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OBSERVATIONS ON EMERGENCE AND LIFE-SPAN OF WHEAT BULB
FLY, *LEPTOHYLEMYIA COARCTATA* (FALL.). UNDER
FIELD-CAGE CONDITIONS.

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In 1956, emergence and life-span of the adult wheat bulb fly, *Leptohylemyia coarctata* (Fall.) were studied by observations on the population of an area of infested wheat enclosed by a large cage of mosquito-netting (Dobson, Stephenson & Lofty, 1958). The enclosed area was searched daily and all newly emerged flies were caught, recorded, marked according to date of capture and liberated in the cage. The survivors were recaptured and reliberated regularly and, from the data obtained, the rate of population decline was estimated. The life-span of individual flies could not, however, be observed directly.

In 1957 and 1958, the work was repeated with improved techniques which reduced experimental hazards and enabled individual life-span to be estimated. As before, the site chosen was Pennell's Piece, a small field adjoining the classical wheat field, Broadbalk, at Rothamsted.

Technique.

The method used to study emergence was the same in all three years. Populations of flies were sparse during 1957 and 1958, and it had been hoped to supplement the natural emergence in the cage with flies obtained from the next field. This proved impossible as local micro-climatic differences had a marked effect (see p. 808). Flies from outside the cage that emerged on suitable dates were, however, used in the cage for the other studies.

The main criticisms of the method of studying population decline used in 1956 are that life-span could not be directly measured and that both flies and wheat suffered from excessive handling. In subsequent experiments the flies were marked so as to be distinguishable individually rather than according to emergence date only and this enabled the histories of individual flies to be studied. The use of individual marks also obviated the need to catch the flies during 'recapturing', because all that was needed was to record the presence of particular individuals. In 1958, the technique was further improved by arranging the experiment so that observations could be made without touching either wheat or flies. This had the advantage that notes on the activities, natural positions and postures of undisturbed flies could be made during routine observations on marked flies.

The 1957 experiment.

The cage used in 1956 (24 ft. long, 12 ft. wide and 6 ft. high) was used again and six paths were cut through the wheat, two lengthwise and four across, to give access to all parts of the enclosure. Both newly emerged and marked flies were searched for daily, the wheat being agitated continuously to make them fly up. The sex and identity of marked flies could be determined by observation from a distance of about 18 inches, so they were usually recorded without being handled and only unmarked flies were actually caught. On certain 'test' days, however, at about ten-day intervals, an attempt was made to catch the entire population

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so that the adequacy of the routine technique could be checked. Usually two people searched independently at the same time, but on some days there was only one person. Each search was continued until it seemed likely that no further flies would be found; the time needed varied between one and three hours, depending on numbers.

Preliminary sampling of immature stages indicated that the natural population was much lower than in 1956, and, to increase the numbers for the study of life-span, many newly emerged flies bred out of pupae obtained from Broadbalk were marked and introduced into the cage.

Nitrocellulose lacquers in five basic colours,* white, violet, blue, red and yellow were used for marking, with two extra shades, orange and green, prepared by mixing yellow with red and blue, respectively. Violet and blue, being transparent, appeared dark when used alone, so they were mixed with a high proportion of white to make them opaque.

These lacquers seemed as durable and as resistant to fading as the artists' oil colours used previously, and were preferred because they dried quickly and did not leave a spreading stain on the integument. Three paint spots, arranged in a triangle, were placed on the dorsum of the thorax of each fly, and with seven colours, 343 (*i.e.*, 7³) different combinations were available. Only three-spot combinations were used, so that all flies carried approximately equal loads. As before, to facilitate marking, the flies were made comatose by chilling, and after marking they were placed in ventilated containers which were opened in the cage. Individuals later found dead in these containers were regarded as marking casualties and were not included.

The 1958 experiment.

The cage was doubled in size to 24 ft. × 24 ft. × 6 ft. high, and the enclosed wheat was divided into sixteen 4-ft. square plots separated and surrounded by paths. As in 1957, the natural population was supplemented by introduced flies and individual marks were used. From the 1957 results, it was suspected that two of the lacquers (yellow and violet) were harmful to the flies, so that only shades mixed from the basic colours blue, red and white were used. Five shades, blue (blue + white), red, white, pink (red + white) and brown (blue + red + white) were available and, by using three different configurations of three-spot combinations, 375 individuals of each sex could be distinguished. The marking technique was standardised by keeping the flies first at 5°C. for 15 minutes, then at 0°C. for 30 minutes (during which time they were marked) and then at 5°C. for a further 15 minutes. Flies were only partially incapacitated by this treatment, and it was hoped that possible harmful effects of sudden changes of temperature would be lessened.

Searches were made daily and, as in 1957, only unmarked flies were captured. At first, while the flies were still few, the wheat was agitated by hand, but after a few days all searching was made without touching either flies or wheat. Every part of the enclosed area was inspected once only during each day's searching, and, to facilitate finding the flies, the crop was kept free from excessive growth of weeds. This method of searching was less efficient (Efficiency = $\frac{\text{No. of flies recaptured}}{\text{No. available for recapture}}$) than the methods used previously but it had two advantages. First, observations on the behaviour and distribution of relatively undisturbed flies could be made, and secondly, counts on different days and under different weather conditions could be compared.

* I.C.I. Necol serial numbers: (1) White—FO. 56-101; (2) Heliotrope—FO. 56/CW/01065 (*i.e.*, violet); (3) Ultra Blue—FO. 56/CW/01066; (4) Scarlet—FR. 56/9920 (*i.e.*, red); (5) Golden Yellow—FR. 56-456.

Depending on the number of flies present, searching took between 35 minutes and 4½ hours each day.

Effects of chilling and marking.

Some effects of chilling the flies and of marking them with artists' oil paint were discussed by Dobson, Stephenson & Lofty (1958). Two spots of paint were apparently not more harmful than one, and it was decided in 1957 that it would be a fair risk to use three spots, the least number needed to give a reasonable range of different combinations. Care was taken, of course, to ensure that the paint spots were small and that they adhered securely to the cuticle of the fly.

In 1957, when nitrocellulose lacquers were substituted for oil paints, the recapture figures showed that higher proportions of both sexes died 'prematurely', that is, within five days of emergence, than would have been expected with random mortality. No particular marking colour appeared to be lethal but the proportion of short-lived individuals was greater amongst those bearing yellow or violet spots than amongst the others. The effect of different colours of paint on the life-spans of the flies was tested statistically. This test was based, for each sex, on 133 different sets of three spots arranged in a triangle, each set comprising not more than two of the seven colours, and each colour thus appearing in 37 different sets. Table I summarises the results: the figures for yellow and for violet suggested

TABLE I.
Survival of flies marked with given colours. 1957.

Colour	Numbers surviving					
	5 days or less			6 days or more		
	♂	♀	Total	♂	♀	Total
White	10	10	20	27	27	54
Red	6	11	17	31	26	57
Orange	8	14	22	29	23	52
Yellow	21	15	36	16	22	38
Green	16	11	27	21	26	47
Blue	13	7	20	24	30	54
Violet	19	11	30	18	26	44
	93	79	172	166	180	346

that these colours were harmful, and those for green supported the suspicion regarding yellow. Significance tests (Table II) appeared to confirm these doubts, so it was decided not to use yellow and violet in the 1958 experiment and to test all the colours in the laboratory when flies became available.

In these laboratory tests, 44 sets of newly emerged flies were observed. Each set consisted of 7 males and 7 females kept in a lamp glass and provided with condensed milk, honey and meat extract as food (*cf.* Bardner & Kenten, 1957) and the following treatments were applied. Five pairs of flies were chilled (using 1958 standard procedure) and marked with a single spot of one of the five colours to be tested, *i.e.*, white, yellow, blue, red and violet; one pair was chilled only and one control pair was neither marked nor chilled. The flies were kept at 20°C. and 45 per cent. relative humidity and subjected to a cycle of 16 hours light (provided by fluorescent tubes) and 8 hours darkness. All sets were examined daily and dead flies were removed. Accidental losses were few. Under these

conditions flies were fairly short-lived, the mean life-span being 8.8 days for males and 24.0 days for females.

The yellow and violet paint seemed no more harmful than the others in this experiment, but females marked with white showed a slightly higher mortality than all other categories for the first 20 days (difference between white and controls significant at $P=0.05$ on 11th, 12th and 13th days). However, the proportions surviving 21 days or more (*i.e.*, approaching maturity) and the expectation of life, even of those marked with white, were not affected.

TABLE II.

Significance tests to show effects of different marking colours, 1957.

Flies marked with	Premature deaths			Survived 6 or more days Total	Comparison with safe colours (white, red & blue) χ^2 test
	♂	♀	Total		
White, red & blue only ..	3	4	7	35	—
Orange and/or green but excluding yellow and/or violet	11	14	25	63	$\chi^2 = 1.53$ $0.30 > P > 0.20$
With yellow	21	15	36	38	$\chi^2 = 10.44$ $P < 0.01$
With violet	19	11	30	44	$\chi^2 = 5.97$ $0.02 > P > 0.01$

Among the males, of which 95 per cent. had died by the 14th day, the groups of differently coloured flies all had similar mortality, but both chilling and painting appeared to be harmful and resulted in higher mortality from the 3rd to the 14th days. Comparing the aggregate of marked and chilled males with the controls, the differences in mortality were significant at $P=0.05$ for the 5th and 6th days and at $P=0.01$ for the 7th–11th days. It was concluded, therefore, that the adult males, which are less robust than the females, are more likely to be injured by marking and chilling but that no particular colours were especially harmful under the conditions of the experiment. The mean life-spans of the three groups of males, chilled and marked, chilled only, and control, were 8.38, 9.36 and 10.19 days, respectively.

A possible cause of the premature mortality observed in 1957 was that some batches of flies might have been subjected to unsuitable conditions during or after marking. For example, from 16th to 19th June, there was a period of hot weather (the daily mean temperature on bare grass being 20°C. or more) and there was an abnormally high premature mortality of flies emerging on these days and an especially high premature mortality of flies marked with yellow or violet (Table III). It seems likely that the sudden chilling by exposing to -5°C . may have been more harmful when the flies were at a high temperature at the outset. During the cooler weather (daily mean temperature less than 20°C.), *i.e.*, before 16th and after 19th June, newly emerged flies marked with yellow or violet still tended to die prematurely but the differences were less and were not significant statistically.

The need for care in marking is obvious, and during a separate field experiment in 1958, in which many flies had to be marked quickly, many individuals were later found to be unable to fly. The mass of paint carried seemed not to be

the deciding factor because some of the incapacitated flies had very small spots whereas others which could fly had large ones. As a result of these observations the flies in the cage were tested for their ability to fly; of 166 males and 221 females, 11 and 17, respectively, could not fly. In both sexes the mean life-span of these disabled individuals was only three-fourths that of normal flies.

TABLE III.

Significance tests showing effects of the marking colours under different weather conditions.

Fly material	Weather condition, or colours used	Number of flies emerged	Number dying within 5 days	χ^2	<i>P</i>
All flies that emerged during periods specified	Hot period 16-19.vi.	178	77	22.30	< 0.001
	Cooler periods 6-15.vi. & 20-27.vi.	160	30		
Males as above	Hot period	93	44	14.92	< 0.001
	Cooler periods	85	16		
Females as above	Hot period	85	33	6.83	< 0.01 > 0.001
	Cooler periods	75	14		
All flies that emerged during hot period	Marked with safe colours	84	26	8.89	< 0.01 > 0.001
	Marked with yellow and/or violet	94	51		
Males as above	Safe colours	39	13	4.34	< 0.05 > 0.02
	Yellow and/or violet	54	31		
Females as above	Safe colours	45	13	3.15	< 0.10 > 0.05
	Yellow and/or violet	40	20		
All flies that emerged during cooler periods	Safe colours	91	14	1.11	< 0.30 > 0.20
	Yellow and/or violet	69	16		
Males as above	Safe colours	54	7	3.45	< 0.10 > 0.05
	Yellow and/or violet	31	10		
Females as above	Safe colours	37	7	0.003	> 0.95
	Yellow and/or violet	38	6		

Results.

Emergence.

In 1956, all the flies under observation were those that had emerged naturally from the infested wheat in the cage. In 1957 and 1958, because populations were low, attempts were made to increase the numbers of flies in the cage by taking pupae from Broadbalk, at a point about 250 yards from the cage, and allowing them to emerge from pots of peaty loam sunk to soil level in the crop near the

cage. This plan failed because the emergence dates of the two populations differed greatly. Table IV summarises results obtained from three different populations observed during 1958; (a) the natural population of Pennell's, (b) flies derived from pupae obtained from Broadbalk between 12th and 27th May and immediately transferred to Pennell's, and (c) pupae obtained from Broadbalk

TABLE IV.

Emergence dates of flies in 1958.

Source of flies		Date of emergence of		
		First flies	50%	Last flies
(a) Natural infestation of cage	♂	17 June	2 July	21 July
	♀	17 June	8 July	22 July
(b) Pupae obtained in Broadbalk but kept by cage	♂	12 June	28 June	19 July
	♀	19 June	30 June	20 July
(c) Pupae obtained and kept in Broadbalk	♂	13 June	20 June	1 July
	♀	14 June	24 June	5 July

but kept there (data kindly supplied by Dr. D. B. Long). The differences observed probably reflect micro-climatic differences between the two sites. The crop on Broadbalk was much less advanced than that on Pennell's so that the soil received more solar radiation and was warmer, and also the soil of Broadbalk was drier than that of Pennell's.

The emergence data of the natural populations of the cage site for 1956, 1957 and 1958 and also the temperature summations in degree-days above 42°F. (5.6°C.) from 1st January are shown in fig. 1. Consistently, males appeared before females, but there were considerable differences from year to year. The immature stages occur in the soil and plants and, as the eggs are fully developed in autumn but do not hatch until after the frosts in early spring, temperature during post-embryonic development is probably the most important factor influencing date of emergence. There is, as yet, no precise knowledge of the relation between temperature and development in wheat bulb fly, but the flies emerged latest in 1956, when the spring was coldest, and earliest in 1957, when it was warmest. Temperature summation is quoted merely to make a broad comparison of the three seasons, and the values given must not be regarded as estimates of the thermal requirements of developing flies.

Life-span of flies.

As the life-span of individual flies could not be measured in 1956, the half-life of the population was estimated indirectly on the assumption that, after the losses caused by marking, mortality was essentially random. In 1957 and 1958, when individual marks were used, direct estimates were possible and it became clear that the 1956 estimates of half-life were too low. The reasons for this can be illustrated by an example. On 28th June 1958, 23 male flies were marked and released in the cage; the recapture data can be expressed in three different ways: (a) the actual numbers observed on the following days; (b) the actual numbers known, from later observations on individually marked flies, to have been alive on that day; or (c) the best estimate of the minimum numbers alive on each day if all had been marked according to emergence date only so that they were not

recognisable individually. The numerical values for recaptures expressed in these ways are given below.

	June										July																									
	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	. . .	28	28	29	30	1	2	3	4	5	6	7	8	9	10	11	12	13	. . .	28
(a)	23	8	6	9	8	6	10	6	12	14	5	6	9	10	5	4	. . .	8	23	23	23	23	22	22	22	22	21	21	20	20	19	19	19	19	. . .	14
(c)	23	14	14	14	14	14	14	14	14	14	10	10	10	10	8	8	. . .	8	23	23	23	23	22	22	22	22	21	21	20	20	19	19	19	19	. . .	14

Method (c) gives a low estimate of the numbers surviving and it is clear that the sharp drop in numbers between marking and first observation, formerly thought to be an effect of marking, is largely an artefact of the technique.

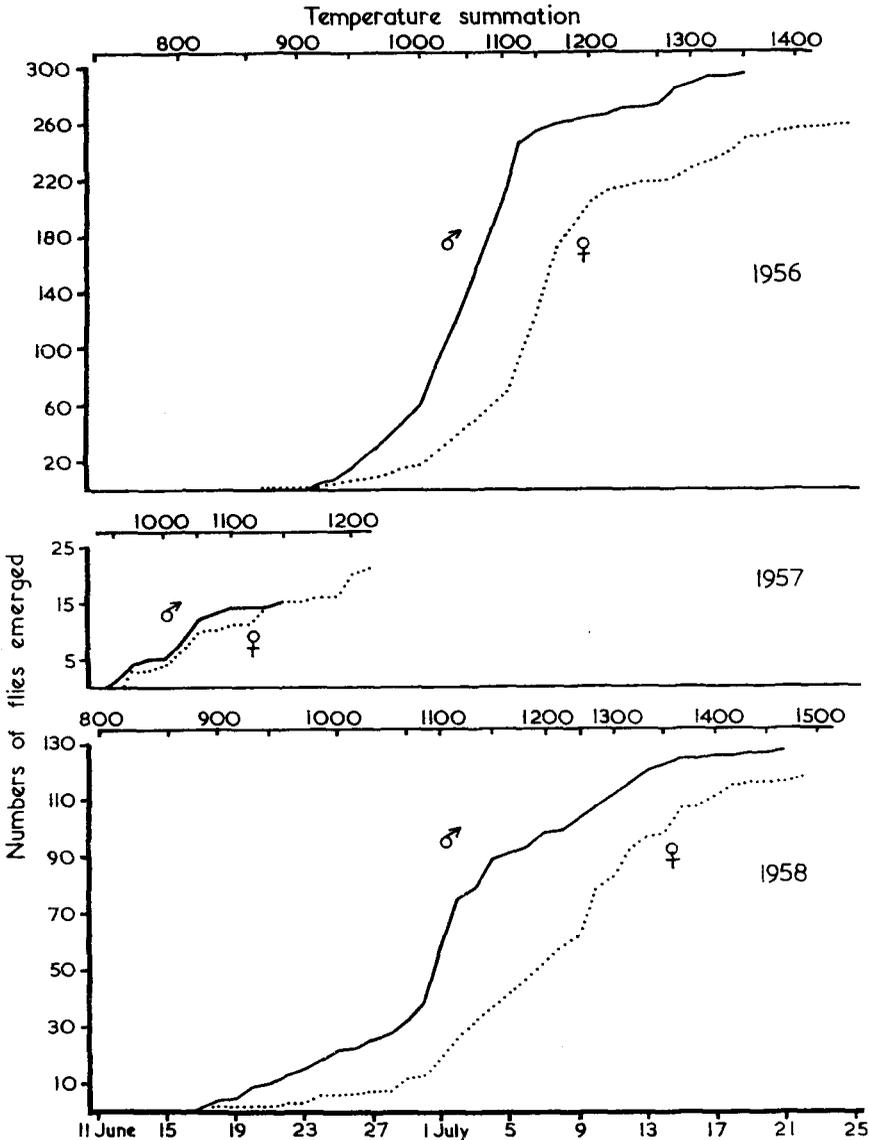


Fig. 1.—Accumulated emergence figures and temperature summations (degree-days above 42°F.) for 1956, 1957 and 1958.

The data for the three years (Table V) show that as the technique was improved so the apparent and real premature mortality decreased and the estimated half-life increased. For this reason, therefore, only the 1958 data will be dealt with in detail.

TABLE V.
Premature mortality and half-lives of flies in 1956, 1957 and 1958.

		% mortality				Estimated half-life of population	
		1 day		5 days		(days)	
		♂	♀	♂	♀	♂	♀
1956	Marking casualties	31.5	31.9				
	Survivors of marking	9.8	5.7	40.2	27.5	7.3	11.1
1957		2.2	2.2	12.5	16.4	12.7	18.0
1958		2.4	2.1	9.3	6.0	33.4	31.4

The frequency distribution of life-span for male and female flies in 1958 is shown in fig. 2. Only a small proportion of flies was actually found dead (7.6% males, 3.6% females) so, in general, life-span had to be taken as the number of days, including those when first and when last seen, that flies were known to have

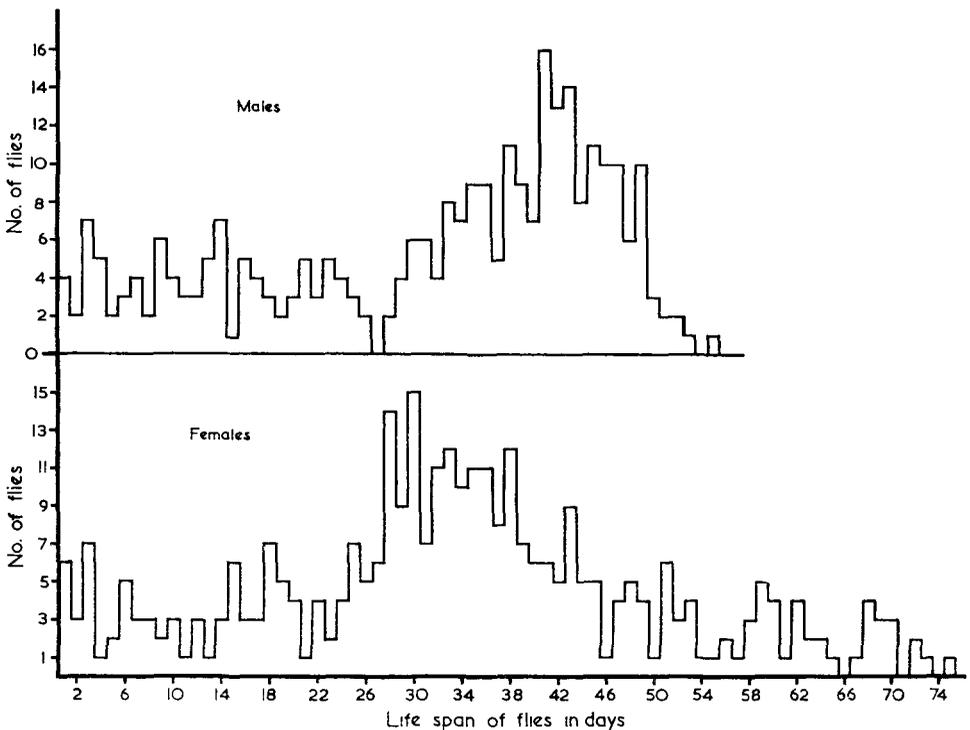


Fig. 2.—Frequency distribution of life-span amongst male and female flies observed in 1958.

lived. It will, of course, be appreciated that this under-estimates the true life-span because the disappearance of a fly does not imply its immediate death. It was obvious that flies often lived for some time after the last appearance recorded during routine searching because on certain days, when prolonged observations were made in connection with studies of behaviour, individuals were found which, according to the standard records, had disappeared and had been presumed dead. As will be shown later, a correction to allow for the difference between observed and true life-span can be calculated.

The frequency distributions of life-span for the two sexes are quite different. Deaths of males were relatively infrequent during the first $4\frac{1}{2}$ weeks, amounting to a mean daily mortality of 1.3 per cent. of the total population. Mortality then increased to a maximum at about 6 weeks and after 8 weeks all were dead. Among females mortality was low during the first four weeks (mean of 1.1% per day), increased from 4 weeks to 6 weeks (2.9% per day) and then decreased again (0.8% per day) until all were dead in the 11th week.

Many of the mature females apparently survive for some considerable time, whereas males die off soon after reaching maturity. This difference is illustrated in fig. 3 which shows the number of flies more than 20 days old (and therefore

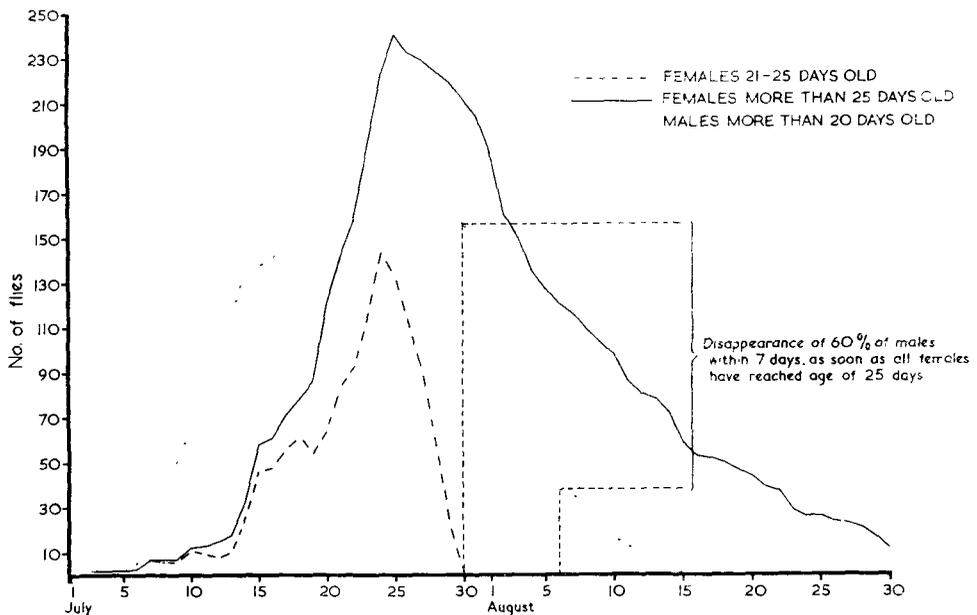


Fig. 3.—Number of flies more than 20 days old present in cage on each day (1958).

approaching maturity) in the cage on each day. Mature males and females co-existed for a while, but then the male population decreased by more than 60 per cent. in one week, at a time when all the females were more than 25 days old. The female population decreased during this time by less than 35 per cent. The observed life-spans of males and females arranged according to date of

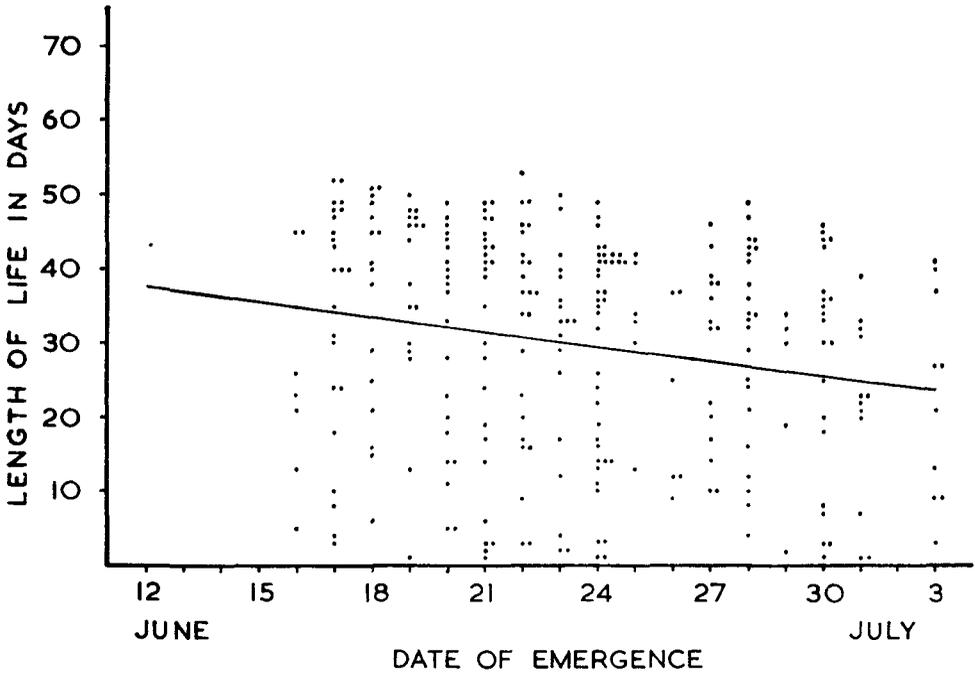


Fig. 4.—Observed life-spans of male flies in 1958.

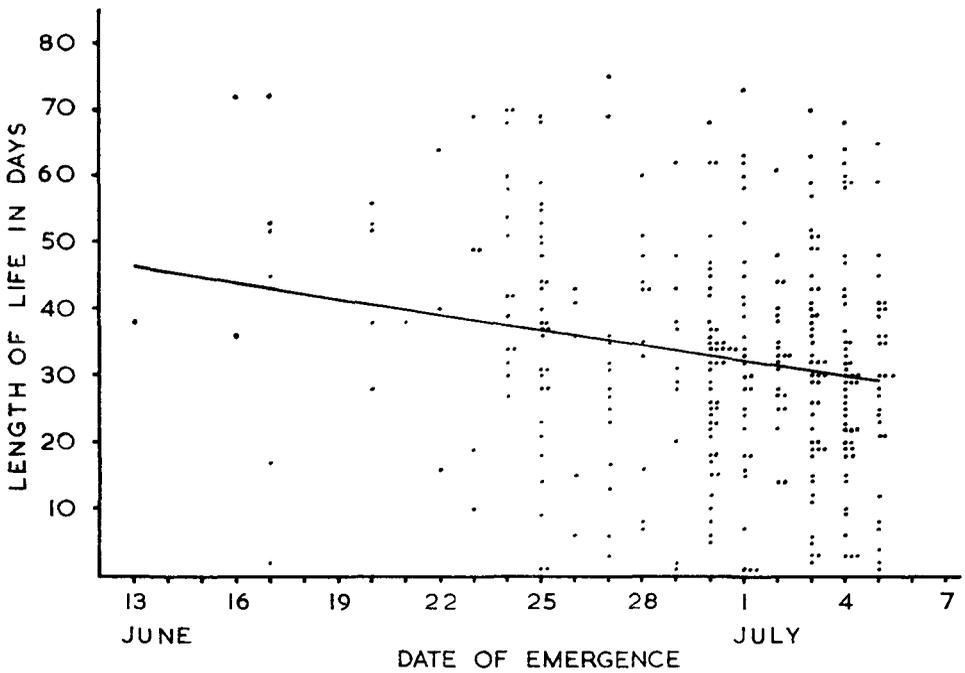


Fig. 5.—Observed life-spans of female flies in 1958.

emergence are shown in figs. 4 and 5. In both sexes, flies that emerged earlier in the season tended to live longer than those that emerged later. The regression lines shown have the equations:—

for males with mean life-span (\bar{y}) of 30.1 days

$$\hat{y} = 38.04 - 0.64x$$

for females with mean life-span (\bar{y}) of 33.2 days

$$\hat{y} = 47.96 - 0.82x$$

where $x=1, 2, 3$, etc. corresponds to the 1st, 2nd, 3rd . . . day of the emergence period for each sex. $x=0$ therefore corresponds to 11th June for males and 12th June for females. The standard errors of the regression coefficients, ± 0.19 for males and ± 0.21 for females show that both coefficients differ significantly from zero ($P < 0.001$). This reduced expectation of life of late-emerging flies was also observed in the females of the 1957 experiment but not in the males. The 1957 data are, however, less reliable because of the high premature mortality and inferior technique.

By 5th June 1958, it was decided that further additions to the already large population of marked flies in the cage would interfere with efficient note-taking, and the regression for the female expectation of life on time is therefore based on an incomplete emergence range. This is unfortunate as there is no way of knowing whether the relation implied by the regression would have continued. There are, however, three possible reasons for the decreased life expectation observed in later emerged flies. First, flies that emerged later may have tended to be intrinsically, less long-lived than those that emerged earlier. This, however, appears unlikely because no such trend was noticed in the data for the laboratory tests on marked flies, in which over 300 individuals of each sex emerging during a period of 16 days were kept in a constant environment. Secondly, there may have been a progressive change in the environment, such as the ripening and drying of the crop gradually diminishing the food supply, or thirdly, there may have been a build-up of predators and disease so that the life expectation of the flies that emerged later was reduced.

The mean life-spans of the two sexes are based on the entire data and must not be compared directly, as their values depend on the proportions of flies from each part of the emergence range considered. The values given by the regression lines for the same dates give the best available comparison.

Efficiency of searching.

The ratio $\frac{\text{Number of flies seen}}{\text{Number known to be alive}}$ gives some measure of the efficiency of searching on each day. The denominator is found by adding the number of flies seen on the day in question to the total number of additional ones seen subsequently and it will always give a low estimate of the true population because some individuals remain undetected. It follows, therefore, that the estimated efficiency of searching is always higher than the true value.

In 1957, there was considerable day-to-day variation in the searching efficiency, and although there were signs that these differences were connected with changes in weather, analysis was impracticable because the technique had not been standardized sufficiently. The mean estimated efficiency (a) with normal searching (*i.e.*, flies not caught, wheat beaten, two workers) was 73 per cent., (b) on 'test' days (flies actually caught) was 79 per cent. and (c) when only one worker took part was 66 per cent. The efficiency also increased greatly as the season progressed, probably because practice sharpened observation.

In 1958, the technique was standardized by the time about 200 flies had been established in the cage and, on 32 occasions between 4th July and 5th August,

a standard search was made through a population consisting of at least 50 flies of each sex. The mean efficiency (males 34%, females 36%) was much lower than in 1957, but variations from varying technique were eliminated and there was no seasonal trend. Daily searching efficiencies were essentially similar for both sexes.

There was no exceptional weather during this period. The mean temperature during the observational sessions varied between 15° and 24°C. and there was no prolonged heavy rain. On some days there were showers or drizzle but these were insufficient to affect the searching efficiency.

Flies were more difficult to find on windy days than on calm ones, and on bright days than on dull ones. As the data were limited it was clearly unprofitable to attempt too fine a distinction between types of weather noted during the searching period so it was decided to consider only more windy, or less windy, occasions with 5 m.p.h. as an upper limit for the latter, and mainly sunny or mainly dull (*i.e.*, less than or more than 50% cloud cover) assigned to one of the cells of a 2 × 2 × 2 classification (summarised in Table VI.)

TABLE VI.

Mean percentage efficiencies, with standard errors, according to weather and sex of flies.

	Dull		Sunny		
	More wind	Less wind	More wind	Less wind	
Males	37.7	42.4	28.0	29.9	(-1.8) 34.3
Females	35.7	43.6	31.5	34.3	36.6
	36.7	43.0	28.7	32.1	35.3 (±1.8)

Analysis of variance gave:—

Source of variation	d.f.	Mean Square	Variance ratio
Sun	1	1310	23.7***
Wind	1	286	5.2*
Sex	1	64	1.2
Sun × Wind	1	56	1.0
Sun × Sex	1	73	1.3
Wind × Sex	1	15	
Wind × Sun × Sex	1	7	
Within Sub-classes	56	55.2	
	63		

* $P < 0.05$

*** $P < 0.001$

The effects of sun and wind are both significant. Although there is no statistically significant interaction, the biological meaning of the differences shown in Table VI is interesting. On dull days, male and female flies were equally easy to find and this was true irrespective of their tending to become less visible during stronger winds. On sunny days, each sex was more concealed than on dull days, both on more windy and less windy occasions, but the differences were much greater with the males and it is this that accounts for the whole difference between the percentages of males and females found. Apparently, because the

flies avoid the sun, they have little need to seek further protection from the wind. In neither sex was the difference due to wind significant on sunny days and in the males the difference was negligible. The absence of males, more obvious when conditions are seemingly adverse, is consistent with their smaller size and apparently greater fragility.

Accuracy of observations on life-span.

Dead flies were quickly destroyed by scavengers and those found could be assumed to have died within the preceding 24 hours. Usually, however, bodies were not found and with such individuals length of life was measurable only up to the last observation. Clearly it is important to try to assess the life expectation of a fly after it has been seen for the last time.

If every fly were seen every day then a reasonable expectation of life after a fly was seen for the last time would be half a day, or if every fly were seen every alternate day it would be reasonable to add half this interval, *i.e.*, one day, to the measured life-span of the flies. An estimate of this unmeasurable part of the life-span can be obtained from the original data, a small section of which is shown in Table VII. Records of the occurrence of each fly (indicated by X)

TABLE VII.

Extract from daily records.

Fly No.	Date																				
	July										August										
	20	21	22	23	24	25	26	27	28	29	30	31	1	2	3	4	5	6	7	8	9
192	X	0	0	0	X	X	0	0	0	X	X	0	0	X	0	X	0	0	0	0	0
193	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	X	0	0	0	0	0
194	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
195	X	0	0	0	0	0	0	0	X	0	0	X	X	0	X	X	0	0	0	X	0
196	X	0	0	0	0	0	X	0	X	0	0	0	0	0	0	0	0	0	0	0	0

X = fly seen; X = fly last seen; 0 = fly not seen.

are separated by gaps of varying length (each day in which is indicated by 0) during which it was not seen. The accumulated frequency distribution of gaps of all lengths for all the data in fig. 6 (based on 1,744 and 2,343 gaps for males and females, respectively) shows that those of short duration were most frequent and that longer ones were progressively less frequent; thus, about 40 per cent. of all gaps were of only one day's duration, 60 per cent. of them were not more than two days long and only 3 per cent. exceeded 10 days. The blank records after the flies were seen for the last time may also be regarded as gaps which differ from the preceding ones only in that the flies failed to reappear, and it seemed likely that these gaps would have a similar frequency distribution, *i.e.*, that 40, 60, . . . 97 per cent. of them would have been of not more than 1, 2, . . . 10 days' duration had the flies reappeared. However, the flies did not

reappear and so it may be supposed that the expected intervals till death, namely, $\frac{1}{2}$, 1, . . . 5 days, followed the same distribution. The mean values for the gaps occurring within the observed life-spans of the flies were 3.05 days for males and 2.82 days for females, so that the unrecordable expectation of life was 1.5 days and 1.4 days, respectively. This method gives a useful approximation on the assumption that gaps of varying length are distributed randomly throughout the data.

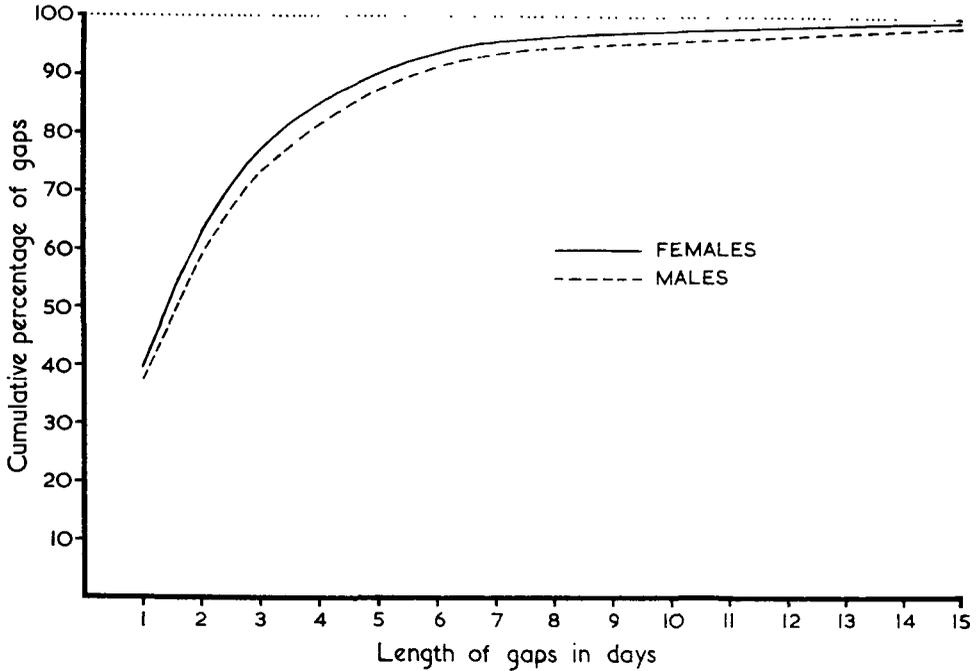


Fig. 6.—Accumulated frequency distribution of gap length in 1958 data.

If p , the probability that any particular fly will be seen on any one day, was, disregarding weather effects, constant, its true value is

$$\frac{\text{Sum, for every day, of all the flies seen}}{\text{Total number of days lived by all the flies}}$$

but the denominator derived directly from the records is too low. In Table VIII. (a) represents flies marked and released on one day. Estimates of p could be made from the complete columns starting from the left representing 1st, 2nd, 3rd . . . days after the flies' release in the cage. The difficulty is to know how many individuals to include in the total where the records show no further reappearance. This is overcome in Table VIII (b), which represents the same data rearranged according to the day on which each fly was last seen. Again the columns give estimates of p . Table IX summarises data from the 1958 experiment arranged as in VIII (b). Because the behaviour of flies that die prematurely as a result of marking is not normal, observations on those living six days or less are excluded. The totals also omit newly marked flies because these would bias the positive

TABLE IX.
Estimates of searching efficiency for the 12 days before final observation.

		Days before final observation												
		12	11	10	9	8	7	6	5	4	3	2	1	F
Males	..	68	73	79	70	77	77	72	61	70	66	75	62	261
	Total	238	242	246	248	254	257	260	261	261	261	261	261	261
	Proportion seen	0.286	0.302	0.321	0.282	0.303	0.300	0.277	0.234	0.268	0.253	0.287	0.238	
Females	..	111	110	101	98	105	100	92	93	101	95	92	97	306
	Total	292	293	296	297	300	301	304	306	306	306	306	306	306
	Proportion seen	0.380	0.375	0.341	0.330	0.350	0.332	0.303	0.304	0.330	0.310	0.301	0.317	

appropriate to the flies' latter days. As before, the expectation of life after the last appearance can be taken as half this interval. The results, Table X, agree with those obtained by the previous method.

TABLE X.

Estimates of mean unrecorded lives of flies and their fiducial limits obtained by exact method.

	Males	Females
Regression coefficient b with S.E. ..	0.00503 \pm 0.00174 (signif. at $P = 0.05$)	0.00609 \pm 0.00133 (signif. at $P = 0.01$)
\hat{Y} (for $x = 0$)	0.2465	0.2915
95% fiducial limits of \hat{Y}	0.2180 — 0.2750	0.2692 — 0.3138
95% fiducial limits of mean expected interval until reappearance ..	2.6 — 3.6 days	2.2 — 2.7 days
Probable unrecorded life of fly ..	1.3 — 1.8 days	1.1 — 1.4 days

Discussion.

The results now described are much better than those described earlier (Dobson, Stephenson & Lofty, 1958) and many of the technical problems discussed previously have now been overcome. The most important change in technique was to use individual marks rather than marks indicating date of emergence only, because this not only made flies recognisable individually but also obviated the need for handling them during recapturing.

In the 1956 experiment, the flies had to be captured for recording and, to minimise handling, marked flies were searched for only once every three days. The present method overcame this difficulty and it had the further advantage that flies could be observed in their natural positions and postures (Dobson, 1959). Individual behaviour and movements will be described in a separate paper.

Although the technique was developed to study wheat bulb fly, it is suitable for studying other insects provided that they can be marked and that their life-histories are not affected adversely by their being confined to a restricted area. Clearly, some previous knowledge of the life-history and habits of the species under study would be an advantage; for example, if a species had a pronounced diurnal rhythm of activity the worker would have to decide on the best time to make his observations.

The accuracy of the estimates of excess over observed life-span depend on efficiency of searching but it is not always necessary or desirable to aim at high efficiency. As a general rule, the shorter the life-span of the species under study, the higher the efficiency desired. Higher efficiency can be achieved by (a) careful design and maintenance of the experimental site so that all parts can be examined easily, (b) employing more labour and searching for longer periods, (c) disturbing the site so that the animals are stimulated to activity. Care should be taken in employing these measures, however. With (a) it is necessary to guard against making the site unrepresentative of field conditions and with (c) the damage inflicted on the animals by disturbance may have adverse effects on the life-span that greatly outweigh the advantages of higher efficiency.

A high proportion of female flies obviously lived long enough to reach sexual maturity and lay eggs, and a high proportion of both sexes lived for over 30 days. This was surprising, because, in the laboratory, males often seem to be much less

long-lived than females (*e.g.*, Bardner & Kenten, 1957, and the laboratory tests of marking paints reported above). Figs. 4 and 5 show that a single statement of the mean life-span of either sex for flies living under field conditions is meaningless because the range of life-span is so great and there is apparently a trend during the season.

In an experiment of this type it is practically impossible to determine whether confining the flies to the crop and preventing their dispersal are harmful. It is not possible to study directly, or measure, the biology of free-living flies; all that can be inferred is that, as far as their occurrence on the crop can indicate, the confined flies appear to behave similarly to free-living ones, that they live for considerable periods and that they reach sexual maturity and lay eggs (Dobson, Stephenson & Lofty, 1958).

The natural food of the adult wheat bulb fly is not yet known, but Long (in Mellanby, 1958, p. 159) points out that flies probably need a source of food containing sugars for continued life and egg maturation, adding that such a source is not freely available in wheat fields, suggesting that the daily dispersion of flies from the crop may be due to their foraging for food. It is interesting to note that in 1958, when the plots in the cage were weeded from time to time and very few plants other than wheat and a few grasses were present, many flies in the cage were long-lived and appeared to mature normally.

Summary.

Emergence and life-span of wheat bulb fly, *Leptohylemyia coarctata* (Fall.), have been studied by the use of a field-cage-marking technique. Emergence was investigated by observing the numbers of flies emerging daily from an area of infested wheat enclosed by a cage of fine mosquito-netting, and life-span by making a daily census of marked and individually recognisable flies which had been liberated in the cage. Flies were handled only when being marked and in the later part of the work all observations were made without touching either them or the wheat.

Flies were chilled to render them comatose for marking and under certain circumstances this and the marking was harmful. Attempts were made to reduce these harmful effects.

Emergence dates varied from year to year depending on the temperatures of spring and early summer, and there were also considerable differences between the emergence dates of populations of adjacent fields in the same year. Consistently, males appeared before females.

The ratio of the number of flies seen to the number known to be alive on each day varied according to weather, flies being more difficult to find on windy days than on calm ones and on bright days than on dull ones.

The observed life-spans of both sexes varied greatly, up to a maximum of 75 days for females and 55 days for males. An exact statement of mean life-span was not possible because there was a tendency for flies emerging later in the season to be less long-lived than those emerging earlier. Most flies of both sexes lived for over 30 days.

The observed life-spans fall short of the true life-spans by amounts that depend on the proportions of living flies seen each day. Two methods are shown by which the mean unrecorded life-span can be calculated.

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