Biological studies on some coprophilous sphaeroceridae (borboridae, diptera)

V. E. G. Edge

BIOLOGICAL STUDIES ON SOME COPROPHILOUS SPHAEROCERIDAE

(BORBORIDAE, DIPTERA)

by V.E.G. Edge B.Sc.

(University College)

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INTRODUCTION

Since Réamur (1740) recorded that cow droppings contained a large number of different types of dipterous larvae and reared several species, including *Mesembrina meridiana* and *Scopeuma stercoraria*, numerous studies have been conducted on flies associated with mammalian dung, particularly from cattle. (Mellor, 1919; Hammer, 1941; Coe, 1942; Mohr, 1943; Hafez, 1948, 1949; Kettle & Lawson, 1952, and Laurence, 1954, 1955). The present work is concerned with certain species belonging to the family Sphaeroceridae (Borboridae) that frequent dung in the adult stage and whose larvae can also be found in dung.

Richards (1930) reviewed the taxonomy of 100 species of British Sphaeroceridae and classified their habitats. The adults are normally found associated with decaying organic matter, including seaweed, fungi, grass, carrion, and dung, and the larvae appear always to be scavengers. Species are not usually confined to one habitat and of the 29 that were captured on dung, Richards concluded that "Most of the dung haunting species are not restricted to the dung of any particular animal", but he observed that certain species exhibit definite preferences for dung from certain mammals, or for dung in a particular state, e.g. manure heaps. This work, together with that of Hammer (1941) who studied flies (including sphaerocerids) associated with pasturing cattle and their excrement in Denmark, and Laurence (1954) who carried out investigations at Rothamsted on the larval inhabitants of cow pats and subsequently also published a paper in 1955 on the ecology of the species of Sphaeroceridae he found in cow pats, has provided the background and impetus for much of the present work.

The basic approach of Hammer (1941) and Laurence (1954, 1955) was similar, in that they used the 'cow pat' as an ecological unit and studied the main groups of flies associated with it. Therefore, necessarily, the information they obtained on the species of Sphaeroceridae encountered was limited by this parameter. To gain further information on the wider biological spectrum of certain species of Sphaeroceridae, the adults of which, although occurring in cow droppings, are in no way confined to this medium, the present investigations are almost entirely restricted to 5 species belonging to the genus Copromyza :-

C.similis Collin

C.equina Fallen

C.hirtipes Robineau - Desvoidy

C.nigra Meigen

C.nitida Meigen

and one of the genus Sphaerocera :- S.subsultans L. (Nomenclature after Richards).

Adults of all these species are abundant in the study area in dung from farm mammals at certain times of the year, and their larvae can also be found in this dung. By concentrating on fewer species it is possible to provide more quantitative data on certain aspects of their biology and to assess more accurately interspecific differences and similarities.

Investigations were carried out mainly at Houghall Agricultural College (Houghall farm) Durham from 1964 to 1966 to estimate the seasonal occurrence of adults, their preferences for dung from different farm mammals, the succession of adults associated with the ageing of dung, locomotory activity over 24 hours, and the influence of weather conditions on movement. The duration of development in the field at different times of the year was also determined. Laboratory investigations were conducted on C.similis and C.equina, the 2 most anatomically and ecologically closely related species, to provide further information on their breeding biology and behaviour.

Duda (1923) recorded C.similis as commoner in Northern Europe than C.equina, and Nielsen, Ringdahl & Tuxen (1954) recorded C.similis as common all over Iceland, but C.equina as rare or absent. However, in Madeira and the Canaries, C.equina is known to occur, but C.similis is not. This suggests that where these species occur together the relative abundance of C.similis compared with C.equina will tend to increase towards the north, or the colder the climate becomes. To determine if this could be demonstrated in England, adults were collected monthly over a period of one year at a lowland site near the study area in Durham, at a lowland site in Dorset, and at a highland site in the Pennines in Westmorland (the climate in this locality has been described by Manley (1936) as "sub-arctic"), and the relative abundance of the species estimated.

An important extension of this work was the investigation of chemical attractants which provides a valuable indication of the nature of the volatile substances present in dung that attract adult sphaerocerids. The method of enquiry consisted of a series of field tests, in which a number of pure chemicals, both singly and in combination, were exposed. As Jacobsen (1966) pointed out, the field of chemical insect repellents and attractants is rapidly expanding and although much work is naturally motivated by economic needs, and hence usually only concerned with insects of economic importance, it should not be overlooked that a chemical which remains attractive over a number of days can be an extremely valuable aid to the insect ecologist, particularly if his work necessitates trapping.

Although considerable general information exists on coprophilous sphaerocerids, quantitative data is almost entirely restricted to species associated with cattle droppings. The present work was carried out to provide further information, quantitative where possible, on these common and abundant members of the dung fauna. Particular attention was paid to annual variations in the number of adults attracted to the dung of farm animals, the effects of ageing of dung on attractiveness, and the chemicals responsible for this attraction.

I. BREEDING BIOLOGY AND HABITS OF C.SIMILIS AND C.EQUINA

(1) BREEDING TECHNIQUES

A fuller understanding of the breeding biology and habits of *C.similis* and *C.equina* could be obtained only by establishing laboratory cultures. Richards (1930) found both species to be common in horse dung and this was also the case around Durham. Adults were readily obtained from fresh horse dung using an aspirator and often large numbers emerged from samples of this dung kept in the laboratory. The identification and separation of adults of these species was only possible after anaesthetization with ether. The majority of individuals treated in this manner recovered and could be used for breeding.

A. Breeding Media

Freeden & Taylor (1964) cultured the small sphaerocerid *Leptocera caenosa* (Rondani) from egg to adult in various organically rich media, usually autoclaved horse or sheep manure. *C.equina* and *C.similis*, however, failed to oviposit in autoclaved horse dung, although they are known from the present work to breed in horse dung in the field. This may be due to the loss of the characteristic fresh dung odour during autoclaving. The problem of killing any sphaerocerid eggs or larvae present in the samples, while still retaining the attractive odour, was overcome by sealing the samples in polythene bags and subjecting them to below $-30^{o}C$ in a deep freeze for several days. Eggs and larvae treated in this manner always failed to survive.

B. Breeding containers

Breeding containers were constructed from tins measuring 22x22x23cm. With the top of the tin removed and the open end upwards, the whole of the front was cut away, except for a 1cm wide framework, and a circular hole 15cm in diameter was also cut in one side. A muslin sleeve was fixed around the circular hole and the front and top covered with polyglaze. The breeding medium on a petri dish was introduced into the cage through the muslin sleeve which could be closed by a spring clip.

It was easily possible to maintain the high humidity that sphaerocerids prefer by placing filter papers on the floors of the containers and occasionally dampening them with a few drops of water. Condensation had to be avoided as the flies were easily trapped or damaged by drops of water on the sides of the containers.

C. Procedure for breeding

Fresh pre-frozen horse dung in petri dishes was normally placed in the containers each day. At the same time any old dung was removed and either discarded or kept under observation in muslin topped jars.

Goddard (1938) experienced difficulty in culturing adults of certain Sphaeroceridae. This he attributed to the presence of fungi and nematodes in the tubes he used. The nematodes destroyed larvae, pupae, and occasionally adults.

These problems were not encountered in the present work, probably due to the larger breeding containers and the daily removal of dung into muslin topped emergence jars.

(2) FEEDING BEHAVIOUR AND FOOD CHOICE

Richards (1930) recorded that "C.equina is the commonest species in horse dung, but is also found more rarely on that of cows and dogs and on carrion", while he states that "C.similis is also common on horse dung, but is not nearly so much confined to it as C.equina. It is also found on cow- and human-dung". Rabbit burrows and mouse runs are also given as places where C.similis occurs. Goddard (1938) found C.equina in decaying lawn mowings, cow and sheep dung, while C.similis was found in cow and deer dung.

To determine if C.similis and C.equina adults exhibit preferences for certain media, the following were compared under laboratory conditions :- fresh pig, sheep, cow, rabbit, and horse dung (collected in the field), vole and mouse dung (obtained from laboratory animals), decaying grass cuttings (from compost heaps), and dead mice. Each type of dung was collected from a number of animals and well mixed to reduce any chance of variability between individual samples. The samples, in sealed polythene bags, were subjected to below -30°C for several days to destroy any sphaerocerid eggs present. The mouse carcasses were allowed to decay for a few days before freezing.

A. Separate exposure of media

Samples of the different types of media were separately exposed to laboratory cultures of both species. After 24hrs the samples were removed, examined, and retained in muslin topped jars. All the media were exposed several times in this way to both species. A high humidity in the cages and a laboratory temperature of approximately 20°C were maintained throughout the investigations.

Both species were observed feeding on all the different types of media, although to a lesser extent on mouse, mole, and rabbit dung, and far less on decaying grass cuttings and carcasses.

B. Multiple exposure of media (observations on all samples)

A direct comparison between the preferences of C.similis and C.equina for certain media could be made only by simultaneously exposing a number of samples to each species. To facilitate this, a large observation cage was constructed, 74cm in height x 51cm x 36cm, from a galvanized metal frame completely covered with polyglaze except for a muslin section in one side. Entrance was gained through a circular hole, diameter 18cm,in the muslin section, surrounded by a muslin sleeve which could be closed by a clip. The floor was covered by damp filter papers to maintain a high humidity and to aid observation. The floor was well illuminated from above by a fluorescent light and from high up on two sides by 60 watt bulbs directed downwards. A laboratory temperature of approximately

$20^{o}C$ was maintained during the observations.

At the onset of the investigations, 500 adults from 1 - 2 weeks old were released into the cage at 17.00hrs and then left without food overnight. At 10.00hrs the following day, samples of cow, sheep, pig, and horse dung, smoothly spread in petri dishes, were placed, one in each corner of the cage. The numbers present on each sample were counted at 5min intervals over a 45min period. Although there was considerable activity, with the flies both flying and walking on to the dung, the good illumination and smoothness of the dung surfaces enabled reasonably accurate counts to be made. 10 repetitions were carried out with the positions of the samples being altered in relation to the corners they occupied, thus reducing any errors that may have occurred through a particular position being more or less favourable.

There was an inherent difficulty in the method of starving the cultures. After each test it was necessary to leave the dung in the cage for a certain length of time to avoid subsequent deaths due to starvation. The length of time that the dung had to be kept in the cage to ensure survival, yet partial starvation, could be found only by trial and error. Even if the dung was left in the cage for a specific period such as 1hr, this did not ensure that the level of starvation the next day would be the same. Thus it was necessary to make a subjective decision on the period of feeding after each test, and consequently there were large differences in the numbers of adults that were recorded on the samples of dung from test to test. In fig.1 the total number of adults of C.similis and C.equina recorded on samples of cow, sheep, pig, and horse dung at each of 9 counts at 5min intervals (10 replicates) are shown. Individuals of both species invaded the dung within a few seconds of exposure, and this is reflected by the high first counts (fig.1). The total number of adults present on the samples rose rapidly over the first 10mins (2 counts), and then moved slowly to reach a maximum after 20mins (4 counts) for both species. Over the remaining exposure time, there was a gradual decrease in the numbers present on the dung samples, although there was a slight increase from the seventh to the eighth count (35-40mins).

In Table 1 the mean number of adults of C.similis and C.equina recorded on samples of cow, sheep, pig, and horse dung at each of 9 counts at 5min intervals (10 replicates) is shown. The great variability in the number of adults recorded at each count is due to unavoidable differences in the levels of starvation of the cultures and hence the number of adults that were attracted to feed on the samples of dung from test to test. Thus, for C.equina feeding on horse dung, the 9 counts for the first test were 56, 80, 90, 90, 90, 80, 75, 66, 35, as compared with 22, 32, 35, 36, 40, 37, 40, 44, 35, for the fourth test.

FIG.1. Total numbers of C.similis and C.equina adults recorded at each of 9 counts at 5min intervals (10 replicates) on cow, sheep, pig, and horse dung

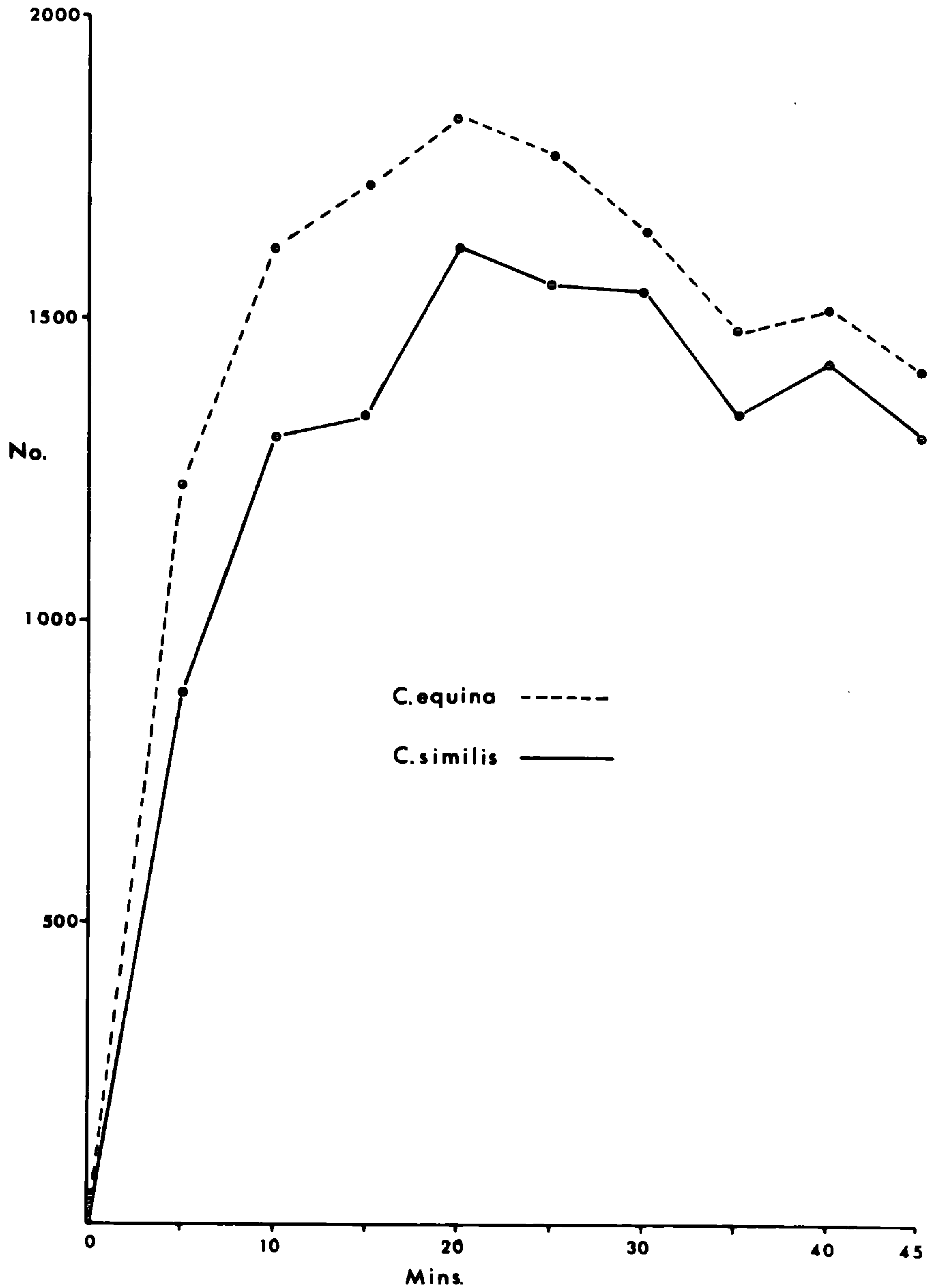

2000
1500
1000
500
No.
C. equina
C. similis
0
10
20
30
40
45
Mins.

TABLE 1. The mean number of adults (± S.E.) recorded on samples of cow, sheep, pig and horse dung at each of 9 counts at 5min intervals (10 replicates, 500 adults present for each species)

	No. of count								
	1	2	3	4	5	6	7	8	9
C.similis									
Cow dung	5.8 ± 3.7	6.8 ± 4.5	8.1 ± 4.7	10.3 ± 4.2	7.0 ± 3.5	9.1 ± 2.8	10.3 ± 3.7	11.6 ± 5.8	12.8 ± 6.0
Sheep dung	14.0 ± 11.2	18.6 ± 11.1	18.7 ± 11.6	26.3 ± 7.4	26.3 ± 7.9	21.5 ± 9.2	18.8 ± 8.9	18.0 ± 9.2	13.6 ± 7.5
Pig dung	28.0 ± 23.8	47.9 ± 17.8	46.7 ± 10.4	55.4 ± 10.8	46.2 ± 14.8	45.0 ± 12.8	38.6 ± 12.2	41.5 ± 14.7	40.3 ± 12.0
Horse dung	40.2 ± 22.3	57.2 ± 13.3	59.8 ± 19.1	70.0 ± 16.6	76.3 ± 13.3	78.9 ± 20.4	66.4 ± 14.3	71.4 ± 21.8	64.0 ± 19.1
C.equina									
Cow dung	6.9 ± 4.5	9.7 ± 6.1	9.8 ± 6.4	10.3 ± 7.0	10.3 ± 5.7	10.3 ± 5.1	8.8 ± 4.4	7.6 ± 4.1	7.7 ± 4.7
Sheep dung	16.0 ± 9.5	18.1 ± 9.3	21.7 ± 7.6	22.8 ± 6.8	24.2 ± 9.6	18.8 ± 5.6	15.2 ± 2.8	16.0 ± 5.9	18.5 ± 5.2
Pig dung	51.1 ± 26.4	72.0 ± 25.4	70.1 ± 12.5	73.6 ± 24.6	67.6 ± 19.8	75.1 ± 18.7	60.9 ± 24.1	59.5 ± 22.8	61.5 ± 24.9
Horse dung	47.9 ± 30.1	61.7 ± 20.9	70.0 ± 25.8	77.1 ± 26.2	75.2 ± 21.4	61.6 ± 21.0	62.9 ± 19.5	68.3 ± 22.1	55.6 ± 22.0

From Table 1 it can be seen that the rise and fall in the number of adults of each species present on the individual samples of dung follows a similar pattern to that shown in fig.1, with a rapid rise during the first 5mins to reach a maximum within 30mins (6 counts), except for <u>C.similis</u> on cow dung where the maximum was attained after 45mins (9 counts).

The rapidity with which each species invaded the various dung samples can be compared by expressing the mean first count on each sample as a ratio of the mean maximum count recorded on that sample (Table 2). The ratios for <u>C.equina</u> were higher and less variable (o.62:1 - 0.67:1) than for <u>C.similis</u> (0.45:1 - 0.53:1) indicating a more rapid invasion rate in the former.

TABLE 2. The mean number of adults present on dung samples from 10 replicates of 9 counts at 5min intervals (500 adults present for each replicate)

<u>C.equina</u>

	Mean No. 1st count	Mean No. Max. count	Mean 1st count / Mean Max. count	Time taken to reach mean max. count Mins
Cow dung	6.9	10.3	0.67	20
Sheep "	16.0	24.2	0.67	25
Pig "	51.1	75.1	0.68	30
Horse "	47.9	77.1	0.62	20

<u>C.similis</u>

Cow dung	5.8	12.8	0.45	45
Sheep "	14.0	26.3	0.53	20
Pig "	28.0	55.4	0.51	20
Horse "	40.2	78.9	0.51	30

In Table 3.i. the total number of adults of each species recorded on samples of cow, pig, sheep, and horse dung in 90 counts is shown. From these results χ^2 values have been calculated and are shown in Table 3.ii. It can be seen from Table 3 that C.similis is significantly more attracted to horse dung than cow, sheep, and pig dung, while pig dung is significantly more attractive than either sheep or cow dung. Sheep dung is also significantly more attractive than cow dung. The χ^2 values for C.equina are similar to those for C.similis except that there is no significant difference between the attractiveness of pig and horse dung.

TABLE 3.i. Total number of adults of C.similis and C.equina recorded on samples of cow, pig, sheep, and horse dung in 9 counts at 5min intervals (10 replicates)

	Cow dung	Sheep dung	Pig dung	Horse dung
C.equina	814	1713	5908	5803
C.similis	818	1758	3916	5822

TABLE 3.ii. χ^2 values have been calculated on the total number of adults recorded on each dung sample, using a null hypothesis that the distribution of adults between the samples compared is equality

Dung samples compared	C.equina		C.similis	
	χ^2	P.	χ^2	P.
Cow and sheep	100+	< 0.001	100+	< 0.001
Cow and pig	100+	< 0.001	100+	< 0.001
Cow and horse	100+	< 0.001	100+	< 0.001
Sheep and pig	100+	< 0.001	100+	< 0.001
Sheep and horse	100+	< 0.001	100+	< 0.001
Pig and horse	0.3	> 0.5	100+	< 0.001

Richards (1930) reports C.equina as being more restricted to horse dung than C.similis, but from these results it would appear that, as far as feeding is concerned, pig dung is just as attractive to C.equina as horse dung, while it is significantly less attractive to C.similis.

Both species exhibited definite preferences for certain media, and by expressing the numbers recorded on each sample as a percentage of the total numbers recorded at that count, the consistency of these preferences over 45mins can be compared (see Table 4).

TABLE 4. The total number of adults recorded on each type of dung at a particular count expressed as a percentage of the total number recorded on all the samples at that time (10 replicates of 9 counts at 5min intervals)

C.equina	Number of Count									
Type of dung	1	2	3	4	5	6	7	8	9	Mean %
Cow	5.7	6.0	5.7	5.6	5.8	6.2	6.0	5.0	5.4	5.7
Sheep	13.1	11.2	12.7	12.5	13.6	11.3	10.2	10.6	12.9	12.0
Pig	41.9	44.6	40.8	39.8	38.2	45.3	41.3	39.3	42.9	41.5
Horse	39.3	38.2	40.8	42.1	42.4	37.2	42.5	42.5	38.8	40.8
C.similis										
Cow	6.6	5.2	6.1	6.4	4.5	5.9	7.7	8.1	9.8	6.6
Sheep	15.9	14.3	14.0	16.2	16.9	13.9	14.0	12.6	10.4	14.3
Pig	31.8	36.7	35.0	34.2	29.7	29.1	28.8	29.2	30.8	31.8
Horse	45.7	43.8	44.9	43.2	48.9	51.1	49.5	50.1	48.9	47.3

With C.equina there was very little variation over the exposure time. Thus, for the number of individuals on cow dung, the mean over the 9 counts was 5.7%, and the difference between the minimum and maximum percentage was 1.2%. For sheep, pig, and horse dung, the means were 12.0%, 41.5%, 40.8%, and the differences were 3.4%, 6.4%, and 6.9% respectively. The results for C.similis were less consistent, particularly for cow and sheep dung. These had means of 6.6% and 14.3%, and differences of

5.4% and 5.5% respectively. However, the maximum value for cow dung, 9.8%, was still less than the minimum for sheep dung of 10.4%. The results obtained for pig and horse dung were less variable, with means of 31.8% and 41.3% respectively, and the difference for both was 7.9%. On the whole, both species showed consistent preferences for certain media over the 45mins, although it was less marked with C.similis than C.equina. From these results it can be concluded that there was no change in the relative attractive powers of the media over 45mins time.

C. Multiple exposure of media (observations on a single sample)

The number of individuals recorded at a particular count was not only dependent upon the numbers that had come on to the dung, but also upon the time they remained. By placing the 4 dung samples (horse, cow, sheep, and pig) in position as before, but restricting the observations to one particular dung sample, it was possible to count the numbers coming on to the samples in 5mins and the numbers that were present at the end of this period. One set of nine 5min counts was carried out for C.similis and C.equina on each of the 4 types of dung. The number of adults that are present at the end of any 5min period is equivalent to the number present at the start of the next 5min period. Thus, the number of adults present at both the beginning and end of a 5min period, and the number of adults that have come on to the dung during this period, are known. Therefore, the number leaving in 5mins (E) can be calculated as follows :-

No. of adults present on dung at start of a 5min period = N_1(e.g.20)
" " " " " " " end " " " " = N_2(e.g.10)

No. of adults arriving on dung 1st 5min period = I_1
" " " " " " 2nd 5min " = I_2(e.g.40)

No. of adults that left the dung in 5min period (E) =

$$N_1(20) + I(40) - N_2(10) = 50$$

The average time (t) an individual remains on the dung in Tmins (e.g. 1st 10mins) can be calculated as follows :-

No. of adults present at the end of the 1st 5mins = 1st N_2(e.g.10)
" " " " " " " " " 2nd " = 2nd N_2(e.g.20)

$$\text{Mean } N_2 = \frac{\text{1st } N_2(10) + \text{2nd } N_2(20)}{2} = 15 \text{ flies}$$

Total No. of adults (Y) that have come on to dung in

Tmins (10) = I_1(e.g.20) + I_2(30) = 50

$$t = \frac{\text{Mean value of } N_2(15) \times T(10)}{Y(50)}$$

= 3mins

TABLE 5.i. Number of adults of C.equina recorded coming on to samples of Dung (I) during nine 5min periods and the number left on at the end of each period (N_2). The number leaving (E) and the total movement during a period (I + E) have been calculated (see text for details)

Copromyza equina	5min periods									
Cow dung	1	2	3	4	5	6	7	8	9	Total no.that came on in 45mins
(N_2)	6.	7	8	11	7	9	10	12	11	32
(I)	8	6	4	3	2	3	2	1	2	
(E)	2	5	3	0	6	1	1	0	3	
(I + E)	10	11	7	3	8	4	3	1	5	
Sheep dung										
(N_2)	14	18	20	24	26	19	17	17	16	59
(I)	20	12	6	8	5	4	2	1	1	
(E)	6	8	4	4	3	11	4	1	2	
(I + E)	26	20	10	12	8	15	6	2	3	
Pig dung										
(N_2)	50	65	72	74	65	70	60	54	52	309
(I)	80	65	30	32	40	50	10	2	0	
(E)	30	50	23	30	49	45	20	8	2	
(I + E)	110	115	53	62	89	95	30	10	2	
Horse dung										
(N_2)	44	62	64	73	79	61	73	65	58	315
(I)	60	57	50	60	35	20	22	8	3	
(E)	16	39	48	51	29	38	10	16	10	
(I + E)	76	96	98	111	64	58	32	24	13	

TABLE 5.ii.

Copromyza similis 5min periods

Cow dung	1	2	3	4	5	6	7	8	9	Total no.that came on in 45mins
(N)	7	9	10	10	8	8	9	10	10	29
(I)	8	5	2	4	3	2	2	2	1	
(E)	1	3	1	4	5	2	1	1	1	
(I + E)	9	8	3	8	8	4	3	3	2	
Sheep dung										
(N)	8	16	14	23	27	22	28	34	38	122
(I)	13	14	4	18	16	10	15	18	14	
(E)	5	6	6	9	12	15	9	12	10	
(I + E)	18	20	10	27	28	25	24	30	24	
Pig dung										
(N)	10	26	39	45	39	39	38	55	50	187
(I)	13	32	33	36	22	17	11	21	2	
(E)	3	16	20	30	28	17	12	4	7	
(I + E)	16	48	53	66	50	34	23	25	9	
Horse dung										
(N)	25	40	47	60	75	77	73	64	55	318
(I)	35	55	40	67	50	33	20	10	8	
(E)	10	40	33	54	35	31	24	19	17	
(I + E)	45	95	73	121	85	64	44	29	25	

(a) Invasion rate (Number of adults coming on to dung)

It can be seen from Table 5 that C.equina again exhibited the more rapid invasion rate with maximum numbers invading the dung during the first 5mins; with C.similis this occurred only on cow dung. With C.equina there was a marked decrease in the invasion rate over the last 15mins; only 18.8%, 7.0%, 3.9%, and 10.4% of the total numbers that came on to cow, sheep, pig, and horse dung respectively did so in this period. The equivalent results for C.similis on to cow, sheep, pig, and horse dung were 17.4%, 34.4%, 18.9%, and 12.0% respectively. Thus, with C.similis there was a less pronounced decrease in the invasion rate, and on to sheep dung there was in fact an increase.

(b) Emigration rate (Number of adults leaving dung)

The maximum numbers of C.equina adults emigrating in 5 minute periods were recorded on the fifth, sixth, fifth, and fourth counts from cow, sheep, pig, and horse dung respectively, and with C.similis on the first, fourth, sixth, and fourth counts from the same samples. The emigration rate for C.equina also showed a marked decrease over the last 15mins of the exposure time. Thus, only 19.0%, 6.8%, 11.7%, and 14.0% of the total numbers leaving cow, sheep, pig, and horse dung respectively did so in this period. The degree of reduction was again less marked with C.similis, as the equivalent results of 15.8%, 25.4%, 12.8%, and 22.8% for the same samples showed.

C.similis exhibited a more gradual increase and decrease in activity (the number of individuals moving on to and off a sample) over the 45mins than *C.equina*. *C.equina* was most active in the first 15mins of the exposure time and least active in the last 15mins, while *C.similis* was most active in the second 15mins of the exposure time (Table 5).

(c) The average time individuals remained on the dung

The average time an individual remained on a sample at any one time has been estimated for the periods 0-15mins, 0-30mins, and 0-45mins (Table 6).

TABLE 6. The estimated average time an individual remains on a sample of dung at any one time, calculated from the results in Table 5 (for method see page 19)

C.equina	Exposure time of samples		
Average time in mins	0 - 15mins	0 - 30mins	0 - 45mins
on - Cow dung	5.8	9.2	12.7
Sheep "	6.8	11.0	14.5
Pig "	5.3	8.0	9.1
Horse "	5.0	6.8	9.2
C.similis			
Cow dung	8.7	10.8	14.0
Sheep "	6.1	7.3	8.6
Pig "	4.8	6.5	9.1
Horse "	4.3	5.8	8.1

As there tended to be a reduction in activity with an increase in exposure time, consequently there was an increase in the average time an individual remained. This increase was similar for both species on cow, pig, and horse dung, but on sheep dung the increase is far greater for C.equina (from 6.8mins in the 1st third to 14.5mins in the last), as opposed to 6.1mins to 8.6mins for C.similis. This reflects a far more uniform activity over the exposure period in the latter.

Individuals of C.equina remained for shorter periods on the samples with the highest densities. Thus, on pig and horse dung with high average densities, the estimated average times over 45mins were 9.1mins and 9.2mins respectively, as opposed to 12.7mins and 14.5mins on the low density cow and sheep dung. It seems probable that these differences are produced by crowding at high densities, causing individuals to be disturbed and to leave the dung, thus reducing the average time, rather than by some inherent difference in the reaction of this species to the samples. Similar results were obtained for C.similis with low average times of 9.1mins and 8.1mins on pig and horse dung, compared with 14.0mins on the low density cow dung. The estimated average time on sheep dung of 8.6mins was less than expected from the mean density, but this may have been due to the more uniform activity on this sample not allowing the flies to become settled. The average time individuals spent on all the samples over the 45mins, estimated from the total numbers of 715 for C.equina and 656 for C.similis, were 9.7mins and 8.7mins respectively. This difference would have been reduced if the results for *C.similis* on sheep dung had followed the same pattern as on the other samples.

D. Combination of results from B and C

The results obtained from observations on a single sample during multiple exposure can be used to interpret those from observations on all samples during multiple exposure. The total number of individuals recorded from observations on all the samples in 90 counts were 14,238 for *C.equina* and 12,314 for *C.similis*. At each count there were 500 individuals present in the cage and therefore the maximum that could have been recorded was 500 x 90 = 45,000. Assuming 100% of the flies visited the dung once in a 45min period, the average time an individual remained would have been :-

$$\frac{14238}{45000} \times 45 = 14.2\text{mins for } C.equina$$

$$\frac{12314}{45000} \times 45 = 12.3\text{mins for } C.similis$$

However, the results obtained from observations on a single sample indicated that an individual of either species would remain for approximately 9mins (9.7mins for *C.equina*, and 8.7mins for *C.similis*). This suggests that some individuals must have visited the dung more than once during the 45mins.

The difference between the total numbers recorded for *C.equina* of 14,238 individuals and the 12,314 for *C.similis* was probably due to the more rapid invasion rate in the former and consequently a greater number would visit the dung in the 45min periods. The rate of invasion is dependent upon the degree of starvation of the flies, and as only one culture of each species was used on consecutive days during the investigations, it is possible that the discrepancy may have been due simply to the culture of C.equina being more starved throughout.

E. Additional food choice observations

Further investigations on food choice were carried out by separately substituting samples of mouse, vole, and rabbit dung, carcasses and decaying grass for cow dung. The same procedure was followed as before with the multiple exposure of media and observations on all samples. However, it soon became apparent that these media were virtually unattractive in the presence of pig, sheep, and horse dung. Apart from being visited by the odd individual, vole, mouse, and rabbit dung remained almost unattractive, even when exposed with 3 samples of cow dung. It seems probable that in the field these media would be only marginally attractive, except when there was a shortage or absence of available cow, sheep, pig, and horse dung in a particular area.

(3) OVIPOSITION IN DIFFERENT MEDIA

To determine if C.similis and C.equina exhibit similar preferences for egg laying as they did for feeding, the following procedure was carried out. The samples of different media that had been separately exposed for 24hr periods in the feeding experiments were examined for eggs and placed in muslin topped jars at 15°C. (This temperature is known to facilitate successful development). These samples were kept under daily observation for 28 days, which is longer than the duration of development of both species at 15°C (see Section I, 5A), and any adults that emerged were recorded.

Adults of both species emerged only from samples of cow, sheep, pig, and horse dung, and as no eggs were detected in the other samples, it can be concluded that oviposition occurred only in cow, sheep, pig, and horse dung. These experiments were carried out to determine whether or not oviposition took place in a particular medium, and direct quantitative comparisons cannot be made when the media are exposed separately.

A direct comparison was made between cow, sheep, pig, and horse dung by simultaneously exposing a sample of each for 24hrs to a mature culture of one species in the large observation cage. The samples of dung were placed in petri dishes so as to resemble as closely as possible the way in which dung occurs normally in the field. Oviposition may have been inhibited if the samples had been smoothly spread, as they were in the food choice experiments. At the end of the 24hr periods the samples were removed, placed in muslin topped jars at 15°C for 28 days, and any emergences that occurred were recorded.

The numbers of adults that emerged from the sample of cow, sheep, pig, and horse dung are shown in Table 7.

TABLE 7. The number of adults of *C.similis* and *C.equina* that emerged from pig, cow, sheep, and horse dung. The χ^2 values have been calculated on the number of adults that emerged from the dung samples, using a null hypothesis that the distribution of adults between the samples compared is equality

	Type of dung			
	Cow	Sheep	Pig	Horse
C.similis				
No.of adults emerging	0	94	256	304
C.equina				
No.of adults emerging	0	130	349	367

	C.similis		*C.equina*	
Dung compared	χ^2	P.	χ^2	P.
Sheep and pig	75.0	<0.001	99.0	<0.001
Sheep and horse	100+	<0.001	100+	<0.001
Horse and pig	4.1	<0.05	0.45	>0.5

There were no emergences recorded from cow dung for both species, nor were any eggs detected after the dung had been exposed to the cultures. It can be seen from Table 7 that horse dung was significantly more attractive to *C.similis* than either sheep or pig dung, while pig dung was more attractive than sheep dung. The results for *C.equina* were similar, but there was no significant difference between the attractiveness of horse and pig dung.

The number of adults that emerged from a sample cannot be equated with the number of eggs laid in it, due to the unknown mortality during development. Previous results had indicated that the mortality in sheep dung was slightly higher than in pig and horse dung, but not sufficiently to significantly affect the results.

(4) MATING, OVIPOSITION AND EGGS

A. Copulation

Prior to copulation the males could be observed darting after females and other males that came into close proximity, but they were not attracted to mature virgin females separated from them by muslin. This indicates that the males are attracted by sight, not smell, and that final recognition is only achieved by touch. Copulation occurred on the sides of the cage and on the dung, but not in flight. During copulation the couple tended to remain immobile and flight was never observed. The flies occupied the same characteristic position as described by Hammer (1941), namely "the male standing over the female which it always holds with the second pair of legs near the root of the wing or at the front edge of the wings; the first pair of legs are usually placed in some part or other of the thorax of the female, most often near the shoulders".

B. The pre-copulation period and duration of copulation

To determine the pre-copulation period (the time from emergence to the commencement of copulation) at 20°C and the duration of copulation, the following procedure was adopted. On emerging, males and females were separated and placed in breeding cages with an adequate food supply. At 24hr intervals, 10 pairs were placed separately in small polyglaze tubes. The number of pairs copulating was recorded and any that failed to do so within 30mins were returned to the cages. The first 30 pairs of each species were timed. To determine if the pre-copulation period varied between males and females, mature males and mature virgin females were placed in tubes with newly emerged males and females. Each tube, therefore, contained either a mature male and a young female, or vice-versa.

The minimum pre-copulation period recorded was 4 days for males and females of both species. The older males attempted to copulate with the young females from thefirst day, but the latter resisted by bending the abdomen away. The young males showed no interest in the mature virgin females until after 4 days. It was observed in breeding cages that the introduction of fresh horse dung produced an increase in activity, with males and females running over the surface of the dung, beating their wings and then copulating. However, the minimum pre-copulation period was not reduced in the presence of fresh horse dung. Copulation also occurred in the dark.

The mean copulation times ($\pm$ S.E.) was 95.5mins $\pm$ 5.2mins, and 86.0 $\pm$ 1.8mins for C.similis and C.equina respectively. The difference is not significant ($t = 1.4$, $P. > 0.1$).

C. Pre-oviposition period for C.equina and C.similis

The pre-oviposition period is the length of time from the female emerging to when the first eggs are laid.

Breeding cages, each containing approximately 200 freshly emerged individuals of C.similis or C.equina, were placed in an incubator at 20°C, with a time switch set to expose them to a 12hrs light, per 24hrs. Fresh pre-frozen horse dung was placed in the cages daily, removed at the end of 24hrs, and retained in muslin topped jars at 15°C. Any emergences that occurred were recorded. Detection of the eggs by examination of the dung proved unsatisfactory as most of them tended to be hidden in crevices in the dung. (The females were reluctant to oviposit in small quantities of dung). The minimum oviposition period for both species was found to be 7 days.

D. Eggs and oviposition

The eggs of C.similis and C.equina are white, approximately circular in cross-section, 1.0 - 1.15mm in length, 0.3 - 0.35mm in diameter at the broadest point, and with one end rounded and the other flattened. The chorion is sculptured by a series of longitudinal ridges which end anteriorly at a flat disc. The eggs are deposited singly or in batches, usually, of 3 or 4, but up to 11 were recorded. The larvae emerge through the flat disc. Hammer (1941) described the eggs of C.equina as being 0.95mm long and 0.28 to 0.29mm broad, with a number of interrupted longitudinal wrinkles and a lid at the anterior end. He presumed that they were laid under cow pats on the soil surface, or on grass. Attempts were made to determine the numbers of eggs individual females laid, but it was found impossible to do this accurately as the females failed to lay in small samples of dung, and in large ones they hid the eggs in crevices. The number of emergences from a sample of dung cannot be equated with the number of eggs that were laid on it due to the unknown mortality. Hammer (1941) found 37-52 eggs (from 3 dissections) in the ovaries of C.equina. (In the present work, however, in 54 dissections of females of this species, a maximum of only 40 eggs was found.)

E. Incubation period at 20°C

Fresh horse dung, freed of any living sphaerocerid eggs by deep freezing, was exposed to laboratory cultures of C.similis and C.equina for 1hr and then removed. Any eggs present were removed and placed on a damp filter paper in a closed petri dish. (Dessication quickly kills the eggs.) This was placed in an incubator at 20°C and examined under a binocular microscope every 30mins. 250 eggs of each species were examined in this manner.

The mean incubation period ($\pm$ S.E.) was 23.7 $\pm$ 0.7hrs and 23.8 $\pm$ 0.8hrs for C.equina and C.similis respectively. This difference is not significant ($t = 0.7$, $P.>0.4$).

(5) THE INFLUENCE OF TEMPERATURE ON THE DURATION OF DEVELOPMENT

A. Duration of development

The duration of development from egg to adult at 5, 10, 15, and 20°C for C.equina and C.similis was determined in the laboratory.

Samples of fresh horse dung freed from any living sphaerocerid eggs by deep freezing were exposed to laboratory cultures of C.equina and C.similis for 24hrs. The samples were then placed in muslin topped jars in constant temperature rooms or incubators at either 5, 10, 15, or 20°C. They were examined daily and any individuals that had emerged were removed, identified, and the duration of development was recorded. This procedure was continued until large numbers of individuals of both species had emerged at each temperature.

TABLE 8. The mean duration of development from egg to adult for C.similis and C.equina. The numbers in brackets are the total no. of adults that emerged at each temperature.

Temp. °C	Mean no. days (Males)	Mean no. days (Females)	Mean No. days (Total)	S.E.
C.similis				
5	62.5 (551)	62.4 (583)	62.5 (1134)	± 0.051
10	31.1 (500)	31.1 (438)	31.1 (938)	± 0.039
15	17.7 (356)	17.6 (427)	17.7 (783)	± 0.036
20	13.0 (714)	13.0 (775)	13.0 (1489)	± .002
C.equina				
5	63.4 (703)	63.6 (709)	63.5 (1412)	± 0.053
10	31.1 (599)	31.1 (563)	31.1 (1162)	± 0.028
15	17.9 (317)	17.9 (313)	17.9 (630)	± 0.056
20	12.9 (877)	12.8 (895)	12.9 (1772)	± 0.002

It can be seen from Table 8 that the duration of development of males and females of each species at all the temperatures was identical, or almost so, and that the duration of development of C.similis and C.equina adults at 10°C was identical, and at 15°C and 20°C was almost so. The one day difference between the duration of development of the 2 species at 5°C is possibly due to experimental error rather than some inherent difference between the species. Errors may have arisen because both species were not simultaneously exposed in the constant temperature rooms, and, therefore, they were not subjected to the same small fluctuations in temperature that may have occurred.

Larsen & Thompson (1940) suggested that, as manure is such an exceedingly difficult medium to work with, humidity, structure, and foodstuff contents varying, minimum values for the duration of development give a more reliable picture. Unfavourable conditions could increase the duration of development considerably. The minimum duration of development at each temperature for C.similis and C.equina is shown in Table 9.

TABLE 9. Minimum duration of development in days

	C.similis		C.equina	
	Males	Females	Males	Females
5°C	59	59	59	59
10°C	29	29	29	29
15°C	16	16	16	16
20°C	11	11	11	11

It is concluded that there is no significant difference in the duration of development at 5, 10, 15, and 20°C between males and females of C.similis and C.equina, or between the 2 species.

B. Sex ratio at emergence

Totals of 2284 males and 2343 females were recorded of C.similis. A χ^2 value was calculated using a null hypothesis that the sex ratio is equality (χ^2 = 0.75 d.f. = 1, P.>0.30). This difference is not significant.

For C.equina a total of 2333 males and 2360 females was recorded. (χ^2 = 0.16, d.f. = 1, P.>0.50). Again the difference is not significant. From these results the sex ratio appears to be 1:1 for both species.

(6) THE EFFECTS OF THE AGE OF DUNG ON LARVAL MORTALITY AND ON THE WEIGHTS OF ADULTS OF C.SIMILIS

Initial observations had indicated that as dung aged it became increasingly less attractive to adults of C.similis and C.equina both as a food source and as a site for oviposition. To determine if this was coupled with a deterioration in its nutrient value the following investigations were carried out.

A large quantity of fresh stable horse dung only a few hours old was collected from one horse over a number of days. This was subjected to a temperature of below -30°C for several days to kill any sphaerocerid eggs present. Sheep dung less than 24hrs old was collected in the field, thoroughly mixed to give as homogeneous a medium as possible and then treated in the same way as the horse dung.

Samples of the fresh horse dung described above were exposed to cultures of C.similis for 24hrs and any eggs present at the end of this period were removed. 25 of these eggs were carefully inserted into crevices in each of three 50gm samples of horse dung that had been left in polythene bags in the laboratory for 24hrs. The samples were then placed in muslin topped jars at 15°C until the adults emerged, and these were then killed, sexed, and weighed.

From the 75 eggs, 39 males and 33 females emerged with mean weights ($\pm$ S.E.) of 2.04 $\pm$ 0.057mgm and 1.99 $\pm$ 0.056 respectively. The difference is not significant ($t = 0.4$, $P. > 0.6$) and, therefore, the sexing of individuals in subsequent experiments was unnecessary.

The mean weight of the adults was not significantly altered by either doubling or halving the quantity of dung per egg and so it was concluded that 2gm of dung per egg was quite sufficient to allow normal development.

To simulate ageing, samples of dung were placed in unsealed polythene bags at 10°C for up to 6 weeks. Eggs were obtained, as previously described, and 25 were placed in two 50gm samples of each of the various ages of horse and sheep dung. These were kept at 15°C in muslin topped jars, and any adults that emerged were weighed. 25 eggs were also placed in each of four 50gm samples of freshly thawed horse dung and also left at 15°C. After 3 days, 50 larvae were isolated from these samples and 25 were carefully inserted into each of two 50gm samples of fresh horse dung. These were then returned to 15°C and any adults that emerged were killed and then weighed.

In Table 10 the larval mortality and the mean weight of adults that emerged from samples of horse and sheep dung of different ages are shown. Values of "t" calculated from the number of adults that emerged from the samples are also shown.

TABLE 10. The effects of the age of dung on larval mortality and on the weights of adults

Sample No.	Type of dung	Age of dung in which eggs are placed	No. of eggs	Larval mortality %	Mean wt. of adults Mgm.	± S.E.
1.	Horse	24hrs at lab. temperature	75	5	2.01	± 0.078
2.	Horse	2 weeks at 10°C.	50	6	1.45	± 0.042
3.	Horse	6 weeks at 10°C.	50	96	0.28	± 0.0002
4.	Horse	Eggs put into fresh dung, 3 days old larvae to fresh dung	100 50 larvae	2	2.70	± 0.035
5.	Sheep	24hrs at lab. temperature	50	16	1.64	± 0.036
6.	Sheep	2 weeks at 10°C.	50	14	1.32	± 0.013
7.	Sheep	6 weeks at 10°C.	50	100	-	-

t. tests on samples	t.	P.
1 & 2	4.7	< 0.001
1 & 3	10.0	< 0.001
1 & 4	6.2	< 0.001
1 & 5	3.2	< 0.01
5 & 6	5.8	< 0.001

It can be seen from Table 10 that as horse and sheep dung increased in age, so there was a significant decrease in the weight of the adults that emerged, and an increase in the larval mortality, except between sheep dung of 24hrs and 2 weeks old, when the mortality in fact decreased from 16% to 14%. Larsen & Thompson (1940) found that very moist dung reduced the weight of the adults emerging, and this may have been the case with fresh sheep dung. However, it can be concluded that as dung ages so its nutrient value to larvae of C.similis decreases. Madle (1934) stated that dung beetles (Aphodiini) feed exclusively on albuminous substances in the dung and that only dissolved albuminous substances, vegetable albumens, and bacterial albumens occur richly enough to satisfy the alimentary requirements of the adults and larvae. Furthermore, he found that the dissolved albumens are quickly broken down by bacterial action. It is possible that C.similis larvae also feed on albuminous substances and that as the dung ages, so these substances are broken down, consequently reducing the nutrient value of the dung.

It can be seen from Table 10 that horse dung appears to be a more suitable medium for the development of C.similis larvae than sheep dung, as the larval mortality was less in horse dung, and the adults that emerged from 24hr old horse dung were significantly heavier than those that emerged from sheep dung of the same age.

From these results it can be seen that under field conditions it would be advantageous for the females to oviposit in dung as soon after deposition as possible.

(7) STARVATION OF *C.SIMILIS* ADULTS AT LOW TEMPERATURE

Observations in the field had shown that *C.similis* could survive the winter in the adult stage. Individuals have been found beneath the snow throughout the winter, even at Moor House Nature Reserve. The climate at Moor House has been described by Manley (1936) as sub-arctic, having many features comparable to those at sea-level in Iceland. The average temperatures from 1953-65 for December, January, February, were -2.0°C, -0.6°C, and -0.9°C respectively. Many adults may have to spend several weeks in these months trapped beneath the snow, possibly unable to feed either through the low temperature or the lack of food.

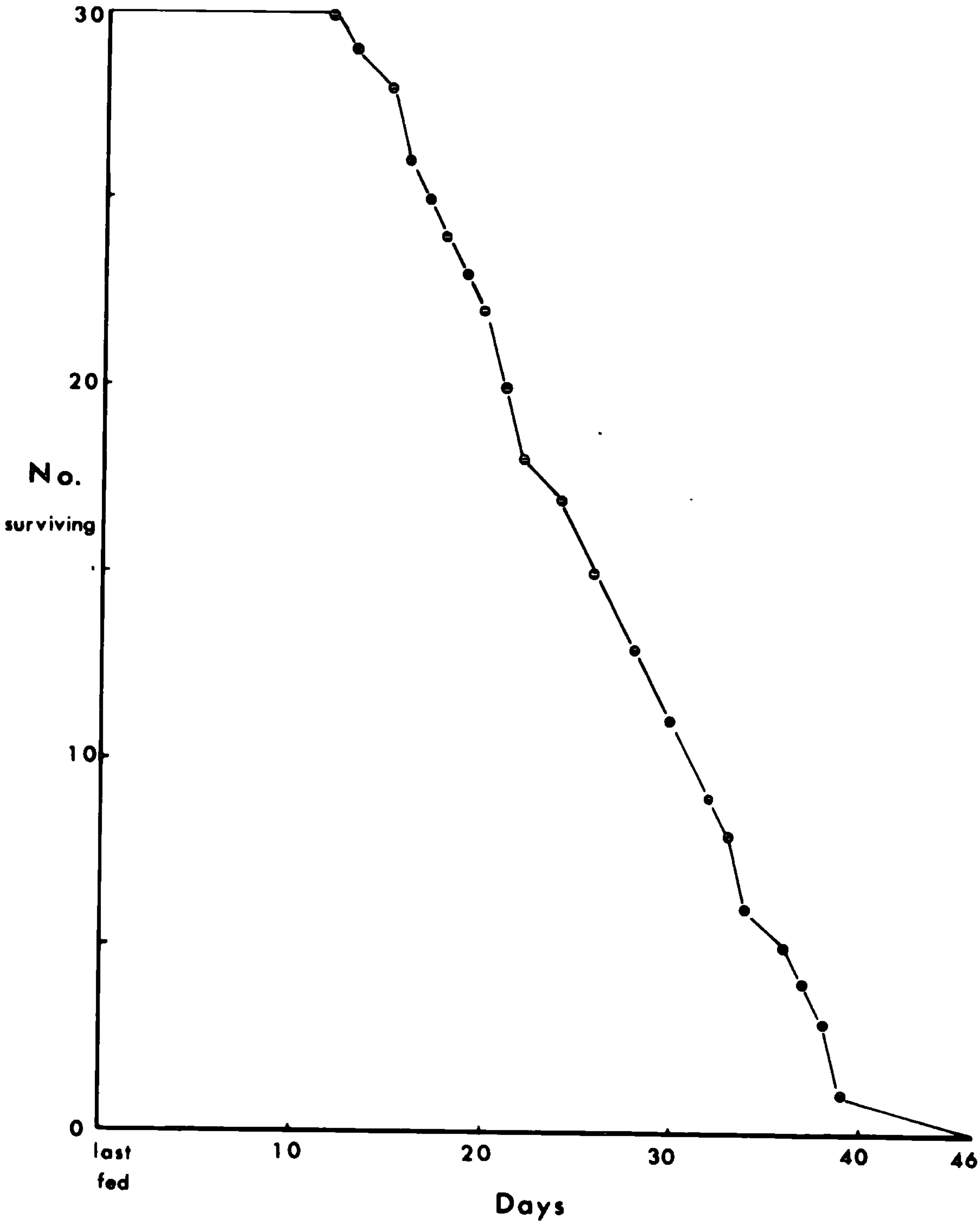
The following laboratory investigations were carried out to determine the ability of adults of this species to withstand starvation at low temperatures. 15 males and 15 females, approximately 2 weeks old, were placed individually in glass specimen tubes sealed with wads of cotton wool. The equivalent numbers of males and females of the same age were also placed in tubes with a small quantity of fresh horse dung. The 60 tubes were put into an incubator at 0.5°C (variations of ± 0.5°C were experienced during the experiment). The cotton wool was kept damp to avoid any dehydration. The tubes were examined each day and the number of deaths recorded. The dung was also inspected and changed every few days.

The survival rate is shown in Fig.2. The mean survival period ($\pm$ S.E.) for males and females was 26.5 $\pm$ 0.63 days and 27.6 $\pm$ 0.53 days respectively. This difference is not significant ($t = 0.97$, $P. > 0.3$). An unequal survival rate between males and females in the field would produce a discrepancy in the sex ratio. The mean survival period for all individuals was 27.0 $\pm$ 1.6 days.

After 46 days all the individuals that had been kept without food were dead, while only one out of those that had been fed had died. It can be concluded that starvation was almost entirely the cause of mortality.

The ability to withstand starvation at low temperatures for several weeks would be advantageous in the field as individuals that were trapped without food beneath the snow could survive until there was a thaw. Individuals that were trapped beneath the snow in dung would be able to feed and survive with only a low mortality.

Fig.2. Effects of starvation on the survival of <u>C.similis</u> adults at low temperature (approx. 0.5°C)

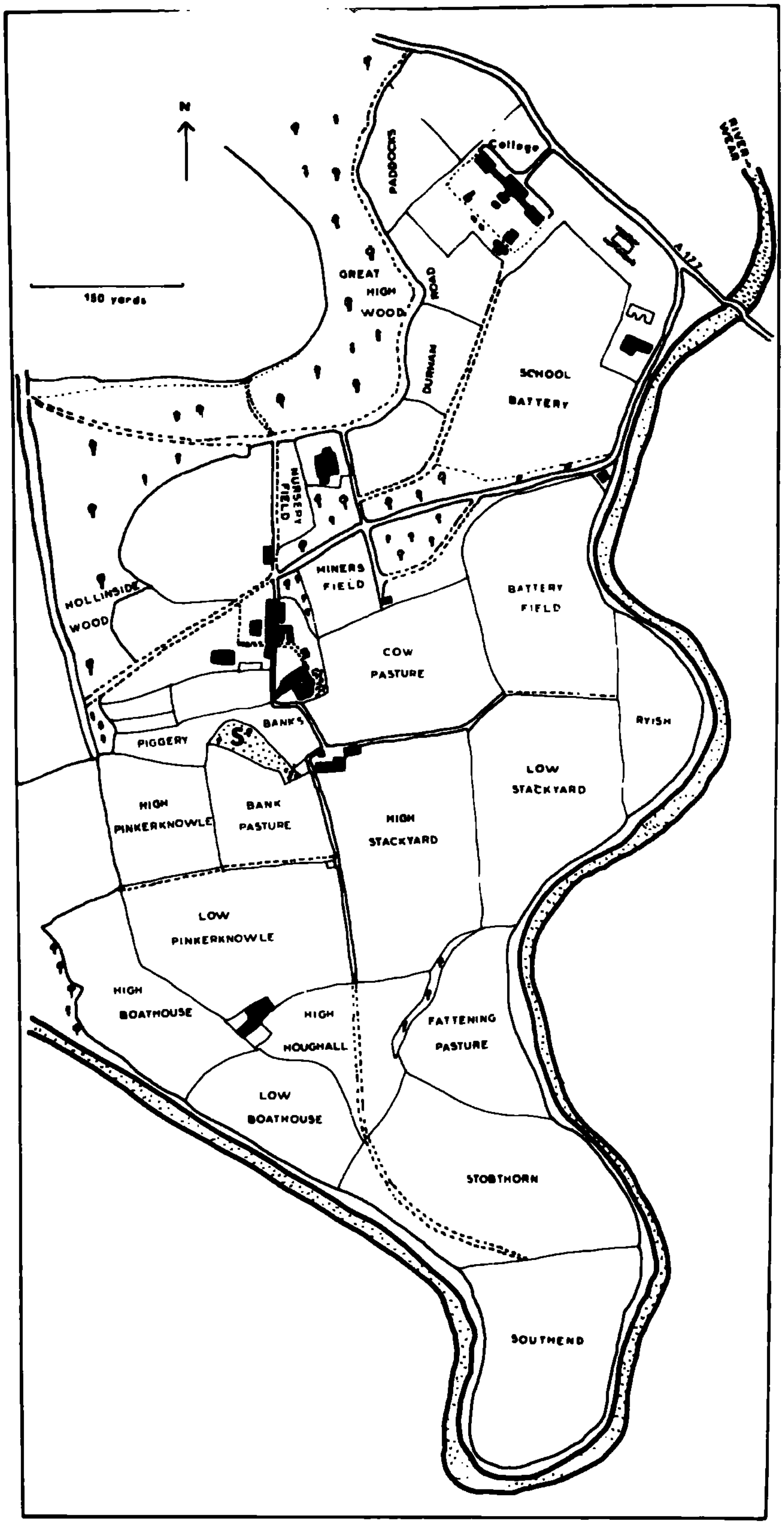

30
20
10
0
No.
surviving
last
fed
10
20
30
40
46
Days

II. STUDY AREA

Most of the present work was carried out at Durham School of Agriculture, Houghall farm (Nat.Grid.Ref. NZ/278405), which consists of a total of 476 acres bounded by mixed woodland to the west and by the river Wear to the south and east (Fig.3). The riverside fields are level and the soil is mainly alluvial in character. The land rises from the river by a series of terraces to the highest point, 250ft above sea level.

Fig.3. Study area : Houghall College of Agriculture,
Durham

HOUGHALL - THE STUDY AREA



III. QUANTITATIVE SAMPLING OF ADULTS

Field investigations were carried out on certain coprophilous Sphaeroceridae to estimate population densities in relation to time and space. The studies may be defined as "intensive" (Morris, 1960). The information required to achieve these objectives could only be obtained by sampling and consequently the choice of an efficient and accurate sampling technique was of paramount importance.

Laurence (1955), working at Rothamsted, studied the seasonal occurrence of larval and adult Sphaeroceridae associated with cow dung, using the "cow pat" as a sampling unit. However, at Houghall it was the policy to move the cattle out of fields during the winter. Thus, at a time when several species of Sphaeroceridae were abundant, the sampling unit was absent.

Laurence's sampling method was simply to collect as many adults as possible in 5mins from a cow pat, using small glass tubes. He maintained that it was possible to do this because the adults were difficult to disturb and did not readily fly. The only droppings present in the field throughout the year that could conceivably be sampled by a direct method such as this were from sheep and one carthorse. The sheep droppings, however, were far too variable in size and shape to be used as a sampling unit and there were insufficient droppings from the one horse. It was also found that the sampling technique suffers from certain disadvantages as its efficiency varies from species to species and according to the time of year. Adults of <u>C.similis</u> and <u>C.equina</u> readily fly during the warmer months, but not in the winter, making it easier to catch them at the latter time. Adults of <u>S.subsultans</u> are always reluctant to fly, making them easier to catch in the summer than the above species. Thus, an alternative sampling technique was required.

(1) ABSOLUTE POPULATION ESTIMATES

A technique was evolved to sample a unit area in the open field. A transparent perspex cylinder of known area (0.2sq.m), 50cms in height, with a muslin top and metal spikes attached to the lower lip, was rapidly pushed down into the vegetation and soil, trapping any Sphaerocerids present. A modified form of battery driven suction apparatus, described by Johnson, Southwood & Entwistle (1957), for sampling organisms inhabiting herb and ground strata, was used to extract the adults. The long rubber nozzle of the unit was inserted into the cylinder through the muslin top and drawn through the vegetation and over any dung present. This method proved to be reasonably successful during the summer, as most of the flies, on being disturbed, tended to fly on to the sides of the perspex cylinder and could easily be caught. However, during the colder months the flies tended to burrow down in the vegetation or dung, and attempts to extricate them usually proved futile. Therefore, the catch varied according to the prevailing weather conditions, rather than to the population density.

Marking methods were used in an attempt to determine the total population (Le Cren, 1965). 500 individuals were marked with aniline dust in an aspirator (Dalmat, 1950) and released in a field containing sheep and cows. 24 hours later 500 individuals were captured, but none were marked. Marked individuals can readily be detected as they leave a trail of the particular colour when dropped into a mixture of absolute alcohol, glycerine and chloroform. Subsequent captures in the same area over the next 2 days also failed to detect any marked individuals. It was obvious that mark and recapture methods were impracticable as adult Sphaerocerids are highly mobile and the population densities were too high.

(2) RELATIVE POPULATION ESTIMATES (POPULATION INDICES)

A. Sweep netting

Sweep netting (Parker, 1949; Linsley, Macswain & Smith, 1952) was tried, but proved unsuccessful, as the number of adults occupying the top of the vegetation was not wholly dependent upon the population density. Thus, in warm weather many sphaerocerids rested in the upper vegetation in the open field, but during the winter the adults tended to stay under the dung, or in the lower layers of the vegetation.

B. Sticky traps

Sticky traps (Broadbent, Doncaster, Hull & Watson, 1948; Lewis, 1959; Cornwell, 1960) were tried. These consisted of aluminium cylinders 18cm high and 5.5cm in diameter, coated with "stiktite" and supported vertically by a stake, with the base of the trap resting on the soil surface. 10 of these traps were placed around the perimeter of a field containing cattle at Houghall.

Adult sphaerocerids were readily caught, but their extrication proved time-consuming and damaging to the flies; consequently identification was difficult. Nelson (1965), working at Moor House Nature Reserve, had used sticky traps to catch adult sphaerocerids, but had later found detergent traps to be more efficient (pers.comm.).

C. Detergent traps

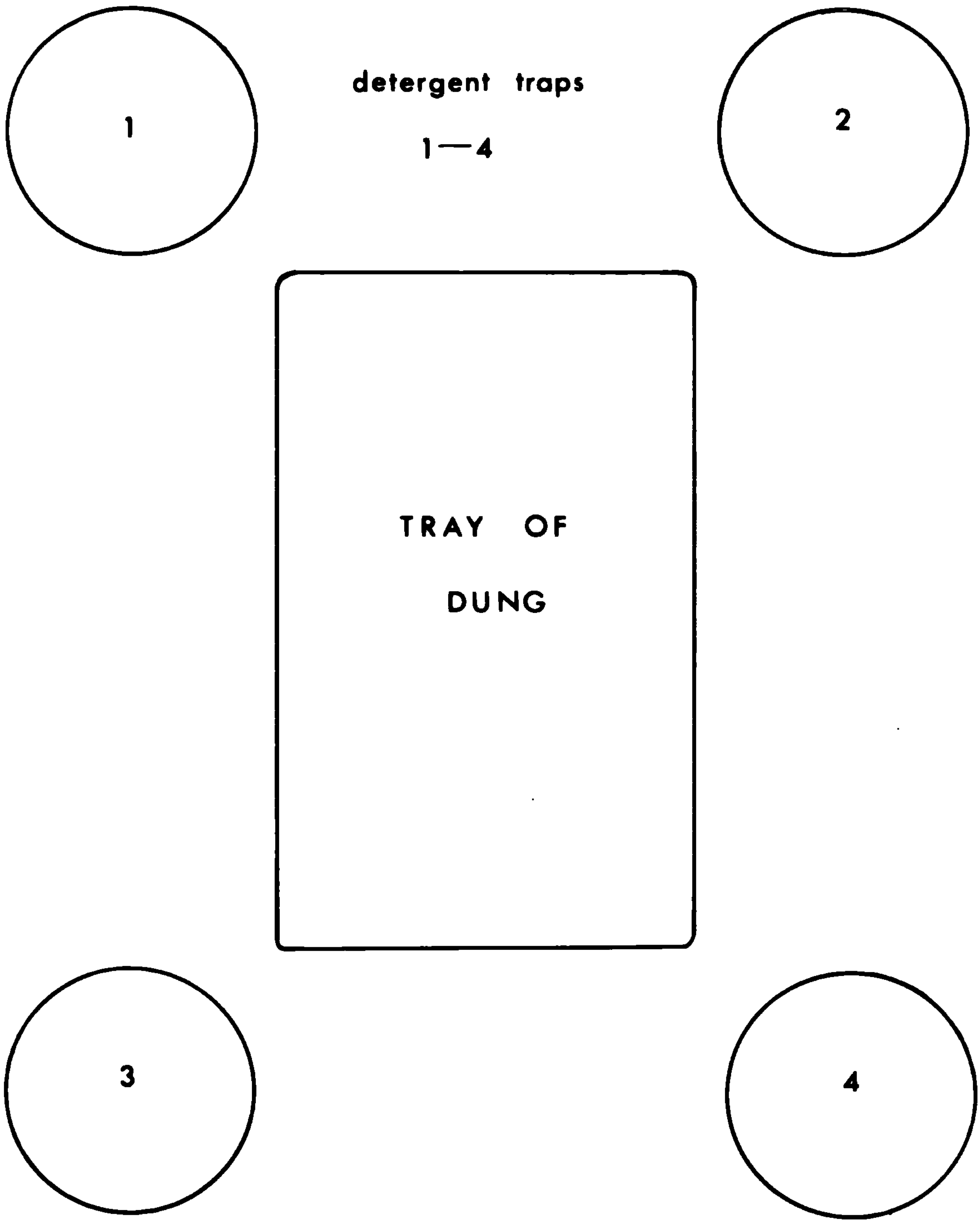
Detergent traps consist of bowls or trays filled with water to which a small quantity of detergent solution has been added to reduce the surface tension of the water. Omission of the detergent markedly reduces the number of insects caught (Harper & Storey, 1962). 24 plastic bowls, 15cm in diameter at the mouth and 11cm deep, were sunk into the ground with their rims level with the soil surface, around fields containing cattle. The traps had to be placed outside the boundary fences as the cattle are always liable to damage them or drink the detergent sample. After 7 days they were emptied, but although adult sphaerocerids were abundant in the field, relatively few were captured.

To increase the effectiveness of the detergent traps, fresh dung, usually horse dung from a nearby stable, but on occasions cow, pig, and sheep dung, were used as bait.

Two methods were employed. Firstly, for studies where the dung had to be left in the field for several days (e.g. studies on the seasonal distribution of adults), plastic trays 36cm x 22cm and 4.5cm deep were sunk into the ground with their rims level with the soil surface. A layer of fresh turf, approximately 3cm in thickness, was placed in each tray, and 1500gms of fresh horse or cow dung, which had previously been subjected to below $-30^{\circ}C$ for several days in sealed polythene bags, was placed on the turf. Plastic bowls (measurements as above) were sunk into the ground with their rims level with the soil surface, 5cm from the corner of each tray (Fig.4). The bowls were filled with water and a little detergent solution, and any flies that were caught were removed by pouring the contents of the bowls through a fine sieve. (These traps will be referred to throughout as type A.)

The second method was used when large catches were required in a matter of hours. The traps consisted of rectangular metal trays, 56cm x 37cm and 6cm deep, filled with water and a little detergent solution. A weighted plastic box, 10cm x 15cm and 7cm deep, was filled with fresh dung and placed in the centre of each tray. The small quantity of dung aged rapidly and required changing every 2 - 3hrs. The traps were not sunk into the ground. (These traps will be referred to throughout as type B.)

Fig.4. Arrangement of 4 detergent traps (15cm in diameter) around a tray containing horse or cow dung


detergent traps
1—4
1
2
TRAY OF
DUNG
3
4

IV. SPATIAL DISTRIBUTION OF ADULTS AT HOUGHALL

Richards (1930) stated that nearly every species of Sphaeroceridae occurs in a range of habitats, and in nearly all cases the flies occur wherever material suitable for their larvae is found. He also pointed out that if carrion and dung were to be examined numerous species would be found that are absent or very rare in the surrounding area when all the other factors are the same.

(1) THE EFFECTS OF HORSE DUNG ON DISTRIBUTION IN THE OPEN FIELD

By introducing quantities of fresh horse dung into an area free from farm animals, and sampling in the immediate vicinity of the dung and at least 10m away from it, the influence of the dung on the distribution of adult sphaerocerids could be estimated. A fenced area next to the "Bank Pasture" field (Fig.3) was used as a sampling site. The area sloped gradually from point A to point C, and steeply from sides CD and DE to side AB (Fig.5). The whole site was covered with dense bracken, except for a peripheral strip of grass varying from 0.5 - 8m wide. Along side EF there was a line of hawthorn bushes, and in corner A,B,C there were a number of small conifers.

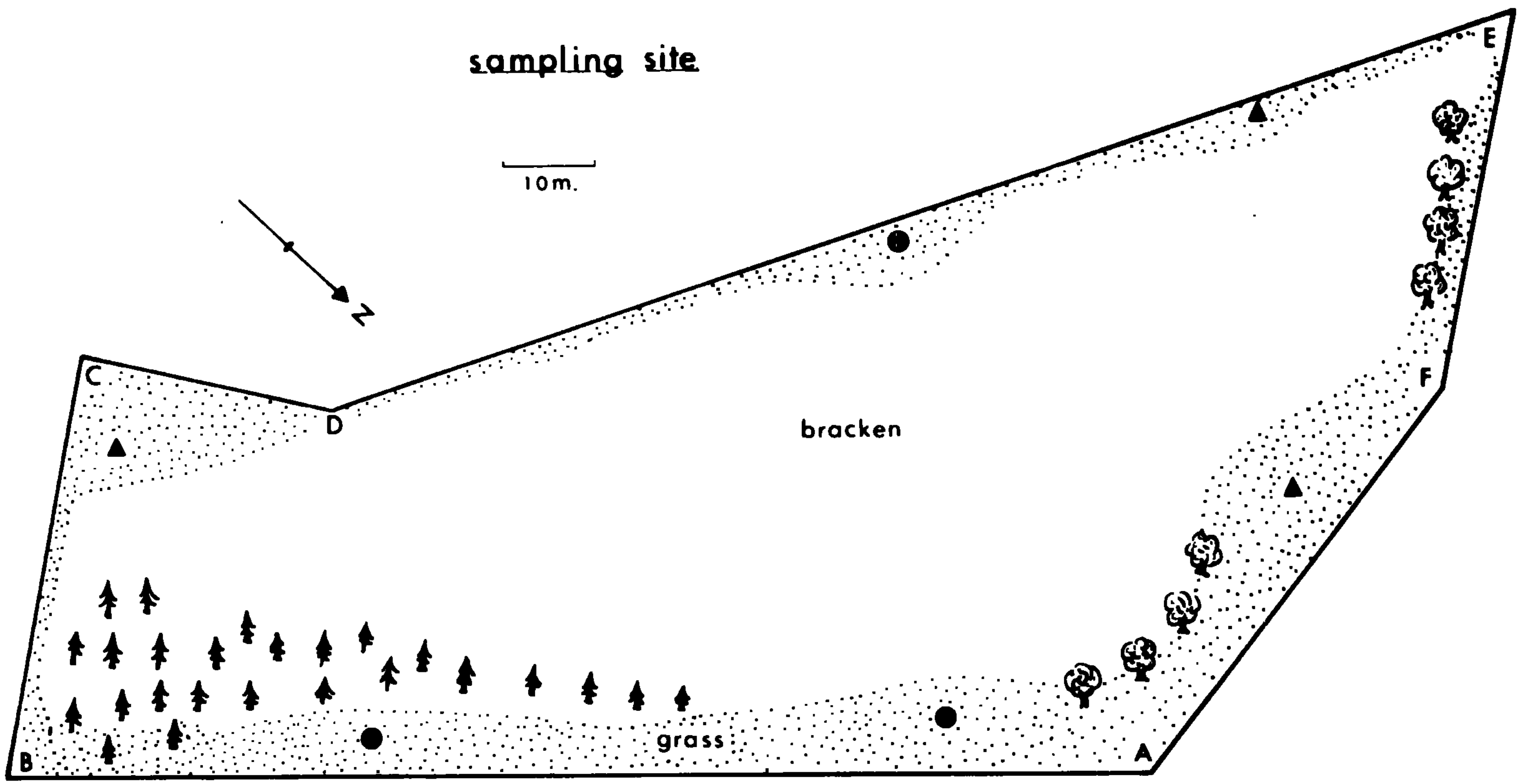
Three sets of 4 detergent traps (type A) were sunk into the soil, around trays of fresh horse dung, in flat areas of the peripheral grass strip, 3 - 5m from the fence (Fig.5). The detergent traps around trays of cow dung, shown in Fig.5, were used in the study of seasonal occurrences of adults and were not

Fig.5. Fenced sampling site at Houghall (shown on Fig.3 as 'S')

● 4 detergent traps around a tray containing horse dung

▲ 4 detergent traps around a tray containing cow dung

sampling site



present in the fenced area at the time of these investigations. 12 detergent traps of the same dimensions were also sunk into the ground, at least 10m apart, in the grass strip. The vegetation was cut short around the detergent traps in case its heterogeneity in the different areas affected the number of adults caught.

Sampling was carried out for 4 weeks continuously in May and June of 1964. The old dung was replaced by fresh dung once a week. The contents of the bowls were sieved off at least once every 3 days, and catches were taken to the laboratory for sorting and identification. The level of the detergent solution was kept within a few mm of the lips of the bowls.

During the 4 weeks, 3820 adults were caught in the traps close to dung, 97.4% of the total number caught. Only 101 adults, 2.6% of the total, were caught in the detergent traps away from dung. It can be seen from Table 11 that significantly more adults of each species were caught close to dung than away from it.

TABLE 11. A comparison between the total numbers of adults caught in 12 detergent traps close to horse dung, and in 12 detergent traps away from dung, May - June 1964. χ^2 values have been calculated using a null hypothesis that the distribution of adults is equality

	No.of adults caught close to dung (T_1)	No.of adults caught away from dung (T_2)	$T_1:T_2$	χ^2	P.
C.similis	739	17	43.4:1	100+	< 0.001
C.equina	1009	16	63.1:1	100+	< 0.001
C.hirtipes	1408	50	28.2:1	100+	< 0.001
C.nigra	551	17	32.4:1	100+	< 0.001
S.subsultans	113	1	113.0:1	100+	< 0.001

The ratio between the number of adults caught in traps near to horse dung, compared with those away from dung, is dependent upon the habits of the species involved. Thus, the greater the tendency to aggregate in and around horse dung, the higher the ratio. This tendency appeared to be more highly developed in adults of C.equina and S.subsultans; ratios of 63.1:1 and 113:1 were recorded respectively. Adults of C.nigra and C.hirtipes were less closely associated with horse dung; ratios of 32.4:1 and 28.2:1 were recorded respectively. C.similis was intermediate in its distribution, with a ratio of 43.4:1. (The ratio for each species was similar over the 4 weeks of trapping).

(2) RELATIVE ATTRACTIVENESS OF DUNG FROM DIFFERENT FARM ANIMALS

To compare the relative attractive powers of cow, pig, sheep, and horse dung to adult sphaerocerids in the open field, and hence the effects on distribution, the following sampling procedure was carried out in August 1965. 4 detergent traps (type B), baited with fresh cow, sheep, pig, or horse dung, were placed at least 20m apart in the "Cow Pasture" field (Fig.3). The traps were left in position for 6hrs and the dung was renewed whenever it showed signs of ageing.

In Table 12 the total number of adults of each species caught in two 6hr periods by detergent traps baited with cow, sheep, pig, or horse dung are shown.

TABLE 12. Total numbers of adults caught in detergent traps in two 6hr periods with different types of dung. χ^2 values have been calculated.

No.of adults caught

	Horse dung 1	Pig dung 2	Sheep dung 3	Cow dung 4	Columns in χ^2 comparisons	χ^2	P.
C.similis	51	8	4	0	1 & 2	31.3	<0.001
					1 & 3	40.2	<0.001
C.equina	271	168	46	13	1 & 2	24.2	<0.001
					1 & 3	100+	<0.001
					1 & 4	100+	<0.001
					2 & 3	69.6	<0.001
					2 & 4	100+	<0.001
					3 & 4	18.6	<0.001
C.hirtipes	387	842	551	561	1 & 2	100+	<0.001
					1 & 3	28.7	<0.001
					1 & 4	31.9	<0.001
					2 & 3	60.7	<0.001
					2 & 4	56.3	<0.001
					3 & 4	0.9	>0.3
S.subsultans	4	4	0	0			

It can be seen from Table 12 that species were attracted to dung in decreasing attractiveness as follows :

C.similis Horse, pig, sheep, and cow dung. (The absence of adults from the traps baited with cow dung was probably due to the low numbers present in the area at the time). Cow dung was found to be attractive to this species by Laurence (1955).

C.equina — Horse, pig, sheep, and cow dung.

C.hirtipes — Pig, sheep, cow, and horse dung.

S.subsultans — The numbers caught were too low to permit any conclusions to be drawn.

From Table 12 it can be seen that C.similis is significantly more attracted to horse dung than to any other type of dung. The low number of adults caught in the traps baited with cow, sheep, and pig dung do not permit any conclusions to be drawn on their significance. However, it is worth pointing out that laboratory investigations on food choice (see Table 3, Section I) showed that pig dung was significantly more attractive than sheep or cow dung, while sheep dung was also significantly more attractive than cow dung. C.equina was similarly attracted to the different types of dung, with horse dung being significantly more attractive than any other type, and cow dung significantly less. Pig dung was also significantly more attractive than sheep dung. The relative attractiveness of the different types of dung to C.hirtipes was markedly different from C.similis and C.equina. Thus, pig dung was significantly more attractive than any other type of dung, while horse dung was significantly less attractive than any other type. The attractiveness of sheep and cow dung was not significantly different.

It appears that the distribution of adults of these species during the summer in the open field at Houghall will be mainly determined by that of the dung from farm mammals. The degree of aggregation around a particular type of dung varying with the species. There was no evidence to suggest that adults of C.equina were more confined to horse dung than adults of C.similis as Richards (1930) had stated. However, the ratio between the number of adults of C.similis and C.equina caught near dung and away from it (Table 11), possibly indicates that C.equina is more restricted to dung from farm animals than C.similis.

(3) DISTRIBUTION OF ADULTS IN SHADED AND EXPOSED SITUATIONS

Laurence (1955) concluded that,as Richards (1930) had recorded adults of the common species of Limosina and Copromyza from a wide range of habitats in most months of the year, their presence on cow droppings in the open field only at certain times in the year must, therefore, depend mainly upon their reactions to temperature and humidity in the field at these times. Laurence (1955) recorded adults of C.similis and C.equina as absent from dung in the field during July and August and the number of adults of C.hirtipes as greatly reduced, presumably in response to the conditions of high temperature and low humidity prevailing at the time.

Trapping was carried out at Houghall in shaded and exposed situations on 11 and 12 August 1965. It was dry and sunny on both days and metereological records at Houghall show that the screen maximum temperatures recorded on 11 and 12 August were 21.6°C and 22.1°C respectively. A temperature of 22.1°C was only exceeded twice during 1965.

Two detergent traps (type B) baited with fresh horse dung were placed 10m apart in the following open areas :

1. The "Cow Pasture" field (Fig.3) containing cows, sheep, and horses.
2. At the west end of the "Piggery Banks" field (Fig.3).

In the following shaded areas :

1. Dense bracken in the fenced area, shown in Fig.5.
2. A small wood adjacent to the "Miners Field" (Fig.3).

These traps were exposed during the periods of highest temperature, i.e. between 12.30hrs and 15.30hrs on 12 August, and 11.00hrs to 16.00hrs on 11 August. The dung was renewed whenever it showed signs of ageing. The detergent traps in the field with the farm animals had to be guarded almost continuously, but it was possible to run to the furthest sampling site to inspect the dung and back in 5mins.

The shade temperatures were recorded at 5cms above ground level and in the open the temperatures were recorded against a white card at 5cms above ground level at 15min intervals. The relative humidity was recorded just above the vegetation in the open field every 15mins and in the wood once every hour, using a whirling hygrometer. The results are shown in Table 13. The total number of adults (males and females) of each species caught during the 2 trapping periods are shown in Table 14.

TABLE 13. Temperatures at 5cms above ground level and relative humidities just above the level of the vegetation. (The temperature measurements were taken in the field)

	Exposed Temp. (°C)			Shade temp. (°C)		
	Average	Max.	Min.	Average	Max.	Min.
11 Aug.	24.1	28.0	21.0	19.2	21.5	16.8
12 Aug.	23.4	26.5	22.0	20.3	22.0	20.0

Relative Humidity (%)

	Open field			Wood		
11 Aug.	71	83	63	93	95	93
12 Aug.	68	71	65	93.5	94	93

TABLE 14. The total numbers of males (M) and females (F) caught in detergent traps on 11 and 12 August 1965

	SITE			
	Field with cattle	Field without cattle	Wood	Bracken patch
C. equina				
M	733	4	1	1
F	812	7	2	2
Total	1545	11	3	3
C. similis				
M	69	1	0	0
F	67	1	0	0
Total	136	2	0	0
C. hirtipes				
M	417	675	29	60
F	631	701	45	79
Total	1048	1376	74	139
S. subsultans				
M	2	1	0	0
F	4	0	1	0
Total	6	1	1	0
C. stercoraria				
M	0	0	0	0
F	1	1	0	0
Total	1	1	0	0
C. suillorum				
M	0	0	4	0
F	0	0	10	0
Total	0	0	14	0

C.similis : 98.6% of the total number of adults were caught by traps in the field containing the farm animals and 1.4% in the open field without animals. No adults were caught in the wood or bracken patch (Table 14).

C.equina : Similar results were obtained for C.equina. 98.9% of the total number were caught in the field with the farm animals. Only 0.2%, 0.7%, and 0.2% of the total number of adults were caught in the field without farm animals, in the bracken and in the wood, respectively.

C.hirtipes : Adults of C.hirtipes were the most abundant; 2637 were caught over the 2 days. It was also the most widely distributed species, but it was far more abundant in the open field. 39.7% of the total number of adults were caught in the field with farm animals and 52.2% in the field without farm animals, compared with only 2.8% and 5.3% in the wood and bracken, respectively.

Copromyza suillorum Haliday : Only 14 adults were recorded; 13 in the wood and 1 in the bracken.

Copromyza stercoraria Meigen : Only 2 adults of this species were recorded and both were in the open field.

S.subsultans : 6 adults were recorded in the field with farm animals, 1 in the field without animals, and 1 in the wood.

It is concluded that the distribution of adults of C.similis and C.equina at Houghall during the periods of trapping appears to have been mainly determined by the distribution of droppings from farm animals and not by the conditions of temperature and humidity prevailling in the open field during these times. It also seems probable that the distribution of adults of S.subsultans was governed by food sources, rather than by conditions of temperature and humidity.

It appears from Table 14 that the distribution of C.hirtipes is not so dependent upon the dung of farm animals as the above species, but more probably on a wider variety of food sources. Richards (1930) recorded that adults of this species had a wide range of habitats. The numbers of adults caught in the field containing farm animals may have been reduced by the large quantity of cow dung in the area as it is significantly more attractive to this species than horse dung (Table 12).

Adults of C.similis, C.equina, C.hirtipes, and S.subsultans were present and active in the open field at temperatures of 24+°C. Although higher temperatures do occur in northern England, the adults could easily avoid their effects by moving down into the vegetation; also, extremely low humidities are not likely to be experienced close to droppings, or low down in vegetation. It would, therefore, appear that these species will be present in the open field in northern England, at least during cool summers, such as that of 1965.

No adults of C.suillorum were recorded in the open field around cow or horse dung during the two and a half years of the present studies. Duda (1923) recorded adults of this species as abundant in damp woods and shady places in Germany, and Richards (1930) found adults to be common in woods on decaying fungus and carrion. As this species does not appear to leave the woods and areas of dense vegetation at any time during the year, it cannot be assumed that the low humidities and high temperatures in exposed conditions during the summer force the adults to remain in shaded situations. It seems more probable that they feed on various organic media which are more abundant in damp shaded places.

Laurence (1955) suggested that males of Limosina lugubris are probably more sensitive to low humidities than the females. It can be seen from Table 14 that there is no evidence to suggest that males of any of the above species are more restricted than females to shady, more humid, situations.

V. THE EFFECTS OF AGEING OF DUNG ON NUMBERS OF ADULTS PRESENT

Several authors have described the effects of ageing on the properties of cow dung and the succession of adult insects associated with this. Hammer (1941) found that species of flies exhibited rather striking differences in their times of arrival on fresh cow pats. Some appeared immediately after the dung had been deposited and others appeared mainly on droppings several hours, or even days, old. C.hirtipes was found on pats a few mins after deposition and under pats a few days old. Mohr (1943) in U.S.A. found that flies attained continual representation as long as the cow pats were occupied by adult insects, rising gradually to a peak in numbers, followed by a decline. Leptocera sp (unidentified) and C.equina adults reached a peak on the first day. He observed that the duration of Leptocera adults occupation of the pats was greatly affected by the prevailing weather conditions and that the whole succession could be 'telescoped'. Laurence (1955) found that adults of Limosina lugubris and L.scutellaris reached their maximum numbers on 2 days old pats and were absent on those 9 days old. However, L.collini was most abundant on pats 8 days old, and adults were still present on those 10 days old. Landin (1961) recorded Scopeuma stercoraria adults as the first species to invade cow droppings.

Handschin (1932) observed a change in the colour and odour of cow dung 4 days after deposition. Previously, the dung attracted *Lyperosia*, but not its parasite *Sphalangia*. Between 4 and 10 days, the dung was only attractive to the latter, but after 10 days it was attractive to neither. It is pertinent at this juncture to point out that insects seem largely attracted to dung by airborne molecules (odours) emanating from the odorous constituents. Any alteration in the attractiveness of the dung, as it ages, will be caused by the loss of volatile constituents to the atmosphere, by biochemical decomposition and by the formation of a crust on certain types of dung, e.g. cow dung, which tends to prevent the odours from escaping. The rate at which these processes occur, for a particular type of dung, will be dependent upon the prevailing weather conditions.

(1) DUNG AGEING EXPERIMENT USING DIRECT SAMPLING

9 trays, containing 1500gms of fresh stable horse dung, were placed at least 10m apart in the "Piggery Banks" field (Fig.3). After 24hrs any adult sphaerocerids present on the dung were collected with an aspirator, killed by sucking in ether, and later identified in the laboratory. Sampling by this method was executed at 24hr intervals up to 10 days from the initial exposure time. A further set of 9 trays, containing 1500gms of fresh horse dung, was placed in the same area 3 days from the onset of the investigations, and similarly sampled. A final set of 9 trays of horse dung was also placed in the area 6 days from the onset of the investigations, and similarly sampled.

This situation represents a simplified version of what would normally occur when cattle or horses are admitted to a field for 6 days, and then removed. 10 days after the cattle were first admitted, there would be a large number of droppings from 4 - 10 days old. After 10 days of these investigations, there were 9 trays of dung 10 days old, 9, 7 days old, and 9, 4 days old.

The rate of ageing of the dung is directly related to the prevailing climatic conditions in the environment close to the dung, referred to by Landin (1961) as the "lococlimate". Accurate measurements of these conditions would have necessitated relatively sophisticated and expensive equipment being left in the field over the period of investigations. This had to be avoided, as the chances of the equipment being damaged or stolen was high. However, the lococlimate is influenced by the "macroclimate" (Geiger, 1950), i.e. the climate that is recognised from the meteorological aspect as that prevailing at about 1.5m or more above the ground surface. The meteorological data for the appropriate periods (from Houghall Observatory) is shown in Appendix 1.

A. Effects of ageing of the dung on the number of adults caught daily

The effects of the ageing of the dung on the number of adults present is shown by summing the daily number of males and females of each species caught on dung 1 - 4 days old (no adults were recorded on dung older than 4 days), and expressing these values as percentages of the total number of adults caught, of the particular species (Fig.6).

C.similis : There was a slight decrease in the percentage of adults caught from day 1 to day 2, but there was actually a slight increase in the percentage of males caught (Fig.6). On the third and fourth days there was a more marked decrease in the percentages caught. (A total of 160 males and 186 females were caught over the 10 days).

C.equina : Unlike C.similis the percentage of adults caught reached a maximum on the second day but, as with C.similis, this was followed by a marked decrease on the third and fourth days (74 males and 92 females were caught).

S.subsultans : There was a progressive decrease in the percentage of adults caught from the first to the fourth day (327 males and 353 females were caught).

C.hirtipes : The progressive decrease in the percentage of adults caught from the first to the fourth days was more dramatic than for C.similis or S.subsultans, and in fact no adults were caught on the fourth day (327 males and 353 females were caught).

Adults of C.similis, S.subsultans, and C.hirtipes were strongly attracted to fresh dung, particularly the latter, with maximum numbers recorded on the first day. Adults of C.equina were also attracted to fresh dung, with maximum numbers recorded on the second day. The results in Fig.6 show that the males and

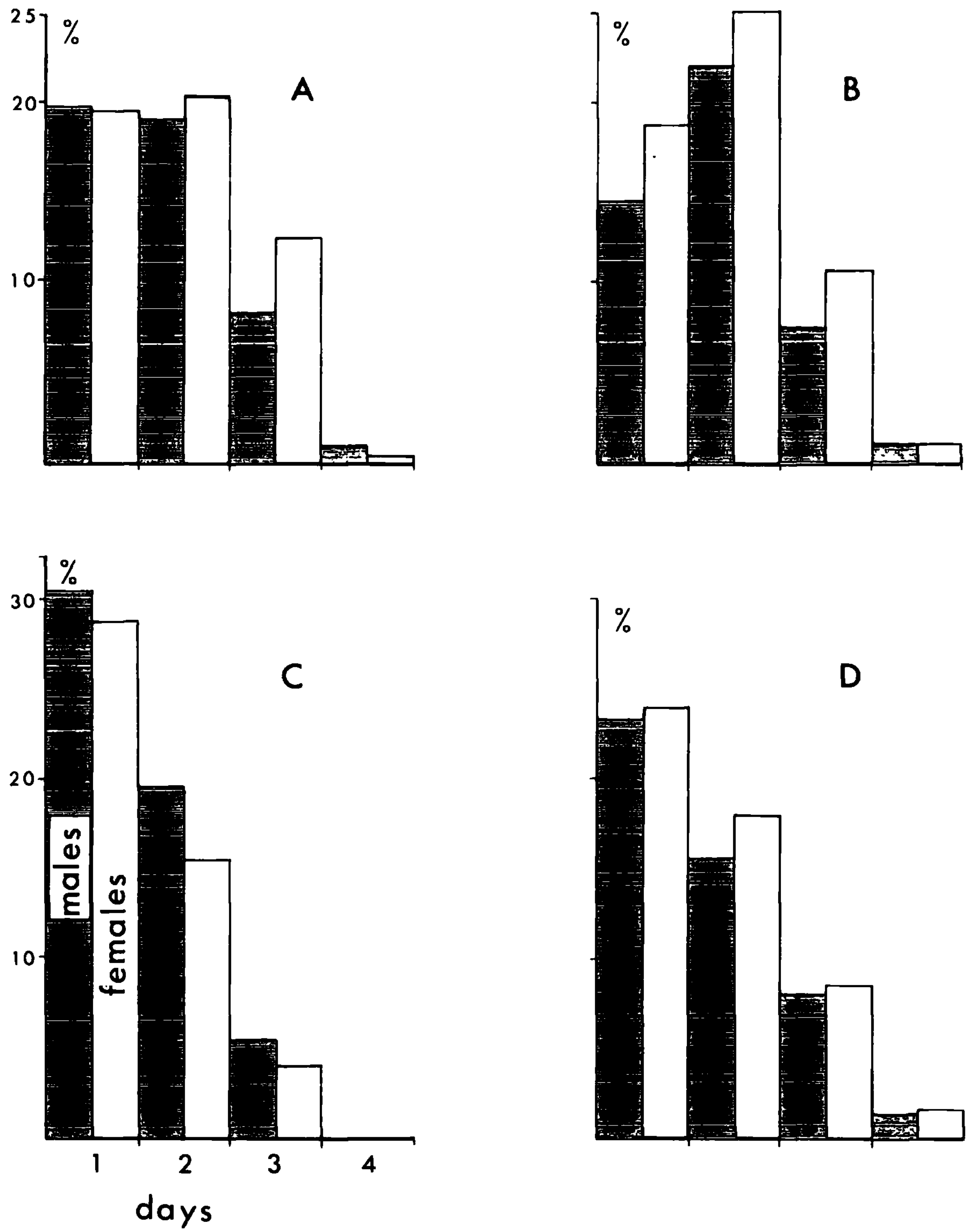
Fig.6. Percentages (males and females) of total number of adults of each species caught daily on dung 1 - 4 days old. June - July 1964

A. C.similis

B. C.equina

C. C.hirtipes

D. S.subsultans



25
%
20
10
A
B
%
%
30
20
10
C
D
males
females
1
2
3
4
days

females of each species reacted similarly to the ageing of the dung.

B. Influence of weather conditions on the rate of ageing of dung

The daily numbers of adults caught is dependent upon the attractiveness of the dung, which is directly related to its rate of ageing. This in turn is controlled by the prevailing weather conditions. The 3 sets of trays of dung were placed in the field at consecutive 3 day intervals, and sampling was carried out daily for 10 days from the time when the first set of trays was placed in the field, but adults were never caught on 2 separate sets of trays at the same time. Thus, as the dung in the 3 sets of trays was initially the same, any differences in the pattern of succession of adults, occupying the dung on the 3 sets of trays, will be mainly determined by differences in weather conditions over the 10 days.

In Fig.7, the numbers of adults of each species caught daily, in each of the 3 sets of trays of dung, are expressed as percentages of the total number of adults of the particular species recorded on that set of trays.

C.similis : With the first set of trays of dung the maximum percentage of the total number of adults was recorded on the first day and the percentages were drastically reduced on the second and third days. No adults were caught on the fourth day. With the second set, the percentage of adults reached a maximum on the second

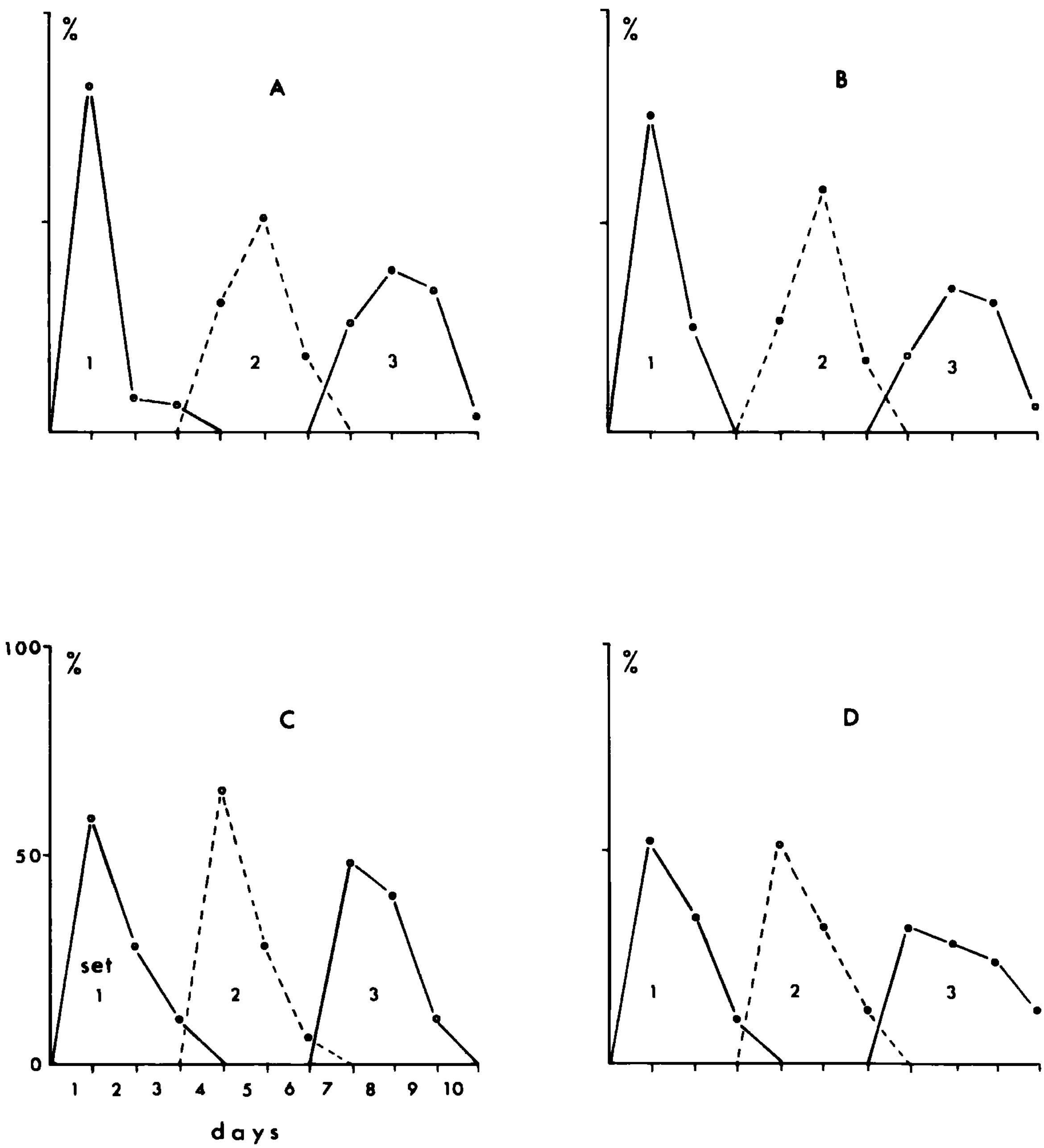
Fig.7. Percentage of total number of adults of each species caught daily on each of 3 sets of trays of horse dung. June - July 1964

A. C.similis

B. C.equina

C. C.hirtipes

D. S.subsultans



%
A
1
2
3
%
B
1
2
3
100
%
C
50
set
1
2
3
0
1 2 3 4 5 6 7 8 9 10
days
%
D
1
2
3

day, followed by marked reduction on the third day. Again, no adults were caught on the fourth day. A lower maximum percentage was recorded on the second day for the third set and there was a less drastic reduction on the third and fourth days than previously experienced.

C.equina : The results for C.equina and C.similis were very similar. Thus, for the first set the maximum percentage was recorded on the first day, while for the second and third sets it was recorded on the second day. As with C.similis the lowest maximum percentage was recorded for the fourth set.

C.hirtipes : The maximum percentage was recorded on the first day for all 3 sets and no individuals were caught on dung older than 3 days. Again, the lowest maximum percentage was recorded for the third set.

S.subsultans : As for C.hirtipes, the maximum percentages were recorded on the first day for all 3 sets and the lowest maximum percentage was recorded for the third set.

The dry, warm (mean daily max.temp., 19.8°C) and sunny (mean daily sunshine, 9.9hrs) conditions prevailing over the first 3 days (see Appendix 1) rapidly dried out the dung, causing it to age quickly. This was reflected by the high maximum counts that were recorded on the first day. The cooler (mean daily max.temp., 17°C), less sunny (mean daily sunshine, 6.5hrs) conditions over the fourth, fifth, and sixth days, and the 0.01ins of rain, tended to reduce the rate of ageing of the dung, compared with the first 3 days. Thus, the maximum daily catch for C.similis and C.equina was recorded on the second day. Although the mean daily max.temp. was 19.4°C over the last 4 days of the investigations, there was less sunshine (mean daily sunshine, 6.1hrs) and the humidity was higher (see Appendix 1), with 0.6ins of rain. The dung dried out more slowly than in the previous periods and consequently the rate of ageing was reduced. Thus, the maximum percentages recorded for the third set of trays were the lowest for any set.

It is interesting to note that with the first 2 sets of trays no adults were caught in the fourth day. This may have been because of the rapid rate of ageing of the dung during these periods, or more likely it was due to the older dung being unattractive in the presence of fresh dung, particularly with the second set of trays. The fact that adults of all species except C.hirtipes were caught on the fourth day, on the third set of trays of dung, was probably due not only to a slow rate of ageing of the dung over the last four days, but also that the older dung was not in competition with fresh dung.

C. Possible factors affecting the number of adults caught

Two days after the dung from the previous experiment had been removed, 9 similar trays of fresh horse dung were placed in the same area. 100 Copromyza spp. (not identified) and 100 S.subsultans adults were collected off the dung on the first day, in 2 aspirators, and marked with red and green aniline dust respectively, (as previously described). They were simultaneously released 8hrs after the dung was first put out, and adults were collected, as before, at 24hr intervals.

In the 10 day experiment, the total numbers of adults of C.similis, C.equina, C.hirtipes, and S.subsultans caught were 352, 166, 522, and 680 respectively. The relationship between these figures and the total number of adults of each species that actually visited the dung was almost certainly not constant. Firstly, individuals of S.subsultans tended to remain beneath the dung and did not readily fly, making them relatively easy to catch, but adults of the Copromyza spp. flew far more readily and tended to move off the dung into the surrounding vegetation. This made adults of the Copromyza spp. more difficult to locate, and they often evaded capture by flying away. Secondly, the mark and recapture investigations indicated that S.subsultans adults tended to remain on, or in the immediate vicinity of the dung for longer periods than the adults of the Copromyza spp. Thus, 16hrs after the marked individuals were released, 99 Copromyza spp. adults were collected, none of which were marked, while 60 individuals of S.subsultans were caught, 3 of which were marked. After a further 24hrs, 76 Copromyza spp. adults were collected, none of which were marked, while 2 of the 42 S.subsultans adults caught were marked. No marked individuals were recorded after this time. This suggests that S.subsultans adults are less mobile than those of Copromyza spp.

Therefore, comparisons cannot be made between the actual numbers of S.subsultans and Copromyza spp. that were caught.

The number of adults of a particular species caught daily on the dung will not only depend upon the effectiveness of the sampling method, but also upon :

(a) The population density at the time.

(b) Activity, i.e. the rate of movement on to the dung.

(c) The presence of alternative food sources in the immediate vicinity of the sampling area.

(d) The attractiveness of the dung.

Any natural changes in population density that were likely to have occurred during the 10 day period would probably have affected the daily number of adults caught only to a minor degree. The results obtained from the mark and recapture investigations showed that the removal of adults (by collecting) would probably not have reduced the population density to a significant extent.

If the population density in the area was reasonably constant over the 10 day period, then the daily level of activity of a particular species will be mainly determined by the prevailing weather conditions. The fluctuations in climatic conditions experienced over the period of investigations cannot account for the dramatic variations in the number of adults caught. There were no farm animals in the immediate vicinity of the sampling site, so the effects of alternative food sources would probably be insignificant.

Therefore, it is concluded that the attractiveness of the dung was probably the main factor in determining the pattern of succession of adults.

(2) DUNG AGEING EXPERIMENTS USING DETERGENT TRAPS

Twelve detergent traps (type A) were sunk into ground around 3 trays of fresh horse dung, and 12 such traps were also sunk in the ground around 3 trays of fresh cow dung. The trays were placed at least 30m apart (Fig.5). The traps were emptied daily until 2 clear days elapsed when no adults had been caught. Such a programme was executed with horse dung in May - June 1964 and with cow and horse dung during Aug. 1964 and Apr. 1965.

The daily Met. records from Houghall Agricultural College Observatory, for the appropriate periods, are shown in Appendix 2.

A. Effectiveness of trapping method

Observations on adults of the *Copromyza* spp. had indicated that they moved on to the dung by running over the vegetation, or by short flights. Often, after spending some time on the dung, they tended to move into the vegetation in the immediate vicinity. These characteristics made them particularly liable to be caught in detergent traps set around dung. However, *S.subsultans* adults mainly moved on to and off the dung by running over the vegetation, and they appeared adept at avoiding the traps, probably due to their powerful hind legs. They also tended to remain on or under the dung once they had reached it. The proportion of adults of this species that visited the dung and were caught in the detergent traps was almost certainly less than for the Copromyza spp. Thus, direct comparisons between actual numbers of adults of S.subsultans and the Copromyza spp. cannot be made.

B. Effects of ageing of dung on the number of adults caught daily

In Figs. 8, 9, and 10, cumulative percentages have been calculated on the number of adults of each species caught daily (when a sufficient number were caught). In Table 15 the total numbers of adults of each species caught in the trapping periods, the number of days over which they were caught, and the day of the maximum catch, are shown. The times in which the first two-thirds of the total numbers of adults of each species were recorded (from Figs. 8, 9, 10), are also shown.

Fig.8. Cumulative percentage of adults of each species caught daily in 12 detergent traps (type A) around horse dung. May - June 1964

A. *C.similis*

B. *C.equina*

C. *C.nigra*

D. *C.hirtipes*

E. *S.subsultans*

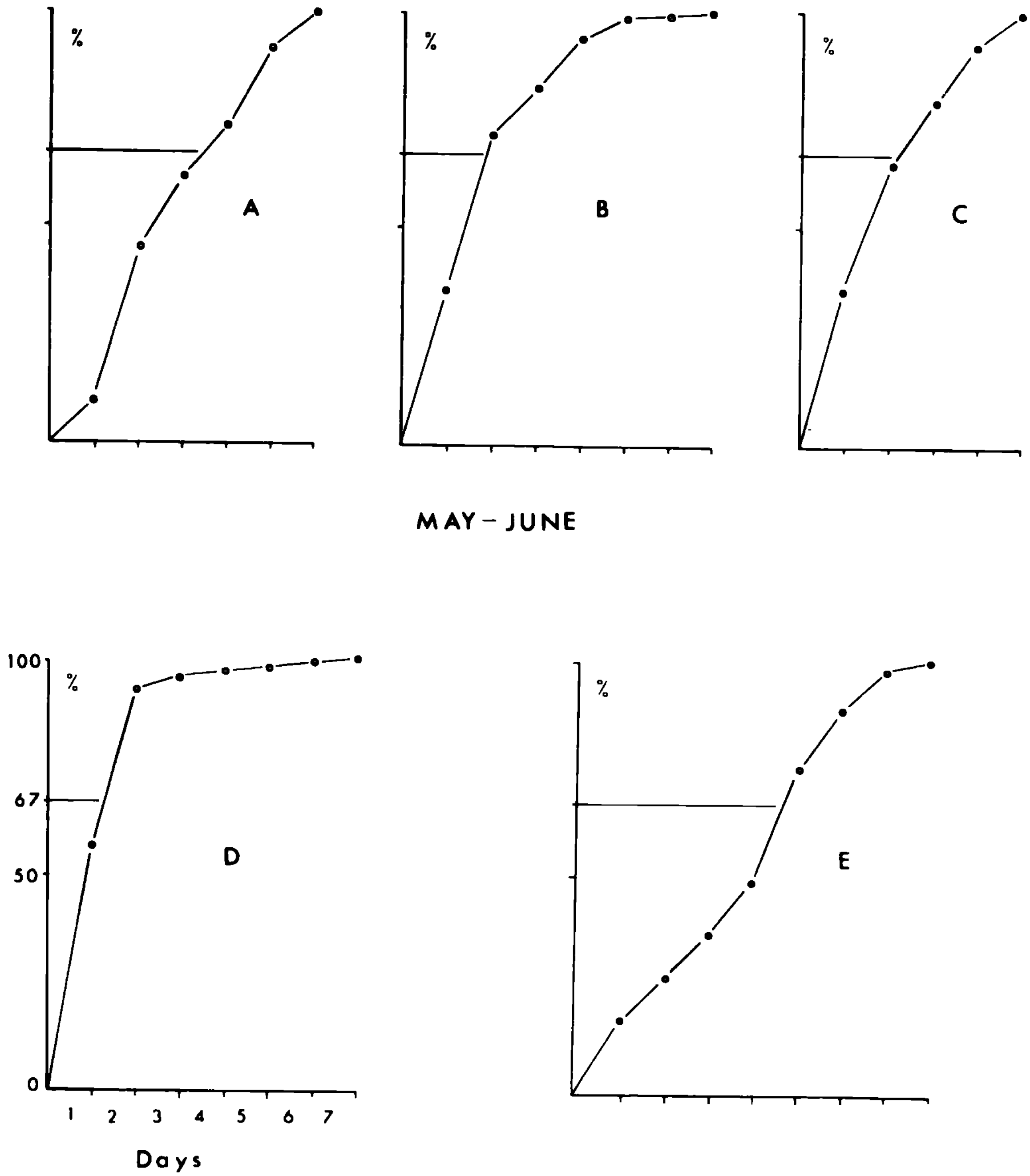

%
A
B
C
MAY – JUNE
100
67
50
0
D
E
1 2 3 4 5 6 7
Days

Fig.9. Cumulative percentage of adults of each species caught daily in 12 detergent traps (type A) around (1) horse dung (2) cow dung. August 1964

(1) horse dung ————————

(2) cow dung - - - - - - - - - - - - -

A. C.similis

B. C.equina

C. C.hirtipes

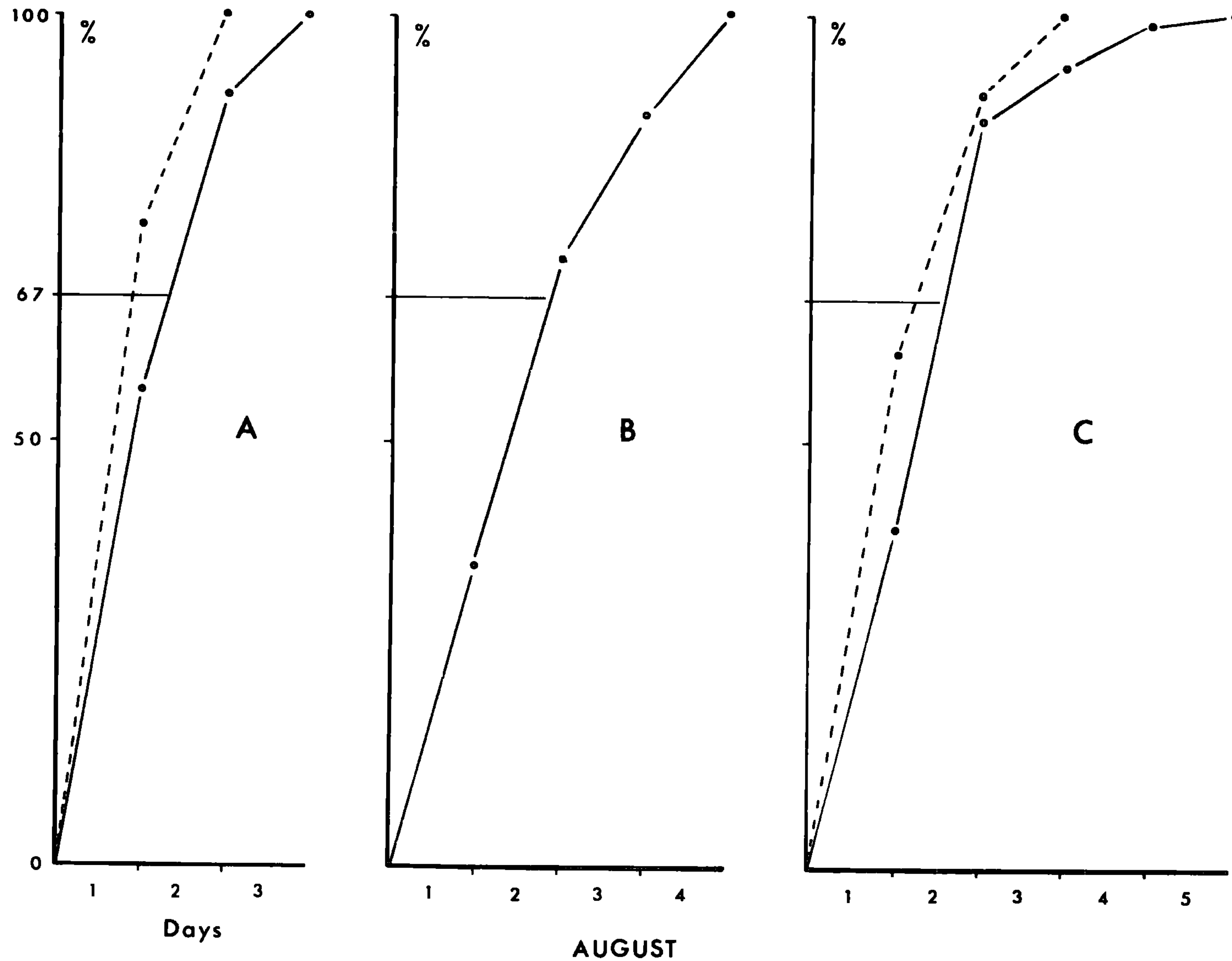

100
67
50
0
%
A
B
C
1
2
3
4
5
Days
AUGUST

Fig.10. Cumulative percentage of adults of each species caught daily in 12 detergent traps (type A) around (1) horse dung (2) cow dung. April 1965.

(1) horse dung ————————

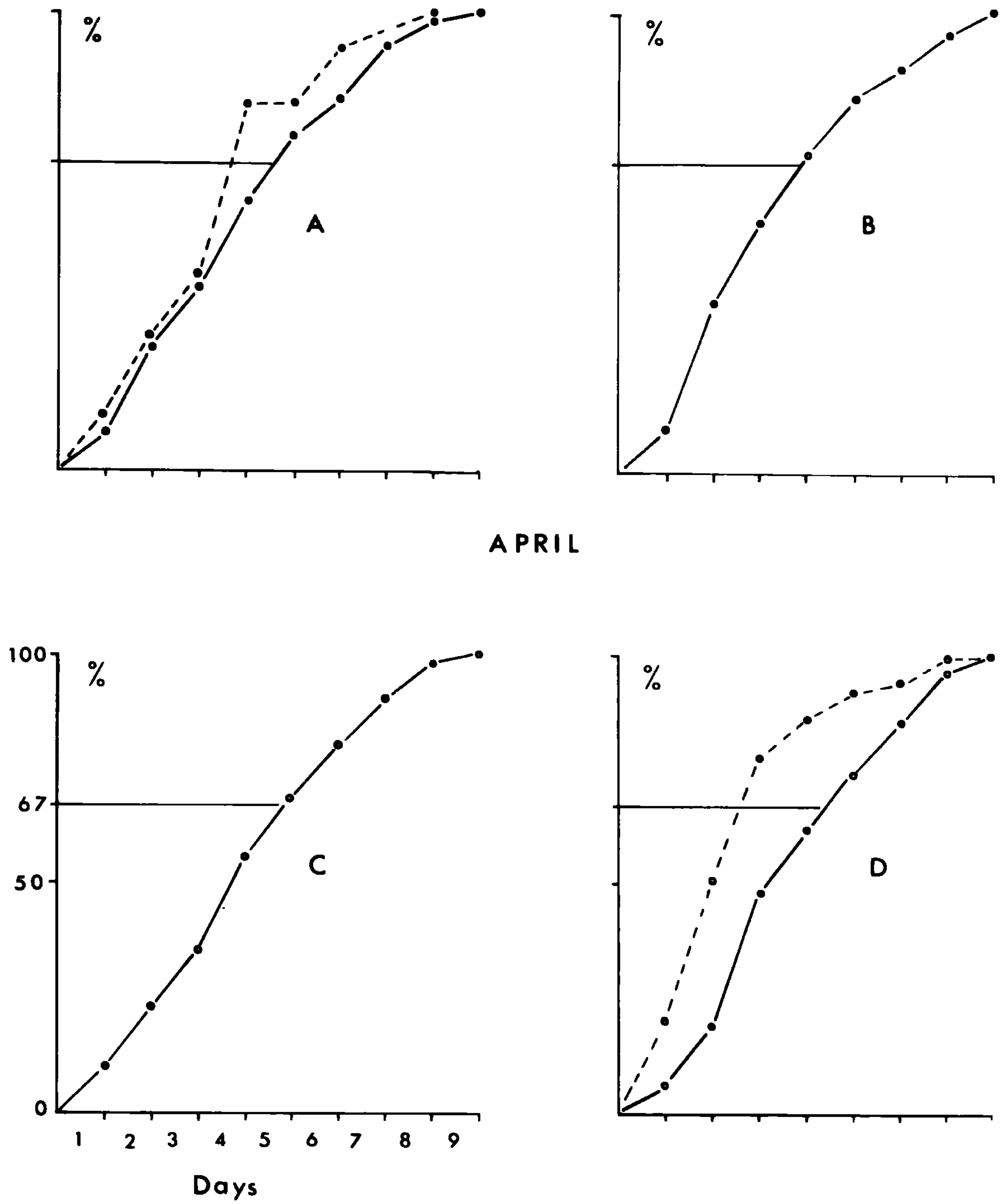
(2) cow dung - - - - - - - - - - - - - -

A. C.similis

B. C.equina

C. C.nigra

D. C.hirtipes



%
A
%
B
APRIL
100
67
50
0
%
C
1
2
3
4
5
6
7
8
9
Days
%
D

TABLE 15. The total numbers of adults caught in detergent traps around (1) horse dung and (2) cow dung in Aug.1964 and Apr.1965, and around horse dung in May - June 1964. The period in which they were caught, the day of the maximum catch, and the time in which the first 67% of the total number of adults was recorded are shown

	Date trapping commenced	No.of adults caught around : Horse dung	Cow dung	Period over which adults were caught (days) Horse dung	Cow dung	First 67% of total number caught (days) Horse dung	Cow dung	Day of maximum catch around : Horse dung	Cow dung
C.similis	1. 8 Apr 1965	220	24	9	8	4.6	3.7	2	2
	2. 29 May 1964	100	-	6	-	3.5	-	2	-
	3. 7 Aug 1964	11	8	3	2	1.4	0.9	1	1
C.equina	1. 8 Apr 1965	79	9	8	6	3.9	-	2	1
	2. 29 May 1964	289	-	7	-	1.9	-	2	-
	3. 7 Aug 1964	17	2	4	1	1.9	-	1 + 2	1
C.hirtipes	1. 8 Apr 1965	357	408	8	8	4.4	2.6	2	2
	2. 29 May 1964	568	-	7	-	1.3	-	1	-
	3. 7 Aug 1964	426	276	5	3	1.6	1.2	2	1
C.nigra	1. 8 Apr 1965	60	11	9	4	4.8	-	4	4
	2. 29 May 1964	100	-	5	-	2.2	-	1	-
	3. 7 Aug 1964	0	0	-	-	-	-	-	-
C.subsultans	1. 8 Apr 1965	1	1	2	2	-	-	-	-
	2. 29 May 1964	41	-	8	-	4.7	-	5	-
	3. 7 Aug 1964	1	0	2	-	-	-	2	-

(11 C.nitida adults were caught in 5 days in April and 6 S.nitida adults in 5 days in May - June)

The results in Figs. 8, 9, and 10, clearly show that adults of the Copromyza spp. were most attracted to fresh dung during all the trapping periods. Thus, at least 58% of the total number of adults caught for any species was recorded in the first half of the time in which the total number were caught. The maximum daily catch was recorded on the first and second days on all occasions, except for C.nigra in April, when it was on the fourth day (Table 15). No adults were recorded after 9 days.

Only 2 S.subsultans adults were recorded in April and 1 in August. In May - June, 41 adults were caught over 8 days, with the maximum daily number being recorded on the fifth day. These results are at variance with those obtained from direct counts, i.e. less S.subsultans adults were caught in detergent traps than would have been expected from direct counts. This may be due to the fact that adults of this species tend to remain on or under the dung for longer periods than adults of the Copromyza spp. The maximum count recorded on the fifth day in May - June could,therefore,have been due to an exodus of adults from the dung. However, it also seems probable that adults of this species are less sensitive to the ageing of the dung than the adults of the Copromyza spp.

In Table 16 the numbers of males and females of each species caught daily in detergent traps around horse dung in May - June 1964 and around cow and horse dung in Aug. 1964 and Apr. 1965 are shown. It can be seen from these results that the males and females appear to react similarly to the ageing of both cow and horse dung. The absence or low numbers of adults of certain species in Table 16 reflects seasonal changes in their abundance (see Section VI).

C. Influence of weather on the rate of ageing

The daily numbers of adults caught in detergent traps around dung is dependent mainly upon the rate of ageing of the dung which is governed by the prevailing weather conditions.

It can be seen from Table 15 and Figs. 8, 9, and 10, that the period over which flies were caught in detergent traps around horse dung became shorter from April to May - June to August, and in detergent traps around cow dung it became shorter from April to August (cow dung was not used in the May - June experiment). The period over which flies were caught around cow dung tends to be less than around horse dung, particularly in August (Figs. 8, 9, 10). This is because cow dung loses its attractive nature more rapidly than horse dung in warm, dry weather, due to the rapid formation of a crust which prevents the odours from escaping. The dung underneath keeps an odour which attracts flies as soon as the crust is broken, even if the dropping is 1 - 2 weeks old (Hammer, 1941).

From Appendix 2 it can be seen that climatic conditions prevailing during the April trapping period were cool (mean daily max.temp. 12.1°C) and wet (0.86ins of rain). In these conditions the dung would age slowly and consequently adults were caught up

TABLE 16. The numbers of males (M) and females (F) caught daily in 12 detergent traps around (1) horse dung, and (2) cow dung

1. HORSE DUNG	Date trapping commenced	Day 1 (M)	Day 1 (F)	Day 2 (M)	Day 2 (F)	Day 3 (M)	Day 3 (F)	Day 4 (M)	Day 4 (F)	Day 5 (M)	Day 5 (F)	Day 6 (M)	Day 6 (F)	Day 7 (M)	Day 7 (F)	Day 8 (M)	Day 8 (F)	Day 9 (M)	Day 9 (F)
C.similis	8 Apr 1965	4	14	10	31	7	22	13	28	9	23	4	13	12	16	1	9	1	3
	29 May 1964	2	8	19	5	4	9	3	5	8	5	1	6						
	7 Aug 1964	3	3	2	2	0	1												
C.equina	8 Apr 1965	2	5	6	16	3	11	3	8	5	5	0	5	2	4	1	3		
	29 May 1964	66	36	55	49	17	16	19	14	9	4	1	2	0	1				
	7 Aug 1964	1	5	4	2	2	1	2	0										
C.hirtipes	8 Apr 1965	16	7	56	24	41	29	17	32	16	27	22	14	27	16	5	8		
	29 May 1964	190	189	71	78	9	4	3	5	4	8	2	2	2	1				
	7 Aug 1964	104	67	114	86	22	8	10											
C.nigra	8 Apr 1965	2	4	2	6	4	3	7	5	4	4	5	2	2	4	3	2	1	0
S.subsultans	29 May 1964	2	5	2	2	2	2	1	4	9	2	1	4	4	0	1	0		
2. COW DUNG																			
C.similis	8 Apr 1965	0	3	0	7	0	4	2	3	0	0	1	2	0	1	1	0		
	7 Aug 1964	2	4	1	1														
C.equina	8 Apr 1965	0	5	0	1	0	0	1	0	0	0	0	2						
C.hirtipes	8 Apr 1965	59	23	106	22	84	26	21	7	19	8	9	5	11	3	3	2		
	7 Aug 1964	89	80	47	40	16	4												

to 9 days, and 67% of the total number of adults was recorded in the first 4 - 5 days. Less than 10% of the total number of adults was recorded on the first day, probably due to the low temperature at the time reducing activity.

The first 2 days of the May - June trapping period were hot (mean daily max.temp. 20.9°C) and sunny (mean daily sunshine 7.7hrs), with only 0.01ins of rain. The next 5 days were much cooler (mean daily max.temp. 13.9°C) and overcast (0.2hrs sunshine daily), with 1.11ins of rain. Thus the dung would age rapidly over the first 2 days, losing most of its attractiveness, but the rate of ageing would then be markedly reduced over the next 5 days. Consequently, 67% of the total number of adults of C.similis, C.equina, C.hirtipes, and C.nigra were caught in the first 3.5, 1.9, 1.3, and 2.2 days respectively. This is a considerable reduction from the equivalent April periods, but the period over which the total number of adults were caught, 5 - 8 days, was far less reduced, due to the cool damp weather after the first 2 days.

The first day of the August trapping period was warm and dry (Appendix 2). Although the second day was still warm, there was a heavy downpour of rain, 0.34ins. The third and fourth days were quite warm and sunny with only 0.03ins of rain. Landin (1961) found that after heavy rain horse dung is liable to rapid dessication which increases the rate of ageing of the dung. This was reflected by adults only being caught over 3 - 5 days and that two-thirds of the total number were recorded in the first 2 days.

3. INFLUENCE OF SHADE ON THE RATE OF AGEING OF DUNG

Investigations on the ageing of dung were restricted to exposed conditions, as droppings are rarely deposited in the shade at Houghall due to the lack of high hedges and trees around the fields. Landin (1961) comprehensively studied the effects of weather on the properties of dung deposited in exposed and shaded conditions. In the shade dung is less liable to rapid dessication, high temperatures and the effects of heavy rain. The rate of ageing of the dung in such a situation is generally less rapid than in exposed situations.

4. OVIPOSITION AND AGEING OF DUNG

Fresh stable horse dung was collected within 2 - 3hrs of it being deposited, sealed in polythene bags, and subjected to below -30°C for several days to kill any sphaerocerid eggs present. 2 trays were filled with 1500gms of fresh horse dung and covered with muslin (fine enough to exclude adult sphaerocerids). These were placed in an area free from farm animals at Houghall, i.e. the "Piggery Banks" field (Fig.3). Subsequently, 2 such traps were placed daily in the area at least 20m apart, over 6 days. On the seventh day (7 May 1965) the muslin was removed and the dung left exposed for 24hrs. The dung was then taken back to the laboratory and placed in muslin topped jars at 15°C. Any adults that emerged were recorded.

Two such muslin covered trays of stable horse dung that had been left in the area for 1 and 7 days respectively, but not exposed, were brought back to the laboratory. 100 C.similis eggs, from laboratory cultures, were inserted into each sample of dung. The samples were then placed at 15°C in muslin topped jars and any emergences were recorded.

In Table 17 the numbers of adults of each species that emerged from the different samples of dung are expressed as percentages of the total number of emergences of that species, from all the samples.

TABLE 17. Percentages of adults of each species that emerged from horse dung which had been exposed in the field at different ages

Age of dung when first exposed	C.similis		C.equina		S.subsultans	
	No. of adult emerg-ences	% of Total	No. of adult emerg-ences	% of Total	No. of adult emerg-ences	% of Total
Fresh	100	46.7	30	34.0	49	35.5
1 day	84	39.3	26	29.5	46	33.3
2 "	12	5.6	16	18.2	22	23.9
3 "	10	4.7	8	9.1	8	5.8
4 "	8	3.7	8	9.1	2	1.4
5 "	0	0	0	0	0	0
6 "	0	0	0	0	0	0

It can be seen from Table 17 that the greatest number of adults of C.similis, C.equina, and S.subsultans emerged from dung which was exposed when it was fresh. As the age of the dung on exposure increased, so the number of adults that emerged from it decreased. No emergences were recorded from dung older than 4 days on exposure. Although adults of other Sphaeroceridae were present in the field at the time of this investigation, it appears that they did not oviposit in the samples of dung.

There was an 8% larval mortality in the dung that was 1 day old when the eggs were placed in it, compared with a 15% mortality in the dung that was 7 days old when the eggs were placed in it. The differences in the number of adults that emerged from the various samples of dung were, therefore, predominantly caused by the females preferring to oviposit in fresh dung. Differential mortality would probably only have had a slight effect on the number of adults that emerged.

VI. SEASONAL DISTRIBUTION OF ADULTS

(1) SAMPLING TECHNIQUE

A sampling regime was carried out from May 1964 to April 1966 in a fenced area at Houghall (Fig.5), using 12 detergent traps (type A) around 3 trays of fresh horse dung (previously deep frozen for several days). The traps were left in the field for a period of 7 days, usually at least once a month, and the dung was removed after each period. Care was taken to keep the vegetation around the traps short at all times, and sodium chloride was added to the detergent solution during the winter to prevent it from freezing. A similar sampling regime, using 12 detergent traps (type A) around 3 trays of fresh cow dung (previously deep frozen), was executed in the same fenced area from March 1965 to April 1966. During this period 6 such traps were sunk into a large manure heap next to the "Cow Pasture" field (Fig.3). From March 1965 to April 1966 all 30 traps were placed in the field at the same time and emptied 7 days later.

Twelve detergent traps (type A) were also placed around 3 trays of fresh horse dung (previously deep frozen) in Hollingside woods (Fig.3) for 7-day periods from 10 May to 6 August 1965. The vegetation around the trays was kept short.

(2) EFFICIENCY OF TRAPPING TECHNIQUE

To justify the use of this trapping technique it is necessary to consider the possible sources of error involved.

The size of the catch will be influenced not only by population changes, but also by the following factors (Southwood, 1966) :

1. Changes in the number of animals in a particular "phase".
2. Changes in activity.
3. Changes in the efficiency of the traps.
4. The responsiveness of a particular sex and species to the trap stimulus.

The "phase" the animal is in will have little or no effect on the catch, as coprophilous sphaerocerids of all ages are attracted to dung. The diurnal cycle of activity will have no effect on the total number of adults caught, as trapping was continued over periods of 7 days. Coulson (1956) concluded that "sticky traps give a measure of activity, but if the insects are grouped into long enough periods, then they also give a measure of abundance". It is considered that the 7-day monthly trapping periods were of sufficient duration to give a measure of the change of abundance from month to month.

Snow is probably the only weather factor that is likely to seriously affect the efficiency of the detergent traps. The effect of wind speed on catch size is probably fairly small, as most of the adults approach the dung, and hence the traps, by running over the vegetation, or by short low level flights. Flies attracted to dung tend to move up wind, but as there were 4 detergent traps set around the dung, the wind direction would be relatively unimportant.

The efficiency of the traps depends upon the attractiveness of the bait, i.e. the dung, which varies according to its age. The rate of ageing is determined by prevailing weather conditions and will be more rapid in dry, warm weather. However, the error that is caused by increased rate of ageing in warm weather is probably partially compensated for by an increase in the rate of movement of the adults on to the dung. Low temperatures reduce both the rate of ageing and the rate movement of adults on to the dung.

The detergent traps used in the present studies act in basically the same way as pitfall traps, and critical studies on the efficiency of these have been made by Mitchell (1963) and Greenslade (1964) working on Carabid beetles. Greenslade (1964) found that the efficiency of traps varied from species to species. It has been observed in the present studies, and discussed previously, that adults of S.subsultans appear to be more adept at avoiding detergent traps than those of the Copromyza spp. Therefore, direct comparisons between actual numbers of the two genera have been avoided. Greenslade (1964) also found the efficiency of the traps varied from habitat to habitat, and that the catch was affected, both qualitatively and quantitatively, by the level of the mouth of the trap and the area of ground around the trap that was free of vegetation.

To minimize these sources of error, the following precautions were taken :

1. All the traps were sunk into the ground with their mouths flush with the soil surface or the surface of the manure heap.
2. The changes in population were estimated mainly from trapping around horse dung and, to a lesser extent, cow dung in the open field.
3. All the traps in the open field were set well apart, but they were sunk into fairly flat areas of a grass strip in a fenced off site.
4. The grass within a 1m radius of the trays was kept short (less than 3cm in height) throughout the two years of trapping. Therefore, the vegetation could not impede the movement of adults towards the traps.

Having taken the above precautions, it is considered that the trapping technique is a valid method of estimating population changes of coprophilous Sphaeroceridae.

(3) TRAPPING RESULTS

A. C.similis

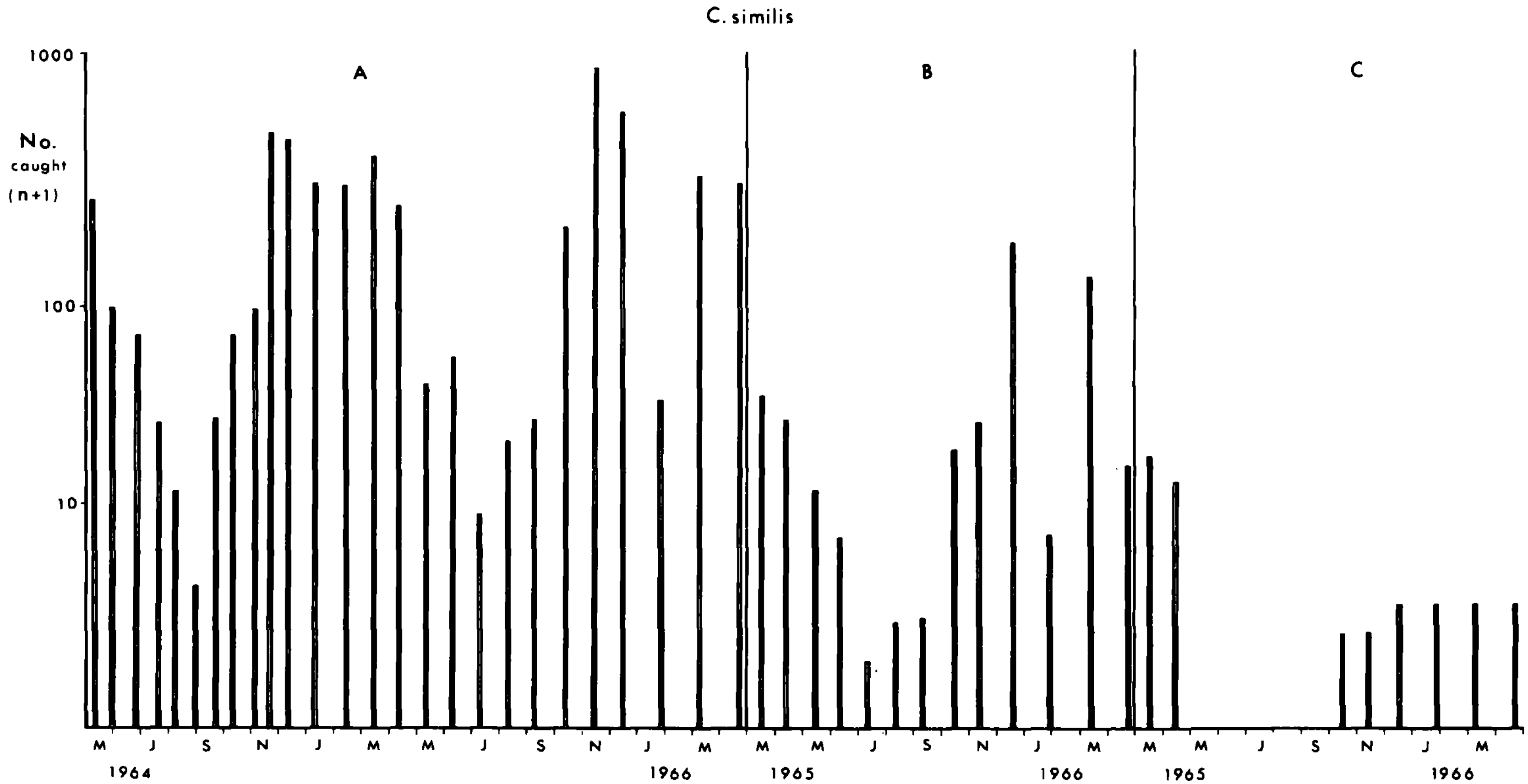
A total of 4668 C.similis adults were caught in two years around horse dung and this was the highest total recorded for any species. In Fig.11 the total number of adults caught in the 12 detergent traps in each 7-day period are shown. It can be seen from Fig.11 that adults were most

Fig.11. Numbers of C.similis adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap March 1965 - April 1966



C. similis
A
B
C
1000
100
10
No.
caught
(n+1)
M
J
S
N
J
M
M
J
S
N
J
M
M
M
J
S
N
J
M
M
M
J
S
N
J
M
1964
1966
1965
1966
1965
1966

abundant in late autumn, winter, and early spring, but there was a marked reduction in the numbers caught in July, August, and September. However, adults were caught on every occasion that trapping was carried out, with the peak numbers in late November and December.

Only 382 adults were caught in 12 detergent traps around cow dung from March 1965 to April 1966, compared with 2773 in 12 traps around horse dung in the same period. It can be seen from Fig.11 that the seasonal occurrence of adults in cow dung was very similar to that in horse dung with numbers low throughout the summer and greatly increased in November and December. The January catch was again low, but the population increased in March.

Adults of C.similis were uncommon in the manure heap, only 42 being caught in 6 detergent traps from March 1965 to April 1966, and 26 of these were recorded in the first two months. Adults were not caught from May to September 1965, but small numbers were recorded from October 1965 to April 1966 (Fig.11).

The seasonal occurrence of adults in the manure heap was not only dependent upon the population at the time, but also upon the quality and nature of the dung that the heap was composed of. The principal components of the manure heap were pig and cow dung, but the proportion of the latter was reduced during the summer. The supply of fresh pig dung, which was regularly added to the heap, was occasionally interrupted in the summer. Variations in the composition of the heap would affect the numbers and species composition of the adults present. The results obtained from trapping in the manure heaps are, therefore, of more value in comparing the number of adults of different species present at various times of the year, rather than for estimating seasonal fluctuations in populations.

A total of 10 adults was caught in 12 detergent traps around 3 trays of fresh horse dung in woods during 4 trapping periods from May to August 1965, compared with 104 caught by the same number of traps around horse dung in the open field during the same period. This indicates that there was no marked tendency for adults to move into woods during the summer.
It can be seen from Table 17 that differences in the sex ratios of flies caught in detergent traps around cow and horse dung and in the manure heap are not significant.

TABLE 17. The number of males and females caught in detergent traps around cow and horse dung and in a manure heap. χ^2 values have been calculated.

	HORSE DUNG				COW DUNG				MANURE HEAP			
	Males	Females	χ^2	P.	Males	Females	χ^2	P.	Males	Females	χ^2	P.
<u>C.similis</u>	2292	2376	0.4	> 0.2	188	194	.09	> 0.70	27	15	1.7	> 0.1
<u>C.equina</u>	640	711	3.7	> 0.05	57	77	3.0	> 0.05	660	674	0.15	> 0.5
<u>C.hirtipes</u>	1951	1818	4.6	< 0.05	1049	788	20.2	< 0.001	5	2	1.2	> 0.2
<u>C.nitida</u>	423	387	1.6	> 0.2	176	103	19.1	< 0.001	0	0	0	0
<u>C.nigra</u>	506	538	1.0	> 0.5	158	158	0	0	74	80	0.2	> 0.5
<u>S.subsultans</u>	67	72	0.2	> 0.5	20	15	0.7	> 0.3	1052	1316	29.4	< 0.001

B. C.equina

Adults of C.equina were less abundant than those of C.similis. 1341 were caught from May 1964 to April 1966 compared with 4668 of the latter, and also the population of C.equina did not fluctuate as markedly. Adults of C.equina were most abundant in spring and late autumn.

It can be seen from Fig.12 that there was a decrease in the number of adults that were caught around horse dung after May 1964, and the minimum catch for 1964 was recorded in early October. The increase in late November was less dramatic than for C.similis, and after a decrease in December only 2 and 4 adults were recorded in January and February 1965 respectively. As for C.similis, there was an increase in the numbers caught in spring. The summer reduction in population was less pronounced than for C.similis, while the maximum catch for 1965 was recorded in October, as opposed to November for C.similis. This was followed by a progressive reduction in the population in November, December, and January, and a slight increase in March and April 1966. The adult population of C.equina is less reduced in the summer and more in midwinter than that of C.similis. Thus, during the autumn, winter, and early spring, adults of C.similis are the more abundant, while in the summer the position is reversed.

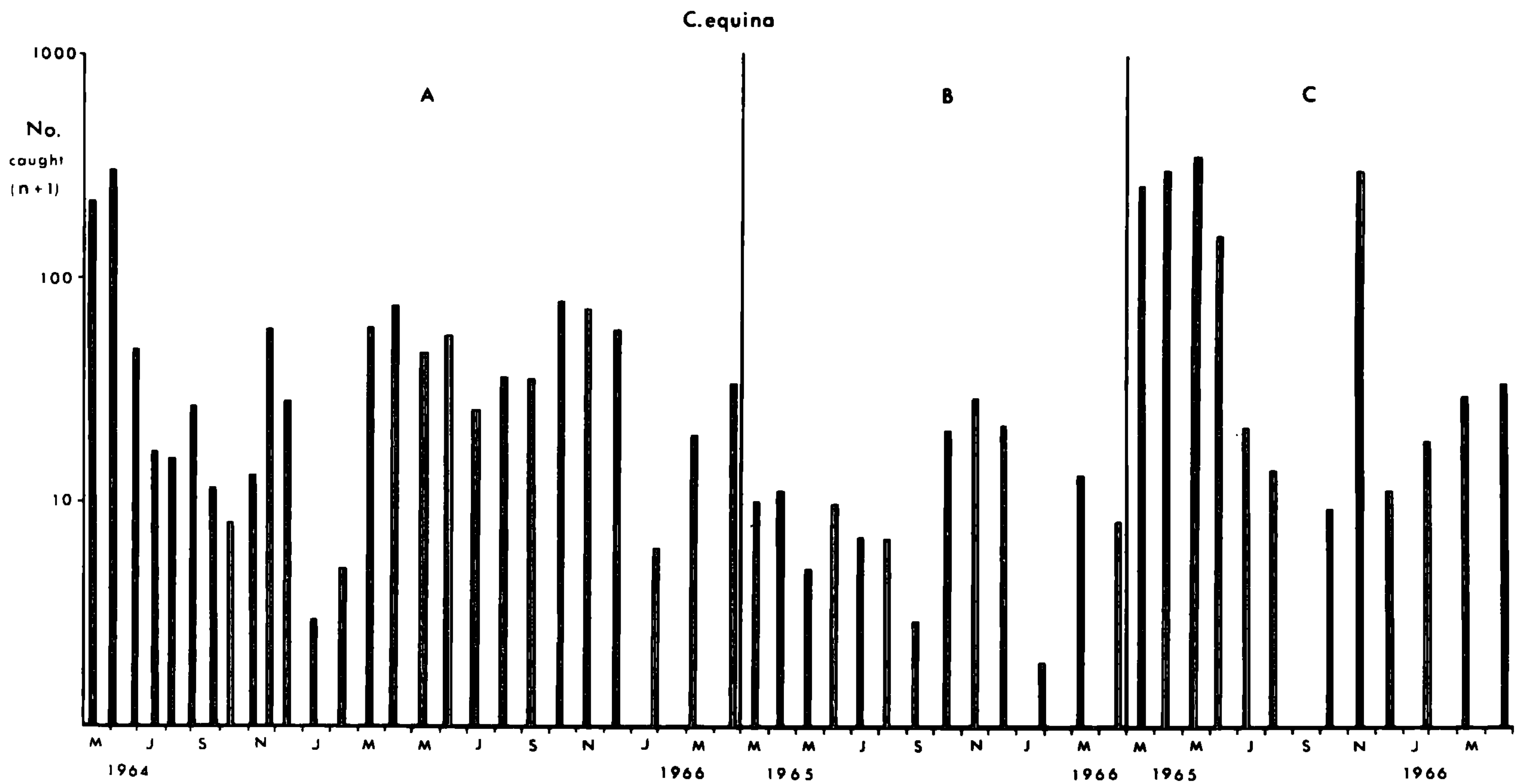
As for C.similis, the total number of adults caught in detergent traps around cow dung, 134, was far less than the number caught around horse dung, 594, in the same period. The seasonal

Fig.12. Numbers of C.equina adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap March 1965 - April 1966



C.equina
A
B
C
No.
caught
(n+1)
1000
100
10
M
J
S
N
J
M
M
J
S
N
J
M
M
M
J
S
N
J
M
M
M
J
S
N
J
M
1964
1966
1965
1966
1965
1966

pattern of the numbers of adults caught around cow dung was similar to that described for horse dung, with a decrease in the population from May to September and an increase in October (Fig.12). The maximum catch for 1965 was recorded in early November and this was followed by a progressive decrease in catch size in December and January. Although there was an increase in population in March, it fell in April.

Adults were abundant in manure, 1334 being caught in 6 detergent traps from March 1965 to April 1966. The greatest numbers were recorded in March, April, May, and November 1965, but adults were scarce from July to October and from December to April 1966 (Fig.12). The marked fluctuations in the number of adults caught at various times of the year are not unexpected, as the numbers caught were dependent not only upon the population density, but also on the state of the dung in the heap. An interesting point is that C.equina was previously thought to be far more restricted to horse dung than C.similis (Richards, 1930), but in the present work adults of the former were much more abundant in the manure heap (composed of pig and cow dung).

Only 7 adults were caught in 12 detergent traps around horse dung in woods from May 1965 to August 1965, compared with 158 caught in 12 such traps around 3 trays of horse dung in the open during the same period. The adults did not, therefore, appear to move into woods during the summer, but remained in the open field.

It can be seen from Table 17 that the differences in the sex ratios of flies caught in detergent traps around cow and horse dung and in the manure heap are not significant.

C. C.hirtipes

A total of 3769 adults were caught in detergent traps around horse dung from May 1964 to April 1966. It can be seen from Fig.13 that in 1964 the population remained high from early May to late September and maximum catches were recorded in late May and early August. From November there was a decrease in the population and adults were not recorded during December and January. After a peak in April, the population fell from May to July, but this was followed by a peak in early August. Again there was a winter decline and adults were not recorded in January, but a high catch was recorded in April.

Adults of C.hirtipes were the most abundant of any species in cow dung. A total of 1837 adults were caught from March 1965 to April 1966. The seasonal occurrence of adults was similar to that described for horse dung, with a peak in April, and the population reduced in May, June, and July, followed by an increase in August and September. Adults were absent in January, but again there was a dramatic rise in the number caught in April. A similar pattern of seasonal occurrence of adults on cow dung was recorded by Laurence (1955).

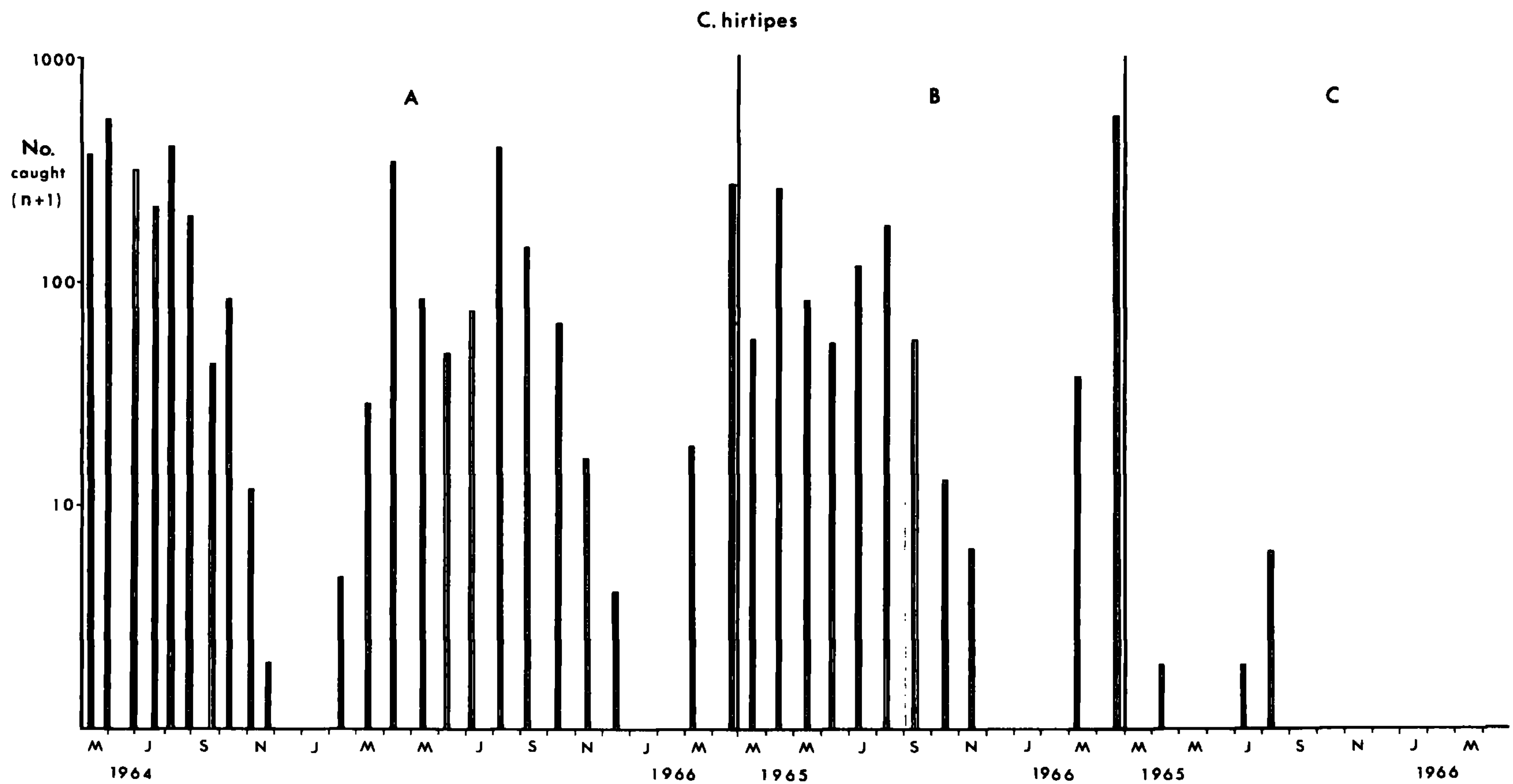
Only 7 adults were caught in 6 detergent traps in the manure heap from March 1965 to April 1966. Richards (1930) recorded

Fig.13. Numbers of C.hirtipes adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap March 1965 - April 1966



C. hirtipes
1000
100
10
No.
caught
(n+1)
A
B
C
M J S N J M M J S N J M
1964
1966
M M J S N J M
1965
1966
M M J S N J M
1965
1966

this species as having a wide range of habitats and as commonest on dung, including that of cows. It appears, from the present studies, to be mainly restricted to dung in the form of droppings, deposited in the open field, and to be rare in manure heaps. Only 48 adults were caught in 12 detergent traps around horse dung in woods from May to August 1965, compared with 641 caught by an equal number of traps around 3 trays of horse dung in the open field during the same period. This indicates that adults tend to remain in the open field during the summer and do not move into the woods.

It can be seen from Table 17 that significantly more males than females were caught around both cow and horse dung. This cannot be accounted for by an excess of males emerging (see Section VII, 3). Laurence (1955) also caught more males than females of this species on cow dung. Richards (1930) examined adult sphaerocerids from many collections and recorded the number of individuals of not only each species, but each sex. He concluded that the sex ratio so obtained has probably some significance, for the specimens were derived from so many collections that in most cases they may be regarded as a random sample of the population inhabiting England. He reasoned that in certain cases the preponderance of one sex is more likely to be due to differences in the length of life, rather than a difference in habits. Richards (1930) identified 135 males and 136 females of C.hirtipes and this difference is not significant. Presumably the life span of both sexes is the same and, therefore, the preponderance of males around horse and cow dung must be due to differences in habits between the sexes.

D. C.nigra

A total of 1044 adults was caught in detergent traps around horse dung from May 1964 to April 1966. It can be seen from Fig.14 that the peak in population for 1964 was in May, but no adults were caught from July to October. Adults were caught in November and December, but not in January. The peak in population for 1965 was also in May, but after this, adults were not caught until October and November. Adults were absent again until April.

A total of 316 adults was caught in detergent traps around cow dung from March 1965 to April 1966, compared with 561 caught around horse dung in the same period. It can be seen from Fig.14 that seasonal occurrence of adults was similar to that described for horse dung, except that adults were caught in December and January around cow dung.

A total of 154 adults was caught in detergent traps in the manure heap from March 1965 to April 1966. Adults were most abundant from March 1965 to May 1965, but none were recorded from July to October 1965 and January to March 1966 (Fig.14).

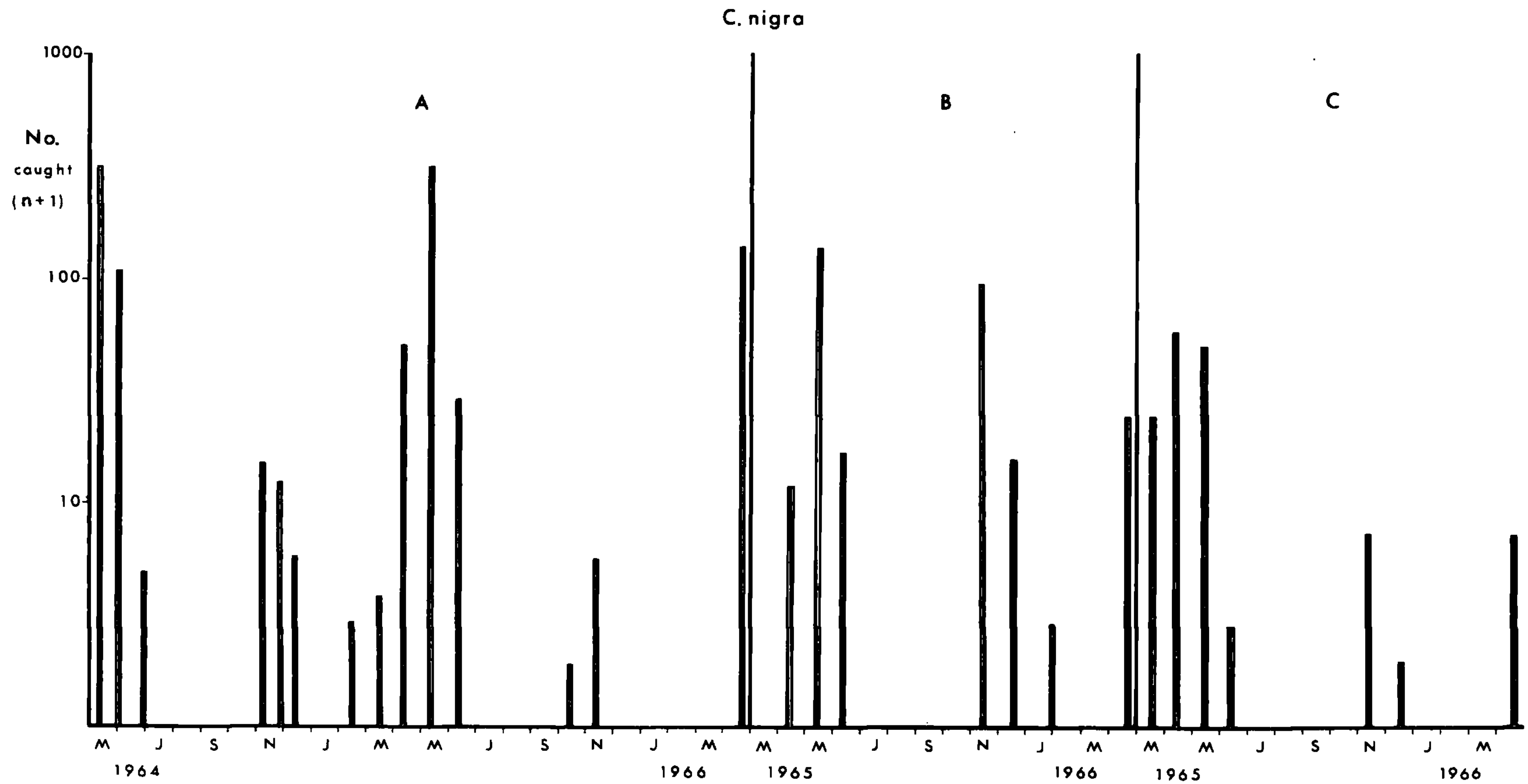
A total of 34 adults was caught from 10 to 17 May and from 27 May to 3 June 1965 in 12 detergent traps around horse dung in woods. None were recorded in July and August. The failure to locate adults from July to September in the present investigation, and from July to August by Richards (1930), may be due to the low population density during those months. However, Richards recorded individuals on dead leaves, presumably in woods

Fig.14. Numbers of C.nigra adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung
May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung
March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap
March 1965 - April 1966


C. nigra
A
B
C
No.
caught
(n+1)
1000
100
10
M J S N J M M J S N J M M M J S N J M M M J S N J M
1964
1966
1965
1966
1965
1966

and if the adults tend to remain beneath the leaves, where it is cool and damp, this would explain why they are difficult to find. It is also possible that this species spends the summer as larvae in a state of diapause. Laurence (1954) found that larvae of *Smittia* and *Trichocera* enter a diapause during the summer when the temperature is high.

It can be seen from Table 17 that the differences in the sex ratios of flies caught in detergent traps around cow and horse dung and in the manure heap are not significant.

E. *C.nitida*

Richards (1930) recorded either males or females for every month of the year, with both sexes most abundant in May. In England adults of *C.nitida* are nearly always found in woods.

A total of 810 adults was caught in detergent traps around horse dung from May 1964 to April 1966, but they were only recorded in the open field during the winter and were absent from May to September (Fig.15). The population in the open field was at its highest in November and December in both 1964 and 1965.

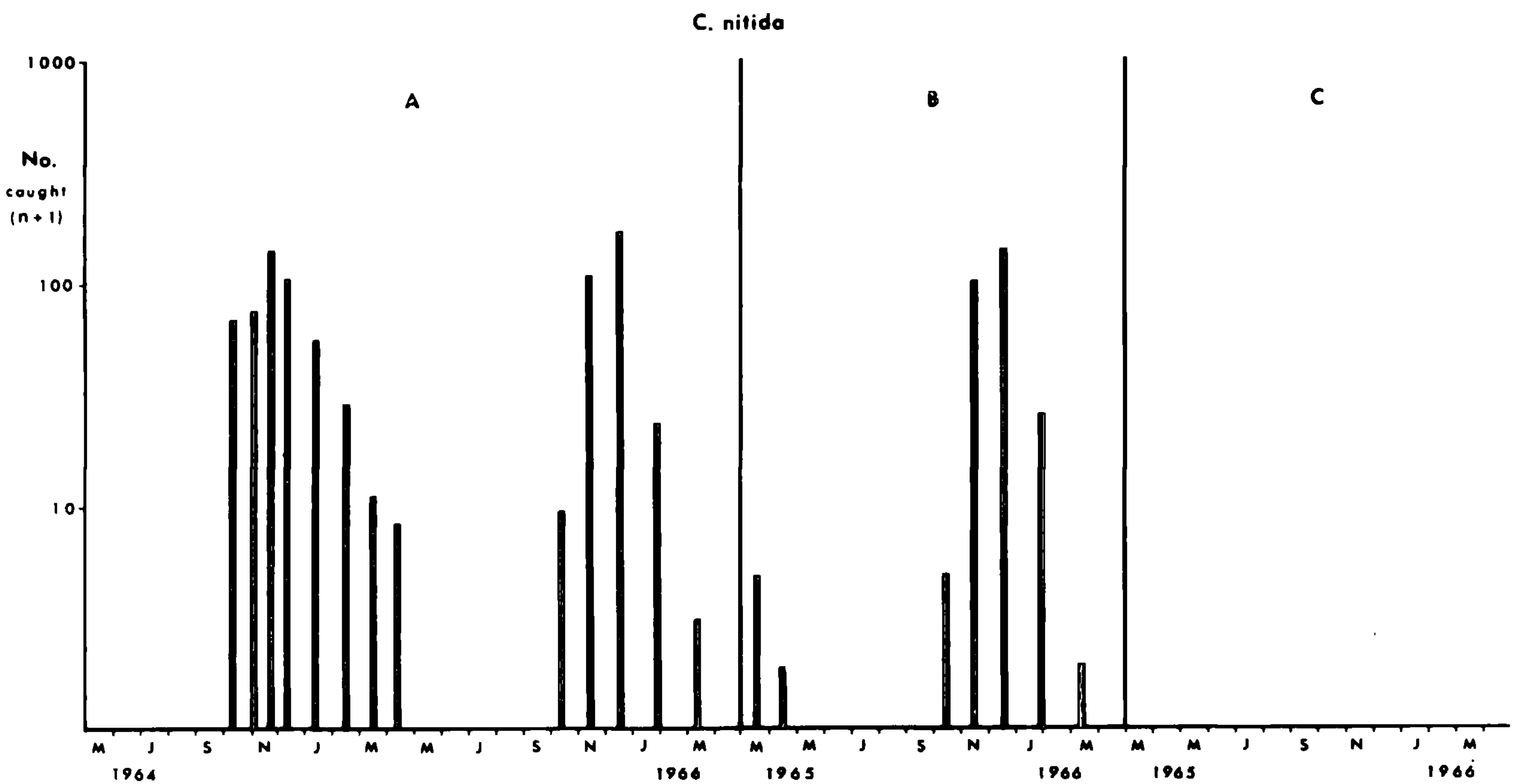
A total of 279 adults was caught in detergent traps around cow dung from March 1965 to April 1966 compared with 334 around horse dung in the same period. The seasonal pattern was very similar to that recorded around horse dung. Adults were absent from May to September and maximum catches were again recorded in November and December (Fig.15).

Fig.15. Numbers of *C.nitida* adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung
May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung
March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap
March 1965 - April 1966


C. nitida
No.
caught
(n + 1)
1000
100
10
A
B
C
M J S N J M M J S N J M
1964
1966
M M J S N J M
1965
1966
M M J S N J M
1965
1966

No adults were recorded in detergent traps in the manure heap.

A total of 20 adults was caught in detergent traps around horse dung in woods from May to August 1965, but adults were recorded for each month. The fact that adults were recorded in the open field in winter and were present in woods, but not in the open, during the summer, must be mainly due to their reaction to low humidity and high temperature in exposed situations during the summer.

It can be seen from Table 17 that significantly more males than females were caught around cow dung ($\chi^2 = 19.1$, d.f. = 1, $P. < 0.001$), but not around horse dung. Laurence (1955), however, collected 21 males and 39 females off cow pats in 12 months. The preponderance of males caught in detergent traps around cow dung, and the excess of females caught on cow dung, may be due to the females spending more time actually on the dung, perhaps for the purpose of egg laying. Richards (1930) recorded significantly more males than females from a number of separate collections, with the greatest excess of males in September and October. In the present investigation the preponderance of males was most marked in October and November, while from January to April 1965 and in December 1966 there was an excess of females around horse dung.

These seasonal irregularities in sex ratio and the results obtained by Laurence (1955) indicate that the preponderance of males is more likely to be due to a difference in habits between the sexes, rather than to differences in life span, as suggested by Richards (1930). The possibility of the difference being caused by an excess of females emerging can be excluded (see Section VII, 5).

F. S.subsultans

A total of 139 adults was caught in detergent traps around horse dung from May 1964 to April 1966. In 1964 adults were most abundant in spring and were absent from October until April 1965 (Fig.16). Low numbers were recorded from April to September, and they were absent from October 1965 until April 1966.

A total of 35 adults was recorded from March 1965 to April 1966, compared with 20 caught around horse dung in the same period. Small catches were recorded from April to November and adults were absent in December and January, but present in low numbers again in March and April (Fig.16).

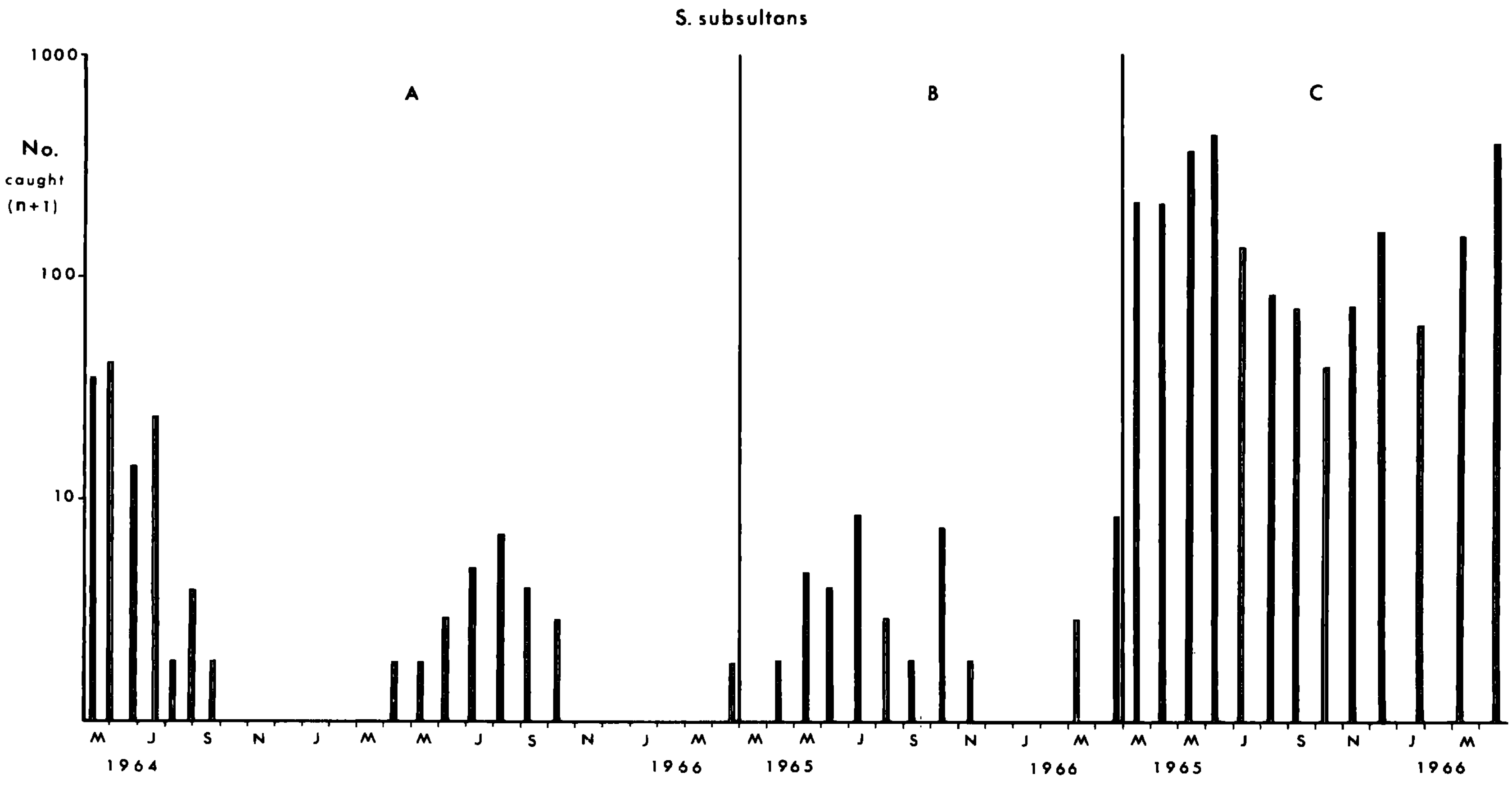
A total of 2368 adults was caught in 6 detergent traps in the manure heap from March 1965 to May 1966. Adults of S.subsultans were the most abundant of any species in the manure heap. It can be seen from Fig.16 that adults were most abundant in April and May, but this species was represented on all the occasions when trapping was carried out. The adults are well adapted for movement in manure with powerful hind legs. Their reluctance to fly, as previously described, is probably also an adaptation to living in large accumulations of dung or other organic matter.

Fig.16. Numbers of *S.subsultans* adults caught in 7-day periods approximately once monthly

A. 12 detergent traps (type A) around 3 trays of horse dung
May 1964 - April 1966

B. 12 detergent traps (type A) around 3 trays of cow dung
March 1965 - April 1966

C. 6 detergent traps (type A) in a large manure heap
March 1965 - April 1966


S. subsultans
A
B
C
No. caught (n+1)
1000
100
10
M J S N J M M J S N J M
1964
1966
M M J S N J M
1965
1966
M M J S N J M
1965
1966

Only 3 adults were recorded in detergent traps around horse dung in woods from May 1965 to August 1965.

There was no significant difference between the numbers of males and females caught in detergent traps around cow and horse dung (Table 17), but there were significantly more females than males recorded in detergent traps in the manure heap ($\chi^2 = 18.1$, $P. < 0.001$, d.f. = 1). Richards (1930) also recorded significantly more females than males from a number of separate collections. The difference may be caused by the females living longer, as suggested by Richards, but the excess of males caught around cow dung indicates that the difference is possibly due to a difference in habits between the sexes. The females may be more restricted to manure heaps or large accumulations of organic matter than the males. The possibility of the difference being caused by an excess of females emerging can be excluded (see Section VII, 6).

G. Other species

a) C.stercoraria : 3 adults were caught around horse dung in the open in August 1965, and 2 around horse dung in woods in July 1965.

b) C.suillorum : 30 adults were recorded around horse dung in woods in July and August 1965.

c) S.nitida : 28 adults of Sphaerocera nitida Duda were recorded around horse dung from May to September.

VII. DURATION OF DEVELOPMENT AND SEASONAL EMERGENCE OF ADULTS

From May 1964 to May 1965, at the end of each trapping period (described in Section VI, 1), a 500gm sample of horse dung was taken from each of the trays. The dung was placed in such a breeding cage as was described in Section I, 1, but with the polyglaze top replaced by fine muslin. The cages acted as emergence traps and were left on the ground just outside the laboratory. Any flies that emerged were removed daily with an aspirator, identified, and the duration of development recorded. The environmental conditions in this situation were obviously somewhat different from those in the field, but the emergence traps could not be left away from the close proximity of the laboratory in case they were interfered with. The temperature close to the laboratory was probably slightly higher than in the field, particularly in the winter, due to the heat emitted from, and reflected by, the buildings.

The effects of the trap on the microclimate within were not investigated, but Southwood & Siddorn (1965) found that shallow metal emergence traps did not reduce the fluctuations in temperature inside as much as deep muslin ones, because the insulating layer of air was smaller. As the emergence traps used in these investigations were made mainly of thin metal and were three-quarters filled with dung, it seems probable that the internal fluctuations in temperature were broadly similar to the external ones.

TABLE 18(i) Numbers of adult emergences from samples of horse dung exposed for 7-day periods in the field and the mean duration of development ($\pm$ S.D.)

Date dung was first exposed	*C.similis* (1)	*C.similis* (2)	*C.equina* (1)	*C.equina* (2)	*C.hirtipes* (1)	*C.hirtipes* (2)
1964						
8 May	74	18.0	40	18.0	4	18.0
29 May	0	-	4	16.0	0	-
26 June, 17 July, 7 Aug, 28 Aug	0	-	0	-	0	-
18 Sept	4	20.0	0	-	0	-
9 Oct	4	27.0	2	27.0	0	-
30 Oct	57	54.0	0	-	0	-
20 Nov	1366	71.1 ± 3.3	175	73.3 ± 4.0	0	-
11 Dec	2495	83.0 ± 4.6	1	86.0	0	-
1965						
8 Jan	0	-	0	-	0	-
9 Feb	1228	53.9 ± 11.6	69	53.1 ± 2.7	0	-
12 Mar	942	37.1 ± 1.4	68	37.1 ± 1.4	4	36.0
8 Apr	400	32.1 ± 0.5	92	32.1 ± 0.6	9	32.0
7 May	59	22.5 ± 0.8	87	21.8 ± 1.4	1	23.0

(1) No. of adults

(2) Mean emergence time ($\pm$S.D.)

TABLE 18(ii) Number of adult emergences from samples of horse dung exposed for 7-day periods in the field and the mean duration of development (± S.D.)

Date dung was first exposed	C.nitida (1)	C.nitida (2)	C.nigra (1)	C.nigra (2)	S.subsultans (1)	S.subsultans (2)
1964						
8 May	0	-	0	-	36	20.0
29 May	0	-	0	-	2	24.0
26 June	0	-	0	-	0	-
17 July	0	-	0	-	1	20.0
7 Aug	0	-	0	-	1	24.0
28 Aug	0	-	0	-	11	26.0±1.6
18 Sept	0	-	0	-	2	25.0
9 Oct	0	-	0	-	0	-
30 Oct	120	165.0±0.45	0	-	0	-
20 Nov	189	141.0±4.5	0	-	0	-
11 Dec	87	123.8±1.6	8	111.0	0	-
1965						
8 Jan	61	107.9±0.63	0	-	0	-
9 Feb	336	82.5±3.5	0	-	0	-
12 Mar	42	61.9±1.3	4	56.0	0	-
8 Apr	12	54.8±0.4	0	-	0	-
7 May	0	-	0	-	0	-

(1) No. of adults

(2) Mean emergence time (±S.D.)

The numbers of adults that emerged from each set of samples of dung and the mean duration of development ($\pm$ S.D.) for each species are shown in Table 18. The duration of development is taken as the interval in days from the deposition of the dung to the emergence of the adults. This does not take into consideration the possibility that eggs could have been laid in dung up to 7 days from the initial exposure time. However, the results in Section V indicate that females tend to oviposit only in fresh dung. The only time when oviposition in dung older than 3 - 4 days might occur would be in winter, and as the duration of development is extended by low temperatures, the error would be proportionally quite small.

(1) C.SIMILIS

A total of 6629 adults emerged from 16 sets of three 500gm samples of horse dung that had been exposed for 7-day periods from May 1964 to May 1965.

No adults emerged from samples exposed from the end of May until the end of August and only a few emerged from those exposed in September and October (Table 18). However, large numbers of individuals emerged from samples exposed in November, December, February, March, and April. The peak in the number of emergences was recorded from the December samples. No adults emerged from the samples of dung that had been in the field from 8 - 15 January although the adult population was high at this time. The low temperatures prevailing at the time may have inhibited egg laying.

The greatest number of adults of C.similis emerged from dung that had been exposed when the population density was at its highest, i.e. from November to April. Although Laurence (1955) also found that no adults emerged from cow dung during the summer, it cannot be concluded that this species does not breed in the summer, as emergences were recorded from cart-horse dung that had been exposed in the field at Houghall during July and August 1964.

A total of 3281 males and 3348 females emerged from samples of horse dung, but the difference is not significant (χ^2 = 0.7, d.f. = 1, P. > 0.3).

(2) C.EQUINA

A total of 538 adults emerged from samples of horse dung. Emergences were recorded from dung exposed in May and early June, but none were recorded after this until October (Table 18). The greatest number of emergences was recorded from dung exposed in late November, February, March, April, and May, and in these months the adult population was also at its highest. Although the number of emergences of C.equina was far less than for C.similis from dung exposed in winter and early spring, more of the former were recorded from dung exposed in late May 1964 and May 1965. As for C.similis, it cannot be assumed that this species does not breed in the summer, as emergences were recorded from cart-horse dung deposited in the field during July and August 1964.

A total of 252 males and 286 females emerged from samples of horse dung but the difference is not significant (χ^2=2.3, d.f.= 1, P. > 0.1).

(3) C.HIRTIPES

Only 18 adults emerged from the samples of horse dung and all of these were from dung exposed in the spring (Table 18). As adults of this species are numerous on horse dung at certain times of the year, it can be concluded that they are attracted to feed rather than to oviposit.

A total of 10 males and 8 females emerged from samples of horse dung, but the difference is not significant (χ^2 = 0.2, d.f. = 1, P.> 0.5).

(4) C.NIGRA

Eight adults emerged in May 1965 from dung exposed in the field during December 1964 and 4 adults emerged in May from dung exposed in March (Table 18). The low numbers of emergences indicate that the females oviposit more frequently in other media. The peak in the adult population in early May was probably due to a large number of adults emerging at the time, and this is supported by the fact that none of the females was gravid. A total of 7 males and 5 females emerged from samples of horse dung, but the difference is not significant (χ^2 = 0.3, d.f. = 1, P.>0.5).

(5) C.NITIDA

A total of 846 adults emerged from samples of horse dung and it can be seen from Table 18 that the greatest number emerged in November and December. Laurence (1955) recorded the duration of development as the interval in days between the deposition of the cow pat and the emergence of the adults. He found the duration of development for <u>C.nitida</u> to be 196-205, 100-112, and 87-107 days in pats deposited in November, January, and February respectively. From examination of the techniques he employed it can be concluded that adults must have emerged from dung deposited in January and probably February before those from dung deposited in November. A similar pattern was observed in the present studies as adults emerged from dung exposed from 30 October to 5 November 1964, in late April 1965, and in early and mid-April 1965, from dung exposed from 20-27 November 1964, and 11-18 December 1964 respectively.

Eggs laid from late November to April appeared to develop normally, but the delay in development from eggs laid in late October and early November could be accounted for by some form of diapause. This is unlikely to occur in the egg or early larval stages, as it has been shown in the present studies that the nutrient value of the dung decreases with age. The larvae probably enter diapause in mid-winter, and this state is broken in spring. The conditions to which the female is subjected prior to egg laying may determine whether the larvae enter a diapause in winter. The determining factor is probably temperature and/or day length. Presumably, the higher the temperature and the longer the days, the more likely females are to lay eggs that hatch to give larvae which enter a diapause in mid-winter. Laurence (1954) recorded a mean grass minimum temperature for November 1950 at Rothamsted of 33.1°F, while at Houghall it was 33.3°F from 7 October - 3 November 1964. The entry of the late larval or pre-pupal stage into diapause could be controlled by the conditions to which the early larval stages are subjected. The larvae that hatched from eggs laid from 30 October - 5 November 1964 were subjected to much higher temperatures during the first 3-4 weeks of development than those that hatched from eggs laid from 20-27 November 1964. The average temperature for November was 6.4°C, compared with 2.2°C for December. (Records from Durham University Meteorological Station). If this suggestion is correct, then temperature is almost certainly the controlling factor, as the larvae develop in an environment where there is little or no light.

A total of 403 males and 443 females emerged from samples of horse dung, but the difference is not significant ($\chi^2 = 1.9$, d.f. = 1, P. >0.1).

(6) S.SUBSULTANS

A total of 53 adults emerged from samples of horse dung. All the adults that emerged were recorded from dung exposed from May - September 1964 (Table 18). Those that emerged from dung exposed in July and August were the only ones recorded of any species.

A total of 31 males and 22 females emerged from samples of horse dung, but the difference is not significant ($\chi^2 = 1.5$, d.f. = 1, P. >0.2).

VIII. RELATIVE ABUNDANCE OF C.SIMILIS AND C.EQUINA IN THREE CONTRASTING LOCALITIES IN ENGLAND

Duda (1923) recorded *C.equina* as very common throughout Europe on horse dung, and Spuler (1925) gave many localities in N. America. Nielsen, Ringdahl & Tuxen (1954) listed the distribution as Europe to northernmost Scandinavia, British Isles, the Azores, Madeira, the Canaries, N. America, and the Faroes. They found adults all over Iceland, except in the central highlands, but rather rare.

Duda (1923) recorded *C.similis* as apparently commoner in Northern Europe than *C.equina* and mentioned particularly the following areas : Lapland, Faroes, Island of Borkum, the Urals, Germany, Austria, and Bosnia. Nielsen, Ringdahl & Tuxen (1954) recorded its distribution as Europe to northernmost Scandinavia, British Isles, Borkum, the Urals, and the Faroes. They found it to be very common all over Iceland.

(1) SAMPLING TECHNIQUE AND LOCALITIES

From May 1965 to April 1966 monthly samples of 150 adults were collected off horse dung in fields where horses had been present for some time in the following localities :

1. Moor House Nature Reserve, Westmorland (Nat.Grid. Ref.NY/758329). This area has been described by Manley (1936) as having a sub-Arctic climate and it is one of the coldest places in England. The samples were taken at about 1800ft.

2. Durham (Nat.Grid.Ref.NZ/274412). Specimens were collected in fields adjacent to the University of Durham Science Laboratories, representing lowland conditions in northern England.

3. Wareham in Dorset (Nat.Grid.Ref.SY/872871), representing lowland conditions in southern England.

The mean maximum, mean minimum, and average monthly temperatures from January 1965 to April 1966, recorded at each site, are shown in Appendix 3. As there was no meteorological station at Wareham, the records from the Poole Observatory, 5 miles north east, were used.

(2) RELATIVE SEASONAL ABUNDANCE OF *C.SIMILIS* AND *C.EQUINA* IN THE THREE LOCALITIES

In Fig.17, the monthly numbers of adults of *C.similis* and *C.equina* collected at each site are expressed as percentages of the whole catch for that month, at the particular site.

Adults of *C.equina* were rare at Moor House; only 22 were collected over the year, compared with 1378 of *C.similis*. The former were only found during the warmer months of the year, June - October, and they were relatively most abundant in June. Snow during November, December, and February prevented collections from being made.

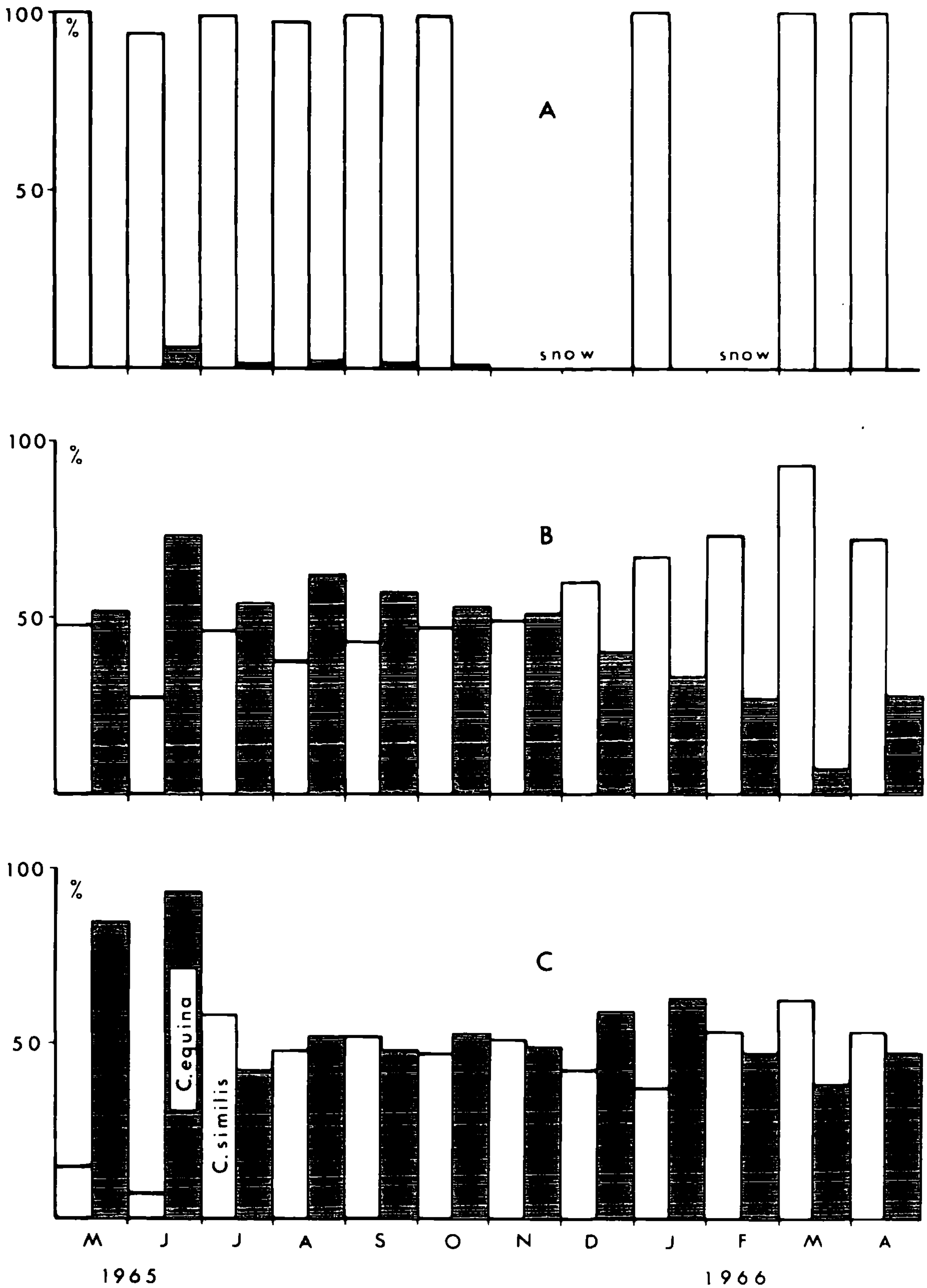
In Durham, adults of *C.equina* were the more abundant from May - October, and their highest percentages of the monthly catches were in June and August (Fig.17). Adults of *C.similis* were the more abundant from November to April, and their proportion of the monthly catch rose from November to reach a

Fig.17. Percentages of *C.similis* and *C.equina* in total monthly catch for both species at each site.

A. Moor House Nature Reserve, Westmorland

B. Durham

C. Wareham, Dorset


100
%
50
A
snow
snow
100
%
50
B
100
%
50
C
C.equina
C.similis
M
J
J
A
S
O
N
D
J
F
M
A
1965
1966

maximum of 83% in March. A total of 992 adults of C.similis and 808 of C.equina were recorded in the year.

In Wareham, adults of C.equina were far more abundant in May and June. However, for the rest of the sampling periods the monthly proportions were irregular, but quite close to unity (Fig.17). A total of 1013 adults of C.equina and 787 of C.similis were recorded in the year.

(3) COMPARISONS OF THE TOTAL NUMBERS OF C.SIMILIS AND C.EQUINA CAUGHT IN THE THREE LOCALITIES

Adults of both species are common in horse dung and as equal numbers were collected each month, the total numbers should give a valid indication of the relative abundance of the two species in the different localities. C.similis is obviously significantly more abundant than C.equina at Moor House, compared with Durham or Wareham. A χ^2 value has been calculated on the total numbers of adults of C.similis and C.equina caught at Durham and Wareham, using a null hypothesis that the distribution is equality. C.similis is significantly more abundant than C.equina in Durham, compared with Wareham (χ^2 = 4.7, d.f. = 1, $P. < 0.05$).

It can be seen from Appendix 3 that the average monthly temperatures recorded at Moor House were consistently lower than those at Durham, which were lower than those at Wareham, while the relative abundance of C.similis compared with C.equina decreased from Moor House to Durham to Wareham. This indicates that as the climate becomes progressively colder from southern England to the mountains of northern England, so the relative abundance of C.similis

increases.

IX. ADULT ACTIVITY

Coprophilous sphaerocerids are attracted to dung to feed and/or oviposit. The present studies have shown that as dung ages so its attractiveness to adults and its nutrient value to both adults and larvae decreases. The rate of ageing is dependent upon climatic conditions and is accelerated during the summer. Thus, the rapid invasion of freshly deposited dung by adults is important, particularly in the summer. Assuming there are individuals within the population that are in a state to be attracted, then the rate at which the freshly deposited dung is colonised will depend, in part, upon its proximity to these individuals and their level of activity. The level of activity of an insect is governed by its diurnal cycle, and the expression of this activity will be conditioned by the prevailing climatic conditions (Southwood, 1966).

(1) MOVEMENT OF ADULTS ON TO DUNG

A. Movement during the summer

Trapping was carried out on 5 occasions, around mid-day, in late July and early August 1965, using detergent traps (type B). Two traps, baited with fresh horse dung, were placed 10m apart in the "Cow Pasture" field (Fig.3) which contained cows, sheep, and a horse. Care was taken to place the traps at least 10m away from fresh dung, deposited by these animals. At 15min intervals any flies that had been caught were removed with fine forceps and placed in tubes of alcohol. Trapping was continued for 3 - 5hrs and the dung was renewed whenever it showed signs of ageing. This technique was employed in preference to direct sampling with an aspirator, as the latter method proved difficult in operation and the investigator influenced the results by continually interfering with the movement of adults on to the dung. The shade temperature, at approximately 5cms above ground level, was recorded at 15min intervals, and the humidity was recorded every 30mins, just above the vegetation level, using a whirling hygrometer. Notes were taken on rainfall, sunshine, and windspeed.

(a) Movement on to dung immediately after exposure

On the 5 occasions that trapping was executed, individuals of C.hirtipes and C.equina were caught within 1 - 4mins of the dung being exposed. This rapid movement towards the dung, immediately after exposure, is also demonstrated by comparing the catches for the first 15mins and the mean 15mins catch for a particular trapping period (Table 19). It can be seen from Table 19 that the first 15min catch was usually greater than the mean 15min catch(for the subsequent 3 - 5hrs). The high numbers of C.hirtipes and C.equina adults caught are indicative of high population densities in the area, while, conversely, the low numbers of C.similis adults were almost certainly due to a low population density.

TABLE 19. The number of adults of each species caught in the first 15mins of trapping, compared with the mean 15min catch, for the whole 3 - 5hrs of trapping

	No. of adults					
	C.similis		*C.equina*		*C.hirtipes*	
	1st 15mins	Mean 15mins	1st 15mins	Mean 15mins	1st 15mins	Mean 15mins
29 July	6	3	55	46	39	25
2 Aug	8	2	12	8	16	12
4 Aug	8	2	47	33	7	4
11 Aug	3	9	62	40	17	18
12 Aug	6	6	52	63	49	55

(b) The influence of climatic conditions

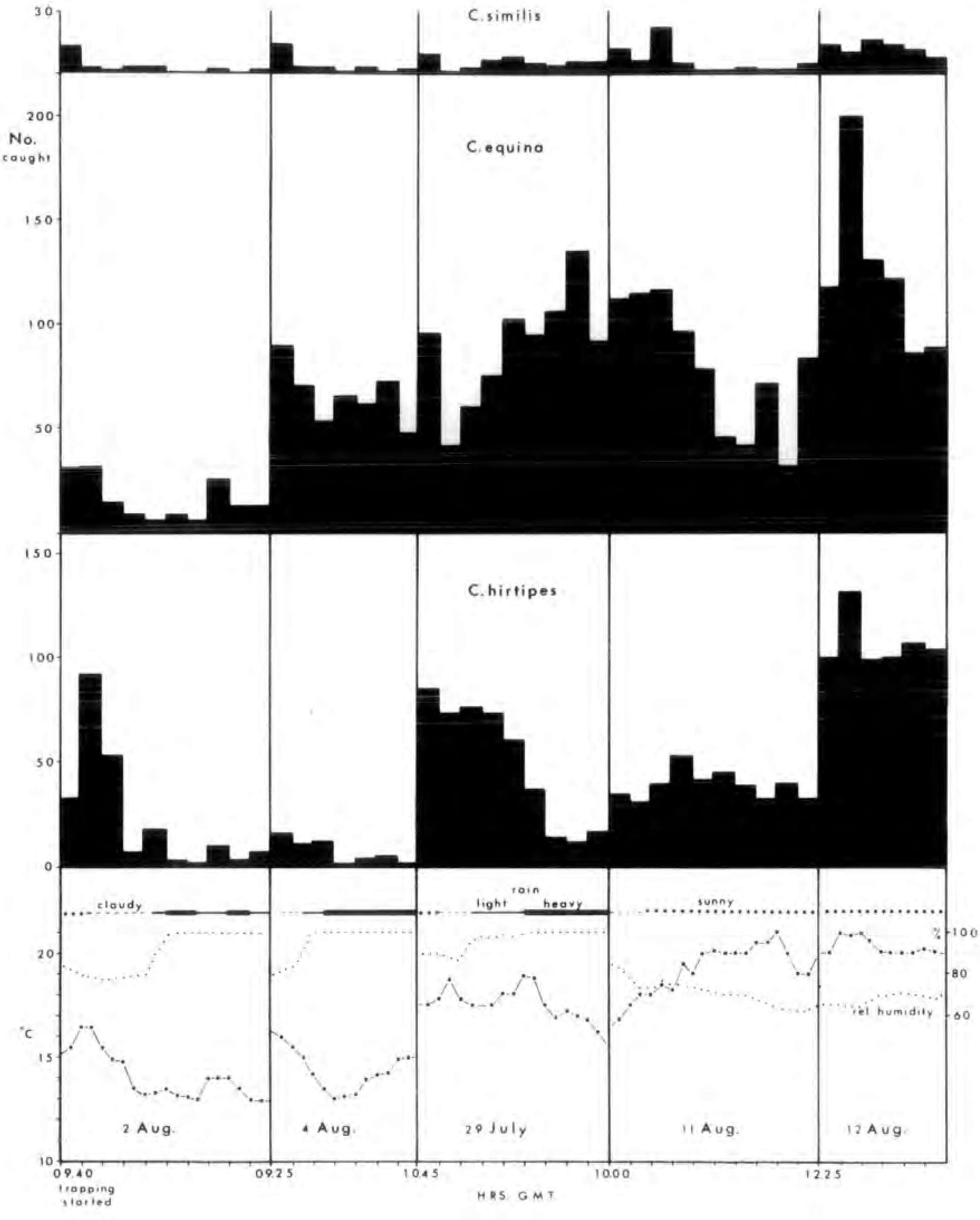
The numbers of adults of each species caught during 30min periods, the temperature, humidity, rainfall, and sunshine are shown in fig.18. The rainfall has been subjectively classified into light and heavy. Only very light winds were experienced and probably the fluctuations in wind speed had little effect on activity within a particular trapping period.

Direct comparisons between levels of activity on different days have been avoided, due to any unknown changes in population in the area and the varying quantities of alternative fresh dung that may have been present. The actual reduction in the numbers of adults present in the area, because of trapping, was probably not significant, as there were very high numbers

Fig.18. Numbers of adults of each species caught in 2 detergent traps (type B) baited with dung during 30min periods from :

10.45 - 15.15hrs 29 July; 09.40 - 14.40hrs 2 August;
09.25 - 12.55hrs 4 August; 10.00 - 15.00hrs 11 August;
12.25 - 15.25hrs 12 August 1965.

Temperature and relative humidity recorded at 15min intervals.
Observations on rainfall and sunshine, continuous.



C. similis
C. equina
C. hirtipes
No. caught
30
200
150
100
50
0
cloudy
rain
light
heavy
sunny
% 100
80
60
rel. humidity
°C
20
15
10
2 Aug.
4 Aug.
29 July
11 Aug.
12 Aug.
09.40
trapping started
09.25
10.45
10.00
12.25
HRS. G.M.T.

of adults associated with the large quantities of dung in the field and the considerable manure heaps close to the edge of the field.

The relationship between relative humidity and activity is difficult to evaluate from these results. Sphaerocerids inhabit damp humid places (Laurence, 1955) and Hammer (1941) pointed out that they are sensitive to low humidities. Therefore, presumably, only low humidities could inhibit activity. However, during the lowest humidities, recorded on 11 and 12 August, activity was still high (Fig.18). This does not preclude the possibility that there may have been greater activity at the same temperature if the humidity had been higher, or that activity would not have been inhibited at lower humidities. High humidities may well favour high levels of activity, but this cannot be assessed from these results, as the highest humidities were associated with rain.

The influence of temperature on activity is also complicated by the fact that reduction in temperature was often associated with rain. Attempts to correlate temperature and activity have, therefore, been limited to dry conditions. The activity of <u>C.hirtipes</u> did not appear to be significantly affected by an increase in temperature from 16.5°C - 21°C on 11 August (Fig.18), but the highest temperatures, recorded on 12 August, coincided with the peak in the numbers caught. The rise and fall in temperature over the first two and a quarter hours of trapping on 2 August was reflected by a rise and fall in the number of individuals caught. It appears from these results that an increase in temperature between 13°C and 21°C tends to increase activity, particularly if the rise is within the 13 - 16°C range.

The fluctuations in the numbers of *C.equina* adults that were caught on a particular day appear to be almost independent of the changes in temperature. Thus, the gradual increase in temperature from 16.5°C - 21°C, on 11 August, was accompanied by a general decrease in the numbers caught, apart from a slight initial rise, while the increase in temperature on 12 August was reflected by an increased catch, and the highest temperatures on 2 August were concomitant with the highest catches. All that can be concluded from these results is that the general level of activity appeared to be slightly higher on the warmer days. Although the numbers of *C.similis* caught were low, the reaction of this species to the temperature changes experienced appears to have been similar to *C.equina*.

Rain normally inhibits the activity of most species of Diptera associated with pasturing cattle and their excrement (Hammer, 1941). D.S. Gibbons (pers.comm.) found that at Houghall *Scopeuma stercoraria* adults were completely absent from cow pats during rain. From Fig.18 it can be seen that rain coincided with a reduction in the number of *C.hirtipes* adults caught. Although the general decrease in temperature associated with the rain may have contributed to this trend, it seems that rain alone inhibits movement. Thus, on 29 July there was a marked reduction in activity during heavy rain, at temperatures between 17°C and 18.5°C, compared with a high first catch which had been recorded at 17.5°C in dry conditions. However, heavy rain on 2 and 4 August in no way appeared to inhibit the movement of C.equina adults, while on 29 July the numbers that were caught actually increased during the 2hrs 30mins of heavy rain (Fig.18). The activity of C.similis also did not appear to be significantly inhibited by rain.

The ability to colonise fresh dung, in conditions that seriously hampers the movement of other coprophilous Diptera, is an obvious advantage to these species, as it allows them access to dung when it is of the highest nutrient value to them and in the absence of many other Diptera.

B. Movement during the winter

Hammer (1941) found that adults of C.equina were active at temperatures as low as 5°C and C.hirtipes at 5°C - 7°C. A chance observation at Moor House Nature Reserve, Westmorland, had clearly indicated that at least C.similis females were active at temperatures below 5°C. On 20 November 1963, at 13.00hrs, with approximately 2ins of snow lying on the ground and an air temperature of 1°C, 8 C.similis females were collected from horse dung that had been deposited less than 2hrs previously. A temperature of 27°C was recorded from the centre of the droppings by inserting a thermometer. The only dung located above the snow within an approximate 50m radius, and inhabited by C.similis adults, was 30m away. A temperature of 3°C was recorded at the centre of this dung.

To substantiate this observation a trapping regime, using 3 sets of 4 detergent traps (type A) sunk into the ground around 3 trays of fresh horse dung, was executed in the grounds of the Science Laboratories, Durham University. Trapping was carried out overnight, i.e. between 19.00 and 07.00hrs from 22 - 26 February 1965. The dung was removed at the end of each 12hr trapping session and replaced by fresh dung at the beginning of the next. The maximum temperature at grass level was recorded during each trapping period.

From Table 20 it can be seen that adults of C.similis and C.nitida were caught on all 4 nights, including the last 2 when sleet fell. The maximum temperature (1.1°C) recorded on the third night shows that both species must still be active at this temperature, or even below it. The population density of C.equina was probably low at this time, but the 1 male that was caught on the first night must have been capable of movement at 2°C or below. The ability of adults of certain species of Copromyza, particularly C.similis and C.nitida, to remain active at low temperatures and during inclement weather conditions must be extremely advantageous to them in winter as adults of both species are abundant and continue to breed during winter.

TABLE 20. The numbers of males (M) and Females (F) caught in detergent traps during 12hr trapping periods (overnight). February 1965. The max.temp. recorded at grass level during each period is shown

Trapping period 19.00hrs. day 1 to 7.00hrs. day 2	Max. Temp. °C.	C.similis		C.equina		C.nitida	
		M	F	M	F	M	F
Day							
1. 22 Feb 2. 23 Feb	2.0	2	7	1	0	1	1
1. 23 Feb 2. 24 Feb	1.5	7	8	0	0	2	5
1. 24 Feb 2. 25 Feb	1.1	1	0	0	0	0	1
1. 25 Feb 2. 26 Feb	1.5	1	0	0	0	1	0

(2) DIURNAL RHYTHMS OF LOCOMOTORY ACTIVITY

A. Introduction

Diurnal rhythms of activity have been demonstrated in numerous living organisms, particularly among arthropods, and the considerable literature has been reviewed by Harker (1958), Cloudsley-Thompson (1961), and Aschoff (1963). The present investigations are not concerned with determining the nature of diurnal rhythms of activity, but only with measuring levels of activity over 24hrs in the field. However, it is worthwhile pointing out that these rhythms can be partly or completely endogenous in origin, being governed by some internal physiological chronometer, or almost completely exogenous, controlled by cyclic variations in some physical environmental factor. Irrespective of the nature of the rhythm, it is essential that it is kept in time with the daily environmental changes, and Aschoff (1963) concluded that generally "there is a coupling between the innate oscillator and the driving agent, the environmental fluctuation." He stated that the driving agent is normally light and there is usually a remarkable independence of temperature.

Cloudsley-Thompson (1961) regards the terms rhythm, cycle, and periodicity as synonymous, and that a rhythm having a frequency of 24hrs is termed a diurnal rhythm, while diurnal activity means activity during daylight. These definitions are accepted in the following text.

Lewis and Taylor (1965) comprehensively studied the diurnal periodicity of flight by insects, using suction traps. As previous observations had indicated that adults of certain species of Copromyza remained active at temperatures below their flight threshold temperature, colonising dung by walking, the measurement of flight activity alone would be of little value in determining the actual diurnal periodicity of locomotory activity. Even at higher temperatures, the short low level flights, which are often characteristic of the movement of sphaerocerids on to dung, would be difficult to detect using a suction apparatus.

Hammer (1961), from direct observations on cow pats, concluded that adults of the species of Sphaeroceridae he encountered were not active between sunset and sunrise, while Laurence (1955) stated that "Sphaerocerids are caught in numbers in light traps, indicating considerable activity at night". To provide information on both nocturnal and diurnal activity, trapping was carried out on a 24hr basis, using detergent traps baited with fresh dung. Harker (1961) stated that any method of trapping may only reveal one particular phase of the general activity pattern, while Williams (1959) pointed out that trapping can only ever be a direct measurement of locomotory activity, but this in itself usually reflects productive activity, i.e. searching for food etc. As coprophilous sphaerocerids both feed and oviposit in dung, the results obtained by the use of detergent traps baited with dung should give a reasonable indication of the general diurnal periodicity of activity.

All the times given are G.M.T. unless otherwise stated.

B. September 1965

A trapping programme was carried out at Houghall farm from 10.00hrs on 13 September to 16.00hrs on 17 September, using 6 detergent traps (type B) baited with fresh horse dung. The trays were arranged at least 20m apart around the perimeter fence of the Cow Pasture (Fig.3) which contained cows, sheep, and a horse. Any flies that were caught were removed at 3hr intervals from 04.00 - 19.00hrs, while the overnight catch was of 9hrs duration. By renewing the dung each time the traps were emptied, the reduction in attractiveness due to ageing was minimized. Although the overnight exposure periods of the dung were longer, this would be compensated for by the reduced rate of ageing in the cooler more humid night conditions.

The meteorological data recorded during the trapping period are shown in Appendix 4. The temperature measurements were taken in the shade (5cm above ground level) and the humidity was recorded just above the level of the vegetation, using a whirling hygrometer.

A total of 619 C.similis, 3478 C.equina, 2134 C.hirtipes, and 209 S.subsultans adults were caught in 102hrs, demonstrating the efficiency of the traps. The differences between the numbers of adults of the 4 species that were caught were probably mainly due to different population densities in the area at the time.

However, it had been previously observed that *S.subsultans* adults were more adept at avoiding small detergent traps than the *Copromyza* spp. and this may also apply to the larger traps that were used in these investigations.

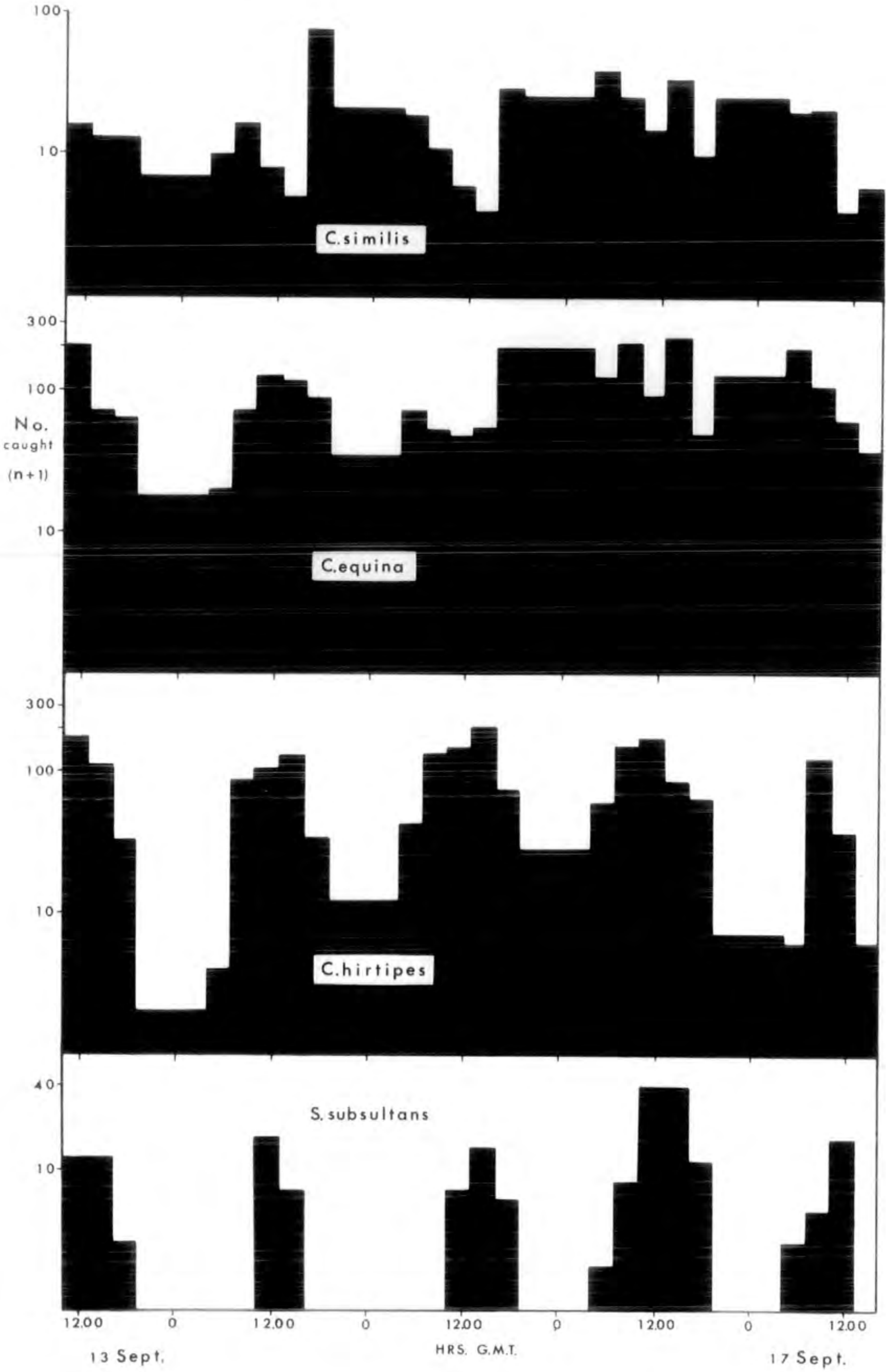
In Fig.19 the numbers of adults of each species caught in the 3hr trapping periods are shown. The 9hr overnight catch for each species has been equally divided into 3, and is thus represented in Fig.19. This has been done to enable the results to be expressed diagramatically, and it is not suggested that the level of activity of any species was constant throughout the night.

a) Nocturnal Activity

As sunset was at approximately 18.25hrs and sunrise at 05.30hrs, all the individuals caught in the 9hr period must have been caught after sunset and before sunrise. It can be seen from Fig.19 that *C.similis* was extremely active during this period, and it is possible that the greatest activity may have been at night, particularly on the third and fourth nights. Similarly, *C.equina* must have been very active overnight, particularly on the third and fourth nights. *C.hirtipes* adults were far less active at night than those of the above species, or compared with their own diurnal activity. No *S.subsultans* adults were caught at night.

The lowest overnight catch was recorded on the first night and the highest on the third for all the *Copromyza* spp.

Fig.19. Numbers of adults of each species caught in 6 detergent traps (type B) baited with dung during 3hr periods. (Overnight trapping period was of 9hrs duration, but represented as 3 equal 3hr catches). 10.00hrs 13 September - 16.00hrs 17 September 1965



100
10
C.similis
300
100
No.
caught
(n+1)
10
C.equina
300
100
10
C.hirtipes
40
S. subsultans
10
12.00
0
12.00
0
12.00
0
12.00
0
12.00
13 Sept.
HRS. G.M.T.
17 Sept.

This coincided with the lowest minimum temperature which was recorded on the first night and the highest, recorded on the third night. Williams (1940), using a light trap, found that an increase in the minimum temperature of $5^{o}F$ was accompanied by a doubling of the number of insects caught. It seems probable that an increase in minimum nightly temperature causes an increase in adult activity of the *Copromyza* spp.

b) Diurnal Activity

From Fig.19 it can be seen that there was no clear activity pattern for *C.similis*. From 10 - 13 September maximum catches were recorded from 10.00 - 13.00hrs, 16.00 - 19.00hrs, 16.00 - 19.00hrs, and 04.00 - 07.00hrs respectively. *C.equina* showed a somewhat similar irregular pattern of diurnal activity over the trapping period (Fig.19). In contrast to these species, *C.hirtipes* exhibited a clearly defined pattern of diurnal activity, with maximum activity between 10.00 - 16.00hrs on all days except 15 September when it was from 07.00 - 10.00hrs. However, as previous observations had indicated, rain tends to reduce activity and the rain which fell intermittently from 10.00 - 16.00hrs was probably responsible for inhibiting activity during this period. *S.subsultans*, after being inactive overnight, showed a clear pattern of activity, similar to *C.hirtipes*, with maximum activity between 10.00hrs and 16.00hrs on all occasions (Fig.19).

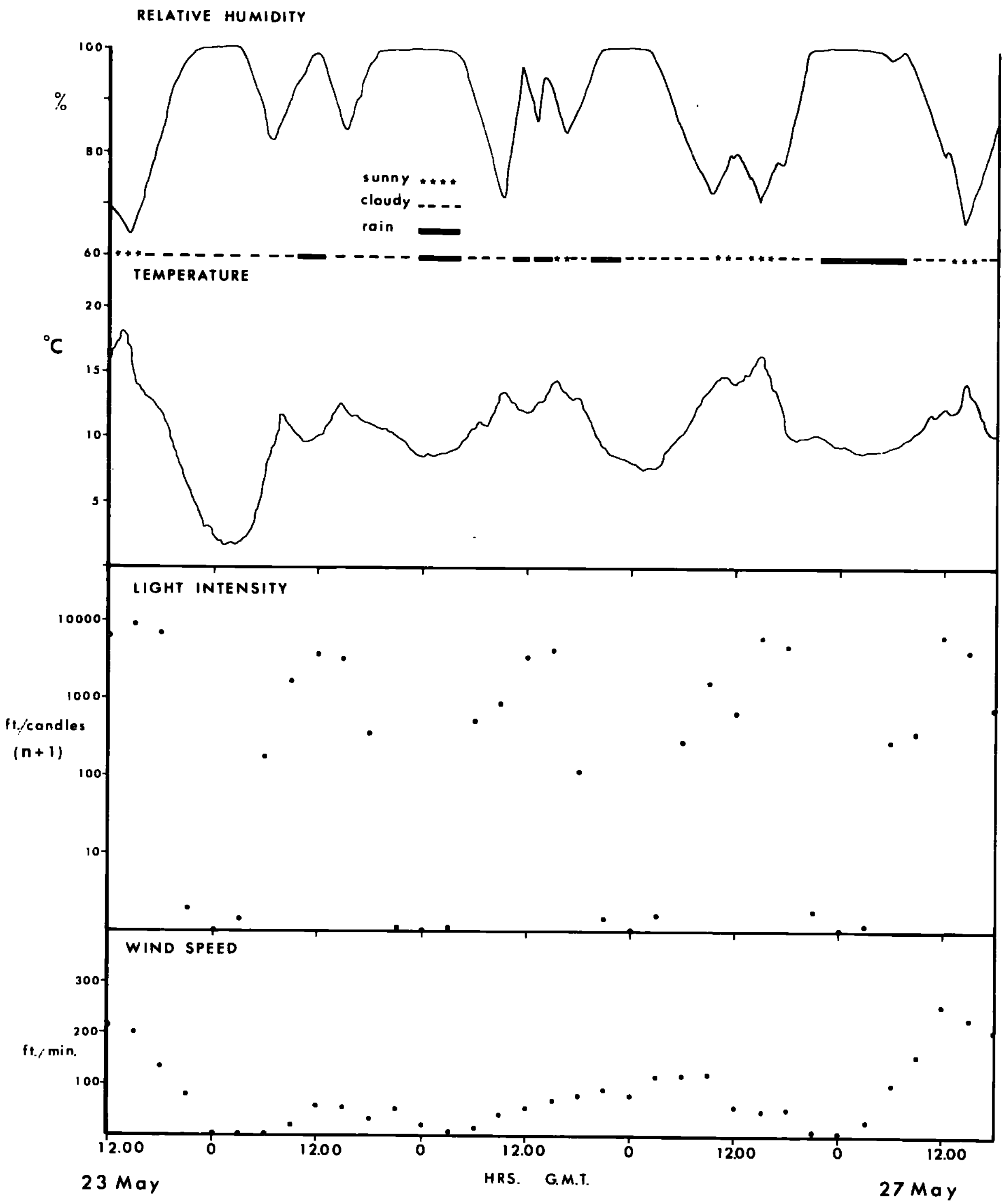
It seems probable that both S.subsultans and C.hirtipes adults are usually most active around mid-day. However, the results obtained from a trapping method in which the unit trapping time is 3hrs must only give an approximate indication of the time of maximum and minimum activity as it is possible that there could be quite considerable variations in activity over 3hrs.

C. May 1966

A more extensive trapping regime was carried out in the same area using 6 detergent traps (type B) baited with fresh horse dung and 3 with pig dung, (arrangement as described for the September investigations), from 12.00hrs 23 May - 16.00hrs 27 May. Any flies that were caught were removed at 3hr intervals and on each occasion the dung was also renewed. It was found necessary to use some fresh pig dung as sufficient supplies of fresh horse dung were not available.

Continuous temperature and humidity readings were obtained using a thermohygrograph (at ground level) protected from rain and direct sunlight. These readings were checked by taking temperature and humidity measurements (as previously described for the September investigations). The temperature and humidity records, together with information on cloud, sunshine, and rainfall, are shown in Fig.20. The wind speed (in ft per min) was measured, at approximately 1m above ground level, by taking the mean of three 1min counts using an anemometer.

Fig.20. Temperature, relative humidity, and observations on rainfall and sunshine, recorded continuously. Wind speed and light intensity recorded at 3hr intervals. 12.00hrs 23 May - 16.00hrs 27 May 1966.



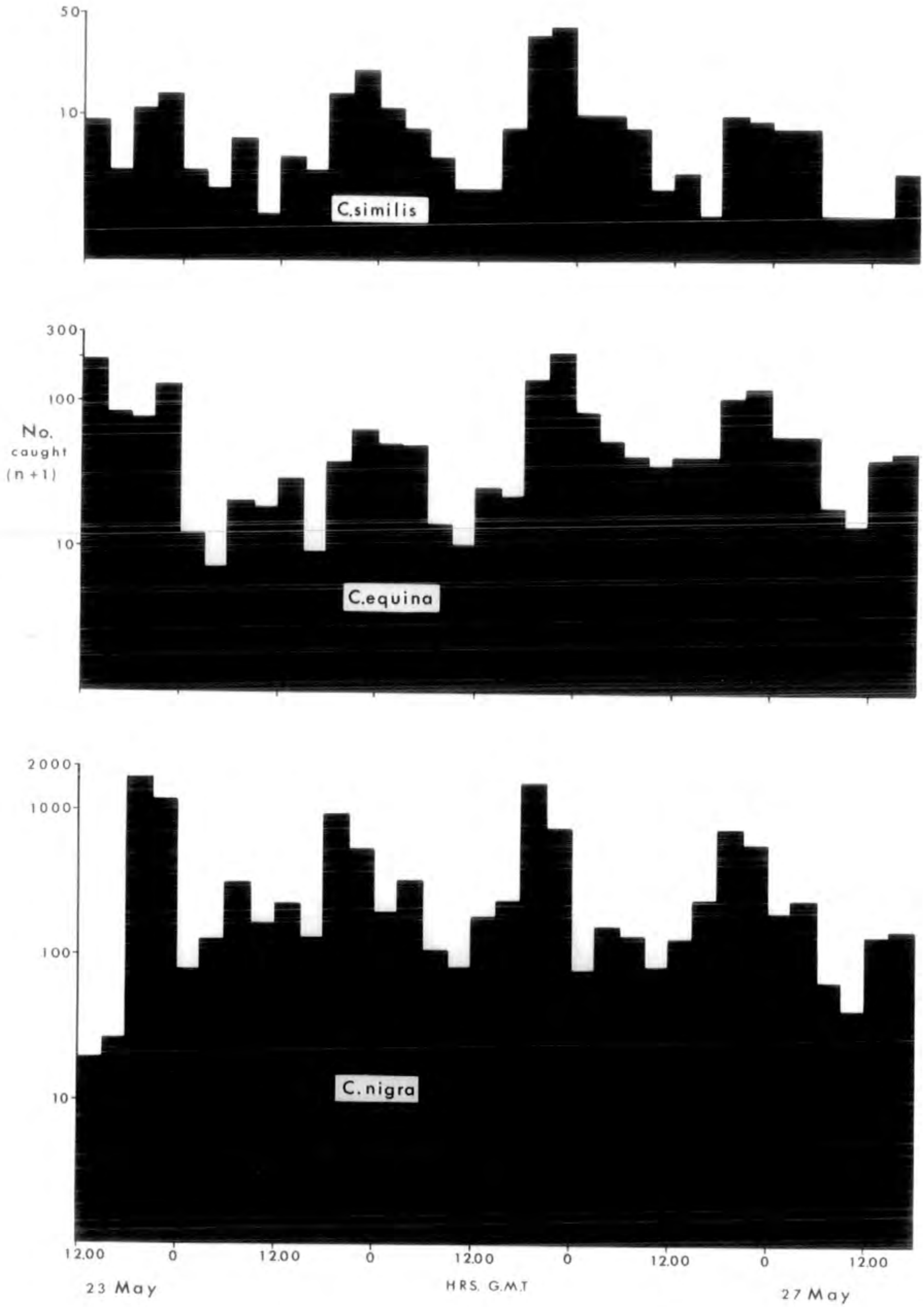
RELATIVE HUMIDITY
%
100
80
60
sunny
cloudy
rain
TEMPERATURE
°C
20
15
10
5
LIGHT INTENSITY
ft./candles
(n+1)
10000
1000
100
10
WIND SPEED
ft./min.
300
200
100
12.00
0
12.00
0
12.00
0
12.00
0
12.00
23 May
HRS. G.M.T.
27 May

The light intensity was recorded with an S.E.I. exposure photometer, accurate from 0.01 - 10,000ft candles, sighted against a white card which had an approximate reflectance value of 80%. These records are also shown in Fig.20. During the trapping period sunset was at approximately 20.20hrs and sunrise at 03.45hrs. The numbers of adults of each species caught in the 3hr trapping periods are shown in Figs. 21 and 22. In Fig.23 the total number of adults of each species caught in four equivalent daily 3hr periods has been expressed as a percentage of the total catch for that species from 12.00hrs 23 May to 12.00hrs 27 May. Thus, activity during a 3hr period is expressed as a percentage of daily activity and consequently the general diurnal rhythm of locomotory activity can more easily be seen.

12,109 C.nigra, 1,985 C.equina, 259 C.similis, 1,913 C.hirtipes, and 511 S.subsultans adults were caught in the 102hrs of trapping. The very high numbers of C.nigra adults that were caught was almost certainly due to the fact that the time of trapping coincided with the peak in seasonal occurrence of adults in the open field. The close proximity of extensive manure heaps probably accounts for the relatively large numbers of S.subsultans adults that were trapped.

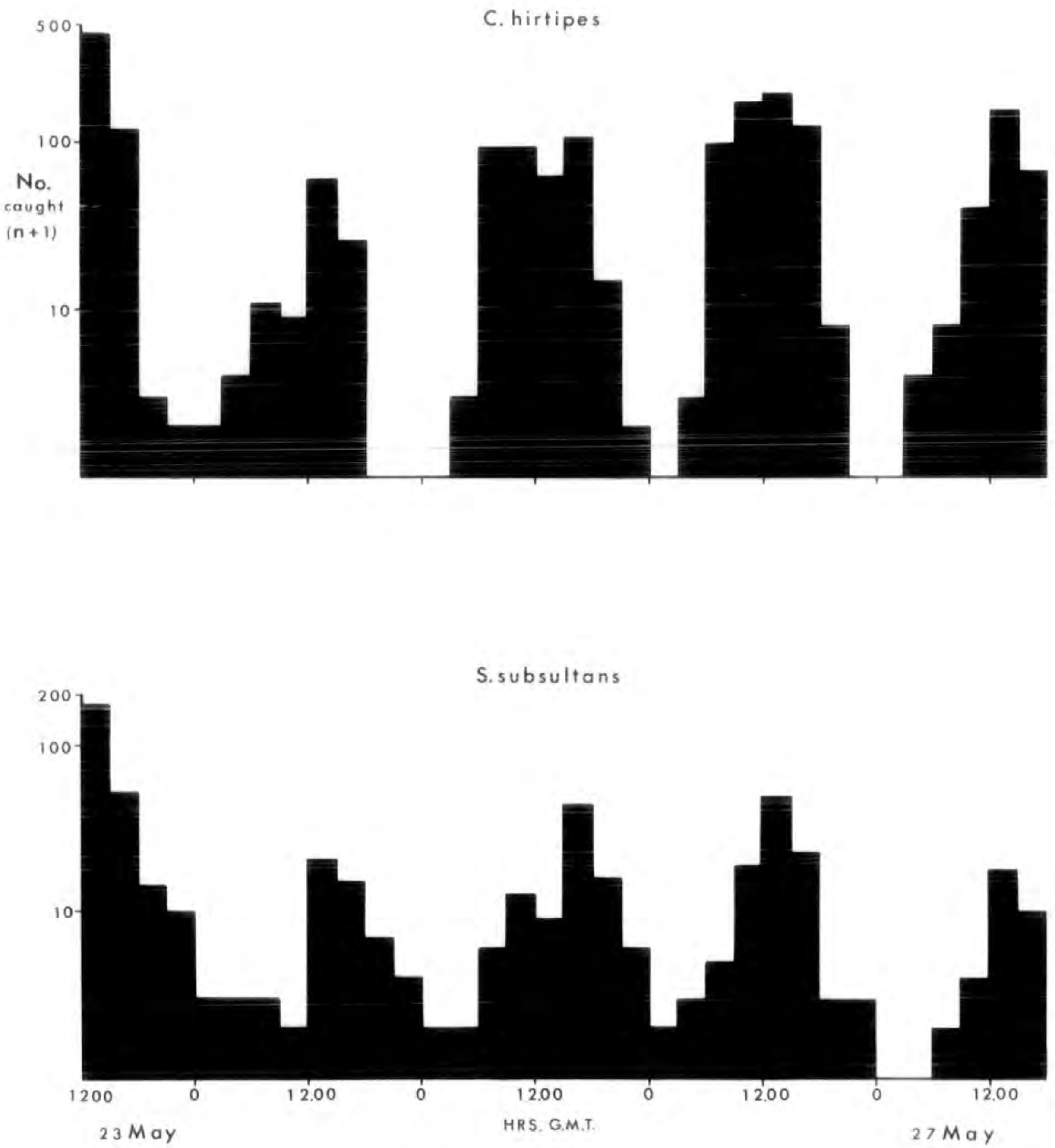
C.nigra : This species showed a definite and quite regular diurnal cycle of activity during the trapping period which did not seem to be appreciately affected by the day-to-day changes

Fig.21. Numbers of C.similis, C.equina, and C.nigra adults caught in 9 detergent traps (type B) baited with dung during 3hr periods from 12.00hrs 23 May - 16.00hrs 27 May 1966



50
10
C.similis
300
100
10
No.
caught
(n+1)
C.equina
2000
1000
100
10
C.nigra
12.00
0
12.00
0
12.00
0
12.00
0
12.00
23 May
HRS. G.M.T
27 May

Fig.22. Numbers of C.hirtipes and S.subsultans adults caught in 9 detergent traps (type B) baited with dung during 3hr periods from 12.00hrs 23 May - 16.00hrs 27 May 1966.



C. hirtipes
500
100
No.
caught
(n+1)
10
S. subsultans
200
100
10
1200
0
12.00
0
12.00
0
12.00
0
12.00
23 May
HRS. G.M.T.
27 May

Fig.23. Percentage of total number of adults of each species caught in 9 detergent traps baited with dung during 4 equivalent daily 3hr periods from 12.00hrs 23 May - 12.00hrs 27 May 1966.

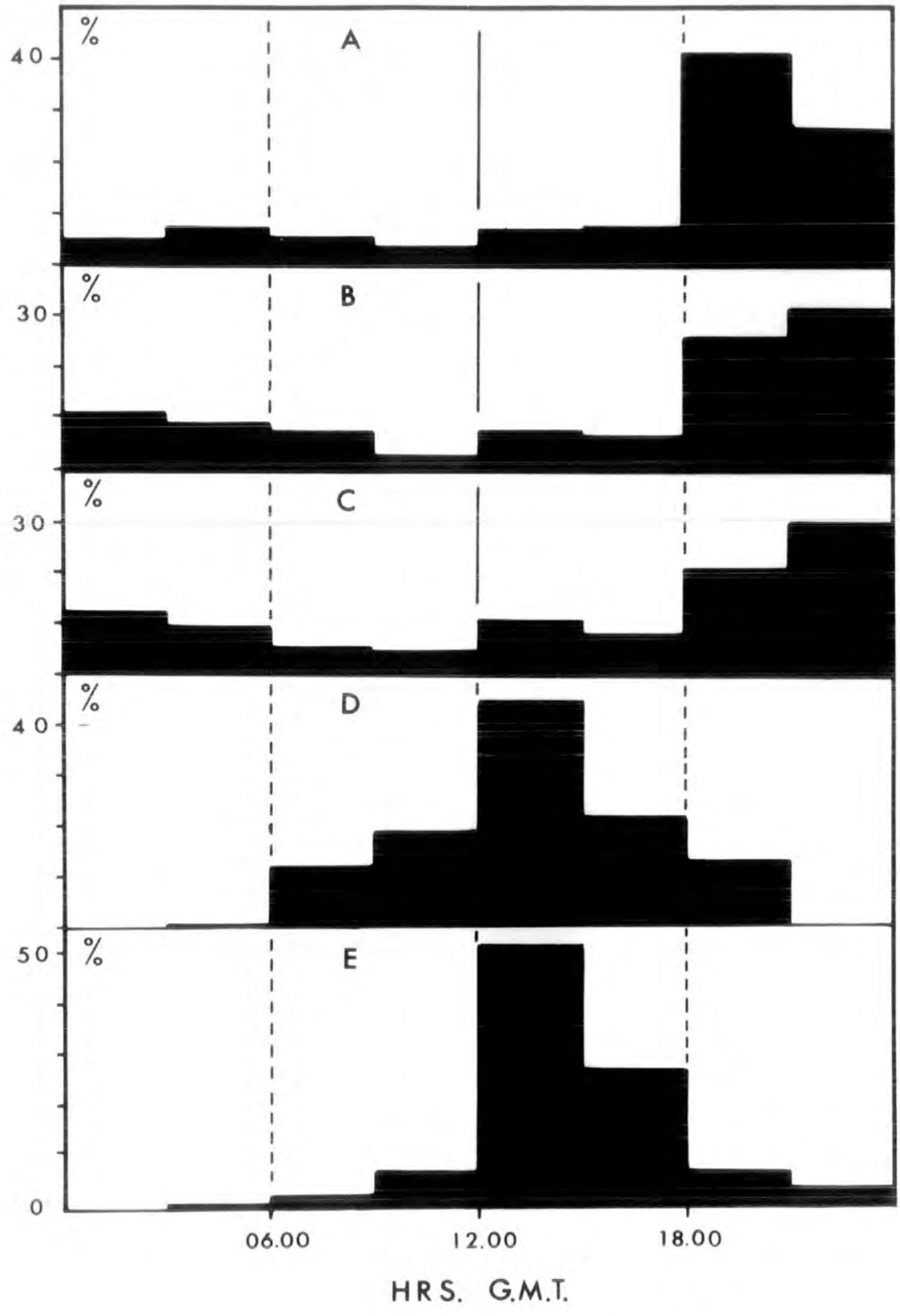
A. C.nigra

B. C.similis

C. C.equina

D. C.hirtipes

E. S.subsultans



%
A
40
%
B
30
%
C
30
%
D
40
%
E
50
0
06.00
12.00
18.00
HRS. G.M.T.

in weather conditions (Figs. 20 and 21). It can be seen from Fig.23 that by far the greatest activity was recorded between 18.00hrs and 21.00hrs. Although activity remained high between 21.00hrs and midnight, there was a marked decrease after the latter time. Activity remained relatively low from 0 - 18.00hrs, with a minimum catch from 09.00 - 12.00hrs, and a slight peak after sunrise.

From Figs. 20 and 21 it can be seen that C.nigra was most active at the times when wind speed, temperature, and light were decreasing, but humidity was increasing, i.e. around dusk. However, just before dawn, when the air humidity is highest and temperature and wind speed are lowest, activity was greatly reduced. Lewis and Taylor (1965) found that the majority of insects feeding on decaying organic matter flew at dawn or, more especially, dusk. This, they suggested, may be due to the still moist air which would aid the detection of food by smell, but the low temperatures around dawn decrease the rate of evaporation of odours. The diurnal cycle of activity of C.nigra adults may be affected either by temperature, humidity, or light, or by a combination of them, but the relative importance of these factors cannot be evaluated from these investigations.

C.similis : Over the trapping period the diurnal rhythm of C.similis was more irregular than that of C.nigra, although the peak in activity was always between 18.00hrs and

24.00hrs, from 23 - 26 May (Fig.21). From Fig.23 it can be seen that there was peak in activity from 21.00hrs to midnight, followed by a progressive decrease in activity to midday. Although activity remained low from 12.00hrs to 18.00hrs, there was a dramatic rise in the number of adults caught between 18.00hrs and 21.00hrs. Again, this rise in activity coincided with a decrease in temperature and windspeed and an increase in humidity.

Lewis and Taylor (1965) did not detect flight activity at night by C.similis, but they found that flight activity was bimodal with a small peak around midday and at a maximum around 17.00hrs. The results obtained in the present work and those obtained by Lewis and Taylor (1965) are not necessarily mutually exclusive. The present work was carried out in an area which contained large quantities of dung from various farm mammals and, therefore, probably a high population density of coprophilous sphaerocerids. Movement on to dung at night might well be by walking,as this has been observed at low temperatures in daylight, or by short low level flights which would not be detected with a suction apparatus. It is quite possible that more sustained flight is mainly diurnal.

C.equina : Apart from a higher first catch, the diurnal cycle of activity of C.equina was similar to C.similis, with maximum activity between 18.00hrs and midnight (Fig.21). Another similarity is that the activity of both species does not appear to be appreciably affected by rain (Figs. 20 and 22). It can be seen from Fig.23 that the general pattern of the diurnal cycles of these species was very much alike.

C.hirtipes : This species exhibited a clearly defined diurnal cycle of activity throughout the trapping period, with greatest activity around midday (Fig.22). As previous investigations had indicated, rain appears to inhibit movement, and lower than expected catches were recorded during periods of rain around midday, i.e. from 09.00 - 12.00hrs on 24 May, and from 12.00 - 15.00hrs on 25 May (Figs. 20 and 21). From Fig.23 it can be seen that this species was virtually inactive between 21.00hrs and 06.00hrs. There was a progressive increase in activity from 03.00hrs, to reach a maximum from 12.00 - 15.00hrs, followed by a progressive decrease.

The periods of maximum activity coincided with maximum temperature and minimum humidity. As the latter can hardly be required for optimum activity of a species that normally inhabits damp places, it appears that the most important environmental factor affecting the diurnal rhythm of activity must be either temperature or light, or a combination of both. However, their relative importance cannot be evaluated from these results.

It must be emphasised that the conclusions drawn from these investigations, concerning the diurnal rhythms of activity of adults of any species, are necessarily bounded by the conditions experienced. Thus, for instance, it is possible that exceptionally low humidities and high temperatures in the field may reduce the activity of C.hirtipes adults. However, it is worthwhile pointing out that on 12 August 1965 C.hirtipes adults were most active at the time when the shade temperature was highest, i.e. 21°C, and the humidity lowest (Fig.18.). The screen maximum temperature of 22.1°C recorded at the Houghall observatory on 12 August was only exceeded on two occasions in 1965 and, therefore, it appears that under normal summer conditions at Houghall activity will rarely, if ever, be inhibited by high temperature and low humidity.

S.subsultans : The diurnal cycle of activity of this species is similar to C.hirtipes. Rain, at the times mentioned for the latter, also appears to inhibit movement (Figs. 20 and 22). From Fig. 23 it can be seen that there was a progressive rise in activity from 03.00hrs to reach a maximum between 12.00hrs and 15.00hrs, followed by a progressive decrease. The 09.00 - 12.00hrs catch was relatively lower than the corresponding catch for C.hirtipes, while the 18.00 - 21.00hrs catch was higher. This indicates that the peak in activity was slightly later for S.subsultans than for C.hirtipes.

There was no significant difference between the diurnal rhythm of activity of the males and females of any species.

The effects of available food on the trapping results:

It was necessary to carry out these investigations in an area where the density of coprophilous sphaerocerids was high.

Obviously, to satisfy this requirement, the area had to contain quantities of dung from farm mammals. Variations in the quantities of fresh dung in the vicinity of the traps could affect the degree of hunger of the flies, and hence the efficiency of the traps. No appreciable quantities of fresh dung were added to the extensive manure heaps close to the traps and as large accumulations of dung tend to age slowly it can be reasonably assumed that this food source remained fairly constant over the trapping period. Therefore, on a 24hr basis, the variations in available food would have been mainly dependent upon the diurnal rhythm of defaecation of the cows and to a lesser extent the sheep, in the Cow Pasture field.

Hammer (1941) found that cows were active from somewhat before sunrise till towards midnight, with numerous resting periods, including a long rest between 11.30hrs and 13.30hrs (C.E.T.), and that each cow deposited dung 7 to 9 times in 24hrs, while Mohr (1943) gave the rate of defaecation as 10 times per day. The only time that Hammer (1941) found a lack of fresh droppings was between 12.30 and 13.30hrs. The weather conditions during the present investigations were generally cool and cloudy and under these conditions the dung would not tend to age rapidly. Thus, it seems unlikely that there would be a shortage of dung suitable for the adults to feed on at the times mentioned by Hammer, and consequently the deposition of dung in the cow pasture probably did not have a significant effect on the diurnal cycle of activity of the coprophilous sphaerocerids in the area.

X. CHEMICAL ATTRACTANTS FOR SOME COPROPHILOUS SPHAEROCERIDAE

Olfactory stimulation in terrestrial insects is accomplished by airborne molecules which impinge on the extremely sensitive olfactory receptors. Any stimulus which produces a positive directive response may be termed an attractant. Normally when the insect is stimulated, it appears to respond spontaneously and moves towards the source of the attractive odours. Natural attractive odours assist insects in various ways, including recognizing and locating a mate, oviposition sites, and food.

Many workers have investigated insect attractants and repellents, particularly for insects of economic importance, e.g. sheep blow-flies (*Lucillia* spp.) (Hobson, 1936; Mackerras and Mackerras, 1944; Cragg and Ramage, 1945; and Cragg, 1950, 1956), and *Musca domestica* adults (Crumb and Lyon, 1921), and larvae (Hafez, 1950).

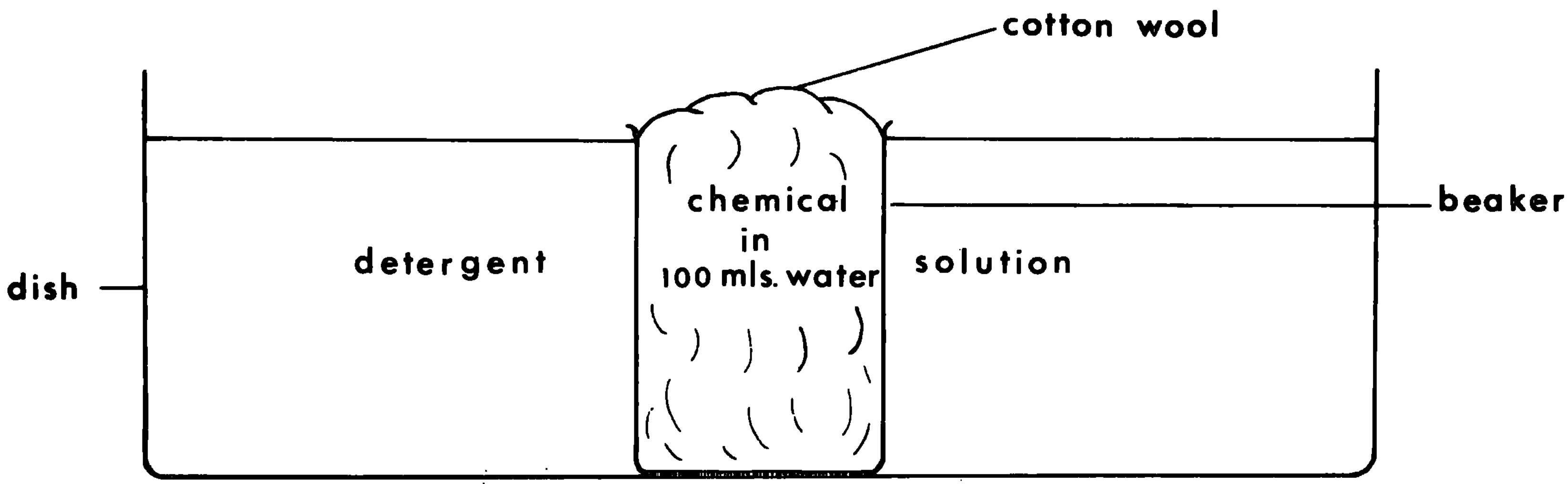
(1) TECHNIQUE FOR ESTIMATING THE RELATIVE ATTRACTIVE POWERS OF CHEMICALS

Coprophagous insects are attracted to dung by odours from protein and fat decomposition products present. Dethier (1947) listed the components of faeces with special reference to the odorous constituents. A number of pure chemicals, from this list, were tested under field conditions to determine if they were attractive to certain species of coprophilous Diptera.

A known quantity of chemical, or a combination of chemicals, was added to 100ml of water and thoroughly shaken in a stoppered bottle. The contents of the bottle were carefully poured into a 100ml beaker containing a wad of cotton wool, and as the level of the liquid rose, so the cotton wool was pulled out above the lip of the beaker. Any undissolved solid tended to lie in the cotton wool, but the odour could still be detected by the observer and, therefore, presumably by the insect with its greater olfactory acuity. Each beaker was placed in the centre of a 15cm diameter, 7cm deep crystallizing dish. The dishes had previously been set out at least 10m apart in a field close to the University of Durham Science Laboratories (Nat.Grid Ref.NZ 277415). Water, plus a little detergent solution, was gradually poured into the dishes to within a few mm of the lips of the beakers (Fig.24). A beaker containing only water was also placed in the centre of a dish of detergent solution as a control. To give some indication of the relative attractiveness of the chemicals compared with dung, a beaker of fresh horse dung in a dish of detergent solution was also simultaneously exposed. The traps were left in position for several days and any flies that were caught were removed and identified. On completion of each exposure the chemicals were disposed of away from the area, and the dishes and beakers thoroughly washed in hot water. This was necessary to avoid contamination in subsequent investigations of chemical attractants.

Fig.24. Detergent trap (15cm diameter) with a beaker containing 100mls of water, a chemical attractant, and cotton wool.

Detergent Trap with Chemical Attractant



(2) THE NUMBERS OF ADULTS CAUGHT IN DETERGENT TRAPS WITH CHEMICAL ATTRACTANTS

In late June and early July 1964 0.2gm of solid and 0.2ml of liquid chemicals were added to 100ml of water and exposed for 5 days. At the end of this period the traps were emptied and the chemicals renewed. 3 such repetitions were carried out. Table 21 shows the numbers of adults of each species that were caught in detergent traps with different chemicals as attractants. Chemicals that had proved to be attractive in 1964 were tested with other chemicals, both singly and in combination with skatole, for three 3-day periods in early May 1965. The quantity of chemical used was reduced by half but, as before, fresh chemicals were used for each exposure (in all subsequent experiments fresh solutions were used for each exposure). In Table 22 the numbers of adults of each species that were caught in detergent traps with different chemicals as attractants are shown. The numbers of Scopeuma stercoraria and Dasyphora cyanella adults that were caught in the detergent traps are also included.

A further three 3-day exposures were carried out with 0.1% solutions of skatole in combination with either n-butyric acid, iso-butyric acid, n-valeric acid, or iso-valeric acid. The total numbers of adults caught in six 3-day periods, when these solutions were simultaneously exposed, are shown in Table 23. To determine if any of the solutions is significantly more attractive to a particular species than another, χ^2 values have been calculated (Table 23).

0.1% solutions of skatole, indole, and n-butyric acid, both singly and in combination, were exposed for three 3-day periods in April 1965. Table 24 shows the total numbers of adults of each species that were caught in detergent traps with these chemicals as attractants. χ^2 values have been calculated and are also shown in Table 24.

TABLE 21. Total numbers of adults caught in detergent traps with chemicals and horse dung as attractants in 15 days (three 5-day exposures). 1 trap to each chemical (0.2gm of solids and 0.2ml of liquids to 100ml of water) Skatole (S), Indole (I). June - July 1964

	C.similis	C.equina	C.hirtipes	S.subsultans	S.nitida
Skatole	0	5	15	1	0
Indole	1	1	7	0	0
Skatole Indole	0	1	8	1	1
iso-Butyric acid	0	1	53	0	0
iso-Valeric acid	0	3	104	1	2
iso-Butyric acid + S + I	7	30	461	10	2
iso-Valeric acid + S + I	3	23	530	15	1
Methylamine	0	2	9	7	40
Dimethylamine	0	0	6	0	0
Trimethylamine	1	0	3	0	0
1, 4-Diamino butane	1	0	15	0	0
1, 5-Diamino pentane	0	0	2	0	0
Phenol	1	0	7	0	0
Ammonium carbonate	0	0	2	0	0
Ammonium hydroxide	0	0	2	0	7
Paracresol	0	0	1	0	0
Benzoic acid	0	0	4	0	0
Indole-acetic acid	0	0	1	0	0
Horse dung	12	29	577	19	6
Water	0	2	2	0	0

(chemical nomenclature is that used by B.D.H.Ltd., the suppliers)

TABLE 22. Total numbers of adults caught in detergent traps with Chemicals and horse dung as attractants in 9 days (three 3-day exposures). 1 trap to each chemical (0.1gm of solids and 0.1ml of liquids to 100ml of water) Skatole (S) May 1965

	C.equina	C.similis	C.hirtipes	C.nigra	Scopeuma	Dasyphora
Acetic acid	0	0	0	4	4	18
Acetic acid + S	0	0	0	0	3	7
Propionic acid	1	0	1	0	1	12
" acid + S	0	1	0	0	2	0
n-Butyric acid	0	1	0	8	10	6
n- " + S	70	159	49	869	42	23
iso-Butyric acid	0	2	1	4	2	2
iso- " + S	43	84	31	734	48	20
n-Valeric acid	0	1	2	3	10	
n- " + S	22	96	11	502	34	5
iso-Valeric acid	0	9	10	7	0	0
iso- " + S	29	85	13	500	22	0
n-Caproic acid	0	0	0	0	13	0
n-Cap " + S	3	6	1	0	14	9
iso-Caproic acid	0	0	0	0	12	1
iso- " + S	5	23	6	136	36	6
n-Octoic acid	0	0	0	0	0	0
n- " + S	0	0	0	0	3	0
n-Decoic acid	0	0	0	0	0	0
n- " + S	0	1	0	0	15	0
Methylamine	0	0	0	0	24	0
Methylamine + S	5	4	3	57	64	1
Ethyl mercaptan	0	0	0	2	0	0
Ethyl " + S	0	0	2	3	3	0
Skatole	0	3	1	12	1	0
Indole	0	1	1	20	2	0
Horse dung	43	117	40	665	15	22
Water	0	1	0	3	0	0

(B.D.H. chemical nomenclature)

TABLE 23. Total numbers of adults caught in detergent traps with 100ml of 0.1% solutions of skatole, plus certain fatty acids, in 18 days (six 3-day exposures) May 1965. χ^2 values have been calculated using a null hypothesis that the distribution of adults between the chemicals compared is equality.

	No. of adults			
	C.equina	C.similis	C.hirtipes	C.nigra
1. n-Butyric acid + skatole	148	369	131	1987
2. iso-Butyric acid + skatole	57	175	76	1009
3. n-Valeric acid + skatole	35	155	46	853
4. iso-Valeric acid + skatole	57	170	75	1002

Totals in χ^2 comparisons	χ^2	P.	χ^2	P.	χ^2	P.	χ^2	P.
1 and 2	40.4	<0.001	69.1	<0.001	14.6	<0.001	100+	<0.001
1 and 3	69.6	<0.001	87.3	<0.001	41.6	<0.001	100+	<0.001
1 and 4	40.4	<0.001	72.1	<0.001	15.2	<0.001	100+	<0.001
2 and 3	5.2	<0.05	1.2	>0.2	7.4	<0.01	13.0	<0.001
2 and 4	0		0.07	>0.7	0.003	>0.95	0.001	>0.95
3 and 4	5.2	<0.05	0.7	>0.3	7.0	<0.01	12.0	<0.001

TABLE 24. Total numbers of adults caught in detergent traps with Skatole (S), Indole (I), and n-Butyric acid (B), singly and in combination in 9 days (three 3-day exposures). Apr. 1965. χ^2 values have been calculated

100ml of H_2O to quantity of chemical	No. of adults *C. similis*	*C. equina*	*C. hirtipes*	*C. nigra*
1. 0.1ml B.	8	3	2	0
2. 0.1gm I.	40	8	9	0
3. 0.1gm S.	30	19	14	6
4. 0.1gm S. + 0.1gm I.	20	9	9	6
5. 0.1gm I. + 0.1ml B.	77	29	22	10
6. 0.1gm. S. + 0.1ml B.	300	94	40	103
7. 0.1gm S. + 0.1gm I. + 0.1ml B.	116	36	20	6

Total in χ^2 comparison	χ^2	P.	χ^2	P.	χ^2	P.	χ^2	P.
5 and 6	100+	< 0.001	34.3	< 0.001	5.2	< 0.05	76.4	< 0.001
5 and 7	7.9	< 0.01	0.8	> 0.3	0.02	> 0.8	1.0	> 0.3
6 and 7	81.3	< 0.001	25.9	< 0.001	6.7	< 0.01	86.2	< 0.001

A. Skatole C_9H_9N and Indole C_8H_7N

Skatole is known to be an attractant to many insects. *Necrophorus orbicollis* and *N.americanus* adults found approximately 54% of objects (meat and clothes) soaked in skatole and buried in sand (Abbott, 1936). Dung beetles of the genus *Geotrupes* are attracted to skatole (Warnke, 1931) and it attracts *Lucilia sericata* Mg. (Hobson, 1936). Indole is also attractive to *L.sericata* (Hobson, 1936) and to *Drosphila* spp. (Hunter, Kaplan and Enzmann, 1937).

In the text, the following terms are used to describe attractants in order of increasing attractiveness : marginal, slight, mild, moderate, strong, and powerful.

It can be seen from Tables 21, 22, and 24, that solutions of indole and skatole, both singly and in combination, were only slightly attractive to adults of the *Copromyza* spp., *S.subsultans*, and *Scopeuma*. However, if skatole and/or indole were combined with certain other chemicals (that in themselves are only slightly attractive), then the resultant solutions were powerful attractants. Thus, 510 sphaerocerids, 34.4% of the total catch, were caught in the traps with indole, skatole plus iso-butyric acid as the attractant, while a solution of indole, skatole plus iso-valeric acid caught 572 adults, 40.9% of the total (Table 21). The *Copromyza* spp. were also strongly attracted to solutions of skatole in combination with either n-butyric acid, iso-butyric acid, n-valeric acid, or iso-valeric acid, although separately these chemicals were only marginally attractive (Tables 22 and 23). This may be due to skatole and indole acting as "fixing agents" to odours from the other chemicals.

From Table 24 it can be clearly seen that solutions of n-butyric acid plus skatole and/or indole were far more attractive than would be expected from the numbers of adults that were caught in traps where these chemicals were used in isolation. A solution of n-butyric acid plus skatole was significantly more attractive to the Coromyza spp. than n-butyric acid plus indole, or n-butyric acid plus indole and skatole (Table 24). A solution of n-butyric acid plus skatole and indole was significantly more attractive to C. similis than a solution of n-butyric acid plus indole, but there appears to have been no significant difference between the attractive powers of these two solutions to other Copromyza spp.

B. Fatty acids

A mixture of volatile organic acids, consisting mainly of short-chain fatty acids, is a characteristic product of fermentation within the alimentary tract of mammals. Elsden, Hitchcock, Marshall and Phillipson (1946) found that the quantities of volatile fatty acids produced by mammals varied from species to species (ruminants producing the largest quantities). They listed the following animals in order of decreasing production : oxen and sheep, horses, pigs, rabbits, and rats. The fate of volatile fatty acids in the intestine has been the subject of a number of investigations (Phillipson and McNally, 1942; Barcroft, McNally and Phillipson, 1944; Elsden, 1946; Danielli, Hitchcock, Marshall and

Phillipson, 1946; Masson and Phillipson, 1952). These investigations showed that although there was a high concentration of volatile fatty acids (mainly acetic, propionic, and butyric acids) in the rumen, due to absorbtion in the rumen, reticulum, and omasum, the concentration in the abomasum was low. Gray, Pilgrim and Weller (1951) found that 1 kilo of wheaten hay, fermented in vitro, gave 200 - 250gm of volatile fatty acids, but they concluded that very little of these acids would be found in the excrement of the animals.

Phillipson (pers.comm., 1965) stated that fatty acids in the faeces of cows, sheep, and horses consist mainly of acetic, propionic, and butyric acids and these amount to about 90% of the total. A.Th.vant't Klooster of the Laboratory of Animal Physiology, Agricultural University, Wageningen, Holland (pers.comm., 1965) found that in the faeces of 4 cows the ratio of acetic acid to propionic and butyric acids was approximately 3:1:1.

a) Acetic acid CH_3COOH

In low concentrations, acetic acid attracts some Diptera, e.g. Musca domestica (Crumb and Lyon, 1921). However, it does not appear to have been attractive to the Copromyza spp., both in isolation and in combination with skatole (Table 22). Scopeuma appears to have been slightly attracted to both acetic acid and acetic acid plus skatole. 15.9% of the total number of Dasyphora that were recorded were caught in the traps with acetic acid as the attractant, but the addition of skatole rendered acetic acid less attractive to this species.

b) Propionic acid CH_3CH_2COOH

Cragg (1950) found propionic acid to be slightly attractive to *Lucilia sericata*. Solutions of this chemical appear to have been virtually unattractive to the *Copromyza* spp. and *Scopeuma* (Table 22). Addition of skatole did not noticeably affect the attractiveness. In Table 22 it can be seen that propionic acid acted as a mild attractant to *Dasyphora*, but in combination with skatole it appeared to be unattractive.

c) n-Butyric acid $CH_3(CH_2)_2$ COOH and iso-butyric acid $(CH_3)_2$ CH.COOH

Dethier (1947) reported that butyric acid is known to act as a feeding and oviposition type of attractant to many Calliphoridae, Sarcophagidae, Muscidae, and Anthomyiidae.

Apart from iso-butyric acid and n-butyric acid which appear to have been mildly attractive to *C.hirtipes* and *Scopeuma* respectively, both acids seem to have been unattractive, or only marginally attractive to the *Copromyza* spp., and *Dasyphora* (Table 21 and 22). However, iso-butyric acid in combination with skatole and indole acted as a strong attractant to the *Copromyza* spp. and a moderate attractant to *S.subsultans* (Table 21). A solution of n-butyric acid plus skatole acted as a powerful attractant to the *Copromyza* spp. and a strong attractant to *Dasyphora* and to *Scopeuma* (Table 22).

In Table 23 it can be seen that n-butyric acid plus skatole was significantly more attractive to the Copromyza spp. than the other solutions. Iso-butyric acid plus skatole was significantly more attractive to C.equina, C.hirtipes, and C.nigra, but not C.similis, than n-valeric acid plus skatole. There was no significant difference between the attractive powers of solutions of iso-butyric acid plus skatole and iso-valeric acid plus skatole to any of the Copromyza spp.

d) n-Valeric acid $CH_3CH_2CH_2COOH$ and iso-Valeric acid $(CH_3)_2\ CH.CH_2COOH$

Dethier (1947) reported that the common isomer of valeric acid present in barnyard manure is attractive to species of Muscidae, Calliphoridae, Sarcophagidae and Anthomyiidae.

As attractants n-valeric and iso-valeric acids acted similarly to the butyric acid isomers. n-Valeric acid appears to have been unattractive or only marginally attractive to the Copromyza spp. and Dasyphora and mildly attractive to Scopeuma (Table 22). A solution of n-valeric acid plus skatole acted as a strong attractant to the Copromyza spp. and Scopeuma, but it was only slightly attractive to Dasyphora. Iso-Valeric acid appears to have been moderately attractive to C.hirtipes (Table 21), but unattractive or only marginally attractive to the other species. A solution of iso-valeric acid plus skatole and indole acted as a strong attractant to the Copromyza spp. and S.subsultans (Table 21). In combination with skatole it was also a strong attractant to the Copromyza spp. and Scopeuma, but unattractive to Dasyphora (Table 22).

A solution of iso-valeric acid plus skatole was found to be significantly more attractive to the Copromyza spp., except C.similis, than n-valeric acid plus skatole (Table 23). The significant differences in attractive powers of solutions of certain fatty acids plus skatole, indicated by these investigations, could only be verified by laboratory experiments using a sophisticated olfactometer.

e) n-Caproic acid $CH_3(CH_2)_4COOH$ and iso-Caproic acid $(CH_3)_2 CH.CH_2CH_2COOH$

n-Caproic acid appears to have been unattractive to the Copromyza spp. and Dasyphora, but slightly attractive to Scopeuma (Table 22). In combination with skatole, it was marginally attractive to the Copromyza spp. and mildly attractive to Dasyphora, but the number of Scopeuma caught was only increased by 1 (Table 22).

iso-Caproic acid also appears to have been unattractive to the Copromyza spp., but marginally and mildly attractive to Dasyphora and Scopeuma respectively. iso-Caproic acid plus skatole acted as a mild attractant to the Copromyza spp. and Dasyphora and was strongly attractive to Scopeuma (Table 22).

f) n-Octoic acid $CH_3(CH_2)_6COOH$

n-Octoic acid, alone and in combination with skatole, seems to have been unattractive to the Copromyza spp. and Dasyphora, but n-Octoic acid plus skatole appears to have been marginally attractive to Scopeuma (Table 22).

g) n-Decoic acid $CH_3(CH_2)_8COOH$

Apart from Scopeuma which appears to have been mildly attracted to n-decoic acid plus skatole, this chemical, singly and in combination with skatole, seems to have been unattractive to the other species.

C. Amines

Krijgsman and Windred (1933) found that Lyperosia was attracted to amines extracted from dung. Kullenberg (1953) showed that the scent from Arum spp. contains amines and ammonia which attract manure insects. Aedes aegypti is as strongly attracted to trimethylamine as arm odour, but methylamine acts as a repellent (Delong, 1954). Steiner (1942) found that dimethylamine is attractive to Phormia regina, but methylamine and Trimethylamine act as repellents.

a) Methylamine $(CH_3)\ NH_2$

Methylamine appears to have been unattractive, or only marginally attractive, to the Copromyza spp., but it acted as a moderate attractant to Scopeuma and S.subsultans (Tables 21 and 22). To adults of S.nitida it was by far the most attractive chemical tested. 69% of the total numbers of adults of this species were caught in the methylamine traps. A solution of methylamine plus skatole was slightly attractive to the Copromyza spp., but to Scopeuma it was the most attractive.

b) Dimethylamine $(CH_3)_2\ NH$

This chemical appears to have been virtually unattractive to sphaerocerids (Table 21).

c) Trimethylamine $(CH_3)_3$ N

This chemical appears to have been marginally attractive to C.similis, C.hirtipes, and S.nitida (Table 21).

d) 1, 4-Diamino butane $NH_2(CH_2)_4$ NH_2 and 1, 5-Diamino pentane $NH_2(CH_2)_5$ NH_2

Both chemicals appear to have been virtually unattractive to the sphaerocerids under investigation (Table 21).

D. Ammonium hydroxide NH_4OH and Ammonium carbonate $(NH_4)_2CO_3$

Ammonia is a well known insect attractant. Wieting and Hoskins (1939) found that Musca domestica is attracted to ammonia in air at a concentration 0.012% by volume, but repelled by concentrations greater than 0.03%.

Ammonium carbonate appears to have been unattractive to sphaerocerids, but ammonium hydroxide was moderately attractive to S.nitida (Table 21).

E. Other chemicals tested

Benzoic acid (C_6H_5COOH) and phenol (C_6H_5OH) appear to have been marginally attractive to the Copromyza spp., while indole-acetic acid $(C_{10}H_9NO_2)$ and paracresol $(C_8H_{10}O_2)$ were unattractive to all species (Table 21).

These investigations indicate that although adults of all the above species are attracted to dung, there is a marked difference in their reaction to certain chemicals. Thus, acetic and propionic acids were only attractive, to any degree, to Dasyphora, while methylamine acted as a powerful attractant to

S.nitida and in solution with skatole to *Scopeuma*, but it was virtually unattractive to the *Copromyza* spp. and *Dasyphora*. However, both isomers of butyric acid, in combination with skatole, were attractive to the *Copromyza* spp., *Scopeuma*, and *Dasyphora*. Generally, species belonging to the genus *Copromyza* reacted similarly to the chemicals tested.

It can be seen from Tables 21 and 22 that the most attractive chemical combinations were comparable in their attractive powers to a small quantity of fresh horse dung exposed in a 100ml beaker, except to *S.nitida* and to *Scopeuma*. Methylamine appears to be at least 6 times as attractive as horse dung to *S.nitida* and methylamine plus skatole seems to be 4 times more attractive to *Scopeuma* than horse dung. It must be pointed out, however, that small quantities of dung age rapidly and that horse dung is only about one-sixth as attractive to *Scopeuma* as cow dung (Gibbons, pers.comm.).

(3) SEX RATIO OF *COPROMYZA* SPECIES CAUGHT

In Table 25 the total numbers of males and females of the *Copromyza* spp. that were caught in detergent traps, using certain chemical attractants, are shown. χ^2 values have been calculated and they are also shown in Table 25. It can be seen from Table 25 that there is no significant difference in the sex ratio of any of the species and, therefore, it appears that these chemicals were equally attractive to both males and females.

TABLE 25. Total numbers of males (M) and females (F) caught in detergent traps with 0.1% solutions of (1) n-butyric acid + skatole (2) iso-butyric acid + skatole (3) n-valeric acid + skatole and (4) iso-valeric acid + skatole as attractants over 18 days (six 3-day exposures). χ^2 values have been calculated.

	C.equina				*C.similis*				*C.hirtipes*				*C.nigra*			
	M	F	χ^2	P.	M	F	χ^2	P.	M	F	χ^2	P.	M	F	χ^2	P.
1.	76	72	0.1	> 0.5	184	185	0.003	> 0.95	71	60	0.9	> 0.3	959	1028	2.4	> 0.1
2.	24	33	1.4	> 0.2	88	67	2.8	> 0.05	39	37	0.15	> 0.8	483	526	1.8	> 0.1
3.	14	21	1.4	> 0.2	87	88	0.005	> 0.9	25	21	0.3	> 0.5	402	451	2.8	> 0.05
4.	24	33	1.4	> 0.2	82	88	0.2	> 0.5	43	32	1.6	> 0.2	475	527	2.7	> 0.1

(4) ATTRACTIVENESS OF DIFFERENT CONCENTRATIONS OF N-BUTYRIC ACID PLUS SKATOLE IN AQUEOUS SOLUTION

Odours are aerial molecular suspensions and the first discernible reaction of an insect to an increase in molecular concentration of an odorous substance is known as the threshold of response. The acceptance or avoidance of the odorous substance at this point determines whether the substance is an attractant or a repellent. Warnke (1931) found that concentrations of 0.003 - 0.009mgm of skatole/litre of water initiated an attractive threshold response from Geotrupes sylvatica and Geotrupes vernalis. An odour, if it is initially attractive, will increase its attractiveness with increased concentration until an optimum is reached. Above this level the attractiveness decreases with increased concentration until the substance acts as a repellent. Wieting and Hoskins (1939) demonstrated this phenomenon by subjecting Musca domestica to different concentrations of chemicals, including ammonia and ethyl alcohol in a stream of air.

The present investigations were undertaken only to give some indication of the optimum concentration of skatole plus n-butyric acid for use as an attractant in the field and to determine the rate at which the attractiveness of different concentrations alters daily. Dethier (1947) emphasised that intricate laboratory apparatus is required to make accurate quantitative determinations of the repellent or attractive qualities of any substance.

Aqueous solutions of skatole, n-butyric acid, and skatole plus n-butyric acid, of different concentrations, were simultaneously exposed in the field in November 1964 and May 1966 (method as previously described). The solutions were exposed for periods of 3 days and the traps emptied at the end of each period, except for one 7-day exposure when the traps were emptied daily. A trap without an attractant was always placed in the area as a control. In Tables 26 and 28 the total numbers of adults of each species that were caught in traps with solutions of different strengths as attractants are shown. In Table 27 the daily numbers of adults and the total numbers of each species that were caught in traps with solutions of different strengths are shown.

TABLE 26. Total numbers of adults caught in detergent traps with skatole (S) and n-butyric acid (B) as attractants over 6 days (two 3-day exposures). 1 trap to each solution. November 1964

Quantity of chemical to 100ml water	No. of adults			
	C.similis	C.equina	C.hirtipes	C.nigra
1.0gm S + 1.0ml B	14	49	1	9
0.1gm S + 0.1ml B	21	38	1	2
0.01 S + 0.01ml B	1	1	0	0
0.001 S + 0.001ml B	0	0	0	0
0.0001 S + 0.001ml B	0	0	0	0
0.1gm S	2	4	0	1
0.1ml B	0	2	0	1
Water	0	0	0	0

TABLE 27(i). Numbers of adults caught daily (and total numbers) in detergent traps with skatole (S) and n-butyric acid (B) as attractants. 2 traps to each solution. May 1966

Quantity of chemical to 100ml of water	*C.nigra* (No. of adults) Day 1	2	3	4	5	6	7	Total
1. 1.0gm S	0	0	1	0	2	1	1	5
2. 0.1gm S	0	0	0	0	1	2	1	4
3. 1.0ml B	0	0	0	0	1	1	1	3
4. 0.1ml B	0	0	0	0	1	0	0	1
5. 1.0gm S + 1.0ml B	22	16	8	22	36	70	60	234
6. 1.0gm S + 0.1ml B	18	6	4	28	14	54	36	160
7. 0.1gm S + 1.0ml B	28	34	25	57	31	95	63	333
8. 0.1gm S + 0.1ml B	24	13	19	75	27	160	110	428
9. 0.1gm S + 0.01ml B	3	6	6	31	17	61	40	163
10. 0.1gm S + 0.001ml B	4	0	2	17	20	41	30	114
11. 0.1gm S + 0.001ml B	0	0	0	5	1	17	13	36
12. 0.01gm S + 0.1ml B	23	3	2	6	10	12	8	64
13. 0.001gm S + 0.1ml B	5	0	0	0	0	0	0	5
14. 0.001gm S + 0.1ml B	2	2	0	0	0	0	0	4
15. 0.01gm S + 0.01ml B	15	4	1	13	8	10	8	59
16. 0.001gm S + 0.001ml B	1	0	0	0	0	0	0	1
17. 0.0001gm S + 0.0001ml B	0	0	0	0	0	0	0	0
18. Water	0	0	0	0	0	0	0	0

TABLE 27(ii). Numbers of adults caught daily (and total numbers) in detergent traps with skatole (S) and n-butyric acid (B) as attractants. 2 traps to each solution. May 1966.

Quantity of chemical to 100ml water	Day 1	2	3	4	5	6	7	Total
	<u>C.similis</u> (No. of adults)							
1. 1.0gm S	0	0	0	0	0	0	0	0
2. 0.1gm S	0	0	0	0	0	0	0	o
3. 1.0ml B	0	0	0	0	0	0	0	0
4. 0.1ml B	0	0	0	0	0	0	0	0
5. 1.0gm S + 1.0ml B	2	2	2	12	2	1	1	22
6. 1.0gm S + 0.1ml B	0	0	0	8	2	1	1	12
7. 0.1gm S + 1.0ml B	2	3	11	3	0	3	1	23
8. 0.1gm S + 0.1ml B	3	1	11	9	2	5	3	32
9. 0.1gm S + 0.01ml B	0	0	3	2	1	1	1	8
10. 0.1gm S + 0.001ml B	1	0	2	2	0	1	0	6
11. 0.1gm S + 0.001ml B	0	0	0	0	0	0	0	0
12. 0.01gm S + 0.1ml B	0	0	2	2	1	0	0	5
13. 0.001gm S + 0.1ml B	0	0	0	0	0	0	0	0
14. 0.001gm S + 0.1ml B	0	0	0	0	0	0	0	0
15. 0.01gm S + 0.01ml B	0	0	0	0	0	1	0	1
16. 0.001gm S + 0.001ml B	0	0	0	0	0	0	0	0
17. 0.0001gm S + 0.0001ml B	0	0	0	0	0	0	0	0
18. Water	0	0	0	0	0	0	0	0

TABLE 27(iii). Numbers of adults caught daily (and total numbers) in detergent traps with skatole (S) and n-butyric acid (B) as attractants. 2 traps to each solution. May 1966.

Quantity of chemical to 100ml water	*C.equina* (No. of adults) Day 1	2	3	4	5	6	7	Total
1. 1.0gm S	0	0	0	0	0	0	0	0
2. 0.1gm S	0	0	0	0	0	0	0	0
3. 1.0ml B	0	0	0	0	0	0	0	0
4. 0.1ml B	0	0	0	0	0	0	0	0
5. 1.0gm S + 1.0ml B	10	4	0	6	4	0	0	24
6. 1.0gm S + 0.1ml B	2	2	2	2	4	0	0	12
7. 0.1gm S + 1.0ml B	16	4	7	3	3	2	1	36
8. 0.1gm S + 0.1ml B	5	1	4	3	2	7	4	26
9. 0.1gm S + 0.01ml B	2	2	2	3	1	2	2	14
10. 0.1gm S + 0.001ml B	2	0	0	0	0	1	0	3
11. 0.1gm S + 0.001ml B	0	0	0	0	1	1	0	2
12. 0.01gm S + 0.1ml B	2	0	1	0	0	1	1	5
13. 0.001gm S + 0.1ml B	0	0	0	0	0	0	0	0
14. 0.001gm S + 0.1ml B	0	0	0	0	2	1	0	3
15. 0.01gm S + 0.01ml B	0	0	0	0	0	0	0	0
16. 0.001gm S + 0.001ml B	0	0	0	0	0	0	0	0
17. 0.0001gm S + 0.0001ml B	0	0	0	0	0	0	0	0
18. Water	0	0	0	0	0	0	0	0

TABLE 28. Total numbers of adults caught in detergent traps with skatole (S) and n-butyric acid (B) as attractants in 3 days. 1 trap to each solution. May 1966.

	No. of adults			
	C.equina	C.similis	C.hirtipes	C.nigra
1. 1gm S	1	0	0	2
2. 0.1gm S	0	0	0	2
3. 1.0ml B	0	1	0	1
4. 0.1ml B	0	0	1	0
5. 1.0gm S + 1.0ml B	5	7	0	11
6. 0.1gm S + 1.0ml B	6	2	0	31
7. 0.01gm S + 1.0ml B	1	0	1	34
8. 0.001gm S + 1.0ml B	1	1	0	40
9. 0.1gm S + 0.5ml B	2	12	0	41
10. 0.1gm S + 0.1ml B	3	1	0	90
11. 0.1gm S + 0.01ml B	4	2	0	69
12. 0.1gm S + 0.01ml B	0	0	0	36
13. 0.1gm S + 0.001ml B	0	0	0	16
14. Water	0	0	0	0

From Table 26 it can be seen that in November 1964 a 1% solution of skatole plus n-butyric acid tended to be slightly more attractive to adults of the *Copromyza* spp., except *C.similis*, than a 0.1% solution, while 0.01% and 0.001% solutions were slightly attractive and unattractive respectively.

It can be seen from Table 27 that the following solutions (in order of decreasing attractiveness) were the most attractive to *C.similis* and *C.nigra* : (1) 0.1% skatole + n-butyric acid (2) 0.1% skatole + 1.0% n-butyric acid (3) 1.0% skatole + n-butyric acid. These solutions were also the most attractive to *C.equina*, but the order of attractiveness was 2, 1, 3. Only 8 *C.hirtipes* adults were caught. The relatively low numbers of *C.similis*, *C.equina*, and *C.hirtipes* that were caught was probably due to low population densities in the area at the time.

It can be seen from Table 28 that in late May 1966 *C.equina* was most strongly attracted to a 1.0% n-butyric acid + 0.1% skatole solution, and *C.similis* to a 0.5% n-butyric acid + 0.1 skatole solution, but both species were attracted to a range of concentrations. Far more *C.nigra* adults were caught by a wider range of concentrations. (The peak in seasonal abundance of *C.nigra* adults in the open field is in May and this probably accounts for the high numbers that were caught). The most attractive solution to this species appears to have been a 0.1% skatole + n-butyric acid solution. The greater attractiveness of the lower concentrations in late May, particularly compared with November, but also mid-May, could possibly be due to the higher temperatures in late May, as the rate at which molecules are emitted from a volatile source increases with a rise in temperature. Higher concentrations may be more effective in colder conditions.

The results obtained from daily catches indicate that the attractiveness of the most attractive solutions to adults of *C.similis* and *C.equina* decreased only slightly over the 7-day period. The *C.nigra* catches were in fact higher over the last two days although this was probably due to greater activity, or an increase in the density of adults in the area, the results clearly indicating that the attractive powers of the most powerfül chemicals did not significantly alter over the 7-day exposure period.

It is worthwhile reiterating that to accurately determine the optimum concentration of an attractant requires comprehensive laboratory studies using a sophisticated olfactometer. The results obtained from the present studies indicate that a wide range of combinations of different concentrations of skatole plus n-butyric acid (in aqueous solution) are attractive to adults of certain *Copromyza* spp. and that the attractiveness may be affected by the prevailing weather conditions. Accepting the variability of the results it is suggested that if a chemical attractant is required for any of the *Copromyza* spp. (mentioned above) a 0.1% solution of skatole plus n-butyric acid should be reasonably attractive all the year round. In cold weather an increase in the concentration, by as much as a factor of 10, would possibly increase the catch. The deterioration of the attractant over exposure periods of 3 - 5 days is unlikely to be significant. The results also indicate that the use of molar solutions instead of percentage solutions, for the comparison of the most attractive chemicals, would not have significantly altered the results.

XI. DISCUSSION

This thesis is primarily concerned with evaluating the biology of 6 species of Sphaeroceridae, 5 of which are cogeneric, living in the same habitat. Firstly, the possible interaction of these species will be discussed in relation to the concept of "competition" and the phenomenon commonly known as "Gause's hypothesis". Secondly, the information obtained from investigations of chemical attractants for coprophilous Sphaeroceridae will be discussed in relation to olfaction and chemical insect attractants in general.

(1) CIRCUMSTANCES OF CO-EXISTENCE AMONG COPROPHILOUS SPHAEROCERIDAE IN RELATION TO THE POSSIBLE REDUCTION OF COMPETITION

Since Darwin's "The Origin of Species" was published in 1859 competition has been regarded as one of the most important forms of the struggle for existence, but Birch (1957) emphasized that due to indiscriminate and often ambiguous usage in biological literature the term has largely lost its scientific usefulness. He, therefore, proposed that the use of the term should be restricted and stated that "competition occurs when a number of animals (of the same or different species) utilize common resources, the supply of which is short". This is essentially the same definition as given by Clements and Shelford (1939), Crombie (1947), Park (1954), Milne (1961), Bakker (1961), and Solomon (1964).

The term "competition" has been used in a broader sense by Odum (1959) who stated that "Competition refers to two organisms striving for the same thing. In ecology, interspecific competition is any interaction between two or more species which adversely affects their growth and survival", and later pointed out that the interaction can involve common space, food, light, waste material action, susceptibility to carnivores, disease, and many other types of interaction. Elton (1946), in a similar interpretation, stated that "Competition is used not merely for direct antagonism, but as an objective interplay of longevity factors of all kinds (known and unknown) favouring one species at the expense of another". However, Elton and Miller (1954) used the term in the restricted sense.

For the sake of clarity it is considered necessary to restrict the concept of competition to the narrow type of definition proposed by Birch (1957). This is close to the etymology of the word, com- (together) and -petere (seek) and is similar to the generally accepted everyday meaning, i.e. where two or more individuals strive for some goal which cannot be completely achieved by all.

At the 1944 British Ecological Society's symposium, devoted to the ecology of closely allied species, an anonymous reporter stated that there was a lively discussion centred about "Gause's contention that two species with similar ecology cannot live together in the same place". This appears to have been the birth of "Gause's hypothesis" for Gause (1934) certainly did not draw such general conclusions from his work, but merely showed that in his cultures the equations developed by Volterra (1926) and Lotka (1932) appeared to hold.

Subsequently, Lack (1945) stated that "Gause contends that two species with similar ecology cannot live together in the same area", while Lack (1946) stated this concept as "two species with the same ecology cannot persist together in the same region". Another variation was given by Allee, Emerson, Park, Park and Schmidt (1949), i.e. "two species with identical ecology cannot persist together in the same region". In an attempt to clarify the situation Gilbert, Reynoldson and Hobart (1952) emphasised that "similar ecology" is objectively meaningless and that two species are hardly likely to be ecologically identical. Subsequently, Park (1954) supported these arguments.

De Bach (1966) regards the term "competitive displacement principle" as being preferable to various other designations, e.g. Gause's hypothesis, Grinnell's axiom (Udvardy, 1959), for the phenomenon. He avoided the use of the terms "identical ecology" and "similar ecology" and defined the competitive displacement principle as "different species having identical ecological niches (that is, ecological homologues) cannot co-exist for long in the same habitat". De Bach (1966) stated that "Ecological niche refers to the role played by an animal based upon its precise food, spatial or habitual requirements in a particular habitat" and that "Individuals of different species which have identical needs for food, shelter, or other essential requisities in the same habitat have identical niches. If only one essential component of the niches of two species is identical, such as food, then the niches are identical as regards food". Weatherley (1963) in fact considers that the niche concept will be of most value if it is restricted to an organism's feeding relations and stated that "The niche is the nutritional role of the animal in its ecosystem, that is, its relation to all the foods available to it".

The "co-existence principle" is the corollary of the competitive displacement principle and De Bach (1966) defined it as "different species which co-exist indefinitely in the same habitat must have different ecological niches, that is, they must not be ecological homologues". There are numerous examples of two or more cogeneric species living in the same habitat, which on superficial examination appear to disprove this theory, but subsequent detailed examination has revealed significant interspecific differences in feeding habits, spatial distribution etc., which show that the species do not occupy the same niche (e.g. Lack, 1945, 1946; Hairston, 1951; Broadhead and Thornton, 1955). It will be subsequently shown that the present investigations have revealed significant biological differences between certain species of coprophilous Sphaeroceridae.

Hammer (1941) concluded that the great mortality among the early stages of coprophagous Diptera in cattle droppings is seldom due to shortage of food and he pointed out that it is fairly common to find droppings which still contain undigested food after the majority of larvae have ceased to feed. However, Laurence (1954) found that the numbers of larvae present in cow pats were much larger than previously supposed, but he was unable to show that there is competition for food among the larvae of coprophagous species, due to the lack of evidence of how much the larvae actually require. Landin (1961), after laboratory experiments on the food and spatial requirements of adults and larvae of certain species of coprophagous Aphodiini, concluded that "interspecific fluctuations occurring in natural populations of dung beetles in dung heaps depend on environmental factors rather than the competition factor". The importance of competition between the species of coprophilous Sphaeroceridae that were studied cannot be directly assessed from the present investigations, but it is possible to demonstrate significant interspecific differences in their biology which probably severely reduce the incidence of competition.

In Table 29 the monthly percentages of adults of each species caught in detergent traps around trays of horse dung at Houghall, from May 1964 to April 1966, are shown (original data presented in Figs.11 - 16). Trapping was carried out for 7-day periods, usually once a month over the two years, but trapping was not attempted in February 1966, due to snow, and during certain months in 1964 trapping was executed on two occasions. Thus, the number of times that trapping was carried out in each calendar month, over the two years, was not constant and, therefore, to give a true representation of the seasonal pattern of abundance the percentages shown in Table 29 were calculated as follows : the mean monthly catch for a calendar month (e.g. November 1964 (2 catches); November 1965

(1 catch), divided by 3 = mean November catch), expressed as a percentage of the total of mean monthly catches for the 12 calendar months.

At the end of each 7-day trapping (described above) from May 1964 to May 1965 samples of the horse dung were placed in emergence traps in the field and any adults that emerged were recorded (for method etc. see Section VII). The monthly emergence percentages shown in Table 29 have been calculated as described above, and the "months" shown in Table 29 refer to the month in which the trays of dung were exposed in the field (original data presented in Table 18).

TABLE 29. The monthly percentages of adults caught in detergent traps around horse dung (%A), May 1964 - April 1966, and the monthly emergence percentages from horse dung (%E), May 1964 - May 1965 (see text for details and method of calculating percentages)

Months in which dung exposed	C.similis		C.equina		C.hirtipes		C.nigra		C.nitida		S.subsultans	
	%A	%E	%A	%E	%A	%E	%A	%E	%A	%E	%A	%E
Jan	6.2	0	0.7	0	0	0	0	0	10.1	7.2	0	0
Feb	10.0	18.8	0.7	14.6	0.2	0	0.4	0	8.1	39.7	0	0
Mar	13.3	14.4	7.1	14.4	1.5	25.0	0.4	33.1	1.5	5.0	0	0
Apr	10.0	6.1	8.1	19.5	18.5	56.2	20.0	0	1.3	1.4	1.8	0
May	5.5	1.0	22.5	13.5	13.3	18.8	64.2	0	0	0	33.9	78.3
June	2.4	0	21.9	0.1	17.6	0	11.6	0	0	0	33.9	4.4
July	0.6	0	3.5	0	8.7	0	0	0	0	0	16.1	2.2
Aug	0.6	0	4.3	0	24.5	0	0	0	0	0	7.1	13.0
Sept	0.9	0.1	3.9	0	11.3	0	0	0	0	0	5.4	4.4
Oct	4.1	.5	8.9	0.1	3.0	0	1.0	0	18.6	14.2	1.8	0
Nov	28.7	20.9	11.3	37.0	0.5	0	1.8	0	32.0	22.3	0	0
Dec	17.8	38.2	7.2	0.1	0.1	0	0.6	66.7	34.5	10.3	0	0

(Over 13 months a total of only 12 C.nigra and 18 C.hirtipes adults emerged from samples of horse dung and so emergence percentages for these species are not reliable)

It can be seen from Table 29 that as far as the attraction to horse dung shows, adults of the different species have periods of greatest abundance as follows : C.similis and C.nitida in November and December; C.equina and S.subsultans in May and June; C.hirtipes and C.nigra in April - June, but C.hirtipes is abundant again in late summer. A similar phasing in the seasonal occurrence of adults of different species was also found to occur in cow dung at Houghall (see Section VI), indicating that a particular pattern of abundance is characteristic of the species irrespective of the kind of droppings. Although the numbers of adult emergences cannot be equated with the numbers of eggs laid, due to unknown developmental mortality, the monthly emergence percentages shown in Table 29 do give some indication of the seasonal breeding patterns of the different species in horse dung in the open field. It can be seen from Table 29 that as far as emergences show, the different species have the following main breeding periods : C.similis in November, December, February, and March; C.equina in November and February - May; C.hirtipes in March and April; C.nitida in November - February; C.nigra in March and December; and S.subsultans in May and August.

The highest emergence percentages recorded for C.similis, C.nitida, and S.subsultans tended to be from dung exposed in months when the adults were most abundant in the open field. The greater proportion of the C.equina emergences were from samples exposed in November and April, but adults were most abundant in the field during May and June. This may have been due to a higher developmental mortality in May and June, or simply that more eggs were laid in April and November. Adults of C.hirtipes were abundant around horse dung in April - June and in August (see Section VI), but a total of only 18 adults emerged from May 1964 to May 1966. The low numbers or complete absence of emergences from horse dung that had been exposed in the field, when adults of a species were abundant, may have been due to a very high developmental mortality, or that the species tends to oviposit in other media. The absence of adult emergences of C.nigra from dung that had been exposed in May, when adults were abundant, is probably due to the fact that most of the adults attracted to horse dung at this time were immature (see Section VII (4). It cannot be concluded that the failure to record adult emergences from samples of horse dung that had been exposed in the field (when the adults were present) was due to the species not ovipositing at the time. However, the monthly numbers of adults attracted to horse and cow dung and the seasonal emergence patterns from horse dung indicate that to a certain extent the species do have different annual cycles of abundance.

Table 30 shows the proportions of adults of each species caught in detergent traps exposed for 7-day periods approximately once a month from March 1965 - April 1966 around (a) cow dung, (b) horse dung, (c) manure heaps (composed of cow and pig dung) (original data presented in Figs.11 - 16).

TABLE 30. Relative distribution of adults (% of total for each species) caught in detergent traps around 3 kinds of dung at Houghall. March 1965 - April 1966.

	Horse dung	Cow dung	Manure heap
	%	%	%
C.similis	86.7	11.9	1.3
C.equina	28.8	6.5	64.7
C.hirtipes	45.6	54.2	0.2
C.nigra	54.4	30.6	15.0
C.nitida	54.5	45.5	0
S.subsultans	0.8	1.4	97.8

From Table 30 it can be seen that there are marked differences in the distribution of adults between different kinds of dung; e.g. C.similis was relatively abundant around horse dung, but rare in the manure heap, while C.equina was more abundant in the manure heap than around horse dung. S.subsultans was virtually restricted to the manure heap, while C.hirtipes and C.nitida were abundant around cow and horse dung, but rare and absent respectively from the manure heap. Variations in the levels of attractiveness of different kinds of dung were also revealed by exposing cow, sheep, pig, and horse dung in detergent traps in August 1965 at Houghall (see Table 31).

TABLE 31. Percentages of total numbers of adults of each species caught in detergent traps baited with different kinds of dung. Houghall August 1965

	Dung			
	Horse	Pig	Sheep	Cow
C.similis	81.0	12.7	6.3	0
C.equina	54.4	33.7	9.2	2.6
C.hirtipes	16.5	36.0	23.5	24.0

It can be seen from Table 31 that horse dung was most attractive to *C.similis* and *C.equina* and cow dung least attractive, while horse dung was least attractive to *C.hirtipes* and pig dung most attractive.

The results shown in Tables 30 and 31 are for adults only, but as the adults feed and oviposit in dung it is suggested that the different preferences exhibited by adults for certain types of dung will also reflect ovipositional preferences. This is supported by the results of laboratory food choice experiment with cultures of *C.similis* and *C.equina* adults and by observations on the number of adults that emerged from samples of different types of dung that had been exposed to these cultures. Table 32 shows the percentage of adults that were observed feeding on cow, sheep, pig, and horse dung. Also shown are the percentages of adults that emerged from the different kinds of dung (original data presented in Tables 3 and 7).

TABLE 32. Relative distribution of adults of *C.similis* and *C.equina* (% of total for each species) feeding on and emerging from different kinds of dung in the laboratory

	Dung			
	Horse	Pig	Sheep	Cow
C.similis				
% Feeding	47.3	31.8	14.3	6.6
% Emergences	46.5	39.1	14.4	0
C.equina				
% Feeding	40.8	41.5	12.0	5.7
% Emergences	43.5	41.2	15.4	0

Thus, the types of dung that were most attractive as food to *C.similis* and *C.equina*, i.e. horse and pig dung, also had the greatest numbers of adults emerge from them, and it may be concluded that feeding and egg laying preferences are similar in these species.

From Tables 30 and 31 it can be clearly seen that *C.similis* adults are markedly more attracted to horse dung than cow dung, while the opposite applies to *C.hirtipes*. Laurence (1955) caught 2.1 *C.hirtipes* adults on cow pats to every 1 *C.similis* adult, while 10.8 *C.hirtipes* adults emerged from samples of this dung to every 1 *C.similis* adult. In the present investigations, from May 1964 - May 1965, 1.2 *C.hirtipes* adults were caught in detergent traps around horse dung to every 1 *C.similis* adult, but only 1 *C.hirtipes* adult emerged from the dung to every 368.3 *C.similis* adults. Thus, it appears that preferences for egg laying and feeding are similarly directed, but the former is more accentuated. This should cause an even greater separation between the larvae of the species than between the adults. From Table 30 it can be seen that adults of C.nigra, C.nitida, and S.subsultans show distinct preferences for different types of dung, and it seems probable that these will also reflect egg laying preferences. If this is so, there will also tend to be a separation of the larvae of these species.

The present investigations on the diurnal periodicity of locomotory activity of adults have clearly shown that there are differences in the times of peak activity between the species. Thus, in May, C.nigra appears to be most active between 18.00 - 21.00hrs, and C.similis and C.equina between 21.00hrs and midnight, while S.subsultans and C.hirtipes were most active between mid-day and 15.00hrs. These results were obtained by the use of detergent traps baited with dung and will, therefore, probably reflect feeding activity, and as all the species oviposit in dung, possibly egg laying activity as well. Egg laying is restricted to fresh dung, and if the above premise is correct, the species composition of eggs laid in droppings deposited at different times of the day will tend to differ. This could produce a separation of larvae of different species between droppings, even from the same animal. The separation of adults due to differences in the diurnal rhythms of activity between species may, consequently, cause a separation of larvae of the species.

The 6 species of coprophilous Sphaeroceridae have to a certain extent different annual cycles in the open field, i.e. C.similis and C.nitida are most abundant in the winter, while C.equina, S.subsultans, C.nigra, and C.hirtipes are mainly spring species, but C.hirtipes is abundant again in late summer. They depend to different extents on dung from various animals and their diurnal cycles of activity also tend to differ. These factors will cause a certain degree of separation between the species in time and in different kinds of dung. Interspecific competition, therefore, is likely to be reduced or very slight. Although a number of the species occur in the same habitat at the same time, i.e. co-exist, none of them occupy the same ecological niche, and hence they are not ecological homologues. These species, therefore, obey the "co-existence principle".

(2) CHEMICAL ATTRACTANTS FOR COPROPHILOUS SPHAEROCERIDAE

True chemical attractants, by definition, may exist only in the form of odours, for they alone can elicit positive directive locomotor responses, while both odours and tastes may act as repellents, for both are capable of producing avoidance reactions. Olfactory receptors possess a low threshold which endows them with a high sensitivity and in terrestrial insects they are stimulated by airborne molecules (odours), emitted from some distant source, while the gustatory receptors have a comparatively high threshold and they can only be stimulated by substances in liquid or solution form (tastes) in close contact with the insect (within the buccal cavity or touching the legs, palpi, or antennae). Normally, in the presence of attractive odours the insect becomes excited and moves towards their source by 'klinokinesis' and in the latter stage this may be assisted by 'klinotaxes' or 'tropotaxes' (for definition of terms see Wigglesworth (1966, p.278).

Naturally occurring chemical insect attractants are extremely numerous and diverse in character, but they may conveniently be placed in two major categories. The first is comprised of attractants that are actually secreted by the insect to attractant members of the same species. Included in this category are sex attractants or sex pheromones (Wilson, 1963) which are substances produced by one sex to attract members of the opposite sex for the purpose of mating. Females of a number of species, including Pothetria dispar L. (Jacobsen and Berozoa, 1963) and Periplaneta americana L. (Jacobsen, Berozoa and Yamamoto, 1963) produce a substance which is incredibly attractive to the males of the species, while males of certain Mecopteran flies (Bornemissza, 1964) produce a substance which attracts females of the species. In several species of insect, as yet found only in the order Coleoptera, family Scolytidae, one sex produces a substance, in certain circumstances, which causes both sexes to assemble for mating. This type of attractant is termed an "assembling scent" and a number of bark beetles produce such substances, e.g. unmated females of Deudroctonus breviconis Le conte and D.pseudotsugue Hopkins, feeding on Douglas fir, produce a substance which attracts both sexes in flight (McMullen & Atkins, 1962). A number of species of social insects produce chemical attractants, e.g. workers of the fire ant Solenopsis saevissima (Fr. Smith) produce a chemical attractant, termed a "trail substance", which assists their fellow workers in locating food.

The production of this type of chemical attractant by an insect is a physiological adaptation, which enables individuals of a species or colony to more readily carry out some vital function, with a consequent saving of time and energy.

As regards the second main category of attractants, Dethier (1947) emphasised how difficult it is "to draw a hard and fast distinction between attractants which direct an insect to oviposition sites and those which direct it to its food". The relationship is by no means constant and this is demonstrated by the study of Diptera associated with dung. Thus, to Scopeuma stercoraria, cow and horse dung are oviposition sites, but the adults are insectivorous, while to C.similis both kinds of dung act as a food source and an oviposition site. Laurence (1955) found that S.subsultans adults are quite frequently attracted to cow dung to feed, but rarely to lay eggs. Dung odours may act as "token stimuli" to certain species, e.g. Mesembrina meridiana is attracted to cattle droppings to oviposit, but the dung itself does not directly provide food for the larvae which are zoophagous, feeding mainly on coprophagous dipterous larvae.

Dethier (1947) considers it necessary to divide chemical attractants, pertaining to feeding and egg laying, into ovipositional-type attractants which only attract gravid females and food-type attractants which direct the insect to its food. A particular medium may provide a source of food and oviposition site for an insect. Therefore, it seems quite possible that a characteristic odour emitted from the medium may act both as a food and oviposition-type attractant and this duality of function would negate such a division.

Many species of insects are lured by odours to their host plants. These are true attractants and are usually food-type in nature, but they may be ovipositional. Thorsteinson (1960) suggested "that a principal effect of odours emanating from food plants is to inhibit locomotory activity (negative chemokinesis) when olfactory thresholds have fallen sufficiently during dispersal movement" and that these are not true attractants. The term "aggregant" was suggested by Thorsteinson (1960), but Beck (1965) regards the term "arrestant" as more appropriate. Thorsteinson (1960) pointed out that "the insect may respond by olfaction, if at all, only to plant odours of a rather general botanical distribution and find its food less by attraction thereto than by avoidance of other plants, the odours of which are presumed to be repellent" and Beck (1965) stated that plant characteristics "that tend to prevent oviposition may do so either by failing to provide the appropriate releasing stimuli for one or more of the behavioural components, or by providing stimuli that inhibit behavioural release". Thus, the relationship between phytophagous insects and their hosts is far more complex than between coprophagous insects and dung. The latter have evolved the ability to recognise certain characteristic dung odours and to locate their source, but in the former situation the host plant is also a dynamic entity and certain plants have evolved defences against insect attack, often in the form of chemical repellents.

Many saprophagous insects are attracted to their food and oviposition sites by odours which are usually products of fat and protein decomposition. Examples of this type of chemical attractant have been cited in Section X.

Numerous species of insects have evolved an extremely sensitive olfactory system which is capable of recognising attractive odours, amongst the multitude of airborne molecules that the terrestrial insect is normally subjected to. Once the olfactory receptors are stimulated, a behavioural response is triggered off which results in the movement of the insect towards the apparent source. The possession of such a concise system of identification and location must have greatly contributed to the success of many species of insect, and it is hoped that this general account gives some idea of the universality and diverse nature of chemical attractants, their mode of action, and the role which they play in nature.

The nature of the chemicals present in dung that attract adults of certain coprophilous Sphaeroceridae are discussed in relation to theoretical considerations and with special reference to the information obtained from the present work on chemical attractants.

Variations in the odorous constituents of dung from different animals endows each with a fairly characteristic odour and laboratory and field investigations have shown that the adults of certain Sphaeroceridae are preferentially attracted to different types of dung. The odours emitted from dung are continually changing both quantitatively and qualitatively, from the moment of deposition until the dung finally becomes odourless, due to molecular dissipation of the original volatile elements and to the further production of odours by bacterial and fungal decomposition of the dung as it lies in the field. The rate at which these processes occur, for a particular type of dung, will be governed by the prevailing climatic conditions and the location of the dung. Thus, the characteristic odour of a particular type of dung will be a function of its original composition and the length of time that has elapsed since deposition.

The present investigations have shown that both feeding and egg laying responses are only stimulated by dung which is below a certain age. By placing C.similis eggs in horse dung that had ceased to be attractive, the developmental mortality was increased from 2 - 5% to as high as 96%, while the weight of the emergent adults was reduced by as much as a factor of 10. This indicates that the loss of attractive powers of dung, due to a decrease in the concentration of attractive odours to below the threshold level, or possibly to the production of some repellent substance, coincides with a marked reduction in the nutrient quality of the dung for the larvae. Thus, the dung odours not only enable the adults to distinguish between different types of dung, but ensure that females searching for an oviposition site are only attracted to dung that is fresh enough to subsequently allow normal larval development.

Of the chemicals tested, only normal and iso-butyric acids and normal and iso-valeric acids, in the presence of skatole and/or indole, proved to be powerful attractants to the 4 *Copromyza* spp. studied. Adults of these species are often to be found together in the same dung, e.g. in horse and cow dung during the spring, and, therefore, it is perhaps not unexpected to find that they are powerfully attracted to the same chemicals and that the relative attractiveness of these chemicals to the different species is similar (Table 33).

TABLE 33. Percentages of the total number of adults of each species caught in detergent traps with different chemical attractants (original data presented in Table 24)

100ml of 0.1% aqueous sol. of chemical attractant	C.equina %	C.similis %	C.hirtipes %	C.nigra %
n-butyric acid + skatole	49.8	42.5	39.9	41.0
iso-butyric acid + skatole	19.2	20.1	23.2	20.7
n-valeric acid + skatole	11.8	17.8	14.0	17.6
iso-valeric acid + skatole	19.2	19.6	22.9	20.7

Another similarity between the Copromyza spp. is that the chemicals shown in Table 33 proved equally attractive to males and females of all species. As there is no evidence to suggest that the sex ratio in the field was anything but equality and as gravid females of C.similis, C.equina, and C.hirtipes were also attracted, it seems reasonable to postulate that the chemicals act as both food and oviposition type attractants.

The mechanism by which skatole and indole "modify" or "activate" the odours of these lower fatty acids to increase their attractiveness, if they do so at all, cannot be determined from the present investigations.

Although certain chemicals proved highly attractive to the *Copromyza* spp., it cannot be assumed that they will attract all coprophilous insects, or that chemicals unattractive to the *Copromyza* spp. will not prove attractive to other species of insects. Thus, although *Scopeuma* was attracted to butyric and valeric acid isomers plus skatole, *Dasyphora* was only attracted to isomers of the former, while both species were found to be attracted to chemicals that were unattractive to the *Copromyza* spp., e.g. *Scopeuma* to methylamine and *Dasyphora* to acetic and propionic acids. Even within the Sphaeroceridae associated with dung there are probably considerable variations in reaction to different chemicals. For instance, *S.nitida* was strongly attracted to methylamine, but not to the chemicals which attract the *Copromyza* spp.

The investigations on chemical attractants have clearly shown that the fatty acids mentioned in combination with skatole are powerful attractants, particularly to the *Copromyza* spp., but it cannot be concluded that they alone provide the actual attractive dung odours. However, these fatty acids do possess the necessary attributes required by an attractant that attracts coprophilous insects which feed and oviposit in fresh dung, particularly from cows, sheep, pigs, and horses. For the large quantities of cellulose present in the diet of these ungulate mammals are broken down by enzymes (cellulases) from symbiotic bacteria and protozoa present in the rumen and reticulum of sheep and cows, and the caecum of pigs and horses. The major products of the fermentation of cellulose are short-chain fatty acids, but due to re-absorption only small quantities are actually excreted in the faeces. These small quantities would soon be lost to the atmosphere after the dung was deposited, thus providing an excellent olfactory indication of the age of the dung and hence its suitability for food and oviposition.

The attractiveness of isomers of butyric and valeric acid, in the presence of skatole and/or indole, to some coprophilous Sphaeroceridae, was comparable with that of small quantities of horse dung. These chemicals may well provide the main attractive stimulus to certain coprophilous Sphaeroceridae and it is conceivable that subtle variations in the quantities present in dung from different animals may also enable the species to distinguish between the different kinds of dung. However, it is also possible that a far wider range of odorous substances present in different kinds of dung are collectively responsible for the characteristic odours.

SUMMARY

1. Laboratory investigations of *Copromyza similis* and *C.equina* have shown that the feeding behaviour and food choice of these species is similar, but *C.equina* is significantly more attracted to pig dung than *C.similis*. Both species prefer to oviposit in the following kinds of dung, in order of decreasing preference : horse, pig, sheep, and cow dung. No significant differences were found between these species in their precopulation and pre-oviposition periods, egg incubation period, or duration of development from egg to adult at 5, 10, 15, and 20°C. *C.similis* adults survived without food, at a temperature of 0.5°C, for 27.0 $\pm$ 1.6 days ($\pm$ S.D.).

2. When eggs of *C.similis* were placed in horse and sheep dung, kept for 2 and 6 weeks at 10°C, the resulting adults were sub-normal in size, weighing as little as 0.28mgm, compared with normal sized adults, which had developed in fresh dung (wt. 1.64 - 2.01mgm). Developmental mortalities of 5, 6, and 96% were recorded in the same horse dung, which was fresh, 2 weeks, and 6 weeks old respectively, compared with developmental mortalities of 16, 14, and 100% in sheep dung of the same ages. When 3-day old larvae were transferred to fresh horse dung the resulting adults weighed 2.70mgm.

3. In the field (Houghall farm, Durham), adults of *Sphaerocera subsultans*, *C.equina*, *C.similis*, *C.nigra*, and *C.hirtipes* were highly aggregated around horse dung, compared with areas

free from dung of farm mammals (species listed in order of decreasing aggregation).

4. Adults of C.equina, C.similis, and C.hirtipes were differentially attracted to dung from different farm mammals, e.g. C.equina and C.similis were most attracted to horse dung, while C.hirtipes was most attracted to pig dung. During August 1965, the distribution of C.equina, C.similis, S.subsultans, and, to a lesser extent, C.hirtipes, appears to have been mainly determined by the distribution of dung from farm mammals. These species were rare in shaded areas, free from farm animals, but C.suillorum was caught only in shaded situations.

5. As cow and horse dung aged, so their attractiveness to sphaerocerids decreased and the rate at which this occurred was dependent upon prevailing weather conditions, being accelerated by dry, warm conditions. The attractiveness of horse dung, as an oviposition site for C.similis, C.equina, and S.subsultans, also decreased with age.

6. By using detergent traps for 7-day periods, approximately once monthly, for 24 months, around horse dung, and for 14 months around cow dung and in a manure heap, it was found that C.similis, C.nitida, and C.nigra adults were most abundant around horse dung, C.equina and S.subsultans in a manure heap, and C.hirtipes around cow dung. The same trapping showed that adults of the different species have periods of greatest

abundance as follows : C.similis and C.nitida in November - December, C.equina and S.subsultans in May - June, and C.hirtipes and C.nigra in April - June, but C.hirtipes is abundant again in late summer.

7. Emergences from horse dung, exposed monthly, indicate that the different species have the following main breeding periods : C.similis in November - December and February, C.equina in November and February - May, C.hirtipes in March - April, C.nitida in November - February, C.nigra in March and December, and S.subsultans in May and August.

8. The relative abundance of C.similis adults, compared with C.equina adults, increased significantly from a lowland site at Wareham in Dorset, to a lowland site in Durham, to a highland site in the Pennines in Westmorland.

9. Adults of the Copromyza spp. moved on to dung within 5mins of deposition, during the summer, while in the winter adults of C.similis and C.nitida were found to be capable of movement at low temperatures (1.1°C).

10. Diurnal rhythm studies showed that C.similis and C.equina were active over 24hrs, but peak activity was between 21.00hrs and midnight, while C.nigra was most active between 18.00hrs and 21.00hrs. C.hirtipes and S.subsultans were virtually inactive at night and peak activity was between mid-day and 15.00hrs. Rain appeared to inhibit the locomotory activity of S.subsultans and C.hirtipes, but not the other species.

11. It was shown that aqueous solutions of isomers of butyric and valeric acids, in combination with skatole and/or indole, are extremely attractive to certain *Copromyza* spp. Various concentrations of n-butyric acid plus skatole were found to be attractive to these species, and it was also shown that n-butyric acid plus skatole is significantly more attractive than n-butyric acid plus indole or plus indole and skatole. It is suggested that butyric and valeric acids are important attractant constituents of dung to these Sphaeroceridae. Of the chemicals tested, methylamine was the most attractive to *S.nitida*, and in combination with skatole, it was most attractive to Scopeuma stercoraria. *Dasyphora cyanella*, like the *Copromyza* spp., was most attracted to n-butyric acid in combination with skatole.

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APPENDIX 1. Met. records from Houghall observatory

1964	Rel.Humidity % at 09.00hrs	Max.temp. °C	Min.temp. °C	Rainfall ins.	Sunshine hrs
29 June	54	19.4	8.3	0	13.6
30 "	76	20.6	11.7	0	3.7
1 July	61	19.4	8.9	0	12.3
2 "	67	19.4	11.1	0	6.3
3 "	53	15.6	8.9	0.01	8.8
4 "	65	16.1	6.1	0	4.3
5 "	77	18.3	5.0	0	9.3
6 "	75	20.0	1.1	0.01	0
7 "	72	20.0	8.3	0.05	6.5
8 "	81	20.0	11.1	0	8.7

APPENDIX 2. Met. records from Houghall observatory

1964	Rel.Humidity % at 09.00hrs	Max.temp. °C	Min.temp. °C	Rainfall ins.	Sunshine hrs
29 May	78	21.1	7.8	0	10.3
30 "	64	20.6	5.0	0.01	5.1
31 "	69	13.3	10.6	0.34	0
1 June	67	9.4	7.8	0.23	0
2 "	88	15.0	5.6	0.30	0
3 "	92	14.4	6.1	0	0.9
4 "	82	17.8	7.2	0.24	0
5 "	78	18.3	12.8	0	1.9
7 Aug	79	19.4	7.8	0	3.7
8 Aug	87	18.3	7.2	0.35	3.4
9 "	84	18.9	5.6	0.03	2.2
10 "	76	16.1	7.2	0	6.9
11 "	82	13.9	11.7	0	0.4
12 "	93	15.6	11.1	0.04	0
1965					
8 Apr	92	8.9	4.4	0.1	0.3
9 "	70	11.7	0.6	0.27	0.1
10 "	81	12.8	6.1	0.03	5.3
11 "	65	9.4	3.9	0.06	9.5
12 "	65	13.9	2.2	0	7.0
13 "	92	11.7	1.7	0	10.9
14 "	80	13.3	0	0.35	0.6
15 "	78	15.0	7.2	0	2.1
16 "	65	12.2	4.4	0.05	7.5

APPENDIX 3. Mean minimum, mean maximum, and average monthly temperatures (^{o}C) from January 1965 to April 1966, recorded at Moor House Nature Reserve in Westmorland, Durham, and Poole in Dorset

	MOOR HOUSE			DURHAM			POOLE		
1965	Mean Max. Temp.	Mean Min. Temp.	Average	Mean Max. Temp.	Mean Min. Temp.	Average	Mean Max. Temp.	Mean Min. Temp.	Average
Jan	1.2	-3.6	-1.2	5.4	-0.68	2.4	7.5	1.4	4.5
Feb	1.4	-2.7	-0.6	6.1	-0.8	3.4	6.5	0.8	3.7
Mar	3.4	-2.6	0.4	7.8	3.7	4.4	10.1	2.5	6.3
Apr	7.7	0	3.8	11.8	2.7	7.3	13.3	4.4	8.9
May	10.5	3.3	6.8	14.5	5.7	10.1	15.8	7.6	11.7
June	13.9	6.6	10.2	18.3	8.4	13.4	18.4	9.6	14.0
July	12.8	5.6	9.4	16.7	8.3	12.2	18.7	11.2	14.9
Aug	13.9	7.2	10.5	18.2	8.7	12.9	19.8	10.9	15.3
Sept	11.1	6.1	8.6	15.4	8.4	11.9	16.7	8.7	12.7
Oct	10.5	4.4	7.4	13.7	6.3	9.9	16.2	8.1	12.1
Nov	2.2	-2.2	0	6.2	-2.1	2.4	9.6	2.9	6.3
Dec	2.7	-4.4	-0.8	5.4	-0.9	2.6	9.4	2.1	5.7
1966									
Jan	1.2	-2.2	-0.5	3.9	-0.8	0.5	6.4	2.0	4.2
Feb	1.7	-1.7	0	6.1	0.6	3.3	9.5	5.0	7.3
Mar	5	-0.3	2.3	10.2	2.1	6.2	11.3	2.9	7.1
Apr	3.4	-0.6	1.4	7.9	2.3	5.1	12.3	5.6	8.9

APPENDIX 4. Temperature recorded at 5cms above ground level and relative humidity recorded just above level of vegetation, at Houghall. 10.00hrs 13 Sept - 16.00hrs 17 Sept 1965 (sunset 18.35hrs, sunrise 05.30hrs)

S = sunny, C = cloudy, W = light wind

Hrs G.M.T.	Temp. °C	Relative humidity %	
10.00	13.1	77	S W
13.00	16.3	67	C
16.00	15.0	68	C
19.00	10.0	83	C
			Min.temp.overnight 3.4°C
4.00	7.5	93	C
7.00	10.5	85	C
10.00	14.9	74	C
13.00	15.5	74	C W
16.00	14.1	80	C
19.00	13.8	82	C
			Min.temp.overnight 7.8°C
4.00	11.0	95	C
7.00	12.0	90	C
10.00	14.4	87	C W
13.00	16.1	86	C W
16.00	15.5	96	Rain
19.00	15.2	100	Rain
			Min.temp.overnight 12.8°C
4.00	13.8	100	Rain
7.00	13.9	100	Rain
10.00	14.3	76	S W
13.00	15.0	68	S W
16.00	14.2	70	S W
19.00	10.5	85	S
			Min.temp.overnight 7.8°C
4.00	9.0	95	C
7.00	10.7	93	C
10.00	14.2	82	C W
13.00	14.0	90	Rain
16.00	10.5	100	Rain