High-altitude migration of Psylloidea (Hemiptera) over England

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Abstract

Some species of psyllid (Hemiptera: Psylloidea) are known to make high-altitude windborne migrations, but compared with their sister superfamily, the Aphidoidea, our knowledge of these movements is rudimentary and unsystematised. Here we have extracted psyllid capture data from day and night aerial sampling carried out at a height of 200 m above ground at Cardington, Bedfordshire, UK, during summers between 1999 and 2007. These records were consolidated with high-altitude psyllid catches made over England during the 1930s and with some other trapping results from northwest Europe which were indicative of migration. Information on aerial densities, diel flight periodicity, and the sex-ratio of the aerial psyllid populations is presented. We also compared our results with those of a recent study which used the Rothamsted Insect Survey network of suction traps (sampling at a height of 12.2 m); this provided confirmative evidence that the suction-traps were indeed detecting migrating psyllids. Finally, both aerial netting and suction trap data were used to tentatively interpret the seasonal timing of migrations in terms of the breeding/overwintering cycles of some common psyllid species.

Key words: Jumping plant lice, aerial trapping, windborne migration, flight, atmospheric transport, seasonal cycles.

Introduction

Psyllids or jumping plant-lice (Hemiptera: Psylloidea) are phloem-feeding Sternorrhyncha which are habitually highly host-specific and include species which are significant pests particularly of fruit and ornamental trees (Hodkinson, 2009; Percy, 2014; Greenslade *et al.*, 2020). Damage to hosts can be due to feeding and excretions, or to the vectoring of plant pathogens (e.g. the bacterium causing Citrus Greening Disease). Some psyllid species appear to move over significant distances by means of windborne migration, as evidenced by their capture high in the air (Berland, 1935; Hardy & Milne, 1938; Freeman, 1939, 1945; Glick, 1939, 1960; Glick & Noble, 1961; White 1970, 1973, 1974; Chapman *et al.*, 2004; Weidel, 2008, 2010), and over the seas, remote from land (Harrell & Yoshimoto, 1964; Holzapfel & Harrell, 1968; Hardy & Cheng, 1986; Peck, 1994); see also Hodkinson's review (2009). Extensive day- and night-time sampling of the upper air (e.g. by Glick, 1939) indicates that psyllids are very largely daytime migrants, and *Trioza urticae* (Linnaeus, 1758), for example, shows a well-defined diel flight periodicity curve with a maximum around noon (Lewis & Taylor, 1965). Thus, it is likely that psyllids make potentially long-distance migrations by utilising lift from turbulent convection (Wainwright *et al*., 2017) as in the related superfamily, the Aphidoidea.

Recently, Greenslade *et al*. (2020) published an analysis of British psyllid diversity and seasonal migration patterns, using the Rothamsted Insect Survey network of suction traps sampling at a height of 12.2 m in England and Scotland (plus a similar trap in Sweden). At least for aphids, trapping at this height largely samples migrant individuals and the sample is representative of the aerial population over a wide area (Taylor, 1974).

The paucity of information on psyllids migrating at altitude over the UK has encouraged us to document captures of these hemipterans from a height of ~200 m above ground, made during eight seasons of sampling over southern England. We integrate these results with catch data from the earlier literature (Hardy & Milne, 1938; Freeman 1939, 1945) which are indicative of high-altitude migratory activity in the British species of Psylloidea. The resulting picture, although still fragmentary, will advance our understanding of migratory propensities and seasonal movements in this understudied group of insects.

Materials and Methods

The aerial sampling methods have been described in detail elsewhere (Chapman *et al*., 2004; Reynolds, Nau & Chapman 2013; Reynolds, Chapman & Stewart 2017), so we provide a brief summary here. Insects flying at *ca*. 200 m above ground level (a.g.l.) were captured in a drogue net of 1-m diameter aperture suspended from a tethered helium-filled kite-balloon (kytoon) (Fig. 1). The sampling site, at Cardington Airfield (52°06´N, 0°25´W), Bedfordshire, in southern England, is in an official aircraft exclusion zone, thus allowing balloon flying above the normal Civil Aviation Authority limit of 60 m. Sampling was carried out over eight seasons (in 1999, 2000, and 2002–2007), in various months between May and early September, but mostly in July (Table 1). Kytoon flying was undertaken opportunistically, in fine weather when there was no significant risk of lightning, rain or very strong winds. Occasionally, winds at altitude were too weak (i.e. below ~3 m/s) for efficient netting. Each 24-h period was generally divided into: 1 h around dusk (~ 21.00–22.00 h BST in July); night-time after the dusk period (various durations, occasionally until dawn); ‘morning’ (10.00–14:00 h), and afternoon (14:00–18:00 h). At the end of each sample period, a radio-controlled net closure device was used to close-off the end of the net, and the kytoon was winched down to near ground level. A detachable net bag containing the catch was unzipped from the end of the net and placed in a plastic killing bottle. The sampling period ‘wind run’ (in kilometres) was read off a meter suspended below the kytoon (Fig. 1); this measurement allowed an estimate of the airflow through the net, from which the aerial density of insects in each sample could be calculated. The catch was sorted and preserved in a mixture of 95% ethanol and 5% glycerol. Psyllids in the samples were later identified by one of us (AFCG); see Greenslade *et al*. (2020) for the taxonomic works used.

Results and Discussion

During the eight seasons of sampling at 200 m a.g.l. at Cardington, a total of 490 psyllids were caught (Table 1). The great majority of these (451) comprised a grouping of *Cacopsylla melanoneura* (Foerster, 1848) and *C. affinis* (Löw, 1880) which were amalgamated because females of these species could not be reliably distinguished (Greenslade *et al.*, 2020).

However, judging by the males of the two species (190 *C. melanoneura* individuals to only two of *C. affinis*), it seems likely that the former species was highly dominant in the collections. The next most numerous species was *Trioza urticae* (L.) with 17 specimens, followed by *Aphalara* spp. and *Cacopsylla pruni* (Scopoli, 1763) with 5 specimens each.

Our catches at altitude were generally in accord with the results of the 12.2 m suction trapping in England (Greenslade *et al.*, 2020) where the *C. melanoneura/affinis* group and *T. urticae* were respectively the first- and third-most numerous, respectively, in the year-long study. *Trioza remota* (Foerster), which was the second-most prevalent species in the 12.2 m suction traps, was not taken in our samples or those of Hardy & Milne (1938) and Freeman (1939, 1945). However, peak numbers of *T. remota* in the suction traps occurred in November and December, which was outside the sampling period of the high-altitude studies.

A comparison of the aerial catches from the present study with those made in England in the 1930s by Hardy & Milne (1938) and Freeman (1939, 1945) is shown in Table 2. The most striking feature of the early studies was the large number (173) of an *Aphalara* sp. caught by Freeman in his higher-level traps (54 and 84 m) mostly in September.

Aerial densities

Considering sampling occasions when psyllids were actually caught, the aerial densities over the eight seasons at Cardington were of the order of one individual per 10^4 cu. m (ranging between 0.26 and 2.20 per 10^4 cu. m; see Table 1). The highest densities recorded were 7.7 - 7.8 per 10^4 cu. m in two samples taken in June 2005 when sizeable numbers of *C. melanoneura / affinis* were flying. In comparison with other hemipteran groups sampled, the psyllid aerial densities were greater than densities of the Heteroptera (~0.3 per 10^4 cu. m) and Auchenorrhyncha (~0.5 per 10^4 cu. m; Reynolds, Chapman & Stewart 2017), but smaller than aphid densities recorded at altitude over Cardington (~5 per 10^4 cu. m ; Berry & Taylor, 1968; Johnson, 1969, fig. 105). Even so, it is clear that at periods of mass emigration (like the June samples mentioned above), psyllid densities can temporarily rival those of aphids at altitude. We also note the aforementioned large numbers of an *Aphalara* sp. recorded by Freeman (1945) near Grimsby, Lincolnshire, flying "in swarms" in the autumn.

Percentage of the total insect catch

In the aerial sampling by Hardy & Milne (1938), Freeman (1939, 1945) and the present study, psyllids comprised about 1- 3% of the total number of insects captured (Table 2). Similarly, in aerial sampling by aircraft over Schleswig-Holstein, North Germany (Weidel, 2010) psyllids comprised 3% of the total catch.

Diel flight periodicity

Psyllids were generally caught at Cardington in the daytime sampling periods (77 samples containing a total of 458 individuals), with a few continuing into the dusk period (12 samples containing 32 individuals); they were not caught in the night samples, i.e. after about 22:00 h.

Sex-ratio

Psyllids usually show sex-ratios of close to 1:1 on adult emergence, but in some species there are indications that females disperse further than males (Hodkinson, 2009). This seems to be the case in our *Cacopsylla melanoneura / affinis* samples, where there were 259 females to 192 males – a significant departure from a 1:1 ratio (chi-square goodness-of-fit = 9.9534, P = 0.001605).

Migration distance

Small insects, such as psyllids, starting to ascend under daytime convective conditions, will be borne upwards if they encounter an updraft. Attaining the 200 m sampling height (assuming an updraft vertical speed of ~1 m/s) even if followed by an (unlikely) immediate descent would involve a flight time of several minutes during which, at the average horizontal wind speeds recorded when psyllids were flying (~5.8 m/s), would transport the migrants at least 2 km. This distance is, of course, the absolute minimum; the presence of psyllids far from any possible sources (see Introduction) indicate much longer flights. For example, Hodkinson (1972) records psyllids including *C. melanoneura*, *C. affinis* and *Trioza urticae*, overwintering on pines in northern England about 13 km from their nearest host plants. Movement over at least tens of kilometres is indicated by the capture of psyllids at quite high altitudes. For example, Berland (1935) caught unidentified psyllids at heights between 500 and 2300 m near Paris, and Weidel (2010) caught *Cacopsylla melaneura* (the dominant species in our study) at heights up to 1520 m over Schleswig-Holstein.

Nonetheless, as pointed out by Chapman *et al*. (2004), the fact that psyllids comprised a very small proportion of the North Sea catches of Hardy & Cheng (1986) suggest that this group is much less likely to make long distance flights in the UK compared to certain species of aphid. Sometimes aphids may continue flying after dark which can greatly increase migration distances (Wainwright, Reynolds & Reynolds 2020), but our results indicate that night-time psyllid migration does not occur to any great extent in Britain (see above).

Phenology and migration

The *Cacopsylla melanoneura / affinis* group (mainly *C. melanoneura* judging by the tally of males) were caught between May and August, but the largest numbers were caught in June and July samples, e.g. 46 individuals in a sample on 18 June 2005 and 43 in a 13 July 2002 sample. This agrees well with the 12-m suction trapping results of Greenslade *et al.* (2020) who also recorded a large peak in June-July. Greenslade *et al.* also recorded small peaks of *Cacopsylla melanoneura / affinis* in February-early April and in the late autumn, i.e. outside the period of our aerial sampling. Nearly all the *Cacopsylla* species caught by us – *C. melanoneura / affinis, C. brunneipennis* (Edwards, 1896) / *pulchra* (Zetterstedt, 1840) and *C. pruni* – overwinter as reproductively-diapausing adults largely on conifers or evergreen shrubs (Hodkinson, 2009) (see Appendix). Some authors have found that *Cacopsylla* spp. do not simply relocate to nearby conifers, but tend to migrate further afield to overwinter on conifers in mountainous areas (Čermák & Lauterer, 2008; Thébaud *et al*., 2009). Therefore, it is highly likely that the early season movement detected by Greenslade *et al.* represents a migration from overwintering sites to host plants on which juvenile development can ensue – Hodkinson (1972) mentions that even in the cool environment of the northern Pennines psyllids had left winter shelters in pine trees by May. Subsequently, as these *Cacopsylla* are univoltine (Hodkinson, 2009), the large summer movement recorded both by Greenslade *et al.* and the present study would appear to be a migration to the wintering sites by the new generation of adults. Although it might seem rather early for such a movement, Thébaud *et al*. (2009) in south-eastern France showed that *C. pruni* migrated to conifers in June, and then spent 8 months there. Also, monitoring of overwintering sites in Moravia (Czech Republic) revealed that the *Cacopsylla* spp. movement can be as early as late May and June (Čermák & Lauterer, 2008). The adaptive reason suggested for this timing was that convective upcurrents necessary for fairly long-range migration would be more likely in June–August; migration later in the year (September-November) would restrict the migrants to shorter distance movements (Čermák & Lauterer, 2008). However, some psyllids show peak flight activity in autumn, e.g. *Aphalara* spp. (see below), or even as late as November and December, e.g. *T. remota* in the 12.2 m suction traps (Greenslade *et al*., 2020).

Conceivably, in these circumstances, upward movement may be less dependent on convective updrafts and more on self-propelled ascent.

Trioza urticae, the second most common species in our samples, was caught only in June, which coincides with the large mid-summer peak recorded by Greenslade *et al*. (2020). The species is multivoltine with at least three generations per year in the UK (Hodkinson & White, 1979), but separate movement events associated with the generations are not evident from the suction-trap record (Greenslade *et al*. 2020). The small peak in November-December presumably represents a late *T. urticae* migration to winter shelter locations. Weidel (2008) caught two *T. urticae,* at heights of 150 and 640 m respectively, in October.

The few *Aphalara* spp. in our aerial samples were from the '*Aphalara calthae* group' of species *sensu* Burckhardt & Lauterer (1997). There are five species known from Britain in this group at the time of publication (Greenslade *et al.* 2020). These *Aphalara* spp. seemed to show a different pattern to the previously-mentioned species, being caught *only* in late August and September. Aerial samples were not taken later in the season, but the 12.2 m suction trapping in 2015 at three sites in England produced the following numbers of the *A. calthae* group: July - 1; August - 4; September - 6; October - 6 and November - 3 (A.F.C. Greenslade, unpublished). This picture of autumn movement is strongly reinforced by Freeman (1945) who caught large numbers of an *Aphalara* sp. in September in his higher-level traps (54 and 84 m) (see Table 2). Lastly, we note that Weidel (2008, 2010) caught 6 *Aphalara crispicola* Ossiannilsson (now considered a synonym of *Aphalara purpurascens* (Hartig, 1841)) between 100 and 1520 m over northern Germany, again in August, September and October.

Aphalara spp. have 1-2 generations per year (*A. polygoni* Foerster, 1848 is bivoltine, for example) (Hodkinson, 2009), and as *Aphalara* "are never found on their true host plant during the winter" (Hodkinson & White, 1979), it seems likely that flights in the autumn represent movement of reproductively-diapausing adults to their winter shelters on conifers or evergreen shrubs (Hodkinson, 2009).

Generally, the phenology of common British psyllid species, as documented by 12.2 m suction traps, does seem to be reflected in our catches at 200 m above ground. This supports the view that the suction trap network is detecting psyllid migration events and indicates that windborne movement may transport psyllids over significant distances.

Conclusion

The present report forms a companion paper to Greenslade *et al*. (2020), who sampled psyllids across Britain at a height 12.2 m above ground, and mirrors many of their findings. This validates the view that the nationwide suction-trap network is suitable for monitoring psyllid movement in the UK, and offers the opportunity for testing for important disease agents, such as '*Candidatus* Phytoplasma prunorum' carried by *C. pruni*. Together the papers provide evidence for the substantial migration capabilities of certain psyllid species over distances of at least several kilometres, and probably tens of kilometres. These studies, although preliminary, have still revealed definite patterns in the syndrome of migratory behaviour in some British Psylloidea, and hopefully will provide a basis for further research.

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References

Berland, L. 1935. Premier résultats de mes recherches en avion sur la faune et la flore atmosphériques. *Annales de la Société Entomologique de France* **104**: 73–96.

Berry, R. E. & Taylor, L. R. 1968. High-altitude migration of aphids in maritime and continental climates. *Journal of Animal Ecology* **37**: 713–722.

Burckhardt, D. & Lauterer, P. 1997. Systematics and biology of the *Aphalara exilis* (Weber & Mohr) species assemblage (Hemiptera: Psyllidae). *Entomologica Scandinavica* **28**: 271–305.

Čermák, V. & Lauterer, P. 2008. Overwintering of psyllids in South Moravia (Czech Republic) with respect to the vectors of the apple proliferation cluster phytoplasmas. *Bulletin of Insectology* **61**: 147–148.

Chapman, J. W., Reynolds, D. R., Smith, A. D., Smith, E. T. & Woiwod, I. P. 2004. An aerial netting study of insects migrating at high altitude over England. *Bulletin of Entomological Research* **94**:123–136.

Freeman, J. A. 1939. Studies in the distribution of insects by aerial currents. A contribution to the study of windborne insects with special reference to vertical distribution and dispersal. PhD Thesis, University College, Hull, UK.

Freeman, J. A. 1945. Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. *Journal of Animal Ecology* **14:** 128–154.

Glick, P. A. 1939. The distribution of insects, spiders and mites in the air. *Technical Bulletin* No. 673. Washington DC, United States Department of Agriculture.

Glick, **P. A.** 1960. Collecting insects by airplane, with special reference to dispersal of the potato leafhopper. *Technical Bulletin* No. 1222, Washington DC, United States Department of Agriculture.

Glick, P. A. & Noble, L. W. 1961. Airborne movement of the pink bollworm and other arthropods. *Technical Bulletin* No. 1255.Washington DC, United States Department of Agriculture.

Greenslade, A. F. C., Carnegie, M., Ouvrard, D., Sjölund, M. J., Highet, F., Sigvald, R., Kenyon, D. M. & Bell, J.R. 2020. Aerial psyllid (Hemiptera: Psylloidea) detection and monitoring using suction traps in Britain: population observations, new species found and a revised British checklist. *Entomologist's Gazette* **71**(3): 151–163.

Hardy, A. C. & Cheng, L. 1986. Studies in the distribution of insects by aerial currents. III. Insect drift over the sea. *Ecological Entomology* **11**, 283-290.

Hardy, A. C. & Milne, P. S. 1938. Studies in the distribution of insects by aerial currents. Experiments in aerial tow-netting from kites. *Journal of Animal Ecology* **7**, 199–229.

Harrell, J. C. & Yoshimoto, C. M. 1964. Trapping of air-borne insects on ships on the Pacific, Part 5. *Pacific Insects* **6**(2): 274–82.

Hodkinson, I. D. 1972. Long range dispersal of certain species of Psyllidae in the Northern Pennines. *Entomologist's Monthly Magazine* **108**: 21-22.

Hodkinson, I. D. 2009. Life cycle variation and adaptation in jumping plant lice (Insecta: Hemiptera: Psylloidea): a global synthesis. *Journal of Natural History* **43**: 65–179.

Hodkinson, I. D. & White, I. M. 1979. Homoptera: Psylloidea. *Handbooks for the Identification of British Insects, vol. II, part 5 (a).* Royal Entomological Society of London, London.

Holzapfel, E. P. & Harrell, J. C. 1968. Transoceanic dispersal studies of insects. *Pacific Insects* **10**: 115–153.

Johnson, C. G. 1969. *Migration and dispersal of insects by flight*. Methuen, London, xxii + 766 pp

Lewis, T. & Taylor, L. R. 1965. Diurnal periodicity of flight by insects. *Transactions of the Royal Entomological Society of London* **116**: 393–479.

Peck, S. B. 1994. Aerial dispersal of insects between and to islands in the Galápagos Archipelago, Ecuador. *Annals of the Entomological Society of America* **87**: 218–224.

Percy, D. M. 2014. *Psyllids of Economic Importance*. https://www.psyllids.org/psyllidsPests.htm . Accessed 1 November 2020.

Reynolds, D.R., Nau, B.S. & Chapman, J.W. 2013. High-altitude migration of Heteroptera in Britain. *European Journal of Entomology* **110**: 483–492.

Reynolds, D. R., Chapman, J. W. & Stewart, A. J. A. 2017. Windborne migration of Auchenorrhyncha (Hemiptera) over Britain. *European Journal of Entomology* **114**: 554–564.

Taylor, L. R. 1974. Monitoring change in the distribution and abundance of insects. *Rothamsted Experimental Station Report for 1973*, Part 2: 202–239. https://doi.org/10.23637/ERADOC-1-34639

Thébaud, G., Yvon, M., Alary, R., Sauvion, N. & Labonne, G. 2009. Efficient transmission of '*Candidatus* Phytoplasma prunorum' is delayed by eight months due to a long latency in its host-alternating vector. *Phytopathology* **99**: 265-273.

Wainwright, C.E., Stepanian, P.M., Reynolds, D.R. & Reynolds, A.M. 2017. The movement of small insects in the convective boundary layer: linking patterns to processes. *Scientific Reports* **7**: article 5438.

Wainwright, C. E., Reynolds, D. R. & Reynolds, A. M. 2020. Linking small-scale flight manoeuvers and density profiles to the vertical movement of insects in the nocturnal stable boundary layer. *Scientific Reports* **10**: article 1019.

Weidel, H. 2008. *Die Verteilung des Aeroplanktons über Schleswig-Holstein*. Doctoral Dissertation, Faculty of Mathematics and Natural Sciences, Christian-Albrechts-University, Kiel, Germany. http://d-nb.info/1019553197/34

Weidel, H. 2010. Das Aeroplankton in der Norddeutschen Tiefebene über Schleswig-Holstein. *Faunistisch-Ökologische Mitteilungen* 9(3/4): 111–129.

White, T. C. R. 1970. Airborne arthropods collected in South Australia with a drogue-net towed by a light aircraft. *Pacific Insects* **12**(2): 251-59.

White, T. C. R. 1973. Aerial dispersal of adult *Cardiaspina densitexta* (Homoptera, Psyllidae) *Transactions of the Royal Society of South Australia* **97**: 29-31.

White, T. C. R. 1974. Semi-quantitative sampling of terrestrial arthropods occurring in the air over South Australia. *Pacific Insects* **16**(1): 1–9.

Fig. 1. Sampling insects at ~200 m above ground by means of a net attached to the tethering line of a 6-m long kytoon. The detachable bag at the end of the net has been closed-off, prior to winching down of the kytoon to ground level and recovery of the sample. A wind-run meter can be seen suspended below the kytoon tail.

Table 1. Psylloidea caught at high altitude (ca. 200 m a.g.l) at Cardington, Bedfordshire, UK, 1999–2007.

	Year	1999	2000	2002	2003	2004	2005	2006	2007	**Total**
	Sampling month(s)	July	July	July	August –Sept.	July	June –July	August –Sept.	May–July	
	Total wind-run (km)†	2847.2	2524.0	2273.0	2922.1	2610.0	3262.0	1370.0	2188.0	
Family	**Species**									
Aphalaridae	*Aphalara* spp.				2			3		**5**
Liviidae	*Psyllopsis fraxinicola* (Foerster)		1							**1**
Psyllidae	*Cacopsylla melanoneura* (Foerster) / *affinis* (Löw)	18	31	101		19	232	2	48	**451**
	Cacopsylla pulchra (Zetterstedt) / *brunneipennis* (Edwards)			1					3	**4**
	Cacopsylla pruni (Scopoli)		1			3			1	**5**
Triozidae	*Trioza chenopodii* Reuter					1				**1**
	Trioza galii Foerster			2						**2**
	Trioza urticae (L.)						17			**17**
Unidentified Psylloidea (missing samples)						2	2			**4**
Total		18	33	104	2	25	251	5	52	**490**
Mean density (numbers/10^4 cu. m^3)		0.69	1.21	1.72	0.34	0.56	2.20	0.26	0.84	

† Total wind-run for all sampling periods in that season (provides a measure of sampling intensity).

Table 2. **Comparison of catches of Psylloidea obtained during some aerial trapping studies over England.**

Study reference		Freeman, 1939, 1945		Hardy & Milne, 1938		Present study		**Totals**
Sampling location		Tetney, near Grimsby		Hull, Thorpeness (Suffolk), and near Dover		Cardington, Bedfordshire		
Year(s)		1934, 1935		1932 – 1933		1999, 2000, 2002-2007		
Sampling Period		May – September		June – October		May – early September		
Time of sampling		Day only		Day only		Day & night		
Height of sampling		54 and 84 m only*		60 – 610 m		c. 200 m		
Psylloidea family & species	**Species name in Freeman, or Hardy & Milne (if different)**	**Number**	**%**	**Number**	**%**	**Number**	**%**	
Aphalaridae								
Aphalara spp.		2	1.07			5	1.02	**7**
” ”	*Aphalara calthae*†	173	92.51	6	75			**179**
Liviidae								
Psyllopsis fraxinicola (Foerster)						1	0.20	**1**
Psyllidae								
Psylla sp.		2	1.07					**2**
Cacopsylla mali (Schmidberger)	*Psylla mali*	2	1.07					**2**
Cacopsylla melanoneura (Foerster) / *affinis* (Löw)						451	92.04	**451**
Cacopsylla pulchra (Zetterstedt) / *brunneipennis* (Edwards)						4	0.82	**4**
Cacopsylla pulchra (Zetterstedt)	*Psylla nigrita*			2	25			**2**
Cacopsylla pruni (Scopoli)						5	1.02	**5**
Triozidae								
Trioza sp.	*Spanioza* sp.	2	1.07					**2**

Trioza chenopodii Reuter	*Spanioza atriplicis*	4	2.14			1	0.20	**5**
Trioza galii Foerster		1	0.53			2	0.41	**3**
Trioza urticae (L.)						17	3.47	**17**
Unidentified Psylloidea		1	0.53			4	0.82	**5**
Total Psylloidea		187	100	8	100	490	100	**685**
Total insects and % Psylloidea		7748	2.41	839	0.95	17752	2.76	

*Freeman’s samples taken at his lowest height (3 m above ground) were omitted.

† *Aphalara calthae* is not on recent checklists of psyllids in Britain (e.g. Greenslade *et al.* 2020) but these individuals probably belong to the ‘*Aphalara calthae* group’ of species.

Appendix

Host plant (on which the species breeds), voltinism, overwintering stage and location of some psyllid species caught at altitude (life-history information from Hodkinson, 2009).
C = conifers and evergreen shrubs

Species	Host plant	Voltinism	Overwintering stage	Overwintering location
Cacopsylla melanoneura	*Crataegus, Malus*	1	Adult	C
Cacopsylla affinis	*Stellaria*	1?	Adult	C
Cacopsylla pruni	*Prunus*	1	Adult	C
Cacopsylla brunneipennis	*Salix*	1	Adult	C
Cacopsylla mali	*Malus*	1	Egg	on host shoots
Cacopsylla pulchra	*Salix*	1	Adult	C
Aphalara spp.		1 - 2. 2 in *polygoni*	Adult	C
Trioza urticae	*Urtica*	1 - 4	Adult	C + grass tussocks near host
Trioza chenopodii (seasonally polymorphic)*	*Chenopodium, Atriplex, Halimione*	2 - 5	Adult	on host shoots
Trioza galii	*Galium, Asperula*	1+?	Adult	C & leaf litter
Psyllopsis fraxinicola	*Fraxinus*	1 - 2	Egg	on host shoots

* Has a long-winged summer form and an autumn-winter form with shorter, broader wings.