

# DISPERSAL BY FLIGHT OF LEAFHOPPERS (AUCHENORRHYNCHA: HOMOPTERA)

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## INTRODUCTION

In the last few years a series of studies on the bionomics and ecology of leafhoppers have been carried out at the Imperial College Field Station, Silwood Park, Berkshire. Results of a survey of the species breeding in acidic grasslands have been reported (Waloff & Solomon 1973). Dispersal by flight of leafhoppers and the catches in the aerial suction traps and in various interference traps, have also been studied. The interest in these problems is two-fold, firstly, because dispersal to and from breeding sites contributes to fluctuations in the sizes of populations (see May 1971; Tay 1972; Solomon 1973) and, secondly, because many of these plant-sucking insects are vectors of plant diseases; transmitting viruses or mycoplasma to various graminaceous crops, clover, strawberries and other plants (Slykhuis & Watson 1958; Watson & Sinha 1959; Raatikainen & Tinnilä 1959; Maramorosch, Shikata & Granados 1968; Fewkes 1969; Nakasuji & Kiritani 1970).

Little is known about the times of the year in which the leafhoppers in Britain disperse by flight, and these aspects have been summarized in this paper. In this country, leafhoppers are considered pests of minor importance only, but in parts of Europe, in North America and in tropical countries the effects of transmitted plant diseases and of direct damage caused by leafhoppers on crops assume a high significance. Recently, the direct effects of feeding, coupled with the intense outbreaks of the delphacid *Saccharosydne saccharivora* (Westw.) on sugar cane throughout the Caribbean have been described (Metcalf 1971).

Closely associated with dispersal by flight are the problems of alary polymorphism, which are both widespread and diversified throughout the Auchenorrhyncha.

## METHODS

### *Flight*

Dispersal by flight was investigated by recording the numbers of Auchenorrhyncha captured in the aerial suction traps (Johnson 1950, 1957; Johnson & Taylor 1955; Taylor 1951, 1955, 1962). Traps II and IV are permanently sited east of Elm Ridge at Silwood, adjacent to one another, with trap II suspended 1.2 m and trap IV 9.1 m above ground level. Both are 46 cm in diameter and the input of air is 71 m<sup>3</sup>/min. A third suction trap, 12.2 m above ground level and 65 m west of the other two, has been operated since 1969. It is referred to as the Rothamsted trap (R.T.).

Supplementary suction traps, 23 cm diameter, were also used in this study. They were located on sites of population studies on *Psammotettix confinis* (Solomon 1973), *Cicadella viridis* (Tay 1972) and *Stenocranus minutus* (May 1971). Another similar trap which





Table 1 (cont'd)

|   | April |   |   | May |   |   | June |   |   | July |    |    | August |    |    | September |    |    | October |   |   |
|---|-------|---|---|-----|---|---|------|---|---|------|----|----|--------|----|----|-----------|----|----|---------|---|---|
|   | a     | b | c | a   | b | c | a    | b | c | a    | b  | c  | a      | b  | c  | a         | b  | c  | a       | b | c |
| TYPHLOCYBINAE   |       |   |   |     |   |   |      |   |   |      |    |    |        |    |    |           |    |    |         |   |   |
| (Records for <i>Z. scutellaris</i> as above, other spp. for 1962 and 1969 only) |       |   |   |     |   |   |      |   |   |      |    |    |        |    |    |           |    |    |         |   |   |
| <i>Atebra albostriella</i> (Fallén)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Dikraneura variata</i> Hardy   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Kybos smaragdula</i> (Fallén)  | .     | . | . | .   | . | . | 1    | 2 | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Empoasca flavescens</i> (Fabricius)  | .     | . | . | 1   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. pteridis</i> (Dahlbom)  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Eurhadina pulchella</i> (Fallén)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Eupteryx atropunctata</i> (Goeze)  | .     | . | . | .   | . | . | 1    | 4 | . | .    | .  | .  | 1      | 1  | 4  | .         | .  | .  | .       | . | . |
| <i>E. aurata</i> (L.)   | .     | . | . | 2   | 7 | 4 | 4    | 4 | 1 | 6    | 1  | 4  | 4      | 4  | 6  | 7         | 15 | 1  | .       | . | . |
| <i>E. collina</i> (Flor)  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. notata</i> Curtis   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. tenella</i> (Fallén)  | .     | . | . | .   | . | . | 1    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. urticae</i> (Fabricius)   | .     | . | . | .   | . | . | 1    | 1 | 1 | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Limnovoiviana decempunctata</i> (Fallén)                                     | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>L. pandellei</i> (Lethierry)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Fagocyba cruenta</i> (Herrich-Schaeffer)                                     | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>F. bifasciata</i> Boheman  | .     | . | . | .   | . | . | 2    | 2 | 4 | 3    | 4  | 3  | 4      | 6  | .  | .         | .  | .  | .       | . | . |
| <i>F. quercus</i> (Fabricius)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>F. lethierryi</i> Edwards  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | 5      | 1  | 5  | 2         | .  | .  | .       | . | . |
| <i>F. nigriloba</i> Edwards   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>F. rosae</i> (L.)  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Ribautiana cruciata</i> (Ribaut)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>R. tenerrima</i> (Herrich-Schaeffer)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Erythroneura parvula</i> (Boheman)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. ribanti</i> Ossianilsson  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. angusta</i> (Lethierry)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. flammigera</i> (Geoff. in Fourc.)   | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. ordinaria</i> Ribaut  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>E. rubrovittata</i> (Lethierry)  | .     | . | . | .   | . | . | .    | . | . | .    | .  | .  | .      | .  | .  | .         | .  | .  | .       | . | . |
| <i>Z. scutellaris</i> (Herrich-Schaeffer)                                       | .     | . | . | .   | . | . | 1    | 2 | 5 | 23   | 18 | 13 | 11     | 16 | 25 | 16        | 31 | 56 | 21      | 9 | 7 |



segregated the catch into hourly samples was erected by traps II and IV in 1972. In addition, water traps and pots containing grasses on which the flying insects landed were suspended at 0.6, 1.2, 1.8 m above the ground level within the area of study (Waloff & Solomon 1973). There were two water traps and ten sets of suspended pots distributed through the 1-ha field.

The catches were removed daily and preserved in 70% alcohol for sorting and identification in winter. The data were supplemented by catches made in 1962. Simultaneously, with sampling of the aerial populations, the seasonal abundance of the acidic grassland species was recorded in the field and the methods used are summarized in Waloff & Solomon (1973).

#### *Flitting*

Flitting was examined in 1968, when ten sets, each of three pots with grasses, which were periodically renewed, were suspended on poles at heights of 0.6, 1.2 and 1.8 m above the ground level. The thirty pots were examined daily and any leafhoppers that settled on them were beaten on to a tray, collected and recorded. It can be seen in Table 2, that as generation time progressed, fewer insects settled on the higher pots and more on the lower ones and this coincided with greater proportions of mature individuals.

Females were dissected and the immature ones given the value of -1, those with developing oocytes -2, and those with fully developed eggs -3 and spent females -4. The indices of maturity being the averages of these values. It may be inferred from these data (Table 2) that mature individuals tend to flit.

#### *Laboratory tests*

Some laboratory tests were made to see whether the leafhoppers would continue to fly on reaching maturation. These were not tests for migratory abilities but they helped to distinguish between the females which retained flight ability throughout their lives from those that lost it with age.

The insects were gently shaken out of a tube at a height of 0.6 m into a container 1.0 m long with muslin sides and roof, a transparent window at one end and an open side at the releasing end. Some flew straight to the window, others dropped on the floor and hopped towards it. This was repeated five times with each individual insect. Secondly, the insects were released on to the floor, one at a time, and gently prodded with a paint brush, some only hopped, while the flyers hopped and flitted. This was also repeated five times with each insect. The flyers and non-flyers were then dissected to ascertain their state of maturation and measurements of their body length, the length of the fore and hind wings and of hind tibia (Table 7). *Macrosteles sexnotatus*, *Balclutha punctata* retained powers of flight to death, whereas in other species, e.g. *Arthaldeus pascuellus*, *Streptanus sordidus*, *Euscelis plebejus*, *Diplocolenus abdominalis*, *Elymana sulphurella*, the older females with abdomens distended with eggs, appeared to lose the ability to fly and only hopped.

## RESULTS

### *The seasonal incidence of flying Auchenorrhyncha*

The seasonal incidence of flight of leafhoppers and froghoppers is summarized in Table 1. One hundred and fifteen species were identified in the catches in the Silwood traps; three Cercopidae, fifty-eight Cicadellidae, twenty-nine plus Typhlocybinae, two Cixiidae and twenty-three Delphacidae. This list constitutes one-third of the British species of Auchenorrhyncha.

Table 2. Numbers of leafhoppers settling on grass in pots suspended at different heights and the indices of maturity of the females in the samples (1968)

| Date       | No. in sample | Height above ground  |       |       | Index of maturity |       |       |
|------------|---------------|----------------------|-------|-------|-------------------|-------|-------|
|            |               | 1·8 m                | 1·2 m | 0·6 m | 1·8 m             | 1·2 m | 0·6 m |
|            |               | Proportion of sample |       |       |                   |       |       |
| 16-31 May  | 17            | 0·88                 | 0·12  | 0·00  | 1·3               | —     | —     |
| 1-15 June  | 42            | 0·67                 | 0·21  | 0·12  | 1·7               | 1·5   | —     |
| 16-30 June | 45            | 0·22                 | 0·51  | 0·27  | 1·9               | 2·5   | —     |
| 1-16 July  | 36            | 0·14                 | 0·28  | 0·58  | 1·8               | 2·0   | 2·7   |

The yearly catches were small, the combined totals from traps II, IV and R.T. ranging between a 1000 and 1400 in 1969 to 1972. Generally, about one-half of each annual catch comprised *Javesella pellucida*, *Macrostes sexnotatus* and *M. laevis* only (Table 3). All are active flyers, but not the most abundant local species and are vectors of plant diseases. *Javesella pellucida* transmits the European wheat striate mosaic virus (Watson & Sinha 1959) and the *Macrostes* spp. carry the 'asters yellow' mycoplasma.

The proportions in which the different families of Auchenorrhyncha formed the monthly catches in aerial traps are given in Table 4. As most delphacid species hibernate as nymphs, their adults were the first to emerge and formed the bulk of the catch in April and May. By June, the Cicadellidae, most of which hibernated as eggs, were the most abundant both in the field and in the air, while the numbers of adult delphacids declined. By mid-July, the second generation of adult delphacids emerged and their incidence in the aerial traps rose. The second generations of cicadellid adults tended to overlap with the delphacids, but whereas the latter died out by the end of August, or in the first week of September, the cicadellids persisted and some species continued to emerge into the adult stage into October. By September and October the numbers of Typhlocybinæ increased and by November, only the Typhlocybinæ and the occasional cicadellids that hibernated as adults (e.g. *Balclutha punctata*, *Mocydiopsis parvicauda*) were caught in the aerial traps.

Table 3 (a). Number of species and individuals of Auchenorrhyncha caught in suction traps II (1·2 m), IV (9·1 m), R.T. (12·2 m) at Silwood Park 1970-71

|                 | Cercopidae | Cicadellidae      | Typhlocybinæ | Cixiidae | Delphacidae |
|-----------------|------------|-------------------|--------------|----------|-------------|
| 1970            |            |                   |              |          |             |
| No. species     | 2          | 31                | —            | 2        | 13          |
| No. individuals | 2          | 634               | 269          | 30       | 343         |
|                 |            | Total catch: 1276 |              |          |             |
| 1971            |            |                   |              |          |             |
| No. species     | 3          | 23                | —            | 2        | 9           |
| No. individuals | 4          | 469               | 437          | 16       | 164         |
|                 |            | Total catch: 1090 |              |          |             |

Table 3 (b). Proportion of total annual catch made of *Javesella pellucida*, *Macrostes sexnotatus* and *M. laevis*

|                      | 1970 |            | 1971 |            |
|----------------------|------|------------|------|------------|
|                      | No.  | % of catch | No.  | % of catch |
| <i>J. pellucida</i>  | 286  | 22         | 140  | 13         |
| <i>M. sexnotatus</i> | 344  | 27         | 278  | 26         |
| <i>M. laevis</i>     | 82   | 8          | 90   | 9          |
| Total                | 712  | 57         | 508  | 48         |

Table 4. Total monthly catches of *Auchenorrhyncha* in aerial traps II (1.2 m) and IV (9.1 m) at Silwood Park, 1969-71

| Month                        | Total catch | Percentage of total catch |            |             |              |             |
|------------------------------|-------------|---------------------------|------------|-------------|--------------|-------------|
|                              |             | Cixiidae                  | Cercopidae | Delphacidae | Cicadellidae | Typhlocybae |
| Apr.                         | 14          | —                         | —          | 100.0       | —            | —           |
| May                          | 349         | 9.5                       | —          | 74.5        | 7.7          | 8.3         |
| June                         | 755         | 1.7                       | 0.1        | 8.7         | 72.7         | 16.7        |
| July                         | 491         | 1.2                       | 0.5        | 29.5        | 46.6         | 22.2        |
| Aug.                         | 507         | 0.6                       | 0.2        | 35.9        | 48.5         | 14.8        |
| Sept.                        | 523         | 0.4                       | —          | 1.3         | 56.9         | 41.3        |
| Oct.                         | 311         | —                         | —          | —           | 12.2         | 87.8        |
| Total for 3 years            | 2950        |                           |            |             |              |             |
| Percentage total for 3 years |             | 1.9                       | 0.1        | 22.8        | 47.0         | 28.1        |

## Patterns of flight

(a) The two permanently sited and adjacent suction traps, one at 1.2 m, the other at 9.1 m above ground level, probably distinguish between the more actively flying grassland species from the poorer flyers. The slopes of the lines of the logarithms of the seasonal catches on the logarithms of heights of traps, provide an index of the ability of the species to disperse. Examples of catches of six common grassland species are given in Fig. 1(a), from which it may be inferred that although the numbers of flying *Macrosteles*

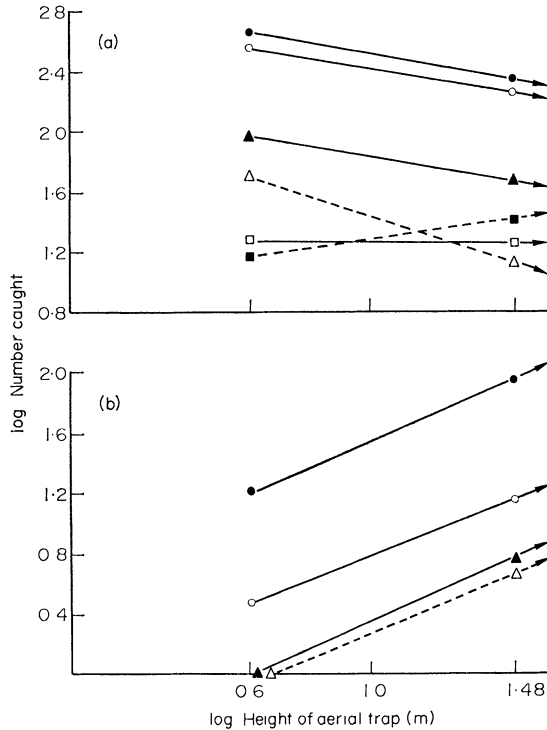


FIG. 1. Differences in dispersal patterns of leafhoppers. (a) Grassland-dwelling species: ●, *Macrosteles sexnotatus*; ○, *Javesella pellucida*; ▲, *Zygina scutellaris*; △, *Arthaldeus pascuellus*; ■, *Balclutha punctata*; □, *Psammotettix confinis*. (b) Tree-living species: ●, *Oncopsis* spp.; ○, *Allygus* spp.; ▲, *Macropsis* spp.; △, *Idiocerus* spp.



*sexnotatus*, *Javesella pellucida* and *Zygina scutellaris* were greater than those of *Psammotettix confinis*, individuals of the latter species may have flown greater distances and that within this group of insects, *Arthaldeus pascuellus* had the lowest power of dispersal. In contrast to these species, the numbers of *Balclutha punctata* were greater in the higher trap. This may have a bearing on its bionomics, as this grassland species hibernates as an adult on pine trees and in the grass tussocks.

(b) The patterns of flight were different in the grass-dwelling and the tree-dwelling Cicadellidae, which formed 10% of the catch of this family. The catches of the cicadellids in the two traps in 1969–71 are shown in Fig. 1(b). Greater numbers of the twenty-six species inhabiting ground vegetation were caught in the lower than in the higher trap, whereas the reverse was true of the seventeen tree-living species, the exception being the grass-dwelling *B. punctata*.

### EFFECTS OF WEATHER ON FLIGHT

To see whether flight, as measured by the daily catches in the suction traps was influenced by weather, multiple correlation analyses were made on the numbers of *Javesella pellucida*, *Macrosteles sexnotatus* and *Arthaldeus pascuellus* with the independent variables which comprised the mean and maximum daily temperatures, hours of sunshine, average wind speed, day of flight (day 1 being the first day of catch), the 'index of abundance' which was measured by the numbers of adults in the field samples and the 'index of maturity'.

From these analyses it may be seen that most of the values of  $R$  are significant (Table 5). However, the values of  $R^2$  indicate that much of the variance is still not accounted for by the independent variables.

Temperature stimulated flight in all the three species (indicated by positive correlations) and higher wind speeds inhibited it as is indicated by negative correlations. No significant effects of the hours of sunshine, nor of abundance in the field and of the day of flight were obtained. It is also probable that insufficiency of data account for the two non-significant correlations with the 'index of maturity', since the inhibiting effects of maturation on flight were seen in laboratory tests on *Javesella pellucida* and *Arthaldeus pascuellus*. Moreover, Nuorteva (1962) noted that the mass migratory flight of *Javesella pellucida* is commonly the first flight of immature adults.

Lewis & Taylor (1965) showed that although *Macrosteles sexnotatus* fly throughout the day, its peak of flight is between 17.00–19.00 hours G.M.T. At Silwood the mean temperature between these hours on the days of flight was 17.5° C, but there was no correlation between variations around this mean and the numbers of *Macrosteles* in traps. The threshold of daily mean temperature on the days of flight was above 14° C and that of the maximum at or above 20° C. Furthermore, in this species there was little flight at wind speeds above 6.2 m s<sup>-1</sup>.

In *Javesella pellucida*, flight occurred when the mean daily and maximum temperatures were at or above 15° and 20° C respectively. Winds above 4.2–4.6 m s<sup>-1</sup> appeared to have an inhibiting effect.

In the three species examined, the hours of sunshine had little influence, as obtained by May (1971) with *Stenocranus minutus*, where temperatures above 15° C and wind speeds below 7.7 m s<sup>-1</sup> low sunshine hours favoured flight.

By contrast, flight in *Cicadella viridis* was positively correlated with hours of sunshine and negatively with a decrease in hours of rainfall (Tay 1972).

Table 5. Multiple correlation (R) between the 'daily catch in traps' and seven independent variables

| Year          | Generation | R     | R <sup>2</sup> | F for analysis of variance |     | Significance of correlations between catches in traps and |                |             |              |                 |                |                    |   |
|---------------|------------|-------|----------------|----------------------------|-----|---|----------------|-------------|--------------|-----------------|----------------|--------------------|---|
|               |            |       |                | Value                      | P   | Mean temp. (°C)   | Max temp. (°C) | Wind speed† | Hours of sun | Index abundance | Day of flight† | Index of maturity† |   |
| 1970          | 1st        | 0.767 | 0.559          | 4.496                      | **  | **  | *              | .           | .            | *               | *              | *                  | * |
|               | 2nd        | 0.603 | 0.304          | 1.634                      | .   | .   | .              | .           | .            | .               | .              | .                  | . |
| 1969          | 1st        | 0.827 | 0.684          | 7.722                      | *** | *   | *              | .           | *            | .               | .              | .                  | * |
|               | 2nd        | 0.632 | 0.399          | 2.559                      | *   | .   | .              | *           | .            | .               | .              | .                  | * |
| 1970          | 1st        | 0.633 | 0.401          | 3.119                      | *   | .   | .              | *           | .            | .               | .              | .                  | . |
|               | 2nd        | 0.583 | 0.340          | 3.954                      | *** | **  | *              | .           | .            | .               | .              | .                  | . |
| 1969 and 1970 | 1st        | 0.538 | 0.239          | 4.138                      | *   | .   | .              | ***         | .            | .               | .              | .                  | . |
|               | 2nd        | 0.520 | 0.267          | 4.992                      | *   | ***   | ***            | *           | .            | .               | .              | .                  | . |
| 1970          | 1st        | 0.607 | 0.368          | 4.946                      | *** | **  | ***            | .           | .            | ***             | .              | .                  | . |
|               | 2nd        | 0.610 | 0.372          | 6.027                      | *** | .   | **             | *           | .            | .               | .              | .                  | . |
| 1970 and 1971 | 1st        | 0.377 | 0.142          | 3.669                      | .   | .   | *              | *           | .            | .               | .              | .                  | . |
|               | 2nd        | 0.405 | 0.164          | 4.860                      | *   | *   | ***            | *           | .            | .               | .              | .                  | . |

\*,  $P < 0.05$ ; \*\*,  $P < 0.01$ ; \*\*\*,  $P < 0.001$ ; ., N.S.; - no correlations tested.

† Significant correlations -ve.

## LIFE HISTORIES AND TIME OF DISPERSAL

Johnson (1969) considers that there are three classes of migration in insects: (1) emigration without return, usually by relatively short-lived adults; (2) emigration and return by the same individuals within a season; and (3) emigration to hibernation and aestivation sites and return by the same individuals after imaginal diapause.

Table 6. *Voltinism, hibernation stage and time of dispersal by flight*

| Hibernation stage | Time of dispersal by flight                             | Species  |
|-------------------|---|--|
| Univoltine spp.   |   |  |
| Egg               | Mainly immature adults                                  | <i>Philaenus spumarius</i> (Cerc.*)<br><i>Neophilaenus lineatus</i> (Cerc.*)<br><i>Cercopis vulnerata</i> (Cerc.*)<br><i>Cicadella viridis</i> (C)<br><i>Graphocephala coccinea</i> (C)<br><i>Doratura stylata</i> (C)<br><i>Diplocolenus abdominalis</i> (C)<br><i>Deltocephalus coronifer</i> (C)<br><i>Graphocraerus ventralis</i> (C)<br><i>Elymana sulphurella</i> (C)<br><i>Conomelus anceps</i> (D) |
| Adult             | Pre-hibernation flight                                  | <i>Mocydiopsis parvicauda</i> (C)<br><i>Stenocranus minutus</i> (D)  |
|                   | Pre- and post-hibernation flight                        | <i>Balclutha punctata</i> (C)  |
| Bivoltine spp.    |   |  |
| Egg               | (a) In 1st generation only                              | <i>Errastunus ocellaris</i> (C)  |
| Egg               | (b) In 1st generation with very small proportion in 2nd | <i>Jassargus pseudocellaris</i> (C)<br><i>Arthaldeus pascuellus</i> (C)<br><i>Streptanus sordidus</i> (C)<br><i>Laodelphax elegantulus</i> (D)   |
| Nymph             | (c) In both 1st and 2nd generations                     | <i>Psammotettix confinis</i> (C)<br><i>Cicadula persimilis</i> (C)<br><i>Macrosteles sexnotatus</i> (C)<br><i>M. laevis</i> (C)<br><i>M. viridigriseus</i> (C)<br><i>Euscelis plebejus</i> (C)<br><i>Javesella pellucida</i> (D)<br><i>Muirodelphax exiguus</i> (D)<br><i>Paraliburnia dalei</i> (D)<br><i>Xanthodelphax stramineus</i> (D)  |
| Polyvoltine spp.  |   |  |
| Nymph and adult   | Flight in successive generations                        | <i>Zygina scutellaris</i> (T)  |

\* Cerc, Cercopidae; C, Cicadellidae; D, Delphacidae; T, Typhlocybinae.

The majority of Auchenorrhyncha examined appeared to fall into class 1. However, some individuals of the cicadellid *Balclutha punctata* hibernate on pine trees and in grass tussocks and may return to the original breeding sites, therefore, this species falls into class 3.

Most of the grassland species studied were either univoltine or bivoltine and the only certain polyvoltine species encountered was the typhlocybid, *Zygina scutellaris*.

The incidence of dispersal by flight within the life cycles is summarized in Table 6 and in Figs. 2-5.

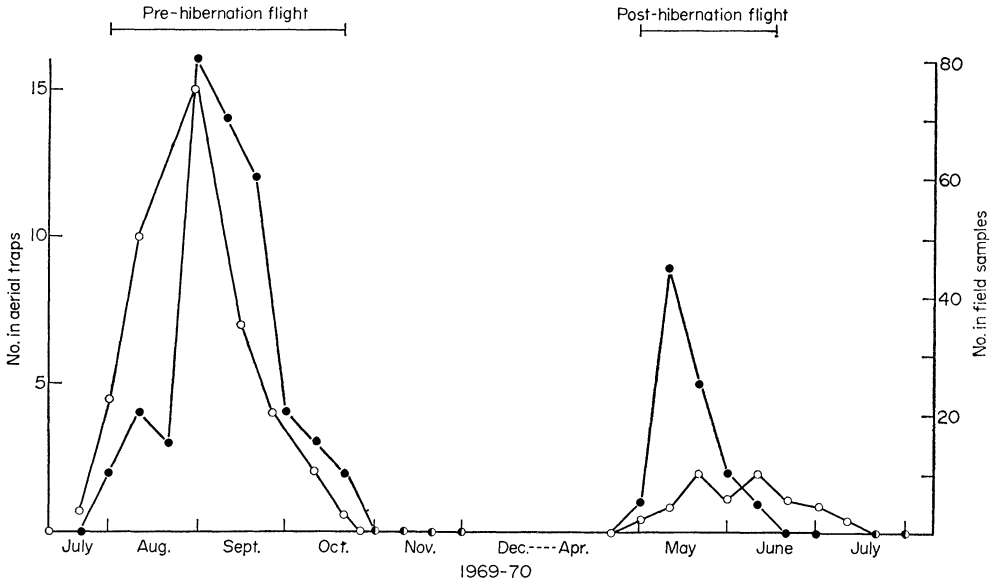


FIG. 2. *Balclutha punctata* (Cicadellidae), a univoltine species that hibernates as adult and disperses by flight before and after hibernation. ○, Numbers of adults in field samples; ●, numbers in aerial traps.

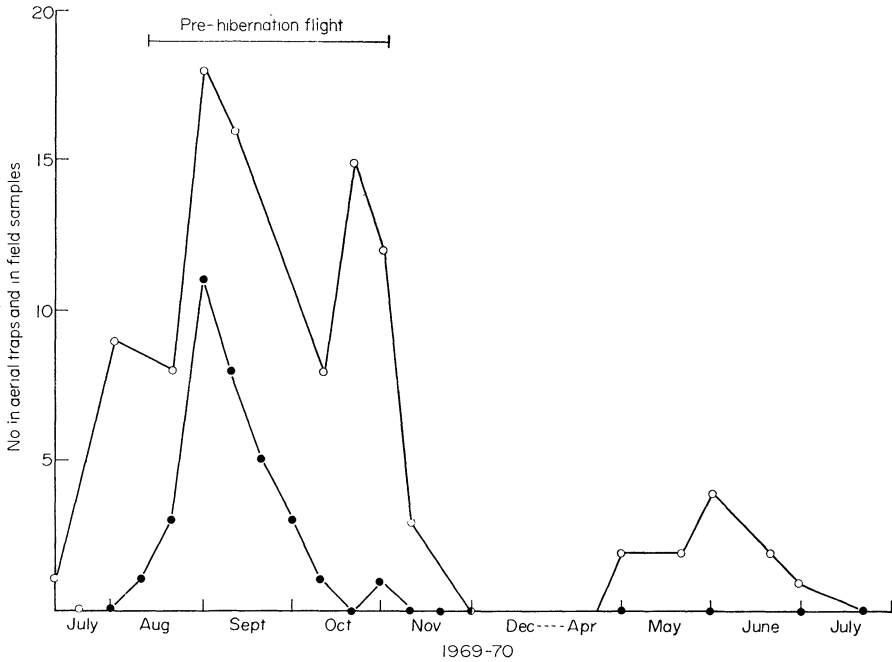


FIG. 3. *Mocydiopsis parvicauda* (Cicadellidae), a univoltine species that hibernates as adult and disperses by flight before hibernation only. ○, Numbers of adults in field samples; ●, numbers in aerial traps.

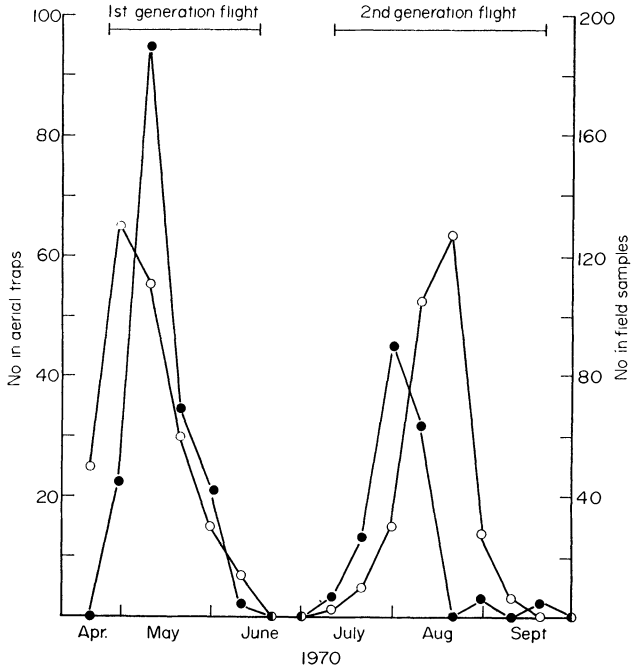


FIG. 4. *Javesella pellucida* (Delphacidae), a bivoltine species which disperses by flight in both generations. ○, Numbers of adults in field samples; ●, numbers in aerial traps.

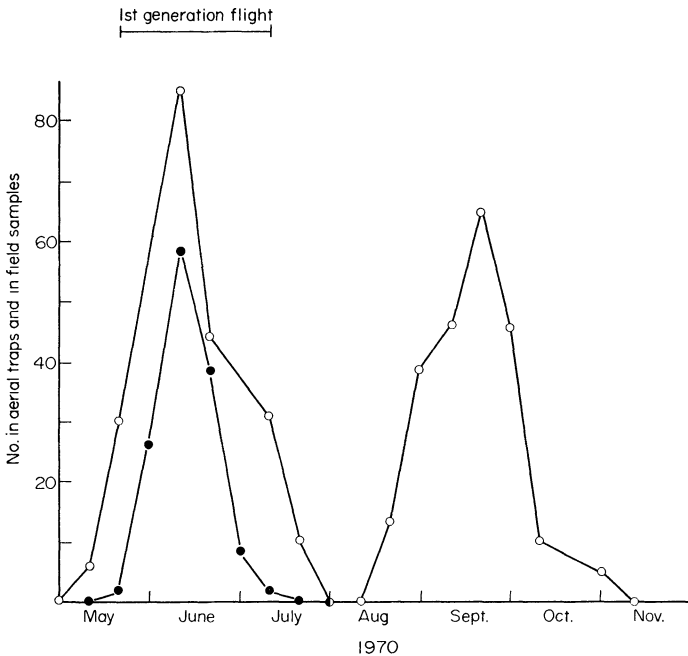


FIG. 5. *Errastunus ocellaris* (Cicadellidae), a bivoltine species which disperses by flight only in the first generation. ○, Numbers of adults in field samples; ●, numbers in aerial traps.

Migratory flight in leafhoppers occurs when the females are teneral and still immature (Lawson, Chamberlain & York 1951; Nuortova 1962; Johnson 1965, 1966, 1969). It is possible, however, that some of the leafhopper species, for instance *Macrosteles sexnotatus*, continue to fly actively between successive ovipositions, whereas others, e.g. *Arthaldeus pascuellus*, *Elymana sulphurella*, become less active on maturation (see below). *Balclutha punctata* has a pre- and a post-hibernation flight and remains completely immature, with thread-like ovarioles, from the time of its emergence in late summer or autumn until the following spring. On the other hand, *Mocycdiopsis parvicauda*, which has only one flight period, preceding the imaginal diapause, may begin to mature in autumn, i.e. its oocytes begin to grow. However, they do not reach full size and the ovaries regress to the thread-like condition in the winter.

In the bivoltine species, and in Delphacidae in particular, the proportions of the flying individuals in the two annual generations are closely linked with alary polymorphism, i.e. with the proportions of populations that are brachypterous.

It was also of interest that some of the more actively flying species were capable of mass exodus from their breeding sites. Thus *Balclutha punctata* which formed a large breeding colony in 'the study area' (Waloff & Solomon 1973), emigrated on reaching its adult stage in 1969. Similarly, *Macrosteles laevis* which colonized a disturbed site in 'the study area' in 1968 and formed a large breeding colony for four generations, took off from this site when it became overgrown by dense vegetation.

#### ALARY POLYMORPHISM IN LEAFHOPPERS

Alary polymorphism is widespread in Auchenorrhyncha, but whereas it is frequent in species living in grasses or other low vegetation, so far, only the macropterous forms of tree-living leafhoppers have been encountered in Britain.

The female flyers and non-flyers are subdivided into five groups, but it is emphasized that the ability to fly is not necessarily synonymous with that to migrate.

*Group 1: macropterous species, in which females retain ability to fly throughout their lives*

The ability to fly was tested as described and by the incidence of individuals in suction traps, e.g. *Macrosteles sexnotatus* and *M. laevis*. Some species of the genus *Macrosteles* are very active flyers and the long-range migrations of *M. fascifrons* (Stål) in North America, have been extensively studied and linked with synoptic meteorology (see Johnson 1969; Chiykowski & Chapman 1965; Medler 1962; Miller & De Lyzer 1960; Westdal, Barrett & Richardson 1961; Wallis 1962). However, even this actively flying species has short-winged forms in isolated populations (Beirne 1956; Severin 1940).

A few, relatively short-winged males of *M. sexnotatus* were encountered in the field samples at Silwood in 1970. They were different from the usual forms, in having shorter bodies as well as wings, and were only recognized as *M. sexnotatus* after examination of their genitalia and sternal apodemes. Equal numbers of males and females of *M. sexnotatus* and *M. laevis* were caught in the suction traps.

*Group 2: macropterous species in which flight ability greatly diminishes, or is lost with maturation and age*

Numerous species fall into this group, e.g. *Elymana sulphurella*, *Diplocolenus abdominalis*, *Cicadella viridis* and the macropterous forms of the delphacid *Javesella pellucida*. In these species flight tends to be inhibited by maturation.

*Group 3: species that can be distinguished into macropterous and sub-macropterous forms*

All individuals of this group are capable of flight, but at Silwood, only the macropterous forms have been caught in the suction traps and are presumed to be the migratory forms. One species within this group is the delphacid, *Stenocranus minutus* (May 1971). Müller (1957, 1958, 1960) found that when its larvae were subjected to a shorter photoperiod than normally experienced, different morphological forms were produced and it is probable that differences in day length and in other environmental conditions may be critical in the production of submacropters and macropters. However, macropterous individuals found by May (1971) have not been previously encountered or described.

Table 7. Means and ratios of fore- and hind-wing lengths of flyers and non-flyers

|                              | No. and sex     | Mean wing length (mm)† |      | Ratio (F)/(H) | Significance of comparison of means |          |       |      |
|------------------------------|-----------------|------------------------|------|---------------|-------------------------------------|----------|-------|------|
|                              |                 | (F)                    | (H)  |               | <i>t</i>                            | <i>P</i> |       |      |
| <i>Errastunus ocellaris</i>  | 15♀♀ Non-flyers | 3.00                   | 2.50 | 1.20          | (F)†                                | 5.749    | ***   |      |
|                              | 17♀♀ Flyers     | 3.49                   | 3.17 | 1.10          | (H)                                 | 7.553    | ***   |      |
|                              | 34♂♂ Non-flyers | 2.94                   | 2.31 | 1.27          | (F)                                 | 0.898    | n.s.  |      |
|                              | 5♂♂ Flyers      | 3.16                   | 2.84 | 1.11          | (H)                                 | 4.257    | ***   |      |
| <i>Arthaldeus pascuellus</i> | 10♀♀ Non-flyers | 3.40                   | 2.58 | 1.32          | (F)                                 | 1.168    | n.s.  |      |
|                              | 8♀♀ Flyers      | 3.54                   | 3.03 | 1.18          | (H)                                 | 3.195    | *     |      |
|                              | 15♂♂ Non-flyers | 2.97                   | 2.34 | 1.27          | (F)                                 | 3.359    | *     |      |
|                              | 15♂♂ Flyers     | 3.23                   | 2.91 | 1.11          | (H)                                 | 6.715    | ***   |      |
| <i>Psammotettix confinis</i> | 1st generation  | 4♀♀ Non-flyers         | 3.52 | 3.02          | 1.17                                | (F)      | 0.603 | n.s. |
|                              |                 | 21♀♀ Flyers            | 3.60 | 3.03          | 1.19                                | (H)      | 0.119 | n.s. |
|                              | 2nd generation  | 14♀♀ Non-flyers        | 3.51 | 2.84          | 1.24                                | (F)      | 0.327 | n.s. |
|                              |                 | 15♀♀ Flyers            | 3.53 | 3.00          | 1.18                                | (H)      | 1.833 | n.s. |
|                              |                 | 10♂♂ Non-flyers        | 3.49 | 2.72          | 1.28                                | (F)      | 0.235 | n.s. |
|                              |                 | 18♂♂ Flyers            | 3.47 | 3.00          | 1.16                                | (H)      | 2.778 | *    |

\*,  $P < 0.05$ ; \*\*\*,  $P < 0.001$ ; n.s., not significant.

† F, Fore-wing; H, hind-wing.

At 25° C tethered and suspended macropters flew on average for 1200 s and submacropters for 240 s. Macropterous forms of *S. minutus* are slightly smaller than submacropters but have longer wings and differ in coloration. In submacropterous forms the fore-wings are 2.25–2.5 times as long as the abdomen, but in macropters they are 2.5–2.75 as long; the length of the hind-wings in submacropters is 1.5–2.0 and in macropters 2.25–2.5 that of the abdomen. The black markings in the macropters are more extensive and the black stripes on the fore-wings more prominent. Moreover the apical cells are more extended and the wing tips more pointed in macropters than in submacropters.

The assumption that macropters are the migratory forms was substantiated by May (1971) not only by trap catches, but also by observations on a localized population on *Dactylis glomerata* L. In 1969, macropters formed 52.5% of the total population before the flight period and in 1970, 48.2%. After the flight period these percentages fell to 19.4 and 17.9, respectively.

At 20° C and 16 h of light, crowded nymphs produced high proportions of macropters on wilting *Dactylis* and equally high proportions of sub-macropters on green and succulent grass. However, isolated nymphs reared on wilting and succulent *Dactylis* gave

rise to submacropters (May 1971). It is therefore possible, that the leafhoppers were affected by the condition of the plant, and also by crowding.

A different type of macroptery and submacroptery has been encountered by Rose (1972b) in *Cicadulina* spp. (Cicadellidae). In *C. mbila* (Naude), *C. storeyi* China and *C. parazeae* Ghauri, the wing lengths in the two forms remained more or less constant, but the individuals were either short-bodied or long-bodied. Tethered and suspended long-bodied individuals flew for 8–15 s, or not at all, the short-bodied *Cicadulina* flew for an average of 500 s. Most of the tests were made on males, to avoid confusion with elongation of the body on maturation in the females. Field experiments and observations also consistently pointed to the existence of two ranges of distances flown by *Cicadulina*. Rose's results indicate also that flight ability in the three *Cicadulina* spp. is inherited, the progeny of non-flyers being mostly non-flyers while those of the long-flyers, mainly flyers.

No experiments have been made on the grassland cicadellid, *Balclutha punctata*, but immature adults, collected in the field prior to winter diapause, showed a considerable variation in their wing lengths and were subdivided into short- and long-winged individuals. This variation, however, is not associated with the colour polymorphism which exists, in this species, since the long- and the short-winged forms have been seen in both the green and the brown individuals.

In a sense, Group 2 and Group 3 intergrade, since in Group 2 females alteration in the proportions of the body to wing lengths occur on maturation, when the abdomen is full of eggs it extends well beyond the wing tips and flight is inhibited.

*Group 4: species in which the ability to fly is linked with the alteration in the ratio of lengths of the fore- to hind-wing*

*Errastunus ocellaris* and *Arthaldeus pascuellus* fall within this group. In both species the mature females lose their flight ability, but some cannot fly, even when immature. *Errastunus ocellaris* provides a particularly good example of such dimorphism, the greater proportion of its populations consisting of non-flyers and the high proportion of flyers being female. The sex ratio of *E. ocellaris* caught in suction traps between 1967 and 1970 was 1 ♂:25 ♀. Measurements of the total body length, the fore- and hind-wing and hind tibia were made on the flyers and non-flyers of *E. ocellaris*, *Arthaldeus pascuellus* and of *Psammotettix confinis*, which was originally suspected of belonging to this group. The most relevant differences were found in the lengths of the fore-wings and hind-wings (Table 7).

In *Errastunus ocellaris* females, there was a difference between the lengths of the fore- and hind-wings of flyers and hoppers. The ratio of the two wing lengths in flyers being 1.10 and that in non-flyers 1.20. In the males, there was no difference in the lengths of the fore-wings of the two groups, but a significant difference in the hind-wings. The ratios of the lengths in the flyers being 1.11 and in non-flyers 1.27. The low number of flying males measured reflects their scarcity. *Arthaldeus pascuellus* was similar, but in contrast to *Errastunus ocellaris*, most individuals were capable of flight, and non-flyers were rare.

In *Psammotettix confinis*, variations in the wing-lengths between the flying and non-flying immature individuals were not significant, suggesting that physiological factors may determine whether an individual is a flyer or a non-flyer.

*Group 5: species exhibiting clear alary polymorphism*

In the brachypterous forms of these species, both pairs of wings are reduced and the skeletal structure of the thorax and the dimensions of the flight muscles are modified.



A distinction between the brachypterous and macropterous forms of the same species is found in many Delphacidae, while the normally short-winged *Doratura stylata* and *Ulopa reticulata* (F.), in which the hind wings are normally absent, provide examples within the Cicadellidae.

The incidence of brachypters and macropters in several species of Delphacidae, is given in Table 8. In the habitat studied, the great bulk of *Javesella pellucida* were macropterous and of the 2063 individuals examined throughout the six generations between 1969 and 1971, 76% of the females and 75% of the males were long winged, the greater

Table 8. *The incidence of macropterous and brachypterous forms in field samples taken at Silwood Park*

| Species                           | Year | Generation | ♀♀  |     | ♂♂  |     |
|-----------------------------------|------|------------|-----|-----|-----|-----|
|                                   |      |            | br* | m*  | br  | m   |
| <i>Javesella pellucida</i>        | 1969 | 1          | 84  | 198 | 167 | 267 |
|                                   |      | 2          | 20  | 106 | 17  | 154 |
|                                   | 1970 | 1          | 66  | 195 | 30  | 222 |
|                                   |      | 2          | 5   | 153 | 3   | 136 |
|                                   | 1971 | 1          | 47  | 56  | 43  | 74  |
|                                   |      | 2          | 4   | 4   | 2   | 10  |
| <i>Laodelphax elegantulus</i>     | 1969 | 1          | 188 | 0   | 151 | 0   |
|                                   |      | 2          | 56  | 1   | 56  | 1   |
|                                   | 1970 | 1          | 443 | 0   | 308 | 0   |
|                                   |      | 2          | 58  | 0   | 53  | 1   |
|                                   | 1971 | 1          | 103 | 0   | 58  | 0   |
|                                   |      | 2          | 13  | 0   | 12  | 0   |
| <i>Muirodelphax exiguus</i>       | 1969 | 1          | 155 | 0   | 136 | 0   |
|                                   |      | 2          | 170 | 0   | 256 | 0   |
|                                   | 1970 | 1          | 129 | 1   | 107 | 0   |
|                                   |      | 2          | 70  | 0   | 67  | 0   |
|                                   | 1971 | 1          | 105 | 0   | 104 | 0   |
|                                   |      | 2          | 18  | 0   | 2   | 0   |
| <i>Ribautodelphax angulosus</i>   | 1969 | 1          | 35  | 0   | 12  | 0   |
|                                   |      | 2          | 21  | 1   | 32  | 0   |
|                                   | 1970 | 1          | 55  | 0   | 44  | 0   |
|                                   |      | 2          | —   | —   | —   | —   |
|                                   | 1971 | 1          | 5   | 0   | 4   | 0   |
|                                   |      | 2          | —   | —   | —   | —   |
| <i>Paraliburnia dalei</i>         | 1969 | 1          | 148 | 0   | 175 | 0   |
|                                   |      | 2          | 219 | 0   | 140 | 0   |
|                                   | 1970 | 1          | 128 | 1   | 93  | 0   |
|                                   |      | 2          | 74  | 1   | 47  | 0   |
|                                   | 1971 | 1          | 16  | 0   | 9   | 0   |
|                                   |      | 2          | 17  | 0   | 10  | 0   |
| <i>Dicranotropis hamata</i>       | 1969 | —          | 36  | 1   | 15  | 0   |
|                                   | 1970 | —          | 15  | 0   | 19  | 0   |
|                                   | 1971 | —          | 34  | 1   | 46  | 0   |
|                                   | 1972 | —          | 99  | 2   | 59  | 1   |
| <i>Criomorphus albomarginatus</i> | 1969 | —          | 13  | 0   | 20  | 3   |
|                                   | 1970 | —          | 8   | 1   | 9   | 0   |
| <i>Xanthodelphax stramineus</i>   | 1969 | —          | 2   | 0   | 5   | 0   |
|                                   | 1970 | —          | 1   | 0   | 3   | 2   |

\* br, brachypterous; m, macropterous.

proportions of macropters in both sexes occurring in the second generation of each year. In the other species (Table 8), brachypterous forms predominated and out of the 1502 individuals of *Laodelphax elegantulus* examined, 0.1% of the females and 0.3% of the males were long winged. A higher incidence of macropterous forms was seen in *Dicranotropis hamata*, *Criomorphus albomarginatus* and in the locally rare species *Xanthodelphax stramineus*.

Macroptery occurred in *Doratura stylata*, a monovoltine species collected in the study area for 5 years. The numbers of adults from similar samples were 45 in 1967, 87 in 1968, 214 in 1969, 1037 in 1970 and 233 in 1971, indicating fluctuation in abundance by a factor of twenty-three. The sample of 1037 in 1970, contained 535 females and 502 males. No macropterous males were seen, but 25 (4.7%) of the females had long wings

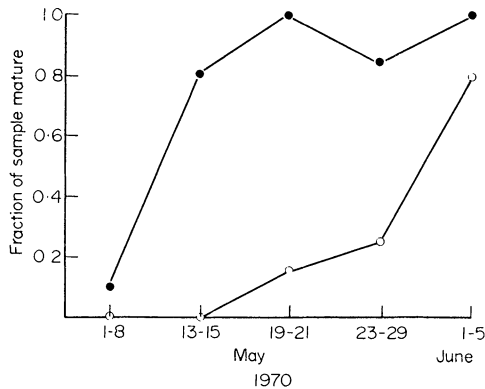


FIG. 6. Delayed maturation in macropters of *Javesella pellucida* (Delphacidae). Proportions of samples of a field population with mature brachypterous (●) and macropterous (○) females.

that extended beyond the abdomen. The macropters caught in the suction traps were also females. As this species was concentrated in a relatively small area and, as in 1970, its nymphs were abundant, the effects of density on production of macropters cannot be dismissed. Comparable effects of crowding on production of long-winged forms of *Delphacodes striatella* (Fallén) and other leafhoppers have been described by Kisimoto (1965).

In some cicadellid species macroptery is very rare and, none has been encountered in *Ulopa reticulata*, where normally the hind wings are absent. However, in 732 adults dissected between 1969 and 1972, there were two fully winged females. Le Quesne (1965) states that in the only other species of this genus in Britain, i.e. in *U. trivialis* Germar, a single macropterous individual has been reported by Duffield (1963).

In addition to the structural differences between the macropters and brachypters, the females of the two forms differ in their reproductive physiology. In macropters the preoviposition period is prolonged, and fecundity may be reduced. In field populations of *Javesella pellucida* and *Doratura stylata* the brachypterous females mature long before the macropterous ones (Figs. 6 and 7). May (1971) has shown that the macropters of *Stenocranus minutus* lay fewer eggs than the submacropters kept under comparable conditions. Similarly, Kisimoto (1965) found that the preoviposition period was prolonged and fecundity reduced in the macropters of *Delphacodes striatella*, *Nilaparvata lugens* Stål and *Sagata furcifera* Horváth.

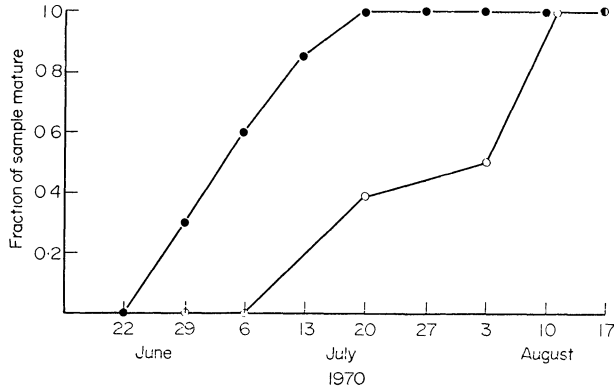


FIG. 7. Delayed maturation in macropters of *Doratura stylata* (Cicadellidae). Proportions of samples of a field population with mature brachypterous (●) and macropterous (○) females.

### SEX RATIOS OF SPECIES IN SUCTION TRAPS

Sex ratios of some species caught in suction traps are given in Table 9, where the size of R.T. is not adjusted to that of the two adjacent traps.

In Auchenorrhyncha there is a considerable variation in the proportions of the two sexes that fly. In many species of Cicadellidae, e.g. *Macrosteles sexnotatus*, *M. laevis*, *Balclutha punctata*, *Arthaldeus pascuellus*, *Mocydiopsis parvicauda*, in the three species of *Cicadulina* studied by Rose (1972a, b), and in the delphacids *Javesella pellucida* and *Stenocranus minutus*, the two sexes fly in approximately equal proportions. These species include some of most active flyers and probably migrants, i.e. those that regularly occur in larger numbers in the aerial suction traps.

In *Cixius pilosus* and in *Psammotettix confinis* there was a consistent excess of flying males in all the traps. The reverse was true of the cicadellid *Streptanus sordidus* and the typhlocybid *Zygina scutellaris*, where the females appear to be the more active sex and are caught in larger numbers. In *Errastumus ocellaris* only a low proportion of the populations are flyers, but there was a great excess of flying females over males, the numbers caught in traps between 1967 and 1970 being 5 ♂:126 ♀.

In the normally brachypterous cicadellid species *Doratura stylata* and *Ulopa reticulata* the only macropterous individuals, capable of flight were all female. In 1970, in *Doratura*, 25/535 females collected in the field population were macropterous. In *Ulopa*, of the 517 individuals examined between 1969 and 1972, two females were fully macropterous.

Table 9. Sex ratio (♂:♀) in total seasonal catches of some species of Auchenorrhyncha caught in suction traps at Silwood Park 1969–71

| Species                       | Height above ground |                  |                | Total |
|-------------------------------|---------------------|------------------|----------------|-------|
|                               | 1.2 m<br>Trap II    | 9.1 m<br>Trap IV | 12.2 m<br>R.T. |       |
| <i>Arthaldeus pascuellus</i>  | 1:1.3               | 1:0.7            | 1:1.1          | 1:1.1 |
| <i>Balclutha punctata</i>     | 1:1.4               | 1:0.8            | 1:1            | 1:1.0 |
| <i>Mocydiopsis parvicauda</i> | 1:1.4               | 1:1              | 1:0.5          | 1:1.2 |
| <i>Cixius pilosus</i>         | 1:0.7               | 1:0.4            | 1:0.3          | 1:0.5 |
| <i>Psammotettix confinis</i>  | 1:0.6               | 1:0.4            | 1:0.3          | 1:0.5 |
| <i>Streptanus sordidus</i>    | 1:1.4               | 1:3.6            | 1:4            | 1:1.9 |
| <i>Zygina scutellaris</i>     | 1:1.5               | 1:1.5            | 1:1.6          | 1:1.5 |

## FLIGHT OF PARASITIZED LEAFHOPPERS

Lewis & Taylor (1965) have shown that the vast majority of Auchenorrhyncha are day flyers. They also point out, that the synchronization of life cycles and distribution of many small parasitic Hymenoptera with their hosts is assisted by flight activity in daytime, when they are subject to the same distributive processes. However, this association is even closer, since parasitized individuals were not uncommon in the aerial suction traps,

Table 10. Number of parasitized *Javesella pellucida* (Delphacidae) caught in suction traps at Silwood Park

| Year | Generation | Metres above ground | No. examined | No. parasitized by |           |              | Percentage parasitized |
|------|------------|---------------------|--------------|--------------------|-----------|--------------|------------------------|
|      |            |                     |              | Strepsiptera       | Dryinidae | Pipunculidae |                        |
| 1960 | 1          | 1.2                 | 371          | 10                 | 3         | —            | 3.5                    |
|      | 2          | 1.2                 | 85           | —                  | —         | —            | 0                      |
| 1962 | 1          | 1.2                 | 318          | 12                 | 9         | —            | 6.6                    |
| 1968 | 1          | 1.2                 | 104          | 10                 | 1         | 1            | 11.5                   |
|      | 2          | 1.2                 | 34           | —                  | —         | —            | 0                      |
|      | 1          | 9.1                 | 34           | —                  | —         | —            | 0                      |
|      | 2          | 9.1                 | 19           | —                  | —         | —            | 0                      |
| 1969 | 1          | 1.2                 | 51           | 4                  | —         | —            | 7.8                    |
|      | 2          | 1.2                 | 75           | 1                  | —         | —            | 1.3                    |
|      | 1          | 9.1                 | 13           | —                  | —         | —            | 0                      |
|      | 2          | 9.1                 | 33           | 2                  | —         | —            | 6.1                    |
|      | 1          | 12.2                | 12           | 1                  | —         | —            | 8.3                    |
|      | 2          | 12.2                | 16           | —                  | —         | —            | 0                      |
| 1970 | 1          | 1.2                 | 101          | 4                  | —         | 1            | 4.9                    |
|      | 2          | 1.2                 | 42           | —                  | —         | —            | 0                      |
|      | 1          | 9.1                 | 50           | 2                  | 1         | —            | 6.0                    |
|      | 2          | 9.1                 | 32           | 1                  | —         | —            | 3.1                    |
|      | 1          | 12.2                | 37           | 1                  | —         | —            | 2.7                    |
|      | 2          | 12.2                | 15           | —                  | —         | —            | 0                      |
| 1971 | 1          | 1.2                 | 33           | 2                  | —         | —            | 6.1                    |
|      | 2          | 1.2                 | 28           | —                  | —         | —            | 0                      |
|      | 1          | 9.1                 | 18           | 2                  | —         | —            | 11.1                   |
|      | 2          | 9.1                 | 14           | —                  | —         | —            | 0                      |
|      | 1          | 12.2                | 8            | —                  | —         | —            | 0                      |
|      | 2          | 12.2                | 3            | —                  | —         | —            | 0                      |

even at 12.2 m. The most common parasites of the nymphal and adult stages of Auchenorrhyncha are the strepsipteran *Elenchus tenuicornis* (Kirby) on Delphacidae, many species of Dryinidae (Hymenoptera) on Delphacidae and Cicadellidae and species of Pipunculidae (Diptera) on delphacids, cicadellids, cercopids and cixiids.

Parasitized individuals were readily detected in the trap catches, since the Strepsiptera and Dryinidae protrude from their hosts and all three sets of parasites tend to give rise to 'intersexes'.

The incidence of parasitized individuals of *Javesella pellucida* in the trap catches is given in Table 10. Catches in 1960 and 1962, i.e. in the years prior to this study, are also included. It is probable that the recorded incidence of the Strepsiptera is accurate, but that of the Dryinidae and Pipunculidae is an underestimate, since it is difficult to detect

young parasitic larvae in the leafhoppers preserved in alcohol. The percentage of the flying *Javesella* of the first generation parasitized by *Elenchus* was 4.2, that by Dryinidae 1.2 and that by Pipunculidae 0.2.

In laboratory tests, the macropterous delphacids parasitized by Strepsiptera flew until the males of *Elenchus* pupated and the females were almost fully grown, delphacids and cicadellids parasitized by Dryinidae and Pipunculidae flew actively when the internal parasites were small, but lost their flight ability when the parasitic larvae reached their full size.

## DISCUSSION

Dispersal by flight of insects is an integral part of their population dynamics (Johnson 1969). Where the exodus by flight from the breeding site is related to density, as in the broom psyllid, *Arytaina spartii* (Guérin-Méneville) (Watmough 1968; Dempster 1968) and in the broom mirid, *Orthotylus virescens* (Douglas & Scott; Waloff & Bakker 1963), density must be considered along with the other processes that not only alter, but regulate populations of insects.

In Auchenorrhyncha, widespread and diversified dispersal by flight is closely linked with alary polymorphism. Frequently populations of the same species are composed of macropterous individuals capable of colonizing new areas and of brachypters that reproduce within the original breeding sites. Thus, not only parts of ontogeny of individuals are 'set aside' for dispersal, but there is functional differentiation between members of populations. This is a type of division of labour in which there is no apparent co-operation between the morphs and alary polymorphism in the leafhoppers is probably akin to, though less highly evolved than, that in the Aphididae.

Lewis & Taylor (1965) have shown that most of the Hemiptera and Auchenorrhyncha are day-flyers. In their analysis of aerial samples of more than a quarter of a million day-flying insects, Auchenorrhyncha comprised no more than 0.9%. By comparison, Aphididae comprised 32% and Phoridae 30% of the total. The small number of leafhoppers in the aerial traps was not due to scarcity, since they are abundant in grasslands, reaching up to a 100–200/m<sup>2</sup> (Whittaker 1969; Morris 1971; Waloff & Solomon 1973). Perhaps this apparent scarcity reflects both the high proportion of brachypterous individuals or of macropters and submacropters that do not migrate. It is possible that the low numbers of leafhoppers caught in the aerial traps in Britain are also related to weather conditions, since there are indications that the daily catches are affected by temperature (Table 5). Moreover, the weather in the British Isles, in most of the years, enables grass to remain turgid even in the summer months, whereas, there is evidence that in some species of leafhoppers, the high incidence of migratory forms is associated with the wilting or drying state of their food plants. Thus, Rose (1972b) found greater numbers of short-bodied migratory forms of three species of *Cicadulina* in perennial grasses than in irrigated Kikuyu grass. Similarly, Kisimoto (1965) considers that the seasonal fluctuations in the numbers of macropters of *Nilaparvata lugens* within field populations, are related not only to crowding, photoperiod and other environmental conditions, but also to the stage of growth of its food plant. In *N. lugens*, the greatest numbers of migrants occurred in the autumn generations and it may be relevant that in the present observations, the proportions of macropterous *Javesella pellucida* were consistently greater in the second generations (Table 8). Although Nuortova (1962) points out, that the mass migratory flight of this species is commonly the first flight after emergence and that it takes place

irrespective of the condition of the food plant, he is probably referring to the thresholds of stimuli for 'take off' and not to the developmental thresholds that may be responsible for the production of the two morphs. May (1971) in experiments on *Stenocranus minutus*, suggested that the production of the macropterous, migratory forms was associated with the interaction of density of nymphs with the state of grass on which they were reared. In many species of the Aphididae, besides density-induced interference which seems to be primarily responsible for the switch from aptera to alate production, many other factors including the state of the host plant may enhance this process (Hughes 1963; Lees 1966, Way 1968, van Emden *et al.* 1969).

The relatively low numbers of Auchenorrhyncha in the air in this country is a local phenomenon, since vast numbers of these vectors of plant diseases (e.g. *Macrostoteles fascifrons* Stål, *Curculifer tenellus* (Baker) and *Empoasca fabae* (Harris) are known to migrate over long distances in North America. These long-range movements, which have been correlated with synoptic meteorology have been discussed by Johnson (1969) and De Long (1971). Moreover, migrations of leafhoppers may occur at different altitudes and Glick (1939) found them at almost every height from 61 to 4267 m.

One-third of all the species of British Auchenorrhyncha were caught in the Silwood traps, but numbers of tree-dwellers were low. This supports Southwood (1962) who suggests that migration occurs most often amongst insects that occupy more temporary habitats. Also, up to 50% of the annual catches included only *Macrostoteles sexnotatus*, *M. laevis* and *Javesella pellucida*, although locally they were not the most abundant leafhoppers in the field. The catches in aerial traps may be related to the considerable power of dispersal of these leafhoppers, which readily arrive to colonize field crops.

Most leafhoppers migrated while they were still immature and did not return to their original habitat. Johnson (1969) and Dingle (1972) emphasize that the development of the reproductive system is minimized while that of the flight system is maximized during migratory flight.

In most species examined readiness to fly was inhibited by maturation. Whether the ability to disperse by flight is also associated with autolysis of flight muscles as in *Sitona* (Jackson 1933) and in Corixidae (Young 1965a, b) is not known. In the bivoltine species dispersal by flight may occur equally in both generations, or with a smaller proportion or absence in the second generation.

Dispersal by flight in leafhoppers is dependent on alary polymorphism which is widespread amongst species living in ground vegetation, but not in tree dwellers. Clearly defined macroptery and brachyptery exists in many Delphacidae and among the cica-dellids examined in *Doratura stylata* and *Ulopa reticulata*. Brachyptery is a synonym for the numerous morphological changes that accompany the shortening of wing length, since there are simultaneous alterations in the skeletal structure of the thorax, and in flight muscles and physiological changes which find expression in higher fecundity (Kisimoto 1965; May 1971).

Much has been said about the evolution of migration and of the behavioural and physiological processes that accompany dispersal by flight (Kennedy 1961; Southwood 1962; Johnson 1969), but it is arguable that the evolution of brachypterous morphs in the Pterygota is as striking and must have been subject to great selective pressure.

In Auchenorrhyncha, differentiation between flyers, including the migratory forms and non-flyers, has been achieved by a variety of means. Various degrees of alary polymorphism are widespread throughout the Insecta, particularly in the qualitatively different forms in locusts (e.g. Uvarov 1961). Among the Hemiptera, long-winged 'good' and

'poor' flyers in the milkweed bug, *Oncopeltus fasciatus* (Dallas) have been identified by Dingle (1965, 1966, 1968), who related the proportions in populations of these behavioural morphs to photoperiodism. Similarly Shaw (1967, 1968) demonstrated differences in flight performance and even absence of flight in the alatae of *Aphis fabae* (Scop.). It is probable that the same phenomenon exists in leafhoppers, e.g. in *Psammotettix confinis*. Moreover, there are members of species which are usually long-winged with some individuals that have extra long wings in proportion to their body length, i.e. submacropters and macropters. All can fly, but the submacropters for shorter distances. Submacroptery may be achieved in two ways, i.e. by shortening the wing length in proportion to the body length, as in *Stenocranus minutus* (May 1971), or by increasing the body length, the wing length in the two morphs remaining relatively constant, as in the *Cicadulina* species (Rose 1972b). The same alterations in the proportions of wing to body length also occurs in ontogeny of female adults of many species, e.g. *Arthaldeus pascuellus*, *Elymana sulphurella*, *Diplocolenus abdominalis* where in immature females the wings extend beyond the abdomen, and mature ones the distended abdomens project beyond the wings. It seems probable that maturation does not only inhibit flight physiologically, but that mature females also become less 'flight-worthy' mechanically.

There are other species of leafhoppers which do not show fully developed brachyptery, the fore wings of non-flyers being only slightly shorter than in flyers but the hind-wings showing a much greater reduction in length. The ratio of lengths of the fore- and hind-wings in *Errastunus ocellaris* determines whether the individuals are able to fly, or only to hop (Table 7). A similar differentiation in lengths of the fore- and hind-wings occurs in *Arthaldeus pascuellus*, but whereas non-flyers form the bulk of field populations or *Errastunus*, they are relatively rare in *Arthaldeus*.

In many species the sexes flew in approximately equal numbers, but in those where macroptery is rare, as in *Doratura stylata* and *Ulopa reticulata*, the only individuals seen with fully developed wings, were all females. It is not difficult to visualize why an excess of long-winged females are produced when macroptery is rare, but the excess of flying males over females of *Cixius pilosus* and of *Psammotettix confinis* (Table 9), needs a further explanation.

Den Boer (1968) formulated a concept of stabilization of animal species by phenotypic variation, later he (Den Boer 1970) applied this concept to the differentiation of carabid populations into alary morphs. Whether alary polymorphism in leafhoppers is genetically fixed is not known. Rose (1972b) considers inheritance of flight ability in the *Cicadulina* spp. suggesting that progeny of non-flyers are mostly non-flyers, those of flyers mainly flyers. Wigglesworth (1962) presented a hypothesis that 'all characters are the product of chromosome constitution and that therefore in a very broad sense all of them are of genetic origin'. He emphasized that although the changes such as those between brachyptery and macroptery of some species may be of genetic origin, they may also be subject to environmental influences.

Differentiation of insect populations into 'good', 'poor' and non-flyers suggests that the switch-mechanisms involved are labile, and that selective pressure must have been operating in opposite directions producing the more sedentary brachypters and more active migratory macropters in the same populations, i.e. by 'spreading of risk' (Den Boer 1968).

Finally, the fact that parasitized leafhoppers are active throughout at least a part of their flight period is interesting, since in colonization of new breeding sites the host populations will transfer some of their regulatory mechanisms with them. This may be

fairly widespread and has been recorded in Miridae that live on broom (Waloff & Bakker 1963).

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### SUMMARY

(1) One-third of the total of British species of Auchenorrhyncha have been identified in aerial traps at Silwood.

(2) The numbers of leafhoppers in annual catches in traps are small compared with those of other insects and about half of them are composed of *Macrosteles sexnotatus*, *M. laevis* and *Javesella pellucida*, which are known vectors of plant diseases.

(3) Patterns of dispersal have been examined in several species and related to voltinism and to the seasonal incidence of adults.

(4) Ten per cent of the Cicadellidae in aerial traps were tree-dwellers; this may be related to permanency of their habitats. Also, tree-dwellers occurred in greater numbers in higher than lower traps, whereas the reverse was true of the grassland species. This indicates differences in dispersal patterns of leafhoppers from different habitats.

(5) Many species show alary polymorphism. (a) Some exhibit extreme brachyptery and macroptery, the long-winged, migratory females showing delayed maturation. (b) In another group, ability to fly was linked with the ratio of lengths of fore- and hind-wings. Flyers and non-flyers were distinguished by laboratory tests. (c) In a third group all individuals were macropterous, but some had extra long wings and were the only morphs caught in aerial traps.

(6) Most, or all species dispersed when they were immature. In many species males and females dispersed in equal numbers. In those where macroptery was rare, the long-winged individuals were all females. In a few species greater numbers of males than females were caught in aerial traps.

(7) Parasitized leafhoppers dispersed by flight, at least while the internal parasitic larvae were still small. Thus in invading and colonizing new breeding sites, some regulatory mechanisms of leafhopper populations were transmitted together with the host species.

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