to allow separate analysis.

Adult Coccinellids in the suction traps.

Further evidence on the changes in populations of adult Coccinellids on the beans and nettles are given by the results from the two suction traps (Table IV). The records for *A. 2-punctata*, shown in fig. 3, reflect the three phases already observed.

During the period weeks 6–20, the numbers of Coccinellids of all species captured in Trap a (Plot A) was 63 (maximum, 23 in one week) while in Trap b (Plot B), 114 Coccinellids (maximum, 22 in one week) were obtained.

Recaptures of marked adult Coccinellids.

Movements of ladybirds between sites selected for study were also investigated by marking the insects with coloured paints before liberation at the sites where they had been captured.

TABLE V.

Records of Coccinellids marked and liberated at sites where first found and recaptured elsewhere.

Date of recapture	Week	Species	Liberated at	Recaptured at	Remarks
16 May	6	*C. 7-punctata*	Site e	Site h	Liberated site e on 12 May. Seen again site h on 24 May
16 May	6	*P. 14-punctata*	Site g	Plot B	
23 May	7	*C. 7-punctata*	Site d, f or g	Plot D	Paint missing
24 May	7	*A. 2-punctata*	Site g	Site h	
9 June	9	*A. 2-punctata*	Site g or Plot B	Plot A	Recovered on mustard near Plot A; paint missing
11 June	9	*A. 2-punctata* *P. 14-punctata*	Site g	Plot C	
18 June	10	*C. 7-punctata*	Site g, Plot B or C	Plot C	Two specimens, probably from site g; paint missing from both specimens
2 July	12	*A. 2-punctata*	Site h	Plot C	

Marked Coccinellids were often found again where they had been liberated; only a few were recovered, however, at other sites (Table V); this is attributed primarily to the fact that the area over which the insects could disperse was very large in comparison with the part studied. Furthermore, the unsatisfactory marking technique was partly responsible for the paucity of the results.

Numbers of Coccinella 7-punctata *and* Propylea 14-punctata *at nettles.*

Changes in numbers of *C. 7-punctata* and *P. 14-punctata* at the three nettle sites were similar to those of *A. 2-punctata* except that in weeks 4 and 5 the numbers of *C. 7-punctata*, already at a high value, had started to decline, due partly to re-dispersal and partly to mortality (several specimens parasitised with the Braconid, *Perilitus coccinellae* (Schr.) were found in early spring). *C. 7-punctata* apparently emerged from hibernation earlier than the other two and appeared at the nettles at least four weeks before them. This is supported by observations at Great Field II nettles where, in week 5, many *A. 2-punctata* were found under dried leaves close to the nettles and in a state of lethargy, not then ready to disperse.

But the second peaks (nettle brood) of *C. 7-punctata* and *A. 2-punctata* coincided; which is explained by the difference in average length of the life-cycles of the species: *C. 7-punctata* 44 days, *A. 2-punctata* 37 days, and *P. 14-punctata* 27 days. The second peak of *P. 14-punctata* was too small to allow any conclusions to be drawn.

Effects of Changes in the Numbers of adult Coccinellids on Numbers of Eggs and Larvae on the Beans.

Numbers of eggs and larvae of Coccinellids on the bean plots corresponded to variations of the adult insects both in phase and in numbers, with the important exception that there was no third phase of the immature stages to correspond to the third phase of adults. In addition, two effects of special significance will be described, namely, cannibalism and the probable death through starvation of many larvae of the second phase.

Counting of eggs and larvae.

The eggs of *A. 2-punctata*, orange in colour, are laid in batches containing an average of 12·5 eggs and usually occur on the undersides of leaves on the middle of the plants, although occasionally near the top. Eggs of *C. 11-punctata* could not be distinguished from those of *A. 2-punctata*. Eggs of *P. 14-punctata* are yellow and the batches have an average of 6·5 eggs, occurring underneath the bottom leaves, frequently on the pair closest to the ground. Eggs of *C. 7-punctata* are orange, larger than those of *A. 2-punctata*, and the batches have an average of 25 eggs although as many as 65 in a batch have been counted; they occur usually underneath the leaves but occasionally on the upper surfaces and sometimes at the tops of the plants.

Despite these differences, some eggs could not be assigned to a species. Eggs of *A. 2-punctata* appeared to form 70–78 per cent. of all eggs counted on the three plots. Eggs of all species have been treated together, especially for comparison with numbers of the larvae.

In the field, species of larvae could not be distinguished in the early instars which often cannot be seen after the insects have dispersed from the egg shells; third and fourth (final) instars are usually readily seen and identified.

Larvae of all species, therefore, have been treated together and were classified as " just hatched " (1st instar larvae still grouped on the empty egg shells before dispersal, a stage lasting up to 24 hours) and as " older larvae " (mostly 3rd and 4th instars with a few earlier-stage larvae).

Egg populations.

Considerable fluctuations in numbers of eggs occurred on all plots (Table III; fig. 4). While two phases may be discerned, corresponding to the first two phases in the populations of adults, there was no third phase to correspond to the third phase of adults.

Phase 1 (weeks 7–11) was characterised by a comparatively low egg density on all plots, synchronous with that of adults. Plot C reached a much higher maximum egg density during this phase than did Plots A and D.

Phase 2 (weeks 11–14 or 15) attained a much higher egg density than the first and corresponded to the second phase of adults; the egg density of Plot D was higher than that of Plot A and almost equal to that of Plot C.

At Plots A and D, the second maximum of eggs was reached in week 12, one

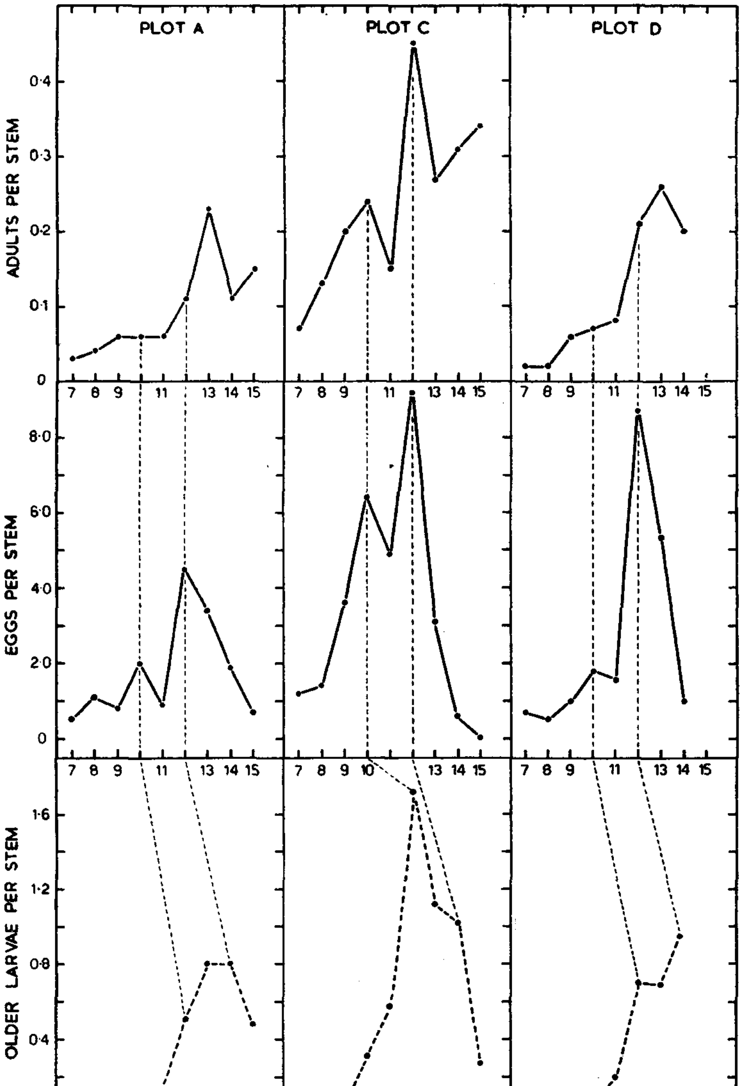

Fig. 4.—Comparison of the numerical changes of adults, eggs and older larvae of all species of Coccinellids for the bean plots A, C and D during the infestations by *Aphis fabae*.

week before the maximum density of adults. These two plots, being remote from nettles, received the nettle brood immigrants over a period of two weeks; the first immigrants laid large numbers of eggs in week 12 but as adults continued to arrive, the numbers of eggs in week 13 were maintained at a comparatively high level. On the other hand, during week 12, Plot C, which was close to nettle sites g and h, was invaded by many ladybirds which at once laid large numbers of eggs; as few immigrants arrived during week 13, the numbers of eggs at this plot, therefore, fell very rapidly.

The absence of a third phase of eggs indicates that the adult Coccinellids, which developed from eggs laid on the beans during phase 1 (bean brood), did not lay eggs; indeed, no third phase adults were observed to mate (Table VI).

TABLE VI.

Records of pairs of Coccinellids seen *in copula* on the bean plots A, C and D.

	Weeks								
	7	8	9	10	11	12	13	14	15
Plot A									
A. 2-*punctata*	0	0	1	2	2	1	2	0	0
P. 14-*punctata*	1	1	0	0	0	0	0	0	0
C. 7-*punctata*	0	0	0	0	0	0	0	0	0
Total ..	1	1	1	2	2	1	2	0	0
Plot C									
A. 2-*punctata*	0	1	11	6	7	10	1	0	0
P. 14-*punctata*	0	1	1	1	0	0	0	0	0
C. 7-*punctata*	0	0	0	0	0	1	0	0	0
Total ..	0	2	12	7	7	11	1	0	0
Plot D									
A. 2-*punctata*	0	0	3	3	2	0	2	0	
P. 14-*punctata*	0	0	3	0	0	0	0	0	
C. 7-*punctata*	0	0	0	0	0	0	0	0	
Total ..	0	0	6	3	2	0	2	0	
Grand Total	1	3	19	12	11	12	5	0	0

The first two phases of adult Coccinellids, then, were reflected by corresponding phases in egg numbers. Plot C had a large number of eggs during both phases while Plot A had a comparatively low density of eggs at all times.

Larval populations.

Counts of larvae (Table III; figs. 4, 5) reveal two facts, (1) the absence of distinct phases to correspond with those of egg populations, (2) that the densities of larvae of the three plots differed from each other. These problems are considered below.

(1) The absence of distinct phases in curves for larvae, which were such a noticeable feature of adult and egg populations, is noteworthy, but the existence

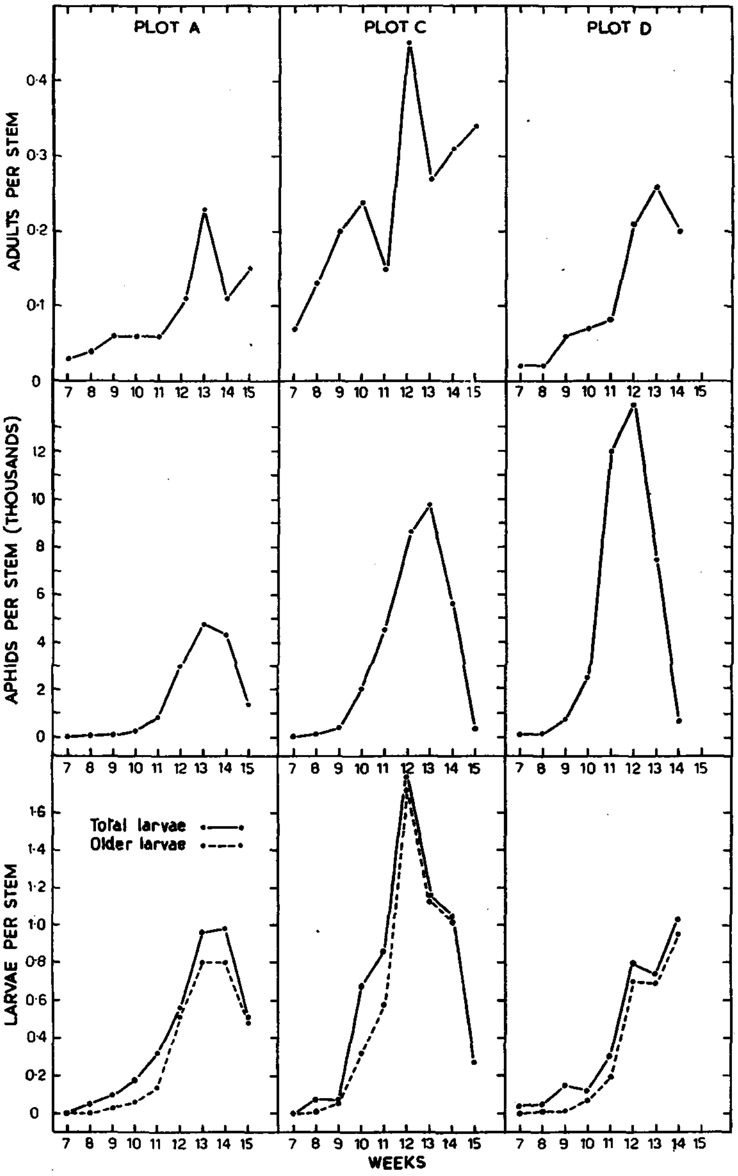

Fig. 5.—Comparison of the numerical changes of adults and larvae of all species of Coccinellids with the changes in numbers of *Aphis fabae* on the bean plots A, C and D.

of these phases may be discerned on Plots C and D. As the egg stage lasts for an average of seven days and the young larvae (1st and 2nd instars) would not be counted for another seven days (" missing stage "), the total lag between counting the eggs and the resulting older larvae would be approximately 14 days. It should, therefore, be possible to associate the eggs counted in one week with the older larvae counted two weeks later. This may be done satisfactorily for Plots C and D, when the peaks of egg numbers in phases 1 and 2 may be seen reflected in the populations of older larvae (fig. 4).

The maximum of eggs in week 10 (phase 1) resulted in a maximum of older larvae in week 12, while the second maximum of eggs (week 12) produced older larvae in week 14, giving a rise in numbers of larvae on Plot D as expected; but on Plot C there was no rise in numbers owing to the high rate of pupation in week 13; instead, there was a check in the decline of older larvae.

The older larvae curve for both Plots C and D is smooth and regular from weeks 7–12; after that it would have dropped rapidly as the larvae pupated. Instead, the fall of the population in week 14 was checked (Plot C) or the density actually rose (Plot D), due to the heavy rate of oviposition in week 12. The drop in numbers on both plots during week 13 was, of course, partly caused by the decline in numbers of eggs in week 11.

For Plot A, however, the phases are obscured. Instead of an expected drop in numbers of older larvae in week 14, numbers remained the same as in the week before, because the eggs laid in week 12 counter-balanced the number of larvae pupating in week 14. The usual drop due to pupation was not recorded, therefore, until week 15; maxima of pupae occurred in week 13 on all plots (Table III).

(2) Densities of total larvae of Plot C were always much higher than those of Plots A and D; this was not unexpected in view of the large populations of adults and eggs recorded on Plot C. There is, however, a positive correlation in both phases 1 and 2 between the maximum densities of adults (of all species), eggs and larvae of each plot (Table VII).

TABLE VII.

Correlations between maximum densities of Coccinellid adults (all species), eggs and larvae of the bean plots A, C and D.

	Plot	Adults per stem	Eggs per stem	Total larvae per stem
Phase 1	C	0·24	6·37	1·79
	A	0·06*	1·98	0·96
	D	0·08*	1·83	0·80
Phase 2	C	0·45	9·19	1·16
	D	0·26	8·70	1·03
	A	0·23	4·49	0·98

* The population densities of adult insects on Plots A and D were very low in phase 1 and these differences are probably not significant.

It may be concluded therefore, that the populations of eggs and larvae were correlated with the populations of adult Coccinellids on each plot, both as regards the phases (1 and 2) and in population densities.

Cannibalism.

An irregularity in the curve for total larvae for Plot C occurred in weeks 10 and 11 (fig. 5). Many just-hatched larvae were counted in those weeks, because of the high rates of oviposition in weeks 9 and 10, respectively. In week 10 there was a greater increase in the density of eggs than in week 9 and it would have been expected, therefore, that the density of just-hatched larvae in week 11 would have been similar to, or even greater than, that in week 10. This was not the case, for there was a marked falling-off in density of just-hatched larvae in week 11. An approximate estimate of this " loss " may be made.

The duration of the egg stage is about seven days and the just-hatched stage lasts from a few hours to one day. An estimate of the numbers of eggs laid on any one day may be obtained by dividing the total number of eggs counted by the duration of the stage (p. 583), thus:

	Eggs counted	Estimate of egg population		Just-hatched larvae counted
Week 9	1,392	199	Week 10	139
Week 10	2,444	349	Week 11	108

If 199 eggs in week 9 produced 139 just-hatched larvae in week 10, then 349 eggs in week 10 might have been expected to produce 244 just-hatched larvae in week 11; as only 108 were counted, there was, therefore, an approximate loss of 136 just-hatched larvae or about 56 per cent. of the expected value.

This loss was attributed to the destruction of the eggs by the larvae, especially by those of the early stages.

On all three plots, larvae of both *A. 2-punctata* and *P. 14-punctata* were seen attacking their own and each other's eggs at various times: this intra-specific and inter-specific predation will be referred to, for convenience sake, as cannibalism.

All instances of larvae and adults seen attacking eggs or other stages are recorded in Table VIII. Predation of eggs by larvae during phase 1 was

TABLE VIII.

Records of cannibalism (destruction of eggs by larvae) on the bean plots A, C and D, with densities of Aphids and coccinellid eggs.

	Week	Frequency of cannibalism	No. of cannibal larvae	Cannibal larvae as proportion of older larvae (%)	Aphid numbers (Aphids/stem)	Coccinellid egg numbers (eggs/stem)
Plot C	7	0	0	0	45	1·19
	8	1	1	25·0	125	1·40
	9	3	6	25·0	403	3·63
	10	16	22	18·8	1,917	6.37
	11	8	12	5·4	4,458	4·90
	12	2	2	0·3	8,628	9·19
	13	1	2	0·5	9,639	3·11
	14	0	0	—	5,738	0·56
	15	0	0	—	331	0·02
Plot A	9	1	1	12·5	90	0·81
	10	2	5	29·4	248	1·98
	13	1	1	0	4,676	3·40
Plot D	9	1	1	25·0	720	0·96
	12	1	3	1·2	13,958	8·70
	13	1	1	0	7,459	5·34

TABLE IX.

Records for Plot C of cannibalism (egg destruction by larvae) on the 30 bean stems on which it was observed.

Week	No. of cannibal larvae	No. of older larvae not cannibals	Proportion of cannibal larvae of all older larvae (%)	No. of stems	Mean Aphids on these stems	Mean coccinellid eggs on these stems	No. of cannibal larvae, no. of stems concerned and class of stem				
							Class of stem O	V	L	M	H
7	0	—	—	—	—	—					
8	1	0	100	1	97	12		1(1)			
9	6	1	86	3	1,212	12		1(1)	5(2)		
10	22	11	67	15	2,212	22	2(2)	11(8)	3(1)	6(4)	
11	12	9	57	8	4,019	15		4(3)	2(2)	5(2)	1(1)
12	2	2	50	2	10,335	18				1(1)	1(1)
13	2	4	33	1	13,010	12					2(1)
14	0	—	—	—	—	—					
15	0	—	—	—	—	—					

frequently observed on Plot C, rarely on Plots A and D. The total occasions seen, during a period of about 6 hours in one day per week, of larvae eating eggs were: Plot A, 4; Plot C, 32; Plot D, 3. Plot C was conspicuous, therefore, also in this respect.

Cannibalism on Plot C resulted from the high population of coccinellid eggs during phase 1 before Aphids had become abundant. In week 9 only 3 per cent. of the stems examined had large, well-developed Aphid populations (classes M and H); in week 10, 17 per cent. of the stems were classified together as M and H, for aphid colonies had increased very rapidly and the Aphids had spread over the plants.

Coccinellid eggs were also increasing in number and in week 10 reached a maximum density of approximately 6·4 eggs per stem (Table VIII). It was from the eggs counted in week 10 that the loss of just-hatched larvae in week 11 was observed. In week 10, nearly 70 per cent. of all larvae seen on the 15 stems concerned were feeding on eggs, yet the average number of Aphids on those stems was 2,212 and the mean number of eggs was only 22 per stem (Table IX).

Although cannibalism was associated with a scarcity of Aphids on the one hand and an abundance of eggs on the other during the first phase, the most important factor was the high density of eggs, associated with the relative locations of eggs and Aphids on the bean stems; Aphids were mostly on the tops of the stems, while coccinellid egg batches were situated on the undersurfaces of the leaves low on the plants; furthermore, egg batches were often laid on uninfested stems. Larvae dispersing from the egg shells after hatching would probably encounter egg batches more readily than they would aphid colonies.

That cannibalism was not just a question of the relative abundance of Aphids or eggs is further supported by the evidence of Table IX. Cannibalism not only occurred on stems where Aphids were scarce (classes O, V and L) but also where they were abundant (classes M and H), although less frequently. For example, on Plot C in week 10, 6 cannibal larvae were recorded on 4 stems of class M, each of which had, on the average, 7,660 Aphids and only 25 coccinellid eggs.

The fate of eggs and larvae of the second phase.

On Plot D, the Aphids reached their maximum numbers in week 12, with an average of approximately 14,000 Aphids per stem. During week 13, many apterae and nymphs had crawled off the plants on to the ground and on to nearby plants, and by week 14 the aphid population of the plot had declined almost to zero. Aphids had been so numerous that the plants were killed and defoliated, many predators falling to the ground.

In order to determine the fate of the large numbers of larvae of week 14, resulting from the high rate of oviposition in week 12, an examined was made of the accumulated litter on the ground at Plot D during week 14, immediately after the last count on the bean stems.

All the dried leaves and some loose soil were collected from a quadrat 13 in. square, four times per row, the 48 samples being equivalent to ⅛th of the area occupied by the bean stems. The samples were enclosed in paper bags and sorted in the laboratory.

In the samples from Plot D, there were 66 adult Coccinellids, 99 larvae and 51 pupae (Table X). The last would probably have survived in the field and indeed did in the laboratory; whether the larvae would also have survived is very doubtful. Some might have been able to do so by preying on other insects or on each other and some would have been ready to pupate; the majority would probably have died.

The 99 larvae were equivalent to a density of 0·30 larvae per stem; the actual density on the stems in week 14 was 1·04; thus, approximately 22 per cent. of the total larvae of week 14 was in the litter on the ground. Similarly, 50 per cent. of the adult Coccinellids and 33 per cent. of the pupae were also in the litter.

Similar samples were taken at Plots C and A in weeks 15 and 16, respectively, but much smaller numbers of Coccinellids were found in the litter. Defoliation of the plants at these plots was slight in comparison with that at Plot D.

TABLE X.

Coccinellids recorded in 48 samples of the ground litter at Plots D, C and A.

	Adults				Eggs	Larvae	Pupae
	A. 2-punctata	*P. 14-punctata*	*C. 7-punctata*	*C. 11-punctata*			
Plot D (week 14)							
Total in litter	13	13	0	40	20	99	51
Equivalent density/stem			0·20			0·30	0·15
Actual density/stem			0·20			1·04	0·31
Per cent. in litter			50·0			22·3	32·8
Plot C (week 15)							
Total in litter	44	3	6	0	0	35	44
Equivalent density/stem			0·12			0·09	0·12
Actual density/stem			0·34			0·27	0·16
Per cent. in litter			26·5			25·6	41·4
Plot A (week 16)							
Total in litter	17	2	1	0	0	1	15
Equivalent density/stem			0·07			0·01	0·05
Actual density/stem			0·15			0·51	0·11
Per cent. in litter			31·4			0·8	32·3

There was no means of telling whether the adult Coccinellids would have overwintered on the soil as, following normal practice, the plots were cleared of the beans a few weeks later. Plot C was cleared during August and no adult Coccinellids were found on the ground during the work.

The large number of eggs laid on Plot D during week 12, therefore, produced a comparatively large number of larvae in week 14, many of which probably died of starvation. The nettle brood had arrived on the beans and laid these eggs when the Aphids there had already reached their maximum numbers. These eggs were probably wasted. On Plots A and C, the decline of aphid numbers was not so rapid and larvae on the bean plots from the nettle brood had a food supply available for a longer period.

Relations between Numbers of Coccinellids and *Aphis fabae*.

The rates of growth, times of reaching maximum densities and the rates of decline of Aphid populations of the three plots differed and adult coccinellid populations were not closely synchronised with them (fig. 5). Furthermore, the numbers of adult Coccinellids entering the plots showed no obvious dependence on the numbers of Aphids there; for, Plot D had a high aphid population and a low population of ladybirds, Plot C, with an intermediate aphid population, had the highest coccinellid numbers of all plots, while Plot A had comparatively few Aphids and low numbers of ladybirds.

Populations of coccinellid larvae depended on the numbers of eggs laid, which in turn were dependent on the numbers of adults coming on to the plots and apparently not on the relative amounts of aphid food available. Where Aphids were more abundant, however, fewer larvae might die as the result of a difficulty in finding prey (Nicholson, 1933, p. 167) and if the quantity of food available was always a limiting factor, the survival rates of the larvae would be correlated with the density of the Aphids. We may not, however, compare the final survival rates of Coccinellids (Table XI) with the aphid densities of the plots, for the causes of mortality were multiple (see below) (Thompson, 1939, p. 361; Ullyett, 1953, p. 78).

The most critical time in the life of the larvae is probably after eclosion when the insects have dispersed from the egg shells; prey density is probably then a limiting factor in survival. When a larva has reached a food supply sufficient for its further development, its chances of survival are probably much enhanced and the importance of food supply as a limiting factor in survival is decreased. Prey density would, then, probably be most important between the just-hatched and older larvae stages; but the mortality rates between these stages were not correlated with the aphid densities of the three plots.

While the presence of *Aphis fabae* on the beans was the cause of the accumulation of the ladybirds on the plots, the levels of populations of the predators

TABLE XI.

Estimation of populations and mortality of immature stages of Coccinellids on the bean plots A, C and D.

Corrections for fauna in litter.

		Plot		
		A	C	D
1. Proportion in litter (%) (Table X)	larvae	0·8	25·6	22·3
	pupae	32·3	41·4	32·8
2. No. in litter (calculated)	larvae	1	35	99
	pupae	15	44	51
3. Total counted week 7–15 (Table III)	eggs	4,385	11,653	6,935
	larvae	1,047	2,285	1,084
	pupae	159	610	276
4. Corrected totals (2+3)	eggs	4,385	11,653	6,935
	larvae	1,048	2,320	1,184
	pupae	174	655	327

Corrections for duration of stage.

	Duration of stage (days)	Estimated populations Plot		
		A	C	D
Eggs	7	4,385	11,653	6,935
Just-hatched larvae ..	0·5	3,304	4,634	2,786
Older larvae	14	406	995	493
Pupae	9	135	509	254

Mortality rates (per cent.).

	Plot		
	A	C	D
Eggs—just-hatched larvae ..	24	60	60
Just-hatched larvae—older larvae	88	79	82
Older larvae—pupae	67	49	49
Eggs—pupae	96·9	95·7	96·3
Survivors to pupal stage ..	3·1	4·3	3·7

Mortality (per 100 eggs).

	Plot					
	A		C		D	
	died	survived	died	survived	died	survived
Eggs	24	76	60	40	60	40
Just-hatched larvae ..	67	9	32	8	33	7
Older larvae	6	3 pupae	4	4 pupae	3	4 pupae

were not determined by the abundance of the prey but by other factors. The high populations of Coccinellids of Plot C were ascribed to its situation between the two nettle sites, Great Field II and Great Field III, with their large populations of ladybirds; the comparatively small coccinellid populations of Plots A and D were associated with the distance of these plots from places harbouring ladybirds; at Plot A, the surrounding trees and buildings probably hindered the ladybirds from reaching the plot.

Estimation of Mortality Rates of Coccinellids on the Bean Plots.

Mortalities of the immature stages of Coccinellids on the bean plots at particular times have already been mentioned; cannibalism at Plot C was responsible for the large loss of just-hatched larvae in weeks 9 and 10 and, on

Plot D, the feeding problems confronting large numbers of larvae of the second phase have been stressed.

It is not possible to link the numbers of adult Coccinellids at the beginning with those at the end of the infestations owing to the complications arising from emigration and immigration; but it is possible to estimate approximately the mortalities between various stages from eggs to pupae and to attempt an explanation of any differences between plots.

Estimates of the actual numbers of individuals of any one stage on any one day may be obtained by dividing the total number counted on a plot during the period of 8 or 9 weeks by the duration of that stage. From these figures, the mortality from stage to stage may be estimated and thus the proportion surviving. The results have been obtained in a similar fashion for each plot and may be compared.

The durations of the various stages adopted for these estimations are as follows (see p. 576): egg stage, 7 days; just-hatched larva, 0·5 day; "missing stage", 7 days; older larva, 14 days; pupa, 9 days. The durations of the stages, which are considered representative for all the species, would probably vary from time to time.

Corrections for the fauna in the litter on the last sampling occasions (from Table X) have been applied to the totals of Coccinellids counted during the weeks 7–15 (from Table III) and these new totals have been divided by the durations of the stages to give the estimated populations for each plot and the mortality rates therefrom (Table XI).

Eggs—just hatched larvae.

Between these stages, mortalities were identical on Plots C and D but considerably lower on Plot A.

There was no pronounced infertility of the eggs, and no extensive destruction of just-hatched larvae was observed. While egg destruction by cannibalism is suggested as a possible contributory cause of the high mortality of Plot C, no satisfactory explanation for the identical loss on Plot D or the lowness of the mortality on Plot A can be advanced.

Just-hatched—older larvae.

On Plot A, Aphids and other food (*e.g.*, coccinellid eggs) were comparatively scarce, especially in the early stages of the aphid infestation, but on Plots C and D, where Aphids were very abundant, mortality rates were almost as high as on Plot A and a shortage of food was probably not the main cause of mortality. There are two other possibilities, both functions of prey density, (1) the difficulty of young larvae in finding the aphid colonies, (2) the large amount of honeydew on the heavily infested plants might hinder feeding and development of the young larvae.

Older larvae—pupae.

Mortalities in these stages were caused apparently by birds. Sparrows (*Passer domesticus*) occurred especially at Plots A and C and at the former four robins (*Erithacus rubecula*) were constantly present. At these two plots numbers of half-eaten pupae were found during the last two weeks of the surveys. At Plot A during the summer of 1953, when larvae tagged with radioactive labels were being studied (Banks, 1954*b*), robins were again present and were held responsible for the loss of several larvae. One robin was captured but was not radioactive; however, one of many masses of bird-droppings near the plot was highly radioactive.

Cannibalism and predation by birds cannot explain all the larval mortality observed and while a shortage of food was probably an important cause at certain times, recent work (Banks, *l.c.*) suggests that many young larvae die of starvation and exhaustion before encountering a food supply on account of the ineffectiveness of their searching behaviour and of the oviposition habits of the adult insects.

Discussion.

The potentialities of the overwintered Coccinellids were not directed entirely against *Aphis fabae* but partly against *Microlophium evansi* on nettles; consequently, populations of *A. fabae* were able to start developing on the beans without large populations of adult and larval Coccinellids to attack them.

On Plot C, where large numbers of ladybirds arrived and laid many eggs when the aphid population was still low, the larvae did not attack the Aphids so readily as they did the unhatched coccinellid eggs. Again, the nettle brood at Plot D laid large numbers of eggs when the Aphids had already reached their maximum density and were about to decline; many of the resulting larvae probably died of starvation for the aphid numbers had fallen almost to zero. Finally, the Coccinellids of the bean brood reached the adult stage by the time that the aphid infestations were over.

The effectiveness of the Coccinellids as predators of *A. fabae* was, therefore, reduced, partly by the arrival of the Aphid on the beans when the overwintered Coccinellids had already emerged from hibernation and partly by the availability of an alternative prey on nettles. To be effective against a polyphagous Aphid like *A. fabae*, any insect enemy would have to attack it on all its host-plants. The effectiveness of predators has been discussed by Varley (1953).

Other authors have emphasised the importance of alternative prey in reducing the effectiveness of a parasite or predator against a particular species (Leopold, 1933; Solomon, 1949; Allee & others, 1949); but the effectiveness is even more reduced if the alternative prey is in a separate habitat, as *Microlophium* was. *M. evansi*, though acting as a " buffer " in diverting the force of the coccinellid attack against *A. fabae*, was, however, a first food supply for the predators recently emerged from hibernation and was probably important for their survival (Leopold, *l.c.*, p. 237).

While some species of Coccinellids are specific in their food habits (Thompson, 1929), aphid-eating members of the family are not restricted to any one species of Aphid for their main food supply (Schilder & Schilder, 1928; Clausen, 1940) and Clausen (p. 573) remarks " In the aphid- and scale-feeding species particularly, there is often a pronounced tendency to vary the diet, and many species will be found to feed at times upon immature stages of Lepidoptera, Hemiptera, etc. Some have been shown to feed extensively at nectar glands of plants and on sap, pollen, fungi, honeydew, etc." The Coccinellids considered in this survey have been recorded as predators of many aphid species (Schilder & Schilder, *l.c.*; Smee, 1922; Smith, 1931).

The abundance of a predator is usually associated with the abundance of its prey (Allee & others, *l.c.*, p. 374); while this is probably true from year to year the present results indicate, when all three plots are considered, that the numbers of adult Coccinellids which came to the plots were not dependent on the abundance of the Bean Aphids but either on the proximity of a plot to nettles harbouring ladybirds, or the remoteness of a plot from such places, or the shelter afforded by trees and buildings which hindered the access of the beetles to the beans. Fenjves (1945) remarked on the influence of surrounding vegetation on the population of coccinellid larvae on a potato field in Switzerland; in one field close to a wood where Coccinellids were numerous, there was a population of 0·4 larvae per plant as against 0·1 larvae per plant elsewhere. Heinze & Profft (1940) noted the effect of sudden immigrations of adult Coccinellids on to potato fields in Germany in 1936 and 1937.

The abundance of coccinellid eggs and larvae of the bean plots depended on the numbers of adult Coccinellids which came to the plots and was not correlated with the density of the Aphids there; nor is there any evidence of a correlation between the survival rates of the various immature stages and the densities of the Aphids of the plots.

Although the adult and larval Coccinellids attacked the Bean Aphids and reduced their numbers, their effect was not noticeable and the populations of the predators apparently varied independently of those of the Aphids. Under other circumstances, Coccinellids might be effective against an abundant polyphagous Aphid like *A. fabae* if they could concentrate their attack on the one species of Aphid as soon as it arrived on its host-plant.

Summary.

Changes in numbers of adult Coccinellids on nettles infested with *Microlophium evansi* (Theo.) and on three experimental bean plots infested with *Aphis fabae* Scop. are described for the spring and summer of 1952 at Rothamsted. Of the three common species, *Adalia bipunctata* (L.), *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.), the first was always the most abundant.

The overwintered Coccinellids produced two broods: one on nettles in the spring and one on beans in early summer.

On bean plots, changes in numbers of the adult insects occurred in three phases: (1) overwintered ladybirds, dispersing from nettles and other places, accumulated on the beans in the early stages of the infestations by *Aphis fabae*; (2) ladybirds, which had developed from eggs laid by the overwintered insects on nettles, emigrated from nettles and accumulated on the beans when *A. fabae* populations were at their height; (3) ladybirds, developed from eggs laid on the beans also by the overwintered insects, reached the adult stage when the bean aphid infestations had finished. The rise and fall of the *A. fabae* populations are discussed.

One of the bean plots had always a high population of Coccinellids, which was attributed to its situation between two of the nettle sites. The other two bean plots were remote from nettles and one was sheltered by trees and buildings; their coccinellid populations were much lower.

Variations in numbers of coccinellid eggs and larvae on the bean plots followed those of the adult insects both in phase and in numbers, with the exception that there was no third phase of eggs and larvae to correspond to that of the adults.

Cannibalism (destruction of eggs by larvae) was frequently observed on the bean plot with the high coccinellid population, where, in one week, a loss of about 56 per cent. of newly hatched larvae was attributed to cannibalism. The evidence suggests that cannibalism was caused partly by a scarcity of Aphids but chiefly by an abundance of eggs and was also influenced by the relative locations of egg batches and of Aphids on the stems; larvae dispersing from the egg shells after hatching probably encountered egg batches on the lower leaves more readily than the Aphids at the tops of the plants.

A very high aphid population was responsible for the early defoliation of the plants on another bean plot and for the consequent accumulation of much of the predator fauna in the ground litter. Many coccinellid larvae from the numerous eggs laid during the second phase probably died of starvation towards the end of the infestation owing to the disappearance of many of the Aphids.

The numbers of coccinellid eggs and larvae of the different plots did not depend on the sizes of their aphid populations but on the numbers of adult Coccinellids coming on to the beans; and the mortality rates of the immature stages were apparently not correlated with the aphid densities of the three plots.

The main factors determining the numbers of adult Coccinellids of the bean plots appeared to be the distance of the plots from nettles harbouring ladybirds and the shelter afforded by trees and buildings.

Coccinellids were ineffective as predators of *A. fabae* because the majority of the overwintered ladybirds and their progeny were already attacking *M. evansi* on nettles when *A. fabae* arrived on the beans. When many Coccinellids did arrive on the beans, the aphid infestations there had already reached their maximum numbers and the effectiveness of these predators was again reduced.

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