An investigation into field population of calliphorine flies with special reference to the age structure of female calliphora

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" AN INVESTIGATION INTO FIELD POPULATIONS OF CALLIPHORINE FLIES WITH SPECIAL REFERENCE TO THE AGE STRUCTURE OF FEMALE *CALLIPHORA*".

A dissertation presented for the Degree of M.Sc. in the University of Durham.

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TABLE OF CONTENTS.

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INTRODUCTION

This study has as its main aim the investigation of the adult ecology of Calliphoridae population; more specifically, C. vomitoria. With special reference to any age changes in the age composition of the female population during the early part of the season of adult occurrence, i.e. May - July.

Sampling Calliphoridae from the natural dispersed population by suction traps or by catching resting flies (trap methods) is impracticable as the natural fly population density is relatively low. Trapping flies for this investigation then necessitated the use of baited traps in order to attract and so concentrate the flies. This method of collecting flies for the investigation does then give a biased sample, as only those flies reacting in a positive manner to the bait will be caught and the variables which may influence any particular fly are numerous, the general physiological condition of the fly being perhaps the greatest single variable factor.

Throughout this study, then, the trapped sample refers not to a random sample from the population, but rather to that sector of the population that has reacted to the bait.

Other workers, notably Maclaed and Donelly (1956,1957), trapped blow flies and found great variability between traps in respect of the numbers of flies actually caught, and as no rational explanation could be found to account for these differences, they called it 'trap idiosyncracy'. Such variability in the number of flies caught in different traps was also found in this study and although it is realized that trapped blow-flies attract other flies to the trap (Cragg and Ramage, 1945), this does not entirely account for trap differences.

This study is, then, essentially concerned with investigating the age structure of those female Calliphora attracted to meat baited traps. From the life history and annual cycles of the Calliphora (see later), one would expect the flies that appeared early in the season to be newly emerged nulliparous flies, and then, as the season progressed one would expect the population in general to age, although nulliparous flies would still be present as second or even third generation flies entered the population.

To see if these expected generalizations were true, the reproductive history and thus indirectly the physiological age of each female was investigated by dissection (details of techniques used are given later); the basis of the age table was the number of dilations found on the ovariale tunica as this indicates the number of previous ovarian cycles since each batch of eggs that is laid leaves one dilation.

THE STUDY AREA.

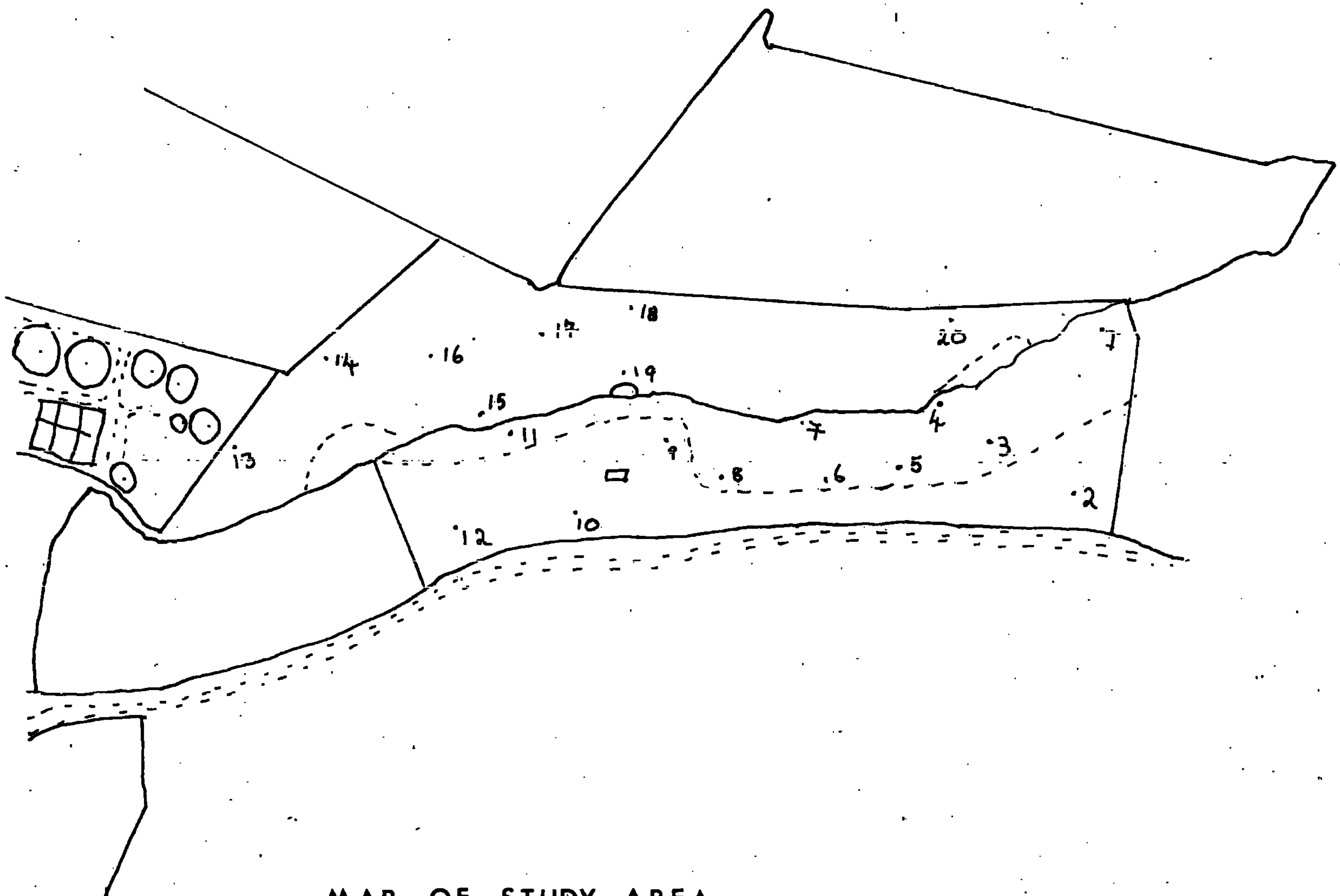
The study area used was the Durham University Zoology Field Station, Grid Reference N.Z. 272408, as shown on the map. The ground of the field station slopes gently to a small stream, the height difference being about 40 feet. The margins of the stream and the general S.E. slope are wooded with birch, beech and oak. The S.W. slope has a more scrub-like vegetational cover of long grass with brambles and hawthorn. The northern sector of the station was once grazed pasture, but grazing ceased five years ago; the main grasses in this area are Agrostis spp., Holcus, and Festuca, which combine to give a rouch, tussocky pasture.

Adjoining the field station is a sewage farm and the adjacent pastures are grazed by sheep and cattle. The woodland to the south of the station is known to contain a good population of small mammals such as Glethrionomus and Apodemus and this area then is likely to provide a reservoir of carrion which will serve as blow fly breeding grounds. The study area is then situated in a position such that one would expect a relatively dense blowfly population.

Twenty trap positions were used, these are shown on the map (Fig.1.) They were chosen so as to cover as wide a range of different types of position as possible in respect of the vegetation and degree of shading.

The basic kinds of trap position could be recognised; shaded by trees, with canopy cover and shelter; exposed sites in the open pastures, and stream bank positions which were also shaded to some extent.

Traps were sited so as to cover adequately all three types of position.



MAP OF STUDY AREA

FIGURE ONE

LABORATORY STUDY.

The aim of this part of the study was to investigate the number of eggs laid by the two species, C. vomitoria, and C. vicina under optimal laboratory conditions, and to obtain some indication as to the correlation between calendar age and physiological age, which is determined by studying the female fly's reproductive history.

Flies for this experiment were reared from stock cultures, eggs were obtained by feeding the stock flies on fresh liver which provided an oviposition site. The eggs then obtained were transferred to fresh liver slices placed on damp sawdust in a crystallizing dish, and incubated at 21 °C. The emerging larvae were able to feed on the liver and pupated after about eight days. The pupae were transferred to a wide-necked conical flask, fitted with sawdust and incubated at 23 °C. Adult images emerged after about ten days, and these were then transferred to box cages and sustained on sugar and water.

The flies obtained were then of known ages. For the purpose of this experiment, one male and one female fly were placed together under a lamp glass and provided with sugar, water and liver. The food was changed daily sc the flies had optimal nutritional supples for oocyte development; Harlow (1954) showed that in Phormia terrae novae although flies could be maintained on sugar and water, protein was essential for dacyte development and oviposition and this seems normally true for the species studied here.

Six pairs of each species, C. vomitoria and C. vicina were set up in this manner; the number of eggs laid on the liver by each fly was recorded each day.

Flies of _G. vicina_ emerged on 8 June, the number of eggs laid by these flies is shown on Table I.

The first eggs were laid on 18 June when the flies were ten days old, the last fly to begin laying was fourteen days old, so there is obviously great variation between individual flies even when kept under identical laboratory conditions. Flies often laid on two consecutive days, these are obviously eggs of the same batch, and so these flies are regarded as having laid just once on such occasions.

The maximal number of times that any fly laid in the twenty-nine days during which the experiment was in progress, was three.

Flies that had laid twice were between sixteen and twenty days old, and those that laid for a third time, twenty-two to twenty-five days old.

There is, then, variation between the calendar age of females which corresponds to their physiological age, and as this experiment only concerned six flies kept under identical conditions, then obviously there is much greater variation in wild flies which are subject to greater fluctuation in conditions.

In one of the flies that laid 3 times, there is variability in the total numbers of eggs laid, ranging from 147 to 250, the individual batches ranged in number from 30 to 156 eggs. Generally speaking, the numbers of eggs laid in this experiment are low; the average number of eggs laid by a female _Calliphora_ is between 100-150 eggs per batch, and a fly may be expected to lay up to five times during its life.

These low results may be caused by the conditions under which the flies were kept; it is known that flies are sensitive to temperature and the temperature in the insectary where these flies were kept tended to rise periodically, and this factor could have adversely affected the laying of eggs.

A similar experiment was set up with pairs of <u>C. vomitoria</u> but these flies never laid eggs. It is thought that they may have been heat sterilized, as originally the stacks were kept in an insectary which became ovdrheated during a sudden warm spell.

These results, then, although sparse, do give some indication as to the calendar age corresponding to the physiological age of female <u>C. vicina</u>. Flies that have laid once will be between ten and fifteen days, those that have laid twice or more will generally be more than sixteen days old, and so these results can be used to tentatively age flies taken in the field trapping experiment.

TABLE I. The number of eggs laid by G. vicina females under laboratory conditions.

Day after emerging:	Fly 1.	Fly 2.	Fly 3.	Fly 4.	Fly 5.	Fly 6.
10	-	-	21	-	-	-
11	-	-	32	-	27	-
12	30	-	-	-	-	-
13	-	-	-	56	-	72
14	-	112	-	-	-	-
15	-	-	Dead	-	156	-
16	56	-		8	-	Dead
17	-	73		4	-	
18	-	-		-	58	
19	-	-		47	9	
20	-	-		32	-	
21	104	40		-	-	
22	22	-		-	-	
TOTAL	212	225	54	147	250	72

OUTLINE OF LIFE HISTORY.

Female Calliphora lay their eggs on carrion or refuse, these eggs are 1.5 mm long, cylindrically oval and white. They hatch after 1 - 2 days, and larval life lasts from 8 - 11 days, depending upon the temperature. The larvae live in carrion and when they are ready to pupate they burrow into the soil. Pupation also lasts for 8 - 11 days and is once again temperature dependent. During the summer months when temperatures tend to vary between 18 and 24 °C, the average duration of the pupal stage is 10 days, but as temperatures fall then conditions are less favourable for pupal development and emergence.

Calliphora vomitoria (Meigen) and Calliphora vicina (Robineau Desvoidy), overwinter as larvae or pupae, not as adults, although observations of adult blow flies have been recorded for almost every month of the year, those adults found in winter are found indoors. It is probable that these flies emerged from pupae that were in a warm microhabitat where conditions were favourable for development and emergence. Isolated warm spells or the onset of warmer weather in the spring both enable the pupae to complete development and so new flies emerge. The development period for C. vomitoria and C. vicina then depends on temperature, during the summer development from egg to image takes 16 - 35 days, but development is slowed by cold weather, and so there is no fly emergence during the winter except for those individuals which were in warmer microhabitats.

The Lucilia (Robineau-Desvoidy) species have a similar life history although on this species the eggs are often laid on living tissues, particularly on sheep, giving the familiar condition of cutaneous miasis. One basic difference, however, is the existence in these species of a prepupal diapause if conditions are unfavourable during the larval or prepupal period. Such unfavourable conditions could be temperature extremes, dessication or overcrowding. The physiological cause of this diapause is the lack of hormone production by the corpus allatum of the larvae (Wigglesworth, 1934) and diapause can only be broken if nervous stimulation activates this gland to produce the requisite hormone. Factors which give the requisite stimulus to break diapause are generally the opposite to those that caused the onset of diapause. Lucilia esp. then, overwinter in a prepupal diapause, then as conditions become more favourable, diapause is terminated, the prepupa is able to pupate and a new fly eventually emerges.

There is, then, an essential difference between the life cycles of Calliphora and Lucilia species, in that diapause occurs only in the latter.

Flies of the Lucilia esp. then tend to appear later in the season than the Calliphora (see later results); Green (1951), reports that Calliphora pupates during the first two weeks of March, but Lucilia does not begin to pupate until the third week of March at the earliest.

The adult life span of both species is 3 - 4 weeks during the height of the season.

METHODS.

Trapping.

The flies were caught using traps of the design first used by Cragg and Ramage (1945). A mosquito netting cylinder about 1' 9" high and 11" in diameter and within this cylinder a cone, the apex of which formed the fly entrance. This net trap was suspended from a metal frame and the bait placed in a petri dish beneath the cone.

The bait used was approximately 35 gms of ox liver that had been left to thaw out for a short time so that it was slightly "off"; fresh liver does not have a smell and was found to be less attractive to the flies.

The traps were put out and baited in the evening before dusk when fly activity was minimal and then collected in the next evening. Trapping was done, on average, once a week. The traps were constructed in such a manner that it was easy to close both ends of the trap and so retain the trapped flies within a muslin bag. The catch could then be conveniently transported to the laboratory.

The flies were killed by placing the trap inside a metal cannister which contained pads of cotton wool soaked in ethyl acetate, this proved to be an efficient killing jar. The dead flies were then sorted into Calliphora; Lucilia species and remaining Diptera, these groups of flies were placed in separate labelled tubes and stored in a deep freeze. This method of storage ensured that there was no deterioration in the condition of the flies, an important factor as the technique used for aging the flies was entirely dependent upon the ovaries being intact.

On days when the catch was high, notably 2nd and 10th June, this basic procedure was varied. The flies were kept alive and emptied into box cages where they were maintained on a diet of sugar and water until such a time as they were required for dissection. This variation in technique was to ensure that the dilations of the tunica of any fly that had laid on its way into the trap had become distinct. In fact, keeping the flies alive was difficult and required too much space; it was therefore discontinued and all flies were killed after capture and placed in a deep freeze.

Dissection.

The main part of this study was concerned with investigating the reproductive history of the female flies as this gave an indication of their physiological age. The technique used was dissection and observation of the ovaries as described by Anderson (1954) and Detinova (1962).

Flies were removed from the deep freeze a few at a time and defrosted. Each fly was examined under the low power of a binocular microscope; identified and sexed. The microscope was used with a glass stage to facilitate rapid changes from direct to reflected light. Such switches were very necessary when examining the ovarioles.

The ovaries of each female were dissected out by making a small longitudinal tear in the abdomen, then placing a dissecting needle on the ovipositor and pulling gently. In this way the reproductive system was removed in one piece and any remnants of fat body or digestive tract could be easily removed.

The female Calliphora has a pair of ovaries joined via two lateral oviducts to a common vagina; these ovaries are composed of a mass of ovarioles in which the oöcytes develop sequentially. In order to see the dacytes clearly, the separate ovarioles were teased out and then the oöcyte stage could be recorded using a six point scale. The scale used was similar to that used by Harlow (1956) with the addition of one stage.

Stage I. Small white ovaries, ovarioles compacted together with no oöcyte development.

Stage II. The dacyte has begun to differentiate.

Stage III. The vitellarium and nurse cells are clearly separated, the oöcyte is elongated and has taken on a whitish, more opaque appearance.

Stage III(b). The process of oöcyte elongation and general growth has continued, the nurse cells are reduced.

Stage IV. The oöcyte now occupies the whole volume of the ovariole, it has reached its maximum size with complete egg shell, but is not yet turgid.

Stage V. The oöcyte has taken up water and is ready to be laid.

In order to examine the oöcytes and determine the number of dilations, the individual ovarioles were stretched slightly. It was easier to distinguish dilations on ovarioles that did not contain a developing oöcyte and so each ovary was 'searched through' until a non-functional ovariole was found. If all the ovarioles contained oöcytes then gravid ~~oöcytes~~ ovarioles had to be examined, the dilations were found nearest the oviduct. Several ovarioles in each ovary were examined; it was important to do this as often an ovariole broke when put under tension. The appearance of ovaries bearing one or two dilations are shown in Figure 2.

FIGURE TWO

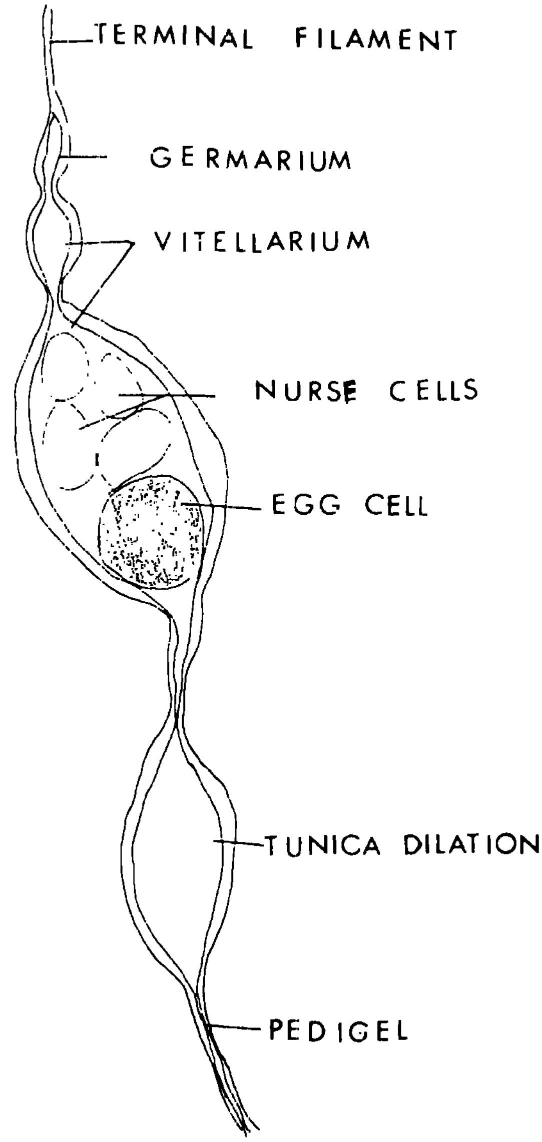


DIAGRAM of

OVARIOLE of FEMALE CALLIPHORA with

ONE TUNICA DILATION

The physiological age of the fly was then taken as the maximum number of dilations found on any ovariole, i.e. the number of egg batches that had been laid.

This technique proved to be perfectly adequate for determining the physiological age of female calliphorids, the only drawback, as found by other workers, was the time taken to complete the dissection, but this was compensated for by the reliability of the results obtained. Nulliparous flies with immature ovaries were, however, easy to recognise and could be dealt with rapidly; these flies had small compact ovaries with a dense supply of close-knit trachae and they were easily distinguishable from any other stage.

The vagina of those flies that had previously laid eggs was also examined for the presence of a retained egg. Flies in this group are known to be ovoviporous, that is they retain an egg within the vagina and here it undergoes embryonic development although it receives no nutrient supply from the mother fly.

In a mature retained egg, the spine-welts and oral hooks of the embryonic larva can be seen; when these eggs are laid they only take minutes or perhaps a few hours to develop and this explains how meat can soon become maggot infested if flies deposit eggs on it that have been retained.

This dissection technique then allowed the general oocyte stage, number of ovariole dilations and the presence or absence of retained eggs to be investigated and so the physiological age of the fly was known. This technique was used to determine the physiological age of G. vomitoria, C. vicina, Cynomya ssp., Sarcophaga spp. and Acrophaga spp.

The Lucilia spp. caught were merely sexed and counted, as there was insufficient time available to dissect them. The other Dipteran species were used as the basis for a separate study.

RESULTS.

Species Composition of the Catch.

The catch totals for each trapping date and the percentage of the total catch represented by each species are given in Table 2 and Figure 3. Individual trap catches for each date are given in Tables 4 - 14. Catches were low at the beginning of the season but as weather conditions improved numbers increased to reach a maximum on 10 June. When trap catches are correlated with the metereological data obtained on each trapping day it is clear that high trap catches correspond with warm, calm weather conditions. (Fig.5.)

Each trap catch can be broken down into its component species, and it is seen that at the start of the season C. vicina predominates. This early domination of C. vicina agrees with the results of Macleod and Donnelly (1957); no other species were caught in any numbers at this time, but it is interesting to note that the two Lucilia specimens caught were both male, as Maclaed and Donnelly reported that the early Lucilia specimens caught were male flies.

As the trap numbers increased from 21 May to 10 June, C. vomitoria is the predominant species, contributing up to 74% of the catch. This predominance of C. vomitoria was never found by Macloed and Donnelly, in fact they reported a C. vomitoria level of on average, 5% of the total catch; however, this difference in the species composition of the catch could be directly attributable to a difference in study areas - Macloed and Donnelly were trapping on a disused aerodrome, essentially an open area, whereas the study area in this instance was partially wooded. It is known that C. vomitoria prefers wooded, sheltered areas, and during this period of C. vomitoria dominance, the traps in which a majority of the flies were caught were located in a wooded area. This area then, probably provides a much better environment for C. vomitoria than the airfield used by Macloed and Donnelly and this could be the reason for the difference in the species composition of the trap catches.

Gynomia and Sarcophaga species also began to appear in the catch at this time, although numbers were generally low and there was no regular pattern of emergence.

After 10 June the C. vomitoria population slumped and the C. vicina numbers increased; there seems to be some sort of reciprocal relationship between the numbers of these two species as one increased, the other decreases (Fig.6.), but this could simply be due to different emergence patterns.

At this time, Acrophaga appeared in the catch, and was taken in increasing numbers as the season progressed. Lucilia species also rose throughout the season, reaching a maximum of 56% of the total catch on 7 July. Macloed and Donnelly (1957) also found that Lucilia had a summer maximum.

The species composition of the catch then changes as the season progresses, the most marked change being the reciprocal relationship between C. vomitoria and C. vicina. If the individual catches for each day are examined, then one finds that in general, C. vomitoria is trapped in the wooded area, C. vicina and Lucilia species in the open areas. (A comprehensive study of the differences between traps in respect of the species caught has been made by A. Frazer.)

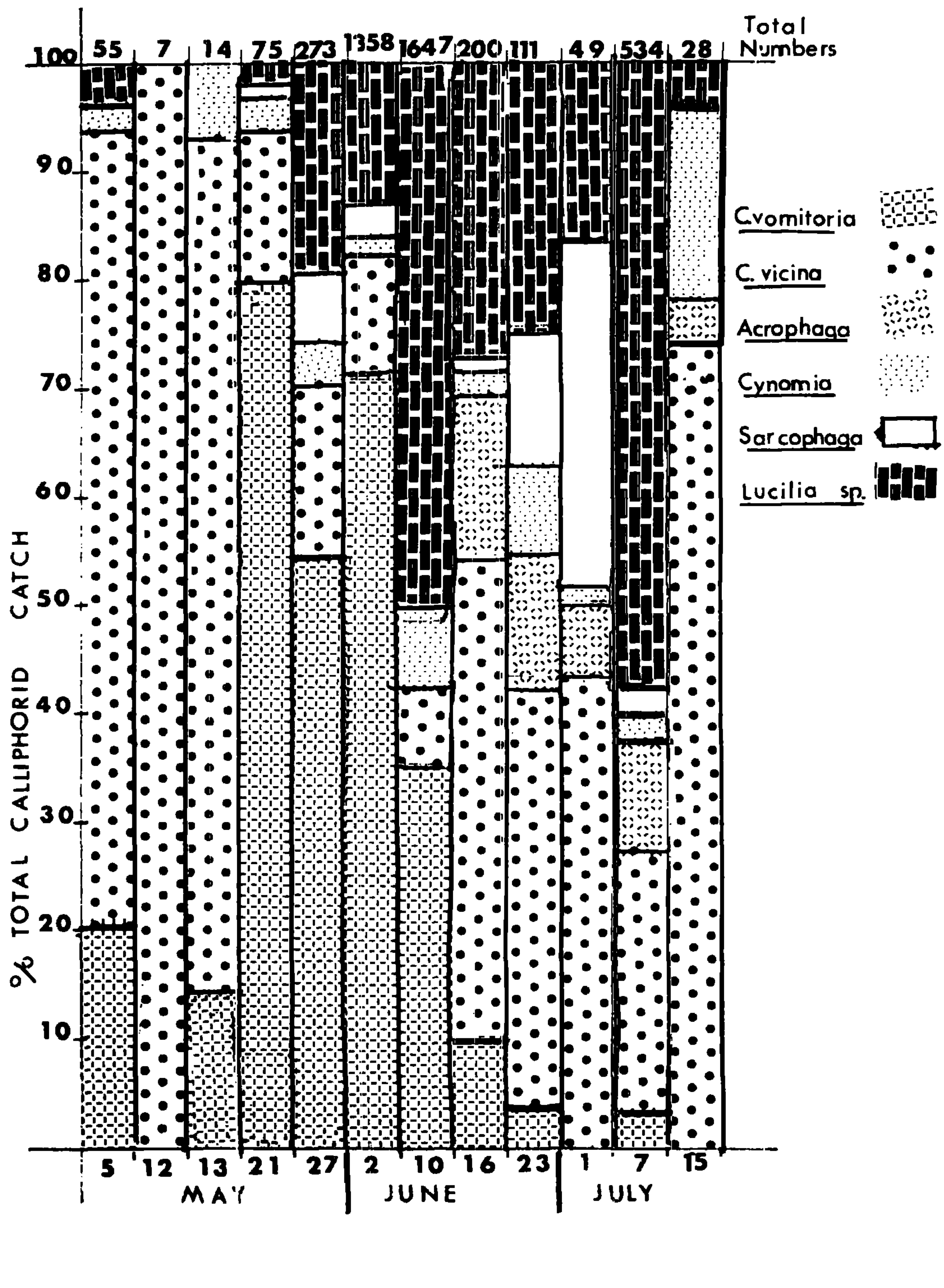
TABLE 2. Species composition of the total *Calliphorid* catches.

Date:	C.vomitoria		C.vicina.		Acrophaga		Cynomia.		Sarcophaga.		Lucilia.	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
5 May	14	25.5	37	67.3	-	-	2	3.6	-	-	2	3.6
12 May	-	-	7	100	-	-	-	-	-	-	-	-
13 May	2	14.4	11	78.6	-	-	1	7.1	-	-	-	-
21 May	60	80.0	11	14.7	-	-	2	2.6	1	1.3	1	1.3
27 May	150	54.9	52	19.0	-	-	1	3.7	18	6.6	52	19.0
2 June	1016	74.8	114	8.3	-	-	6	0.4	52	3.8	170	12.5
10 June	585	35.5	130	7.8	36	2.4	11	7.6	14	0.8	871	50.0
16 June	20	10.0	70	35.0	31	15.5	5	2.5	20	1.0	54	27.0
23 June	6	3.4	44	38.3	14	12.2	10	8.7	15	13.1	28	24.3
1 July	-	-	21	43.8	7	14.5	1	0.2	12	25.6	8	16.4
7 July	18	3.4	128	24.1	52	9.7	15	2.8	18	3.4	303	56.7
15 July	-	-	22	78.5	-	9.6	5	17.9	-	-	1	3.6

Figure 3.

Species composition of the total *Calliphorid* catch.

Each species given as a percentage of the total *Calliphorid* catch.



Total Numbers
55
7
14
75
273
1358
1647
200
111
49
534
28
100
90
80
70
60
50
40
30
20
10
% TOTAL CALLIPHORID CATCH
C.vomitoria
C. vicina
Acrophaga
Cynomia
Sarcophaga
Lucilia sp.
5
12
13
21
27
2
10
16
23
1
7
15
MAY
JUNE
JULY

Figure 4.

Graph showing total trap catches of *Calliphorid* flies for each trapping date.

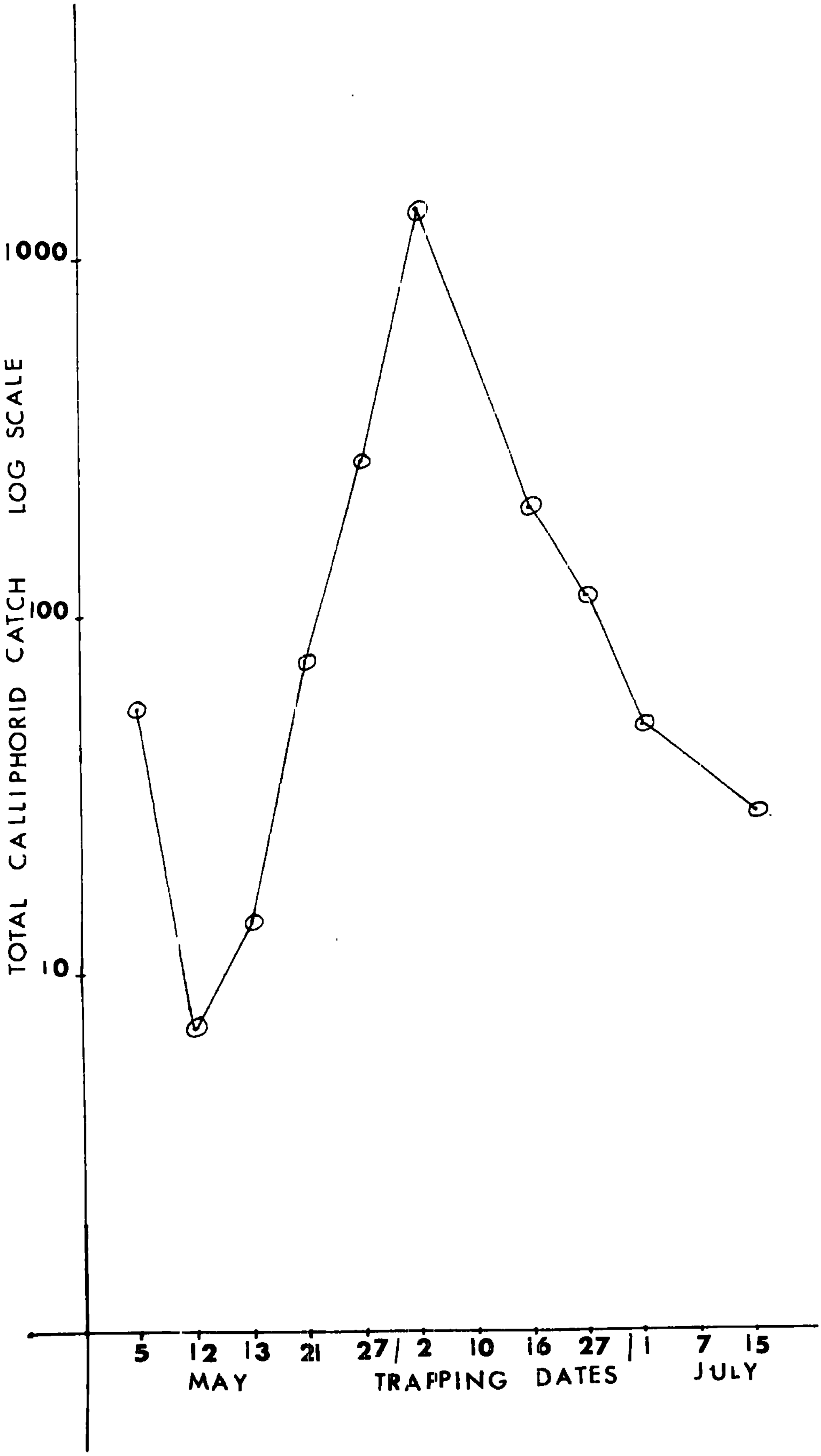

TOTAL CALLIPHORID CATCH LOG SCALE
1000
100
10
5
12
13
21
27
2
10
16
27
1
7
15
MAY
TRAPPING DATES
JULY

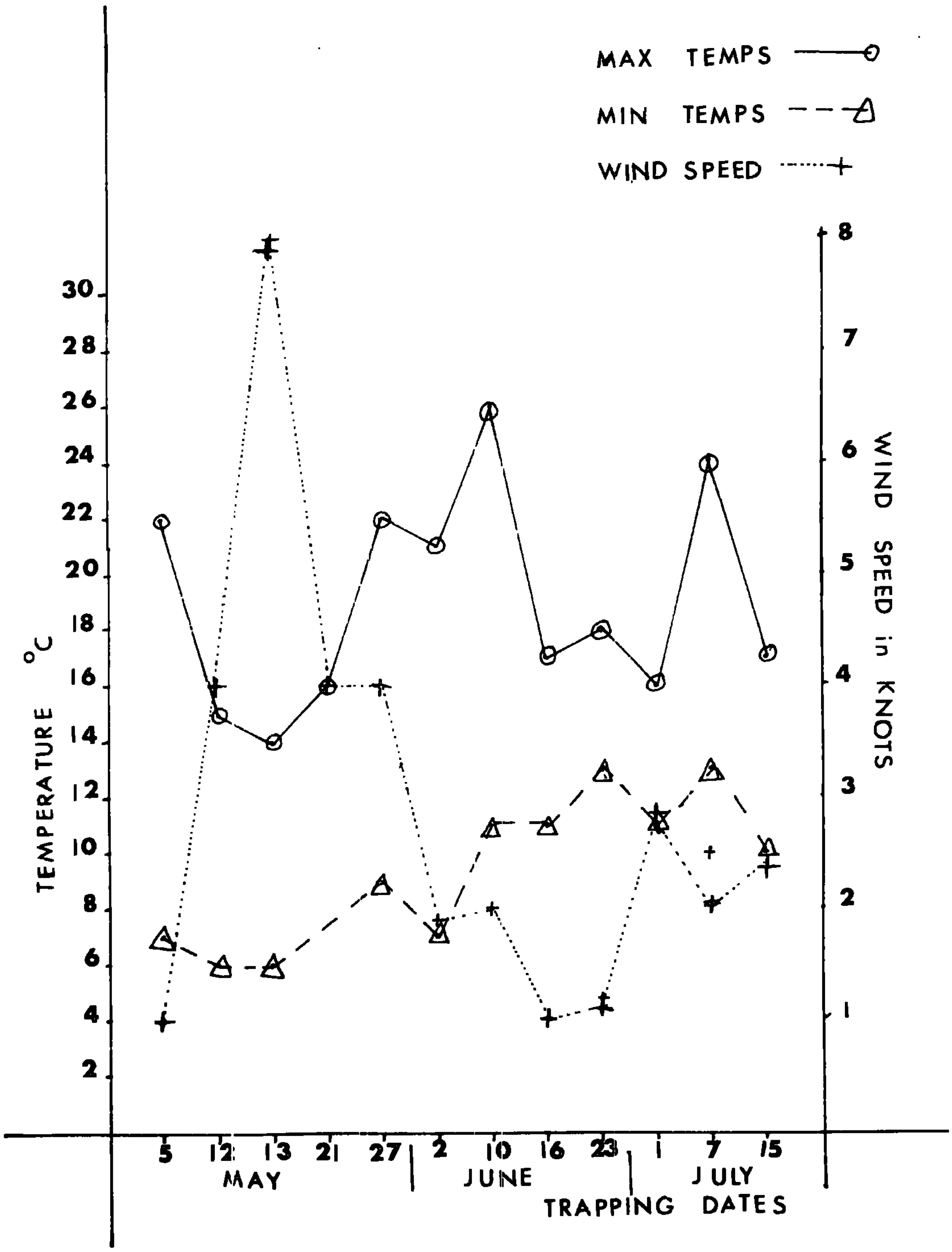
TABLE 3. Metereological Data as recorded by Durham University Observatory.

Date.	Maximum. Temp. °C.	Minimum. Temp. °C.	WIND Speed(Knots)	SUNSHINE Hours	RELATIVE. Humidity. %
5 May	22	7	1.0	9.8	97
12 May	15	5	4.0	10.7	70
13 May	14	5	8.0	8.9	79
21 May	16	4	4.0	12.0	61
27 May	22	9	4.0	12.0	73
2 June	21	7	1.8	7.3	62
10 June	24	11	2.0	13.7	67
16 June	17	11	1.0	8.1	76
23 June	18	13	1.2	4.9	84
1 July	16	11	2.8	6.0	77
7 July	24	13	2.0	9.8	68
15 July	17	10	2.4	3.8	68

Figure 5.

Metereological Data as recorded by Durham University

Observatory for each trapping date.



MAX TEMPS
MIN TEMPS
WIND SPEED
TEMPERATURE °C
WIND SPEED in KNOTS
30
28
26
24
22
20
18
16
14
12
10
8
6
4
2
8
7
6
5
4
3
2
1
5
12
13
21
27
2
10
16
23
1
7
15
MAY
JUNE
JULY
TRAPPING DATES

TABLE 4.

5.5.70 Trap.	C.vomitoria ♀	♂	C.vicina ♀	♂	Acrophago. ♀	♂	Cynomia. ♀	♂	Sarcophaga. ♀	♂	Lucilia. ♀	♂
1	2	-	6	-	-	-	-	-	-	-	-	-
2	1	-	-	-	-	-	-	-	-	-	-	-
3	-	-	1	1	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	1	-	-	-	-	-	-	-	-	-
6	-	-	5	2	-	-	-	-	-	-	-	-
7	-	-	1	2	-	-	1	-	-	-	-	-
8	1	-	3	1	-	-	-	-	-	-	-	-
9	-	-	-	1	-	-	-	-	-	-	-	1
10	-	-	1	-	-	-	-	1	-	-	-	-
11	6	1	5	2	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-
15	2	-	2	1	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	1	-	-	-	-	-	-	-	-	1
18	-	-	-	-	-	-	-	-	-	-	-	-
19	1	-	1	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-
Total	13	1	27	10	-	-	1	1	-	-	-	2
	14		37				2				2	

TABLES 4 - 15.

These tables give the species caught in each individual trap on each trapping day. Where a species column has been omitted, as in Tables 5 & 6, this means that no individuals of that species were caught.

TABLE 5.

12.5.70	*C. vomitoria*		*C. vicina*.	
Trap.	♀	♂	♀	♂
1	-	-	-	-
2	-	-	-	-
3	-	-	-	-
4	-	-	1	-
5	-	-	1	-
6	-	-	-	-
7	-	-	1	-
8	-	-	-	-
9	-	-	1	-
10	-	-	-	-
11	-	-	6	-
12	-	-	-	-
13	-	-	-	-
14	-	-	-	-
15	-	-	-	-
16	-	-	1	-
17	-	-	1	-
18	-	-	1	-
19	-	-	-	-
20	-	-	-	-
Total	-	-	7	-
			7	

TABLE 6.

12.5.70	C. vomitoria		C. vicina.		Cynomia.	
Trap.	♀	♂	♀	♂	♀	♂
1	-	-	-	-	-	-
2	-	-	-	-	-	-
3	-	-	-	-	-	-
4	1	-	1	-	-	-
5	-	-	-	-	-	-
6	-	-	-	-	-	-
7	-	-	1	1	-	-
8	-	-	-	1	-	-
9	-	-	1	1	-	-
10	-	-	-	1	-	-
11	-	-	-	-	-	-
12	-	-	-	-	-	-
13	-	-	-	-	-	-
14	-	-	-	-	-	-
15	-	1	2	-	-	-
16	-	-	-	-	-	-
17	-	-	-	1	-	-
18	-	-	1	-	-	-
19	-	-	-	-	1	-
20	-	-	-	-	-	-
Total	1	1	6	5	1	-
	2		11		1	

Table 7.

21.5.70	C.vomitoria.		C.vicina.		Acrophaga.		Cynomia.		Sarcophaga.		Lucilia.	
Trap.	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂	♀	♂
1	5		-	-	-	-	-	-	-	-	-	-
2	2		-	2	-	-	-	-	-	-	-	-
3			1	-	-	-	-	-	-	-	-	-
4	9	7	1	-	-	-	-	-	1	-	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-
7	19	3	3	-	-	-	-	-	-	-	-	1
8	-	-	-	-	-	-	-	-	-	-	-	-
9	2	-	-	-	-	-	-	-	-	-	-	-
10	2	-	-	-	-	-	-	-	-	-	-	-
11	7	1	2	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	1	-	-	-	-
13	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	1	-	-	-	-	-	1	-	-	-	-	-
18	2	-	2	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-
20	1	-	-	-	-	-	-	-	-	-	-	-
Total	49	11	9	2	-	-	1	1	1	-	-	1
	60		11				2		1		1	

TABLE 8.

27.5.70 Trap	G.vomitoria ♀	♂	G.vicina ♀	♂	Acrophago ♀	♂	Gynomia ♀	♂	Sarcophaga ♀	♂	Lucilia ♀	♂
1	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	1	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	34	12	6	5	-	-	-	-	-	-	8	2
5	-	-	-	-	-	-	-	-	-	1	-	-
6	1	-	[illegible]	-	-	-	-	-	-	-	-	-
7	31	8	1	-	-	-	-	-	4	-	3	6
8	1	-	3	1	-	-	-	-	-	-	-	-
9	-	-	[illegible]	-	-	-	-	-	-	-	-	-
10	15	3	3	5	-	-	-	-	4	-	5	1
11	22	13	4	-	-	-	-	-	4	-	3	5
12	-	1	1	-	-	-	-	-	2	-	3	-
13	1	-	1	-	-	-	-	-	1	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-
15	2	2	-	-	-	-	1	-	-	-	2	2
16	-	-	-	-	-	-	-	-	-	-	-	-
17	1	1	1	1	-	-	-	-	-	-	1	-
18	-	-	-	-	-	-	-	-	-	2	-	-
19	-	-	7	1	-	-	-	-	-	-	-	-
20	1	3	-	-	-	-	-	-	-	-	7	3
Total	109	41	29	13	-	-	1	-	15	3	33	19
	150		52				1		18		52	

TABLE 9.

2.6.70 Trap	C.vomitoria ♀	♂	C.vicina ♀	♂	Acrophaga ♀	♂	Cynomia ♀	♂	Sarcophaga ♀	♂	Lucilia. ♀	♂
1	177	71	6	4	-	-	-	1	-	-	1	1
2	5	1	6	-	-	-	-	-	7	5	-	2
3	3	4	1	3	-	-	-	-	2	-	10	6
4	224	90	4	1	-	-	-	-	-	1	4	2
5	5	1	6	-	-	-	-	-	-	-	4	3
6	22	4	10	3	-	-	-	-	3	2	6	3
7	77	35	5	5	-	-	-	-	-	-	25	10
8	3	-	10	2	-	-	1	1	1	-	6	-
9	7	1	10	5	-	-	-	-	5	4	7	4
10	24	6	4	4	-	-	-	-	-	-	9	7
11	92	31	7	1	-	-	-	-	-	4	5	2
12	2	-	-	-	-	-	1	1	-	3	2	2
13	89	19	-	-	-	-	-	-	-	2	9	6
14	-	-	1	-	-	-	1	-	1	-	1	1
15	6	-	4	2	-	-	-	-	1	2	-	-
16	-	-	-	-	-	-	-	-	-	1	4	2
17	13	-	3	-	-	-	-	-	-	-	2	1
18	1	1	5	-	-	-	-	-	1	1	4	1
19	-	-	-	-	-	-	-	-	3	2	5	4
20	2	-	2	-	-	-	-	-	-	-	9	-
Total	752	264	84	30	-	-	3	3	23	29	113	57
	1016		114				6		52		170	

TABLE 10.

10.6.70 Trap	C. vomitoria ♀	C. vomitoria ♂	C. vicina ♀	C. vicina ♂	Acrophaga ♀	Acrophaga ♂	Gynomia ♀	Gynomia ♂	Sarcophoga ♀	Sarcophoga ♂	Lucilia ♀	Lucilia ♂
1	131	44	32	5	-	-	-	-	3	-	83	20
2	1	-	1	-	1	2	-	-	-	-	2	1
3	-	-	-	-	-	-	-	-	-	1	9	3
4	5	1	1	1	-	-	-	-	-	-	-	-
5	6	2	10	4	2	3	1	1	2	-	27	16
6	4	1	7	1	1	-	1	-	-	-	14	9
7	174	88	22	8	-	-	-	-	-	-	116	81
8	2	-	9	-	-	-	-	-	-	-	23	1
9	1	-	3	1	1	1	-	-	-	-	30	35
10	-	-	2	2	-	-	-	-	-	3	61	22
11	57	15	8	3	4	7	-	-	-	1	17	11
12	-	-	-	-	1	-	-	-	-	-	1	2
13	9	6	5	-	3	-	-	-	-	1	6	2
14	-	-	-	-	-	-	-	-	-	-	15	2
15	-	-	2	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	37	7
17	-	-	2	1	3	2	-	-	-	-	55	17
18	-	-	-	-	-	-	1	1	-	-	11	3
19	-	-	4	-	1	3	1	-	2	1	28	15
20	-	-	3	-	1	-	-	5	-	-	65	20
Total	328	57	111	19	18	18	4	7	7	7	604	267
	585		130		36		11		14		871	

TABLE 11.

16.6.70 Trap	C.vomitoria ♀	♂	C.vicina ♀	♂	Acrophaga ♀	♂	Cynomia ♀	♂	Sarcophaga ♀	♂	Lucilia ♀	♂
1	8	2	8	4	-	-	-	-	-	1	6	1
2	-	-	-	-	2	1	-	-	-	-	1	1
3	1	-	9	3	-	-	-	-	-	-	2	-
4	2	2	6	2	-	1	-	-	-	-	-	-
5	-	1	4	-	1	1	-	-	-	-	2	-
6	-	-	1	3	-	1	1	-	-	-	3	-
7	2	-	4	2	-	1	-	-	-	-	5	2
8	-	-	1	-	1	-	-	-	-	-	1	1
9	-	1	1	1	2	-	-	-	1	4	-	2
10	-	-	-	-	1	2	-	-	-	1	1	1
11	-	1	4	3	1	1	-	-	-	1	-	-
12	-	-	-	-	1	3	-	-	-	-	2	-
13	-	-	-	1	-	-	-	-	-	-	1	-
14	-	-	2	1	-	-	1	-	2	2	1	-
15	-	-	-	-	1	3	-	-	-	-	-	-
16	-	-	-	-	1	1	-	-	1	-	1	-
17	-	-	3	1	1	-	-	-	-	-	3	1
18	-	-	1	-	1	-	2	1	-	1	7	1
19	-	-	2	2	3	-	-	-	2	3	6	-
20	-	-	-	-	-	2	-	-	-	-	2	-
Total	13	7	46	24	16	15	4	1	6	14	44	10
	20		70		31		5		20		54	

TABLE 12.

23.6.70 Trap.	C.vomitoria ♀	C.vomitoria ♂	C.vicina ♀	C.vicina ♂	Acrophaga ♀	Acrophaga ♂	Cynomia ♀	Cynomia ♂	Sarcophaga ♀	Sarcophaga ♂	Lucilia ♀	Lucilia ♂
1	2	-	-	1	1	-	-	-	-	-	2	-
2	-	-	-	-	-	-	-	-	-	1	-	-
3	-	-	3	-	-	-	-	-	-	-	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-
5	-	-	1	-	-	-	-	-	-	-	-	-
6	-	-	9	-	-	1	-	-	-	-	-	-
7	4	-	4	-	3	-	-	-	-	-	3	-
8	-	-	3	-	1	1	-	-	1	1	1	-
9	-	-	2	1	1	2	-	-	2	3	2	-
10	-	-	-	-	-	2	-	-	-	-	-	-
11	-	-	3	1	-	-	-	-	-	-	4	-
12	-	-	-	-	-	-	1	-	-	1	-	-
13	-	-	1	-	-	-	-	-	-	-	-	-
14	-	-	2	-	-	-	-	-	-	2	1	-
15	-	-	-	-	-	-	-	-	-	1	1	-
16	-	-	2	-	1	-	-	5	-	-	2	-
17	-	-	2	-	-	-	-	2	-	-	1	-
18	-	-	1	-	-	-	-	2	-	2	1	-
19	-	-	4	-	2	1	-	-	1	1	6	1
20	-	-	3	1	-	-	-	-	-	1	4	1
Total	6	-	40	4	7	7	1	9	4	11	26	2
	6		44		14		10		15		28	

TABLE 13.

1.7.70 Trap.	G.vomitoria ♀	♂	C.vicina ♀	♂	Acrophago ♀	♂	Cynomia ♀	♂	Sarcophagao ♀	♂	Lucilia ♀	♂
1	-	-	2	-	-	-	-	-	-	-	1	-
2	-	-	3	-	1	-	-	-	2	-	2	-
3	-	-	2	-	1	-	-	-	-	-	-	-
4	-	-	1	-	-	-	-	-	-	-	-	-
5	-	-	1	-	-	-	-	-	-	-	-	-
6	-	-	-	-	-	-	-	-	-	-	-	-
7	-	-	2	-	-	1	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	3	-	-	-	-	-	3	1	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	1	-	1	-	-	-	1	-	-	-
12	-	-	1	-	-	-	-	-	1	1	-	-
13	-	-	-	-	-	-	-	-	-	-	-	1
14	-	-	-	-	-	-	-	-	1	-	2	-
15	-	-	4	1	-	-	-	-	1	-	1	-
16	-	-	-	-	1	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	1	-	-	1	-	-	1	-
19	-	-	-	-	-	-	-	-	-	1	-	-
20	-	-	-	-	1	-	-	-	1	-	-	-
Total	-	-	20	1	6	1	-	1	9	3	7	1
			21		7		1		12		8	

TABLE 14.

7.7.70 Trap.	C.vomitoria ♀	♂	C.vicinia ♀	♂	Acrophaga ♀	♂	Cynomia ♀	♂	Sarcophaga ♀	♂	Lucilia ♀	♂
1	2	-	10	-	1	3	-	-	-	-	13	1
2	-	-	5	1	2	4	-	1	-	-	-	-
3	-	-	15	1	3	2	-	-	-	-	3	-
4	2	-	4	-	-	3	-	-	-	-	3	-
5	-	-	7	-	4	-	-	-	-	-	4	-
6	-	-	11	1	-	-	-	-	-	-	2	-
7	3	-	9	-	-	3	-	-	-	2	15	-
8	-	-	7	-	2	2	-	-	-	1	2	-
9	1	-	1	-	-	-	-	-	1	1	4	-
10	2	-	4	1	-	4	-	-	-	4	17	-
11	8	-	17	1	2	5	-	-	-	-	9	-
12	-	-	2	1	1	1	-	-	-	-	3	-
13	-	-	5	-	2	-	-	-	-	1	47	1
14	-	-	9	-	-	-	2	4	1	-	13	-
15	-	-	-	-	-	-	-	-	1	-	-	-
16	-	-	3	-	-	3	-	4	-	-	33	7
17	-	-	2	1	-	-	-	1	-	-	1	-
18	-	-	4	1	-	1	-	3	-	3	86	1
19	-	-	7	2	-	-	-	-	-	1	16	1
20	-	-	-	-	-	-	-	-	1	1	20	1
Total	18	-	118	10	20	32	2	13	4	14	291	12
	18		128		52		15		18		303	

TABLE 15.

17.7.70 Trap	C. vomitoria ♀	C. vomitoria ♂	C. vicina ♀	C. vicina ♂	Acrophaga ♀	Acrophaga ♂	Cynomia ♀	Cynomia ♂	Sarcophaga ♀	Sarcophaga ♂	Lucilia. ♀	Lucilia. ♂
1	-	-	1	-	-	-	-	-	-	-	-	-
2	-	-	1	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	-	-	1	-	-	-	-	-	-	-	-	-
5	-	-	2	-	-	-	-	-	-	-	1	-
6	-	-	4	-	1	-	-	-	-	-	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-
9	-	-	1	1	-	-	-	-	-	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	-	-	1	-	-	-	-	-	-	-	-	-
14	-	-	1	-	-	-	1	-	-	-	-	-
15	-	-	1	-	-	-	-	-	-	-	-	-
16	-	-	1	-	-	-	1	1	-	-	-	-
17	-	-	1	-	-	-	-	-	-	-	-	-
18	-	-	4	-	-	-	-	-	-	-	-	-
19	-	-	1	-	-	-	-	1	-	-	-	-
20	-	-	1	-	-	-	-	1	-	-	-	-
Total	-	-	21	1	1	-	2	3	-	-	1	-
			22				5					

FIGURE 6.

Percentage of *C. vicina* and *C. vomitoria* in the catch as the percentage *Calliphora* catch.

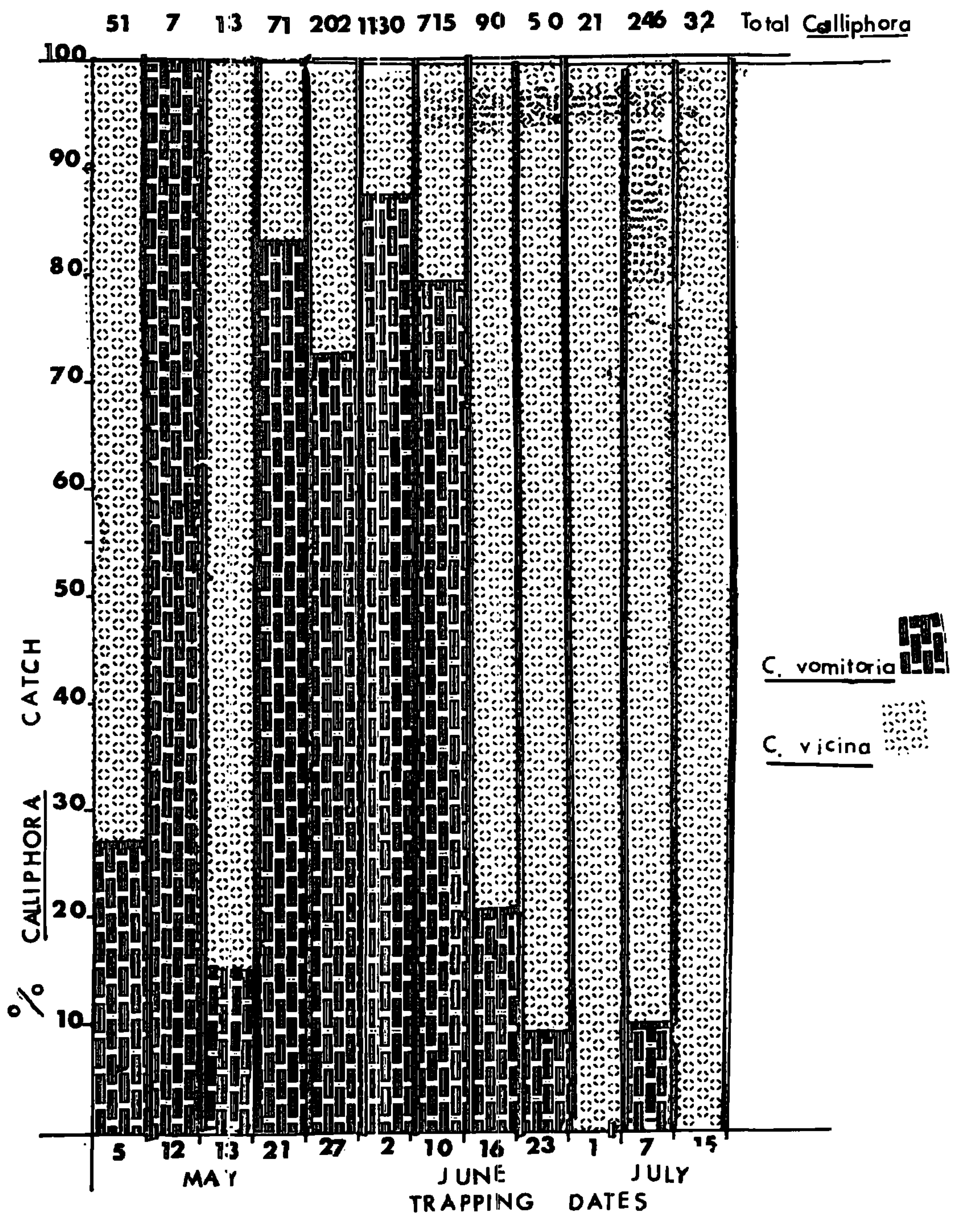

51 7 13 71 202 1130 715 90 50 21 246 32 Total Calliphora
100
90
80
70
60
50
40
30
20
10
% CALLIPHORA CATCH
5 12 13 21 27 2 10 16 23 1 7 15
MAY
JUNE
JULY
TRAPPING DATES
C. vomitoria
C. vicina

TABLE 16. Sex ratio of flies caught on each trapping date, given as the percentage of females caught for each species.

Date:	C. vomitoria			C. vicina			Acrophaga			Cynomia			Sarcophaga			Lucilia.		
	♀	♂	%♀	♀	♂	%♀	♀	♂	%♀	♀	♂	%♀	♀	♂	%♀	♀	♂	%♀
6.5.70	13	1	92.8	27	10	72.9	-	-	-	1	1	50	-	-	-	-	2	0
12.5.70	-	-	-	7	-	100	-	-	-	-	-	-	-	-	-	-	-	-
13.5.70	1	1	50	6	5	54.5	-	--	--	1	-	100	-	-	-	-	-	-
21.5.70	49	11	81.6	9	2	81.8	-	-	-	1	1	50	1	-	100	-	1	0
27.5.70	109	41	72.6	29	13	69	-	-	-	1	-	100	15	3	83.3	33	19	63.4
2.6.70	752	264	71.2	84	30	73.6	-	-	-	3	3	50	23	29	45	113	57	66.7
10.6.70	328	57	85.1	111	19	85.3	18	18	50	4	7	36.3	7	7	50	604	267	69.3
16.6.70	13	7	65	46	24	65.7	16	15	51.6	4	1	80	6	14	30	44	10	81.4
23.6.70	6	-	100	40	4	90.9	7	7	50	1	9	11.1	4	11	26.6	26	2	92.8
1.7.70	-	-	-	20	1	95.2	6	1	85.7	-	1	0	9	3	75	7	1	87.5
7.7.70	18	-	100	118	10	92.1	20	32	38.4	2	13	13.3	4	14	28.5	291	12	96.0
15.7.70	-	-	-	21	1	95.4	1	-	100	2	3	40	-	-	-	1	-	100

Figure 7.

Percentage Female flies caught on each trapping date in

C. vicina

C. vomitoria

Acrophaga

Lucilia

The number of females is expressed as a percentage of the total number of flies of a species caught on that trapping date.

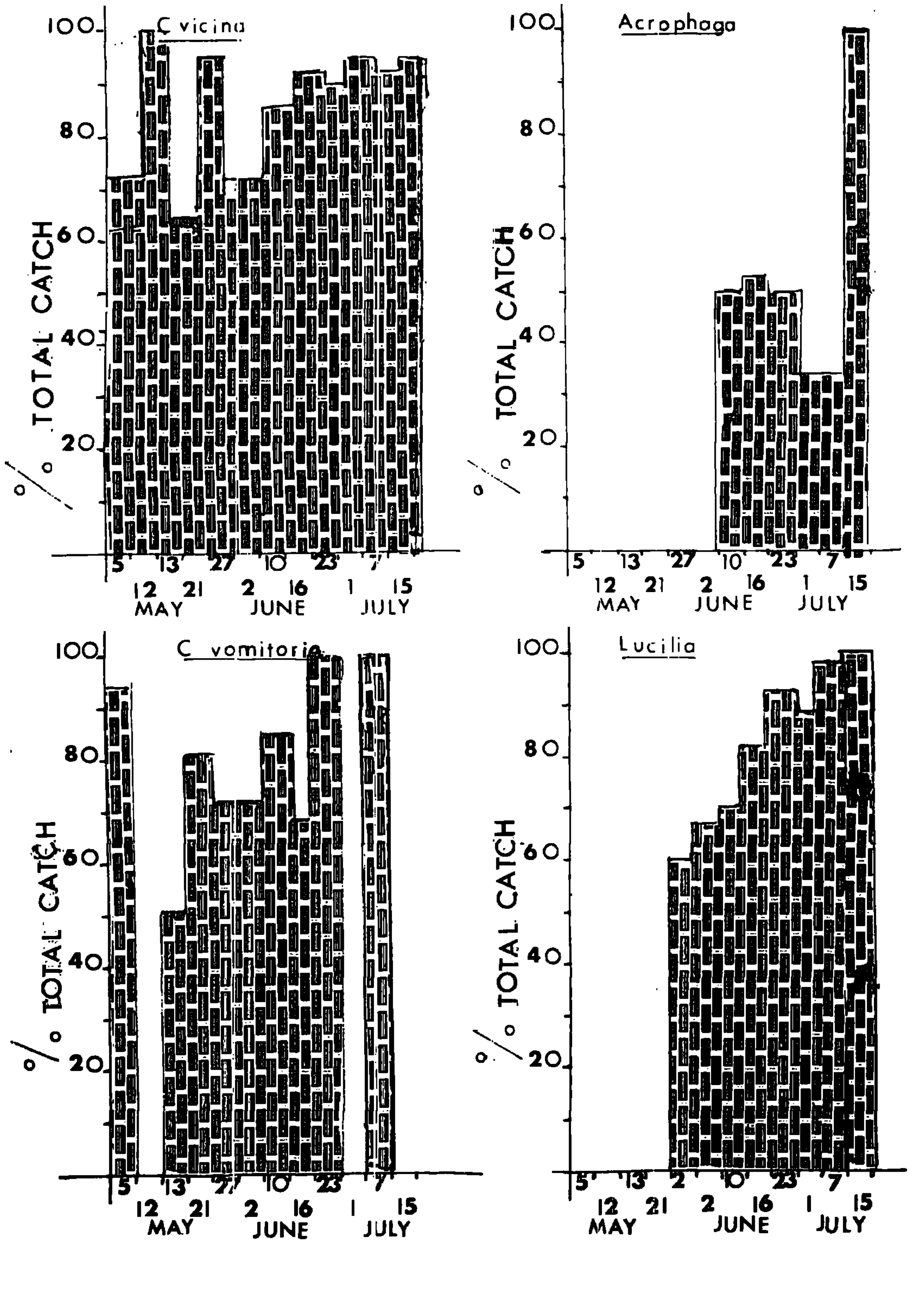

C vicina
Acrophaga
C vomitoria
Lucilia
% TOTAL CATCH
100
80
60
40
20
5
12
13
21
27
2
10
16
23
1
7
15
MAY
JUNE
JULY

TABLE 17. χ^2 test between individual trap catches, using sex ratios.

2.6.70 Trap.	G.vomitoria. ♀	♂	χ^2	p.
1 4	177 224	71 90	0.003	0.95
1 7	177 77	71 35	0.09	0.95
1 10	177 24	71 6	0.24	0.95
1 11	177 92	71 31	0.32	0.95
1 13	177 89	71 19	0.42	0.95
4 7	224 77	90 35	0.06	0.95
4 10	224 24	90 6	0.06	0.95
4 11	224 92	90 31	0.04	0.95
4 13	224 89	90 19	4.57	0.05
7 10	77 24	35 6	0.96	0.95
7 11	77 92	35 31	0.10	0.95
7 13	77 89	35 19	4.82	0.05
10 11	24 92	6 31	0.04	0.95
10 13	24 89	6 19	0.001	0.95
11 13	92 89	31 19	0.16	0.95

10.6.70 Trap.	C. vomitoria. ♀	♂	χ^2	p.
1 7	131 174	44 88	0.0004	0.99
1 11	131 37	44 15	0.045	0.95
1 13	131 9	44 6	0.961	0.95
7 11	174 37	88 15	0.028	0.95
7 13	174 9	88 6	0.00086	0.99
11 13	37 9	15 6	0.076	0.95

Table 16; Figure 7 shows the sex ratios of the total catches; with C. vomitoria and C. vicina one can see that the female flies predominate, although the number of males attracted to the traps does, in fact, increase as the season progresses. The proportion of males caught in each trap is subject to great variation.

In the case of Acrophaga, this female domination is not so well marked, whilst male dominated. The Lucilia species started the season with a male dominated population, but as the season progressed the proportion of females gradually increased.

? meaning
wrong word
preponderance of male
not dominance

Female flies are attracted to the meat-baited traps, either to obtain a protein meal so they could mature their eggs, or to lay their eggs; the males may have been directly attracted to the bait, or by the concentration of female flies, or perhaps they were trapped by chance.

The sex ratios of individual traps were compared for 2nd and 10th June, using a χ^2 test. (These dates were chosen because adequate numbers of flies were taken for a comparison to be made). The results are given on Table 17, and it was seen that there was no significant difference between traps in respect of the sex ratio of trapped flies.

Marked changes, then, occur in the species composition and the sex ratio of those species of Calliphorid flies attracted to meat baited traps during the early part of the season, May - July.

Age Structure of C. vomitoria and C. vicina catches.

The dissection results giving the oocyte stages, the number of retained eggs and ovariole dilations for each trapping date are given on Tables 21-34, in the Appendix.

The reproductive history of each female gives some indication of its physiological age, and as was seen in the laboratory work, this can be correlated to a certain extent with calendar age. A fly that has laid once willthen be roughly between ten and fifteen days old, one that has laid twice may be between twelve and twenty-one days old; great variation was found in the laboratory flies, so one would expect a similar variation, possibly an even greater one, to occur in the field.

The percentages of C. vomitoria and C. vicina which had 0, 1 or 2 plus dilations are given on Table 18 and Figure 8.

In C. vomitoria, the overall picture is one of a young population at the beginning of the season with 85% of the trapped population nulliparous, i.e. they had never laid eggs, and at the end of the trapping period, 47% of the population had laid once, and 12% twice or more, superficially then, the population has aged considerably .

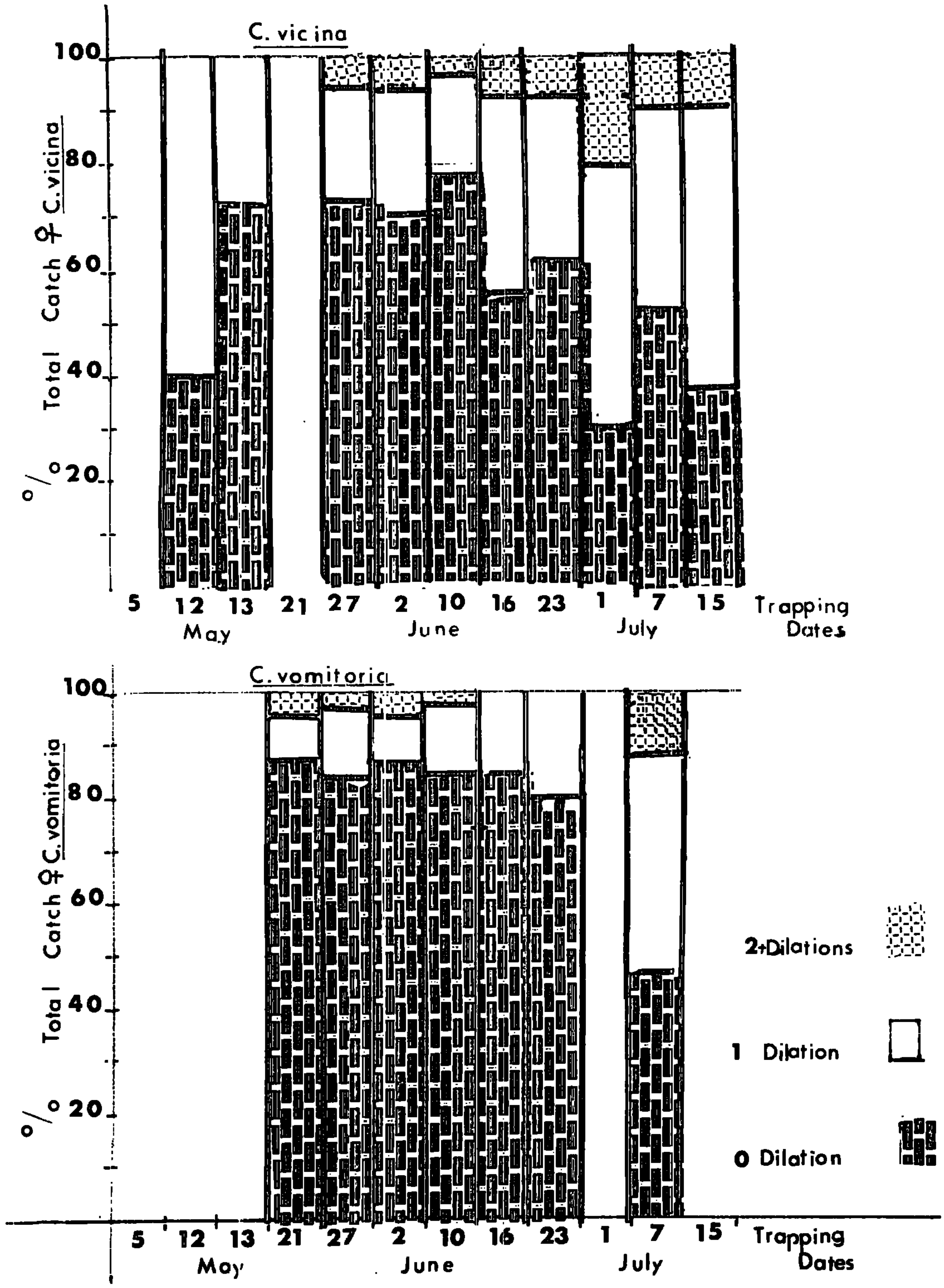
A closer inspection of these results reveals that there was very little change in the population structure between 21 May and 10 June, although total numbers increased markedly. There must, at this time then, have been a great emergence of young flies,

TABLE 18. Number and percentage of dissected female flies with 0, 1 and 2+ ovariole dilations.

DILATIONS	*G. vomitoria*							*G. vicina*						
	0		1		2+		No	0		1		2+		No
Date	No.	%	No.	%	No.	%	Dissected.	No.	%	No.	%	No.	%	Dissected.
5.5.70	-	-	-	-	-	-	-	-	-	-	-	-	-	-
12.5.70	-	-	-	-	-	-	-	2	40	3	60	-	-	5
13.5.70	-	-	-	-	-	-	-	5	71.5	2	28.5	-	-	7
21.5.70	38	88.5	4	9.3	1	2.2	43	-	-	-	-	-	-	-
27.5.70	91	85	15	14	1	1	107	21	72.5	7	24	1	35	29
2.6.70	609	86.5	82	11.5	14	2.0	705	27	71	9	24	2	5.0	38
10.6.70	262	85	42	13.6	4	1.4	308	83	80	19	18.4	2	1.9	104
16.6.70	11	85	2	15.0	-	-	13	22	525	17	40.5	3	7.0	42
23.6.70	4	80	1	20	-	-	5	20	62.5	10	31.2	2	6.3	32
1.7.70	-	-	-	-	-	-	-	6	30	10	50	4	20	20
7.7.70	8	47	7	41	2	12	17	73	57	47	36.4	8	10.6	129
15.7.70	-	-	-	-	-	-	-	8	38	11	52.5	2	9.5	21

Figure 8.

Percentage Dissected female flies with 0, 1 and 2+ dilations for C.vomitoria and C.vicina.


C. vicina
% Total Catch ♀ C. vicina
100
80
60
40
20
5
12
13
21
27
2
10
16
23
1
7
15
May
June
July
Trapping Dates
C. vomitoria
% Total Catch ♀ C. vomitoria
100
80
60
40
20
5
12
13
21
27
2
10
16
23
1
7
15
May
June
July
Trapping Dates
2+Dilations
1 Dilation
0 Dilation

especially around 2 June, as numbers increased seven-fold between 23 May and 2 June. If such an emergence had not taken place then the numbers of trapped flies would not have risen and, more importantly, the population would have gradually aged - it is this continuous influx of new flies that keeps the population young.

The weather during this period was warm, maximum temperatures rising to 26 °C and so conditions were favourable for the rapid development of larvae and pupae to adults and consequently new flies were emerging in vast numbers.

From 10 to 16 June, the proportion of parous flies increased to 20% of the total catch, this ageing of the population could be due to several factors. A differential rate of mortality in the young flies would give such an ageing pattern, but it is unlikely as there is no explanation as to why young flies should die at a faster rate than old ones, and one would expect the converse situation. A decrease in the number of flies actually emerging would, however, give this apparent ageing of the population; weather conditions had deteriorated somewhat during this period, the maximum temperature attained was 21 °C, this could then affect the rates of larval and pupal development, giving a decline in the number of flies emerging. Total catch numbers fell dramatically during this period from 705 flies on 2 July to only 13 flies on 16 July; what then was the reason for this fall? Mass mortality is unlikely, a more reasonable explanation may be found by considering the habits of <u>C. vomitoria</u>. This species is known to prefer wooded areas (Macleod and Donnelly, 1958), which provide shade, and although the field station is partially wooded the trees are somewhat scattered and so the canopy cover is somewhat intermittent. The nearby woodland, however, provides much greater cover and shade and it is possible that many of the flies have migrated into these woods; this migration could have started between 2 and 10 June, the temperature on 10 June was the highest recorded during the trapping period, but already the numbers of C. vomitoria were beginning to drop. The newly emerged flies could then be 'hiding' in the wooded area and so not influenced by the traps.

The catch on 1 July was zero, but weather conditions were unfavourable for blow fly activity, and although conditions had improved by 7 July the catch was still relatively low; 17 flies. This catch had aged considerably, over 50% of the flies caught were parous, it is then possible that the old flies were more active at this time, and therefore came under the influence of the traps, while most of the young flies had migrated from this population.

To return to C. vicina, catches were at first very low and so little can be interpreted from them. However, as the weather conditions improved, numbers increased and the population on 27 May was found to consist of both nulliparous and parous flies. The population remained almost the same on 2 June, indicating that new flies must have emerged and then on 10 June when temperatures reached maximum, there was an increase both in the actual numbers of C.vicina caught and in the percentage of young flies within the population. This, then, indicated a sudden emergence of young flies into the population.

After this date the population was seen to age, flies that had laid once reached a maximum of 50% of the population, and those that had laid twice 20%, on 1 July, when the population had the lowest percentage of young flies recorded during the trapping period. It would seem, then, that between 16 June and 1 July, there was a decreased rate of emergence of young flies, total catch numbers had also begun to fall as this ageing of the population was possibly due to a decrease on the numbers of flies emerging. C. vicina is a fly of open spaces, so the migration of young flies to an alternative area is not a good explanation for this decline in the number of young flies. Around 7 July, however, weather conditions had improved, the maximum temperature was 21 °C and the catch numbers again increased, once more there appeared to have been an influx of young flies into the population.

These results can be contrasted with those obtained by Ovazzo et al (1965), (cit. Muirhead, Thomson, 1968) in their study on black-fly populations. They found a similar ageing of the female population as the season progressed, but there was one important difference. They found that as total catch numbers fell the population became younger, i.e. there was a decrease in the percentage of parous flies in the population. In the case of C. vicina, however, as numbers decreased, the physiological age of the population increased, i.e. the parous flies formed a greater percentage of the population than the nulliparous flies. In C. vicina this was explained by the fact that young flies were not emerging on a sufficient scale and entering the population. This decrease was due to a worsening of the weather conditions, for as soon as temperatures rose again the catch total increased, andsso did the percentage of nulliparous flies. In contrast, the fall on the population numbers of black-fly was due to increased mortality or decreased life expectancy of the young flies, so that they never reached the parous state.

It would be interesting to continue this study, trapping the blow flies until the end of the season to determine the age composition of the declining population. One would theoretically expect it to become older and older as fewer and fewer new flies emerged until such time as the adult flies disappeared completely.

A comparison can be made between the populations of C. vicina and C. vomitoria in order to see if there were any differences between the two species in respect of their age composition.

C. vicina was the first species to emerge, and although total catches were small, both nulliparous and parous flies were found within the population. By 21 May, C. vomitoria had appeared in the population, and by 27 May, both species were caught in sufficient numbers for a comparison to be made. A χ^2 test was done to compare the age structure of the two species populations on this date, a χ^2 value of 4.12 was obtained, showing that there was a significant difference between the two species at the 5% level in the proportion of parous flies in each population. The C. vicina population was significantly older than C. vomitoria, but one might expect this, as it was the first species to appear in the field. This situation remains unchanged, on 2 June, C. vicina is still significantly older, (χ^2 = 5.68), although the catch number of C. vomitoria is 7 larger than the C. vicina catch. The number of C. vomitoria flies emerging was presumably then vastly in excess of the numbers of C. vicina emerging. On 10 June, however, as has already been discussed, the number of nulliparous C. vomitoria decreased, whilst conditions seem favourable for the emergence of C. vicina, and on this occasion there was no significant difference in the age composition of the two species populations (χ^2 = 0.04). In fact, after this date, the

the age composition of these two species populations was never significantly different, and this would suggest that new flies of both species were entering the population proportionally at the same rate. This is not to say that they were emerging in equal numbers, as this was obviously not so, but rather the relative proportions of young flies are the same in both species.

The dramatic drop in the number of C. vomitoria caught at the end of the trapping period makes it difficult to compare the populations meaningfully, the reasons for this drop in C. vomitoria numbers has already been discussed.

The only other species obtained in sufficient numbers to analyse for age changes was Acrophaga (Table 19), even so, this species never contributed more than 15% of the total catch. The age composition of this species changed only very slightly, but as it did not enter into the catch until late in the season, data is only available for four trapping dates. Flies that had laid more than once were never found and the proportion of flies that had laid once varied from 10 to 40% of the catch. Obviously, no conclusions as to age trends within the population can be drawn from this data.

Generally, then, at the beginning of the season the numbers of both Calliphora species were low, and the females were mostly nulliparous. As the season progressed, parous flies entered the population, which consequently aged. This ageing of the population was not a continuous process as young flies were constantly entering the population.

TABLE 19. Dissection data for Acrophaga.

			OOCYTE STAGE						OVARIOLE DILATIONS.		
Date:	♀	♂	I	II	IIIa	IIIb	IV	V	0	1	2+
16.6.70	16	15	8	1	4	-	1	2	14	2	-
23.6.70	9	6	4	3		1	1		8	1	
1.7.70	5	1	3	2					3	2	
7.7.70	16	28	6	1	2		4	3	11	5	

These results, then, support the general hypothesis that the blow-fly overwinters as larvae or pupae, as the first flies caught were predominantly nulliparous. If this species overwintered as adults, one would expect old parous flies that had laid several times to be caught early in the season. It was at no time possible to separate distinct generations, nulliparous flies always formed the largest single age group, as flies breed continuously, as long as conditions are favourable. A large emergence of flies during any one period indicated that there had been favourable conditions for the development of the larval stages and for pupal emergence. Similar conclusions were drawn by Gibbons (1968) in his studies on the age composition of field populations of the dung fly, Scopeuma. He, too, found that the population had a stable age structure at the height of the season, whilst as numbers began to decline, he found that the population aged. These results were then directly comparable with those obtained in this study.

TABLE 20A. χ^2 test comparing numbers of Nulliparous and Parous flies caught in different traps.

Date.	Trap.	Nulliparous.	Parous	χ^2	p.
2.6.70	1	149	28	0.08	0.75
	4	184	40		
2.6.70	1	149	28	1.15	<0.05
	7	70	7		
2.6.70	1	149	28	0.39	0.95
	11	86	6		
2.6.70	4	184	40	0.019	0.75
	7	70	7		
2.6.70	4	184	40	0.36	0.95
	11	86	6		
2.6.70	7	70	7	0.118	0.95
	11	86	6		
10.6.70	1	79	22	0.003	0.95
	7	113	35		
10.6.70	1	79	22	0.0002	0.99
	11	29	7		
10.6.70	7	113	35	0.092	0.95
	11	29	7		

Individual trap catches were compared for 2 and 10 June, to see if there was any difference in the age composition of the flies caught in different traps. A χ^2 test was used (Table 20A), and no significant difference was found between the trap catches, all the traps compared caught the same proportions of young and old flies.

Stage of oocyte development in the age-studied *Calliphora* populations.

The oocyte stage of each dissected *Calliphora* female was also recorded and these results were analysed to see if there were any changes in the stage of development of the ovaries of the population that could be correlated with changes in the age structure. Tables 35-40 in the Appendix give the oocyte stages corresponding with each number of ovariole dilations. In fact, no clear changes in the general oocyte stage a pattern could be seen and all stages were found on each trapping occasion. This is to be expected, as blow flies lay continuously as long as there is protein nutrient available for the maturation of eggs and conditions are generally favourable. Flies with ovaries in every stage of development then occur within the population. When the oocyte stages are compared in nulliparous and parous flies, there is a predominance of nulliparous flies with Stage I immature ovaries in both *C. vomitoria* and *C. vicina*. In flies that had laid once, the predominant oocyte stages were IIIb and IV, whilst Stage IV oocytes were found most frequently in flies that had laid twice or more.

English !

From this it would seem that the more times a fly has laid then the quicker its oocytes mature again; alternatively the more times a fly has laid then the later in the cycle does it require protein for final maturationof the oocytes prior to oviposition.

Although it has been shown that protein is essential for maturation of the eggs past stage III (Harlow, 1956), no work has been done on the differences, if any, in the development of oocytes in relation to feeding in parous flies.

Occurrence of Retained Eggs.

Each parous fly was also examined for the presence of a retained egg within the vagina. Table 20B shows the percentage of parous flies with retained eggs found on each trapping date.

In the case of C. vomitoria it was a relatively rare occurrence, only 7.8% of the flies that had laid once had a retained egg. In C. vicina, however, it was a commoner occurrence than in C. vomitoria, since 26% of the total number of flies that had laid once also had a retained egg. The occurrence of retained eggs in C. vicina fluctuated somewhat, but did seem to rise as the season progressed and at the end of the trapping period, 64% of those flies that had laid once had a retained egg; this percentage is, however, only 7 flies as the catch on that date was low.

The phenomenon of ovarparity then seems to be more common in C. vicina than in C. vomitoria. This difference is statistically significant, when the number of flies with one dilation, with and without retained eggs in the two species, a χ^2 value of 11.2($p=0.001$).

This ovoviparity is an advantageous adaptation as although the egg receives no direct nourishment from the mother, it is nevertheless protected from predators and the effects of dessication. The latter factor is obviously most important during the summer when the surface of the available carrion is likely to dry out and thus the egg will perish. The retained egg, however, is able to undergo embryogenesis within the shelter of the vagina. Here the egg develops almost

Figure 9

Oocyte stages for C. vomitoria and C. vicina with 0, 1 and 2 + dilations given as % dissected ♀

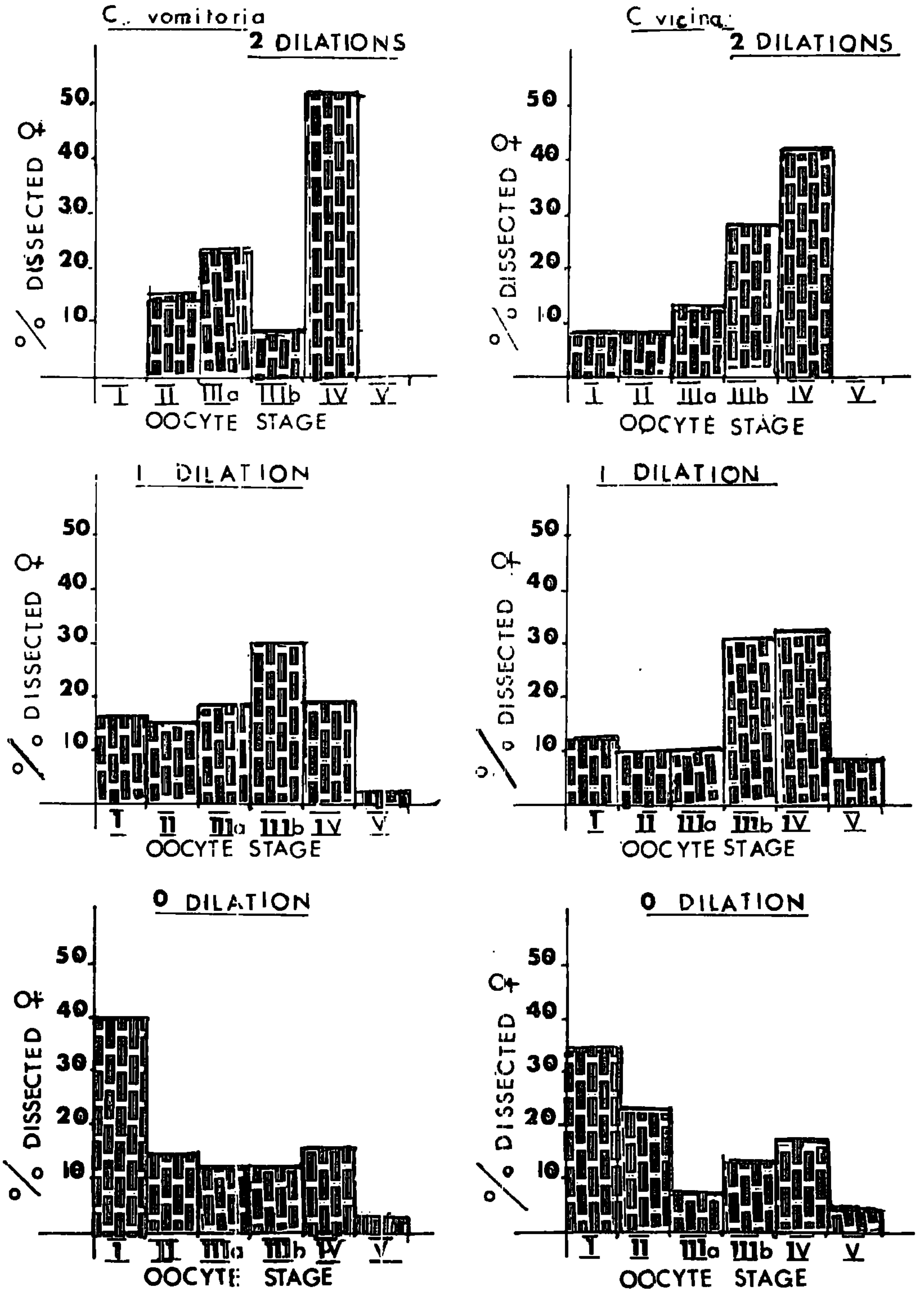

C. vomitoria
C. vicina
2 DILATIONS
1 DILATION
0 DILATION
% DISSECTED ♀
10
20
30
40
50
I
II
IIIa
IIIb
IV
V
OOCYTE STAGE

TABLE 20B. Occurrence of Retained Eggs in parous flies.

C. vomitoria.

Date.	No.with 1 Dilation.	No.with retained eggs.	% with retained eggs.
12.5.70	-	-	-
13.5.70	-	-	-
21.5.70	4	0	0
27.5.70	15	1	6.5
2.6.70	82	6	7.3
10.6.70	42	4	9.5
16.6.70	2	0	0
23.6.70	1	0	0
1.7.70	-	-	-
7.7.70	7	1	14
15.7.70	-	-	-
Total	153	12	7.8

C. vicina.

Date.	No.with 1 Dilation.	No.with retained eggs.	% with retained eggs.	No.with 2 Dilations.	No.with retained eggs.
12.5.70	3	0	0	0	0
13.5.70	2	0	0	0	0
21.5.70	-	-	-	-	-
27.5.70	7	2	28	1	1
2.6.70	9	5	55	2	2
10.6.70	19	3	15	2	1
16.6.70	17	2	11	3	0
23.6.70	10	2	20	2	1
1.7.70	10	3	30	4	2
7.7.70	47	11	23	8	1
15.7.70	11	7	64	2	0
Total	135	35	26	24	8

APPENDIX.

Tables 21-27.

These give the dissection data for G. vomitoria for each trapping date. Generally, only the larger trap catches were kept separate so that the reproductive history of the flies caught in specific traps was known. However, in each case the total figures refer to all the flies that were dissected from the twenty trap catches, this is not necessarily the sum of the individual trap catches as shown on the table, it will also include the flies from the 'pooled' trap catches which cannot be distinguished from each other.

Tables 28-34.

These give the dissection data for G. vicina, the total results only are given for 12 May to 2 June on Table 28; Tables 29-34 give the individual trap catch results from 10 June to 15 July.

Tables 35-40.

These give the oocyte stages corresponding to 0, 1 and 2+ dilations found in the dissected females of G. vicina and G. vomitoria.

TABLE 21.

21.5.70	*C. vomitoria.* ♀	♂	(OOCYTE STAGE) I	II	IIIA	IIIB	IV	V	(OVARIOLE DILATIONS) 0	1	2	RETAINED EGGS.
1	5	-										
2	2	-										
3	-	-										
4	9	7										
5	-	-										
6	-	-										
7	19	3										
8	-	-										
9	2	-										
10	2	-										
11	7	-										
12	-	-										
13	-	-										
14	-	-										
15	-	-										
16	-	-										
17	1	-										
18	2	-										
19	-	-										
20	1	-										
Total	49	11	18	10	9	5	1	0	38	4	1	1

TABLE 22.

27.5.70 Trap.	*G. vomitoria.* ♀	♂	I	Oocyte Stage. II	IIIa	IIIb	IV	V	0	1	2	Retained Eggs.
1	-	-	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	34	12	46	2	7	2	6	1	30	4	-	-
5	-	-	-	-	-	-	-	-	-	-	-	-
6	1	-	-	-	-	-	-	-	-	-	-	-
7	31	8	13	1	5	7	4	-	28	2	1	-
8	1	P	-	-	-	-	-	-	-	-	-	-
9	-	-	-	-	-	-	-	-	-	-	-	-
10	15	3	-	-	-	-	-	-	-	-	-	-
11	22	13	6	1	4	5	6	-	16	6	-	-
12	-	1	-	-	-	-	-	-	-	-	-	-
13	1	-	-	-	-	-	-	-	-	-	-	-
14	0	-	-	-	-	-	-	-	-	-	-	-
15	2	2	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	1	1	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-
20	7	1	-	-	-	-	-	-	-	-	-	-
Totals	109	41	47	16	17	20	6	1	91	15	1	1

TABLE 23.

2.6.70 Trap:	*C. vomitoria.* ♀	♂	Oocyte Stage. I	II	IIIa	IIIb	IV	V	Ovariole Dilations. 0	1	2	Retained Eggs.
1	177	71	51	8	24	32	43	3	149	26	2	2
2	5	1										
3	3	4										
4	224	90	62	20	34	31	39	4	184	31	9	1
5	5	1	1	9								
6	22	4										
7	77	35	23	8	11	16	17		70	5	2	
8	3	-										
9	7	1										
10	24	6	13	4	-	4	3	-	20	4	0	1
11	92	31	18	9	15	22	26	3	86	6	0	2
12	2	-										
13	89	19	22	10	5	22	20	5	79	10	0	-
14	-	-										
15	6	-										
16	-	-										
17	13	-										
18	1	1										
19	-	-										
20	2	-										
Total.	752	264	206	66	112	141	164	16	652	82	14	6

TABLE 24.

10.6.70. C. vomitoria. Trap.	♀	♂	Oocyte Stage. I	II	IIIa	IIIb	IV	V	Ovariole Dilations. 0	1	2	Retained Eggs.
1	131	44	51	28	8	4	9	1	87	15	1	-
2	1	-	-	-	-	1	-	-	1	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	2	1	-	1	-	1	-	-	2	-	-	-
5	5	2	1	1	1	1	1	-	3	1	1	1
6	4	1	2	2	-	-	-	-	4	-	-	-
7	174	88	82	31	11	11	13	-	128	19	1	-
8	2	-	-	-	2	-	-	-	2	-	-	-
9	1	-	-	1	-	-	-	-	1	-	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-
11	37	15	17	12	5	-	2	-	32	4	1	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	9	6	8	-	-	-	-	-	5	3	-	1
14	-	-	-	-	-	-	-	-	-	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-
Total	366	157	161	76	27	18	25	1	262	42	4	2

TABLE 25.

16.6.70	*C. vomitoria.*		Oocyte Stage.						Ovariole Dilations			Retained Eggs.
Trap.	♀	♂	I	II	IIIa	IIIb	IV	V	0	1	2	
1	8	2	6	2					5	1	0	
2	-	-								0	0	
3	1	-			1				0	1	0	
4	2	2	1	1					2	0	0	
5	-	1										
6	-	-										
7	2	-	1	1					2			
8	-	-										
9	-	1										
10	-	-										
11	-	1										
12	-	-										
13	-	-										
14	-	-										
15	-	-										
16	-	-										
17	-	-										
18	-	-										
19	-	-										
20	-	-										
Total	13	7	8	4	1				11	2	0	0

TABLE 26.

23.6.70

Trap.	C.vomitoria ♀	♂	Oocyte Stage. I	II	IIIa	IIIb	IV	V	Ovariole Dilations. 0	1	2	Retained. Eggs.
1	2		2									
2												
3												
4												
5												
6												
7	3	-	1	2					2	1	-	
8												
9												
10												
11												
12												
13												
14												
15												
16												
17												
18												
19												
20												
Totals	5	-	3	2					4	1		-

TABLE 27.

7.7.70

Trap.	*C. vomitoria* ♀	*C. vomitoria* ♂	Oocyte Stage I	II	IIIa	IIIb	IV	V	Ovariole Dilations 0	1	2	Retained Eggs.
1	2	-		1		1			2			
2	-	-							-			
3	-	-							-			
4	2	-	2						2	-		
5	-	-							-			
6	-	-							-			
7	2	-		1			1		0	2		
8	-	-							-	-		
9	1	-		1								
10	2	-	1	1					0	2		1
11	8	-	3	2		1	1	1	4	3	1	
12	-	-										
13	-	-										
14	-	-										
15	-	-										
16	-	-										
17	-	-										
18	-	-										
19	-	-										
20	-	-										
Total	17	-	6	6	-	3	3	1	8	7	2	1

TABLE 28.

Dissection Data for total *C. vicina* females, 12.5.70 - 2.6.70.

Date	Numbers. ♀	♂	OOCYTE STAGE. I	II	IIIa	IIIb	IV	V	OVARIOLE DIL. 0	1	2+	Retained Eggs.
12.5.70	7	-	-	-	-	2	3	-	2	3	-	
13.5.70	6	4	3	-	-	1	1		3	2		
21.5.70	9	2										
27.5.70	29	13	6	6	8	5	4	-	21	7	1	
2.6.70	84	30	6	6	2	8	13	3	29	7	2	

TABLE 29.

10.6.70 Trap.	C. vicina ♀	C. vicina ♂	Oocyte Stage. I	II	IIIa	IIIb	IV	V	Ovariole Dilations. 0	1	2	Retained Eggs.
1	36	5	12	10	8	2	4	-	24	10	1	2
2	1	-	-	-	1	-	-	-	-	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	-	1	-	-	-	-	-	-	-	-	-	-
5	10	4	3	5	-	-	2	-	10	-	-	-
6	7	1	-	-	-	-	-	-	-	-	-	-
7	22	8	7	4	2	4	4	-	21	-	-	-
8	9	-	5	3		1	-	-	-	2	-	-
9	3	1	-	1	1	1	-	-	1	1	1	-
10	2	2	-	2	-	-	-	-	-	-	-	-
11	8	3	1	3	1	1	2	-	5	3	-	1
12	-	-	-	-	-	-	-	-	-	-	-	-
13	5	-	1	1	1	1	-	-	-	2	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-
15	2	-	-	1	-	1	-	-	-	1	-	-
16	-	1	-	-	-	-	-	-	-	-	-	-
17	1	2	-	-	-	1	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-
19	4	-	2	-	-	-	2	-	-	-	-	-
20	3	-	1	2	-	-	-	-	-	-	-	-
Totals:	114	28	32	32	14	12	14	0	83	19	2	3

TABLE 30.

16.6.70 Trap.	*C. vicina* ♀	*C. vicina* ♂	Oocyte Stage. I	II	IIIA	IIIB	IV	V.	Ovariole Dilations. 0	1	2	Retained Eggs.
1	8	4	2	3	-	-	-	1	2	4	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-
3	9	3	1	2	1	2	3	-	6	3	-	2
4	6	2	4	2	-	-	-	-	6	-	-	-
5	4	-	2	2	-	-	-	-	0	0	1	-
6	1	3	1	-	-	-	-	-	-	-	-	-
7	4	2	3	-	-	-	1	-	5	1	-	-
8	1	-	-	-	-	1	-	-	-	1	-	-
9	1	1	-	-	-	1	-	-	-	1	-	-
10	-	-	-	-	-	-	-	-	-	-	-	-
11	4	3	1	-	1	1	1	-	1	3	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	-	1	-	-	-	-	-	-	-	-	-	-
14	2	1	-	-	-	1	1	-	-	2	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	1	3	-	-	-	-	1	-	1	1	1	-
18	1	-	1	-	-	-	-	-	-	-	-	-
19	2	2	1	-	-	-	1	-	1	1	1	-
20	-	-	-	-	-	-	-	-	-	-	-	-
Totals	44	24	16	9	2	6	8	1	22	17	3	2

TABLE 31.

23.6.70 Trap.	C.vicina ♀	♂	Oocyte Stage. I	II	IIIa	IIIb	IV	V	Ovariole Dilations. 0	1	2	Retained Eggs.
1	0	1	-	-	-	-	-	-	-	-	-	-
2	-	-	-	-	-	-	-	-	-	-	-	-
3	3	-	-	-	1	1	1	-	2	1	-	-
4	-	-	-	-	-	-	-	-	-	-	-	-
5	7	-	-	1	-	-	-	-	0	1	-	-
6	2	-	-	-	-	-	1	1	2	-	-	-
7	3	-	2	1	-	-	-	-	3	-	-	-
8	3	-	2	1	-	-	-	-	3	-	-	-
9	2	1	-	-	1	-	-	1	1	-	1	1
10	-	-	-	-	-	-	-	-	-	-	-	-
11	3	1	-	1	-	1	1	-	2	1	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	1	-	-	-	-	-	1	-	-	1	-	-
14	2	-	-	-	-	1	1	-	2	-	-	-
15	-	-	-	-	-	-	-	-	-	-	-	-
16	2	-	-	-	-	1	1	-	0	2	-	-
17	2	-	-	1	-	-	1	-	1	1	-	-
18	1	-	-	1	-	-	-	-	0	1	-	-
19	4	-	-	-	1	-	2	1	2	2	-	-
20	3	-	-	1	-	1	1	-	2	-	1	-
Totals:	32	4	4	7	3	5	10	3	20	10	2	2

TABLE 32.

1.7.70 Trap.	*C. vicina* ♀	 ♂	Oocyte Stage. I	 II	 IIIa	 IIIb	 IV	 V	Ovariole Dilations. 0	 1	 2+	Retained Eggs.
1	2	-	-	2	-	-	-	-	0	1	1	-
2	3	-	-	-	-	2	-	1	1	1	1	2
3	2	-	-	-	-	-	1	1	1	1	-	1
4	1	-	-	-	-	-	-	1	-	1	-	-
5	1	-	-	-	-	-	1	-	-	-	1	1
6	-	-	-	-	-	-	-	-	-	-	-	-
7	2	-	-	1	-	-	1	-	-	2	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-
9	3	-	1	1	-	1	-	-	2	-	1	-
10	-	-	-	-	-	-	-	-	-	-	-	-
11	1	-	-	1	-	-	-	-	-	1	-	-
12	1	-	-	-	-	-	1	-	-	1	-	1
13	-	-	-	-	-	-	-	-	-	-	-	-
14	-	-	-	-	-	-	-	-	-	-	-	-
15	4	1	1	1	-	1	1	-	2	2	-	-
16	-	-	-	-	-	-	-	-	-	-	-	-
17	-	-	-	-	-	-	-	-	-	-	-	-
18	-	-	-	-	-	-	-	-	-	-	-	-
19	-	-	-	-	-	-	-	-	-	-	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-
Totals.	20	1	2	6	0	4	5	3	6	10	4	5

TABLE 33.

7.7.70 Trap.	*C. vicina* ♀	♂	Oocyte Stage I	II	IIIa	IIIb	IV	V	Ovariole Dilations 0	1	2	Retained Eggs.
1	11	-	3	3	-	-	3	2	4	4	1	2
2	6	1	2	2	-	-	-	2	2	2	-	-
3	16	1	5	1	-	3	6	1	14	2	-	2
4	3	-	-	1	1	1	-	-	2	1	-	-
5	10	-	5	-	-	2	3	-	5	4	1	1
6	9	-	2	1	-	2	2	2	4	4	1	2
7	11	-	2	1	-	3	3	2	4	6	1	-
8	7	-	3	-	-	1	3	-	5	1	1	1
9	2	-	1	1	-	-	-	-	1	-	1	
10	4	1	2	-	-	-	2	-	-	2	2	-
11	17	1	6	2	1	2	4	2	14	3	-	-
12	2	1	-	-	-	-	2	-	-	2	-	-
13	5	-	1	-	-	1	2	1	3	2	-	2
14	9	-	-	-	2	3	3	1	-	9	-	2
15	-	-	-	-	-	-	-	-	-	-	-	-
16	4	-	1	-	-	1	2	-	3	1	-	-
17	2	1	1	1	-	-	-	-	-	-	-	-
18	4	1	2	-	1	-	1	-	-	-	-	-
19	7	2	1	-	-	2	3	1	3	4	-	-
20	-	-	-	-	-	-	-	-	-	-	-	-
Totals	129	9	37	13	5	21	39	14	73	47	8	12

TABLE 34.

15.7.70 Trap.	*C.vicina* ♀	♂	Oocyte Stage I	II	IIIa	IIIb	IV	V	Ovariole Dilation 0	1	2	Retained Eggs.
1	1	-	-	-	1	-	-	-	-	1	-	1
2	1	-	-	1	-	-	-	-	1	-	-	-
3	-	-	-	-	-	-	-	-	-	-	-	-
4	1	-	-	-	-	1	-	-	0	1	-	-
5	2	-	1	-	1	-	-	-	-	2	-	1
6	4	-	-	1	-	-	3	-	3	1	-	-
7	-	-	-	-	-	-	-	-	-	-	-	-
8	-	-	-	-	-	-	-	-	-	-	-	-
9	1	1	-	-	1	-	-	-	-	1	-	1
10	-	-	-	-	-	-	-	-	-	-	-	-
11	-	-	-	-	-	-	-	-	-	-	-	-
12	-	-	-	-	-	-	-	-	-	-	-	-
13	1	-	-	-	-	1	-	-	-	1	-	-
14	1	-	-	-	1	-	-	-	0	1	-	1
15	1	-	-	-	1	-	-	-	-	-	1	-
16	1	-	-	-	-	1	-	-	-	1	-	1
17	1	-	1	-	-	-	-	-	-	-	1	-
18	4	-	2	-	-	1	1	-	3	1	-	1
19	1	-	-	-	-	1	1	-	-	1	-	-
20	1	-	-	-	-	-	1	-	1	-	-	-
Totals	21	1	4	2	5	5	5	0	8	11	2	6

TABLE 35.

G. vicina. Oocyte Stages. O Dilation.

Date:	I No.	I %	II No.	II %	IIIA No.	IIIA %	IIIB No.	IIIB %	IV No.	IV %	V No.	V %
5.5.70	-	-	-	-	-	-	-	-	-	-	-	-
12.5.70	-	-	-	-	-	-	1	50	1	50	-	-
13.5.70	3	60	-	-	-	-	1	20	1	20	-	-
21.5.70	-	-	-	-	-	-	-	-	-	-	-	-
27.5.70	6	28.5	5	23.8	5	23.8	3	14.3	2	9.5	-	-
2.6.70	5	17.9	3	10.7	-	-	7	25.0	10	35.7	3	10.7
10.6.70	30	36.1	29	34.9	10	12.0	6	7.2	8	9.6	-	-
16.6.60	12	54.6	8	36.4	-	-	1	4.5	6	2.7	-	-
23.6.70	4	20	4	20	2	10	3	15	4	20	3	15
1.7.70	1	16.7	1	16.7	-	-	2	16.7	-	-	3	50
7.7.70	28	38.4	13	17.8	3	4.1	11	15.0	13	17.8	4	5.8
15.7.70	3	37.5	2	25.0	1	12.5	1	12.5	1	12.5	-	-
Total %s.		34		23.8		7.7		12.8		17		4.8

TABLE 37.

Date	*C. vicina* Oocyte Stage, 2 Dilations. I No.	%	II No.	%	IIIa No.	%	IIIb No.	%	IV No.	%	V No.	%
27.5.70	-	-	-	-	1	100	-	-	-	-	-	-
2.6.70	-	-	-	-	1	33	1	33	1	33	-	-
10.6.70	-	-	-	-	-	-	1	50	1	50	-	-
16.6.70	1	33	-	-	-	-	1	33	1	33	-	-
23.6.70	-	-	-	-	1	50	-	-	1	50	-	-
1.7.70	-	-	2	50	-	-	1	25	1	25	-	-
7.7.70	1	12.5	-	-	-	-	-	-	5	87.5	-	-
15.7.70	-	-	-	-	-	-	1	50	1	50		
Total %		8.3		8.3		12.5		29		42		

TABLE 38.

G. vomtiroai. Oocyte Stage - Flies with 0 Dilations.

Date	I		II		IIIa		IIIb		IV		V	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
5.5.70	-	-	-	-	-	-	-	-	-	-	-	-
12.5.70	-	-	-	-	-	-	-	-	-	-	-	-
13.5.70	-	-	-	-	-	-	-	-	-	-	-	-
21.5.70	17	43.5	9	23	7	17.9	5	12.8	1	2.6	0	-
27.5.70	46	50.5	15	16.4	12	13.2	13	14.3	4	4.4	1	1.1
2.6.70	200	32.8	57	9.4	91	14.9	112	18.4	134	22.0	15	2.5
10.6.70	147	54.8	65	24.2	26	9.7	9	3.4	20	7.4	1	0.4
16.6.70	8	72.7	3	27.3	-	-	-	-	-	-	-	-
23.6.70	3	60	2	40	-	-	-	-	-	-	-	-
1.7.70	-	-	-	-	-	-	-	-	-	-	-	-
7.7.70	4	44.4	4	44.4	-	-	1	1.2	-	-	-	-
15.7.70	-	-	-	-	-	-	-	-	-	-	-	-
Total %		40		14.5		13.1	[illegible]	13.5		15.4		1.6

TABLE 39.

C. vomitoria, Oocyte Stage 1 Dilation.

Date:	I No.	I %	II No.	II %	IIIa No.	IIIa %	IIIb No.	IIIb %	IV No.	IV %	V No.	V %
5.5.70	-	-	-	-	-	-	-	-	-	-	-	-
12.5.70	-	-	-	-	-	-	-	-	-	-	-	-
13.5.70	-	-	-	-	-	-	-	-	-	-	-	-
21.5.70	1	25	1	25	2	50	-	-	-	-	-	-
27.5.70	1	6.6	1	6.6	4	26.6	7	46.6	2	13.3	-	-
2.6.70	6	7.31	8	9.8	18	21.9	28	34.1	21	25.6	1	-
10.6.70	14	37.8	10	27.0	1	27	8	21.6	4	10.8	-	-
16.6.70	-	-	1	50	1	50	-	-	-	-	-	-
23.6.70	1	100	-	-	-	-	-	-	-	-	-	-
1.7.70	-	-	-	-	-	-	-	-	-	-	-	-
7.7.70	2	28.6	1	14.3	-	-	1	14.3	2	28.6	1	14.3
15.7.70	-	-	-	-	-	-	-	-	-	-	-	-
Total %		16.4		15		17.6		30		19.8		1.4

TABLE 40.

G. vomitoria, Oocyte Stage, 2 Dilations.

Date	I		II		IIIa		IIIb		IV		V	
	No.	%	No.	%	No.	%	No.	%	No.	%	No.	%
27.5.70	-	-	-	-	1	100	-	-	-	-	-	-
2.6.70	-	-	1	72	3	21.4	1	7.2	9	64.3	-	-
10.6.70	-	-	1	25	1	25	1	25	1	25	-	-
16.6.70	-	-	-	-	-	-	-	-	-	-	-	-
23.6.70	-	-	-	-	-	-	-	-	-	-	-	-
1.7.70	-	-	-	-	-	-	-	-	-	-	-	-
7.7.70	-	-	1	50	-	-	-	-	1	50	-	-
15.7.70	-	-	-	-	-	-	-	-	-	-	-	-
Total %				14.3		24		9.5		52		

DISCUSSION.

The results of this study are divided into two main sections, changes in the age-composition of the population and changes in the species-composition during the early part of the blow-fly season, namely May - July.

Total catch numbers were profoundly affected by weather conditions and maximal trap numbers, which presumably indicated high blow-fly activity were obtained on warm, calm days (Fig.4.) The numbers of C. vomitoria fell dramatically on 10 June, although the maximum temperature on this day was the highest recorded during the trapping period. It is possible that this fall in the trap catches was attributable to mass emigration of flies away from the study area, Such an emigration from the study area could have been attributable to the nature of the area; it is only partially wooded, and as C. vomitoria prefers wooded, shaded areas, the nearby woodland would provide a more preferable habitat for this species. The fall in trap catches of C. vomitoria could then be due to the emigration of these flies from the study area into the nearby woodland. Macloed and Donnelly recorded a marked preference of C. vomitoria for wooded areas.

When considering the results obtained in this study, it must be remembered that they are based on flies caught in meat-baited traps. These then, are flies which displayed a positive reaction to the bait. Factors influencing a fly's response to the bait are complex, for instance, an adequate supply of carrion in the area may affect the number of flies taken in the traps, as many of the flies will have obtained their essential protein from these natural supplies.

The complexity of the response of blow flies to baited traps was also seen in the differences in response of flies of different physiological age. The difference emerged when the oocyte stages of the parous and nulliparous flies were examined (Fig.6.) The nulliparous flies attracted to the traps had immature ovaries, with oocytes predominantly in Stage 1, whereas the parous flies caught had more mature oocytes, predominantly Stages III-IV. This implies that having visited carrion (in the present case the liver-baited traps), nulliparous flies tended not to be caught as their ovaries matured over the following days. On the other hand, parous flies it seems, were attracted to meat-baited traps during the later stages of oocyte maturation. It seemed then that the reproductive history of the fly profoundly affected its response to the attraction of a baited trap.

The results obtained as to the age-composition of the females caught in the traps do, then, refer only to the age structure of that contingent of the population which responds to the trap bait. It is likely that the age-composition of the trap catch does not simply reflect the age of the population as a whole, since various sections or ages of the population may not equally respond to the trap bait, and so are excluded from the 'census'. The age-changes in the trap catches recorded in this study were then those changes which occured in that proportion of the population which responded to the bait.

The flies responding to the bait were predominantly female; this is to be expected as female flies require a protein meal for the maturation of oocytes. The numbers of males caught in the traps was variable and always relatively small. In the total catch of

C. vomitoria, 23% were males, in C. vicina males contributed 19% of the total catch numbers, while in Lucilia the proportion of males was 24% overall. The sex ratios varied during the season (Fig.16). C. vomitoria and C. vicina were female dominated throughout the season, showing only small variations, Lucilia, on the other hand, had a much higher percentage of males at the beginning of the season (37% as compared with 19% in the two Calliphora species). The percentage of males in the Lucilia catches did, however, fall as the season progressed and the sex ratios became comparable with the Calliphora species (5 - 15% males).

This variability in the number of males caught, further serves to illustrate the fact that trap catches are not representative of the general population. In laboratory reared blow-flies, the sex ratio is 1:1, but males have a slightly shorter life, one would then reasonably expect the sex ratio in the wild population to be almost 1:1, with only a slight predominance of females, trap catches, however, indicate a female dominated population. Steiner (1949), showed that in Phormia regina, optical factors introduced differences in the reactions of the sexes to baited traps, and considering the marked differences between the compound eyes of the male and female Calliphorids (the distinction is so great that it is used as a convenient method of sexing these flies), one would expect sight to play some role in the choice of habitats and possibly the response to traps.

The age structure of the population, as indicated by the reproductive history of the flies is seen in Fig.8. If the situation were simple, one would expect the population to be composed entirely of nulliparous females that had just emerged; (Calliphora spp. overwinter as larvae or pupae), until enough time had elapsed for these early emerged flies to reach maturity and lay eggs (about 10-14 days) and to reach a physiological state such that they respond to the bait. Obviously parous flies would be present in the population before they were actually taken in the traps as the chance of catching parous flies is low when the total number of such flies is small. For example, one might have to catch as many as 200 females before a parous fly was taken. If there were descrete generations of Calliphora, then there would be no emergence after the initial appearance of young flies and the proportion of parous flies could be expected to increase to nearly 100%.

However, when one considers the results obtained during this study, it is clear that the situation is far more complex. Nulliparous flies are always found within the population and the proportion of parous flies never rose above 53% in C. vomitoria and 70% in C. vicina.

These results, then, indicated that flies must have been emerging continuously throughout the season in sufficient numbers to prevent continuous increase in the proportions of parous flies. In C. vicina the proportion of parous flies fell 10% on 10 June, indicating a sudden emergence of nulliparous flies.

The population of both C. vomitoria and C. vicina began to age when total catch numbers started to fall, 10 - 16 June; this fall in numbers is due to a decrease in the number of young flies that emerged and consequently as the proportion of young flies dropped, the population aged.

The results of this study, then, show that marked changes occur in the species composition of the Calliphorid population attracted to meat-baited traps during the early part of the season, May - July. These changes are due to the different life cycles and emergence patterns of the individual species. The age changes that occur in the female population also support the general hypothesis that C. vomitoria and C. vicina overwinter as larvae or pupae and consequently the first flies to enter the population are immature adults, old parous flies were not taken until later in the season. The laboratory study indicated that flies that had laid once were between at least 10 and 14 days old, whilst those that had laid twice were more than at least 16 days old.

Nulliparous flies caught at the beginning of the season have then emerged from overwintering pupae, these flies matured and laid eggs to give rise to parous flies as the season progressed. Nulliparous flies taken later in the season were those that had emerged from eggs laid by the first adults of the season.

The techniques used in this study then allow an estimate to be made of the age composition of the female Calliphora population that is attracted to meat baited traps. This study also revealed the degree of complexity of such a response to an attractant bait, one factor affecting the response being the reproductive history of the female fly.

A study such as this could obviously be carried on right through the blow-fly season, which lasts until October. This would enable one to study both species and age changes as the population numbers declined, one would expect from the trends observed in this study, that the population would age as fewer flies emerged when the weather became worse during the autumn. A complete study would, however, be necessary to see if this hypothesis was correct.

A further line of development could be an investigation of the suspected movements of C. vomitoria out of the study area and into the nearby woods. Obviously one would have to run one or two traps continuously within the wooded area, these trap catches could then be compared with those taken in the study area. Any movements of flies c uld then be determined by comparing the species composition of the trap catches taken in the two areas.

SUMMARY.

1. 20 liver baited traps were set in a partly wooded, partly open, study area. The following Calliphorids were caught in total for 12 trapping days, between 5 May and 15 June, 1970.

1,951 Calliphora vomitoria.

647 Calliphora vicina

1,490 Lucilia spp., predominantly of the L. ceasar group.

147 Acrophaga.

2. The species composition of the catches changed during the above period, C. vicina was moderately abundant at the beginning of the trapping period and contributed 67 - 100% of the catches taken from 5 May - 13 May. C. vomitoria did appear in significant until 21 May, when it was 80% of the total catch, and the numbers of this species rapidly rose to a peak number of 1,016 specimens on 2 June, numbers declined thereafter. This marked decline in the numbers of C. vomitoria caught was probably due to emigration of the population from the study area into the nearby extensive woodlands.

3. The age composition of the two Calliphora spp. was investigated by dissection and observation of the presence or absence of dilations on the ovariole tunica. The stage of development of the oocytes was also recorded. Changes in the proportions of parous females were as follows; in C. vicina parous flies increased from 27% on 27 May to a maximum of 70% by 1 July, but in general the numbers of parous C. vicina fluctuated between 20-50% during the trapping period. In C. vomitoria parous flies increased from 11.5% on 21 May to a maximum of 53% on 7 July, but generally numbers of parous flies fluctuated between 11-25% during the season.

4. The frequency of flies with retained eggs was also recorded, it was found to be more common in C. vicina than in C. vomitoria and also the proportion of parous flies with a retained egg increased as the season progressed.

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