Ecological studies on flies associated with dung, with particular reference to scopeuma species (diptera)

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by

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Introduction.

The main purpose of this study was to elucidate the adult ecology of the Yellow Dung Fly, Scopeuma stercoraria (L) with particular reference to seasonal population changes. Hammer(1941) and Darwish(1954) had described adults of this species as being present on dung from May to November, with marked spring and autumn peaks in numbers, but occurring only rarely during summer. The study was carried out in the vicinity of a herd of dairy cattle on a lowland farm at Houghall, near Durham.

direct estimates of the populations by mark and recapture methods were impracticable, so mature male and females attracted to fresh dung, to copulate and oviposit, were counted on and around 40 cow pats. Immature adults and older females in the course of maturing their ovaries for the second, or subsequent gonotrophic cycles, frequented long grass and other vegetation away from fresh dung. Regular standardised sweep-netting was carried out in these areas. In order to ascertain the reasons forthe seasonal changes in numbers, the age-structure of the females from each catch was investigated by dissection. Counting dilatations on the ovariole tunica was found to be the most accurate method of determining the number of previous ovarian cycles, as was the case with Anopheline mosquitoes (Detinova(1962) and others).

Laboratory cultures of Scopeuma stercoraria, S.squalida(Mg) and S.suilla(Fabr.) were maintained to provide essential background information in addition to the facts found by Cotterell(1920). The last 2 species were present at Houghall in low numbers while *S.squalida* was more numerous on the Pennine moors at Moorhouse, where some comparative observations were carried out in the early months of the study. Many details of breeding biology, such as the length of the preoviposition period, amount of insect food eaten in relation to egg production etc., were determined from these laboratory reared flies.

Eggs from these *Scopeuma* in the laboratory were kept to investigate the effects of humidity and temperature on them, to compare with Larsen and Thomsen(1940), and Larsen(1943). The effect of temperature on the pre-imaginal development and subsequent adult emergence was investigated in detail. This information for all 3 species was required to answer some of the problems arising from the field studies, particularly with respect to the spring and autumn peaks, generations and duration of development at different times of the year.

The counting method used to assess changes in numbers of mature adults also provided information on the diurnal activity of these flies, in relation to weather conditions and cow behaviour. Incidental information on other dung-frequenting flies was also obtained during the counts.

In the course of the dissections for the age-structure studies of the field populations, castrated males and females were found which led to a study of the variety known as *S.stercoraria* var. *merdaria* Fabr. A more general study of the taxonomic relationships of some of the species of the genus *Scopeuma* was then made.

Information on the life history and breeding biology of the 3 *Scopeuma* species, obtained largely from laboratory work, is presented in Section 1. This is followed, in Section 2, by the results of the field studies on the population fluctuations together with analyses of age-structure results and survival rates. Diurnal activity and other aspects of behaviour of *Scopeuma* are presented in Section 3. Section 4 is concerned with temperature and humidity studies on eggs and larvae, and with patterns of adult emergence at different temperatures. Taxonomic investigations into *Scopeuma* species comprise Section 5 while Section 6 is concerned with information on other species encountered during the study. The general discussion considers the theories of population control and examines which, if any, are applicable to *Scopeuma*.

Section 1. FEEDING BEHAVIOUR AND BREEDING BIOLOGY OF *Scopeuma* SPECIES

a) LABORATORY EXPERIMENTS

1. Life history and definition of terms:

During the course of population studies on the Yellow Dung Fly, *Scopeuma stercoraria* (L), 2 other *Scopeuma* species were found. These were *S. suilla* (Fabr) and *S. squalide* (Mg.), and both were much less frequently found than *S. stercoraria*. The proportions of the 3 species varied in different habitats (see p.15) but there seemed to be no obvious differences in behaviour which would account for the discrepancies in numbers.

The 3 species were therefore studied in the laboratory as well as in the field to try to ascertain the points of difference between them. The general features of the life history were found to be the same for each species, so the following description will apply to all 3.

The eggs are creamy white at first, about 1.4mm. long, by 0.4mm. wide. They are laid in the excrement of mammals or birds, but dung of pasturing cattle is preferred. The eggs are pushed into the dung obliquely so that the respiratory apparatus projects almost parallel with the dung surface. After being laid the egg assumes a darker, more yellow appearance and hatches in 1 - 2 days.

The newly hatched larva emerges through the projecting part of the egg on to the surface of the dung and then attempts to burrow into the soft medium. If the dung has formed a hard crust the larvae may not be able to penetrate the surface. Death, by dessication or predation is then likely. Once inside the dung, however, the larvae consume the semi-liquid medium and pass through three instars lasting nearly 2 weeks altogether at about 20°C.

Pupation then takes place either in the dung or in the soil beneath. In laboratory conditions at about 20°C the pupal stage usually lasts 10-15 days, giving a total pre-imaginal period, from egg to newly-emerged adult, of 21-26 days.

On emergence from the pupa the adult has very little fat body and the gonads are immature, i.e. they are anautogenous, and both sexes must eat live food in order to mature their gonads. The amount of fat body also increases as the adults become mature. During this period from eclosion to sexual maturity, which is termed the preoviposition period, the males show no interest in the females, except as possible sources of food. Immature flies will only be found on or near dung during the preoviposition period in very small numbers. Immature *Scopeuma* are mostly found in vegetation, which suggests that the presence of immature individuals on dung is accidental or that they are only there to hunt insects. No evidence has been found that the smell of dung attracts immature *Scopeuma* in the same way that it attracts mature flies.

The adults of all three *Scopeuma* species catch their prey, usually any small insects, by pouncing on them. The prey is held by the forelegs and sometimes also by the midlegs, and the stiffened proboscis penetrates the cuticle by means of its prestomal teeth. The body contents are then sucked out and the largely empty husk of the prey is dropped when it is finished with. The adult *Scopeuma* do not catch their prey in flight, nor do they actively hunt. They sit on the vegetation waiting for an insect to alight nearby, whereupon they will attack it. If the insect escapes it is rarely chased.

When the adults become mature their habits change and they are attracted to fresh dung. The males then mate readily on or near the dung and when copulation completed the female is usually ready to lay eggs. The male removes his abdomen from that of the female and moves back a little, holding the female around the waist with his forelegs. The female then moves around the dung selecting sites to lay her eggs and, as she does so, the male moves with her, fending off other males by raising one or both of his midlegs. When the female has finished laying, the male lets go and usually mates with another female while his previous mate attempts to leave the dung.

Because of the usual preponderance of males she may be mated again immediately, or she may be fortunate enough to leave the dung.

This behaviour on the dung has been mainly confirmed in northern Califonia by Foster (1967), although with slight differences from my own observations. He states that copulation usually occurs in the vegetation within 1 metre of the pat, lasting about 30 minutes, due to the females drawing the males off the pats into the vegetation. From my observations on many thousands of pats, mating usually takes place wherever the female lands near a male, whether on the grass around the dung, or on the pat itself. Mating pairs may move from the dung to the vegetation, or vice versa at any time before oviposition. Foster then states that oviposition takes place with the male in the mounted position for about another 30 minutes, after which the female flies away. This is much longer than I have observed.

Mating or ovipositing pairs are often attacked by one or more males trying to mate with the female. The original male may be displaced by another, which then resumes copulation. Foster says that he has only seen this happen twice, and that the new partners flew back to the vegetation. I have seen it happen many times, particularly when there were many more males than females, and the new partners usually remain on the dung. A female ovipositing alone was only seen once by Foster but in my studies it happened many times particularly when there were few males in the vicinity. The male does not inevitably protect the female during oviposition. He may leave her immediately after mating.

The males may stay on the dung for two or more hours but the females are usually only on long enough to mate and lay eggs, which takes 30-45 minutes. The females then leave the dung to hunt for insects in order to develop the next batch of eggs. Females which have laid eggs are termed parous, those which have not are nulliparous, or nullipars.

A brief summary of the life history so far described is given: after emergence from the pupa both sexes of Scopeuma are highly carnivorous, and hunt insects in the vegetation to mature their gonads, some nectar is also taken from flowers. This behaviour lasts from 1-2 weeks, during which neither sex is attracted either to each other or to fresh dung. This part of the life history is referred to as the preoviposition period. When both sexes become mature they are attracted to dung for the first time, usually about 2 weeks after eclosion. Mating takes place on or near fresh dung and this is usually followed by oviposition. Females gravid for the first time may not lay immediately after mating, but may leave the dung and oviposit a day or two later.

When a female has laid her first batch of eggs she enters the oviposition period which lasts until her death which, in the field, may be anything up to two months later, having laid up to seven or eight batches of eggs. Each time a female matures a batch of eggs she returns to fresh dung and is usually mated before ovipositing. She then leaves the dung for the vegetation to hunt insects to mature the next batch of eggs. The females may occasionally return to dung before they are fully gravid, the purpose of which appears to be for mating.

Males also leave the dung to hunt insects in the vegetation but they do not eat as much as the females. They may return to the dung several times in a week, and probably more than once a day. This difference in behaviour between the sexes is probably correlated with the difference in the gonads and production of the germ cells. Eggs take about a week to mature and all ovarioles mature together, whereas sperms are being produced all the time. The large amount of material needed for a batch of 50-60 eggs requires that the female must be away from the dung for long periods. Both mature and immature flies have been taken sucking nectar on flowers so that this feeding habit is not confined to any age group.

The life-span of adult Scopeuma in the field may be as much as ten weeks, and the pre-imaginal period is 3-4 weeks, giving a total life-span of 13-14 weeks. Flies kept in the laboratory can live longer than this.

A final summary of the life history of Scopeuma stercoraria is given as follows:

Eggs laid on dung hatch in 1-2 days. The larvae, feeding on the semi-liquid medium, pass through 3 instars before pupating about 11 or more days after hatching. The pupal stage lasts 10-15 days at $20^{\circ}C$ in the dung or in the soil. After emergence from the pupae, the adults hunt insects and suck nectar for 1-2 weeks during the preoviposition period. When mature the adults are attracted to dung where they mate and lay eggs. After oviposition the female leaves the dung and hunts insects for about a week while the next batch of eggs is being developed. Males spend most of their time on fresh dung, but do leave for the vegetation to hunt insects and suck nectar. When females are gravid for the second time they return to the dung and are usually mated before ovipositing. Again the females leave the dung after laying to mature the third batch of eggs. This cycle is repeated throughout the oviposition period. Adult females may live at least as long as 10 weeks in the field, and males can probably also live this long.

2. Review of the literature.

The literature on the feeding behaviour and breeding biology of only Scopeuma stercoraria, the Yellow Dung Fly, can be referred to since S. squalida and S. suilla, being much rarer, have not attracted the same attention as has S. stercoraria.

Cotterell (1920) dealt with the life history and habits of S. stercoraria, based on laboratory pbservations of breeding cultures. He said that "Sexual maturity is not achieved until after 21 days of life". He also stated that: "No females were observed to lay more than 120 eggs. It is probable that one female is capable of laying from 100 to 150 eggs and then dies. Eggs are laid in one batch of from 40 to 80 and afterwards 10 or 20 at a time at intervals".

Larsen and Thomsen (1940) give the preoviposition period as about 14 days at 20-21°C, and said that it was presumably much dependent on the quantity of food present.

Hammer (1941) quotes both of these figures for the preoviposition period but says that Cotterell's figure presumably applied to the field. This is not so as Cotterell's paper was almost completely based on laboratory studies.

The most important statement concerning the biology of S. stercoraria was made by Larsen and Thomsen (1940 p.50): ".....it seemed, however, that when pairing and oviposition had commenced the flies ceased to feed". Hammer (1941 p.69) elaborated on this point: "The feeding habits of Scopeuma stercorarium are rather peculiar; it seems as if from being carnivorous it changes to be a peaceable honey-eater. In the laboratory where Bro Larsen and Thomsen (1940) kept Scop. through 7 to 8 generations, it appeared that Scop. is highly carnivorous in the preoviposition period and must have several small *Musca domestica* daily, while after oviposition had begun it did not take any food. In the cultures it was usual for big males to suck out smaller females, a feature which also Cotterell (1920) pointed out".

On p.71, Hammer then says: "I believe that I have ascertained in the field that *Scopeuma* in the oviposition period catches many other flies, which are all released again except females of its own species.... This feature which needs a closer examination is very curious, as it is in fact a peculiar alteration of the habits of a rapacious animal simultaneous with the beginning of sexual ripeness".

Darwish (1954 unpublished thesis) noted, in his description of *S. stercoraria* that the adults fed on nectar and were blood-sucking predators of other insects. He stated that the change from blood to nectar sucking had been shown by Larsen and Thomsen (1940) to be associated with the achievement of sexual maturity.

3. Field and laboratory observations.

In the present work *S. stercoraria* were kept in muslin cages in the laboratory. The adults were given a constant supply of small insects (mostly Drosophila melanogaster Mg) and sucrose solution. If there was a lack of insect food cannibalism was observed, but not solely males eating females. After sexual maturity was achieved there did not seem to be any increase in the drinking of the sugar solution provided, nor was there a cessation of the predacious habit, although cannibalism ceased. Both male and female S. stercoraria were observed to catch and eat insects throughout their lives.

I was able to observe on several occasions that feeding in the oviposition period also occurred in the field, the most outstanding occasion was at the Moorhouse National Nature Reserve on 6th November, 1963, when numerous Borborids were feeding and laying eggs on horse dung. At the same time there were also large numbers of S. stercoraria and a much smaller number of S. squalida, also on the horse dung. Both species of Scopeuma were eating the Borborids, the females whilst copulating or ovipositing, and the males caught their prey either on the dung after the males had finished copulating, or on the grass around the dung.

4. Experiment to show the necessity for insect food

In order to clarify some of the details of the feeding and breeding biology of S. stercoraria, a simple experiment was carried out using laboratory reared virgin females and males which had not previously mated. Having seen mature Scopeuma adults eating insects I wanted to know if this was obligatory or facultative, i.e. was it essential for the flies to have an insect diet during the oviposition period, as opposed to a diet of nectar? Could the extra batches of eggs mentioned by Cotterell be produced on a nectar diet or was insect food necessary?

These questions had to be answered unequivocally but I wanted to make a further investigation. Cotterell (1920) recorded that oviposition occasionally took place with the male 'in situ' i.e. the male was on top of the female, holding her with his forelegs. Both in the laboratory cages and in the field I had only seen oviposition take place with the male 'in situ' and I wanted to know whether the presence of the male was necessary to stimulate oviposition, or if he was merely incidental.

In order to answer these questions, four categories were needed:

1) Male and female given insect food and sugar solution.
2) Male and female given sugar solution only.
3) A female, mated once, given insect food and sugar solution.
4) A female, mated once, given sugar solution only.

The procedure for all these catagories was basically the same: a mature, i.e. gravid, female was pootered out of the cage of virgin females, and a mature male was sucked into the same pooter. After they had mated they were knocked out of the pooter into a glass jar containing a small tube of sugar solution, and with sheep dung spread over half of the bottom of the jar. The dung had been collected fresh from the field, was then deep-frozen, and was freshly thawed when needed. In the case of the two categories of solitary females it was quite easy to separate the female after one mating and put her in a jar, the males being returned to the cage of males. Drosophila melanogaster were given to the flies in categories 1) and 3).

As soon as any eggs had been laid the flies were removed to another jar containing freshly thawed dung, and their eggs were then kept for studies on larval development. When any of the flies being studied died they were replaced by other flies which were kept under the same conditions.

The results of this experiment are presented in Table 1.

Discussion of results:

a) Presence of males:

This is clearly not necessary to stimulate oviposition as both the solitary females laid eggs, one laying three batches. Since this experiment was carried out I have noticed, on several occasions, solitary females laying eggs even when

TABLE 1

Results of Egg-Laying Experiments with <u>Scopeuma</u> <u>stercoraria</u> at 19-21^{o}C

Category	No. of eggs in 1st Batch	Time from mating to Laying Days	No. of eggs in 2nd Batch	Time Between Batches Days	No. of eggs in 3rd Batch	Time Between Batches Days	Total Number of eggs
1/. ♂ and ♀ Given Insects and Sugar	52	1 (Died, replaced)	57	4	57	4	166
2/. ♂ and ♀ Given Sugar only	66	1	(Died)				66
2/. ♂ and ♀ Replacement pair. Given Sugar only.	9	6	(Died)				9
3/. ♀ only. Given insects and Sugar	50	3	53	4	21 (Died)	4	124
4/. ♀ only. Given Sugar only	43	7	(Died)				43

males were present on the same dung.

b) The necessity for an insect diet after maturity:

All three females (including one which was a replacement) which were starved of insect food after maturity died after laying the first batch of eggs although they had had ample food during the preoviposition period.

The males were less indicative of the need for insect food, as the male being fed (category 1) died 7 days after the first mating. Because of the small number of individuals being studied it was not possible to conclude with certainty that an insect diet was necessary during the oviposition period.

c) Successive batches of eggs:

Table 1. shows that successive batches of eggs can be laid by females which are receiving a diet of insects as well as sugar solution. It should also be noted that all three batches of eggs laid by the solitary female, in category 3/., were fertile, showing clearly that the spermathecae are capable of storing sufficient spermatozoa, from one mating, to fertilise over 100 eggs over a period of 11 days.

The constant interval of 4 days between batches may indicate the time necessary at about 20°C for the maturation of successive oocytes, provided that there is no shortage of food. The second batch of eggs laid by both females receiving insect food was slightly larger than the first, so that there is not necessarily a decrease in the number of functional ovarioles with each gonotrophic cycle (cf. Anderson 1964, p.235). The third batch of eggs laid by the female in category 1. was the same as the second batch, showing that there had been no degeneration of ovarioles. The total number of eggs laid by the two females receiving insect food (124 and 166) were larger than had been recorded by Cotterell (1920).

It appeared, from this experiment, that female Scopeuma were capable of laying successive large batches of eggs throughout their mature lives (i.e. in the oviposition period), and for this to happen it is probably necessary that they have a diet of insects.

5) Detailed comparison of three species of Scopeuma in culture.

A series of investigations into the feeding and breeding biology of three species of Scopeuma was carried out during the winter of 1964-1965. The three species studied were S. stercoraria, S. suilla and S. squalida. Because these studies had to be left until winter there was not a readily available source of the flies. Individuals therefore had to be taken as they emerged from eggs laid by laboratory cultures of the three species.

As well as confirming and elucidating further the results described above, I wished to determine the amount of food needed to achieve maturity, the time this took, and whether there were any differences between the three species in these details. Hitherto, nothing has been published about the food requirements or breeding of S. suilla or S. squalida. This information was required because I had never seen either of these species in anything like the same number as S. stercoraria in the field. Both on the dung and in vegetation S. stercoraria is the most abundant species and, in comparison, S. suilla and S. squalida are extremely rare.

At Moor House only a few specimens of S. suilla have been recorded (Nelson pers. comm.), but S. squalida is more common, several individuals may be seen together. Near Durham City S. suilla is more numerous than S. squalida, but S. stercoraria vastly outnumbers both species in both areas.

Method of study:

When females (and occasionally males also) emerged from cultures they were immediately put into separate hurricane lamp glasses. These glasses were inverted on to a Petri dish and the upper, open, end was covered by a piece of perforated polythene held in place by an elastic band. Plastic tops of 2 x 1 specimen tubes, containing cotton wool soaked in a sugar solution, were placed on the Petri dishes and could be replaced easily. Insect food was provided by knocking known numbers of vestigial-winged Drosphila melanogaster into the lamp glasses from a pooter. The numbers of Drosophila eaten each day were counted and more added as necessary. Water was sprayed in occasionally to maintain a reasonable humidity.

Vestigial winged Drosophila were used because they were easy to handle in pootering and transferring from their culture bottles to the Scopeuma jars. By using these Drosophila of the same age throughout the studies it was hoped that these insects would provide a reasonable constant unit of food.

6) Method of finding the preoviposition period, and the treatment of eggs laid:

The preoviposition period was ascertained by removing the immature females a few days after eclosion and putting them, separately, with mature males from the culture cages. This was repeated at daily intervals until copulation took place. After copulation had taken place the females were put back into their jars and dung was provided in plastic tops like those containing the sugar solution. The time from eclosion to the date of the first eggs laid was taken as the preoviposition period. In order to count the numbers of eggs easily the freshly thawed dung was put into plastic 1" diameter vessels and smoothed to a flat surface, and replaced as necessary.

Removing the females from the jars entailed a risk of injury, and so mating was sometimes facilitated by putting a mature male into the jar with a virgin female when trying to determine the preoviposition period. If the female refused to mate the male was removed to prevent him from being eaten, and he would then be put with the female at daily intervals until mating took place. After copulation the male was removed and either kept in a separate jar, where the number of *Drosophila* eaten would be recorded, or he was put back into one of the culture cages.

By knowing, from the first experiment, that the spermathecae could store sperm for long periods it was not necessary to reintroduce a mature male until several batches of eggs had been laid, or when the female showed signs of being unable to lay. The main disadvantage of leaving a male with the female was that the mature males also eat *Drosophila*, and so an accurate record of the number of *Drosophila* eaten by the female could not be obtained when a male was present for more than the duration of copulation. There was also the possibility that the female might eat the male, which happened once.

When eggs had been laid the dung was removed from the jar, the eggs were counted and recorded. The dung, with the eggs, was carefully removed from the plastic vessel and put into a larger plastic container with some more thawed dung.

These containers, with perforated polythene on the top, were then put at different temperatures for separate studies on development. The perforated polythene reduced water loss from the dung to a minimum. The plastic vessels were then refilled with freshly thawed dung and put back into the jars for any further eggs. If no more eggs were laid within two days the dung lost its freshness and was replaced. Once a female had begun to lay eggs she was kept supplied with dung.

The biggest difficulty experienced in this study was to have a reservoir of mature fertile males of all three species. Mature males sometimes could not be obtained from the culture cages and on one occasion the only mature male S. stercoraria available was infertile. This is an important point to watch if any further work on this subject is carried out.

The number of Drosophila supplied to the Scopeuma individuals was altered as required, and the effect of lack of insect food on the preoviposition period and on egg laying was studied.

7) The preoviposition period:

Six S. stercoraria females had an abundance of insect food after eclosion and there were mature males available. Their average preoviposition period was 13.3 days at 19-20°C with a range of 8-21 days. Those females with an artificially extended preoviposition period were excluded from this calculation. The four S. squalida females kept at room temperature had a mean preoviposition period of 9.75 days, with a range of 8-11 days. A mature male was only available for one S. suilla female which laid her first eggs 12 days after eclosion. No mature males were available for the other five females for a long time after they were gravid. One female in the group became gravid 11 days after eclosion, but as there was no male she died 13 days later without laying. The mean preoviposition period for the five S. suilla females was 26.6 days, with a range of 12-36 days.

From these observations it seemed that mating was necessary before oviposition could take place, which agrees with Anderson's (1964) observations on Fannia canicularis L. Some S. stercoraria females became gravid after about two weeks, but there was only one mature male in the culture cages. They all mated but did not lay any eggs. When another mature male became available they all mated with it and laid eggs almost immediately. This pointed to the fact that the stimulus for oviposition must be a fertile mating. No unmated females were ever observed to lay eggs. The infertile mating explains the greatly delayed oviposition periods of 37 and 38 days as given in Table 2.

No definite conclusions can be made about any specific differences in the preoviposition period because of the small number of individuals studied. Close attention should be paid to elucidating this possibility in any future work because S. squalida females may be able to develop at a faster rate, on the same amount of food, than the other 2 species.

The lengths of the preoviposition period for the 3 species are presented in Table 2 together with the number of Drosophila eaten during this time. The number of eggs laid are also presented for the purpose of examining any possible relationships between the length of the preoviposition period and these other factors.

8) Numbers of Drosophila eaten during the preoviposition period, the early rates of feeding and the effect of starvation:

The mean total number of Drosophila eaten during the preoviposition period by: a) 10 S. stercoraria females was 122.5 with a range of 63-206; b) by 5 S. suilla females was 119.2 with a range of 80-156; c) by 4 S. squalida females was 77.0 with a range of 62-93. Reference to Table 2 shows that, although the flies are arranged in order of lengthening preoviposition period, there is no corresponding series of decreasing amount of food eaten. This would be

TABLE 2/. Comparison of preoviposition periods and numbers of insects eaten by three *Scopeuma* species:

Female Reference Number	Preoviposition Period (days)	*Drosophila* eaten during preoviposition period Total No:	No: per day.	Number of eggs laid at end of 1st cycle	Maximum number of eggs laid in any cycle.
S. stercoraria					
7	8	63	7.9	56	56
8	12	113	10.3	64	70
14	13	92	7.7	48	49
12	13	103	8.6	45	45
13	13	113	9.4	50	50
5	21	206	9.8	73	76
2	37	115	3.1	69	74
4	37	151	4.1	65	65
3	37	181	4.9	84	84
1	38	88	2.3	66	66
S. suilla					
	gravid after 11				
4	No eggs	102	9.3	-	-
1	12	103	8.6	63	100
2	26	156	6.0	67	75
3	28	116	4.1	15	37
5	31	80	2.6	36	63
6	36	141	3.9	50	53
S. squalida					
2	8	62	8.9	80	80
1	9	72	9.0	43	51
3	11	81	8.1	53	53
4	11	93	9.3	62	73

expected from the suggestion of Larsen and Thomson (1940) that the amount of food eaten probably determined the length of the preoviposition period.

The numbers of Drosophila eaten per day during the preoviposition period for the last four S. stercoraria females, in Table 2., are artificially low because there was no fertile male available when they became gravid. After they had become gravid they ate very little, and the rates of feeding during the pre-gravid period (from eclosion to the gravid state) for females No. 2, 4, 3 and 1 were 5.3, 8.0, 6.5 and 3.9 respectively.

The shortest preoviposition period of 8 days was recorded for one S. stercoraria female, with a feeding rate of 7.9 Drosophila per day, and for 1 S. squalida female with a rate of 8.9 insects per day. Feeding rates both greater and less than these figures were achieved by females with longer preoviposition periods. This eliminated the possible correlation between feeding rate and length of preoviposition period.

There remained the possibility that the length of the preoviposition period might be partly governed by the number of eggs which were being matured. This was on the assumption that a large number of developing eggs would require a larger amount of food than would a smaller number. This would be reflected either in a higher feeding rate or in a longer preoviposition period. Examination of column 5 of Table 2, however, shows that the number of eggs laid at the first gonotrophic cycle is independent of the amount of food eaten or the length of the preoviposition period.

The problem is a little clearer from studies on two series of females of the same age, one of *S. stercoraria* and the other *S. suilla*. In both series the females were given a different number of insects each day so that, for instance, one female would never have more than 4 *Drosophila* in the jar each day, another no more than 8, another no more than 16, and so on. Whether the females ate all or none of the *Drosophila* in any day, the same number would be maintained at the next inspection by adding more flies as required, e.g. if 6 out of 8 had been eaten, another 6 would be added. If 8 out of 8 had been eaten another 8 would be added. This method was used because it was not possible to force the flies to eat a required number per day, so it was arranged that they could not eat more than a certain number. This experiment was to see if those *Scopeuma* eating the highest numbers of flies per day matured first.

Unfortunately, mature males were not available for either series and so the time was recorded at which the females became fully gravid, i.e. the outlines of the eggs could be seen through the stretched membranes of the abdomen.

This was then termed the pre-gravid period, from eclosion to the fully gravid condition.

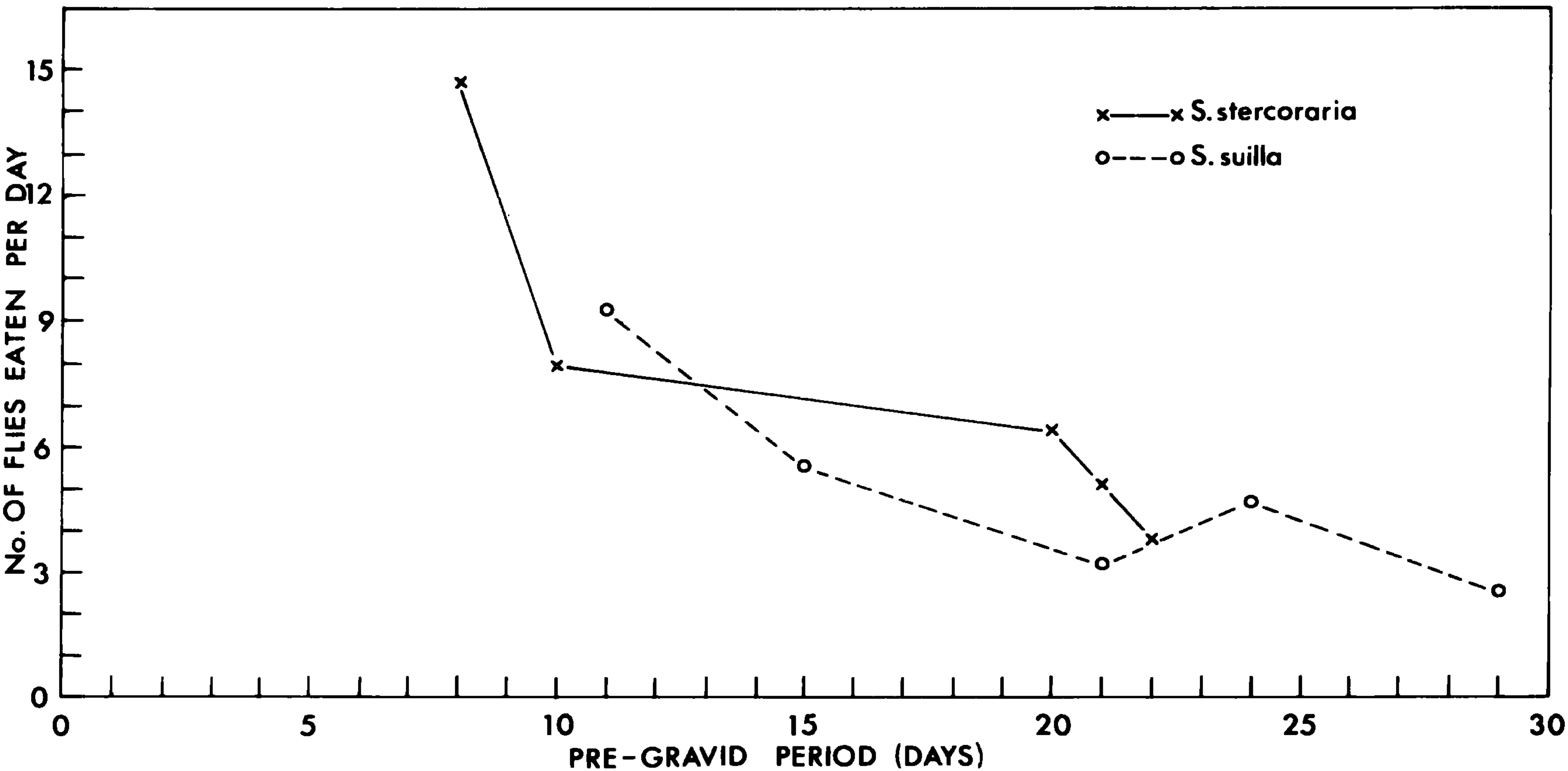
In S. stercoraria for pre-gravid periods of 8, 10, 20, 21 and 22 days, the corresponding feeding rates were, respectively, 14.8, 8.0, 6.5, 5.3 and 3.9, Drosophila per day. In S. suilla, including two other females, for pre-gravid periods of 11, 15, 21, 24 and 29 days, feeding rates were 9.3, 5.7, 3.2, 4.7 and 2.6 Drosophila per day.

Although the relationship is not truly linear (Fig. 1.) it can be seen that, in general, as the feeding rate increases, the pre-gravid period decreases. It seems that the rate at which maturity is reached depends on the amount of food eaten only when food is in short supply. When food is in excess it is possible that the amount extracted from each insect is less than maximum. This could be checked by examining the remains of all insects eaten, but it would be a very lengthy procedure. This possibility could, however, explain the anomalous figures for the number of Drosophila eaten and the length of the preoviposition period.

The necessity for live food for immature Scopeuma of both sexes of all species was easily demonstrated by keeping them on sugar solution only, or with liquid meat extract and sugar solution. All the individuals lived for a few days but then showed decreasing activity and general weakening, and died.

Fig. 1. The relationship between the number of *Drosophila* eaten per day and the time taken to become gravid in two *Scopeuma* species.

FEEDING RATE AND MATURITY IN *Scopeuma* SPECIES



Early rates of feeding:

There is surprisingly little feeding in the very first days after eclosion. By the 8th day after emergence, 7 out of 19 flies had not even eaten 10% of the total number of insects they eventually consumed. Some females did not eat at all during the first 2 or 3 days of adult life, and even when they had started to feed they did not eat very much, but this did not have any adverse effect on the egg production or life-span. The highest percentage of the total insect consumption eaten by the end of the first day was only 4.6%. The highest percentage of all Drosophila eaten up to the end of the 8th day of adult life was 48.6% of total consumption, by an S. stercoraria female. Figures showing the accumulated totals of flies eaten up to the 8th day of adult life are shown in Table 3.

This early phase when little feeding takes place could be the time when the greatest dispersal, away from the place of emergence, occurs, as the flies seek a suitable environment in which to feed and mature. This would agree with the dispersal behaviour of immature flies as described by Johnson (1966).

Feeding usually stops, or is very much reduced, when the female is fully gravid, but recommences at a high rate as soon as the eggs have been laid. In calculating the

Table. 3. Feeding during the first 8 days of adult life af 3 Scopeuma species. Figures are the accumulated totals of Drosophila eaten up to each day specified in the column headings.

Days after emergence (eclosion)

Female Reference Number.	1	2	3	4	5	6	7	8	Total Flies Eaten	Lifespan in Days
S. stercoraria										
2	2	2	6	9	10	12	17	26	499	117
1	0	0	8	8	10	15	20	27	137	76
14	0	2	6	12	16	21	32	45	548	80
(escaped) 13	0	3	3	12	17	20	31	48	266	26+
12	0	3	8	14	20	26	37	53	109	15
3	4	10	16	23	31	39	46	54	550	87
4	8	8	16	31	42	52	58	65	175	54
7	7	24	36	47	59	63	63	73	158	23
8	5	9	9	23	42	69	85	93	322	56
5	3	15	36	37	54	75	94	118	470	68
S. squalida										
A	2	8	13	22	29	35	46	62	228+	57
2	3	5	13	21	38	46	62	67	534	45
1	3	9	22	29	40	48	59	72	1168	150
B	6	14	21	30	39	47	59	73	276+	44
S. suilla										
5	0	1	3	6	10	11	14	15	316	65
6	1	3	7	8	13	14	18	22	248	56
2	0	0	0	10	23	28	43	44	640	98
3	2	7	20	35	46	50	57	66	256	47
1	6	15	27	33	50	65	81	85	502	56

rate of feeding per day during the preoviposition period, in Table 2., the number of insects eaten before the first oviposition was divided by the number of days before the first eggs were laid, i.e. for a preoviposition period of 9 days, the denominator is 8. In nearly all gonotrophic cycles oviposition is preceded by a period of inactivity and followed by renewed feeding.

9) The effects of starvation after maturity:

Starvation during the preoviposition period was shown (Fig. 1.) to delay the achievement of maturity, and so I decided to investigate the effect of starvation after maturity (i.e. during the oviposition period) on the length of time needed to mature the next batch of eggs. Because of the shortage of experimental flies this was carried out only on two female *S.stercoraria* nos. 1 and 4, chosen because of the difference in their feeding rates during the preoviposition period. Both females were allowed to feed on the day they laid their first batch of eggs, but were given sugar solution only after that.

The first positive result was from female no. 4 which laid 2 eggs, but only empty shells, 9 days after laying the first eggs. Five days later she died. Female no. 1 was not so conclusive because she laid 36 eggs 15 days after laying the first batch. This interval is nearly 2½ times the mean interval between the first and second batches (6.4 days) in S.stercoraria. The number of eggs was about half that laid in the first batch (66). After 9 more days (24 days after the first batch) no more eggs had been laid, so I decided to see if providing Drosophila again would restore normal egg-laying. Within two days of being given insects she laid 30 eggs, and seven days later she laid a fourth batch of 53 eggs. Both forelegs broke off at the femur-tibia junction three days after this last batch and she died.

Although these results are not absolutely conclusive they suggest, combined with the results of the starved flies described in Table 1., that starvation after maturity probably restricts egg production and reduces the lifespan. If insect food is supplied again the life expectancy is lengthened and egg production is restored. More studies are needed to allow any confident conclusions.

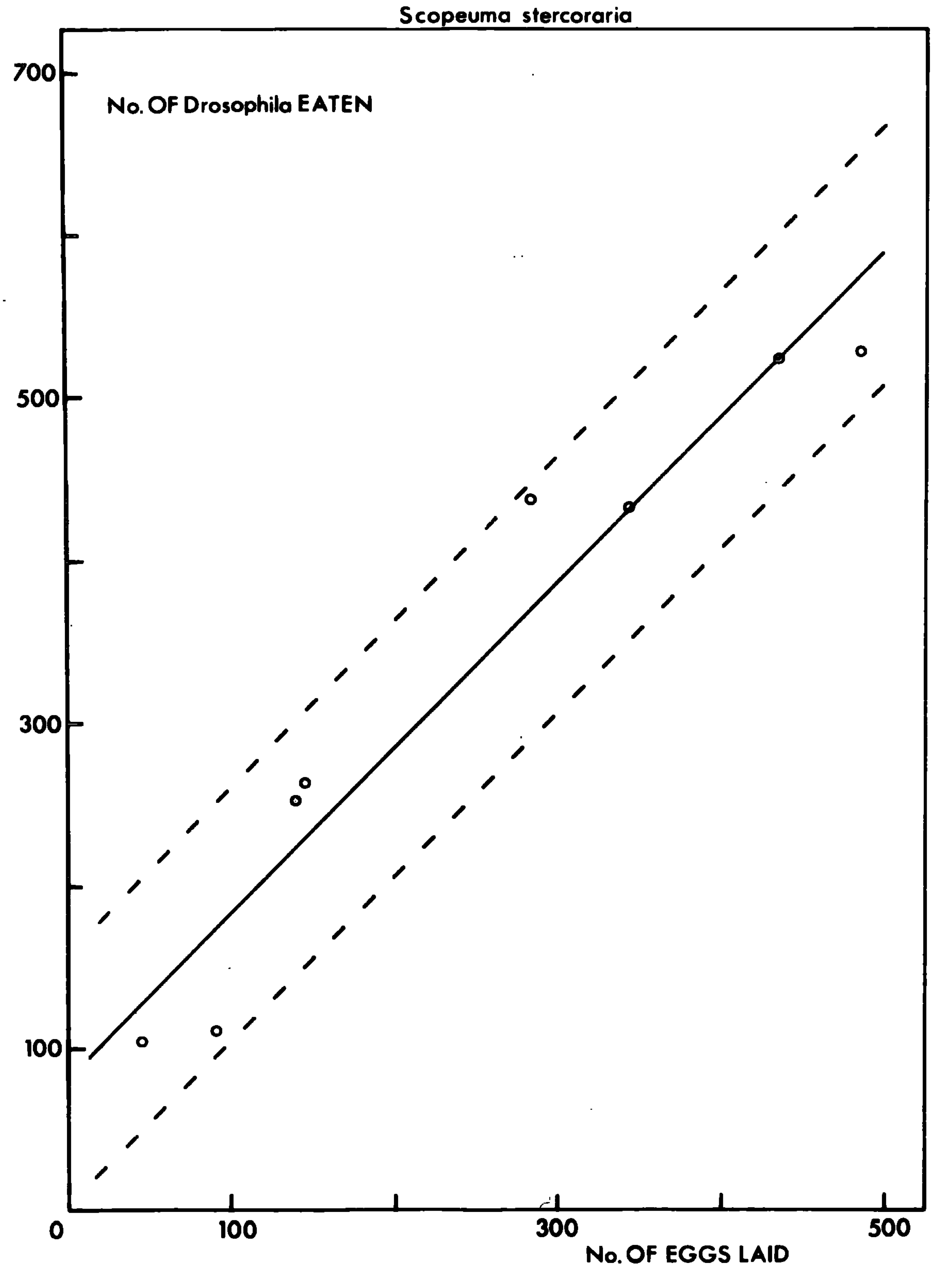
10) The relationship between the numbers of insects eaten and the numbers of eggs laid throughout life, in three Scopeuma species:

After the Scopeuma had achieved maturity they were still examined every day to record the number of Drosophila eaten, and the number of any eggs laid. The eggs were dealt with as described on P. 17. To investigate any relationship between the amount of food eaten and the numbers of eggs laid, the results were analysed as follows: The total number of eggs laid by each female was plotted against the total number of Drosophila eaten up till the first day of the last batch of eggs. This date was chosen because any flies eaten between that day and death could not contribute to eggs already laid. Correlation coefficients and regression equations were calculated from these figures for the three Scopeuma species separately, and only for females kept under normal conditions. Those which were deliberately starved were excluded from these calculations.

For S.stercoraria females, Fig 2. shows the regression line $y=81.68 + 1.014x$, with confidence limits of two standard errors, fitted to the points representing the numbers of eggs laid and insects eaten by each female. The correlation coefficient for this relationship is $r=0.97$ ($P<.001$)

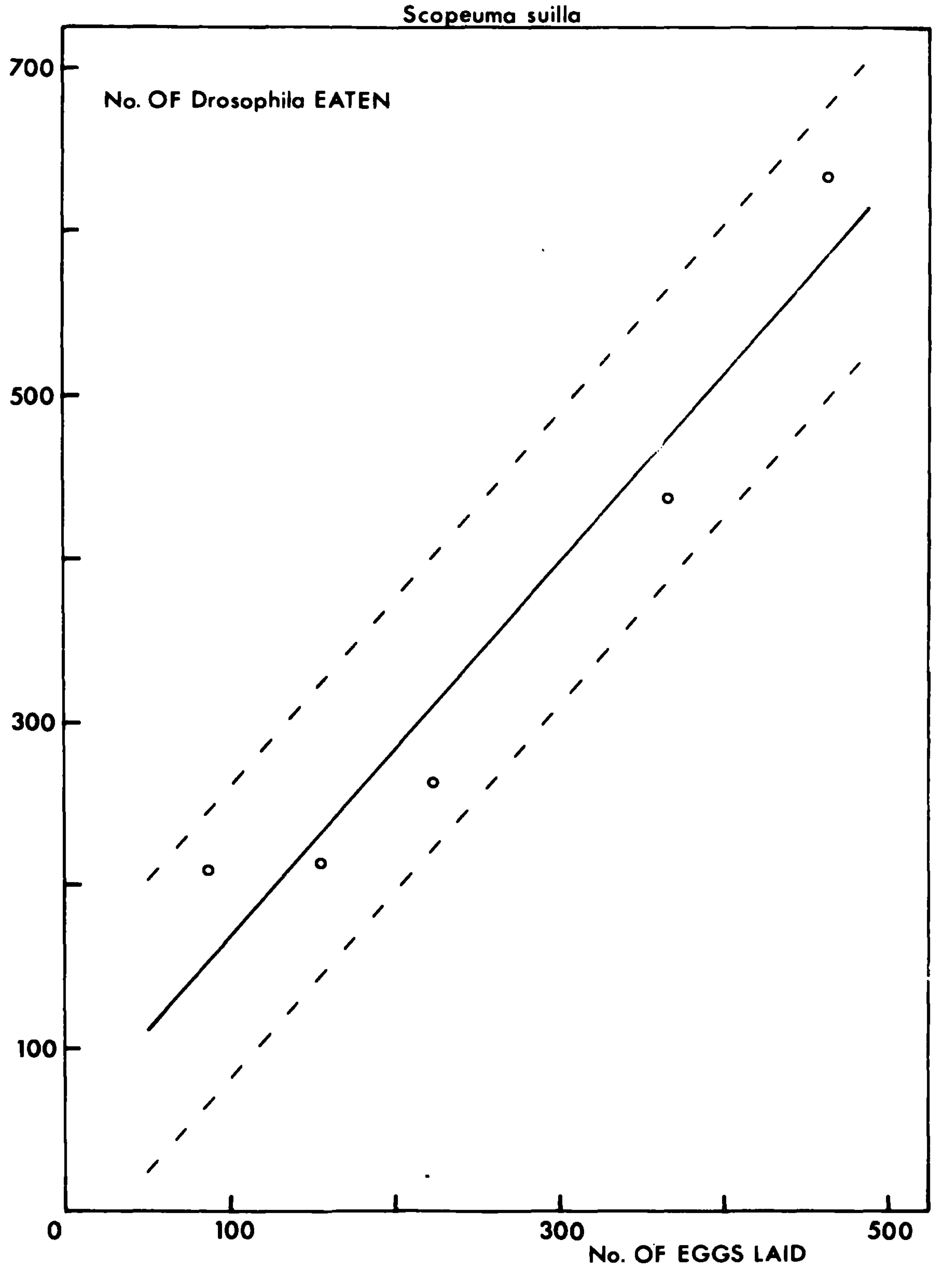
Fig. 3. for S. suilla females shows the regression line $y=54.96 + 1.15x$, with confidence limits $r=0.96$ ($P<.01$) Fig 4 for S. squalida females is the regression line $y=1.70x - 381.96$ with confidence limits $r=0.96$ ($P<.02$). This figure needs some explanation because the number of insects eaten by two of the females was not recorded between the first and fifth batches

Fig. 2. Numbers of _Drosophila_ eaten and numbers of eggs laid by _Scopeuma stercoraria_ females Regression line $y = 81.68 + 1.014\,x$ drawn with confidence limits of 2 standard errors. Correlation Coefficient = 0.97 for the relationship of numbers of insects eaten and eggs laid.



Scopeuma stercoraria
No. OF Drosophila EATEN
700
500
300
100
0
100
300
500
No. OF EGGS LAID

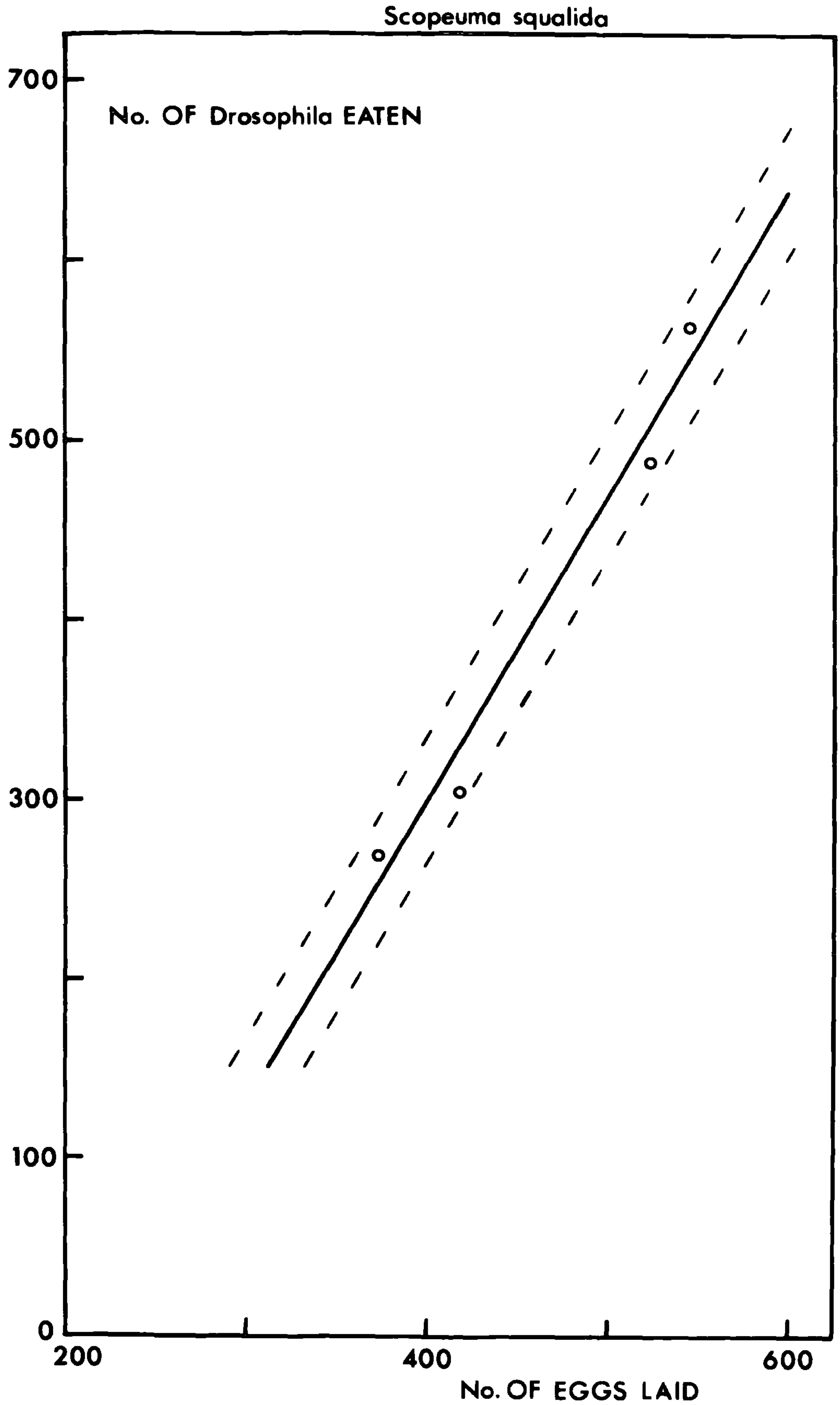
Fig. 3. Numbers of *Drosophila* eaten and numbers of eggs laid by *Scopeuma suilla* females. Regression line $y = 54.96 + 1.15\,x$ drawn with confidence limits of 2 standard errors. Correlation coefficient = 0.96 for the relationship of numbers of insects eaten and eggs laid.



Scopeuma suilla
700
No. OF Drosophila EATEN
500
300
100
0
100
300
500
No. OF EGGS LAID

Fig. 4. Numbers of *Drosophila* eaten and numbers of eggs laid by *Scopeuma squalida* females. The lowest points have had 4 times the average of insects eaten between batches added to the observed figure, and the highest point is up to the 12th egg batch only. Regression line $y = 1.70\ x - 381.95$ drawn with confidence limits of 2 standard errors.

Correlation Coefficient = 0.96 for the relationship of numbers of insects eaten and eggs laid.


Scopeuma squalida
No. OF Drosophila EATEN
700
500
300
100
0
200
400
600
No. OF EGGS LAID

of eggs. In order to obtain some estimate for the total number of insects eaten, the mean number of *Drosophila* eaten between later batches was calculated. These figures for the two females were inserted between each of the batches for which there was no recorded figure. As there were four gaps in the results, four times the mean was added to the observed figure to estimate the total number of insects eaten.

Of the other two females represented on this graph (Fig. 4), one is plotted for the number of eggs laid and insects eaten up till the 12th batch only. This was an extraordinarily long-lived female, but after laying 13 batches of eggs, the frequency and size of the batches were very erratic although the numbers of insects eaten seemed to be quite normal. Until the 12th batch she laid 544 eggs and had eaten 563 *Drosophila* whereas, after the 12th batch until death, she laid only 258 eggs but ate 605 *Drosophila*. The graph therefore shows for this female, the results of the first 50 days, of a total lifetime of 150 days.

It is possible that the processes of ageing affected the reproductive behaviour far more than the feeding behaviour since there was an interval of 29 days after the 13th batch during which no eggs were laid. A complicating factor, however, was the fact that there were no mature males available during this interval. When a male was put with the female eggs were laid the next day. Since the last previous mating 4 egg batches had been laid so that the sperm supply had probably been used, which might explain the absence of eggs during the long period after the 13th batch.

It is unfortunate that more S. squalida females were not available for study as the regression line (Fig. 4) is different from those of the other two species. This regression line cannot be extrapolated in a linear manner below the lowest point; since it would imply that more than 200 eggs could be laid without any food being eaten. However, on the few reliable results, it seems that S. squalida may have a more efficient mechanism for the conversion of food to eggs than the other two species.

11) The relationship between the numbers of insects eaten during the oviposition period and the total eggs laid after the first batch.

The figures for this analysis were obtained by comparing the number of insects eaten after the first batch of eggs until the first day of the last batch, and the total number of eggs laid in all cycles except the first. This was done for all females kept under normal conditions and which laid more then one batch of eggs.

Fig. 5. shows the results for S.stercoraria females. The correlation coefficient is 0.97 ($P<.001$) and the regression line is $y = 51.4 + 0.88x$.

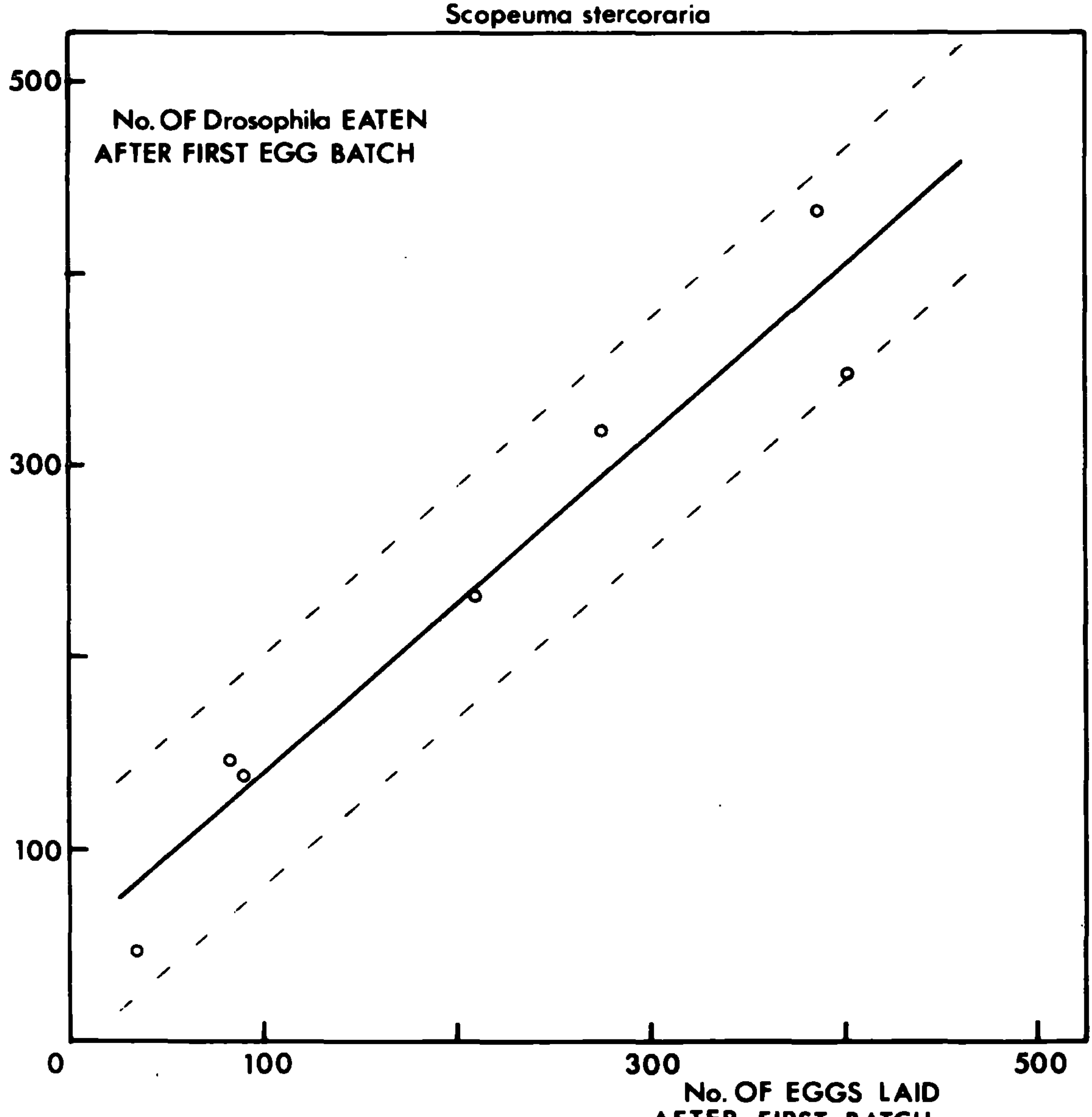
Fig. 6. for S.suilla females is the regression line $y = 1.25x - 32.85$ with a correlation coefficient $r = 0.987$ ($P<.01$). It is probably not valid to compare the regressions for the two species as so few individuals were studied.

Fig. 7. shows the corresponding figures for S.squalida females. The correlation coefficient is 0.986 ($P=.01$) and the regression line is $y = 1.70x - 358.98$. It must be noted again that the two lowest points on this graph have had 4 means added to their observed insect totals, and that the top point is one individual represented only by figures until the 12th batch. The interesting point is that the slope of the regression line ($dy/dx = 1.70$) is identical with that of the regression for total eggs and total insects (Fig. 4.).

S.squalida was the only species studied in which there were no delayed preoviposition periods and so it is doubtful whether, in this species, the food eaten during the

Fig. 5. Numbers of *Drosophila* eaten during the oviposition period and numbers of eggs laid after the first cycle by *Scopeuma stercoraria* females.

Regression line $y = 51.4 + 0.88 x$ drawn with confidence limits of 2 standard errors. Correlation coefficient = 0.97 for the relationship of numbers of insects eaten and eggs laid after the first cycle.

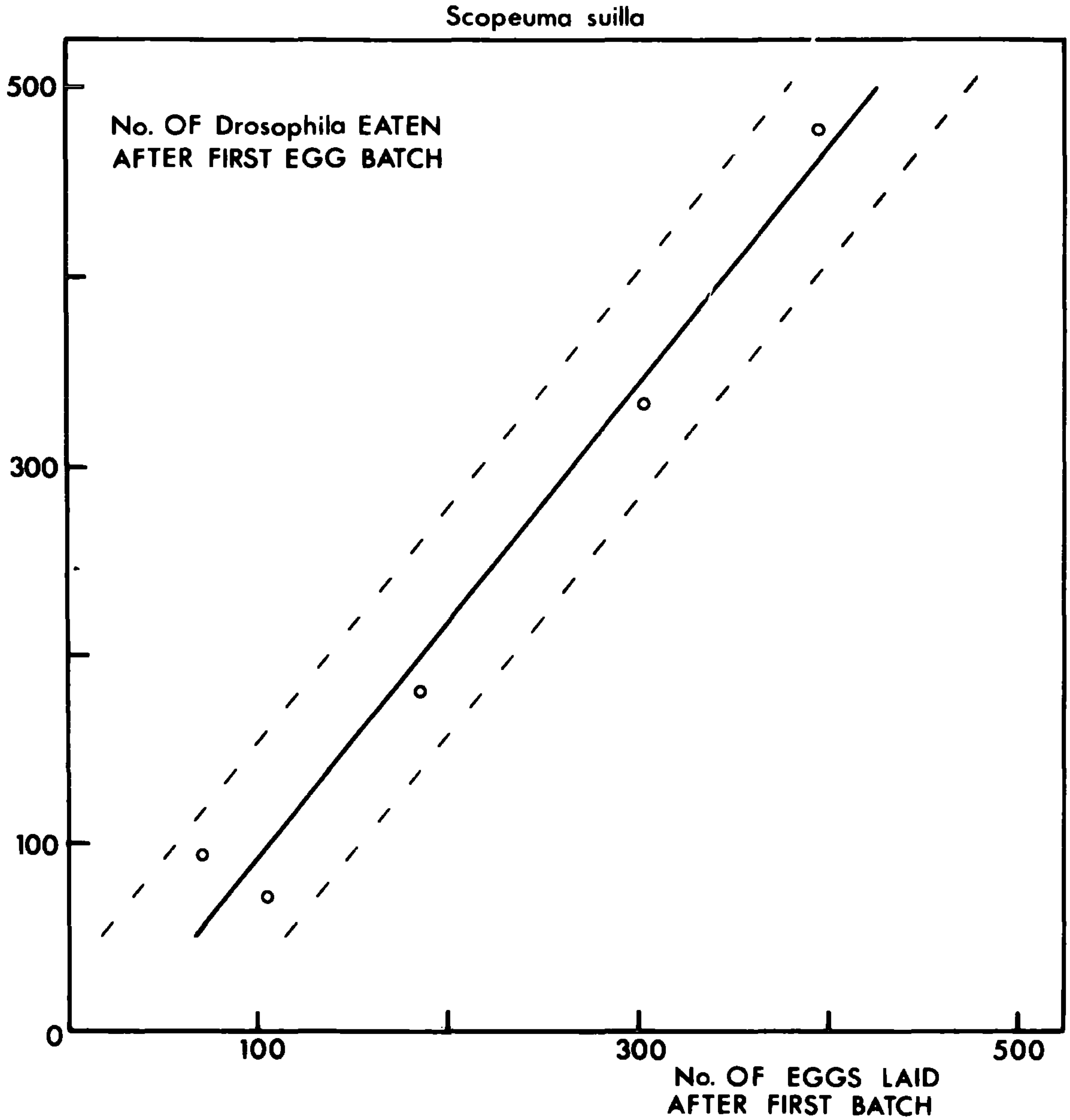


Scopeuma stercoraria
No. OF Drosophila EATEN
AFTER FIRST EGG BATCH
500
300
100
0
100
300
500
No. OF EGGS LAID
AFTER FIRST BATCH

Fig. 6. Numbers of *Drosophila* eaten during the oviposition period and numbers of eggs laid after the first cycle by *Scopeuma suilla* females.

Regression line $y = 1.25x - 32.85$ is drawn with confidence limits of 2 standard errors.

The correlation coefficient is 0.987 for the relationship of numbers of insects eaten and eggs laid after the first cycle.

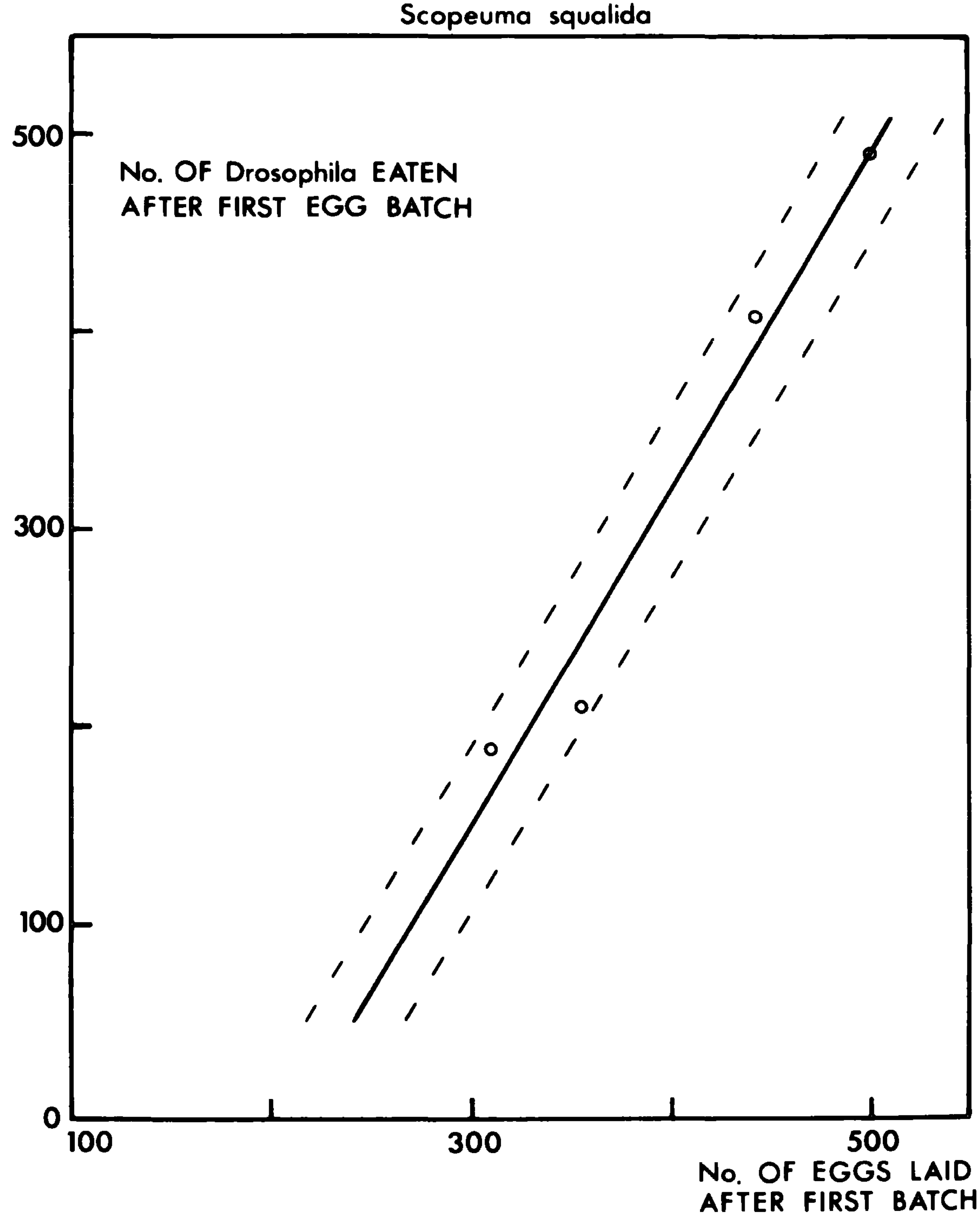


Scopeuma suilla
No. OF Drosophila EATEN
AFTER FIRST EGG BATCH
500
300
100
0
100
300
500
No. OF EGGS LAID
AFTER FIRST BATCH

Fig. 7. Numbers of *Drosophila* eaten during the oviposition period and numbers of eggs laid after the first cycle by *Scopeuma squalida* females. The lowest 2 points have had 4 times the average of insects eaten between batches added to the observed number, and the highest point represents the first 12 batches only.

The regression line $y = 1.70x - 358.98$ is drawn with confidence limits of 2 standard errors.

The correlation coefficient is 0.986 for the relationship of numbers of insects eaten and eggs laid after the first cycle.

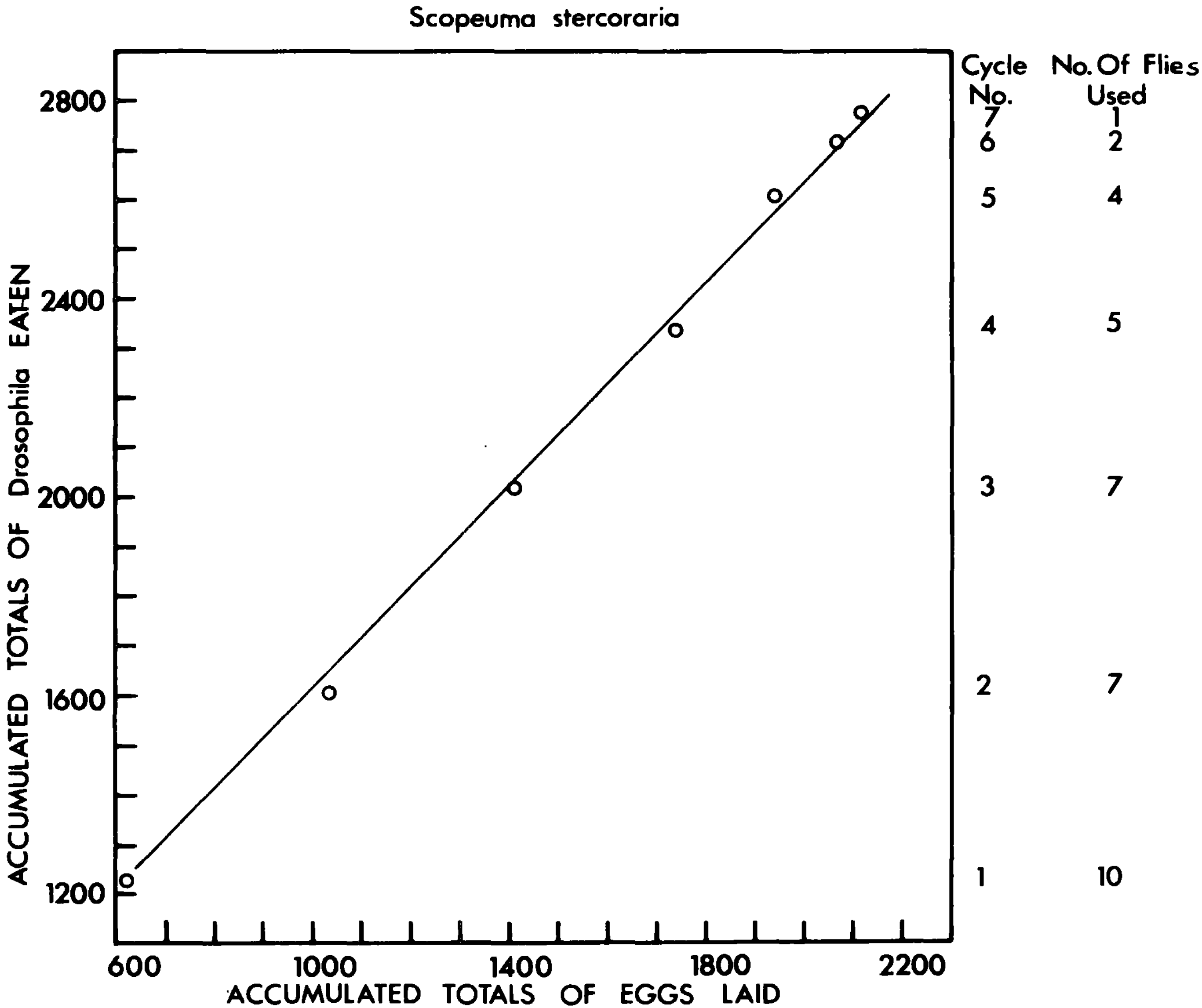

Scopeuma squalida
No. OF Drosophila EATEN
AFTER FIRST EGG BATCH
500
300
100
0
100
300
500
No. OF EGGS LAID
AFTER FIRST BATCH

preoviposition period could contribute to later egg batches. The possibility that this happened in S.stercoraria and S.suilla cannot be dismissed as there were several unavoidably delayed preoviposition periods because of lack of males. The fact that the correlation coefficients are so good, however, indicates that the effect of preoviposition period food has a minimal, if any, effect on the oviposition period feeding and egg production. It seems, therefore, that eggs laid after the first batch are dependent upon the amount of food eaten during the oviposition period.

12) The demonstration of the continuous process of feeding and egg-laying in S.stercoraria:

For S.stercoraria there are sufficient results to demonstrate the relationship between the number of insects eaten and numbers of eggs laid in successive cycles in a cumulative manner. To show this, the total number of Drosophila eaten during the preoviposition period by all the females added together was plotted against the total number of eggs laid in the first batch by all the females. The total number of insects eaten between the first and second batches by all the females was then added to the total number eaten during the preoviposition period.

Fig. 8. The demonstration of the continuous processes of oviposition and feeding in *Scopeuma stercoraria*.


Scopeuma stercoraria
Cycle No.
No. Of Flies Used
7 1
6 2
5 4
4 5
3 7
2 7
1 10
2800
2400
2000
1600
1200
ACCUMULATED TOTALS OF Drosophila EATEN
600
1000
1400
1800
2200
ACCUMULATED TOTALS OF EGGS LAID

For the second point on the graph this accumulated figure was then plotted against the sum of the total number of eggs laid in the second batch by all the females, plus the total number of aggs laid in the first batch.

A similar accumulation of eggs laid and insects eaten is carried out for successive cycles until the 7th., when only one female was left. The results are shown in Fig. 8., which also shows the numbers of females from which each point was calculated. If more females had been available, the points on the graph would have been much further apart.

The main value of this graph is that it shows how egg batches laid after the first are equally dependent upon the amount of food eaten between each batch. If the females had stopped eating, or drastically reduced their intake of insect food, after maturity, but still laid further egg batches by using up their food reserves, the curve would have flattened out soon after the first point. The processes of both oviposition and insect eating are thus seen as being continuous throughout the life of the female and not discontinuous as stated by previous authors (Hammer (1941), Larsen and Thomsen (1940) and Darwish (1954).)

13) <u>The feeding biology of male *Scopeuma* species:</u>

A study of the feeding requirements of males, similar to that described for females, is difficult to carry out unless a large reservoir of virgin females is available. These females are necessary in order that the males can be put with gravid virgin females, at daily intervals, to see when they are mature. During the winter months, when only experimental females were available, it was too risky to put young males with the females in case they were not mature and ate the females. Until male *Scopeuma* are sexually mature they will eat females, making no attempt to copulate with them.

A few males were kept in individual jars after emergence, supplied with *Drosophila* and sugar, and were killed at intervals of up to 8 days after emergence. Immediately after killing, the testes were dissected out and stained with acetic orcein. The squashed preparation was then examined for meioses, developing sperm and mature sperms. Developing sperms were found as early as 2 days after emergence, and mature sperms were present by 5 days after emergence. More studies are necessary to give more exact figures for the stages of spermatogenesis. The shortest time after emergence when the males would copulate was found to be 7 days, so the achievement of maturity does not seem to depend solely on the completion of spermatogenesis.

After reaching maturity, male Scopeuma do not eat very much and they are not very active. Most of the activity of mature males in the field is in flying to fresh dung and, once there, they wait for females to come and then they mate. If no females arrive they remain waiting on the dung. The production of spermatozoa is probably continuous throughout life and no periods of feeding activity are expected.

During this study of the food requirements of males before and after maturity, males were kept individually in the culture jars, (hurricane lamp glasses) and the numbers of Drosophila eaten per day were recorded. Indications of maturity are stretched abdominal membranes, abdomen 'bobbing', and a reduction in feeding. After mating had taken place they were usually put back into their individual jars and kept supplied with Drosophila and sugar solution.

Only 4 S.squalida males were kept in culture jars and the number of flies eaten per day was recorded for the first 10 days prior to the Christmas break. Over the Christmas break they were put into an incubator at 10°C with a good supply of Drosophila. The two males which survived had eaten an average of 5.9 and 6.0 flies per day in the first 10 days of adult life. On the other hand, the two males which died during the Christmas break had eaten an average of 4.2 and 4.5 flies per day during the same period. The amount of food eaten per day might have a strong influence on the ability to survive difficult times during the early period. It might also affect the time taken to achieve maturity, but this is a special study of its own.

Because there were only two mature male S.squalida available after Christmas they were kept in the culture jars with females 3 and 4. This is why the numbers of Drosophila eaten were not recorded as it was not known how many had been eaten by the males and how many by the females.

From the 4 S.stercoraria males, for which rates of feeding before and after maturity are available, it can be seen (Table 4.) that there is a considerable decrease in the feeding rates after maturity. Approximately 5 times as many insects were eaten before maturity than after, but mature males did not cease feeding altogether. I have seen mature males on dung eating a wide variety of insects but the occurrence of this is not very frequent.

The figures of feeding rates before and after maturity, for males and female, are shown in Table 4. Females which were deliberately starved, or died after the first egg batch, have been excluded. No male S.suilla were available for these studies but, from observations at other times in culture cages and in the field, the males behave in the

Table 4

<u>To Compare Rates of Feeding Before and After Maturity in Males and Females of Three Scopeuma species.</u>

Female Reference Number	Number of Flies Eaten per day: Preoviposition Period	Ratio	Oviposition Period
S. stercoraria			
2	3.11	1: 1.54	4.80
3	4.89	1: 1.51	7.38
14	7.67	1.13 :1	6.81
7	9.00	1.42 :1	6.33
13	9.42	1: 1.25	11.76
5	9.81	1.81 :1	5.43
8	10.27	2.20 :1	4.75
S. suilla			
5	2.58	1: 2.69	6.94
6	3.92	1: 1.36	5.35
3	4.14	1: 1.78	7.37
2	6.00	1: 1.12	6.72
1	8.58	1: 1.06	9.07
S. squalida			
2	8,86	1: 1.44	12.76
1	9.00	1.16 :1	7.77

Male Reference Number	Number of Flies Eaten per da: Before Maturity	Ratio	After Maturity
S.stercoraria			
3	6.80	4.93 :1	1.38
1	7.20	5.41 :1	1.33
2	7.20	5.41 :1	1.33
4	7.30	4.93 :1	1.48
S. squalida			
2	4.20		Died
4	4.50		Died
3	5.90		-
1	6.00		-

same way as those of the other two species.

The table also illustrates some of my evidence against the reported change of feeding habit after maturity. Of the 14 females, only 5 ate fewer insects after maturity than before, but the differences are never so great as to suggest a change from the rapacious habit.

14) The numbers of eggs laid in successive cycles:

The constancy in the numbers of eggs laid in successive batches by all three *Scopeuma* species is quite striking and contrasts with the sudden reduction in numbers laid after the first batch, suggested by Cotterell (1920). The numbers of eggs laid in each gonotrophic cycle are given in Table 5. The maximum number of batches laid by *S.suilla* was 7; by *S.stercoraria*, 10 (much higher than expected from Cotterell's work), and by *S.squalida* 21 although, for convenience, only 12 batches are shown in the table.

It can be seen from the table that the total number of eggs laid by each female are usually much higher than the largest total recorded by Cotterell (1920). From the results of 10 dissections, Hammer gave the maximum number of eggs found in *S.stercoraria* females as 45, with an average of 32.9. Most of the batches laid by the laboratory

Table 5.

The numbers of eggs laid in successive gonotrophic cycles, total eggs laid and lifespan of three *Scopeuma* species.

Female Reference Number	Gonotrophic Cycle Number 1	2	3	4	5	6	7	8	9	10	11	12	Total Eggs	Lifespan (Days)
S.stercoraria														
7	56	35											91	23
13	50	50	39										139	26+
8	64	70	12										146	56
1	66	36	30	53									185	76
5	73	60	68	76	6								283	68
2	69	69	74	65	68								345	117
3	84	80	78	81	81	82							486	87
14	48	45	46	49	49	42	47	45	46	19			436	80
S.suilla														
3	15	34	37										86	47
6	50	53	52										155	56
5	36	61	63	63									223	65
1	63	69	69	65	100								366	56
2	67	71	70	75	70	58	51						462	98
S.squalida														
4	62	73	56	71	66	63	26						417	44
3	53	41	50	52	50	51	51	24					372	57
2	80	56	58	61	60	51	53	46	57				522	45
1	43	48	47	48	45	46	43	46	48	46	44	40	802	150

females were higher than this maximum, and the results of my dissections of approximately 4,000 S.stercoraria females from the field, showed that Hammer's maximum of 45 was frequently exceeded even in old females. The maximum number of 84 eggs, laid during the present studies, was also exceeded once by a wild female.

Anderson (1964), in presenting the number of eggs laid at each oviposition by Fannia canicularis L., drew attention to exceptions in the general rule of diminishing numbers of eggs produced in successive gonotrophic cycles. Six of his flies had laid more eggs in one cycle than in the preceding cycle, but the possibility of previously non-functional ovarioles becoming functional again was dismissed as the explanation. He suggested, from the results of dissections, that the females did not lay all the mature eggs at one oviposition but 'held over' some until the next cycle or even later ones. Analysis of Anderson's figures in reference to his female no. 4., reveals the fact that there must have been 46 eggs which were not laid when the other 66 eggs were laid at the first oviposition. If Anderson's explanation is correct these 46 eggs must have been retained in the ovary for periods varying from 3 - 24 days until the ninth cycle was completed. In Anopheles a retained egg causes the follicle lying above it to degenerate (Detinova 1962), which is likely to be rather general in the Diptera.

The present study on Scopeuma species showed that females can retain ripe eggs for a few days after laying the first eggs af any particular cycle. It may also take a few days to lay all the eggs of one cycle, especially by old females. It cannot, however, be inferred that any cycle which results in more eggs than in the previous one is exclusively the result of retaining eggs from the previous cycle. I believe that non-functional ovarioles in Scopeuma can become functional again at a later cycle. This is reported to happen in Anopheles (Detinova 1962). My evidence for this comes partly from the results of starving a female S.stercoraria after the first oviposition, and later supplying her with insect food again. This has been described previously for female no. 1. She laid 66 eggs in the batch, was starved and laid a second batch of 36 eggs 15 days later. Starvation was continued for 9 more days and, 2 days after feeding began again, she laid 30 eggs. After eating more insects a fourth batch of 53 eggs was laid.

It is doubtful whether, in view of the extensive starvation, this last larger batch was produced by including eggs matured during either of the two previous cycles. Fresh dung was always in the culture jar so that the female could have laid at any time. It seems more probable that some ovarioles were non-functional in the 2nd and 3rd cycles, due to the starvation, and became functional again when food was supplied. Table 5. shows 8 cases out of 17 where the 2nd batch of eggs was larger than the 1st, and 3 cases where the 3rd batch was larger than either of the two preceding batches.

In my own dissections I did not find any evidence of mature eggs being retained while another batch was developing. I can therefore only suggest that these examples in Table 5. are instances where some ovarioles have become functional only at later gonotrophic cycles.

Table 5. also shows the lifespan of all the females. The maximum for S.suilla is 14 weeks, for S.stercoraria it is 16 weeks, and over 21 weeks for S.squalida. Examination of Cotterell's figures for S.stercoraria gives a maximum adult lifespan of about 4 weeks for females, in the first 3 of which they are immature. The life of the male is reported as being considerably longer than that of the female. I have had instances of both males and females living for 16 weeks, and found no difference in longevity in the laboratory between the sexes.

15) <u>Numbers of insects eaten during successive gonotrophic cycles</u>:

The numbers of *Drosophila* eaten by each female during successive cycles (from one oviposition to the next) remain markedly constant, as shown in Table 6.

<u>Table 6.</u> <u>Mean numbers of eggs laid, and mean numbers of *Drosophila* eaten in successive gonotrophic cycles by three *Scopeuma* species:</u>

	Gonotrophic Cycle Number								
Species	1	2	3	4	5	6	7	8	
<u>S. stercoraria</u>									
Eggs Laid	62,0	58.4	52.8	64.8	51.0	62.0	47.0		
Insects eaten		59.0	68.2	63.0	67.5	56.0	60.0		
No. of females	10	7	6	5	4	2	1		
<u>S. suilla</u>									
Eggs Laid	46.2	57.6	58.2	67.7	85.0				
Insects eaten		52.0	74.4	75.0	106.0				
No. of females	5	5	5	3	2				
<u>S. squalida</u>									
Eggs Laid	59.5	54.4	52.8	58.0	55.3	52.8	43.3	38.7	52.
Insects eaten		36.0	43.5	38.5	46.0	42.8	42.3	52.7	52.
No. of females for eggs	4	4	4	4	4	4	4	3	[illegible]
No. of females for insects		2	2	2	2	4	4	3	[illegible]

For this table, successive means had to be calculated from fewer individuals as the cycle number progressed, but this does not affect the general pattern. In calculating the mean numbers of insects eaten during each cycle, females which had been starved were excluded.

This table shows that S.squalida seems to have a more efficient conversion of insects into eggs than the other 2 species.

16) Time intervals between successive egg batches:

The interval between successive ovipositions was measured from the date of the first eggs of one batch to the date of the first eggs of the next batch. When the figures for these intervals in the three species are compared (Table 7.) specific differences can be seen similar to those figures for the rate of conversion of food eaten to eggs laid (e.g. Table 6.). This could be due to the small number of individuals studied, or it could be additional evidence of a physiological difference in S.squalida from the other two species. It could explain why S.squalida is the only species studied which is more common in the harsher environment of the high Pennine moors than in the lowlands (P.15.). The mean preoviposition periods were calculated by excluding females which, due to partial starvation or lack of males, had a delayed preoviposition period. The mean intervals between egg batches may include such females which showed normal behaviour after the first oviposition.

Table 7. Mean intervals in days between successive egg batches in three *Scopeuma* species:

	Preoviposition Period	Gonotrophic Cycle Number							
	1	2	3	4	5	6	7	8	9
S.stercoraria	13.3	6.4	8.7	7.8	7.0	7.5	10.0	4.0	
No. of females	6	7	7	5	3	2	1	1	
S.suilla	12.0	5.4	10.4	7.7	17.0				
No. of females	1	5	5	3	2				
S.squalida	9.8	3.0	3.5	3.3	3.5	3.8	4.0	5.7	4.5
No. of females	4	2	2	4	4	4	4	3	2

Table 7. shows that in *S.stercoraria* the preoviposition period is approximately twice as long as any succeeding cycle, an important point in the analysis of field work data. The preoviposition period in *S.squalida* is about 3 times as long as other cycles, but the figures for *S.suilla* are inconclusive. Many more individuals must be studied in order to obtain more accurate estimates for the intervals between egg batches.

17) <u>The effect of temperature on the intervals between egg batches:</u>

The shortage of *Scopeuma* females made the comparative study of the effect of temperature on feeding and breeding biology impracticable. The opportunity was taken of studying two *S.squalida* females which had reached maturity at 10°C. They were seen mating in their cage about 33 days after eclosion. The two females were put into separate culture jars at 10°C one with a male from the same cage, and the other with one of the laboratory reared (20°C) males. Unfortunately, two of the flies (♂and ♀(B)) were accidentally killed during their third egg batch. The results of the two females (A) and (B) are shown in Table 8., together with the means of the laboratory reared *S.squalida* females kept at 19-21°C for comparisons.

There were no marked differences in the amount of food eaten or numbers of eggs laid by the females at 10°C, compared with those reared and kept at 19-21°C in the laboratory. The main difference was in the length of the interval between egg batches which was much longer at 10°C than at 19-21°C. This also meant that the feeding rate of insects eaten per day was less at 10°C although the total number eaten between batches was about the same at both temperatures. The reason for this could be a direct effect

Table 8. Intervals between egg batches, numbers of eggs laid and *Drosophila* eaten by 2 *S. squalida* females at $10^{\circ}C$, compared with the means for females reared and kept at about $20^{\circ}C$.

Gonotrophic Cycle No.	No. of Eggs laid in each cycle.			No. of Drosophila eaten between each egg batch.			Interval in days between each egg batch		
	2 ♀s @ 10^oC A	B	Mean for ♀s @ 20^oC	2♀s @ 10^oC A	B	Mean for ♀s @ 20^oC	2♀s @ 10^oC A	B	Mean for ♀s @ 20^oC
	49	56	59.5						
1				31	37	36.0	8	8	3.0
	56	56	54.5						
2				43	32	43.5	7	8	3.5
	58	15	52.8						
3				39	-	38.5	8	-	3.3
	59		58.0						
4				47	-	46.0	15	-	3.5
	58		55.3						
5									

of the lower temperature reducing the activity of the Scopeuma, or it could be the indirect effect of putting Drosophila, reared at 25°C, into 10°C and so reducing their activity. This would then lengthen the time taken for Scopeuma to mature each batch of eggs. This possibility of indirect effects can only be excluded by feeding Scopeuma on flies which have been acclimatised to the various temperatures.

In other studies, S.stercoraria were kept in a cage at a constant temperature of 5°C. The Scopeuma showed very little activity at all, and Drosophila which were put into the cage were virtually inactive. No flies survived to maturity.

FEEDING BEHAVIOUR AND BREEDING BIOLOGY OF *Scopeuma* SPECIES

b) EXAMINATION OF OVARIES

1) Introduction.

The population studies of *Scopeuma* in the field had to be supported by studies of the age composition of the flies in order to answer the controversy about the number of generations in a season (Hammer 1941, Darwish 1954, Laurence 1954). From the laboratory studies on the breeding biology, already described, some idea of the probable behaviour of the flies in the field was emerging. It remained to be seen whether the flies in the field behaved in the same manner. In order to study the age composition of the population, flies were caught in the field at weekly intervals so that the ovaries could be dissected.

Detailed descriptions of age determination in mosquitoes and other flies have been given by Detinova (1962), after the discovery of the dilatations of the ovariole tunica by Polovodova in 1947. This discovery stimulated research by Detinova, Beltiukova and Lineva into mosquitoes, particularly *Anopheles maculipennis* Mg., Simuliids, Muscids and other flies to see if accurate age determinations could be carried out. In all the flies studied there were dilatations in the tunica, or follicular tube, of all parous flies, indicating that eggs had been matured and laid. Each dilatation corresponded to one egg. By dissecting out the ovary and examining the ovarioles it was then possible to count the number of dilatations in each ovariole and, hence, the number of egg batches laid. This was possible because these flies laid all the eggs of one batch together.

If there is simultaneous development of all the follicles in each ovary, and if the interval between batches is known, then it is possible to determine the age of females with some degree of accuracy. Since it is often difficult to determine the interval between batches under field conditions, particularly if the flies are active for a long season, the age determination is often referred to as the physiological age. This simply means that it is possible to count the number of gonotrophic cycles which a fly has gone through, but it is not possible to calculate the calender age from this. The physiological age therefore refers to the number of gonotrophic cycles.

Gillies and Wilkes (1965) showed that the method of determining the age of *Anopheles maculipennis* could also be applied to *A. gambiae* Giles and *A. funestus* Giles. The process was more difficult in these two species because of the impossibility of examining individually isolated ovarioles. Gillies and Wilkes were also able to relate the physiological age to the calender age, as a result of marked mosquitoes which they released and recaptured later. Dissections then showed how many gonotrophic cycles had developed during the time they were at liberty.

Several methods of age-determination in flies (e.g. Detinova 1962, Anderson 1964) have been described and the purpose of my dissections was to see which methods were applicable to Scopeuma species. During this study I was unable to relate physiological age to calender age, except from laboratory results which gave the relationship of different cycles to each other.

2) Dissection techniques

The Scopeuma to be dissected were caught mainly by sweep-netting and killed in the field, either by putting the catch into a cyanide bottle or by spraying the net contents with a fly-spray. The flies were then put in specimen tubes and labelled. At the end of the day the tubes were placed in a deep-freeze refrigerator at about -20^{o}C. In this way the flies can be kept for up to two years.

Females to be dissected are taken out of the specimen tube a few at a time and placed in 0.7 % saline. The specimen tube is left in the refrigerator so that the flies remain frozen until a few minutes before they are dissected. Each female is first examined under the low power (X35) of a binocular microscope with revolving objectives, then at X75 or X100 as required. A glass stage, with a mirror below was found to be most suitable to enable rapid changes to be made from direct to reflected light.

The females were first examined for the presence of mites or other external parasites. In the examination of several thousand Scopeuma of both sexes, no external parasites were ever found. The fly was then cut at the waist and the abdomen was retained on the slide in the saline. The anterior, cut, part of the abdomen was held down by a fine bent needle whilst the ovipositor was cut off with entomological scissors. Using the scissors the whole length of the abdomen was cut along the sternites and then along the mid-tergites. By means of fine forceps and needles the two halves of the cuticle, together with most of the attached tracheae and fat body were then removed, leaving the reproductive and alimentary systems with a little excess of fat body and tracheae. The alimentary canal was removed carefully, to avoid staining the reproductive system with its contents. As much fat body and tracheae as possible were then removed to clear the reproductive system.

A gravid female was dissected first, to investigate the structure of the ovary. The few ripe eggs were pressed out of the ovaries and a coverslip was then pressed down on one ovary and sealed. Fig. 9. shows the appearance of this ovary. All the follicles are at the same stage of development and most ovarioles have a clearly visible dilatation attached to the second follicle. Also attached to the second follicle in each ovariole is a third follicle and a germarium. The ovariole in the bottom right hand corner shows the transparent ovariole sheath enclosing the follicle and dilatation of the tunica. The ovarian sheath, which encloses the whole ovary, can be seen running from the top right to the mid-left of Fig. 9.

In order to dissect the ovaries to determine the number of dilatations the ovarian sheath was broken so that the ovarioles lay fairly loosely. Fig. 9. shows the positions of the points of very fine entomological forceps used to extract the follicle and its attached dilatations. The points of the forceps were firstly put around the narrow neck which separates (in this Fig.) and 2nd and 3rd follicle. If pulling at this point did not pull the follicle and dilatation out, the points of the forceps would be placed at the junction of the dilatation and the follicle to which it was attached. By pulling against the follicle it was usually possible to pull the follicle and its dilatations clear of the ovariole sheath.

This dissection technique was applied to all the ovarioles in the ovary because, the ovarian and ovariole sheaths were

Fig. 9. Squash of an ovary of a mature female *Scopeuma stercoraria* showing the basic structures. Dilatations can be seen attached to some developing follicles.


1·0 m.m.
ovarian sheath
tunica dilatation
ovariole sheath

not transparent enough to facilitate counting the dilatations on each tunica. The connection between the follicle and its dilatation sometimes broke whilst it was being pulled out. All the ovarioles, therefore, had to be examined to find the maximum number of dilatations in any one ovariole. The dissection of the ovaries of gravid females was very similar except that the egg had to be gripped by the forceps near to the developing follicle. This was then pulled out carefully and any dilatations would be attached to the end of the egg nearest to the oviduct. The physiological age of any fly was thus the maximum number of dilatations found in either ovary. This was represented in all the figures as the number of egg batches laid.

The technique described above was found to be very good for the purpose of obtaining an accurate determination of the physiological age of the flies. The only difficulty was the time taken to do the dissecting. The words of Detinova (1962 discussing Liniova) applied to this work: "The number of dilatations in the ovarioles enables us to determine with accuracy the number of ovipositions completed by each female. However, the dissection of the ovaries of house-flies to count the number of dilatations is technically more difficult than in the case of mosquitoes and other Diptera." Detinova's next sentence did not apply to _Scopeuma_, for reasons which will be discussed later: "The physiological age of female house-flies is determined mainly by the number, colour and position of the yellow bodies and by the condition of the tracheal system of the ovaries."

The only time when it was possible to dissect the Scopeuma quickly was when there was a catch of newly-emerged flies which had soft abdomens. It was possible to examine these flies at the rate of one a minute, but older flies sometimes took up to 15 minutes or more. If a slide was made of part of the reproductive system, then the time taken was extended further. The numbers of any eggs present were recorded, as was the presence of nematodes.

Slides were made by withdrawing the saline solution with a pipette and then adding a drop of Aquamount medium, staining being unnecessary. There was occasionally a slight contraction in the ovariole when the mounting medium was added.

3) The development of the ovaries after eclosion.

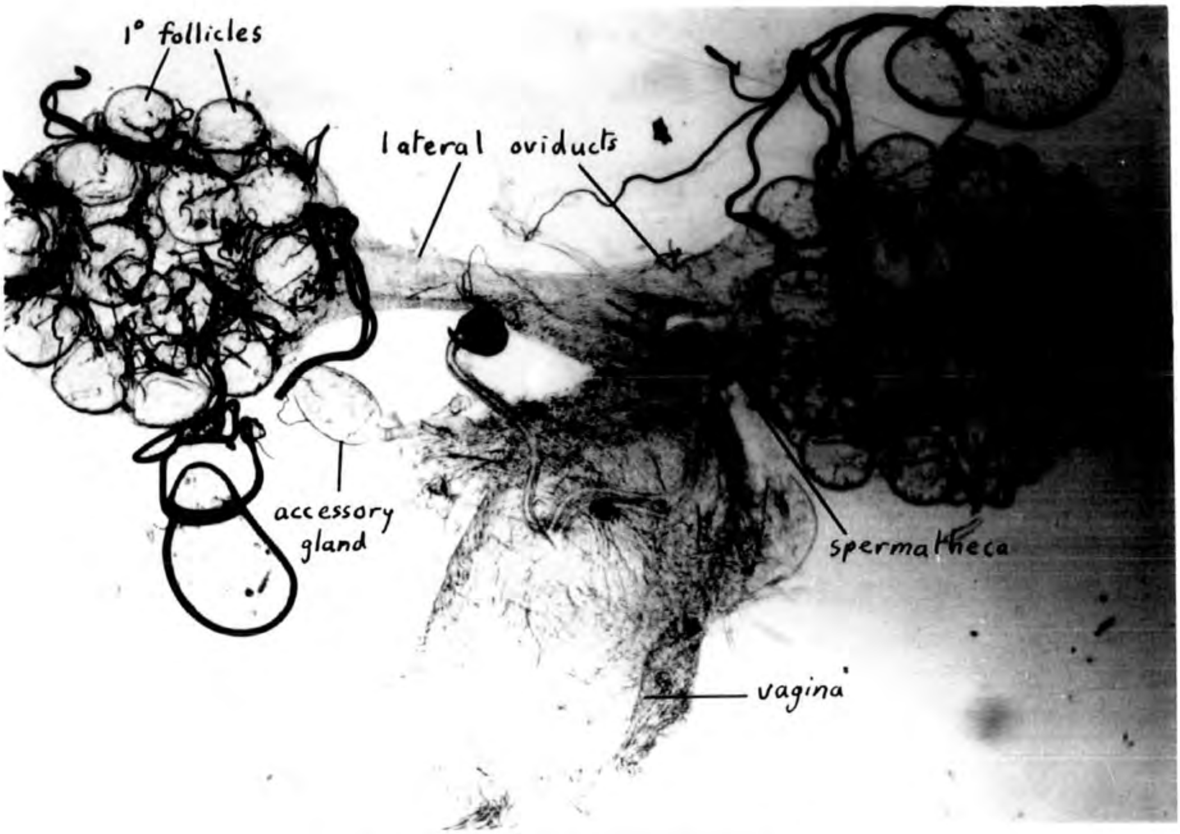
When female Scopeuma adults emerge from the pupa their ovaries are extremely small, being composed of small first follicles, germaria and short ovariole pedicels. The young ovary is thus a very compact body and its component parts cannot be easily identified because of the dense supply of tracheae. As the newly-emerged female grows older the follicles increase in size and the ovary develops the appearance of a bunch of grapes. Fig.10. shows two reproductive systems of female _Scopeuma stercoraria_ dissected a few days after emergence. These two photographs show the variation in compactness and tracheal supply. The ovaries at the top, although very immature, have the appearance of those of a fly which has oviposited several times. The external appearance of an ovary and its tracheal supply are not reliable indications of its age.

The top photograph in Fig. 10. also shows the typical number and arrangement of the spermathecae and accessory glands. The three spermathecal tubes all open together into the dorsal surface of the vagina, between the two openings of the accessory glands. In the overwhelming majority of females examined, two spermathecae were joined together on the right side. Much more rarely they were joined on the left side.

As the ovary grows larger the follicles lengthen and become differentiated into the darker, lower, oocyte region and the lighter coloured upper nurse cell region. Fig. 11. shows this in a _Scopeuma stercoraria_ about half way through the preoviposition period. With the increase in volume of the growing ovary, the tracheal supply becomes stretched and so more of the ovary is readily visible.

Fig. 12. shows the ovaries of a _Scopeuma suilla_ female which had laid one batch of eggs. "Yellow bodies", or

Fig. 10. Reproductive systems of two immature *Scopeuma stercoraria* females, showing variation in compactness of follicles and in the amount of tracheae present.



1° follicles
lateral oviducts
accessory gland
spermatheca
vagina

1·0 m.m.

trachea

Fig. 11. Ovary of an immature Scoepuma stercoraria female several days old. The nuclei of the nurse cells can be seen in the lighter regions of the follicles above the darker oocyte region.


1·0 m.m.

Fig. 12. Reproductive system of a uniparous *Scopeuma suilla* female, showing "Yellow bodies" in the ovarioles.


1·0 m.m.
"yellow bodies"

follicular relics were present in the ovary, but it was not possible to determine, without dissection, how many relics were in each ovariole.

Fig. 13. top picture, was an interesting case of a degenerated ovary. The right ovary (upper in photo) seemed to have developed only one follicle which did not mature. An empty sac-like structure (probably a degenerated egg) can be seen in the ovary with no evidence of follicles. The left ovary, (lower in photo) however, contained 51 ripe eggs and three ovarioles which had not developed eggs in this cycle. Each had two dilatations, indicating that the fly was gravid for the third time, having laid 108 eggs already. The left ovary occupied nearly all the volume of the abdomen so that there was no external appearance of abnormality. As the left ovary contained as many eggs as are usually contained in two ovaries, this seemed to be a case of compensation for the unproductive right ovary.

4) The appearance of dilatations on ovariole funicles in *Scopeuma stercoraria* and numbers of eggs in ovaries.

When ovarioles were dissected out of the ovary they were pulled out of their ovariole sheath so that any dilatations would be clearly visible as described on P.41. Slides were made of all different types of ovarioles having varying

(i) Degenerated right ovary of a gravid 2-parous female *Scopeuma stercoraria*. The left ovary had 51 ripe eggs and 3 non-functional ovarioles.

Fig. 13.

(ii) Compact ovaries of a uniparous *Scopeuma stercoraria* After oviposition the ovary contracts to the immature size. Only dissection of the right ovary indicated that the fly was mature.

1·0 m.m.

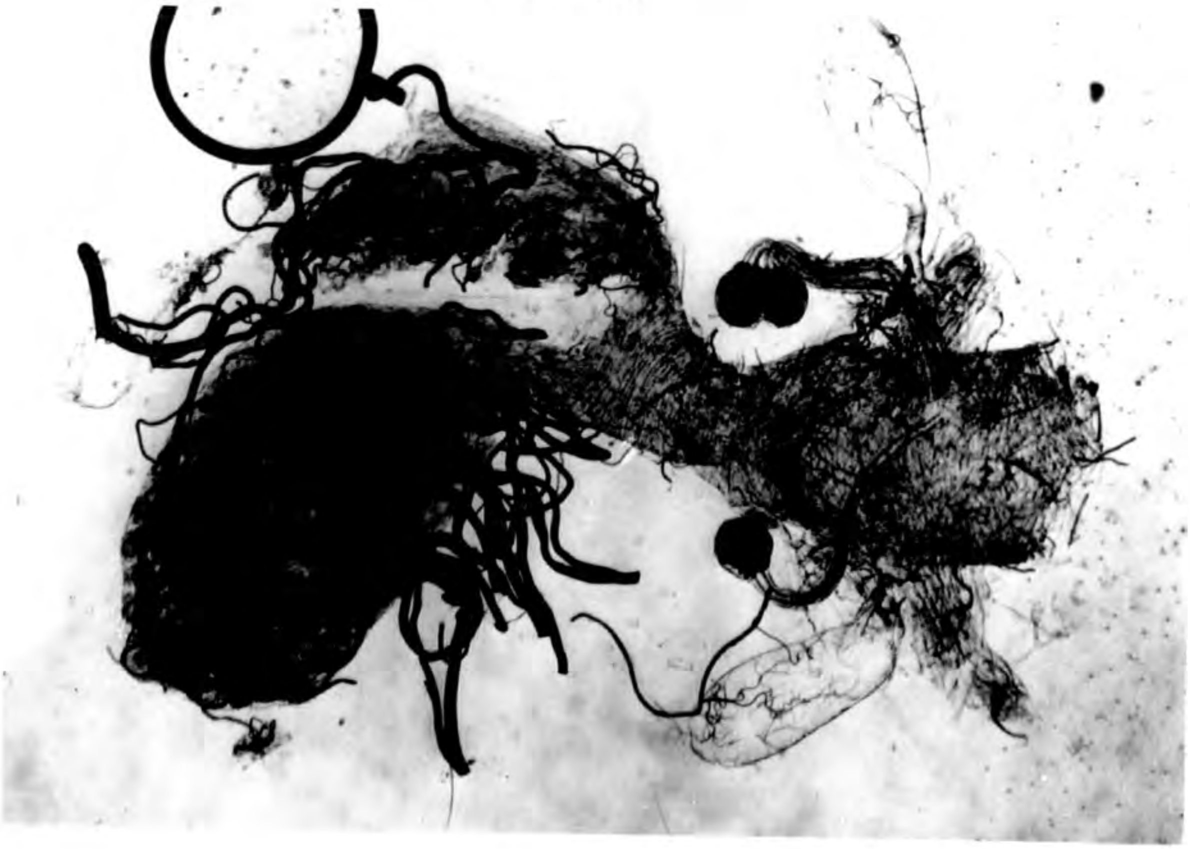
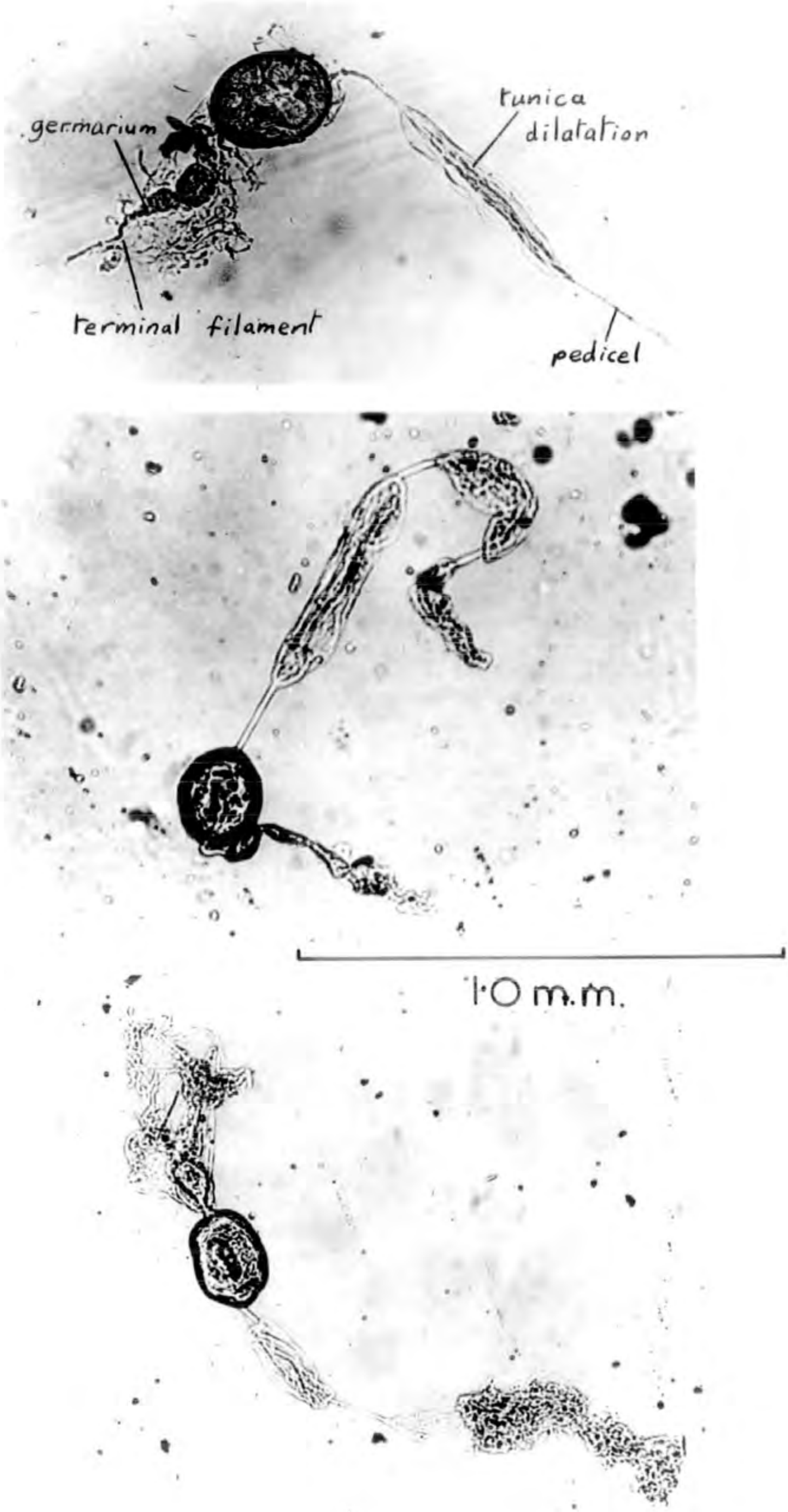


Fig. 14.

(i) Ovariole of a uniparous Scopeuma stercoraria with 1 dilatation.

(ii) Ovariole of a 3-parous S. stercoraria with 3 dilatations.

(iii) Ovariole of a 2-parous S. stercoraria with 2 dilatations.


germarium
tunica dilatation
terminal filament
pedicel
1·0 m.m.

numbers of dilatations. Fig. 16. gives an indication of the degree of shrinking which takes place when the aqueous mounting medium is added, as this ovariole was photographed whilst in saline and, again, after it had been stretched and mounted.

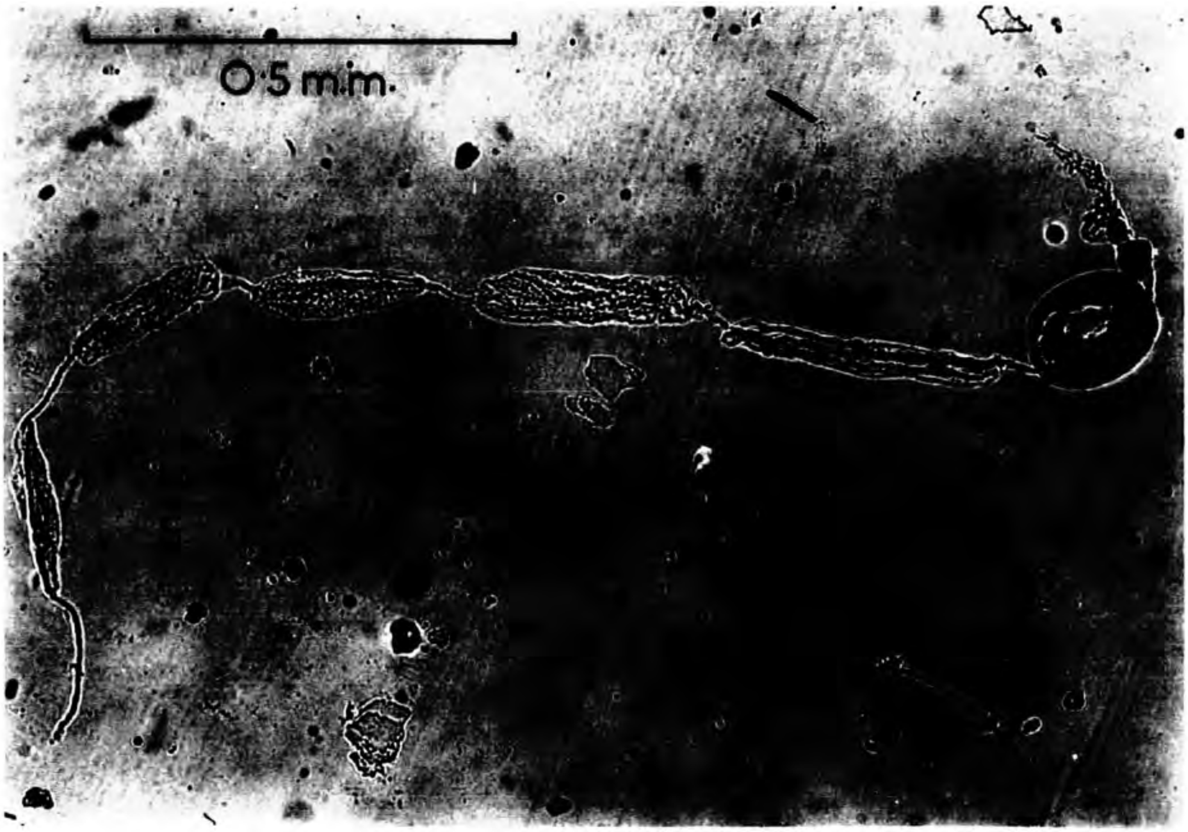
Fig. 14. shows 3 ovarioles having, from top to bottom, 1, 3, and 2 dilatations respectively. The top picture shows the terminal filament, germarium, young third follicle, second follicle ready to develop, and the dilatation left by the ripe egg of the first gonotrophic cycle. The frayed piece of tissue around the germarium in this and other pictures is the portion of the ovariole sheath, torn during dissection. The bottom picture is rather unusual in that the dilatation left from the first egg laid is much larger than that left by the second egg. The centre ovariole is more typical in showing a gradation in size from the smallest first dilatation to the largest (3rd) and most recent dilatation.

Two ovarioles are shown in Fig. 15. the top one having 4 dilatations, and the bottom one with 5. As the number of dilatations increases beyond 3, those distal to the developing follicle become twisted around the more proximal dilatations. Great care has to be taken in dissecting these ovarioles and

(i) Ovariole of a 4-parous _Scopeuma stercoraria_ with 4 dilatations.

Fig. 15.

(ii) Ovariole of a 5-parous _Scopeuma stercoraria_ with 5 dilatations.


0·5 m.m.

in trying to straighten the tunica, with fine entomological forceps, to see the number of dilatations. This has to be done under the X10 objective, with reflected light.

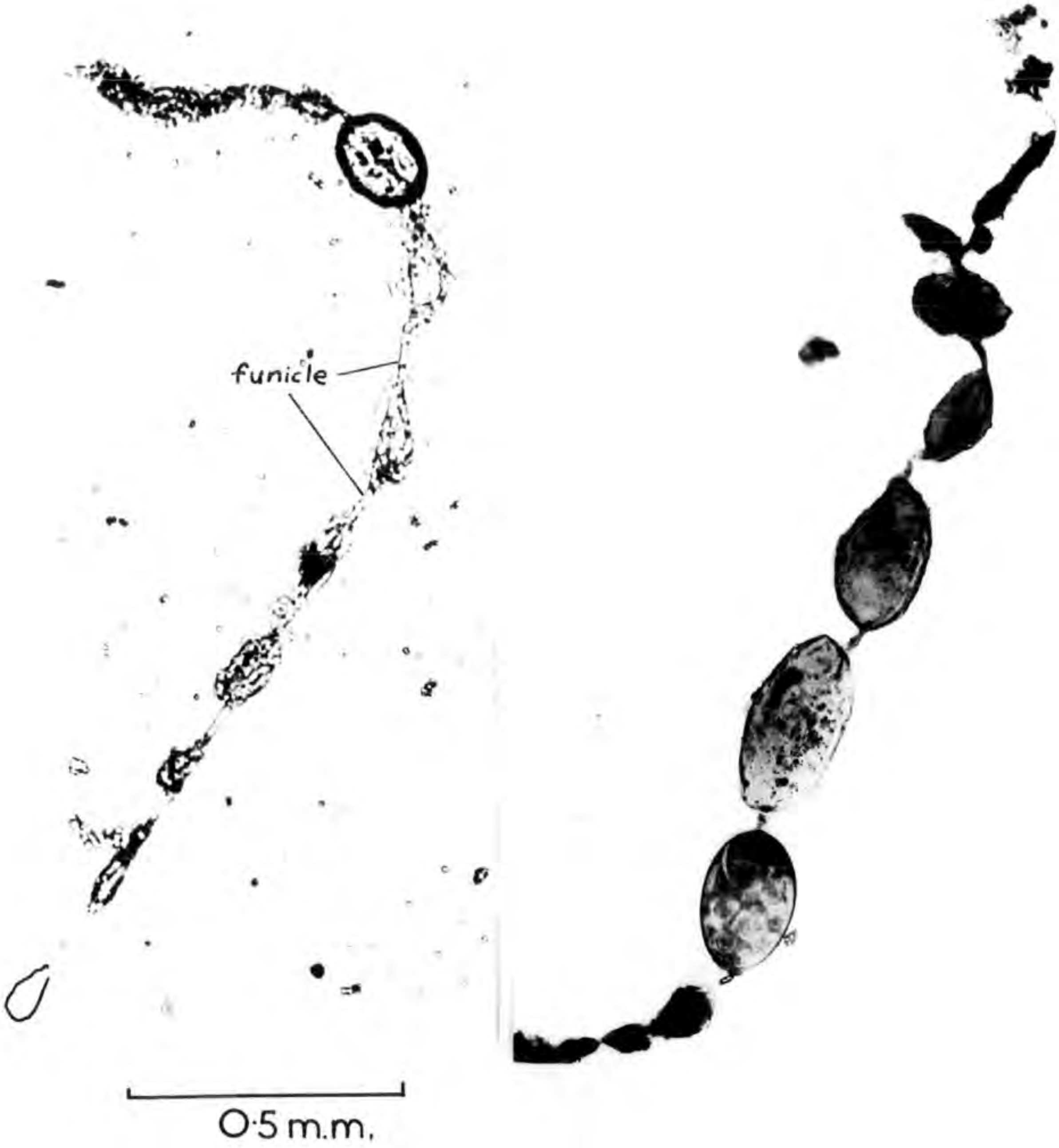
There is no photograph of an ovariole with 6 dilatations for two reasons. All but one of the ovarioles with 6 dilatations were so twisted that some dilatations were torn in the process of trying to straighten the pedicel. Only one ovariole was successfully transferred to a slide ready for mounting, and the saline was withdrawn. There was an unavoidable delay in transferring the mounting medium, and the slide quickly dried out, so that the dilatations became indistinguishable from each other.

Fig. 16. shows an ovariole of one of the oldest flies caught in the field, having seven definite dilatations (there was the possibility of an eighth being present, but this was not clear). The picture on the right shows the ovariole in a late stage of being straightened out in saline. When first dissected out of its sheath it had the appearance of only having three dilatations. With further manipulation it became clear that there were more. When the stage had been reached at which four dilatations were quite clear and that there were others which were less clear, I decided to have the ovariole photographed before proceeding further. After this had been done the straightening out proceeded.

Fig. 16. Ovariole of a 7-parous Scopeuma stercoraria

Right: Ovariole at a late stage in dissection before final straightening and mounting.

Left: The same ovariole after straightening and mounting in Farrants medium. The spirally twisted nature of the funicle between the dilatations can be seen.


funicle
0·5 m.m.

Unfortunately, the ovariole collected quite a lot of dust during the four hours when it was being dissected. When it had been straightened, a permanent slide was made of it and the photograph on the left was taken. It revealed 7 clear dilatations (and possibly an 8th). The female was therefore gravid at least for the 8th time and was caught on 12th October 1965. By allowing 3 weeks larval and pupal development, 2 weeks preoviposition period, and one week for each successive cycle, this gives a calendar age of about 12 weeks. The egg from which the fly developed must have been laid sometime in mid-July.

Whilst the results of the dissections were being recorded for the number of dilatations, any mature eggs present were counted and recorded. Any large numbers of follicles were also counted in non-gravid females. It was thus possible to obtain an estimate of the number of eggs laid previously by multiplying the number of eggs by the number of gonotrophic cycles already passed. As the number of cycles was usually determined by counting the number of dilatations on non-functional ovarioles, the number of eggs already laid is a minimum estimate, as these non-functional ovarioles would have been functional in previous cycles.

The highest number of eggs or functional follicles counted in any female, was 85, in a uniparous female.

This was not an isolated high number as 78, 74, 73, 72 and 71 were also recorded, some more than once. Many numbers in the 50's and 60's were also recorded. Numbers less than 20 also occurred, showing a wide variation. The highest number of eggs recorded in dissected <u>Scopeuma</u> by Hammer (1941) was 45, but he did not say where his flies had been caught. Flies taken off cow dung usually have lower numbers of eggs because they have usually already laid part of the batch. The highest numbers of eggs were recorded from females caught in the vegetation. These were flies which had almost completely matured the next egg batch but had not yet left the vegetation to lay on the dung.

The highest number of eggs in the various gonotrophic cycles, and the minimum number of eggs calculated as having been already laid can be seen from the following table. - Table 9 - Table 9.

Cycle No.	Highest no. Eggs encountered	No. of Eggs already laid
2	85	85
3	63	126
4	73	215
5	57	228
6	55	275

This last figure for 5-parous (6th gonotrophic cycle) was the highest calculated number of eggs laid by any female, but is probably an underestimate as the number of functional ovarioles usually decreases with age.

It was not possible to calculate a mean number of eggs for all the females or even to give a mean figure for the eggs in each gonotrophic cycle. This was because the number of eggs in the ovaries cannot always be assumed to be the maximum number produced in that cycle by all the females. Some females caught in the vegetation may have laid part of a batch and then were disturbed, retreating to the vegetation. It would have taken too much time during the dissection to look for ovarioles which had just released an egg. The main purpose of the dissection was to determine the age structure of the flies as accurately as possible, without trying to obtain accurate figures for the mean numbers of eggs. The figures quoted above are intended to give an idea of the reproductive potential of these flies. These figures also show that the high number of eggs laid by the laboratory-reared flies were not artefacts of that environment. The decrease in the proportion of functional ovarioles in older flies is not so great as to discount this older section of the population from contributing to the future generations. Their longevity and high reproductive potential are most important in maintaining the population during times when the climate is unfavourable for the hatching of eggs and larval survival.

5) Aberrations in structure, and the parasites of the reproductive systems of *Scopeuma*.

The aberrations in structure of the reproductive system fall into two main categories: variations in the spermathecae, and variations in the ovaries and testes.

As already mentioned (P.52) the occurrence of two joined spermathecae on the left instead of the right is very rare. A more frequent abnormality is that shown in Fig. 17. where there are four spermathecae, both left and right sides having two joined together. These occurrences may indicate the ancestral position, of two spermathecae fused on each side. The whole question of spermathecae is discussed in relation to taxonomy and phylogeny in Section 5. (P.200).

These variations in spermathecal number and arrangement do not seem to have altered any other features of the flies. A much more significant aberration in wild flies is that of castration, in both males and females. The castrated males had no testes, and castrated females no ovaries, but the rest of the reproductive systems were intact. This can be seen in Figs. 48 and 49 (Section 5. P. 195) where normal reproductive systems of males and females are shown for comparison.

In these females there was no trace of an ovarian membrane, the lateral oviducts ended bluntly. There were

Fig. 17. Female reproductive system of Scopeuma stercoraria, showing the abnormal occurrence of 4 spermathecae, with two on the left side instead of the usual 1.


1·0 m.m.

no remnants of the testes in the male, and no stages of degeneration have been seen in either sex. The degenerate ovary in Fig. 13. (top) cannot be considered as a stage in this castration, because of the functioning left ovary, and the normal external appearance of this female. In every one of the castrated flies, the external genitalia of the females resembled those of males, and the male genitalia had a tendency towards the female appearance. In addition, the external appearance of the castrated males, in size, colour and bristle arrangement, resembled that of normal females very closely. In both sexes causation may have been genetic affecting more than the primary sexual characteristics, but see the discussion Section 5, P. 199.

Parasites seem to be excluded from offering an explanation for castration because: 1) no evidence has been found of any sort of parasite in or on the flies concerned: 2) flies parasitised by nematodes or the fungus _Empusa muscae_ Cohn. have had normal reproductive systems and external appearance.

In 1964, 2 male _Scopeuma stercoraria_ were found at Moor House, clinging to _Juncus_ stems, killed by _Empusa_. In 1965, one male killed by _Empusa_ was found at Houghall, clinging to a Groundsel (_Senecio vulgaris_ L). All 3 were found with the head upwards, in contrast to the findings of Hammer (1941) who found all flies killed by _Empusa_, with the head downwards.

These three flies were the only ones found parasitised by _Empusa_ during the whole of the study. (4 _Scopeuma_ (3 with head upwards) were found so parasitised clinging to plants on a saltmarsh near Borth in west Wales in July 1967). Hobby and Elton (1935) found large numbers of _Scopeuma_ killed by the fungus, and Hammer (1941) recorded finding a few scores. Hammer suggested that this fungus may play an important part in the summer decline of adults in the field. Darwish (1954) found no evidence to suggest that this fungus could have accounted for the summer decline in _Scopeuma_ which he observed in 1952 and 1953. In the present study only one parasitised fly was found in the study area (in 1965) and, consequently, I do not think the fungus had any effect on the adult population.

Fig. 18. shows two photographs (top X100, bottom X400) of nematodes found in the ovaries of _Scopeuma stercoraria_. The nematodes were found inside the ovarian membrane amongst the ovarioles, often protruding through the membrane into the body cavity. Six female _Scopeuma stercoraria_ thus parasitised were found in 1964 and 1965 out of a total of about 4,000 females. Of these 6, 3 were nulliparous and the other 3 were uniparous, including one gravid one. One of the flies also had these nematodes in the proventriculus. The same sort of

i) X100

Fig. 18. Nematodes found in bodies of Scopeuma stercoraria. They can be seen actually inside the ovary and projecting through its membrane.

ii) X400

nematodes were found in the reproductive systems of some coprophilous Sphaeroceridae (Edge. pers. comm.). The description of the appearance and life cycle of *Heterotylenchus aberrans* (sub. fam. Anguillulininae) given by Bovien (1937), show some sililarities with these nematodes in *Scopeuma*.

Heterotylenchus aberrans is a heterogonic parasite of the Onion Fly, *Hylemyia antiqua* Meig. which is present in the fly as a few large bisexual females and numerous parthenogenetic females. This situation appears to be true in *Scopeuma*, but there are two main differences between the two flies. In *Scopeuma* the eggs of the nematode are produced within the ovaries of the fly, whereas in *Hylemyia* the nematode eggs are produced in the body cavity, followed by migration of larvae into the reproductive system. The *Scopeuma* females did not appear to have been sterilised by the nematodes as *Hylemyia* females were by *Heterotylenchus*.

No details could be found about the life history of these nematodes, or of their effect on the individual flies. The infection was only discovered at a late stage in this study and so further research was not possible. An infection rate of about 0.15% of females is unlikely to have had any effect on the reproductive potential of the population.

Dissections of *Scopeuma* have shown that much of the information obtained from the laboratory studies also applied to flies in the field. Table 5. shows the numbers of eggs laid in successive cycles by laboratory-reared *Scopeuma*. Only Female no. 14 laid more batches of eggs than any caught in the field (i.e. 10, as opposed to 7 from wild flies). The numbers of eggs laid per batch by the laboratory flies were very similar to those laid by wild flies. The fairly long period spent eating insects to mature eggs is probably why egg batches of *Scopeuma* are relatively small when compared with many Muscid flies. Important information on the behaviour of flies in the field was obtained from the dissections of the flies caught in vegetation away from the cows, when compared with the flies caught on the dung. Between 90 - 100% of the females caught on dung were fully gravid and had often laid part of their batch when caught. Three other categories of females were caught on dung, in small numbers; castrated, immature, and others in the process of maturing further eggs.

Females caught in the long grass, on the other hand, were nearly all in the process of developing eggs, whether nulliparous or parous. Few were fully gravid or castrated. All stages of ovarian development were found in the females from long grass in the fields and from woodland vegetation.

This suggests that after gravid females had laid their eggs they moved away from the grazed areas, into the vegetation where they could mature the next egg batch. As the strip method of grazing was employed at Houghall there was always a large area of ungrazed grass nearby providing large numbers of small insects as food.

The long grass was particularly suitable for the parous females to mature their next batch of eggs, as it provided some protection from dry winds and sun, as well as an abundant food supply. The flies here were also close to their oviposition medium.

Non-gravid parous flies were sometimes caught mating on dung and it is probable that females return to the dung to mate when their sperm supply is exhausted. However the small number of immature flies caught on dung were probably there by chance, perhaps to hunt, as no evidence was found to suggest that immature males or females are attracted by the smell of dung.

The oviposition cycle observed in the laboratory, lasting about a week from one oviposition to the next, certainly seemed to take place in the field.

Dissection enabled the ages of flies caught sucking nectar to be determined. These females came under the following age categories: 4 immature, 2 uniparous, 3 biparous and 1 castrated. Of the few flies seen sucking nectar there was no preponderance of mature flies, as expected from other authors' statements (see Section 1 a).)

Detailed week by week analysis (Section 2) of the age composition of the S. stercoraria population was possible due to the facility of determining the physiological age of the females, paralleling studies on mosquitoes (Detinova, 1962; Gillies and Wilkes, 1965; Gillies, 1966). Females of Scopeuma suilla and S. squalida were dissected on the few occasions when they were caught. Their ovarian structure and development, and their behaviour, did not differ from S. stercoraria.

The rate of maturation of the gonads and the development of successive batches of eggs was very closely related to the quantity of food eaten. It is possible that there is a physiological difference between S. squalida and the other species in relation to the conversion of food material into eggs. If this proves to be so it could be the major factor affecting the ecology of this species, since S. squalida is more numerous in harsh moorland conditions than in low lying agricultural land.

6) DISCUSSION

The methods of age-determination of a wide variety of flies has progressed considerably since Perry (1912) suggested a method for mosquitoes, which depended on the degree of damage to the wings. The presence of 'yellow bodies' in the ovaries had been recorded as early as 1825, but it was not until 1942 that Kuzina, working on Stomoxys calcitrans L. suggested that the number of these 'corpora lutea' (remnants of the follicle cells) might be used in age determination. The discovery of dilatations by Polovodova (1949) and of their formation by Detinova enabled entomologists to make accurate determinations of the physiological ages of female flies.

It is interesting to compare some of the processes associated with the maturation of the ovaries in Scopeuma stercoraria with those described for some Muscidae by Anderson (1964).

Anderson described newly emerged females of Fannia canicularis L., Musca domestica L., and Muscina stabulans Fall. as having hundreds of fat body 'balls' in the haemocoel which gradually diminished until fully mature eggs were formed, by which time all the fat body had disappeared. Anderson said that as the fat body never reappeared once it had disappeared the presence of fat body balls was "unequivocally characteristic of the nulliparous state", and assumed that this would be typical of the Cyclorrhapha.

My studies on Scopeuma species have shown that the situation, with regard to the fat body, is quite different. Newly emerged flies had very little fat body but, as they aged, the amount of fat increased. There seemed to be a slight depletion of fat body as the eggs approached maturity, but not complete loss. Unless starvation occurred after maturity the fat body continued, and was also found in multiparous field flies. If starvation occurred the fat body became depleted. The presence or absence of fat body balls cannot therefore be used in age determination for Scopeuma species. The situation in Scopeuma is more like the hunger cycle in Glossina (Wigglesworth 1953), where fat body is produced after each blood meal and used up before the next.

The presence of follicular relics (yellow bodies or 'corpora lutea') could not be used to gauge the physiological age of Scopeuma species. Only rarely were any relics clearly visible, and these were not distinct enough to facilitate counting. Relics, when found, were yellow or white and were concentrated in the ovaries. They were more commonly found amongst older flies.

Another characteristic of the nulliparous state described by Anderson (1964), was that the ovarioles were tightly bunched, and became loosely bunched in the parous state. The degree of compactness of ovarioles in nulliparous Scopeuma females was very varied. After each batch of eggs has been laid the ovary shrinks and the tracheae, which previously had been spread out, now become closer together again and obscure much of the ovary. The ovaries often seem to revert to their immature size and compactness. Fig. 13. (bottom picture) shows an example of this. The ovary looked so compact that I thought it was immature, but on dissection it proved to be uniparous (i.e. laid one batch of eggs).

Lineva (1953) described the prescence of tracheal skeins on the ovary as characteristic only of nulliparous flies. Anderson (1964), however, reported seeing them also on parous flies. In the Simuliidae, the extensive tracheal system supplying the ovaries does not undergo any changes with age (Prokofieva 1957).

With increasing numbers of ovipositions the ovaries contain fewer functional ovarioles in Musca domestica (Lineva 1953), and Muscina stabulans, Fannia caricularis and Cryptolucilia caesarion (Anderson 1964). In Scopeuma, however, ovarioles which are non-functional in one cycle can become functional in another. I have been unable to find, from the dissections, any examples of degenerated follicles which leave dilatations (c.f. Lineva, 1962).

Section 2. <u>FIELD POPULATION STUDIES</u>

a) THE STUDY AREA.

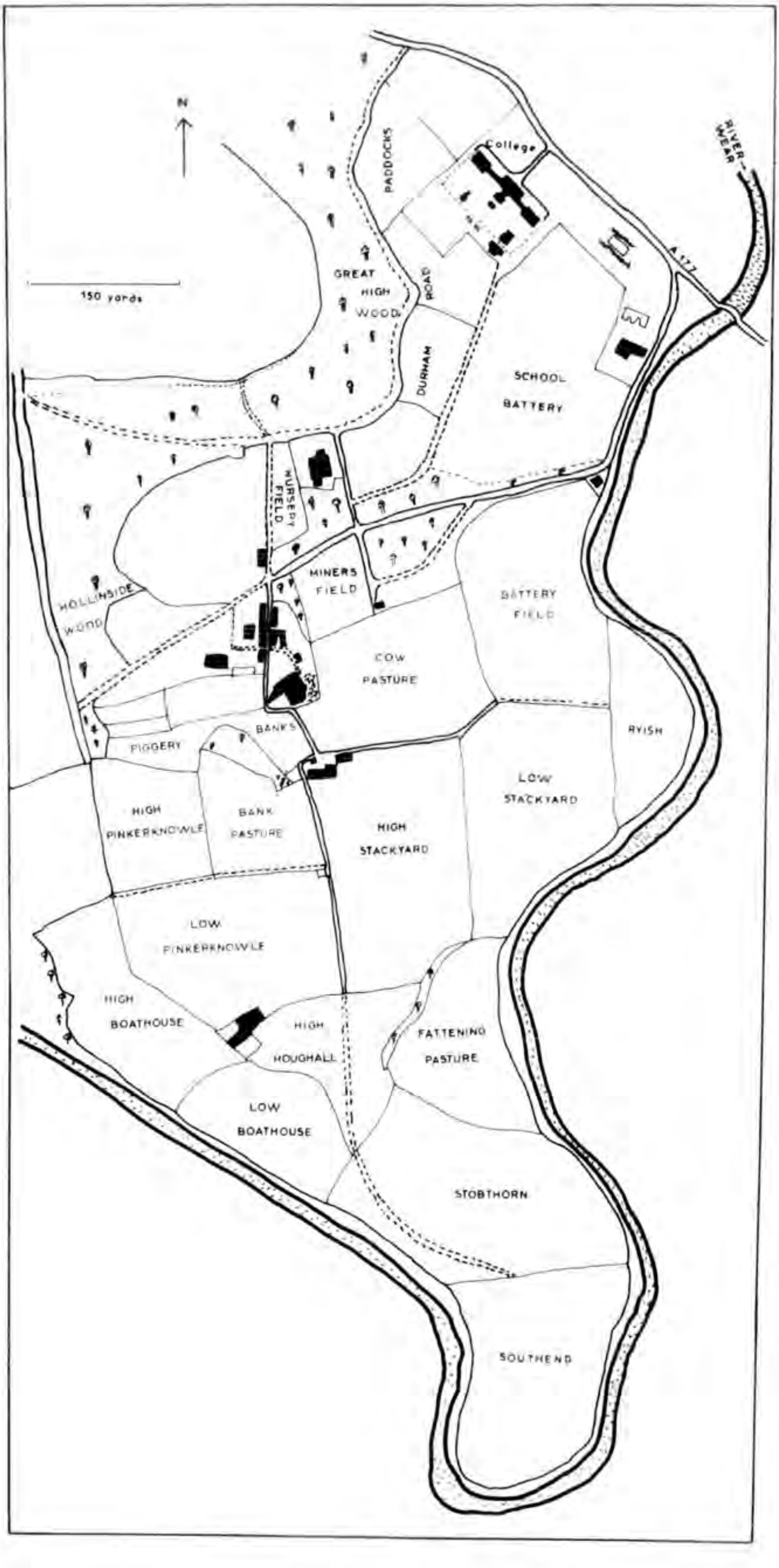
The population studies were carried out during 1964 and 1965 on Houghall Farm, Nat. Grid ref. NZ 280403, one mile south of Durham City. The farm is part of the Durham County School of Agriculture, and is shown in Fig. 19.

Most of the land from the river almost to the Western boundary lies between 100 and 150 feet above sea level. The main area of the farm lies in the shallow river valley, the sides of which rise to over 300 feet in Great High Wood and also in Croxdale Wood on the East.

Work was mainly carried out in the southern half of the Farm where the main dairy herd was kept, namely the fields Cow Pasture, Battery field, Low Stackyard, High Stackyard, Bank Pasture, High Pinkerknowle and Low Pinkerknowle. High Houghall and Piggery Banks are permanent pastures often grazed by sheep or cows, but not on the forward creep grazing system which is used in other fields. In other fields, and also in parts of the fields used for grazing, cereals and rootcrops are grown. After harvest the cattle and sheep are turned on to the stubble and also graze kale.

Fig. 19. Sketch of the study area.

HOUGHALL - THE STUDY AREA



The teaching herd of 20 Ayrshire cows was kept on part of the 33 acres used for experimental work. This small herd was utilised for the Scopeuma studies in the spring of 1965, as they were the only cows out and had all the Scopeuma associated with their grazing area.

The main herd of dairy cows comprised 50 to 60 grazing cows and in calf heifers, mainly Ayrshires, with a smaller number of Friesians. The number grazing at any one time was fairly constant. Fewer fields were used in 1965 because a more efficient grazing technique (the back fence method) was used than in 1964, and the weather was also more favourable for the grass. There was thus no shortage of grass as there had been in 1964.

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b) FIELD STUDIES ON *Scopeuma stercoraria*

1). Introduction.

The seasonal variation in numbers of adult *Scopeuma stercoraria* has been studied by Hammer (1941) and Darwish (1954). Graham-Smith (1916), Larsen and Thomsen (1940), and Coulson (1956) show evidence for a summer decline in numbers of this species. Laurence (1954) made some very interesting contributions to the problem in his studies of larvae in cow pats.

The main purpose of this study was to try to explain the reason for the summer decline in the adult population, as the explanations suggested by Hammer and Darwish were contradictory. Hammer plotted the course of his adult populations using the maximum number found on any cow pat as an index of the population size. Darwish used the results of emergences from cow pats collected in the field as indicators of the span of generations, but did not present any figures for the number of adults in the field.

In order to ascertain the reasons for the seasonal variation in numbers it is necessary to be able to measure the size of the population, both on the dung and in the vegetation away from the dung. Immature flies are not attracted to dung and so form the majority of the *Scopeuma* in the vegetation. During spring 1964, attempts were made to calculate the size of the population by mark and recapture methods. As only two flies were recovered from two experiments the method was abandoned. Various methods of trapping the flies on the dung were also tried, but were unsuccessful.

An attempt was therefore made to count the adults on the cow pats as it was found that if the pats were approached carefully, the numbers of flies could be counted accurately. When the flies first arrive at the pat there is a lot of movement between the fresh dung and the grass around, particularly if the dung has a very liquid consistency. When the dung is in this condition the flies alight and leave almost as soon as they touch the surface. As more flies arrive in the vicinity the numbers actually on the dung increase and in a short time the flies mate and the activity is stabilised and the numbers remain fairly constant. From this point the flies are very easy to count and even the watcher's shadow can pass slowly across the pat and the flies are not disturbed. Any sudden movement, however, will cause the flies to disperse into the grass, but they return to the dung very quickly.

The flies in the grass around the pat are as much a part of the cow pat community as those actually on the dung because of the interchange of flies between the dung and the grass.

Most of the males fly to the dung and are there before the females which tend to arrive by crawling over the vegetation rather than by flying. As the females come towards the dung they have to pass through a circle of males waiting around the dung. They are usually mated here and then pass onto the pat with their mate. If the female gets through to the dung unmolested, then she is invariably mated by one of the males waiting on the dung. Some males waiting on the dung may not be successful in finding a female and so they leave the dung and wait on the grass.

When one or more males try to interpose themselves between a mating couple, males on the grass are attracted to fly onto the dung. As more males join in the fray, more are attracted from the grass. The mating pair may succeed in breaking away from the others, or the original male may be forced off by another which replaces him. The female may be killed by being forced into the liquid dung, and the male may die from exhaustion.

The zone of influence of a particular pat varies according to its consistency and the climatic conditions. In still conditions the flies may be spread around the pat up to a radius of about a yard from the centre of the pat. When there is any appreciable wind there is usually a concentration of males up wind of the pat. These flies have overshot the pat and presumably partly lost the smell of the dung, so they remain where they are.

For the purposes of measuring the population of adult Scopeuma I first tried to count the numbers of flies on and around twenty pats, and then determine what proportion of the total pats in the study area that this represented at each count. Thus, by estimating the area of field containing these twenty pats and, by estimating the total area of field enclosing all available pats, the total population of Scopeuma should be calculable. For example, if there were 200 flies on 20 pats occupying 1/10 of the total area, the population would be 2,000.

This method was soon abandoned for several reasons. Choosing an area at random in which to count the flies did not take into account the behaviour of the flies. The erroneous assumptions were therefore made that the pats were dropped at random all over the field and that the flies had a normal, or poisson, distribution on the pats. As the flies aggregate on certain pats this area method would give an overestimate or an underestimate of the population. It was impracticable to cover the whole field to ascertain the nature of the dispersion of the flies at the time that the count was being made. The final assumption in this area method was that the numbers of Scopeuma in a particular field constituted a discrete population and that if emigration and immigration occurred they would be equal.

After several days of experimenting with different sampling methods I decided that it would be impossible to calculate the size of the population of Scopeuma because there was no discernible limit to the range of the population. The immature flies could not be sampled in the same way as the mature flies and their population could not be estimated by the usual methods. Marking techniques were impracticable for the immature flies because they were damaged by sweep - netting and could not be baited by traps. The distribution of immature flies in the field did not seem to conform to any particular pattern and so area methods were ruled out. Any long term experiments on population longevity could be upset by the movement of the cows out of the field into another, and also by the spraying or cutting of the grass, or by ploughing.

2). Counting methods.

I decided to study adult Scopeuma in the field by using two basic methods: (1) to obtain an index of the variation in numbers by counting the flies on and around 40 pats which had an appreciable number of flies on and, (2) to record the ages and numbers of flies away from the dung by standard sweep - netting in the vegetation. Other methods were also tried to supplement these studies, but more explanation of the two main methods is needed first.

As the electric fence was moved twice a day, a long strip of fresh grass, 5 - 15 yards wide, was made available to the cows each time. The cows spent most of their time feeding in this strip and so the greatest number of fresh pats were present here and attracted the greatest number of *Scopeuma*. By walking carefully along the new strip of grass it was possible to count the number of males and females on and around the pats which had most flies on. It was usually possible to find 40 pats in this strip with large numbers of *Scopeuma*. When there were fewer than 40 pats in this strip a search had to be made in the rest of the field. By watching the movements of the cows whilst I was counting, I could see where the fresh pats would be in the rest of the field.

40 pats was found to be the optimum number on which to count *Scopeuma*, as this could be managed in an hour with 5 - 10 minutes to spare for sweeping in the grass and recording temperatures etc. ready for the next count. Patterns of

diurnal activity for each day could be discerned by counting the flies each hour. From these figures an index could be obtained of the population sizes at different times of the year. Before each count commenced ground and air temperatures, and other climatic conditions were recorded. When, later in the year, the cows had regular periods of rest followed by mass defaecation, there was a corresponding increase in the numbers of *Scopeuma*. The behaviour of the cows was therefore noted, mainly the proportion standing.

In spring the cows did not show any marked tendency to move around the field away from the fresh strip of grass. Each succeeding count was therefore usually made in the same area, as fresh pats were being constantly dropped in the fresh strip of grass. Later in the year the cows spend much less time eating the fresh grass and they move to another part of the field to lie down. The cows may lie down together, in two or three groups, or occasionally the herd is spread out over the whole field. When the cows are grazing the fresh grass or starting to lie down for the first time after the morning milking, the counting is done mainly in the fresh strip. If the cows are still lying down at the start of the next count, the area searched will be practically the same as on the previous count, as no new pats will have been dropped. When the cows have finished ruminating they tend to rise almost in unison and defaecate before they move away to start grazing again. The parts of the field where the cows were lying down then become the areas of attraction for Scopeuma, and must be searched first to find the largest numbers of these flies.

Some cows, after ruminating, walk to the drinking trough before grazing and usually defaecate whilst drinking or just before moving away from the trough. In very hot weather a large proportion of the herd usually goes to the trough to drink before grazing again after rumination. On these occasions, the best method for counting Scopeuma is to search the areas where the cows were lying down and, when there are no cows either at the trough or heading for it, count the flies around the trough. The reason for this is that there are, at these times, extremely large numbers of Scopeuma attracted to the large amount of dung dropped around the trough. One cow coming to drink, or just leaving the trough, can scatter the flies by walking over them or, whilst standing, by shaking its head and flicking its tail. To obtain an accurate number of flies around the trough it is therefore necessary to do the counting when there is no risk of disturbance. This also allows the flies time to settle down on the dung so that they can be more easily counted.

The problem of disturbance is very much less in the open field because the flies are not upset by the usually placid and deliberate movements of the cows when grazing. If the flies on a particular pat might be disturbed by an oncoming cow , it is possible to position oneself between the pat and the cow and, if necessary, to fend off the cow with one hand, whilst counting. If the cow is intent on licking one's back or even rubbing its head, careful balancing can maintain a position which does not disturb the flies.

Cows may defaecate whilst moving and the resulting pat is a string of smaller pieces of dung, separated by intervals of several inches or feet, depending on the speed at which the cow was moving. Each piece of dung acts like a separate pat, but with a smaller number of flies. These strings of dung were dealt with by carefully moving along the pieces of dung, counting the numbers of males and females on and around each piece, and recording the total numbers in these categories for the whole 'pat'. The relative attracting powers of strung-out pats and pats dropped in one piece will be discussed later. If the dung is shot out at defaecation on a horizontal trajectory, a strung-out pat results, but the pieces are usually fairly close together.

The maximum period of activity of Scopeuma, particularly in summer, was during the one or two hours after the cows had been taken away for the afternoon milking (see section 3/.).

The cows had usually had a long lie down prior to this and as they were all roused together, nearly 50 pats would be dropped at the same time. Most of the pats would be where the cows had been lying, some would be at the water trough and some at the gate where the cows congregated before being taken for milking. There were then three main areas of high numbers of <u>Scopeuma</u> on dung. If 40 pats could not be found in these areas a search was made over the rest of the field. The areas between the trough and the gate, and between either of these and wherever the cows had been lying down were particularly searched for pats. As no fresh dung would be dropped for the next 2 - 3 hours, studies on ageing of the dung in relation to its attracting power could be made.

Flies were not counted on freshly dropped pats because the considerable movement of the flies approaching fresh dung made accurate counting extremely difficult. The activity of the flies on a fresh pat stabilises after a while and so a fresh pat can be included in a count when its flies have settled down. By systematically covering an area where I knew there were a lot of pats with high numbers of <u>Scopeuma</u>, no pat was counted twice. If, for any reason, there was the slightest doubt whether a pat had been included in a count, I disregarded the pat. When the pats are spread over a very wide area it is possible to cover that area systematically by sighting on a point in the boundary of the field, such as a fence post, tree or part of a hedge, and walking straight towards it. When this point has been reached a right angle turn is made for about 5 - 10 yards and the walk continues on a course parallel to the previous one, but in the opposite direction. Pats were only counted to one side of the walk to avoid possible recounts. Whilst the cows were lying down they could also be used as markers for fixing a systematic search. If one or two moved the positions of the adjacent cows would indicate this. This method was reliable as I knew all the cows individually.

Because of the aggregation and localisation shown by the flies it was necessary to adopt this rather subjective approach to counting, so that error would be as constant as possible. 40 pats with reasonable numbers of flies gave a good index of the population, as even in the highest population periods the vast majority of flies were on fewer than 40 pats. The flies counted on 40 pats probably comprised about 90% of the total number of flies in the field. In a herd of about 50 cows, not every pat dropped will attract flies, either because of the nature of the dung or the place where it was dropped.

After 40 pats had been counted I returned to the recording instruments, making observations on the pats to see how the flies were distributed, and on the cow behaviour to see where the next count should be made. There were nearly always a few pats with one or two males or the occasional mating flies, but generally the majority of flies had been included in the 40 pats.

During very low populations of Scopeuma, 40 pats often included every fly which could be found on the dung in that field. The index for the population at low levels would thus be an almost absolute number of the flies at that time whereas, at extremely high population levels there would be several pats remaining after 40 pats with the highest numbers had been counted. The index would then be an underestimate in comparison with that for low populations.

It must be remembered that these counts were only done in the field where the main dairy herd was at the time. There was also a smaller dairy herd, small groups of calves and sheep, all with their smaller populations of Scopeuma. No attempt was made to include these flies because of the extreme difficulty in counting small numbers of flies over a large area. At the start of the season in 1965 the experimental dairy herd was put put to graze before the main herd, and it immediately attracted fairly large numbers of Scopeuma. Counts were made on these pats as described for the main herd, until the main herd was put out to graze, after which counts were made exclusively on the pats of this herd.

The presence of flies away from the main herd means that at times of low numbers, when 40 pats would include all the flies on the dung in the field being studied, there are always some Scopeuma on pats in other fields. There might also be larger numbers of Scopeuma on other farms in the area, and at high population times at Houghall there are large numbers of flies in fields other than that occupied by the main herd. The totals on 40 pats can therefore only be used as an index of the way in which the population is varying throughout the year, and not as actual sizes of the population. As I have indicated before, the index cannot be expected to be equally representative of the population at all levels of abundance.

Diurnal activity was studied in detail by using the figures obtained from successive counts of flies on 40 pats. Each count was started an hour after the previous count unless something happened to delay it. If this did happen the fact was always recorded and subsequent counts were retimed accordingly.

I had planned to continue observations on individual pats, as described on P. 86 , throughout the year at different population levels and in different weather conditions.

Continuous bad weather in 1965 made this impossible, as the counts and sweep-netting had to take priority. These were particularly important because the weather in 1965 was so different from that in 1964.

I was not solely concerned with Scopeuma stercoraria, but also with S. squalida and S. suilla. These other two species were never very common and for both, the numbers of males and females were recorded when they were seen. This was more difficult than for S. stercoraria because they showed much less sexual dimorphism. I also included in my counting any of the following species: Mesembrina meridiana L, Dasyphora cyanella Mg., Rhingia campestris Mg., and Cryptolucilia caesarion Mg., as these flies were easily identifiable and were never very numerous. Little can be done with the results other than to record their maximum numbers for each day, to examine diurnal activity and distribution over the field. Dasyphora and Cryptolucilia were fairly constant in their numbers on pats from hour to hour and their diurnal activity was studied in a little detail. Mesembrina and Rhingia, on the other hand, are extremely mobile and a total of these two species on 40 pats could well include flies counted more than once. Seasonal occurrence and maximum numbers per pat were the only items of information which could be reliably obtained. These flies were occasionally cought by sweep-netting in grassland and in woodland, and they were recorded when caught.

3). The length of time adult Scopeuma spend on pats:

Counting the number of flies on and around cow pats is only valid if, for the period of counting at least, the flies associated with each pat remain there and do not fly away from pat to pat. When there are large numbers of Scopeuma and the pats are close together, it is possible to stand and see the numbers remain constant on several pats, each with over 100 flies.

Male Scopeuma are attracted to a fresh pat by its smell, which will also attract females to come to mate and oviposit. The longer a male remains on a fresh pat the greater are his chances of mating. If females are slow in coming to the pat, or if there are too many males, the males which have not found a female will attempt to mate with each other and with other flies, from Sepsids to Myiospila F., and Dasyphora. Records in the literature (Hammer 1941, Darwish 1954) of Scopeuma waiting on the dung to eat other flies, and even trying to eat Mesembrina, are probably misinterpretations of the behaviour of male Scopeuma. If the sex ratio of Scopeuma on a particular pat is near to unity all the males stand at least one chance of mating, and other flies can come on to the dung unmolested.

If a male mates successfully he is automatically precluded from leaving the pat for at least half an hour, since mating lasts half an hour or longer. If the female is going to lay eggs after mating, as is usually the case, the male then holds on around her waist with his forelegs and walks around with her using his midlegs to ward off other males. Oviposition usually takes several minutes because the female walks around inspecting the dung, and may only lay one or two eggs before moving on, looking for another suitable site (cf. Foster 1967).

Pats which were counted hour after hour had approximately constant numbers of Scopeuma. Detailed watches on individual pats, recording the numbers pesent at regular intervals, were necessary to determine the constancy of Scopeuma numbers.

The results from 3 pats studied in this way provided the information required. For the first 5 minutes after each pat was dropped, the numbers of males and females on the dung and in the grass around were counted at one minute intervals (no count was made at the 4th minute on pat B). After this counts were made at 5 minute intervals.

Counts were made on pat A. at 5 minute intervals for the first 2 hours after it was dropped, and at less regular intervals for the remaining 135 minutes until the cows returned and scared off the flies. On pat B. counts were made at 5 minute intervals for the first 50 minutes and at intervals for the remaining 130 minutes before the flies were scared off by returning cows. Counts were made on pat C. for the first 45 minutes at 5 minute intervals and then less regularly for the remaining 75 minutes when rain forced the abandonment of the counting. The counts are shown in Fig. 20. The maximum total number of flies were present on the pats after the following times:

Pat A. 15 minutes, Pat B. 25 minutes, Pat C. 75 minutes.

The highest number of males and females were present on each pat after the following times:

Pat. A. Males - 20 minutes, Females - 25 minutes

Pat. B. Males -40 minutes, Females - 110 minutes

Pat. C. Males - 75 minutes, Females - 75 minutes

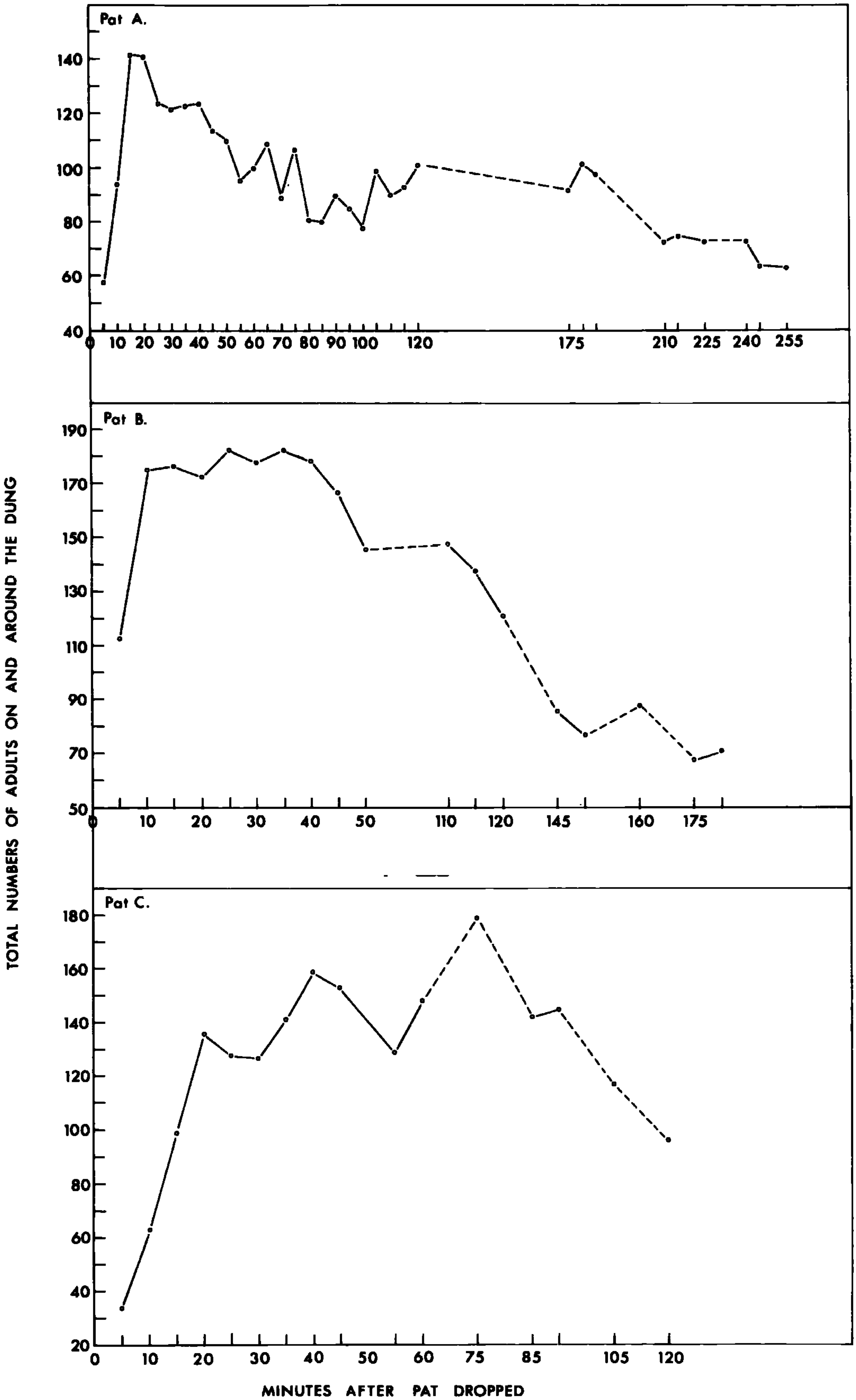
The sex ratios on the pats came nearest to unity at the times indicated below:

Pat A. - 245 minutes, Pat B. - 175 minutes, Pat C. - 60 minutes

The time scale for Pat A. (Fig. 20) is more compressed than for the other two pats. It can be seen that, even if

Fig. 20. To show the numbers of *Scopeuma stercoraria* on three pats from the time they were dropped; until the flies were scared off.

TIME SPENT ON COW PATS BY *Scopeuma stercoraria*



all the pats were dropped at the same time, in the succeeding count the numbers of Scopeuma on 40 pats should represent a good index of the population. Pats were not normally included in a count until 10-20 minutes after being dropped. If no further pats were dropped, and a further count was to be carried out on the same 40 pats, the index should still be true as some pats would have increasing numbers (e.g. pat C.) while others would have decreasing numbers (pats A. and B.). In effect, the pats are never dropped completely in unison, even when the cows are being taken in for milking, and there are nearly always older pats with large numbers of flies.

Fig. 20. also shows the variations in numbers over the first hour. During the first 10-20 minutes there is a rapid rise in numbers. This may then be followed by a gradual increase or decrease in numbers (pats C. and A.) or the numbers may remain constant (pat B.). The early rapid rise may be seen by comparing the numbers in the first 10 or 15 minutes for the three pats:

Pat A. Dropped 12.01 P.M. G.M.T. Ground temperature 20.5°C Sunny periods, moderate West wind, Dung watery.

Mins. after pat dropped	Dung Males	Dung Females	Grass Males	Grass Females
1			4	1
2			30	6
3	1	1	38	8
4	5	2	39	8
5	5	1	43	9
10	17	3	61	13

Pat B. Dropped 1.07 P.M. G.M.T. Ground temperature 19.5°C

Sunny periods, moderate West wind, Dung very watery.

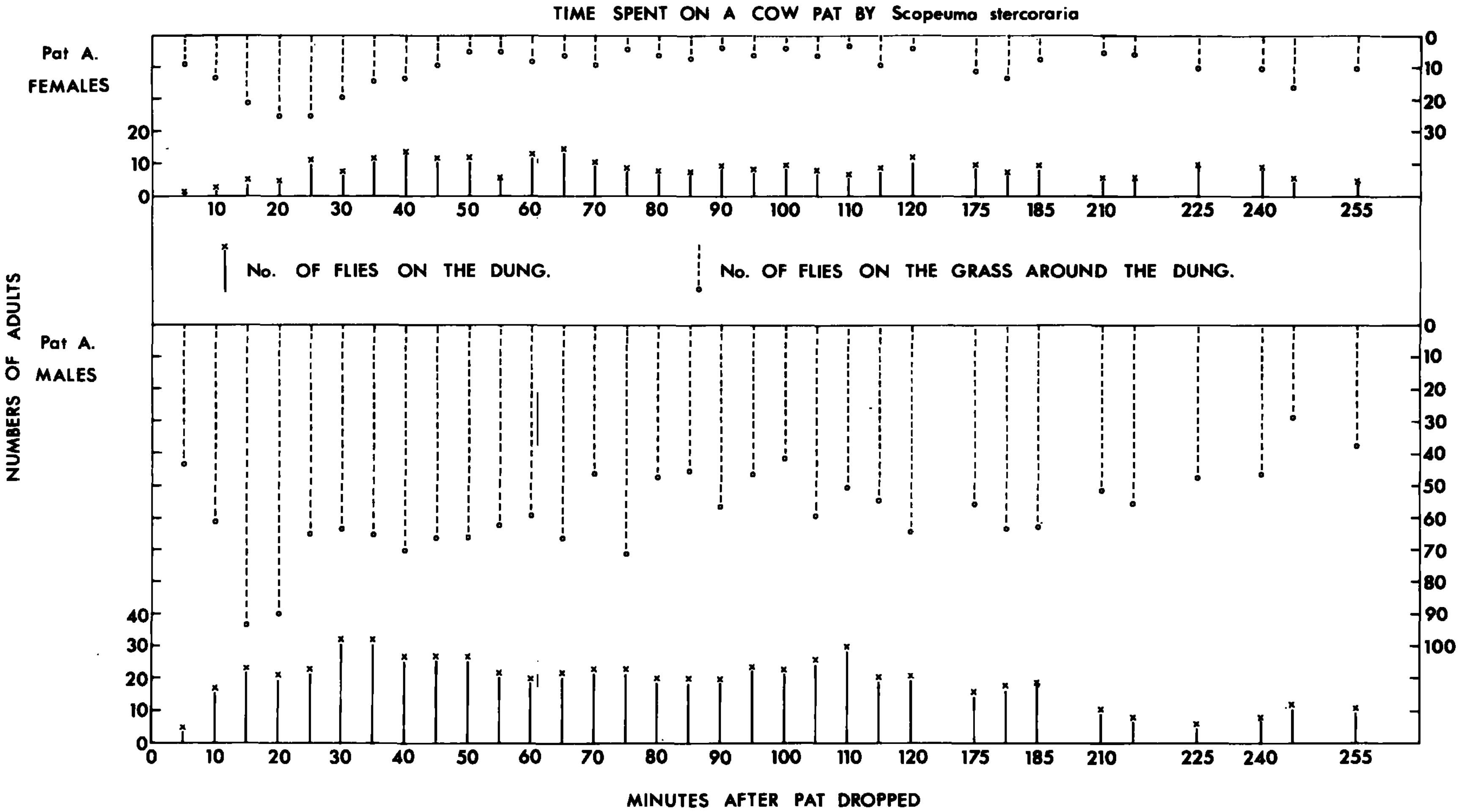
Mins. after pat dropped	Dung Males	Dung Females	Grass Males	Grass Females
1	1	0	75	4
2	1	0	101	7
3	2	0	95	6
4				
5	9	2	91	11
10	10	3	143	19

Pat C. Dropped 1.09 P.M. G.M.T. Ground temperature 16.5°C

Cloudy, Light West wind. Dung solid and rather dry.

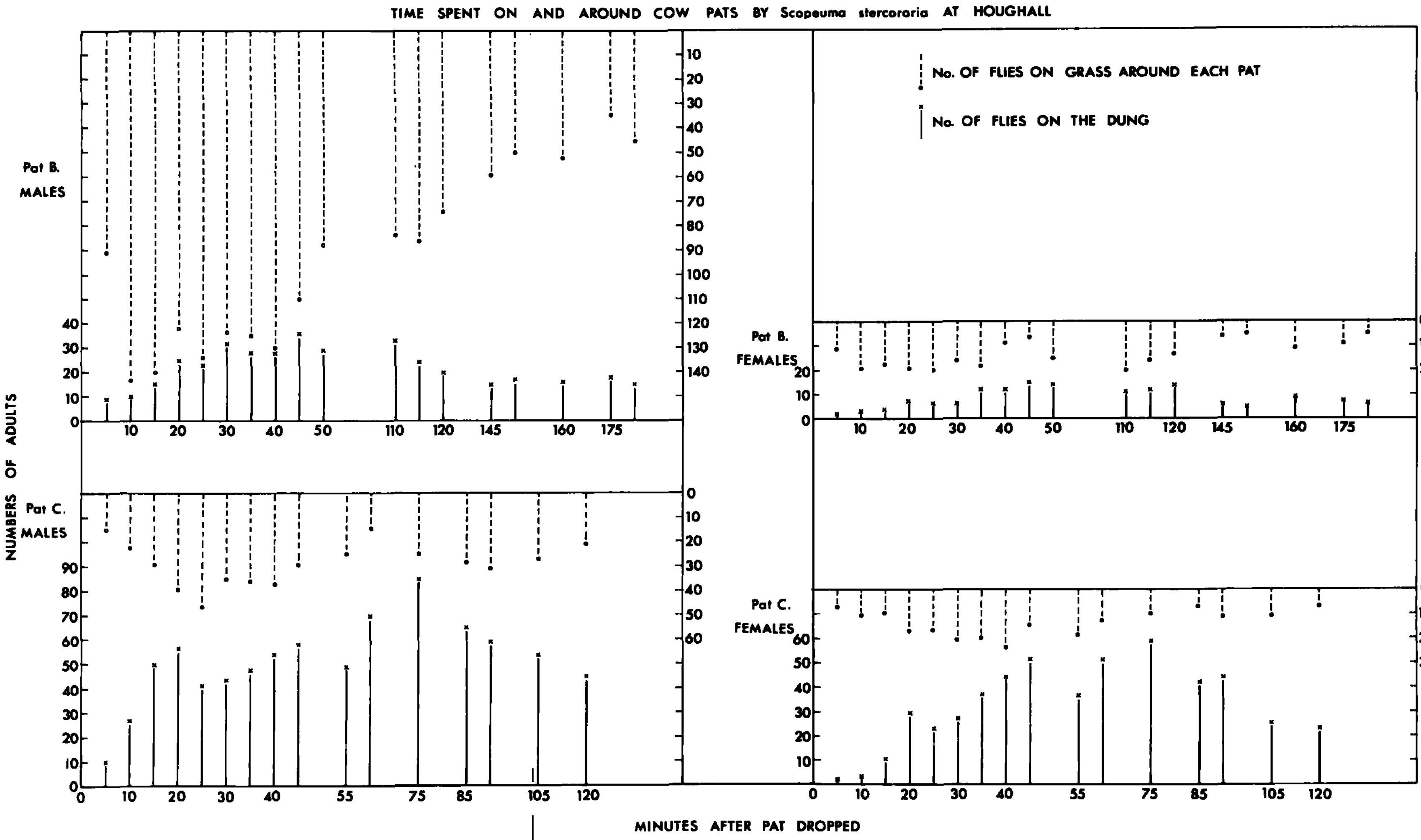
Mins. after pat dropped	Dung Males	Dung Females	Grass Males	Grass Females
1			0	1
2	1	0	2	1
3	4	0	3	3
4	9	3	9	4
5	10	2	15	7
10	27	3	22	11
15	50	10	29	10

Fig. 21. To show the numbers of male and female *Scopeuma stercoraria* on and around a cow pat at intervals after the pat was dropped.



TIME SPENT ON A COW PAT BY Scopeuma stercoraria
Pat A. FEMALES
Pat A. MALES
NUMBERS OF ADULTS
No. OF FLIES ON THE DUNG.
No. OF FLIES ON THE GRASS AROUND THE DUNG.
MINUTES AFTER PAT DROPPED

Fig. 22. To show the numbers of male and female *Scopeuma stercoraria* on and around cow pats at intervals after the pats were dropped.


TIME SPENT ON AND AROUND COW PATS BY Scopeuma stercoraria AT HOUGHALL
No. OF FLIES ON GRASS AROUND EACH PAT
No. OF FLIES ON THE DUNG
Pat B. MALES
Pat C. MALES
Pat B. FEMALES
Pat C. FEMALES
NUMBERS OF ADULTS
MINUTES AFTER PAT DROPPED

Figs. 21. and 22. show separate analysis of males and females on the dung and in the grass around. These figs. show an interesting aspect of the behaviour of females with regard to the relative numbers on the grass and on the dung. For some time after the pats were dropped the numbers of females in the grass around the dung were higher than those actually on the dung (10 minutes for pat C. and 35 minutes for each of pats A. and B.). The numbers of females on the dung then exceeded those on the grass. This excess of females on the dung lasted for 85 minutes on pat A., 100 minutes on pat C. but was more variable on patB. The reason for this behaviour is that females have to pass many male Scopeuma waiting on the grass, where mating usually takes place. As mating may take up to 30 minutes or more, it is often some time after a pat has been dropped before a female can reach the dung in order to lay. Pats A. and B. were both of very watery dung and at every count on these two pats the number of males in the grass was considerably greater than the number on the dung. Pat C. on the other hand was solid and rather dry, and after 5 minutes there were more males on the dung than on the grass. This meant that it was easier for the females to reach the dung quickly on pat C. than for either of the other two pats.

Very watery dung always had the effect of keeping an excess of males on the grass. However, whatever the consistency of the dung, the numbers of males remained relatively constant throughout the counts, whether they were on the grass or on the dung. This behaviour of males and females was noted throughout the two years, although no other detailed counts were made of individual pats over long periods as described above. It would be useful to do this at different times of day, in different weather conditions, seasons and also on pats of different consistencies.

4) Catching adult *Scopeuma*

In order to obtain comparable results of *Scopeuma* caught in vegetation I first tried to standardise the sweep-netting technique by sweeping for 5 minutes. Different types of vegetation offered different degrees of resistance to the net and so comparisons between sweeps could not easily be made. I therefore decided that each sample should be from 200 sweeps, each sweep being 3 - 4 feet through the vegetation from one side to the other. If the vegetation offered much resistance to the net, it simply took longer to do the 200 sweeps than if there was little resistance, but the volume of vegetation sampled would be approximately the same.

The sweeping was always done as quickly as possible because *Scopeuma* tends to fly in front of a moving object for a few yards and then resettle. By moving quickly it was possible to catch the flies either before they started to fly off, or to catch them soon after resettling because they do not usually fly off again immediately. If the wind caused increased vegetation resistance to the net it also increased the reluctance of *Scopeuma* to fly away, so that the reduced speed of sweeping did not catch fewer flies. 200 sweeps was the figure decided because if the flies showed anything other than a random distribution, a strip of about 200 yards by 3 - 4 feet should catch any pockets of flies to compensate for patches where there were no flies. The flies caught were all killed and kept in a deep-freeze refrigerator at about -20°C for dissection to determine the age-structures of the population in the vegetation.

Some flies were also taken off cow pats for dissection, eith by putting various traps over the pat and then extracting all the flies, or by pootering the flies directly off the pats. If both of these methods failed flies were scared into the grass around the dung and then swept rapidly. These were not maintained as regular techniques because of the difficulties of catching the flies off dung in any numbers. Flies taken off different cow pats at the same time did not have the same age-structures. For example, on 6th May 1964, one pat had 2.3% immature, 7.0% gravid for the first time, and 88.4% uniparous females. 2.3% of females were castrated. On a nearby pat there were 8.2% gravid for the first time, 80.8% uniparous, 8.2% 2-parous and 2.8% castrated females.

The disadvantage of dissecting flies caught on dung is that the majority of the females are fully gravid, and as explained on P. 50 , it is not often possible to say with any certainty which gonotrophic cycle they are in. The results obtained from sweep-netting are however, comparable, giving information on sex ratios and numbers of females in all age groups.

I had to decide the area of vegetation to be sampled by sweeping, having regard to wind direction, the previous movement of the cows and the nature of the vegetation itself. Between counts of flies on dung sweeps were usually made in the long ungrazed grass on the other side of the electric fence from the cows. Sweeps were also made in Great High Wood, which bordered the north west edge of the farm (see Fig. 19.), because this was the largest area of woodland nearby. Other areas were sampled by sweep-netting, to see if Scopeuma showed any habitat preference.

5). Other methods of studying *Scopeuma* populations.

During 1964, the counting of flies on cow pats, and sweep-netting methods were supplemented by two other techniques. One was to study the flies in small woodland areas within the farm boundaries and the other was to study the pupal mortality in the cow pats.

The woodland study involved the use of detergent traps on the ground placed at 5 yard intervals, in a transect in one wood, and in a grid formation in the other. The traps were emptied twice a week, and the flies preserved in 95% alcohol.

This method was eventually abandoned because the effort involved in collecting the flies was not justified by the very small number of *Scopeuma* caught. The main reason for this was that the vegetation in the woods grew extremely quickly. The traps catch flying insects which accidentally drop in but *Scopeuma* rarely flies other than when disturbed, so the taller the vegetation, the less likely it is to drop in.

To study pupal mortality in dung ten fresh cow pats were collected from the field each week. Pats were only taken if they had *Scopeuma* eggs, and were kept under conditions designed to allow fly emergence.

This method was abandoned because rooks attacked and dispersed the pats. Rooks were also observed to attack pats in the field as Elton (1966) observed, even very fresh ones which could not have contained any larvae or worms. On some occasions every pat in the field was attacked and spread out.

It is difficult to know what effect this has on the Scopeuma larval populations. Although a cow pat can lose its attraction to Scopeuma in about an hour on a very hot dry day, by early formation of a crust, this attraction can be restored by damaging or removing the crust, exposing the more liquid dung beneath. The damage to pats by rooks can therefore have two possible effects, depending on the extent of the damage. If a fresh pat is completely spread around it undergoes very rapid and complete dessication, thus preventing any further development of larvae. If a pat of the same age was only slightly damaged it would enable newly hatched larvae to enter the liquid dung and so complete their development. Slight damage to a pat also attracts mature adult Scopeuma to oviposit on the exposed liquid dung. If the pat had not been damaged, no further eggs would have been laid because of the undisturbed crust.

One important fact emerged from the collection of these cow pats which lent support to my criticism of the hypothesis suggested by Darwish (1954). Darwish stated that oviposition by *Scopeuma* did not take place during the hot summer months, since he found no larvae in the pats which he collected. At Houghall in 1964 the numbers of *Scopeuma* were very low in the summer months but I still managed to collect 10 pats each week without difficulty which had large numbers of eggs laid on them. The eggs may not have hatched or the newly-hatched larvae may have died because they were unable to penetrate the crust of the pat. The fact remains, however, that eggs were laid throughout the season irrespective of the temperature or the size of the population. Probably there were very few, if any, larvae or pupae in the pats which I collected, but high mortality in the early stages, and not absence of oviposition, was responsible.

c) SEASONAL VARIATIONS IN NUMBERS OF *Scopeuma* ON DUNG

1). Methods of analysis of counts.

The main difficulty in analysis of numbers counted on dung was due to the fact that males and females spent different lengths of time on the dung. Females came on to the dung, and after mating and oviposition lasting up to about 45 minutes they left the dung for the vegetation. They remained in the vegetation for about a week while they matured the next batch of eggs. From the results of dissection only a negligible proportion of females came on to the dung for mating before they were gravid. When, however, they were gravid they came back to the dung for a period lasting from a few minutes to nearly an hour whilst they oviposited, where upon they left the dung once again. The length of time the females spent on the dung depended upon whether or not they were mated before they could oviposit. If they were not mated at that visit they laid their eggs in a few minutes and then left the dung.

Males, on the other hand would stay on the same pat for up to 3 hours and possibly longer. When the pat had lost its attraction, or when the number of females was declining rapidly, the males would seek a fresh pat. Whereas females probably spend a maximum period of about one hour per week on the dung, males are capable of spending at least two successive day on the dung, and there seems no reason why they should not spend longer. Males kept in the laboratory, whether caught in the field or reared in the laboratory, remained on the dung in the cages for hours day after day and their low food requirements (P.34 .) means that they can obtain their food easily by eating other insects which come to the dung. The greater amount of food required by the females to mature their eggs can only be obtained in vegetation.

This difference in behaviour between the sexes means that in successive hourly counts, the males are mainly the same individuals throughout the day, but the females will be different. Assuming that the mean duration of stay on the dung for females is less than one hour, the female counts for each hour are summed for any day. This will be the total number of females visiting the pats counted, but this total is probably a slight underestimate as very few females probably stay for a full hour. In order to obtain some index of the number of males and females visiting the pats each day, the total number of females counted throughout the day is added to the maximum total number of males counted in any hour during the day.

The next problem of presentation was the length of interval between the points on the graph. It was eventually decided to have a 4-day period because of the length of the gonotrophic cycle in females. To have had a shorter interval would have meant too many periods when no counts were made because of bad weather. A longer interval would have included females more than once, since with an approximately weekly ovarian cycle any period of more than 4 days would include females which might be counted right at the beginning of the period and again at the end of the period as they returned to lay the next batch of eggs, or possibly for mating.

Because the number of hourly counts made varied, it was necessary to find some means of standardising the figures. This was done by expressing the figures as the mean daily total for each 4 day period. The maximum number of males on 40 pats for each day's count on each 4 day period were added to the sum of the females counted in that period. This total was then divided by the number of days on which counts were made, to give the mean daily population index.

It was hoped, by this mean daily figure, to obtain a comparable result for males and females. It is not suggested that the males counted at the time of their maximum activity were the total number of males out on each day. As there is usually a gradual increase in the numbers of males, reaching a maximum in the early afternoon, there are obviously many males which come on the dung later than others. The maximum number of males is probably an underestimate because it is probable that the males spend less than 1 whole day on the dung and then leave for the vegetation. Exposure on the cow pats for several hours, mating, and fighting, must impose a strain. It was not possible to follow the movements of the mature males after they had left a pat. The index of population as described above is presented in Fig. 23 for 1964 and 1965.

The population variations of males and females were then analysed separately. The male index used was the mean daily maximum number of males on 40 pats for each 4-day period. The index for females was the mean number per 40 pat count for each 4-day period.

A final analysis was carried out, namely the mean log of the maximum numbers of males and females counted on 40 pats on each day over 4-day periods. The graphs obtained by this method are presented in Fig. 26 where it can be seen that the pattern obtained for the variations in numbers is very similar to that obtained by the method used in Fig. 23. This has an important implication for the work involved in counting the flies in the field. If the counts could be reduced to the time when the maximum number of flies is likely to occur, there would be more time for other types of field work. This would provide an easier method for plotting the course of the total population throughout the year, but would not provide a means of studying the female component of the population.

2). Graphs of the population changes:

The change in the index of numbers of adult Scopeuma at Houghall in 1964 and 1965 are shown in Fig. 23. It can be seen from the graph that the studies in 1964 began much later than in 1965 and also that there was an interval of 18 days in August when no counts were made.

Studies had begun at Houghall before the first point on the graph for 1964, but the 16th May was the first date on which the counting method produced any results. Before this date there had been very large numbers of Scopeuma which were obviously part of the spring peak of numbers of unknown size.

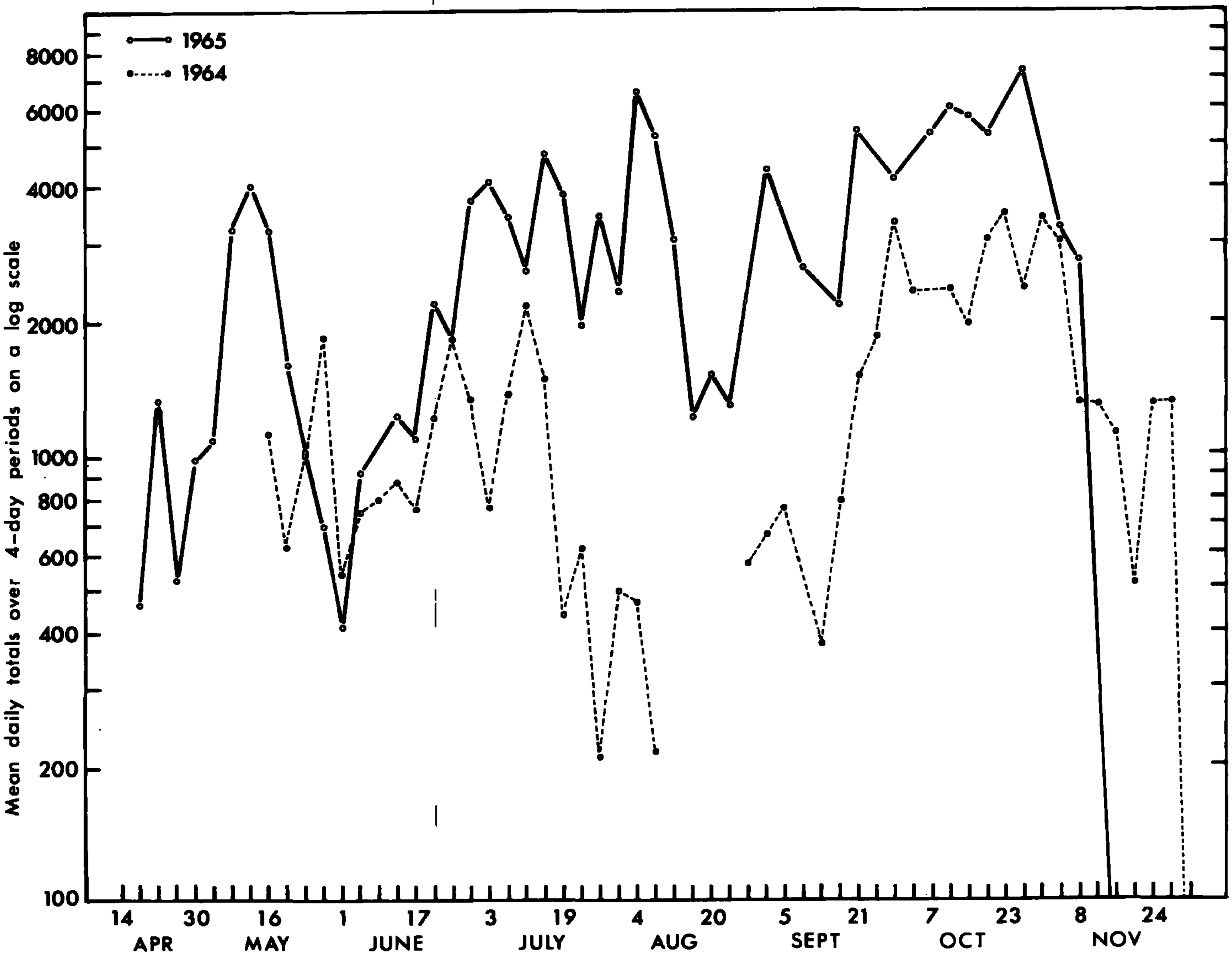
The weather from the last week in May onwards was mainly sunny, warm and windy. Rain was infrequent but came in concentrated periods. The dung, consequently, quickly formed a crust on the surface and soon lost its attraction to Scopeuma. The adult population remained at a fairly low level until after 17th June when it rose rapidly, reaching a peak in the 4-day period ending 25th June. The mean daily total for this period was 1,816 - 600 higher than the previous

Fig. 23. Index of seasonal variation of male and female Scopeuma stercoraria numbers, 1964 and 1965.

Index = mean daily maximum number of males plus mean daily sum of females on 40 pats, calculated for each 4-day period.

For details see text.

SEASONAL VARIATIONS IN *Scopeuma stercoraria* NUMBERS AT HOUGHALL



period and 500 higher than the next. The highest number counted on 40 pats in this period was 2,244 flies.

The population then fell rapidly until the first week in July. After this it rose sharply to a level slightly higher than the June peak having a mean daily total of 2,169 during the period ending 11th July. The weather remained, for the most part, very warm, with temperatures frequently over 20°C. After the July peak the population dropped steadily, reaching its lowest level by 27th July. After a slight rise the population dropped again in the first week in August.

When counts were restarted in the last week of August the flies were numerous and increasing steadily. There was a sudden drop in numbers for about a week, after which the flies increased to the highest numbers recorded in the year. The numbers then remained very high for over a month, producing the autumn peak.

During Novemner the flies were less abundant than in October, but they were still quite numerous. There was no sign that the population was undergoing any serious decline prior to winter although the temperatures were very rarely above 10°C. The season's flies were brought to an abrupt end on 27th November when there was continuous rain which later turned to snow. The evening was clear and there was a frost. Snow, frost, and ice were still present on 28th

November although it was sunny. No Scopeuma could be found after this date, until early spring of 1965. A few adults survived part or the whole of the 1964-65 winter as some were caught in the detergent traps maintained by Edge among a lot of dead bracken, where they perhaps found shelter from the sudden drop in temperature.

In the year as a whole, the Scopeuma populations showed a spring peak, an early summer peak, a late summer trough and an autumn peak. The lack of rain during the year resulted in a shortage of grass for the cows which were given free range over whole fields as strip grazing was impracticable under these conditions. The consequences to the Scopeuma were twofold. The dung was being dropped over wide areas, which made it more difficult to find. The warm dry weather in the summer caused the early formation of a crust which reduced the time during which the dung was attractive to Scopeuma and also prevented the newly hatched larvae from entering the dung.

Although the numbers of Scopeuma were low during the summer, it was observed that numerous eggs were being laid all the time. There was, however, a very high mortality of newly hatched larvae. It is probable that only pats dropped in shade or near the drinking trough, where they would be splashed with water, could provide a refuge for the larvae.

In 1965 the first mature adults were seen on sheep dung in late March, but it was not until mid-April that they were present in any numbers. They first appeared in large numbers when the small experimental herd of dairy cows was put out to graze. These cows were out on 13 April and it was not until 5 May that the main dairy herd was put out to graze, whereupon most of the flies became associated with this herd. There then began a sudden rise in numbers, reaching a peak about the middle of May.

The drop in numbers after the spring peak was about as rapid as the rise prior to the peak. Heavy rain and a drop in temperature probably helped to accelerate the decline in numbers.

The peak in the first week in August was followed by a drop in numbers. This was mainly due to the fact that the wind changed direction and blew the wrong way for the flies to be attracted to the dung area.

High Boathouse had a hedge along its northern border and a wood, leading down to the river, on its western boundary. While the cows were in this field there were very large numbers of Muscids both on the dung and pestering the cows. Dasyphora, Mesembrina and Cryptolucilia were also very common on the dung. The Muscids were more numerous on dung dropped within about 10 yards of the hedge and the wood, and the Scopeuma were more common on the pats further away from the boundaries. This was observed in the summer of 1964 in Cow Pasture where the Muscids aggregated on the pats by the hedge. In both years it was apparent that the *Scopeuma* did not like to go on to pats where they were outnumbered by Muscids, although they were quite capable of killing these flies.

The reason for this seemed to be that the *Scopeuma* were disturbed too much by the Muscids. They normally keep fairly still whilst waiting for a female or mating and are disturbed by other flies moving around the pat. *Scopeuma* were nevertheless tolerant of the large numbers of Sepsids and the sphaerocerid *Copromyza hirtipes* (R-D) which colonised the same pats as the *Scopeuma* in mid-field. This separation of species on to pats in different areas of the field, when *Scopeuma* populations are low and Muscid numbers are high, needs further investigation.

The other interesting effect on the *Scopeuma* during late August 1965 was that this was the only time during the two years when they suffered any heavy predation. Only 3 cases of predation were seen in 1964. However in August 1965 *Scopeuma* and other Muscids on the dung were attacked by wasps (*Vespula vulgaris*(L)) on a considerable scale. Sometimes the wasps ate them on the dung and at other times flew with them.

Many male flies were left dying after wasps had attacked them, and a few were bitten in two and left.

Male Scopeuma were the most numerous victims but females were taken on occasions and a few Cryptolucilia were carried off. Although only a few dozen cases of flies being attacked by the wasps were seen, there was evidence of other attacks by the presence of parts of bodies and dying flies on or around the pats. There certainly seemed to be no severe reduction in numbers due to the wasps and the main effect was the disturbance of the Scopeuma on the dung as the wasps came flying around the pats just above the surface. It is probable that there was a wasps' nest in a nearby wood. The only other victim seen was a female Scopeuma in a spider's web on Piggery Banks.

By 1 September 1965 (Figure 23) the Scopeuma population index was about 3 times greater than in mid-August but it soon fell again. The main reason for this drop was a large quantity of semi-liquid pig dung which had been sprayed in lines in the north-east corner of Low Stack Yard on 8 September. This dung did not lose its attraction for over a week and the numbers of Scopeuma going to it increased as the numbers on the cow pats decreased.

The dung was spread out in 23 lines, each line starting with a large volume of dung spread out almost in a circle.

This was due to the machine starting to empty before it moved off in a straight line. All these expanded ends of the lines were adjacent to each other and the lines of the more thinly spread dung ran parallel to each other. It was therefore possible to walk along all the expanded ends of the lines of dung counting the *Scopeuma* on them as they were rather like large cow pats. The dung along the lines, being thinner than at the ends, lost its attraction more quickly than the ends, but even so, *Scopeuma* was present in fairly large numbers. It was not practicable to walk along the lines counting the *Scopeuma* because they were disturbed too easily.

On 10 September a count was made of the flies on the expanded ends of the dung (termed blobs). There were 2,348 males and 749 females, making a total of 3,097 *Scopeuma*. On the same blobs counted four days later there were 5,934 males and 2,909 females making a total of 8,843. This figure included 509 flies on two blobs separate from the others which had not been included in the first count. There must have been over 10,000 flies on the pig dung altogether, including those, not counted, along the lines of dung.

On 13 September at the first count on one blob of dung there were 364 males and 181 females. Females were removed by pooter for 30 minutes, after which time there were still scores of females left, although 196 had been removed. Flies were therefore being attracted all the time. At 1.10 p.m. G.M.T there were 260 males and 179 females of which 144 were removed. By 2.50 p.m. there were only 148 males and 76 females of which 37 were removed, but by 4.30 p.m. the numbers present had increased to 211 males and 100 females. As 377 females had already been removed and killed, at least 477 had visited this piece of dung in about 5 hours.

The flies present at 3.30 p.m. G.M.T. were scared off the dung and counts made at intervals to see how they returned. The results are shown below.

Mins. after clearing	No. of Males	No. of Females
1	10	8
2	23	26
3	24	23
4	42	32
5	67	50
10	148	62
15	150	68
20	146	51
40	172	73

The count ended at 4.20 p.m. G.M.T. as the numbers of flies on all the dung around were decreasing.

I had hoped to investigate the effect of these large numbers on the sex ratios and to see if there was any social stimulation in large numbers of males which might attract large numbers of females. Unfortunately, from the pootering experiment on 13 September of the 377 females taken from the dung, only 30 proved to be normal females. Of the remaining 347 flies, 213 were castrated females and 134 were castrated males.

On 14 September many females were seen running around on the pig dung. Males frequently caught them but let them go again almost immediately. It was clear from dissections that the males were releasing castrated flies. This is supported by the fact that I had 32 normal females which were probably the result of pootering copulating pairs. All the other flies were probably the free running castrated ones as I did not attempt to catch solitary males.

After the pig dung had lost its attraction, the numbers of Scopeuma on the cow pats rose rapidly and continued to rise until they reached their highest point in the 4 day period ending 27 October. At a mean daily total of 7,301, this was the highest number recorded in the two years. At 2.5 p.m. on 26 October the total number counted on 40 pats was 8,058 - the highest number ever counted on 40 pats. Numbers then decreased, following a similar pattern to the decrease in 1964, but the population was killed much earlier than in 1964 by a large fall of snow on 14 November. Snow remained for a long time and no more flies were seen after this date. One or two were caught in mid-winter in detergent traps.

The area where the pig dung had been was quite clear afterwards because of the lines of long green grass. On the day when the adult Scopeuma were reaching their highest number (26/10/65) large numbers of flies were seen in this long grass and a sweep was made. Over half the females caught were immature and mainly teneral. Clearly these flies were the first to emerge from the eggs laid in mid-September.

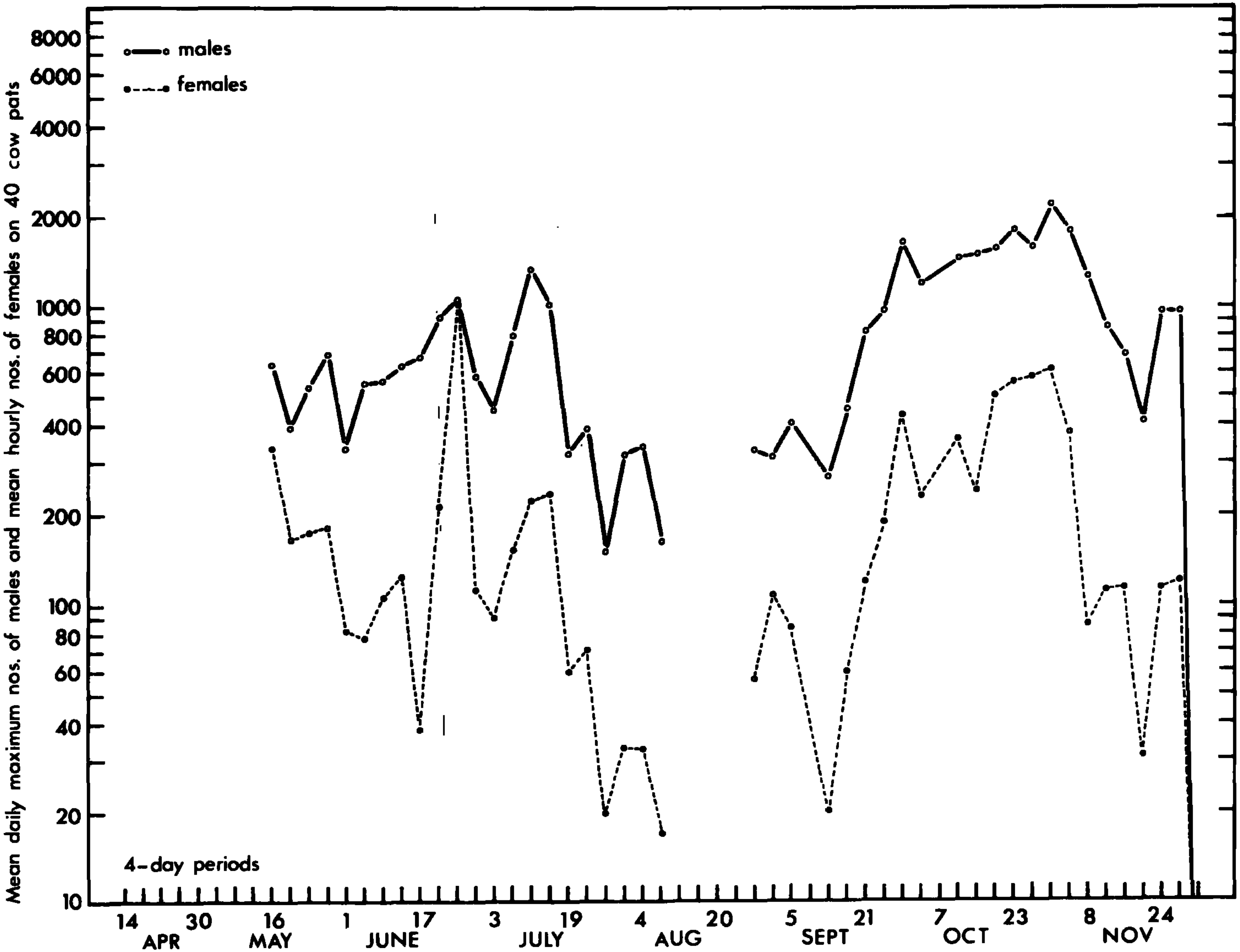
In 1964 (Fig.24) the decline of the spring peak was shown most clearly by the females which declined for over 4 weeks before the numbers rose rapidly for the peak of late June. The male numbers were much more erratic and started their increase at the beginning of June. This difference in the number of the two sexes probably accounts for the irregular way the mean daily totals moved at the end of May (see Fig.23). Fig.24 also shows that the peak of July was mainly due to males, as the females were only a fifth of the numbers present in the late June peak, whilst the males were 1½ times more numerous in the July peak than in the June one.

In the second half of July both sexes declined in numbers and for the rest of the year fluctuations in index numbers of each sex followed each other very closely. Although the total numbers in autumn were higher than at any time previously this was again due mainly to the males. Even at their highest numbers in autumn the females were only 3/5 of the numbers

Fig. 24. Index of numbers of <u>Scopeuma stercoraria</u> in 1964.

Index is mean daily max. nos. of males, and mean hourly nos. of females, given separately, on 40 cow pats.

NUMBERS OF *Scopeuma stercoraria* AT HOUGHALL IN 1964



in the late June peak. The males however were twice as numerous as they had been during the peak of late June.

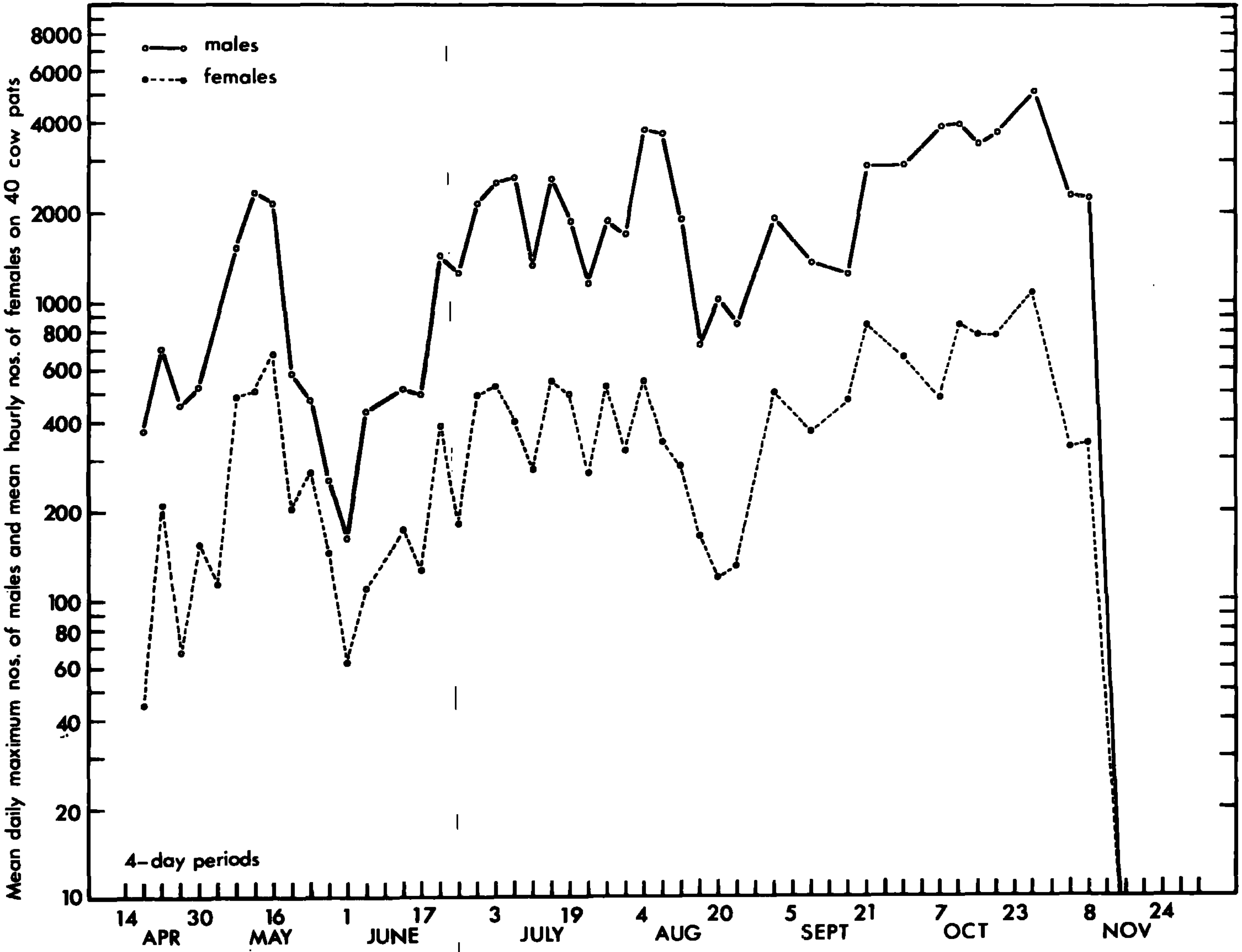
The 4 day period ending 25th June, when the peak occurred, was warm and sunny with no rain. The maximum temperature of 21.7°C occurred twice and was the highest for 6 weeks. Under these circumstances the flies would be expected to occur mainly in early morning and late evening according to Hammer's observations. On the contrary, however, the flies were most numerous around midday in the warmest temperatures. If the flies had avoided activity during the warmer temperatures in the middle of the day an artificial summer trough in their population graph might be expected, even though the numbers then might be higher than in spring or autumn because of the number of hours of daylight in the different seasons. In late autumn there may be only 4 hours when temperatures rise high enough to allow fly activity whereas in summer there may be 15 hours available. It would be expected that the number per hour in autumn or spring would be greater than in summer, but this was not so.

Fig. 25, for 1965, shows the number of males and females following each other more closely than in 1964. In particular the rise and fall of the spring peak is very similar in both sexes. The rise for the summer 'peak' started at the same time in males and females although there are very slight

Fig. 25. Index of numbers of <u>Scopeuma stercoraria</u> in 1965.

Index as in Fig. 24.

NUMBERS OF *Scopeuma stercoraria* AT HOUGHALL IN 1965



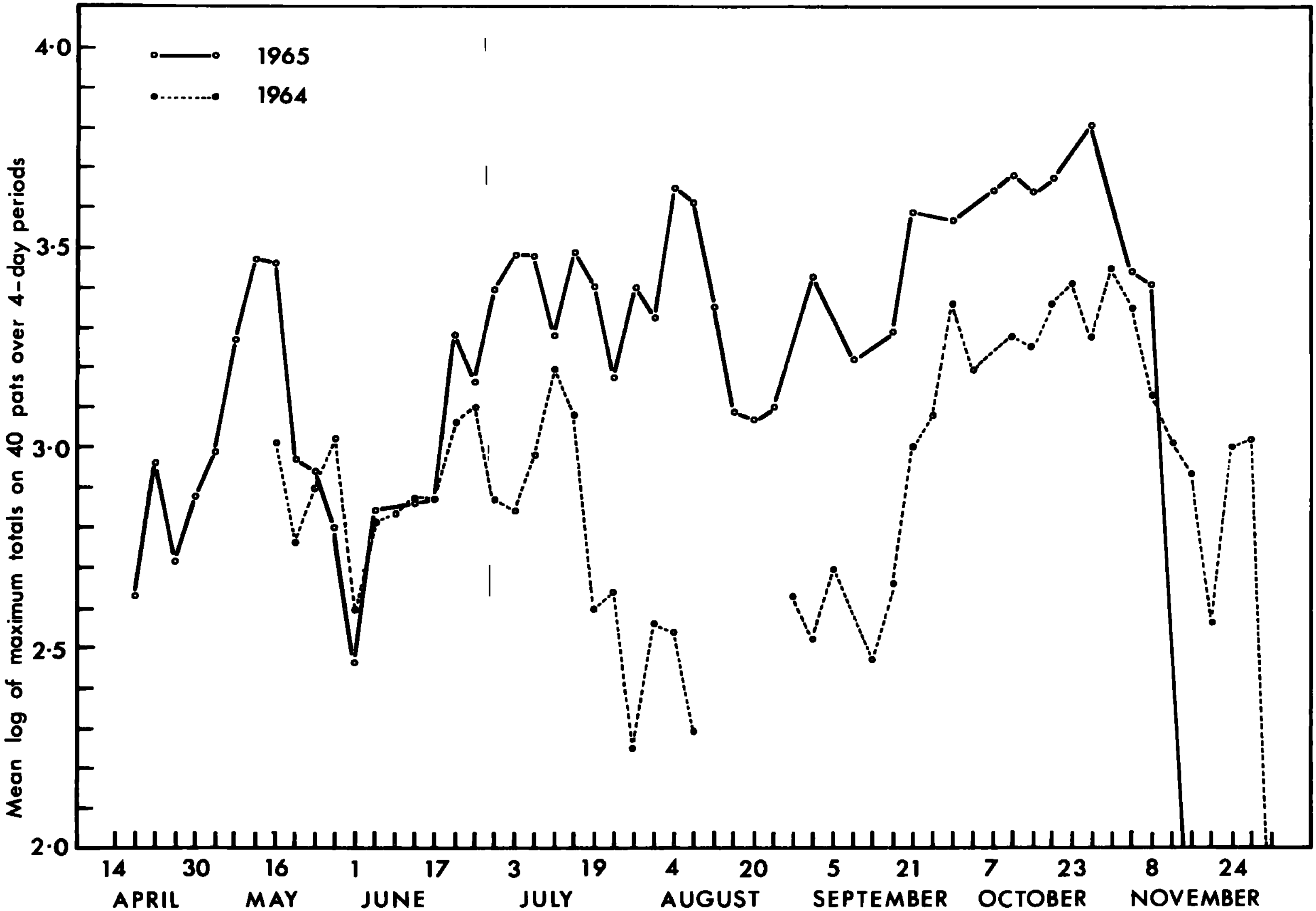
differences in the fluctuations later on in summer. Although the total numbers during most of the summer peak were higher than at the spring peak, this was due mainly to the males. The females never quite reached the highest numbers of their predecessors in the spring.

A clear differences from 1964 can be seen in the length of the summer peak. In 1964 females were present in fairly high numbers from the 4-day period ended 21 June to 15 July - a length of nearly 4 weeks. In 1965 they were consistently high from the 4-day period ended 21 June to 11 August - a length of over 7 weeks. The weather was cool and wet in 1965 as opposed to the warm dry windy weather after the 1964 spring peak. The larvae then had a greater chance of entering the dung before a hard crust formed whereas, in 1964, hard crusts formed within hours of the pat being dropped.

After the drop in numbers during August, the autumn peak started in early September and lasted until the population was killed off by the snows in mid-November. The numbers during the autumn peak were generally higher than they had been at any time previously which again probably reflected the effects on the eggs of the cooler wetter weather during the summer. The pattern of the fluctuations in number during

Fig. 26. Index of numbers of _Scopeuma stercoraria_ in 1964 and 1965. Index is the mean log of the maximum numbers during the 4 day periods.

SEASONAL VARIATIONS IN *Scopeuma stercoraria* NUMBERS AT HOUGHALL



the autumn peak of both years follow each other quite strikingly, apart from the earlier finish in 1965.

Fig. 26 shows the result of considering only the hours during which the maximum totals on 40 pats occurred. By using the mean log of these maxima instead of the arithmetic means any effect of very high totals is minimised. The pattern of the fluctuations shows a very striking similarity to that seen in Fig. 23, when mean daily totals were considered.

d) AGE STRUCTURE STUDIES ON FEMALES

1). <u>Numbers of females caught in vegetation</u>

Fig. 27 shows the numbers caught by net, plotted as the highest number of <u>Scopeuma</u> caught in any 200 sweeps in each week. If several sets of sweeps were made in a week, only the highest number caught in any of them was used for this graph.

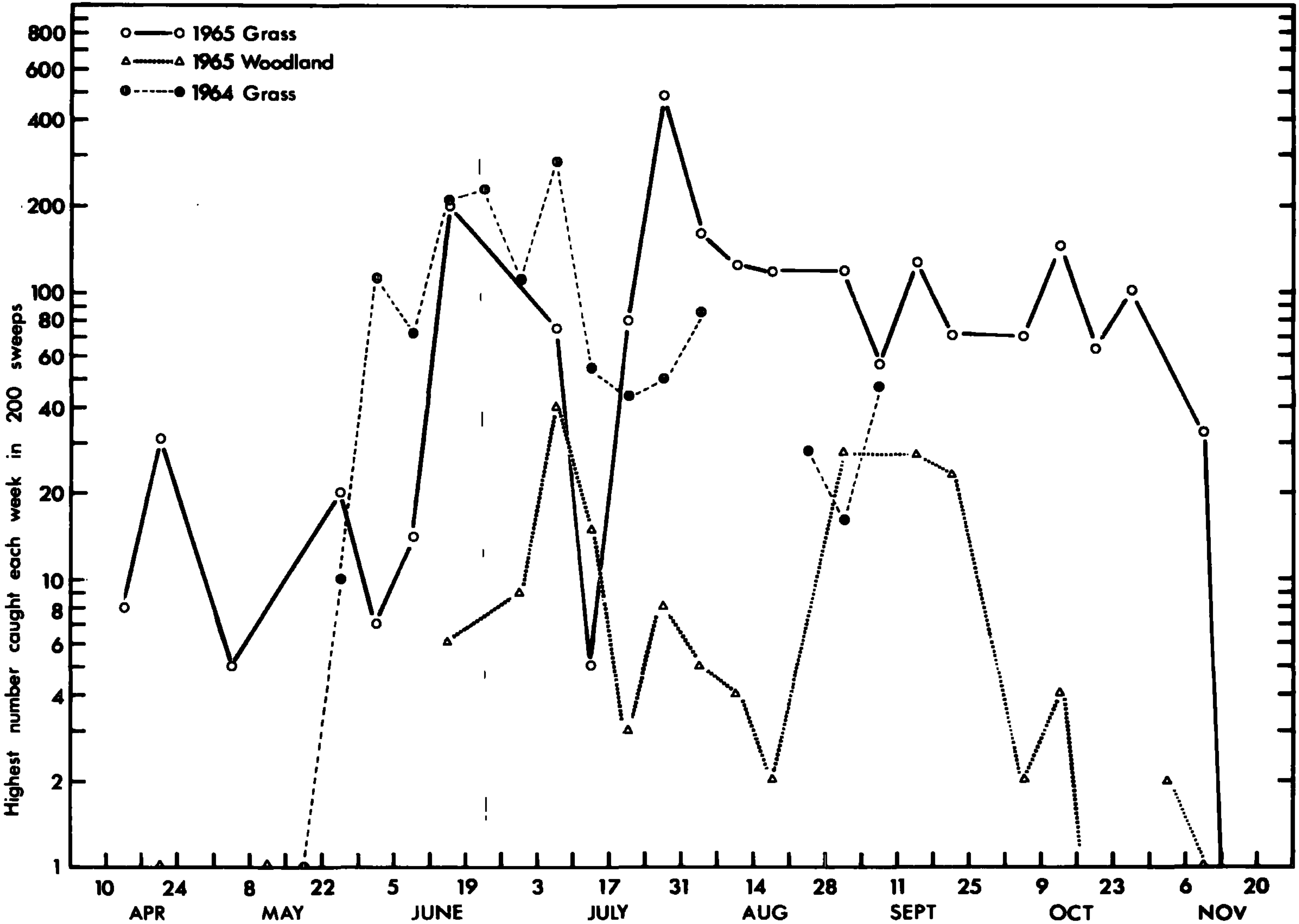
The graph therefore provides some index of the highest levels reached by the population of flies away from the dung. These results are not analysed into 4-day periods to compare with the graphs of counts on the dung, because the technique was more dependent upon weather than the counting since it could not be done when the grass was wet after rain.

As the numbers on the dung fell to the very low level in the period ending 17 June 1964, the numbers in the vegetation rose, reaching their second highest point at the same time. There was a further rise in the first week in August, at a time when the numbers on the dung reached their lowest point.

No more sweeps were done until the end of August. After three weeks it became impossible to continue the standard sweep-netting technique because there was no long grass as a result of the very dry weather throughout summer 1964.

Fig. 27. The highest numbers of _Scopeuma stercoraria_ caught in 200 sweeps each week in grass and woodland at Houghall in 1964 and 1965.

WEEKLY CATCHES OF *Scopeuma stercoraria* IN GRASS AND WOODLAND AT HOUGHALL



The only places away from the dung where Scopeuma were visible were in hedges and in kale - neither habitat amenable to being swept. Even the vegetation in the woodland was very short.

The perpetual rain during 1965 ensured that there was no shortage of grass, so that sweeps could be made throughout the year. The wet vegetation imposed its own restriction so that sweeps were only possible in 23 out of the 31 weeks.

It was not until mid-June that large numbers of Scopeuma were caught by sweep-netting. Earlier in the spring, fairly large numbers were in evidence, but because the grass was still short, they were not easy to catch. The flies either burrowed down into the grass or flew away quickly when attempts were made to sweep them.

After the peak of mid-June the numbers fell to a much lower level than in 1964, but rose again rapidly at the very end of July to the highest point recorded during the two years. As these flies were mainly immature they would probably have maintained the high population on the dung during the drop in numbers during August 1965, which has been described (P.104). From early August to the end of the year the population in the grass remained at a constant fairly high level.

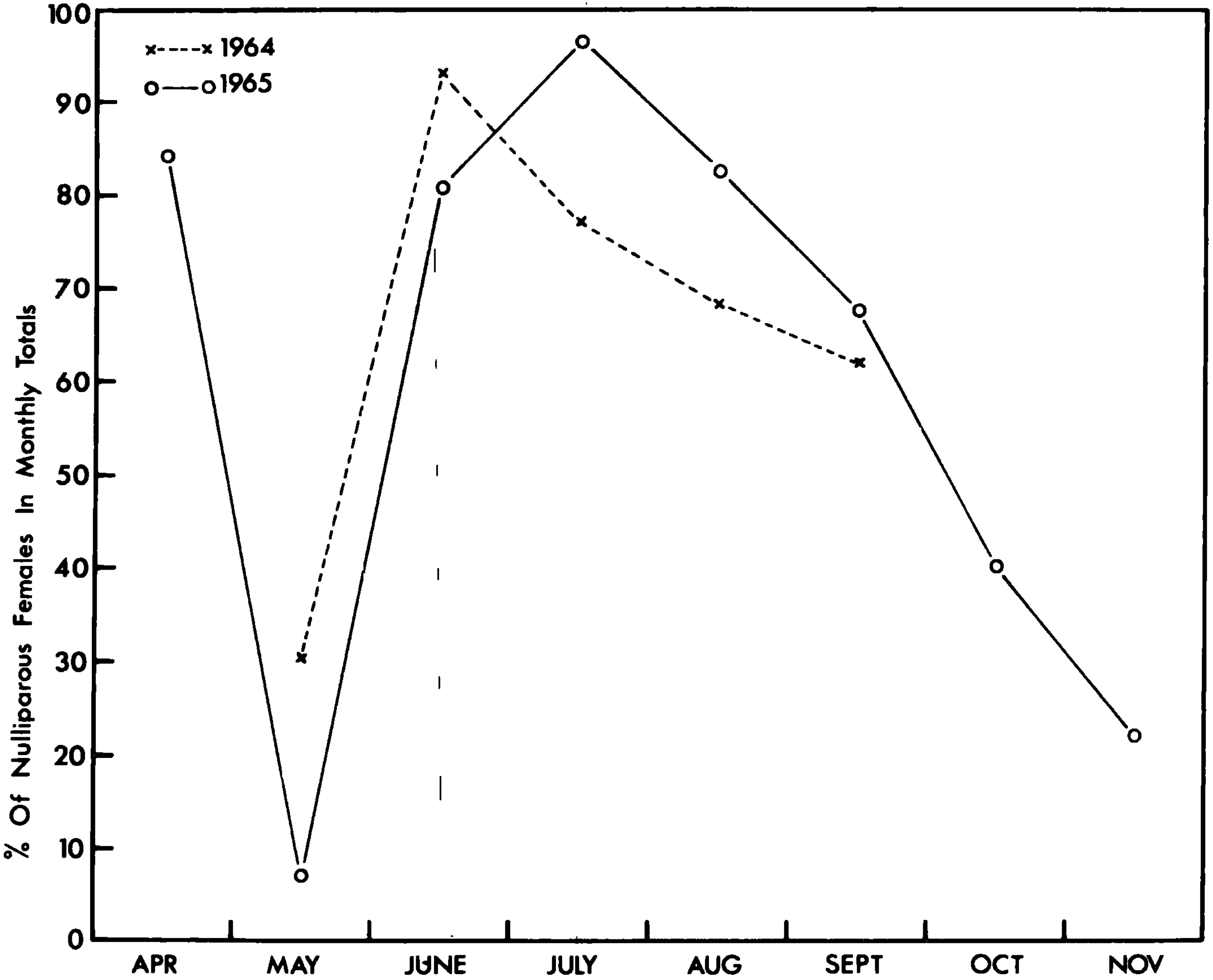
The Scopeuma in the woodland in 1965 (mainly Great High Wood) showed completely dissimilar population changes from those in the long grass. One fly was caught in April, one in early May and there was a gap of nearly five weeks before any more were caught. The highest numbers werw caught in the first week of July after which the numbers dropped to very low levels in late July and August, at the time when the numbers in the grass outside the woodland were at their highest. Throughout September the *Scopeuma* were more numerous but dropped again in October and disappeared from the woods for two weeks. Three flies were caught in November.

The flies in the woods did not form a significant contribution to the population as a whole and it is difficult to know where they came from. It is possible that the higher humidity in woods attracts flies, or it may be that fairly random dispersal of *Scopeuma* takes place and some find their way into woodland. Woods do provide a reservoir of flies which could keep the population going at times of low numbers on the dung, but it does not seem possible to interpret the numbers found there.

The flies in the vegetation begin to offer an explanation of the total population changes when their age structure is examined. Fig. 28 gives the monthly proportion of immature females. For each month all the females caught away from dung have been added, and the numbers of nulliparous females have been expressed as a percentage of this total. This seperates the immature from the mature females, giving a very

Fig. 28. The changes in the percentage of nulliparous females in catches in vegetation each month in 1964 and 1965.

FEMALE *Scopeuma stercoraria* CAUGHT IN VEGETATION



clear picture of what is happening to the adult population.

Both 1964 and 1965 can be considered together even though no results are available from 1964 in April, October or November, females caught in April 1965 were mainly immature, as is to be expected as the population must overwinter largely as pupae. A very few flies manage to overwinter in the adult stage and these probably formed at least part of the 15.9% of parous flies caught in this month. There is also the possibility that some flies emerged early in February and matured by April.

The figures for the flies caught in May in both years show that most of the flies which emerged over winter had matured and moved on to the dung, producing the spring peak. Nulliparous flies in May 1965 formed only 7.0% of the flies in vegetation. The proportion in May 1964 was 30.3%, but this is probably because flies were only caught in the second half of the month, and included immature flies from eggs laid early in spring.

No parous females were caught in the woods until June in 1964 and not until July in 1965. All hunting to mature further egg batches in spring thus seemed to take place in grass in the fields near to the cows.

The population caught in vegetation in June was composed of mainly immature flies, obviously the offspring of the flies comprising the spring peak. This indicates a large mortality of the flies of the spring peak, although some flies caught in June were as old as 6-parous and 7-parous.

As many females were caught in July 1964 as in June, but the proportion of nulliparous flies dropped from 90.6% in June to 75.5%. In July 1965, on the other hand, the numbers of females caught were 4 times greater than in June and the proportion of nulliparous flies rose from 81.0% in June to 95.8%. This is probably due to the fact that in May 1965, when the flies were at their peak, the weather was very hot and dry, probably causing a large mortality of eggs. In the last half of May and the first half of June, when numbers were low, the weather was cooler and wetter, which provided the best conditions for the survival of the newly hatched larvae. Most of the flies in the early summer peak in 1965 were, therefore, probably a result of eggs laid after the spring peak of adults on the dung.

Females caught in August 1965 were more numerous than those caught in 1964, and comprised 81.5% nulliparous flies as opposed to 67.9% in August 1964. In the first week of August 1964 nulliparous females were more numerous than parous females, but in the last week the reverse situation existed. This probably reflected again on the hot dry weather in late July causing heavy mortality of eggs. During the same period in 1965, however, the climate was more favourable to young stages and there was a more continuous influx of immature flies into the population.

The proportion of nulliparous females in September of both years was approximately the same - 63.4% in 1964 and 67.3% in 1965. It appeared that the two years were converging again at this point. The rather wet August in 1964 must have ensured a greater survival of eggs than there had been for some time previously.

Results are only available for October and November 1965 and show a decreasing % of nullipars because the female population ages towards the end of the season and fewer flies emerge, as more larvae prepare to overwinter.

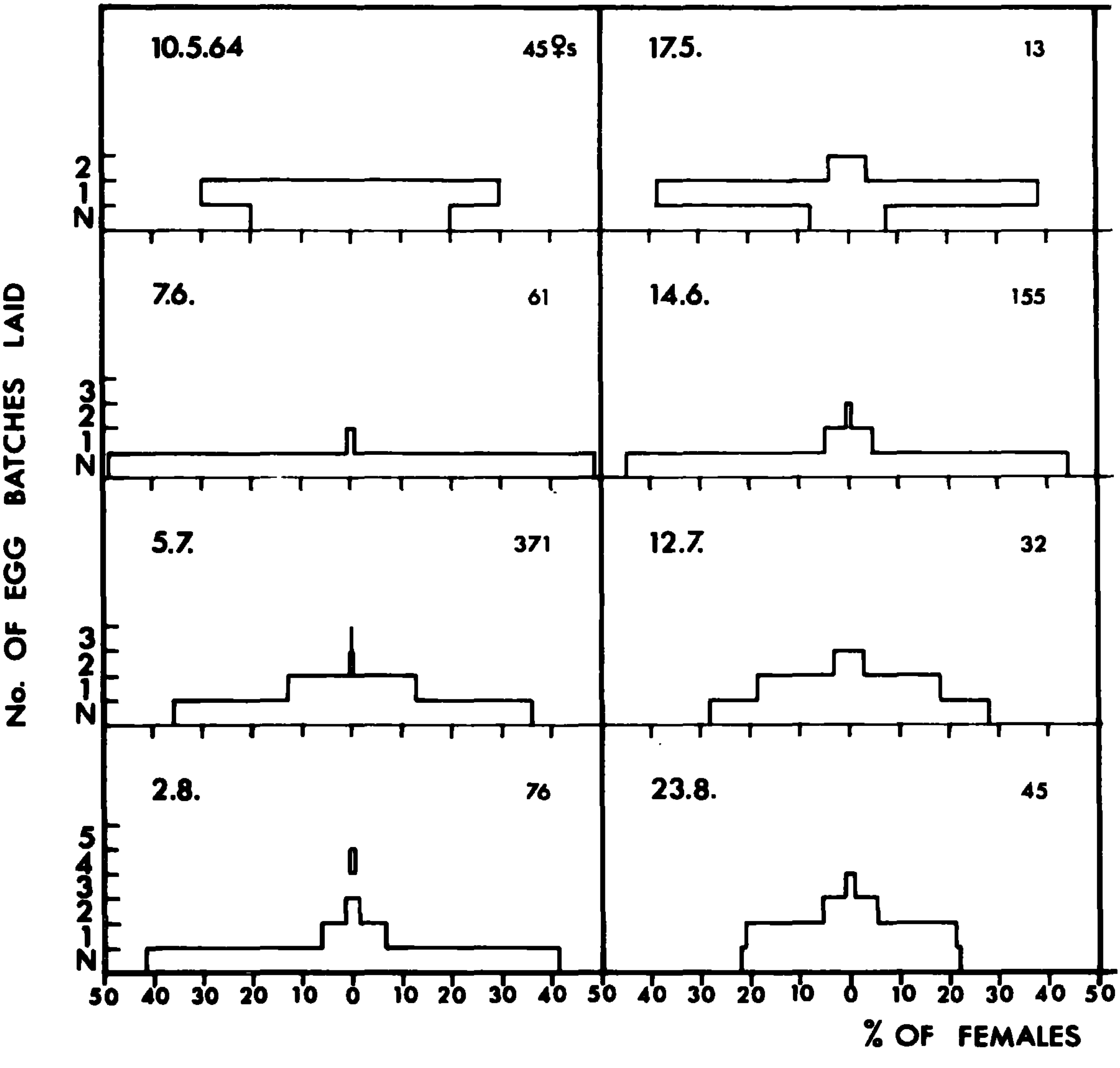
2). Age-structure histograms for weekly catches of females from vegetation.

Age-structure kite diagrams of females in vegetation away from dung for each week during the two seasons when sweeps were carried out are presented for 1964, (Fig.29) and 1965, (Fig.30). For both years the method of presentation is the same.

The results for each week are in separate squares, the vertical axis of each is marked off according to the physiological age of the flies. The horizontal axis in each case is marked off in percentage intervals. The date of the

Fig. 29. Kite diagrams showing the percentage of female Scopeuma stercoraria in each age group for each week in the 1964 season when sweeps were made in vegetation.

WEEKLY CATCHES OF *Scopeuma stercoraria*



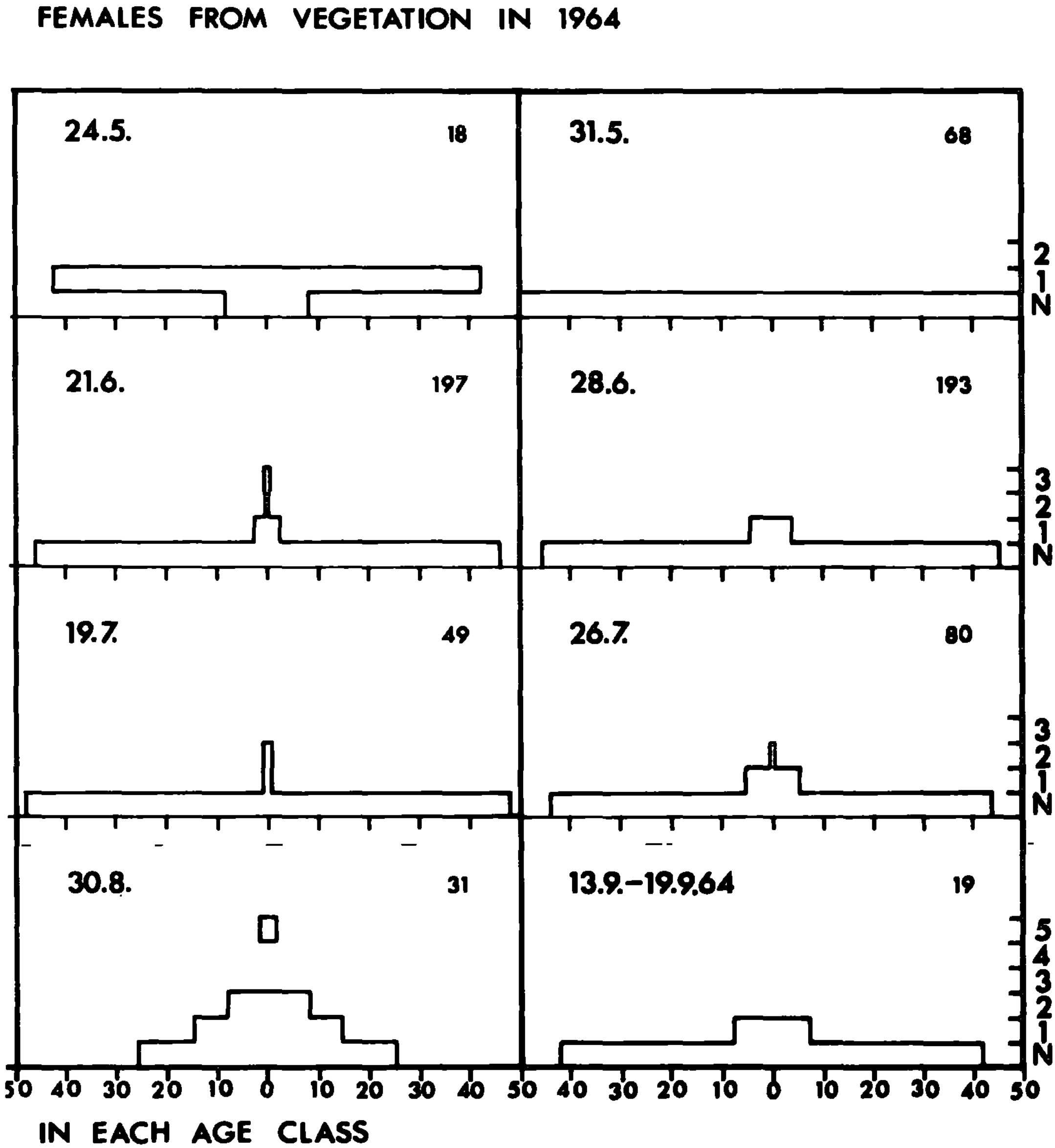
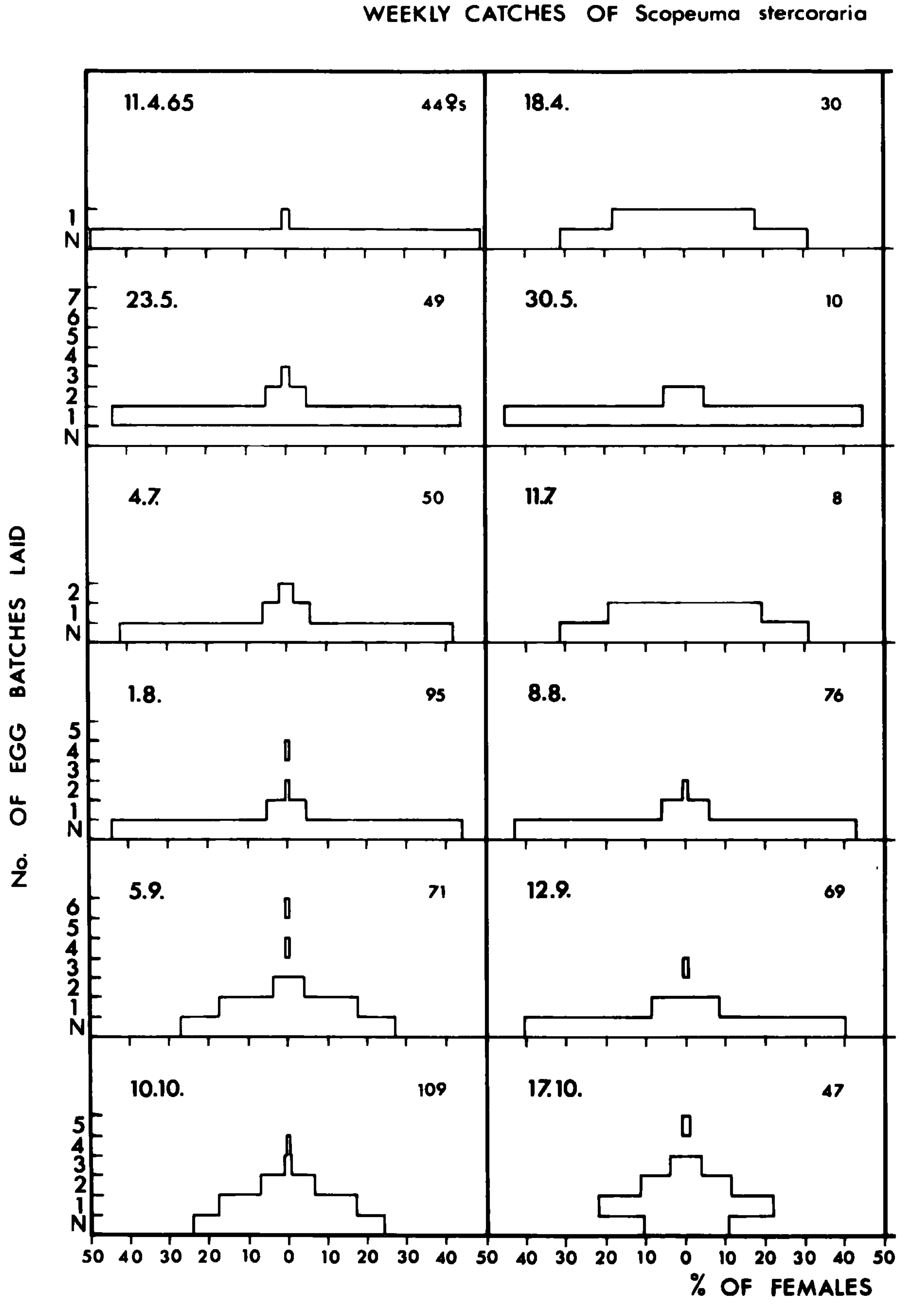
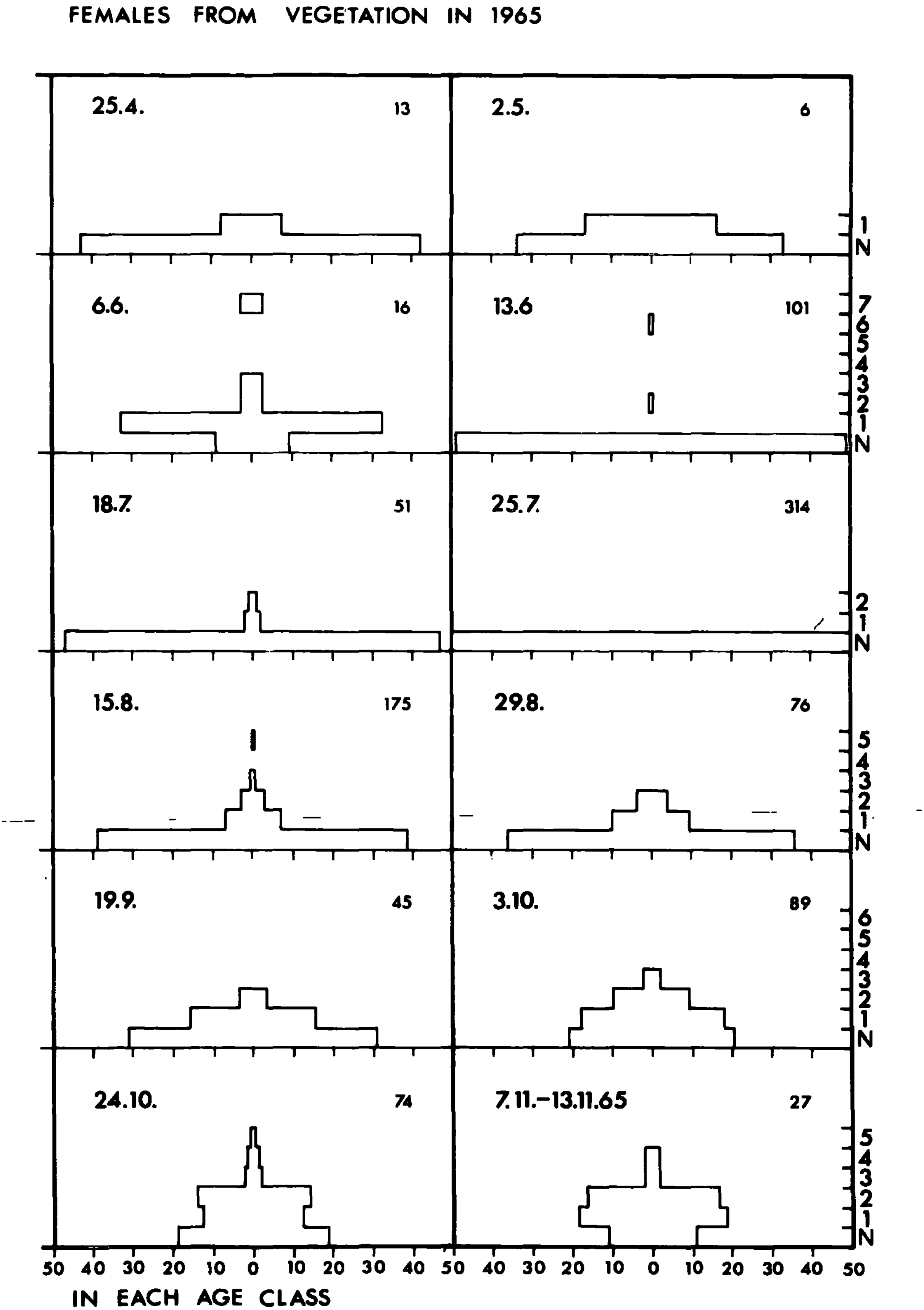

FEMALES FROM VEGETATION IN 1964
24.5.
18
31.5.
68
21.6.
197
28.6.
193
19.7.
49
26.7.
80
30.8.
31
13.9.–19.9.64
19
N
1
2
3
4
5
50 40 30 20 10 0 10 20 30 40 50
IN EACH AGE CLASS

Fig. 30. Kite diagrams showing the percentage of female *Scopeuma stercoraria* in each age group for each week in the 1965 season when sweeps were made in vegetation.



WEEKLY CATCHES OF Scopeuma stercoraria
11.4.65
44♀s
18.4.
30
23.5.
49
30.5.
10
4.7.
50
11.7.
8
1.8.
95
8.8.
76
5.9.
71
12.9.
69
10.10.
109
17.10.
47
No. OF EGG BATCHES LAID
N 1 2 3 4 5 6 7
50 40 30 20 10 0 10 20 30 40 50
% OF FEMALES


FEMALES FROM VEGETATION IN 1965
25.4.
13
2.5.
6
6.6.
16
13.6
101
18.7.
51
25.7.
314
15.8.
175
29.8.
76
19.9.
45
3.10.
89
24.10.
74
7.11.–13.11.65
27
1
2
3
4
5
6
7
N
50 40 30 20 10 0 10 20 30 40 50
IN EACH AGE CLASS

beginning of each week is shown in the top left hand corner of each square, and the number of females caught each week is shown in the top right hand corner.

One of the most important aspects to note is that nulliparous females were present in the population virtually all year. There were only two weeks, in late May and early June 1965, when there were no immature flies. This was at the time of lowest numbers after the spring peak, before the eggs lai laid earlier had had time to complete development. There was a gap of two weeks in the middle of May 1965 when no flies were caught in the vegetation.

The first two weeks of catches, in mid April 1965 (Fig. 30) show firstly a large proportion of nulliparous flies among the first emergences after winter, and in the second week an increase in the proportion of parous females as more of these flies became mature. In the next two weeks the numbers caught were very small but in both cases there was a larger proportion of nulliparous females.

There were no results for the next two weeks, but in the same period in 1964 (mid-May), 1-parous females were more numerous than either 2-parous or nulliparous flies. This was also true for the last week in May. This situation , together with the last two weeks in May, 1965, reflected the gradual disappearance of immature flies from the population as the spring peak drew to an end. This is indirect evidence to support the theory that the majority of overwintering Scopeuma do so in the larval or pupal stage. If a large proportion overwintered in the adult stage, by May large numbers of immature flies should be entering the population as a result of eggs laid by hibernated flies in late March and April.

The first occasions when large numbers of immature flies (the first generation) entered the population were the first week in June 1964 and the third week in June 1965. After these two dates it was not possible to separate generations as the nulliparous females always formed the largest single age group, except in the week beginning 17 October 1965 and the week beginning 7 November 1965.

This absence of clearly defined generations is contrary to what would be expected if either Hammer (1941) or Darwish (1954) were correct in their estimations of 5, and 2 or 3 generations respectively. Eggs were being laid all the time and any large numbers of flies emerging reflects favourable conditions at the time when the eggs were laid. Heavy rain may deter Scopeuma from coming to dung in large numbers but may nevertheless enable a very high percentage of eggs to hatch and enter the dung. Once inside the dung the larvae are safe from adverse climatic conditions unless the crust is broken and the dung spread out, leading to dessication.

From 31/5/64 until 6/8/64 nulliparous comprised 50% or more of the catches, declining to 44.4% in late August but rose to over 80% by mid September.

After spring 1965 nulliparous females formed more than 50% of total females caught each week from 13 June to 25 September. After this date nulliparous females were always less than 50% of each week's catch although they formed the largest single class apart from the two weeks already mentioned.

The age-structure histograms in late summer and autumn show a change from the expanding age pyramid which typified most of the weeks up till this time. In late summer and early autumn there is a reasonably stable age structure, but in the last weeks of October and November excess old flies give an ageing pyramid.

3). <u>Age structure histograms for seasons of the year</u>.

It was possible to group the weekly catches in 1965 into spring, summer and autumn, and then each season into 'early' and 'late'. In 1964, however, for reasons already described, the weekly catches could only be grouped into late spring, early summer , late summer and early autumn.

The top diagram (late spring 1964) Fig. 31, shows 1-parous flies as the lrgest category. This contrasts with summer (middle diagram) when nullipars dominated. By early autumn (bottom) a stable age structure was found. In spring, 2-parous flies were the oldest caught whereas, by autumn, 5-parous females were in the population.

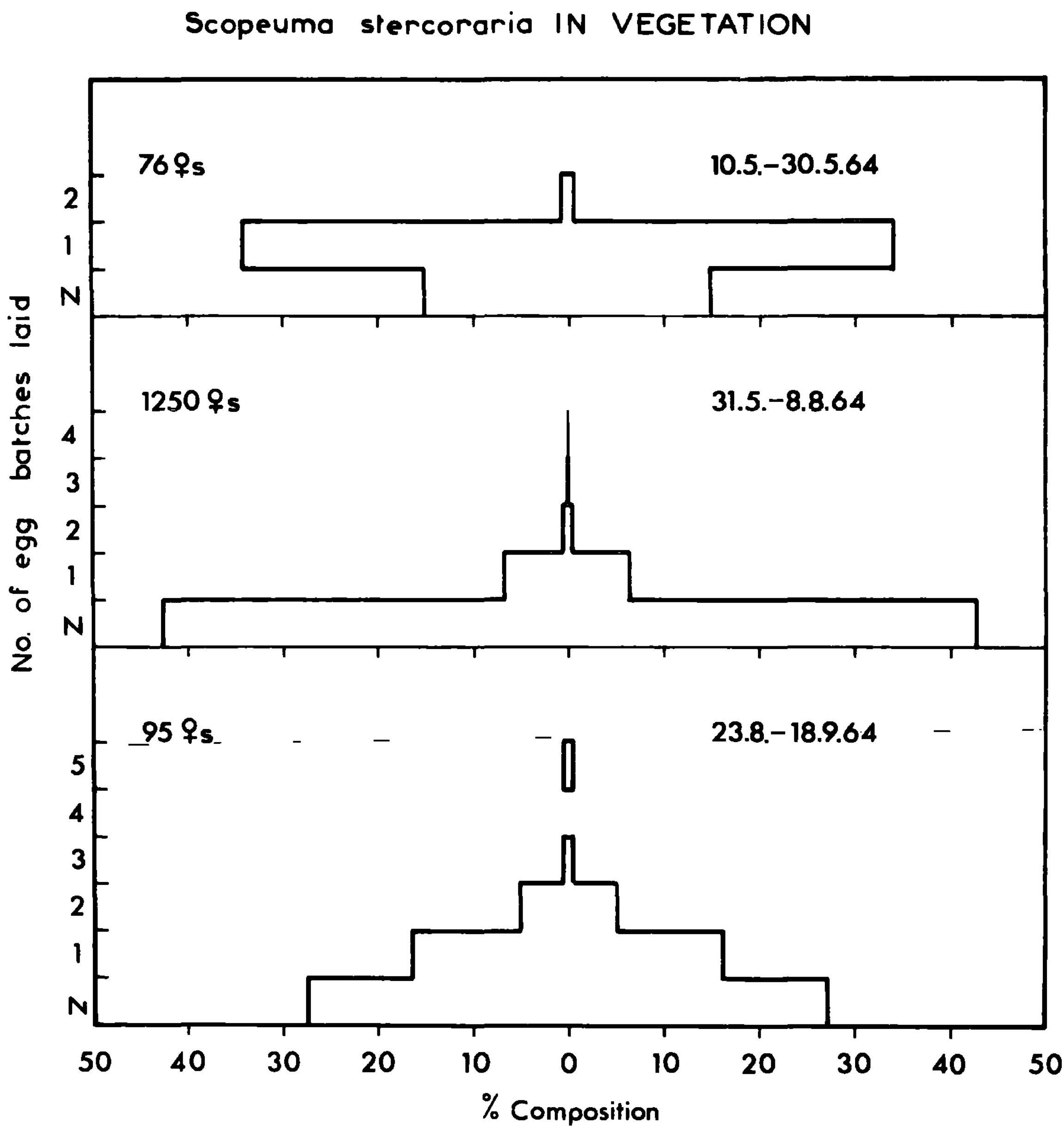
Fig. 32 shows the flies caught in summer 1964 (top) then divided into early and late summer (centre and bottom histograms). In early summer more nullipars and fewer old flies were present than in late summer.

The female populations caught in spring, summer and autumn 1965 are shown in Fig. 33. The spring population was composed of almost equal numbers of nulliparous and 1-parous females, with a few 2- and 3-parous. In summer, nullipars made up 89.9% of the population, but flies of all ages up to 7-parous were also present. The composition of the autumn population formed a stable age pyramid.

Further analysis of these results into the early and late components of each season was made, shown in Fig. 34. The three seasons are presented side by side, but with the early part of each season above, and the late below.

The population in spring 1965 was composed of two distinct age groupings. In early spring 82.8% of females were immature and the rest 1-parous. The large numbers of

Fig. 31. Kite diagrams for Scopeuma stercoraria females caught in vegetation during late spring, summer and early autumn in 1964.



Scopeuma stercoraria IN VEGETATION
76 ♀s
10.5.–30.5.64
1250 ♀s
31.5.–8.8.64
95 ♀s
23.8.–18.9.64
No. of egg batches laid
N
1
2
3
4
5
50
40
30
20
10
0
% Composition

Fig. 32. Analysis of the age structure of females caught in early and late summer 1964 (lower 2 histograms). Flies caught throughout summer are shown in the top histogram.

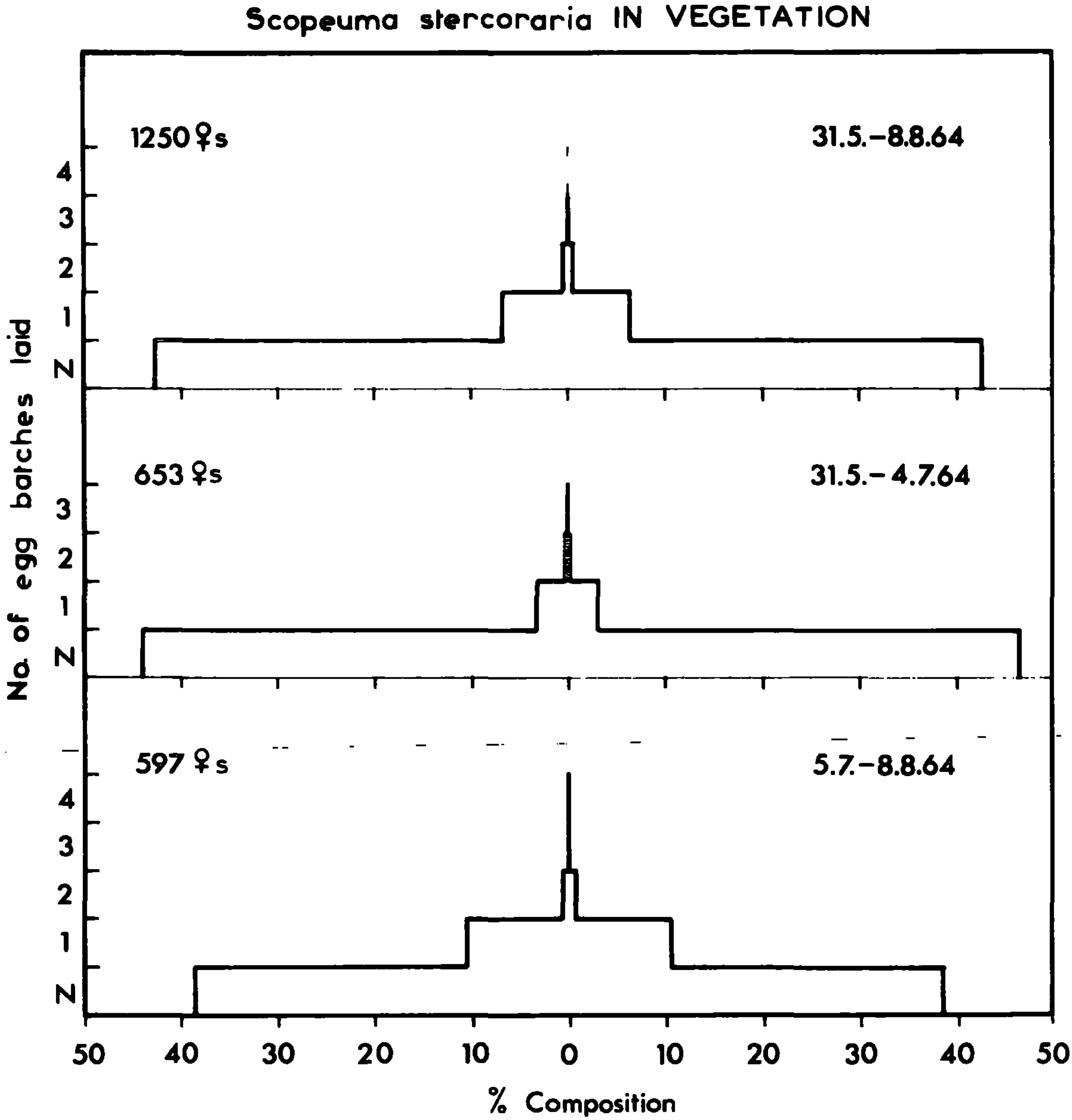

Scopeuma stercoraria IN VEGETATION
1250 ♀s
31.5.–8.8.64
653 ♀s
31.5.– 4.7.64
597 ♀s
5.7.–8.8.64
No. of egg batches laid
N
1
2
3
4
50
40
30
20
10
0
% Composition

Fig. 33. Age-structure histograms of *Scopeuma stercoraria* females caught in spring, summer and autumn 1965.

Scopeuma stercoraria IN VEGETATION

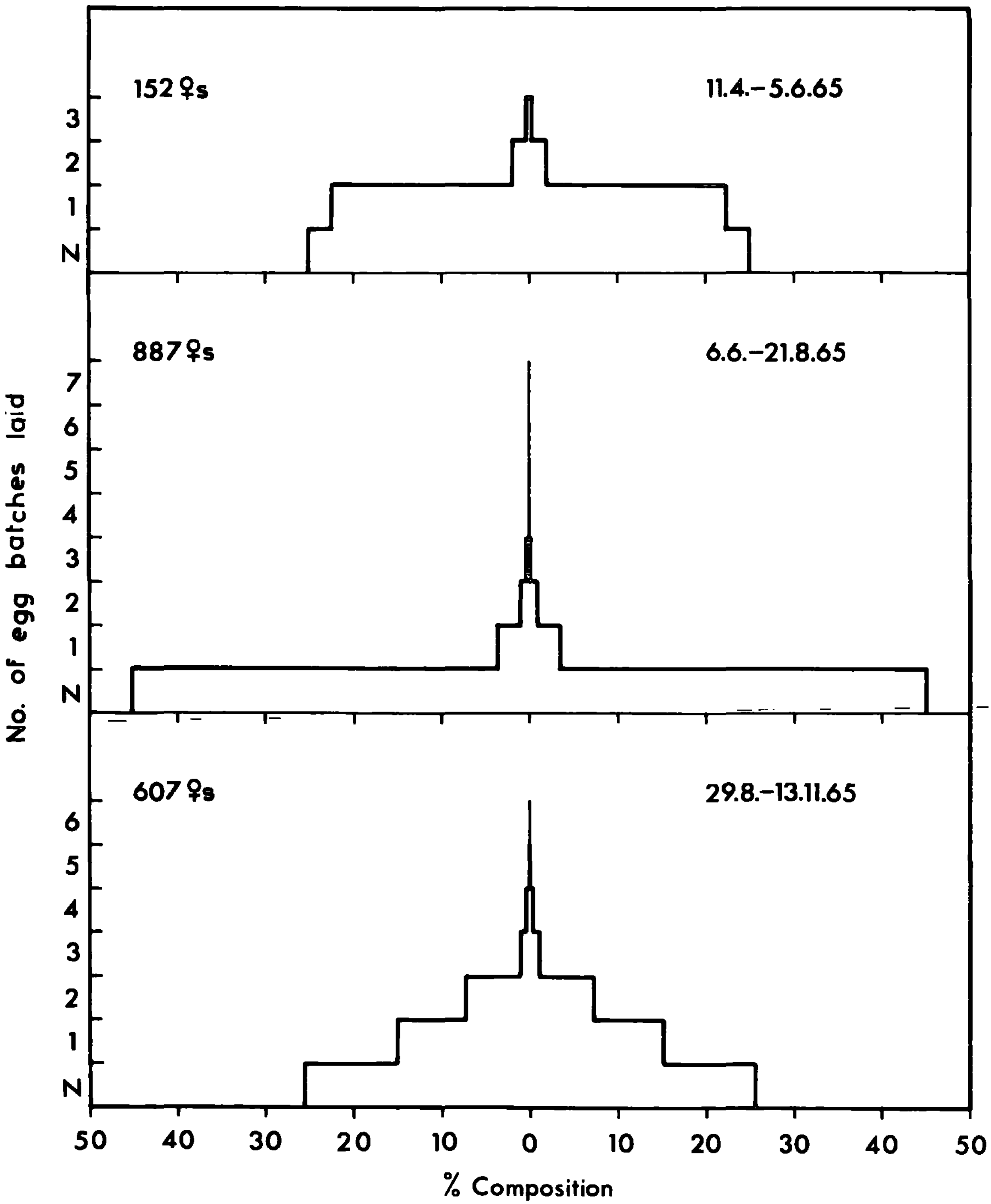
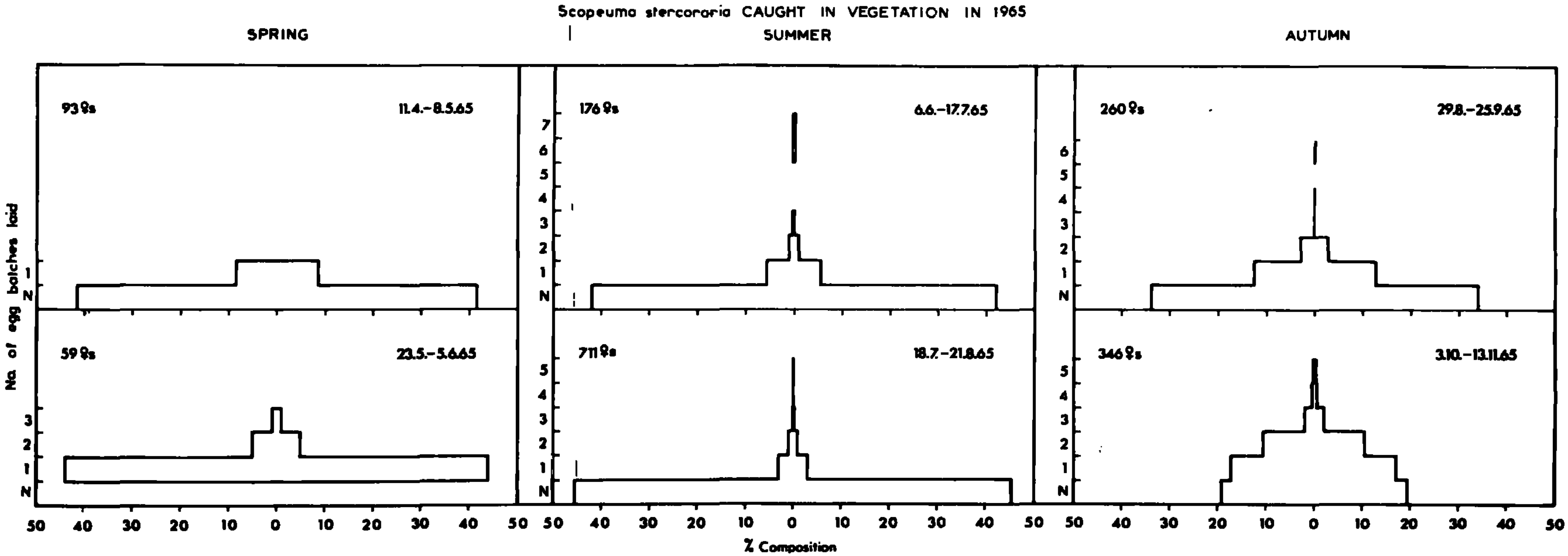


Fig. 34. Age composition of flies caught in 1965, arranged into early and late seasons. For each season the top histogram is for the first half, and the lower histogram is for the second half of that season.



Scopeuma stercoraria CAUGHT IN VEGETATION IN 1965
SPRING
SUMMER
AUTUMN
93♀s
11.4.–8.5.65
176♀s
6.6.–17.7.65
260♀s
29.8.–25.9.65
59♀s
23.5.–5.6.65
711♀s
18.7.–21.8.65
346♀s
3.10.–13.11.65
No. of egg batches laid
% Composition

immature females were obviously emerging from hibernation from pupae or larvae. Their survival however, was not recorded beyond the 1-parous stage. This could have been due to low temperatures, combined with a lack of insect food to eat.

No nulliparous females were found in late spring, although it must be remembered that no sweeps were possible for two weeks at the time of the spring peak and the start of its decline. For the period when sweeps were possible, 1-parous females comprised 88.1% of the total, with 10.7% 2-parous and 1.7% 3-parous females. As the spring peak drew to a close, all the hibernating individuals had emerged and matured so that the population was an ageing one in the sense that the first generation of the year had not yet started to emerge.

The summer population in 1965 showed a very interesting comparison with that in 1964. As can be seen from Fig. 34, both early and late summer populations in 1965 were expanding, but the late summer population contained a higher proportion of immature flies (91.1%) than the early summer population (84.8%). The reverse situation was found in 1964 and this undoubtedly reflects the much greater hatching success of eggs laid in the early summer in 1965 when compared with the same period in 1964.

The continued success in hatching of eggs laid in late summer is reflected in the age composition of early autumn females, which comprised 68.1% nullipars compared with 54.7% in 1964. The early autumn population is therefore an expanding one when compared with that of late autumn which has only 38.7% nullipars. The young females of early autumn survived well into late autumn as can be seen from the shape of the age-pyramid.

4). Survival of female *S. stercoraria* adults.

Survivorship curves, similar to those for *Anopheles gambiae* and *A. funestus* (Gillies and Wilkes, 1965), were constructed for *Scopeuma stercoraria*, based on females caught in vegetation. Modifications in constructing the curves were made because of the differences in general biology between *Scopeuma* and *Anopheles*. The curves are based on the % of each adult age group of the total flies caught over a period of time, the first age group (nullipars) being the 100% survival base.

Survival of 1-parous females is given by the number of parous flies as a % of the total females. That of 2-parous females is the % of 2-parous and older flies of the total, and so on for each age group.

A discrepancy in the presentation of the proportions of the numbers of Scopeuma arose because the mean length of the preoviposition period is 2.07 times the length of the 2nd ovarian cycle (Table 7). All cycles except the first are taken to have a mean duration of 1 week, and there was no evidence that old females were less mobile than young ones. Only a very small number of 1st cycle gravid females were caught and this lack, plus the difference in duration between the 1st and all subsequent cycles, was allowed for by dividing the total number of nullipars by 2.07.

The method of obtaining a survivorship curve maybe explained by taking the actual figures for one of the curves. The curve for early summer 1965 (Fig. 38) was based on "cohorts" of immature females caught between 6 June and 24 July, and all older flies caught which were immature between these dates.

Between 6 June and 24 July 197 immature females were caught. This figure divided by the correction factor 2.07 gives 95. In the analysis two weeks are left at the start and end of this period allowing for immature females moving into the vegetation again as 1-parous females and 1 week for each subsequent age group. The figures for the different age groups caught between the stated dates are given overleaf.

Dates	Age-group	Numbers
6.6 - 24.7.65	nulliparous	197/2.07 = 95
20.6 - 7.8	1-parous	20
27.6 - 14.8	2-parous	3
4.7 - 21.8	3-parous	3
11.7 - 28.8	4-parous	1
18.7 - 4.9	5-parous	1
25.7 - 11.9.65	6-parous	1

Total flies = 124 (using the corrected figure for nullipars).

Survival of nullipars = 100%

Survival of 1-parous flies = 29/124 x 100 = 23,4%

Survival of 2-parous flies = 9/124 x 100 = 7.3%

Survival of 3-parous flies = 7/124 x 100 = 4.8%

Survival of 4-parous flies = 3/124 x 100 = 2.4%

Survival of 5-parous flies = 2/124 x 100 = 1.6%

Survival of 6-parous flies = 1/124 x 100 = 0.8%

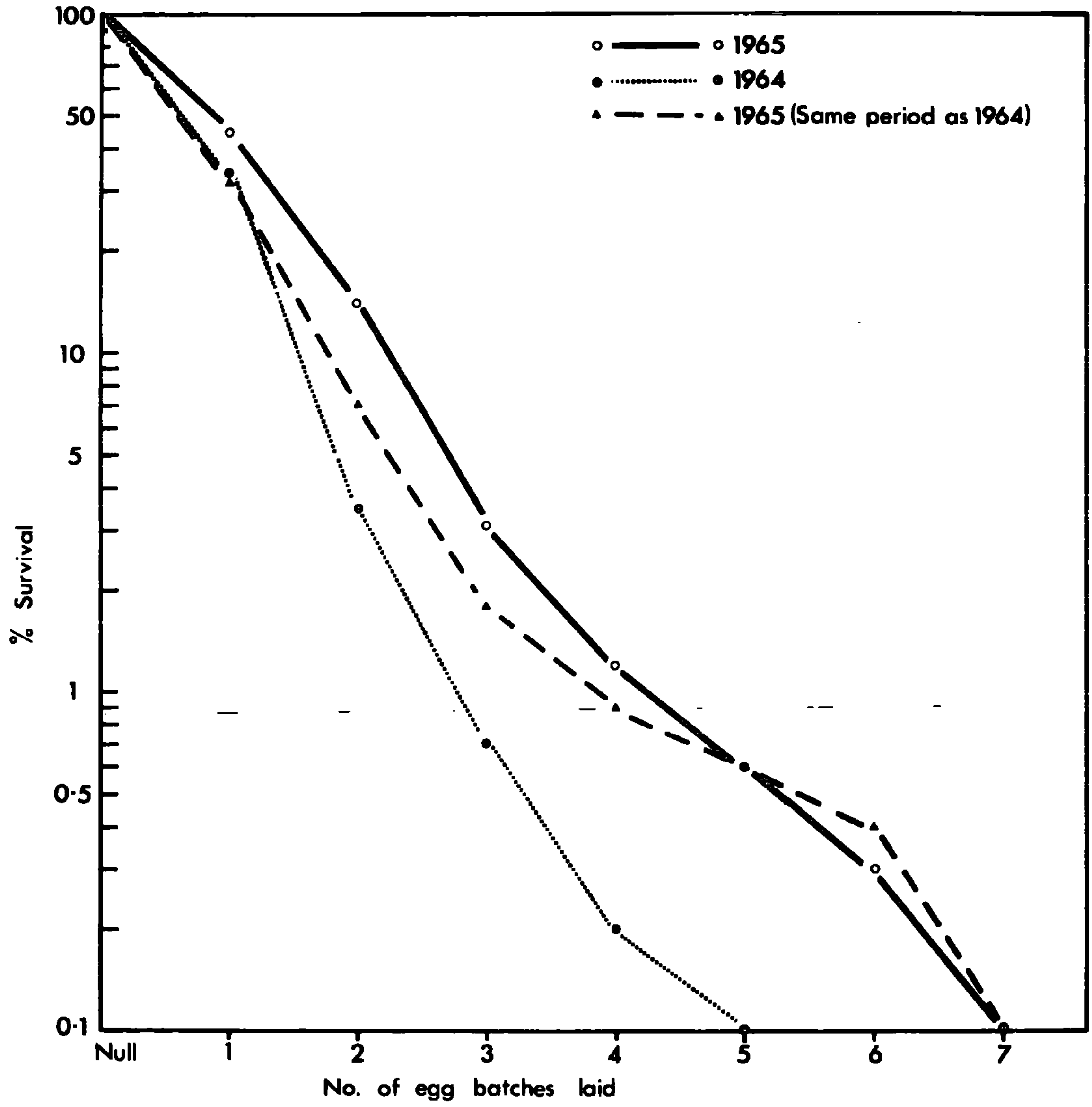
Fig.35) is a comparison of the survival rates for 1964 and 1965. Because flies were collected during a shorter period in 1964 than in 1965, a survivorship curve was calculated for 1965 for the same period as in 1964.

In 1965 as a whole the survival rates were higher for each age group than in 1964. When the shorter period in 1965 is considered, the survival rate for 1-parous females is fractionally lower (32.1%) than in 1964 (33.7%). All other age groups, however, have higher survival rates in 1965 than in 1964.

Fig. 35 Survivorship curves (log. scale) for *Scopeuma stercoraria* females caught during 1964 and 1965 (nulliparous females plotted as 100% survival). A curve for 1965 between the same dates as 1964 is also presented.

For details see text.

SURVIVORSHIP CURVES FOR *Scopeuma stercoraria* IN VEGETATION



When 1964 is considered by itself (Fig.36), the survivorship curves for immature flies (and their descendants) caught in late spring, summer and early autumn are compared. Full results are not available for spring or autumn, but the striking point is that the survival rate of each age group in summer was considerably lower than the corresponding rate in spring or autumn. The survival of 1-parous females was greater in spring 1964 than in autumn, but 2-parous females had about the same survival rates in the two seasons. No 3-parous females were caught in autumn, but the survival of this age group in spring (10.9%) was much higher than in summer (0.6%).

As Fig.37) shows, for 1965, the survival of females in spring and autumn was greater than in summer for all age groups. Once again, 1-parous females had a higher rate of survival in spring (71.1%) than in autumn (61.6%), but the difference was smaller than in 1964. 2-parous flies had a much greater survival in autumn (24.6%) than in spring (10.2%). 3-parous flies also survived better in autumn than in spring, but no further comparisons can be made because no 4-, or 5-parous females were found in spring, and no 6-parous females found in autumn.

The shape of the curve for flies in summer 1965 suggests that mortality is fairly constant for different age groups.

Fig. 36. Survivorship curves for cohorts of immature females caught in late spring, summer and early autumn 1964.

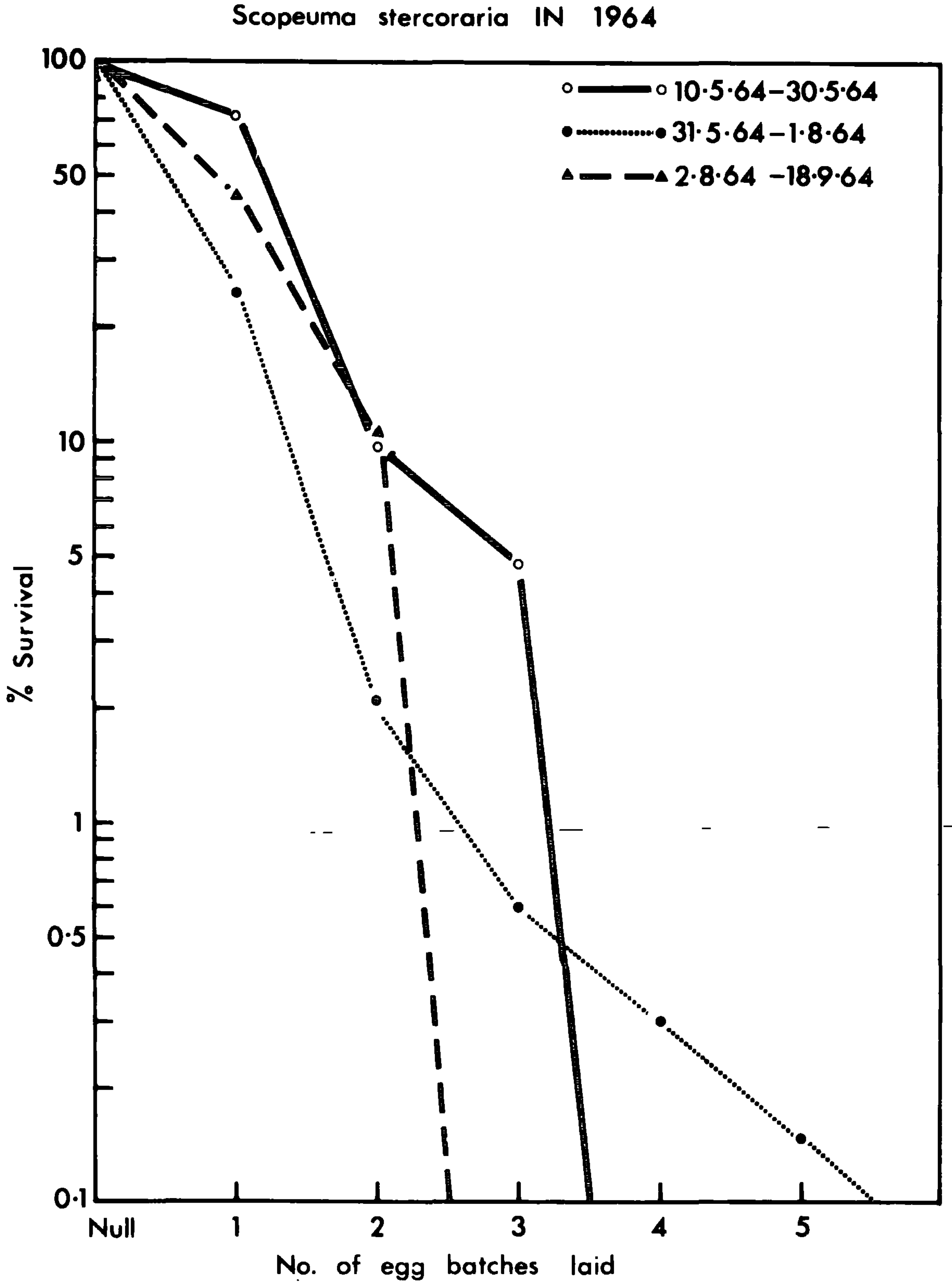

Scopeuma stercoraria IN 1964
10·5·64–30·5·64
31·5·64–1·8·64
2·8·64 –18·9·64
100
50
10
5
1
0·5
0·1
% Survival
Null
1
2
3
4
5
No. of egg batches laid

Fig. 37. Survivorship curves for cohorts of immature females caught in spring, summer and autumn 1965.

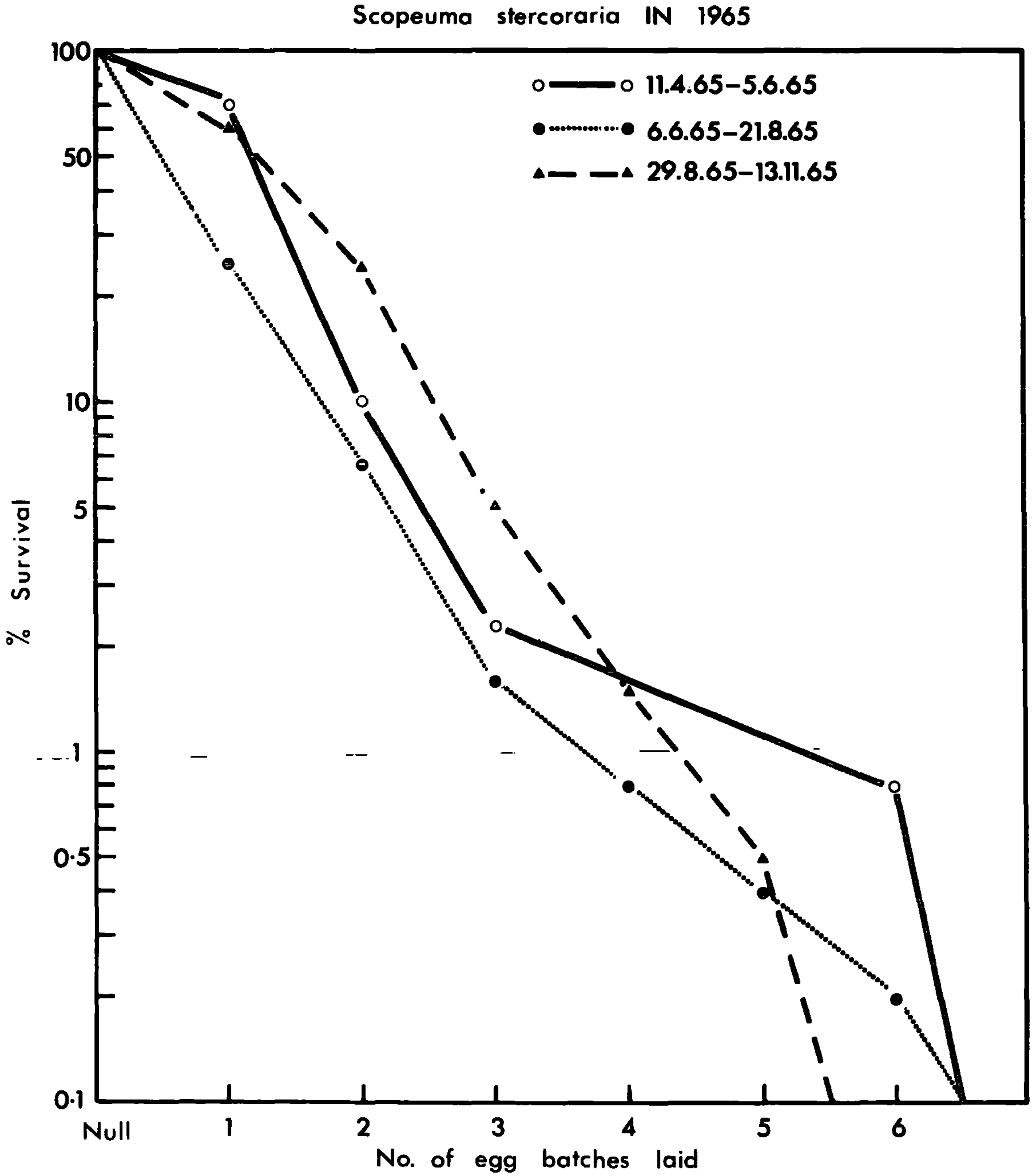
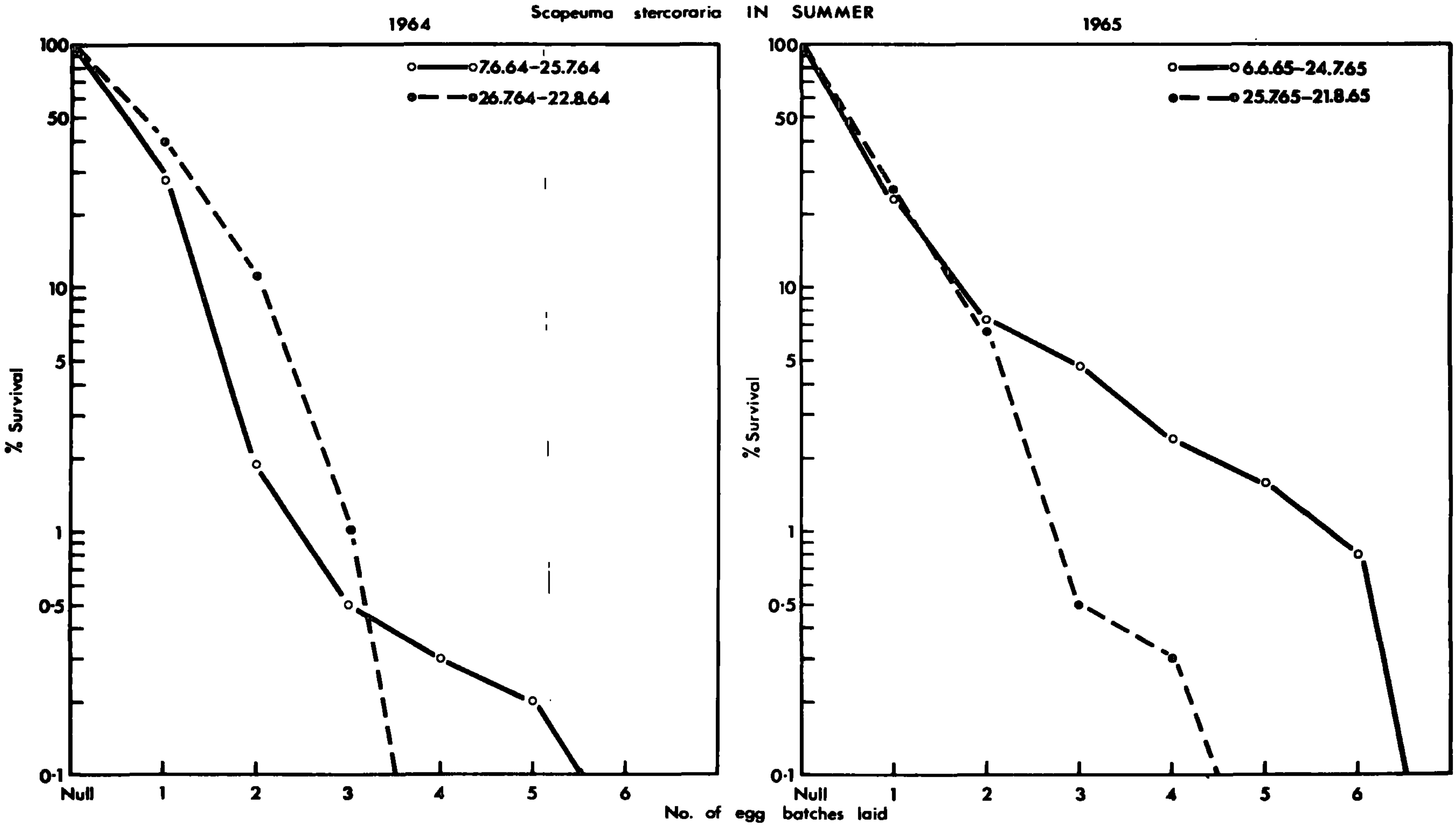

Scopeuma stercoraria IN 1965
11.4.65–5.6.65
6.6.65–21.8.65
29.8.65–13.11.65
100
50
10
5
1
0·5
0·1
% Survival
Null
1
2
3
4
5
6
No. of egg batches laid

Fig. 38 Comparison of survivorship curves for cohorts of immature females caught in early and late summer in 1964 and 1965.



Scapeuma stercoraria IN SUMMER
1964
1965
7.6.64–25.7.64
26.7.64–22.8.64
6.6.65–24.7.65
25.7.65–21.8.65
% Survival
100
50
10
5
1
0·5
0·1
Null
1
2
3
4
5
6
No. of egg batches laid

Until more information on the lengths of different gonotrophic cycles in the field has been obtained, it is not possible to present figures for mortality rates as Gillies and Wilkes (1965) did for Anopheles species.

In Figs.36) and 37), the dates for summer in each year do not correspond very well because of the two week gap in August 1964. For Fig.38) the dates for the end of summer are the same, as the purpose here is to compare the relative survival of cohorts of immature females in early and late summer. In 1964 all age groups had higher survival rates in late summer than in early summer.

Flies emerging in early autumn in 1965 showed a steady decrease in survival, in contrast to those emerging in late autumn and living beyond the 2-parous stage. As Fig.39) shows 1-, and 2-parous flies have very similar survival rates, but that of 3-parous flies emerging in late autumn is one tenth that of flies which emerged in early autumn. The survivorship curve for the flies emerging between 3 October and 13 November 1965 is incomplete in that early snows killed off the adult population and so there are no flies caught after 13 November 1965.

Fig.40) compares the survival rates for 1-, 2-, and 3-parous females in spring, summer and autumn. A comparison is also made between flies caught in 1964 and 1965.

Fig. 39. Survivorship curves for immature females caught in early and late autumn in 1965.

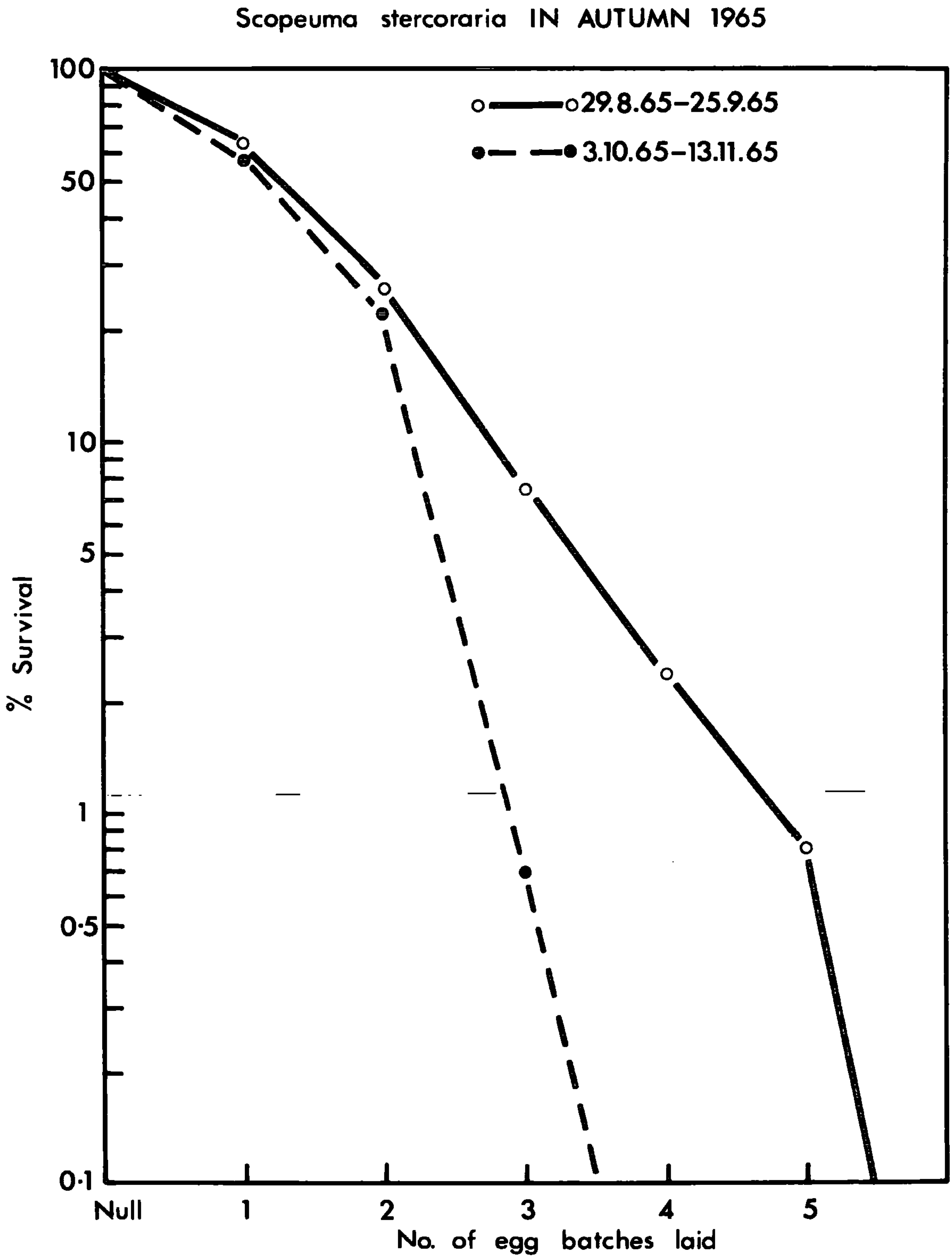
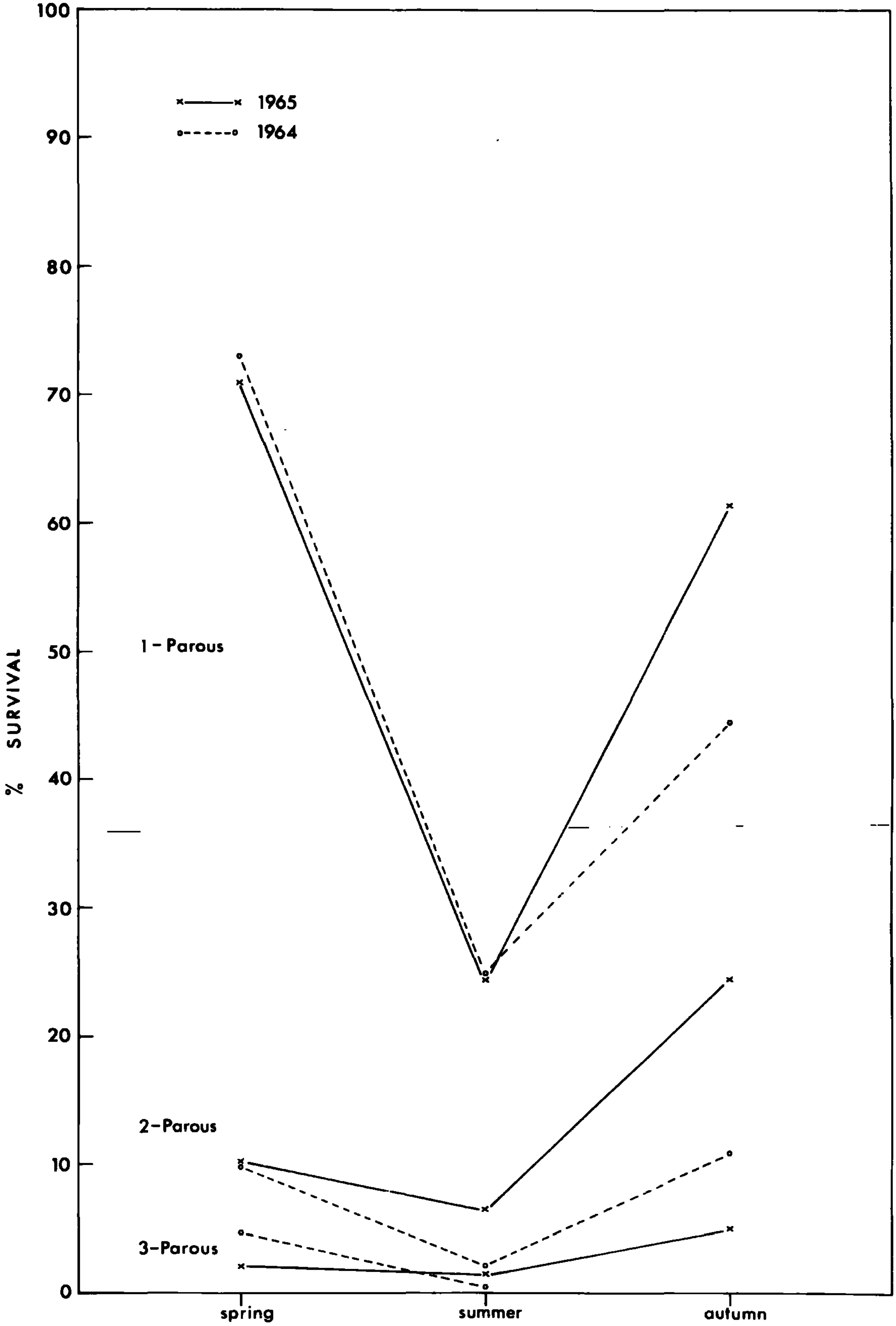

Scopeuma stercoraria IN AUTUMN 1965
29.8.65–25.9.65
3.10.65–13.11.65
100
50
10
5
1
0·5
0·1
% Survival
Null
1
2
3
4
5
No. of egg batches laid

Fig. 40. Comparison of the survival rates of female *Scopeuma stercoraria* of different ages during spring, summer and autumn, for 1964 and 1965.

SURVIVAL OF *Scopeuma stercoraria* FEMALES IN DIFFERENT SEASONS



It can clearly be seen that survival in spring and autumn is higher than in summer for all ages. This difference is most clearly shown for 1-parous flies but it is also true for older flies. Survival in spring was almost equal for females in 1964 and 1965 for 1-, and 2-parous flies, but better for 3-parous flies in 1964 than in 1965.

1-, and 3-parous females had almost equal survival rates during summer in both years, but 2-parous flies did better in 1965 than in 1964. The cooler, wetter summer of 1965 was probably responsible for this, but why the 2-parous flies should have been affected differently is difficult to understand. It may be that this age is the most vulnerable, and that once the 2-parous stage has been passed only the fittest are left.

The figures for autumn are probably biased against the flies caught in 1964 as no sweeps were possible after mid-September. The survival rates for autumn 1964 are therefore probably underestimates, but they are nevertheless higher than the summer figures.

5). <u>Age composition of flies caught on dung.</u>

About half of the <u>Scopeuma</u> taken from dung were caught by various traps and the other half were caught by cautiously approaching a pat and simply pootering as many flies as possible.

The age-structures of flies taken from different pats at the same time, or from the same pat at different times, always differed. It was thus not possible to construct age-structure histograms for the year as there was no method of standardising catches.

When the results of the dissections of these flies were tabulated; it was seen that flies in their first cycle were grossly under-represented. The figures for all the catches off dung are shown overleaf, castrated flies excluded.

Table 9. Age composition of female *Scopeuma stercoraria* caught on dung:

Place and year		Age in Cycles								
		Imm.	1st	2nd	3rd	4th	5th	6th	7th	8th
Houghall 1963 (sheep dung)	Total 53	1	5	45		1	1			
	%	1.9	9.4	84.9		1.9	1.9			
Moorhouse 1963 (sheep and horse dung)	Total 30	2	8	18	2					
	%	6.7	26.7	60.0	6.7					
Houghall 1964 (cow dung)	Total 144	1	12	120	9	2				
	%	0.9	8.3	83.3	6.5	1.4				
Houghall 1965 (cow dung)	Total 292	9	69	125	51	25	8	2	2	1
	%	3.1	23.6	42.8	17.5	8.6	2.7	0.7	0.7	0.3

When these results are totalled, the figures are as shown below.

Table 10. Total numbers and percentage of all females caught on dung :

Age:	Imm.	1st	2nd	3rd	4th	5th	6th	7th	8th
Total	13	94	308	62	28	9	2	2	1
%	2.5	18.1	59.2	11.9	5.4	1.7	0.4	0.4	0.02

The females gravid for the first time (i.e. all the figures under the column heading 1st) ought to form the largest group, with all other ages showing a similar pattern to that seen for 2nd cycle and older. One possible explanation for the lack of these 1st cycle gravid females was that they might be mainly in the vegetation. The figures for flies caught in the vegetation were therefore checked for the % of gravid females in each age class. The following figures were obtained.

Table 11. % of gravid Scopeuma in each age class of females caught in vegetation.

1964	1st	2nd	3rd	4th	5th	6th
Total	1141	251	23	4	1	1
% gravid	8.23	15.60	30.43	50	100	100

1965	1st	2nd	3rd	4th	5th	6th	7th	8th
Total	1185	317	112	20	6	3	2	1
% gravid	4.98	24.61	35.71	60.00	33.33	33.33	100	100

Thus, although females in the 1st cycle form the largest age-class, the percentage of 1st cycle females that are gravid is the lowest. The answer to the problem presumably therefore lies in dispersal. Females gravid for the first time must disperse and are thus poorly represented on any one pat.

Johnson (1966) suggests that in insects generally most dispersal occurs during the first preoviposition period and that immature adults make the longest flights. After Scopeuma females emerge from the pupa they may fly long distances in their preoviposition period and will not necessarily mature in the vicinity of the herd.

6). The occurrence of castrated flies throughout the year.

Dissections for age structure studies revealed castrated males and females throughout most of the year but they were exceptionally abundant in September 1965.

To study seasonal variations in occurrence of castrated flies the % of such flies in both sexes are given for each month. If more than one sweep in any month contained castrated flies, the results were combined. Figures for dung and vegetation catches were kept separate and are shown in Table 12.

Asterises have been placed by the sides of the figures with 5% or more castrated. The main times of occurrence are thus June (females only in 1964, males only in 1965), August 1964, September 1964 (females only), and 1965 (both sexes), October 1963 (males), and November 1965 (for flies caught on dung). It thus seems that autumn was the time of greatest abundance with a slight peak in June. It is difficult to understand, however, how the differences between the sexes occur, and why, in September 1965, castrated females were rare in the vegetation but abundant on the dung, whereas castrated males were common in both habitats. Why also was the one sex not represented at all in the June figures for 1964 and 1965?

One possible explanation for the occurrence of castrated flies is suggested by their abundance in June and autumn. They may have occurred as a result of overcrowding, with resulting partial starvation, in the larval stage during the spring peak (for the June figures) and during summer (for the autumn figures). More careful studies on laboratory reared flies may throw further light on this problem but the reason why castrated flies occur is still obscure.

Table 12. The Occurrence of Castrated Scopeuma stercoraria throughout the year.

		Total flies	Castrated flies	% Castrated
1963				
Houghall dung.				
October	males	37	3	8.1*
	females	55	2	3.6
Moorhouse dung.				
November	males	59	1	1.7
1964				
Houghall dung.				
May	males	157	1	0.6
	females	116	3	2.6
Houghall vegetation.				
June	females	420	29	6.9*
July	males	192	5	2.6
	females	480	13	2.7
August	females	18	1	5.5*
September	females	20	1	5.0*
1965				
Houghall vegetation.				
April	females	31	1	3.2
May		0	0	0
June	males	19	1	5.3*
July	males	78	2	2.6
	females	419	4	0.95
August	males	227	8	3.5
	females	275	5	1.8
September	males	142	8	5.6*
	females	147	2	1.4
October	males	84	2	2.4
	females	213	3	1.4

Table 12. The Occurrence of Castrated Scopeuma stercoraria throughout the year (continued).

		Total flies	Castrated flies	% Castrated
1965				
Houghall vegetation.				
November		0	0	0
Houghall dung.				
September	males	312	264	84.6*
	females	403	345	85.6*
October	females	126	3	2.4
November	males	97	13	13.4*
	females	126	24	19.1*

Discussion:

1) The annual pattern of events in *Scopeuma* populations.

The explanation for the fluctuations in numbers of *Scopeuma* has previously been given in terms of generations. Hammer's interpretation (1941) was that a number of generations succeed each other but with the reservation that climate influences newly hatched larvae and also adult flies. Darwish (1954) deduced the development of 2 or 3 generations in a year, a summer with diapause in the adult stage to explain low numbers during the summer.

In view of the fact that the flies from one hatch of eggs emerge over a period of at least 5 - 7 days, and that each female lays eggs at weekly intervals, distinct generations cannot exist. My observations have been that eggs are laid every day throughout the season except when the weather is so bad that it prevents the adults from coming to the dung. This in itself precludes the possibility of definite generations developing.

Overwintering takes place mainly in the larval or pupal stages, with very few adults overwintering and occasionally emerging during warm spells to lay eggs. When the weather improves as spring approaches, adults start to emerge, and any overwintered adults appear on dung of any animals out at that time (usually sheep). As there are few small insects about in February and March it takes these immature adults a long time to mature. The majority of adults emerge during April so that the main part of the population has matured and moved on to the dung in May, forming the Spring 'peak'.

Numerous eggs are laid during this time of abundance of adults but the usual hot sunny weather at this time causes many pats to harden before the eggs have a chance to hatch. After the spring peak the flies tend to die off and this mortality may be increased by a sudden lowering of temperature and rain, as happened in 1965.

No flies older than 3-parous have been found during the Spring peak which indicates that hibernating adults could form only a minor component of the overwintering population. This is contrary to the view held by Cotterell (1920). This absence of old flies in spring poses the question of a possible physiological difference between flies which emerge after winter and those emerging throughout the rest of the year.

A spring peak, followed by a fairly rapid decline in numbers, seems to be one of the most significant features of *Scopeuma* population fluctuations. The extended pre-imaginal development period and the nature of the weather during spring, with its extremes of frosty nights and hot days, are probably mainly responsible for the mortality which causes the end of the spring peak. In the weeks that follow this decline the adult population is mainly derived from eggs which were laid before the spring peak. Strictly speaking these flies are the first generation of the season, for by the time of the early summer peak, there is a wide age range in the population.

The nulliparous females in late spring 1964 (Fig. 31) were mostly caught in the first week of that period and were probably the last of the overwintering stages to emerge. Those nullipars caught at the end of the period were probably the first to emerge from eggs laid in early spring since only immature females were caught in the week following that period.

After the spring peak has passed the fate of the population throughout the rest of the year probably depends on the weather as it determined the number of first instar larvae which enter the dung each day. A hot dry day will cause the early formation of a crust over the surface of the dung which forms an impenetrable barrier to newly hatched larvae. A cool wet day will ensure that the dung remains liquid and consequently there will be easy penetration by the young larvae. Once inside the dung larvae and pupae are virtually immune from the effects of the weather after the formation of a crust, since this ensures the continued semi-liquid nature of the medium.

The extension of the first peak in early summer depends upon the weather after the decline of the spring peak. The weather in late May of both years was sufficiently good to allow the development of enough eggs to produce a second peak in mid-July. The pattern of events in the two years diverged from this point onwards. As can be seen from Figs. 23 and 26 the numbers of flies fell away markedly after the July peak in 1964, but actually increased to a higher peak in early August in 1965. The reasons for this difference can be traced to the weather from early June.

Table 13. Comparison of meteorological data for 1964 and 1965 from first week in May to first week in August. Relative humidities and temperatures are weekly means. Rainfall and hours of sunshine are weekly totals. Mean daily totals of <u>Scopeuma</u> over 4-day periods between the same dates are also shown.

Shaw week	R.H% '64	R.H% '65	Max. '64	Max. '65	t°C Min. '64	Min. '65	Rain " '64	Rain " '65	Hrs. sun '64	Hrs. sun '65
29.4-5.5 26	64.1	74.3	14.4	13.3	5.0	3.9	0.14	0.66	54.4	44.9
6-12.5 27	70.1	65.0	16.7	17.8	8.3	6.1	0.31	0.15	34.5	52.8
13-19.5 28	63.3	74.1	17.8	14.4	6.7	4.4	0.18	1.07	55.9	39.3
20-26.5 29	72.1	73.1	17.2	16.1	5.0	5.6	0.06	0.45	45.1	22.3
27.5-2.6 30	78.7	67.9	16.7	13.3	7.2	5.0	0.88	0.13	35.4	27.2
3-9.6 31	73.0	79.9	17.8	17.8	7.8	6.1	0.49	0.18	28.0	43.3
10-16.6 32	75.0	77.0	18.3	19.4	8.9	7.8	0.22	0.45	39.2	37.8
17-23.6 33	77.3	77.9	13.9	17.2	7.2	10.6	1.01	0.72	27.1	36.8
24-30.6 34	66.4	75.6	20.0	19.4	9.4	8.3	0.04	0.07	52.5	35.3
1.7-7.7 35	66.7	67.7	18.3	13.3	6.7	6.7	0.01	0.33	48.8	20.7
8-14.7 36	73.1	77.4	18.9	15.6	8.9	7.2	0.18	0.82	43.5	15.4
15-21.7 37	78.6	81.3	20.0	18.3	10.6	6.7	1.76	0.21	34.4	29.4
22-28.7 38	68.9	83.4	21.1	17.2	9.4	10.6	0.02	2.52	35.0	14.0
29.7-4.8 39	67.0	77.7	21.1	17.2	11.1	6.1	0.05	0.94	35.6	40.8

Mean daily totals

Date	1964	1965
4.5		1074
		3252
		4025
16.5	1120	3199
	619	1599
	1002	1022
	1846	696
1.6	539	411
	755	911
	798	
	878	1221
17.6	752	1082
	1205	2202
	1816	1819
	1334	3758
3.7	766	4106
	1362	3424
	2169	2582
	1473	4792
19.7	440	3858
	619	1955
	210	3457
	493	2325
4.8	468	6555

Table 13 shows the main details of the climate at Houghall between May and August in 1964 and 1965. During this 14 week period the mean weekly relative humidity was greater in 1965 except for 2 weeks. The rainfall was also greater in 1965 except for 5 weeks. Heavy rain during this time in 1964 usually came in short spells, followed by warm dry weather which quickly dried out the soil and vegetation. Higher mean weekly temperatures in 1965 were recorded 3 times for maximum and 3 times for minimum. In only 4 weeks in 1965 there were more hours of sunshine than in 1964.

From 10 June to 4 August 1964 there were generally high temperatures and low rainfall. This was particularly true of the period 24 June to 14 July, which was also the time of the late June and early July peaks of Scopeuma. The high numbers of Scopeuma in 1965 started at about the same time, but there were lower tempratures and higher rainfall.

In the week 17 June to 23 June 1964, 1.01 in. rain fell, 0.48 in. of this was on 1 day. From 15 July to 21s July 1964 1.76 in. rain fell, of which 1.44 in. fell on one day. Very few flies went on to the dung on those days, and only for a short time so that the effect which this rain might have had on egg survival was negligible.

Rainfall in August 1964 was 1.96 in., spread over 15 of the 31 days and this was probably the month with greatest egg survival, to produce the autumn peak of mature adults. Total rainfall in August 1965 was 2.10 in., spread over 16 days which also probably increased egg survival.

These details are to try to show that weather conditions mainly affected eggs and therefore the size of the mature adult populations 5-6 weeks later, rather than the numbers of adults at the time. Very hot or wet weather reduced the numbers of adults going to dung, but this seemed to be mainly a result of avoiding behaviour by the flies (see section 3).

The termination of the spring peak in numbers seemed unrelated to weather conditions and was almost certainly due to heavy mortality of adults which had overwintered as larvae and pupae. After the spring peak had passed the numbers of mature adults at any time depended on how the weather affected eggs laid previously. Because of this, the population variation cannot be interpreted in terms of generations.

In 1964, because of the lack of large numbers of immature adults entering the population in summer the future of the *Scopeuma* depended upon the small numbers of old females still alive and ovipositing when the weather improved (for the flies). This longevity of *Scopeuma* obviously is of considerable importance for ensuring the continuation of the species during drought conditions, when weeks may pass without any eggs hatching and surviving to maturity.

From August onwards in both years the weather was fairly similar and the fly populations showed similar patterns of abundance. The long autumn peaks of both years were initially due to good survival of eggs laid during August, and afterwards the continued survival of eggs ensured a long period of high numbers of adults. During typical autumn weather cow dung takes a long time to form a crust because of the lower day temperatures, cooler damper nights and more rain. There are also large numbers of insects about during autumn so that the immature adults which keep entering the population have a ready supply of food, and mature females have no difficulty in maturing further egg batches. The autumn climate also ensures a higher rate of survival of adults than was possible during summer (see Fig. 40).

All these factors during autumn ensure that there are large numbers of eggs being laid for a long time, most of which will have a good chance of successful development. This therefore ensures that there will be a large population in the spring of the following year.

The end of the season for the adults came with the first heavy frosts or snow. It would be very interesting to see how long the autumn population could continue in a mild autumn. Mating and oviposition will take place in the field between 3 - 5°C so that in a very mild winter there might only be a slight drop in numbers. The greatest limiting factors under such circumstances would be the availability of dung and the food supply of small insects. Borborids could supply the food requirements during winter (Edge pers. comm) and manure heaps would be an egg-laying medium.

Although predation on adults and larvae, by both animals and fungi, will play some part in affecting the population, there is no doubt that weather is the most important factor. Apart from the spring peak, nothing is predictable about Scopeuma populations. Persistent drought could keep the flies at a very low level, and if severe enough could even exterminate local populations. Only dung dropped in shaded or permanently damp areas could offer any hope for survival of eggs under these conditions. Perpetual cool damp weather on the other hand could mean a continuous geometrical increase in numbers until winter.

Peaks in the population are not due simply to the appearance of successive generations, but depend on the times of weather suitable for eggs to hatch and the larvae to enter the dung. Such occurrences mean that about 5 - 6 weeks afterwards there will be large numbers of adults on the dung. The fact that eggs are being laid throughout the day and every day means that Scopeuma are providing the maximum number of opportunities for the continuation of the species.

Another insurance which Scopeuma has against extinction is its very wide distribution. These flies can be found everywhere and by this means they can utilise dung as a breeding medium wherever it is. Grouse dung on moors and even dog and donkey dung on sea shores or badger dung in woods may all be used. Under very severe drought conditions, isolated pockets of survivors may be found because of this dispersal and versatility. A food supply for the adults can be found everywhere so that the presence of dung is the only limiting factor.

2). The study of Scopeuma populations.

This discussion is an attempt to collate the findings of other workers on Scopeuma stercoraria and to compare their methods and conclusions with my own. The works of Hammer (1941) and Darwish (1954) contain the most detailed studies and most controversial interpretations on Scopeuma adults, while Lawrence's studies (1954) on the larvae of cow pats provide additional information.

Graham-Smith (1916) records _Scopeuma_ _stercoraria_ as overwintering as pupae in soil and presents tables showing the number of flies caught in traps baited with excrement and placed in different situations. These figures for 1915 showed that high numbers of _Scopeuma_ were caught in May, July, August and October, with low numbers in April, June, September and November.

Mellor (1919) reported finding _Scopeuma_ pupae in cow manure in January 1917 which emerged in May. He also recorded _Scopeuma_ breeding in horse manure, in contrast to the findings of Cotterell (1920) and thought to be accidental by Thomsen and Hammer (1936), said that the adults occurred in two periods, possibly representing two generations, namely in April-May and from late August to the beginning of October. From late June to mid August they had disappeared or only a few were seen.

Such a two-peaked occurrence was also recorded by Coulson (1956) from 6 sticky traps set on the high moors of the Moor House National Nature Reserve in Westmorland in 1955. The first peak lasted from late May to mid August, with a drop in late July. There was a much smaller peak in October and November, with a few flies caught in September. Although sticky traps are not a very good way of studying *Scopeuma* populations, this result deserves further consideration in view of the environment in which the study was carried out.

The climate at Moor House (1840 ft.) has been described by Manley (1936) as sub-Arctic. The mean July temperature is only 53°F and rainfall is very high (about 120 inches per year). The main breeding medium for *Scopeuma* is sheep dung on the alluvial grassland, grouse dung in the heather moor, and a little horse dung. Although *S. stercoraria* does breed in the horse dung, this medium was preferred by *S. squalida* which was more successful at Moor House than at Houghall. Sheep dung was the main breeding medium for *S. stercoraria* but this is very susceptible to hot dry days.

In the summer of 1963 there were quite long spells of clear sunny days making the sheep dung hard and dry and impossible for *Scopeuma* to oviposit. 1955 was a year of very hot weather at Moor House, with very little rain in June, July and August, although there was heavy rain in the first half of May. This probably explains the very small autumn peak, as this dry summer weather would quickly prove fatal to any eggs laid in fresh dung.

The extended spring peak which occurred in 1955 is probably typical of *Scopeuma* on most high moors. The cooler temperatures obtaining at high altitudes will not only delay pupal emergence, but cause the adults to live longer and also lengthen the larval development period. The climatic conditions probably impose a reduction in the breeding potential of these flies so that only two, or perhaps three, generations are possible. Nelson (1965), records highest catches of _Scopeuma_ at Moor House in July, with quite high numbers also in August. This could be due to immature flies, the progeny of the June population, hunting and getting caught on the sticky traps. Mature flies are less mobile. _S. stercoraria_ was twice as common as _S. squalida_.

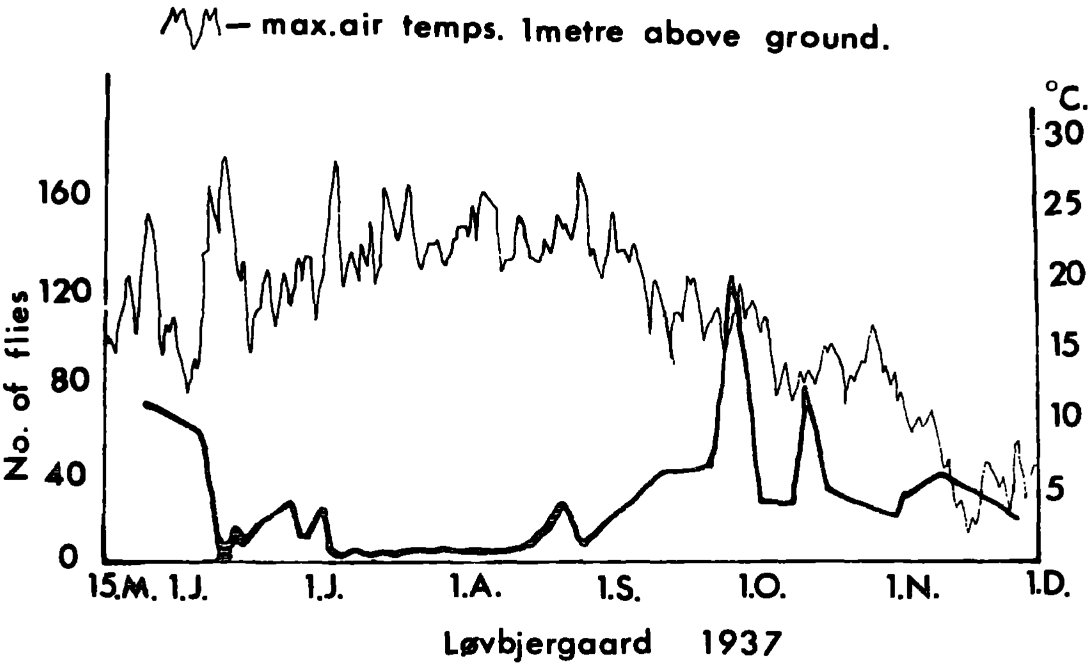
Mohr (1943) recorded _Scatophaga furcata_ Say (= _Scopeuma squalida_ Mg.) as being more numerous than _Scopeuma stercoraria_ in Urbana, Illinois. He presents _S. furcata_ as being present on the dung from the beginning of March until early June after which it disappears, then reappearing from early September to the end of October. No explanation is offered for the summer absence. _Scopeuma stercoraria_ was recorded in very small numbers (always in the company of _S. furcata_) in April, early May, late September and October. It was not found on cow dung in open pastures at all. Again, no explanation was offered for the summer absence of the fly.

Oldroyd (1964), like Cotterell, describes _Scopeuma stercoraria_ as breeding smoothly from April to October, with four or five generations. He also states that larvae pupate in the soil beneath the dung, as do Graham-Smith (1916), Colyer and Hammond (1951), Cotterell (1920), and Darwish (1954). Mohr (1943) says that larvae of Scatophaga furcata pupate in the dung. Larsen and Thomsen (1940) and Hammer (1941) say that pupation of Scopeuma stercoraria takes place in the dung. I have known pupation of both species occur both in the dung and in the soil beneath.

Larsen and Thomsen (1940) suggested that the probable explanation for the summer depression in Scopeuma numbers was that certain stages, particularly the pupae, were killed by heat on very hot days. This does not answer the problem as death of pupae would have to continue over a long period prior to the decline in numbers of mature adults in order to be the factor responsible for this decline. This explanation makes it difficult to understand how there could be a resurgence of the flies in the autumn. Larsen (1943), however, describes the vulnerability to death by dessication of a newly hatched larvae and even quotes Hammer's (1941) description of cow pats covered with dead newly hatched larvae in wind and sun. This, surely, is the main factor responsible for determining the number of mature adults on the dung at a later stage.

Hammer's work (1941) was concerned with flies associated

Fig. 41. Population curves for Scopeuma as given by Hammer (1941). The number of flies is presented as the highest number found on one cow pat.



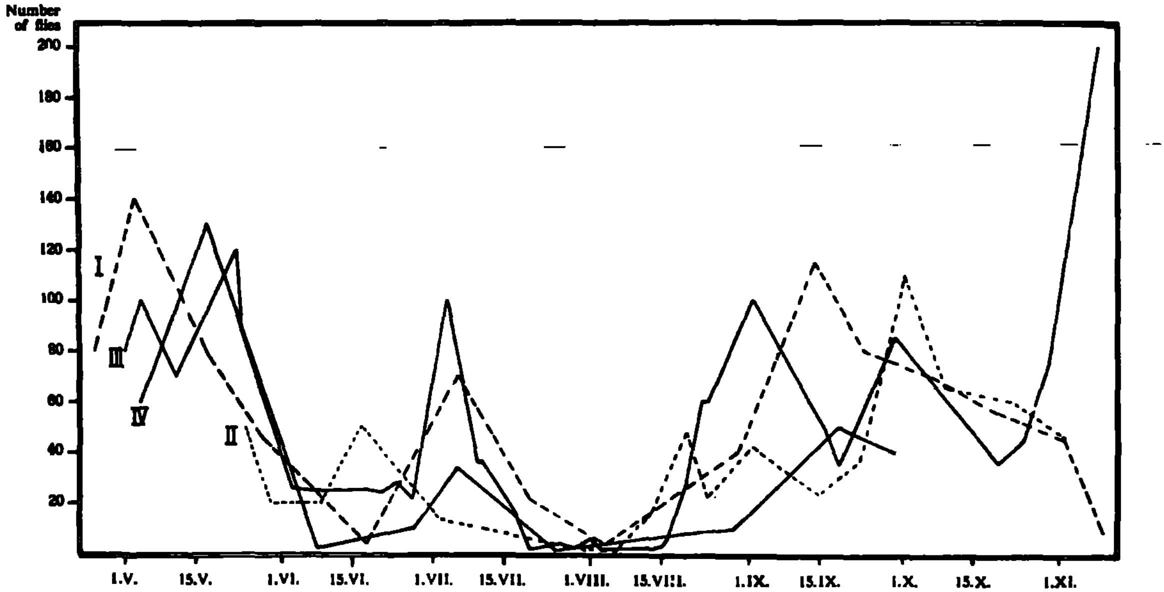


Fig. 49. Occurrence of *Scopeuma stercorarium* through the year in three localities (I and II Villingerød 1938 and 1937, III Løvbjerggaard 1938, IV Grønholt I 1938).

with cattle as well as with dung, and his method of counting Scopeuma was to record the highest number observed on a single pat. His results for three localities in 1937 and 1938 are shown in Fig. 41.

The disadvantage of this method of counting is that it takes no account of the dispersion of the flies on the other pats. This is illustrated in Hammer's curve for Løvbjerggaard 1938 (Fig. 41, Hammer's Fig. 49.), where the increase from the end of October was due to the fact that the cows were kept inside after 25 October, leaving only 5 heifers in the field. The number of droppings was accordingly reduced to about a quarter of the previous total and the flies congregated on the few droppings that remained. Thus, although the actual number of flies probably decreased, the number on any one pat was higher than when there were many more pats.

Another possible source of error in Hammer's method was that he said that in the summer months the flies are only seen when the sun is not too bright. This is contrary to my own observations that Scopeuma was usually abundant during the hottest time of the day, in the early afternoon.

Hammer (1941) suggested that the low numbers of flies in summer was due to the adults being killed by the heat when the temperature was over about 25^{o}C, and that possibly death was brought about by the accumulative effect of a succession of hot days. Hammer also recorded the fatal effect of high temperature on newly hatched larvae.

In early summer (mid June - end of July) at Løvbjergaard in 1937 Hammer made sweeps in the grass with a net and dissected the catch. Only ten sweeps were made each time and so numbers caught were rather small. The results showed that immature flies were present in the vegetation during the low numbers of mature adults. The presence of mature adults also showed that they moved into the vegetation after oviposition.

No explanation is offered as to how such a high autumn peak could have been achieved with such mortalities of eggs, pupae and adults in the two months previously. This autumn population is regarded as comprising flies of the third, fourth and fifth generations.

Hammer's work was very strongly criticised by Darwish (1954) who proposed completely new theories to account for the summer decline in numbers of Scopeuma. Hammer's suggestion that attacks by Empusa muscae were partly responsible for the decline was discounted by Darwish as playing any part in the summer decline in either 1952 or 1953 in Midlothian. Predation on the eggs of Scopeuma by the staphylinid Philonthus marginatus was also discounted as being significant.

Darwish gave no indication of what the adult Scopeuma population on the dung was like. His concepts of the succession of events in 1952 and 1953 are shown in Fig. 42.

Darwish only discerned two generations in 1952 (Fig. 42), presumably corresponding to a 2-peaked curve, with an intervening phenomenon of aestivation by the adults. From the diagram presented for 1953 Darwish recognised a peak of population during July as well as the spring and autumn peaks. Aestivation (described as aestival imaginal deapause) was deduced to have taken place in adults of part of the second generation and in the whole of the third generation.

The information from which Darwish produced these summaries of events was obtained from the results of emergences of adults in cone traps from cow pats collected in the field. It must be emphasised that the adult diapause postulated was not a proven fact, but merely a hypothesis to explain the results obtained from his methods.

One important statement which greatly influenced Darwish's interpretation of his own results was that no individuals completed development from eggs laid on or after 6 August 1952, nor from eggs laid on or after 14 August 1953. He unfortunately equated the absence of adult emergence with

Events in 1952

Fig. 42. Succession of generations of *Scopeuma stercoraria* as described by Darwish (1954).

Events in 1953.

WINTER Preimaginal Development Interrupted.
(=Hibernal Pupal Diapause)

↓

Adults Mature Directly.

↓

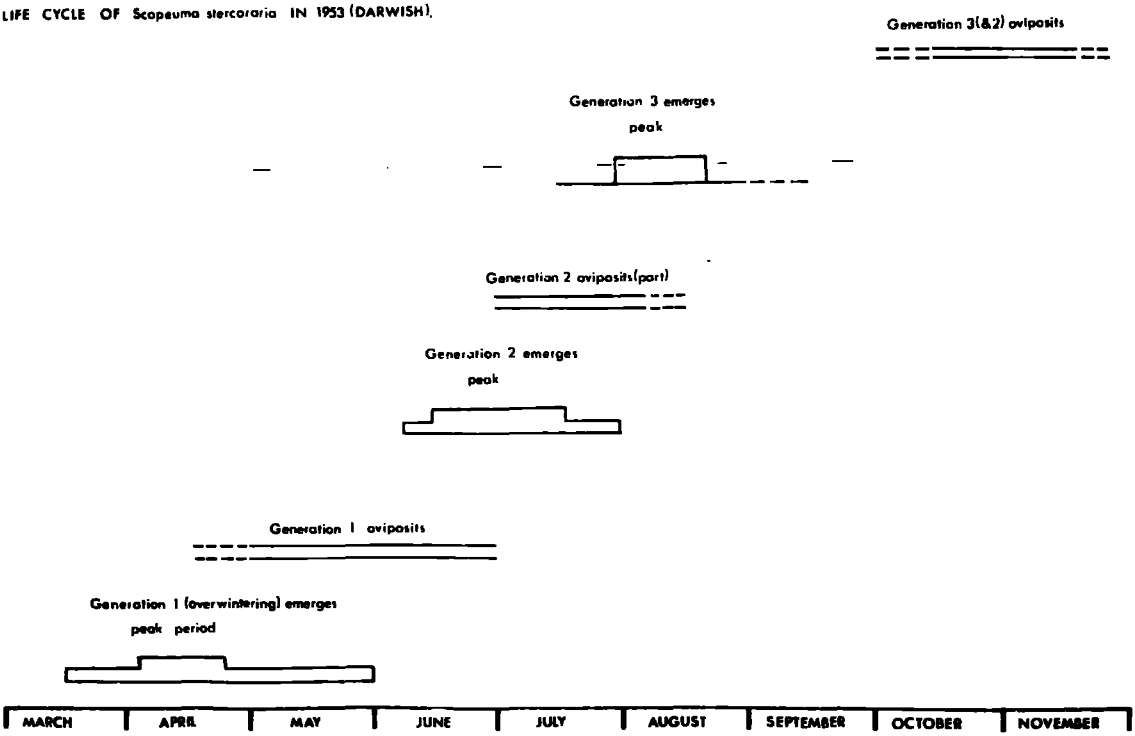
Preimaginal Development Uninterrupted.

↓

SUMMER Adults With Delayed Maturity.
(=Aestival Imaginal Diapause)

Probable Succession Of Events For Scopeuma stercoraria In 1952. (Darwish)

LIFE CYCLE OF *Scopeuma stercoraria* IN 1953 (DARWISH).



a lack of oviposition. The presence of immature flies well after these dates in both 1964 and 1965 showed that this situation did not occur at Houghall.

No dates are given for the duration of the generations in 1952, but Darwish states that there were two peaks and there was no June peak. To explain this situation he postulates that the adults emerging from eggs laid in spring must delay their achievement of sexual maturity until the autumn. The appearance of a third generation in 1953 presented Darwish with a problem. Because of his statement against the possibility of any emergence after August 14, he deduced that the flies of the autumn peak must have emerged before the end of August and spent late summer as adults. This third generation was smaller than either the first or second generations and unlikely to represent the whole progeny of the second generation. It was not large enough to account for the large autumn population and so a more complex explanation was produced. This was that part of the second generation was assumed to have matured normally and produced the July peak, but the rest of this generation delayed its sexual development until October. The whole of the third generation delayed its sexual development until October so that the autumn population was composed of a mixture of the third and part of the second generations. I only observed a delay of sexual maturity in conditions of starvation, and the maximum delay was about 1 month. Starvation is unlikely to occur naturally in summer. Darwish found no evidence of either the mode of location of adult aestivation so that its postulation is to try to explain an absence of emergence of adults from dung.

Both Darwish and Hammer seemed unaware of the fact that eggs are being laid continuously and that only the spring peak emerges as anything like a generation. My age-structure histograms show that immature flies can be found all through the season.

Lawrence (1954) studied the larvae of coprophilous insects, by obtaining 4, one-inch cores of dung from each of 10, pats per month, the pats having previously been marked on deposition. He admits that only marking pats in the open deposited during the day will not give a true picture of the insects studied. In his Fig. 41, Lawrence presents histograms of the percentage of pats containing larvae throughout the year. April and May, October and November have the highest infestation rates, while December, July and August have no larvae in the pats at all. This figure is only for pats in the open. He states that larvae of Scopeuma, Copromyza and Psychoda were, however, found abundantly in summer in pats in almost continuous shade.

Lawrence criticises the suggestion that a two peaked curve (Hammer 1941) is caused by two generations as the duration of development is only 20 - 30 days. He says that the summer decline may be more apparent than real, due to a change in habit of the adults which continues to breed in the shade or in woodland. He supports this contention by quoting figures of Williams (1935) where high numbers were caught at night in light traps in July and August as well as in spring and autumn. Some individuals were caught in the first 3 months of the year and as many as 71 in December. Most of the Scopeuma caught by Williams entered the traps one and a half hours after sunset and than at a steady lower level for the rest of the night.

The chief factor which determines the numbers of immature individuals entering the adult population must be the climate, affecting hatching success by its effect on dung crust formation. The changes in size of the mature Scopeuma population depend on the proportions of each age group and their mortality rates.

Section 3. BEHAVIOUR STUDIES ON Scopeuma stercoraria.

1). Diurnal activity from counts.

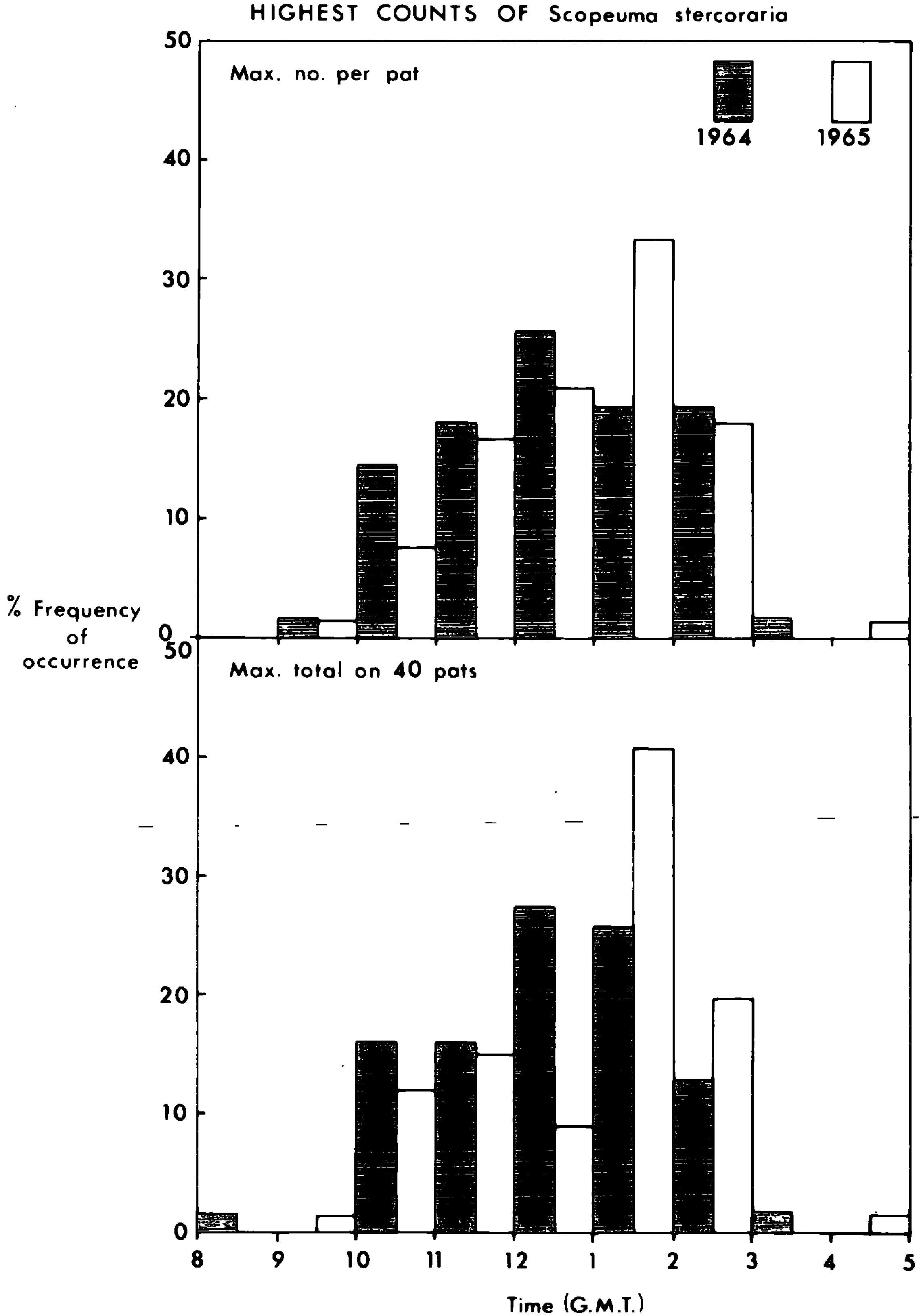
Counts of S.stercoraria on cow pats were made for several hours each day throughout the 2 seasons of the study to obtain an index of the population fluctuation. During these counts information on the diurnal activity of the flies was also obtained.

The frequency distribution of the hour at which the highest number of Scopeuma on any pat, and the maximum count on 40 pats occurred is shown in Fig.43. for the 2 seasons. The peak of activity occurred most frequently in the early afternoon, which corresponds mainly with the time at which the cows were taken to be milked. This was usually at about 1.15p.m. G.M.T. during summer and about 2,15p.m. G.M.T. when B.S.T. ended. As described on P. 80, just before the cows are taken to be milked there is usually mass defaecation as the cows rise from their midday rest. This large amount of fresh dung dropped at one time usually attracted large numbers of Scopeuma. These tended to remain on the pats longer than usual since no more pats would be dropped until after the cows returned, nearly 3 hours later.

The drop in frequency of maximum numbers between 12.00 and 1.00p.m. in 1965 was mainly due to the frequent occurrence of the cows' midday rest. In 1964 the hour between 12.00 and 1.00p.m. had the highest frequency of maximum numbers. The absence of a drop in frequency like that in 1965 was probably a). Frequency distribution (%) of the hours during which the highest no. of _S. stercoraria_ occurred on any pat in 1964 and 1965.

Fig. 43

b). Frequency distribution (%) of the hours during which the maximum count of _S. stercoraria_ on 40 pats, occurred in 1964 and 1965.



HIGHEST COUNTS OF Scopeuma stercoraria
Max. no. per pat
1964
1965
Max. total on 40 pats
% Frequency of occurrence
0
10
20
30
40
50
8
9
10
11
12
1
2
3
4
5
Time (G.M.T.)

because the warm dry weather in early summer not only caused the flies to appear earlier in the day but also reduced the growth of the grass. The cows had larger areas of field available to graze throughout summer and rarely rested together as they did in 1965. Consequently there was no mass defaecation before they were taken to be milked. The more frequent rain in 1965 probably caused the flies to concentrate their breeding activity into a shorter period in the day thanin 1964.

The effect of cow behaviour on Scopeuma activity in 1965 can be seen in Table 14. The % frequency of the occurrence in each hour of maximum numbers of Scopeuma on 40 pats was compared with the % of these hours when counts were made with all or most of the cows lying down at the start of the count.

Table 14. Relation between cow behaviour and maximum numbers of Scopeuma in 1965.

Time G.M.T.	9.10.	10.11	11.12	12.1	1.2	2.3
% hours at each time started with cows resting at start of count.	70	52.6	45.8	58.0	41.9	0
% frequency of max. no. on 40 pats counted at same times.	1.5	12.1	15.1	9.1	40.9	19.7

Cows were put back into the field about 8.00a.m. after the morning milking and usually grazed for an hour or so before resting. Of the counts made between 9 and 10.00a.m., 70% were started when the herd was resting. Corresponding with this high figure the maximum numbers of Scopeuma only occurred during this hour with a frequency of 1.5%. This frequency increased throughout the morning as the cows grazed more actively, producing increasing amounts of fresh dung. The midday rest is clearly shown by the rise in frequency of counts made with the herd resting and its effect by the drop in % of maximum numbers. Although the cows were usually out of the field between 2 and 3.00p.m. G.M.T., high numbers of Scopeuma frequently occurred at this time. This was partly due to the variation of the time when the cows were taken to be milked, and partly to an increase in flies moving on to pats dropped early in the previous hour.

There was a slight difference in the latter half of the season, 1965, in the time of the morning rest. From April to July, 100% of counts between 9 and 10.00 a.m. were started when the cows were resting. The figure for counts between 10 and 11.00 a.m. was 27.7%. From August to November only 40% of counts between 9 and 10.00 a.m. started with the herd resting whereas the figure for counts between 10 and 11,00 a.m. was 68.7%. This mainly reflected on the colder weather later in the year and possibly also on the shorter grass, causing the cows to graze for a longer period before they took their first rest.

2). <u>Effect of climate on numbers of flies during the day.</u>

A general principle of the behaviour of *Scopeuma* is that numbers on the dung increase as temperature increases, and they leave the dung when the temperature falls. A simple increase in numbers until the maximum temperature occurred followed by a decrease, was rarely found, mainly because of the irregular deposition of fresh dung. Increases in speed or change of direction of the wind can modify temperature-related increases in *Scopeuma* numbers. Rain showers for even a short period can interrupt a normal pattern of diurnal activity, which is not usually resumed after the rain has stopped.

The counts of *Scopeuma* on 40 pats were analysed as to whether or not the maximum number of flies occurred at the same time as the maximum temperature. The days when these two maxima did not coincide are listed with reasons for the deviation.

Table 15 shows that 1964 and 1954 showed similar patterns for each season. In spring and autumn of both years there was a slight excess of days when the highest number of *Scopeuma* on 40 pats was recorded at the same time as the maximum temperature. The days during the summer months of both years when the two maxima coincided were much fewer than the days when maximum numbers occurred at a "lower" temperature.

Table 15.

Diurnal Activity of S. stercoraria

	Days when counts made	Days when max. nos. coincided with max. temps.	Days when max. nos. did not coincide with max. temps.	Days with insufficient data.
1964				
May and June	45	15	14	16
July, August and September	57	19	32	5
October and November	27	11	11	5
1965				
April, May and June	35	16	11	8
July, August and September	41	12	19	10
October and November	12	6	3	3

Out of a total of 217 days when counts were carried out there were 47 days with insufficient data for the factors affecting diurnal activity to be analysed. The main reasons for this lack of data were persistent, heavy rain, insufficient records of temperatures or because other work had priority over counts.

Mass defaecation occurred in many of the counts when maximum numbers coincided with highest temperatures so that it is not easy to separate the response to heat from the response to the smell of fresh dung. Tables 16 and 17 show the analysis of reasons for lack of correlation between numbers and temperature.

In May and June 1964 (Table 16), one possible factor responsible for erratic diurnal activity in Scopeuma on most days was low relative humidity. This possibly accounted for 5 out of the 14 days in this period when maximum numbers did not coincide. Low relative humidity may have accounted for 5 of the 32 days of unusual diurnal activity during the late summer months. This contrasts sharply with 1965 (Table 17) where low relative humidity perhaps accounted for only 1 out of the 33 days of abnormal diurnal activity in the whole year.

Rain showers whether short or long, heavy or light, disturbed behaviour of Scopeuma so that even when conditions returned to normal after the shower the flies rarely resumed

Table 16. Probable reasons for lack of coincidence between maximum numbers of Scopeuma and max. temps. in 1964

	Probable Reason		Nos. of Days This Occurred.
May and June	1). Max. nos. after mass defaecation; max. temp. earlier or later in the day		2
	2). Rain disturbed behaviour of flies		3
	3). Low relative humidity (51-69% R.H.).		5
	4). Cows moved into another field		1
	5). No obvious reason.		3
		Total	14
July, August and September	1). Max. nos. after mass defaecation; max. temp. earlier or later in the day.		10
	2). Rain disturbed behaviour of flies		4
	3). High winds reduced fly nos. before max. temp. reached,		2
	4). Low relative humidity		5
	5). No obvious reason		11
		Total	32
October and November	1). Max. nos. after mass defaecation; max. temp. earlier in the day.		4
	2). Rain disturbed behaviour of flies		2
	3). Sky became overcast as temp. rose to maximum. Flies fewer.		2
	4). Cows taken in very early, pats aged as temp. increased.		1

.... Table 16 continued.

Probable Reason	Nos. of Days This Occurred
5). No obvious reason	2
Total	11

Table 17. Probable reasons for lack of coincidence between maximum Numbers of Scopeuma and maximum temperatures in 1965.

	Probable Reason.	Nos. of Days This Occurred.
April, May and June.	1). Max. nos. after mass defaecation; max. temp. earlier or later in the day.	5
	2). Rain disturbed behaviour of flies.	2
	3). Low relative humidity (54% R.H.).	1
	4). No obvious reason.	3
	Total	11
July, August and September.	1). Max. nos. after mass defaecation; max. temp. earlier or later in the day.	13
	2). No obvious reason.	6
	Total	19
October and November.	1). Max. nos. after mass defaecation; max. temp. earlier or later in the day.	3
	Total	3

their previous numbers. The flies to be found on dung during fairly heavy rain were usually ovipositing females.

Mass defaecation by the cows was the main factor responsible for the occurrence of the highest numbers of Scopeuma at temperatures lower than the maximum. Large amounts of fresh dung always attracted large numbers of flies, irrespective of the climatic conditions. Although Scopeuma usually arrived very quickly on fresh pats there were occasions when, because of the position of the dung, and the wind direction, the maximum numbers did not arrive on the dung until the second hour after its deposition.

Mass defaecation was responsible for the lack of coincidence between maximum numbers and temperatures on 16 out of 57 days in 1964. This factor accounted for 21 of the 33 days of irregular activity in 1965. Because the cows had more grass and behaved more as a herd in 1965, mass defaecation occurred more frequently than in 1964 when there was a shortage of grass.

Other factors which probably prevented Scopeuma from being most numerous at the time of highest temperatures are listed in Table 16 and 17. There were, however, 25 days in the two years when there was no apparent reason why Scopeuma did not respond to an increase in temperature. Temperature may have played an important part in this since it was not possible to measure either the radiant heat actually received by the insects, or the changes in relative humidity in the immediate vicinity of the flies, both on and off the dung. Nothing was known of the effect of age on diurnal behaviour and the age structure of the flies on the dung at any one time was not known.

3). Diurnal activity experiment.

a). Introduction.

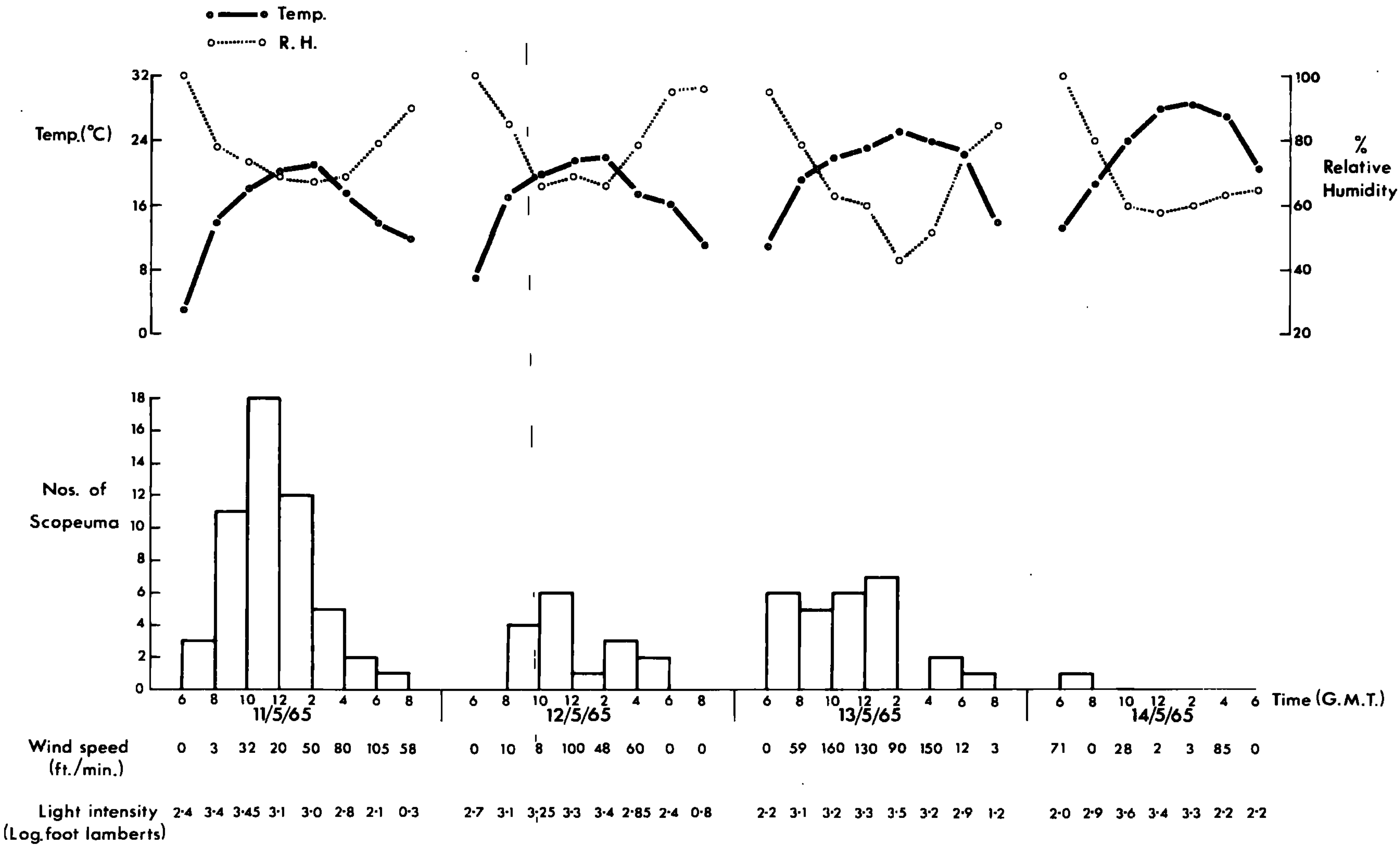
An investigation into the diurnal activity of coprophilous flies was carried out in May 1965 by Edge and myself. The experiment took place in a farm field adjacent to the Science Laboratories (Nat. Grid Ref. NZ 277415).

The flies were attracted to 30 beakers of horse dung, each placed in a glass dish containing detergent solution. The detergent was added to lower the surface tension of the water and so ensure that flies alighting on the surface would sink. The traps were first baited with dung at 6.00 p.m. G.M.T. on 10 May and were emptied at 2 hour intervals, day and night, until 6.00 p.m. on 13 May. Before each trap-emptying session records were taken of the wind speed, temperature, relative humidity (using a whirling hygrometer) and light intensity (using an exposure photometer).

Fresh horse dung had been collected and frozen and was thawed as required to replace dung which was ageing in the traps. Horse dung was used because the main purpose of the experiment was to attract coprophilous Sphaeroceridae. Continuous supplies of fresh dung were used in order to analyse the diurnal activity of the flies in relation to climatic conditions only, since the effect of cattle behaviour was eliminated.

Fig. 44. Numbers of <u>Scopeuma</u> <u>stercoraria</u> caught in baited detergent traps. For details see text.

DIURNAL ACTIVITY OF *Scopeuma stercoraria*



b). Results.

The numbers of *S. stercoraria* caught during the 4 day experiment are shown in Fig. 44. The climatic conditions recorded each time the traps were emptied are also shown for the period that *Scopeuma* were caught. The numbers of flies caught seemed to be mainly correlated with temperature. Apart from 14 May. the highest numbers of flies caught were at, or near, the highest temperature recorded.

The last day of the experiment, 14 May, may be disregarded since catches of all species were at their lowest on that day. This was probably because the majority of the local supply of insects had been caught during the first 3 days.

More flies were caught in the morning than in the afternoon, but the period of time during which they were caught was longer in the afternoon than in the morning. Equal numbers of male and female *S. stercoraria* were caught over the whole period, but there was a difference in the times at which they were caught. Two thirds of all the males were caught in the first day whereas females were caught in small number all the time, and were more numerous than the males on both the second and third days. This supports my view that the females only come on to dung to oviposit, which does not last very long, whereas males may stay on dung for long periods and may return each day.

When the accumulated percentages for each catch, based on each day's total were analysed, it was found that 50% of the flie were caught by the period 10.00 a.m. to 12.00 noon. There were not sufficient numbers of each sex for separate analysis of males and females. Between 2 and 6 S. squalida were caught each day at irregular intervals. No analysis was thus possible for this species, nor for S. suilla, of which only one individual was caught. This was the only occasion when S. squalida outnumbered S. suilla near Durham.

c). Discussion.

The captures of Scopeuma during this experiment showed a similar pattern to the results obtained from suction traps by Lewis and Taylor (1965). Their results fitted a normal distribution curve from 6.00 a.m. G.M.T. with the mean flight time at 1.09 p.m. for females and 1.20. p.m. for males. The flies caught in these suction traps probably included immature Scopeuma, whereas the ones caught in our baited detergent traps were almost entirely mature. Lewis and Taylor do state, however, that old flies of S. stercoraria, fly most at 13.00. hours. Williams (1935) caught fairly large numbers of Scopeuma during the night in light traps during the period March to February 1933-34, most flies arriving in the first 1½ hours after sunset. In the same period, 1934-35, only 17 individuals were caught, arriving in small numbers throughout the night. Edge (pers. comm.) caught a very small number of Scopeuma during the night in another diurnal activity experiment. As before, dung-baited detergent traps were used.

From all investigations on the diurnal activity of _Scopeuma_ it appears that they are usually most active during the middle of the day, but may be found at any time during the day or night. The numbers of adults found on dung are usually highest at the warmest times of the day, but their behaviour may be affected by other climatic conditions. The availability of large amounts of fresh dung may attract very large numbers of _Scopeuma_ during sub-optimal weather conditions. It was not possible to carry out continuous counts on cow pats at the same time as a trapping experiment, but it would be interesting to know how rain during the day affected the behaviour of the flies at night.

4). _Ageing of dung and its effect on Scopeuma numbers._

The study of the effect of ageing of dung on the population of _Scopeuma_ which it supports, is rarely possible in isolation from climatic factors. The afternoon of 11 October 1964, presented an opportunity for this, since the climatic factors remained nearly constant for just over 3 hours after the cows were taken from the field. Three counts were carried out during this period of constant conditions. The numbers of flies can therefore be examined with relation to the ageing of dung only, since no fresh dung was dropped during this time.

With a ground temperature of 9.1°C, a very light N.E. wind, and a sunny sky with only a few clouds, the total numbers of _Scopeuma_ fell from 2,016 in the first hour, to 1,625 in the second and finally to 427 in the third. After this third count the temperature dropped to 5°C and to 1.9°C within an hour. The numbers of Scopeuma had, by then, dropped to 2. No fresh dung was dropped after the counts started because the cows were put into another field after being milked.

The sex ratio in the 3 counts dropped from 2.95 males : 1 female at first, to 2.77 : 1, and finally to 2.75 males : 1 female in the last count. There was thus a fairly constant reduction of numbers of both sexes.

Three pats were noted in the second and third counts, and were examined again at the end of the third count. At the start of the second count, begun at 2.25 p.m. G.M.T. the 3 pats bore 129, 74 and 18 flies. By 3.40 p.m. these numbers had dropped, respectively, to 48, 30 and 13 flies and by 4.20 p.m. to 5, 5 and 0.

Investigations into the effects of strung-out pats on Scopeuma had not yielded any consistent results on normal days. Sometimes there was a higher mean of flies on pats which had been dropped as a line of small pieces than on pats dropped in one piece. At other times the reverse situation would occur, or the 2 means would be the same. On the afternoon of near-constant climatic conditions, however, a constant pattern emerged. Although the number of strung-out pats recorded with flies dropped from 11, to 8 in the second count, and finally to 4, the mean numbers of flies on these pats was higher than the means for normal pats in all 3 counts. This is shown by the following data:

Time:	12.55p.m.	2.22p.m.	3.40p.m.
mean nos. on strung-out pats:	76.73	53.88	14.00
mean nos. on normal pats;	40.41.	37.31.	10.31.

The reduction in numbers of flies from the first count to the next was greater on the strung-out pats than on normal pats. This might be due to the fact that smaller pieces of dung dried out more quickly because of their greater surface area in relatio to their volume. From the second to the third count, however, the reduction was slightly greater on the normal pats. This suggests the possibility that the presence of fairly large numbers on the strung-out pats may have acted to stimulate the individuals to stay, even though the attractiveness of the dung was declining.

The possibility of some sort of social interaction by large numbers stimulating the flies to remain longer on one piece of dung, deserves further study. Many cases were noted during the study where a few pats maintained large numbers of Scopeuma, or even increases then, while other pats were losing their flies. These pats often kept their high numbers when fresh pats were dropped quite near.

5). Aggregation of *Scopeuma* on cow pats.

The dispersion of animals within a habitat can be assessed quantitatively and analysed particularly to examine any departure from randomness. Such non-random distributions have been termed under and over-dispersed. Confusion arose over which term to apply to a particular dispersion. Salt and Hollick (1946) used Fisher's 'coefficient of dispersion' to examine wireworm populations, and found that the coefficient was high for young larvae which were under-dispersed, or aggregated. This was attributed to the fact that eggs were laid in clumps and the young larvae did not move far. As they grew older the larvae dispersed more until the coefficient approached unity, indicating random dispersion.

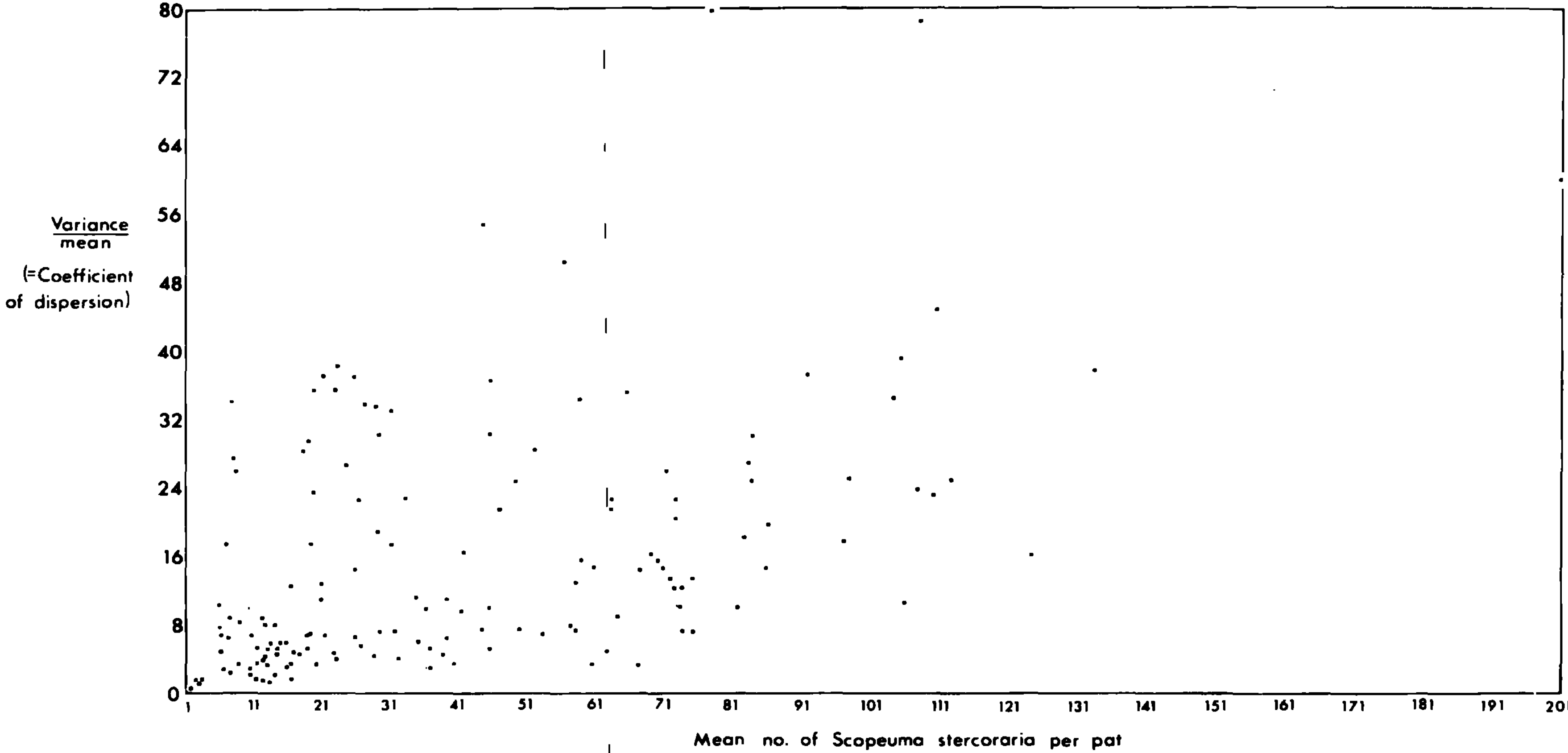
Greig-Smith (1952) and Goodall (1952) described as over-dispersed the situation where the coefficient of dispersion (= variance : mean ratio) was greater than unity - the same as Salt and Hollick's under-dispersed population. To try to avoid this ambiguity, Goodall(1952) suggested that 'aggregated' would be a better term to describe grouping. 'Even' dispersion might be an alternative to 'under-dispersion'.

The variance : mean ratio for indicating non-random dispersions has proved useful in both animal and plant ecology where it has been the method of analysis for numbers of plants or animals in quadrats. Skellam (1952) criticised this method on the grounds that it depended on the size of the sample. Clapham (1936) pointed out that although this relative variance (= variance/mean) was a useful tool, its value increased with an increase in mean density and then decreased at very high densities.

This system of analysis was used to examine the dispersion of adult Scopeuma on cow pats for any 40 pat count, while at

Fig. 45. Relation between the coefficient of dispersion (= Variance/mean) and mean nos. of Scopeuma on cow pats.

Relationship between the coefficient of dispersion and the mean.



the same time appreciating the limitations due to the method of study. Adult flies attracted to fresh pats are obviously aggregated within any area. Even if the cow pats were distribute at random, the flies on them could not be considered to be distributed at random within the field. For counting purposes cow pats were not chosen at random nor selected by a random technique. The flies were counted on the pats where they were most abundant. The analysis was carried out by treating the pats counted as if they were all contiguous and then seeing whether the flies were randomly distributed over these pats.

The size of a pat did not seem to have any bearing on the number of flies attracted, so that the unit of sampling was taken as the whole cow pat, and not any particular size of pat. To see whether the coefficient of dispersion increased with the mean, Fig.45 shows the variance : mean values plotted against the means of numbers of flies per pat. As can be seen, there is no clear increase, and in many cases there is a wide range of values for the coefficient for the same mean, thus eliminating the necessity for log. transformation of data (Quenouille,1950).

The main point of this exercise was to see how, for successive counts, the dispersion changed as the numbers increased or decreased. If there had been some system of random sampling the departure of the coefficient from unity could have been tested by the standard error which (as suggested by Bartlett, in Greig-Smith, 1952) is

$$s = \sqrt{\left(\frac{2}{N-1}\right)}.$$

For 40 pats, 2 standard errors would be ± 0.45. Only 2 values fell within the range 0.55 - 1.45, indicating random dispersion, and 1 was 0.22, indicating an even dispersion. This last value occurred at a time of very low numbers when nearly all the pats had only solitary flies on. In the vast majority of cases the flies were fairly highly aggregated so that comparisons would be a matter of degree.

Examination of the coefficient of dipersion for all counts on selected days indicated that the degree of aggregation showed very little correlation with the number of flies. In some cases the flies became more aggregated as the numbers increased, but in other cases reduced aggregation accompanied increased numbers. Where the change in aggregation followed a change in numbers, the rate of change was rarely the same. For a twofold increase in flies, there were up to tenfold increases in the coefficient of dispersion.

From an inspection of distributions of numbers of flies per pat, the presence of a few pats with very large numbers produced a high coefficient of dispersion. The pattern of the majority of pats was often almost a normal distribution curve with respect to the numbers of flies. This was true for most days, but even 2 or 3 pats with large numbers of flies would result in a vastly different situation in one count from the preceding count carried out before these particular pats had been dropped. The presence of such pats maintaining their *Scopeuma* numbers while the numbers on other pats decreased, ensured that a high level of aggregation would be maintained.

Although it is recognised that the proper use of the variance:mean ratio to detect non-randomness in a population depends on a random sampling technique, it has been employed in this study to detect excessive aggregation. Much of the aggregation in *Scopeuma* can be attributed to differences in quality of different cow pats. There were occasions, however, when very high degrees of aggregation pointed to some type of behaviour of the flies rather than to abnormal chemical constituents of certain pats. The possibility of some form of social interaction seems to be the only explanation whereby a few pats can maintain very high numbers of flies while other pats of the same age lose their flies. It did seem that the presence of large numbers of flies stimulated the flies to remain longer than they would have otherwise done. This may have been due to high numbers of females causing unpaired males to remain in the 'hope' of acquiring a mate.

The fact that *Scopeuma* were not distributed at random on the pats which they infested was one factor which would have worked against a mark and recapture technique. The distribution of pats bearing *Scopeuma* was another factor which was unpredictable and often varied considerably from one count to another. The importance of the wind direction added to the impracticability of estimating the population parameters by marking the flies.

Section 4.

LABORATORY STUDIES ON Scopeuma EGGS AND LARVAE.

1). Methods of culture.

Scopeuma adults were kept in 2 x 1.5 x 1.25 ft. cages of stiff muslin round a metal frame on a solid tray base. One side of each cage was of transparent plastic while another had a muslin sleeve of 6 in. diameter. A bottle of cotton wool soaked in sugar solution was always kept in each cage and renewed as necessary. Water was regularly sprayed through the muslin to maintain the humidity at a suitable level, to keep any dung moist and to provide drinking water.

The small mesh of the muslin prevented the escape of Drosophila, cultures of which could be opened inside the cage through the wide sleeve. Dishes of freshly thawed dung for breeding purposes could also be placed easily inside the cages. The cages could accommodate over 100 adult Scopeuma for long periods.

2). The effect of humidity on hatching success.

In order to assess the probable effects of dry weather on Scopeuma eggs it was necessary to test their ability to hatch when dried for various intervals. It is dificult to remove eggs from dung undamaged so the opportunity was taken of experimenting with 71 S. stercoraria eggs which were layed on the surface of very watery dung. These eggs had not been

Table 18.

Table of events of 71 eggs.

Hrs. after laying.	No. of eggs dried.	Hrs. after drying.	No. of eggs wetted	hours after wetting 1st. hatched.	hours after wetting last hatched.	total hrs. after laying.
24.15.	20	12.00	10	19.00	41.00	77.15
27.15	20	9.00	10	19.00	37.15	73.30
31.15	10	5.00	5	12.00(all)		48.00
34.15	10	2.00	5	00.15(all)		36.30

35.20 - 11 hatched

All eggs which had remained dry from 24.15 - 34.15 hours after laying were wetted 55.15 hrs. after laying, but none hatched.

pushed into the medium and so were easily removed.

The eggs were placed on a piece of muslin and washed free of any particles. The muslin was supported on a piece of metal gauze resting on 2 corks in water in a jar. The eggs and muslin were then given a final sprinkling before the lid was screwed on tightly. This was to preserve an atmosphere of high humidity around the eggs.

At various intervals after laying, some of the eggs were removed from the jar and placed on dry muslin in an open jar. When the few remaining eggs had hatched, half of each group of dried eggs was wetted and the time noted for these to hatch. The results are given in Table 18.

The results showed that larvae were unable to emerge from eggs dried up to within 1 hour before they were due to hatch. Rewetting the eggs within a few hours after drying enabled the larvae to emerge and limited success was even possible with eggs dried eleven hours before they were due to hatch, and then rewetted. ,

The inability of any larvae to emerge from eggs which were not rewetted for over 20 hours is in accordance with the observations of Larsen (1943) who found that no eggs hatched at or below 83% R.H. Larsen recorded only a 20% hatch at 93% R.H., which illustrates the susceptibility of this species to dessication.

Experiments on eggs of the blow fly, Lucilia sericata (Mg.)

by Davies and Hobson (1935) and Davies (1948) showed that although egg development was retarded by reduced humidity, a fairly large proportion of eggs completed development even at 25% R.H.. The ability of fully developed larve to withstand imprisonment within the hardened chorion of the egg-shell was about 3 hr. at 37°C, having been incubated in moist conditions to within 20 min. of hatching. Hatching, on return to moist conditions, was quite high, but after longer periods of dryness greater mortality occurred, and 4 hours of dryness seemed the limit.

The resistance of Scopeuma larve to imprisonment within the egg seemed higher than that recorded for Lucilia but more work is needed. My experiment did show, however, that warm dry weather, with the consequent formation of a hard crust on the cow pats, would be lethal to Scopeuma eggs unless rain occurred within a few hours. Larsen (1943) showed that newly hatched Scopeuma larvae are alsohighly prone to dessication, so that the egg and first instar larval stages seem to be the most vulnerable in the life history of Scopeuma species.

3) The Effect of Temperature on the duration of development from egg to adult.

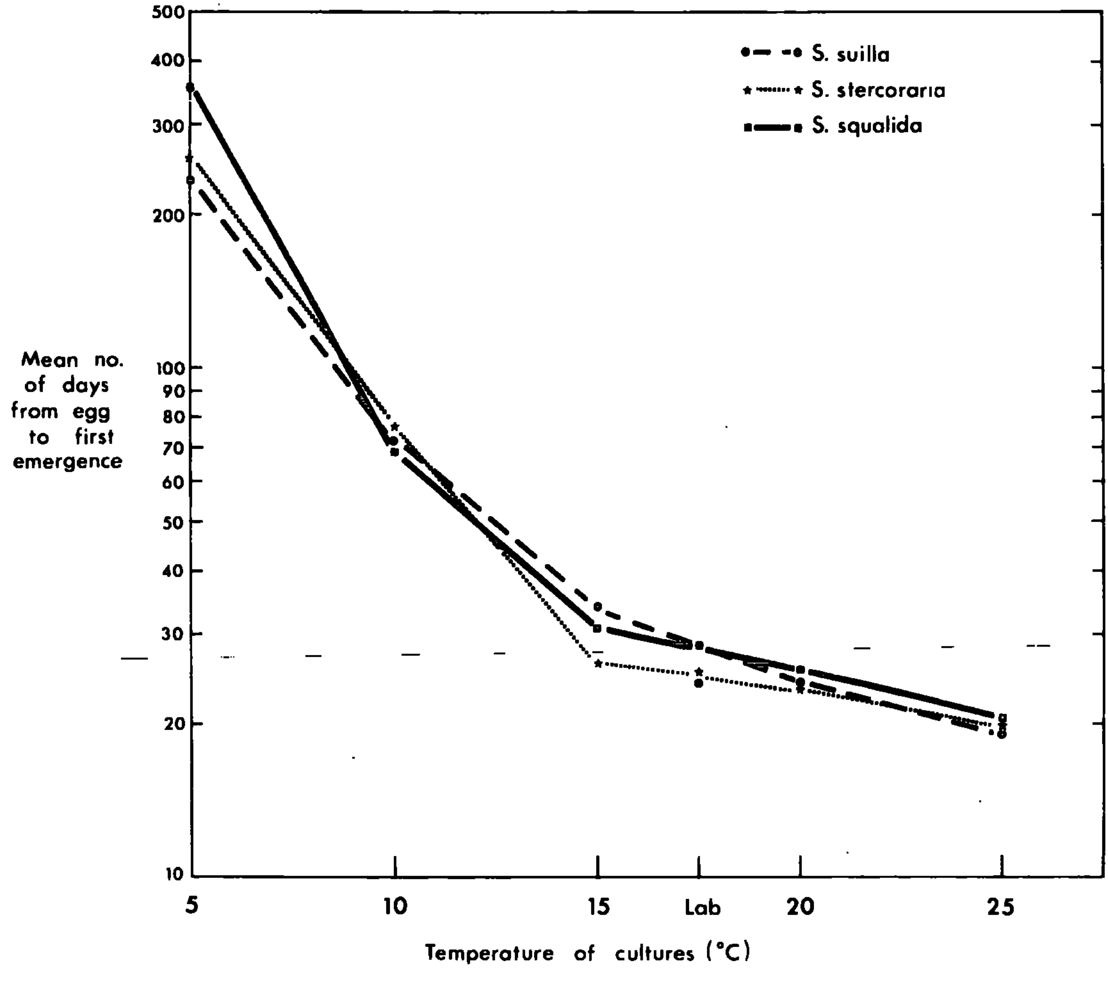
Eggs and subsequent stages from all 3 species of Scopeuma were kept to maintain breeding stocks. The original purpose of keeping the eggs was to see if there was any deviation from equality in sex ratios on emergence which might account, partly at least, for the excess of males in the field. Although this investigation proved negative it did lead to other studies to investigate the possible difference between the 3 species with respect to the times of development at different temperatures.

Constant temperature of 5, 10, 15, 20, and 25°C were used for the temperature studies, but many batches of eggs were also kept in the laboratory where there was a less constant temperature of about 18 - 20°C, occassionally dropping below 18°C. Flies were removed from the containers each day as they emerged and the sex and date of emergence were recorded. The flies had to be removed as soon as possible after emergence because if left they ate the adults emerging later. Each fly was sexed for information for a study on the patterns of adult emergence, to be described later.

Fig. 46 shows the mean times of first emergences from egg batches of all 3 Scopeuma species. The results show that there is no straight line relationship between temperature and pre-imaginal development. Development at 5° and 10°C is very much slower than at temperatures of 15° and above, There is only a difference of 6 days between the times from oviposition to the first eclosion at 15°

Fig. 46. Mean times of first adult emergences from egg batches of 3 Scopeuma species at different temperatures.

TEMPERATURE AND DEVELOPMENT IN *Scopeuma* SPECIES



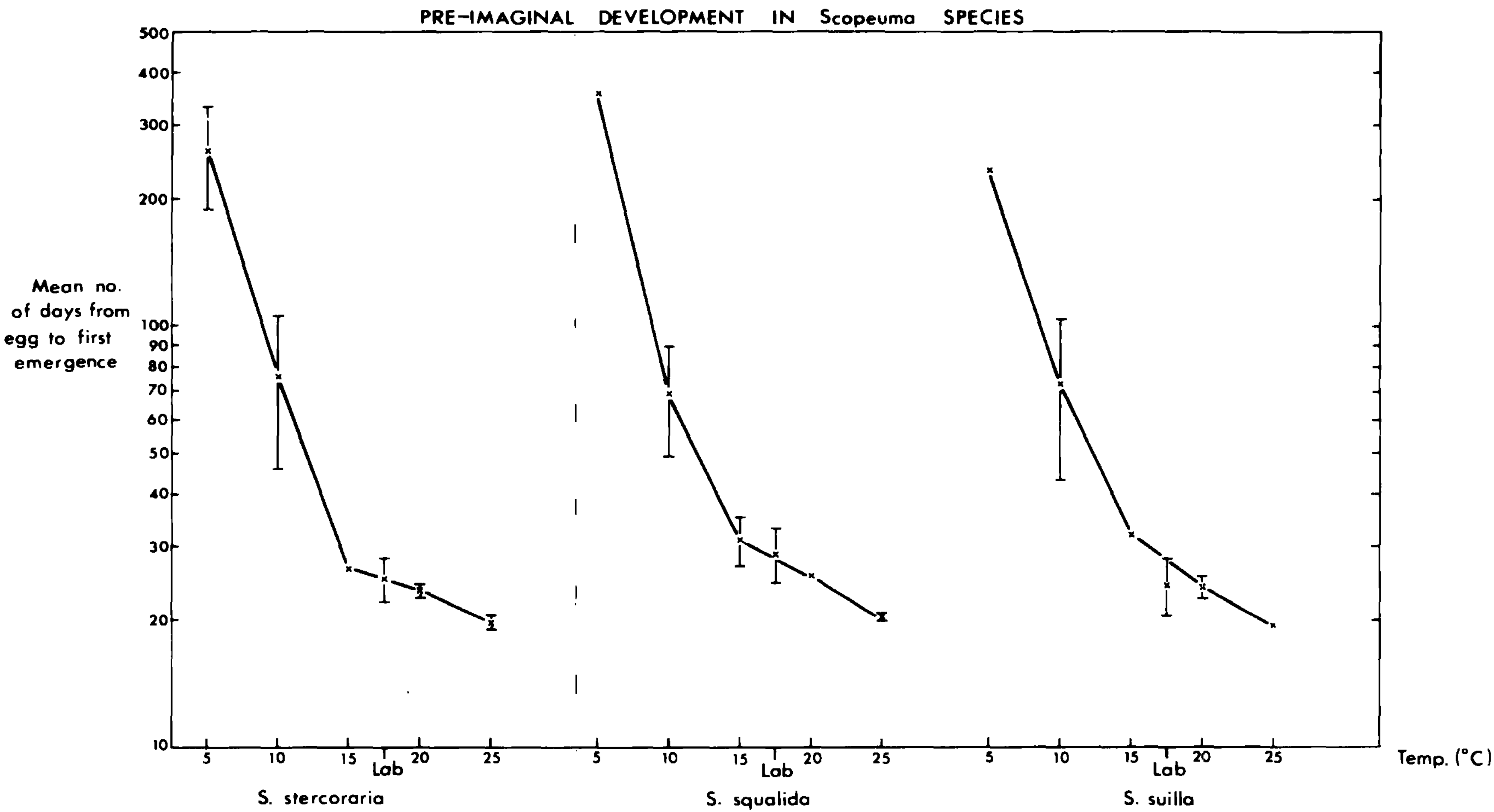
and 25°C. Pre-imaginal development at 10°C varied from 2-3 times as long as at 15°C in the 3 species. S. suilla takes 7 times as long to develop at 5°C as at 15°C whereas S. stercoraria and S. squalida take, respectively, 10 and 12 times as long.

The shortest time taken for an adult to emerge at 10°C was 31 days, and at 5°C was 92 days. The figure for 10°C was obtained from a batch of eggs laid by a female which had been reared at 10°C. Any possible effect of maternal acclimatisation on the development of the eggs only affected the first emergences because it was another 156 days before the last adult emerged.

The mean times taken for eggs to start emerging as adults at laboratory temperatures are also shown on Fig.46, midway between 15 and 20°C. The figure for S, suilla is very near to the development time at a constant 20°C. S. suilla was only cultured on a large scale later in the study and the laboratory temperatures may have been closer to 20°C than they were when the other 3 species were kept.

Fig. 47 shows the curves for times of development from egg to adult at different temperatures for the 3 species separately. Where sufficient results were obtained, the standard deviations are also shown. The main feature from these figures is that S. squalida has, at 10°C, a much smaller standard deviation (± 20.65 days) than either

Fig. 47. Means and standard deviations for times of development from egg to first adult appearance for 3 *Scopeuma* species at different temperatures.



PRE-IMAGINAL DEVELOPMENT IN Scopeuma SPECIES
Mean no. of days from egg to first emergence
500
400
300
200
100
90
80
70
60
50
40
30
20
10
5
10
15
Lab
20
25
Temp. (°C)
S. stercoraria
S. squalida
S. suilla

S. stercoraria (± 31.38) or *S. suilla* (±30.61). This could indicate a closer adaptation to life in low temperature areas such as the high Pennine moors around Moor House where it is the only one of the 3 species that is more abundant than in lowland areas,

There were no significant differences between the 3 species with regard to the mean pre-adult development times at each temperature. Under laboratory conditions (~18-20°C) however, both *S. stercoraria* and *S. suilla* had significantly shorter development times than *S. squalida*. The difference between the mean pre-adult development times at laboratory temperatures of *S. stercoraria* and *S. squalida* was 2.9 times the standard error of the difference. When *S. suilla* was compared with *S. squalida*, the difference between the means was only just significant, being 2.08 times the standard error.

These differences might explain why *S. stercoraria* and *S. suilla* are more numerous than *S. squalida* in lowland areas. No difference in times of development at any temperature were found between *S. stercoraria* and *S. suilla*. More results are needed for all 3 species so that more tests may be applied.

At 10°C adults of most egg batches started to emerge about 60 days after the eggs were laid. There were a few batches from all 3 species, where eclosion did not take place until after 103-155 days after oviposition. In case these batches had undergone diapause at some stage, the development times were analysed in 2 ways. All the results were included to give the following means and standard deviations: S. stercoraria ($\bar{x}$ = 76.39 ± 31.38 days), S. squalida ($\bar{x}$ = 69.15 ± 20.65 days), and S. suilla ($\bar{x}$ = 73.6 ± 30.61 days). These means were compared and no significant differences were found. All development times of more than 100 days were then excluded, and the remaining results gave the following figures : S. stercoraria ($\bar{x}$ = 58.5 ± 14.97), S. squalida ($\bar{x}$ = 63.54 ± 5.21) and S. suilla ($\bar{x}$ = 60.6 ± 5.95). No significant differences were found between any of these smaller means.

Larsen and Thomsen (1940) found the times of development from egg to adult fly to be 31.08 days at 14°C, and 17 days at 23,9°C, with a threshold of development at 2.05°C. Their lowest temperature for development studies was 5.8°C at which adults appeared after 93 days. I obtained this result once at 5°C, only the first adult emerging after 92 days, others of the same batch of eggs continued to emerge for a further 90 days. Apart from this batch of eggs no adults emerged at 5°C in less than 213 days. The longest period to first emergence was 381 days for S. stercoraria, 428 days for S. squalida and 249 days for S. suilla. Darwish (1954) doubted the wisdom of extrapolation to the lower temperatures, of curves relating development rates to temperature.

One case of diapause for over 2 months in the pupal stage was discovered by Larsen and Thomsen (1940) at 15°C but the first adults emerged 1 month after the eggs were laid. I did not obtain any delayed emergence at this temperature. At 25°C the shortest duration of development which I found for S. stercoraria was 18 days, and 19 days for the other 2 species; Larsen and Thomsen (1940) found 15.58 days to be the shortest development at 25.3°C.

Although about 25°C may be the temperature at which Scopeuma species develop most rapidly, there are dangers in the more rapid drying up of the dung. Slightly slower rates of development at temperatures down to 15°C are compensated by reduced risk of dessication of the medium. Development at 10° and 5° may be greatly retarded, especially if diapause occurs, but the adults are as large and vigorous as those which develop at higher temperatures.

4) The effect on adult emergence of changing temperatures during the development period.

While the effects of temperature on development were being studied it was decided to investigate any possible susceptibility to changes of temperature by different instars. Some egg batches were therefore placed in different constant temperatures and then moved to another temperature after various intervals. This was done in order to subject one or other instars, or the pupae, to the change in temperature, and to see what effect increases and decreases of temperature had.

In most cases the adults first emerged about the same time as they would have in a constant temperature of that to which they were moved as larvae. When pupae were moved from a low temperature to a higher one, the adults emerged as if they were still in the low temperature. When the reverse situation occurred the new low temperature delayed emergence from the date expected at the constant higher temperature. The delay was not great enough to bring it near to the time expected from a constant low temperature.

Some examples will illustrate the development rates under these conditions. S. stercoraria eggs moved from 5°C to 10°C after 1, 2 and 3 weeks emerged in 60-69 days. These results fall within the range of the mean and standard deviation of emergences at a constant 10°C ($\bar{x}$ = 76.38 ± 31.38 days). Eggs kept in 10°C for 39 days and then moved into the laboratory emerged 7 days later. This result again comes within the range for a constant 10°C. When eggs kept in the laboratory for 29 days were transferred to 5°C, eclosion was delayed for a further 25 days. This result was much longer than emergences from cultures kept at laboratory temperatures ($\bar{x}$ = 25.23 ± 2.67 days), but was far short of the range for a constant 5°C ($\bar{x}$ = 259.75 ± 69.28).

One result, of emergence after 34 days, came from a batch of eggs kept in the laboratory for 2 weeks, put at 10°C for 2 weeks and then moved back to the laboratory. This figure is outside 2 standard deviations from the laboratory temp. mean, and nearly 1½ standard deviations from the 10°C mean.

All experiments involved a change from one temperature to another and occasionally back to the original temperature again. One batch of eggs however was subjected to 3-5 days in each of 10°, 15° and 20°C and then placed in 25°C for the last 10 days. The first emergence was 22 days after the eggs were laid which is more then 2 standard deviations from the mean for 25°C ($\bar{x}$ = 19.89 ± .98 days).

Other studies were carried out on the effect on all larval stages at various periods at -20°C. This was carried out by placing different cultures in the deep-freeze refrigerator for periods from 15 minutes to 18 hours, and then putting them back in the laboratory. All batches treated in this emerged within the range of one standard deviation either side of the mean development time atlaboratory conditions in S. stercoraria and S. squalida. No cultures of S. suilla were available for these experiments. The only occasion where this low temperature affected the development was in the case of a batch of eggs, laid on 9 February, 1964, which was put in the deep-freeze for 1 hour on every other day, from 11 February to 2 March, 1964, inclusive. The first adults emerged on 11 March, 1964, 32 days after the eggs were laid. This treatment only delayed emergence for 7 days beyond the mean for lab. temps.

Further experiments, involving both the effect of sub-zero temperatures and fluctuating temperatures, are needed to understand the effect of climate on all pre-imaginal stages. The experiments using the deep-freeze were carried out because I had observed in the field that successive hard frosts did not seem to delay significantly larval growth and subsequent pupation. Scopeuma larvae are certainly frost hardy and have a very wide temperature tolerance which is true also of the adults. This probably explains the very long season during which they may be found in the field.

5) Adult emergence in Scopeuma species.

Emergence of adult Scopeuma has previously only attracted attention in relation to the times at which the adults emerge each day, and the fact that females start to emerge before the males. Lewis and Bletchley (1943), found that S. stercoraria adults emerge between 06.00 hours and 20.00 hours, reaching a peak between 09.00 and 14.00 hours.

Larsen and Thomsen (1940) concluded that male S.stercoraria larvae fed for 1 day longer than female larvae which caused the earlier appearance of the females, and also the greater size of the males.

In my studies of 3 Scopeuma species, the features of adult emergence which seemed most interesting were the greatly increased periods of emergence at low temperatures, and the similarity between the species of the patterns of emergence of the 2 sexes.

1) The duration of adult emergence at different temperatures:

Many cultures of eggs of all 3 Scopeuma species did not produce adults after the first day of emergence, at high temperatures, or after up to 2 weeks at low temperatures. There are not enough figures to give standard deviations to the means. It is, however, possible to give some idea of the range of emergence spread at different temperatures, as shown in Table 19.

There was considerable overlap in the duration of emergence over the temperature range of 25-15°C, as can be seen in Table 19. The widest range was in cultures of S.stercoraria where there were up to 33 days between the first and the last adults to emerge from 1 batch of eggs at lab. temps.. There were probably some cases of diapause since the last adults to emerge from this batch did so 59 days after

Table 19. Duration of adult emergence from cultures of eggs of 3 Scopeuma species. Figures given are the mean number of days of emergence spread, and the range.

Temperature. °C	S. stercoraria. mean	S. stercoraria. range	S. suilla. mean	S. suilla. range	S. squalida. mean	S. squalida. range
25	3.78	2 - 5	3	-	2.5	2 - 3
20	6.4	3 - 12	7.17	4 - 15	3.25	2 - 4
15	8.5	4 - 14	13.5	11 - 16	5.67	4 - 9
Lab. temps.	10.65	2 - 33	5.8	3 - 11	7.1	3 - 12
10	111.56	46 - 241	113.65	33 - 327	1.77	69 - 310
5	165.88	90 - 254	189.67	178 - 208	-	-

the eggs were laid. There were 2 other cases of delayed emergence, one af 25 days and another of 24 days duration. The last adults of these 2 batches emerged after intervals of 50 and 51 days respectively after the eggs were laid.

It is difficult to see any advantage to the flies in the extended spread of emergence of this sort of magnitude at quite high temperatures. The situation at lower temperatures is much more easily understood. The mean emergence spread at 10°C was about 10 times that at 15°, and at 5°C the mean figure was about half as much again as that at 10°C.

There were examples for all 3 species of intervals from 9-11 months between the first and last emergences from any one culture at 5° and 10°C. The longest spread of emergence at 5°C was only a few days longer than that at 10°C for _S.stercoraria_ but much shorter for _S.suilla_. Only one culture of _S.squalida_ at 5°C emerged over any period, but this was for 46 days. As this was in a culture of only 19 eggs it has been omitted from the table.

The advantage to the flies in delayed emergence can be seen in relation to hibernation, especially at high altitudes. As the late winter-early spring weather is so changeable it is probable that many flies emerge during an early warm spell, only to be killed by severe late frosts or even snow. If all the hibernating pupae emerged as soon as the temperature rose above a certain point, it would be possible for almost entire populations to be wiped out by severe weather. By extending the period over which pupae will emerge a considerable proportion of adults will still survive even though all the early adults may have been killed.

The important point to note is that these cultures were all kept under constant conditions of temperature and, as far as was possible, humidity. A light in the constant temperature rooms and cabinets was on during the day to attract newly emerged adults to the top of the containers so that they could be seen easily. As Larsen and Thomsen (1940) pointed out, the factors inducing diapause in Scopeuma are unknown. From my records of irregular emergences of adults over a period of up to 10 months, it is difficult to see how the diapause is broken. Constant temperatures like those studied will not occur in nature, so that diapausing pupae in the field will probably respond to fluctuating temperatures. It seemed from the results of my dissections that immature flies were entering the adult population in spring over a period of several weeks.

There seemed no difference in size or viability between adults emerging from any culture over a long period of time. For example, in the widest emergence spread, that of a batch of S.suilla eggs, adults which emerged 389 days after the eggs were laid were no different from those which emerged first, 62 days after the eggs were laid. For this to have happened there must have been almost complete cessation of development, since metabolic processes at even a slow rate over such a long period of time would have depleted the food reserves of the larvae or pupae, resulting in much smaller or otherwise inferior adults.

There seemed to be no unified response by the pupae at any stage to any change, however slight, since the adults emerged continually over the whole of these long emergence periods. The pattern of emergence at 10°C and 5°C resembled an enormous extension of that at 15, 20 or 25°C.

The transfer of cultures from 1 temperature to another as described under heading 4) in this section did not have much effect on the emergence spread. The period over which adults emerged at the new temperatures always fell within the range recorded for those constant temperatures, with 2 exceptions. One involved the transfer of 1 culture of each of the 3 species of Scopeuma from 20°C to 5°C. The transfers were all carried out on the same day, but the cultures were at slightly different stages. Adults had started to emerge on the previous day in the S.stercoraria culture; they had just started to emerge in the S.suilla cultures, but no emergences of S.squalida had occurred. S.squalida adults emerged over a period of 17 days, while S.stercoraria adults had an emergence spread of 15 days. Both these results were outside the range for 20°C. S.suilla adults, on the other hand, completed their emergence in a period of 6 days, well within the range for 20°C.

The other exception was a batch of eggs transferred from 10° to 5°C 1 week after the eggs were laid. The only adult to emerge from these 12 eggs was a female which appeared after 535 days-the longest development recorded.

Two cultures of S.stercoraria were transferred to 10°C for 2 weeks after 2 weeks at lab. temps., and were then put back to lab. temps. for the rest of their development. Adults emerged from these cultures over periods of 94 and 84 days, falling in the range for a constant 10°C.

When 2 day and 7 day larvae were exposed to -20°C for ¾ and 1 hour respectively, in 2 S.stercoraria cultures, the adult emergence spread was extended to 52 and 44 days. Both these figures are well outside the range for at lab. temps. The 2 cultures were kept in the laboratory apart from the short period in the deep freeze. No explanation is offered for these extended emergence periods since other cultures with similar exposures to to low temperature emerged well within the normal laboratory range.

11) The patterns of adult emergence in Scopeuma species:

Larsen and Thomsen (1940) found from 12 cultures at 20°C that S.stercoraria females emerged over a period of 4 days and males over a period of 3 days, no males emerging on the 1st day. Most males emerged on the 3rd day of their emergence spread, which corresponded to the 4th day of the females' emergence. By weighing the larvae and pupae at intervals during the development of 20 eggs the Danish workers found that 10 larvae fed for 1 day longer than 10 others. Those larvae which stopped feeding first emerged as 10 females, mean weight 12.1mg. The 10 larvae which fed for 1 day longer emerged as 9 males and 1 female, mean weight 19.9mg..

The difference in weight between the 2 groups of larvae at the time they stopped feeding was about 2.2mg.. From the graph of Larsen and Thomsen it seems that the difference in weight of the adults was due more to the excess loss in weight by the female larvae after they stopped feeding, than to the increased weight in male larvae resulting from longer feeding.

It is open to question whether this extra day's feeding by the male larvae is the cause of the later emergence of the males. From over 100 cultures of the 3 Scopeuma species I found that the majority resulted in females and males emerging over 4-6 days, with the largest number of each sex emerging on the 3rd day of their respective periods of emergence. The pattern of frequency of emergence was that of 2 superimposed normal distribution curves, with the female emergence 1 day ahead. This pattern was generally true for constant temperatures of 15° and 20°C, and at lab. temps. Extended periods of emergence were due to small numbers of adults emerging at irregular intervals after the majority had emerged in the pattern described.

The most important point about these results is that both S.squalida and S.suilla have identical emergence patterns to S.stercoraria but there is no difference in size between the sexes of the first 2 species. This points to a genetical control of the time of emergence which may be typical of the genus. A difference of 1 day's feeding by male larvae can not be expected to account for more than 1 day's delay in emerging. It was rare for more than a very small proportion of females to emerge on the first day so that it was not a question of all the females emerging on 1 day and all the males on the next.

At 10° and 5°, the patterns of emergence of the 2 sexes of all 3 species were similar to the situation at higher temperatures, but over a longer period (1-2 weeks), followed by very long periods with occasional emergences of either sex. Where only small numbers of adults emerged, some cultures obviously did not show any particular pattern of emergence. This situation was also the case with cultures at a constant 25°C where no discernible pattern was obtained because of the small numbers of flies emerging.

The conclusions to be drawn from comparing the 3 species are that either: 1) the male larvae of *S. squalida* and *S. suilla* do not feed for longer than female larvae, or 2) the delay in male emergence in all 3 species is controlled by some factor other than time spent feeding. It was not true of all cultures however that females emerged first. Of 258 cultures studied at different temperatures, females emerged first in 166, males emerged first in 33 cultures and males and females emerged together on the first day in 59 cultures. There was no difference in the size of the males in cultures where males emerged first or at the same time as females.

Changes in temperatures during development, or exposure to periods of intense cold or even different constant temperatures had no effect on the patterns of emergence. One possibility of determining the causes of emergence patterns would be to separate each egg from several batches and study the emergence of adults from single egg cultures. More detailed weighing studies with experiments on varying conditions might throw some light on the reason why Scopeuma adults emerge over a period of a few days, the males 1 day out of phase with the females.

This section may be concluded by stating that laboratory studies did not produce any concrete reasons why Scopeuma squalida should be more abundant at high altitudes than at low altitudes, or why S.stercoraria should be more abundant than S.squalida or S.suilla wherever it was found. Tentative suggestions have been made where appropriate but more studies are needed before this problem is solved.

Section 5.

ASPECTS OF THE TAXONOMY OF *Scopeuma* SPECIES

a). The status of *Scopeuma stercoraria* var. *merdaria* Fabr.

In descriptions of *Scopeuma* species in the literature reference is usually made to a species *S. merdaria* Fabr. (Wingate 1906, Poulton, 1906), or a variety *S. stercoraria* var. *merdaria* Fabr. This variety is usually described as being dark or dirty green, the male less hirsute than *S. stercoraria* and closely resembling the female e.g. Colyer and Hammond (1951).

Several other descriptions of this variety may be found, none of which are complete. Cotterell (1920), Séguy (1934) and Collin (1958) all describe this form as a variety of *S. stercoraria*. This status is accepted by Hobby (1931), Albuquerque (1953) and Hackman (1956). Verrall (1901) and Hammer (1941) regarded all individuals as belonging to the same species *S. stercoraria*, though whether for taxonomic reasons or for ecological convenience is uncertain.

During the course of my studies I found a wide variation in size and colouring in *S. stercoraria*, both in the field and in flies emerging from laboratory cultures. No individuals were seen which were sufficiently different to warrant the description of a variety. The size, colour, length and arrangement of bristles in adults probably depend largely on the amount of food eaten by the larval stages and the conditions in which they develop. Larsen (1943) showed that even 4 days old larvae can pupate but do not emerge very successfully. Adults from these larvae can hardly be expected to be as big and vigorous as those which emerge from fully sized larvae. Field conditions, under which the larvae develop, vary considerably in different areas and at different times of the year, so that considerable variation can be expected.

When female Scopeuma, caught on dung on 13 and 15 September 1965, were dissected, some of these supposed females had male genitalia, but the external appearance of the abdomen was flattened, green and with sparse dark hairs. When these female-like males were dissected they were found to lack testes. Most females examined in this series had no ovaries, the lateral oviducts ended blindly. In both sexes thus affected tha accessory reproductive organs, fat body and gut appeared normal. The absence of the primary reproductive organs was the only defect apart from the external appearance of castrated males. Fig. 48 shows the reproductive system of castrated females and Fig. 49 that of castrated males. Normal systems are shown for

a) Normal System

Fig. 48 Female reproductive system of S. stercoraria

b) System found in castrated females, lateral oviducts ending blindly.

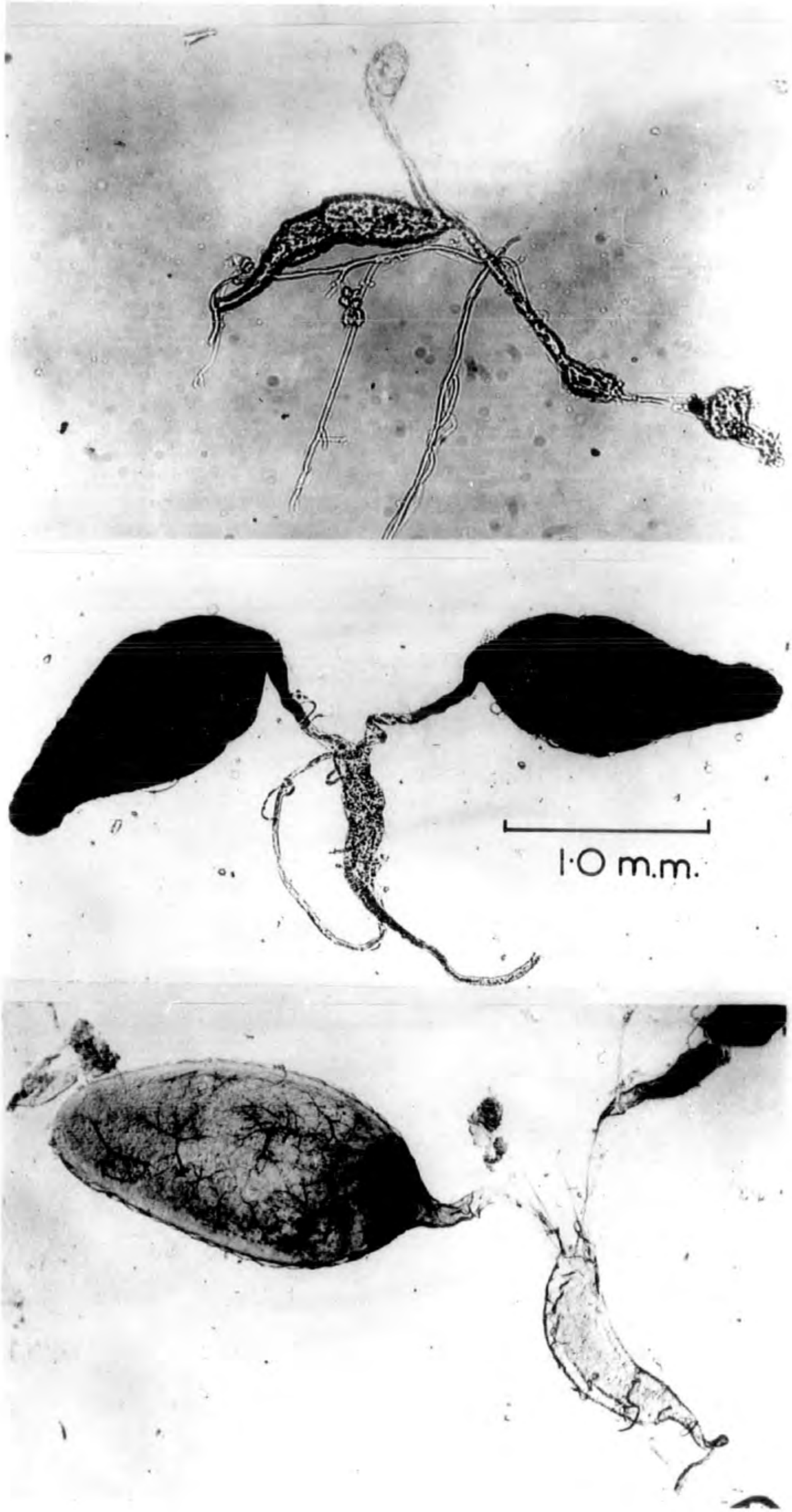

0·5 m.m.

a) System found in castrated males.

Fig. 49 Male reproductive system in S. stercoraria

b) Normal System

c) Normal System.


1·0 m.m.

comparison in each case.

Normal males and females were present in these catches. The castrated males were all small and green and superficially resembled females, only the external genitalia indicated otherwise. These males agreed with the described features of var. merdaria. It seemed as if the explanation for the var. merdaria had been found, but the causes still remain obscure. No intermediate stages of break down of the gonads have been found. It is not known how the castration affects the life of these insects apart from the fact that these individuals were found in large numbers on fresh dung at particular times.

Details of the chaetotaxy on which descriptions of both the normal form of S. stercoraria and the merdaria variety are based seem to be inaccurate. Wingate (1906) describes Scatophaga merdaria as having acrostichal bristles distinctly 2-rowed, whereas they are more than 2-rowed in S. stercoraria. Normal specimens of this species in fact usually have 2 rows of acrostichal bristles but there may be a few irregularly placed bristles between the 2 rows in the anterior region. From the large number of flies which I have examined, there is a complete gradation from a lack of bristles between these 2 rows, to more than a dozen bristles which rarely are in 2 short rows on the prescutum. Vockeroth (1958) noted the variation in acrostichal bristles from 2 rows in small specimens to 3-4 very irregular rows in large specimens. In females there are normally only 2 rows of acrostichals but sometimes there are also a few bristles between the rows on the prescutum. On this basis the description of the variety is, in fact, a description of many normal Scopeuma.

Cotterell (1920) distinguishes the variety from S. stercoraria in that both sexes are dirty green and there are only 2 rows of dorso-central bristles on the thorax, but he does not say how many rows there are in the normal forms. All the specimens I have examined, including the castrated ones had 4 rows of dorso-centrals.

Collin (1958) describes var. merdaria as a smaller, grey-haired species, the male abdomen having dark hairs mixed with pale ones. Dark hairs only being present on the hypopygium in the normal form. There is in fact a variation from 0 to more than 12 black hairs on the abdomen of normal males, mostly on the posterior edges of the abdominal tergites. Large robust males rarely have dark hairs on the abdomen, but as the colour and length of the abdominal hairs become less intense, the number of dark hairs increases. Normal and castrated females have many dark hairs on the abdomen, mostly on the posterior edges of the tergites.

Séguy (1934) describes var. merdarium as having a large vibrissa and the stercorarium form with 3 large vibrissae. All normal and castrated males I have examined have 1 large vibrissa and several smaller ones. The wings of var merdarium are more transparent than in the normal stercorarium according to Séguy. Wingate, on the other hand, describes the wings of S. merdaria as evenly coloured dirty yellow-brown.

It seems that var. merdaria applies to castrated individuals and this not a taxonomic variety but a class of teratological specimens. I have no explanation for the causes of castration or for the effect this has on the external appearance of the flies. No obvious causative agents, such as a fungus or other micro-organisms were found in my specimens. There is usually thickening around the external genitalia so that they are not easy to 'sex' without a lens. If my conclusions are wrong I have not yet found the variety, although the literature describes it as common, or it is possible that the descriptions of the variety have in fact applied only to the smaller specimens of the normal form?

b) PHYLOGENETIC RELATIONSHIPS WITHIN THE GENUS *Scopeuma*

In the classification of the species in the Genus *Scopeuma*, Séguy (1934) proposed the sub-genus *Scopeuma* to include all species having a plumose arista, and the sub-genus *Scatina* (Desv.) for those without a plumose arista. *S. litorea* Fall. was placed in a separate genus - *Scatophaga*. Collin (1958) proposed a sub-genus *Scatina* for the species having a bare or microscopically pubescent arista.

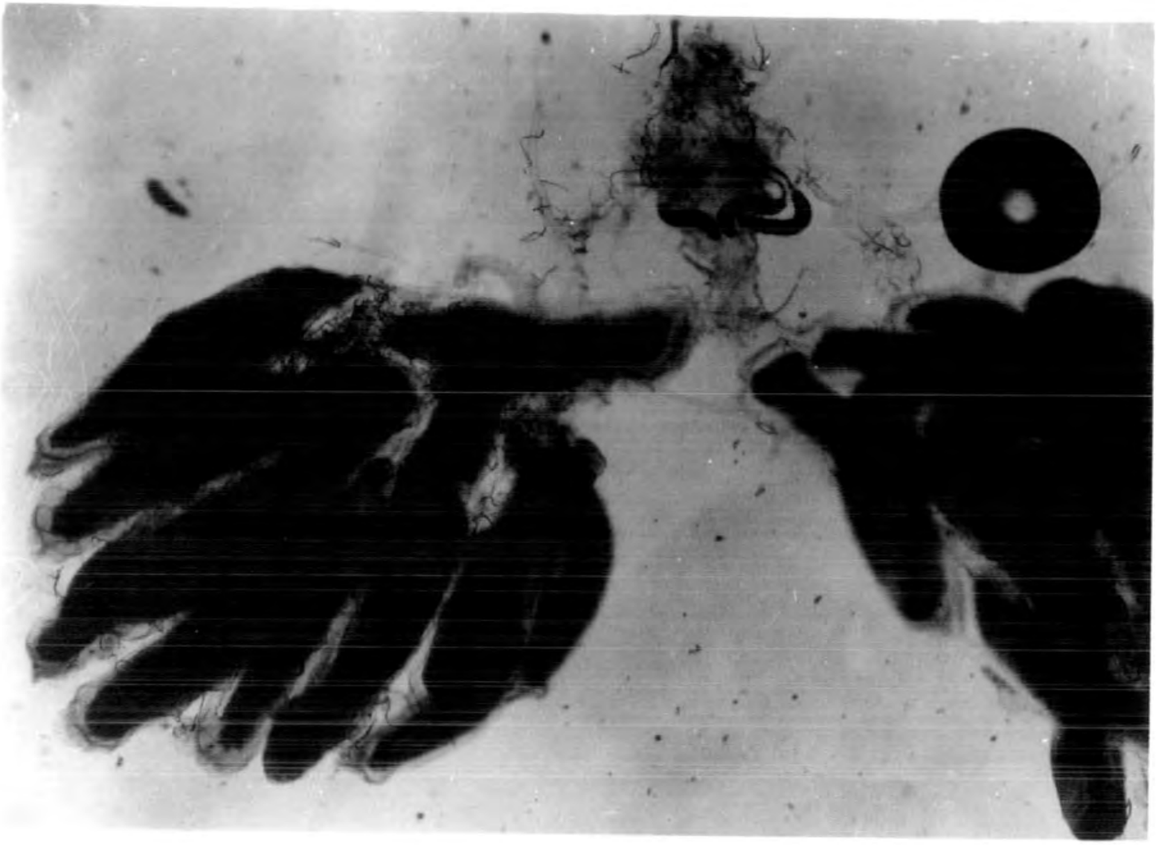
Of the four species which I have examined, *S. stercoraria* and *S. suilla* are placed in the sub-genus *Scopeuma* of Séguy and *S. squalida* and *S. litorea* in the sub-genus *Scatina* of Collin. During the course of dissections I noticed that the spermathecae of *S. squalida* and *S. suilla* were identical in shape, size and arrangement, as shown in Fig. 50. In *S. stercoraria* the spermathecae are small and spherical, two always being joined, usually on the right side. The spermathecae of *S. litorea* are almost spherical, with a slight protruberence distally, and although two are often associated together on one side, they are not joined. The colouring, vibrissae (2 large ones) and degrees of sexual dimorphism in *S. suilla* and *S. squalida* are also very similar and they appear to be more closely related to each other than to either *S. stercoraria* or *S. litorea* (See Table 20).

Whilst discussing this with Mr. P. L. Pearson, he

S. suilla

Fig. 50 Female reproductive systems of *Scopeuma suilla* and *S. squalida* to show nature of spermathecae.

S. squalida



1·0 m.m.

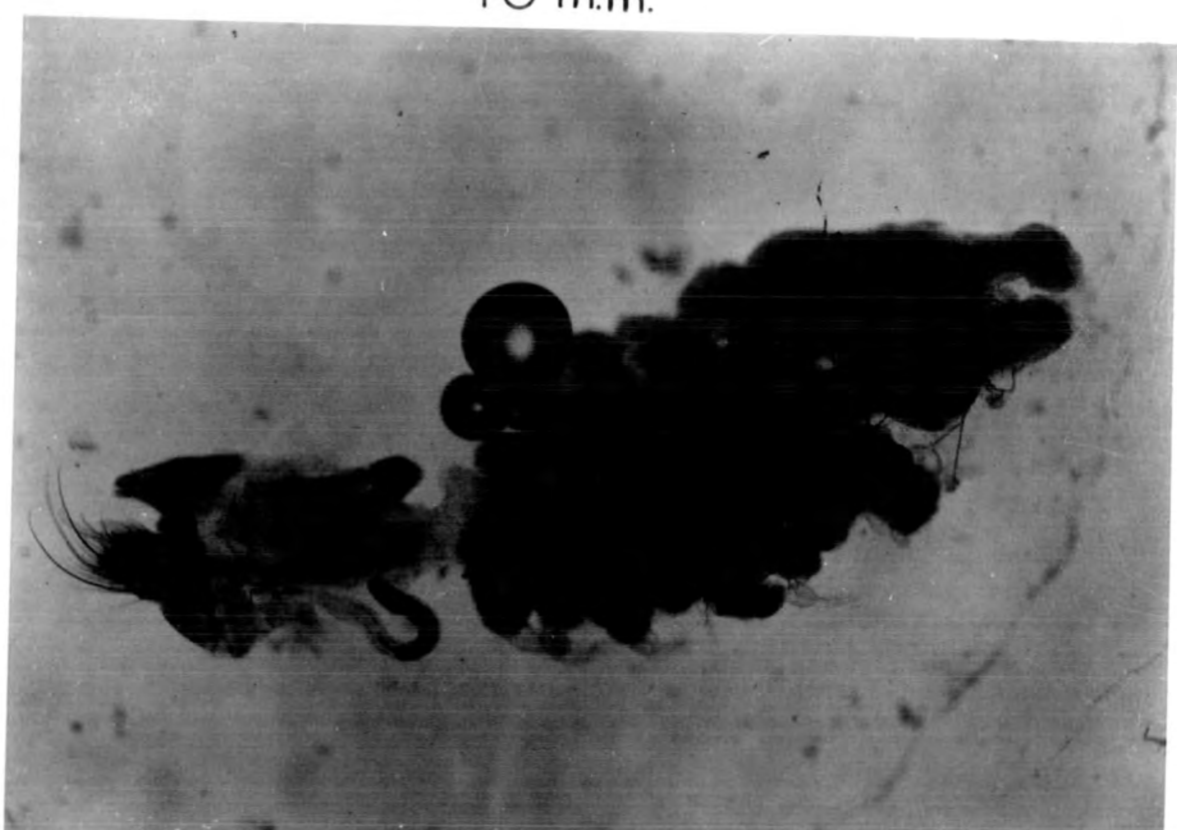


Table 20 To compare the characteristics of 4 species of *Scopeuma*.

Species	Sexual Dimorphism	Vibrissae	Spermathecae	Chromosomes	Arista
. *stercoraria*	male large, yellow female small, green	1 large	3 spherical, 2 joined	n=7 (large)	plumose.
. *suilla*	male and female almost same size, both brown	2 large	3 long, separate	n=6 (5 large, 1 small)	plumose.
. *squalida*	male and female almost same size, both brown, black patch on fore femora	2 large	3 long, separate		short pubescence
. *litorea*	male and female almost same size, both black.	1 large	3 almost spherical separate		plumose.

offered to examine the chromosomes. At the time I only had S. stercoraria and S. suilla, but the results were quite surprising as both species are in the same sub-genus. S. stercoraria had a haploid number of n=7, all large chromosomes, while S. suilla had a haploid number of n=6, five large chromosomes and one small. These two species have differences in colour, sexual dimorphism, numbers of vibrissae, size, shape and arrangement of spermathecae, and the number and types of chromosomes.

I have not yet been able to examine the chromosomes of S. squalida or S. litorea, nor have I been able to dissect females of any other species. From specimens of S. inquinata (Mg), S. lutaria (Fabr) and S. taeniopa (Rond), kindly sent by Dr. J. R. Vockeroth, I have compared their aristas with those of the four species which I have collected. All aristas are plumose to a greater or lesser extent and none are completely bare. It therefore seems artificial to erect a sub-genus based solely on the length of pubescence on the arista. If a sub-genus is to indicate some close phylogenetic relationship between the species in that group, many other features need to be considered. I am not proposing any new taxonomic divisions for the genus Scopeuma, only that any sub-genera should take several characteristics into account. Examination of the nature of the spermathecae and of the chromosomes could be of help in this taxonomy.

I have used the generic name Scopeuma Mg. rather than Scatophaga Mg. for temporary convenience. It may be thought that one genus should not contain members with such different characteristics as described for the above species. I forsee the possible reorganisation of the genus into 2 or possibly more genera, more truly reflecting the phylogenetic relationships of the species.

Section 6.

OBSERVATIONS ON OTHER FLIES ON DUNG.

1). Occurrence of flies throughout the year.

During counts of Scopeuma stercoraria on cow pats, numbers of Mesembrina meridiana, Dasyphora cyanella, Rhingia campestris and Cryptolucilia caesarion were also noted. No detailed studies were made on the behaviour of these flies so that it was not possible to interpret the figures for population analysis. The observations on these species are summarised in Tables 21 and 22.

The totals for all these species are a simple addition of the numbers of individuals counted on cow pats. It was not possible to be sure that the same flies were not counted more than once. The highest numbers per pat and the number of pats infested at each count gave the same relative rate of abundance as the total figures. More detailed observations are needed to see how long individuals remain on the same pat, and whether the flies move from one pat to another.

The most significant point to arise from these observations was that Mesembrina Cryptolucilia and Rhingia were up to 5 times more abundant in 1964 than in 1965, even though this was a shorter season. The inaccuracy due to the counting method was constant and the recorded figures confirmed my general impression at the time that 1965 was a poor year for the dung fauna other than Scopeuma. 1965 was expected to have been a more favourable year for Rhingia since the larvae, on hatching,

Table 21.

Occurrence of 2 species on cow pats.

	Mesembrina meridiana 1964	*Mesembrina meridiana* 1965	*Dasyphora cyanella* 1964	*Dasyphora cyanella* 1965
1st. appeared	last wk. May	last wk. May	last wk. May.	3rd.wk. April
last appeared	1st. wk. Nov	last wk. Oct.	last wk. Sept.	2nd.wk. Sept.
Total seen	1354	298	645	603
No. of pats	831	236	399	366
Month with max. no. seen	September	August	May	June
Max. No.	622	164	392	202
Max. per pat.	15	4	9	29

Table 22.

Occurrence of 2 species on cow pats.

	Rhingia	campestris	Cryptolucilia	caesarion
	1964	1965	1964	1965
1st. appeared	last wk. May.	last wk. May.	last wk. May.	3rd.wk. April
last appeared	3rd.wk. Sept.	1st. wk. Oct.	3rd.wk. Sept.	2nd. wk. Sept.
Total seen	195	40	1105	354
No. of pats	143	38	626	231
Month with max. no. seen	May	June	July	August
Max. no.	123	35	637	128
Max. per pat	4	2	18	7

drop on to the dung and have to burrow in, like Scopeuma larvae. No explanation can be offered for its very rare occurrence in that year.

Dasyphora was almost equally abundant in the 2 seasons but it was not apparent why this species was not affected in the same way as the other species, even allowing for the possibility of more flies occurring earlier than mid-May,1964. Over half the year's total were counted during the 3rd week in May 64, which seems too high a figure to be the first of overwintering adults to appear on the dung.

More sophisticated techniques of population analysis and life history studies are needed to explain the seasonal fluctuations of these flies.

2). Summary of previous work on these species

Thomson (1937) found Mesembrina meridiana in Ayrshire from early May to the end of October. He also saw it mating and ovipositing, but neither activity was observed during the present study. Hammer (1941) found M.meridiana from early May to early November with the peak of numbers from the end of August to early October. Hammer's observation that the fly does not appear in bright sunshine because of its presumed need of humidity was not supported in this study. The high numbers of 12-15 per pat were all found in midfield far from shade and in warm sunny weather.

The numbers of Dasyphora cyanella which I recorded at Houghall were much higher than those obtained by Thomson (1937) who said they were never common and only occasionally were 2 females on the same pat. He found the species in the field from early April until mid November.

Hammer (1941) suggested that most of the first generation of Rhingia campestris hibernated, while only a few emerged to produce the second generation. Coe (1942), on the other hand, found 2 peaks of abundance, one from mid June to early July and the other in early August. The adults are very mobile and were more often seen away from the dung at Houghall than those of the other 3 species.

Cryptolucilia caesarion was found by Hammer (1941) from early April to early November, with a peak in late April and early May. The absence of this fly during the summers of 1935, 1936 and 1939 was tentatively attributed to climate and predators. During my studies there was no summer depression in either of the 2 years although the difference in climate in the 2 seasons was considerable, and no significant predation was observed.

Thomsen (1937) recorded C. cornicina (F) from April to early September, being most numerous in August. Although Colyer and Hammond (1951) regard this as more abundant than C. caesarion, I did not find any specimens during the whole study. It is possible that the 3 species are not able to coexist.

3) Diurnal activity of Dasyphora cyanella

It was not possible to discern the factors controlling the diurnal activities of the 4 species from the counts of numbers on cow pats, because of the deficiencies of the counting methods already described. In the diurnal activity experiment carried out by Edge and myself, described in Section 3, a large number of Dasyphora were caught, as shown in Fig. 51. Only 1 female Cryptolucilia caesarion was caught in this experiment.

The Dasyphora caught over the 4 days were rather erratic as regards the numbers caught each day, but the range of time during which they were caught was very similar for each day. Unlike Scopeuma, which occurred in equal numbers of each sex, female Dasyphora predominated. Of the 1,315 Dasyphora caught, 1,274 were females and only 41 were males, 32 of which were caught during the first day,

The highest numbers were caught between 12.00 noon and 2.00 p.m. on the first day, and from 10.00 a.m. to 12.00 noon on the next 2 days, On the 4th day only 30 females and 1 male were caught, the highest number being caught between 8.00 a.m. and 10.00 a.m. As suggested for the low numbers of Scopeuma caught on this last day, the local population had probably been almost completely removed so that not much significance is attached to these last figures.

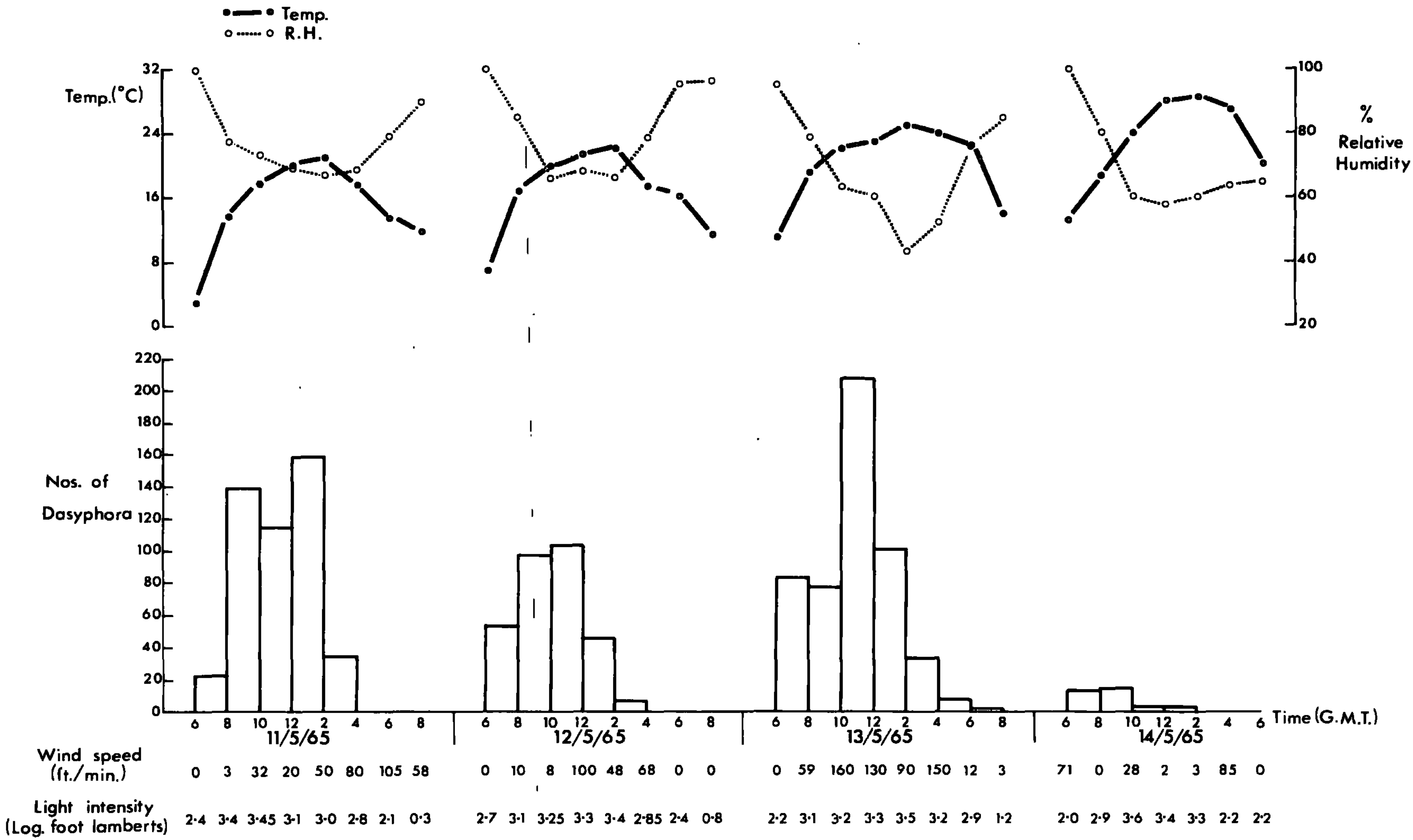
The numbers of Dasyphora caught throughout the day tended to increase as temperature increased, but started to decrease before the maximum temperature was reached. The exception to this was on the first day when the maximum number of flies occurred at the same time as the maximum temperature. Before this, however, the numbers caught had dropped slightly from the previous catch but there seemed no apparent reason for this. As the early temperatures of each succeeding day became higher, the first catch of each day increased progressively, from the first to the third day, but after that the numbers were erratic. From the calculated accumulative percentage, 50% of each day's catch were trapped between 10.00 a.m. and 12.00 noon, except for the last day when 50% were caught between 8.00 and 10.00, a.m.

Perhaps the most important point about this experiment was that more Dasyphora were caught in these 4 days than were seen in 2 years at Houghall, although the site of the experiment was only half a mile away from the main study area. Since so many Dasyphora were attracted to each trap, any one of which was only a few feet from its nearest neighbour, the species was behaving quite differently in this habitat. The farm where the experiment was carried out was small, with only a few cattle and with very few Scopeuma

The experiment was carried out at the time of the spring peak in numbers of Scopeuma at Houghall. Only 31 Dasyphora

Fig. 51. Numbers of Dasyphora cyanella caught in baited detergent traps. For details see text.

DIURNAL ACTIVITY IN *Dasyphora cyanella*



were seen at Houghall which was the reverse of the situation at the site of the experiment. This suggests that interspecific competition for oviposition sites occurs between the 2 species. This possibility deserves further investigation.

4) The feeding habits of Scopeuma stercoraria on cow pats

Some attention has been paid to Scopeuma falling prey to other insects, particularly to Mellinus arvensis L. (Hamm and Richards, 1930) and Dioctria rufipes De. G. (Hobby, 1932). Far greater attention, however, has been paid to listing the insects which fall prey, to Scopeuma, particularly by Poulton (1906) and Hobby (1931, 1933, 1944). To these lists I should like to add Copromyza hirtipes R-D, Dasyphora cyanella, Rhingia campestris, and Cryptolucilia caesarion. This last species had been recorded as a prey of S. scybalaria by Hobby (1931), but not of any other Scopeuma species. According to Darwish (1954), Dasyphora was regularly eaten by S. stercoraria early in the season, but I only saw 2 individuals being eaten.

During the present study predation on dung was predominantly by male Scopeuma, only 6 females were seen eating on the pats, The actual amount of predation was very small indeed, in 1964, 56 flies were seen eating prey, comprising less than 0.02%

of the numbers of Scopeuma observed on the dung. In 1965, when Scopeuma numbers were much higher, only 51 males were seen eating, 1 of which was eating a female Scopeuma.

The majority of insects eaten werePsychodids, Sepsids and Sphaerocerids, particularly Copromyza hirtipes, but occasionally Sphaerocera subsultans Meig.. These flies were usually attracted to fresh cow pats and were often present on pats in larger numbers than Scopeuma. There was rarely much determination on the part of Scopeuma to pursue any prey which escaped or even to spend long actually feeding. One male did, however, spend 50 minutes eating what looked like a Morellia, before flying off with it.

Feeding took place either on the dung or in the grass nearby and no more than 2 flies were ever seen feeding on one pat. It did not appear that S. stercoraria was a significant predator of flies on the cow pats, but the numbers of insects eaten by both immature and mature flies in the vegetation must be very considerable indeed,. Some indication of the potential of Scopeuma is given by the numbers of Drosophila eaten in the laboratory, as described in Section 1.

DISCUSSION

The main object of this study was to elucidate the facts behind the population changes of Scopeuma stercoraria throughout the year. The complex life history and behaviour of the adult flies made quantitative assessments of birth and mortality rates impracticable. In spite of this, however, the investigations of the age composition, of adult females, and other studies enabled me to obtain some idea of why the numbers changed at different times throughout the year.

Animal populations are held by various authors to be controlled by either density dependent or density independent mortality factors, or both. In trying to establish the factors responsible for mortality in a population which one is studying, all possibilities must be considered. If particular factors have been found to cause mortality, they must be examined in relation to the population. Each factor may be classed as either density dependent or density independent. It is at this point that one is inevitably drawn into the argument as to what sort of factors control populations.

Varley (1963) commented on the semantic nature of the argument between the advocates of density independent factors and those who hold that only density dependent factors can control, populations. Much of the argument has, in fact, been caused by confusion over terminology, The words 'control', 'regulate', 'govern' and 'legislate' have meant different things to different people. There even seems to be some confusion over the terms 'density dependent' snd 'density independent', so that some explanation is necessary.

A density dependent mortality factor is one which causes increasing mortality as the density of the population in question increases. Factors which cause mortality of individuals irrespective of the size of the population are called density independent. Those factors classed as density dependent include intraspecific competition, predation, parasitism and disease, of which intraspecific competition is generally held to be the most important. Milne (1956, 1957) regarded intraspecific competition as the only perfectly density dependent factor, and the others as only imperfectly density dependent and, hence, incapable of controlling a host of prey population. Density independent factors are usually various climatic conditions which are detrimental to one or more stages in a life history. Mortality may be a direct effect by the climate, or an indirect one as a result of the effect of climate on the food or shelter.

The principle of density dependent factors determining population numbers was originally expounded by Howard and Fiske (1911), particularly with regard to parasitism. The most important development of this principle has come from Nicholson who originally discussed his ideas in 1927.

His most controversial statements, however, were made concerning the compensation of mortality at one stage to survival at another (1954, a), and his general theory of population control (1954, b).

Uvarov (1931) and Bodenheimer (1938) regarded climate as the most important factor controlling insect population dnsities. The main proponents of density independent mortality factors were Andrewartha and Birch (1954) whose views were opposed to those of Nicholson. Since 1954 ecologists have tended to agree with one theory or the other.

Andrewartha (1957) pointed to some of the difficulty over the term 'density' by quoting one of Nicholson's statements which indicated that variation in numbers was not the same as variation in population density. Nicholson held natural oscillations in density to be responsible for population changes-even though they might be obscured by variations in numbers due to climatic factors. To those who believed in control by density independent factors, an observed change in numbers was the real change and the factor which caused this change was controlling the population. Nicholson's view of the effect of weather is that it is legislative only and cannot control or govern populations. Control, on the other hand must be by density dependent factors alone which stabilise populations and prevent them from going too high or too low (Nicholson, 1954, b).

Thompson (1956) tried to simplify the problem of terminology by using 'control' in the sense that "... no organism increases without limit".

From field observations on a parasite-host system in the Knupweed Gall-Fly, Urophora jaceana, Varley (1947, 1953, 1963) proposed that parasites acted in a delayed density dependant manner. The general rule in such a system is that as a host increases in numbers its parasites also increase, eventually reaching a density when they start to deplete the host population. The host density then dwindles to such a low figure that the parasites are not able to find them easily and so also decrease in numbers. The reduction in the rate of parasitism allows the host to increase again. Such systems and their terminology have been reviewed by Hassell (1966).

Varley and Gradwell (1956), and Varley (1963) accepted the importance of weather as well as that of density dependent factors, whether delayed or not. Richards (1961) gave a more detailed account of the various ways in which climate could act. One interesting point which he brought up both directly and indirectly concerns the fate of a small population which might suffer from a catastrophe, especially if outside the climatic zone for its species. This situation, where small numbers are at risk to climatic factors is one which has been stressed by Cragg (1961) with respect to moorland species.

Milne (1957) tried to combine the various theories of population control and was strongly supported by Dempster (1963), since Milne's theory seemed to explain the situation in acridid populations. Milne's division of density dependent factors into perfect and imperfect was criticised by Clark _et al._, (1967). Solomon (1957) brought out the very important point that populations are not necessarily being regulated continuously. Weather conditions might keep population densities below the level at which density dependent factors would act.

In the light of these views on population control, it is necessary to examine the life history and population changes of _Scopeuma_ _stercoraria_ to see which, if any, might explain how these populations were controlled. In spite of the absence of really long term studies on the populations of _Scopeuma_ it is possible to use our limited knowledge to suggest some answers to the problem of control.

In any population growth the initial factor of importance is the birth rate, since mortality factors must have some initial figure to reduce. Nicholson's (1954,a) concepts of compensatory reactions may apply to the numbers of eggs laid in many biological systems, but the numbers which hatch at one time, or over a period of time, may be more important. Thus, if a small population of adults laid a large number of eggs, or if many adults laid few eggs, the fecundity would not be denied as being density dependent. After being laid, however, the fate of the eggs must depend upon the environment and not on their density. A favourable environment will ensure that a high proportion hatch, whereas an unfavourable environment will reduce the numbers hatching independently of the original density of eggs. A physical catastrophe or severe climatic conditions could kill all the eggs in one locality. It is not difficult to see biotic factors which act in a similar capacity. A young cuckoo in the nest of another bird will eject all the eggs or newly hatched birds irrespective of the number initially present.

Scopeuma eggs are left unprotected by the adults and thus completely exposed to the physical environment. The factors which probably determine whether the eggs hatch are temperature and humidity. Predation on eggs, particularly by Staphylinid beetles has been recorded by Hammer (1941) and Darwish (1954), but this did not seem to be an important factor. Some female Scopeuma laid their eggs on the surface of the dung but did not insert them. Such eggs were doomed to 100% mortality in all but persistently wet conditions. These eggs were laid by solitary females as well as by females on a pat infested by large numbers of other Scopeuma, so this seemed to be independent of density.

When the eggs hatch the larvae are exposed on the surface of the dung and must enter the pat in order to feed on the semi-liquid dung. This appeared to be the most important stage in the life history of Scopeuma, since the presence or absence of a hard crust, or of cracks in the crust, determined whether any of the larvae could enter the pat. If hot or windy weather had caused the dung surface to harden, larvae would crawl around until killed by heat or dessication. In this position the larvae would also be exposed to predation or parasitism. Although Smith (1951) recorded a few instances of parasitism by Ichneumonids, parasitism did not appear to have any significant effect upon *Scopeuma* populations.

Mortality due to predation of newly hatched larvae on the surface of a hard crust, might well increase in higher densities of larvae, but this would not matter since the larvae would die anyway. If the crust on a pat is broken, revealing soft dung, the numbers which penetrate the dung will be determined by the chance result of a fairly adjacent position to the exposed region.

In wet or cold humid weather the dung did not form a hard crust so that a high proportion of larvae succeeded in entering the dung. This was reflected in large numbers of adults on the dung 4-6 weeks later which were unaffected by the climate. The proportion of larvae which enter the dung at any time is dependent on the nature of the dung as it is affected by climatic conditions, and not on the density of eggs or larvae.

Weather thus appeared to act as the key factor affecting the population at this stage in a manner similar to that suggested by Morris (1959) and Birch (1957). Widespread and persistent drought conditions could cause continued mortality of all eggs laid, and eventual local extinction of the species as soon as the last adults died. Immigration would be the only means of repopulating such an area. This susceptibility to hot or dry weather presumably explains why Scopeuma is almost exclusively found in north temperate zones.

Once inside the dung Scopeuma larvae become largely independent of the climate, particularly if a hard crust forms later. Intra-specific competition may occur here with respect to the amount of food available and the numbers of larvae present. Inter-specific competition is probably severe at times, not only with other insects, but also with earthworms (Svendsen, 1957). Until more is known about the amount of food eaten by larvae the existence of competition for food, and its possible effect on size and fecundity of the adults, cannot be more than speculation at the moment. From my laboratory studies with constant volumes of dung I found no evidence to suggest that increased numbers of larvae reduced the numbers of adults which emerged.

It is possible to envisage, for Scopeuma populations, the same situation which arose in the Lucilia cuprina Wied. populations of Nicholson (1954,a). High larval densities in dung might result in fewer eggs being laid by the adults which develop from these larvae. This need not act as a controlling factor since none of the eggs may hatch in unfavourable conditions. Scopeuma larvae are, however, immune from the feed back described for Lucilia by Nicholson (1954,a), since adults emerging from one pat will not lay their eggs in the same pat. It is uncommon for eggs to be laid on the same pat after a period of a few hours from the time it was dropped.

Larval predation may be high at times but it is not certain that this is related to the density of Scopeuma larvae. The main predator, Myiospila meditabunda F. was more abundant in summer 1964 than at any time during the higher densities of Scopeuma in 1965.

Pupal mortality has been reported as being mainly due to either high temperatures (Larsen and Thomsen, 1940) or low humidity (Larsen, 1943). Larsen (1943) showed that 4 days old larvae could form puparia. Size was therefore less important than the physical conditions, since no flies emerged below 80% R.H..

Scopeuma adults are obliged to hunt insects within the first few days of emergence, both to survive and to mature their gonads. If large numbers of Scopeuma emerged at a time of small numbers of insects, intraspecific competition would occur, but how often will this occur under natural conditions? Large numbers of Scopeuma in early spring and late autumn have no difficulty in maturing, and the vast insect numbers in summer presents the species with ample food. A catholic diet of insects is one method by which Scopeuma has avoided the problem of food shortage.

Flight is well developed in Scopeuma and direction appears to be random. Movement away from the site of emergence will occur if there is not enough food there. This cannot act as a controlling factor, since areas of deposition of fresh dung may be quite independent of previous areas from which the flies might have emerged. Movement towards dung is by attraction to the volatile compounds contained in it. Dung can attract flies from a large area, thus negating any disadvantage to immature flies which had to disperse from their site of emergence.

The spread of emergence over several days might be another adaptation to avoid high densities of immature flies since, by the time the last flies have emerged, the first flies to emerge will have moved away. The widespread occurrence of adult Scopeuma in almost every environment, noted also by Nielsen, Ringdahl and Tuxen (1954), makes it very unlikely that the species will suffer from food shortage. Competition for shelter does not occur since Scopeuma will alight anywhere.

The highest densities reached by adult Scopeuma are found on fresh dung, when pats may be covered by copulating and ovipositing flies, It is at this point that one might expect some interference, due to density, as described by Klomp (1964). It appeared, in fact, that the interference decreased as the density of females increased. As males are usually the first to arrive on a pat there are several ready to pounce on the first females to arrive. With increasing numbers of females arriving the excess males, which caused the initial interference, find their own mates and activity is correspondingly reduced.

High densities of adults on cow pats can help to ensure copulation so that solitary females can oviposit at a later date with the store of sperm they have received. The separation of the main sites of feeding and oviposition has removed the possibility of competition between mature adults acting to reduce their fecundity.

Any density dependent factor acting during the larval stages to reduce adult fecundity will not necessarily be able to act as a controlling factor because of the longevity of Scopeuma adults. The wide range of ages found in the field will act to maintain the rate of oviposition at any one time. Continual oviposition throughout the season has eliminated the appearance of seperate generations and also the ability of one generation to determine the size of the next. Continual oviposition serves mainly as an insurance against extended weather conditions inimical to egg hatching and larval survival.

Adult mortality posed one of the more difficult problems since the causes were rarely observed. The only significant predation, by wasps, took place not at high Scopeuma densities but at what was apparently a high density of Vespula. Since Scopeuma was obviously not a regular prey of Vespula these attacks, in August 1965, could not be regarded as controlling the population. Males were the most usual victims so that the effect of these predators on oviposition was slight. Predators thus seemed to act as non-governing mechanisms, as suggested by Huffaker (1956). Cannibalism might have been expected to increase in higher densities, but only 3 cases were seen during the entire study of field populations.

It is appropriate at this point to briefly summarise the population fluctuations in adult Scopeuma and the factors responsible, as deduced from the age structure studies. The spring peak of adult Scopeuma on cow pats was composed of large numbers of fairly young flies with high rates of survival to the 2- or 3- parous stage. Most adults in this peak had over-wintered in the larval or pupal stages and emerged in large numbers in early spring.

The end of the spring peak may be the only time when there are no immature flies entering the adult population. As the mature adults die there may thus be no replacement for a time, until the eggs laid in the spring peak have developed into mature adults. In favourable (i.e. cool, wet weather) years there may be large numbers of adults on the dung in summer, reflecting successful hatching and development in the months of April, May and June. Although some flies may reach quite old ages (6- and 7- parous) the survival rates of most flies in summer is much lower than in spring. This means that in warm dry years there will be low numbers of adults on the dung partly, also, due to the fact that there may have been fewer emergences from eggs laid in spring.

The autumn peak is mainly caused by much better survival rates of old flies. Large numbers of old adults may thus persist on the dung quite late in the year. As autumn progressed fewer young flies were found in the population since more larvae overwinter instead of completing development in late autumn.

The presence of large numbers of adults at the hottest times of the day suggested that high temperature was not as deleterious to adults as Hammer (1941) suggested and, thus, not responsible for any summer drop in numbers. The occurrence of immature flies throughout almost the entire season and the continual oviposition, were strong evidence that adult diapause did not occur, as suggested by Darwish (1954). The occurrence of distinct generations was obvious only at the start of the season when the spring peak ended and the first early summer peak started. Further developments were due to a combination of variable hatching success and differential survival rates of adults, high in spring and autumn, but much lower in summer.

The main conclusion to be drawn from this discussion is that although the possibility of density dependent factors acting at various stages in the life history has not been denied, their role in controlling *Scopeuma* populations has not been proved. The life history of *Scopeuma* is such that the weather conditions on any day determine the number of newly hatched larvae which enter the dung successfully. This obvious weak point in the life cycle has its counterpart in the first instar larvae of *Tipula* species (Coulson, 1962), eggs of *Tipula* species (Milne, Laughlin and Coggins, 1965) and young adults of *Neophilaenus* species (Whittaker,1965). The importance of natality, as opposed to mortality factors, in contributing to subsequent population size has been stressed by Southwood and Jepson (1962) and Southwood (1967).

Consideration of these facts leads me to suggest a possible division of life cycles into either open systems or closed systems. An open system life cycle is one in which the population is not normally controlled by density dependent factors because of the vulnerability of one or more stages to unfavourable physical factors. If the density of any stage reached excess proportions it is recognised that intraspecific competition would occur. Species falling in this division would be expected to eat a variety of foodstuffs and/or have a variety of predators.

If a species does not contain a stage which is vulnerable to the physical environment, it will increase geometrically unless controlled by competition, predators or parasites. Such species are therefore classed as having closed system life cycles in that they are maintained in some state of balance by factors acting in a density dependent manner.

Scopeuma stercoraria would be classed in the open system life cycle and the facts presented by Richards (1961) for the desert locust, *Schistocerca gregaria* (Forskål), and by Andrewartha and Birch (1954) for *Austroicetes cruciata* Sauss. would classify these species similarly. Beaver's (1967) discussion of the bark beetle, *Scolytus scolytus* (F.) and Lack's (1954, 1966) analyses of bird populations would qualify these to join *Lucilia cuprina* in being classed as having closed system life cycles.

My analysis and suggestion is designed to propose that all populations might be affected by both density dependent and density independent factors. The control of populations, however, will be by only one of either class of mortality factors. No population is immune from catastrophic physical factors, as many marine populations showed in the winter of 1962-'63 (Crisp et al., 1964).

Animals such as Scopeuma which have an open system life cycle may be at risk of local extinction but they are equipped with various adaptations of behaviour to reduce this risk. Animals heavily predated or parasitised at high densities may not risk extinction but their mode of life is restricted to a predictable pattern.

If a mutation occurred in Scopeuma so that the larvae hatched out of the inserted end of the egg, straight into the semi-liquid dung, instead of the exposed end, the weak point in the life cycle would be eliminated. The fecundity of this specie is such that the population would be able to grow at a much faster rate and would have to be controlled by density dependent factors. At the moment, however, the population of S. stercorari is controlled primarily by the physical environment obtaining at the time of the hatching of the egg.

Summary.

1). Adults of *Scopeuma stercoraria*, *S.suilla* and *S.squalida* must eat insects to attain sexual maturity and they remain entomophagous throughout life. Males probably eat fewer insects during the mature phase than when they are maturing their gonads. The first gonadotrophic cycle, or preoviposition period, in females in the laboratory took about 10-14 days in well fed flies, when 8-10 *Drosophila* were eaten per day. Subsequent cycles were about 7 days duration in *S.stercoraria* and *S.suilla*, but only 3-4 days in *S.squalida*. Both *S.stercoraria* and *S.suilla* ate about 50-70 Drosophila in each cycle to produce 50-60 eggs. *S.squalida*, on the other hand, needed only 30-40 *Drosophila* to produce the same number of eggs.

2). Counts were made, at Houghall in 1964 and '65, of adults on and around 40 cow pats having reasonable numbers of *Scopeuma stercoraria*. Several counts were made on each day that counts were possible. A spring peak of numbers was due to large numbers of adults, which had overwintered in the larval or pupal stage, maturing and going on to the dung to breed. The numbers dropped towards the end of May and rose in the second half of June and first half of July to 1 or more early summer peaks. In 1964 the numbers then dropped, due to the hot dry weather at the end of May causing heavy mortality of newly hatched larvae. In 1965 the high numbers persisted until mid August when they dropped for a short time and then rose again. Autumn peaks in

numbers were features of both years, persisting until severe frost or snow killed the majority of the flies.

3). Dissection of female Scopeuma caught in vegetation and on dung was carried out to count the dilatations of the ovariole tunica, thus giving the physiological age of each fly. The age composition studies for these females showed that immature flies were present all the time except for a short time at the end of the spring peak, 1965. Old flies were found during the summer months, but survival rates for most, if not all, ages were lower in summer than in spring or autumn. The higher survival of a wide age range in autumn was mainly responsible for the autumn peak lasting so long. First cycle gravid females were much less common than uniparous females and it was therefore assumed they dispersed more widely.

4). The highest number of Scopeuma tended to occur at the hottest time of the day, but adverse weather conditions and mass defaecation at other times could upset the normal diurnal activity of increase in numbers with increase in temperature.

5). Scopeuma eggs could hatch after a few hours of dessication if rewetted, but the enclosed larvae could not escape if permanent dessication occurred only 1 hour before they were due to hatch. Pre-imaginal development at 10°C and below was very slow (70 days to 200-400 days at 5°C), whereas there was little difference in the duration of development at 15°C and at 25°C (30-20 days). Adults emerged over a period of 2-5 days from cultures maintained at 25°C but at 10°C and less the emergence was spread over several months.

6). The variety S.stercoraria var. merdaria F. was thought to be due to castrated individuals of which the males resembled normal females. The description of such a variety is thus not thought to be valid. It is suggested, from anatomical studies, that S.suilla is more closely related to S.squalida than to S.stercoraria, so that subgenera should not be erected without more study.

7). The occurrence of Mesembrina, Dasyphora, Cryptolucilia and Rhingia throughout the year was described, with information on the diurnal activity of D. cyanella.

8). It was suggested in the discussion that Scopeuma populations were not controlled by density dependent mortality factors but by the effect of the weather on the eggs and the dung, affecting the success of newly hatched larvae to enter the cow pats.

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