THE HEMIPTERA AND COLEOPTERA OF STINGING NETTLE (*URTICA DIOICA* L.) IN EAST ANGLIA

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Stinging nettle (*Urtica dioica* L.) is a very widespread and abundant plant in Britain. Around buildings and in agricultural grassland it is usually considered an undesirable weed because it forms dense stands, spread by rhizomes and is difficult to eradicate. It can apparently persist for long periods on sites of human habitation and has been associated with ancient earthworks and the sites of mediaeval hearths (Greig-Smith 1948; Beresford 1971, p. 62). In the past it enjoyed a rather higher status as a source of fibres for textiles and as a basis for various culinary recipes (Grigson 1958; Masefield *et al.* 1969). An account roll of Ely's manor at Lakenheath for 1429 quotes 'And for 8d for nettles in the garden sold this year'. It has also long been known as a food plant for a large and diverse fauna and is commended by lepidopterists like Newman (1967) for the vanessids dependent on it.

The biology and ecology of *Urtica* in Britain have been described by Greig-Smith (1948). With minor revisions to O. W. Richards' list of insects in that paper, twenty-seven species may be considered more or less confined to nettle, plus a further nineteen oligophagous species and a few predators closely associated with it. The fauna has not been the subject of any intensive study, perhaps because nettle is considered such a common-place plant. As a characteristic member of field margins and waysides, however, it makes a significant contribution to the faunal diversity and biomass of intensively farmed agricultural areas. The diversity of the fauna, moreover, raises questions of how and why there is such full exploitation of this host plant and its widespread occurrence makes it possible to study this in most parts of the country and to compare different habitats and soil types. Because nettle establishes itself fairly quickly under favourable conditions and rapidly achieves its full performance, it is a useful experimental plant with great advantages over annuals or slower growing woody plants.

The present work was done to elucidate the life cycles of the commoner elements of the fauna of nettle and some of the more important habitat factors determining their distribution. This was considered a necessary background to studies on insect dispersal and host colonization in relation to factors such as isolation and the effects of sprays, all of which are particularly relevant to wildlife conservation in lowland Britain. These more applied aspects will be dealt with in subsequent papers. Because of the different sampling techniques required for different groups of insects, this paper is devoted to the Hemiptera (except aphids) and the Coleoptera. A few of the less common monophagous species are not covered, but several polyphagous species which were found to be locally common and important components of the fauna have been included. Nomenclature follows Kloet & Hincks (1964) for the Hemiptera and Kloet & Hincks (1945) for other groups.

GROWTH CHARACTERISTICS OF STINGING NETTLE

Phenology

During 1969 two 'standard' sites were visited at roughly weekly intervals between early April and early November and six other sites less frequently or for only part of this period. All were on clay soils in arable or grassland habitats within about 10 km of Huntingdon. Phenological observations were made to supplement the major features described by Greig-Smith (1948). When observations started the nettle was about 10 cm high. At the end of April it was around 20 cm high but then the growth rate increased and by the end of the third week in May the nettle reached 80 cm. During June the plants came into flower and by the end of this month they achieved their maximum height of 120–150 cm. The male flowers were shed early in July and ripe seed during July and August. By mid-July many of the lower leaves had also been shed, so that the nettle patches took on a more open appearance. Secondary growth of lateral shoots with many small leaves took place during August and by the beginning of September the top 20 cm of the plants had gained a very bushy appearance. This occurred more at some sites than others and the growth of lateral shoots was sometimes confined to stems which had fallen over. The only change during September and October was the gradual loss of old leaves leading to a more open appearance at most sites.

One of the two standard sites (Alconbury) was visited regularly again during 1970 and much the same pattern was observed. Owing to a prolonged hot dry spell for several weeks from the middle of May, some wilting was noted early in June and male flowers were shed nearly a fortnight earlier than in 1969. Most of the nettle did not grow above 100 cm and during July large areas were blown over and pulled down by bellbine (*Calystegia sepium* L.) which encouraged fresh growth from the lower parts of the stems during August. This second flush reached about 75 cm, produced more flowers and retained its lush appearance until November.

A patch of nettle growing on peat was visited during 1971 and this again showed similar features. Growth of lateral shoots occurred over a greater proportion of the stems and even the main stems produced some new growth in August. Falling seed was noted on 26 August at the same time as new flowers were being produced on the terminal and lateral secondary growth. In general, it was noted that nettle which is cut down during June or July produces vigorous new growth and flowers 4–6 weeks later. This does not grow as tall as the uncut nettle and by retaining the large primary leaves later in the year it often shows up as a denser stand. Repeated cutting weakens the plants and is a recommended measure for controlling nettles.

Variability between contrasting sites

Visits were made to nineteen sites during 1970 which were chosen to represent clear-cut differences with respect to soil type and shade. Eight of the sites were on clay soils in central and north-west Huntingdonshire, six were on peat in the fenland district of Huntingdonshire and five were on sandy soils in the Suffolk breckland. On each soil type, pairs of shaded, woodland sites and open, unshaded sites were chosen within 4–5 km of each other. One breckland site was unpaired. Although shaded from above, it was open to oblique light from the east and west and was therefore somewhat intermediate.

On 21 and 22 July, estimates were made of the density of plant stems per unit area, height of plants and size of fully expanded primary leaves. Fig. 1(a) illustrates the scatter diagram obtained when median height is plotted against leaf length. The median heights

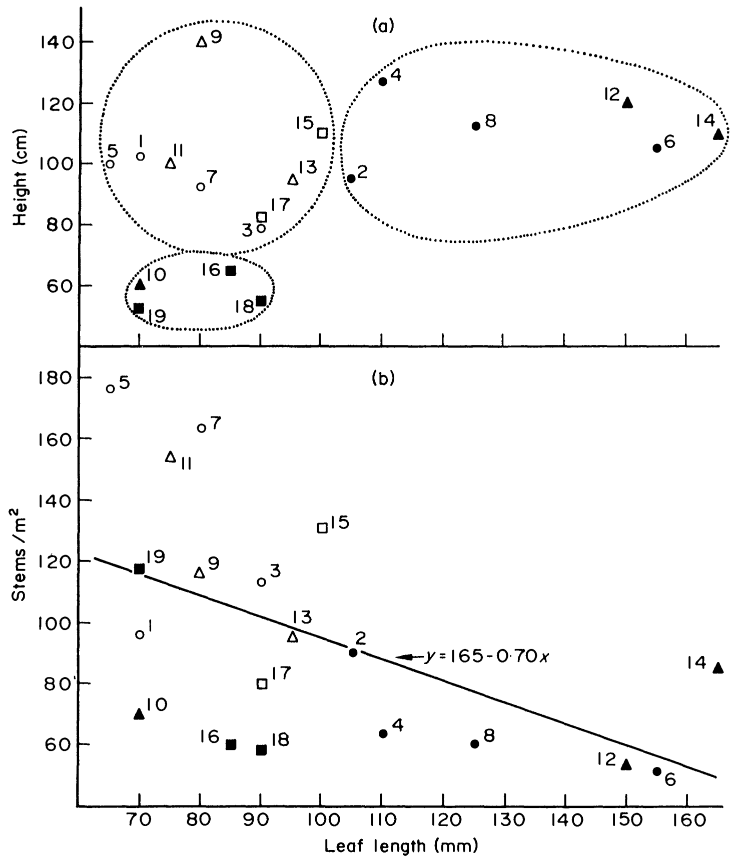

FIG. 1. Scatter diagrams for nineteen nettle sites based on growth characteristics. (a) Nettle height plotted against leaf length. (b) Density of stems per m^2 plotted against leaf length. Pairs of sites differing with respect to shade are numbered 1 and 2, 3 and 4, etc. Circles represent clay soils, triangles peat soils and squares sandy soils. The solid symbols represent shaded sites.

ranged from 52–140 cm and leaf lengths from 65–165 mm. The sites are classified by symbols into six categories according to soil type and situation and can be loosely grouped into three clusters. One cluster included all the sites in open situations with medium to tall plants and small-to-medium-sized leaves, while the shaded sites fell into two distinct groups with respect to these measurements. Fig. 1(b) shows the scatter diagram for mean stem density plotted against leaf size. Stem density varied by a factor of over three. As well as a significant difference between pairs of shaded and open sites with respect to density ($P<0{\cdot}005$), there was an overall inverse relationship between density and leaf size (correlation coefficient $r = 0{\cdot}55$; $P<0{\cdot}02$). Soil type did not show up as an important factor in the grouping of sites, but it is clearly a multifactorial situation. Soil moisture and nutrient status (nitrate and phosphate) were not measured, but these are important factors in growth (Greig-Smith 1948; Piggot & Taylor 1964) and may have accounted for many of the differences. Flower and seed production was also very variable but was not assessed quantitatively. The intermediate status of the unpaired site, number 19, is seen by comparing its position in the two diagrams. The relative condition of the Alconbury site (number 1) used for the intensive faunal studies, may also be noted.

Table 1. *Chemical analyses of nettle leaves from different habitats (means ± twice standard errors expressed in terms of oven-dry weights)*

Habitat category	% total N	Extractable N mg/100 g	% soluble carbohydrate	% soluble tannin
Shaded	3·97 ± 0·25	1·06 ± 0·10	7·38 ± 0·88	0·72 ± 0·11
Open	3·88 ± 0·25	1·33 ± 0·23	8·51 ± 0·90	0·79 ± 0·11
Clay	3·64 ± 0·20	1·30 ± 0·21	8·34 ± 1·05	0·79 ± 0·10
Peat	3·98 ± 0·32	1·23 ± 0·31	7·48 ± 1·26	0·73 ± 0·18
Sand	4·16 ± 0·31	1·06 ± 0·12	7·66 ± 0·89	0·75 ± 0·16

Chemical analyses were carried out on samples of mature primary leaves collected in July after these had been dried at 35° C and ground in a mill. Results (Table 1) were corrected to an oven-dry basis after making moisture determinations on sub-samples. When classified according to soil type, the sites showed no significant differences in nitrogen, soluble-carbohydrate or soluble-tannin figures. However, open sites had noticeably greater amounts of soluble carbohydrate compared with shaded ones. Taking the plots in pairs the mean difference was 1·26% and using a one-tailed *t*-test, on the assumption that any difference due to sunlight would be in this direction, this is significant at the 5% level. A difference in soluble tannins, though small, was also significant at this level when analysed in the same way, but a one-tailed test is less obviously applicable in this instance. Individual sugars and various secondary compounds like tannins have been associated with insect feeding preferences, a subject which is discussed by Thorsteinson (1960).

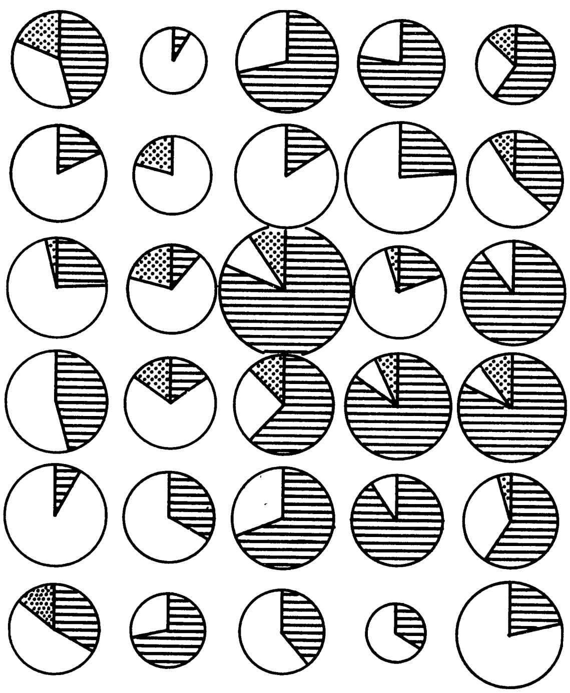

FIG. 2. Variation in density of stems per $\frac{1}{4}$ m^2 quadrat and in the proportions of male stems (hatched) and female stems (white) over an area of $2\frac{1}{2} \times 3$ m. Stems without male or female flowers are shown stippled.

Variability within a nettle bed

In many places nettles are interspersed with other plants like *Lamium album* L., but even in pure stands there is intrinsic variability owing to its dioecious nature and to competition between rhizomes and stems. One such extensive nettle bed on peat near Holme Fen was examined on 1 September 1971. It had been cut towards the end of June and was now starting to set seed on female plants. An area of $3 \times 2\frac{1}{2}$ m was surveyed using a $\frac{1}{2} \times \frac{1}{2}$ m quadrat and counting the number of male and female stems in each. The quadrat fitted on to and was moved along a 2·6-m aluminium bar which was supported at each end by vertical rods pushed into the ground. The whole frame was moved forward $\frac{1}{2}$ m at a time after each row had been completed.

The total number of stems per quadrat varied between nine and forty-four with a mean and standard deviation of $22{\cdot}6 \pm 6{\cdot}6$. The spatial variation in stem density is shown by the size of the circles in Fig. 2. If adjacent quadrats are combined in fours, the density can be given as 70–116 stems/m^2. The proportions of male and female flowering stems are shown in Fig. 2 by sectors, with sometimes a third category of stems which lacked flowers and could not be assigned to either sex. There was clearly an intimate mixture of both sexes in this patch and the overall proportion of male to female stems was 1 : 1·1. However, there was marked local patchiness of the sexes, reflecting growth centres for individual plants, which was relatively greater than that for the two combined. This is shown quantitatively by expressing standard deviations for quadrat counts of male, female and total stems as percentages of the means, viz. 80, 60 and 39% respectively. Sampling for insects which favour one sex, as in the case of *Brachypterus* spp., must take this into account.

Occasionally plants were found in which the upper part of the inflorescence bore female flowers and the lower part male flowers in a slightly more advanced condition. At one site on the edge of Monks Wood such a clone extended over an area of about 1 m^2.

INSECT SAMPLING METHODS

The Dietrick (1961) suction sampler was used to collect Hemiptera and Coleoptera and the following procedure was adopted. The 1 ft^2 (0·09 m^2) sampling head was placed over a group of nettle stems for about 5 s and shaken gently to help dislodge and catch the insects there. When the nettles were less than about 50 cm tall, the sampler was placed on the ground but was raised progressively as the nettles grew with the result that the lower and generally leafless stems were not within the sampler. Two sets of ten such sample units were taken at each site. The distance between sample units depended on the extent of the nettle bed but care was taken not to disturb an area before it was sampled. The nylon mesh bags from the suction sampler were put into 1-litre plastic jars and taken to the laboratory. There the insects were killed with ethyl acetate, brushed from the leaves and larger plant debris over a sieve and picked out into vials of 70% alcohol.

Variation between suction samples

As assessment of sampling variation was made at one site on 7 August 1970 by taking ten suction samples each consisting of ten subsamples in the usual way. The number of nettle stems enclosed by the sampling head was counted in a proportion of the subsamples the mean being 13·8 (standard deviation 3·8).

Twenty-four species of insect associated with nettle were obtained altogether in the ten samples (*c.* 9·3 m^2) and individual samples contained 14–19 species. Table 2 gives the

Table 2. *Frequency of occurrence and density of Hemiptera and Coleoptera species in suction samples from nettle at Easton, 7 August* 1970

Species	Numbers of samples (out of 10)	Numbers per sample (0·9 m²) mean ± standard deviation Adults	Larvae
Trioza urticae (L.)	10	67·6 ± 24·4	0·8 ± 1·3
Liocoris tripustulatus (Fab.)	10	47·1 ± 15·6	44·4 ± 19·3
Eupteryx urticae (Fab.)	10	44·4 ± 12·4 }	4·6 ± 2·6
E. aurata (L.)	10	26·9 ± 11·9 }	
Plagiognathus arbustorum (Fab.)	10	23·3 ± 5·6	
Anthocoris nemorum (L.)	10	13·8 ± 5·6	8·4 ± 6·7
Scolopostethus thomsoni Reut.	10	7·7 ± 3·4	10·5 ± 7·7
Ceuthorhynchus pollinarius (Forst.)	10	5·8 ± 3·9	
Brachypterus urticae (Fab.)	9	6·4 ± 3·9	
Cidnorhinus quadrimaculatus (L.)	9	2·7 ± 1·8	
Lygocoris spinolai (Meyer-Dür)	9	2·6 ± 2·0	
L. pabulinus (L.)	9		3·8 ± 2·6
Orthonotus rufifrons (Fallén)	8	4·4 ± 3·8	
Heterogaster urticae (Fab.)	7	0·5 ± 1·1	3·9 ± 7·9
Orthotylus ochrotrichus Fieb.	5	1·0	
Crepidodera ferruginea (Scop.)	5	1·0	
Heterotoma planicornis (Pallas)	5	0·7	
Deraeocoris ruber (L.)	3	0·3	
Brachypterus glaber (Steph.)	3	0·3	
Lygus rugulipennis Poppins	2	0·2	
Risophilus atricapillus (L.)	2	0·2	
Calocoris norwegicus (Gmelin)	1	0·3	0·1
Scolopostethus affinis (Schill.)	1	0·1	
Eupteryx cyclops Matsum.	1	0·1	

frequency of occurrence of these species which follows the logarithmic distribution typical of this type of sample (Williams 1964, p. 79). Only four other species are dealt with in this paper, namely *Macrosteles variatus* (Fallén), *Macropsis scutellata* (Bohem.), *Phyllobius pomaceus* Gyll. and *Apion urticarium* (Herbst). These are arranged taxonomically in Table 2.

The number of species which could be expected on this occasion by taking two samples —the usual sampling regime—can be estimated by taking the samples in pairs, i.e. 1 and 2

Table 3. *Aggregated distributions of insects on nettle determined* by comparison of numbers in ten suction samples*

		λ
Heterogaster urticae	Larvae	4·00
Trioza urticae	Adults	2·97
Liocoris tripustulatus	Larvae	2·90
Scolopostethus spp.	Larvae	2·36
Anthocoris nemorum	Larvae	2·30
Eupteryx aurata	Adults	2·30
Liocoris tripustulatus	Adults	2·27
Eupteryx urticae	Adults	1·87
Ceuthorhynchus pollinarius	Adults	1·62
Anthocoris nemorum	Adults	1·51
Eupteryx spp.	Larvae	1·45
Scolopostethus thomsoni	Adults	1·21
Plagiognathus arbustorum	Adults	1·16
Cidnorhinus quadrimaculatus	Adults	1·11

$\lambda > 1{\cdot}28$, significant at 5% level
$\lambda > 1{\cdot}56$, significant at 1% level

* Using the index: λ = standard deviation/$\sqrt{\text{mean}}$.

together, 3 and 4 together. . . . 9 and 10 together. The mean of these five pairs is 18·2 which is 73% of the number obtained by the more intensive sampling of the area. The estimates of mean density for these species are also shown in Table 2 with standard deviations for the more frequently occurring species. All immature stages are combined under the heading larvae. The most common nettle insects can be several hundred times as abundant as the less common ones and this imposes difficulties for any single sampling technique.

One cause of variation between samples is due to aggregation of adults or larvae. Dense aggregations of *Heterogaster* were frequently seen during 1970; they are also characteristic for larvae of the Lepidoptera *Aglais urticae* (L.) and *Nymphalis io* (L.). This effect is considerably reduced by combining sub-samples, but an estimate of overdispersion in the sample populations can be obtained from the index $\lambda = s/\sqrt{m}$ (where s is the standard deviation and m is the mean) (Debauche 1962). In populations which are distributed at random λ will tend to unity while a higher value denotes a negative binomial or one of the contagious distributions. Significance is tested by $\chi^2 = \lambda^2 (n-1)$ with $n-1$ degrees of freedom (where n is the number of samples). From Table 3 it is clear that suction samples of most species showed overdispersed distributions and that this applied especially to larvae, notably of *Liocoris*, *Scolopostethus* and *Anthocoris*. Such frequency distributions can result from biological causes other than family aggregates, so no single interpretation of Table 3 can be assumed.

Efficiency of suction sampling

Assessments were made of sampling efficiency for the suction sampler by several comparisons with hand collecting. The first comparison was made with the suction samples described above. In this a hundred randomly chosen nettle stems were cut with secateurs and placed in polythene bags in groups of ten. After fumigation with ethyl acetate these were carefully searched.

Fewer species and fewer individuals of most species were actually obtained by the cutting method, but this was because of the smaller sample size. The only addition to the fauna was a single adult specimen of *Lygocoris pabulinus* (L.)—in suction samples only larvae were present. Table 4 compares the mean numbers of adults and larvae of the more common species obtained by the two methods. The third column gives the difference between the weighted means (using the scale factor 13·8 referred to above) arranged in sequence. Significance was tested by the statistic

$$d = (\bar{x}-\bar{y}) \Big/ \sqrt{\frac{s_x^2 - s_y^2}{n}}$$

which is distributed as t with 9 to 17 degrees of freedom (where s_x^2 and s_y^2 are the variances of the weighted variables) (Bailey 1959, p. 50).

More direct assessments were made by cutting and searching groups of nettle stems which had actually been sampled with the suction apparatus. For this purpose five or ten suction units were taken individually at three sites and compared with the cut-stem samples taken immediately afterwards (Table 5). Here asterisks are used to denote instances where the suction method obtained less than 50% and 25% of the total populations present (ignoring populations below ten).

Evidently the suction method is most efficient for insects which are very active or are readily dislodged like the weevils. Adult *Eupteryx* are active fliers, as are *Trioza* and some Miridae on hot days. Callow *Trioza* are much less active; they were common in the

Table 4. *Comparison between suction sampling and cut-stem sampling for insect populations on nettle (means of ten samples in each case and difference between means after multiplying cut-stem values by scale factor)*

Species	Stage	Suction sample (no./0·9 m²)	Cut stem sample (no./10 stems)	Suction (cut stem × 13·8)	
Eupteryx spp.	Adults	71·3	1·0	57·5	**
Brachypterus spp.	Adults	6·7	0·2	3·9	NS
Scolopostethus spp.	Larvae	10·5	0·5	3·6	NS
S. thomsoni	Adults	7·7	0·3	3·6	NS
Heteroptera (nine spp.)	Adults	9·3	0·5	2·4	NS
Cidnorhinus quadrimaculatus	Adults	2·7	0·1	1·3	NS
Ceuthorhynchus pollinarius	Adults	5·8	0·4	0·3	NS
Lygocoris pabulinus	Larvae	3·8	0·5	−3·1	NS
Plagiognathus arbustorum	Adults	23·3	2·8	−15·3	**
Anthocoris nemorum	Adults	13·8	2·6	−22·1	*
Eupteryx spp.	Larvae	4·6	2·3	−27·1	**
Liocoris tripustulatus	Adults	47·1	5·8	−32·9	*
Trioza urticae	Adults	67·6	7·4	−34·5	*
Anthocoris nemorum	Larvae	8·4	3·6	−39·3	not tested
Liocoris tripustulatus	Larvae	44·4	11·6	−115·7	not tested
Trioza urticae	Larvae	1·3	10·4	−142·2	not tested

NS, Not significant; *, significant at 5% level; **, significant at 1% level.

Table 5. *Numbers of insects obtained from nettle in suction samples and by subsequent examination of cut stems (total numbers are obtained from the sum of the two methods of collection)*

		Monks Wood, 15 July 1971 (5)		Easton, 20 July 1971 (5)		Holme Fen, 5 Oct. 1971 (10)	
		Suction	Cut	Suction	Cut	Suction	Cut
Anthocoris nemorum	Adults	11*	16	5*	14	37	8
	Larvae	7*	20	1†	22	1	–
Liocoris tripustulatus	Adults	–	–	1	–	37	6
	Larvae	–	3	2	1	18	4
Plagiognathus arbustorum	Adults	27	9	9	1	–	–
	Larvae	3	–	–	–	–	–
Other Heteroptera	Adults	2	–	1	–	1	–
	Larvae	4	5	–	2	2	–
Trioza urticae	Adults	1783	401	674	112	–	–
	Larvae	28*	71	–	2	10†	414
Eupteryx urticae	Adults	43	6	76	14	105	–
E. aurata	Adults	1	–	4	4	33	1
Eupteryx spp.	Larvae	–	–	–	–	7	1
Cidnorhinus quadrimaculatus	Adults	2	1	1	–	16	–
Ceuthorhynchus pollinarius	Adults	–	1	–	–	2	–
Apion urticarium	Adults	–	–	–	–	1	–

Site: Monks Wood, Easton, Holme Fen; Date (number of samples); Method of collection.

* Less than 50% of total number obtained by suction sampling.
† Less than 25% of total number obtained by suction sampling.

Monks Wood sample (Table 5) where 18% remained on the plants. *Anthocoris nemorum* (L.) is particularly under-sampled by the suction method. Its habit of entering leaves rolled up by caterpillars provides good protection from any sampling technique other than searching. The larvae of several species are also poorly sampled. *Trioza* is an extreme example as the larvae are usually found adhering to the undersides of leaves or to the grooves in the stems even after fumigation with ethyl acetate. Dense foliage is also likely to hinder efficient capture of insects but measurements of this factor were not made.

LIFE HISTORIES AND HABITATS OF HEMIPTERA AND COLEOPTERA ASSOCIATED WITH NETTLE IN EAST ANGLIA

Methods

A reconnaissance was made during 1969 at eight sites referred to earlier in the description of nettle phenology. The seasonal occurrence of insect species in suction samples was used as a basis for an intensive sampling programme at Alconbury, near Huntingdon, in 1970 and for a survey of nineteen contrasting sites. A few samples were also taken during winter months to determine the overwintering condition of species. The results are all based on the totals of twenty sampling units (two samples of ten units each). Occasionally samples of cut stems were examined for specific purposes. Cultures of *Ceuthorhynchus pollinarius* were kept to elucidate certain aspects of the life cycle.

The Alconbury site was an extensive bed of nettle about 120 m long by 10 m wide with a stream on the south side and an arable field on the north. A few tall willows (*Salix alba* L.) on the far side of the stream cast patches of light shade over the plot and a broken hawthorn hedge along the edge of the field gave some protection from winds. Weekly samples were taken from 21 April to 2 December. Twenty-three species were studied of which eight are considered to be more or less restricted to the Urticaceae. Except for *Brachypterus* spp., all adults were sexed and females were dissected for eggs. Heteroptera larvae were identified and counted using Southwood & Scudder's (1956) key, but the different instars were not usually separated. Other species taken, like *Orius minutus* L. and *Propylea 14-punctata* (L.), were considered to be outside the scope of this study though they may be important predators in some contexts. Aphids were also omitted since they require special sampling methods; *Microlophium evansi* (Theob.) was abundant in 1971.

The nineteen nettle sites visited were those whose growth and chemical properties were described earlier. They were divisible into six categories on the basis of three soil types and whether or not they were heavily shaded. Suction samples were taken on 16–17 June, 21–22 July, 25–26 August and 20–21 October, these dates being selected so as to cover the periods of peak adult populations for as many species as possible (see Fig. 3).

Results

The results of these series of samples are summarized in Figs. 3–5 and Tables 6–8 and are analysed together for each species in turn. The occurrence of nine out of the twenty nettle insects taken during the pilot survey is shown in Fig. 3. The sampling dates at roughly weekly intervals are shown along the horizontal axis with the number of sites visited in that week. Circle sizes indicate the proportion of sites visited in which adults of a species were present. The extraction of *Trioza* and *Eupteryx* spp. from samples was suspended at some sites during part of July with the arrival of the bulk of adult mirids; these gaps are represented by NE. Within the three groups Heteroptera, Homoptera and

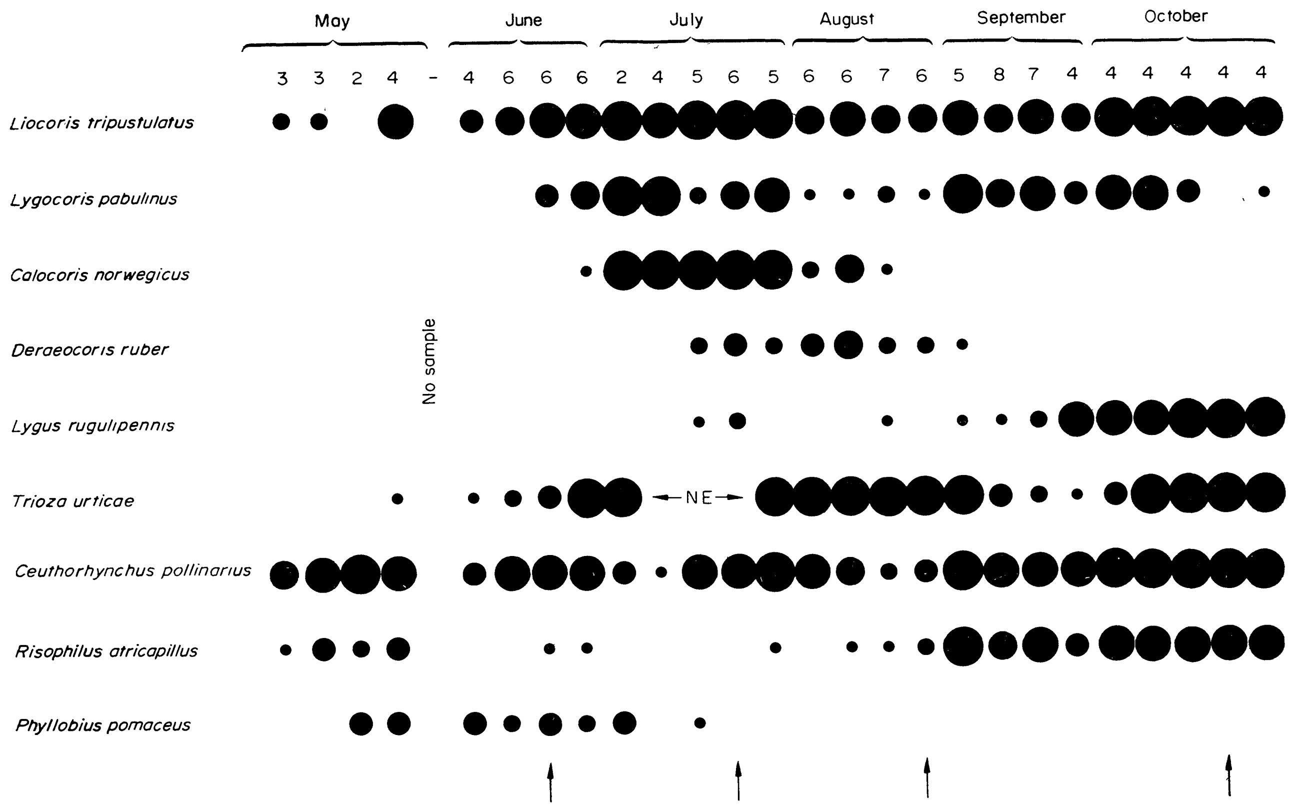

FIG. 3. Representatives of insects associated with nettle selected to show the main phenological variations in adult occurrence in 1969. The number of sites sampled each week is shown at the top, presence and absence being represented on a six point scale. NE = not extracted. Arrows at the bottom indicate sampling dates chosen for comparison of sites in 1970.

Coleoptera the species have been arranged so as to display the sequence of appearance of adults.

The population fluctuations for fifteen species at Alconbury in 1970 are illustrated in Figs. 4 and 5. Total adult numbers and total egg-bearing females are shown above the lines and larval counts in the Heteroptera below the line. Different vertical scales are used depending on the relative abundance of each species. In the case of *Eupteryx urticae* and of *Trioza urticae* the scales have to be adjusted between generations. The species are again arranged so as to reveal the different phenological patterns.

The mild winter of 1971/72 made it easier than usual to collect large numbers of insects from nettle because the aerial parts had not all been killed off by frosts. Table 6 gives the results of samples from two sites taken in January and February.

Comparisons between the six contrasting habitat types are given for twenty-seven species in Table 7. The figures give totals over the four sampling occasions and include larvae in the case of the Heteroptera. The number of sites in each category, from two to

Table 6. *Winter samples of nettle insects (totals of twenty suction sample units)*

	17–19 January		24 February	
	Brampton	Monks Wood	Brampton	Monks Wood
Scolopostethus thomsoni	5	–	1	4
S. affinis	9 (1 larva)	2 (2 larvae)	3	1 (1 larva)
Anthocoris nemorum	6	1	–	1
Liocoris tripustulatus	3	–	3	–
Trioza urticae	779	215+1 larva	121	31
% females having eggs	0*	0†	87	93
Eupteryx urticae	6	–	1	–
Risophilus atricapillus	3	1	1	–
Cidnorhinus quadrimaculatus	3	1	9	2
Ceuthorhynchus pollinarius	–	–	1	–

* In sample of 150 females examined.
† In sample of fifty females.

four, is shown and also an index of mean stem density (see Fig. 1(b) for values at individual sites). Although the density of nettle growth is an integral feature of habitat condition, this index can be used as an approximate factor for assessing the density of insects per plant as distinct from density per unit sampling area. Table 7 also gives the number of sites in which each species occurred, the overall proportions of adults taken on the four sampling occasions and the proportions of larvae in the case of the Hemiptera.

Heteroptera

Scolopostethus thomsoni and *S. affinis* (Lygaeidae) have been studied by Eyles (1963a, 1964) who showed that both species have a single annual generation. Eggs are laid on the inflorescence of nettle and some other plants and he claimed that both species needed unripe seed for growth of young instars and for maturation and egg laying in adults. However, the large numbers of third to fifth instar larvae and adults sometimes found at Alconbury in April suggest that other food is used at this time of year. Both species, but especially *S. affinis*, occur commonly on the ground and hence are probably not well sampled by the suction method, or by examining cut stems. The Alconbury data (Fig. 4) illustrates the long oviposition period from June to September for *S. thomsoni* which is

Table 7. *Total numbers from suction catches taken on four occasions from nineteen sites divided among six habitat categories (Heteroptera figures include larvae)*

	Habitat category									
	Clay		Peat		Sand					
	Shaded	Open	Shaded	Open	Shaded	Open				
	Number of sites in each									
	4	4	3	3	3	2	Total no. of sites	% adults	% of totals caught in June:July:Aug:Oct adults	larvae
	Relative density of stems									
	1·1	2·3	1·3	2·1	1·0	1·9				
HEMIPTERA										
Lygaeidae										
Heterogaster urticae	–	32	–	231	–	331	5	67	3:<1:97:0	0:15:85:0
Scolopostethus thomsoni	48	426	265	418	925	167	19	32	14:10:72:5	<1:17:81:2
S. affinis	2	54	–	16	10	9	8		13:2:84:1	
Cimicidae										
Anthocoris nemorum	352	425	305	250	169	125	19	41	1:16:65:18	23:12:58:7
Miridae										
Deraeocoris ruber	1	52	–	3	–	–	7	11	0:50:50:0	98:0:2:0
Orthonotus rufifrons	27	45	31	–	12	2	12	58	0:94:6:0	98:0:2:0
Plagiognathus arbustorum	38	487	49	255	93	125	17	78	0:79:21:<1	68:31:1:0
Heterotoma planicornis	5	12	8	3	1	2	12	68	0:86:14:0	10:90:0:0
Orthotylus ochrotrichus	120	36	53	12	76	2	18	81	0:100:<1:0	85:15:0:0
Lygus rugulipennis	58	18	21	6	11	16	18	90	0:2:3:95	8:0:77:15

Licoris tripustulatus	37	951	32	272	99	441	19	57	8:21:53:18	2:47:48:3
Lygocoris pabulinus	110	69	34	108	20	19	19	60	44:7:49:0	87:3:10:0
L. spinolai	10	61	16	53	4	38	17	64	4:47:49:0	0:20:80:0
Calocoris norwegicus	18	157	1	39	4	3	13	15	47:53:0:0	96:4:0:0
Cicadellidae										
Macrosteles variatus	42	4	115	80	111	121	14		15:45:29:11	
Eupteryx urticae	1598	2544	1727	2059	2529	1027	19		34:6:23:37	
E. cyclops	6	9	367	539	23	394	15		24:9:33:34	
E. aurata	49	1181	61	1509	73	253	19		17:2:74:7	
Psyllidae										
Trioza urticae	830	1454	735	2388	3010	7393	19		4:13:8:75	
COLEOPTERA										
Carabidae										
Risophilus atricapillus	2	21	1	1	1	1	9		0:0:59:41	
Nitidulidae										
Brachypterus urticae	139	382	346	455	132	439	19		59:28:13:<1	
B. glaber	2	263	–	468	5	115	12		88:11:1:0	
Apionidae										
Apion urticarium	–	2	14	36	1	4	8		7:9:49:35	
Curculionidae										
Cidnorhinus quadrimaculatus	63	166	104	202	147	284	19		37:15:35:13	
Ceuthorhynchus pollinarius	35	54	2	41	17	39	16		17:15:54:14	
Phyllobius pomaceus	–	16	2	2	–	–	6		100:0:0:0	

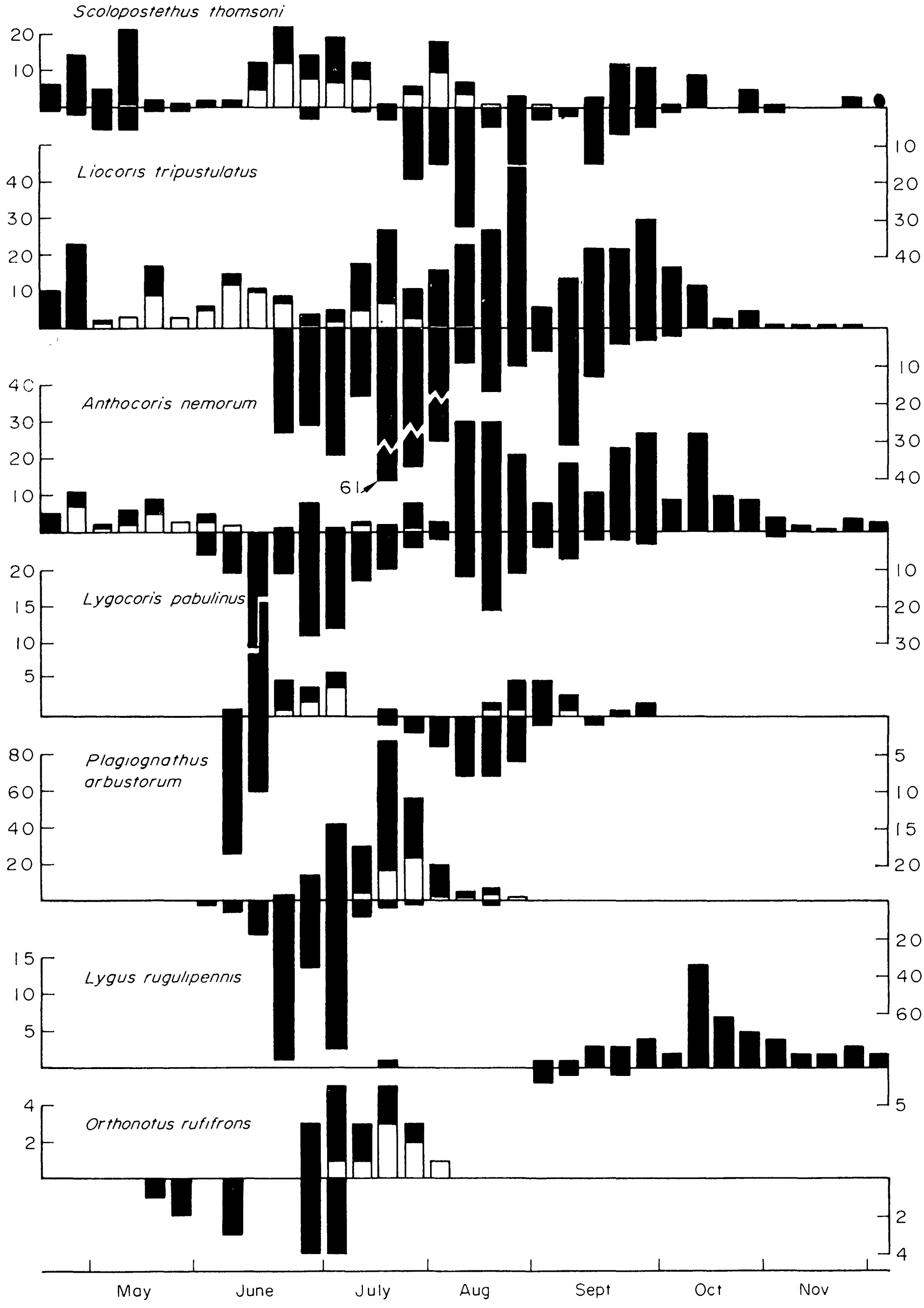

FIG. 4. Seasonal fluctuations in numbers of Heteroptera at the Alconbury site in 1970. Larval catches below the lines, adult catches above. Open columns represent females with eggs.

characteristic of several species of this genus (Southwood & Leston 1959). Adults of *S. affinis* were taken throughout the year from January to December.

Larvae of these two species are separable statistically in the fifth instar by using an index of shape based on ten measurements (Eyles 1963b) but identification of individuals is not reliable and those that were collected were assumed to be predominantly *S. thomsoni*. A few fourth and fifth instar larvae were collected during the winter months (Table 6) as well as April and May establishing the fact that they overwinter as in *S. pictus* (Schilling) (Southwood & Leston 1959).

S. thomsoni was common at all nineteen sites sampled in 1970 though clay woodland sites were less favoured than other habitats. *S. affinis* was probably more common and widespread than the suction samples suggest.

Heterogaster urticae (Lygaeidae) also has a single annual generation with overwintering adults. It is, however, a much more local species in Huntingdonshire and only one specimen was taken at Alconbury in the two years 1969 and 1970. During the survey it was found at five sites, all in sunny situations and mainly on peat and sand. Breeding adults frequently form dense aggregations (Southwood & Leston 1959) and this was seen in the succeeding generation. One sample taken at Brandon, Suffolk, on 22 July contained 2nd, 3rd, 4th and 5th instar larvae with 1, 3, 19 and 5 individuals respectively, while another from Farcet, near Peterborough, taken on 25 August contained 2nd to 5th instar larvae and adults with 1, 3, 21, 85 and 76 individuals respectively. These suggest that egg laying extends over a considerable period but is very localized, thus enabling young larvae to join up with older ones for protection.

Anthocoris nemorum (Cimicidae) is probably one of the most abundant and widespread predators on nettle (Table 7) especially since the suction catches may represent only a half or a third of the actual numbers present (Table 5). This species has been studied in detail by Anderson (1962). Adults overwinter and the two summer generations overlapped to some extent at Alconbury (Fig. 4). 1969 and 1970 were both 'good' summers in south-east England, but in neither year was there clear evidence of a third generation as suggested by Southwood & Scudder (1956) though a fifth instar larva was taken as late as 5 November.

Seven of the species of Heteroptera studied on nettle have very similar life cycles, namely the Miridae *Deraeocoris ruber*, *Orthonotus rufifrons*, *Plagiognathus arbustorum*, *Heterotoma planicornis*, *Orthotylus ochrotrichus*, *Lygocoris spinolai* and *Calocoris norwegicus*. These are all univoltine and overwinter as eggs. Fig. 4 shows the appearance of larvae and adults of *Orthonotus rufifrons* and *Plagiognathus arbustorum* at Alconbury between June and early August; the catches of the other species fell within this range, both in abundance and timing. Apart from *Orthonotus rufifrons* they are found on a range of other plants and their occurrence on nettle does not necessarily represent their overall distribution and abundance. *Heterotoma planicornis* and the predatory *Deraeocoris ruber* were the least common and widespread species in the survey. The most abundant species, *Plagiognathus arbustorum*, favoured open sites as did *Lygocoris spinolai*, while *Orthonotus rufifrons* and *Orthotylus ochrotrichus* favoured shaded ones. Relatively few adults of *Calocoris norwegicus* were obtained in this set of samples.

Liocoris tripustulatus (Miridae) is like *Scolopostethus thomsoni* in having a single, long breeding season and adults that overwinter. Egg-bearing females were found for fifteen consecutive weeks from 4 May onwards. Peak larval numbers at Alconbury occurred towards the end of July followed by a peak of new adults at the end of August. Although numbers at Alconbury did not reach the peak of abundance achieved by *Plagiognathus* *arbustorum* this was one of the most consistently common species here and at other open sites on all soil types. Like many other mirids, *Liocoris* will sometimes feed on aphids.

The mirids *Lygus rugulipennis* and *Lygocoris pabulinus* are both bivoltine but have very different phenological patterns (Fig. 4). Overwintered adults of *Lygus rugulipennis* were not taken on nettle in the spring in 1969 or 1970. The first summer generation was also scarcely represented (Table 7), while the characteristically larger second generation (Southwood & Leston 1959) showed up clearly at Alconbury and at most of the other sites in the October sample. The difficulties of separating members of the *L. pratensis* complex have recently been clarified by Woodroffe (1966). Individuals of *L. wagneri* Rem. or *L. maritimus* Wag. would probably not have been recognized in these samples, but it is unlikely that they occurred in any numbers, if at all.

Lygocoris pabulinus alternates between woody and herbaceous hosts. Late instar larvae of *L. pabulinus* appeared on the Alconbury nettle quite suddenly in June at about the same time as young larvae of the *Deraeocoris–Orthonotus* group; the first sample in Fig. 4 consisted of two fourth instar and twenty-nine fifth instar larvae. Second generation larvae appeared towards the end of July and egg-bearing females of the summer generation left the nettle for woody hosts in September and October. No marked habitat preference was noted in the survey.

Homoptera

The life cycle of *Trioza urticae* (Psyllidae) has been studied by Lal (1934) in Scotland and by Zangheri (1954) in the Italian Apennines. Adults overwinter and, according to Zangheri, there are three generations starting with mass emergence of adults from winter quarters in June. Fecund females were found as early as February (Table 6) followed by eggs in March and larvae until early June when large numbers of callow adults first started to appear at Alconbury (Fig. 5), i.e. these were the first summer brood as indicated by Lal and not overwintering adults. The wave-like pattern of peaks in the Alconbury catches supporters Zangheri's theory of two further generations rather than the three proposed by Lal, but breeding experiments are needed to settle this question. A small proportion of the autumn population may attempt an extra generation since copulation was observed among a few pairs in the second half of November and a fifth instar larva was found in the middle of January (Table 6). Lal also found mature larvae overwintering.

Adult numbers varied considerably from generation to generation and year to year, possibly as a response to changes in predation. In 1969 the peak numbers caught at two sites in August were higher than those caught at the beginning of November while in 1970 the November peak was twenty times the August figure (Fig. 5). The capacity for increase in this species is evidently very high for Lal noted an average of 176 eggs laid per female. Leaf curling, which Zangheri noted as a characteristic of infested plants, was not seen by Lal and was found in Huntingdonshire only in August and September when larval populations were high. One badly affected leaf (*c.* 15 mm long) was found to carry twenty-nine second instar larvae.

As shown by Table 7, *T. urticae* was one of the most abundant species found on nettle. At one Breckland site, a sheltered sunny clearing in a wood, the catch exceeded 5000 in the October sample and was estimated by counting aliquot subsamples. The numbers in open sites were two to three times as great as in shaded ones but this difference could be directly related to plant density.

The life cycles and co-occurrence of *Eupteryx urticae*, *E. cyclops* and *E. aurata* (Cicadellidae) on nettle have been described by Le Quesne (1972). All three species have two

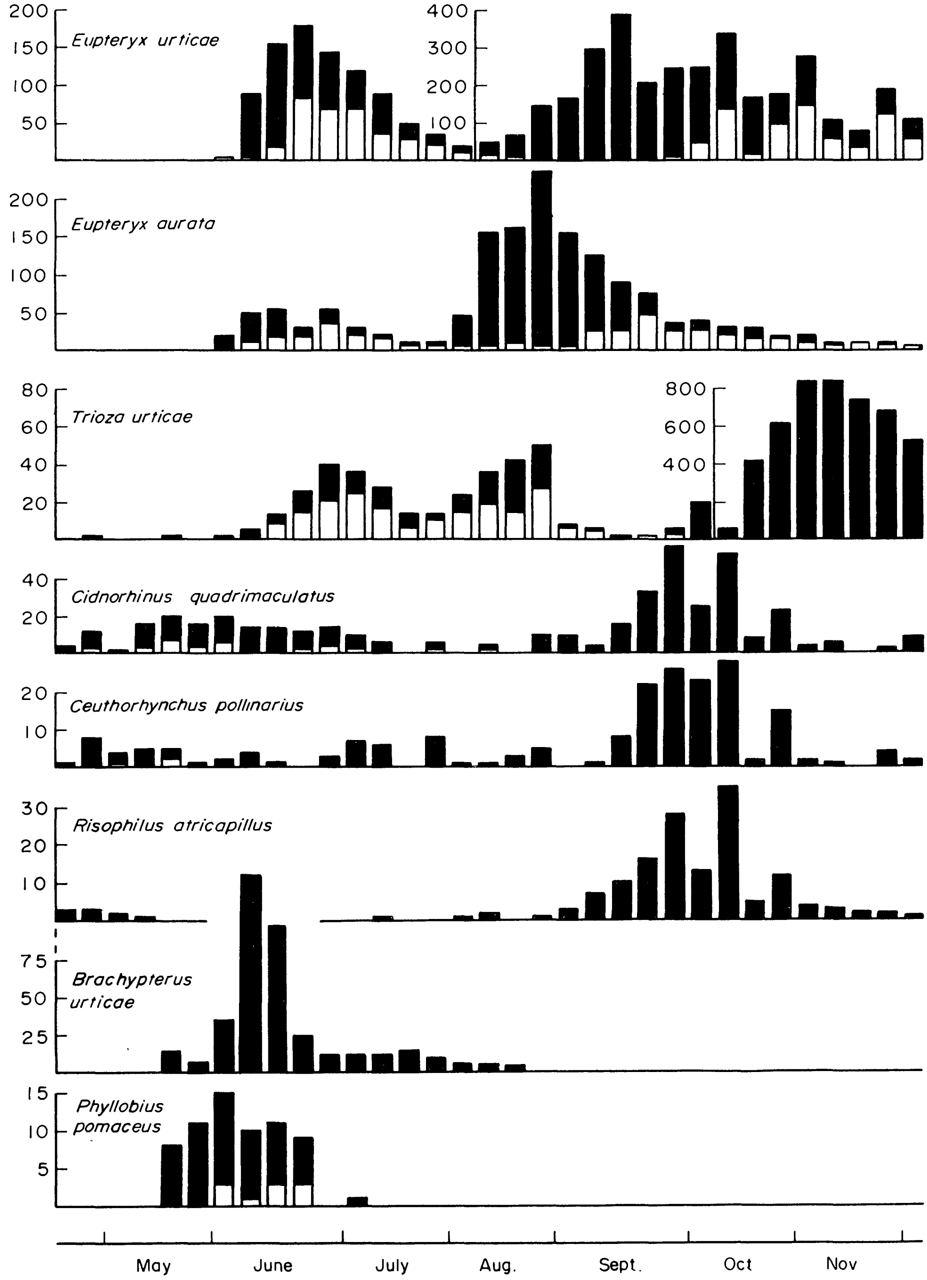

FIG. 5. Seasonal fluctuations in numbers of adult Homoptera and Coleptera at Alconbury in 1970. Open columns represent females with eggs.

distinct annual generations and overwinter as eggs, apart from a few adults which may survive a mild winter (Table 7). *E. urticae* was the most abundant species in all six habitat types, followed by *E. aurata* which showed a distinct preference for open habitats. *E. cyclops* was evidently less associated with clay soils than with peaty and sandy soils. It was virtually absent from the Alconbury site even though this was the only site situated near a stream. Marshy and obviously humid habitats near water which are favoured by this species (Le Quesne 1972) were not sampled at all in this study.

The second-generation peak for *E. aurata* at Alconbury came a few weeks earlier than in *E. urticae* and dropped off more quickly. According to Le Quesne (1972) this can vary from year to year. In both species the first generation was much smaller than the second but this again may alter with weather conditions, predation and parasitism. Table 8 summarizes the incidence of parasitism in 1970 by Dryinidae and by unidentified internal parasites which could include early stages of dryinids as well as pipunculids and Strepsiptera (Ribaut 1936). As in Le Quesne's study, both generations were attacked, but particularly the second. At Alconbury 20–40% of individuals were affected within the dates given. Males and females of both species were equally affected.

Table 8. *Parasitism in* Eupteryx urticae *and* E. aurata *at Alconbury in* 1970

Species	Sex	Period	Total adults	% with Dryinidae	Period	Total adults	% with unidentified parasites
E. urticae	♂	16–30 June	222	8·1	23–30 June	142	2·1
	♀		253	7·1		181	3·9
	♂	18 Aug. to 29 Sept	789	19·0	11–29 Sept	595	5·7
	♀		735	25·0		548	3·7
E. aurata	♂	16–30 June	60	1·7	6 July	12	–
	♀		80	1·3		20	10·0
	♂	5 Aug. to 22 Sept	506	37·0	1–22 Sept	178	2·3
	♀		535	36·7		262	2·7

Macrostetes variatus (Cicadellidae) was taken in most weeks between the middle of June and the end of October. It was recorded at fourteen of the nineteen sites but, as noted by Le Quesne (1969), seldom occurred in large numbers. It was least common at open sites on clay soils. Egg-bearing females were found in almost every week between the middle of July and the end of October, 82% of all females examined, but numbers were too low to show how many generations there were.

Macropsis scutellata (Cicadellidae) was found in small numbers only at two shaded sites in the Breckland during July and August. Adults are recorded between July and October (Le Quesne 1965).

Coleoptera

Risophilus atricapillus (Carabidae) overwinters as an adult and the larvae live on the ground in grass tussocks, etc. between June and August (M. Luff, personal communication). During the spring, the numbers on nettle were low but the appearance of new adults in September was clearly shown by suction catches (Figs. 3 and 5). Table 7 would suggest that this species is uncommon and virtually confined to open clay sites, but the timings of the four samples fit badly with its phenology and a mid-September sample would reveal a much clearer picture of habitat preferences. Laboratory observations showed that it feeds readily on aphids.

Of the four species of weevil restricted to nettle, *Cidnorhinus quadrimaculatus* is the most common and widespread. It appeared to have a slight preference for sandy soils, at least compared with clay ones. The somewhat larger catches in open, as compared with shaded sites, may just reflect the greater stem density there. Pairing was commonly observed between April and the middle of July and females with eggs were found at Alconbury from April to early August indicating a more protracted oviposition period than that given by Sherf (1964). Larvae live on the roots and produce new adults in the autumn. The late August collection from nineteen sites yielded fifty-one callow adults, nearly 16% of the sample, and a few callow adults were found up till 10 November. Hoffmann (1954) refers to overwintering larvae, but his description of the life cycle in other respects points to confusion with another species.

Declining catches during July and August can be attributed partly to mortality but also to summer diapause. Out of fifty individuals caged during June, seventeen were recovered in October and had resumed feeding. The increased catches in September are therefore probably due to a combination of new and old adults. This suggests that a proportion may survive to breed a second year as in the chrysomelid *Phytodecta olivacea* (Forster) (Waloff & Richards 1958).

Ceuthorhynchus pollinarius was found on average to be about one-fifth as numerous as *C. quadrimaculatus* though almost as widely distributed. The numbers taken at Easton (Table 2) were exceptionally high. Very few individuals were taken in shaded sites on peat, but shading appeared to make little difference in the case of clay soils.

Sherf (1964) quotes Hoffmann (1954) in saying that eggs are laid in stems and petioles in May and June and that larvae overwinter and pupate in March and April the following year. This life cycle is not supported by the evidence obtained at Alconbury where the weekly catches indicated a life cycle very similar to *C. quadrimaculatus*. No callow adults were found in the autumn or spring samples, but adult survival in cages was demonstrated for the period June to mid-October and from early October until the following March. Some females collected and dissected in early November had thin undeveloped ovarioles and may have been newly emerged adults, while other females with plump ovarioles and egg calyces or corpora lutea resembled the condition of those which had been kept since June. Two more had developing eggs in their ovarioles and oviducts similar to those seen in specimens collected in late March. Out of nineteen species of *Ceuthorhynchus* for which life histories are given by Sherf (1964), seventeen pupate and emerge as adults in the summer or autumn and only two pass the winter as larvae or pupae apart from *C. pollinarius*. Further studies are being made to resolve the life history of this species.

Phyllobius pomaceus has a relatively brief and clear-cut adult period from May to early July (Fig. 5 and Table 7) after overwintering as a larva in the roots and pupating in the spring (Roberts 1926; Sherf 1964). Pairing was seen in June and females with eggs were found for four consecutive weeks in June. One female contained thirty-six eggs.

This is a rather local species in Huntingdonshire. It was almost restricted to the Alconbury site among the nineteen surveyed in 1970, but was more common and widespread in 1971 appearing to favour sunny situations.

Apion urticarium is considered a very local species (Joy 1932) but was taken in small numbers at five of the six peaty sites in the Huntingdonshire fens, at one clay site on the edge of the fens near Sawtry and at two of the sandy sites in Suffolk. There is one generation a year and larvae develop in the stems between July and August according to Sherf (1964) though Hoffmann (1958) considered that two annual generations were likely. Adults were found on all four sampling occasions during the survey, but more commonly in August and October. This very small species could be easily underestimated in samples containing any considerable bulk of other insects, nettle seed or plant fragments.

The two Nitidulidae, *Brachypterus urticae* and *B. glaber*, are both closely geared to nettle flowering. Observations in 1971 showed that these beetles are restricted to male flowers where they aggregate in large numbers for short periods while conditions are right. Eggs are laid in the male inflorescences and older larvae could be seen crawling over the surface of flower buds. Five male and five female nettle stems were collected on 25 June at Holme Fen and stood in jars of water over white trays. Within the following six days 281 larvae were collected off the male plants and none from the female. Similar results were obtained at two other sites with mature larvae appearing between 24 June and 5 July. Attempts to get larvae to pupate were largely unsuccessful, but a few pupated after a few days in damp sand and in damp vermiculite. These produced adults of both species between 19 and 26 July. On 11 August beetles were again seen swarming on flowers at Holme Fen where nettles had been cut in June. From twelve selected male stems 637 *B. glaber* and 228 *B. urticae* were obtained. Although no larvae appeared this time, indirect evidence points to a second generation of larvae and overwintering pupae. Neither species has been collected as hibernating adults during the winter, unlike several *Meligethes* species (P. C. Hammond, personal communication). Also, well-developed eggs were found in four out of thirty female *Brachypterus urticae* examined from collections made on 25 and 26 August.

The weekly frequencies in suction samples from Alconbury were practically identical in the two species and so only *B. urticae* is shown in Fig. 5. The single peak of adults gives a misleading impression of the life cycles of these species since it probably reflects flowering conditions at Alconbury rather than beetle numbers at large. Adult populations of both species, especially *B. glaber*, declined after June in the 1970 survey (Table 7) though the high numbers given above for early August 1971 suggest that dispersal to other sites with late flowering nettle may normally account for some of this decline. *B. glaber* is said to be more common than *B. urticae* in the Midlands and southern England (Fowler 1889), and also to visit other plants. In the Huntingdonshire area the two species were present in very similar numbers in the open sites, but *B. glaber* was virtually absent from the shaded ones. *B. urticae* was somewhat reduced in numbers in the shaded sites but not as much as the lower stem density and flower production might suggest.

Crepidodera ferruginea (Chrysomelidae), which Richards (1948) refers to as common on nettle as well as thistles, was taken only in June and July in the Breckland sites and in early August at one site near Huntingdon (Table 2). This species was not listed by Richards (1964) among the more characteristic insects of nettle in the London area.

Sex ratios

The proportions of males and females were noted for all species except *Brachypterus* spp. and is summarized by months for the more common ones in Table 9. The high proportion of female *Anthocoris nemorum* in the spring is well known (Southwood & Leston 1959); this ratio was reversed at Alconbury in the August and September populations. Similar disparities in sex ratios before and after periods of mating were also observed in *Eupteryx urticae* and in *E. aurata*. In Fig. 6 the declines in percentage males are seen to correspond with egg production in females. In contrast, *Trioza urticae*, had roughly equal numbers of males and females at all periods including the February sample (Table 6). Among the Coleoptera the three species of weevils showed a small predominance of males in most months when adults occurred, particularly May and September. Differences

Table 9. *Monthly sex ratios for the more common insects taken at Alconbury in* 1970

Species	April	May	June	July	August	September	October	November
	♂:♀	♂:♀	♂:♀	♂:♀	♂:♀	♂:♀	♂:♀	♂:♀
Scolopostethus thomsoni	11:9	12:17	25:29	18:20	15:18	14:13	6:9	3:1
Anthocoris nemorum	3:13	0:20	8:8	8:6	57:27	63:25	29:26	7:4
Liocoris tripustulatus	21:12	9:16	10:35	34:27	55:55	50:44	17:20	2:2
Plagiognathus arbustorum	–	–	15:4	132:85	15:19	–	–	–
Trioza urticae	2:0	0:1	39:48	32:59	74:86	1:17	584:545	1632:1490
Eupteryx urticae	–	–	293:272	76:207	103:142	681:334	375:516	183:430
E. aurata	–	–	101:112	20:45	312:278	189:286	36:82	15:33
Risophilus atricapillus	3:3	2:1	–	1:0	3:1	35:29	34:31	7:4
Cidnorhinus quadrimaculatus	11:5	35:17	39:34	6:13	6:7	82:35	52:50	2:8
Ceuthorhynchus pollinarius	7:2	11:4	7:4	10:11	6:4	41:16	42:26	4:3
Phyllobius pomaceus	–	13:6	32:13	1:0	–	–	–	–

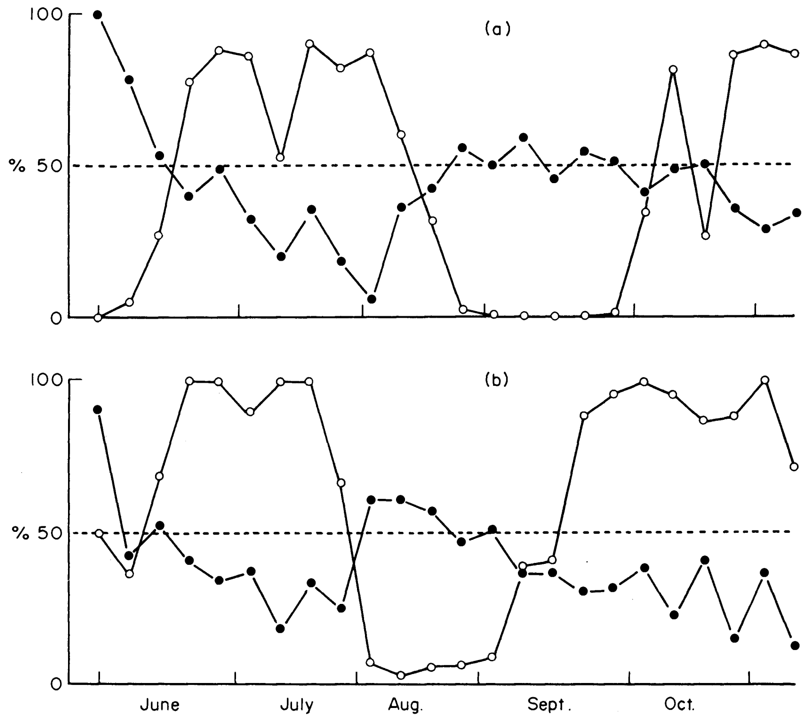

FIG. 6. Comparisons of % fecund females (○) with % males (●) in the population for (a) *Eupteryx urticae* and (b) *E. aurata* at Alconbury in 1970.

in catchability of the sexes cannot be ruled out, but egg-laying behaviour in the females would only provide a partial explanation since it would not apply to the September populations.

Comparison of habitats and sampling dates

Samples taken in June, July and August from the nineteen sites produced on average 14–15 species while in October this dropped to nine. Over the four occasions the numbers of species found at individual sites ranged from 16–24 out of the 26 in Table 7, with mean and modal values of 20. Sites in open situations had consistently more species than their counterparts in shaded situations. Thus the numbers at shaded sites varied from 16–20 while at open sites 20–24 were taken. There was virtually no difference, on the other hand, between mean numbers of species found on different soil types.

DISCUSSION

The use of the Dietrick vacuum sampler allows a quantitative approach to the sampling of insects on herbage which is otherwise difficult to achieve. Although the efficiency is not always very high for tall dense herbage like nettles, it is possible to estimate this efficiency and thus to interpret the results with greater confidence. With standardized plots it would be possible to detect quite small differences, but nettle beds are usually such variable entities that only gross differences are likely to be of interest. Interspersion with other plants is a common feature but the ability to form locally dominant stands makes it especially suitable for experimental work and allows one to concentrate on other variables.

The majority of Hemiptera and Coleoptera associated with nettle have life histories which fall into one of four broad categories when classified by overwintering stage and number of annual generations. Those which overwinter as eggs and have one generation a year are the Miridae *Deraeocoris ruber*, *Orthonotus rufifrons*, *Plagiognathus arbustorum*, *Heterotoma planicornis*, *Orthotylus ochrotrichus*, *Lygocoris spinolai* and *Calocoris norwegicus* and probably the cicadellid *Macropsis scutellata.* The three *Eupteryx* species, (Cicadellidae), are bivoltine and probably *Macrosteles variatus* is as well. The third group consists of adult overwintering, univoltine species such as *Heterogaster urticae* (Lygaeidae), *Liocoris tripustulatus* (Miridae), *Risophilus atricapillus* (Carabidae) and the weevils *Cidnorhinus quadrimaculatus* and *Ceuthorhynchus pollinarius*. Three other Heteroptera, *Anthocoris nemorum*, *Lygus rugulipennis* and *Lygocoris pabulinus* have two generations and make up the fourth group. *Apion urticarium* belongs in the third or fourth group. This leaves the psyllid *Trioza urticae* which has three or more generations a year and the weevils *Phyllobius pomaceus* which is univoltine and overwinters as a larva. *Scolopostethus thomsoni* and perhaps *S. affinis* (Lygaeidae) combine the features of the first and third groups described above by having both adults and larvae which overwinter. If Sherf (1964) is correct about the overwintering of larvae of *Ceuthorhynchus pollinarius*, this would be in a similar category. The blossom beetles *Brachypterus urticae* and *B. glaber* may belong in the fourth group but if, as suspected, they overwinter as pupae they would represent yet another type of life cycle.

The coexistence of so many insect species implies a high degree of productivity and nutrition on the part of the host plant which seldom appears to be adversely affected by its fauna. It also implies a highly competitive situation in which there has been selection for species which have adopted many minor differences in feeding habits and variations in phenology, or are particularly well adapted to certain habitats. This can be seen even within the phytophagous Hemiptera and Coleoptera; the Lepidoptera and Diptera fill further niches which will be considered separately. All parts of the plants are utilized. For example, the roots, rhizomes and stems are used by Curculionid larvae, leaves by Curculionid adults, male inflorescence by *Brachypterus* spp., fruit by *Scolopostethus* spp., and the sap from stems and leaves by all the phytophagous Hemiptera. Within these groups some subtle feeding differences are apparent: among the weevils, for example, the Ceuthorrhynchinae bite holes in the lamina of leaves, while *Phyllobius pomaceus* eats around the edges. Intensive studies like those done on *Scolopostethus* by Eyles (1964) would doubtless reveal further subtle requirements including the use of seeds by other species to a greater or lesser extent.

Those with a long adult phase and prolonged oviposition period like *Liocoris tripustulatus*, *Scolopostethus thomsoni* and *Cidnorhinus quadrimaculatus* differ markedly from those which have brief, highly synchronized adult periods, such as *Orthonotus rufifrons* and *Phyllobius pomaceus*. As shown in Figs. 3–5 there is a succession of peaks for adult populations most clearly seen by comparing species with one generation like *Calocoris norwegicus* and *Deraeocoris ruber* or with two generations like *Lygocoris pabulinus* and *Lygus rugulipennis*. Le Quesne (1972) has observed such differences between the three *Eupteryx* species over a period of 6 years and in this case temporal separation is combined with partial separation by habitats (*E. cyclops*) and with oligophagy (*E. aurata*). The synchronization of breeding periods is inevitable for the two *Brachypterus* species and here habitat advantages (*B. urticae* in woodlands) are balanced against oligophagy (*B. glaber*).

Many such details remain to be clarified. For instance it is not clear precisely how much overlap there is in the requirements of *Cidnorhinus quadrimaculatus* and *Ceuthorhynchus pollinarius*. Population studies would also need to consider predation, parasitism and disease as well as annual changes in plant biomass and nutritional status. The analysis of these interactions could only be made by intensive autecological studies comparable to those described by Waloff (1968) for insects on broom (*Sarothamnus scoparius* (L.)).

Soil type appears to be of less importance than shading in its effect upon the performance of nettle and on habitat selection by insects. Although nutritional factors can be important for insects, notably aphids, it is more likely that temperature, humidity and shelter from wind are among the most important factors. The surprisingly small variation in numbers of insect species found on nettle patches suggests that predictions can be made of other sites. Regional differences must be expected, but sites which are found to have more than twenty-four species may be considered especially favourable in terms of locality and microclimate, while those that have less than twenty (in open situations) or sixteen (in shaded situations) may indicate adverse conditions. The sites sampled in this study were all rather large dense stands and other differences may be found for nettles which are dispersed amongst grass or other vegetation. Human influences, such as cutting or spraying, and the effects of pollutants in the environment can also be evaluated.

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SUMMARY

Aspects of the phenology and growth characteristics of stinging nettle are described which could be important for insects. Six habitat categories were contrasted by selecting nettle patches in shaded and unshaded conditions on clay, peat and sandy soils. The efficiency of suction sampling for Hemiptera (except aphids) and Coleoptera was examined and compared with the searching of cut-stem samples.

Suction sampling was used to build up a general phenological picture of adult insects in preparation for an intensive study of one site and a comparison of nineteen sites in contrasting habitats. The life histories and habitat preferences of fourteen Heteroptera, five Homoptera and seven Coleoptera are described, including monophagous and polyphagous plant feeders and a few predatory species common on nettle in East Anglia. Several gaps in the information still remain and these are pointed out. The repuirements of the phytophagous species are discussed in relation to the successful exploitation of nettle by so many species. The comparison of insect faunas in different habitats in this study provides a basis for comparing other sites with respect to regional, climatic and biotic factors.

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