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Seasonal Changes and Alternation of Food Plant Preference in Some Mesophyll-Feeding Leafhoppers

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Summary. The life histories of two bivoltine mesophyll-feeding leafhoppers, *Lindbergina aurovittata* (Douglas) and *Edwardsiana rosae* (L.), in South Wales are described. *L. aurovittata* alternates between evergreen *Rubus* and *Quercus* in the first generation and various deciduous broad-leaved trees in the second. Experiments on nymphal food preferences and adult oviposition behaviour show that nymphs of both generations tend to prefer older to younger leaves, but show little species specificity. However, adults are discriminating in oviposition preferences, which change regularly and completely in alternating generations. Similar results were obtained with *E. rosae*. Such obligate seasonal changes in host preferences and utilization are well known amongst aphids, but previously have not been reported in leafhoppers.

Introduction

Phytophagous insects may be characterised by the degree to which they are restricted to a narrow range of plant species for their food and development. Some species have a very wide tolerance, others may be restricted to only one species, and yet others may be intermediate in their requirements. We have previously (Claridge and Wilson, 1976) described the mesophyll-feeding leafhoppers associated with woodland trees in Britain. Of the 31 species found commonly enough for reliability to be placed on the field data, 16 were regarded as monophagous, and three polyphagous, with 12 oligophagous – that is associated with a few different tree species – though these categories grade into each other.

In this paper, we examine the life histories and seasonal responses to food plants of a common bivoltine species – *Lindbergina aurovittata* (= *Youngiada pandellei*, see LeQuesne, 1977) – and also give less detailed information on another, *Edwardsiana rosae* (L.), in order to explore the nature of food specificity in this group.

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Materials and Methods

Life history data were accumulated as described previously (Claridge and Wilson, 1976) by regular sweep net sampling, but primarily by hand collecting, from woodland areas in South Wales. All insects used in feeding and oviposition experiments were taken from field populations.

For experimental purposes, field collected adults and nymphs were kept in the laboratory in ventilated perspex box cages, which could take two similar plant stems of different species, placed horizontally (as described by Claridge et al. 1977).

Lindbergina aurovittata (Douglas)

Life Cycle

L. aurovittata, together with *Ribautiana tenerrima* (Herrich-Schaeffer), is commonly found feeding on brambles, *Rubus* species, during early summer in South Wales. We have previously also recorded it later in the season as common on oak, *Quercus robur* L., and present in smaller numbers on alder, *Alnus glutinosa* (L.), hornbeam, *Carpinus betulus* L., and beech, *Fagus sylvatica* L., and noted its apparent alternation of generations between bramble in the spring and oak and other trees in the summer (Claridge and Wilson, 1976).

Results of hand sampling every one or two weeks from bramble and oak at a woodland site near Cardiff between April and November, 1977, are presented in Table 1. Regular collecting from other sites and over at least eight seasons, confirm the pattern of host distributions.

Overwintering eggs are laid in the under (abaxial) surfaces of evergreen bramble leaves (Table 1) during early autumn and hatch by about the end of April of the following year. In southern England we have also found first generation nymphs and overwintering eggs on the evergreen Holm Oak, *Quercus ilex* L. Five nymphal instars occur, with adults usually appearing in early June. The adults disperse to woodland trees, and, by late June, very few are to be found on brambles. The second generation of eggs are laid in the leaf lamina of various trees, most commonly oak and beech, but also alder, *Alnus glutinosa* (L.), hazel, *Corylus avellana* (L.), birch, *Betula pubescens* (Ehrh.) and the other deciduous oaks, *Quercus cerris* L. Coste and *Q. petraea* (Mattuschka) Liebl. Nymphs of various ages are found through August and September, together with small but increasing numbers of adults. During this period no eggs, nymphs or even adults have been found on brambles. In South Wales, adults begin to reappear on brambles in early October and eggs may then be found. Large numbers of adults can usually be collected well into November, after which they decline with the onset of autumn frosts.

Nymphal Feeding

Field observations of feeding nymphs on bramble leaves strongly suggested a preference for old leaves over newly opened ones. The term "old leaf" here

Table 1. Presence (+) of life history stages of *Lindbergina aurovittata* on *Rubus* and *Quercus* during 1977, at Cefn On, near Cardiff, South Wales

Sampling dates	*Rubus*							*Quercus*						
	Adults	Eggs	Nymphs					Adults	Eggs	Nymphs				
			I	II	III	IV	V			I	II	III	IV	V
23. IV. 1977		+	+											
2. V.				+										
18. V.					+									
31. V.	+					+	+							
8. VI.	+						+							
15. VI.	+						+							
21. VI.	+						+	+						
30. VI.	+							+						
7. VII.								+						
20. VII.								+	+					
1. VIII.								+	+	+	+			
15. VIII.								+	+	+	+	+		
31. VIII.								+	+	+	+	+		
13. IX.								+	+				+	+
5. X.	+							+						+
12. X.	+	+						+						+
23. X.	+	+												
2. XI.	+	+												

Table 2. Field distributions of 3rd and 5th instar nymphs of *L. aurovittata* on "old" and "new" leaves of *Rubus* in the first generation

	Old	New
3rd instar 13 leaves	84	0
5th instar 26 leaves	126	10

refers to leaves formed during the previous growing season and which have overwintered on the plant in the field. "New leaf" refers to young, but fully opened, leaves formed during the same season.

In the springs of 1976 and 1977, field counts of nymphs of *L. aurovittata* on new and old brambles were made (Table 2). The earliest instars were found exclusively on old leaves. Even 5th instars were overwhelmingly on old leaves despite apparent overcrowding (with up to 30 nymphs on a single leaf). Such old leaves showed extensive feeding damage in the form of large whitish-yellow patches.

Since the overwintering eggs of *L. aurovittata* are laid in leaves, it could be argued that the nymphs do not show any definite preference for old leaves, but simply stay near to the egg sites. A series of experiments was made to test both this and also possible preferences for different potential food plants.

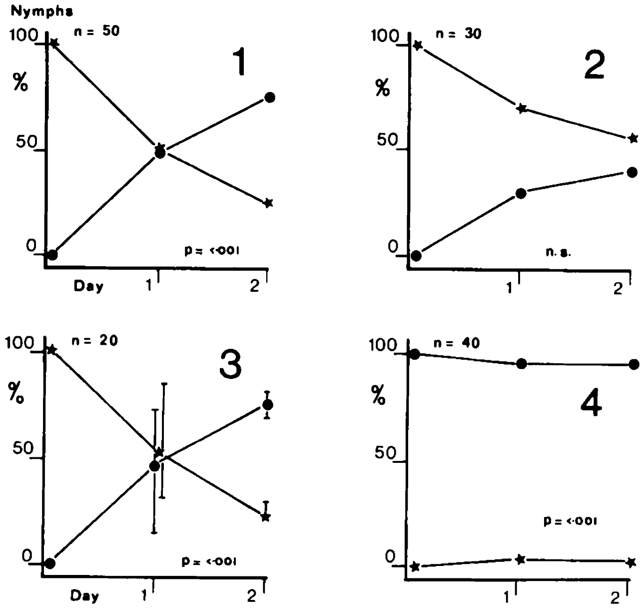

Fig. 1–4. Results of experiments on feeding preferences of *L. aurovittata* between "old" and "new" leaves of *Rubus* (see text) over 2 days: 2nd–3rd instars (**Fig. 1**), 3rd–4th instars (**Fig. 2**), and 5th instars (**Fig. 3**) placed initially on young leaves; and 3rd–4th instars placed initially on old leaves (**Fig. 4**). * Indicates numbers on new leaves and ●numbers on old leaves after 1 and 2 days. Significance levels of χ^2 for differences between numbers after 2 days are given

Experiments on Nymphal Feeding

1. Old and New Bramble Leaves. Experiments were done with nymphs released either on to young or old leaves on stems with about equal numbers of both. The results (summarised in Figs. 1–4) clearly demonstrate a preference for old leaves by nymphs of *L. aurovittata*, and a tendency to migrate from new to old.

2. Bramble and Oak Leaves. Oak and other woodland trees are the host plants of second generation nymphs. Feeding choice experiments were made, using first generation nymphs from bramble with a combination of choices of mature oak and both new (Fig. 5) and old bramble leaves (Figs. 6–8). In all of these the nymphs showed no clear preferences and certainly no strong tendency to return to bramble.

3. Bramble and Rose Leaves. Two first generation nymphs were on one occasion collected in the field from leaves of *Rosa* species. It is likely that they had wandered there from nearby brambles. Two experiments were done to test preferences between rose, and young and old bramble.

In experiment 1, 15 3rd to 4th instars were placed on rose with young bramble as an alternative. They showed a very significant preference to remain on the rose ($P < 0.001$).

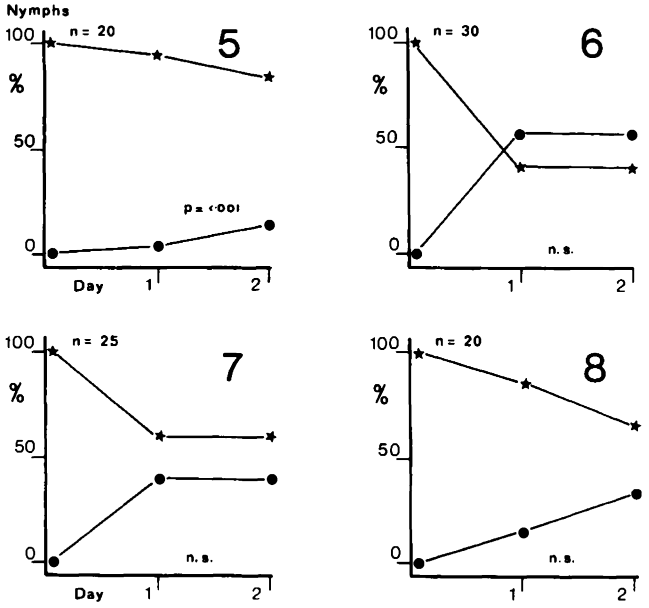

Fig. 5–8. Results of experiments on feeding preferences between mature leaves of *Quercus* and "new" (**Fig. 5**) and "old" leaves of *Rubus* over two days (**Figs. 6–8**), using 3rd–4th instars (**Figs. 5 and 6**), 4th instars (**Fig. 7**) and 4th–5th instars (**Fig. 8**) of *L. aurovittata*—all placed initially on *Quercus*. * Indicates numbers on *Quercus* and ● numbers on *Rubus*. Significance levels of χ^2 for differences between numbers after 2 days are given

In experiment 2, 20 4th instars were placed on rose with old bramble as an alternative. After 2 days, there was no significant difference, with about equal numbers on both plants.

4. Birch, Beech, Alder and Bramble Leaves. 30 5th instar nymphs were placed on Birch (*Betula pubescens* Ehrh.), 20 on Beech and 20 on Alder in separate tests, each with old bramble as an alternative. In all three experiments, the nymphs showed no significant tendency to move back to bramble ($P < 0.001$).

It is clear from these experiments that first generation nymphs of *L. aurovittata* show no clear-cut preference for bramble, the host upon which they are usually found in the field. Also, there is a definite indication that a preference for older leaves overrides any taxonomic preferences. No experiments were done with second generation nymphs, but in view of the results described here, it is unlikely that they would show great differences in behaviour.

Oviposition Behaviour

Since first generation nymphs show no clear preference for brambles, it is likely that adult females, in distributing their eggs, discriminate strongly between the leaves of different tree species.

Table 3. Results of oviposition experiments with adult females of the first and second generation of *L. aurovittata*. – indicates plant not tested

		Rubus	*Fagus*	*Quercus*
1st Generation	1.	1	17	–
	2.	2	–	23
2nd Generation	1.	84	–	0
	2.	144	–	0

Two experiments were conducted to test this hypothesis. In the first, 15 females and 5 males of first generation adults, reared from bramble, were liberated into a cage with bramble and beech stems, with about equal numbers of mature leaves. After 2 weeks, the leaves were removed. 29 eggs were found on the beech and none on bramble.

In a second experiment, similar bred adults were liberated into a cage and given a choice between beech and bramble. After a week, the numbers of eggs were counted. The same adults were then given a choice between oak and bramble and, again, left for 1 week before eggs were counted. Results are given in Table 3.

In the second experiment, 96% of the eggs laid on oak were deposited on the upper (adaxial) surface, whilst only 12% of those laid on beech were adaxially placed. The three eggs laid on bramble were all on the upper surface. In the field, eggs on beech were mostly found on the lower abaxial surface, whilts those on oak were on the upper surface. All field eggs on bramble have been found on lower surfaces only. It seems that the three eggs laid in bramble in the experiments were the result of aberrant oviposition behaviour.

Second generation adults were collected from oak and given a choice for oviposition between oak and bramble leaves. In two experiments, each with 20 females, after 7 days a total of 228 eggs were laid in bramble and none in oak. In further experiments with females isolated on oak, no eggs were laid.

It is thus clear that there is a complete switch of preferences in oviposition behaviour between the two generations of *L. aurovittata*.

Edwardsiana rosae (L.)

E. rosae is a common bivoltine species in Britain and is a well known minor pest of various Rosaceous fruit and ornamental trees in Europe and N. America (Knight, 1966; Massee, 1941; Raine, 1960). We have previously recorded it as breeding on *Rosa* species and rowan, *Sorbus aucuparia*, in mixed woodlands of South Wales (Claridge and Wilson, 1976). Various authors have suggested that *E. rosae* overwinters mainly on wild and cultivated species of *Rosa*, but attacks a wider variety of hosts, especially cultivated apples and cherries, in its second summer generation (Childs, 1918; Chiswell, 1964; Dirimanov and

Kharizanov, 1964; Evenhuis, 1955; Simm, 1928). There is some confusion in the literature, undoubtedly due to the difficulties of identifying both nymphs and adults of *E. rosae* and of separating them from other species which may attack some of the same plants. Only males of most species of the large genus *Edwardsiana* can be certainly identified and then only by examination of the genitalia.

In South Wales, we have found *E. rosae* nymphs of the first generation hatching only on *Rosa* species, often in large numbers. In the second generation, a wider range of hosts is attacked. It is clear that *E. rosae* significantly expands its host plant range during this generation. It must be supposed that ovipositing females change their behaviour in a manner similar to *L. aurovittata* from generation to generation. We have made no oviposition experiments with *E. rosae*, but continuous field sampling of *Rosa* species and *Sorbus aucuparia* growing in close association, has confirmed that no nymphs hatch on *S. aucuparia* in the spring, whilst large numbers are to be found on *Rosa*. In mid-summer, first instar nymphs have been found in numbers on both *Rosa* and *S. aucuparia*, together also with nearby cultivated apples, *Malus* species, and strawberries, *Fragaria* × *ananassa*. Thus, there is no indication that *E. rosae* lays overwintering eggs on apple (as claimed by Childs, 1918; Dirimanov and Kharizanov, 1964) or any other plants than species of *Rosa*.

Some experiments were done with first generation *E. rosae* nymphs. Preference tests using four species of Rosaceous plants – Rowan (*Sorbus aucuparia* L.), a known regular second generation host, Blackthorn (*Prunus spinosa* L.), a doubtful, but possible host, and Hawthorn (*Crataegus monogyna* Jacq.) and Birdcherry (*Prunus pradus* L.), both non hosts in South Wales – as alternatives to *Rosa*. In all experiments the insects were put onto the test plant and after two days, some, but not all, had moved back to *Rosa*. Only with the *Rosa*/*P. spinosa* choice had significantly more nymphs moved to *Rosa* than had remained on the test plant after 2 days ($P < 0.001$). In the other three choice tests there was no significant difference between the numbers on the pairs of plants after 2 days.

Thus, it is clear that first generation nymphs of *E. rosae* do not reject plants other than rose as a food. In other tests, first generation nymphs were transferred to a non host, bramble (*Rubus* species), and adults emerged successfully. As in *L. aurovittata*, it seems that the pattern of host relations in the field is determined by discriminatory oviposition.

Discussion

We have here demonstrated seasonal changes in oviposition preferences, and hence host plant ranges, in both *Lindbergina aurovittata* and *Edwardsiana rosae*. In *L. aurovittata*, there is a distinct alternation of generations with a complete change of oviposition plants, and hence nymphal food plants. In *E. rosae*, the change is not so exclusive, in that the host range is widened in the second generation, and still includes the overwintering oviposition plant. Previously, little indication of such obligate seasonal food plant changes in leafhoppers has been published, though there are some descriptions of seasonal changes in polyphagous, multivoltine species (De Long, 1965). For example, the well known Beet leafhopper, *Circulifer tenellus* (Baker), in North America has between three and five broods annually which migrate to seasonally suitable hosts, including cultivated crops (Cook, 1967). Similarly the Blue Green Sharpshooter, *Hordnia circellata* (Baker), changes its host plants seasonally in an opportunistic manner (Purcell, 1976).

Obligate seasonal alternations of food plants are well known in aphids (Dixon, 1977). For example, winged adults of *Rhopalosiphum padi* (L.) migrate from the overwintering host tree, bird cherry (*Prunus padus*), during summer to feed and reproduce on various grasses. They then return to feed and lay overwintering eggs on bird cherry in the late summer and autumn. Such alternation is clearly associated with seasonal changes in the food value of tree foliage to phloem-feeding aphids (Dixon, 1971). The significance of seasonal alternations and changes of oviposition plants in mesophyll-feeding leafhoppers is not so obviously correlated with changes in nutrient availability. Little is yet known of the nutritional requirements of such leafhoppers, and nothing is known of the environmental cues responsible for switching oviposition behaviour preferences. However, in the not too distantly related planthopper (Delphacidae), *Muellerianella fairmairei* (Perris), Drosopoulos (1975) has demonstrated a switch in oviposition preferences depending on the photoperiod experienced during nymphal development. Similar changes in photoperiod would be experienced in the field by both *L. aurovittata* and *E. rosae*, and could also provide suitable cues for them. It is interesting that Günthart (1971) has been able to rear successive generations of *E. rosae* on *Malus* using a continuous daily photoperiod of 18 h.

The experiments on nymphal feeding with both species studied here demonstrate that nymphs show less discrimination in their feeding preferences than do adult females in oviposition. Indeed in many instances nymphs were able to survive and develop on hosts which are not attacked in the field. Similar, but less extreme, results have been reported previously for phloem-feeding leafhoppers (Claridge et al., 1977).

The selective advantage of these seasonal changes in host plant preferences is not obvious. However, in *L. aurovittata*, eggs of both generations are always laid in the leaf lamina of oviposition plants. Overwintering eggs, therefore, will only survive on hosts with evergreen foliage. Of the known host range of this species, only the evergreen species of *Rubus* and *Quercus* are known to be used as first generation hosts. Because of the precise method of oviposition in this species alternation allows the exploitation of a wider range of food plants, but it is not clear why brambles should not be suitable hosts also during the second generation.

In *E. rosae*, the precise site of oviposition differs in the two generations. Overwintering eggs are laid in the young stem growth before leaf abscission. Second generation eggs are laid in the mid-ribs and major veins of leaves, whatever the oviposition plant species. Such changes also have obvious survival value, in that overwintering eggs can only survive in the non-leaf structures of deciduous hosts, but again it is not clear why only a restricted range of oviposition plants, here species of *Rosa*, are suitable for overwintering.

Ecological studies on leafhoppers often refer, in a general way, to food plant ranges (e.g. Claridge and Wilson, 1976; Waloff and Solomon, 1973). It is clear that work on individual species may reveal complicated patterns of preferences and seasonal changes, which may otherwise be masked under the general categories of oligophagous and polyphagous species.

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