THE SEASONAL FREQUENCY OF CALLIPHORINE BLOWFLIES IN GREAT BRITAIN.

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(With 4 Charts.)

CONTENTS.

I.

The relative proportions and the number of generations of *Calliphora*, *Lucilia* and *Protocalliphora*.

The British genera of blowflies, if the term be restricted to members of the Muscid subfamily Calliphorinae, are *Calliphora*, with the two species *erythrocephala* Mg. and *vomitoria* L., *Lucilia*, with several species, of which the commonest in the Manchester area are *caesar* L. and *simulatrix* Pand., and *Protocalliphora*, with two species *azurea* Fln. and *groenlandica* Ztt., of which the latter alone concerns us.

Evidence concerning the relative proportions of these genera in a non-industrial locality, Cambridge, has been put forward by Graham-Smith (1916), his conclusions being based upon the examination of 51,000 Calliphorine flies captured in traps during the period April 25–November 30, 1915.

The following evidence concerns the proportions occurring in an industrial locality, and is based upon the examination of 26,000 of these flies, trapped at a particular point in the Fallowfield district of Manchester, within three miles from the centre of the city, during the period April 20–October 30, 1926.

It is not suggested that the proportions obtained hold good for the Manchester area as a whole. It is highly probable that they represent merely the proportions, in a trapped sample, of the blowfly population of this particular district.

The flies were trapped always in the Hodge or Balloon type of fly trap, baited with ox-liver. The traps were emptied and rebaited at intervals of

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several days. Three such traps were placed in the "Sun," that is to say in an open situation exposed to sun temperature, rain and wind. Three other traps were placed in the "Shade," *i.e.* in a shed, protected from rain and to a large extent from wind and sunshine. The curves representing the number of flies captured under these two sets of conditions will be referred to for convenience as the *Sun Curve* and the *Shade Curve* respectively.

The shade traps were not placed in position until some weeks after the sun traps so that the shade curves start somewhat later in time on the figures than the sun curves. Three traps also were placed for several weeks in almost total darkness but were discontinued as no flies ever entered them.

The figures recorded in Table I indicate the percentage proportions of the three genera obtained at Manchester, and for comparison, at Cambridge, for the whole period.

Table I.

Locality	Conditions	Number of flies	*Calliphora*	*Lucilia*	*Proto-calliphora*
Manchester	Sun	11696	71%	21%	8%
1926	Shade	14390	82%	16%	2%
Cambridge	Sun	49116	56%	43·7%	0·2%
1915	Shade	1916	86%	14%	0%

The figures given in Table I indicate that:

(1) The proportions of *Calliphora* and *Lucilia* in the shade were about the same for both localities, but in the sun, the percentage of *Lucilia* in the industrial area was less than half that in the much sunnier non-industrial area.

(2) The percentage ratio of flies captured in the sun to those captured in the shade was 45 : 55 in Manchester, as against 93 : 7 in Cambridge. Graham-Smith's recommendation as to the advisability of placing garbage tins in the most shady situations available so as to attract as few flies as possible, would not therefore hold good for Calliphorine flies in the Manchester area.

The difference in the behaviour of *Calliphora* and *Lucilia* to sun and shade conditions has been previously described (Herms, 1907; Wardle, 1921) and has been attributed to differences in phototropic habit between the two genera, but another explanation will be put forward later in this paper.

The percentage proportions of the respective genera in the Manchester locality, at intervals of a few days, throughout the whole period, are indicated in Chart 1.

Reference to the curves there shown will indicate that:

(1) Although in the shade, *Calliphora* was the dominant genus, there were several periods during which the proportion fell below 82 per cent., notably the three periods June 7–13, July 11–18 and August 10–28. The fall in the proportion of *Calliphora* was not caused by any unusual diminution in the number of individuals captured, but was due to the capture of unusually large numbers of *Lucilia*.

(2) Although in the sun *Calliphora* was for the greater part of the summer the dominant fly, there were three periods when its percentage proportion fell

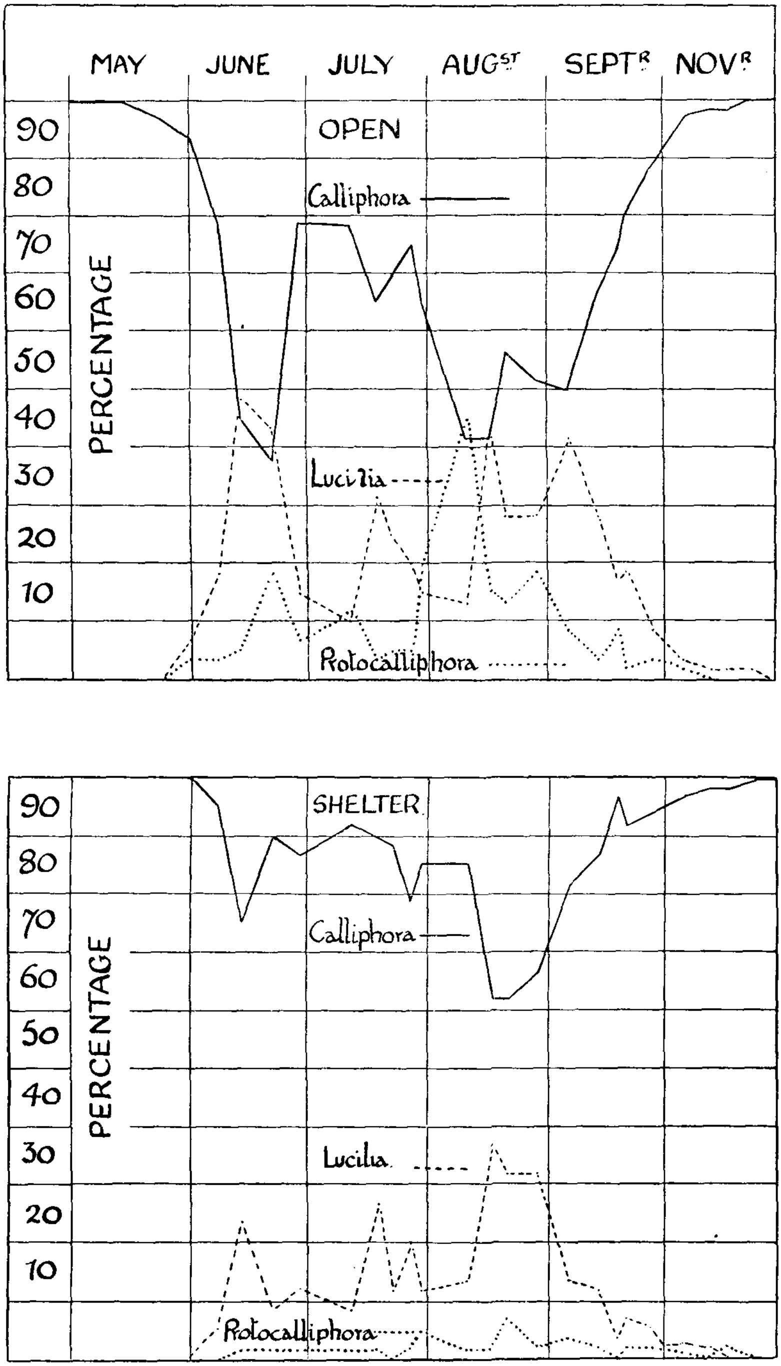

Chart 1. Percentage proportions of *Calliphora*, *Lucilia* and *Protocalliphora*, in the Fallowfield district of Manchester during 1926.

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below 71 per cent., namely June 7–21, July 11–22, and July 27–September 13. Here again, the fall was occasioned by the exceptional number of *Lucilia* individuals captured, rather than by any marked drop in the number of captured *Calliphora* individuals.

In fact, the percentage proportion of *Lucilia* under both sun and shade conditions attained maxima during June 7–13, July 11–22 and August 10–16.

The percentage proportion of *Protocalliphora* attained its maximum under sun conditions during July 31–August 10. The numbers under shade conditions were insignificant.

Curve of trap captures.

The curves in Chart 2 represent the actual numbers of the three genera in question, trapped under sun and shade conditions.

In each case, the curve consists of a number of major and minor peaks separated by depressions. That is to say, if the trap captures afford any indication as to the numbers of each genus in the locality throughout the period, then such numbers do not increase gradually through the summer to a culminating maximum in late summer or autumn, just before the flies begin to disappear, but fluctuate in somewhat irregular fashion from day to day.

Four possible explanations of such curves may be put forward:

(1) That the peaks merely indicate periods when no local counter-attraction to the baits was present, and the depressions indicate the existence of such counter-attractions.

(2) That the peaks indicate periods of time when meteorological conditions were most favourable to the movements of blowflies, and to the attraction of the baits for such flies.

(3) That the curves express the emergence of successive generations, the peaks indicating the maximum emergence of each generation, the depressions indicating the diminution in numbers of the generation brought about by various mortality factors.

(4) That the curves express the variations in the numerical abundance of blowflies in the locality.

As regards the first of these explanations, it may be stated that the bait used was always ox-liver in a high state of putrefaction, and in the author's experience there is no substance more attractive to blowflies than this. The temporary attraction of over-ripe fruit, human faeces, or even a small dead animal, would be very unlikely to outweigh the very positive attraction of putrescent ox-liver.

Further, it may be noted that similar peaks were obtained by Graham-Smith on a curve expressing the descendants from about 100 female *Calliphora erythrocephala* reared in captivity, but under open air conditions, through the summer and autumn of 1915, and on curves expressing the numbers of wild flies of various species captured in traps during the same period.

The first explanation therefore is unlikely.

The remaining explanations however merit careful examination.

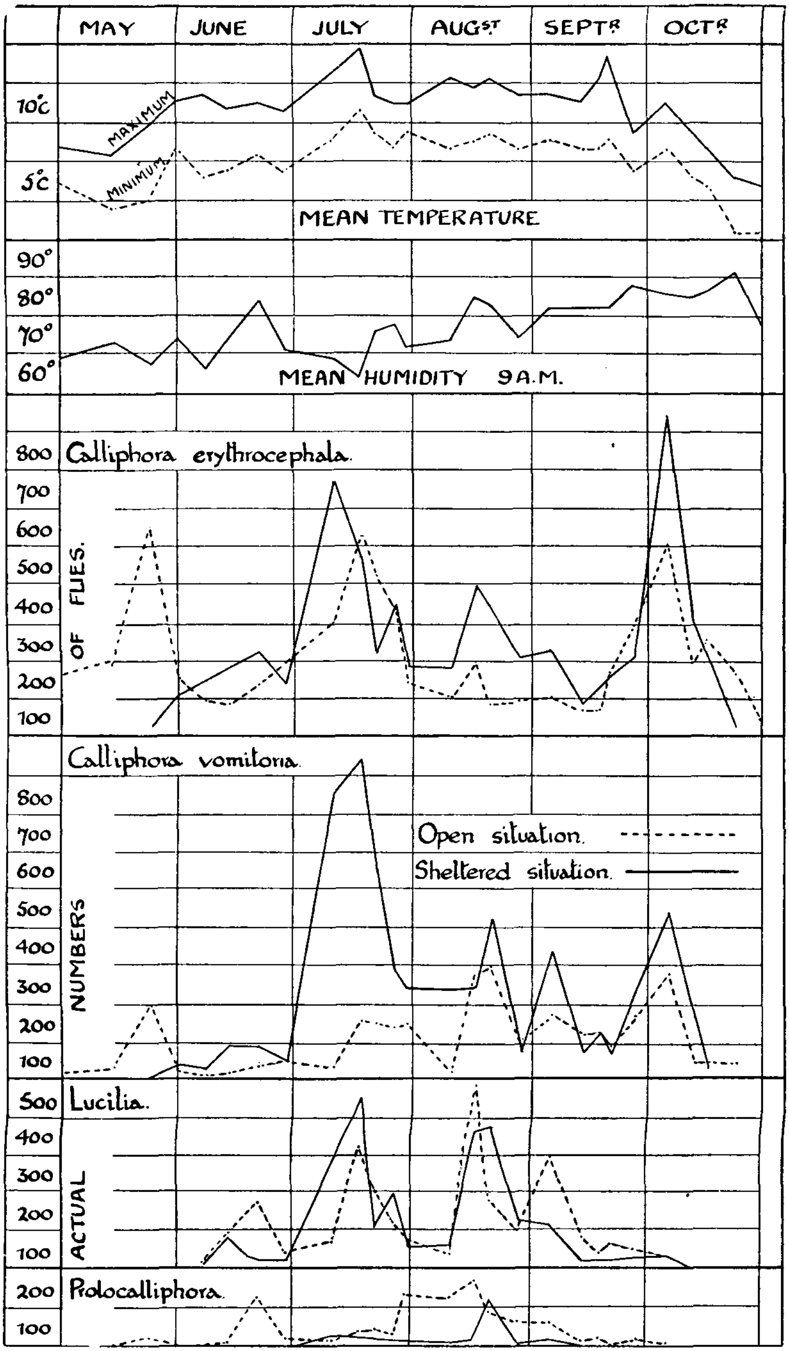

Chart 2. Actual numbers of blowflies trapped under open and sheltered conditions in the Fallowfield district of Manchester during 1926.

Duration of the blowfly life cycle.

For *Calliphora erythrocephala*, evidence as to the period of time which may elapse between parental oviposition and the imaginal emergence of the ensuing generation, based on the observation of flies under controlled laboratory conditions, and at temperatures within the range of English summer temperatures, has been supplied by Saunders (1915) who suggests a period of 21–30 days at 4·5–15·5° C.: by Cousin (1926) who suggests 25–27 days at 18–20° C.: and by Hewitt (1914) who suggests 22–23 days at 23° C. To these periods must be added the time elapsing between imaginal emergence and maturation, a period of time about which there is little accurate information beyond the assertion by Cousin that at 18–20° C. the period is 8–10 days.

At the mean temperatures prevailing in England throughout the summer, therefore, the average period of time between parental emergence and filial emergence is between 33 and 38 days, and the absolute minimum is almost certainly not less than 29 days.

Similarly, in the case of *Lucilia caesar* and *sericata*, the evidence of Herms (1907), MacDougall (1909), Hewitt (1914), Saunders (1915), Johnston and Hardy (1923), would suggest that the average period between one generation and another under laboratory conditions is about 38 days, and the absolute minimum may be as low as 21 days.

Under field conditions, however, it seems certain that some individuals of a generation of either *Calliphora* or *Lucilia* emerge considerably later than is usual. Whilst, admittedly, retardation of development of the egg, larva or pupa can be caused by lowering of the temperature, there is a general concensus of opinion among workers on the subject, that the main cause of prolonged life cycle is a retardation, through certain extrinsic causes, of the prepupal stage, that is to say, of the period between cessation of larval feeding and commencement of pupal immobility.

Under laboratory conditions, the passage of the nontrophic wandering stage into pupal immobility, which occurs 3–4 days after cessation of feeding, at 20° C., may be delayed by subjecting the prepupa to intense light, to tactile disturbance, to sudden changes of temperature, to contact with dry earth or sawdust.

Under field conditions the factors producing such delay are somewhat obscure.

Roubaud (1922), discussing the subject of retardation of life cycle in Muscid flies generally, postulates two causes:

(1) Low temperature (*athermobiosis*) or low humidity (*anhydrobiosis*) which in one physiological group, the homodynamic flies, exemplified by *Musca domestica* and *Stomoxys calcitrans*, influence all the generations of the year; that is to say, homodynamic flies can produce a rapid succession of generations throughout the year if conditions of temperature and humidity be suitable.

(2) Uraemic intoxication, occasioned by a progressive inability, increasing from generation to generation, of the Malpighian tubules to eliminate the uric excretory products, so that they accumulate in the adipose tissue; at the end of a number of generations, which can be retarded or accelerated by temperature or humidity, this degree of intoxication eventually reaches a point at which further development of the animal is inhibited; only prolonged exposure of the organism to low temperature or low humidity will, by reducing metabolism to a minimum, permit this accumulation to be transferred to the Malpighian tubules and so eliminated, in the which case development recommences; uraemic intoxication characterises, according to Roubaud, a physiological group of flies which he terms heterodynamic, and in which he includes *Calliphora* and *Lucilia*.

As is shown by the curves in Chart 2, the appearance of *Lucilia* and *Protocalliphora* in the traps was more than a month later than that of *Calliphora*, and their disappearance occurred about a month earlier than this genus. The appearance of *Calliphora* coincided with the rise of the mean daily minimum temperature beyond 5° C., and the disappearance coincided with the autumn drop of the minimum temperature to a value less than this. The appearance and disappearance of the other two genera, on the other hand, seemed to be independent of rise or fall of mean minimum temperature, an observation which supports the view that they are heterodynamic. It may be pointed out that both genera are typically flies of open situation habit; Luciliine flies are characteristically part of the fauna of tropical and subtropical savannah or semi-desert areas, where short periods of high humidity alternate with longer periods of very low humidity; *Protocalliphora* is characteristically sub-arctic, living under conditions where a short but hot summer alternates with a prolonged period of very severe cold.

Calliphora, on the other hand, is more typically a fly of shady situations, probably in origin a fly of wooded country, and characteristically not tropical nor arctic in distribution, but occurring in regions where alternation of extreme high and low temperature or humidity values is not usual. It would not therefore be expected to be heterodynamic, and Roubaud's statement to this effect is somewhat surprising.

Individual specimens of *Calliphora* frequently appear during sunshiny days in winter but there is no evidence of copulation or oviposition on the part of these individuals, although Whiting (1914) claims to have bred *Calliphora* during the entire year at Forest Hill, Massachusetts.

The author's own observations suggest that *Calliphora* is homodynamic, but that, owing to the conditions of winter, at any rate in northern England, no generation is produced between autumn and spring. Many of the late emerging autumn imagines do not copulate, and may hibernate in sheltered situations as far as the end of the year, possibly longer, and emerge from hibernation during warm, sunny spells. The progeny of the autumn generation, however, remain until early spring chiefly in the prepupal stage, pupate in

March and April, and emerge as soon as the mean minimum ground temperature has exceeded 5° C.

Prolongation of the prepupal stage seems to be brought about by a combination of low temperature and high humidity. Thus, larvae which hatched on September 14, 1926, were full fed by September 20, but pupation did not occur for nearly a fortnight, and the imagines emerged about the middle of October. Larvae hatched at the end of October 1926, are, at the time of writing (February 14, 1927) still in the prepupal condition.

It may be noted that, at the onset of a period of low temperatures, larvae cease to feed and crowd together under a piece of stone or similar shelter on the ground surface. The crowding and consequent tactile disturbance may also tend to delay the onset of pupation.

Numerical abundance of blowflies.

The numerical abundance of blowflies throughout the year is a function of two variables, namely the rate of imaginal emergence, and the rate of mortality.

The number of generations throughout the year will depend upon the rapidity with which the periods elapsing between the initial emergence of successive generations can be passed through. The minimum inter-generation period will be equivalent to the mimimum interval between parental emergence and initial filial emergence, a period which, under northern England field conditions, is certainly not less than 29 days for *Calliphora erythrocephala*.

The maximum period over which the individuals of a generation can emerge is equivalent to the maximum interval between parental emergence and initial filial emergence. Thus it would seem that, even if we limit the maximum emergence period to fifty days, the succession of generations throughout the year should overlap considerably and should number about twelve.

Actually, however, the period between the emergences of successive generations, and consequently the number of generations in the year, is affected by two factors, namely prolongation of the prepupal stage, and prolongation of the interval between the emergence of a female fly and its subsequent oviposition.

The first of these factors is the main cause for the absence of any generations between late autumn and spring. That it is a serious factor in prolonging the emergence period of other generations is less probable. Individual flies of every generation may have a life cycle prolonged beyond the normal, particularly under early autumn conditions, and the maximum of emergence of the autumn generation may be delayed somewhat, but between May and September the great majority of the individuals of a generation have probably a life cycle from egg to mature fly varying between 29 and 38 days. The second factor is of more importance.

According to data derived from laboratory observations, a female blowfly should oviposit about 8–10 days after emergence, at English summer temperatures.

Under outdoor conditions, however, this interval between emergence and oviposition may be prolonged, firstly by limitation of opportunities for copulation, secondly by low sun temperatures which delay maturation.

Low sun temperature as an inhibition factor is more potent in spring and autumn so that the interval between the early and the late summer generation may be expected to be shorter than the interval between the spring and the early summer generation, or between the late summer and the autumn generation.

Further, the majority of the early emerging individuals of a generation are dwarfs, for reasons which will be discussed later, and among these the rate of pre-maturation is probably high. The first date of oviposition of a generation therefore, instead of occurring about 8–10 days after the commencement of emergence, will be delayed until cessation of the rate of pre-maturation mortality permits the appearance of mature flies.

The following conclusion may now be put forward.

On a curve expressing the emergence of consecutive blowfly generations the maxima of emergence will be separated by a longer interval than the average period that elapses under laboratory conditions between parental emergence and filial emergence, owing to the extension of the interval between initial emergence and initial oviposition in each generation by two factors, low sun temperature and pre-maturation mortality.

Among laboratory reared flies, the number of emerging imagoes of a generation is not greatly in arrears of the number of eggs laid by the parental generation. On the other hand, as Graham-Smith has indicated, among flies reared in open air cages, the actual numerical strength of each generation of imagoes is far short of the calculated strength. This observer estimates the actual number of descendants from each female of the spring generation to be 130 by autumn instead of a possible 1012 millions.

Every stage of the blowfly life cycle is liable to be affected by mortality factors.

The chief danger to which the egg stage is liable is that of desiccation. During the summer periods of high sun temperature and low humidity, egg masses very readily dry up, particularly if competition for oviposition media is keen and eggs consequently deposited on exposed surfaces of the medium. The liability is greater when the surface area of the medium is restricted, and since winds play a considerable part in bringing about desiccation, the danger is greater under open than under sheltered conditions.

Larval stages are usually fairly well protected from the direct influence of meteorological conditions but are affected indirectly by desiccation of the food medium, and are liable to a considerable degree of mortality from rain storms. Probably desiccation of, and flooding of, the medium are the chief causes of larval mortality. The prepupal and pupal stages are not fatally affected to any great extent by extrinsic causes. In the case of *Calliphora erythrocephala*, and possibly of the other genera, however, there occurs a considerable degree of

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parasitism of the autumn prepupal stages by Braconid Hymenoptera belonging to the genera *Alysia* and *Aphaereta*, especially under shade conditions, and a considerable number of the spring pupae are attacked by the Chalcid Hymenoptera *Melittobia* and *Nasonia*, especially under sun conditions (Graham-Smith, 1916).

Pre-maturation imagoes suffer from a high degree of mortality whose causes are as yet not satisfactorily explained. Graham-Smith, who regards this early imaginal mortality as one of the most important factors in limiting the numerical abundance of flies, associates it with cold windy and rainy periods, and again with sultry oppressive weather.

Whilst agreeing that this mortality may be due to abnormal weather conditions, the author's own observations would suggest, for *Calliphora erythrocephala* at Manchester, that, judging by the number of flies which seemed to die soon after entering the traps:

(1) The pre-maturation mortality was low among emerging individuals of the spring generation, high among the early summer generation, low again among the late summer generation, and high in the autumn generation.

(2) It was high among the early summer generation and the autumn generation owing to a spell of east and north-easterly winds during six days of July, and a spell of north-north-easterly winds accompanied by a sudden fall of 7° F. and 5 mm. of rain on September 20, 1926.

(3) It was low among the late summer generation because the winds during August were chiefly south and south-westerly; low among the spring generation because in this generation dwarf flies were scarce and the pre-maturation mortality seems to concern chiefly dwarf flies, that is to say, flies whose length between frons and abdominal tip is less than 9 mm. Such dwarfs are uncommon in spring but markedly numerous among emerging flies during the summer.

Post-maturation mortality of imagines is due chiefly to predatory animals and does not appear to be a serious factor, judging by the large number of apparently aged flies which come into the traps. In September and October, however, the fungus *Empusa* takes heavy toll.

Now although these various mortality factors cannot affect the actual number of generations, nor, with the exception of the imaginal pre-maturation mortality, can they affect the intervals between generations, they can and do affect the numerical abundance of imaginal flies very seriously, the net result being that the maximum of abundance of any generation occurs earlier in time than would be the case if the only mortality factor was old age.

For if the imaginal mortality was absolute, reaching 100 per cent. during each day of the emergence period, maximum abundance would coincide with maximum emergence. If the rate of mortality, apart from the general causes of old age, were zero, maximum abundance would occur on the last day of the emergence period. Thus, whatever the mean rate of imaginal mortality per day, the interval between maximum emergence and maximum abundance will be some fraction of the emergence period. The higher the rate, the smaller the

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fraction and the nearer will be the maximum of abundance to the maximum of emergence.

Graham-Smith estimated the mean longevity of the individuals of his parental generation of *Calliphora erythrocephala*, in open air captivity, as 30 days, and the emergence period of this generation was 22 days, so that the mean rate of mortality per day was nil. Under field conditions, however, even if the imaginal mortality among the first generation of the year is low, it is high among later generations, especially among the newly emerged flies. Further, if, as seems possible, the great majority of summer individuals of *Calliphora erythrocephala* have a period between parental oviposition and filial emergence of 21–30 days, then the great majority of individuals of a generation emerge over a period of 9 or 10 days, although of course the whole emergence period owing to prolongation of individual life cycles may be considerably longer. Thus the interval between maximum abundance and maximum emergence, even if the rate of mortality is zero, should not exceed 10 days, but, since there is every reason to assume that the imaginal mortality is high, the interval separating the respective maxima cannot be more than a few days.

The following conclusion may therefore be put forward:

On a curve expressing the numerical abundance of a blowfly species throughout the year, the maxima of numerical abundance of successive generations will occur a few days later in time than would be the case if they coincided with the maxima of emergence of successive generations.

Influence of weather upon seasonal frequency.

If the sun curve (Chart 2) expressing the trap captures of *Calliphora erythrocephala* in Manchester be examined, the four peaks on it will be seen to be separated by intervals of 55, 29 and 50 days respectively; on the shade curve, the three highest peaks, which correspond to peaks 2, 3 and 4 of the sun curve, are separated by intervals of 36 and 50 days respectively.

The intervals, therefore, between the major peaks of the curve of trap captures agree fairly well with the assumption that these peaks represent maxima of numerical abundance and so correspond with maxima of imaginal emergence of successive generations, although occurring a little later in time.

There is, however, one difficulty. The interval of 29 days between the July and August peaks seems too short to represent an interval between two generations, since there was not during that period any marked meteorological phenomenon which would favour rapidity of blowfly development.

It will be noted on the sun curve that a low peak occurs in early September, but obviously too near to the August peak to represent a generation. This peak is much more prominent upon the curves for *Calliphora vomitoria* and *Lucilia*, but here again the interval between it and the August peak is too short to represent an inter-generation interval.

It may be suggested, however, that the depression between the August peak and this early September one, corresponding as it does on every curve to the period August 16–September 5, represents either a sudden increase in the rate of mortality during the emergence of a generation, or more probably, since it occurs on both sun and shade curves of all three genera, represents an interruption to the number of flies visiting the baits, and that the two peaks really represent one peak of numerical abundance occurring about the end of August. Such a view would make the interval between the July and August generation maxima longer than the very short one shown on the curve.

It is of interest to note that although this period, August 16–September 5, was not characterised by any abnormal phenomena of temperature, sunshine, humidity or rainfall, yet there occurred within it five consecutive days, August 18–22, during which the wind velocity was continuously 13–24 miles per hour; it was the windiest spell of the whole period April–November. It may be suggested that it was this strong windy weather which interrupted the visitation of flies to the traps.

It will be noted, further, that, on the curves, the major peaks show a tendency to be broken up into minor peaks, produced undoubtedly by some factor which interrupts the continuous attraction of flies to the traps.

That such interruptions are caused by weather phenomena, such as strong wind or rain, seems opposed by the fact that a minor peak on a shade curve is not necessarily accompanied by a similarly situated peak on the sun curve. Thus, during the period June 21–28, the number of *Calliphora erythrocephala* and *Calliphora vomitoria* individuals captured under both conditions was approximately the same as was captured during the preceding period June 13–21. Whereas in the period June 13–21, however, the majority of captures occurred in the shade traps, during June 21–28 the reverse condition occurred, so that the shade curve shows a depression corresponding to the period.

If adverse weather conditions were the cause, the depression should occur in both curves. If the cause were a temporary acceleration in the rate of imaginal mortality, both curves should show the depression.

Similarly, during the period July 18–22, whilst both sun and shade curves show that the number of trap captured individuals of *Calliphora* and *Lucilia* was falling, the number fell more rapidly in the shade traps than in the sun traps. Again, during September 18–20, the number of individuals of *Calliphora* was less as compared with the previous period, whereas the sun traps showed an increase. That is to say, the causative factors of these minor peaks would seem to be phenomena which affect the attractiveness of baits.

Whilst unable to offer a precise explanation as to the nature of these factors, the author would suggest that it is a question of surface desiccation of the bait. In the Manchester area, where absolute calm spells of several hours are rare, small pieces of liver, and possibly of other meat stuffs, more readily undergo surface desiccation and so lose their powers of attraction, under sun conditions than under shade conditions, so that when the baits are unchanged for several days, the number of flies attracted to the shade traps is on the whole more considerable than the number attracted to the sun traps.

During periods of moist west and north-west winds, however, the sun baits remain attractive for some days, and if the weather is also sunny and warm, the number of flies attracted to them is slightly greater than to the shade traps. This is certainly the case when the bait is a small unskinned animal. High sun temperature and low humidity, however, cause the flies to go more readily to shade traps where the bait retains its attraction to the olfactory powers of the fly longer than do the sun trap baits.

Thus the cause of the interruption to the attraction of flies to shade traps probably lies in some combination of weather factors, including the prevalence of westerly and north-westerly winds, during which the rate of surface desiccation of the baits in the sun traps was not so rapid as usual.

There is a certain amount of evidence for the view that the major peaks of the curves, although corresponding in the author's opinion to maxima of numerical abundance and so to transposed maxima of imaginal emergence, are influenced somewhat in position by weather factors.

Table II records the temperature, humidity, rainfall and sunshine during the periods when the major peaks occurred.

Table II.

Period	Maximum temp.	Minimum temp.	Humidity	Rain	Sunshine
Calliphora.	° C.	° C.	°	mm.	hrs.
May 14–24	15	5	67·7	1·1	5·6
June 28–July 11	22	13	69	1·8	6·5
July 11–18	25	17	64	0·4	5·0
Aug. 16–20	21	14	83	2·6	4·0
Sept. 28–Oct. 5	18	12	86	0	3·0
Lucilia.					
June 13–21	18	11	84	1·6	2·1
June 11–18	25	17	64	0·4	5·0
Aug. 10–16	20	13	85	6·0	3·0
Aug. 28–Sept. 5	19	13	82	2·0	2·5
Protocalliphora.					
June 13–21	18	11	84	1·6	2·1
Aug. 10–16	20	13	85	6·0	3·0

It will be observed that all the periods have a relatively high daily mean sunshine value, and that, with the exception of May 14–24 and June 28–July 18, all have a high mean daily humidity value. The first of these periods only concerns *Calliphora* and may be taken to represent the emergence of the first generation from the overwintering stage and so determined rather by accumulated soil temperatures than by humidity.

The period June 28–July 18 is characterised by a moderate humidity value, but during this period there were 5 days on which the mean morning humidity exceeded 80°.

A combination of high sunshine and high humidity values is attained during a sunny morning following a wet night, or a sunny afternoon following a wet morning. That such conditions particularly favour blowfly oviposition has been previously recorded by the author (Wardle, 1921), and it may be pointed out that in areas so separated as Queensland, Cumberland and Montana, a correlation has been observed between frequency of attack by blowflies on living sheep, and warm damp weather.

Hot humid weather seems unfavourable to blowflies in open situations, and under such conditions they show a tendency to seek shady situations.

Conclusions.

1. The curve of seasonal frequency of a blowfly species, as shown by trap captures, consists of a number of major and minor peaks. The major peaks, although representing the actual maxima of flies visiting the traps, correspond to maxima of numerical abundance and so indicate maxima of emergence of successive generations. The minor peaks are caused by interruptions to the attraction of the baits for flies, such interruptions being brought about by variations in the rate of surface desiccation of the bait.

2. Low wind velocity, high sunshine value, high temperatures and high degree of humidity favour the attraction of flies to the baits but their influence upon the curve of seasonal frequency is marked only when these periods of favourable weather factors coincide with maxima of numerical abundance.

3. The number of generations through the year of *Calliphora*, *Lucilia* and *Protocalliphora* is believed to be four, the maxima of emergence occurring in May, late June, August and late September in the case of *Calliphora*; in June, July, August and September in the case of *Lucilia* and *Protocalliphora*. The September generation exists through the winter principally in the prepupal stage.

Calliphora is considered to be homodynamic, the other genera to be heterodynamic.

II.

THE NUMERICAL DISPROPORTION BETWEEN *CALLIPHORA ERYTHROCEPHALA* MG. AND *C. VOMITORIA* L.

When two species of a genus of animals, taxonomically separable only by characters which do not appear to have any utilitarian value, and with a common geographical and environmental distribution, occur in marked disproportion one to the other, there should be forthcoming some rational explanation to account for the phenomenon. An example of this disproportion is seen in the case of the two common British species of blowfly, *Calliphora erythrocephala* and *C. vomitoria*. These species are separated by the systematist on certain slight, but presumably constantly occurring features of colour, namely the possession by *erythrocephala* of reddish brown jowls provided with black bristles, as contrasted with the greyish black jowls with coppery red bristles of *vomitoria*. The exact function, if one occurs, of these cheek bristles is unknown, and no speculation has yet been put forward as to the advantage of black bristles over red ones. It has already been shown in Part I of this paper, that the two species emerge together from winter inactivity, and disappear together in the autumn; their feeding habits and oviposition habits presumably are similar; at any rate no difference has as yet been recorded.

Actually, the ratio of one species to the other is probably not so disproportionate throughout the whole period April to November as has been stated by various authorities.

Thus, among 29,256 specimens of *Calliphora* captured by Graham-Smith in Cambridge during 1916, the percentage ratio of *erythrocephala* to *vomitoria* was 64 : 36. Again, among 20,089 specimens captured by the author in Manchester during 1926, the ratio was 58 : 42.

Thus, although in both rural and industrial localities, the ratio of *vomitoria* was certainly less than that of its fellow species, the difference was hardly such as to suggest that *vomitoria* "is much less common" (Hewitt, 1914) or "not nearly so abundant" (Graham-Smith, 1913) in relation to *erythrocephala*.

If however the curves in Chart 3, expressing the percentage ratio of one species to the other throughout the period April to November 1926 in Manchester, be examined, it will be apparent that during May and June, and again during October, the ratio of *vomitoria* was much lower than that of *erythrocephala* under both open and sheltered conditions. During the summer months, however, *vomitoria* was on the whole the predominant fly. It predominated in the shade traps during June 29–August 10; it predominated in the sun traps during August 10–September 18.

Now during each of these periods, the number of *vomitoria* individuals captured did not differ greatly from the number of *erythrocephala* individuals. Thus during June 29–August 10, 3795 *erythrocephala* were captured as against 3594 *vomitoria*. That is to say, the former species was actually superior in numbers, but as only 57 per cent. went into the shade traps as against 83 per cent. of *vomitoria*, the latter species was apparently predominant under shade conditions. Similarly, during August 10–September 18, 1970 *erythrocephala* individuals were captured as against 1976 *vomitoria*, and again the greater proportion of flies went to the shade traps, but whereas 70 per cent. of *erythrocephala* were recorded there, and only 62 per cent. of *vomitoria*, the latter species predominated in the sun traps.

Therefore to understand why *Calliphora vomitoria* is predominant over *Calliphora erythrocephala* in traps during July, August and September, we must explain why:

(1) *Vomitoria* should be approximately equal in numbers to *erythrocephala* in the middle of the summer, although so markedly inferior in spring and autumn.

(2) *Vomitoria* was more markedly attracted than *erythrocephala* to shade traps during July 1926.

(3) It was less so attracted in August and September.

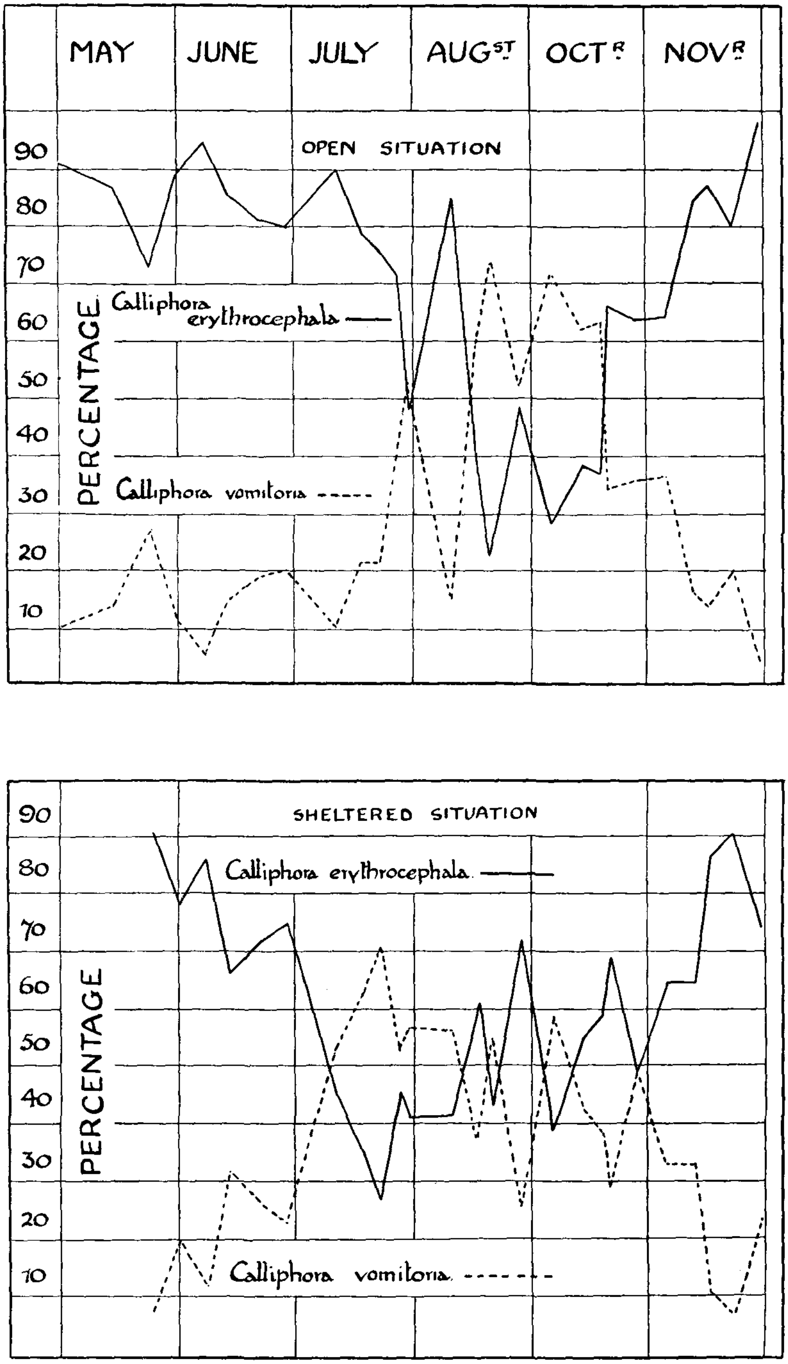

Chart 3. Percentage proportions of *Calliphora erythrocephala* and *Calliphora vomitoria* trapped in the Fallowfield district of Manchester during 1926.

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The greater rapidity of the rate of increase of *vomitoria* as compared with that of *erythrocephala* during the period April to July may be due to a shorter life cycle and consequently greater number of generations, or to greater female prolificacy, or it may result from a lower rate of mortality throughout the life cycle.

It has already been indicated that the number of generations, the duration of the emergence periods of successive generations, and the lengths of the life cycle in both species are probably about the same, although there is no published evidence, to the author's knowledge, as to the duration of the life cycle stages of *Calliphora vomitoria*. It is a fly less easy to rear in captivity than is *Calliphora erythrocephala*. Repeated attempts in Manchester to induce oviposition by female *vomitoria* individuals in captivity were unsuccessful, and at no time were *vomitoria* individuals ever reared from pieces of liver exposed to oviposition by wild flies. It can however be reared from large slabs of carrion which has been exposed to oviposition by wild flies, and among the maggots that can be purchased from dealers in anglers' requisites, those of this species seem to predominate. The statement by Dexler (1916), therefore, that this species feeds but does not oviposit upon meat stuffs is somewhat surprising and is undoubtedly incorrect. It may be noted that *Lucilia* is also a fly very difficult to rear from small pieces of meat, though easily bred from carcases that have been exposed to sunny, open conditions. *Calliphora vomitoria* may very well be a blowfly which oviposits for preference on carcases under shade conditions.

Such a habit at any rate would explain one morphological feature of *Calliphora vomitoria* that seems to have eluded the notice of systematists, and that is the marked difference in size between the average *vomitoria* individual and the average *erythrocephala*. *Calliphora vomitoria* is on the whole a bigger, more active, more noisy fly than *Calliphora erythrocephala* and dwarf specimens are relatively uncommon. In the case of the latter species, although individuals may often occur which are equal in size to the biggest *vomitoria*, the mean size is less, and dwarf individuals are abundant during the summer generations.

Occurrence and cause of dwarf individuals of Calliphora.

That blowflies vary greatly in size is of course a well observed fact, although, apart from the data concerning *Lucilia* published by Tothill, no statistical data concerning this variation in size have, to the author's knowledge, been published.

The curves in Chart 4, indicating the length-frequencies per thousand, for male and female individuals of both species of *Calliphora*, are based upon the measurement of about 11,000 individuals of *C. erythrocephala* and about 8000 individuals of *C. vomitoria*, trapped between April 20 and October 30, 1926 in the Fallowfield district of Manchester under both open and sheltered conditions.

In each fly, the distance between frons and abdominal tip was measured to the nearest millimetre.

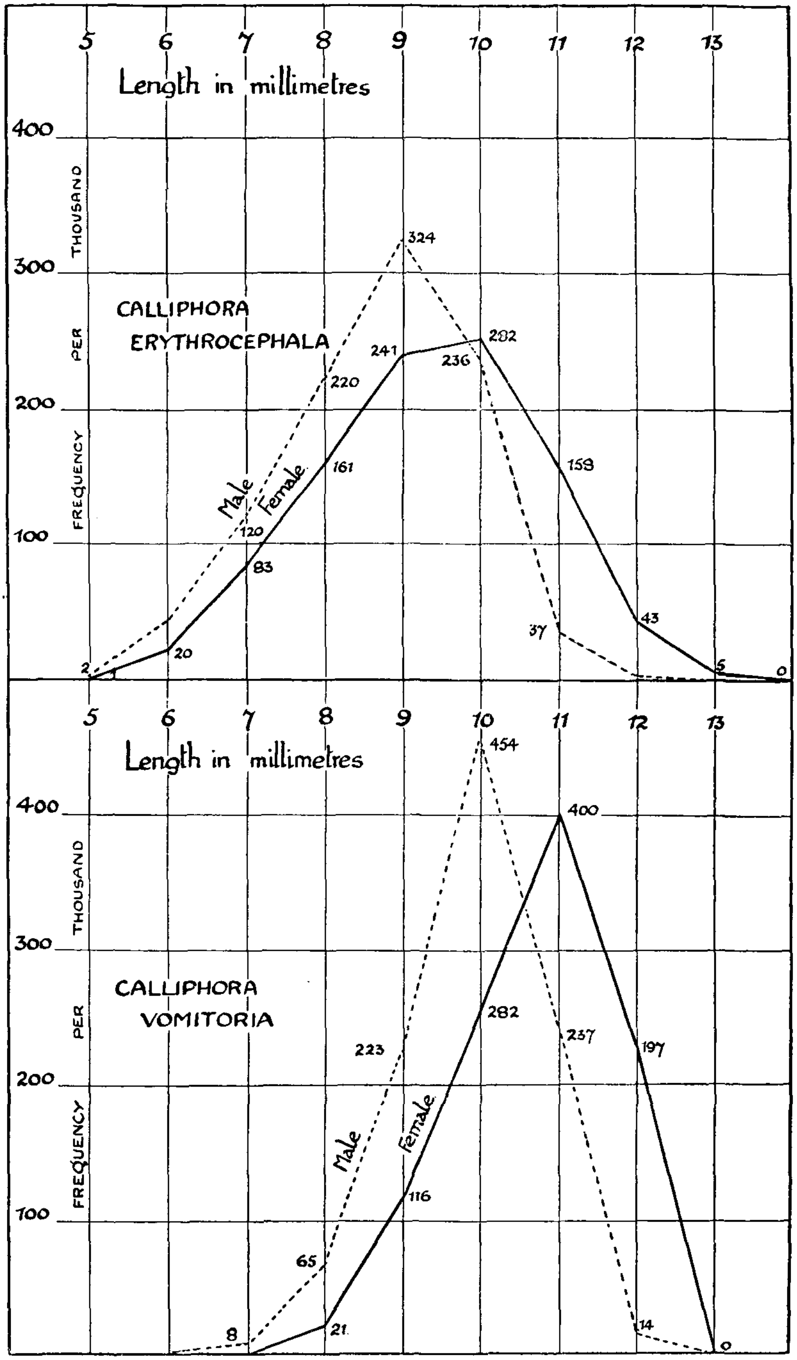

Chart 4. Length-frequencies per thousand of male and female individuals of *Calliphora erythrocephala* and *C. vomitoria* in Manchester.

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As the curves show, the flies ranged in length between 5 and 13 mm. In the case of *C. erythrocephala*, however, the majority of males had a length of approximately 9 mm., the majority of females a length of 10 mm.; in the case of *C. vomitoria*, the majority of males were approximately 10 mm. long, the females 11 mm. In the latter species, no fly occurred with length less than 6 mm. and there was a much larger number of 11 mm. males and 12 mm. females than was the case with *C. erythrocephala*.

In each species, dwarf individuals—of length 8 mm. or less—occurred. These dwarfs apparently do not constitute a distinct race, since the curves have each only one peak. Other observers have stated that such dwarf individuals can produce normal-sized progeny. The frequencies per thousand of these dwarf sizes were as follows:

Calliphora erythrocephala.					
Length in mm.	5	6	7	8	
Male	2	42	120	220	=384 } individuals per thousand
Female	1	20	83	161	=265 } individuals per thousand
Calliphora vomitoria.					
Male	0	0	8	65	= 75 } individuals per thousand
Female	0	0	1	21	= 22 } individuals per thousand

There was thus a striking discrepancy between the frequencies per thousand of dwarf individuals in each species.

It may be added that, in both species, the greatest number of dwarfs occurred in July and August.

The view that this dwarfed condition of blowflies results mainly from insufficient larval nutrition is almost certainly correct. Such forms can be obtained under laboratory conditions by removing larvae from their food before they are full fed. They can be obtained also, according to Bogdanow, by feeding larvae on sterilised meat.

The conclusion, however, from laboratory experiments that such forms arise also in nature through actual shortage of food material, may be objected to. The number of full fed larvae that may be reared under laboratory conditions from a small piece of meat is relatively enormous, and it would seem doubtful whether, even under rural conditions where competition for oviposition media must be more intense than in a town, the actual quantity of food media is insufficient for the larvae which find themselves therein.

The author's own observations would suggest that unsuitability of food rather than insufficiency is the cause, and that this unsuitability is produced by certain weather conditions. During dull cool windy weather, or during very sunny dry weather, small pieces of meat desiccate rapidly. Desiccation first affects the outer surface and discourages further oviposition since the power of attraction of the meat becomes lost. Then, since the mean humidity in Manchester rarely falls below 60° and east and north-east winds are the chief agents in producing desiccation, the interior of the medium desiccates very slowly and larvae tend to crowd together in the moister portions. Some wander about the medium and pupate prematurely within it; the author's experience of such pupae is that they do not hatch. Other larvae migrate and eventually give rise to dwarf imagoes. During May 19–24, 1926, for example, a period when numerous larvae from the spring generation were feeding, the winds were chiefly from the east and the baits rapidly desiccated. During July 6–11, exceptional numbers of small *Calliphora erythrocephala* individuals appeared in the sun traps.

In very humid weather, similar restriction of larval food sources is brought about by fungous growth.

An objection may be raised also against the view that larval starvation prolongs the prepupal period, the period of active wandering between the cessation of larval feeding and the onset of pupal immobility.

If larvae are not permitted to become full fed but are removed from the food medium within 48 hours of emergence from the egg, they very soon die.

If removed after the lapse of 48 hours, they wander restlessly about but do not undergo pupation until, in the author's experience, after a period varying between 9–12 days. Although the bulk of the pupae eventually hatch, the greater number of flies have difficulty in emerging and their wings do not readily dry. This however was in laboratory jars. Under sunny dry outdoor conditions this may not be the case. Imagoes of *Calliphora erythrocephala* obtained by the author from larvae removed from food between 50 and 70 hours after hatching showed scarcely any appreciable variation in body length, the mean length being 7 mm.

Larvae removed after the lapse of 4 days from hatching again varied little in size and had a mean length of 8 mm. Imagoes were never obtained so small as were captured in traps. The ratio of males to females was 50 : 46.

It is difficult to be sure of the exact time when pupation commences so that the author is unable to confirm or oppose the statement of Cousin (1926) that such dwarfed larvae have a pupal period of approximately the same length as normal flies. Such evidence as was obtained suggested that the pupal period of the dwarfs was slightly shorter, a result possibly of the greater susceptibility of such pupae to temperature, owing to the thinner pupal case.

Now to call the period of 9–12 days, between cessation of feeding and commencement of pupation, in dwarf flies, a prepupal period, is incorrect. Only the last 4–5 days of it can represent the true prepupal period. The first 5–7 days is a period when the larvae would normally be feeding and will in fact continue to feed if transferred back to the medium within this period. It may be noted that if so transferred, and allowed to complete normal development, the ultimate date of pupation is later than that of the untransferred larvae by approximately the length of the temporary abstinence. If larvae are transferred to the food medium after the lapse of 5 days' abstinence, they do not recommence to feed but wander away and eventually pupate.

Cousin induced such larvae to recommence feeding even after the lapse of 15 days but they had been subjected to intense light and to rise of temperature from 18–20° C. When such stimuli were not employed, 25 per cent. of the larvae pupated after 4 days, 25 per cent. after 5 days, and the rest by the 8th day. It may be suggested therefore that compulsory abstinence from food does not necessarily prolong the life cycle unless the larva is able to recommence feeding within the limits of its normal trophic period, for that temperature. Otherwise, the larva is very active for a period equivalent to the length of time that its normal trophic period has been curtailed; during this period it may wander up the sides of a containing vessel; then it becomes less active and distinctly geotropic, and after 4–5 days passes into pupal immobility.

The disparity between the two species of *Calliphora* as regards the occurrence of dwarf forms has been already commented upon. It is to be expected that larvae of *Calliphora erythrocephala*, notoriously a breeder in small scraps of animal protein matter, would be more liable to experience food difficulties owing to desiccation than would larvae of a fly that bred in carcases, such as *Calliphora vomitoria* may do. *Lucilia*, a carcase fly, admittedly shows considerable range of body length, but *Lucilia* breeds in carcases under sunny, open conditions where a certain amount of desiccation is to be expected.

The lower frequency of dwarf forms among individuals of *Calliphora vomitoria* as compared with *Calliphora erythrocephala* throws light upon its more rapid multiplication during the early summer.

The view has already been expressed in the earlier part of this paper that pre-maturation mortality among imagoes of blowflies occurs chiefly among dwarf forms. On this view, the pre-maturation mortality of *vomitoria* will be lower than in the case of its fellow species, and the proportion of mature flies in each generation will be greater.

Further among the imagoes of *erythrocephala* that arrive at maturity, copulation may be more restricted than among *vomitoria* individuals owing to the greater variation in imaginal size. The sex ratio among individuals of the former species captured at Cambridge during 1915 and at Manchester during 1926 was 1 : 2·3; among *vomitoria* individuals it was 1 : 3. Among the *erythrocephala* males however were more dwarf forms, which may not reach maturity, than among the *vomitoria* males, so that the ratio of *sexually mature* males to females among *vomitoria* is possibly higher than in the case of *erythrocephala*.

Disparity in sex ratios would however not account for the more rapid rate of increase of *vomitoria* if the assertion by Parker that *Calliphora erythrocephala* is polyembryonic could be substantiated. Keilin has discredited the possibility, and numerous experiments carried out at Manchester in early summer have convinced the author that polyembryony is unlikely among *Calliphora erythrocephala* at any rate between May and August.

Influence of weather on Calliphora.

Throughout the period when captures in traps under open and sheltered conditions were made, individuals of each species of *Calliphora* were more numerous in traps in the sheltered situation than in the other traps. Allowing for the disparity in the sex ratio, there seemed to be no great difference of habit between males and females in this respect. That is to say, the baits in the shade were not attracting chiefly pregnant females.

The numerical difference between the individuals captured in sun and shade respectively was greatest between June 29 and September 18. This period was characterised by a high value of mean daily sunshine. During the period June 29–August 10, when the predominant fly in the shade traps was *Calliphora vomitoria*, and particularly during the week July 11–18, there was in addition a very high sun temperature, and a low mean value of daily rainfall —only 2·8 mm. of rain fell during the whole week, so that the humidity was low, lowest for the whole year in fact.

It is interesting to note therefore that during this week the numbers of each species captured were:

	Calliphora erythrocephala	*Calliphora vomitoria*
Sun traps	531	144
Shade traps	466	831

That is to say, under conditions of high sun temperature and low humidity, more than 85 per cent. of the *vomitoria* individuals were in shade traps.

It might be suggested therefore that *Calliphora vomitoria* is less tolerant of high sun temperature than is its fellow species. Close comparison however of the meteorological conditions prevailing during July, as against those prevailing during August and September, and of those prevailing during periods when the sun temperature was high, suggest that what really brings about disparity between shade and sun captures is surface desiccation of the baits.

If during the first 24 hours of bait exposure, weather conditions comprise high sunshine, temperature and low wind velocity, and so favour activity of flies, the baits will be visited freely under both sun and shade conditions. The disparity between trap captures under both conditions will be small but will be in favour of the sun traps.

If during the first 24 hours of bait exposure, there occurs strong wind or rain or low sunshine, or low temperature, activity of flies is restricted. When weather conditions permit activity again, the baits will have begun to desiccate superficially. Again, the disparity between captures under both conditions may not be great, but since surface desiccation is more rapid in the sun than in the shade, the disparity will favour the shade captures. If during the period of bait exposure, there occur winds of a dry character, such as east and north-east winds in this area, the disparity will be much more marked and will favour greatly the shade captures.

There is some evidence to suggest that susceptibility to the lessened olfactory attraction shown by desiccating baits is more marked among male than among female flies, and is more marked in *Calliphora vomitoria* than in *Calliphora erythrocephala*. I am indebted to my colleague Miss Macgill for the following unpublished data from her work on the antennae of higher diptera (see Patton & MacGill, 1925) concerning the number of antennal pits, generally regarded as olfactory, in four random specimens of each sex of the two species.

	Number of antennal sense pits			
Calliphora erythrocephala male	43	55	45	44
Calliphora erythrocephala female	62	74	60	69
Calliphora vomitoria male	36	28	29	32
Calliphora vomitoria female	33	44	65	40

It would seem therefore that the tendency of *Calliphora* to seek shade baits more than sun baits is due to a difference in the powers of attraction of the respective baits brought about by weather conditions, and that *C. vomitoria* is more susceptible to this difference owing to a lower degree of olfactory perception rather than to any difference in phototropic susceptibility.

Conclusions.

1. The disparity between the numerical abundance of *Calliphora erythrocephala* and *Calliphora vomitoria* in Great Britain is not such as to suggest that the latter species is rare or uncommon except in spring and autumn. During the summer the number of both species are approximately equal.

2. *C. vomitoria* shows a more rapid rate of increase during early summer than does *C. erythrocephala.* This seems to be correlated with a lower number of dwarf forms, and a consequently lower prematuration mortality of imagoes.

3. The greater response, on the whole, of both species to trap baits under sheltered conditions than under open conditions is due not to phototropism but to a susceptibility to lessened attraction of baits. This lessened attraction is brought about by the superficial desiccation induced by weather conditions. Such desiccation is less rapid under sheltered conditions than under open conditions.

4. This susceptibility is more marked among males than among females, and among *Calliphora vomitoria* individuals than among *Calliphora erythrocephala* individuals, owing to lesser powers of olfactory perception.

In conclusion, I must express my indebtedness to my colleague, Miss E. Macgill, for very much help in the securing and examination of the material used.

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