

THE ECOLOGY OF THE BRITISH SPECIES OF
PSYCHODA (DIPTERA: PSYCHODIDAE)

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(With 2 Text-figures)

A study of the dispersal of the sewage-filter Psychodids requires a knowledge of the breeding haunts and seasonal incidences of the local species of the genus. Field dung, decaying vegetable matter and organic mud form the breeding places to one of which some species confine themselves, whilst others, e.g. *Psychoda severini* Tonn., breed in a variety of materials. *P. alternata* Say is more restricted in its choice of breeding grounds and proved the best indicator of dispersal from sewage filters. With this fly, invasion of farms and woodland was apparent at a distance of $\frac{1}{2}$ and 1 mile respectively from the filters, but not at a distance of $1\frac{1}{2}$ miles in the direction of the prevailing wind.

INTRODUCTION

The genus *Psychoda* Latr. includes sixteen species and two subspecies in Britain (Tonnoir, 1940), and their larvae inhabit a variety of decaying organic materials such as dung, mud and rotting vegetation. Three species, *P. alternata* Say, *P. severini* Tonn. subsp. *parthenogenetica* Tonn. and *P. cinerea* Banks, have succeeded in colonizing the bacteria beds of sewage purification works, and *P. alternata* is so commonly present that it has become known as the trickling filter fly. *P. severini* is also frequently found in filter beds, but *P. cinerea* is less commonly present. These sewage-breeding species of *Psychoda* are sometimes so abundant that they become a household nuisance, especially when the sewage works are near towns (Lloyd, 1943), and Ordman (1946) has reported cases of bronchial asthma caused by inhaling the dust resulting from the disintegration of their bodies. No other specific association with disease has been reported for *Psychoda* flies, but insects from such highly contaminated environments must always come under suspicion.

No attempt at assessing the dispersal of the *Psychoda* flies from the sewage works can be made, however, until the abundance and seasonal incidence of the sewage-breeding species in the wild *Psychoda* fauna have been studied. Flies have, therefore, been collected both near to the sewage works and at such a distance away that dispersal from the works was unlikely to affect the fauna. As *Psychoda* flies are, apart from *P. alternata*, indistinguishable in the field, they must all be collected for identification in the laboratory. These collections have yielded information on the relative abundance of the non-sewage-breeding species of *Psychoda* and have shown that different species of *Psychoda* are common at different localities, depending on larval food supply. This latter point has also been studied by recording fly emergence from samples of likely breeding materials brought to the laboratory.

MATERIALS AND METHODS

In the identification of the species of *Psychoda* the descriptions of Tonnoir (1940) have been used, supplemented by those of Del Rosario (1936). The tip of the antenna is a feature of great diagnostic value, but it is readily damaged if the flies are roughly handled. They have, therefore, been collected by tubing them off trees and fences, and a definite area of ground has been worked over each week. This method of collecting is not fully adequate in periods of peak abundance, when it is virtually impossible to collect all the flies present.

To investigate the breeding places of the flies, media such as cow-dung, horse-dung, mud from mud flats and ditch bottoms, decaying grass and decaying leaves have been kept in the laboratory for a month to allow time for all the *Psychoda* flies to emerge. Longer retention led to the production of a second generation.

The collecting sites

Flies were collected by the author at three farms and three areas of woodland bordering on pasture, near Leeds. Collections were made weekly from October 1942 to July 1944. The collecting site at Meanwood Valley was a strip of woodland about 100 × 10 yd. lying between a pasture and a stream. This site lies in a public park, about 5½ miles north-west of the Leeds sewage works at Knostrop. The site at Temple Newsam Park consisted of a row of trees with woodland on one side and pasture on the other, and included a stream and a small mud flat. This site was 1½ miles east of the sewage works, in the direction of the prevailing wind. These two localities both proved to be sufficiently far from the sewage works to have a *Psychoda* fauna uninfluenced by dispersal of the sewage-bred flies, and they can be contrasted with the following four localities, all of which are nearer to the sewage works. Golf-Course Wood lay about ¼ mile due east of the sewage works. The collecting site was a row of trees where the wood bordered on a pasture. Adjoining Golf-Course Wood was farm A, where flies were collected in the outbuildings and dairy. Farm B lay south-west of the works just short of a mile away and flies were collected in the outbuildings. Farm C lay about a mile due west of the works and flies were collected from the outbuildings and around a silo.

The author is indebted to Dr L. Lloyd for data of other *Psychoda* collections taken at three localities all distant from the sewage works. Farm D, 4 miles north of the sewage works, provided a comparison with the three farms near the works. At Roundhay Park collections were made from trees surrounding a rubbish tip of kitchen waste in dense woodland, about 4½ miles north-west of the sewage works. Lastly, Gledhow Valley, a site including a brook and a mud flat in which most of the sewage bacteria bed fauna occurred (Lloyd, 1944, 1945), lay about 4 miles north-west of the sewage works. The valley was wooded and there was pasture nearby.

To compare the composition of the *Psychoda* fauna at these localities the collections during each month were averaged and the resulting monthly indices for January to December 1943 were added together. The abundance of each species was then calculated as a percentage of the year's total.

The Psychoda fauna of pasture land

The *Psychoda* faunas of Meanwood Valley and Temple Newsam Park are alike (Table 1) and are recruited mainly from flies that breed in cow dung in the adjacent pastures. Table 2 gives a more detailed analysis of the fauna of Temple Newsam Park. Although slightly fewer flies were taken during 1943 at Meanwood Valley than at Temple Newsam Park, 859 against 1066, *P. phalaenoides* L. subsp. *elongata* Tonn. constituted just over half the total with 55% at Meanwood Valley and 61.4% at Temple Newsam Park. At both localities *P. setigera* Tonn. constituted just over 17%, whilst *P. albipennis* Zett. came third with 12.9 and 11.0% respectively. The remaining 10-15% was shared amongst the other nine species of the local fauna (Table 2). The three sewage-breeding species were extremely scarce and *P. alternata* was not taken at Meanwood Valley during 1943, and only once at

TABLE 1. The percentage composition of the *Psychoda* fauna of nine localities near Leeds

Locality	Total	<i>P. alternata</i>	<i>P. severini</i>	<i>P. cinerea</i>	<i>P. albipennis</i>	<i>P. phalaenoides</i>	Other species
Meanwood Valley	859	—	0.6	0.2	12.9	55.0	31.3
Temple Newsam Park	1066	0.1	2.0	0.4	11.0	61.4	25.1
Roundhay Park	451	—	14.9	1.9	33.1	33.6	16.5
Golf-Course Wood	329	29.9	20.8	0.2	12.3	12.5	24.3
Farm A	678	48.5	47.6	—	3.6	0.3	—
Farm B	653	3.7	95.2	—	1.0	—	0.1
Farm C	500	15.8	81.7	—	1.6	0.4	0.5
Farm D	1933	—	1.7	0.1	19.5	49.5	29.2
Gledhow Valley	1327	10.9	47.3	14.5	8.0	11.7	7.6

TABLE 2. The monthly indices of the species of *Psychoda* taken at Temple Newsam Park during 1943

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Total	%
<i>P. alternata</i>	—	0.2	—	—	—	—	—	—	0.2	0.1
<i>P. severini</i>	1.0	0.7	1.0	0.8	1.0	—	0.2	0.2	4.9	2.0
<i>P. albipennis</i>	7.0	3.2	2.7	2.0	1.0	—	6.8	4.0	26.7	11.0
<i>P. phalaenoides</i>	—	2.5	29.5	78.8	12.0	5.0	4.0	16.6	148.4	61.4
<i>P. setigera</i>	4.0	9.7	11.0	7.6	1.2	7.0	1.5	—	42.0	17.4
<i>P. brevicornis</i>	—	—	0.7	—	—	0.5	0.3	—	1.5	0.6
<i>P. cinerea</i>	1.0	—	—	—	—	—	—	—	1.0	0.4
<i>P. gemina</i>	—	—	—	—	0.2	0.5	—	—	0.7	0.3
<i>P. trinodulosa</i>	—	—	1.2	2.4	0.5	4.0	0.3	—	8.4	3.4
<i>P. griseus</i>	—	0.7	1.2	1.4	1.0	—	2.8	0.2	7.3	3.0
<i>P. spreta</i>	—	—	—	0.2	0.2	—	—	—	0.4	0.2
<i>P. lobata</i>	—	—	—	—	—	—	0.5	—	0.5	0.2
No. of collections	1	4	4	5	4	2	6	6		
No. of flies caught					1066					

Temple Newsam Park. *P. severini* constituted only 2% at Temple Newsam Park and 0.6% at Meanwood Valley, whilst *P. cinerea* was under 1% at both localities. Together the three sewage-breeding species accounted for just under 3% of the total flies.

At Golf-Course Wood (Table 3) only 329 flies were taken during 1943, and the influence of the adjacent sewage works was very apparent. *P. alternata* constituted 29.9% of the total and was the most abundant species, in marked contrast to the condition in the pasture-land fauna, where it was the scarcest (0.1%). *P. severini* was the second most abundant species, constituting 20.8% of the total. *P. albipennis* and *P. setigera* were approximately as common as in the pasture-land fauna (Table 2), whilst *P. phalaenoides* dropped to 12.5%. At Golf-Course Wood the fauna is thus seen to be largely dominated by flies dispersing from the sewage works. *P. cinerea* is scarce at the Golf-Course Wood because this species has not colonized the bacteria beds at Knostrop.

TABLE 3. The monthly indices of the species of *Psychoda* taken at Golf-Course Wood during 1943

	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Total	%
<i>P. alternata</i>	—	—	6.7	2.4	13.7	1.0	0.4	—	24.2	29.9
<i>P. severini</i>	1.0	2.2	5.0	2.2	4.2	—	1.6	0.6	16.8	20.8
<i>P. albipennis</i>	—	1.5	1.5	2.2	0.5	1.5	0.8	2.0	10.0	12.3
<i>P. phalaenoides</i>	—	0.7	1.0	5.4	0.7	0.5	0.2	1.7	10.2	12.5
<i>P. setigera</i>	—	4.0	5.7	1.2	0.2	0.5	0.2	—	11.8	14.6
<i>P. brevicornis</i>	—	—	—	—	0.2	—	—	—	0.2	0.2
<i>P. cinerea</i>	—	—	—	—	—	—	0.2	—	0.2	0.2
<i>P. trinodulosa</i>	—	—	0.2	—	—	—	—	—	0.2	0.2
<i>P. griseescens</i>	—	0.2	3.2	0.6	0.2	1.0	1.2	1.0	7.4	9.1
<i>P. spreta</i>	—	0.2	—	—	—	—	—	—	0.2	0.2
No. of collections	1	4	4	5	4	2	5	3		
No. of flies caught					329					

The *Psychoda* fauna of farms

The fauna of the three farms near the sewage works consisted almost entirely of sewage-breeding species (Table 1), but their abundance was not entirely due to dispersal from the sewage works. *P. alternata* breeds only in very wet and foul environments and is not a normal inhabitant of farms, but *P. severini* feeds on almost any moist decaying vegetable material. As there is a constant infiltration of adults from the sewage works to the farms any suitable breeding site may support a population of *P. severini* larvae. Consequently, the numbers of this species found on the farms is an index of their state of cleanliness rather than of their distance from the sewage works. Farm A (Table 1) showed approximately equal numbers of *P. severini* and *P. alternata*; it was within a $\frac{1}{4}$ mile of the sewage works, and dung was not left lying about the cow sheds to elevate the *P. severini* population. Farm C (Table 1) had many more *P. severini*, for, though this farm was equally close to the sewage works, this species colonized a layer of dung and straw left at one end of

a cow shed. Farm B (Table 1), nearly a mile away from the works, had *P. severini* present throughout the year. The species constituted 95.2% of the year's total, as a layer of dung and straw was left around the margins of a cow shed in which enormous numbers of the flies bred. It was observed that *P. severini* did not breed in stacked dung, but only in the material left in the sheds. At all these farms there was a large stack of dung, but no *P. severini* emerged from samples brought into the laboratory. On the other hand, dung collected from the floor margins of cow sheds at farm B produced numerous *P. severini*.

The fauna of these three farms may be compared with that of farm D, which was not only remote from the sewage works but free from conditions suitable for the breeding of *P. severini*. *P. alternata* was not taken at all during 1943 and *P. severini* constituted only 1.7% (Table 1). The fauna was very similar to the pasture-land fauna of Meanwood Valley and Temple Newsam Park, except that *P. albipennis* was rather more plentiful. The farm was surrounded by pasture containing numerous deposits of cow dung from which most of the farm *Psychoda* population evidently originated.

P. severini may be abundant at localities other than farms, and it constituted 14.9% of the total at Roundhay Park (Table 1). Here its prevalence was due to the suitable larval pabulum provided by a rubbish tip receiving kitchen waste. *P. albipennis* was also abundant at this locality (33.1%), and this species probably breeds in rubbish and decaying vegetation. Though it constitutes some 12% of the pasture-land fauna it has only twice emerged from field dung. It has, however, emerged from samples of decaying grass cuttings, rotten cabbages and rotten carrots. It was also very abundant (63.2%) in fourteen collections made by Dr L. Lloyd in his garden near Leeds in 1943, where its abundance was probably associated with a stack of rotting straw and manure.

In the Gledhow Valley mud flat many of the insects characteristic of the sewage bacteria bed occur (Lloyd, 1944, 1945). The *Psychoda* fauna, as judged by collections from the trees, consisted mostly of flies that had bred in the mud flat, plus some that had dispersed from the adjacent pasture land. *P. alternata* constituted 10.9%, *P. severini* 47.3% and *P. cinerea* 14.5% of the total, the remainder being pasture-land species (Table 1). Samples from the mud flat produced all three sewage-breeding species, and of 452 flies, *P. alternata* constituted 47.1%, *P. severini* 45.1% and *P. cinerea* 7.5%. The only non-sewage-breeding species was a single specimen of *P. grisescens* Tonn.

The seasonal incidence of *Psychoda* species

Fig. 1 illustrates the seasonal incidence of four species of *Psychoda* in the field. The two breeders in field dung, *P. phalaenoides* and *P. setigera*, each show a summer maximum followed by a depression, and the latter species shows a tendency to increase again in the autumn. The maximum follows the return of cattle to the pastures, but the reasons for the late summer depression and the autumn increase

are not evident. It may be an effect of competition due to the maximum activities of the higher Diptera in the dung deposit at this time. *P. albipennis*, breeding mainly in decayed vegetable matter, is most abundant in October when potential food is coming to its maximum, but before temperature has fallen seriously. *P. severini* shows a maximum in May and a steady decline towards autumn interrupted by a slight rise in August, at the Gledhow Valley mud flat. The abrupt rise in spring indicates a high winter survival, and the low-temperature threshold of larval development of this species, 0.6°C . (Lloyd, 1937), enables it to continue its

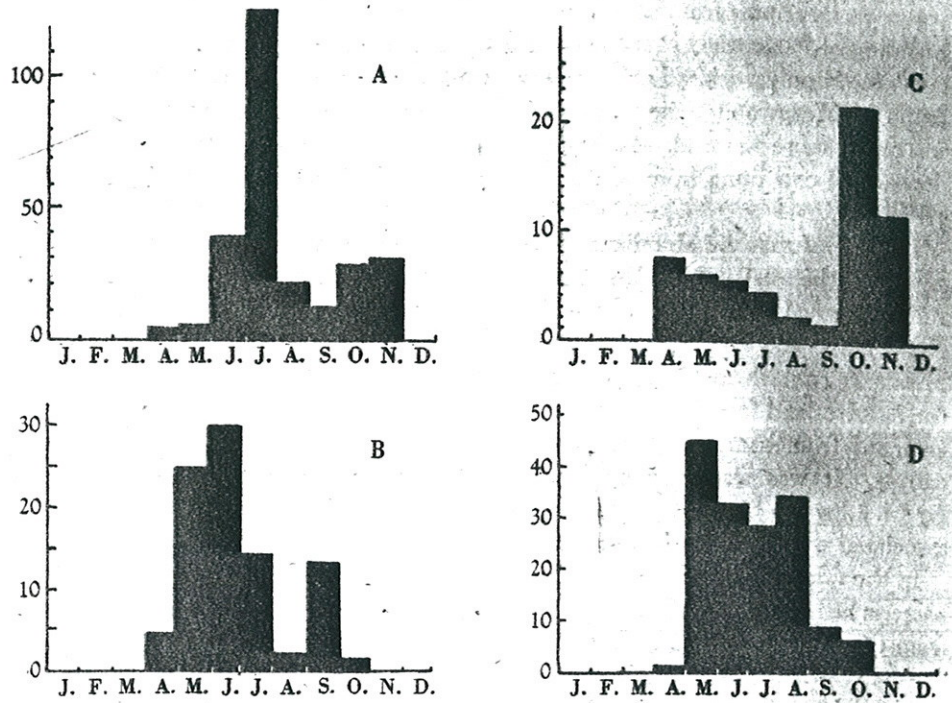


Fig. 1. The seasonal incidence of four species of *Psychoda*. A, *P. phalaenoides*; B, *P. setigera*; C, *P. albipennis*; D, *P. severini*. Ordinate: number of flies. Abscissa: months of the year.

development in all but the very coldest weather. At Gledhow its spring appearance is later than at the filter beds, where the warmth gives the species an early start; also it does not show the intense summer-autumn depression imposed on filter-bed *P. severini* by competition with Chironomids (Lloyd, 1937). This contrast between the natural and filter-bed seasonal incidence is also seen in *P. alternata* (Table 4), which increases steadily from spring to autumn at Gledhow, but at the filter bed exhibits a saddle-back curve of incidence, or a steady decline from an early summer maximum, due to the effects of competition (Lloyd, Graham & Reynoldson, 1940).

TABLE 4. The monthly indices of the three sewage-breeding species of *Psychoda* at Gledhow Valley during 1943

	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.
<i>P. alternata</i>	—	—	1.7	2.0	2.0	9.5	9.7	10.8
<i>P. severini</i>	—	0.3	45.3	32.3	28.0	34.2	8.7	5.7
<i>P. cinerea</i>	0.5	—	1.7	2.3	4.0	13.5	5.3	19.8
No. of collections/month	2	3	3	3	4	4	6	6

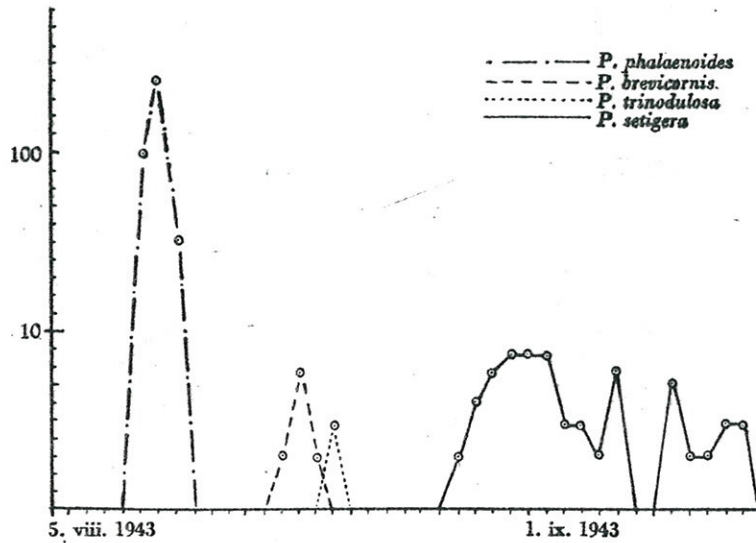


Fig. 2. Graph showing the emergence of *Psychoda* sp. from a sample of cow dung (collected 5 August 1943 near Leeds). Ordinate: log of number of flies ($\log n + 1$). Abscissa: time in days from date of collection.

The breeding media of Psychoda flies and the succession of species in the field dung deposit

By recording the fly emergence from eighty-nine samples of cow dung it was found that eight of the fourteen species of *Psychoda* taken in the field breed in this medium. The species emerge in a definite order, though not every sample of dung had all the members of the succession in it, and many samples were collected after the earlier emerging species had gone. This succession is well shown by a sample collected 5 August 1943 at Temple Newsam Park (Fig. 2). To elucidate this succession, the length of life cycle of a number of species was ascertained by setting up fertile females on scalded dung. The figures given refer to the time elapsing between oviposition and the emergence of the adults, and does not include the time taken for the maturation of the female, as a number of species would not mate in the laboratory.

In the twenty samples of cow dung from which *P. phalaenoides* was recorded this species was always the first to emerge. It has the shortest life cycle of any of the

species tested, 8 days at 20° C. Of the fourteen samples from which *P. grisescens* appeared, it emerged after *P. phalaenoides* on thirteen occasions and with it on one. Its length of life cycle at 20° C. is 12 days, which would account for its relegation to second position in the succession. *P. grisescens* is followed by two species, *P. brevicornis* Tonn. and *P. trinodulosa* Tonn., but it has not proved possible to ascertain the length of the life cycle of these species owing to the shortage of fertile females in the collections. Following these, *P. setigera* emerges; it has a life cycle of 21 days at 20° C. *P. albipennis* does not normally occur in the dung deposit, but on the two occasions when it did emerge, it was once just before *P. setigera* and once just after. Its life cycle at 20° C. takes 19 days.

In addition to the six species of *Psychoda* already mentioned as breeding in cow dung, *P. surcoufi* Tonn. and *P. crassipennis* Tonn. are known to breed in this medium. *P. surcoufi* emerged from two samples collected during November 1943, though only a single specimen of this fly was ever taken in the collections. Its length of life cycle at 20° C. is 15 days. *P. crassipennis* was found by Dr Lloyd breeding in a sample of cow dung collected at Appleby in September 1943, but the species has not emerged from this medium collected near Leeds.

There remain six species of *Psychoda* taken in the collections which do not normally breed in the field dung deposit, and the records of their emergences from various media have been dealt with in a previous paper (Satchell, 1947). *P. severini* does not often emerge from field deposits of cow dung, and of the eighty-nine samples collected, it was present in only two. It does, however, breed in decaying vegetable materials and has emerged from horse and chicken dung, decaying leaves, cabbage stalks, carrots, and mangolds, the slime adhering to the sides of drains, mud from mud flats, and the bacteria beds of sewage works. *P. alternata* has never emerged from the samples of field dung. It tends to be restricted to foul and wet environments such as privies, urinals, drains, rotting straw and dung in disused feeding troughs, carrion, mud flats and bacteria beds. *P. cinerea* has also never emerged from samples of field dung, and has been recorded from drains, a water trough containing algae, mud flats and bacteria beds.

P. gemina Eaton has twice emerged from samples of mud and leaves from a ditch, and *P. spreta* Tonn. appeared in a sample of rotting lawn mowings exposed at Meanwood Valley for a week. *P. lobata* Tonn., a scarce species around Leeds, has never emerged from any of the samples of material collected, and its larval food is unknown.

Parasites of Psychoda flies

Whilst examining the various species of *Psychoda* a number of parasites have been found. Bovien (1937) observed that *Psychoda* flies commonly carry the larval stages of species of *Rhabdites*. The worms wrap themselves tightly round the abdomen of the adult in the grooves between the segments, and were frequently found on flies collected in the field, and on specimens emerging from dung samples. The species most commonly infected was *Psychoda phalaenoides*, the only other infected species

found being *P. grisescens*. In the laboratory any species will pick up the worms if enclosed over a dung sample containing them. One culture was examined by Dr Goodey who identified it as *Rhabdites curvicaudata* Schneider (Goodey, 1943).

An internal parasitic nematode which almost fills the body cavity with its eggs and larvae was encountered on five occasions, four times in *Psychoda grisescens* and once in *P. spreta*. Dr Goodey kindly inspected a preparation and gave his opinion that this worm is allied to *Tylenchinema oscinella* Goodey (Goodey, 1930).

A protozoan parasite, a species of *Glaucoma*, probably *G. piriformis*, was encountered as a massive infection of the body cavity in five flies, three times in *Psychoda severini* and once each in *P. gemina* and *P. cinerea*. Watson (1946) has surveyed the versatile habits of *Glaucoma piriformis*, noting it as polysaprobic, coprophilic, and a potential parasite of invertebrates and cold-blooded vertebrates. In addition to these records in *Psychoda*, Lloyd (unpublished) has observed it in the Chironomid *Spaniotoma minima* Meig. from the filters.

DISCUSSION

The *Psychoda* fauna of pasture land, exemplified by that of Meanwood Valley and Temple Newsam Park, was shown to be dominated by *P. phalaenoides*, a species that has frequently emerged from samples of field dung, but never from any other material. The totals for the three other exclusively dung-breeding species, *P. setigera*, *P. trinodulosa* and *P. brevicornis*, when added to that of *P. phalaenoides*, are found to account for over 80% of the pasture-land fauna. The only species of any numerical importance that is not usually a dung breeder is *P. albipennis*.

Of the few sewage-breeding *Psychoda* in the pasture-land fauna, *P. severini* is the most abundant, constituting 2% at Temple Newsam Park, and when suitable breeding sites are available it may be common. At Roundhay Park, a rubbish tip containing kitchen waste provided it with suitable larval food and it constituted 14.9% of the total. The abundance of this species at the three farms near the sewage works was in part due to dispersal from the filter beds and in part to fly breeding in the cow-shed litter. *P. severini* is probably a common farm insect, passing unnoticed because of its small size. It occurred at ten other farms visited during 1943 (five in Cumberland, three in Yorkshire, two in Shropshire), but is not mentioned by Thomsen & Hammer (1936) in their study of farm-breeding flies in Denmark.

Though *P. severini* is thus seen to be a common species which may be present wherever damp and decaying vegetable material abounds, *P. alternata* is much more restricted in its breeding sites, and consequently in its occurrence. It was common at Gledhow Valley where samples of mud showed it to be breeding in the mud flat, and at Golf-Course Wood, farm A and farm C. Here, however, its presence was due to dispersal, for not only were the bacteria beds within $\frac{1}{4}$ mile, but other suitable breeding grounds were absent. Further, it was observed that peak emergencies of *P. alternata* at the bacteria beds were followed by the appearance of

the species in abundance at the farms and at Golf-Course Wood. The abundance of this species at the farms reflects their distance from the sewage works, farm D, 4 miles away, showing none, farm B, 1 mile away, showing 3.7%, farm C, 1/4 mile west, showing 15.8% and farm A, 1/4 mile east, showing 48.5%. This species has, however, but feeble powers of migration, for at Temple Newsam Park, only 1 1/2 miles away, only a single specimen was taken during almost 2 years' collecting. It is impossible to determine the dispersal powers of *P. severini*, for odd stragglers may colonize some naturally occurring habitat near the works and provide a new focus of abundance of the species, and the wide variety of vegetable matter that will serve this species as food makes it unsuitable as an index of sewage fly dispersal. A series of naturally occurring breeding sites at increasing distances from the sewage works may give the appearance of a very widespread dispersal when, in fact, the distance has been covered in stages.

Since the warmth of the beds during the winter promotes early emergence, a sewage works may be indirectly responsible for a severe fly nuisance even when the flies in question have not emerged from the works but from some naturally occurring breeding site. The early production of a species from the bacteria bed ensures a supply of fertile females ready to oviposit in any naturally occurring habitat, and this early start in the outside breeding foci may result in the species reaching troublesome proportions later in the year. This does not apply so much to species like *P. alternata* and *P. cinerea* which are restricted to wet and foul environments of a rather specialized type, for such species will be less able to find outside breeding foci of a suitable type within the dispersal range of the species from the sewage works. It does apply, however, to species like *P. severini* which is not so restricted. It is thus of importance to the sewage works operator to know, when complaints of sewage fly dispersal are received, not only the species of fly concerned, but also its natural breeding habitats and the extent to which such habitats are likely to be present within the dispersal range of the sewage works.

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