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Source: *Journal of Applied Ecology*, Vol. 8, No. 3 (Dec., 1971), pp. 835-844

Published by: [British Ecological Society](#)

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ASPECTS OF THE BIOLOGY OF *PSYCHODA ALTERNATA* (SAY.) AND *P. SEVERINI PARTHENOGENETICA* TONN. (DIPTERA) IN A PERCOLATING FILTER

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INTRODUCTION

The fly populations of percolating filters treating sewage have been described by Lloyd (1937), who gave details of the general biology and seasonal incidence of both species of *Psychoda* and the effect of temperature on the duration of their life cycles. In later studies (Lloyd 1943b), he examined intraspecific competition in *P. alternata*. The inter-relations of *Psychoda* with other members of the filter fauna were discussed by Lloyd, Graham & Reynoldson (1940), Lloyd (1943a), and Hawkes (1963). Tomlinson *et al.* (1949) examined possible control measures to prevent fly nuisance from filters and certain beneficial effects of *P. alternata* on the purification of an artificial sewage were studied by Williams & Taylor (1968).

This paper is the third in a series describing the fauna of an experimental filter of 12 m³ volume. Previous papers described the whole macro-invertebrate fauna, including the population dynamics of *P. alternata* and *P. severini*, particularly with reference to filter maturation and the effect of animals on the settlement of humus solids (Solbé, Williams & Roberts 1967), and a more detailed study of the enchytraeid worm population (Williams, Solbé & Edwards 1969).

The present work considers the annual change in the balance of *Psychoda* species, changes in population density as the filter matured, and the extent of the contribution to overall filter metabolism made by *Psychoda* respiration. This contribution is compared with that made by the respiration of the enchytraeid worms.

METHODS

The filter contained 11.9 m³ (15.6 yd³) of 5.1 cm (2 in.) blast-furnace slag. Domestic sewage was applied at 5-min intervals at a rate of 0.47 m³/m³ medium/day (80 gal/yd³/day). Sixteen perforated metal canisters, 16.3 cm (6½ in.) diameter and 150 cm (5 ft) long, were set vertically into the filter. Each canister was packed with six perforated metal baskets 15 cm (6 in.) in diameter which contained the filter medium. The bottom four baskets were 30 cm (12 in.) deep and the top two 15 cm (6 in.).

At monthly intervals baskets were removed from the canisters. Canisters were at first sampled in a random order, but once all had been sampled the sequence established was maintained, canisters being left undisturbed for at least 5 months between samples. From March 1964 until May 1965 all the baskets from three canisters were taken; from May 1965 until August 1966 the whole of one canister and the top three baskets of another were sampled; from August 1966 until December 1967 the sample was reduced to all the baskets from a single canister.

The organic material removed from the medium in a rotary washer (Hawkes 1965)

was divided into two parts, one half being used for the determination of the dry weight of film, its content of carbon and nitrogen and the proportion of volatile matter present (Solbé *et al.* 1967). The other half of the sample was used for animal counts and assessing the size-class structure of the population, using the sub-sampling techniques described by Allanson & Kerrich (1961).

In order to establish the number of larval instars, the widths of the head capsules of 203 *Psychoda alternata* larvae and 237 *P. severini* larvae over the whole size range were measured.

Respirometric studies were made on groups of larvae, pupae and adults between January and March in a Warburg constant-volume respirometer (Umbreit, Burris & Stauffer 1964) after acclimation to the test temperature for about 2 h. The number of animals used in each vessel approximated to the average number occupying a similar void space in the filter.

RESULTS

The psychodid population in the filter consisted of two species, *Psychoda severini parthenogenetica* Tonn. and *P. alternata* Say., which can be recognized at all stages after the egg. Larvae were identified by examining the dorsal plates (Satchell 1947) and pupae by the shape of the respiratory horns (Satchell 1949).

The polymodal distribution of larval head capsule widths is shown in Fig. 1 from which the population was accordingly divided into four instars (as is usual in the Nematocera) whose mean widths are indicated. The greater spread of the *P. alternata* distributions may be connected with sexual differences, since the male imagines are much lighter than the females (males $107 \mu\text{g}$ dry weight $\pm 7 \mu\text{g}$ ($n = 1000$), females $208 \pm 20 \mu\text{g}$ ($n = 300$)). *P. severini* is parthenogenetic, the males being unknown in this country (Coe, Freeman & Mattingley 1950).

Table 1 shows the ratios of the widths of head capsules of successive instars; the ratios seem sufficiently close to preclude intermediate instars.

The average dry weight of each instar and of the pupae is shown in Table 2. Although their head capsule widths were very similar, the dry weights of each instar show very large interspecific differences, especially instars II and III. *P. alternata* larvae of any given instar were always heavier than *P. severini*. *P. alternata* pupae were lighter than fourth instar larvae, but this was not so with *P. severini*. Despite a wider range of fourth instar weights than is shown in Table 2, the increased weight of pupae is inexplicable.

The principal feature of the *Psychoda* population data is the peak in numbers of larvae around May each year (Fig. 2). As the filter matured, enchytraeids and lumbricids became established and the *Psychoda* peak decreased each year; in May 1964 the average density of second, third and fourth instar larvae exceeded 14 000/litre, in 1965 nearly 8000, and in 1966 less than 6000. In 1965 and 1966 there were around 1500 enchytraeids/litre in the filter, and in 1966 there were, in addition, eighty lumbricids/litre.

In general, the figures for pupae and adults followed the same pattern as those for the larvae, but there were relatively more pupae in the winter. For both species the lowest value of the ratio of larvae to pupae occurred in January, but while that for *P. alternata* increased slowly from 1.8 to 5.1 in July, the ratio for *P. severini* rapidly increased from 0.5 to 11.1 by May. This difference may well be connected with the success of *P. severini* at lower temperatures, discussed by Lloyd (1937) who found that *P. severini* could com-

plete its life cycle in 85 days at 7° C while *P. alternata* took 218 days at 8° C, pupation not occurring below 7.7° C.

Fig. 2 also shows the numbers of *P. severini* in the population for the period November 1965–October 1966. As expected, *P. severini* made up more than half of the March–May 1966 population of larvae and almost disappeared from the filter during mid-summer and the autumn, the numbers not rising until March. The mechanism of winter survival and the rapid population increase in spring are not yet understood. Small numbers of

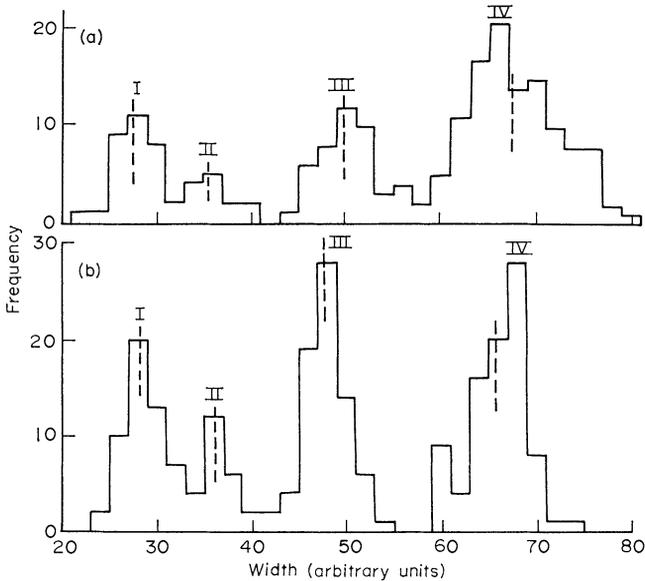


FIG. 1. Frequency distribution of widths of larval head capsules. (a) *Psychoda alternata*; (b) *P. severini*.

Table 1. Ratio of widths of head capsules of successive instars

Species	Instar	Ratio
<i>P. alternata</i>	I	
	II	1.29
	III	1.41
	IV	1.32
<i>P. severini</i>	I	
	II	1.275
	III	1.31
	IV	1.375

most developmental stages of *P. severini* are found in February. There may be a slow accumulation of eggs during the winter which hatch almost simultaneously in the spring, but this is unlikely since Lloyd (1937) found that the fully favourable range for this species was 6–20° C and the sewage temperature, which largely determined the temperature of the filter (Bayley & Downing 1963), only fell below 7° C on 7 days during the period November 1965–March 1966. Lloyd also gives data for *P. alternata* whose favourable range is given as 16–25° C and lower threshold temperatures for larvae and pupae as 5.5 and 7.7° C respectively. In the filter *P. alternata* dominated the *Psychoda*

Table 2. Average dry weight of larvae and pupae and standard deviation between groups within classes

Species	Instar	No. weighed	Groups of	Weight (μg)
<i>P. alternata</i>	I	125	25	8.3 ± 1.4
	II	100	20	187 ± 18
	III	160	20	237 ± 34
	IV	100	20	436 ± 37
	Pupae	125	25	310 ± 26
<i>P. severini</i>	I	120	25+20	2.1 ± 0.3
	II	100	20	12.4 ± 1.4
	III	50	10	33 ± 3.5
	IV	50	10	266 ± 36
	Pupae	125	25	378 ± 20

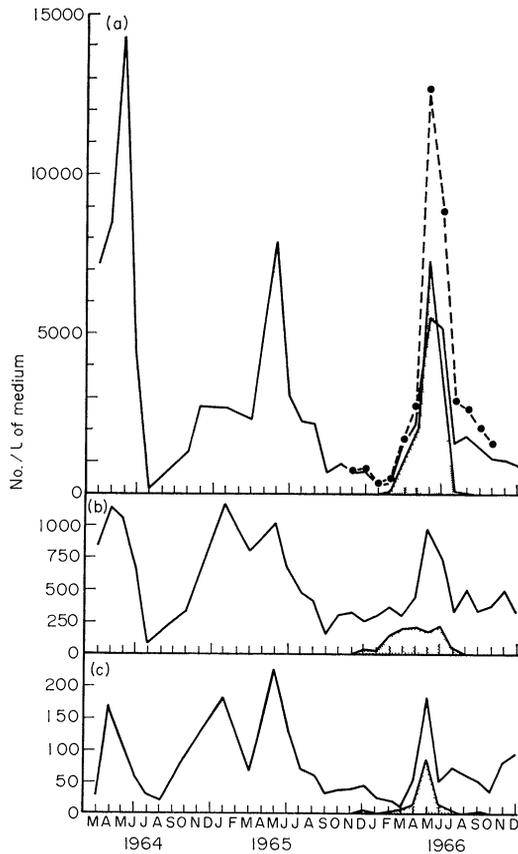


FIG. 2. Average numbers of *Psychoda*: (a) larvae (second, third and fourth instars); (b) pupae; and (c) adults per litre of medium. ●, Including first instars; stippled areas, *P. severini*.

population for 9 months of the year, during which the monthly average sewage temperatures varied between 7.8 and 17.9° C, i.e. only just high enough to reach the lower end of the favourable range and not low enough to inhibit metamorphosis.

Figs. 3 and 4 show the monthly average numbers/litre for each instar from November 1965 to October 1966. *P. alternata* first instar larvae averaged 673/litre over the whole period, seconds 511, thirds 478 and fourths 304. The numbers of all instars rose in the summer, but they remained much nearer their mean values than did those of the *P. severini* larvae, which were virtually absent from the filter except between March and

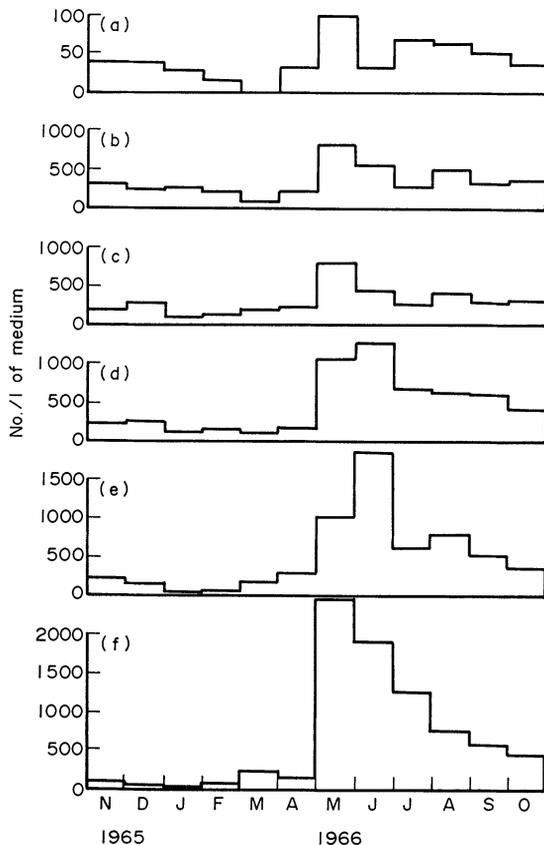


FIG. 3. Numbers of *Psychoda alternata* per litre of medium in each development stage, November 1965–October 1966. (a) Adults; (b) pupae; (c) fourth instar; (d) third instar; (e) second instar; (f) first instar.

June. Again, *P. severini* first instars were most numerous at 511/litre with progressively fewer of the larger larvae: 290 seconds, 194 thirds and 160 fourths/litre.

It has been suggested that the number of adults emerging from the filter reflects the size of the population within the filter (Solbé *et al.* 1967) and that in this filter the *P. severini* population probably declines abruptly around June. This is now verified for the period November 1965–October 1966 and the decline in egression is matched by a decline in the *P. severini* population. Solbé *et al.* calculated the time of establishment of the *P. alternata* population in 1964 and suggested that it followed, and thus did not cause, the reduction of *P. severini*. It now seems likely that *P. severini* decreases to a similar extent at the same time each year, with or without *P. alternata* being present.

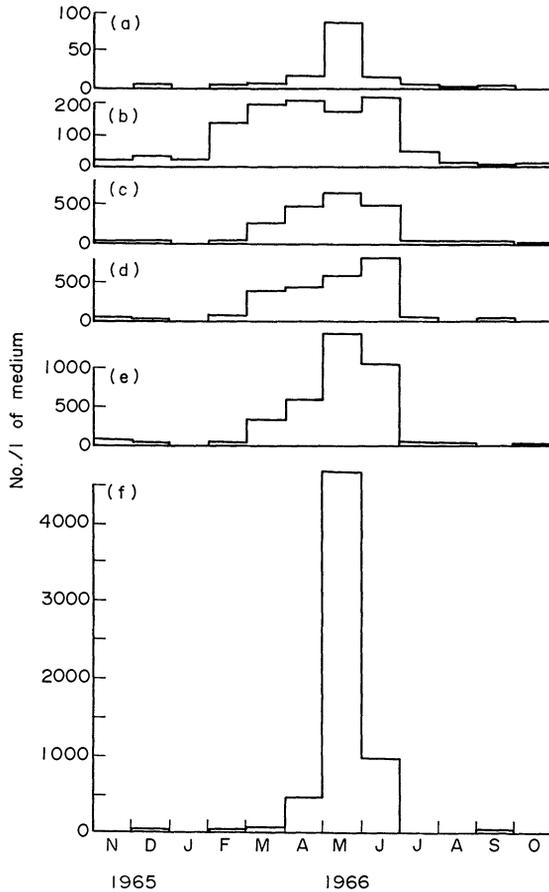


FIG. 4. Numbers of *Psychoda severini* per litre of medium in each development stage, November 1965–October 1966. (a) Adults; (b) pupae; (c) fourth instar; (d) third instar; (e) second instar; (f) first instar.

In both species the distribution throughout the depth of the filter varied little with the time of year. *P. alternata* larvae and pupae were most numerous between 15 and 30 cm (6 in. and 12 in.), except for first instar larvae, maximum numbers of which were found between 0 and 15 cm. The *P. severini* population was also most dense between 15 and 30 cm, except for the adults, which occupied the top 15 cm, and the pupae, at a median depth of 35 cm. The median depths of the two larval populations did, however, differ slightly (Table 3), *P. severini* occupying a lower zone.

The oxygen consumption by *Psychoda* larvae and pupae at three temperatures is shown in Fig. 5. *P. severini* consumed more oxygen per unit weight than *P. alternata* of any given instar, as might be expected from the smaller size of the former. The increase in respiratory rate from 10 to 20° C averaged 2.86 for *P. alternata* and 3.49 in the case of *P. severini*, both values being greater than was found for the enchytraeids whose

Table 3. Median depths (cm) of *Psychoda* larvae and pupae

	Larval instar				
	I	II	III	IV	Pupae
<i>P. alternata</i>	9.1	15.3	12.2	10.7	15.3
<i>P. severini</i>	18.3	19.0	27.4	26.0	35.0

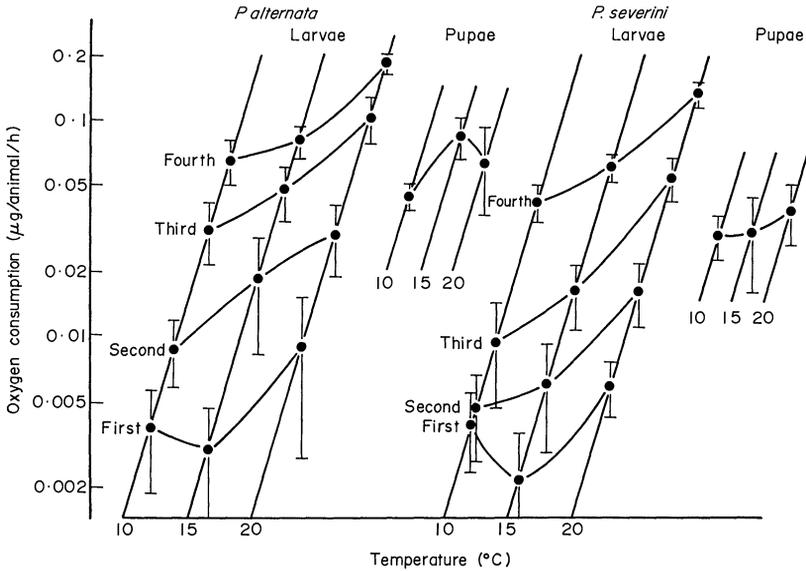


FIG. 5. Oxygen consumption by *Psychoda* larvae and pupae.

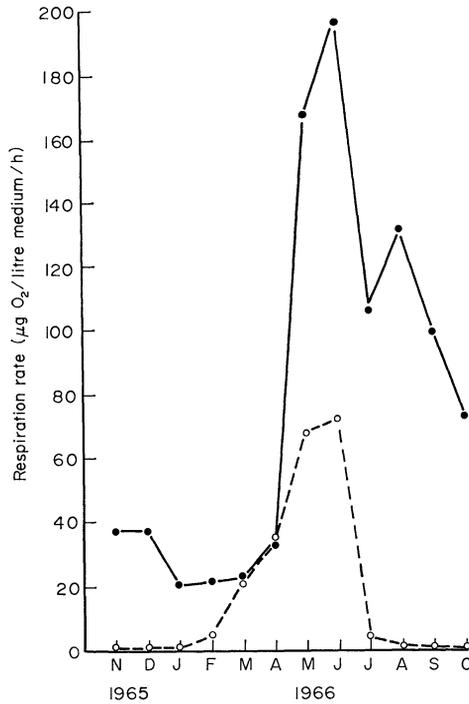


FIG. 6. Respiration of *Psychoda* population, November 1965–October 1966. ●, *P. alternata*; ○, *P. severini*.

average Q_{10} was 1.62 (Williams *et al.* 1969). Some of these results may reflect differences in the acclimation of the animals to temperature and may not represent the seasonal rates that obtain in the filter.

The oxygen consumption data have been used to estimate the respiration of the

Psychoda population from November 1965 to October 1966 (Fig. 6), and from this it can be calculated that *P. alternata* consumed more than $100 \mu\text{g O}_2/\text{litre of filter medium/h}$ from May to September, reaching almost $200 \mu\text{g}$ in June, but *P. severini* only reached as high as $70 \mu\text{g O}_2/\text{litre/h}$ in May and June. In the absence of any data, a respiratory quotient of 0.8 has been assumed in converting oxygen consumption into carbon dissipation. This is compared with that attributable to the enchytraeid worms in Fig. 7. The total dissipation of carbon from the filter has been calculated using the method of Solbé, Ripley & Tomlinson (in preparation). *Psychoda* respiration accounted for from 0.162 (January 1966) to 2.052 (June 1966) mg C/litre of medium/day.

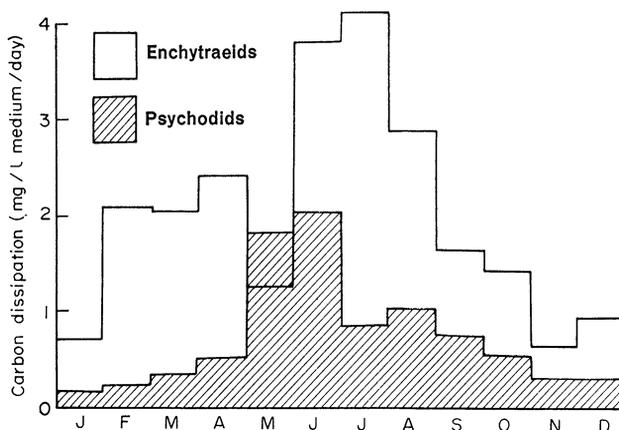


FIG. 7. Comparison of the rate of carbon dissipation by psychodids (closed columns) with that by enchytraeids (open columns).

DISCUSSION

In general the insects respired less carbon than the enchytraeids (Table 4), accounting for only 1% of the total carbon dissipation. Both groups dissipated carbon at their highest rates in summer, although the worms varied less since their numbers did not decline rapidly at the end of June, as was found with *P. severini*. Williams & Taylor (1968) have shown that, given time, a percolating filter in which enchytraeid worms are the only grazers will produce a good quality effluent. Since the worms, unlike the flies, seem never to present any nuisance, their existence in filters appears wholly beneficial.

It is interesting to note the change in the efficiency of the grazing populations in dissipating carbon from a maturing percolating filter which from March to July 1964 (its first summer of operation) supported only *Psychoda* and developed populations of enchytraeid and lumbricid worms in the succeeding 2 years. Table 5 relates this changing efficiency to the changes in the content of volatile matter in the filter over the period. More carbon was dissipated from the filter as time passed and the population became more complex. This increased efficiency is reflected not only in the decrease in volatile material within the filter but also in the results of analysis of the effluent quality in terms of reduction of both BOD and concentration of ammonia (Solbé *et al.* 1967).

It is unlikely that the numbers and species of macro-invertebrates present in a filter are ever stable, especially in the first few years of operation. Nevertheless, various

dynamic patterns of balance may be observed, and one of these is exemplified by *Psychoda*—*P. severini* cannot maintain high numbers in the warmer weather. Others are seen in the enchytraeid worms (Williams *et al.* 1969), the numbers of the two species in the filter changing in the same way from month to month, and in the lumbricid worms (Solbé 1971) where for 12 months one species alone was present, which then decreased as a second species colonized the filter and became dominant.

The filter was allowed to mature without deliberate inoculation and the first species of fly to colonize the filter (*P. severini*) and the first earthworm (*Eiseniella tetraedra*) were obligatory parthenogens. The second earthworm, *Dendrobaena rubida*, was a facultative parthenogen. The advantages of such a method of reproduction in the early stages of the colonization of a filter are obvious. The earthworms, particularly, would otherwise

Table 4. *Average population density, biomass and metabolic rate of psychodid flies and enchytraeid worms in the filter (November 1965–October 1966)*

	Population density/litre of medium	Biomass (g dry matter/litre)	Metabolic rate (mg C/litre/day)
Psychodidae	Larvae 3120 Pupae 450 }	0.547	0.736
Enchytraeidae	1069	0.514	1.993

Table 5. *Change in efficiency of the animal populations in dissipating carbon from a percolating filter*

Year (March–July)	Animals present	Mean dissipation of carbon (mg/litre/day)	Change in content of volatile matter from March to July (g/litre)
1964	Psychodids	2.300	+1.725
1965	Psychodids and enchytraeids	4.179	–2.549
1966	Psychodids, enchytraeids and lumbricids*	4.989	–4.170

* Lumbricid data from Solbe (1971).

have been at a disadvantage, since the population was so sparse in the early stages of maturation of the filter that the chances of two worms being close to one another in the filter were very low.

With only the respiration of the earthworms remaining to be taken into account the rôle of macro-invertebrates in dissipating carbon directly from a percolating filter is seen to be relatively minor, the psychodid flies and enchytraeid worms being responsible on average for only 4% of the dissipation from the whole filter. The less direct effects of animals in percolating filters, protecting the filter against accumulation of too much film and increasing the settleability of humus solids, are likely to be much more important.

ACKNOWLEDGMENTS

The authors wish to thank Professor R. W. Edwards (Department of Applied Biology, University of Wales Institute of Science and Technology, Cardiff) for his advice and helpful criticism.

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SUMMARY

(1) The population dynamics of two species of *Psychoda* in a percolating filter have been examined from the point of view of species balance, depth-distribution, and the change in proportion of larvae and pupae over a year. *P. alternata* was generally the dominant species, although *P. severini* increased considerably in May and June, declining abruptly in July. They occupied almost the same vertical position in the filter, the median depth of the *P. severini* population being slightly greater than that of *P. alternata*. The ratios of the numbers of larvae to the numbers of pupae decreased in winter.

(2) The customary number of four larval instars for dipterans was established by examining the frequency-distribution of head-capsule widths.

(3) Respiratory rates of larvae and pupae were determined in a Warburg constant-volume respirometer and the results were used to calculate population metabolism.

(4) Estimates of the carbon dissipation by *Psychoda* were made and compared with that of the enchytraeid worms and with the total dissipation from the filter. *Psychoda* were responsible for only 1% of the dissipation, so that, with the enchytraeid worms, 4% of the carbon leaving the filter as carbon dioxide has now been assigned to animal respiration.

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