THE DISTRIBUTIONS OF COCCINELLID EGG BATCHES AND LARVAE IN RELATION TO NUMBERS OF *APHIS FABAE* SCOP. ON *VICIA FABA*.

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In the simplest case of interaction of a parasitic insect with its insect host the ife-cycles of the interactants are synchronised, no alternative host is available and the parasite can increase only at the expense of the host.

A more complex type of interaction exists when aphid-eating Coccinellids attack an Aphid like *Aphis fabae* Scop. on beans. The prey undergoes several generations in a few weeks while its predators have but one, or perhaps two, generations a year. The Coccinellids multiply at the expense of many Aphid species throughout the year and any increase in their numbers on, say, bean plots infested with *A. fabae*, may not be attributed entirely to reproduction at the expense of this particular prey species.

It is the purpose of this paper to present additional results from a survey of Coccinellid predators and Aphids on three bean plots to illustrate the different ways in which the predator and prey populations varied, the Coccinellids by mmigration, the Aphids by reproduction.

The survey was carried out at Rothamsted during 1952 (Banks, 1955). Although the populations of *A. fabae* on the three plots of *Vicia faba* varied considerably in size and in rates of development and decline, no correlation was ound between the numbers of Aphids on a plot and the number of Coccinellids adults and immature stages) on it. The main factor determining the numbers of adult Coccinellids was considered to be the distance of the plot from nettles harbouring ladybirds which immigrated to the beans. The numbers of Coccinellid eggs and larvae occurring on the beans depended on the numbers of adult Coccinellids which arrived there and not on the numbers of Aphids. The observaions suggested that the populations of Coccinellids and of Aphids on these plots varied independently of each other.

It is often stated that adult Coccinellids lay their eggs in places close to the prey and it is assumed, therefore, that the larvae are near their food when they have hatched from the eggs. If female Coccinellids instinctively lay their eggs close to colonies of Aphids, then, in the early stages of the infestations by *A. fabae* when colonies are few, we would expect to find egg batches on aphidnfested stems only; but when all the stems are infested and Aphids very numerous, egg batches would be laid at random. The present study of the distributions of coccinellid egg batches and larvae at various stages of development of the aphid infestations of the beans would, therefore, throw light on the oviposition behaviour of the adult Coccinellids.

Methods.

Details of the methods of estimation of numbers of Aphids and Coccinellids have appeared in two previous papers (Banks, 1954*b*, 1955). A fixed number of stems in each of the 12 rows of each of the three bean plots was examined egularly at weekly intervals for the duration of the infestations by *A. fabae*, he numbers of such stems so examined being Plot A, 288; Plot C, 384; Plot D,

336. Each stem was examined from the ground upwards and all predators seen were recorded but not removed from the plants. At the same time, the stem was classified according to its degree of infestation by *A. fabae* into one of five classes: without Aphids (O), very light (V), light (L), medium (M) and heavy (H). Estimates of the numbers of Aphids in each of these classes are given in Table I.

TABLE I.

Estimates of numbers of *Aphis fabae* in classes of infested bean stems with other information concerning the aphid infestations.

Class of stem	Plot		
	A	C	D
V	100	97	190
L	984	1769	1511
M	5205	7660	9736
H	12833	13010	19413
Proportion of stems infested in week 7 (%) ..	23	37	54
Mean Aphids per stem in week 7	20	45	93
Week when maximum aphid nos. reached ..	week 13	week 13	week 12
Maximum numbers of Aphids per stem	4676	9639	13958

Three species of Coccinellids were common on the bean plots, *Adalia bipunctata* (L.), *Coccinella septempunctata* L. and *Propylea quatuordecimpunctata* (L.), the first forming approximately 70 per cent. of all the species, while about 70 to 78 per cent. of the eggs appeared to be of this species.

Eggs as well as larvae of all species have been treated together, for many young larvae of the various species could not be distinguished from each other in the field. Larvae were classified as '*just-hatched*' (the stage after eclosion, with the young larvae still grouped on and around the empty egg shells, which lasts from a few hours to 24 hours) and as '*older*' larvae (mostly 3rd and 4th instars).

Primary migrants of *A. fabae* arrived on the beans during the week ended 21st May (week 6 of the survey). In week 7, the plots differed in their levels of aphid infestation, Plot D having 54 per cent. of the stems infested, Plot C, 37 per cent., and Plot A, 23 per cent. Maximum aphid numbers, attained in week 12 (Plot D) and week 13 (Plots C and A), were in the approximate ratio D:C:A::3:2:1. The maxima were followed by rapid declines, and by weeks 14 (Plot D) and 15 (Plots C and A) the infestations had completely died out.

Distributions of Coccinellid Egg Batches.

Two questions relating to the oviposition behaviour of the adult Coccinellids must be considered; first, before all the stems had become infested, were egg batches laid more frequently on aphid-infested stems than can be explained by chance, that is, was there any significant association between the presence of eggs on a stem and the presence of Aphids. Secondly, when all the stems had become infested, the female Coccinellids could only lay their eggs close to aphid colonies. We then have to consider whether the egg batches were laid on the stems with the most Aphids, that is, what was the extent of any correlation between the numbers of egg batches and the numbers of Aphids on individual bean stems.

TABLE II.

Mean numbers of coccinellid egg batches per class of stem.

	Class of stem	Mean egg batches per stem for week							
		7	8	9	10	11	12	13	14
Plot A	O	0·07	0·14	0·08	0·08	0	0	—	0
	V	0·09	0·18	0·17	0·22	0·06	0·11	0·04	0
	L	—	—	0·09	0·69	0·15	0·24	0·21	0·08
	M	—	—	1·00	0·50	0·38	0·58	0·33	0·18
	H	—	—	—	1·00	0	1·44	0·57	0·56
Plot C	O	0·14	0·13	0·20	0·27	0	—	0	0
	V	0·17	0·21	0·40	0·45	0·22	0	—	0
	L	0·33	0·36	0·62	0·63	0·30	0·18	0	0·05
	M	—	0	0·75	0·83	0·50	0·60	0·24	0·03
	H	—	—	0·50	0·72	0·67	0·86	0·36	0·38
Plot D	O	0·08	0·06	0·06	0·33	—	—	0	0
	V	0·08	0·06	0·12	0·15	0	—	0	0·03
	L	—	0·14	0·20	0·15	0·21	0·50	0·17	0·11
	M	—	—	0·20	0·49	0·16	0·52	0·43	1·25
	H	—	—	0	0·15	0·21	0·73	0·46	—

The mean numbers of egg batches on each class of stem for the three plots are given in Table II. In the first week of the survey of beans (week 7), 48 to 71 per cent. of all egg batches occurred on uninfested stems, although 46 to 77 per cent. of the stems were infested with Aphids. As more and more stems became infested, the proportion of egg batches on uninfested stems, of course, decreased (Table III) and after week 10 (Plot D), week 11 (Plot C) and week 12 (Plot A), all stems had become infested.

TABLE III.

Distributions of coccinellid egg batches on infested and uninfested stems before all stems had become infested with *Aphis fabae*.

Week	Plot A		Plot C		Plot D	
	% egg batches on Class O	% stems uninfested	% egg batches on Class O	% stems uninfested	% egg batches on Class O	% stems uninfested
7	71	77	59	63	48	46
8	58	63	39	53	30	32
9	38	57	26	44	12	24
10	17	46	8	15	3	2
11	0	19	0	1	—	0

TABLE IV.

Numbers of infested and uninfested bean stems with or without coccinellid egg batches, before all stems had become infested with *Aphis fabae*.

	Week							
	7		8		9		10	
	eggs present	eggs absent	eggs present	eggs absent	eggs present	eggs absent	eggs present	eggs absent
Plot A								
Aphids present	6	61	18	89	19	103	37	119
Aphids absent	15	206	25	156	15	153	9	123
χ^2	0·11		0·27		3·52		14·00	
P	0·74		0·60		0·06		<0·001***	
Plot C								
Aphids present	20	123	35	146	78	138	131	198
Aphids absent	34	207	25	178	29	139	13	42
χ^2	0·34		3·07		3·61		4·60	
P	0·56		0·07		0·06		0·03*	
Plot D								
Aphids present	10	171	14	214	32	224	—	—
Aphids absent	14	141	6	102	5	75	—	—
χ^2	2·12		0·001		1·83		—	
P	0·15		0·98		0·18		—	

* = significant of association ($P<0·05$)
*** = highly significant of association ($P<0·001$)

Regarding the first question mentioned above, the numbers of infested and uninfested stems observed with and without egg batches are given in Table IV for the bean plots for the first three or four weeks of the survey. During weeks 7, 8 and 9, when many stems were uninfested, there were no significant associations of the egg batches with the Aphids ($P > 0{\cdot}05$).

On Plot D in week 10 all the stems were infested; on Plots A and C, although a few stems remained uninfested in weeks 10 and 11, egg batches were significantly associated with the presence of Aphids, for, during weeks 9–11, the aphid colonies on many stems had become so large that the adult Coccinellids were able to find them readily; eggs were laid more often on such stems, for the beetles tended to stay and feed on the Aphids.

The second question, whether there was a positive correlation between the numbers of egg batches and the numbers of Aphids on bean stems, has been examined by the calculation of linear regressions for those weeks before the aphid populations of the plots started to decline, the two variables being mean egg batches per class of stem (y) and mean Aphids per class of stem (x). To reduce the variability of the data and to permit the inclusion of stems without eggs or Aphids, the transformations $\log(y+0{\cdot}001)$ and $\log(x+0{\cdot}001)$ have been used to calculate the equation

$$\log(y+0{\cdot}001)=b.\log(x+0{\cdot}001)-\log a$$

which may be written

$$(y+0{\cdot}001)=\frac{(x+0{\cdot}001)^b}{a}$$

The results are given in Table V; no regressions could be calculated for Plot A (weeks 7 and 8) and Plot D (week 7), for stems of only two classes occurred. The regressions with the highest values occurred when aphid numbers were at or near their maxima (Plot A, week 13; Plot C, week 12; Plot D, week 11). Three of the regressions are negative and are for those plots where aphid numbers were high (Plots C and D).

TABLE V.

Weekly regressions (b) of mean coccinellid egg batches on Aphids per class of stem.

	Week						
	7	8	9	10	11	12	13
Plot A							
Regression (b)	—	—	0·100	0·141	0·205	0·424	0·524
S.E. ±	—	—	0·094	0·030	0·215	0·023	0·066
P.	—	—	—	<0·05	—	<0·001	<0·05
Plot C							
Regression (b)	0·047	−0·158	0·071	0·064	0·395	0·787	—
S.E. ±	0·035	0·279	0·015	0·141	0·033	0·086	—
P.	—	—	<0·05	—	<0·01	—	—
Plot D							
Regression (b)	—	0·039	−0·065	−0·023	1·070	0·122	—
S.E. ±	—	0·050	0·184	0·045	0·483	0·103	—
P.	—	—	—	—	—	—	—

The majority of the regressions are positive, indicating that the adult Coccinellids tended to lay their eggs on the most heavily infested stems.

The relative changes in numbers of coccinellid eggs and Aphids on the plots over the period of the survey may be compared by measuring the extent to which the weekly regressions of each plot are positive.

Common regressions " ($\bar{b}$) " for each plot have been calculated (Table VI). They are all positive, but the slope is greatest for Plot A, with the lowest aphid population, and smallest (in fact, negligible) for Plot D where the aphid population was largest.

TABLE VI.

" Common " regressions of coccinellid egg batches on Aphids and of older larvae on Aphids, compared with the maximum numbers of Aphids recorded.

Plot	Common regression for egg batches and Aphids ($\bar{b}$)	P.	Maximum Aphid numbers recorded (Aphids per stem)
A	0·229±0·056	<0·01	4676
C	0·102±0·057	<0·05	9639
D	0·005±0·072	>0·05	13958
	For older larvae and Aphids ($\bar{b}$)		
A	0·271±0·050	<0·001	4676
C	0·153±0·044	<0·01	9639
D	0·185±0·070	<0·05	13958

These common regressions may be interpreted in the following way. On any one plot, as Aphids increased by 1·0 (on the logarithmic scale), coccinellid eggs increased by 0·229 (Plot A), 0·102 (Plot C) and 0·005 (Plot D). In other words (taking the antilogarithms), a 10-fold increase in Aphids on a plot was accompanied by an increase of eggs of 69 per cent. (Plot A), 26 per cent. (Plot C) and 1 per cent. (Plot D).

Distributions of older Larvae.

When studying the distributions of larvae on the bean plots, it is necessary to consider the older larvae alone, for the distributions of just-hatched larvae would resemble those of egg batches. The distributions of older larvae on each class of stem, with the mean number of larvae per class of stem, for the three plots are given in Table VII.

Weekly regressions (b) of log mean larvae (log (y + 0·001)) on log mean Aphids per class of stem (log (x + 0·001)) have been calculated (Table VIII). All but one of these regressions are positive, 8 of the 17 being significant ($P<0·05$). Older larvae, therefore, tended to occur more often on stems where Aphids were most numerous.

The average slopes of common regressions ($\bar{b}$) of the weekly regressions (Table VI) are all positive and significant ($P<0·05$). Again, the slope is greatest for Plot A where the aphid population was the lowest and the meaning of the common regressions is as follows. As Aphids increased by 1·0 (on the logarithmic scale) on any of the plots, the older larvae increased by 0·271 (Plot A), 0·153 (Plot C) and 0·185 (Plot D); that is, an increase of 10 times the aphid numbers on any one plot was accompanied by an increase in older larvae of 87 per cent. (Plot A), 42 per cent. (Plot C) and 53 per cent. (Plot D).

TABLE VII.

Mean numbers of older coccinellid larvae per class of stem.

	Class of stem	Week								
		7	8	9	10	11	12	13	14	15
Plot A	O	—	—	0·01	0·02	0·06	—	—	—	0·04
	V	—	—	0·06	0·09	0·10	0·19	0·06	0·06	0·37
	L	—	—	—	0·04	0·28	0·21	0·32	0·42	0·49
	M	—	—	1·00	0·50	0·07	1·00	0·87	0·81	0·91
	H	—	—	—	1·00	1·00	1·28	2·00	2·18	—
Plot C ..	O	—	0·01	0·08	0·05	—	—	—	0·13	0·18
	V	—	0·01	0·02	0·32	0·40	—	—	1·63	0·44
	L	—	—	0·21	0·30	0·58	0·93	0·40	0·71	0·40
	M	—	—	0·13	0·55	0·61	1·62	1·06	1·14	—
	H	—	—	—	0·61	1·25	2·19	1·28	0·81	—
Plot D	O	—	—	—	—	—	—	0·25	0·62	
	V	—	0·02	0·01	0·04	—	—	0·28	0·99	
	L	—	—	—	0·69	0·16	—	0·67	1·20	
	M	—	—	—	0·08	0·15	0·58	0·67	2·00	
	H	—	—	—	0·39	0·31	0·87	1·31	—	

Discussion.

The changes in numbers of Coccinellids relative to the aphid populations will first be considered.

It was seen that the extent to which the weekly regressions of egg batches on Aphids for each plot were positive, varied inversely with the size of the aphid

TABLE VIII.

Weekly regressions (b) of mean older larvae on Aphids per class of stem.

	Week					
	9	10	11	12	13	14
Plot A						
Regression (b) ..	0·119	0·190	0·103	0·432	0·703	0·450
S.E. ±	0·281	0·091	0·102	0·031	0·028	0·049
P.	—	—	—	<0·001	<0·01	<0·01
Plot C						
Regression (b) ..	−0·088	0·145	0·425	0·419	0·600	0·121
S.E. ±	0·177	0·016	0·046	0	0·070	0·046
P.	—	<0·01	<0·01	<0·001	—	<0·05
Plot D						
Regression (b) ..	—	0·283	1·142	2·812	0·078	0·060
S.E. ±	—	0·202	0·413	0·599	0·036	0·021
P.	—	—	<0·05	—	—	—

populations on the plots. Thus on Plot D, where the Aphids were always very numerous, egg-laying by the Coccinellids could not keep pace with the high rate of aphid increase; the common regression, although positive, was not significant; that is, although there was a tendency for the eggs to occur more often on the stems with the most Aphids, the results were so variable that any correlation could be ascribed to chance. On Plots C and A, however, Aphids increased less rapidly and oviposition by the ladybirds was at a higher rate than on Plot D. The common regressions were positive and significant, the value of the regression and its significance level being higher where the Aphids were fewer and had the lower rate of increase (Plot A).

The degree of correlation between the coccinellid egg batches and Aphids (the values of the common regressions), therefore, appeared to be determined by the rate of increase of the aphid numbers. A situation may be imagined in which the Aphids multiplied so slowly that the numbers of coccinellid eggs could have increased at the same rate. That they did not on any of the plots considered here is because the egg numbers varied directly with the numbers of adult Coccinellids, which increased *additively* (by immigration to the beans) and independently of the aphid numbers which increased *multiplicatively* (by reproduction) and at a much higher rate. In the situation imagined above, the rate of increase of coccinellid eggs by addition would have to equal the rate of increase of the Aphids by multiplication.

Some entomophagous Coccinellids are restricted to a particular kind of prey (Schilder & Schilder, 1928; Thompson, 1929), notably those species predacious on Coccids and mites. Balduf (1935) noted that the small species of Coccinellids exhibit a noticeable tendency towards a parasitic relationship with the larger Coccids. Clausen (1940) has pointed out that while most Coccinellids may be regarded as predators, some species have developed habits similar to those of parasites, for a specialisation in oviposition behaviour is combined with a restriction to a particular food. Thus *Rodolia cardinalis* (Muls.), which attacks *Icerya purchasi* Mask., lays its eggs upon the body of the female Coccid or on the egg mass, and the larva preys on this one host whose progeny usually suffice for the whole development of the predator. *Rodolia limbata* (Motsch.), referred to by Clausen (*loc. cit.*) as *Novius limbatus* Mats., attacks the enormous Coccid, *Drosicha corpulenta* (Kuw.), in Japan, sometimes laying its egg beneath the scale, the larva attaching itself to the body of the host (Clausen, *loc. cit.*).

Other Coccinellids, particularly the aphid-eating forms, are less specialised in their feeding and oviposition behaviour, and although they usually lay their eggs in surroundings where the prey occurs, they have been observed to oviposit in places where there is no prey. Thus, *Hyperaspis vinciguerrae* Capra, a predator of mealybugs in Egypt (Hafez & El-Ziady, 1952) has been seen to lay its eggs in places where the newly-hatched larvae had no prey to feed on (El-Ziady, private communication). At Harpenden in April 1952 *Coccinella septempunctata*, emerging from hibernation in grass, laid many eggs on clover and grass leaves and on cigarette cartons although no Aphids were present in the surroundings (Banks, 1954*a*). Similar observations were made by Hawkes (1920) for *Adalia bipunctata.*

It was suggested at the beginning of this paper that, if female Coccinellids instinctively lay their eggs close to aphid colonies, then, in the early stages of infestations by *A. fabae* when aphid colonies are few, egg batches may be expected on aphid-infested stems only; when all the stems are infested, egg batches will be laid at random.

This argument is not supported by the results of the survey for, during the early stages of the three infestations, any association of coccinellid egg batches with the aphid-infested stems was attributable to chance; but when the infestations had reached an advanced state and all stems were infested, the egg batches tended to occur most frequently on the stems with the most Aphids. The results suggest, therefore, that the aphid-eating Coccinellids of the species considered here do not need the stimulus of the presence of Aphids before laying their eggs on beans; this is also the impression one gets during fieldwork and the behaviour of the various species does not seem to differ in this respect.

It is, of course, possible that the females laid their eggs on infested stems and then themselves ate the few Aphids present, so that an observer recorded the eggs on uninfested stems, but this suggestion is not supported by observation; for example, on Plot D, oviposition occurred before the arrival of any Aphids, for egg batches and well-developed larvae were found on the beans during week 6 when Aphids first arrived (Banks, 1955).

The correlation of numbers of egg batches with numbers of Aphids when the infestations are well advanced is explained by the concentration of the adult Coccinellids on well-infested stems where they would tend to stay to feed on the Aphids and probably to lay their eggs.

The positive correlations between the older larvae and Aphids were to be expected, for the young larvae, after dispersal from the egg shells, would wander until they encountered an aphid colony. But the correlations were not always significant; the eggs from which the larvae hatched were not always laid close to Aphids and larvae would probably have stayed on the nearest infested stem rather than on the most heavily infested stem in the vicinity.

When aphid-infested stems are few, the young larvae might not be able to find them and under such conditions many probably die of starvation and exhaustion unless they can live for the time being on other food such as coccinellid eggs and larvae or other small insects. Those larvae able to find a small amount of food quickly would probably be able to live longer and thus be able to search a larger number of plants to find a food supply sufficient for their growth requirements; and those larvae hatching from eggs laid on infested stems might start with an advantage. The proportion of young larvae able to reach an aphid colony is probably higher when the aphid infestation on a bean plot is well-advanced than when it is in its early stages.

Summary.

Further analysis of results obtained from a study of populations of Coccinellids on three plots of *Vicia faba* infested with *Aphis fabae* Scop. at Rothamsted during 1952 are presented. The distributions of coccinellid egg batches and older larvae (mostly 3rd and 4th instars) on bean stems of five arbitrary classes of aphid infestation, emphasise the differences in the manner of increase of the predator and prey populations considered here; at the same time, the results throw light on the oviposition behaviour of the adult Coccinellids.

The degree of correlation between coccinellid egg batches and Aphids on the plots (as indicated by regression analysis) varied inversely with the size of the aphid populations on the plots. On one plot, where Aphids were extremely numerous, this correlation was negligible; on the two other plots, where Aphids were less abundant, the correlation was more marked, being highest at the plot where the aphid numbers were lowest. The degree of correlation between egg batches and Aphids was determined apparently by the rate of increase of aphid numbers. It is pointed out that while these coccinellid populations increased additively (by immigration of ladybirds to the beans), populations of *A. fabae* increased multiplicatively (by reproduction) and at much higher rates.

During the early stages of the aphid infestations on the bean plots, when aphid-infested stems were comparatively few, there was no statistically significant association between coccinellid eggs and the presence of Aphids on the bean stems; but when all stems had become infested, egg batches tended to occur

most frequently on the stems with the most Aphids. From these and other observations it is concluded that the female Coccinellids do not need the stimulus of the presence of Aphids before laying their eggs on beans, and that they concentrate on well-infested bean stems where they tend to stay and feed on the Aphids and probably oviposit on those stems. The distributions of older coccinellid larvae (3rd and 4th instars) indicate that they, too, tend to concentrate on well-infested stems.

The oviposition habits of the female Coccinellids are discussed in relation to the feeding problems of the newly-hatched larvae.

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