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T. R. NEW

**Observations on the Biology of Psocoptera Found in Leaf Litter
in Southern England**

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PART VII

OBSERVATIONS ON THE BIOLOGY OF PSOCOPTERA FOUND IN LEAF LITTER IN SOUTHERN ENGLAND

By T. R. NEW

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Introduction

Many groups of small arthropods are found in leaf litter, and the fauna is in many ways intermediate in character between that of soil and that of low vegetation. Numerous studies of soil fauna have been made in recent years (see Kevan, 1955, 1962), but there are fewer accounts of leaf litter arthropods. Psocoptera are part of the active mesofauna (*sens* Fenton, 1947) of the litter, in which they comprise only a small proportion of the total arthropod fauna. There have been no ecological studies of Psocoptera in this habitat, but a number of edaphic Psocids have been described from various parts of the world.

Several workers on other groups have enumerated small numbers of Psocids extracted from soil or litter in Europe, but these have not in many instances been identified (see Salt *et al.*, 1948). Stringer and Herrington (1963) recovered a few specimens of *Lachesilla pedicularia* (L.) and *Liposcelis* sp. from black currant litter at Long Ashton, Bristol. Strickland (1947) recovered species of *Ectopsocus*, *Liposcelis*, and *Psocatropos* from litter under Cacao in Trinidad, and Salt (1952) and Belfield (1956) both obtained small numbers of unidentified Psocids from pasture soils in Africa by flotation methods. Two specimens of *Lachesiella* (*sic.*) were found in soil from Giza by El Kifl (1959).

The aims of the present work were to discover the range and numbers of Psocids in leaf litter throughout the year, and to examine the distribution of Psocids in different kinds of litter. All work was carried out at Silwood Park, Ascot, Berkshire.

Extraction Methods

Two methods of extraction were used in the present study. Tullgren funnels were used for the bulk of the extractions, and a Kempson Bowl Extractor (Kempson, Lloyd and Ghelardi, 1963) was also used. Both methods depend on downward movement of the animals in response to heat applied from above, but the latter provides for maintenance of a high humidity towards the bottom of the sample and in the air immediately under it. Comparative calibrations of the two methods should give a measure of the loss of animals caused by desiccation in the Tullgren

funnels. Funnels of 25 cm diameter were used and were heated by 60 w bulbs suspended 15-20 cm above the samples. The funnels and the four-chambered Kempson extractor were calibrated by the following method (after van der Drift, 1951). All Psocids were extracted from samples of *Pinus* and *Quercus* litter by treatment in the funnels for 14 days, after which extraction was assumed to be complete. The 'clean' litter was left in the funnels for a few days to cool thoroughly, and then damped from the top. Known numbers of Psocids of different species and stages were introduced near the top of the samples, which were then extracted for ten days. The collecting jars, which contained 70 per cent alcohol, were changed daily, and the rates of extraction were thus found. Comparison of the total numbers of Psocids extracted with the numbers introduced was taken as a measure of the extraction efficiency of the funnels. Samples of Psocid-free litter from the funnels were transferred to the Kempson bowls, and the above procedure repeated. The bowls of picric acid were changed daily, and all sample bowls were covered to prevent the escape of Psocids. Ten samples of each kind of litter were examined in most cases for each Psocid tested and for each extraction method. Results of these extraction tests are summarised in Table 1. The different types of Psocids were

TABLE 1

Extraction efficiencies of Tullgren funnels and Kempson Bowl Extractor for various Psocoptera from leaf litter

<i>Litter</i>	<i>Psocid species</i>	<i>No. of psocids</i>	<i>Stages</i>	<i>No. of replicates</i>	<i>Total psocids extracted</i>	<i>% extracted</i>
<i>(a) Tullgren funnels</i>						
Oak leaves	<i>Liposcelis</i> sp.	50	Ad + N	10	380	76.0
Oak leaves	<i>E. briggsi</i>	100	Ad	10	726	72.6
Oak leaves	<i>E. briggsi</i>	50	N	10	347	69.4
Oak leaves	<i>C. flavidus</i>	100	Ad	10	886	88.6
Oak leaves	<i>C. flavidus</i>	50	V-VI	10	424	84.8
Oak leaves	<i>C. flavidus</i>	50	II-IV	10	309	61.8
Oak leaves	<i>E. lucifugus</i>	50	Ad - N	5	227	90.8
Pine needles	<i>C. guestfalica</i>	40	Ad	10	278	69.5
Pine needles	<i>E. briggsi</i>	50	Ad	10	396	79.2
Pine needles	<i>E. briggsi</i>	50	N	10	417	83.4
Pine needles	<i>C. flavidus</i>	50	Ad	6	260	86.7
Pine needles	<i>C. flavidus</i>	50	V-VI	10	403	80.6
<i>(b) Kempson Bowls — covered</i>						
Oak leaves	<i>E. briggsi</i>	50	Ad	10	468	93.6
Oak leaves	<i>C. flavidus</i>	50	Ad	10	483	96.6
Oak leaves	<i>C. flavidus</i>	50	V-VI	10	398	79.6
Oak leaves	<i>C. flavidus</i>	50	II-IV	8	316	79.0

extracted more efficiently by the Kempson method, and some variations were seen in the Tullgren extractions. The young nymphs of Psocids (such as *C. flavidus* (Stephens)) are more susceptible to desiccation than the later stages, and were extracted less efficiently.

The amount of water in the ground litter varied considerably; during the winter, especially, drying samples to constant weight reduced the original weight by up to 85 per cent. A comparison of the extraction efficiencies of Tullgren funnels for dry and sodden litter was made by the above method, where ten samples of each were extracted. The results are given in Table 2, and

TABLE 2

Comparison of extraction of efficiencies funnels with dry and wet oak litter

Litter	Psocid	No. of psocoids	Stages	No. of replicates	Total psocids extracted	% extracted
Dry oak leaves	<i>C. flavidus</i>	50	Ad	10	390	78.0
Dry oak leaves	<i>C. flavidus</i>	50	V-VI	10	406	81.2
Dry oak leaves	<i>C. flavidus</i>	40	II-IV	10	293	70.3
Sodden oak leaves	<i>C. flavidus</i>	50	Ad	10	306	61.2
Sodden oak leaves	<i>C. flavidus</i>	50	V-VI	10	397	79.4
Sodden oak leaves	<i>C. flavidus</i>	40	II-IV	10	260	60.5

indicate that a higher proportion of Psocids is extracted from dryer than sodden litter. It is likely that many small active animals become entrapped in water films in wet litter, and drown in the large amount of free water. Corpses of introduced Psocids were found in the sodden litter on subsequent examination, but no conclusions could be drawn as to the cause of death.

The collecting tubes under the Tullgren funnels were changed daily and the numbers of Psocids in them were counted (Table 3).

TABLE 3

Times of extraction of psocids from leaf litter by Tullgren funnels

Litter	Psocid	Stage	Numbers extracted on Day:									
			1	2	3	4	5	6	7	8	9	10
(a) Calibration Tests												
Oak	<i>C. flavidus</i>	Adults	86	230	216	133	189	2	8	—	—	—
Oak	<i>C. flavidus</i>	Nymphs	109	204	138	159	48	51	20	—	4	—
Oak	<i>E. lucifugus</i>	All	31	106	19	26	35	5	4	—	—	1
Oak	<i>E. briggsi</i>	Adults	57	200	308	89	50	3	—	17	2	—
Oak	<i>E. briggsi</i>	Nymphs	72	115	29	21	103	7	—	—	—	—
Pine	<i>E. briggsi</i>	Adults	84	186	44	26	34	2	9	11	—	—
Pine	<i>C. flavidus</i>	Adults	59	107	16	70	6	—	2	—	—	—
(b) Natural samples — 1966												
Oak	<i>C. flavidus</i>	All	2	7	7	18	12	2	3	—	—	—
Oak	<i>E. lucifugus</i>	All	86	37	15	11	9	15	7	—	—	—
Oak	<i>E. briggsi</i>	All	4	2	2	3	3	38	17	—	—	—

Most of the Psocids were extracted in the first three days, and only a very small number was found after seven days. The figure given for *Ectopsocus briggsi* McLachlan may appear anomalous; this was due to a large incidence of first instar nymphs from eggs hatching in the litter, which may be dissociated confidently from the Psocids present in the litter at the time of collection. The duration of the first instar of *E. briggsi* is usually

one to three days, and the presence of this instar after the fourth day of extraction must result from the hatching of eggs. This misleading trend may be found also in other species which have eggs in the litter.

The extraction time for all samples was standardised at seven days.

Kinds of Litter Sampled

The kinds of leaf litter sampled are listed in Table 4. The sample unit was standardised as the amount of litter covering a 30 × 30 cm square of ground. This sample is accurately replicable, although the actual amount of litter varies throughout

TABLE 4
Types of leaf litter sampled, and numbers of sample units extracted

Litter	1966	1967	Total no. of sample units	Months sampled												
				J	F	M	A	M	J	J	A	S	O	N	D	
Oak leaves under large trees	372	360	732	*	*	*	*	*	*	*	*	*	*	*	*	*
Oak leaves under small trees	280	256	536	*	*	*	*	*	*	*	*	*	*	*	*	*
Oak leaves between trees	280	256	536	*	*	*	*	*	*	*	*	*	*	*	*	*
Pine needles	48	180	228	—	—	*	*	*	*	*	*	*	*	—	—	—
Cupressus needles	—	220	220	—	—	—	—	*	*	*	*	*	*	*	—	—
Hawthorn leaves	36	76	112	—	—	*	*	*	*	*	—	*	—	—	—	—
Beech leaves	—	84	84	—	—	—	—	*	*	*	*	*	*	*	*	—
Broom litter	—	63	63	—	—	—	*	*	*	—	*	*	—	—	—	—
Bracken litter	—	40	40	—	—	—	—	*	*	*	*	—	*	—	—	—
<i>Juncus</i> litter	—	48	48	—	—	—	—	*	*	*	*	*	*	*	—	—
<i>Dactylis</i> tussock	—	30	30	—	—	*	*	*	*	*	*	*	*	*	—	—
<i>Holcus</i> litter	—	32	32	—	—	*	*	*	—	—	—	*	*	—	—	—

*samples taken

the year. The main alternative, a known weight of litter, is inconvenient to use as the samples cannot be sized until after extracting the Psocids and drying to constant weight.

Each sample extracted in the Kempson bowls consisted of one of the above units. The funnels each contained four samples and were used for comparative bulk extractions from different types of litter. Extractions from oak litter were continued throughout the year, but most of the other kinds of litter were sampled only from March to November.

The Psocoptera Obtained

All Psocids extracted from leaf litter were identified to species and, where possible, to instar. The total numbers obtained are shown in Table 5, which shows that the great majority of Psocids were from oak litter (41.3 per cent) and Cupressus litter (52.4 per cent), and that many types of litter yielded very few of these insects.

Sixteen species of Psocoptera were recovered, most of them in very small numbers. Three species, *C. flavidus*, *E. briggsi* and *Epipsocus lucifugus* (Ramb.), together formed 98.6 per cent of the

succession of instars throughout the period April to early June, and after this time the occurrence of *C. flavidus* in the litter was sporadic. The first generation of this species is passed in the litter, and the resulting adults fly onto trees (New, in prep.). Individuals found later in the season are likely to have been washed or blown off the trees, or result from eggs on leaves which enter the litter.

E. briggsi was found in the litter in small numbers for most of the season, and there was a succession of instars in early summer. Adults fly onto trees in August, and from that time only a few are found on the ground.

E. lucifugus was found from June to September (Table 7). It is univoltine and apparently confined to litter. All stages of the species are readily distinguishable from all other British Psocids by the form of the lacinia (figured in Badonnel, 1943).

The Psocids found in leaf litter can be conveniently divided into three ecological groups:—

1. Primary litter dwellers, such as *E. lucifugus*, which spend their whole life history in the litter, and do not frequent other types of habitat.
2. Secondary litter dwellers, which have generations in two distinct habitats with at least one in litter and others elsewhere. All the British species which oviposit on the leaves of deciduous trees are in this category, which is exemplified by *C. flavidus*.
3. Casual litter dwellers, which do not normally breed in the litter. Individuals of many arboreal species are knocked off the trees in bad weather and enter the litter. Nymphs can complete their development in the litter and adults then re-enter the trees. This category includes most of the species found in very small numbers, and in late summer, species included in category 2 above are also casual in the litter.

The two species of *Lepinotus* and *Liposcelis* are believed to be primary litter frequenters. *Lepinotus* is normally a stored-products Psocid, but Guetmonprez (in Donisthorpe, 1927) considered that the natural habitat of *L. inquilinus* Heyd. was in 'the nests of ants and other insects'. The primary habitat of *Pteroxanium kelloggi* (Ribaga) has not been clearly defined. Pearman (1927) considered that this species feeds on a grey *Pleurococcus* on trees. The few specimens obtained at Silwood were from litter under *Cupressus*; none were found by beating the trees and it seemed the *P. kelloggi* was confined to the litter in this area. It has been beaten from Box (*Buxus*) in Bucks. (Pearman, 1952), and at Wokingham, Berks., and has been recorded also from other trees and bushes. Adults of this univoltine species were found in July and August.

Distribution in Different Types of Litter

Table 5 indicates that many species of Psocids are limited to a few kinds of litter at Silwood, and are absent from others which appear to be equally suitable habitats. Psocids included as 'casual litter dwellers' are largely limited to the litter under or near the canopies of the trees they normally frequent, and this is partially true of the 'secondary litter dwellers'. These latter species normally overwinter as eggs in the litter, and much mixing and redistribution of the litter occurs both during and after leaf-fall. The changing compositions of the litter near a large oak tree and a large pine tree are shown in Table 8. These changes

TABLE 8

Composition of litter from under oak and pine trees at different times of the year at Silwood Park, 1966

Constituents	Percentage (± 2)									
	Mar.	Apr.	May	June	July	Aug.	Sept.	Oct.	Nov.	Dec.
(a) Oak litter (15 sample units/month)										
Oak leaves	90	94	80	75	68	65	80	90	94	94
Beech leaves	8	4	20	23	30	30	15	10	3	5
Birch leaves	2	0	0	0	2	2	5	0	3	1
Sycamore leaves	0	2	0	2	0	3	0	0	0	0
(b) Pine litter (5 units/months)										
Pine needles	98	96	96	96	100	99	94	95	90	98
Broad-leaved	2	4	4	4	0	1	6	5	10	2

in amount and composition of the litter are largely dependent on climatic conditions, but the figures given are sufficient to show that Psocid eggs attached to leaves may come to be in a litter type different from that of the 'parent' tree. An attempt was made to assess the proportion of leaves on a large oak tree which remained under or near it throughout the winter, by marking large numbers of leaves at different heights with coloured paints. The results were sufficient only to indicate that in calm weather the majority of leaves from the lower branches are deposited in the litter under the tree, and that the proportion of leaves from higher up the tree decreases. It is likely that even under calm conditions populations of eggs of Psocids from different trees and tree species become mixed. *C. flavidus* was virtually absent from pure grass litter and the *Juncus* litter, neither of which contained many tree leaves but otherwise appeared to be a suitable habitat for this species. In laboratory experiments newly-hatched nymphs of *C. flavidus* were placed on *Juncus* leaves and on constituents of oak litter, and their survival compared. Table 9 shows that there was a high survival rate on dead oak leaves, rather less on dead grass, and heavy mortality on *Juncus* leaves, living grass (*Holcus*) and bare soil. The nymphs at first fed from the soil, but did not survive for more than one or two days. None were seen feeding on *Juncus* or *Holcus*, but the leaves appeared dirty and the food suitable. The nymphs seemed unable to reach

TABLE 9

Survival of *C. FLAVIDUS* nymphs on different constituents of leaf litter

Constituent	Unfed 1st instar nymphs	Alive after 7 days	Reached adult stage
Dead oak leaves	130	116	93
Dead grass	76	70	50
Live grass	180	8	0
Bare soil	150	0	0
<i>Juncus</i> leaves	55	3	0

the food on the surfaces of these leaves, because of the dense coating of short hairs. There appears to be a limitation in the litter distribution of this species linked with availability of suitable food; it is only able to take food from comparatively 'smooth' surfaces. The same limitation probably applies to some other arboreal Psocids.

Young nymphs of *E. lucifugus*, which has a wider distribution in the litter, are able to feed from hairy and rough surfaces. This species was abundant in loose coniferous litter in which complete leaves predominated to a depth of 15 cm. Vertical cores of this litter of depths 0-5, 5-10, 10-15 cms were extracted in small Tullgren funnels for seven days. The numbers of *E. lucifugus* extracted from ten samples of each stratum (Table 10) showed that it was almost completely confined to the top 5 cm of litter.

TABLE 10

Vertical distribution of *E. LUCIFUGUS* in *Cupressus* litter

Depth of litter	No. of 7.5 cm diameter cores	Number of <i>E. lucifugus</i>	% total <i>E. lucifugus</i>
0-5 cm	10	64	92.7
5-10 cm	10	5	7.3
10-15 cm	10	0	0

Strickland (1947) sampled soils separated into 0-3.75 and 3.75-7.5 cm strata. Most of the few Psocids he recovered were from the upper layer, and many of the Psocids from his 'cacao' plot were in the shallow litter above the soil surface. Belfield (1956) found a similar tendency for Psocids to be in the upper layer of soil.

The abundance of *E. lucifugus* varied greatly in different kinds of litter, but it was never completely absent (Table 11). The fac-

TABLE 11

Numbers of *Epipsocus lucifugus* extracted from different kinds of litter from June to August 1966-67 at Silwood Park

Litter:	Oak	Pine	Cup- pressus	Haw- thorn	Beech	All others	Total
No. of sample units	144	80	106	28	52	76	486
No. of <i>E. lucifugus</i>	308	14	782	5	28	8	1145
No. expected	339	188	250	66	122	180	1145
X ² sig. [†] at 5% level		—	+	—	—	—	

†significantly more than expected assuming uniform distribution.

—significantly less than expected assuming uniform distribution.

tors affecting the distribution of this species are not at present understood.

Temporal Separation in Litter

The three most abundant species of Psocids were clearly separated in time in oak litter. The first nymphs of *E. lucifugus* hatched when only large nymphs and adults of *C. flavidus* were present. Most *E. briggsi* were found in July and August. The numbers of species taken in different months are shown in Table 12, and show that the greatest diversity occurred at the time of

TABLE 12

Numbers of psocid species in leaf litter at different times of the year

Litter/Month	J	F	M	A	M	J	J	A	S	O	N	D
Oak leaves	—	—	1	1	2	4	4	12	6	2	—	—
Beech leaves	—	—	—	1	1	3	3	4	1	—	—	—
Conifer litter	—	—	—	—	1	3	3	6	—	1	—	—

least abundance, towards the end of the summer. The whole of the litter-Psocid populations are then of casual origin, and because of the extremely low density of these insects, competition is unlikely to occur.

An attempt was made during 1966 to assess the numbers of Psocids dropping into litter from trees, both as insects and as eggs attached to leaves. Ten polythene covered frames, each 60 × 60 cm were covered with a film of banding gum and placed on the ground beneath or between oak trees. These frames were examined at weekly intervals from June until October, and the numbers of Psocids and of fresh leaves on them were recorded. A few fresh leaves were found on the frames every week; there was a small amount of casual leaf-fall throughout the summer. The numbers of leaves rose sharply in mid-October. A few eggs of *C. flavidus* would therefore re-enter the litter during the summer.

The numbers of Psocids recorded on the frames are shown in Table 13. Most of these were *C. flavidus*, but several bark-frequenting species were also obtained. Numbers of foliage-

TABLE 13

Psocids captured on gum-covered frames under or near oak trees, summer 1966

Psocid		Month				
		June	July	Aug.	Sept.	Oct.
<i>C. flavidus</i>	Adult	4	0	15	5	1
<i>C. flavidus</i>	Nymphs	0	1	7	1	0
<i>L. fasciata</i>	Adult	0	0	0	1	0
<i>E. hyalinus</i>	Adult	1	1	0	0	1
<i>Ph. picicornis</i>	Adult	0	0	1	0	0
<i>E. briggsi</i>	Adult	0	0	3	2	2
<i>E. briggsi</i>	Nymphs	0	1	0	2	0

frequenting Psocids are 'knocked' off trees during bad weather, and will be regarded as 'mortality' when samples from the trees are alone considered. Most of the nymphs will complete development in the litter, and the adults re-enter the trees before laying. All the species found on the frames have been reared on damp dead leaves from litter.

Summary

Psocoptera were extracted from various kinds of leaf litter at Silwood Park, Berkshire, by using Tullgren Funnels and a Kempson Bowl Extractor. Only three species (*C. flavidus*, *E. briggsi*, *E. lucifugus*) were common at particular times of the year, but individuals of other species were frequently encountered. The species found can be divided into three ecological categories based on their degree of dependence on the litter as a habitat. The distribution of 'secondary' and 'casual' litter dwellers is related to that of the trees they predominantly frequent. That of a 'primary' litter dweller, *E. lucifugus*, was broader and limited to the surface region of the litter. Psocids were usually found at very low densities in leaf litter, and competition for food is unlikely to occur.

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