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A QUANTITATIVE STUDY OF A POPULATION OF WHEAT BULB FLY,
LEPTOHYLEMYIA COARCTATA (FALL.), IN THE FIELD.

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(PLATE II.)

Extensive studies of adult populations of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), in Britain were carried out by Gough (1946) using a standardised sweeping technique. Irregularities of distribution suggested considerably differing habits and activities of the sexes, but the data could not be fully explained as the numbers caught depended both on the size of the population and on the degree of activity of its members at the time. This difficulty in evaluating data obtained by sweeping alone has also been pointed out by Long (1958). Clearly, knowledge of the absolute sizes and compositions of the populations would have assisted interpretation of these data.

The main purpose of the present work was to estimate the absolute numbers of flies of each sex and of every age present in a natural population during the whole period of adult life. Some observations on immature stages were also made so that natural mortality from egg to imago could be estimated.

The work was carried out during 1956 at Rothamsted, on Pennell's Piece, a small area of land adjoining the classical wheat field, Broadbalk. The soil type of Pennell's Piece is a heavy loam derived from the geological deposit "clay with flints".

After lying fallow for two years, the site had been sown during autumn 1955 with wheat (variety Cappelle) at the rate of two bushels per acre. Preliminary inspection during the spring of 1956 showed that this wheat was moderately infested.

Methods.

The work consisted principally of a study of the development and decline of a population of adult flies. This was supplemented by observations on the populations of the immature stages.

To study emergence, a large cage of terylene netting, 24 ft. long, 12 ft. wide and 6 ft. high, was used (Pl. II, figs. 1 & 2). It was erected over a plot of infested wheat in mid-June shortly before the flies were expected to appear and was searched twice daily, at approximately 10–11 a.m. and shortly before sunset. To avoid unnecessary damage to the plants, paths were cut through the wheat. Full details of the construction of the cage and of the effect it had on the climate of the enclosed area are given in the Appendix.

In order to find the flies, the wheat was gently beaten by hand. This caused many of them to fly up to the walls and roof of the cage where they could easily be captured with a mouth-suction apparatus (Poos, 1929). After this the soil surface and plants were searched but very few additional flies were found. Searching usually took about an hour but was always continued until it seemed unlikely that any more flies would appear.

Population decrease was investigated by the method of marking, releasing and recapturing. Every day the newly emerged flies caught in the cage were removed to the laboratory, and after light anaesthetisation by chilling (six minutes

in a tube placed in a refrigerator at $-5^{\circ}\text{C}.$) were marked with either one spot or two spots of Artist's oil colour applied to the dorsum of the thorax with the head of a fine pin. The colour or combination of colours was changed daily so that the marks indicated dates of emergence. After being marked, the flies were immediately returned to the cage.

A search for marked flies was made on every third day during the morning search for unmarked ones and the numbers, marks and sexes of those captured were recorded. The flies were then released again. Marked flies were sufficiently conspicuous to make it possible to avoid capturing them except when required. Searches were carried out regularly until 4th September, nine days after the last flies had been seen.

Effects of Anaesthetisation and Marking.

Although flies appeared to recover quickly after marking, there were frequently large differences between the numbers of newly marked flies released in the cage and the corrected * numbers recaptured for the first time. This difference was greater for flies marked with two spots of paint than for those marked with one spot; of 143 males with one spot, 60.3 per cent. were known to be alive on the day after marking and, of 150 males with two spots, 46.5 per cent. were alive. The corresponding figures for females were 78.4 per cent. of 47 with one spot and 58.7 per cent. out of 211 with two spots. It seems likely from the above figures that the initial loss was due to the harmful effect of marking.

A laboratory experiment was therefore carried out to test the effects of marking and anaesthetisation on the length of life of Wheat Bulb Fly. Neither treatment appeared to have any effect, and all groups survived equally well. However, the flies used in this experiment differed from those marked and released in the cage in that having been obtained by general field collecting they were of mixed ages whereas the latter were all newly emerged.

It was not possible to repeat the laboratory experiments using newly emerged flies, but there is evidence from the literature that very young insects are frequently less robust than older ones. Jackson (1948) found that marking with oil paints appeared to be more harmful to newly emerged tsetse flies than to older ones, and insecticide workers have frequently found very young insects to be relatively highly susceptible to toxic substances (Morrison, 1943; Mukerjea, 1953; Craufurd-Benson, 1938; Kerr, 1954). There are grounds therefore for believing that the initial losses in the cage were due to marking.

It is equally important to know whether the length of life of marked flies which did not die shortly after marking was affected. Again, this could not be tested directly with newly emerged flies but there is reason for supposing that there was no appreciable effect. In the field cage there was no apparent difference in the survival rate of flies which had survived the initial loss whether they were marked with one spot of paint or with two, and, in the laboratory experiment, marked and unmarked flies survived equally well. In support it may be noted that Jackson (1952, p. 16) found that there was no difference in survival between marked and unmarked groups of tsetse flies over the six weeks following that of release.

The nature of this supposed marking effect is unknown. None of the paints contained poisonous pigments, but the solvent, which tended to spread and leave a permanently blackened area, may have been toxic. It is unlikely that the weight of the paint (approximately 0.5 mg. per spot) was of importance as, although it amounted to between 5 and 12 per cent. of that of the flies, there were no differences in length of life between individuals marked with one spot and those marked with two.

* This is explained later on p. 102.

TABLE II.
Marking and recapture data for female flies.

Date	No. of emerged	No. of days after marking	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21	22	23	24	25	26	
June 21	1		0	0	1	0	1	1	0	0	1	0	0	1	1	0	0	0	0	1	0	0	0	0	0	0	0	0	
22	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	0		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	1		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	2		2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26	2		2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27	2		2	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28	2		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29	5		3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30	2		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July 1	10		6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2	10		6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3	10		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4	11		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5	11		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6	29		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7	35		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8	37		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9	17		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10	17		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11	8		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12	2		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13	4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14	0		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15	3		7	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16	7		1	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17	4		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18	6		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19	10		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20	2		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21	4		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22	1		0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25	1		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

TABLE II—continued.

Marking and recapture data for female flies.

Date	No. of days after marking	No. emerged	27	28	29	30	31	32	33	34	35	36	37	38	39	40	41	42	43	44	45	46	47	48	49	50	51	
June 21		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
26		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
27		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
28		2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
29		5	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
30		2	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
July 1		10	3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
2		10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
3		10	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
4		11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
5		11	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
6		29	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
7		35	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
8		37	2	3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
9		17	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
10		17	0	4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
11		8	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
12		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
13		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
14		0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
15		3	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
16		7	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
17		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
18		6	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
19		10	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
20		2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
21		4	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
22		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
23		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
24		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
25		1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0

Results.

Flies were first seen in the field outside the cage on 20th June, and the first was caught inside on 21st June. From that date, regular collections were made and searching was continued until 4th September, nine days after the last fly had been seen. The entire data for male and female flies are shown in Tables I and II, respectively. The first entry of each line shows the number of flies originally marked, and the succeeding entries the numbers recaptured on successive days. The numbers caught showed a sharp reduction between the first capture and first recapture and thereafter a gradual fall until no more flies were caught.

The proportion of the total population captured each day depended both on the activity of the flies and on the efficiency of the searching technique. Deficiencies amongst newly emerged flies were minimised by carrying out two searches a day, and amongst recaptured flies by correction of the data.

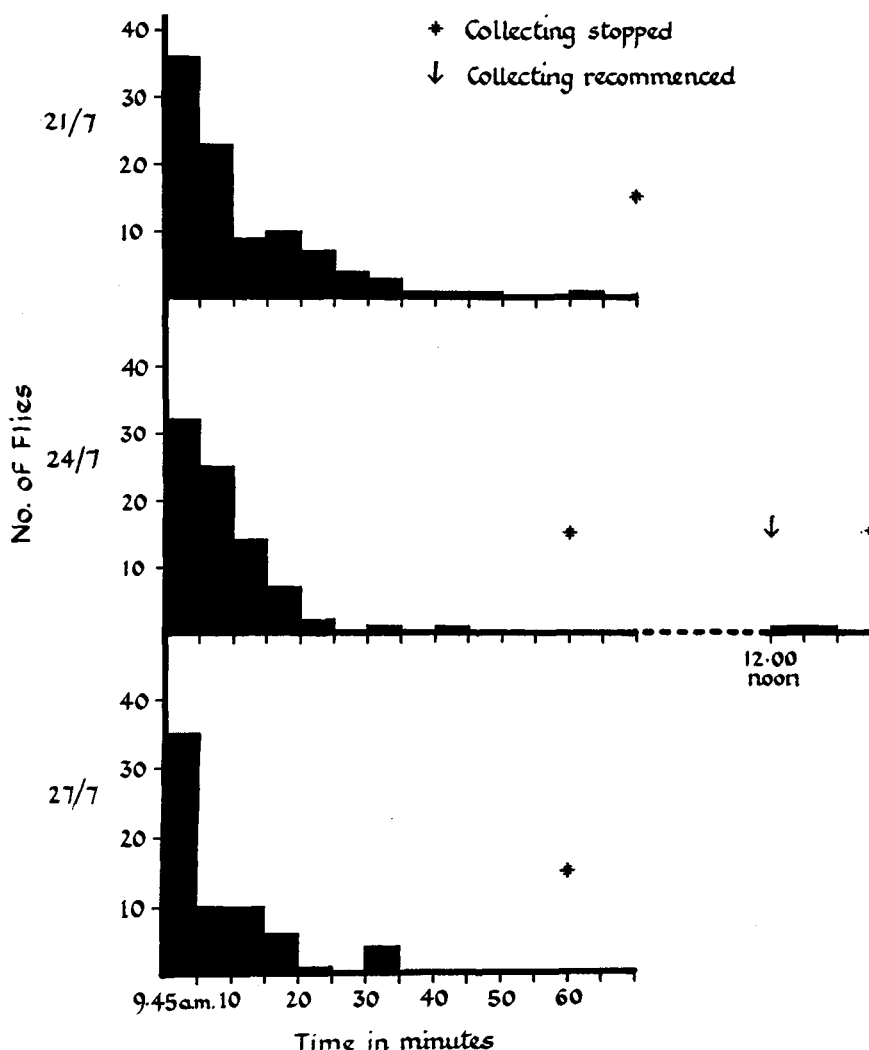


Fig. 1.—The numbers of *L. coarctata* caught at five-minute intervals during the mornings of three separate days.

The technique was tested by carrying out timed collections of at least an hour's duration on 21st, 24th and 27th July. On each date, most of the flies were caught during the early part of the search; after half an hour over 90 per cent. of the final total had been caught, and after 45 minutes only isolated individuals were found (fig. 1). On 24th July a second search, of 15 minutes' duration, carried out 1½ hours after finishing the first, revealed only two more flies. It is thought, therefore, that losses due to inefficient searching were not serious. Further evidence of this was afforded by the constant reappearance of several flies which could be recognised individually, *e.g.*, the female first captured on 21st June was seen 23 times in 25 successive searches before it disappeared finally, and two females first captured on 28th June were both seen in seven out of ten searches, and one of them was seen on two of the remaining occasions.

Errors due to differences of activity, although partly compensated by thorough searching, could not be completely avoided. Their effect could however be minimised by the statistical treatment.

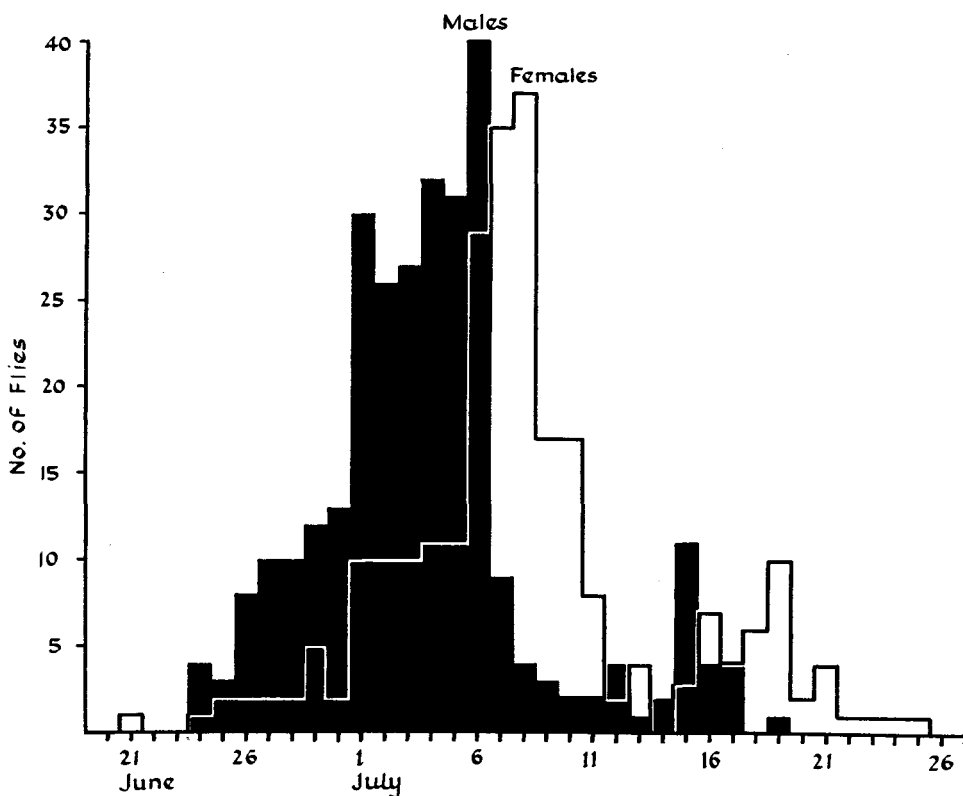


Fig. 2.—The daily emergence figures for males and females of *L. coarctata* in the cage.

Emergence pattern.

The first entries in each line of Tables I and II show the daily emergence figures for males and females. These are illustrated as day to day frequency diagrams in fig. 2 to show the emergence pattern.

Male flies were first seen on 24th June. After this, apart from temporary checks, the daily catch of males increased, reaching a maximum of 40 flies on

6th July. The catches then decreased, and apart from a sharp increase on 15th July remained low until the last freshly emerged fly was caught on 19th July. In all, 293 males were caught during 26 days, and of these, 186 (63%) emerged between 1st and 6th July. This period of six days may therefore be termed the "period of maximum emergence". The highest single day's catch occurred at the mid-point of the emergence period, but the distribution of values around this was markedly asymmetrical, 206 flies (70%) occurring in the period before it, and only 47 (16%) occurring in the period after it.

The first female was found on 21st June, but very few appeared until 1st July when there was a sharp increase. Remaining steady for the next few days, the catch increased again on 6th July and reached a maximum of 37 flies on 8th July. Thereafter there was a rapid decrease, and except for a small increase between 16th and 19th July, numbers remained low until the last freshly emerged fly was caught on 25th July. In all, 258 females were caught during 35 days, and the period of maximum emergence, during which 135 flies (52%) were caught, was from 6th to 10th July inclusive. As with the males, the highest catch occurred at the mid-point of the emergence season and the distribution was asymmetrical, 133 flies (52%) being caught before the maximum and 88 (34%) after it.

The emergence patterns of the sexes, although similar in general form, differed in timing and in degree of asymmetry. The maximum emergence period of the male pre-dated that of the female by some five days, and a greater proportion of the males emerged before the mid-point of the emergence season. Female emergence also spread over a longer period than that of the males. The small increases in the daily emergence figures which occurred in both sexes about a week after the period of maximum emergence are of interest. They suggest that at some stage of development a small portion of the population may have been delayed and that this delay had persisted. This division of the population was also evident amongst the larvae on 31st May when, except for a small minority which were still in their second instar, most had completed their growth and had left the plants.

The check to the rising daily catches of both sexes which occurred between 2nd and 5th July is also of interest. The reason for this is not known, but as it occurred in both sexes simultaneously it may have been the result of some event about the time of emergence.

The final totals, 293 males and 258 females, were sufficiently close to suggest that the sexes are fundamentally equal in numbers.

Population decline.

Rate of population decline was estimated from recapture figures of marked flies. The number of recaptures depended partly on the activity of the flies and partly on the efficiency of searching, so that sometimes not all the flies subsequently found to be alive were captured. Errors due to this were reduced by correcting the figures to show the numbers known to be alive on each day rather than the numbers actually recaptured. For example, the values for male flies marked on 5th July before and after correction are as follows:—

Date	July	5	6	9	12	15	18	21	24	27	30
Uncorrected		11	2	4	6	3	3	1	3	1	0
Corrected		11	6	6	6	3	3	3	3	1	0

When summed for all dates and expressed as percentages of the numbers marked, the corrected recapture figures show that there was a heavy loss of flies during the first day followed by a gradual decrease in numbers. As this high initial loss was believed to be due to marking, the rate of population decline was estimated from corrected recapture figures alone, that is, without reference to the original numbers marked. If the gradual decrease is due solely to random

mortality, then the number of flies will decrease logarithmically with time, that is, there will be a straight-line relationship of the form " $y = a - bx$ " where " y " is the logarithm of the numbers of flies, and " x " is the number of days after marking. The slope of the line, " b ", estimates the rate of decrease and is independent of the intercept at the " y " axis, " a ",—the estimated logarithm of the number of flies at the start. Comparison of the antilogarithm of " a " with the number marked enables the size of the initial loss to be estimated.

The data were insufficient for each day's emergence to be dealt with separately, so a mean rate of decrease based on the entire data for each sex was calculated. As observations were made every three days, the data fell into three groups, depending on whether observations started one, two or three days after marking. Taking each group separately, the logarithm of the summed corrected recaptures was plotted against time. In each case the points at first fell approximately on a straight line but later, as the numbers of flies decreased, they became erratic. In calculating the regression lines, therefore, only points based on ten or more flies were used. The group regressions were used to estimate initial mortality, but to estimate rate of population decrease they were combined into a common regression. From this the half-life of the population could be calculated, and was estimated to be 7.3 days for males and 11.1 days for females. The equations and deductions from them are shown in Table III. (The data for males were more variable than those for females and the slopes of the lines differed significantly—variance ratio, 2/12 d.f., 4.2. It is not thought however that the use of the common regression in this case was misleading.)

Population size and composition.

As the regression coefficients expressing rates of population decrease are independent of the numbers of individuals in the population, they can be applied to the daily emergence figures to estimate the numbers of flies left after any period of time. This enables a general picture to be obtained of the size and composition of the population at any time during the period of adult life.

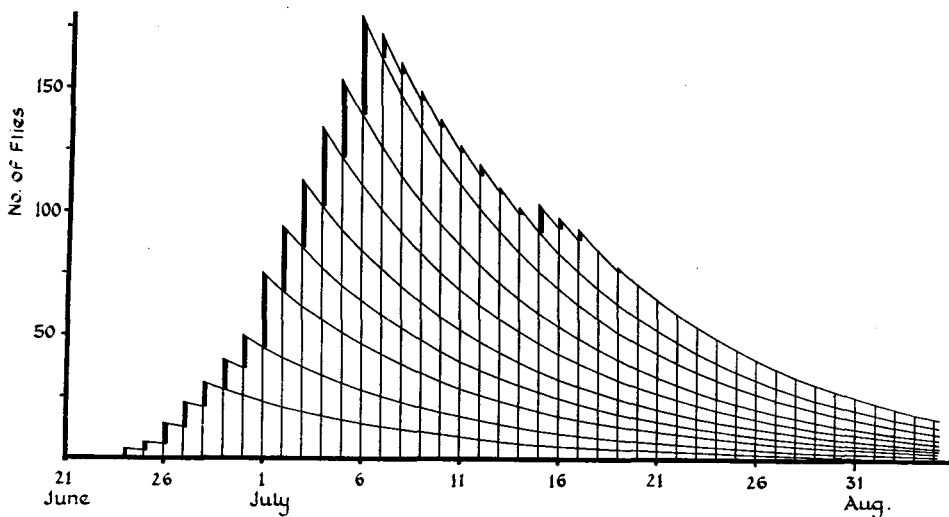


Fig. 3.—The theoretical structure of the male population of *L. coarctata* in the cage.

TABLE III.

Analysis of recapture data.

Sex	Group	Regressions*	Nos. marked	Estimated nos. surviving 1 day	% deaths through marking**	Common regression	Half-life of population
Females	1, 4, 7, etc., days after marking	$y = 1.80 - 0.031x$	81	63	36	$y = 1.74 - 0.27x$	11.1 days
	2, 5, 8, etc., days after marking	$y = 1.75 - 0.025x$	100	56			
	3, 6, 9, etc., days after marking	$y = 1.66 - 0.025x$	77	46			
Males	1, 4, 7, etc., days after marking	$y = 1.66 - 0.034x$	89	46	38	$y = 1.75 - 0.04x$	7.3 days
	2, 5, 8, etc., days after marking	$y = 1.81 - 0.048x$	92	65			
	3, 6, 9, etc., days after marking	$y = 1.85 - 0.049x$	112	71			

* $y = \log$ no. flies.

x = No. days after marking.

** Pooled for flies marked with one spot and with two spots. The proportion of females marked with two spots was higher than that of males.

The reconstructed populations for males and females, respectively, are shown in figs. 3 and 4. The figures show for each day:

- (1) The total number of flies (heights of vertical lines).
- (2) The number of new emergences (thickened portions of vertical lines).
- (3) The number of flies of each age (portions of vertical lines between successive converging curves).

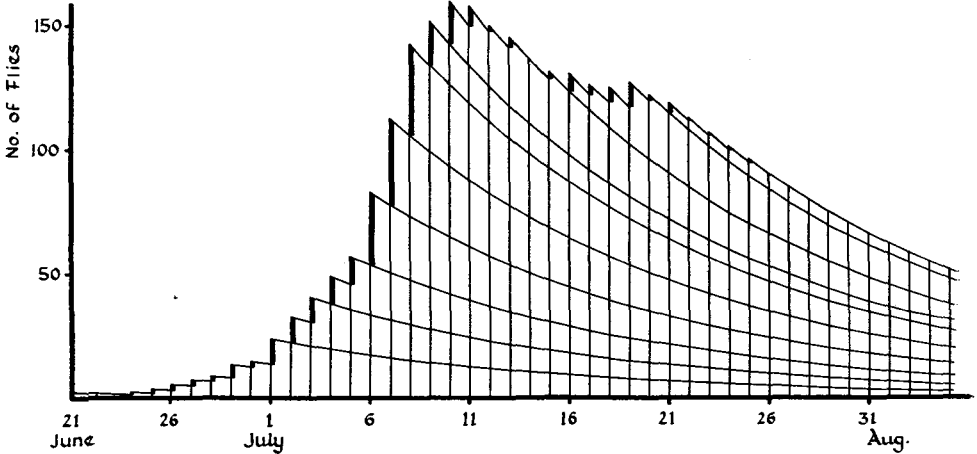


Fig. 4.—The theoretical structure of the female population of *L. coarctata* in the cage.

Populations of males and females showed similar trends (fig. 5). There was a rapid increase in total numbers to a sharp maximum and then a more gradual decrease. The male maximum (179 flies) occurred on 6th July and the female maximum (159 flies) on 10th July. From 24th June until 8th July males were predominant

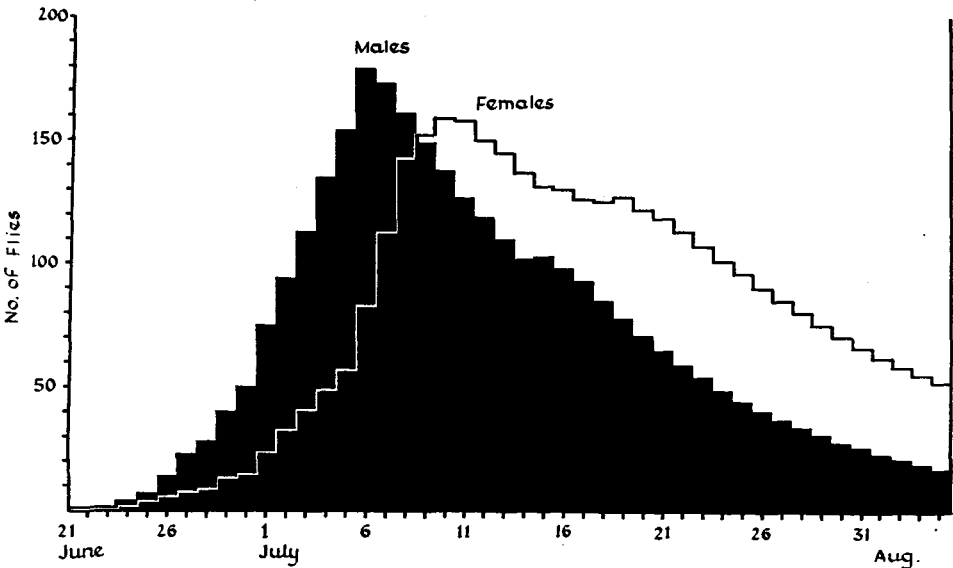


Fig. 5.—The theoretical total population of males and females of *L. coarctata* in the cage.

and between 26th June and 6th July were always more than twice as abundant as females. On 9th July, the sexes became equal in number, and subsequently the relative number of males to females gradually decreased until by the first week of August females were three times as abundant as males. This confirms the observations of previous authors. Gemmill (1927) stated that, on the average, males appear about a week earlier than females, and while this may not be entirely true, males are certainly at first by far the more abundant. Similar observations were also made by Gough (1946) and Long (1958) both in the field and in the laboratory. The early predominance of males was due to their more rapid build-up of population and their later scarcity due to their dying off sooner than the females.

It has been suggested (Gough, 1946), that the eggs require about a month for maturation. If the appearance of mature flies in the field follows a pattern roughly similar to that of emergence, but a month later, one would expect to find mature females first about the third week of July. They would not become numerous until the end of July and then the majority of the population would come to maturity during the next week or so. The appearance of eggs in the soil might be expected to follow a similar course. Taking mortality into account, one would expect that roughly between one-fifth and one-sixth of the females that emerged would come to maturity.

Absolute numbers of all stages.

The population estimates for all stages are shown in Table IV. Sampling for eggs was carried out on 12th March, the earliest date after the frosts on which

TABLE IV.
Populations of various stages of Wheat Bulb Fly.

Date	Sampling method	Stage	Mean population (1000's/acre)	Mean* standard error
12.iii.56	Soil cores	Eggs	1,556	± 199
12.iv.56	Plants	Larvae	227	± 45
31.v.56	Plants	Larvae	30	± 5
13.vi.56	Plants	Larvae	0	
	Soil cores	Pupae	377	± 106
21.vi.56– 25.vii.56	Emergence cage	Adults	83	—
19.vii.56– 22.viii.56	Estimated from recaptures inside cage	Mature females	7	
.ix.56	Soil cores inside cage ..	Eggs	226	± 95

* Analysis carried out on $\sqrt{n+1}$ transformation, hence standard error asymmetrical around arithmetic mean. Mean value given here.

it was possible to take discrete cores of soil. Twenty samples, each consisting of five cores of soil, $2\frac{1}{2}$ inches in diameter and six inches deep, were taken at random and eggs were extracted by a flotation process similar to that of Salt & Hollick (1944). As many eggs had hatched, the population estimates were based partly on empty shells, hence they may be somewhat high, as well preserved shells

persisting from the previous year (also fallow) would be indistinguishable from those recently hatched.

Larval populations were estimated on 12th April, 31st May and 13th June by counting numbers in random samples of 100 plants and multiplying the mean number of larvae per plant by the mean number of plants per square foot. (The latter was estimated by taking plant counts from 20 one-foot-square random samples.)

On 12th April, 42 plants out of the hundred showed signs of infestation. There were 66 damaged tillers, but only 30 larvae, mostly in their second instar, were recovered. The estimate of larval population was lower than that subsequently found for pupae, but at this time secondary migration was in progress so the low estimate was possibly due to many larvae having temporarily left the plants. On 31st May, amongst 30 plants showing signs of infestation, 48 damaged tillers were found. Only four larvae were recovered, all in their second instar. The development of these seemed to have lagged considerably behind that of the majority of the population, as examination of the soil round the roots of the plants on the same day showed that almost all the larvae had by now pupated. On 13th June, eight plants showed a total of nine damaged tillers; no larvae were found. Soil samples were therefore taken and examined for pupae, the method of sampling and examining being similar to that used for eggs.

The adult population was estimated from the total number of flies emerging. It seemed possible that trampling might reduce the numbers emerging from the soil of the paths, so this was investigated by examining 10 soil samples (each consisting of five 2½-in. cores to depth of 6 in.) taken from the paths and an equal number from the untrampled soil amongst the wheat. If trampling had prevented flies from emerging, then it might have been expected that their remains would have been found in the soil from the paths. From each series of samples two dead pupae were recovered. This is roughly equivalent to about 330 in the whole of the cage. Originally there must have been a total of some 2,500 pupae of which about 550 emerged as flies. About 1,600 therefore still remained unaccounted for, and the soil sampling could not be regarded as providing any information on the effect of trampling on emergence.

The soil samples were also examined for eggs. None was found in those from amongst the wheat, but 20 were found in those from the paths. This is equivalent to 956 eggs in the whole of the cage and suggests a mean production of 33 eggs per mature female (*cf.* the estimate of Gough (1946) 30 to 50 eggs/female). However, about 36 per cent. of the females are believed to have been killed by marking, so this figure must be corrected to what it would have been if no deaths due to marking had occurred. This gives a new total of 1,500 eggs which is equivalent to 226,000 per acre or roughly 1/7th of the population of the previous year (see Table IV).

Observations on another part of Pennell's Piece (R. Bardner, private communication) suggested that egg populations there were roughly equal during the two years. This suggests that the reduction of population observed in the cage was probably due to the experiment. The mortality between pupation and emergence of flies was high (78%) and may have been partially due to trampling the soil of the paths. If no adults had emerged from the paths (which occupied 1/3rd of the area of the cage) then to compensate, the potential number of eggs should be increased by one-half and the reduction from 1955 to 1956 decreased from 1/7 to 2/9. Even so, about 70 per cent. of the pupae are still unaccounted for.

Factors which may have influenced the survival rate and fecundity of the adults are handling, disturbance and possible inadequacy of the food supply within the cage. These could not be investigated in the present experiment but will have to be taken into account in future work.

Discussion.

This is believed to be the first application of the marking and recapture technique to a closed insect community. With refinement and development the method may prove of value for the study of other insects as well as Wheat Bulb Fly. The method has three advantages:

- (1) All the flies are of known age.
- (2) Dispersal is prevented and a high proportion of marked flies is recaptured. Hence relatively low numbers are needed and labour requirements are low.
- (3) Immigration of flies into the area is also prevented.

At present the technique is undeveloped but it can be improved. The high initial mortality attributed to marking should be reduced, and if possible insects should be labelled individually rather than according to date of emergence only. Handling may be harmful and should be minimised, therefore a balance between harming the flies through excessive handling and running the risk of having too little data must be found.

Although in the present study the mean rate of population decrease was found for the data as a whole, it would have been preferable to have treated each day's emergence separately. For this, however, much greater numbers of flies, say 30 to 50 a day, would have been needed.

More should be known of the effect of confining the flies. The area of the cage was large and a fair sample of the field was enclosed, but it is possible that not all the food substances available to the free-living fly were present. If so, this may have had an effect on the rate of maturation or on length of life.

Summary.

During the summer of 1956, a quantitative study of a field population of Wheat Bulb Fly, *Leptohylemyia coarctata* (Fall.), was carried out at Rothamsted.

The work consisted principally of a study of the development and decline of a population of adult flies. This was supplemented by observations on the populations of the immature stages.

Emergence was investigated by the use of a cage of fine terylene netting, 24 ft. long, 12 ft. wide, and 6 ft. high. This was erected in an infested wheat field shortly before flies were expected to appear, and was searched twice daily, at 10 a.m. and shortly before sunset.

A total of 293 male flies was caught during the 26 days from 24th June to 19th July. Of these, 186 appeared between 1st and 6th July. The highest day's catch was 40 flies on 6th July, by which date (inclusive) about 84 per cent. of the final total had emerged.

A total of 258 female flies was caught during the 35 days from 21st June to 25th July. Of these, about half emerged between 6th and 10th July. The highest day's catch was 37 flies on 8th, by which date (inclusive) 66 per cent. of the final total had emerged.

Population decrease was investigated by the method of marking and recapture. The newly emerged flies caught in the cage were marked with Artist's oil colours and released in the cage. The colour of the mark was changed daily so that the age of marked flies could be ascertained. A search was made for marked flies every three days and their numbers, marks and sex were recorded. From the recapture figures, estimates of the numbers of flies surviving at different times after marking were obtained. Mortality during the first day was very high, but after this numbers decreased at a steady rate. This initial high mortality was believed to be due to marking. The length of life of marked flies which survived this immediate effect was, however, not impaired, therefore the rate of population decrease was estimated from the recapture figures alone, that is, without reference to the numbers originally marked. The half-life of male and female populations was estimated as 7.3 and 11.1 days, respectively.

Application of the estimated rate of population decrease to the observed emergence figures enabled a general picture of the size and structure of the population to be obtained. The predominance of males over females during the early part of the season and the later predominance of females over males were explained.

Observations on the populations of the various stages showed that the mortality between pupation and maturation of adults was high, and that the egg populations inside the cage during the autumn of 1956 was only about 1/7th of that of the previous year. This reduction was not observed outside the cage and may have been due to the survival rate and fecundity of the flies being affected by the experiment. Further work will be necessary before this can be elucidated.

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It is a pleasure to record our gratitude to Dr. Marjory G. Morris and Dr. K. Mellanby for discussing and criticising the work at all stages. We are also grateful to Mr. D. Burton for making the field cage, to Messrs. F. Alston and M. Mann for assistance in the field, to Mr. V. Stansfield for photography and to Miss A. Simpson and Mr. B. Slater for assistance in preparing the figures.

APPENDIX.

Description of the Cage and Notes on the Climate within it.

The supporting framework consisted of jointed galvanised tubes and rods of the type used by horticulturalists for supporting fruit nets, etc. A rigid structure 24 ft. long, 12 ft. wide and 6 ft. high was constructed and covered with white terylene netting of mesh 18 holes per inch. Seams and corners were reinforced with strips of cotton binding which was treated with Granger's "Tropsol" solution to prevent rotting. The bottom of the cage was sealed by burying the foot of the net in the soil and an entrance was made by leaving an opening 44 inches long at one corner which could be closed by a zip fastener.

The cage remained in the field for three months, during which time much bad weather occurred. In spite of this, little damage was observed. During a period of gale-force winds the framework became bent, but this did not impair the efficiency of the cage. Small runs in the fabric were patched with pieces of netting stuck on with cellulose cement.

During the period 28th August to 1st September 1956, observations were made on temperature, relative humidity and windspeed both inside and outside the cage. Readings inside the cage were taken near the centre, those outside it, in the adjacent crop some 30 ft. from the cage. Temperature recordings were made on a Short and Mason continuous-recording thermograph, the thermometer bulbs being 4 ft. 2 in. above the ground, some 6-7 in. above the crop. Windspeeds inside and outside the cage were measured simultaneously by means of a pair of balanced Casella 3-cup anemometers. Three runs of two minutes each were made at each observation and their means compared. Anemometer readings were taken at two levels, namely 4 ft. 2 in. and 12 in. above ground. Relative humidity was determined by means of a Casella whirling hygrometer 5 ft. 6 in. and 12 in. above ground. Mean values of three readings were compared.

On cloudy or overcast days, temperatures inside and outside the cage differed little. On clear days, however, temperatures outside exceeded those inside by 2-3.5°C. at noon. At night no temperature differences were noted. In the mornings the rate of warming up within the cage was less than that outside, and in the evenings the rate of cooling was less.

In general, the relative humidity inside the cage was greater than that outside. At 5 ft. 6 in., the differences were slight, but at low windspeeds, when mixing of the air was poor, differences of 2-6 per cent. were observed.

Windspeed inside the cage was reduced, and within the range observed, was directly proportional to that outside (fig. 6). At 4 ft. 2 in. it was reduced by about one-half, and at 12 in. by about one-third.

The effect of the netting on light intensity was measured in the laboratory. There was a reduction of approximately 10 per cent. when the netting was new

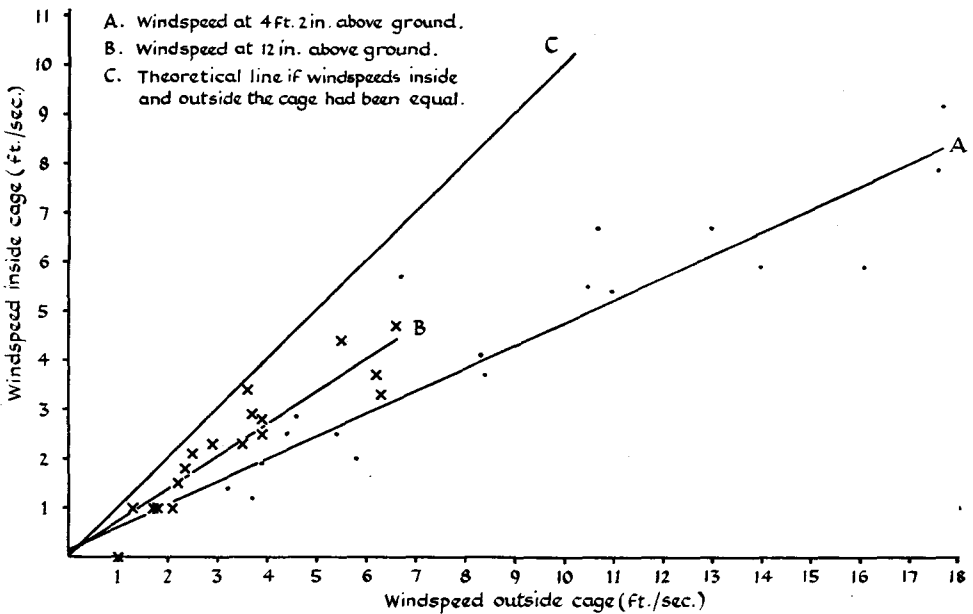


Fig. 6.—The relationship between windspeed inside and outside the cage.

and approximately 15 per cent. when it had become discoloured through standing in the field for three months.

Despite the differences between the climate of the cage and that of the field outside, there was no noticeable difference between the wheat inside and that outside.

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FIG. 1. General view of emergence cage.



FIG. 2. The interior of the emergence cage.

A STUDY OF *LEPTOHYLEMYIA COARCTATA*.