A comparative study of the syrphidae (diptera) from different habitats within Bernwood Forest

John Oliver Watts (1983)

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A COMPARATIVE STUDY OF THE SYRPHIDAE (DIPTERA) FROM DIFFERENT HABITATS WITHIN BERNWOOD FOREST

John Oliver Watts

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ABSTRACT

1. Syrphidae were chosen as indicators of diversity in samples from five Malaise traps chosen to represent the transition from deciduous to coniferous woodland. 20, 234 syrphids of 115 species were captured between 1 April and 30 September 1980 - 1982.

2. Seasonal distribution is bimodal, with abundance peaks in May and late July through August. This contrasts with unimodal distribution in other habitats. Seasonal variation in aphid quality is proposed as the explanation.

3. Hoverfly species show enormous variation in abundance over the years, but, with one exception, the number of individuals and species at each site gives a consistent ranking each year. More species were caught in the first half of the sampling period whereas more individuals were captured in the second half.

4. Variation in species' abundances each year inhibits the identification of indicator species along the coniferization gradient.

5. Species diversity indices are used to estimate site quality and community structure. The former indices give site rankings in agreement with the number of species present and confirm the relative diversities of the two sampling periods. The latter indices demonstrate community changes over the three years, which is ascribed to the fluctuating nature of the species populations involved.

6. Principal components analysis isolates the catches from all sites according to season. High-diversity sites show more seasonal variation than low-diversity ones.

7. 75% of the syrphids captured have aphidophagous larvae but all five trophic categories are represented. Each site has a distinct trophic composition and this apparent trophic stability questions the over-reliance on the species as the fundamental ecological unit.

8. Chaotic phasing of species abundances, mediated through climatic control, is proposed as a non-equilibrium theory of population control which maximizes niche exploitation whilst minimizing intra-guild competition, thus maintaining species diversity.

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CHAPTER ONE

INTRODUCTION

The advent of large scale commercial forestry plantations has brought about the biggest single change to the landscape in Britain this century. The area of land covered by forest has doubled since the birth of the Forestry Commission in 1919 and today extends over almost 2 million hectares (Grainger 1981). This however represents only 8% of the land area and makes Britain one of the least-afforested countries in Europe, on a parallel with densely populated lowland countries such as Denmark but with significantly less woodland cover than, for example, Germany and Sweden, where 28% and 58%, respectively, of the land is forest (Tubbs 1974).

The scarcity of woodland as a wildlife habitat in Britain is further enhanced by the nature of much of the woodlands. Two-thirds of the woodland area has been established by deliberate planting, a practice begun in the latter part of the seventeenth century and which has culminated in the modern, massive operations of the Forestry Commission and forestry investment companies (Tubbs 1974). Almost half of Britain's woodlands are coniferous (Mellanby 1981) and the disappearance of ancient, semi-natural woodland continues apace. It is estimated that 30 to 50% of such woodland has disappeared since 1947, which is equivalent to the losses sustained during the previous four centuries (Goode 1981). Much of this loss is attributable to the conversion of woodland to conifer plantations.

Britain's traditional woodland wildlife is thus under pressure from greatly diminished available habitat, and yet the actual area of the countryside under forestry is increasing. This increase in commercial forestry clearly represents a potential increase in habitat for some of the native wildlife and some plantations possess features that are favourable to a wider range of the native flora and fauna than others. The identification of such features and the design of commercial forests to maximize their potential as viable habitats for as wide a range of native woodland wildlife as possible would be a major contribution to ecological conservation in Britain.

Bernwood Forest offers a unique situation in which to study the impact of commercial forestry practices. Bernwood consists largely of primary woodland in that the site has had a continuous history of woodland since man first began to make clearings in the forests from 2500 B.C. onwards. Although the Forest has been extensively managed, the heavy Oxford clay on which much of it stands has prevented ploughing, which, due to the primitive tools employed, was restricted to the lighter soils which surround it.

This freedom from disturbance has enabled Bernwood to maintain a rich flora and fauna to the present day, in spite of the recent disturbances concomitant with the advent of large scale forestry. Bernwood is best-known for its famous butterfly community and has been recognised as a rich butterfly site since Victorian times. Today, with forty-two species, Bernwood is the best site in Britain for butterflies, with thirty-nine resident species, including the black hairstreak (*Strymonidia pruni*) and the purple emperor (*Apatura iris*). The extraordinary richness of the butterflies, and casual observation and collecting of other groups of insects, hinted at the overall entomological richness of the Forest and this has been borne out by detailed investigation.

Bernwood is unique in other ways than simply being a primary forest of exceptional entomological richness. Since the Forest was acquired by the Forestry Commission in 1950 much of the old woodland was cleared and replanted, but the planting was not carried out with the uniformity typically associated with Forestry Commission woodlands. This has resulted in a great diversity of woodland habitat types on the ground at the present time. These range from old, deciduous coppice areas to old conifer plantations, with a full complement of intermediate stages in between.

Age mosaics are the best way to solve the commercial forester's problem of uniform stands, but in Bernwood this is further enhanced through the variety of tree species that has been used in the replanting. Norway spruce (*Picea abies*) and oak (*Quercus spp.*) mixed stands dominate the forest but western hemlock (*Tsuga heterophylla*), western red cedar (*Thuja plicata*) and Lawson's cypress (*Chamaecyparis lawsoniana*) have all been widely planted and in addition there are extensive relics of the pre-Forestry Commission days, including larch (*Larix*) and scots pine (*Pinus sylvestris*) plantations, many sweet chestnut (*Castanea sativa*), wild service tree (*Sorbus torminalis*) and aspen (*Populus tremula*), and an area of atypical beech (*Fagus sylvatica*) woodland in addition to oak (*Quercus robur*) and hazel (*Corylus avellana*) coppice. This variety of coniferous species, planted over a series of years and existing together with many deciduous 'relics', has resulted in a mosaic of woodland habitats representing many seral stages and geographical zones.

This habitat diversity enables comparisons of different woodland types to be made simultaneously within a single forest complex. This minimizes community differences that might arise from monitoring insect populations in different localities and in attempting to compare different sites with different years' data. This latter is especially hazardous in view of the dramatic population changes many insects are subject to from year to year, which is one of the features of the Malaise trap samples from Bernwood.

Largely on account of the butterfly community present within the Forest, Bernwood has been the focus of much conservation attention, in particular from the Nature Conservancy Council (N.C.C.). From the first Site of Special Scientific Interest scheduling within the Forest in 1951 to the latest Forest Nature Reserve agreement in 1981 the N.C.C. have taken an active interest in the management of Bernwood Forest, and have been successful in instilling conservation measures into the Forestry Commission's commercial management schemes. There are many advantages to pursuing further ecological studies in an area which has already received such attention but it is also vitally important that new management schemes such as the N.C.C. have instigated at Bernwood are properly monitored to confirm their success and provide further data on how they might be improved. Bernwood is viewed as something of a conservation showpiece by the Forestry Commission and it is important that the conservationists use this opportunity to its fullest in the hope that general conservation measures can be reached that may then be recommended to commercial foresters in other situations which are not so tolerant of investigative conservationists.

Malaise traps have been used to monitor insect abundance at sites selected to represent the transition of the Forest from deciduous to coniferous woodland. No method of trapping insects can hope to catch all families with equal probability but the Malaise trap provides the entomologist with samples of low-flying insects with probably the least sample bias of any such technique. The trap does not rely on an attractant and is not subject to human bias in its catching efficiency, which often results in over-representation of rare species in the catches. Its continual operation produces large samples of insects but the catching efficiency is nevertheless low in comparison to the total available population and thus does not have a depletion effect upon the community.

Disney *et al.* (1982) have advocated the use of coloured water trays as a possible standardized method of obtaining samples of aerial insects, but the Malaise trap not only provides larger samples without recourse to eliciting an attraction response within the insect, but also provides a better indication of relative abundance and community structure than do water traps. Disney *et al.* note that

Malaise trap samples of a particular family are frequently dominated by relatively few species, which they regard as a hindrance to sorting out the rare species, but how can a particular trap be more or less efficient than an other at catching common or rare species? J-shaped community distributions abound in the ecological literature and Malaise traps are, through their non-attractant mode of operation, more likely to give a truer indication of community structure than the smaller sample sizes of the water traps.

The choice of the Syrphidae as the family to represent insect diversity has several reasons for commendation. Syrphids are abundant in Malaise trap samples and thus complement the trapping technique used. The syrphids form a distinctive family, which aids their sorting from the trap samples, and their identification to species is taxonomically feasible. Their general abundance has invited study and the potential economic benefit from the aphidophagous species has further encouraged research into these species, and the family contains a wide diversity of larval lifestyles that gives the ecologist information of widely different aspects of the community. This feature is enhanced by the similar lifestyles of the adult syrphids, which, with the exception of *Microdon*, are all feeders upon nectar and pollen.

In spite of these features, little is known of the community structure of hoverflies. Owen, J. (1981) has analyzed Malaise trap samples of syrphids from a Leicester garden and there have been several studies of syrphids in agricultural situations but little is known of their community structure in semi-natural habitats.

This study thus has two principal aims: to investigate the community structure of woodland hoverflies; and to monitor the abundance and diversity of flying insects, as represented by the Syrphidae, along a series of sites chosen to represent the 'coniferization' of Bernwood Forest. The present work is part of a wider research programme being undertaken at the Department of Biology, Oxford Polytechnic, into the insect ecology and conservation of Bernwood Forest.

CHAPTER TWO

Bernwood Forest - the Historical Background

This chapter on the history of Bernwood has been compiled largely from Rowell (1979), an unpublished dissertation held at the Biology Department, Oxford Polytechnic.

Bernwood Forest consists of two distinct pieces of woodland, separated by a field and a road, which also serves as the boundary between Oxfordshire and Buckinghamshire. To the south of the road, in Oxfordshire, lies Waterperry Wood and to the north in Buckinghamshire is a group of woodlands collectively known as the Shabbington complex. This is made up of Shabbington Wood itself, Oakley Wood to the north, York's Wood and Hell Coppice. The Forest covers an area of 399 hectares of generally flat ground between 60 and 90 metres above sea level, to which Waterperry Wood contributes 144 hectares. The woods lie 10 kilometres east north-east of Oxford.

In common with the other woods in the immediate vicinity Bernwood is on Oxford clay, an Upper Jurassic formation whose underground boundaries are often faithfully reproduced by woodland boundaries above (Fig. 2.1). To the west and east Bernwood is bounded by later rocks, including brickearth and oolite (Arkell 1947). Oxford clay is a heavy but fertile soil, subject to compaction in wet

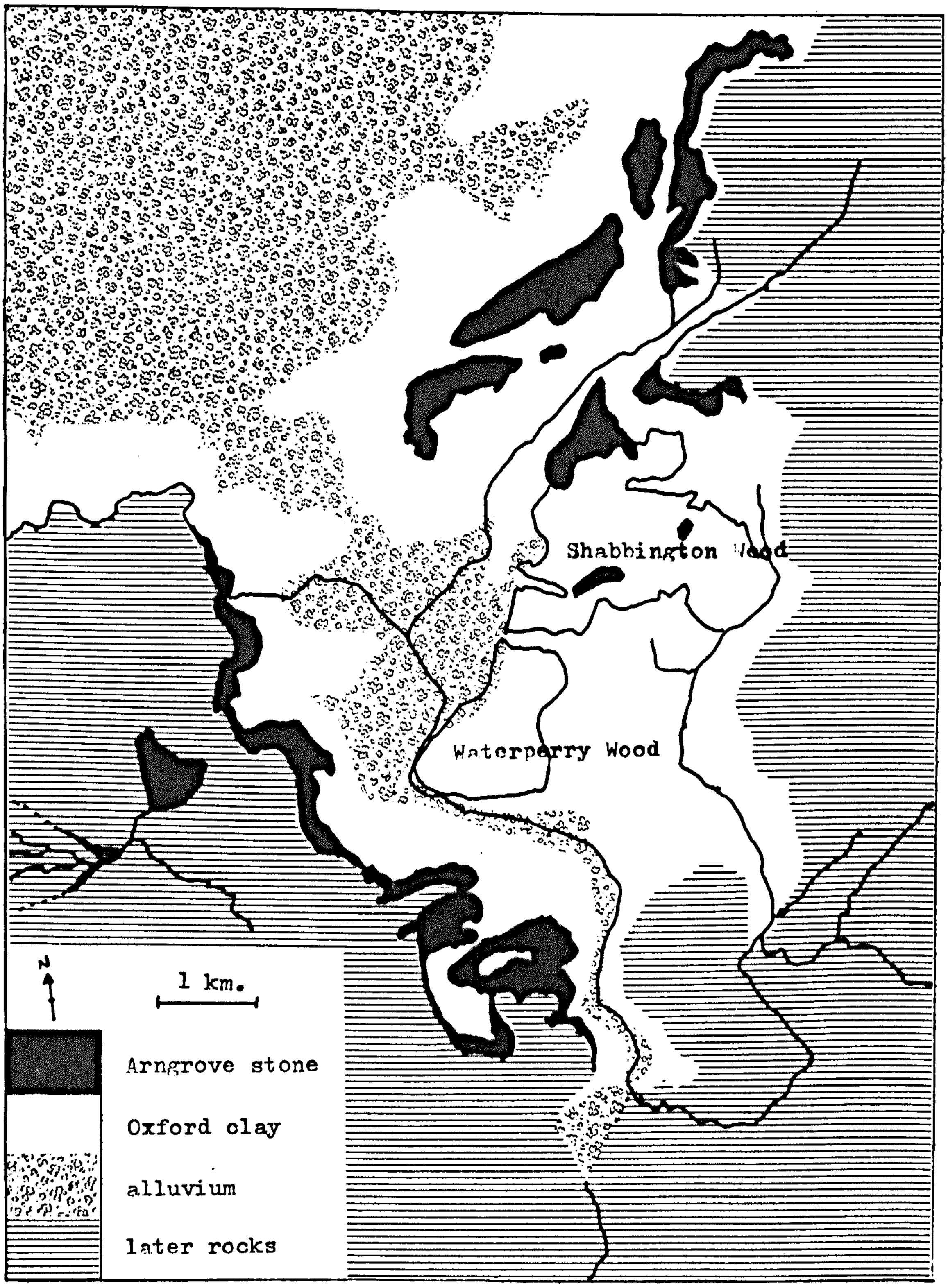


FIG. 2.1 THE GEOLOGY OF THE BERNWOOD FOREST AREA

weather and to drought in dry summers. Annual rainfall in the area ranges between 66 and 76 centimetres.

Most woodland clearance up until and including Saxon times took place only on light soils and thus it is unlikely that much of Bernwood was cut down by man before the Norman Conquest. There is evidence of coppicing within the Forest during Roman times and large amounts of hazel (*Corylus avellana*) are suggested from pollen analyses in Iron Age sumps and wells around Oxford (Robinson 1978). Even in its simplest and most primitive forms coppicing changes the structure and composition of the woodland flora by opening up the canopy and allowing a rich variety of herbs to establish themselves, and further changes to the woodland vegetation would have been brought about by changes in the surrounding vegetation due to agriculture.

The Shabbington complex probably became a separate woodland block during Saxon times. This can partly be assumed from the number of surrounding villages with names ending in "-ley", which in Saxon times denoted a woodland clearing: Wheatley, Beckley, Oakley, Thomley and Studley are all local examples. It was also in Saxon times that the Royal Forest of Bernwood was created as an area to be set aside for the King's hunting, which suggests an open landscape with plenty of cover for game.

Throughout the Middle Ages (1100 - 1600) it is likely that much grubbing up of the Forest occurred; certainly by

1325, one-third of the area of forest present in 1250 had disappeared. Estimates of woodland clearance prior to this date are unreliable due to the vague namings of the woods in the Domesday Book. The primary uses of coppice products in the Middle Ages, namely fencing, poles and firewood, kept the coppicing cycles short at around 4 to 6 years, although some at least must have been carried out on at least two cycles to allow for the growth of longer poles. Standard trees also were left, although these timber trees would have been widely spaced so as not to overshade the understory, which provided the main income. Thus the overall picture is one of open, airy woodland which would have favoured the development of a rich insect fauna. The introduction of the rabbit from France or Spain around the twelfth century may also have had a profound effect upon tree regeneration.

The first Woodland Preservation Act in 1543 was designed to discourage grubbing up of woodland; although previous penalties were exceedingly harsh, they were rarely enforced. This Act required fencing after felling to aid regeneration and to prevent development to pasture. It also laid down a minimum of twelve standards per acre, although even this figure would lead to only around 30% canopy cover (Rackham 1976). Overall, the Middle Ages saw a shift in emphasis in management from pannage to coppicing.

The seventeenth century was a time of great anxiety about the future of timber and really saw the beginnings of modern forestry practices; it was also however a period of great devastation in which many areas lost their standards.

The great demand upon timber for shipbuilding had begun and prices remained high. Shabbington wood was plundered from 1822 to 1824 for timber for the French wars (see Fig. 2.2 for the changing shape of the woods during the 18th and 19th centuries).

Coppicing probably continued in Bernwood until the early 1900s when the demand for coppice products declined rapidly due to the advent of coal, the railways and cheap foreign imports. From this time Bernwood was recognised to be of poor quality, with a hazel rotation of 9 years and oak of 10, and the area would have been further depleted during the Great War of 1914-1918, which also was a period of timber shortage. Ownership of the whole of Bernwood Forest passed to Magdalen College, Oxford, in 1925 with the sale of Waterperry Wood; prior to this sale there was a serious felling of oak standards, with the total oak value over the whole 1000 acres being put at only £7000. Hazel regrowth was also suffering from severe rabbit damage. Perhaps the "best" piece of the forest at this time was Hell Coppice, which had been famous to entomologists since Victorian times; a recollection of this part of Bernwood in the 1930s described it as being "almost entirely of oaks, with a thick undergrowth of sallow, blackthorn and hazel, and a certain amount of aspen and birch: brambles and honeysuckle were abundant" (Symes 1956).

In 1943 Magdalen College sold off all of Bernwood to a timber merchant, which resulted in total devastation of the

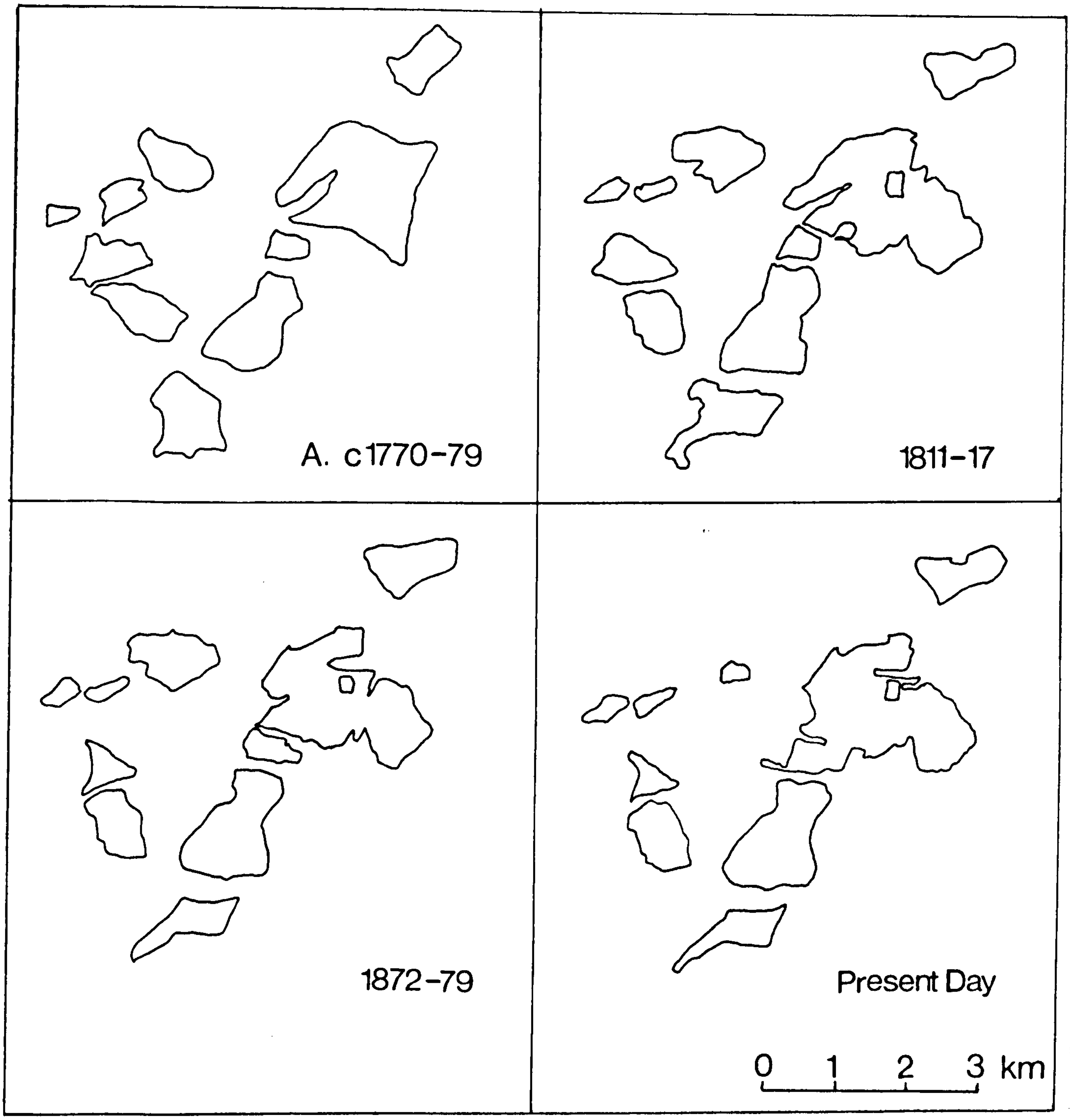


FIG. 2.2 THE CHANGING SHAPE OF BERNWOOD FOREST, 1700 - 1900

woods, removing "practically every tree that can be called a tree" (Forestry Commission records). Most of the felling was completed by 1946 and the woods passed into the hands of the Forestry Commission in 1950-51, needing a drastic rehabilitation of which only a large, Government funded, organisation such as the Forestry Commission could be capable. Ten acres of Hell Coppice were retained by Magdalen College in 1943 because of their unique entomological interest and were not included in the original Forestry Commission purchase, but these too found their way into the hands of a timber merchant and were clear-felled before the Commission acquired them. It was actually during the period of felling that Hell Coppice became a Site of Special Scientific Interest (S.S.S.I): the scheduling was retained by the Nature Conservancy because they thought that the butterfly community present there would not be significantly affected by the felling operations.

The period 1953 - 1960 again was one of great change within Bernwood, with much of the Forest being cleared and then planted up. The first plantings were of oak (*Quercus robur*) and Norway spruce (*Picea abies*), the latter providing a nurse crop for the oak and also some earlier financial return for the Forestry Commission. However, severe spring frosts and the lush growth of grass forced a change in silviculture to the use of overhead cover, by thinning the coppice and planting beneath it. This provoked concern from the conservationists that the range of seral stages present would be removed with a potentially disastrous effect upon the wildlife and lead towards the creation of a Forest

Nature Reserve (F.N.R.) of 60 ha. in Waterperry Wood in 1955. Ten glades were cut the following year under Charles Elton's supervision and thirteen blackthorn areas were selected in the Shabbington Complex to be managed for the black hairstreak (*Strymonidia pruni*) by the Nature Conservancy.

The immediate effect of all these forestry operations upon at least the butterfly community was not significant; however, the 1960s saw greater changes in management with apparent detriment to the entomological fauna. The herbicide 2,4,5-T was introduced to reduce competition for the growing conifers and 1968 saw a major policy change to concentrate on the growing of softwoods. This was followed by further aerial spraying of 2,4,5-T over the Shabbington woods, with some of the valuable deciduous trees being carefully protected. Waterperry Wood was spared from this herbicide onslaught because of its F.N.R. status.

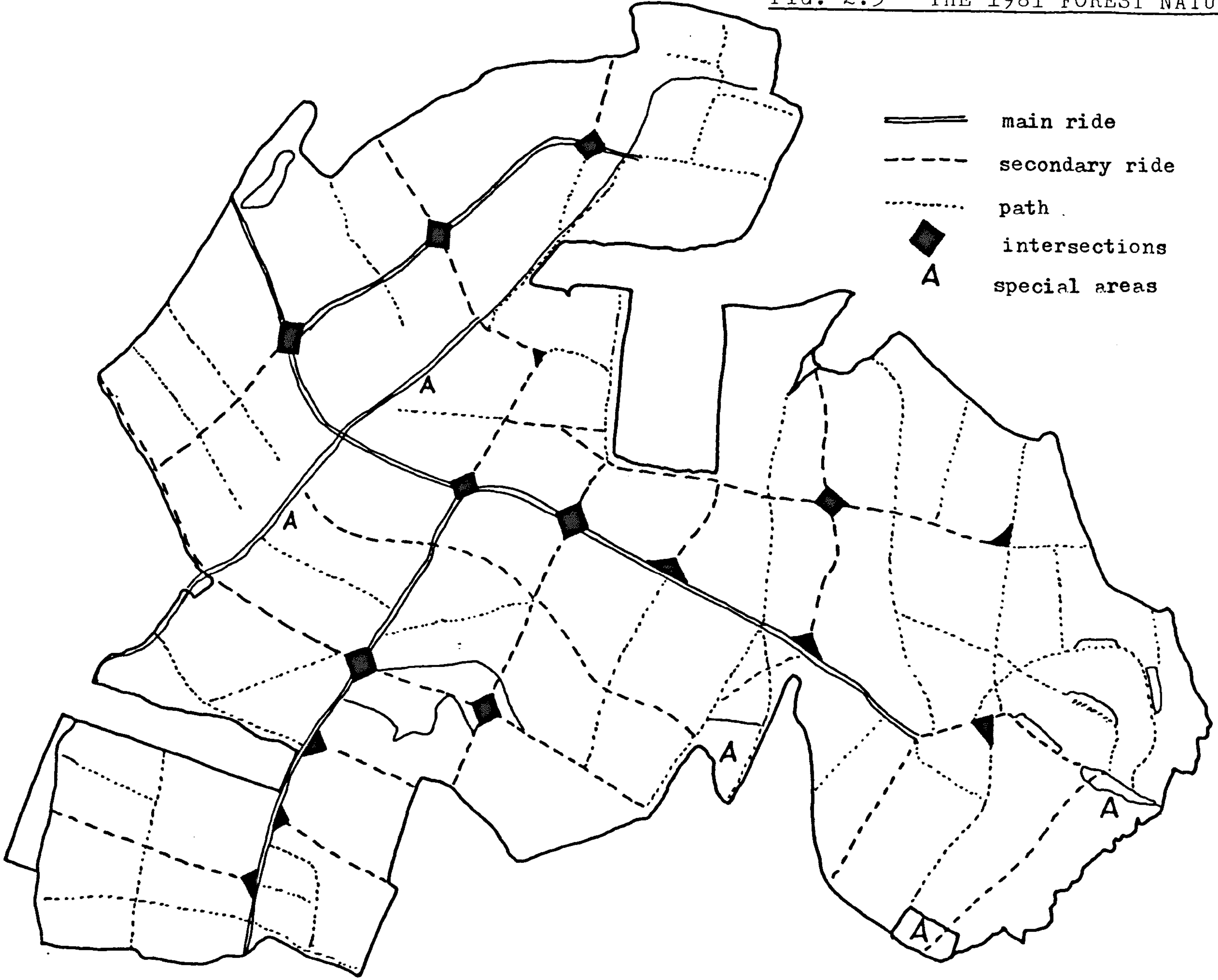
By the early 1970s conifers planted in the 1950s were starting to shade out the narrow rides. Hell Coppice suffered particularly badly in this respect and was deleted from S.S.S.I. status in 1972. The last plantings were done in 1973 with conifers now covering some 80% of the whole area of the Forest and the forestry management now consists of maintenance in anticipation of the felling to follow. This consists mainly of ride cutting although some thinning has also occurred, for example in the larch/oak plantation in Compartment 36 which was carried out during the winter of 1981/82.

The Nature Conservancy Council has maintained a watchful eye over Bernwood since its acquisition by the Forestry Commission, although actual management practices have been difficult to implement due to the lack of labour and finance. The "Elton" glades in Waterperry Wood were initially intended to be cut on a five or ten year cycle, to maintain the range of seral stages; however there was no further cutting after their inception in 1956 until 1963-65, when the growth of the glades and the thinning of the forest around them had effectively caused a reversal in their roles. When they were recut, a zone of scrub was left around the edge and so they are now rather smaller than the originally intended size of one acre. Indeed Waterperry Wood was itself an odd choice of site for the F.N.R; Hell Coppice was traditionally the best site and the smaller Waterperry Wood can be expected to harbour fewer species than Shabbington.

In 1972 a new Forest Nature Reserve agreement was reached which strengthened the N.C.C.'s position regarding the use of herbicides and stressed the importance of the woodland edge as an important entomological habitat. This agreement has been further strengthened by a subsequent agreement in November 1981, which extends throughout Shabbington Wood, with enlarged ride intersections and the maintenance of saucer-shaped rides to provide the seral habitats (see Fig.2.3).

The Berkshire, Buckinghamshire and Oxfordshire Naturalists' Trust have also long been interested in

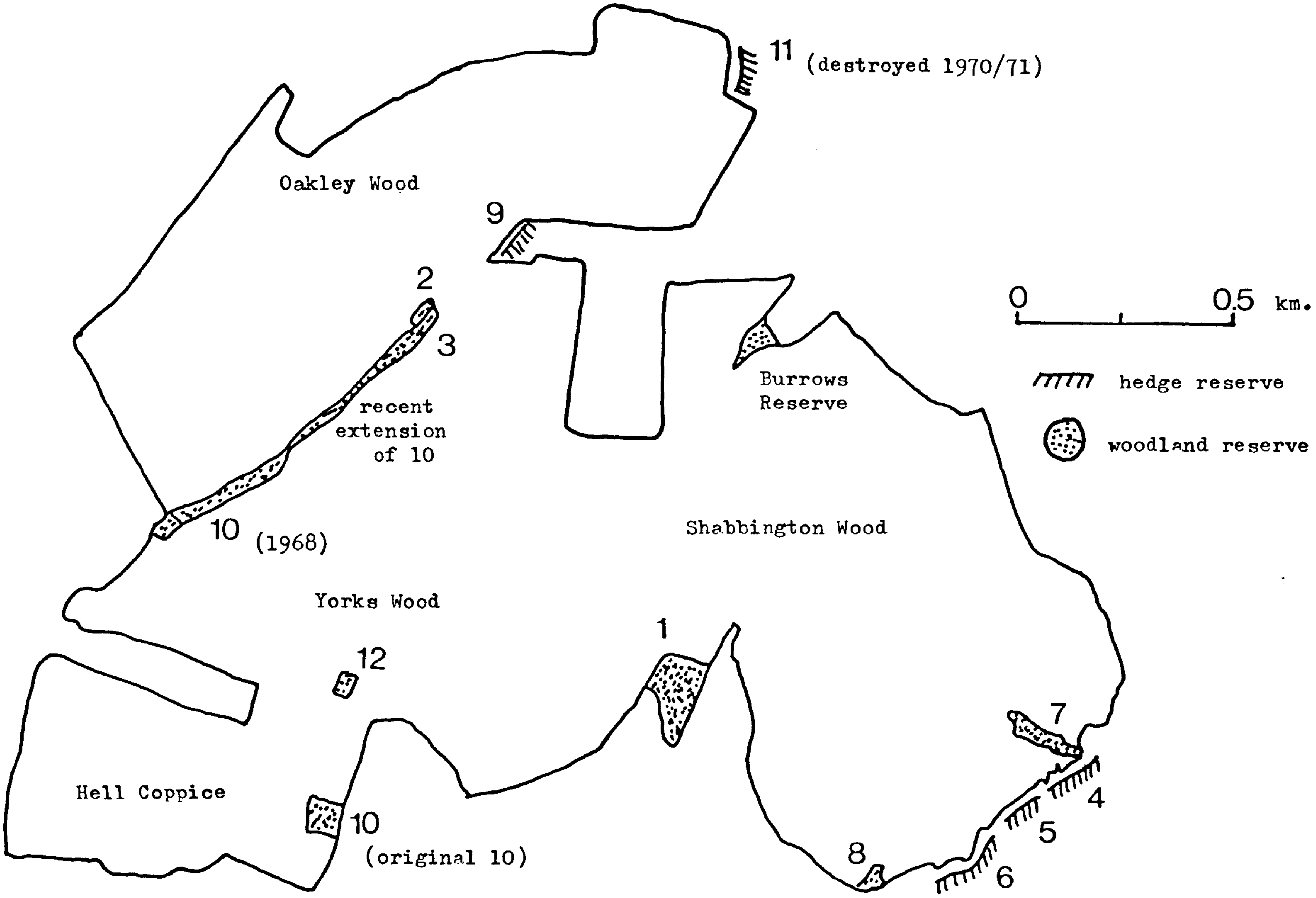
FIG. 2.3 THE 1981 FOREST NATURE RESERVE RIDE SCHEME



Bernwood Forest, with the purchase of the Burrows Reserve in 1966 (Fig. 2.4). This was followed in 1968 by the leasing of seven "Goddard" reserves from the Forestry Commission to manage blackthorn (*Prunus spinosa*) primarily for the black hairstreak, in addition to having five other stretches of hedgerow in gentleman's agreements with the farmers concerned. These reserves all suffer from being small, isolated and expensive to manage and the problems of management aims are compounded by the lack of knowledge about the ecology of the black hairstreak itself.

Despite a turbulent history, especially in recent times, Bernwood has maintained a richness of entomological diversity encountered only rarely within the British Isles. Much of this is undoubtedly due to the wide range of habitats available within its boundaries and also in its position in relation to its outlying woods; both of these facets of its history need to be maintained if Bernwood is to retain its unique status of entomological interest for future generations.

FIG. 2.4 NATURE RESERVES OF THE BERKSHIRE, BUCKINGHAMSHIRE AND OXFORDSHIRE NATURALISTS' TRUST IN THE SHABBINGTON COMPLEX



CHAPTER THREE

Description of the Five Sites

3.1 Site Selection Criteria

The five sites were chosen primarily to reflect the transition in woodland type from old, deciduous to commercial conifer plantation. The mosaic of woodland types and age classes of plantations at Bernwood at the present time makes the site an ideal location in which to study the effects of 'coniferization' of the woodlands on the local insect populations.

Although the main criterion for site selection was the deciduous/coniferous transition, several other factors had to be considered when selecting the five sites. The first constraint was the actual availability of the right kind of site on the ground. The oldest Forestry Commission plantations of *Picea abies* and other typical commercially-used species were less than thirty years old at the commencement of the study and thus an atypical stand of *Pinus sylvestris* was chosen to represent mature coniferous plantations.

The sites were chosen to be within plantation compartments of a similar size, so as to allow for the effects of habitat size on the expected number of species. The old conifer site suffered in this respect in being in a plantation of only 2 to 3 ha. compared with approximately 8 ha. for the other sites. It was impossible to standardize the vegetation surrounding the sites, but placing the traps within the centre of each stand minimised the influences from the vegetation surrounding the site. The sites were also chosen to be fairly close to each other to enable the collections from each site to be made at a similar time of day.

The structure of the vegetation within the sites also influenced selection. Flying insects tend to patrol along borders of vegetation and Malaise traps operate most efficiently when backed up against a vegetation border and placed across an insect flyway. The sites were chosen to have identifiable flyways suitable for trap placement and which might be expected to give comparable catches. The old *Pinus* plantation suffered in this respect because there is no vegetational structure at this site that might channel insects into a flyway; choosing a well-structured site in this respect was the most subjective of the selection criteria.

Bernwood is much frequented by the general public as a recreation area and care was taken to hide all the traps from public view. The sites did however have to have easy access routes and it was important not to create new footpaths which might encourage the public to trespass off the rides. It was not possible to monitor a really young plantation as these were all too open to the public view, interest and possible vandalism.

The Nature Conservancy Council were keen to include one of the Elton glades in the project. These have been managed as conservation areas since 1956 and the present study offered an opportunity to assess their value as conservation areas in relation to the rest of the Forest.

3.2 Description of the Five Sites

The five sites are named according to their relative positions on the deciduous - conifer gradient, with S1 the old deciduous coppice site and S5 the old *Pinus sylvestris* plantation. Photographs of each site, taken on 29 April and 19 August 1981, are given in Figs. 3.1 to 3.10.

S1 lies in Oakley Wood in the north-west of the Shabbington complex, in the Forestry Compartment number 12 (grid reference SP 616118, Ordnance Survey Sheet 164, 1:50,000 series). It covers 9.5 ha. of old, remnant coppice that has seen little management since the advent of the Forestry Commission in Bernwood. The few standards that remain are of poor quality, consisting predominately of *Quercus robur*, with *Corylus avellana* and a few *Betula pendula*; isolated *Fraxinus excelsior*, *Acer campestre* and *A.pseudoplatanus* are also present. There are several fine old *Crataegus monogyna* shrubs, together with *Malus sylvestris* and *Rosa canina*; *Rubus fruticosus* is also abundant. The site is relatively poor in herbaceous plants, with only *Potentilla erecta*, *Viola riviniana*, *Lonicera periclymenum* and *Hypericum spp.* present in any

FIGS. 3.1 AND 3.2 SITE S1, APRIL AND AUGUST 1981

FIGS. 3.3 AND 3.4 SITE S2, APRIL AND AUGUST 1981

FIGS. 3.5 AND 3.6 SITE S3, APRIL AND AUGUST 1981

FIGS. 3.7 AND 3.8   SITE S4, APRIL AND AUGUST 1981

FIGS. 3.9 AND 3.10 SITE S5, APRIL AND AUGUST 1981

abundance. The grasses too are poorly represented, being dominated by *Deschampsia caespitosa* and *Festuca rubra* and the sedge *Carex sylvatica* is also present in restricted abundance. The physical structure of the vegetation layers is weakly defined and there are large areas of bare ground covering almost a quarter of the woodland floor.

S2 is situated in the Clearsale area of Waterperry Wood (grid reference SP 607096). This part of Bernwood was included in the original Forest Nature Reserve agreement and has been designated as a Site of Special Scientific Interest (S.S.S.I.) since the early 1950's. The entomological value of the area was further enhanced in 1956 by the cutting of the Elton glades, although the area was subsequently felled and replanted by the Forestry Commission in 1961. The Nature Conservancy Council were anxious to include this site in the study on account of its history of conservation management. The site lies in Compartment 40 of the Forestry Commission stock maps and covers an area of 9.5 ha.

The trees in S2 consist mainly of*Quercus robur* and *Betula pendula*, together with *Picea abies* which was originally planted along with the *Quercus*; *Corylus avellana* is also present. The shrubs include *Crataegus monogyna* and *Prunus spinosa* with *Rosa canina* and *Cornus sanguinea*, together with an almost continuous carpet of *Rubus fruticosus*. The herbaceous plants include *P.erecta*, *V.riviniana*, *Betonica officinalis* and *Ajuga reptans*, together with rather fewer *Stachys sylvatica*, *Epilobium angustifolium* and *Euphorbia amygdaloides*. *Festuca rubra*, *Dactylus glomerata* and *Deschampsia caespitosa* dominate the grasses, although both *Anthoxanthum odoratum* and *Luzula campestris* are also frequently encountered. Structurally the site is more diverse than S1, with better developed layers and the adjoining glade providing further structural diversity.

S3 is in Compartment 9 of the Forestry Commission plan, in Oakley Wood of the Shabbington complex (grid reference SP 612114). The compartment covers an area of 9.5 ha. The site was planted with *Picea abies* in 1962 and these occur together with *Sorbus torminalis* and lesser numbers of *Corylus*, *Betula* and some *Quercus*. The conifers are planted in dense stands although the trap is situated in a small clearing, which is dominated by a clump of young *Sorbus*. These provide effective shade for the glade once in leaf and must be in part responsible for the lack of shrub and herb layers, the latter of which is particularly sparse. The grasses, however, show more diversity. *Deschampsia caespitosa* is the dominant species but *Brachypodium sylvaticum*, *Anthoxanthum odoratum*, *Festuca rubra* and *Holcus lanatus* are all common, as is *Juncus effusus*.

S4 lies in Foresty Compartment 15, where Oakley Wood merges into York's Wood (grid reference SP 616113). The 6.5 ha. were planted up in 1959 with a mixture of *Picea abies* and *Quercus robur*, supplemented in 1970 by a border of *Tsaga heterophylla*, which does not occur within the vicinity of the trapping area. The plantations occur in dense blocks separated by grassy avenues approximately 3 m. wide. The shrub layer consists largely of *Crataegus*, with some *P.spinosa* and a small amount of *Rosa canina*, together with large amounts of *Rubus*. The overgrown, grassy avenues support a variety of flowering plants, including *Angelica sylvestris*, *Cirsium palustre*, *Succisa pratensis*, *Lonicera* and *Hypericum spp*. The structure of this site thus consists of two distinct components : dense stands of conifers interplanted with a few *Quercus* and the overgrown grassy avenues separating the plantations. The avenues also contain a considerable diversity of grasses, *Festuca rubra*, *Deschampsia caespitosa* and *Anthoxanthum odoratum* all being common, together with smaller amounts of *Arrhenathenum elatus*, *Calamagrostis epigejos* and *Holcus lanatus*; both *Carex* and *Juncus* species are also present.

The fifth site, S5, consists of an older *Pinus sylvestris* plantation planted by Magdalen College in 1939 in what is now Compartment 23, in York's Wood (grid reference SP 612108). The tree layer is composed exclusively of *Pinus* and there is no shrub layer, resulting in a site with almost no structural diversity other than the trunks of the trees reaching up to the canopy 7 m. above. The ground flora is, however, relatively well developed. In May and early June the forest floor is a carpet of *Endymion non-scriptus* and *Lamiastrum galeobdolon*, *Stachys sylvatica*, *Lapsana communis*, *Circaea lutetiana* and *Geranium robertianum* are all common. *Rubus* trails over much of the forest floor and there is much bare ground; of the grasses only *Brachypodium sylvaticum* is abundant, although *Deschampsia caespitosa* and *Festuca rubra* also occur here.

3.3 Methods of Sampling the Five Sites

Each of the five sites was sampled to obtain data on three aspects of the vegetation present: floral composition; vegetational structure; and seasonality of flowering. These three aims of the sampling necessitated different approaches.

The floral composition of each site was determined by obtaining presence/absence data from 40 0.5 m. square quadrats thrown randomly with a 10 m. radius of each trap, 10 quadrats being thrown in each quadrant. This sampling was carried out in August of both 1980 and 1981, but not in 1982. These data are presented in Appendix 1 and are used in the site ordinations.

Vegetational structure was determined through systematic sampling along a 20 m. grid positioned with the Malaise trap at the grid's centre. The height of the vegetation above ground was measured at 1 m. intervals, together with presence or absence of overhanging canopy. These data were converted to height classes from which percentage frequency for each vegetational layer was calculated.

Seasonality of flowering was assessed semi-quantitatively each week by ranking by eye the plants actually in flower on a five-point scale. This gives an indication of each species' potential as a food source each week of the trapping season, to determine whether or not syrphid abundance is correlated with the amount of available food for the adult flies.

3.4 The Distribution of the Five Sites Along the Deciduous - Coniferous Gradient

The data from the 20 m. by 20 m. grid contain the species of tree encountered during sampling and these can be converted to simply deciduous or coniferous, or mixed if both types of tree intercept the point quadrat, to place each site along the deciduous - coniferous gradient. This sequence of sites is clearly demonstrated in Fig. 3.11.

S1 is almost exclusively composed of deciduous trees whereas S5 contains no deciduous trees at all. S4 is also heavily dominated by exclusively coniferous point quadrats. Half of the tree-containing quadrats at S2 are exclusively deciduous with the other two categories sharing similar proportions of the remaining points, giving a total deciduous value of 75% overall. The three categories are present in roughly equal proportions at S3. The number of tree containing quadrats within the grid ranges from 118 at S2 to the maximum possible of 400 at S5.

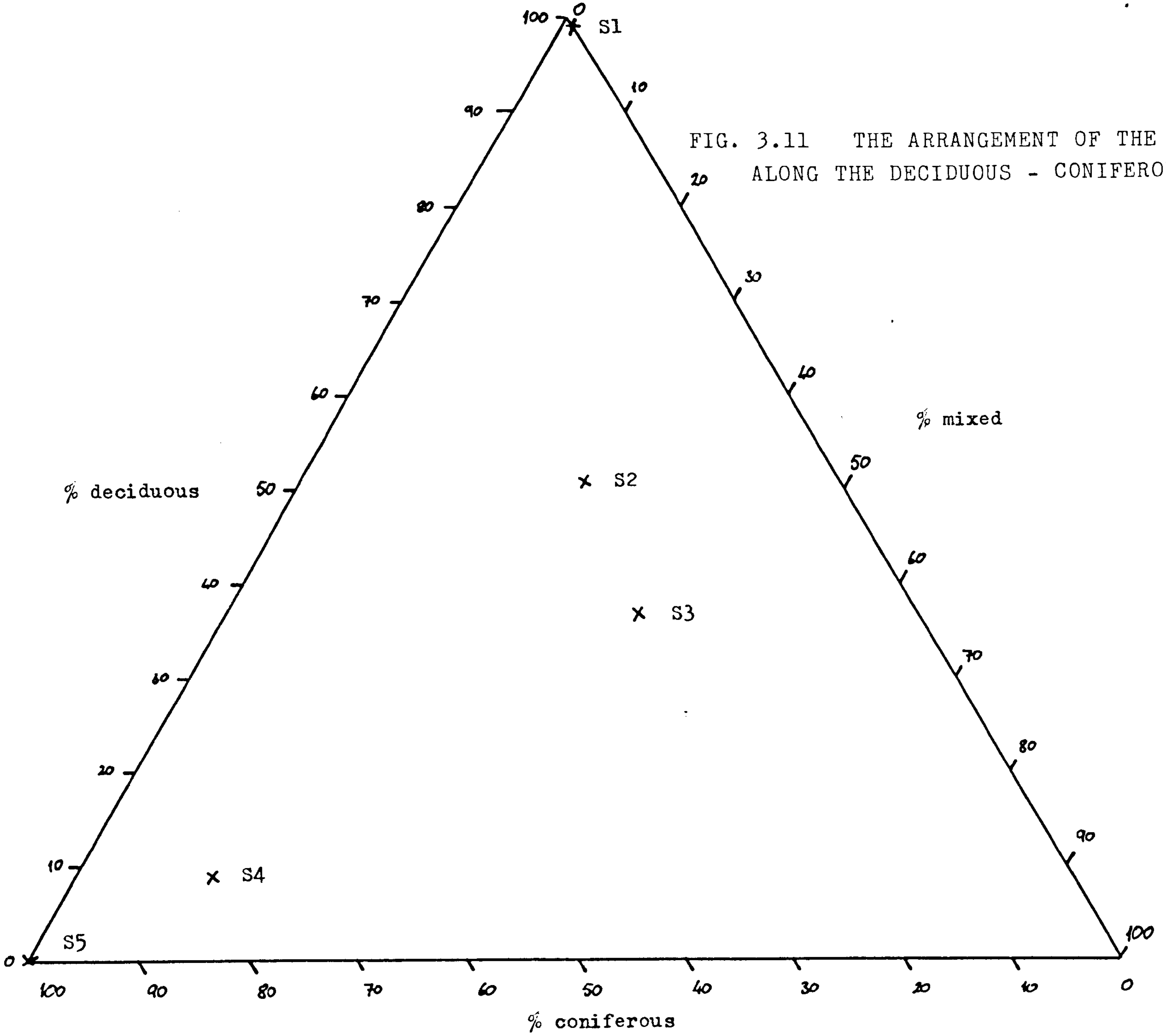


FIG. 3.11 THE ARRANGEMENT OF THE FIVE SITES ALONG THE DECIDUOUS - CONIFEROUS GRADIENT

3.5 Site Similarity Indices

Table 3.1 gives both Sorensen's and Gleason's similarity coefficients calculated from the random quadrat data from 1980 and 1981; the former uses only presence and absence data whilst the latter takes into account the relative abundance of the species present.

The Sorensen index shows S2 and S4 to be the most similar sites for each of the two years' data. S1 is the most similar site to S2 for both years but both S3 and S5 are calculated to be most similar to a different site in each year.

The Gleason index results show more variation than do the Sorensen index between the two years, but the similarity of the actual values requires caution in the interpretation. Only S3 and S5 appear markedly different to the other sites and to each other.

Ranking of the sites by their similarity to both S1 and S5 in turn gives a reasonably good fit with the transition from deciduous to coniferous sites (Table 3.2) Gleason's index gives a more consistent ranking than does Sorensen's but S3 and S4 have exchanged places with regard to the expected order along the transition of the sites: only Sorensen's 1980 data give the expected ranking. S4 clearly bears more relation to the two deciduous sites than is apparent simply from the type of tree found there.

TABLE 3.1

SITE SIMILARITY INDICES FOR THE FIVE TRAPPING LOCATIONS S1-S5 BERNWOOD FOREST, 1980 AND 1981

1980

SØRENSEN

S2	60.9				
S3	58.8	52.4			
S4	55.0	70.8	61.1		
S5	15.4	17.6	27.3	28.6	
	S1	S2	S3	S4	S5

GLEASON

S2	56.8			
S3	46.1	41.9		
S4	58.8	55.0	41.9	
S5	16.6	17.3	23.0	20.8
	S1	S2	S3	S4

1981

SØRENSEN

S2	63.0			
S3	59.6	69.1		
S4	61.1	73.7	64.0	
S5	22.2	37.7	34.8	25.0
	S1	S2	S3	S4

GLEASON

S2	66.2			
S3	55.7	53.6		
S4	58.5	60.0	54.1	
S5	24.6	24.9	32.0	22.2
	S1	S2	S3	S4

TABLE 3.2

SITE RANKINGS FROM SIMILARITY INDICES

a. Starting from S5 : Sites ranked in order of increasing similarity with S1

SØRENSEN	1980	S5 -- S4 -- S3 -- S2 -- S1
	1981	S5 -- S3 -- S4 -- S2 -- S1
GLEASON	1980	S5 -- S3 -- S2 -- S4 -- S1
	1981	S5 -- S3 -- S4 -- S2 -- S1

b. Starting from S1 : Sites ranked in order of increasing similarity with S5

SØRENSEN	1980	S1 -- S2 -- S3 -- S4 -- S5
	1981	S1 -- S4 -- S3 -- S2 -- S5
GLEASON	1980	S1 -- S2 -- S4 -- S3 -- S5
	1981	S1 -- S2 -- S4 -- S3 -- S5

3.6 Principal Components Analysis

A standardized Principal Components Analysis (PCA) was run using each of the two year's plant abundance data. The latent vectors from the principal species accounting for the majority of the variation are given in Table 3.3 and the ordinations from the correlation matrices in Figs. 3.12 and 3.13 for 1980 and 1981 respectively.

The ordinations for each of the two years are almost identical. This is to be expected because the essential floral characteristics of the sites ought not to change over the course of a single year but it does demonstrate that the sampling procedure was adequate to produce replicate results. The principal species accounting for the variation are the four tree species which dominate the sites' characters: these are *Pinus sylvestris*, *Picea abies*, *Sorbus torminalis* and *Quercus robur*. These species all have high latent vectors in the analysis in both years as do *Lonicera periclymenum* and *Festuca rubra*.

S1, S2 and S4 are characterized by *Quercus*, *Lonicera* and *Festuca*, with S4 separated slightly from the other two sites along the second principal component (PC II) by *Picea*. Both S4 and S5 are clearly separated from this group and from each other, the former by *Sorbus* and *Picea*, the latter by *Pinus*. The sequence of sites across both ordinations does not fit the transition of woodland type from deciduous to coniferous faithfully, with S4

TABLE 3.3

LATENT VECTORS FOR THE FIRST TWO PRINCIPAL COMPONENTS OF THE SITE VEGETATION PRINCIPAL COMPONENTS ANALYSIS

1980

PC I 46.29% variance		PC II 29.17% variance	
Pinus sylvestris	-.5440	*Sorbus torminalis*	+.6976
Quercus robur	+.4284	*Picea abies*	+.3540
Lonicera periclymenum	+.3589	*Pinus sylvestris*	-.3509
Festuca rubra	+.3475	*Quercus robur*	-.3233

1981

PC I 46.83% variance		PC II 26.13% variance	
Pinus sylvestri	-.4712	*Sorbus torminalis*	+.5882
Lonicera periclymenum	+.4067	*Picea abies*	+.5179
Quercus robur	+.3446	*Quercus robur*	-.3155
Festuca rubra	+.3325	*Pinus sylvestris*	-.2480

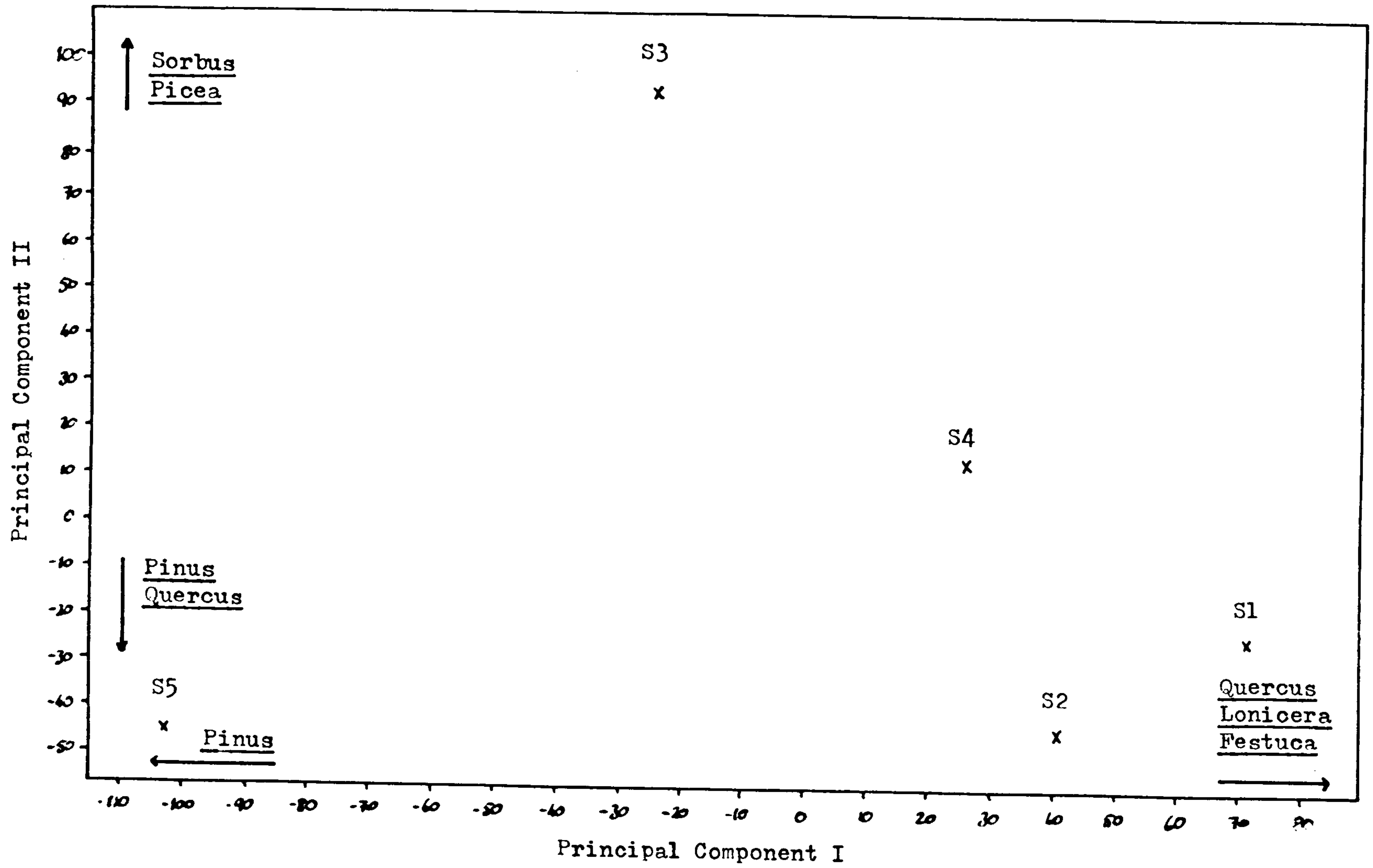


FIG. 3.12 PRINCIPAL COMPONENTS ANALYSIS OF PLANT ABUNDANCE AT THE FIVE SITES, 1980

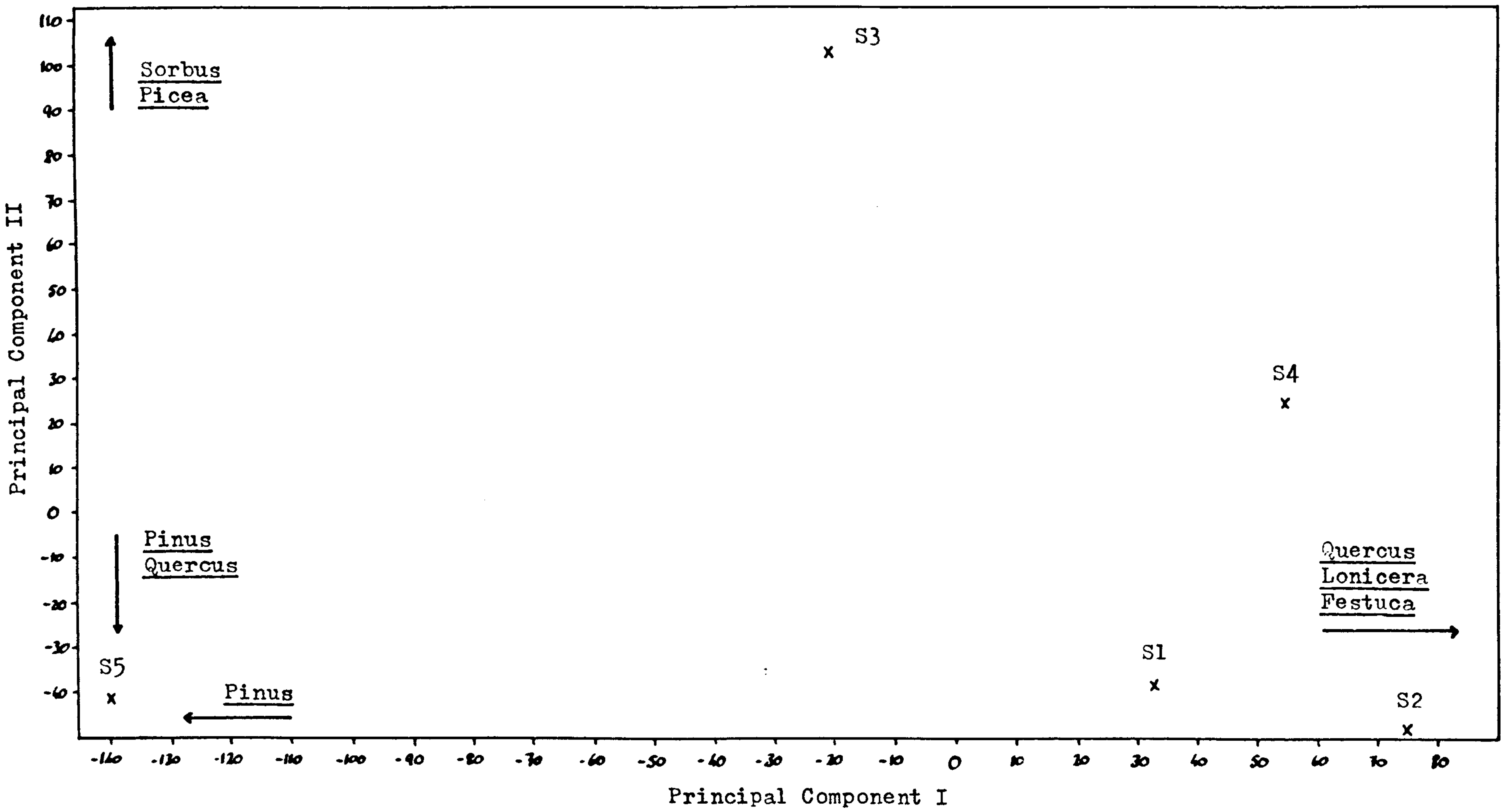


FIG. 3.13 PRINCIPAL COMPONENTS ANALYSIS OF PLANT ABUNDANCE AT THE FIVE SITES, 1981

associating with the two deciduous sites. This is in line with the results of the Gleason index for both years and the Sorensen index for 1981. The presence of the avenues between the dense plantings at S4 clearly allows certain of the essential features of deciduous woodland to be retained in this conifer-dominated site.

3.7 Seasonality of Flowering

Kite diagrams of the flowering phenology for all three years are given in Appendix 1. These data are summarized in Table 3.4, which gives the number of species and overall flowering abundance for the three years.

Site ranking by flower abundance is similar in all three years, with 1981 and 1982 giving identical rankings. S4 is the best site in these two years whereas in 1980 flowering was most abundant at S1. S3 produced consistently poor records of flowering abundance in all three years, as did S1 in the latter two years and S5 in 1981.

3.8 Site Structural Characteristics

The vegetational structure of each of the five sites is presented diagrammatically in Fig. 3.14, which gives the proportion of the vegetation falling within each of six height classes, which range from bare ground to overhanging canopy. The sites separate out into two groups.

TABLE 3.4

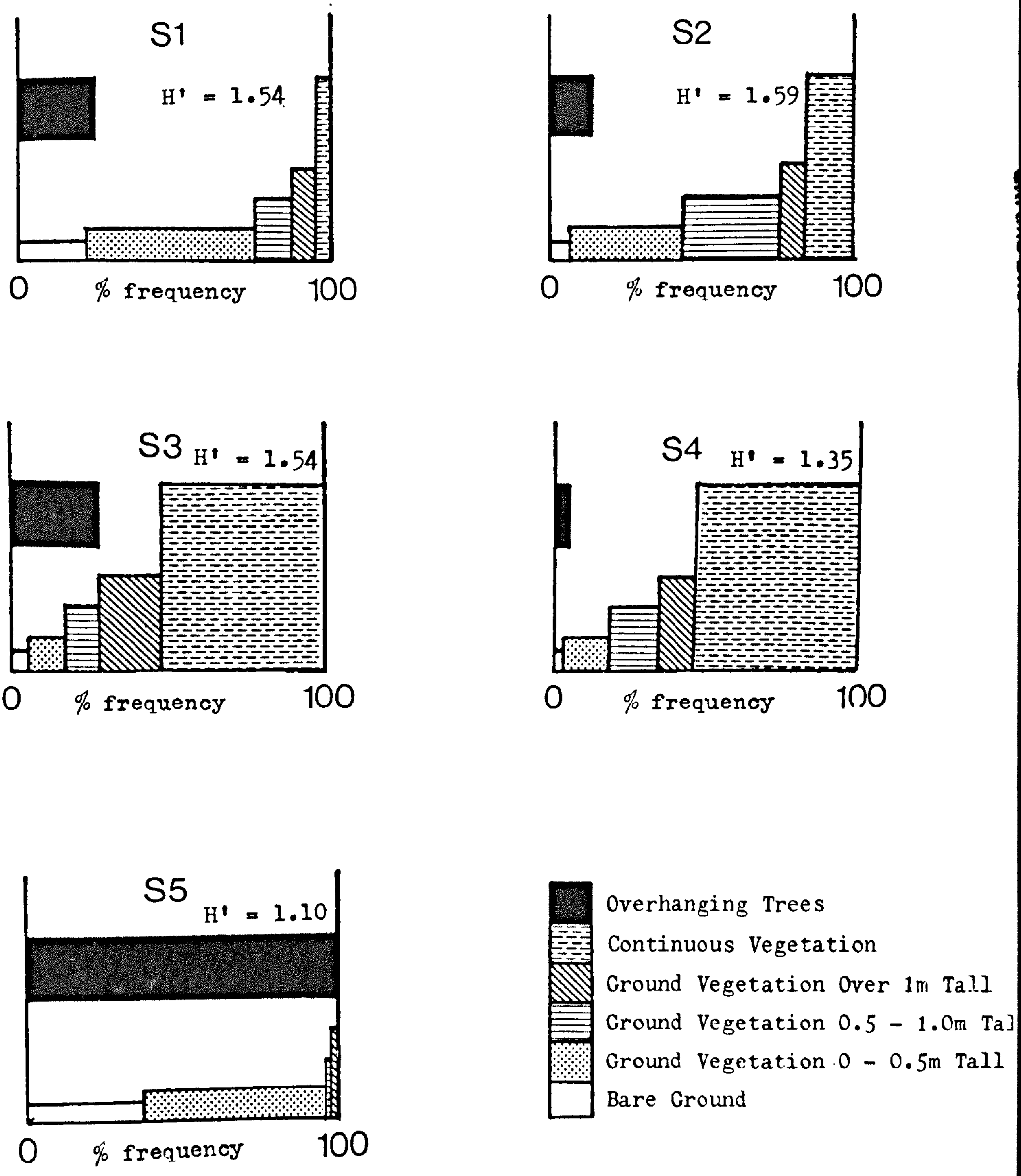
FLOWERING SUMMARY AT THE FIVE SITES

BERNWOOD FOREST 1980-1982 : NUMBER OF SPECIES AND ABUNDANCE

	No.of Spp.	Abundance	No.of Spp.	Abundance	No.of Spp.	Abundance
S1	11	119	8	70	7	74
S2	14	183	10	135	12	120
S3	10	79	9	41	9	30
S4	12	169	11	141	10	132
S5	11	135	9	81	8	112

The abundance figures are the product of weekly estimations of flowering abundance on a five point scale, from 'very scarcely abundant' giving 1 flowering credit to 'abundant' giving 5.

FIG. 3.14 SITE VEGETATION STRUCTURE: THE PERCENTAGE FREQUENCIES OF VEGETATION IN SIX VERTICAL ZONES AT THE FIVE SITES



The closest similarity from this structural analysis is shown between S3 and S4. Approximately 50% of the vegetation at both these sites forms a continuous layer from forest floor to canopy. The three classes of ground vegetation occur in similar amounts and there is little bare ground at either site. The major difference in structure between the two sites is in the amount of overhanging canopy. S4 receives the least shade of any of the five sites whereas S3 has more than 25% of its point quadrats overhung by tree canopy.

The second group of sites does not feature the large proportion of continuous vegetation but is dominated by the low vegetation less than 1 m. tall. S5 is different from the other sites in having a continuous canopy cover over the whole site, with bare ground accounting for 30% of the ground area and low herbs less than 0.5 m. tall a further 60%. This site is almost totally devoid of tall herbs and shrubs.

S1 and S2 share a similar structure, although the former site has more bare ground and low herbs that the latter. S2 on the other hand has a greater proportion of taller herbs and continuous vegetation, and a more even spread of the five ground layers. Both sites have a similar amount of overhanging canopy.

Overall, the two deciduous sites share a similar structure as do the two *Picea*-dominated sites, with S5 being somewhat different, with its continuous canopy and poorly developed taller herbs and shrubs. These structural summaries do however take no account of the spatial arrangement of the different layers on the ground, which is an important factor governing the abundance of insects.

CHAPTER FOUR

Sampling the Five Sites : Malaise Traps

A Malaise trap was used to collect the insect samples at each of the five sites in Bernwood and no attempt was made to supplement this technique. The trap is the invention of Rene Malaise, a Swedish entomologist and traveller who published the details of his new trap in 1937. Malaise had often noticed that whenever insects had entered his tent, they tended to accumulate at the ceiling corners rather than escaping through the open door. On one occasion there happened to be a small hole in the roof of his tent, through which all the insects managed to escape, in spite of being unable to find their way out of the open tent door. Thus the idea occurred to Malaise that "if insects could enter a tent and not find their way out, and persistently tried to reach the ceiling, a trap, made as invisible as possible and put up at a place where insects are wont to patrol back and forth, might catch them much better than any tent and perhaps better than a man with a net, as a trap could catch all the time, by night as well as by day, and never be forced to quit catching when it was best because dinner-time was at hand" (Malaise 1937).

The Malaise traps used in Bernwood are the design of Townes (1972) and were manufactured by Marris House Nets of Duxford, Cambridge (Figs. 4.1 and 4.2). These traps are made from a fine mesh terylene gauze of a dark red-brown colour, with white roofs. The collecting jar attachment is improved over the original Townes design (Fig. 4.3) enabling

FIGS. 4.1 AND 4.2 THE MARRIS HOUSE 'TOWNES' LIGHTWEIGHT MALAISE TRAP

FIG. 4.3 THE COLLECTING TUBE OF THE MARRIS HOUSE 'TOWNES' MALAISE TRAP

the trap to be erected using poles of any diameter rather than the particular size required by the metal sleeve on the Townes model and the attachment of the cloth roof to the metal connector plate is by a jubilee clip rather than by bolts perforating the cloth, which are more likely to cause the material to tear. The trap samples an air space of 2.6 m^3 with each open side offering a capture area of 1.82 m^2.

All the samples were collected in 70% alcohol rather than by using a dry knockdown agent, such as 'Vapona' strips, which is favoured by some entomologists because of the ease of identifying dry specimens. Alcohol does however possess its own advantages. Because it acts as a preservative, the traps only need to be emptied once a week, offering a valuable time-saving over the more frequent trap visiting required to procure good quality specimens from dry collecting methods. The handling and storage of wet specimens is considerably easier because the need to pin out every specimen is eliminated, affording considerable savings in the time, space and money for the curating of the samples.

The siting of the trap in each stand is of crucial importance for the quantitative assessment of the five sites. The traps were located with the small end backed up against vegetation with the front end (containing the collecting jar) toward the open and toward the light, the position which Townes (1972) recommends for optimum catching efficiency. This however proved impossible at S5 where there is no well developed vegetation against which to back the trap up and the lack of any physical channelling of the insects in this site by the vegetation may have adversely affected the collections from S5. The trap at S4 was located out of the main avenue for the opposite reason: the strongly defined avenues through the dense *Picea* stands are likely to act as migration channels for insects atypical of the site. It was impossible to orientate the five traps on a common compass bearing due to the physical constraints of the vegetation at each site, but the exact microlocation and orientation within each site was used for each year's sampling.

Malaise traps have many features which commend them to the long term study of insect communities. The lack of attraction to a bait is an important feature of the traps that enhances the random nature of the catches. This means that insects from many orders are captured with similar probability, dependent only upon the degree of flight activity. The lack of bait also ensures that the captured insects are of local origin, which is important when using the traps to describe the aerial insect fauna of a particular locality or habitat. The colour of the traps does markedly affect the catches obtained and must therefore introduce some bias amongst the collection. Townes (1972) found that the combination of a white top and black sides increased the catch by 70 to 80% over an all-white trap but the least ambiguous ecological interpretation ought to favour the use of an invisible trap.

Malaise traps operate continuously day and night without any need for attention from a human operator. This enables large samples to be obtained with minimum of effort, which allows the operator the large amounts of time necessary in the laboratory to sort the samples. It is this continuous operation that contributes largely to the efficiency of the trap, with the annual catch from a Kampala garden estimated at 113,538 insects belonging to 13 orders (Owen D. 1983). Diptera, Hymenoptera, Hemiptera and Lepidoptera accounted for at least 90% of collections from four zoogeographic regions; Diptera vastly outnumbered the other orders, being 2.5 to 7.5 times as abundant as the second place order, which is typically Hymenoptera (Matthews and Matthews 1971). Coleoptera and Hemiptera tend to be under-represented in Malaise trap samples because they show less tendency towards free flight and a greater tendency to drop when disturbed.

As a tool for investigating the entomological diversity of a site the Malaise trap has few equals. A trap operated at the intensively studied site of Evans' Old Field, Michigan, dramatically increased the species list, particularly of Diptera and the smaller Lepidoptera, at a site where it was believed that the insect fauna was well known (Evans and Owen 1965). Similarly, Breeland and Pickard (1965) found that of 29 species of mosquito known to occur in their study area, Malaise traps collected 27, compared with 19, 16 and 13 species collected by more traditional methods. Indeed Owen D. (1983) believes that the trap could be the surest method of obtaining scientific immortality, because by running a Malaise trap for long enough, particularly in tropical regions, one is bound to collect species new to science which might then bear one's name!

The trap's most useful virtue is that it is eminently suitable for providing quantitative data for a variety of ecological investigations. This potential was probably first recognised by Evans and Owen (1965) who used the trap to measure flight activity, relative abundance and seasonal changes in numbers and sex ratios. Owen has further used Malaise trap samples to compare the catches of tropical Sphingidae with those from light traps (Owen, D. 1969a); to provide evidence in understanding the seasonal cycles in equatorial vertebrates (Owen and Owen 1974); and to quantify insect movements and migrations (Owen, D. 1983). Malaise traps have been used to quantify the direction of insect movements, from the movements of Trichoptera along a small Swedish stream (Svensson 1974) to the migrations of butterflies in Florida (Walker 1978). Long term studies of insect abundance include those of Denlinger (1980), who has monitored the seasonal and annual variation of insects in the Nairobi National Park over five years, and the ten year monitoring of insects in a Leicester suburban garden (Owen, J. 1981,1983)

Despite this diversity of applications, the Malaise trap was largely ignored for 25 years, until 1962, when two designs were published independently by Gressitt and Gressitt (1962) and Townes (1962). The former design has a collecting tube at each end of the trap and the catch is separated according to the direction from which the insect entered the trap. Townes' design collected insects from four sides, representing a considerable refinement over Malaise's original unidirectional trap, and it became commercially available. It was, however, heavy and difficult to make and several variations followed by various authors (see Steyskal (1981) for a partial bibliography). The most widely used design today is that of Townes (1972) which, although two-sided, is similar in efficiency to his previous design of 1962 (Townes 1972). Four-sided designs continue to be used, however, and Yano *et al.* (1975) have modified that of Nishida *et al.* (1970) and used it extensively in faunal studies of paddy fields in Thailand, the Philippines and Hong Kong. No doubt it is this amenability to an almost infinite variety of modifications that is partly responsible for its continued and increasing acceptance (Matthews and Matthews 1971), but widespread acceptance of a standard design would enable better comparisons to be made between different studies.

In summary, the Malaise trap is an efficient tool for catching large and relatively unbiassed samples of flying insects which are representative of the habitat in which the trap is located. Standardized designs allow the replication and comparison of samples from different areas which may be put to a variety of ecological applications.

CHAPTER FIVE

Taxonomy of the Bernwood Syrphidae

5.1 Introduction

The Syrphidae were first clearly separated from the rest of the Diptera by Moses Harris in 1776 with their inclusion as orders II and III of his five orders of *Musca* L. Full family status was not recognised until Latreille's grouping of the genera of Diptera into twelve serially numbered families in 1802-05, where his *Syrphiae* formed family number ten. Meigen used the family name *Syrphici* in his major work on the European Diptera in the early 1800s after its introduction in 1817 by Fallén. The present family name of Syrphidae was introduced by Leach in 1819 and was immediately adopted by Samouelle in the same year and thereafter passed into general use (Goffe 1952).

The Syrphidae form one of the six families of the Aschiza section of the sub-order Cyclorrhapha. Members of these families do not possess a ptilinum with which to escape from the puparium and thus the adults do not have the frontal suture characteristic of the Schizophora. The Syrphidae are one of the most sharply defined families of Diptera, possessing the characteristic wing features of a false vein lying between Veins 3 and 4, and a false margin formed by the two marginal cross-veins running almost parallel to the hind edge of the wing. These two features, in particular the latter one, enable hoverflies to be readily sorted from the Malaise trap samples; doubtful specimens can be checked using Unwin's (1981) key to the families of British Diptera.

The 250-odd species of hoverflies found in Great Britain are placed into two subfamilies, the Syrphinae and the Milesiinae. The Syrphinae in particular have been subjected to many classification revisions of creation and deletion of genera; current views follow the former trend and the nomenclature used in this study follows that of the Biological Records Centre Checklist (1977). This classification recognises 25 genera of Syrphinae and 45 in the Milesiinae, with 95 and 146 species respectively. This species list is by no means a complete one but it is the most workable of the various classifications; indeed one species not on the B.R.C. list, *Dasysyrphus friuliensis*, was captured at Bernwood in 1980.

Identification of the British hoverflies is still centered around the Royal Entomological Society of London key (Coe 1953), although an entirely new key, of which I have a manuscript copy, is currently being prepared by Alan Stubbs. Considering the level of interest in the Syrphidae in recent years, Coe's key has proved to be remarkably robust, although it does have its problem areas: the new key is designed for a 'popular' audience in that it uses only fairly readily discernable features. Coe's key also suffers from extensive lumping of genera, especially within the

Syrphinae: in total Coe recognises 13 genera of the Syrphinae and 41 genera of the Milesiinae. In reality this is a minor problem that can be readily sorted out, with both Vockeroth (1969) and Speight *et al.* (1975) providing clear generic keys and nomenclature.

Coe's key thus provided the backbone work from which the Bernwood syrphids were identified. The key was, however, used in conjunction with the manuscript copy of Stubbs' key and with recent papers on hoverfly taxonomy: amendments and comments to the standard work are given below. My identifications were checked against the specimens held in the Hope Collections in the University Museum of Oxford; troublesome specimens have kindly been checked by Alan Stubbs, Philip Entwistle and Martin C.D. Speight.

5.2 Notes on the Generic Determinations of Syrphidae

The chief problem of Coe's generic keys lie within his genus *Syrphus*, which contains nine genera recognised in the B.R.C. checklist. Nomenclature apart, Coe's *Syrphus* contains two major divisions that are based upon features that are tricky to ascertain with specimens stored in alcohol.

The lateral beading of the tergites used in couplet 7 can often become slightly deformed with wet specimens, making it difficult to ascertain whether the beading extends for the entire length of the tergite. Couplet 28 makes use of 'obvious' hairs on the anterior portion of the mesopleura, immediately behind the prothoracic spiracle. These are often extremely difficult to recognize on wet specimens, even under good lighting conditions. Some of Coe's other section-splitters within his *Syrphus* are tricky for the beginner until one has become familiar with both alternatives; an example is the presence or absence of a series of minute chitin strips on the actual hind margin of the wing used in couplet 29.

Stubbs' generic key overcomes these difficulties. His tribe Syrphini, which encompasses all of Coe's *Syrphus*, is split largely on the patterns of the yellow markings on the tergites and on obvious differences in wing venation; the use of the shape of the yellow spots on the second abdominal tergite is particularly effective. One of Stubbs' characters does, however, need considerable caution, especially with wet specimens: this is the distinction between pale or dark posterior humeri. *Melangyna*, *Meliscaeva*, *Parasyrphus* and the subgenus *Meligramma* all benefit from Stubbs' use of the second abdominal tergite, together with other features, such as the predominately black legs and stigma of *Parasyrphus*. This genus also has black markings on the sternites, a useful characteristic that the keys do not mention. *Epistrophe* too benefits from Stubbs' key, which uses the combination of the point of contact of Vein R 4+5 and yellow femora, together with the slightly dubious posterior humeri feature already mentioned; nevertheless, this is a more confident separation than Coe's.

Male *Melanostoma* and *Platycheirus* specimens can easily be distinguished by the curiously flattened and dilated fron tibiae and/or tarsi of *Platycheirus*, as Coe suggests. The 'noticeably broad and flattened' tarsi and tibiae of the females are however tricky to distinguish and the females of these two genera are best separated by the characteristic triangular-shaped yellow markings on tergites 3 and 4 of *Melanostoma*. Melanic females can be separated using the differing extent of scelerization on the hind coxae, a feature which has caused the transfer of Coe's *Melanostoma ambiguum* to *Platycheirus* (Andersson 1970).

Coe's other generic separations work well, although Stubbs' treatment of the Cheilosiinae, with its split inot three tribes, is rather easier to use: Coe's features of fine bristles, as opposed to fine hairs, along the leading edge of the wing (couplet 3) and of long hairs between the prothoracic spiracle and the convex, swollen part of the mesopheura (couplet 12) need care and experience. Stubbs' key overall is very much easier to use and it works well; it must be borne in mind that the minor criticisms are directed to a pre-correction manuscript copy of this key and not to a well-proven finished product.

5.3 Notes on the Specific Determinations of Syrphidae

It is during the separation into species, rather than for generic determination, that the ease of the modern style, 'non-scientific' key is readily appreciated, especially when dealing with relatively large numbers of syrphids. Caution is, however, necessary, because the features that make Stubbs' key so easy to use, namely the lack of several and often painstaking features of identification, may also be the causes of misidentification. Coe may be slower to use than Stubbs' newer key, but the more detailed couplets it contains provide a more confident identification, even in view of the wide range of variation in the phenotypes of many adult syrphids. Thus Stubbs' key, especially because of its prototype nature, was treated with caution until proven safe to use, by checking back with Coe, the various updates of difficult genera, and named specimens from the Hope museum.

The following comments concern species whose identification, in my experience of the Bernwood hoverfly fauna, does not follow directly from Coe's (1953) key: where they do, no comment has been made.

5.3a Syrphinae

The number of species of *Baccha* present in the British Isles is in some doubt. Coe (1953) recognises two species, *B. elongata* and *B. obscuripennis* and distinguishes the males on minor differences in shape of the lobe of the penis sheath, different degrees of dusting on the frons and other small such features that show considerable variation within one species. He divided females on the relative extent of the dusting along the sides and base of the frons. Kloet and Hincks (1975) recognise *B. elongata*, with *B. obscuripennis* existing as a possible synonym. The Biological Records Centre evade the problem by acknowledging *Baccha spp.*, whilst Stubbs recognises one species in Britain, *B. obscuripennis*. Current opinion favours one species (J.R. Vockeroth, M.C.D. Speight and F.C. Thompson, *in litt.)* ; the only recent case for two species is that of Violovitsh (F.C. Thompson, *in litt.*). He uses wing colour as a major feature, which is sexually dimorphicand thus only males of *B. obscuripennis* key out; he distinguishes colour of the frons as either "golden-bronze or argentate-white" and he also uses antennal colour- however the second part of this couplet is not present in the key. Furthermore Violovitsh's Russian is said to be poor and so until a better attempt is made, the case for a single species carries the most weight. From the Bernwood material it is possible to distinguish Coe's differences in the dusting of the frons, but it seems doubtful as to whether this can be used to confidently separate the two species, especially with alcohol-stored specimens in which dusting patterns can be notoriously unreliable.

Dasysyrphus is a distinctive genus of hover-flies which can readily be identified using either Coe or Stubbs and all four species listed in the keys occur in Bernwood. In addition a female of *Dasysyrphus friuliensis* was captured. This is another distinctive species, with oblique yellow spots on the abdominal tergites, first found in Britain in May 1980.

The four *Epistrophe* species all turned up in Bernwood. Of these, only *E. eligans* could be said to be easy to recognise, although again Stubbs' key makes the separation into species more positive than does Coe's. Stubbs splits *E. nitidicollis* from *E. diaphana* and *E. grossulariae* on antennal colour, the former species having predominantly orange antennae whereas they are predominantly black in the latter two species. *E. diaphana* has entirely yellow front femora and the yellow markings on Tergites 3 and 4 are indented at the margins by the black area; in contrast, *E. grossulariae* has a narrow blackening of the front femora at the base and the yellow bands on tergites 3 and 4 sweep back at the margin.

Melangyna remains a difficult genus to identify in spite of recent efforts to clarify its species. The two British species in the sub-genus *Meligramma* can most confidently be separated using Vockeroth (1980) : Stubbs' characters appear to be straightforward, but I only have experience of *M. triangulifera* and thus cannot comment on their reliability. Coe splits them on the darkening of the front tarsi in *M. triangulifera* but provides a useful feature of the purple reflections from the frons of *M. triangulifera* females, which also readily distinguishes it from the similar *Epistrophella euchroma*.

The sub-genus *Melangyna* is less straightforward. *M. lasiophthalma*, the only member of the genus commonly encountered in Bernwood, is however easily recognisable: the males by their pale hairs on the thoracic dorsum and the black wedge-shaped spots and line around the sides and base of the scutellum, the female by the black scutellar markings and the thin, narrowing dust spots on the frons. *M. lasiophthalma* can be confused with another early spring species, *Parasyrphus punctulatus*, which does however bear the characteristic marks of its genus. These include black stigma, yellow golf club shaped markings on the second abdominal tergite, and by the faded-looking triangular black markings on the abdominal sternites, which contrast with the much crisper, rectangular markings on the sternites of *M. lasiophthalma*. This latter feature is the simplest to use when confronted with large numbers of flies. Stubbs' character of the yellow bars on tergites 3 and 4 only reaching the side margins in *P. punctulatus* is not reliable.

The other *Melangyna* species are best separated using Stubbs' key and then checking against Speight *et al.* (1975) until one is familiar with them. *M. compositarum* and *M. labiatarum* in particular are hard to separate. Collin (1946) remarks that they can only be distinguished when both are present; to which Speight *et al.* (1975) add that it is difficult to decide when one has got both present! The key provided in Speight *et al.* (1975) does not attempt to split these two species; Stubbs splits the males on "eyes feebly hairy" (*M. labiatarum*) and "eyes virtually bare" (*M. compositarum*) and the females on thorax colour - "slightly brighter greyish black" (*M. labiatarum*) in contrast to "duller bronzy" (*M. compositarum*). Coe also uses the difference in the hairiness of the eyes of the males, in addition to *M. compositarum* having a slightly narrower and more shining face than *M. labiatarum;* for the females, thorax colour again is used.

Melanostoma species are best separated using the features given in Speight (1978b), which are much quicker to use than those of Coe, and it is these characters which Stubbs uses. Males are separated by the relative lengths of the abdomen: in *M. mellinum* the second tergite is at the most one-and-a-half times as long as it is wide whereas in *M. scalare* it is twice as long as it is wide; Coe merely states the abdomen of *M. scalare* to be long and narrow. Females are distinguished by the dust spots on the frons. In *M. mellinum* these are confined to the sides of the frons and at their maximum extent extend for no more than a quarter of the width of the frons whereas in *M. scalare* they are much larger, as wide as they are deep and spreading for half the width of the frons. The third British species of *Melanostoma*, *M. dubium*, is a rare montane species which has been much confused in the past - Coe recognised it as "*M. mellinum* var *dubium* Ver." and his features embrace at least melanic *M. mellinum* and typical *M. dubium* females (Speight 1978b). *M. dubium* was not found in Bernwood. As already mentioned, Coe's *M. ambiguum* is now placed in the genus *Platycheirus* (Andersson 1970).

Both British species of *Meliscaeva* occur in Bernwood, with *M. cinctella* more numerous than *M. auricollis*. The typical forms of each are easy to distinguish, *M. cinctella* having a straight, broad yellow on tergites 3 and 4 and *M. auricollis* having separated wedge shaped spots; this is var. *Maculicornis* in Coe. However, there is an intermediate form having an incised yellow band which can often be difficult to place. If the band is deeply incised, then Coe denotes *M. auricollis*; but this discrimination can become arbitrary. Stubbs gives the feature of yellow frontal lunules in *M. auricollis* as opposed to black ones in *M. cinctella.* I have not been able to detect a difference; and his other characteristic of at least a black facial prominence in *M. auriccollis* also appears to be unreliable. The extent of darkening of both the face and the legs is variable and thus most of Coe's features are uncertain; furthermore, spring and autumn specimens tend to be rather darker than summer ones. Speight *et al.* (1975) note that the abdominal markings of *M. cinctellus* are orange compared to the greyer ones of *M. auricollis* but this distinction is blurred by specimens that have been stored in alcohol for several weeks, and to add to the confusion, some clearly-marked *M. auricollis* individuals have either pale yellow markings or more orange ones!

Metasyrphus can be a confusing genus to sort out, despite additional keys from Speight *et al.* (1975). Only *M. corollae* is readily distinguishable, males having a noticeably large pre-genital abdominal segment and distinctive yellow markings; females have a heavily yellow-dusted frons with the black ground colour exposed for only a quarter to a third of the distance between the front ocellus and the base of the antennae. Stubbs' couplet separating female *M. luniger* and *M. nitens* uses the differing extent of the Y-shaped dusting on the frons and needs care, as does the separation of male *M. latifasciatus* from *M. latilunulatus* and *M. luniger* by the width of the lower half of the occiput. Stubbs also lists *M. nielseni* which is not found in Coe; one female of this species was captured at Bernwood in 1980 and identified by the former.

Paragus is another difficult genus, with three British species, split into two sub-genera. Coe's key does not work, indeed he only recognised two species, *P. tibialis* and *P. bicolour* (= *P. albifrons*). Speight (1978a) provides a useful supplement to Stubbs' key, with a key to the British species and to those likely to turn up. Only two individuals of *Paragus* were captured at Bernwood, females which have at present defied identification, although Philip Entwistle has placed them in the *Pandasyopthalmus* sub-genus.

Coe's key to *Parasyrphus* is rather confusing to use and does not separate male of *P. nigritarsis* at all - they run down to *P. malinellus* (Speight *et al.* 1975). These authors provide an alternative key which works well and Stubbs' key is really a simplification of this, using only the readily discernable characteristics - to little detriment. Possible confusion of *P. punctulatus* with *Melangyna lasiophthalma* has already been mentioned; all the other species of *Parasyrphus* have yellow bands rather than spots and so this problem does not occur.

The number and status of *Sphaerophoria* species present in Britain has long been the source of much confusion, and the review of this genus by Speight (1973) is the most useful source of reference. Speight's key, recognising seven species, supercedes Coe's (1953) four species and Alan Stubbs has added a further two, *S. virgata* and *Sphaerophoria* sp.A. Only male *Sphaerophoria* can at present be identified, using the lobes of the genitalia which Stubbs' key relies wholly upon; Speight includes other characteristics in addition. Not many *Sphaerophoria* were caught at Bernwood and most of these are females; the males are of two species, *S. menthastri* and *S. scripta*, of which the former is the more numerous.

Syrphus species are readily identified using Coe's or Stubbs' keys, although with specimens in alcohol the hairy eyes of *S. torvus* may sometimes require careful observation: good lighting of the specimen greatly aids the visibility of fine hairs. *Syrphus* species are readily distinguished from other Syrphini by the presence of abundant pale hairs on the upper surface of the lower lobe of the squama.

5.3b *Milesiinae*

Cheilosia is the largest genus of syrphids in the British Isles with 32 species, all of which are small to medium sized black flies without abdominal markings. Inevitably therefore they can be rather tedious to identify in comparison with other hoverflies, although Coe's key works well for nearly all the British species and only one species, *C. sahlbergi*, has been added (see Speight 1974). Possible confusion using Coe can arise with *C. fraterna* and *C. bergenstammi*; these can however be separated on the length of the scutellar bristles, which are shorter than the scutellum in the former species and at least as long, and often longer than the scutellum in *C. bergenstammi* (Speight *et al.* 1975). Coe also mis-identified *C. semifasciata* (as *C. fasciata*) following on from Collin (1931) and Speight *et al.* (1975) warn that this too is a difficult species to identify, giving a brief description. It was not found at Bernwood. Alan Stubbs' key to the *Cheilosia* species (at least my early version of it) was not trustable on checking back with either Coe or reference material and thus I did not persevere with it.

Ferdinandea is a distinctive genus of two rather similar, bristly, dark hoverflies with a striped thorax. *F. cuprea* is not uncommon in Bernwood whereas *F. ruficornis* is a rare hoverfly, a single individual being caught in 1980, two the following year and ten in 1982. The two species can readily be told apart by the presence of conspicuous bristly black hairs on the femora and tibiae of the first and second pairs of legs. The pattern of the shining band at the base of the tergites is also different in the two species, it being much more extensive in *F. ruficornis* than in *F. cuprea*, where it forms only a very narrow basal strip.

Only two of Coe's ten species of *Helophilus* were caught in the Malaise traps at Bernwood; Coe's genus is now recognised as four genera, *Helophilus*, *Lejops*, *Anasimyia* and *Parhelophilus*. *H. pendulus* is easily distinguished from the much rarer *H. hybridus* by having yellow hind tibiae with a black apical band as opposed to having black hind tibiae with the basal third yellow. The abdominal markings also differ, although this is not as simple a character as the tibiae. *Anasimyia* species should be referred to Speight (1981b), which supercedes the now-unusable Coe.

Coe's key to *Neoascia* relies heavily on male genitalia and Stubbs' key is much simpler to use. Stubbs recognises two sub-genera, based on the extent of the chitin bridge across the hind end of thorax: this is useful in distinguishing between *N. podagrica* and *N. obliqua*, although only the former has as yet been found in Bernwood.

It is not currently possible to identify females of *Neocnemodon* (*Cnemodon* of Coe) although the males, which possess a distinctive spur on the hind trochanter, can be separated using Stubbs' key. Coe (1953) recognises three species occurring in Britain whilst Stubbs lists five; both the Biological Records Centre, Kloet and Hincks (1975) and Speight *et al.* (1975) recognise four species. *N. brevidens* is the new addition (Stubbs 1980) which can be recognised by a "dark, flap-like projection" on the basal segment of the first tarsus. Two species of *Neocnemodon* have been caught in Bernwood, *N. pubescens* and *N. vitripennis*, which can be separated on the colour of the dorsal hairs on the thorax, these being mostly black in the former species and pale in the latter. Rather more females were caught than males and no attempt was made to try to match these to Coe's three species.

Four species of *Pipiza* were identified from Bernwood, none of which was at all common. *P. austriaca* is the easiest to recognise, with its distinctively thickened hind femora, but *Pipiza* is a difficult genus. Coe is confusing to use due to indistinct use of the degree of thickening of the hind femora (Speight *et al.* 1975) and does not separate the females adequately (Speight, pers. comm.) and thus all my *Pipiza* have been identified using Stubbs' key; Seguy (1961) makes too much use of colour characters, which can be variable. Stubbs separates male *P. bimaculata* and *P. noctiluca* on the shape of the small, flat shining area of the frons, which is not easy to see; similarly the differences in hair colour on tergites 4 and 5 used to separate female *neofenestrata* from *noctiluca* and *bimaculata* need a careful eye, especially once again with alcohol-stored specimens.

Pipizella species can be readily identified using either Coe or Stubbs, the latter being a simplification of the former, adding no new characters. Both these authors, along with Kloet and Hinks (1975) and the Biological Records Centre, place *P. heringi* in a separate genus, *Heringia*: neither Goffe (1952) nor Speight *et al.* (1975) however find any justification for this. Two females of *Heringia* were caught from Bernwood in 1982.

Since Coe's key was published in 1953 the world Xylotini have been the subject of a major revision (Hippa 1978). Three genera are now recognized from Britain. Coe's *Xylota lenta* and *X. nemorum* are now placed in *Brachypalpoides* and *Chalcosyrphus* respectively, but both Kloet and Hinks (1975) and the B.R.C., which pre-date the revision, place these two species in the genus *Xylotomima*, which I have followed. A new species, *Xylota coeruleiventris*, has been added to the British list and Speight (1981a) has provided a new key to the British species in the wake of all this activity, including *X. ignava* in case of its turning up. All these keys work well with those species that have turned up in Bernwood.

5.4 Comment

Coe's key remains, at least up until the publication of Alan Stubbs' new key, the standard taxonomic work on the British Syrphidae. Used in conjunction with the various revisions that have appeared in the thirty years since its publication, it must remain the standard by which the new is judged, and this is the approach that I have used with regard to Stubbs' manuscript. As a newcomer to the family, it was also essential to check my determinations with named specimens, both in the Hope Museum and in the private collections of other individuals; for the latter privilege, I am particularly thankful to Jennifer Owen and Philip Entwistle.

CHAPTER SIX

Hoverfly Richness and Abundance at Fives Sites, Bernwood Forest, 1980 - 1982

6.1 The Overall Catch

A total of 20,234 hoverflies were caught at the five sites selected in Bernwood Forest for the experiment over the three seasons, from 1st April to 30th September 1980 to 1982. These flies belong to 115 species of Syrphidae, which represents 46% of the British hoverfly fauna. 1980 was the richest of the three years with 95 species caught although 1982 produced the largest catch, with 8616 hoverflies captured. 1981 was the poorest year in terms of both the number of species and individuals, with 5107 flies belonging to 87 species caught. The abundance of each species in each year is given in Appendix 2.

Episyrphus balteatus is the most abundant hoverfly present in the sample with 2853 individuals captured, accounting for 14.1% of the total collection. This is due largely to the 1982 catch, which contained 2200 *E. balteatus*, 439 of which were caught in a single week at one site; this species is well known for having years of super-abundance and it is a migrant (Speight *et al.* 1975, Johnson 1969). It is ubiquitous in a wide range of habitats all over England and Bankowska (1980) notes that in Poland it is the first dominant species of pine and mixed forests: the relative absence of *E. balteatus* in the first two years of sampling at Bernwood is thus surprising, particularly in 1981 when only 170 individuals were caught.

Meliscaeva cinctella, the second commonest hoverfly in the collection, is much more abundant in the 1982 sample compared with the previous two years. Overall, 2543 individuals were captured, 1523 of these being recorded in 1982. Again this is a widely encountered species in sheltered patches of scrub woodland and hedgerows whereas the much less common *M. auricollis* is associated with young larch and pine plantations: this latter species proved to be rather scarcer than anticipated in Bernwood.

The third most encountered hoverfly is *Melanostoma scalare* with 2310 individuals captured, representing 11.4% of the total catch. This is a hoverfly with a wide distribution over the British Isles and it is found over a wide range of habitats. It usually occurs with *M. mellinum*, as at Bernwood; *M. scalare* is rather more of a woodland species, typically found near low scrub and forest edges whereas *M. mellinum* is generally associated with more open environments such as meadows, roadsides and forest edges and it also extends higher into montane habitats (Leerveld, Meeuse and Stelleman 1976, Speight *et al.* 1975). This habitat distinction is demonstrated by the relative abundance of the two species in the Bernwood collections. In contrast with the two previous species, *M. scalare* has occurred in similar abundances in each of the three years.

These three most abundant species account for 38.1% of the total catch and the species distribution follows the familiar J-shaped curve of Batesian diversity. Thirty three of the species (28.7%) are represented by five or fewer individuals over the three years and fourteen of these have only one specimen present. Several interesting and rare species have been found at Bernwood, including *Dasysyrphus friuliensis*. This species is one of the newest on the British list, being first noticed by Crossley from Timble Ings, an upland conifer forest near Otley in Yorkshire, in May 1980. The Bernwood record is for June 1980, but subsequent checking of collections has put the earliest known specimen in Britain from Hafren Forest in upland mid-Wales in 1975 (Entwistle 1982). In Poland *D. friuliensis* is one of two dominant syrphids of the upper montane zone (Bankowska 1980) and while all the records from Britain are from conifer plantations, Bernwood at least has no other connection with montane environments.

The Bernwood collection contains several other species that are more normally associated with upland forests. *Metasyrphus nielseni* is a rare species from the Scottish Highlands, although a specimen was taken on Brownsea Island, Dorset, in May 1976, adjacent to *Pinus sylvestris* woodland (M.C.D. Speight, *in litt.*). *Megasyrphus annulipes* is also a species of Scottish pinewoods (Stubbs and Chandler 1978). *Parasyrphus malinellus* is given a disjunct distribution in Coe (1953), with records from two localities in the Scottish Highlands and two from southern England but it is now emerging that the true distribution is rather more general (Entwistle 1982). This species seems to be strongly associated with conifers and its expanding distribution appears to be linked with expanding foresty practice; certainly it is no longer particularly rare. 177 specimens of *P. malinellus* were caught at Bernwood, spread fairly evenly over the five sites but with rather more caught in 1980 compared with the other two years.

Twelve of the syrphids from Bernwood are listed on a provisional Nature Conservancy Council Red Data List of species threatened with the British Isles in 1980 (Table 6.1). *Ferdinandea ruficornis* is the only one of these to be listed under the 'endangered' category of species actually threatened with extinction. The larvae of *F. ruficornis* feed on sap runs from tree wounds infested by the larvae of the goat moth *Cossus cossus* whereas the common *F. cuprea* has larvae that feed rather more generally on tree sap (Stubbs and Chandler 1978). *F. ruficornis* was present at Bernwood in all three years but was more abundant in 1982, when 10 individuals were captured.

Both *Cheilosia chrysocoma* and *Microdon eggeri* are listed in the 'vulnerable' category of the N.C.C. list and both these species were caught in all three years. *C. chrysocoma* is usually encountered only in woodlands with a long history of afforestation, although in Poland it appears to be a predominately montane species (Speight *et al.* 1975, Bankowka 1980). *M. eggeri* is also principally

TABLE 6.1

HOVERFLY SPECIES CAPTURED AT BERNWOOD LISTED UNDER THE NATURE CONSERVANCY COUNCIL'S PROVISIONAL RED DATA LIST

Species	Status	N80	N81	N82	Total
Epistrophe diaphana	rare	2	-	-	2
Epistrophella euchroma	rare	9	4	3	16
Melangyna ericarum	rare	1	-	1	2
M. triangulifera	rare	40	17	9	66
Metasyrphus nielseni	rare	1	-	3	4
M. nitens	rare	1	1	-	2
Platycheirus discimanus	vulnerable	2	-	-	2
Cheilosia chrysocoma	rare	4	5	6	15
C. nebulosa	rare	8	2	2	12
Criorhina asilica	endangered	2	-	10	12
Ferdinandea ruficornis	vulnerable	1	2	10	13
Microdon eggeri		11	6	6	23
		82	37	50	169

found in ancient woodlands and is restricted to southern England, where it is scarcer than *M. mutabilis*, which has not been recorded from Bernwood (Colyer and Hammond 1968).

Melangyna triangulifera is by far the most common of the 'rare' category species of the Red Data list with 66 specimens captured, 40 of these being in 1980. *Melangyna* species are normally found close to trees and *M. ericarum* is reputably commoner in coniferous woodlands (Speight *et al*. 1975). Both *Criorhina asilica* and *Platycheirus discimanus* are spring species, the former being associated with ancient woodland whereas the latter is distributed locally along woodland edges.

The hoverflies of Bernwood form a rich collection with several rare and interesting species: in total, 121 species have been recorded from the Forest. This places Bernwood among the richest sites for syrphids in Britain. Monks Wood, near Huntingdon, Cambridgeshire, has produced 103 species of hoverfly (Steele and Welch 1973), with Hayley Wood, the largest surviving ancient woodland in that county giving 61 species, with only a further 9 species expected to occur there (Gilbert and Perry 1982). 79 species have been recorded from Hafren Forest, a large, upland conifer forest with a good age mosaic in mid-Wales (P.F. Entwistle, *in litt*.). Other rich hoverfly sites in Britain include Bookham Common, Surrey, with 115 species registered with the Nature Conservancy Council's Invertebrate Site Register, and a suburban garden in Leicester, from which 91 species have been recorded (Owen, J. 1983).

Bernwood is thus the best-known site in Britain for Syrphidae, but this must in part be due to the intensity of the collecting effort. It was Gilbert White (1788) who first noted that "it is, I find, in zoology as it is in botany: all nature is so full, that that district produces the greatest variety which is the most examined" and he also noted that "new occurences still arise as long as any inquiries are kept alive". Such remarks, although pertinent, can devalue neither the richness of the observed entomological fauna of Bernwood nor the importance of these woods as a site of national interest.

6.2 The Total Catch at Each Site

More hoverflies of more species were caught at S4 than at any of the other four sites, with a total of 6396 syrphids captured of 100 species. This site accounts for 32% of the overall catch and 87% of all the species caught during the three years from the whole Forest were recorded here. The next best site is S2 with 5501 individuals of 87 species captured, with the deciduous site, S1, producing a catch of similar size, with 4233 syrphids representing 77 species. S3 and S5 by contrast produced markedly poorer catches than these three sites, with S5 giving the smallest catch of 1636 hoverflies of 38 species.

The most abundant hoverflies at each site, those represented by 100 or more individuals over the three years, are listed in Table 6.2. Each site has a

TABLE 6.2

HOVERFLIES FROM BERNWOOD FOREST REPRESENTED BY ONE HUNDRED OR MORE INDIVIDUALS AT ONE OF THE FIVE SITES

S1

Meliscaeva cinctella	827
Episyrphus balteatus	746
Melanostoma scalare	440
Ferdinandea cuprea	235
Rhingia campestris	235
Platycheirus albimanus	207
Dasysyrphus venustus	171
Helophilus pendulus	164
Melanostoma mellinum	151
Platycheirus peltatus	125

N = 3301, S = 10, %N = 77.98, %S = 12.99

S2

Episyrphus balteatus	1087
Meliscaeva cinctella	803
Melanostoma scalare	362
Syrphus ribesii	339
Rhingia campestris	334
Helophilus pendulus	333
Platycheirus albimanus	261
Ferdinandea cuprea	211
Dasysyrphus venustus	200
Melanostoma mellinum	174
Parasyrphus lineolus	136
Melangyna lasiophthalma	129
Eristalis pertinax	111

N = 4480, S = 13, %N = 81.44, %S = 14.94

TABLE 6.2 CONTINUED

S3	
Syrphus ribesii	550
Melanostoma scalare	469
Melanostoma mellinum	284
Meliscaeva cinctella	245
Melangyna lasiophthalma	132
Episyrphus balteatus	100

N = 1780, S = 6, %N = 72.12, %S = 10.71

S4	
Melanostoma scalare	874
Helophilus pendulus	856
Melanostoma mellinum	603
Episyrphus balteatus	431
Rhingia campestris	390
Meliscaeva cinctella	284
Platycheirus albimanus	262
Eristalis pertinax	241
Parasyrphus lineolus	210
Syrphus ribesii	159
Cheilosia paganus	152
Metasyrphus corollae	121
Chrysotoxum bicinctum	118
Ferdinandea cuprea	118
Platycheirus peltatus	100

N = 4919, S = 15, %N = 76.91, %S = 15

S5	
Episyrphus balteatus	489
Meliscaeva cinctella	384
Baccha elongata	166
Melanostoma scalare	165
Rhingia campestris	110

N = 1314, S = 5, %N = 80.32, %S = 20

different species as its most common hoverfly, with the exception of S2 and S5, which both have *Episyrphus balteatus* as the top-ranking syrphid. The number of species represented by 100 or more individuals varies considerably between the sites, from S4 with 15 such species to S5 with only 10; this number of species does however represent a consistent proportion of the total number of species collected from each site, between 10% and 20% of the total. These species also represent a similar proportion of the overall catch at each site, accounting for between 72% and 82% of the total number of syrphids caught.

The top-ranking syrphids are all common at each of the five sites and consequently cannot be used as effective indicators of habitat type. Some of the common species do, however, show some preferences for certain sites. *Episyrphus balteatus*, *Meliscaeva cinctella*, *Ferdinandea cuprea and Dasysyrphus venustus* all show a preference for the deciduous sites, although the first two of these species are also relatively common at other sites: nevertheless, they are twice as numerous at S1 and S2 than at S4 and S5. *Ferdinandea cuprea* occurs at S4 but is twice as abundant at each of the two deciduous sites; *Dasysyrphus venustus* in contrast appears more as a deciduous-associated species. The low overall abundances at S3 make simple comparisons of syrphid abundance along the deciduous-coniferous gradient difficult. Some species, for example *Platycheirus albimanus*, occur in similar abundances at S1, S2 and S4 and thus appear to reflect simply the overall abundance of hoverflies at a particular site, and are of no use as potential indicator species.

Several species show a preference for the mixed sites. *Syrphus ribesii* and *Melangyna lasiophthalma* are both more abundant at S3 than at S4, in contrast with the overall abundances at these sites; *M. lasiophthalma* is also common at S2. *Parasyrphus lineolus* and *Eristalis pertinax* show a preference for S2 and S4 and thus appear to select against purely deciduous habitats. *Helophilus pendulus* shows a bias towards the more conifer-dominated mixed sites, being twice as abundant at S4 than at S2, where in turn it is twice as abundant than at S3. *Helophilus* is also moderately abundant at S3 but is is uncommon at S5.

The two *Melanostoma* species are very much more abundant at S4 than at the other sites, although considerable numbers of these common syrphids were captured at all of the sites, with the exception of S5, where *M. mellinum* is a rare hoverfly. *M. scalare* is the more common of the two species and it occurs in similar numbers at S1, S2 and S3, whereas *M. mellinum* is rather more abundant at S3 than at either of the two deciduous sites.

Baccha elongata is the only hoverfly which is more common at S5 than at any of the other four sites. It is principally a species of shaded woodland and thus is not particularly associated with conifers; it is present at all of the sites, with S1 producing the next-largest sample.

6.3 The Number of Individuals and Species at Each Site 1980 - 1982

1982 produced the biggest catches of hoverflies of all the three years at all of the five sites, with the exception of S3, where more were caught in 1980. This apparent anomaly is the result of an influx of *Syrphus ribesii* at this site in May, 1980. Annual totals of both the number of individuals and species caught at each site are given in Table 6.3.

1980 saw the largest number of species captured of the three years, although the differences are slight. 95 species of hoverfly were captured in the first year compared with 87 in 1981 and 92 in 1982. 1981 was a poor year overall, with the lowest numbers of both individuals and species captured at all sites save S5 and S2, where similar numbers were captured as in the previous year. This decline in numbers is particularly noticeable at S1, where only 711 syrphids of 47 species were caught in 1981 compared with 1602 flies of 60 species in the previous year.

Ranking the sites by both the number of species and the number of individuals captured at each site produces a consistent ordering of sites with only one exception in the three years: in 1980, more hoverflies were caught from S1 than from S2. Each individual year therefore confirms the ordering of the sites from the combined data, with S4 the richest and S5 the poorest, with S2, S1 and S3 producing the intermediate catches in that order of decreasing richness and abundance.

TABLE 6.3

THE NUMBER OF INDIVIDUALS AND SPECIES OF AT 5 SITES, BERNWOOD FOREST, 1980 - 1982

Year		Sites	S1	S2	S3	S4	S5	TOTAL
1980	N		1602	1383	970	2065	491	6511
	S		60	67	39	79	30	95
1981	N		711	1564	649	1666	517	5107
	S		47	64	39	72	25	87
1982	N		1920	2554	849	2665	628	8616
	S		60	66	43	74	25	92
TOTAL	N		4233	5501	2468	6396	1636	20,234
	S		77	87	56	100	38	115

6.4 Hoverflies at the Five Sites, 1980 - 1982

The striking impression from the abundances of the ten most common hoverflies from each site (Table 6.4) is the lack of apparent order. Most of the sites have a different species at the head of the table in each year and although many of the species are repeated from site to site and from year to year, the abundances of many species change dramatically at a particular site between different years.

6.4a S1

Meliscaeva cinctella was the most abundant hoverfly at S1 in both 1981 and 1982, as well as in the overall abundance for the site. Its numbers do however fluctuate considerably over the three years and more were caught in 1980, when it ranked third, than in 1981, when it was the most numerous hoverfly at the site. 1981 was a poor year at S1, with fewer than half the numbers of syrphids captured as in the previous year, and this is reflected in both the number of species caught and in the abundances of the common species. There are only 575 individuals within the ten most abundant species in 1981 compared with 1609 in the following year; in all three years, these species account for approximately 80% of the total catch.

Episyrphus balteatus is the most common hoverfly in the 1980 collection from S1, with 231 specimens captured. A dramatic decline in 1981, with only 39

TABLE 6.4

THE TEN MOST ABUNDANT SYRPHIDS AT EACH OF THE FIVE SITES 1980 - 1982

	1980		1981		1982	
S1	*Episyrphus balteatus*	231	*Meliscaeva cinctella*	133	*Meliscaeva cinctella*	511
	Melanostoma scalare	197	*Melanostoma scalare*	104	*Episyrphus balteatus*	476
	Meliscaeva cinctella	183	*Rhingia campestris*	77	*Melanostoma scalare*	139
	Platycheirus albimanus	119	*Ferdinandea cuprea*	60	*Helophilus pendulus*	130
	Platycheirus peltatus	110	*Platycheirus albimanus*	58	*Ferdinandea cuprea*	117
	Dasysyrphus venustus	109	*Episyrphus balteatus*	39	*Rhingia campestris*	65
	Rhingia campestris	93	*Baccha elongata*	37	*Dasysyrphus venustus*	53
	Melanostoma mellinum	86	*Helophilus pendulus*	27	*Melanostoma mellinum*	40
	Syrphus ribesii	65	*Melanostoma mellinum*	25	*Eristalis pertinax*	39
	Ferdinandea cuprea	58	*Xylotomima lenta*	15	*Xylota segnis*	39
	%N = 78.09%	1251	%N = 80.87%	575	%N = 83.80%	1609
S2	*Syrphus ribesii*	212	*Meliscaeva cinctella*	211	*Episyrphus balteatus*	995
	Rhingia campestris	138	*Platycheirus albimanus*	180	*Meliscaeva cinctella*	455
	Meliscaeva cinctella	137	*Rhingia campestris*	154	*Helophilus pendulus*	243
	Dasysyrphus venustus	104	*Melanostoma scalare*	140	*Melanostoma scalare*	119
	Melanostoma scalare	103	*Syrphus ribesii*	90	*Parasyrphus lineolus*	72
	Melanostoma mellinum	74	*Helophilus pendulus*	80	*Ferdinandea cuprea*	69
	Ferdinandea cuprea	74	*Melangyna lasiophthalma*	74	*Rhingia campestris*	42
	Episyrphus balteatus	72	*Melanostoma mellinum*	69	*Dasysyrphus venustus*	41
	Platycheirus albimanus	63	*Ferdinandea cuprea*	68	*Didea fasciata*	38
	Parasyrphus lineolus	46	*Eristalis pertinax*	60	*Eristalis pertinax*	38
	%N = 73.97	1023	%N = 71.99%	1126	%N = 82.69%	2112

TABLE 6.4 CONTINUED

	1980		1981		1982	
S3	*Syrphus ribesii*	448	*Melanostoma scalare*	192	*Meliscaeva cinctella*	176
	Melanostoma mellinum	153	*Melangyna lasiophthalma*	77	*Melanostoma scalare*	155
	Melanostoma Scalare	122	*Melanostoma mellinum*	74	*Episyrphus balteatus*	72
	Melangyna lasiophthalma	27	*Meliscaeva cinctella*	55	*Syrphus ribesii*	61
	Rhingia campestris	24	*Syrphus ribesii*	41	*Melanostoma mellinum*	57
	Platycheirus scutatus	23	*Platycheirus albimanus*	27	*Helophilus pendulus*	53
	Parasyrphus malinellus	17	*Parasyrphus punctulatus*	23	*Parasyrphus lineolus*	51
	Dasysyrphus albostriatus	15	*Baccha elongata*	20	*Melangyna lasiophthalma*	28
	Meliscaeva cinctella	14	*Rhingia campestris*	17	*Ferdinandea cuprea*	22
	Platycheirus tarsalis	14	*Episyrphus balteatus*	16	*Criorhina berberina*	20
	%N = 88.35%	857	%N = 83.35%	542	%N = 81.86%	
S4	*Melanostoma scalare*	326	*Melanostoma scalare*	327	*Helophilus pendulus*	549
	Rhingia campestris	251	*Helophilus pendulus*	200	*Episyrphus balteatus*	360
	Melanostoma mellinum	215	*Melanostoma mellinum*	189	*Melanostoma scalare*	221
	Syrphus ribesii	132	*Platycheirus albimanus*	134	*Melanostoma mellinum*	199
	Helophilus pendulus	107	*Eristalis pertinax*	69	*Meliscaeva cinctella*	198
	Platycheirus albimanus	100	*Rhingia campestris*	62	*Eristalis pertinax*	144
	Parasyrphus lineolus	68	*Chrysotoxum bicinctum*	57	*Parasyrphus lineolus*	122
	Platycheirus peltatus	67	*Eristalis nemorum*	55	*Rhingia campestris*	77
	Sphaerophoria	62	*Cheilosia paganus*	53	*Cheilosia paganus*	67
	Ferdinandea cuprea	60	*Meliscaeva cinctella*	46	*Didea fasciata*	63
	%N = 67.21%	1388	%N = 71.55%	1192	%N = 75.05%	2000

TABLE 6.4 CONTINUED

	1980		1981		1982	
S5	*Episyrphus balteatus*	122	*Meliscaeva cinctella*	168	*Episyrphus balteatus*	297
	Baccha elongata	71	*Melanostoma scalare*	76	*Meliscaeva cinctella*	183
	Rhingia campestris	61	*Baccha elongata*	75	*Melanostoma scalare*	46
	Melanostoma scalare	43	*Episyrphus balteatus*	70	*Baccha elongata*	20
	Meliscaeva cinctella	33	*Rhingia campestris*	37	*Helophilus pendulus*	12
	Platycheirus albimanus	23	*Platycheirus albimanus*	14	*Rhingia campestris*	12
	Dasysyrphus venustus	22	*Criorhina berberina*	13	*Criorhina berberina*	8
	Platycheirus scutatus	21	*Melangyna lasiophthalma*	9	*Dasysyrphus venustus*	6
	Platycheirus tarsalis	16	*Melanostoma mellinum*	9	*Xylota segnis*	6
	Ferdinandea cuprea	14	*Xylota sylvarum*	6	(*Leucozona lucorum*	5
	%N = 86.76%	426	%N = 92.26%	477	(*Melanostoma mellinum*	5
					(*Ferdinandea cuprea*	5
					%N = 94.74%	595

individuals caught, was followed in 1982 by a huge increase to 476 individuals captured. Both *E. balteatus* and *M. cinctella* follow similar patterns of abundance over the three years, with more captured in 1982 than in the previous two years combined. Both the *Melanostoma* species share this abundance pattern, although their recovery in 1982 does not quite reach the numbers attained in 1980. *M. scalare* is much more common than *M. mellinum* in all three years. *Dasysyrphus venustus* shares a similar fate of abundance over the three years as *Melanostoma*.

Helophilus pendulus steadily increased its abundance at S1 in each successive year, from only 7 individuals in 1980 to 130 in 1982, when it was the fourth most common syrphid at the site. *Ferdinandea cuprea* was also much more abundance in 1982 than in the previous two years, whereas *Platycheirus albinmanus*, a common species in 1980 with 119 individuals captured, declined progressively over 1981 and 1982, with only 30 specimens captured in the latter year.

6.4b S2

A different species heads the abundance list in each year at S2, with *Episyrphus balteatus* topping both the 1982 and overall rankings. *E. balteatus* follows similar fortunes of abundance over the three years at S2 as at S1, but the fluctuations between the years are more extreme, with a decline to 20 individuals in 1981 followed by an increase to 995 the following year. 439 of these individuals were captured in a single week, between 29 July and 5 August.

Meliscaeva cinctella was the most abundant syrphid in 1981, although twice as many individuals were captured in the following year. *Ferdinandea cuprea* and *Melanostoma scalare* maintained steady abundances over the three years whereas *M. mellinum*, again much less common than *M. scalare*, was scarcer in 1982 than in the previous two years, in contrast with overall abundances.

Helophilus pendulus once more shows a progressive increase in numbers over the three years, from 10 in 1980 to 243 in 1982, whereas *Dasysyrphus venustus* declined in 1981 to half of its abundance in the previous year, a position maintained into 1982. *Platycheirus albimanus* doubled its numbers to 180 in 1981 before crashing to only 18 individuals the following year; *Parasyrphus lineolus* declined in 1981 only to recover to 72 individuals in 1982, rather more than were caught in 1980. The proportion of the whole catch taken by these ten most common species remained steady at approximately 73% for the first two years but rose to almost 83%, when the common species were twice as numerous than in the previous years.

6.4c S3

Syrphus ribesii, *Melanostoma scalare* and *Meliscaeva cinctella* were the most abundant species at S3 in 1980, 1981 and 1982 respectively. 448 individuals of *S. ribesii* were caught in 1980, with 233 of these captured in the week 27 May to 3 June; catches in the subsequent years were low at around 50 per annum, but it nevertheless is the most numerous syrphid in the combined data for all the years. The abundance of the most common syrphid in the collections is very much lower in 1981 and 1982, with 192 *M. scalare* captured and 176 *M. cinctella*. The ten most abundant species account for 82% of the total catch in these two years compared with 88% in 1980, and there tend to be fewer common species at S3 than at S1, S2 or S4.

M. scalare and *Melangyna lasiophthalma* both show similar abundance patterns for the three years, with an increase in 1981 followed by a fall back to the 1980 levels of abundance in 1982; the latter species is subject to greater fluctuations than the former, which is more abundant. *M. cinctella* and *E. balteatus* progressively increased in abundance over the three years whereas *M. mellinum* declined. *Rhingia campestris* maintained a steady population of around 20 individuals each year.

6.4d S4

Melanostoma scalare is the most common hoverfly from S4, both in the overall total and for 1980 and 1981, with 326 caught in the former year and 327 in the latter. In 1982 it declined somewhat to be the third-ranking syrphid, with 221 specimens captured, in spite of increased general abundances in the third year. *Helophilus pendulus* was the most common species in 1982 with 549 individuals caught and once more this species showed a progressive increase in abundance over the three years. The ten most abundant species contributed 2000 individuals to the annual total in 1982, almost twice as many as in the previous years, and this is reflected in the increasing contribution of these ten species to the total over the three years, from 67% in 1980 to 75% in 1982. Even this latter contribution is lower than the average of 81% for all the sites and this is a measure of the richness of the catches from S4, which typically contain more species of moderate abundance than at the other sites.

Along with *H. pendulus*, *Eristalis pertinax* increased in abundance each year, rising from 28 to 144 individuals captured. *Parasyrphus lineolus* and *Meliscaeva cinctella* were also much more numerous in 1982 than in 1980, but their 1981 abundances were either lower or similar to those the previous year. *Rhingia campestris*, *Ferdinandea cuprea* and *Sphaerophoria* were all much more common in 1980 than in subsequent years.

6.4e S5

Episyrphus balteatus was the most numerous hoverfly at S5 in both 1980 and in 1981, with over twice as many individuals captured in the latter year as in the former. 1981 was again a poor year for *E. balteatus* with 70 specimens caught; *Meliscaeva cinctella* was once more the most common hoverfly in this year, although more individuals were captured in 1982. The final year produced a larger catch than the previous years and this is reflected in the total number of the ten most common syrphids, although the difference in numbers caught between this year and the others is not as great as at other sites. These ten most common hoverflies contribute a much greater proportion of the total than at other sites, ranging from 87% in 1980 to 95% in 1982: again the trend is of the increasing importance of these ten flies in succeeding years.

Few species of hoverfly are common at S5, although it is the best site for *Baccha elongata*, with 167 individuals captured. 1982 was a poor year for *Baccha*, with only 20 individuals caught whereas the previous two years had each produced over 70 specimens. *Rhingia campestris* also declined, but with a more even loss of numbers over the three years. *Melanostoma scalare* was caught in much lower numbers than elsewhere in Bernwood but again 1981 produced the largest catch; *M. mellinum* is represented by only 19 individuals from this site over the three years.

6.5 Comment

The hoverfly samples from each of the five sites form distinct collections that retain features special to that site. Site rankings both by the number of individuals and species give a consistent sequence in all three years, with only one 'misplaced' site, but this ranking bears little relation to the transition of woodland type from deciduous to coniferous.

Three sites give markedly richer and larger samples of hoverflies than do the other two, with S4 consistently producing the best catches. S1 and S2 produce catches of a similar quality to S4, with the purely deciduous site giving the poorest samples of these three rich sites. In comparison with these three sites the catches from S3 and S5 are markedly smaller and less rich in species, with S5 the poorest of all the sites.

The abundances of individual hoverflies are subject to enormous variation between the three years in an apparently chaotic manner. None of the sites has the same species as the most common syrphid in all three years and two have a different such species in all three years. This lack of stability of species populations does not allow the identification of indicator species amongst the woodland hoverflies that might serve as indicators of environmental quality, although some species, for example *Baccha elongata*, are indicative of a certain type of habitat.

Overall, the Bernwood hoverflies form an extremely rich collection and contain several species of national rarity. The suspected entomological richness of the site, as suggested both by the butterfly community present and by casual observation, has been borne out by detailed survey. The site is at present the richest-known in Britain for Syrphidae and although some of the habitats within the Forest are not especially rich in hoverflies, they all contribute to the overall richness of the woods.

CHAPTER SEVEN

Hoverfly Seasonality in Bernwood Forest

7.1 Seasonal Distribution of the Overall Hoverfly Catch

The seasonal distribution of abundance of hoverflies in Bernwood is bimodal, with peaks in May and in the second half of July through much of August. These two peaks of abundance are split by a two-to-five week period in late June and July when less than 100 syrphids were captured each week by all of the five Malaise traps (Fig. 7.1).

The best-defined bimodality is found in the 1980 sample, with sharp abundance peaks in the weeks of 13 - 20 May and 22 - 29 July. The early peak of 1124 syrphids captured is larger than the late peak in July, when 796 individuals were caught, but 1980 was the only year in which the early peak was the larger of the two. The decline from the early peak into the June/July abundance trough is broken in the 1980 sample by a resurgence of hoverfly abundance in the week of 3 - 10 June, when 417 syrphids were caught before populations plunged into the midsummer dearth, averaging only 87 individuals from all of the five traps over the following five weeks. The recovery to the late season abundance peak is as rapid as the fall from it, to 302 hoverflies captured in the week 5 - 12 August, followed by a decline in numbers until mid-September which marks the close of the hoverfly year, with a small number of syrphids still captured in early October.

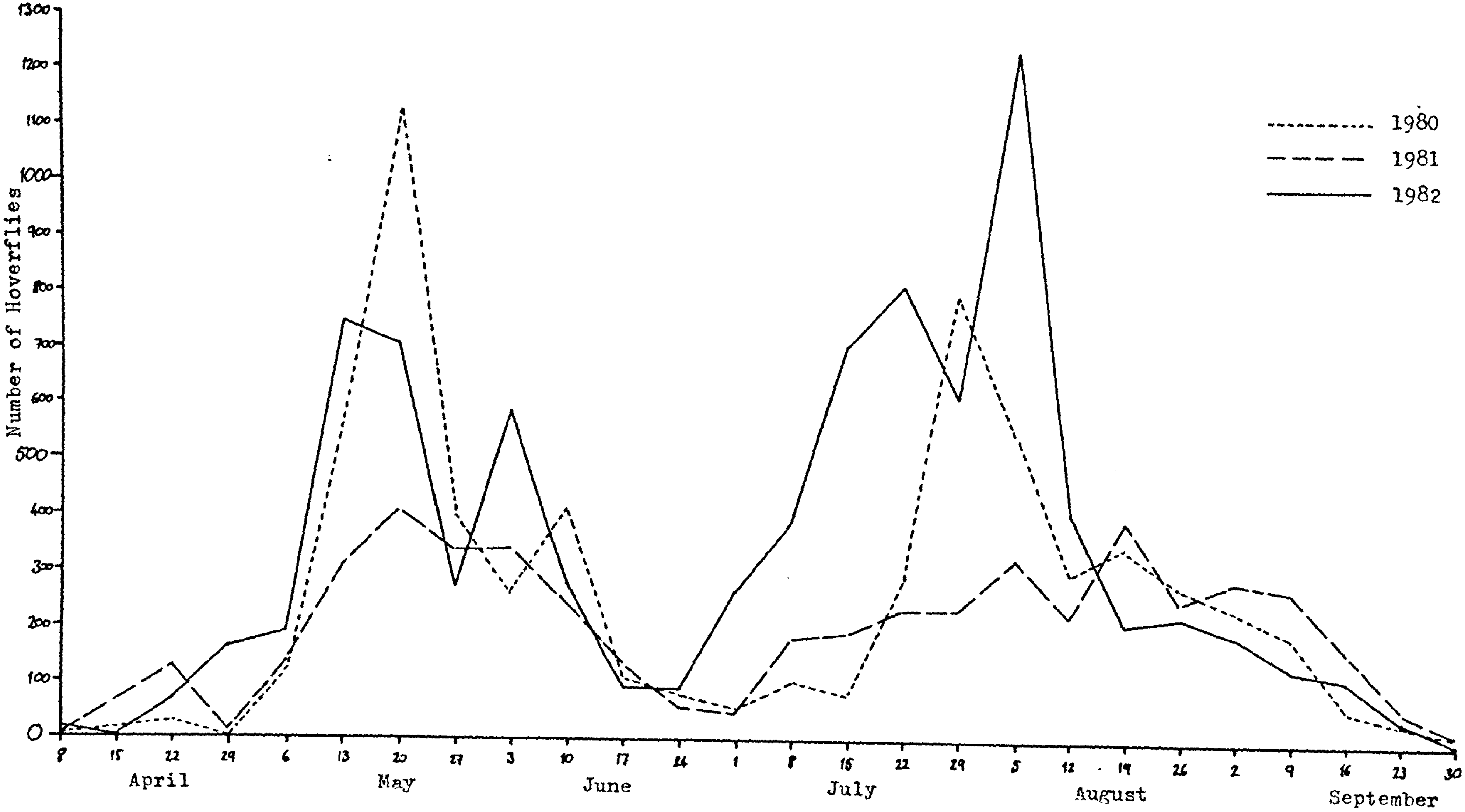


FIG. 7.1 SEASONAL ABUNDANCE OF HOVERFLIES AT BERNWOOD FOREST, 1980 - 1982

The 1981 season did not reproduce the sharply defined peaks of the previous year but the trough of low abundance in the middle of the year confirms the bimodality of the distribution. The early season peak occurred in the same week as in the previous year but only 411 hoverflies were caught, less than half of the previous year's peak. The mid-May peak is preceded by a small peak in mid-April but there is no subsidiary peak preceding the June period of low abundance. This trough of hoverfly scarcity lasts only three weeks in the 1981 sample but the subsequent recovery does not reach the early-season peak, hovering between 250 and 400 individuals each week until early September, when the numbers decline to 28 individuals in the final week of September.

Two clearly-defined abundance peaks are again present in the 1982 collection, although the pattern of abundance is different from that in 1980. The early peak occurs in the week of 6 - 13 May with 747 hoverflies captured but the following week, that of the early peak in the 1980 and 1981 data, maintains this level of abundance with 710 individuals caught. This is followed by a sharp decline between 20 - 27 May to only 275 hoverflies caught, with a recovery to 590 syrphids captured in the following week, before the decline to the mid-summer crash of just below 100 individuals caught in the two weeks of 10 - 24 June. This is the shortest of the three abundance troughs and the following late-season peak includes the best week of all the three year's catches, with 1230 hoverflies caught between 29 July and 5 August. This peak follows a poor week in which 200 fewer syrphids were caught than in the previous week and swiftly declines to 412 hoverflies caught in the week following. The next three weeks see around 200 syrphids each week and then a decline down to 10 syrphids at the end of September, the lowest number in the final weeks of all the years.

All three years thus show a bimodal distribution of hoverflies, with 1980 and 1982 having clearly defined peaks of abundance in both May and late July/early August. Sharply defined abundance peaks are not apparent in the 1981 data in which the bimodality is characterized rather by the mid-season abundance trough than by the preceding and succeeding abundance peaks. This trough, with less than 100 individuals captured in each week, is a feature of all three years collections. The later period of syrphid abundance is of a longer duration than the early one in each of the three years.

7.2 Seasonal Distribution of Hoverflies at the Five Sites

The weekly abundance of hoverflies at the five sites follows the general pattern of the overall abundance for each year (Figs. 7.2, 7.3 and 7.4). A different site contributes the most hoverflies to the early-season peak in each of the three years whilst S2 contributes the most to the late peak in both 1981 and 1982. S4, the richest site with the highest number of individuals in each year, does not contribute the most individuals to any of the six main peaks.

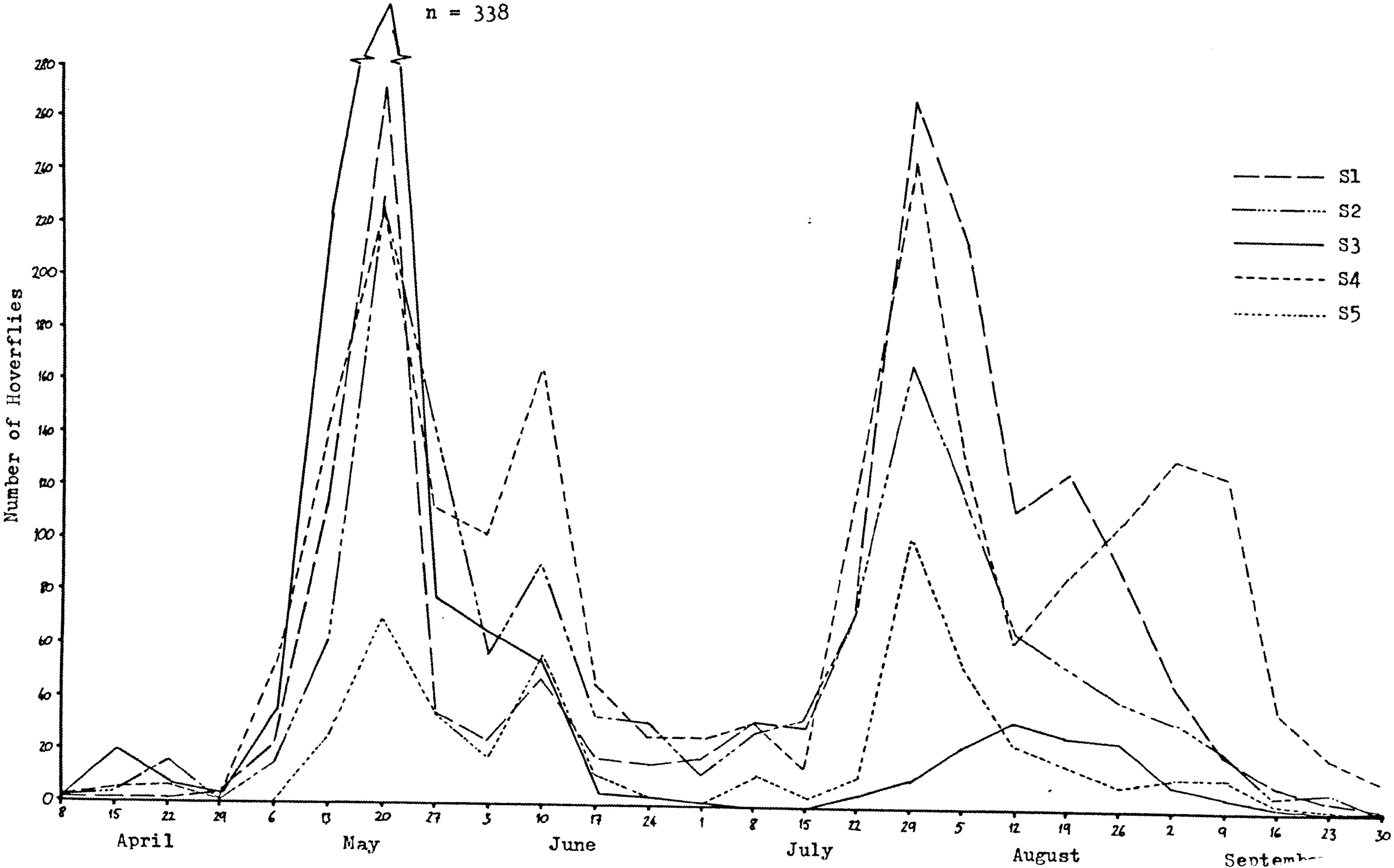


FIG. 7.2 SEASONAL ABUNDANCE OF HOVERFLIES AT THE FIVE SIT
BERNWOOD FOREST 1980

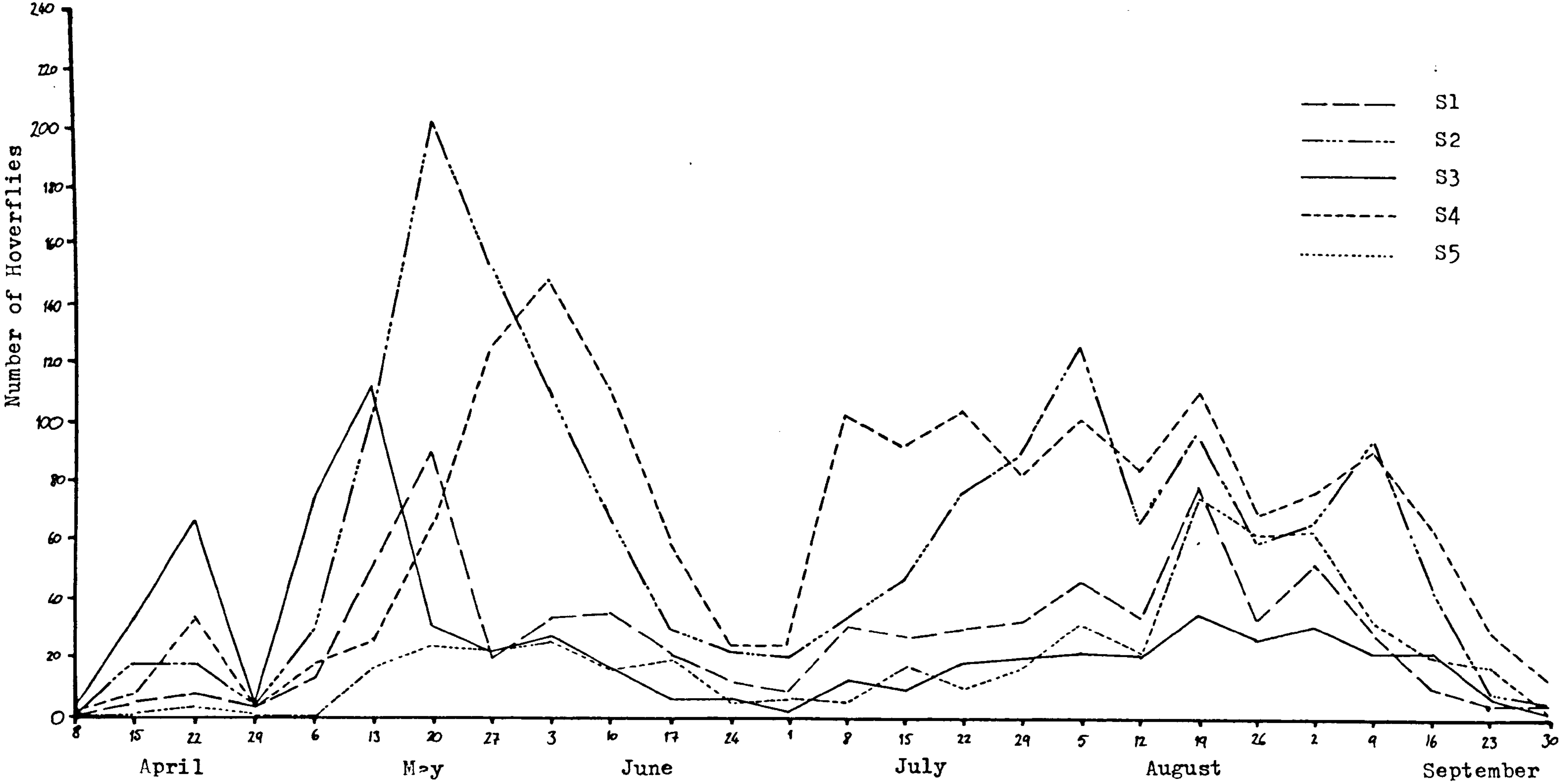


FIG. 7.3 SEASONAL ABUNDANCE OF HOVERFLIES AT THE FIVE SITES, BERNWOOD FOREST 1981

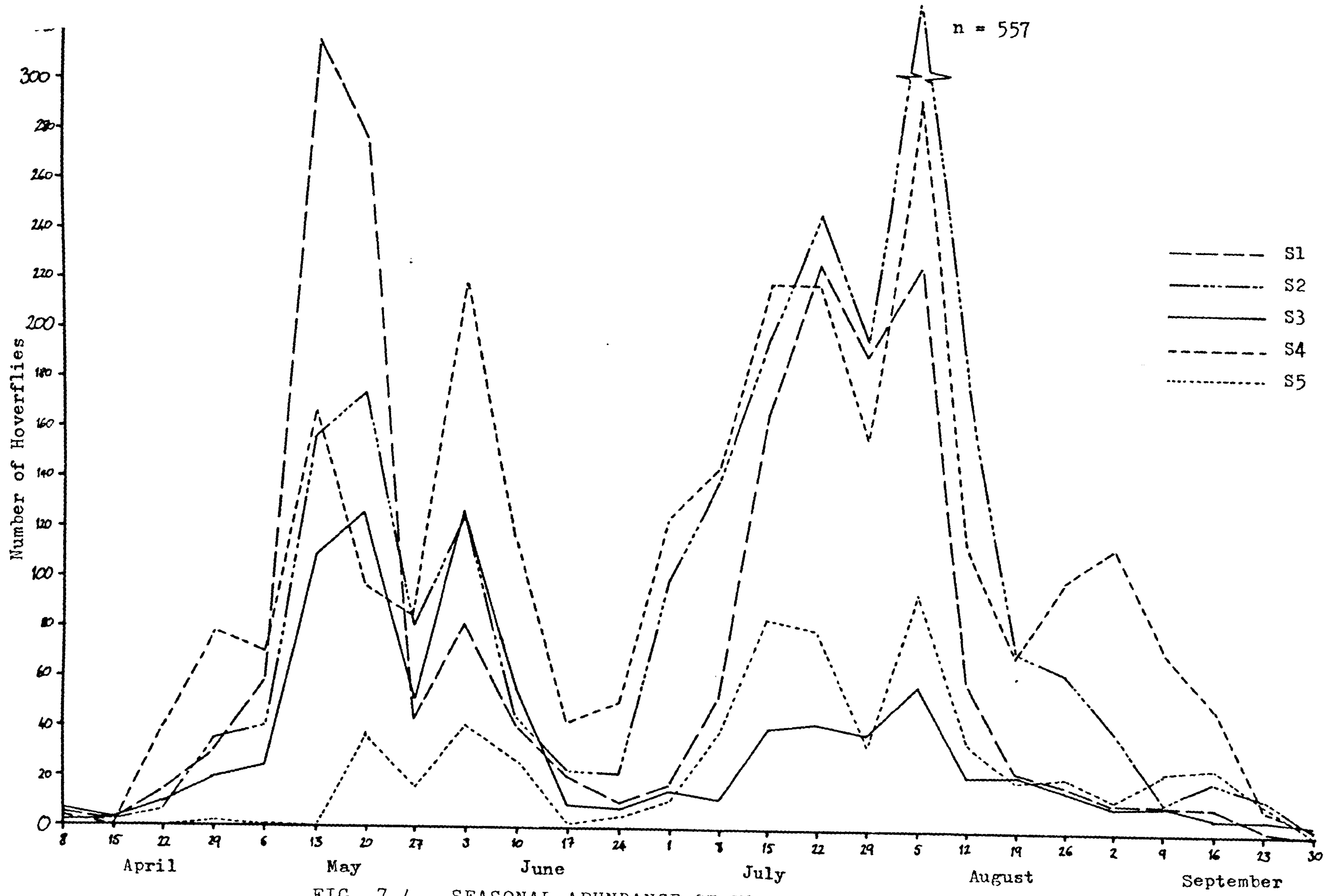


FIG. 7.4 SEASONAL ABUNDANCE OF HOVERFLIES AT THE FIVE SITES BERNWOOD FOREST 1982

The synchrony of the relative abundance of syrphids at the five sites in 1980 is the closest of the three years (Fig. 7.2), which is reflected in the sharp peaks of the overall abundance for this year. S3 contributes the largest number of hoverflies to the main May peak, followed by S1 and then S2 and S4 together; S5 peaks with only 71 individuals in this week. The subsidiary early peak in the first week of June is headed by S4 but all the sites show a marked increase in abundance before crashing the following week into the mid-summer slump. Recovery from the slump is synchronised at all the sites with the exception of S3, which reaches a peak two weeks later than the other four sites. S1 has the most syrphids in this late peak with 268 individuals with S4 having 246; these two samples are clearly the largest. This main late peak is followed five weeks later by a further peak at S4, which occurs whilst the other sites decline to the end of the season. S1, S2 and S4 all have a similar number of hoverflies in the early and late peak weeks whereas S3 only peaks at all in the early peak, with 338 individuals compared with a maximum of 33 in the second half of the year. S5 in contrast has a bigger peak in the late period than in the earlier one.

The weekly abundances of hoverflies at the five sites in 1981 show little of the focussing of abundance seen in 1980 (Fig. 7.3). The early-season peaks span four weeks, with S3 peaking first in the week of 6 - 13 May, S2 and S1 in the following week and S4 two weeks after that; S5 does not achieve a clear peak of abundance, with around

25 hoverflies caught each week between 13 May and 3 June. S2 has the biggest peak with 202 hoverflies captured followed by S4 with 148. S3 has only 112 hoverflies compared with 338 in the previous year's peak, although this site has a small peak of 66 syrphids in 15 - 22 April.

The duration of the mid-season abundance trough varies between the sites. S4 shows the quickest recovery with only two weeks of low abundance whereas S3 falls to 30 syrphids caught in the week of 13 - 20 May and does not exceed this number until the 12 - 19 August. S1 has a long period of low abundance whereas S5 does not have a period of higher abundance before the trough. The second period of abundance shows much fluctuation in the number of syrphids caught at each site and little synchronization between the sites, although all sites show an increase in abundance in the week of 12 - 19 August and a decrease in the following week. The highest number of individuals caught in any one week is at S2 between 29 July and 5 August with 126 syrphids captured although the period of syrphid abundance is greater at all sites for the late season and thus the overall abundance is not reflected in the small peaks. S5 is the only site to have a larger peak in the later half of the season and S1 has similar peaks in both periods, the other three sites having greater peaks in the early season.

1982 shows a return to the well-synchronized peaks of 1980 (Fig. 7.4). The season starts earlier than in the previous two years although the mid-season trough begins at the same time, between 10 - 17 June. The early season is characterised by two peaks of similar abundance, split by a single week of poor catches. The first of these peaks spans two weeks. S1 peaks in the first of these two weeks and produces the largest weekly sample of the early season with 316 hoverflies captured. S2 and S3 peak in the following week, that of 13 - 20 May, as does the smaller sample from S5. The second of the early peaks is topped by S4 which is the only site to have more hoverflies caught in this week than in the previous ones, although the syrphids at both S3 and S5 have similar abundances.

The 1982 abundance trough is the shortest of all the three years, lasting for two weeks and with abundances rising steeply into the late-season abundance peaks. These again are split by a week of poor catches, between 22 - 29 July, which precede the largest catches of the year at S2, S4 and S5. The first week of August in 1982 produced the largest catch at a single site during the three years of the experiment, with 557 syrphids caught at S2. This is followed by a sharp decline in abundance at all of the five sites into the poorest September samples of all the three years, broken only by the familiar late August/early September resurgence of hoverfly abundance at S4. The samples from S2, S4 and S5 all peak higher in the later season than in the early one, in contrast with those from S3 and S5 which reach their weekly maxima in the early season. The late season spans two more weeks than the early one and therefore the peak abundances are the product of a larger population than in the early season, with the exception of S3.

The bimodal pattern of seasonal abundance of hoverflies is reflected in the number of species caught each week at each site (Figs. 7.5, 7.6 and 7.7), although the peaks are obviously not as pronounced as those for the number of individuals. The abundance troughs in the middle of each year show a greater number of species than might be expected from the numbers of hoverflies caught, indicating that this period shows little of the dominance of the community characteristic of the periods of high abundance.

The 1980 samples show clear synchronization of the number of species present at each site for the first half of the trapping season but not in the second half (Fig. 7.5). The two abundance peaks in May and June have a similar number of species, in contrast with the abundance of hoverflies and the early season is richer in species than the later one. The highest number of species in a week occurs at S4 in the early season, followed by S1 and S2 and this ordering of the sites is repeated in the late season, where the difference between the sites is small, being spanned by two species. S3 peaks higher than S5 in the early season but lower in the later one, which reflects the abundance of syrphids at these sites over the year.

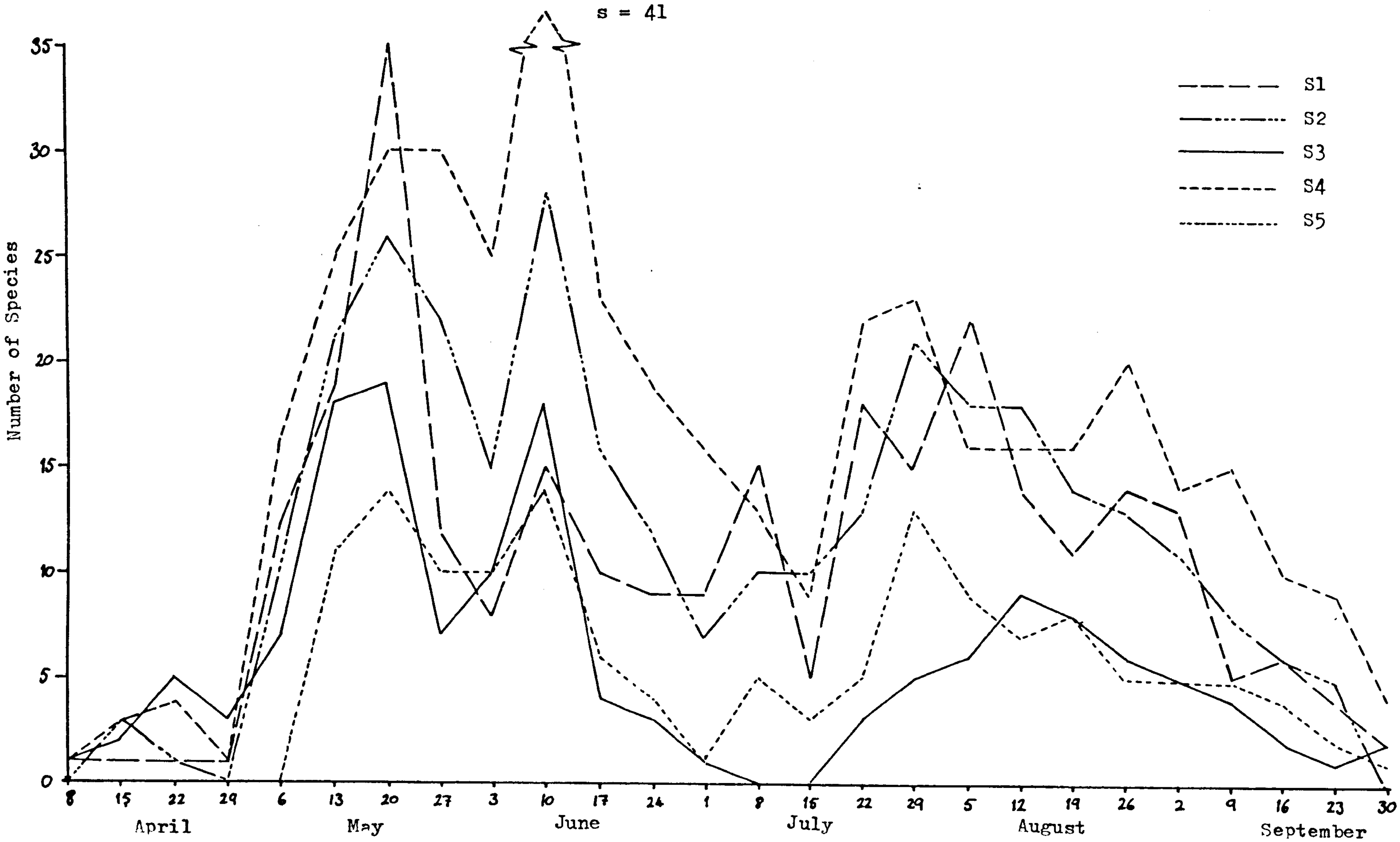


FIG. 7.5 WEEKLY ABUNDANCE OF SPECIES AT THE FIVE SITES, BERNWOOD FOREST 1980

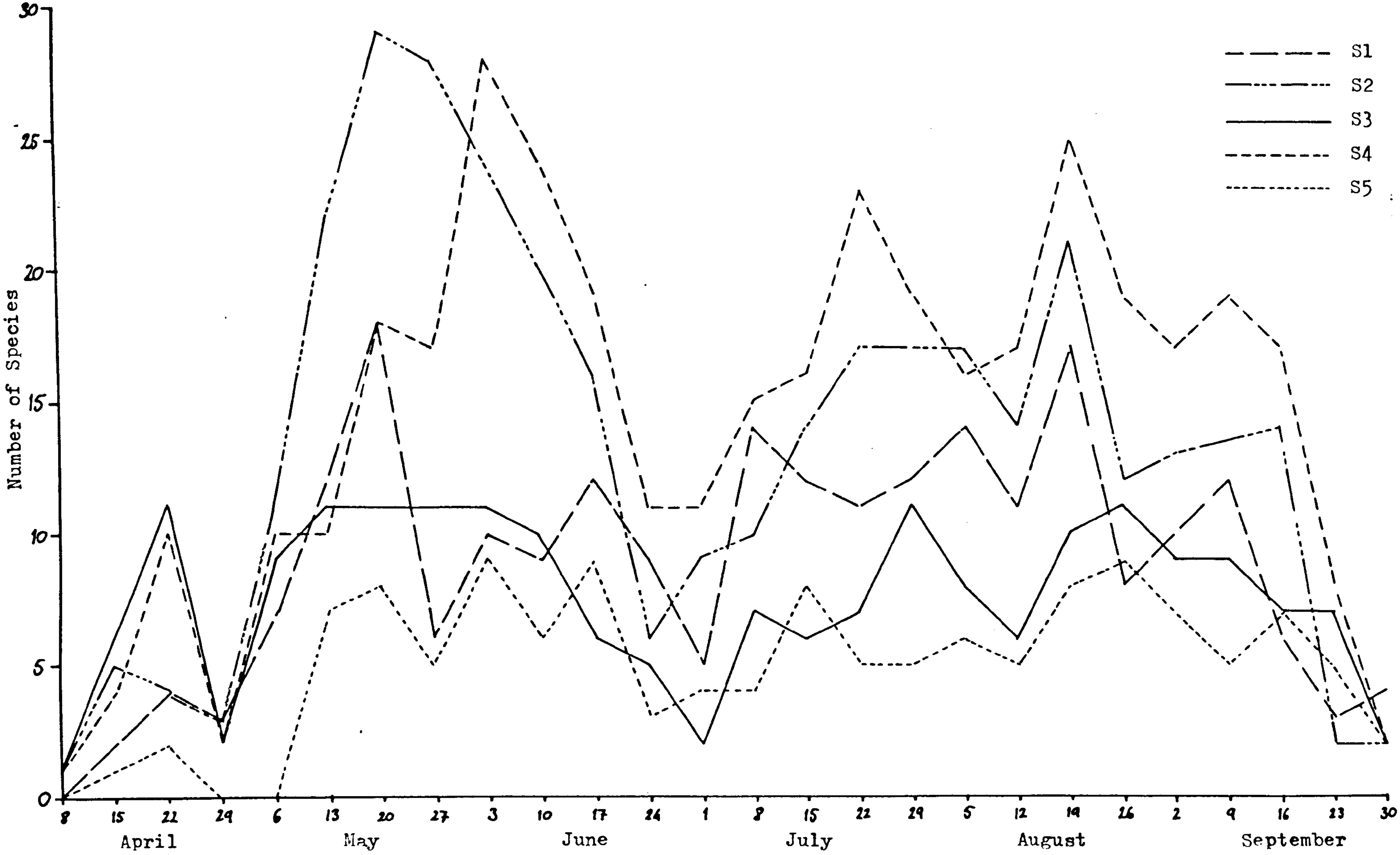


FIG. 7.6 WEEKLY ABUNDANCE OF SPECIES AT THE FIVE SITES, BERNWOOD FOREST 1981

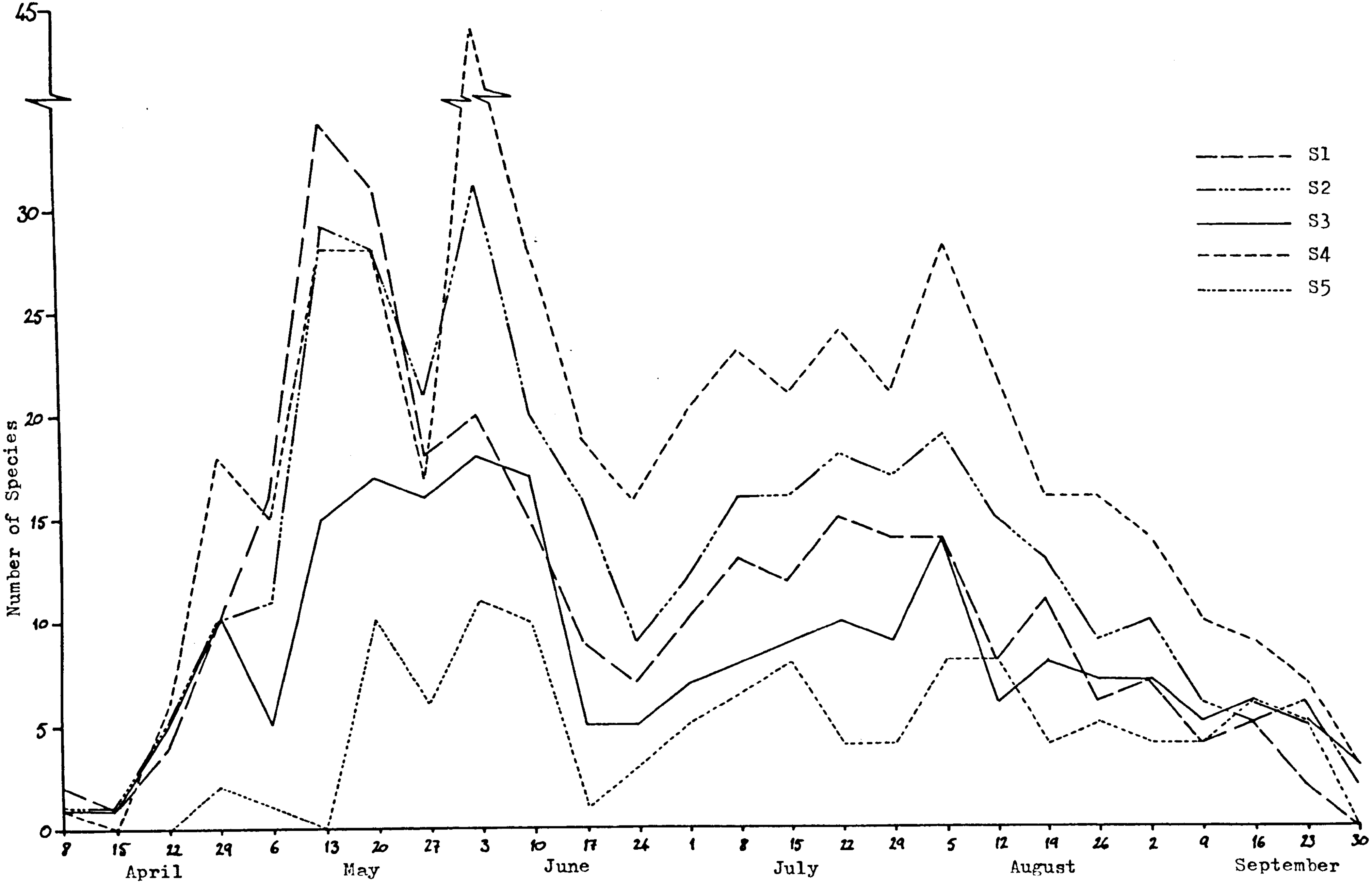


FIG. 7.7 WEEKLY ABUNDANCE OF SPECIES AT THE FIVE SITES, BERNWOOD FOREST 1982

The build-up of species richness at the five sites in 1981 is well synchronized up until mid-May and is not regained until the week of 5 - 12 August, when all the sites suffer a reduction in richness before peaking the following week (Fig. 7.6). S2 and S4 peak highest in the early season with S1 conspicuously species-poor. The species richness at S1 in the late season achieves this same peak whereas both S2 and S4 suffer a peak reduction relative to the early peak, although they both maintain a higher species richness than S1, with S4 the highest. S3 peaks higher than S5 in each season, which does not reflect the abundance of individuals during the late season.

Synchrony of species richness amongst the sites returns in the 1982 collections of hoverflies, especially at the three richest sites (Fig. 7.7). The early season is richer for all the sites, with S4 having the most species in one week, above S1 and S2. S4 is again the richest site in the late season with the places of S1 and S2 reversed. The low abundances in September of this year compared with the previous two are reflected in a lower species richness at the sites.

7.3 Analysis of the Two Seasonal Periods

The bimodal seasonal distribution of abundance of syrphids, with the periods of low abundance occurring in the middle of the summer, allows the six month trapping period to be conveniently split into two 13-week periods.

The 'early season' runs from April until July and the 'late season' from July to September. Each 'season' thus contains one of the two annual abundance peaks and the periods of low abundance that precede and succeed it. Very few hoverflies have been caught at Bernwood before April and after September and so the two 13-week 'seasons' encompass virtually the entire syrphid flight period at Bernwood.

7.3a The Number of Hoverfly Species and Individual Caught in the Two Seasons

The number of individuals and species of hoverflies captured in each of the two sampling seasons at each site over the three years is given in Table 7.1. The major trend is for more individuals, but fewer species, to be caught in the late period than in the early one.

The major exceptions to this trend are the samples from S3. More individuals are captured in the early season than in the late one in each of the years, by as much as five times in 1980, although less spectacularly but nevertheless still significantly in the other two years. The same number of syrphids was captured in each of the two samples from S2 in 1980 and in the following year the late sample contained only 7% more individuals, in contrast with the 1982 collection in which more than twice as many hoverflies were caught in the late season than in the early one.

TABLE 7.1

THE NUMBER OF INDIVIDUALS AND SPECIES OF HOVERFLIES IN THE EARLY AND LATE SAMPLING SEASONS AT FIVE SITES BERNWOOD FOREST 1980 - 1982

		S1		S2		S3		S4		S5	
		E	L	E	L	E	L	E	L	E	L
	1980	576	1026	690	693	820	150	905	1160	222	269
N	1981	299	412	755	809	402	247	647	1019	139	378
	1982	917	1003	812	1742	559	290	1091	1574	142	486
	1980	52	37	58	34	35	13	70	40	24	18
S	1981	29	34	56	41	31	23	50	47	17	18
	1982	56	23	58	37	36	22	65	46	20	16

The actual number of hoverflies caught is extremely variable, even within a particular site, either between the same season in different years or between the two seasons in a particular year. No prediction of syrphid abundance in the following season is possible given any previous season's abundance apart from the trend at four sites of higher abundance later in the year; this increase in abundance ranges from 0.43% at S2 in 1980 to 342% at S5 in 1982 and occurs in an apparently haphazard manner.

The trend of the early season having a richer species assemblage than the late one is more robust than the trend of abundance of individuals between the two seasons. The only major departure from this pattern occurs in the 1981 sample from S1, in which 29 species of syrphid were caught in the early season compared with 34 in the late one. Two other sites in 1981 had a similar number of species caught in each of the two sampling periods; these are S4 and S5.

7.3b Hoverfly Species Composition of the Two Seasonal Samples

The common species that account for the majority of the hoverfly catch at each site and year are given in Table 7.2 for the early season and in Table 7.3 for the late one. Most of these common species

TABLE 7.2

THE ABUNDANT HOVERFLIES FROM THE EARLY SAMPLING SEASON, 1 APRIL TO 1 JULY, FROM FIVE SITES, BERNWOOD FOREST, 1980 - 1982

S1		S2		S3		S4		S5	
				1980					
D. venustus	109	*D. venustus*	104	*S. ribesii*	379	*M. scalare*	189	*Baccha*	45
M. scalare	69	*S. ribesii*	97	*M. mellinum*	148	*M. mellinum*	94	*R. campestris*	32
F. cuprea	53	*R. campestris*	72	*M. scalare*	90	*F. cuprea*	59	*D. venustus*	21
R. campestris	43	*F. cuprea*	66	*M. lasiophthalma*	27	*Sphaerophoria*	56	*P. scutatus*	18
M. mellinum	36	*M. scalare*	51	*P. malinellus*	17	*S. ribesii*	44	*P. tarsalis*	16
P. malinellus	29	*M. lasiophthalma*	33	*P. scutatus*	17	*Neocnemodon*	28	*M. scalare*	15
		M. mellinum	32			*P. lineolus*	27		
						P. malinellus	27		
				1981					
M. scalare	67	*R. campestris*	145	*M. scalare*	136	*M. scalare*	225	*M. scalare*	41
R. campestris	67	*M. scalare*	76	*M. lasiophthalma*	77	*M. mellinum*	55	*R. campestris*	31
F. cuprea	55	*M. lasiophthalma*	74	*M. mellinum*	53	*F. cuprea*	35	*B. elongata*	13
		F. cuprea	66	*P. punctulatus*	23	*H. pendulus*	35		
		D. venustus	55	*P. albimanus*	20	*E. pertinax*	33		
		P. punctulatus	38			*R. campestris*	28		
		M. mellinum	34			*C. paganus*	27		
						M. lasiophthalma	25		

TABLE 7.2 CONTINUED

1982

M. cinctella	211	*H. pendulus*	126	*M. cinctella*	127	*H. pendulus*	233	*M. cinctella*	64
F. cuprea	109	*M. cinctella*	100	*M. scalare*	94	*M. scalare*	147	*M. scalare*	19
M. scalare	95	*M. scalare*	70	*S. ribesii*	55	*E. pertinax*	121	*B. elongata*	12
H. pendulus	95	*F. cuprea*	61	*M. mellinum*	46	*M. cinctella*	75		
R. campestris	55	*D. venustus*	41	*P. lineolus*	35	*M. mellinum*	61		
D. venustus	53	*S. ribesii*	36	*M. lasiophthalma*	28	*M. corollae*	37		
M. lasiophthalma	38	*E. pertinax*	33			*M. lasiophthalma*	30		
E. pertinax	38					*C. paganus*	27		
						P. lineolus	26		

TABLE 7.3

THE ABUNDANT HOVERFLIES FROM THE LATE SAMPLING SEASON, 1 JULY TO 30 SEPTEMBER, FROM FIVE SITES. BERNWOOD FOREST, 1980 - 1982

S1		S2		S3		S4		S5	
				1980					
E. balteatus	228	*M. cinctella*	123	*S. ribesii*	69	*R. campestris*	225	*E. balteatus*	120
M. cinctella	172	*S. ribesii*	115	*M. scalare*	32	*M. scalare*	137	*R. campestris*	29
M. scalare	128	*R. campestris*	66			*M. mellinum*	121	*M. scalare*	28
P. albimanus	116	*P. albimanus*	60			*P. albimanus*	93	*M. cinctella*	28
P. peltatus	88	*E. balteatus*	54			*H. pendulus*	93	*B. elongata*	26
M. mellinum	50	*M. scalare*	52			*S. ribesii*	88		
R. campestris	50	*M. mellinum*	42			*P. peltatus*	49		
		P. lineolus	41			*E. balteatus*	44		
				1981					
M. cinctella	123	*M. cinctella*	183	*M. scalare*	56	*H. pendulus*	165	*M. cinctella*	160
P. albimanus	50	*P. albimanus*	152	*M. cinctella*	40	*M. mellinum*	134	*E. balteatus*	70
E. balteatus	39	*H. pendulus*	72	*S. ribesii*	36	*P. albimanus*	126	*B. elongata*	62
M. scalare	37	*S. ribesii*	65	*M. mellinum*	21	*M. scalare*	102	*M. scalare*	35
B. elongata	33	*M. scalare*	64			*C. bicinctum*	57		
		E. pertinax	53			*E. nemorum*	49		
		M. mellinum	35			*M. cinctella*	36		
						E. pertinax	36		
						R. campestris	34		

TABLE 7.3 CONTINUED

1982									
S1		S2		S3		S4		S5	
E. balteatus	460	*E. balteatus*	973	*E. balteatus*	70	*E. balteatus*	355	*E. balteatus*	297
M. cinctella	300	*M. cinctella*	355	*M. scalare*	61	*H. pendulus*	316	*M. cinctella*	119
M. scalare	44	*H. pendulus*	117	*M. cinctella*	49	*M. mellinum*	138	*M. scalare*	27
H. pendulus	35	*P. lineolus*	52	*H. pendulus*	24	*M. cinctella*	123		
X. segnis	34	*M. scalare*	49			*P. lineolus*	96		
P. lineolus	33	*D. fasciata*	32			*M. scalare*	74		
		X. sylvarum	25			*R. campestris*	60		
						D. fasciata	57		
						X. sylvarum	54		
						C. paganus	40		

show great variation in their abundance between sites, seasons and years but little of this variation is consistent or predictable and the overall impression is of a haphazard occurrence of the abundances. Each season does however have its unique species and certain patterns are consistent between different years.

Nine common species are found only in the collections from the early season of sampling although three of these, *Metasyrphus corollae*, *Sphaerophoria spp.* and *Neocnemodon spp.*, are common at only one site and in a single year. *Parasyrphus malinellus*, *P. punctulatus* and *Platycheirus scutatus* are only common in 1980, which leaves just three species which can be justifiably termed characteristic of the early season. *Ferdinandea cuprea* is encountered at S1, S2 and S4 in all three years although only 18 were captured at S4 in 1982. The two deciduous sites provide the best habitat for this species and for *Dasysyrphus venustus*, which is the most common of the early season species at both S1 and S2 in 1980, when it is also moderately abundant at S5. *Melangyna lasiophthalma* is characteristic of the early-season catches from all the sites save for S5, where it is recorded, albeit by few specimens, in each of the three years. It is most common at S3, the only site where it is common for all three years and unlike either *F. cuprea* or *D. venustus* it has never been captured in the late season.

With only one exception, all of the sites have a different species as the most common syrphid present in the early season collection in each of the three years. This exception is *Melanostoma scalare*, which heads the S4 catches in both 1980 and 1981. This species is more abundant in the early season than in the late, when it is nevertheless still a common species.

Dasysyrphus venustus was the most common syrphid in the early catches at both S1 and S2 in 1980, with *Syrphus ribesii* heading the S3 collection and *Baccha elongata* the one at S5. *Rhingia campestris* is common at S1, S2 and S5; *Melanostoma mellinum* at S1, S2, S3 and S4; and *Syrphus ribesii* at S2 and S4 in addition to at S3.

Melanostoma scalare, which was abundant at all the sites in 1980, is the most common syrphid at all the early 1981 sites apart from at S2, where *Rhingia campestris* is twice as abundant with 145 individuals captured; and at S1, where 67 individuals of both species were caught. S4 is the most dominated site, with 225 *M. scalare* caught compared with 55 of *M. mellinum*, the next-most abundant species which is also common at S2 and S3.

The 1982 catch is dominated by different species than in the previous two years, with *Meliscaeva cinctella* heading the S1, S3 and S5 collections and being common at the other two sites. *Helophilus pendulus* is the most abundant syrphid at both S2 and S4 and is also common at S1 and *Eristalis pertinax* is common at these three sites. *Dasysyrphus venustus* is again common at both of the deciduous sites, as is *Ferdinandea cuprea* with the remainder of the common species being site specific, although *Melanostoma mellinum* is moderately abundant at both S3 and S4.

Seven syrphids are common only in the late season of trapping although six of these are abundant only in one year and at one or two sites. Thus *Episyrphus balteatus* is the sole species to be widespread only in the late season and its abundance fluctuates dramatically between the three years. In 1980 it was the most common of the late species at both S1 and S5 and occurred at all the other sites, albeit only as a rare species at S3. The following year it was common only at S1 and S5 but in 1982 became the most abundant hoverfly at each of the five sites, with S2 producing the largest catch, of 973 specimens.

Meliscaeva cinctella, *Syrphus ribesii* and *Rhingia campestris* are the most common syrphids in the late 1980 collections from S2, S3 and S4 respectively. *Melanostoma scalare* is the only species to be abundant at all five sites with *M. mellinum* and *Platycheirus albimanus* common at S1, S2 and S4. *S. ribesii* is common at S2 and S4 besides S3 and

M. cinctella at S1 and S5 in addition to S2; *Rhingia* is common at all the sites apart from S3, where only 11 specimens were caught despite it being the third-ranking hoverfly.

S1, S2 and S5 all have *Meliscaeva cinctella* the most abundant syrphid in the 1981 late collections and it ranks second at S3, with only 36 individuals captured at S4. *Melanostoma scalare* heads the S3 sample and is a common species at all the five sites whereas *Helophilus pendulus*, the most common species from S4, is common elsewhere only at S2. *Platycheirus albimanus* is abundant at S1 and at S2 although the relative abundance between the two sites is different from the previous year, with the latter site having three times as many individuals present. *Episyrphus balteatus* is rare, only featuring at S1 and S5, as does *Baccha elongata*, whereas *Syrphus ribesii* is common only at S2 and S3.

The late 1982 samples are dominated by *Episyrphus balteatus* which occurred in spectacular numbers throughout the Forest. The second-place species at each site is the same as the previous year's most abundant species and both *Melanostoma scalare* and *Meliscaeva cinctella* are common at all of the sites, although further similarities between the two years are of little significance. *Helophilus pendulus* is common at all the sites except for S5, *Parasyrphus lineolus* is common at the two deciduous sites and at S4 and *Didea fasciata* is abundant at S2 and S4, the latter site having the largest number of common species of the three years.

7.4 Discussion

7.4a Abundance Peaks and Species Composition

The patterns of hoverfly abundance contained within the bimodal distributions are different for each of the three years and whilst this can be appreciated from the syrphid abundances within the two trapping seasons in each year, a closer breakdown of the actual peak weeks' abundances yields further insight into the mechanics governing the structure of these hoverfly assemblages. Abundances of individual hoverfly species for each week of the major peaks are given in Table 7.4 for the early peak and Table 7.5 for the late one.

The early 1980 peak is well-defined, narrow and well-synchronised between the five sites. The major feature of this season is the large number of *Syrphus ribesii* captured, with 233 individuals caught at S3 between 13 - 20 May. 115 *Melanostoma mellinum* were caught in the previous week at this site but only one other species, *M. scalare*, was at all common during this period. This pattern of species abundance is untypical of the other four sites, which show less dominance by the most abundant species and

TABLE 7.4

EARLY SEASON PEAK: THE ABUNDANT SPECIES AT FIVE SITES, BERNWOOD FOREST, 1980 - 1982: WEEKLY ABUNDANCES

1980

		May		
		6-13	13-20	20-27
S1	*D. venustus*	16	79	5
	S. ribesii	4	16	0
	F. cuprea	14	11	5
	M. mellinum	15	19	0
	M. scalare	13	30	6
	R. campestris	10	17	3
	P. noctiluca	5	15	0
S2	*D. venustus*	0	55	29
	S. ribesii	5	55	23
	F. cuprea	1	1	34
	M. mellinum	12	16	1
	M. scalare	5	13	17
	R. campestris	10	17	13
S3	*S. ribesii*	17	235	65
	M. mellinum	115	21	0
	M. scalare	36	17	5
S4	*S. ribesii*	1	15	14
	F. cuprea	1	1	24
	M. mellinum	38	39	4
	M. scalare	25	64	27
S5	*R. campestris*	5	12	3
	B. elongata	3	9	6
	D. venustus	1	12	0

TABLE 7.4 CONTINUED

1981

			May			June	
		29-6	6-13	13-20	20-27	27-3	3-10
S1	*M. scalare*		4	15	10		
	F. cuprea		11	21	2		
	R. campestris		18	28	4		
S2	*D. venustus*		5	17	20		
	M. lasiophthalma		15	12	11		
	M. mellinum		6	21	2		
	M. scalare		13	19	11		
	P. malinellus		1	14	5		
	P. punctulatus		11	20	3		
	S. ribesii		5	11	7		
	F. cuprea		3	8	13	21	
	R. campestris		25	30	34		
S3	*M. mellinum*	8	29	2	3		
	M. scalare	41	51	14	7		
	P. punctulatus	3	11	2	1		
S4	*M. mellinum*		2	13	12	12	10
	M. scalare		7	20	65	73	36
	F. cuprea		0	1	7	6	15
S5	*M. scalare*		9	5	8	8	
	R. campestris		2	10	11	5	

TABLE 7.4 CONTINUED

1982

		6-13	13-20	20-27	27-3
S1	*D venustus*	20	26	1	4
	M. scalare	32	20	6	10
	M. cinctella	105	66	7	6
	F. cuprea	48	22	7	5
	H. pendulus	28	33	2	17
	R. campestris	7	34	1	7
S2	*D. venustus*	3	20	9	8
	M. scalare	17	16	6	7
	M. cinctella	15	41	11	13
	F. cuprea	14	13	16	3
	H. pendulus	12	6	0	20
S3	*M. mellinum*	32	8	2	0
	M. scalare	32	18	7	16
	M. cinctella	14	32	19	31
	P. lineolus	4	17	2	7
	S. ribesii	4	28	5	9
	E. pertinax	2	0	1	12
	H. pendulus	4	2	1	16
S4	*M. mellinum*	38	10	6	2
	H. scalare	33	20	28	31
	M. cinctella	15	16	9	14
	M. corollae	1	0	0	20
	E. pertinax	18	2	9	21
	H. pendulus	15	7	4	39
S5	*M. cinctella*	0	20	5	15
	M. scalare	0	6	7	5

TABLE 7.5

LATE SEASON PEAK: THE COMMON HOVERFLIES AT FIVE SITES, BERNWOOD FOREST 1980 - 1982: WEEKLY ABUNDANCES

1980

		July			August			
		15-22	22-29	29-5	5-12	12-19	19-26	26-2
S1	*E. balteatus*	5	99	77				
	M. cinctella	5	55	40				
	M. mellinum	1	19	14				
	M. scalare	6	18	22				
	P. albimanus	23	29	15				
S2	*E. balteatus*	1	13	13				
	M. cinctella	12	42	18				
	P. lineolus	7	8	10				
	S. ribesii	24	44	17				
	M. mellinum	4	18	10				
	M. scalare	3	10	9				
	P. albimanus	15	12	17				
	R. campestris					28		
S3	*S. ribesii*	2	4	8	17	15	19	
	M. scalare	1	4	11	3	4	4	
S4	*E. balteatus*	2	17	17				
	M. cinctella	2	14	7				

TABLE 7.5 CONTINUED

				July				August		
1980		8-15	15-22	22-29	29-5	5-12	12-19	19-26	26-2	2-9
S4	*M. latifasciatus*		0	21	0					
	S. ribesii		46	23	0					
	M. mellinum		6	58	26					
	M. scalare		4	36	33					
	P. albimanus		15	34	16					
	R. campestris							46	81	69
	H. pendulus							12	12	26
S5	*E. balteatus*		0	63	36					
1981										
S1	*M. cinctella*					6	32	12	20	
S2	*M. cinctella*			21	27	15	26	18	17	27
	P. albimanus			21	32	17	17	16	16	10
	S. ribesii							4	11	20
S3	*M. scalare*					9	11	9		
S4	*M. mellinum*			21	14	26	12	14		
	M. scalare				10	16	8	13		
	P. albimanus				15	11	22	3		19

TABLE 7.5 CONTINUED

					July				August			
1981		1-8	8-15	15-22	22-29	29-5	5-12	12-19	19-26	26-2	2-9	9-16
S4	*H. pendulus*				11	19	5	8	6	15	11	20
	R. campestris							3	9	14	6	1
S5	*B. elongata*							5	11	12	9	
	E. balteatus						1	27	12	9	6	
	M. cinctella					18	12	32	32	30	11	
1982												
S1	*E. balteatus*		119	93	48	130	30					
	M. cinctella		17	97	109	40	13					
S2	*E. balteatus*		121	125	105	439	104	18				
	M. Cinctella		21	67	49	59	49	31				
	H. pendulus	63	21	16	9	8	1	0				
S3	*E. balteatus*		13	16	9	14	4					
	M. scalare		1	3	11	16	10					
	M. cinctella		7	14	10	7	0					
S4	*E. balteatus*		105	33	46	108	16					
	M. mellinum		20	42	10	44	11					
	M. cinctella		9	43	14	20	9					

TABLE 7.5 CONTINUED

					July			August			September
1982		1-8	8-15	15-22	22-29	29-5	5-12	12-19	19-26	26-2	2-9
S4	*P. lineolus*		22	23	7	3	5				
	H. pendulus	59	21	16	18	16	19	21	37	50	31
	R. campestris								8	23	18
	E. balteatus		69	40	15	72	24				
	M. cinctella	12	9	36	17	14	2				

a greater number of common species. S1 is dominated by *Dasysrphus venustus* but *M. scalare*, *M. mellinum*, *Rhingia campestris*, *Ferdinandea cuprea*, *Syrphus ribesii* and *Pipiza noctiluca* are all common and this pattern of species abundance is reflected at S2 and S4, with S5 having a small sample of hoverflies consisting mostly of *Rhingia campestris*, *Baccha elongata* and *Dasysyrphus venustus*.

The early 1981 samples do not show the sharp focussing into short periods of high abundance of the 1980 early season. The biggest abundance peak is that of the S2 hoverfly sample, in which 9 species are common of which none is represented by 100 individuals in the whole of the three week peak period. S4 by contrast, which shows the next-largest peak, has the bulk of the catch in one species, *Melanostoma scalare*, with only two other common species. S1 has three common species of similar abundance and S5 two but both these sites have poor catches of around half the previous year's abundance.

The 1982 samples show a return to, and in most cases above, the 1980 levels of abundance and the early peak is clearly defined and well synchronised between the five sites. S1 has the largest catch dominated by *Meliscaeva cinctella*, but *Dasysyrphus venustus*, *Melanostoma scalare*, *Ferdinandea cuprea*, *Helophilus pendulus* and *Rhingia campestris* are all common. This pattern is repeated at S2 but neither

S3 nor S4 show strong domination by one species in any particular week, with many species common. The small peak at S4 between 22 - 29 April is due largely to a single species, *Eristalis pertinax*, but only 26 individuals were caught in that week. S5 has only two common species, *Meliscaeva cinctella* and *Melanostoma scalare*, which occur in similar numbers.

The late 1980 peak is the product of several species rather than one in particular and none of the sites save for S5 is heavily dominated by one species. S5 has only one common species, *Episyrphus balteatus*, which is more numerous at this site than at the others, with the exception of S1, where it is also the most abundant syrphid of the early season. *E. balteatus*, *Meliscaeva cinctella*, *Melanostoma mellinum*, *M. scalare* and *Platycheirus albimanus* form a 'pool' of species that are all common but with changing relative abundances at S1, S2 and S4. *Syrphus ribesii* is also common at S4 and at S3, where, although scarce, it is the most abundant syrphid of the season. *Rhingia campestris* is responsible for the small peaks during the tail end of the year at both S1 and S4, with *Helophilus pendulus* also present in the peak at the latter site.

The lack of clear late-season peaks in the small catches of 1981 is reflected in the low weekly abundances of the species in these samples, with 32 individuals of one species caught on four occasions but never exceeded. The richness of the samples is also lower than in the previous year with fewer common species at each site, both S1 and S3 having only one common species, in *Meliscaeva cinctella* and *Melanostoma scalare*, respectively. *M. cinctella* and *Platycheirus albimanus* are the two equally-common species at S2, with *Syrphus ribesii* becoming as common later on in the season; *Melanostoma mellinum*, *M. scalare*, *Platycheirus albimanus* and *Helophilus pendulus* are all common at S4, with the latter species continuing late on in the season, when it is joined by *Rhingia campestris*. *Meliscaeva cinctella* is the most abundant species at S5, followed by *Episyrphus balteatus* and then *Baccha elongata*, which gives a more even species distribution than that of the previous year.

The late 1982 season samples contain the largest weekly catches of the whole three year period and witness a return to the sharply defined and well synchronised peaks of 1980. *Episyrphus balteatus* dominates the catches from all of the five sites except for S3, where it is nevertheless the most numerous hoverfly, although both *Melanostoma scalare* and *Meliscaeva cinctella*, the only other common species, are present in similar numbers. *Meliscaeva cinctella* is the only other syrphid that is common at all the sites, and there are fewer common species than during the late season of 1980, despite greatly increased numbers. S2 captured the bulk of the

E. balteatus explosion, with 439 individuals caught in the week of 29 July to 5 August and 894 over the five-week peak period. *M. cinctella* and *Helophilus pendulus* are the only other common species at this site and at both S1 and S5 the former species is the only other common species with *E. balteatus*. *M. cinctella* and *Melanostoma mellinum* are the next-most abundant species at S4 to *E. balteatus* and do not show the population slump of the dominant species in the week 15 - 22 July. *Parasyrphus lineolus* is also common as is *Helophilus pendulus*, which once more maintains a long flight period and is largely responsible for the end-of-season peak in 26 August - 2 September, when *Rhingia campestris* also becomes common.

The biggest abundance peaks in the Bernwood hoverflies are thus seen to be due to the influence of a single species, although this extreme community dominance does not happen regularly or in every year. The *Episyrphus balteatus* outbreaks of 1982 seemed to depress the potential of other normally common species, apart from *M. cinctella*, as did the *Syrphus ribesii* explosion at S3 in 1980, when fewer species were common than in 1982. Moderate dominance in the hoverfly assemblages appears to produce the richest communities which extreme dominance does not allow. The 1981 samples, particularly those from the early season, are poor in both the number of species and individuals compared with the other years, though the early catch from S2 contains the greatest number of common species obtained from that site. Only 19 of the 115 species caught during the three years appear in the lists as common species during these abundance peaks.

7.4b Weather and Hoverfly Seasonality

The number of insects caught in a Malaise trap depends on the activity of the insects as well as on the total populations present in the sampling area. Banks (1959) attributed the weekly variation in the number of hoverflies caught in suction traps mainly to changes in population size and notes that the differences in catch sizes between years is even more dependent upon population size (Williams 1940). Although no association was found between changes in the weather and changes in the abundance of either syrphid species or the total catch, weather did seem to affect the abundance of syrphids. Most were caught when the annual temperatures were high, although aphidophagous Syrphidae were more abundant in cool, wet summers than in warm, dry ones (Banks 1959).

Weather records for maximum and minimum temperature, hours of sunshine and daily rainfall were obtained from the Radcliffe Meteorological Station in Oxford, which lies 10 km. west-south-west of Bernwood Forest. These are presented in Figs. 7.8 -

7.10 for the temperature data and Figs. 7.11 - 7.13 for the sunshine and rainfall data for the three years.

The increase in syrphid abundance in the week of 6 - 13 May in all three years corresponds with a large increase in both the maximum temperature and in the hours of sunshine, particularly in 1980 and 1982 when the hoverfly numbers increased dramatically into the first abundance peak. The fall in abundance two weeks later mirrors a decline in the hours of sunshine and an increase in rainfall, again in the two years when the abundance peaks are the most pronounced, but the trough period from 10 June onwards is not accompanied by any corresponding weather changes.

The late peak in 1980 mirrors two weeks of increasing maximum temperatures and hours of sunshine and the fall in hoverfly abundance is accompanied by a fall in both of these climatic variables. In 1981 the hoverflies do not show a distinct late abundance peak and the hours of sunshine are more stable from week to week in the late season, with on average a similar amount of sunshine as in the previous year. The peak in 12 - 19 August is in a dry week following two wet ones, with similar temperatures and sunshine as in the previous two weeks. The late 1982 syrphid peaks do not fit obvious weather patterns although the week of the

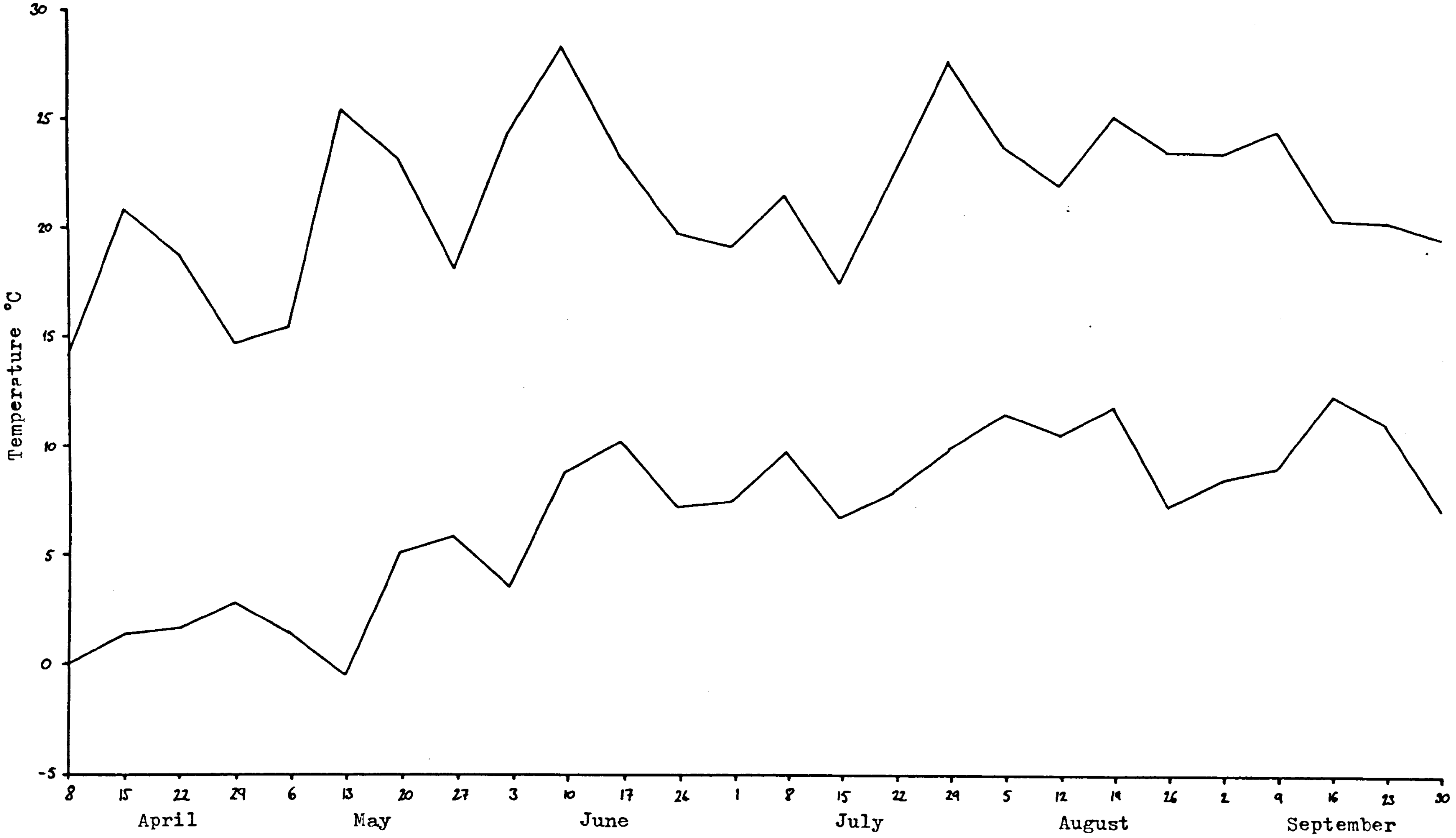


FIG. 7.8 WEEKLY MAXIMUM AND MINIMUM TEMPERATURES, 1980

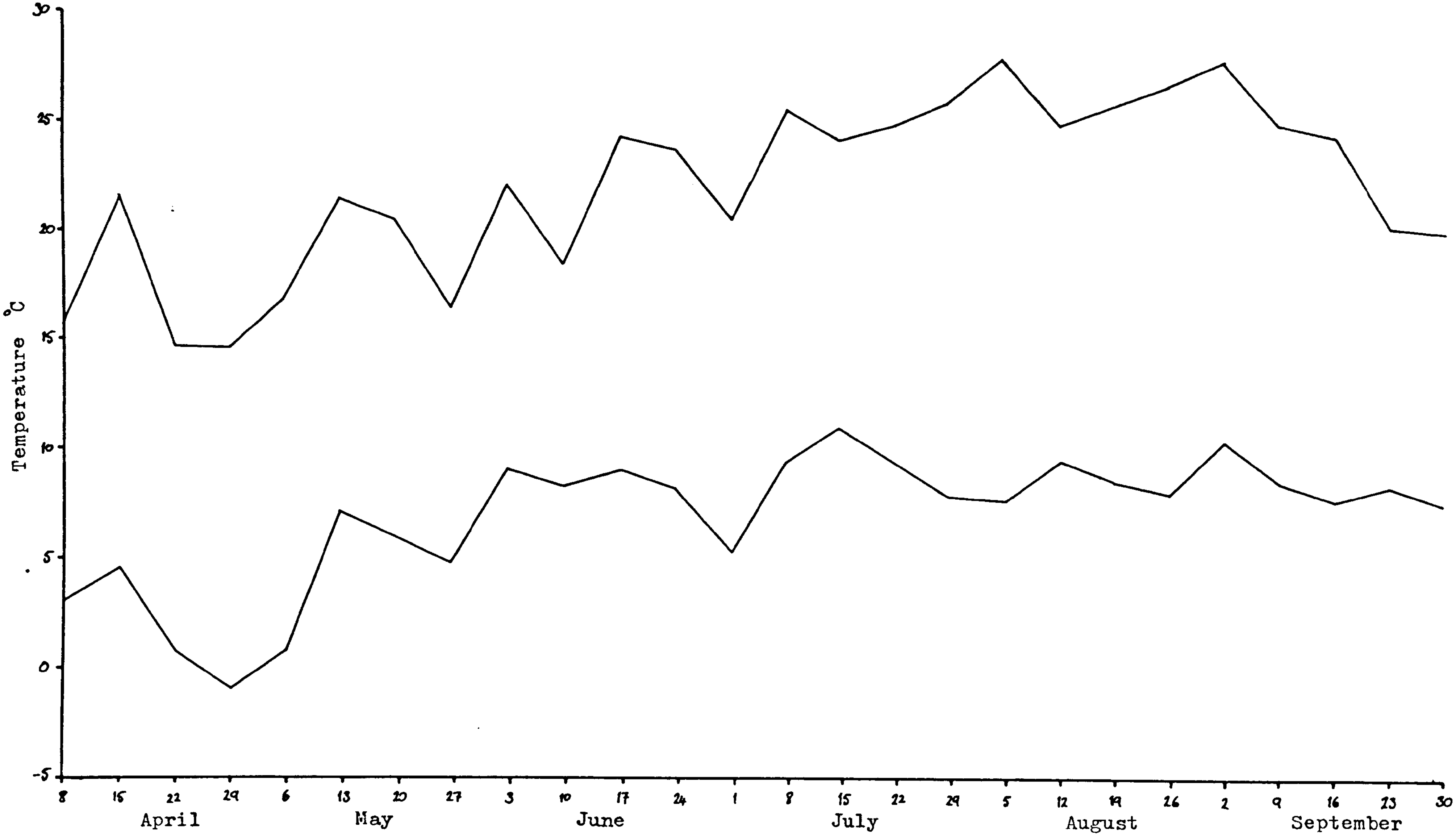


FIG. 7.9 WEEKLY MAXIMUM AND MINIMUM TEMPERATURES, 1981

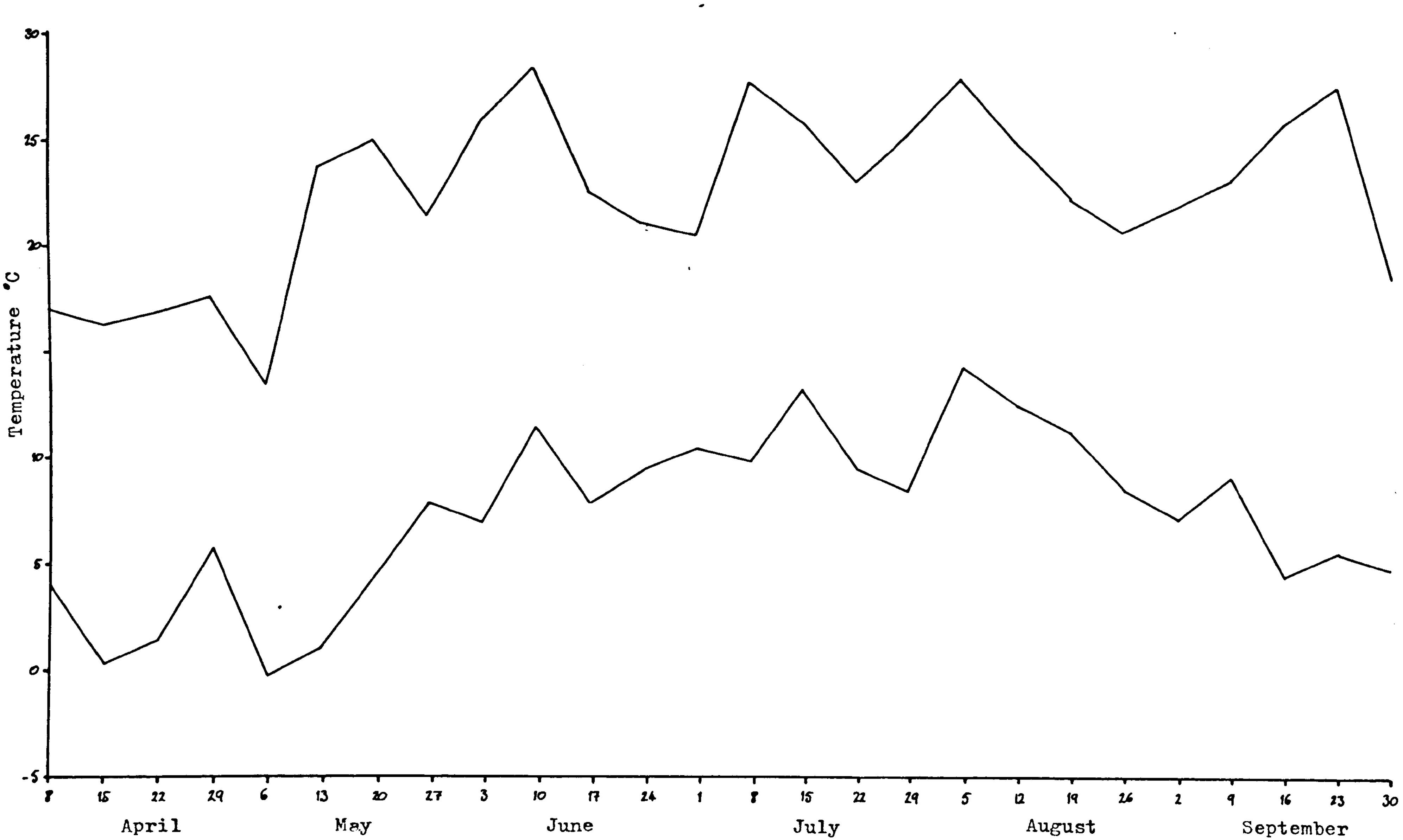


FIG. 7.10 WEEKLY MAXIMUM AND MINIMUM TEMPERATURES, 1982

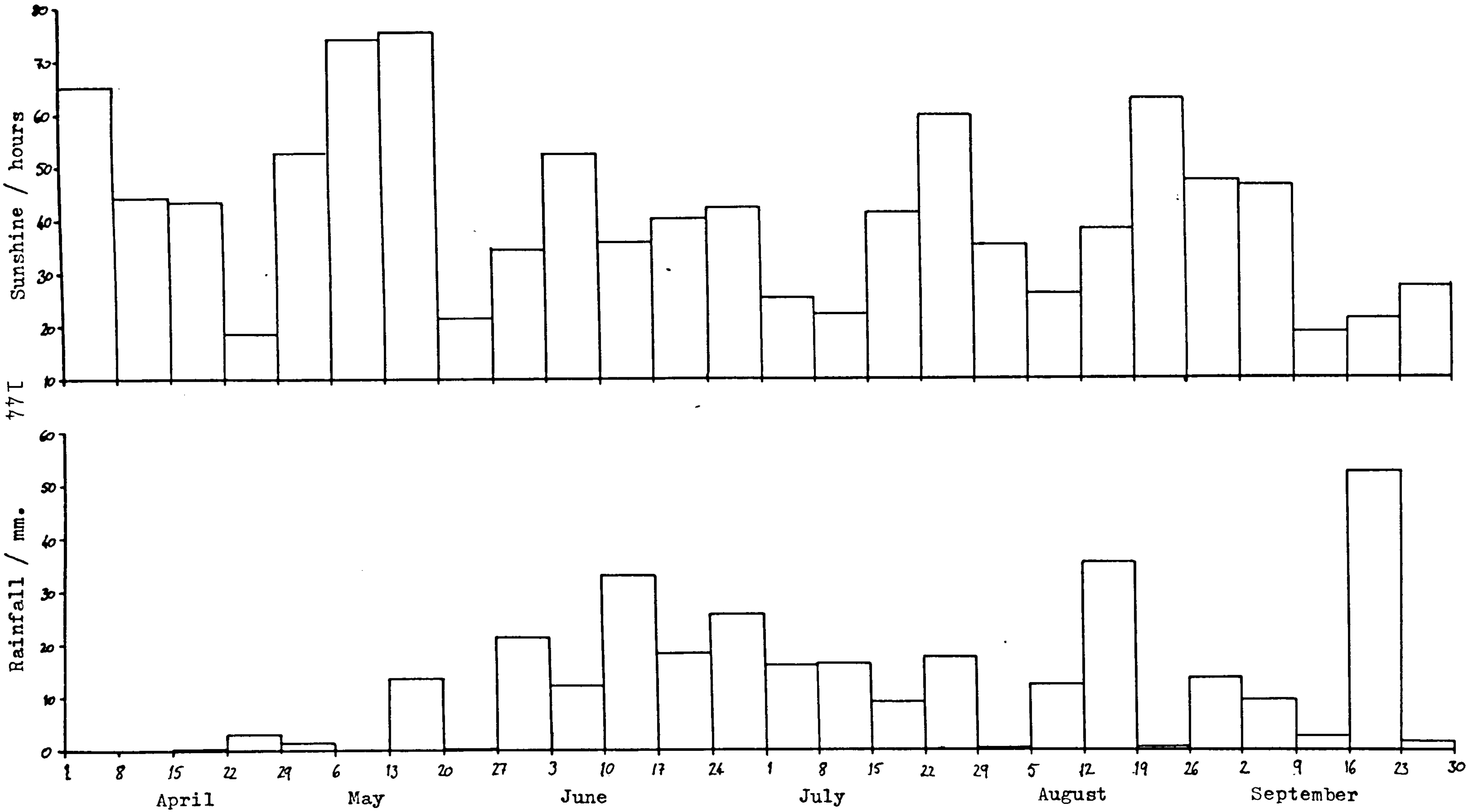


FIG. 7.11 WEEKLY RAINFALL AND HOURS OF SUNSHINE, 1980

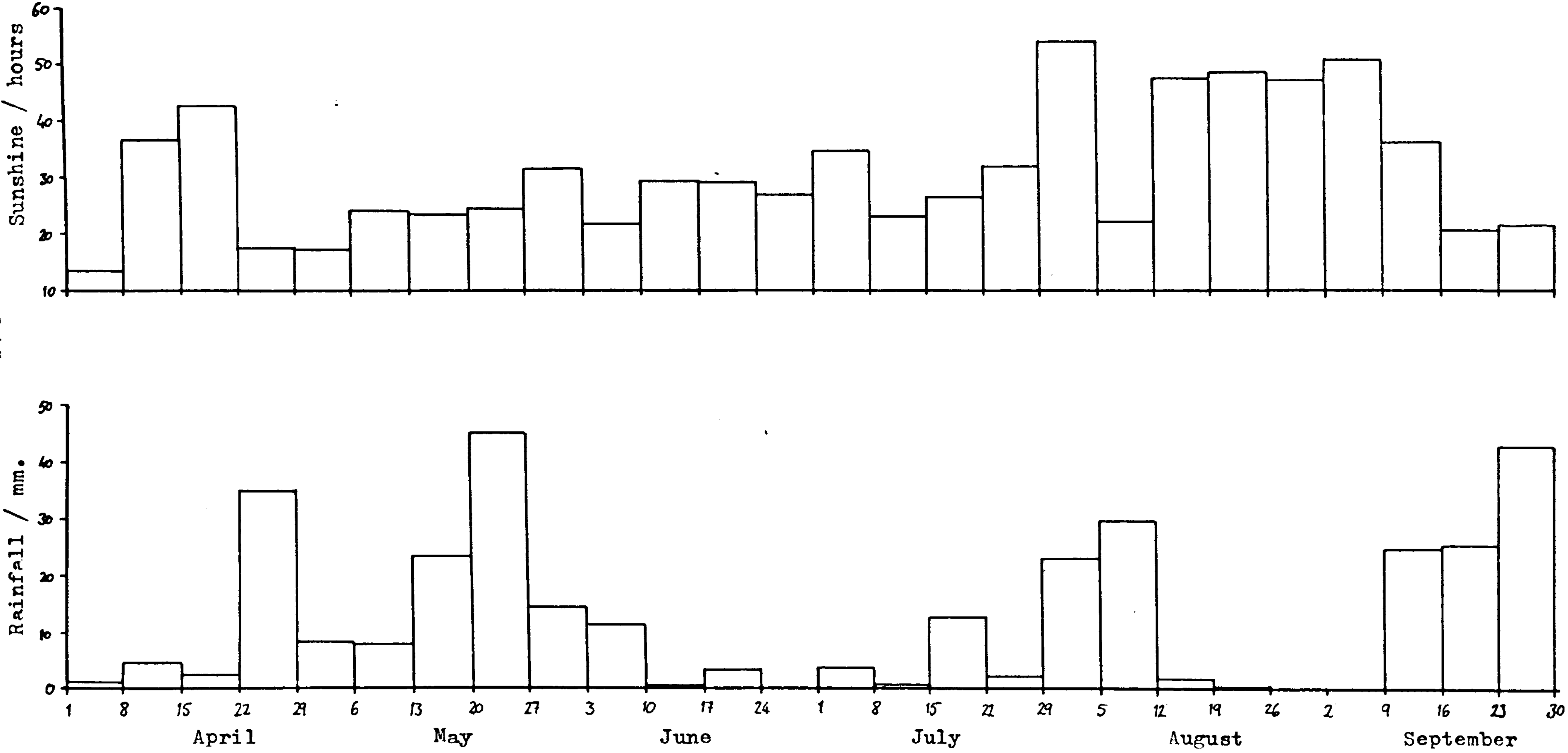


FIG. 7.12 WEEKLY RAINFALL AND HOURS OF SUNSHINE, 1981

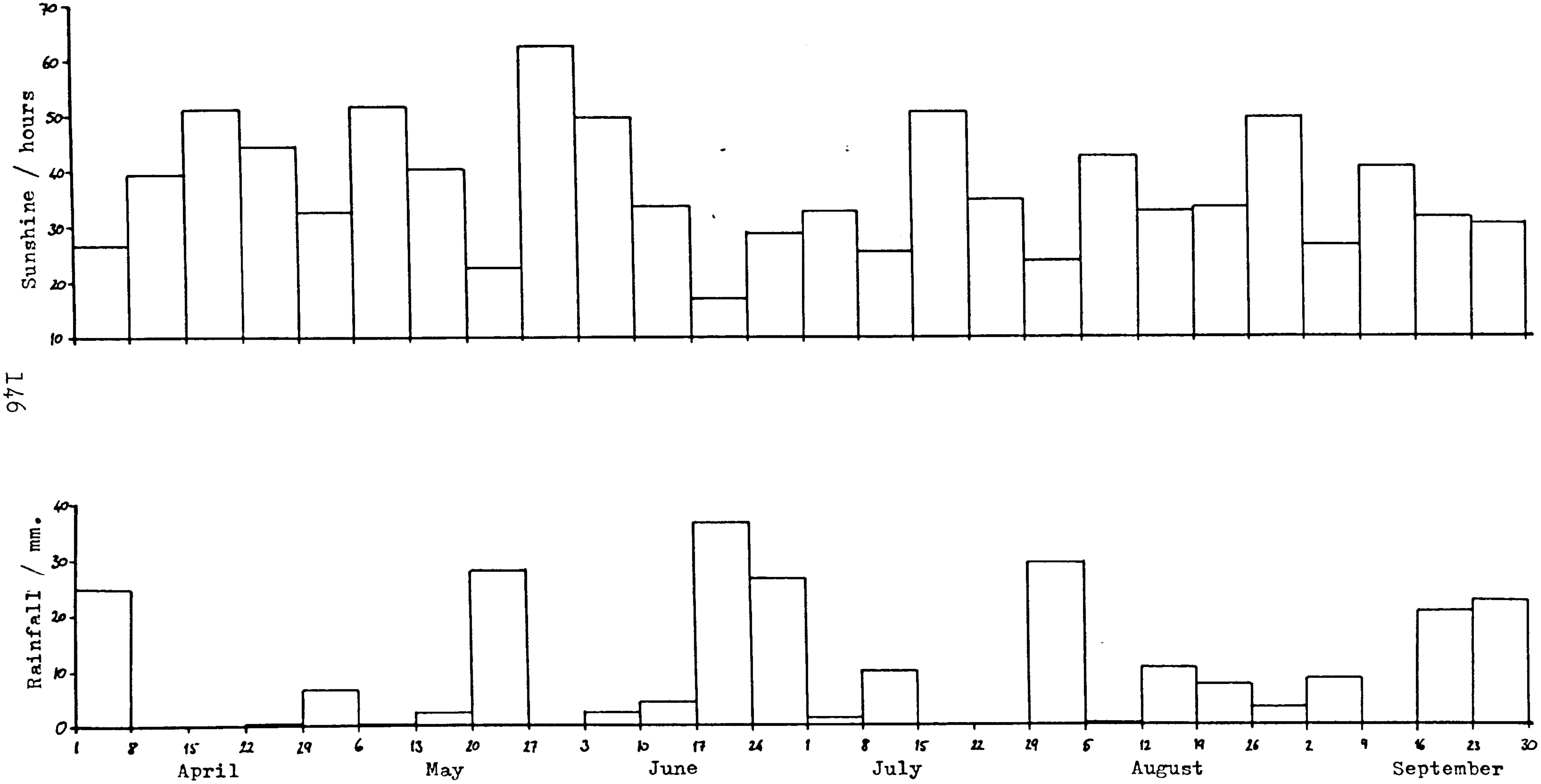


FIG. 7.13 WEEKLY RAINFALL AND HOURS OF SUNSHINE, 1982

Episyrphus balteatus outbreak between 29 July and 5 August follows a sharp increase in the minimum temperature, following two weeks of progressively lower minimum temperatures. This week sees a further substantial drop in the amount of sunlight, to only 23 hours in the week, which does not appear to have adversely affected syrphid abundance, although the weekly figures of both hoverfly abundance and weather records might well obscure the daily fluctations.

Weather, as any collector knows, obviously affects the abundance and activity of Syrphidae, but it is doubtful if this effect is as important as that of the total 'available' population. It is possible that weather conditions might focus hoverfly abundance into short peak periods if the potential abundance is present in the population and this appears to have occurred in at least the early peaks of 1980 and 1982, when the peaks of hoverfly abundance correspond with those of more favourable weather. However the bimodal seasonal distribution of hoverfly abundance cannot be explained simply by climatic phenomena, although certain of the details within the overall trend might well be.

7.4c Adult Hoverfly Food Supply and Hoverfly Seasonality

Adult hoverflies feed on the nectar and pollen of flowering plants for the bulk of their diet, although other sources of fluids rich in sugars, salts and amino acids, such as aphid honeydew, are exploited. Schneider (1948) found that the times of appearance and abundance of hoverflies is associated with the times of flowering of plants whose pollen and nectar is needed for the maturation of their ovaries. Banks (1959) however discovered that the kind of vegetation immediately around a suction trap did not affect the size and composition of the captured hoverflies, although it did affect the catch of the Heteroptera. The seasonality of flowering at the five Bernwood sites is given in Appendix 1 and has little in common with the abundance, diversity or seasonality of the capture of adult Syrphidae.

7.4d Larval Hoverfly Food Supply and Hoverfly Seasonality

Seventy five per cent of the adult hoverflies caught in Bernwood have larvae which prey upon aphids (see section 10.1) and thus the seasonal pattern of aphid abundance might affect the phenology of adult Syrphidae. Shapiro (1975) notes the problems of inferring adult flight periods from larval feeding times but adult aphidophagous hoverflies have also to lay their eggs in thriving aphid colonies to ensure the successful development of the larvae and thus the adults need to be in synchrony with the larval food supply.

Shrubs and trees cease to be a good source of food for aphids after the first flush of spring growth because the phloem sap contains relatively high concentrations of amino acids only during active growth or senescence. The sycamore aphid, which lives upon sycamore (*Acer pseudoplatanus*) throughout the year, produces smaller adults with lower fecundity over the summer period than in either the spring or in the autumn, and this seasonal variation in the quality of their food supply has led to the evolution of host plant alternation, from a woody to a herbaceous species, in some aphids. *Aphis fabae* for example uses spindle (*Euonymus europaeus*) as the primary host but appears on bean and sugar beet crops in late May, returning to spindle in the autumn when the woody plants once more become a favourable supply of nutrients (Dixon 1973, Blackman 1974).

Aphids dwelling upon woody plants are thus either absent from the primary host or present as small, slowly reproducing adults during the summer period from early June until late August or early September. This corresponds with the period of low syrphid abundance in all three years' trapping data and it is reasonable to suggest that adult hoverflies ought to be scarce when suitable oviposition sites are few relative to the early and later portions of the flight period. Unfortunately host plant selection in syrphids has a sparse literature apart from a handful of species which have been found ovipositing on aphid colonies upon commercial plant species, but the pointers are that the common aphidophagous species are able to use a wide spectrum of potential host situations (Dusek and Laska 1966, Laska and Stary 1980, Ghorpade 1981). Bombosch (1966) collected syrphids from a variety of habitats and found that the peak numbers were found in potato fields, along roadside edges and in sugar beet fields in July, which corresponded with a dramatic decline in the numbers of woodland edge hoverflies from a peak in June to almost complete absence in July. The Bernwood data support these findings as regards the July dearth of Syrphidae but also indicate a second period of abundance in late July and early August, which Bombosch did not find.

7.4e Phenology of Hoverfly Aposematic Mimics

Waldbauer and Sheldon (1971) proposed that specialized mimics of aculeate Hymenoptera are absent during most of the summer because they have been selected not to fly when large numbers of inexperienced juvenile birds are still learning to avoid the hymenopteran models. They believe that insectivorous birds are the main selective agents for the phenogical relationships of mimetic hoverflies and the absence of mimics during the period of avoidance-learning by young birds enhances the learning process, allowing the mimics to outnumber the models at other times of the year when only experienced predators are present. This hypothesis is tested further by Waldbauer, Sternburg and Maier (1977) by investigation of a different ecosystem and the same phenological relationships were found to hold. Palatability experiments with certain of the mimic species showed the mimicry to be Batesian and the learning response and memory of the insectivorous birds was found to be capable of allowing mimics freedom from predation during the syrphid abundance peak of the spring following the initial learning period. Maier (1979) explains why the evolution of this phenological response evolved principally in the subfamily Milesiinae and suggests that Batesian mimicry is prevalent in forest-inhabiting syrphids due to increased exposure to avian predators in these habitats.

Syrphidae of the subfamily Milesiinae do not have predatory larvae and thus the seasonal quality of aphids will not affect their phenology. Only four species are consistently common in Bernwood but the subfamily as a whole does appear to be seasonally distributed away from the middle of the trapping season in June and July. *Rhingia campestris* and *Ferdinandea cuprea* are both common but are doubtful mimics. *Rhingia* has a strong bimodal distribution, being absent from the catches typically from the second half of June until August, whereas *Ferdinandea* is common only in the first period of abundance, although its decline in numbers often continues into July. *Eristalis pertinax* and *Helophilus pendulus* are both more convincing mimics and both have bimodal seasonal distributions, but *Helophilus* generally begins its population increase into the second peak from early July or even from late June. This is the period when other hoverflies are scarce and thus *Helophilus* is conspicuous at a time when it ought to be rare or absent to expedite learning by birds - unless it is itself unpalatable.

The hypothesis that syrphid phenology might be regulated by avian predators and aculeate Hymenopteran models is interesting but it requires further study if it is to be invoked as a probable controlling factor of the seasonality of forest hoverflies. The theory depends on the identification of species complexes of models and mimics and excludes the general mimics which do not have the behavioural and anatomic adaptations of mimicry, such as *Metasyrphus* and *Syrphus* species (Waldbauer *et al.*1977). Certain species of southern English woodlands have been found to be specific mimics, for example species of the genus *Eristalis* (Heal 1979a, 1979b, 1981) but it is only in such species that the hypothesis can be invoked and it is unlikely to be an important factor governing the general seasonal abundance of woodland Syrphidae.

7.5 Seasonality : Comment

The seasonal distribution of Syrphidae in Bernwood Forest is bimodal, with peaks of abundance in May and late July/early August, with a period of extremely low abundance in the second half of June. The biggest abundance peaks are the product of the outbreak of one species which tends to suppress the diversity and abundance of the rest of the hoverfly community. Several factors contribute to this phenological pattern of syrphid abundance. The weather conditions might be in part responsible for focussing the two periods of abundance into sharp peaks, and must have a general effect upon insect activity. The seasonal abundance of the adult food supply does not affect the abundance of adult syrphids caught in the Malaise traps, but the seasonal quality and abundance of larval food most likely does affect adult phenology. The majority of the Bernwood hoverflies have aphidophagous larvae and the scarcity of aphids on trees and woody shrubs from June until late August allows only a small number of oviposition sites for adult syrphids during this period, which few hoverflies exploit. The seasonal bimodality of certain specialised aculeate Hymenopteran mimics may be an adaptation to expedite learning in and escape predation from inexperienced insectivorous birds learning the avoidance of aculeate Hymenoptera.

CHAPTER EIGHT

Species Diversity of the Bernwood Hoverfly Collections

8.1 Introduction

The erratic fluctuations in abundance of most of the common hoverflies, both between sites and between years, and the sheer volume of data make the use of some form of community analysis desirable in order to identify trends within the data. Two different types of analysis have been employed; this chapter concentrates on the use of species diversity indices whilst the one following examines a Principal Components analysis of community structure.

8.2 Measuring Species Diversity

The dual nature of ecological diversity, of it being the product of individuals and species, was first recognised by Henry Walter Bates towards the end of the nineteenth century. His interest, which was focussed on the adult, day-flying Lepidoptera, was intuitive and aesthetic and he made no attempt to define the distribution of individuals amongst the species of a community. This problem had its first solution in 1943 in a classic paper by Fisher, Corbet and Williams who described a log-series distribution to fit a sample of 15,200 moths captured in a light trap. This had the important distinction of being the first 'random' collection of animals to be subjected to statistical distribution analysis (Taylor 1978).

The diversity statistic α derived from the log-series is given in the equation $S = \alpha \log (1 + (N/\alpha))$ where S = number of species in the sample and N = number of individuals. The term of (N/α) is solved by reference to a table of values given in Fisher, Corbet and Williams (1943). α has been widely used as a diversity index and it has several desirable properties that make it an attractive index. The most important of these is that it is theoretically independent of sample size. Values of α have been found to be remarkably consistent over a series of years at environmentally stable sites: the site ordering of 14 sites over 6 years for Macrolepidoptera has proved to be consistent, with the only changes being attributable to deviations from the log-series model (Kempton and Taylor 1979).

The problem of deviation of collections of animals from convenient statistical distributions is an important one. There is no theoretical justification as to why ecological distributions should fit statistical ones and this is highlighted in the literature which contains many, often conflicting, justifications for using various distributions (Pielou 1969, Kempton and Taylor 1974, MacArthur 1957, Preston 1962, May 1975). Whilst it is true that a given ecological distribution can be fitted to some kind of mathematical distribution it does not follow that a particular mathematical distribution can be relied upon to fit a series of ecological samples even from the same taxocene and from similar locations over successive years. Most animal populations are fluid and a particular site is able to support a range of populations and it is this variability that parametric statistics cannot account for.

Despite these problems, α diversity has been widely employed by ecologists and the choice of the log-series in preference to other models of species distribution has been widely justified, up to the point at which its use is justified unless proven otherwise (Taylor, Kempton and Woiwood 1976). It is the simplest of the distribution models advocated and has been found to give a good description of the species frequency distribution for a wide range of taxonomic groups; in addition, α is not much affected by moderate deviation from the log-series (Williams 1964, Kempton and Taylor 1974, Kempton, Taylor and Woiwood 1976).

Historically, the 1940s also saw the birth of the two most popularly used non-parametric diversity indices, those of Shannon (1948) and Simpson (1949), although Shannon's information theory statistics were not brought into the study of diversity and trophic complexity of ecological systems until the initial works of MacArthur (1955) and Margalef (1958). Shannon's index, which had variously been ascribed to Shannon, Shannon and Weaver or to Shannon and Weiner, has been shown in a recent paper that it should be credited to Shannon alone (Perkins 1982).

Shannon's index is a measure of the entropy within a code or language and its relevance to ecology has been widely questioned, particularly with relation to the cybernetic systems to which information theory is ancillary. Even the method of calculation of entropy is unclear, there being two possible equations, those of Shannon, where

$$H' = \xi_{i=1}^{s} p_i \quad \log_e p_i$$

or that of Brillouin

$$H = \frac{1}{N} \log \frac{N!}{\pi N_\tau !}$$

where p_i is the proportion of the sample represented by the i.th species: N is the number of individuals in the sample: and S is the number of species present.

The former equation is the one that is more commonly employed and it has been used to estimate the diversity of the Bernwood hoverflies, but there is uncertainty as to which of the two equations is the most appropriate (Peet 1974). The Shannon equation also gives the sum of a series of prime numbers, a property which Yapp (1979) seriously doubts as having any relevance to the distribution of his woodland birds. Whether or not entropy relates to ecological heterogeneity, H' has other, more practical shortcomings as a diversity index. It has been shown to be logarithmically related to the number of species present in the sample and hence to be dependent on the size of the sample (Alatalo and Alatalo 1980, Cousins 1977); furthermore, it is a poor discriminator of sites with differing equitability (Solem 1979).

If Shannon's index can be said to be a measure of heterogeneity, then Simpson's index is a measure of dominance concentration (Peet 1974). Simpson's index is estimated by the equation

$$\lambda = \sum_{i=1}^{s} p_i^2$$

where λ is defined as the probability that two individuals chosen at random and independently from the population will be of the same species and p_i are the proportions of individuals in each species. The resulting index is strongly affected by the abundance of the two or three most common species (DeJong 1975) and in common with Shannon's index it is not an efficient discriminator of sites with samples of differing equitability (Solem 1979).

Doubts as to the validity of these indices and the subsequent proliferation of diversity statistics led to scepticism amongst ecologists as to their usefulness, particularly since the explanation as to why there is such a variety of organic life has evaded so many ecologists for so long (Brown 1981). Even by 1971, the concept of species diversity had been seriously doubted, as containing too many definitions to convey accurate information: it had become a 'non-concept' (Hurlbert 1971). The empirical study of species diversity was in need of some kind of unifying notation that was unambiguous to interpret. This was provided by the diversity series of Hill (1973).

Hill's Numbers consist of a family of diversities which measure, in units of species, the number of species present if the community is examined down to a certain depth amongst its rarities. Thus they have a natural, intuitive interpretation, albeit rather a vague one. They have been recommended by several authors as the most applicable of all the diversity indices available (Peet 1974, Alatalo and Alatalo 1977, Routledge 1979, Daget 1980).

The three measures of diversity N_0, N_1 and N_2 give increasing weight to the most abundant species: N_2 is the least sensitive to the presence of rare species and gives the lowest diversity value. N_2 is derived from Simpson's index, where

$$N_2 = 1 / \lambda.$$

Routledge (1980) comments that N_2 is to be preferred to N_0 and N_1 because there is less sampling bias incurred in the estimation of Simpson's index than for the other two diversity measures; but it is as a series of diversity numbers that Hill's indices are most innovative.

N_1 is a function of Shannon's diversity where

$$N_1 = \exp (H')$$

and this gives the number of 'moderately abundant' species, whereas N_2 gives the number of common species. The origins of N_1 are thus in information theory but this should in no way detract from the validity of N_1 as a diversity measure; "diversities are mere numbers and should be distinguished from the theories they support" (Hill 1973).

The third diversity number in the series, N_0, is simply the total number of species present in the sample and thus is dependent partly on the size of the sample.

It does however give a measure of the overall richness of the sample which most other diversity indices ignore. Together, the three diversity numbers effectively characterise a community by reference to the number of common, not-quite-so-common and rare species it contains and "without being perplexed by apparent lapses into thermodynamics and entropy ... it enables us to apply measures of diversity with as much confidence to dry weights as to counts" (Hill 1973).

The few common species of a community, upon which both Simpson's and Shannon's indices heavily rely, are often prone to violent and erratic fluctuations in abundance over successive years. This is especially true of insect populations and the Bernwood hoverfly data are characterized by such fluctuations. Kempton and Taylor (1976) considered indices based largely upon these erratically fluctuating species abundances to be unsatisfactory when attaching a diversity measure to a species habitat and proposed that the mid-abundant species would provide a better guide to site quality. The diversity of this portion of the species distribution curve can be measured using their Quartile Statistic, Q where $Q = S / 2 \log_e (R_2 / R_1)$ S is the total number of species in the sample and R_1 and R_2 are the lower and upper quartiles of the species abundance distribution (Kempton and Taylor 1976).

Q has been shown to be much more stable than either Shannon's or Simpson's indices with different models of species abundance and it gives a smaller variability for samples taken from the same site in successive years. This makes it a more efficient discriminator of between-site diversity than other indices (Kempton and Wedderburn 1978). It has the further advantage that its calculation is straightforward and thus ecologically relevant interpretations are more forthcoming than from indices cloaked in mathematical and conceptual uncertainty.

The dependence of Q upon only the mid-abundant species raises an important consideration in the interpretation of species diversity statistics. Hurlbert (1971) correctly commented that there is a common failure to distinguish between abundance and importance in ecological communities. Rare species may be of considerable importance to conservationists but they are usually insignificant in terms of community structure and function. The few common species, which affect both the Shannon and Simpson indices so strongly, may also be of little importance in terms of community stabilization and function because they are prone to violent and unpredictable population fluctuations (Kempton and Taylor 1976, Kempton and Wedderburn 1978, Owen 1983). Thus it may well be that the mid-abundant species contribute an importance to the community structure that is not reflected by their relative abundance.

8.3 Measuring Community Evenness

The evenness of the distribution of individuals amongst the species in a community can be measured as a separate entity from the overall diversity. The simplest approach is that of the Berger Parker dominance index, which expresses the proportion of the catch that is due to the most dominant species: $d = N_{max} / N_t$

where N_{max} is the abundance of the most numerous species and N_t is the total number of individuals in the sample. Thus it is a pleasingly simple index from both conceptual and computational viewpoints and it seems to charaterize species distributions "as well as other indices and better than most" (May 1975). It is also not influenced by the total number of species for 'reasonably' sized communities (Southwood 1978).

In common with the overall concept of species diversity, evenness has been widely defined and the concept remains a loose one (Alatalo 1981). One of the earlier definitions was that of Lloyd and Ghelardi (1964), who defined it as the ratio of the number of hypothetically 'equitably distributed' species that would be needed to produce the observed species diversity (S') to the total number of species in the sample (S). Thus $E = S' / S$

This ratio has been widely applied to the Shannon entropy H' to give the equitability component J where

$$J = H' / H'_{max} = H' / \log S \quad \text{(Pielou 1975)}$$

Although it has been widely employed, the evenness measure J has several shortcomings. The most serious of these is that it is correlated with species richness and sample size for purely mathematical reasons (DeBenedictus 1973) whereas evenness values should be comparable in communities with markedly different species richness (Alatalo 1981).

It thus cannot be relied upon in the comparison of different sized communities. In addition to this, it is difficult to interpret, being an extrapolation from information theory.

Hill's Numbers can be used to measure evenness, which is defined as any ratio of N_0, N_1 or N_2. N_0 is no less reputable than either N_1 or N_2 but the latter is usually more stable and may assume a fairly constant value over a wide range of sites (Hill 1973). Alatalo (1981) recommends a modification to the ratio of N_2 / N_1 :

$$e = (N_2 - 1) / (N_1 - 1)$$

This measure has advantages over the other possible Hill's ratios because the species richness of the community is often underestimated; indices using the total number of species are thus not recommended. This measure 'e' is to be recommended over all other equitability measures (Alatalo 1981).

8.4 Diversity of the Bernwood Hoverflies

Species diversity of the annual totals of the hoverflies collected from each of the five Bernwood sites are given in Table 8.1 and Fig. 8.1. These diversity calculations can be put to two distinct uses: to assess site quality and to explore the population structure of the hoverfly assemblages.

8.4a Site Quality and Hoverfly Species Diversity

Site quality is, in ecological terms, most often

TABLE 8.1

HOVERFLY DIVERSITY AT FIVE SITES, BERNWOOD FOREST 1980 - 1982

	S1			S2			S3			S4			S5		
	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
α	12.28	11.30	11.79	14.76	13.41	12.36	7.62	9.12	9.59	16.26	15.37	19.96	7.06	5.51	5.21
Q	15.96	12.20	15.93	19.28	17.54	17.57	8.51	9.44	10.64	21.86	19.46	20.91	6.60	6.30	5.9
Hill's N_0	60	47	60	67	64	66	37	39	43	79	72	74	30	25	25
Hill's N_1	19.62	16.75	12.28	22.85	22.78	10.76	7.68	12.98	14.94	25.83	22.02	20.21	12.62	8.91	5.14
Hill's N_2	13.24	12.26	6.64	14.50	20.67	5.04	3.89	7.45	9.50	15.05	12.12	11.33	8.36	5.74	3.16

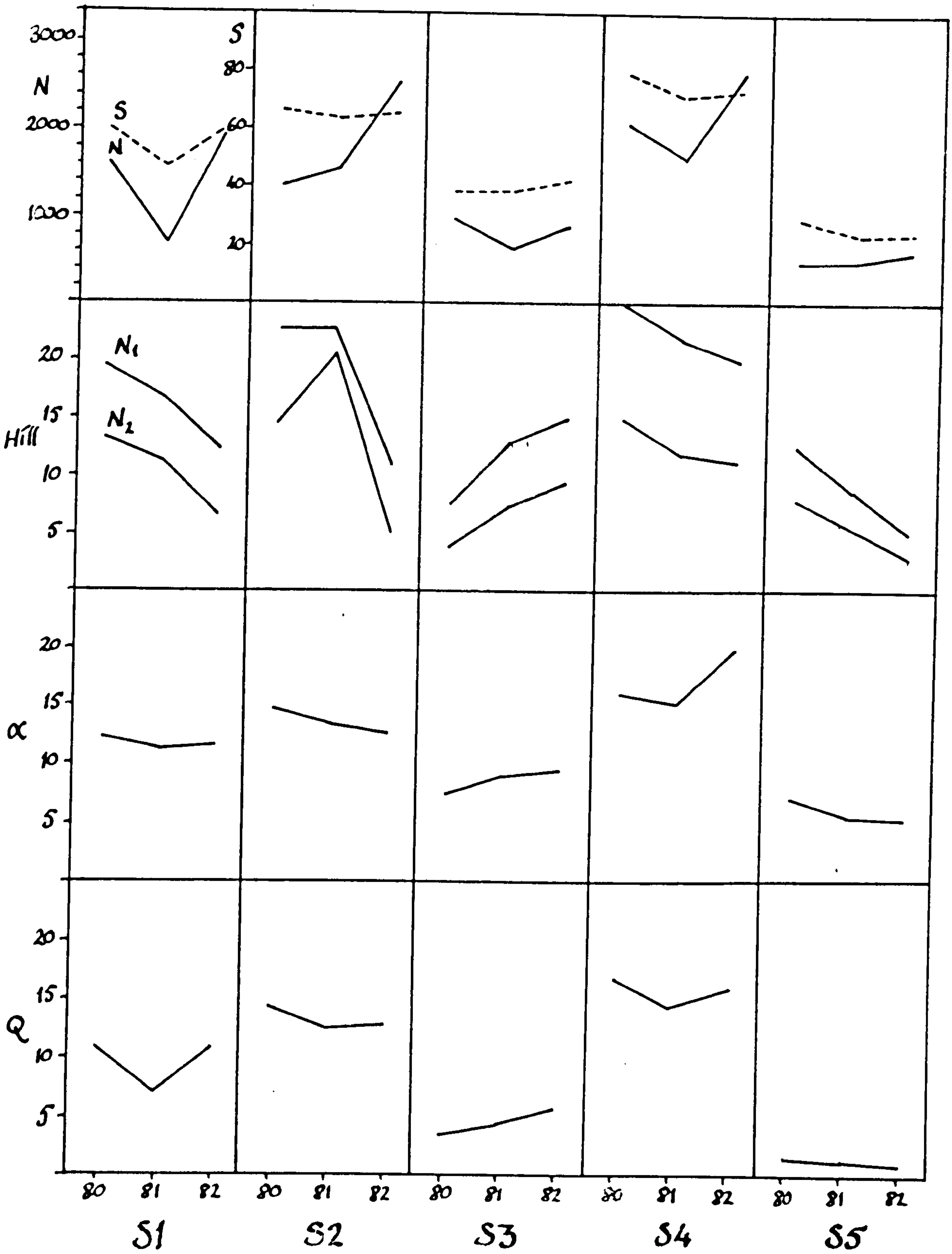


FIG. 8.1 SPECIES DIVERSITY OF THE BERNWOOD HOVERFLIES 1980 - 1982: HILL'S, α AND Q DIVERSITIES, AND NUMBER OF INDIVIDUALS AND SPECIES AT THE FIVE SITES

associated with the variety and abundance of life able to persist at a particular location. Diversity is an important criterion in the assessment of sites for conservation (Ratcliffe 1977, Margules and Usher 1981) but many of the methods used in its estimation are unsuitable as site discriminators.

Hill's diversity (N_1 and N_2) gives a different site ranking for each of the three years, although the ordering is consistent within each year for both Numbers. Their poor suitability as site discriminators is a consequence of the heavy weighting they give to the few common species in the sample: this is demonstrated by the high Hill's diversity at S2 in 1981, which is associated with high equitability of the community rather than high diversity *per se*.

In contrast, Fisher's α index and the Q statistic both give a consistent ranking of the five sites for the three years. These indices rank S4 the most diverse site, followed by S2, S1 and S3, with S5 the poorest site: the rankings are therefore consistent with those by number of species and number of individuals, and they do not give the 'anomalous' placings of S1 and S2 in the rank of the number of individuals for the 1980 data.

The use of one of these two indices in preference to the other cannot be recommended, although Q gives a better separation of the sites than α. Q relies only on those species present in the mid-range of the species distribution whereas the idealized log-series curve upon which α is founded takes into account all the species present in the sample. This difference is reflected in the stability of each index across the five sites. Q is the more stable index at S4 and S5, the richest and poorest communities of those sampled: S4 has the highest number of common species and S5 the smallest. On the other hand, α is more stable than Q at S1 and S2, where the changing relative abundance of the mid-abundant species affects the stability of the values of the latter index. This 'noise' in the value of Q is however small in comparison to the changes within the Hill's diversity numbers and, particularly when used together, α and Q are efficient tools of site discrimination.

8.4b Structure of Hoverfly Communities and Species Diversity

The changing abundance of the hoverflies over the three years is reflected in diversity changes between the years, although the overall significance of such short-term trends must be questioned. Both α and Q are calculated from the relatively stable elements of the species distribution and thus are relatively insensitive to these between-year changes in diversity whereas Hill's Numbers, being weighted to the common species, are subject to fluctuations in their abundance.

S1, S4 and S5 all show decreasing N_2 and N_2 diversity over the three years; these trends are not apparent from either α or Q. S3, by contrast, shows a progressive increase in Hill's diversity. These four sites all share similar trends in the two measures of Hill's diversity, N_1 and N_2: there is a common relationship between the number of moderately common species and the number of common ones, with the distance between the two lines on Fig. 8.1 giving an indication of the richness of the community. S2 however shows a significant increase in the number of common species to moderately common ones in 1981. This is due to the lack of dominance at this site in 1981, a result of the low numbers of hoverflies captured. High diversity in this case is the product of high equitability and a smaller catch of fewer species than in either the preceding or following years. In 1982 the values of Hill's diversity fall dramatically, associated with large increases in both the number of species and individuals captured and strong dominance of the sample by its two most common species.

Hill's diversity does not directly measure diversity: it measures the number of common species and the number of moderately common species. These are useful ecological parameters which provide a simple description of species distribution but they must not be confused with the assigning of a diversity value to a particular site. Hill's diversities give an assessment of the structure of the community in terms of the relative status of its component species and they do not attempt to ascribe an absolute value of diversity to the sample.

8.5 Equitability of the Bernwood Hoverflies

Values of the Berger Parker, Shannon and Hill's estimations of community evenness for the Bernwood hoverflies are given in Table 8.2 and Fig. 8.2. These indices are of little value in site discrimination but they do provide an indication of the population structure of the samples.

The Berger Parker dominance index clearly shows the degree of domination of a sample by its most abundant species. Three samples in particular show strong such domination, those from S3 in 1980 and from S2 and S5 in 1982 and these correspond to the presence of a superabundant species in each case, by *Syrphus ribesii* in the former instance and by *Episyrphus balteatus* in the latter two. S1, S2 and S5 all show increasing domination by one species over the three years whereas dominance in the samples from S3 steadily declined. S4 remained steady over the three years at a relatively low level of dominance, which is a reflection of the rich species structure of these samples.

The two evenness measures, J and e, both show the same pattern of structure the samples from each site with

TABLE 8.2

HOVERFLY COMMUNITY EVENNESS AT FIVE SITES, BERNWOOD FOREST 1980 - 1982

	S1			S2			S3			S4			S5		
	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982	1980	1981	1982
Berger Parker d	0.144	0.187	0.266	0.153	0.135	0.390	0.461	0.298	0.207	0.158	0.196	0.206	0.248	0.325	0.473
J	0.727	0.732	0.612	0.744	0.752	0.567	0.565	0.700	0.719	0.744	0.723	0.698	0.745	0.679	0.508
Hill's	0.657	0.715	0.500	0.618	0.903	0.414	0.433	0.538	0.610	0.566	0.529	0.538	0.633	0.599	0.522

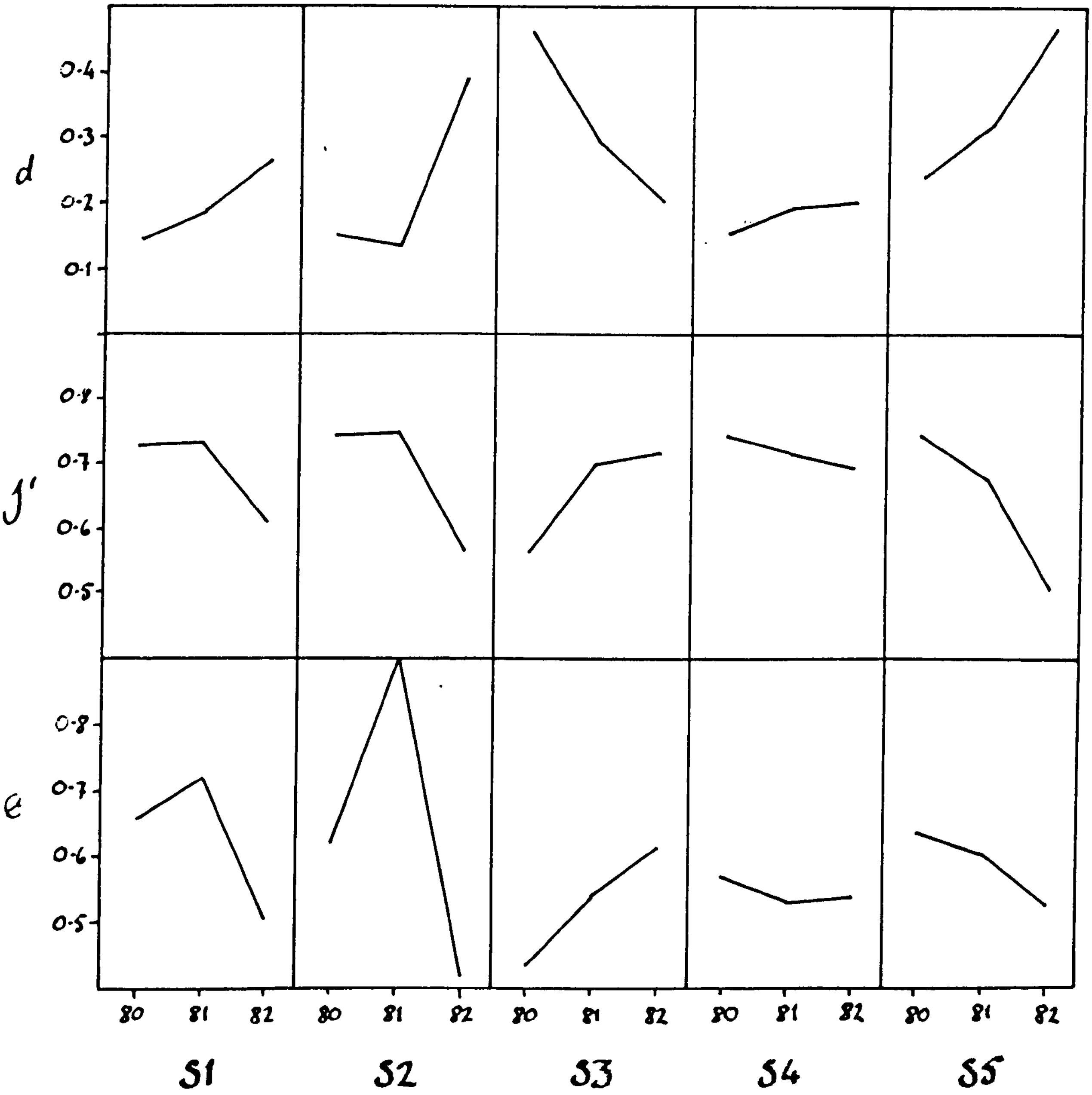


FIG. 8.2 COMMUNITY EVENNESS OF THE BERNWOOD HOVERFLIES, 1980 - 1982: THE d, J AND e EVENNESS INDICES AT THE FIVE SITES

the exception of S2. The samples from S1 show a slight increase in evenness in 1981 over the previous year, which is associated with depressed abundances in 1981, particularly among the common species. This is followed by a decline in sample evenness in 1982, when *Meliscaeva cinctella* and *Episyrphus balteatus* were both abundant. S3 shows a progressive increase in evenness over the three years, with the low evenness in 1980 ascribed to the super-abundance of *S. ribesii*. S4 maintains consistent evenness of each year's samples, with the J index giving a higher value in relation to the other sites than does Hill's ratio of common species to moderately common ones; and S5 shows a progressive decline in sample evenness, particularly in 1982 when *Episyrphus balteatus* and *Meliscaeva cinctella* strongly dominate the collection.

The J index shows a similar pattern of evenness at S2 as at the other deciduous site, S1: a steady value over 1980 - 1981 preceding a marked decrease in 1982, associated with high abundances of *E. balteatus* and *M. cinctella*. This pattern is greatly exaggerated by the e index, which describes a large increase in the ratio of common to moderately-common species in 1981 over the previous year. The cause of this is the low dominance of the 1981 sample with the top four species all occurring in similar abundances, with N_1 containing only 2 more species than N_2. This is followed in 1982 by a dramatic plunge in evenness to the lowest level recorded over the five sites from the highest, with the super-abundance of *E. balteatus*, and to a lesser extent *M. cinctella*, being the principal cause.

8.6 Seasonal Changes in Hoverfly Diversity

Species diversity for each of the two sampling seasons, from 1 April to 1 July to 30 September, are given for each year in Table 8.3. There is a strong overall trend in the samples of higher diversity in the early season than in the later one, which is typically characterized by high abundances of only a few species. This trend is associated with the generally greater species richness of the early season evident at all sites save for S1 and S5 in 1981 (section 7.3a; Table 7.1).

The trend of higher diversity in the early season is weakest for the 1981 samples, where it is strongly noticeable only at S2. Hill's N_1 and N_2 diversities actually give higher values for the late season at S3 and S4 in this year, caused by the lack of a single dominating species at these sites. The least change in all of the diversity statistics is shown by N_2, the number of common species, whereas the number of moderately common species, N_1, varies considerably and is a reliable guide to the equitability and dominance of the samples.

Site rankings using either the early or the late diversity results are more variable than those using the total data from each site in each year. The early period gives a better estimation of the overall annual catch than does the later period, because of the fewer species present and stronger sample domination of the late period.

TABLE 8.3

HOVERFLY DIVERSITY IN THE EARLY AND LATE SEASONS AT FIVE SITES, BERNWOOD FOREST 1980 - 1982

		1980		1981		1982	
		Early	Late	Early	Late	Early	Late
S1	N_0	52	37	29	34	56	23
	N_1	17.94	11.34	11.35	12.83	17.06	5.26
	N_2	12.57	8.19	6.44	7.47	9.79	3.27
	N_R	0.6830	0.6954	0.5256	0.5469	0.5473	0.5329
	α	13.91	7.53	7.95	8.81	13.19	4.20
	Q_e	14.13	8.95	7.00	8.17	15.91	4.70
S2	N_0	58	34	56	41	58	37
	N_1	21.20	14.55	20.06	17.50	25.09	4.96
	N_2	12.88	10.25	12.38	8.53	15.36	2.77
	N_R	0.5881	0.6827	0.5971	0.4564	0.5961	0.4470
	α	15.15	7.49	12.41	9.15	14.26	6.65
	Q_e	16.44	8.41	14.93	10.20	15.01	8.86
S3	N_0	33	13	31	23	36	22
	N_1	7.40	5.63	9.54	11.67	14.01	9.75
	N_2	3.82	3.67	5.60	8.33	9.05	6.75
	N_R	0.4406	0.5767	0.5386	0.6870	0.6187	0.6617
	α	6.92	3.06	7.85	6.20	8.60	5.53
	Q_e	7.91	1.81	7.61	4.65	8.41	4.53

TABLE 8.3 CONTINUED

		1980		1981		1982	
		Early	Late	Early	Late	Early	Late
S4	N_0	70	40	50	47	65	46
	N_1	25.40	16.14	15.99	18.31	22.96	13.72
	N_2	13.53	11.18	6.90	9.20	11.12	8.50
	N_R	0.5135	0.6724	0.3936	0.4737	0.4608	0.5896
	α	17.73	8.04	12.66	10.16	15.20	8.89
	Q_e	19.62	8.45	13.12	10.90	15.03	10.55
S5	N_0	24	18	17	18	20	16
	N_1	12.86	6.58	10.38	5.98	7.83	3.30
	N_2	10.15	4.09	6.22	3.99	4.20	2.29
	N_R	0.7715	0.5538	0.5565	0.6004	0.4685	0.3909
	α	6.81	4.36	5.09	3.94	6.35	3.18
	Q_e	4.98	3.44	3.85	3.78	6.28	3.14

These two features combine to give greater variability in the diversity calculations and the actual calculated values are numerically too similar to provide clear and reliable rankings.

8.7 Hoverfly Diversity in Bernwood Forest: Comment

The site rankings of the α and Q diversity indices confirm the relative quality of sites as suggested by both the number of individuals and species of syrphids captured at each of the five sites. Site quality is an intuitive and subjective criterion which can in this instance be made more objective by recourse to the abundance and richness of the hoverflies caught at the site. The population structure of the sampled community also lends objectivity to an assessment of quality, with a good gradation of common to rare species being preferable to strong domination by a very few species, and with many rare species present in the sample. Such assessments of quality of the five Bernwood sites do not fit the simple gradient from deciduous to coniferous woodland.

Hill's diversity numbers N_1 and N_2 do not measure diversity *per se* but give an objective guide as to the number of common and moderately common species present in the sampled community. These numbers are functions of Shannon and Simpson diversity respectively and as such are highly weighted to the abundances of the few most abundant species present in the sample. Low Hill diversity results from relatively high abundances of the most common species in the sample, even though the community maybe rich: this accounts for the unusually low diversity from S2 in 1982 when *Episyrphus balteatus* accounts for almost 40% of the total catch: the mean contribution of the most abundant species in the annual totals is 25.7%. High abundances of *Syrphus ribesii* at S3 in 1980 and *E. balteatus* at S5 also account for over 40% of the total catch and thus heavily weight the estimation of Hill's diversities, although such catches can be regarded as 'extra additions' to the 'normal' community present.. The resulting low Hill's diversities for these sites thus has a simple explanation.

The equitability indices are a good guide to the quality of the sample because they directly measure the spread of the individuals across the species present in the collection. Once more, S4 is distinct from the other sites in having a steady evenness over the three years. This is an indication of a more stable syrphid population structure than at the other sites, although it may simply be a direct result of the richness and diversity of this site. The high equitability at S2 in 1981 is the result of the four most common species, *Meliscaeva cinctella*, *Platycheirus albimanus*, *Rhingia campestris* and *Melanostoma scalare* all occurring in similar abundances, which usually did not occur in the samples, in which a single species is usually clearly more numerous than any other.

The apparent anomalies found within the diversity calculations are thus attributable to changes in the relative abundance of the most common syrphids present in the sample. Hoverfly diversity can be used to rank and judge site quality but the potential for dramatic population changes makes the use of only the common species in such rankings unreliable. This element of unpredictability also makes short sampling periods unreliable in estimating a site's overall potential and quality, although samples from the early half of the season give a more reliable estimate than those from later on.

CHAPTER NINE

Principal Components Analysis of the Bernwood Hoverfly Collections

9.1 Introduction

A Principal Components Analysis (PCA) was carried out on the syrphid abundance data as a further tool of community analysis to complement the species diversity study. PCA is a method of ordination, in this case of the five sites in terms of hoverfly species abundance. These abundances are projected into multidimensional space, through which the PCA selects a new axis that accounts for the maximum possible variance. This axis is called Principal Component I (PCI).

PC II is selected perpendicular to PC I to account for as much as possible of the remaining variation; further axes are derived in rigid rotation and equal in number to the number of variables, in this case syrphid species, in the data set. In practice the first two axes account for between 40 and 80% of the total variation and thus ecological interpretation may be restricted to the ordination of PC I and PC II (Greig Smith 1964, Gauch 1982).

9.2 Methods

The PCA was carried out from a correlation matrix, which has the advantage over a co-variance matrix of having standardized values for the analysis. This is necessary for quantitative data (Field *et al.* 1982). Six matrices were analysed in three ordinations to give an ordination each year for the early and late seasons of hoverfly abundance. Rare species were excluded from the analysis because of the risk of these species assuming a greater importance in the ordinations than in the living community: thus a minimum limit of ten individuals captured in any one of the sites per season was imposed. This gave amatrix of 50 species.

9.3 Results

9.3a Percentage Variances

The percentage variances for all three runs were good, with PC I accounting for a mean of 34.9% (d=1.95) of the variation and PC II 28.4% (d=2.84). This gives a combined average of 63.3% of the total variance accounted for by these two axes, with a standard deviation of 4.50, which justifies restricting the analysis to the first two principal components only.

9.3b Latent Vectors

The latent vectors or loadings identify which syrphids are affecting the ordination and the amount which each species contributes to the final eigenvector.

The loadings for the ten most influential species in each principal component are given in Table 9.1 and it is immediately noticeable that there is little domination of the eigenvectors by only a few species. The only exception to this is the PC II for 1981 in which four species affected the axis considerably more than the other species.

None of the syrphid species is consistently influential in the ordination of the communities although *Melangyna triangulifera*, *Parasyrphus malinellus* and *Xylota sylvarum* all appear in the 'top five' most influential species for PC I in both 1980 and 1981. These five species are entirely different for 1982 from the previous two years. None of the species appear in the lists for the 'top ten' species in all three years although seven appear twice in the three years; the additional four species are *Chrysotoxum bicinctum*, *Leucozona lucorum*, *Cheilosia fraterna* and *Volucella pellucens*.

The species that contribute most to the PC II loadings similarly show few consistencies between the three years. Only *Syritta pipiens* and *Cheilosia paganus* appear in the top five species for more than one year although nine species occur in the top ten twice; once again, none of these species is listed in all three years. The PC II loadings for 1981 are different from all the other loading series in that four species, *Platycheirus scutatus*, *Melanostoma mellinum*, *P. clypeatus* and *Cheilosia paganus*,

TABLE 9.1

LATENT VECTORS OF THE TEN SYRPHIDS ACCOUNTING FOR THE MAJORITY OF THE BETWEEN SITE VARIATION IN THE TRAP SYRPHID SAMPLES FROM THE FIVE SITES. BERNWOOD FOREST, 1980 - 1982, FOR THE FIRST TWO PRINCIPAL COMPONENTS

1980

PC I (33.0%)		PC II (27.6%)	
Xylota sylvarum	-.2122	*Eristalis pertinax*	.2504
Melangyna triangulifera	.2058	*Syritta pipiens*	.2442
Parasyrphus malinellus	.2045	*Cheilosia paganus*	.2371
Melangyna lasiophthalma	.1995	*Melanostoma scaoare*	.2327
Platycheirus albimanus	-.1929	*Metasyrphus corollae*	.2214
Ferdinandea cuprea	.1903	*Eristalis nemorum*	.2194
Chrysotoxum bicinctum	-.1863	*Platycheirus scutatus*	.2163
Xylotomima lenta	.1831	*Sphaerophoria*	.1929
Volucella pellucens	-.1816	*Neoascia podagrica*	.1857
Criorhina berberina	.1793	*Xanthogramma pedissequum*	-.1822

TABLE 9.1 CONTINUED

1981			
PC I (34.7%)		PC II (26.1%)	
Parasyrphus malinellus	.1970	*Platycheirus scutatus*	.2444
Volucella pellucens	-.1956	*Cheilosia paganas*	.2436
Xylota sylvarum	-.1917	*Platycheirus clypeatus*	.2345
Chrysotoxum bicinctum	-.1912	*Melanostoma mellinum*	.2217
Meoangyna triangulifera	.1902	*Helophilus pendulus*	.1874
Xanthogramma pedissequum	-.1878	*Eristalis nemorum*	.1808
Leucozona lucorum	.1857	*Dasysyrphus tricinctus*	.1759
Parasyrphus lineolus	-.1852	*Metasyrphus corollae*	.1752
Dasysyrphus venustus	.1843	*Eristalis pertinax*	.1741
Cheilosia fraterna	.1835	*Platycheirus peltatus*	.1741

TABLE 9.1 CONTINUED

1982

PC I (36.9%)		PC II (31.6%)	
Platycheirus scutatus	-.2293	*Platycheirus peltatus*	-.2365
Eristalis pertinax	-.2170	*Chrysotoxum bicinctum*	-.2243
Cheilosia fraterna	-.2125	*Syritta pipiens*	-.2223
Parasyrphus punctulatus	-.2089	*Xylota segnis*	-.2198
Pipiza bimaculata	-.2031	*Didea fasciata*	-.2173
Melanostoma scalare	-.2021	*Volucella pellucens*	-.2173
Neocnemodon	-.1997	*Xylota sylvarum*	-.2163
Leucozona lucorum	-.1933	*Parasyrphus lineolus*	-.2149
Dasysyrphus tricinctus	-.1896	*Xanthogramma pedissequum*	-.2070
Baccha elongata	.1840	*Melanostoma mellinum*	-.1991

contribute significantly more weight to the eigenvector than do the next six species (Table 9.1). Nine species occur in the top ten loadings for both principal components.

The latent vectors give confidence to the resulting ordinations because they show that none of the principal components, with the possible exception of PC II for 1981, is strongly dominated by a small number of species. The signs of the loadings are however heavily biassed towards one sign or the other in all of the components save two. This allows only a poor interpretation of these axes and it is fortunate that the two exceptions to this are the first principal components for 1980 and 1981.

9.3c Site Groupings

Each year's ordination shows the clustering of certain sites which the PCA identifies as being similar (Figs. 9.1, 9.2 and 9.3). This grouping pattern is different for all three years although some of the sites are associated together in all the ordinations.

The 1980 data fall into three clusters (Fig. 9.1). The most similar communities are the late samples from S1 and S2 as well as from S3 and S5, with the early collection from S5 grouped together with the latter pair. The early samples from S1, S2 and S3 form the third grouping, with both the S4 communities distinct

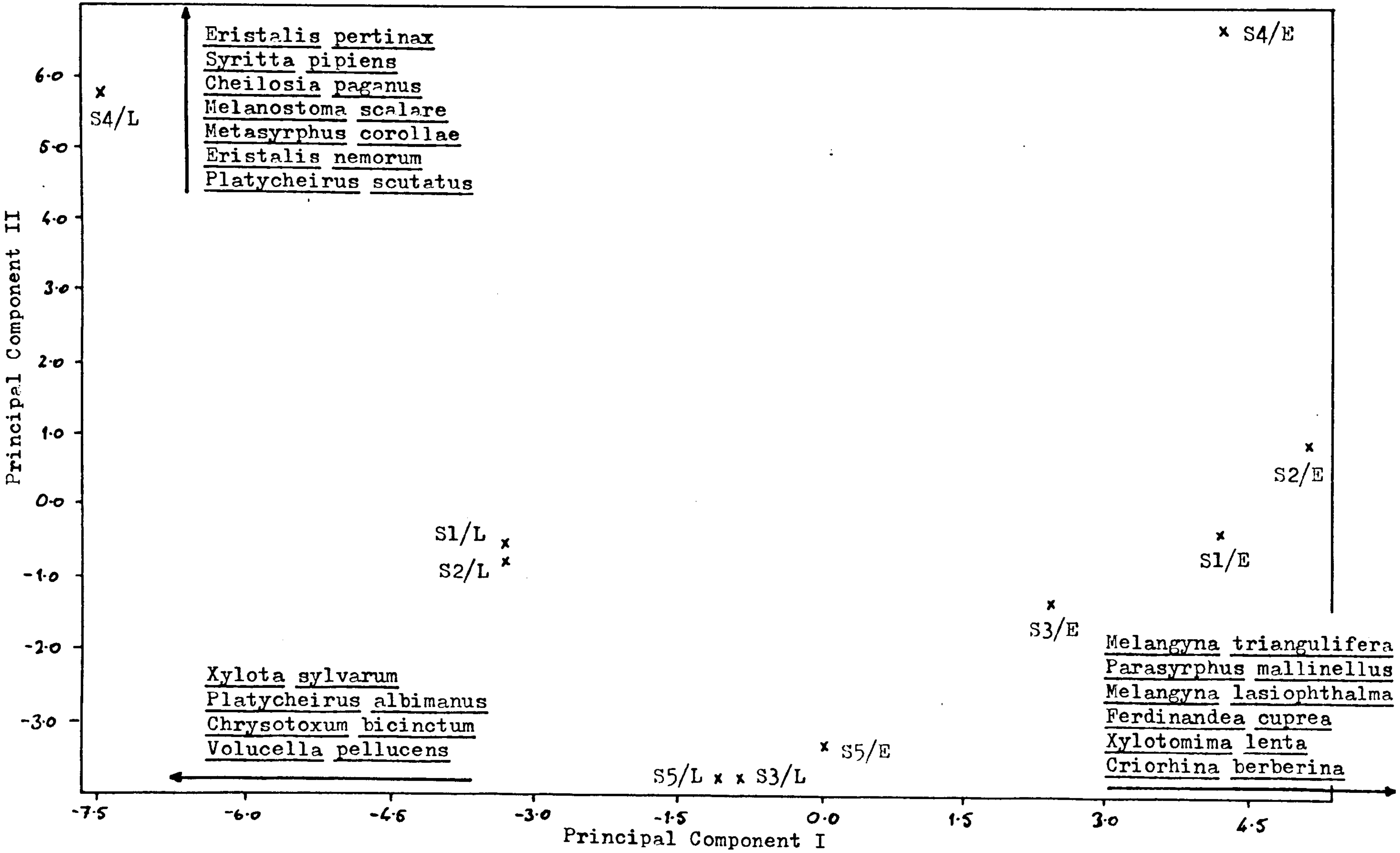


FIG. 9.1 PRINCIPAL COMPONENETS ANALYSIS OF THE EARLY AND LATE SEASON HOVERFLY COMMUNITIES, 1980

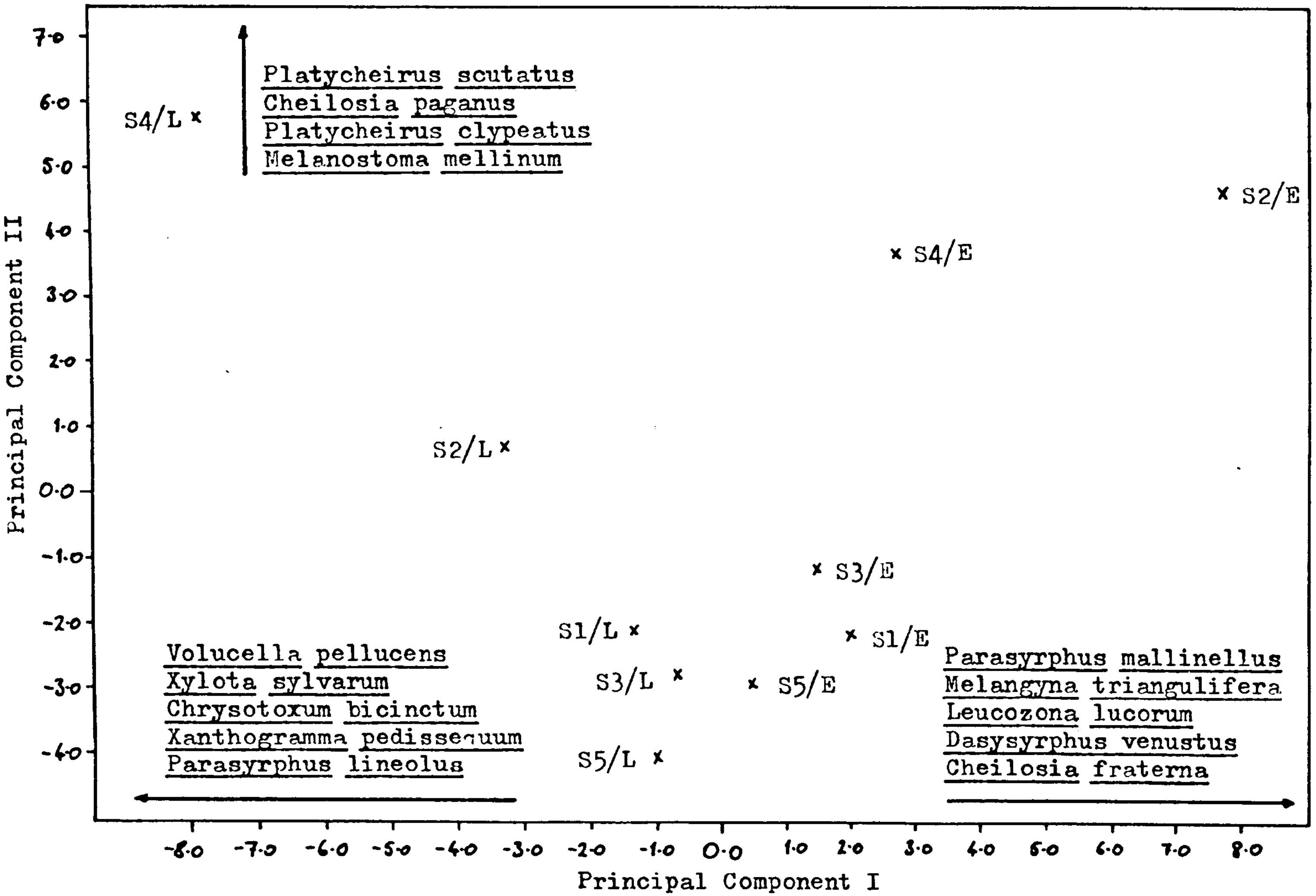


FIG. 9.2 PRINCIPAL COMPONENTS ANALYSIS OF THE EARLY AND LATE SEASON HOVERFLY COMMUNITIES, 1981

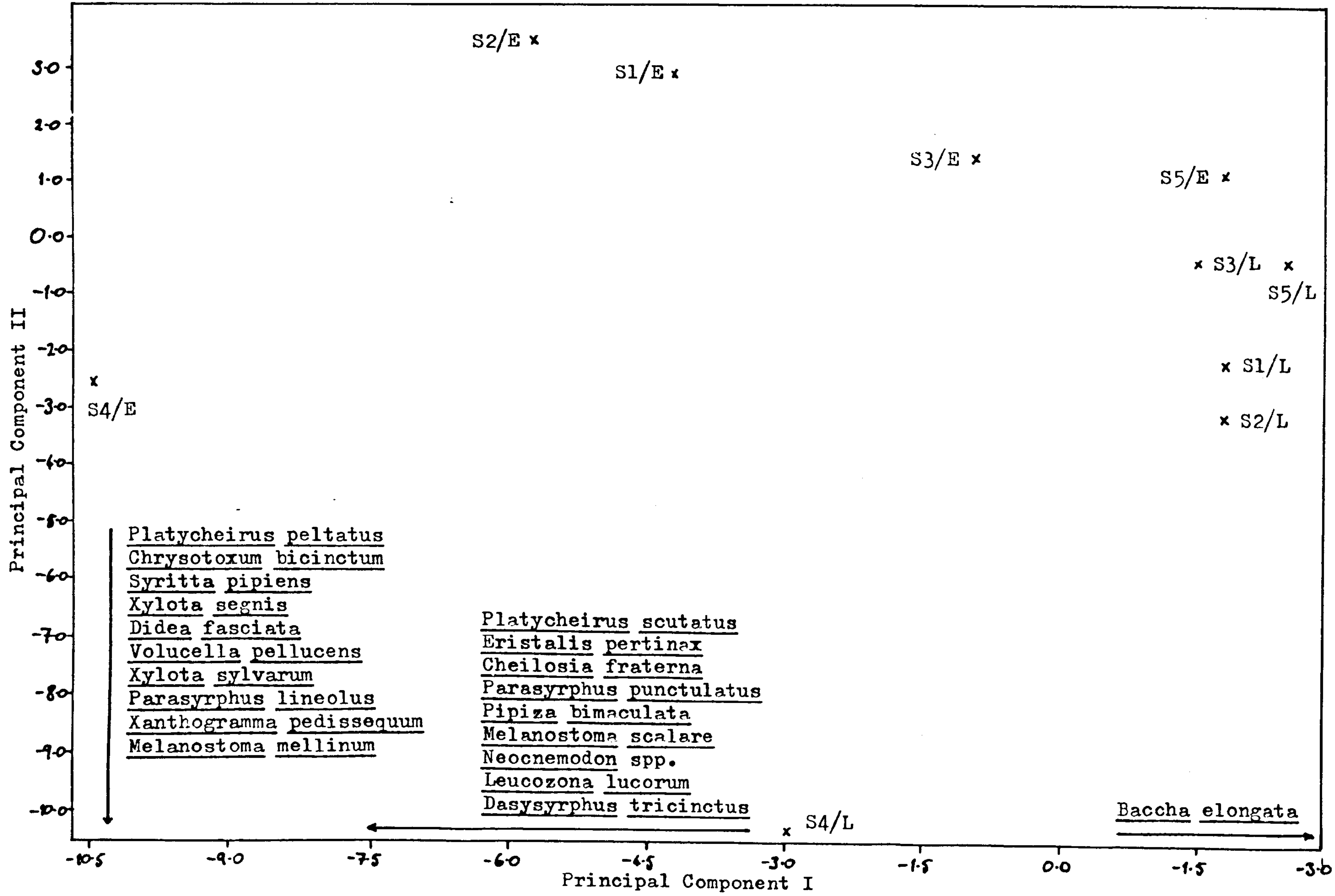


FIG. 9.3 PRINCIPAL COMPONENTS ANALYSIS OF THE EARLY AND LATE SEASON HOVERFLY COMMUNITIES, 1982

both from each other and from the other sites.

The single close grouping within the 1981 ordination contains the early and late collections from S1, S3 and S5, with the remaining four samples isolated both from this grouping and from each other (Fig. 9.2). The 1982 ordination again shows only one distinct cluster, containing the late samples from S1, S2, S3 and S5, together with the early collection from the latter site (Fig. 9.3). The early communities from S1 and S2 fall together, with the early S3 sample sandwiched between these two collections and the main group. The two S4 communities are once again distinct from each other and from the rest of the samples.

9.3d Comparison of the Early and Late Communities

The PCA ordinations associating the two samples from each site are shown in Figs. 9.4, 9.5 and 9.6. The trends in 1980 and 1982 are similar to each other, with only the two S5 samples closely associated. The communities at S1, S2 and S4 are very different for the two sampling periods, with the two S3 collections being neither particularly close to each other nor markedly dissimmilar.

The 1981 ordination shows more similarity of both the catches from S1 and S3, which are clustered together with the catches from S5. The early and late samples from the remaining two sites once more show no similarity to each other.

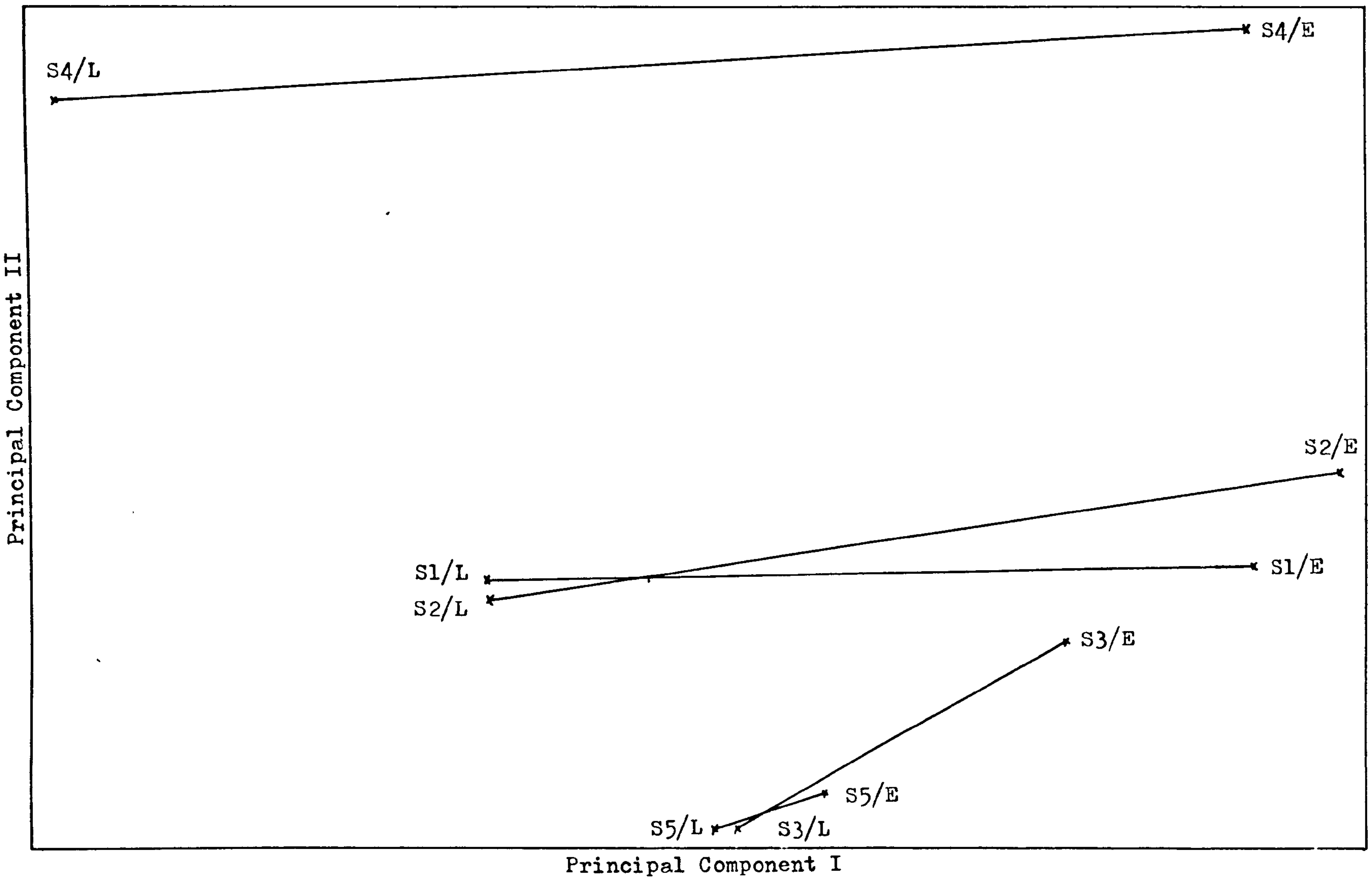


FIG. 9.4 THE SEASONAL SEPARATION OF THE EARLY AND LATE HOVERFLY COMMUNITIES BY PRINCIPAL COMPONENTS ANALYSIS, 1980

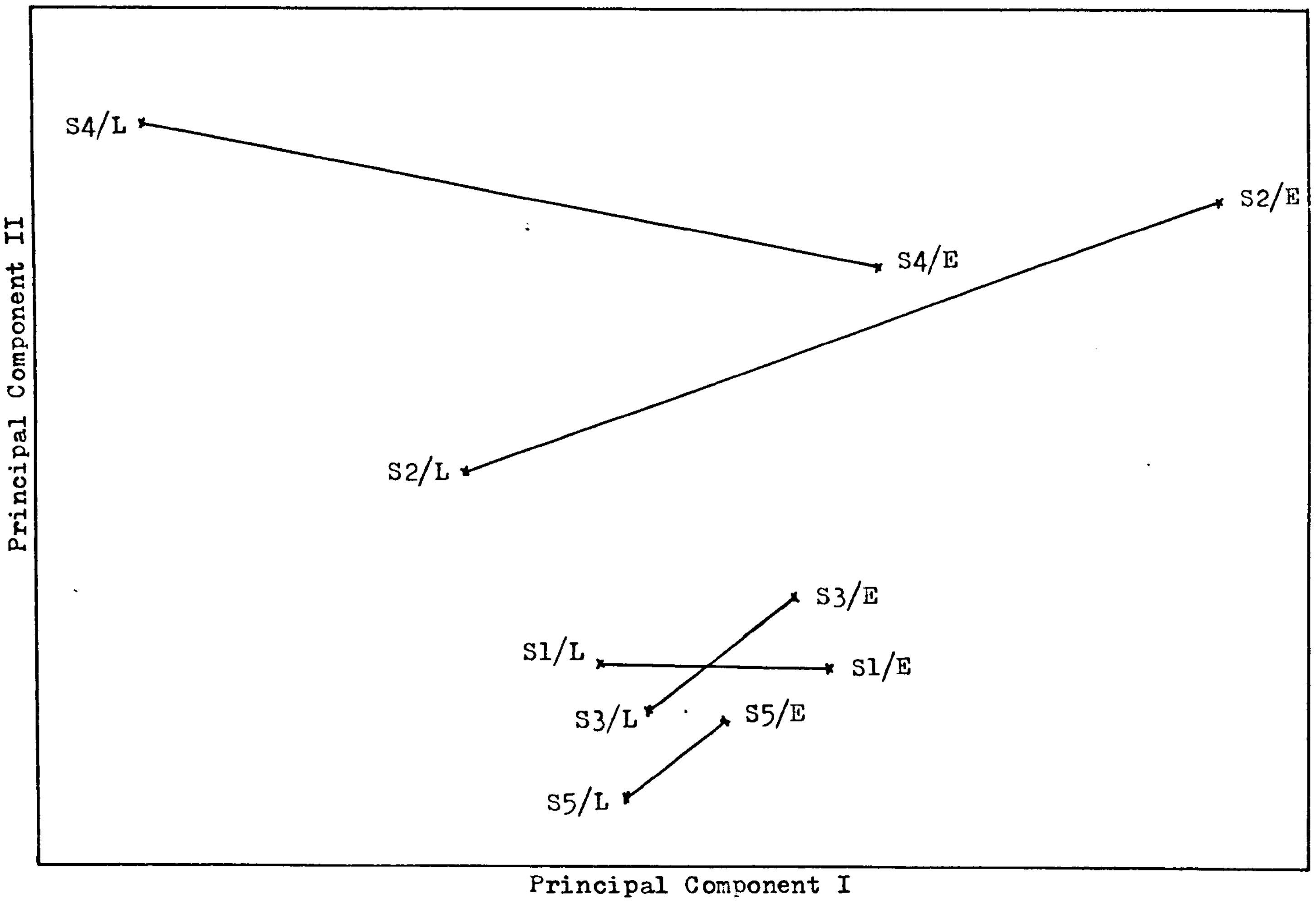


FIG. 9.5 THE SEASONAL SEPARATION OF THE EARLY AND LATE HOVERFLY COMMUNITIES BY PRINCIPAL COMPONENTS ANALYSIS, 1981

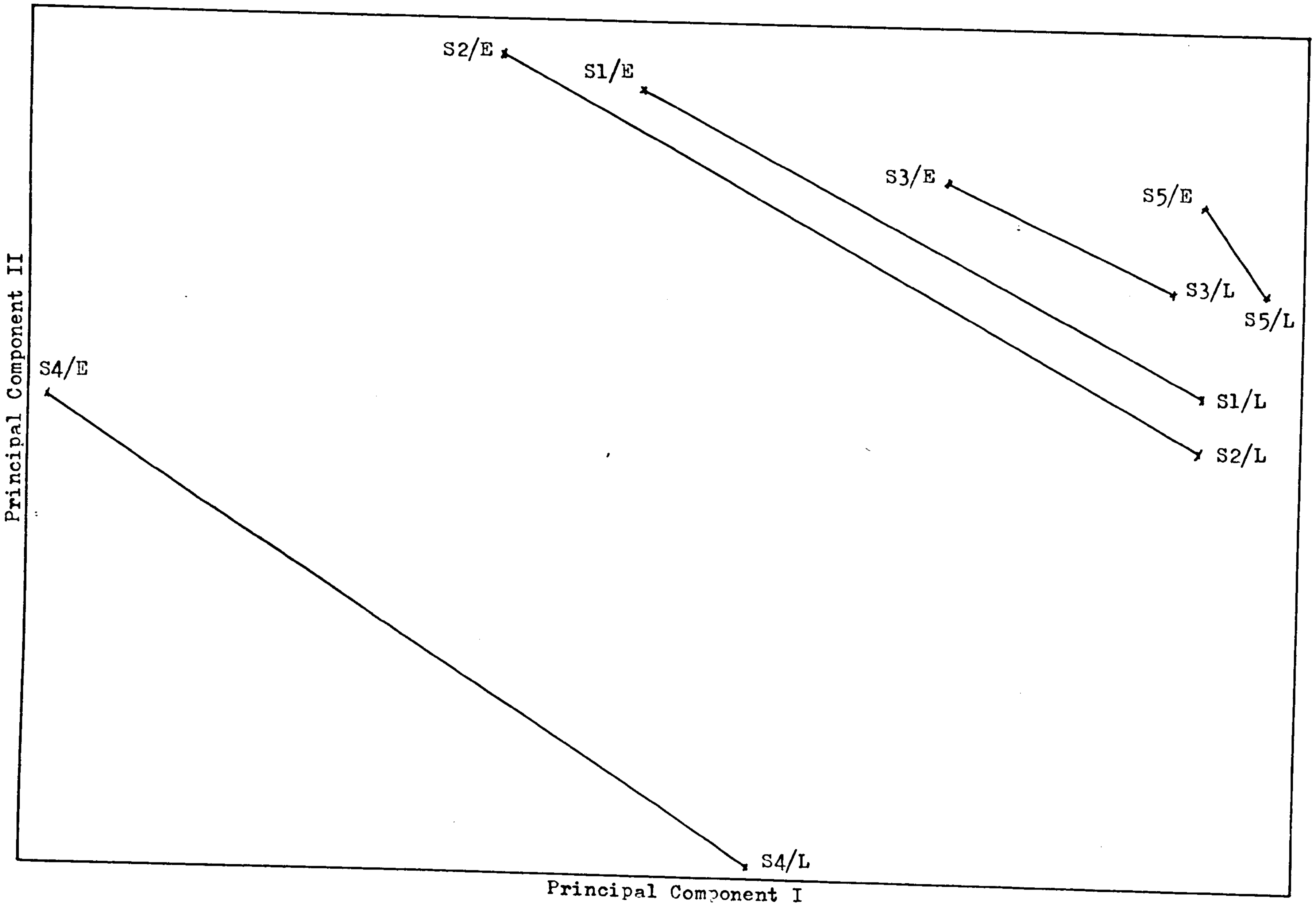


FIG. 9.6 THE SEASONAL SEPARATION OF THE EARLY AND LATE HOVERFLY COMMUNITIES BY PRINCIPAL COMPONENTS ANALYSIS, 1982

9.3e Hoverfly Ordinations and Coniferization

There is apparently no relation between the sequence of increasing coniferization between the sites and the PCA ordinations (Figs. 9.7, 9.8 and 9.9). This is consistent with the ordering of sites from the abundance of syrphids, the number of species present and from the overall syrphid diversity, none of which bear relation to the degree of coniferization at a particular site.

9.3f Hoverfly Ordinations and Hoverfly Species Diversity

The α and Q diversities of the thirty hoverfly communities have been plotted onto the PCA ordination in Figs. 9.10, 9.11 and 9.12. The superimposition of the diversity statistics imposes a pattern on the ordination that aids their interpretation but the close association of the two data sets should come as no surprise, since both have their origins in the abundances of the species present at each site.

The early and late season hoverfly communities in 1980 are seen to be separated by PC I (Fig. 9.10), with the high diversity sites for each season polarised at opposite ends of the axis and the low diversity sites for both seasons lying across the middle of the axis. *Melangyna triangulifer*, *Parasyrphus malinellus*, *M. lasiophthalma*, *Ferdinandea cuprea*, *Xylotomima lenta* and *Criorhina berberina* are the important species in

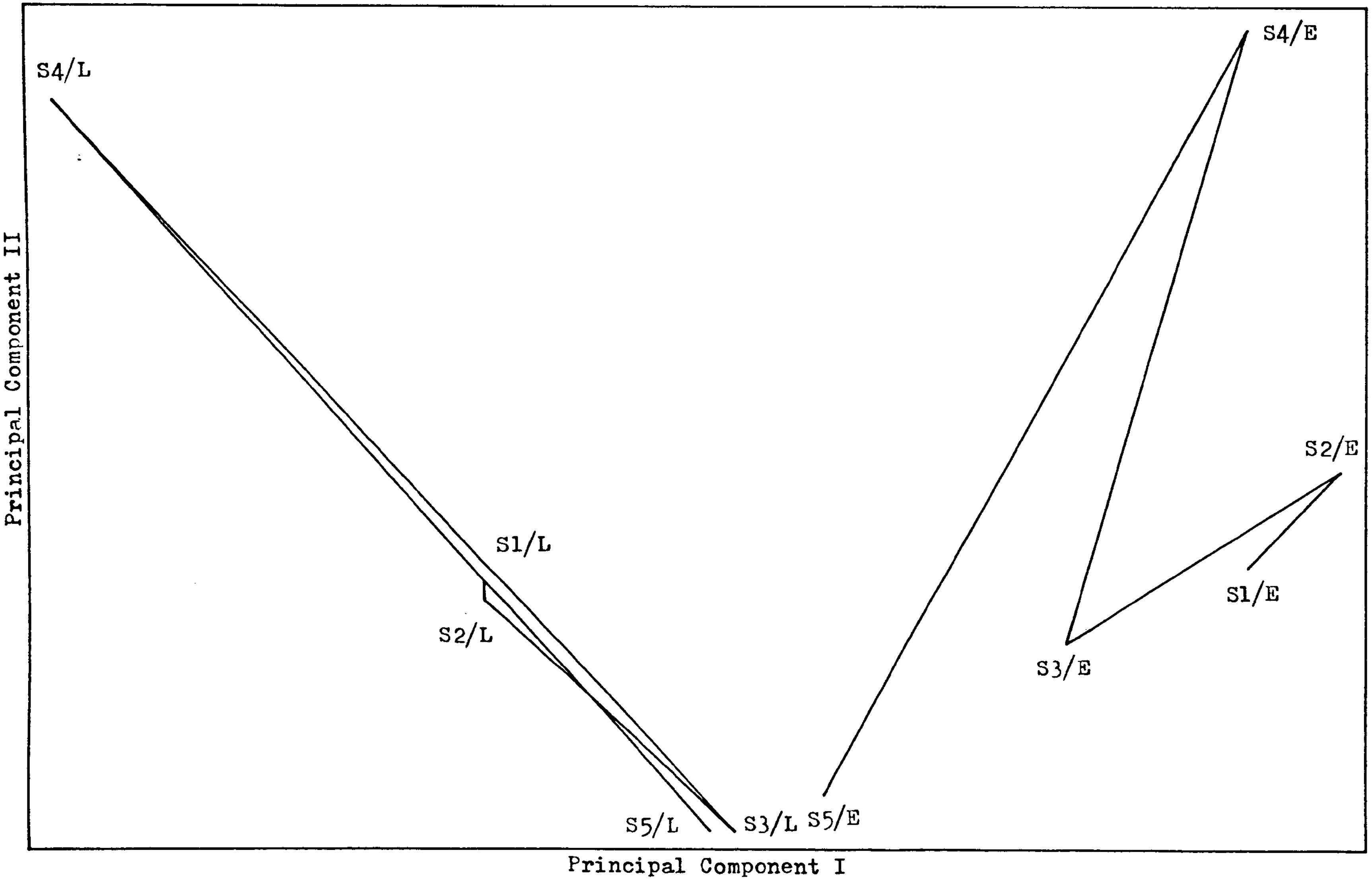


FIG. 9.7 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND THE DECIDUOUS - CONIFEROUS GRADIENT, 1980

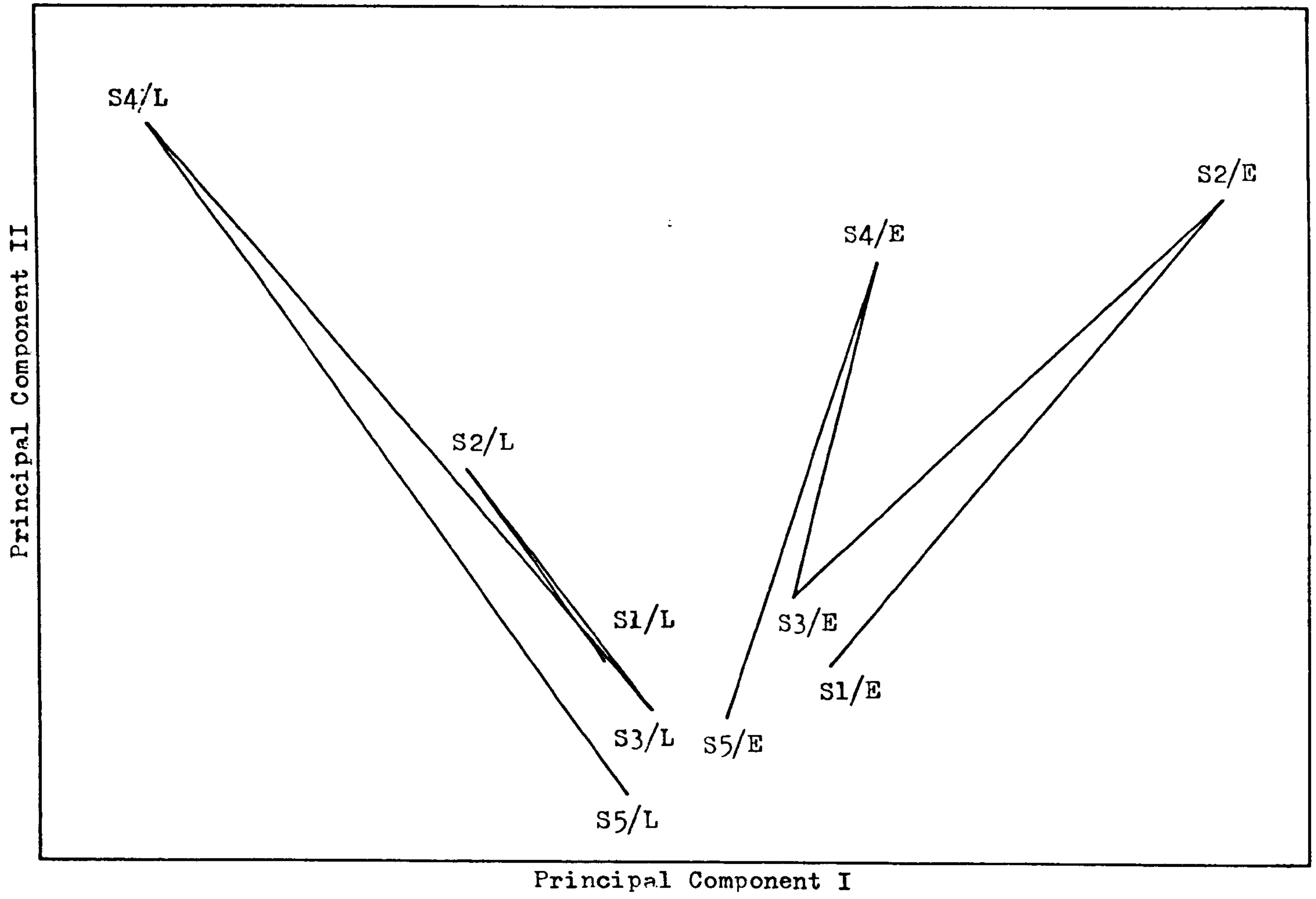


FIG. 9.8 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND THE DECIDUOUS - CONIFEROUS GRADIENT, 1981

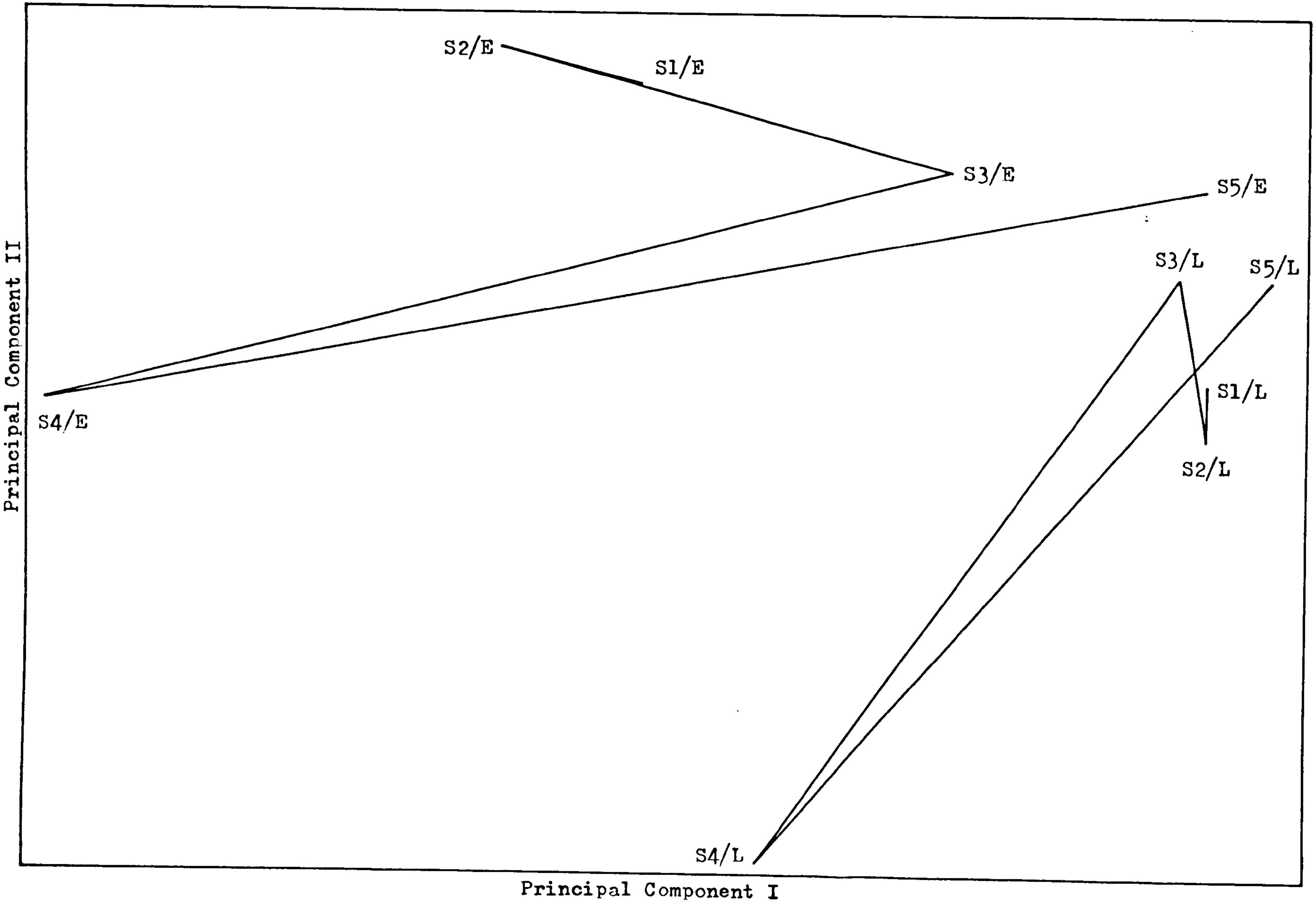


FIG. 9.9 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND THE DECIDUOUS - CONIFEROUS GRADIENT, 1982

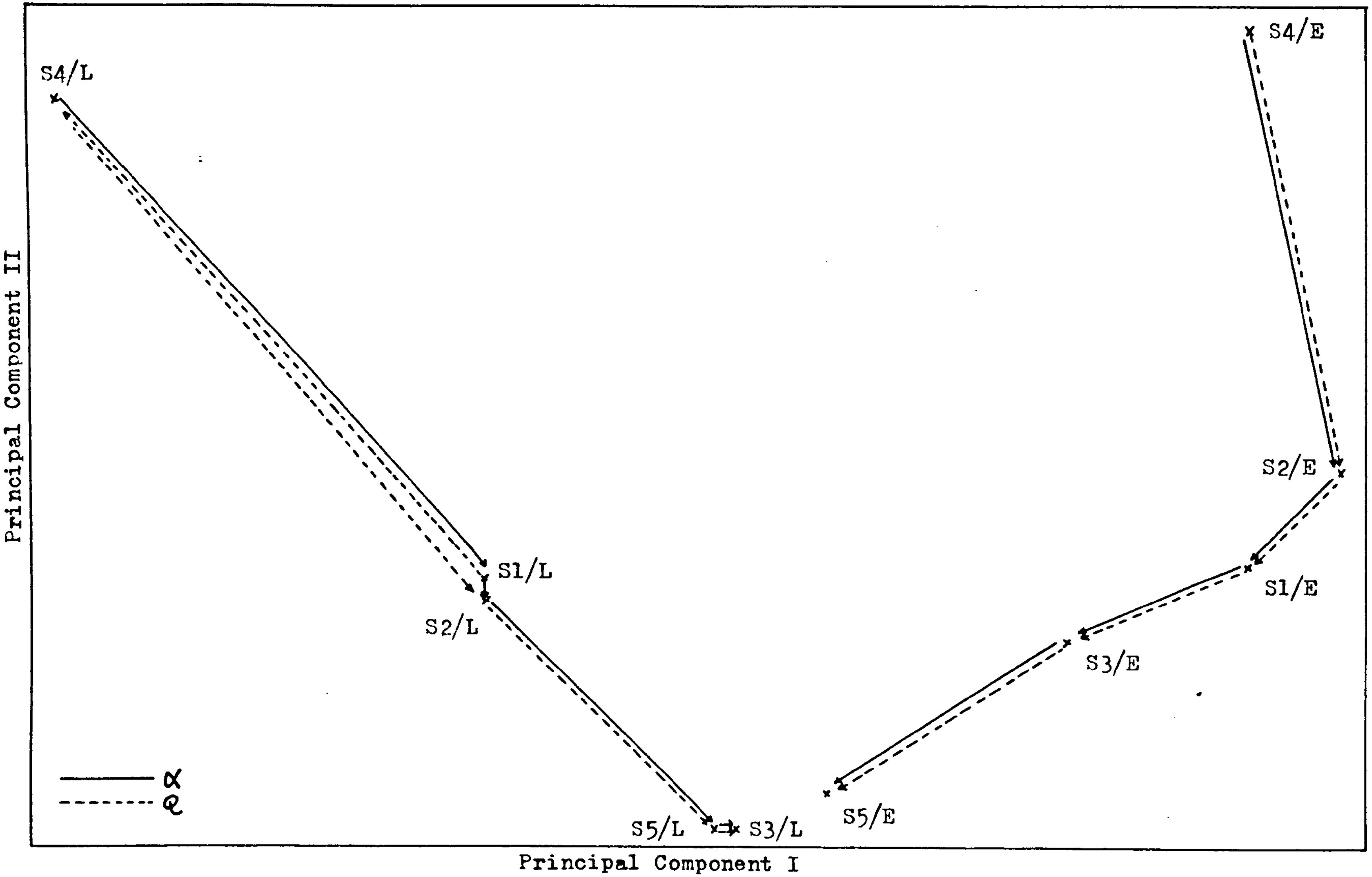


FIG. 9.10 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND HOVERFLY SPECIES DIVERSITY, 1980

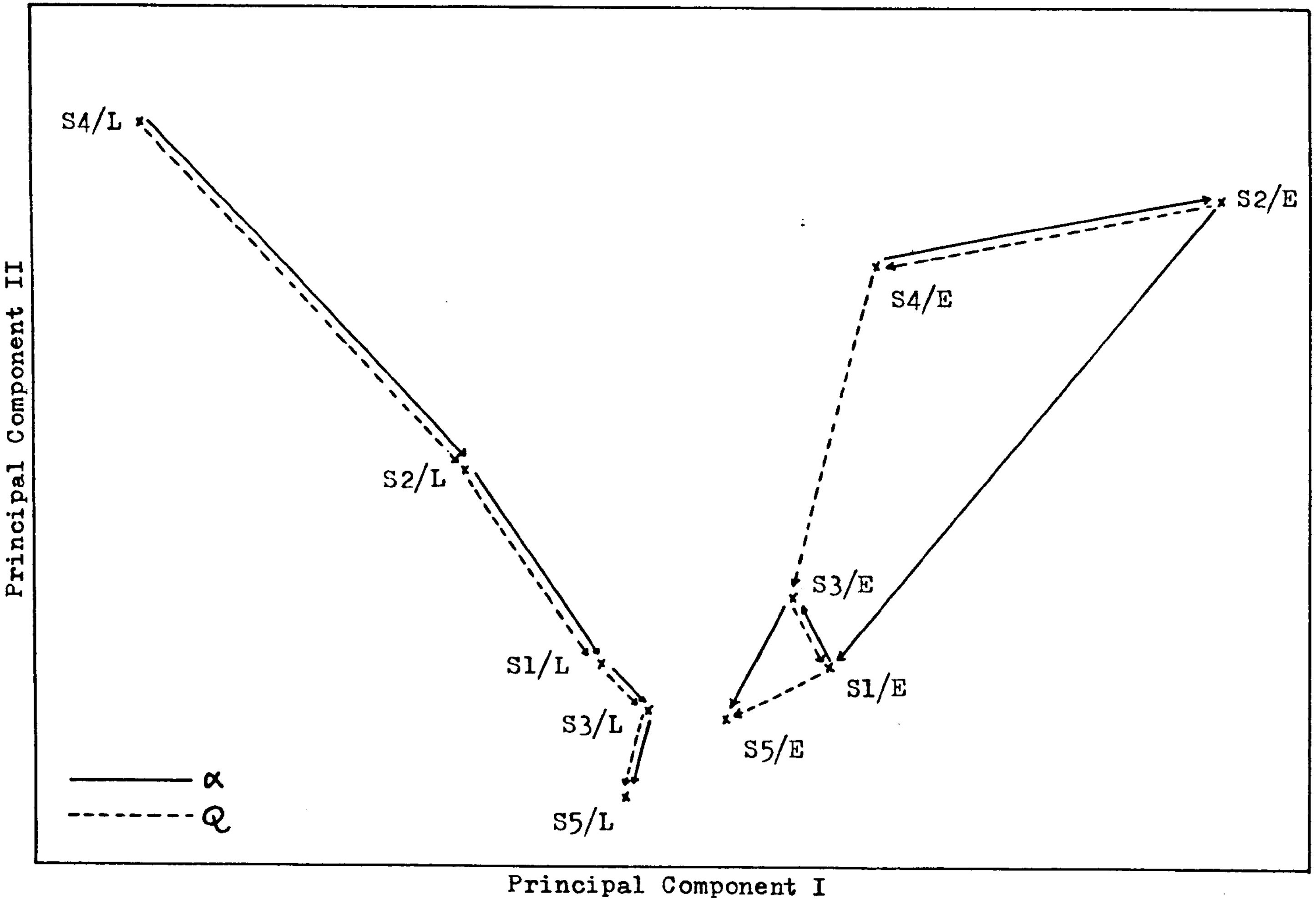


FIG. 9.11 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND HOVERFLY SPECIES DIVERSITY, 1981

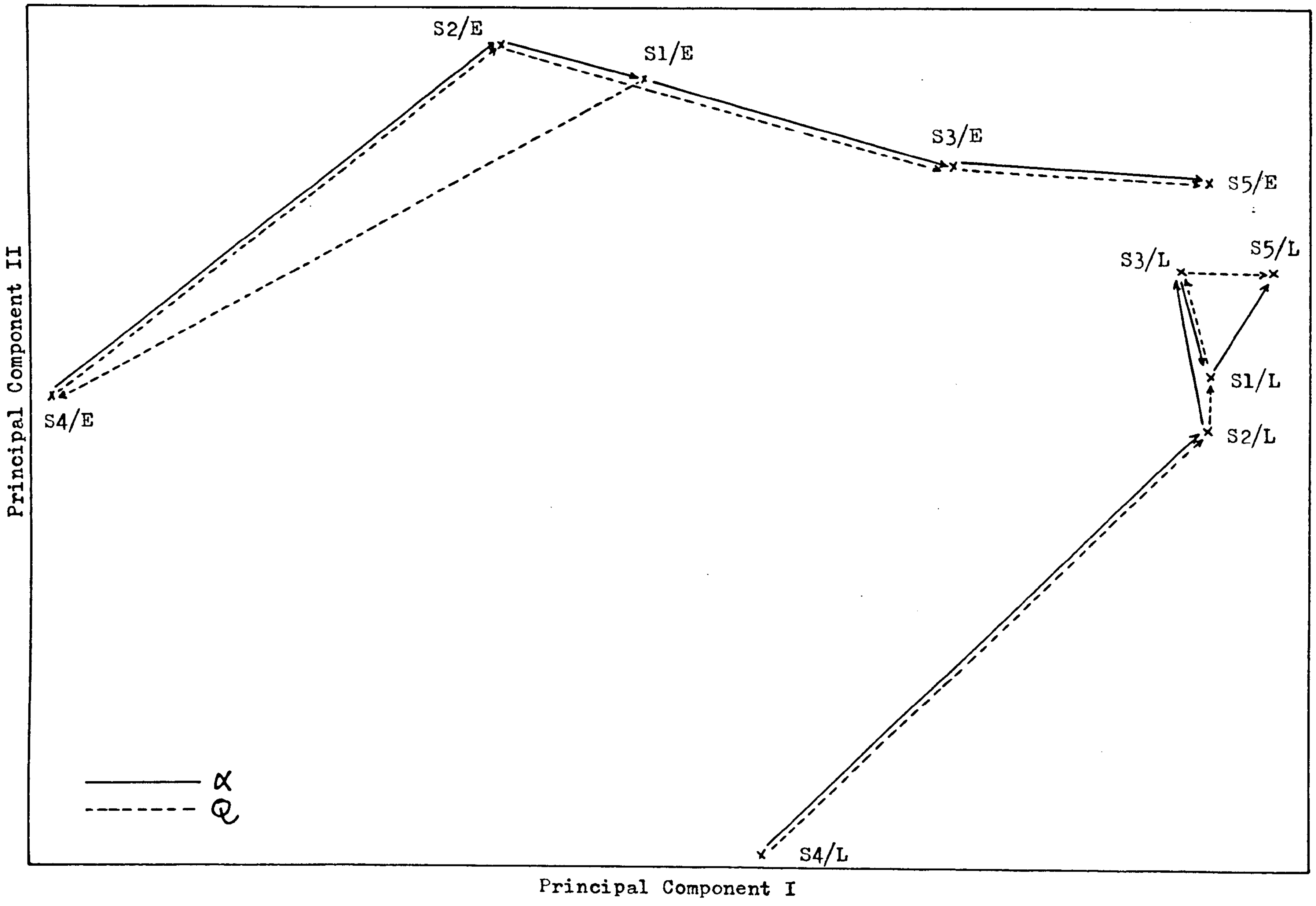


FIG. 9.12 HOVERFLY PRINCIPAL COMPONENTS ANALYSIS AND HOVERFLY SPECIES DIVERSITY, 1982

the early half of the year whilst *Xylota sylvarum*, *Platycheirus albimanus*, *Chrysotoxum bicinctum* and *Volucella pellucens* are characteristic of the late period. The two samples from S5 and the late catch from S3 fall at the interface of the two seasons and these are the three sites with the lowest diversity in 1980.

Species diversity for the early 1980 samples is separated out by PC II, with S4 showing strong associations with *Eristalis pertinax*, *Syritta pipiens*, *Cheilosia paganus*, *Melanostoma scalare*, *Metasyrphus corollae*, *E. nemorum* and *Platycheirus scutatus*. S3 and S5 are further separated by PC I. The late samples for this year are separated by both PC I and PC II. S4 is clearly isolated from the other sites by both the -ve PC I 'late' species and by the +ve PC II 'high diversity' species. S1 and S2 are tightly clustered as are S3 and S5; the species diversity of the two sites within each cluster is almost identical.

The 1981 ordinations show a similar arrangement of the sites, with PC I clearly splitting the early and late season catches, despite a cluster of all the catches obtained from S1, S3 and S5 (Fig. 9.11). *Parasyrphus malinellus* and *Melangyna triangulifera* are again characteristic of the early season, together in this year with *Leucozona lucorum*, *Dasysyrphus venustus* and *Cheilosia fraterna*. The late season species include *Volucella pellucens*, *Xylota sylvarum* and *Chrysotoxum bicinctum* in common with the previous year in addition to *Xanthogramma pedissequum* and *Parasyrphus lineolus*. The catches from S3 and S5 once again fall in the middle of the axis as do the samples from S1, indicating little change in the fauna between the two periods at these three sites.

PC II again separates the sites in terms of their species diversity, although the fit for the early period is not a particularly good one because the two diversity indices give different site rankings. The PCA ordination is in line with Q diversity and not with α; Q diversity is correctly ranged along PC II. *Platycheirus scutatus*, *Cheilosia paganus*, *P. clypeatus* and *Melanostoma mellinum* account for the majority of the variation along this axis, being more common at the more diverse sites. The segregation of S2 and S4 from the other sites along PC II is reflected in the values of diversity for the five early season communities. The most diverse site in each season is again strongly influenced by PC I in relation to the other samples from the same sampling period.

The 1982 ordination gives a different pattern than the two previous years (Fig. 9.12). The early and late periods are not split simply along PC I but by the product of both of the axes, with PC II being the predominant one; they do however still fall into discrete groups. Both of the S4 samples are clearly segregated from the other communities towards the lower end of both of the axes; but the ordination is an unusual one in that all but one of the latent vectors for the ten most influential species for each principal component have a negative sign. The only positive loading is for *Baccha elongata*, which ranks tenth of the PC I species.

Species diversity of the early season samples is spread along PC I, with the only anomaly arising from the Q statistic ranking S1 the most diverse site. α diversity follows precisely the sequence of sites described by the PCA. *Platycheirus scutatus*, *Eristalis pertinax*, *Cheilosia fraterna*, *Parasyrphus punctulatus*, *Pipiza bimaculata* and *Melanostoma scalare* are all characteristic of the more diverse sites, with only *Baccha* exhibiting a preference for the less diverse collections.

The late season samples are not separated out along PC I but form a cluster distinguishable only by PC II. Only S4 lies outside this cluster, displaced by both principal components. In addition to the PC I species listed above, this site is also influenced by *Platycheirus peltatus*, *Chrysotoxum bicinctum*, *Syritta pipiens*, *Volucella pellucens* and *Xylota sylvarum*, all of which have near-identical loadings. Diversity rankings within the cluster are confused and reflect the similarity between the four sites, the PCA giving a better fit to Q diversity. Overall, the diversity of these sites is low and the PCA groups them with the poorest early season site.

9.4 The Principal Components Analysis: Comment

The main aim of PCA is to group together data sets sharing similar attributes and to attempt to identify these common features. The analysis of successive years' data from a particular site can identify persistent trends and their underlying component features, though the model cannot test as to whether these features are in any way causal to the observed trends. The principal components are not real variables but are simply mathematical components of the model, based on correlation evidence which cannot substantiate a theoretical speculation without experimental proof, because an infinite number of models could be constructed that predict the same correlation.

PCA of the Bernwood hoverflies shows both consistent and changing patterns in the relationship of the samples to each other. All the catches from S3 and S5 tend to be ordinated in a group, whilst early and late samples from S4 are always very different both from each other and from all the other sites. The early samples from S1 and S2 appear close to each other on both the 1980 and 1982 ordinations, as do the late samples, but their relation to the other sites is fluid and this similarity breaks down in 1981.

The clear separation of the early and late season catches from all the sites is a consistent feature in all three years (Figs. 9.10, 9.11 and 9.12). This split is achieved cleanly across PC I in 1980 and 1981, but not in the rather different ordination of 1982; the relation of the two catches within each site is the same in 1980 and

1982 but not in 1981.

The species diversity gradient of both α and Q in most cases give a perfect fit with the PCA ordination sequence, which can be used to lend weight to one or the other of the two indices in the instances in which they give different site rankings. In such cases, the PCA does not favour overall either the α or Q, each index giving a 'wrong' ranking on two occasions. PCA can thus be used as a further tool in the ranking of sites by species abundance and diversity.

The two seasonal samples from the high-diversity sites are widely separated in the PCA ordinations, whereas those from low-diversity sites are clustered together at the seasonal interface. Species composition of the rich sites is thus strongly influenced by season, unlike that at the poorer sites, where the sites do not maintain seasonal identity.

The shifting nature of the species populations that underlie these relatively stable communities is confirmed by the principal latent vectors of each of the principal component axes. These axes are the result of the near-equal importance of many species rather than from the domination of only a few, and the identity of these species changes markedly from year to year. The PCA thus cannot identify indicator species whose consistent presence at a particular type of site thus characterizes it: it is the whole assemblage of syrphids that characterizes a particular site and the component species play fickle roles within the overall samples.

CHAPTER TEN

Trophic Analysis of Bernwood Hoverflies

10.1 Larval Trophic Categories of the Bernwood Hoverflies

Adult Syrphidae are all principally feeders upon pollen and nectar, although they also occasionally utilize other sources of fluids rich in sugars, salts and amino acids, such as honeydew, rotting fruit and carrion (Banks 1959, Gilbert 1981, Owen J. 1981). Their larvae however display a wide range of feeding habits and five distinct categories can be recognised: consumers of living plant material, largely of stems, bulbs, roots and fungi; predators of aphids and of other Homoptera; dwellers in, and thus feeders upon, sap runs from tree wounds and in rotting wood; dwellers in and feeders upon soft and liquid decomposing organic material, usually of animal origin but including detritus-rich ponds; and scavengers of the nests of social Hymenoptera. The Bernwood hoverflies, broken down into these trophic groups, are given in Table 10.1. In common with the adults, many of the larvae are probably opportunist feeders to some extent and thus aphid feeders, for example, will sometimes attack other insects, such as Lepidoptera larvae; those hoverfly larvae associated with tree sap will most likely also feed upon those small insects attracted to the sap and thus become secondary consumers,as would the scavengers of Hymenoptera nests occasionally consuming live larvae and pupae (Owen 1981).

TABLE 10.1

TROPHIC CATEGORIES OF THE BERNWOOD HOVERFLIES, 1980 - 1982

Categories	Feeding Site	Trophic Level	Representatives	S	N	%N
1	Stems, roots bulbs	1°C	*Cheilosia*	16	392	
			Eumerus	1	16	
			Merodon	1	1	
				18	409	2.02
2	Plants infested with aphids, aphid galls	2°C	*Syrphinae*	62	15,040	
			Heringia	1	2	
			Neocnemodon	2	73	
			Pipiza	4	81	
			Pipizella	2	13	
				71	15,209	75.16
3	Tree sap, rotting wood	1°C, 1°D	*Criorhina*	2	187	
			Ferdinandea	2	630	
			Myathropa	1	22	
			Xylota	4	366	
			Xylotomima	2	61	
				11	1,266	6.26

TABLE 10.1 CONTINUED

Categories	Feeding Site	Trophic Level	Representatives	S	N	%N
4	Decaying organic matter - usually of animal origin	1-N order decomposers	*Eristalis*	6	539	
			Helophilus	2	1,436	
			Neoascia	1	109	
			Rhingia	1	1,128	
			Syritta	1	23	
				11	3,235	15.99
5	Ant, bee and wasp nests	2-N order decomposers	*Microdon*	1	23	
			Volucella	3	92	
				4	115	0.57
					20,234	

From the Bernwood collection, eighteen species, contained within three genera, fall into the first trophic category of primary consumers and these account for 2% of the total catch. Of these eighteen species, sixteen belong to the genus *Cheilosia*. Several *Cheilosia* species use thistles (*Carduus* spp. and *Cirsium* spp.) as the larval food source. Of the Bernwood species, *C. albipila* and *C. chrysocoma* utilize the stems whereas *C. variabilis* eats the buds and stalks (Smith 1979). *C. variabilis* has also been found in the roots of common figwort (*Scrophularia nodosa*) and mining galleries in the leaves of ransoms (*Allium ursinum*) (Bankowska 1980). *C. albitarsis* and *C. paganus* are both species largely of pasture, with the adults commonly to be found around the flowers of buttercups and celandines (*Ranunculus* spp.) (Speight *et al.* 1975). *C. bergenstami* uses the roots and crowns of ragwort (*Senecio jacobaea*) for larval feeding sites and Smith (1979) comments upon the possible use of this species as a biological control agent against ragwort. Two of the *Cheilosia* species captured at Bernwood have larvae that feed on fungi, although both are rare within the Forest. *C. soror* feeds on truffles (Tuberales) whereas *C. scutellata* consumes a wide variety of rotten fungi (Smith 1979).

In many cases the larval food of *Cheilosia* species is not known, although none of them appears to feed upon crop plants. There is also evidence that the adult flies sometimes frequent the flowers of the same species which provide larval food (Smith 1979).

Eumerus ornatus and *Merodon equestris*, the remaining two primary consumers found at Bernwood, both feed by burrowing into living bulbs and both can be horticultural pests. *E. ornatus* is the least common of the four British *Eumerus* species and has the least pest potential, being principally a species of open woodlands. It is also restricted to the south of England whereas *E. strigatus* and *E. tuberculatus*, which both mine *Narcissus* bulbs, have been recorded as far north as Scotland (Speight *et al.* 1975). *Eumerus* larvae attack and enter bulbs around the damp neck whereas *Merodon* burrows through the basal plate (Oldroyd 1964). *Merodon* also has a predilection for *Narcissus* bulbs although its larvae have been found in the bulbs of wild hyacinth (*Scilla nutans*) (Coe 1953). It is very much a suburban hoverfly and has probably been spread by man over the length and breadth of the British Isles (Speight *et al.* 1975) and to North America (Bankowska 1980). The larvae are stout and fleshy and there is usually only one per bulb, which becomes soft, rotten and useless: *Merodon* is a serious horticultural pest.

The great majority of the Bernwood hoverflies have predatory larvae for which aphids form the principal prey. The 71 species in this trophic group contribute 75% of the total hoverfly catch and include all the 62 species of the subfamily Syrphinae, which accounts for 98.9% of all the predators captured.

The larvae show considerable variation in their prey specifity and this is in part linked to the selection of oviposition sites by the adult syrphid. Eggs are usually laid on plants infested with aphids and in the vicinity of the prey; there is a close correlation between the number of syrphid eggs and larvae and the numbers of aphids on individual bean plants (Banks 1952). Site selection is the result of a balance between olfactory stimuli from the aphids and visual stimuli from the plants (Chandler 1966). There is considerable variation in the degree of dominance of the aphid stimulus over the plant stimulus. Some syrphids, for example *Metasyrphus corollae*, *M. luniger* and *Syrphus ribesii*, exhibit a strong dependence on the presence of aphids prior to oviposition (Chandler 1966); *Scaeva pyrastri* and *S. selenitica* apparently always need aphids to be present to lay eggs (Lyon, in Hodek 1966). Laboratory-reared *Episyrphus balteatus* do not lay on uninfested plants but as the females age, there is a gradual loss of restraint and discrimination in selecting sites for oviposition (Chandler 1966). Although the Syrphinae generally lay single eggs, batches may often be laid on uninfested plants (Chandler 1968).

Platycheirus peltatus on the other hand shows a strong response to the host plant itself and commonly lays on uninfested plants - even gravid females have been observed laying without the presence of aphids. Such eggs laid in advance of aphid attack are usually laid in small batches and the first-emerged larvae may turn cannibal upon the rest of the batch in the absence of aphids upon hatching (Chandler 1966). *Metasyrphus corollae* can also lay eggs in the absence of aphids. This is brought on by an intense drive to oviposit after long periods in the absence of aphids - eggs have been laid in dirty breeding vials, in honeydew, in dead *M. corollae* and in sweated hands but rarely upon clean aphid-free leaves (Bombosch and Volk 1966).

The larval preferences of syrphids also show varying degrees of host specificity, with the species common as adults usually taking a wide spectrum of suitable prey. *Syrphus ribesii*, *S. vitripennis*, *M. luniger* and *Episyrphus balteatus* are all polyphagous and are also largely indifferent to location, whereas *Syrphus torvus* for example is associated with trees and shrubs and *Sphaerophoria* spp. with herbaceous plants. A certain host specificity is shown by *Scaeva pyrastri* and *Sphaerophoria scripta*, both of which prefer *Dactynotus cichorii* on *Crepis biennis* and on *Cichorium intybus* to *Aphis fabae* on *Cirsium arvense* and also in laboratory rearings (Dusek and Laska 1966). The larvae of *Baccha elongata* attack other Homoptera in addition to aphids and *Scaeva*, *Xanthandrus* and *Metasyrphus luniger* have all been recorded attacking the larvae and pupae of moths (Speight *et al.* 1975). Records of the larval habits of the Syrphinae are peculiarly sparse and further investigation would probably reveal more opportunist feeding.

Larvae of the genera *Melanostoma* and *Platycheirus* are particularly polyphagous in that they feed on plant material in addition to, or in place of, insect nutrient sources. Larvae of both these genera have been found in and reared upon rotting vegetable matter (Coe 1953, Oldroyd 1964) and Davidson (1922) found that three Californian

Melanostoma species developed faster on decaying chick-week than on aphids. Both these genera are nocturnal, which Davidson suggests may be symptomatic of an ancestral line living within plant tissues away from light and he speculates that these genera may be in a transition from phytophages to entomophages. *Melanostoma mellinum* larvae have been found feeding on *Psyllopsis fraxini* (Psyllidae) which galls leaves of ash (*Fraxinus)* in addition to a variety of aphids (Stubbs and Chandler 1978).

In contrast, some predatory syrphid larvae have quite specific food requirements, especially amongst the Milesiinae. *Melangyna* however is one genera of the Syrphinae with a narrow feeding range. The adults are rarely encountered far from trees and the larvae too are arboreal; *Melangyna cincta* has only been found on *Phyllapsis fagi* on *Fagus sylvatica* (Speight *et al.* 1975 Dusek and Laska 1966). *Chrysotoxum* larvae appear to be specific in microhabitat if not in actual prey species. They have been found in a variety of situations: in ants' nests (Colyer and Hammond 1968), under stones and loose turf and in a compost heap (Coe 1953) and are presumed to feed upon root aphids, since the larvae are morphologically of the aphidophagous type (Speight *et al.* 1975) *Xanthogramma* larvae prey upon root aphids raised by ants in the underground tunnels and corridors of the nests of *Lasius* spp. (Bankowska 1980).

The predatory Milesiinae syrphids collected from Bernwood all belong to the tribe Pipizini, which together account for only 1.1% of all of the hoverflies in this trophic category. *Neocnemodon* larvae are host-restricted to aphids that produce a waxy or fluffy flocculent secretion, such as woolly aphids, and the larvae live on the dense colonies of these aphids in trees and shrubs (Evenhuis 1966, Speight *et at.* 1975). Contrasting accounts of the larval habits of *Pipiza* exist. Coe (1953) states that these larvae eat various species of aphid both above and below the ground, prefering colonies of aphids that produce a waxy flocculence. Dusek and Laska (1966) however regard *Pipiza* as having a narrow feeding range, primarily on aphids that gall or roll plant leaves. *P. bimaculata* feeds on aphids that roll leaves, regardless of species, whereas *P. festiva* is common only on *Pemphigus* spp. aphids, which produce various forms of gall on poplars (*Populus*).

Pipizella larvae also apparently have contrasting lifestyles. *P. varipes*, which occurs over a wide range of habitats from heathlands and boggy moorlands to pondsides and woodland edges, has larvae which feed on root aphids and it has been found in the roots of both the Graminae and the Umbelliferae (Coe 1953, Bankowska 1980). *P. virens* however apparently feeds on *Pemphigus spirothecae*, which produces petiole galls on *Populus nigra* (Stubbs and Chandler 1978). *Heringia heringi* larvae also live in the galls of this aphid in addition to those of *Tetraneura ulmi* and *Schizoneura lanuginosa* on *Ulmus* and *Pemphigus spirothecae* on *Populus*; all these aphids belong to the family Pemphiginae (Coe 1953, Dusek and Laska 1966, Stubbs and Chandler 1978 and Bankowska 1980).

Eleven hoverfly species in the Bernwood collection have larvae that are associated with wood, feeding either on sap runs from wounds in the tree or within rot-holes. This trophic category accounts for 6.25% of the total catch, *Ferdinandea cuprea* being by far the most common species with 617 individuals taken. *Ferdinandea* larvae are found in holes both of oaks and other broad-leaved trees (Bankowska 1980) and they feed primarily on the sap that runs from tree wounds, especially those infested by the goat moth *Cossus cossus* (Coe 1953). Larvae of this moth feed in the solid wood of various trees, especially in *Ulmus*, *Fraxinus*, *Betula* and *Salix* and take three to four years development to the pupal stage. The larvae form large burrows with sappy detritus and are especially important in that they produce sap runs in the autumn as well as in the spring: most seepages flow best in the spring and early summer and are often dry at other times of the year (South 1948, Stubbs and Chandler 1978). The rare *F. ruficornis* is entirely restricted to *Cossus* sap runs.

The larvae of the Xylotini utilise both sap runs and rotting wood as food resources, with the latter probably the more important. They are most often found under the bark of damp and rotting logs of deciduous trees, with *Xylota sylvarum* associated more with *Quercus* and *Fagus* and the more catholic *X. segnis* has been found in stumps and rot-holes, in yew (*Taxus*) and in silage; both these species also occur in sawdust (Speight *et al.* 1975, Stubbs and Chandler 1978). Both the *Xylotomima* species are associated with *Fagus* (Stubbs and Chandler 1978).

Criorhina and *Myathropa* larvae are confined to rot-holes and not utilise the sap runs. *Myathropa* has the rat-tailed larva characteristic of the Eristalini: however, unlike the other members of this tribe it feeds entirely within rotting wood. They are found in a range of wood detritus sites but especially in *Fagus* and *Quercus*, in wet rot-holes, under damp bark and in other small, woodland bodies of water, such as in the leaf filled water pockets found amongst the surface roots of large deciduous trees (Coe 1953, Speight *et al.* 1975, Stubbs and Chandler 1978).

With the exception of *Rhingia campestris*, all of the decomposers of the soft organic material, which is usually of animal origin, belong to the tribe Eristalini, which have the characteristic "rat-tailed" larvae with their long, extensible breathing siphons. This is the second largest trophic category after the predators and accounts for 16% of the total catch. *Helophilus pendulus* is the most abundant hoverfly within this category, accounting for 44% of the total. Its larvae are aquatic and usually found in foul or stagnant water; it has also been seen laying its eggs around the rim of a bucket of liquid manure (Coe 1953). *Eristalis* species also have aquatic larvae which crawl along the bottom of pools using the ventral prolegs. They are found in a wide range of habitats, from deep water to piles of sodden vegetables and farmyard manure heaps (Oldroyd 1964). When fully grown, the larvae leave the water to find a drier location, in earth or mould, in which to pupate (Colyer and Hammond 1968).

Neoascia podagrica and *Syritta pipiens* both have short-tailed larvae. *Neoascia* adults are rarely found far from water and the larvae also appear to be aquatic (Speight *et al.* 1975). *Syritta pipiens* is a particularly anthropogenic species, often found in back-garden compost heaps as well as in various animal manures and other rotting vegetable matter. It is occasionally found in rotting *Narcissus* bulbs, although the larvae are merely scavengers and do not attack healthy bulbs. It is often found together with the larva of *Eumerus* in these bulbs, which do possess the powerful toothed sclerites with which to enter the bulb (Coe 1953).

Rhingia campestris is the second most common of the non-tree decomposers and its larvae live within cowpats. The eggs are laid on grasses, clover and on other low plants overhanging the dung and the larvae hatch out and crawl or drop onto the pat, seeking a crevice in the drying crust through which to enter into the warm, moist interior of the pat (Colyer and Hammond 1968). *Rhingia* accounts for 35% of this trophic group.

Hoverflies of the fifth trophic category have larvae which scavenge the nests of social Hymenoptera. Only four species representative of this group have been caught at Bernwood and none of them are common: together they account for only 0.5% of the total catch. *Microdon eggeri* has larvae that scavenge the nests of ants (*Lasius* spp. and *Formica* spp.), feeding principally on pellets dropped by the ants. The larvae are unlike any other syrphid larvae, being small, flattened underneath and without visible segments - they were first described as molluscs (Wheeler 1908). If the larvae turn over on their backs, they are attacked by the ants as unfamiliar objects but although a laying female will be driven away by the ants, they do not destroy the eggs (Oldroyd 1964, Speight *et al.* 1975). Adult *Microdon* too are unusual and do not show typical syrphid behaviour. They neither hover nor visit flowers, but spend their lives close to the ant colonies from which they emerged (Duffield 1981).

Volucella larvae live, according to species, in the nests of bees and wasps. The female fly enters the nest unharmed to lay her eggs on the papery nest envelope and on hatching, the larvae fall into the nest cavity, where they wander about unchecked. In addition to eating dead Hymenoptera they also stimulate their host larvae to produce excretion, which they feed upon. Some larvae remain in the comb and migrate to the cells, feeding on faecal and salivary excretions extruded from mature aculeate larvae; they are also known to be partly predatory. *Volucella bombylans* larvae live in the nests of *Bombus* species bees and in *Vespula vulgaris* and *V. germanica* whereas *Volucella pellucens* only inhabits the nests of the wasps *V. vulgaris*, *V. rufa* and *V. germanica* (Colyer and Hammond 1968, Speight *et al.* 1975, Stubbs and Chandler 1978).

These five trophic categories contain all the British hoverflies, although placement of some of the species has to be done by inference from descriptions and from the known habits of other species within the same genus. Certain genera, for example those within the tribe Pipizini, still retain the secrets of their life histories and it is surprising how many of the commoner Syrphinae are covered only by patchy records. However most of this uncertainty lies within the realm of each of the trophic categories and not between them, as does most of the opportunistic feeding and the categories thus constitute a useful framework into which the vast majority of the Bernwood hoverflies can be placed with confidence.

10.2 Trophic Categories of the Overall Catches from Five Sites

The combined records of all syrphids caught at each site over the three years are broken down into the five trophic categories and presented in Table 10.2 and Fig. 10.1. The greatest diversity of larval lifestyles is represented in the adult syrphids of S4, where all five trophic categories are regularly encountered. The poorest site is S5 where both the primary consumers and the hymenopteran commensals are absent and the catch is strongly dominated by the predators. The trophic diversity of the sites follows the same pattern of site richness as species diversity and abundance.

The hoverflies from S1 and S2 share a common pattern of trophic structure. The predators account for 76% of each catch, with the filth-inhabitors the next-largest category contributing13% of the catch, with slightly more

TABLE 10.2

OVERALL NUMBER OF INDIVIDUALS AND SPECIES OF HOVERFLIES IN EACH TROPHIC CATEGORY AT EACH OF THE FIVE SITES, BERNWOOD FOREST

	TROPHIC CATEGORIES														
	1			2			3			4			5		
Site	S	N	%	S	N	%	S	N	%	S	N	%	S	N	%
S1	10	36	0.85	47	3296	77.86	10	408	9.64	7	476	11.24	3	17	0.40
S2	13	134	2.44	51	4125	74.99	11	369	6.71	8	844	15.34	4	29	0.53
S3	7	16	0.65	39	2211	89.66	5	85	3.45	4	155	6.20	1	1	0.04
S4	15	223	3.49	62	4143	64.80	7	328	5.13	12	1634	25.54	4	68	1.05
S5	-	-	-	30	1436	87.59	5	76	4.71	3	126	7.70	-	-	-
		409			15209			1266			3235				

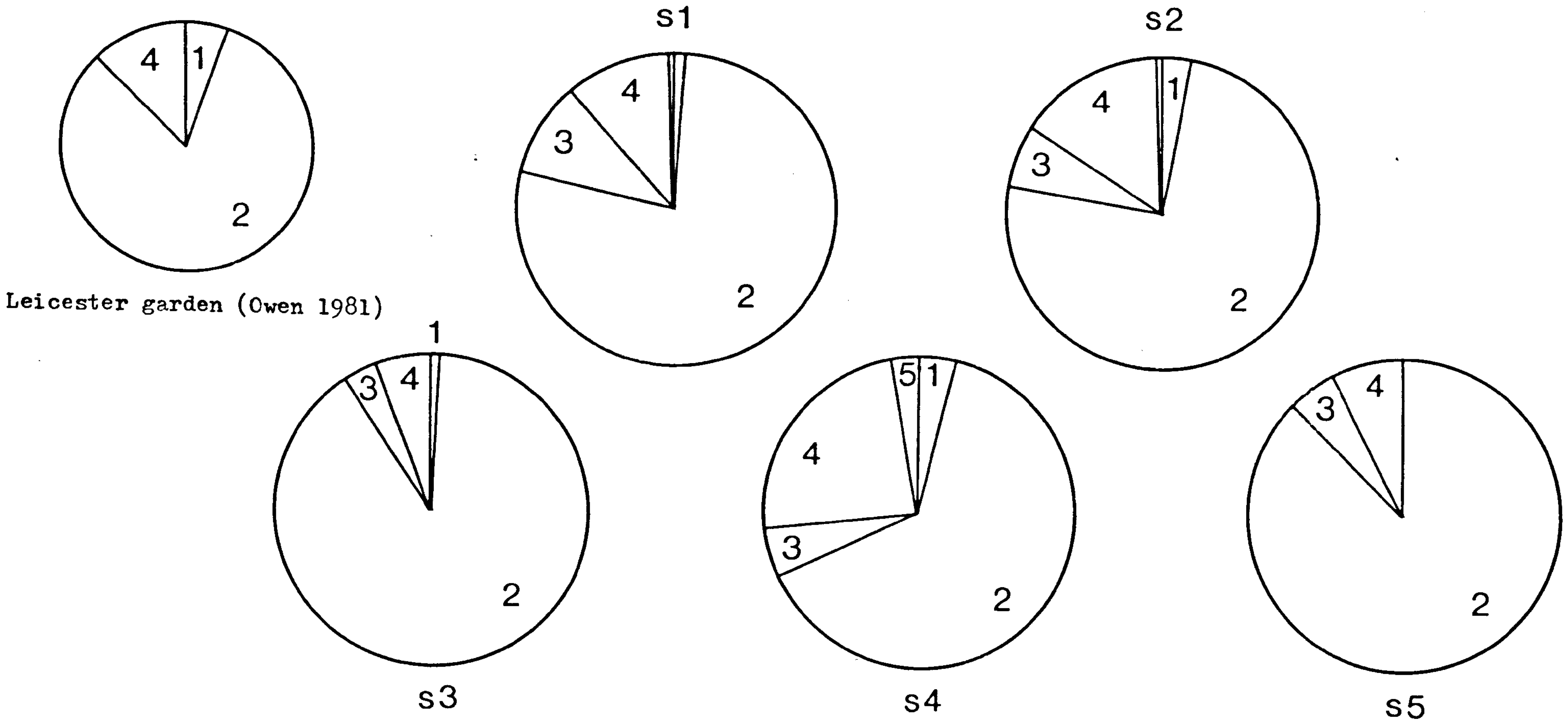


FIG. 10.1 OVERALL RELATIVE ABUNDANCE OF HOVERFLIES IN THE FIVE TROPHIC CATEGORIES FROM THE FIVE SITES, BERNWOOD FOREST AND A LEICESTER GARDEN

at S2 than at S1. This is balanced by the wood decomposers which are more common at S1 than at other sites and account for almost 10% of the catch there, compared with less than 7% at S2. Primary consumers are more common at S2 than at S1, but nevertheless they only account for less than 3% of the total catch from the former site. The hymenopteran commensals contribute only 0.5% of the individuals in the overall catches at each site but they were captured in all three years and are thus a regular feature of these sites.

The S3 and S5 syrphid collections also share a similar trophic composition. Only three of the five trophic categories are properly represented and the predatory syrphids account for nearly 90% of the catches from both sites. The filth-inhabitors contribute 7% to each site's community with the wood decomposers adding a further 4%. Neither the primary consumers nor the hymenopteran commensals have been caught from S5 and only one individual from the latter category has been captured from S3, where the primary consumers however make a regular if minor contribution of 0.6% to the samples from this site, with 16 individuals from 7 species captured.

The S4 syrphid collection shows the least domination by the predators, which account for 65% of the total catch and are represented by 62 species, 11 more than at S2, which is the next-richest site. The filth-inhabitors are relatively almost twice as common at this site than elsewhere, accounting for 25% of the whole sample and S4 is also the best site for the primary consumers, with

15 species captured which contribute 3.5% to the sample from this site. The hymenopteran commensals contribute 1% to the total syrphid catch and thus are still rare, although more were caught at S4 than at all the other sites put together. Only the wood decomposers are better represented elsewhere than at S4, due to the association of these species with old deciduous woodland.

10.3 Trophic Categories at the Five Sites 1980 - 1982

The data from each of the three years' samples for the number of species, individuals and relative abundance of syrphids in each trophic group from each site are given in Table 10.3 and the relative abundances in Fig. 10.2. The two deciduous sites follow a similar sequence of changes over the three years as do S3 and S4 whilst S5's samples follow a different pattern from either of these four sites.

The predatory syrphids at S1 and S2 are relatively less abundant in 1981 than in either of the other two years. This is more pronounced in the S1 collection, where the 1982 catch does not return to the same level of dominance as in 1980, unlike the 1982 S2 sample. This decline in dominance of the predators is balanced by a relative increase in the filth-inhabitors at both sites and by the wood decomposers at S1 in 1981 compared with the other two years. The decline in the relative abundance of the predators at S1 in 1981 is caused by an almost three-fold decline in their actual numbers, with a restoration to their 1980 abundance in 1982, when the filth-

TABLE 10.3

THE NUMBER OF SPECIES AND INDIVIDUALS OF ADULT HOVERFLIES REPRESENTING THE FIVE LARVAL TROPHIC CATEGORIES FROM THE FIVE SITES, BERNWOOD FOREST, 1980 - 1982

		TROPHIC CATEGORIES														
Site	Year	1			2			3			4			5		
		S	N	%	S	N	%	S	N	%	S	N	%	S	N	%
S1	1980	6	13	0.81	39	1369	85.46	8	98	6.12	5	115	7.18	2	7	0.44
	1981	3	4	0.56	29	470	66.10	8	109	15.33	5	125	17.58	2	3	0.42
	1982	8	19	1.00	36	1457	75.88	9	201	10.47	5	236	12.29	2	7	0.36
S2	1980	11	37	2.67	41	1065	77.01	9	110	7.66	4	162	12.00	2	9	0.65
	1981	7	44	2.81	41	1086	69.44	8	95	5.88	6	335	21.61	2	4	0.26
	1982	7	53	2.07	39	1974	77.29	11	164	6.42	6	347	13.59	3	16	0.63
S3	1980	3	3	0.31	29	934	96.30	3	8	0.82	2	25	2.75	-	-	-
	1981	2	5	0.77	29	589	91.01	4	14	2.17	4	41	6.05	-	-	-
	1982	5	8	0.94	28	688	81.04	5	63	7.42	4	89	10.48	1	1	0.12
S4	1980	9	52	2.52	52	1485	71.91	7	101	4.89	8	409	19.81	3	18	0.87
	1981	9	74	4.44	47	1083	65.10	6	86	5.16	8	409	24.50	2	14	0.78
	1982	9	97	3.64	46	1575	58.99	7	141	5.29	8	816	30.62	4	36	1.35
S5	1980	-	-	-	24	405	82.48	4	24	4.89	2	62	12.63	-	-	-
	1981	-	-	-	18	450	87.04	5	27	5.22	2	40	7.74	-	-	-
	1982	-	-	-	18	579	92.04	5	25	4.14	2	24	3.82	-	-	-

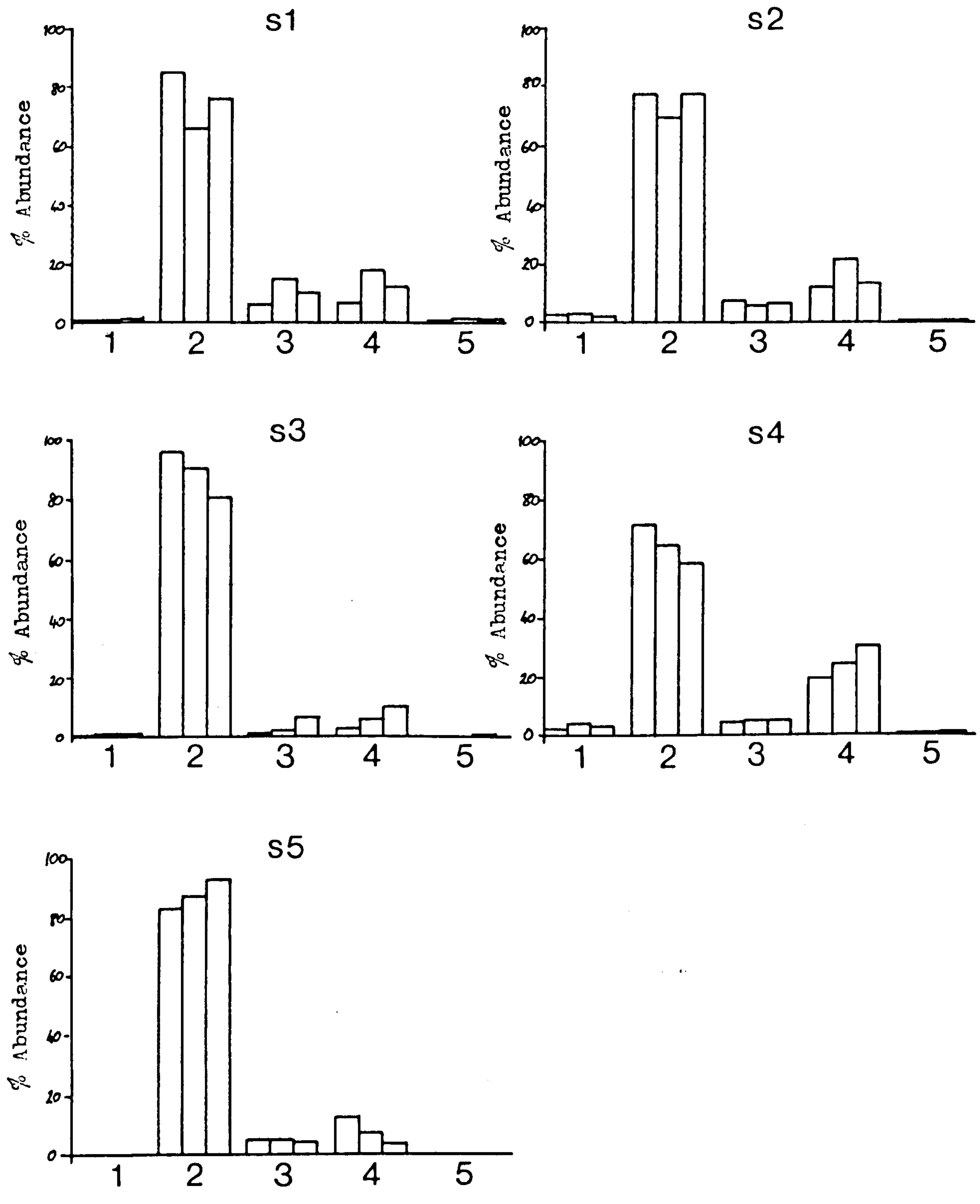


FIG. 10.2 RELATIVE ABUNDANCE OF HOVERFLIES IN THE FIVE TROPHIC CATEGORIES: A COMPARISON OF THE THREE YEARS AT FIVE SITES, BERNWOOD FOREST

inhabitors increase their abundance by two-fold relative to the previous two years. The number of species of both primary consumers and predatory hoverflies (at S1) is lower in the 1981 sample than in the previous year, with a recovery of species richness in 1982; these two trophic groups maintain their species through all three years at S2, as do the remaining trophic categories at both these sites. This is in contrast with S2 where a similar number of predators were caught in 1980 and in 1981, before a doubling of numbers in 1982; the filth-inhabitors doubled their numbers in 1981 compared with the previous year and maintained this high level of abundance in 1982, when the wood decomposers were also more numerous.

At both S3 and S4 the predatory hoverflies decline in relative abundance in each successive year accompanied by an increase in the relative abundance of the wood decomposers at S3 and the filth-inhabitors at both sites in all years. There are fewer predators in the 1981 samples compared with those of the previous year but 1982 saw a recovery in the actual abundance, to slightly above their former level at S4 but rather fewer at S3. Both the wood decomposers and the filth-inhabitors increased in abundance over the three years at S3, although the former category species were rare in the first two years. Exactly the same number of filth-inhabitors were caught at S4 in 1980 and in 1981 with twice as many caught in the final year, whereas the number of wood decomposers in the trap oscillates between 86 and 141, with no apparent trend. The primary consumers show a gradual increase in numbers over the three years at S4 and more hymenopteran commensals were caught in 1982 than in the previous years at this site. The number of species in each trophic category remains steady at both sites over the three years although 5 more species of predatory syrphid were caught in 1980 at S4 than in 1981 or 1982.

In contrast with the other four sites the predatory hoverflies at S5 increase in relative abundance over the three years, balanced by a decline in the relative abundance of the filth-inhabitors. The wood decomposers maintain steady relative abundance over the three years. These relative abundances are a reflection of the true numbers of syrphids at S5 and do not mask more complex changes in the abundance of hoverflies as they do at the other sites. Four more predatory species were caught in 1980 than in either 1981 or 1982 but otherwise the number of species captured in each of the trophic categories remains stable over the three years.

10.4 Trophic Differences Between the Early and Late Sampling Seasons

10.4a Overall Numbers, 1980 - 1982

The number of hoverflies caught over the entire forest in each of the two sampling seasons in each year is given in Table 10.4. The early season is more diverse trophically than the late one when only the predatory syrphids are relatively more common than in the early season; this is to be expected from

TABLE 10.4

THE NUMBER OF HOVERFLIES IN EACH TROPHIC GROUP IN EACH SEASON AT BERNWOOD FORES, 1980 - 1982

EARLY	1980		67	2634	265	231	16	
	1981		86	1510	232	408	6	
	1982		111	2172	360	852	26	
			264	6316	857	1491	48	
		%	2.94	70.36	9.55	16.61	0.53	N =8976
LATE	1980		38	2624	76	542	18	
	1981		41	2168	99	542	15	
	1982		66	4101	234	660	34	
			145	8893	409	1744	67	
		%	0.13	78.99	3.63	15.49	0.59	N =11,258
ANNUAL	1980		105	5258	341	773	34	
	1981		127	3678	331	950	21	
	1982		177	6273	594	1512	60	
			409	15209	1266	3235	115	
		%	2.02	75.16	6.26	15.99	0.57	N =20,234

the higher species diversity in the early seasons.

The primary consumers are more common in the early season than in the late one in all three years and account for 3% of all the early season hoverflies. The only common species is *Cheilosia paganus* which has a peak of abundance in each of the two seasons although it is generally more common in the early season. The early season contains the majority of the rare *Cheilosia* species which account for most of the diversity of this trophic group, which accounts for only 0.1% of the late season catch.

The predatory syrphids are more abundant in the late season catches of 1981, 1982 and the overall total catch, with the same number being caught in each of the two seasons in 1980. More species are present in the early season catches of all the years. *Dasysyrphus venustus* and *Melangyna lasiophthalma* are common predatory hoverflies caught only in the early season, and this trophic category contains the species capable of spectacular population outbursts, most notably *Episyrphus balteatus*, *Syrphus ribesii* and *Meliscaeva cinctella*. Overall the predators account for 70% of the early season samples and almost 80% of the late ones.

More than twice as many wood-decomposing hoverflies have been captured in the early season than in the late one, but the individual years show a progressive decline in this seasonal preference with 1.5 times as many syrphids of this trophic group caught in the early season than in the late one in 1982, compared with almost 3.5 times as many in the early season of 1980. *Ferdinandea cuprea and the two Xylotomima* species are present in the early season whereas *Xylota* spp. are characteristic of the late sampling period and thus each season has its distinct fauna of wood-associated syrphids, with the later season recording slightly fewer species.

The filth-inhabiting hoverflies are more common in the late season than in the early one in all years save for 1982, when the wet summer provided more suitable conditions for the larvae earlier on in the year than normal. Only three species are consistently abundant in the Bernwood collections. *Helophilus pendulus* has early and late season population peaks with the second peak the larger, as does *Eristalis pertinax*. Both these species appeared earlier in 1982 than in previous years, with *H. pendulus* becoming abundant in late June and early July and maintaining numbers until late September. *Rhingia campestris* has a peak in May and in the second half of August through until late September, considerably later than the main late season peak. The filth-inhabitors contribute around 16% of the total catch in each season.

The small number of Hymenopteran commensals captured account for 0.5% of each season's catch, with slightly fewer caught in the early season. They are absent from the early season catches in three cases where they are present in the late season although the low overall numbers preclude a clear seasonal preference.

10.4b Seasonal Trophic Changes at the Five Sites, 1980 - 1982

The seasonal trophic variations at each of the five sites over the three years are given in Tables 10.5 and 10.6 and in Figs. 10.3, 10.4 and 10.5. The two deciduous sites, together with S5, follow a similar pattern of trophic diversity and S3 and S4 once again resemble each other in their trophic trends in the first two years, but not in 1982.

The predatory hoverflies are relatively more common in the late season than in the early one at S1, S2 and S3 in all three years, although the degree of disparity between the two seasons shows considerable variation over the years. This is balanced by the wood decomposers and the filth-inhabitors being relatively more abundant early on in most cases, the principal exceptions being the latter trophic category at S2 and both 1980 and 1981, when a similar proportion in the catch in both seasons is attributable to these syrphids. The low dominance of the predators in the early samples from S1 and S2 in 1982 is caused by the increased abundance of filth-inhabiting and wood-associated syrphids and at S1 in 1981 by a poor catch of predators. The 1981 early season at S5 also showed a dramatic reduction in the

TABLE 10.5

THE NUMBER OF SPECIES AND INDIVIDUALS OF HOVERFLIES REPRESENTING THE FIVE TROPHIC CATEGORIES CAUGHT AT EACH OF THE FIVE SITES IN THE EARLY SEASON, 1 APRIL - 1 JULY, 1980 - 1982

		TROPHIC CATEGORIES														
SITE	YEAR	1			2			3			4			5		
		S	N	%	S	N	%	S	N	%	S	N	%	S	N	%
S1	1980	5	9	1.56	36	440	76.39	6	79	13.71	4	47	8.16	1	1	0.17
	1981	2	3	1.00	17	133	44.48	6	80	26.76	4	83	27.76	-	-	-
	1982	8	18	1.96	34	558	60.85	8	150	16.36	5	190	20.72	1	1	0.11
S2	1980	10	23	3.33	38	500	72.46	6	84	12.17	3	80	11.59	1	3	0.43
	1981	7	35	4.64	37	474	62.78	7	80	10.60	5	166	21.97	-	-	-
	1982	7	41	5.05	35	452	55.66	9	111	13.67	5	201	24.75	2	7	0.86
S3	1980	1	3	0.37	29	797	97.19	2	7	0.85	1	13	1.58	-	-	-
	1981	2	5	1.24	23	370	92.04	2	4	0.99	4	23	5.72	-	-	-
	1982	4	6	1.07	24	456	81.57	4	37	6.62	4	60	10.73	-	-	-
S4	1980	9	32	3.54	46	727	80.33	6	75	8.29	6	59	6.52	3	12	1.33
	1981	6	43	6.65	34	436	67.39	4	57	8.81	5	105	16.23	1	6	0.93
	1982	6	46	4.22	42	588	53.89	7	47	4.31	7	392	35.93	3	18	1.65
S5	1980	-	-	-	21	170	76.58	2	20	9.01	1	32	14.41	-	-	-
	1981	-	-	-	14	97	69.78	2	11	7.91	1	31	22.30	-	-	-
	1982	-	-	-	14	118	83.1	4	15	10.56	2	9	6.34	-	-	-

TABLE 10.6

THE NUMBER OF SPECIES AND INDIVIDUALS OF HOVERFLIES REPRESENTING THE FIVE TROPHIC CATEGORIES CAUGHT AT EACH OF THE FIVE SITES IN THE LATE SEASON, 1 JULY - 30 SEPTEMBER, 1980 - 1982

		TROPHIC CATEGORIES														
SITE	YEAR	1			2			3			4			5		
		S	N	%	S	N	%	S	N	%	S	N	%	S	N	%
S1	1980	3	4	0.39	23	929	90.55	4	19	1.85	5	68	6.63	2	6	0.58
	1981	1	1	0.24	20	337	81.80	6	29	7.04	5	42	10.19	2	3	0.73
	1982	1	1	0.01	14	899	89.63	4	51	5.08	3	46	4.59	1	6	0.60
S2	1980	4	14	2.02	20	565	81.53	6	26	3.75	3	82	11.83	1	6	0.87
	1981	1	9	1.11	27	612	75.65	5	15	1.85	6	169	20.89	2	4	0.49
	1982	2	12	0.69	19	1522	87.37	8	53	3.04	5	146	8.38	3	9	0.52
S3	1980	-	-	-	10	137	91.33	1	1	0.67	1	12	8.00	-	-	-
	1981	-	-	-	16	219	88.66	4	10	4.05	3	18	7.29	-	-	-
	1982	2	2	0.69	13	232	80.00	4	26	8.96	2	29	10.00	1	1	0.34
S4	1980	3	20	1.72	23	758	65.34	4	26	2.24	8	350	30.17	2	6	0.52
	1981	5	31	3.04	29	647	63.49	4	29	2.85	8	304	29.83	1	8	0.78
	1982	6	51	3.24	26	987	62.71	4	94	5.97	7	424	26.94	3	18	1.14
S5	1980	-	-	-	14	235	87.36	2	4	1.49	2	30	11.15	-	-	-
	1981	-	-	-	12	353	93.39	4	16	4.23	2	9	2.38	-	-	-
	1982	-	-	-	11	461	94.86	3	10	2.06	2	15	3.08	-	-	-

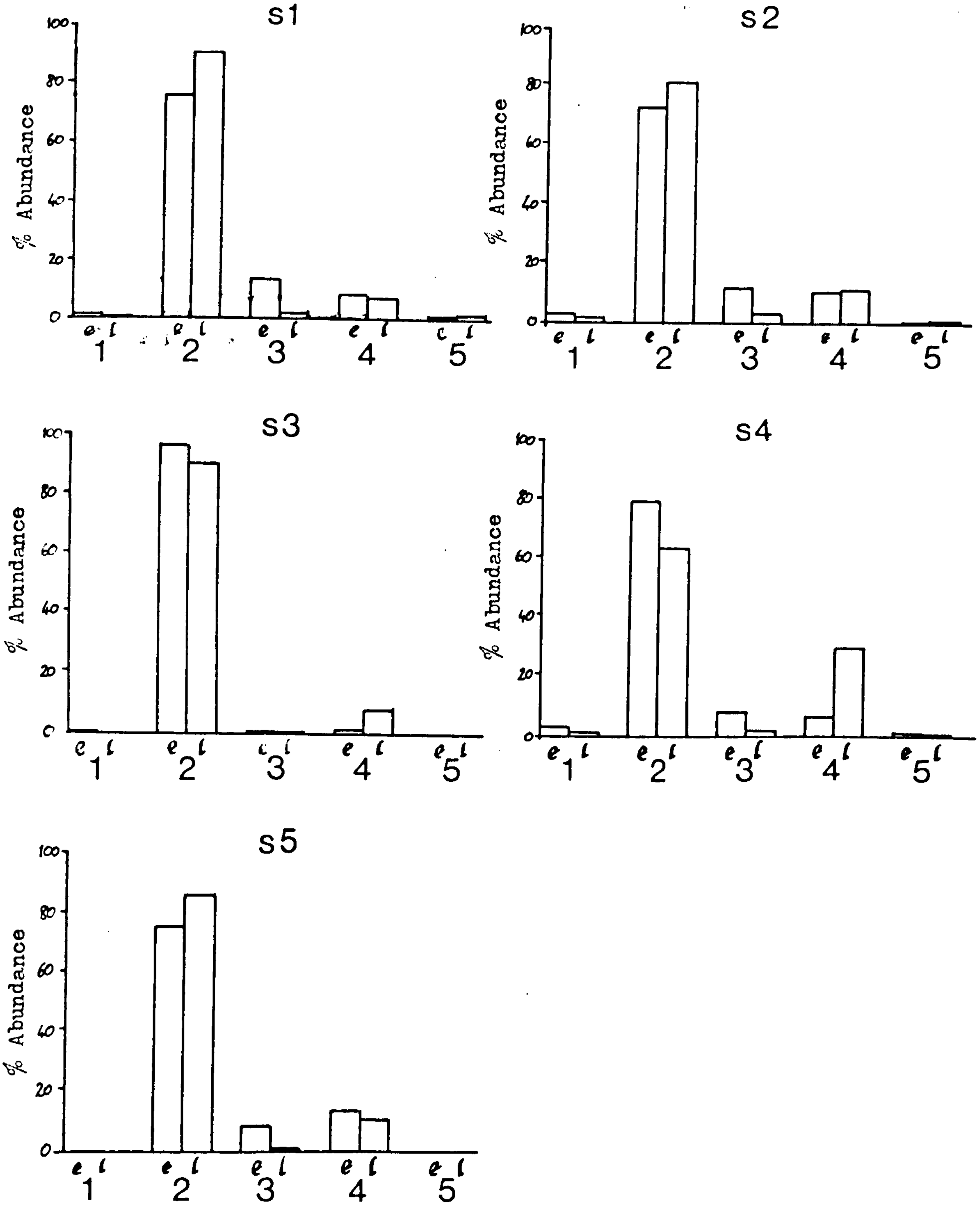


FIG. 10.3 RELATIVE ABUNDANCE OF HOVERFLIES IN THE FIVE TROPHIC CATEGORIES: COMPARISON OF THE EARLY AND LATE SEASONS, 1980

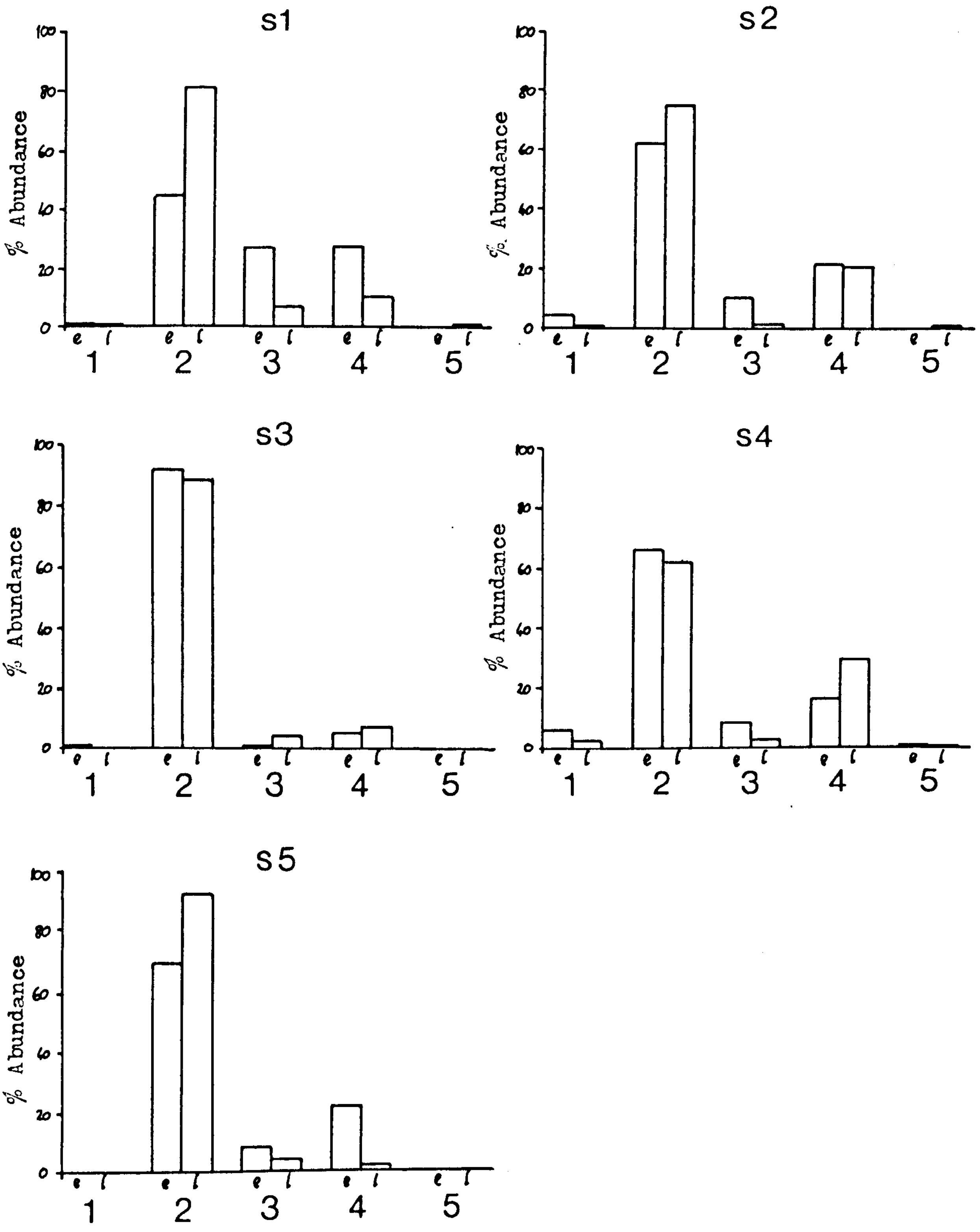


FIG. 10.4 RELATIVE ABUNDANCE OF HOVERFLIES IN THE FIVE TROPHIC CATEGORIES: COMPARISON OF THE EARLY AND LATE SEASONS, 1981

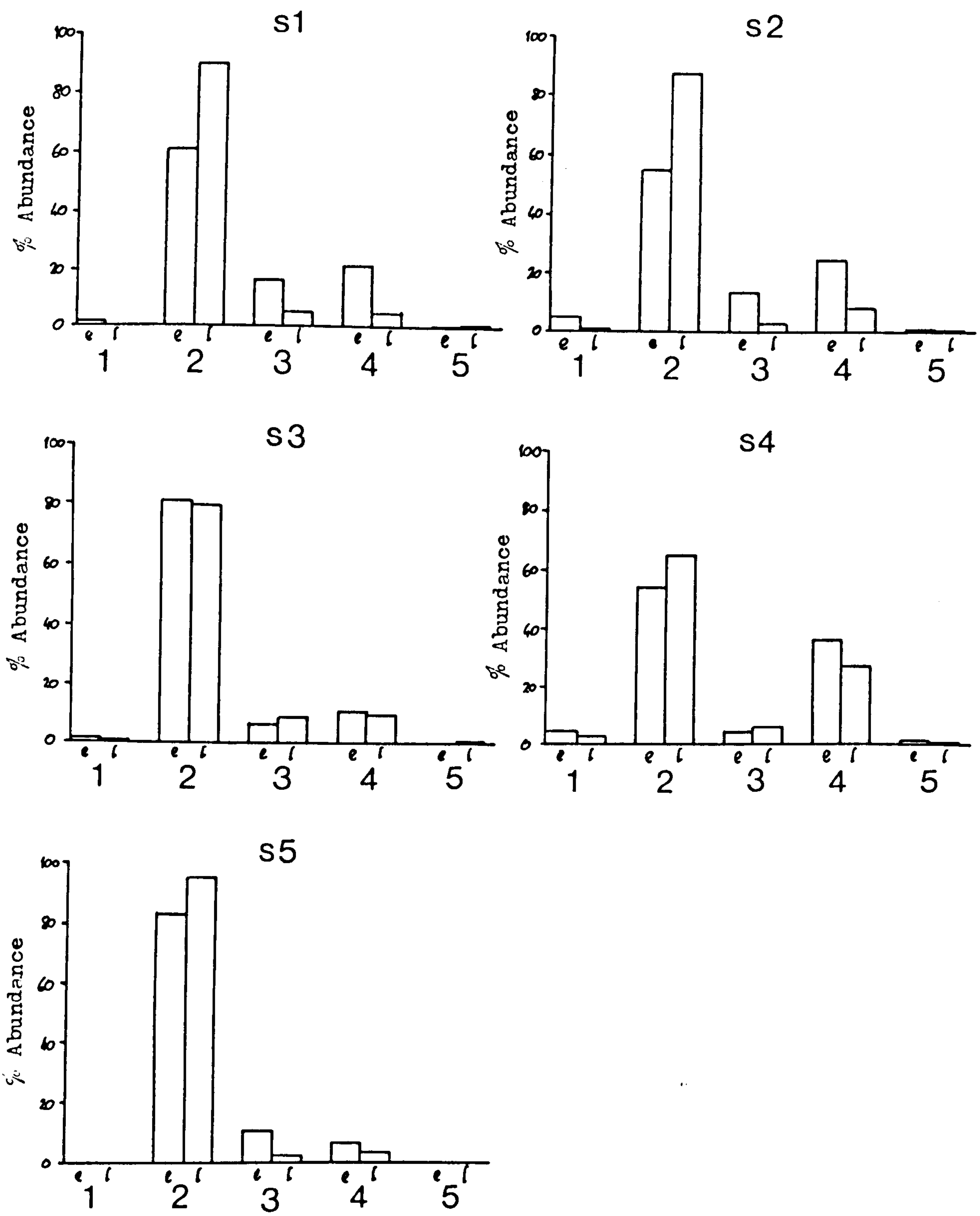


FIG. 10.5 RELATIVE ABUNDANCE OF HOVERFLIES IN THE FIVE TROPHIC CATEGORIES: COMPARISON OF THE EARLY AND LATE SEASONS, 1982

numbers of predators, whereas in the late season they are more numerous than in 1980; this is followed in 1982 with a stabilization of the predators in the early period but a decline in the abundance of filth-inhabiting hoverflies.

S3 and S4 have a lower relative abundance of predators in the late season than in the early one in 1980 and 1981, although this is less pronounced at S3 than at S4. The high domination of the predators at S3 is a consequence of the scarcity of any syrphids other than predators, particularly in the first two years. In 1982 the S3 predators account for 80% of the catch in both seasons and both the wood-associated hoverflies and the filth-inhabitors are substantially more abundant than in the previous years, accounting for similar proportions of the catch in both seasons.

The decline in the relative importance of the predatory syrphids at S4 in the late sampling season compared with the early one in 1980 and 1981 is due to the large increase in both the actual and relative abundance of the filth-inhabitors later on in the year. The wood decomposers are also less numerous and less important in the second sampling period than in the first. A different pattern emerges from the 1982 catches with the predators being more abundant in the late season than in the early one and with their overall dominance lower than in the previous years. The filth-inhabitors occur in similar numbers in both sampling seasons which gives them increased importance in the early season compared with 1980 and 1981, when the actual abundances were lower. The wood associated syrphids are more numerous in the late 1982 season than the early one in contrast with the previous years, but they nevertheless contribute only 6% to the total catch in that season.

10.5 Trophic Analysis: Comment

All five of the trophic categories in which syrphid larvae can be placed are represented in the Malaise trap samples of adult hoverflies. The predatory species account for 75% of the catch and for 62% of the species richness of the whole catch and thus form by far the largest trophic group, but the domination of the predators at Bernwood is not as great as in other situations. Malaise trapping in a Leicester garden over eight years gave a catch of which 82.7% of the individuals were predators, although their contribution to the species richness was exactly the same as for the Bernwood sample (Owen 1981). The hoverflies feeding on decaying organic matter, those associated with trees and wood and the hymenopteran commensals are all relatively more abundant in the Bernwood fauna than that of the garden, although more species of filth-inhabiting syrphids have been caught in the garden. Although the garden primary consumers account for a greater proportion of the total catch than they do in the woodland samples the latter are represented by over twice as many species, despite being four times less abundant. The wood associated species in particular are much more common at Bernwood than in the garden, as would be expected from the available habitat, and they demonstrate this habitat preference within the Forest, being more abundant at the two deciduous sites than at the conifer-dominated stands. Bernwood is thus more trophically diverse than the garden habitat, which must in part stem from the larger sampling area and from the diversity of habitats. The samples from S1, S2 and S4 individually all show greater trophic diversity than the garden fauna (Fig. 10.1).

It is the predatory species that give the overall flavour to the hoverfly samples and it is these species that are capable of sudden and dramatic population outbreaks. *Episyrphus balteatus*, *Meliscaeva cinctella* and *Syrphus ribesii* all occurred in 'super abundance' at some of the sites in one or more years and these three species are all general aphid predators, rather than having more specific prey requirements such as *Melangyna lasiophthalma*, which is only associated with arboreal aphids. *Melanostoma* and *Platycheirus* species also occur in large numbers in the Bernwood samples and these too are genera without the constrictions of a specific larval food source: the more general predators appear to be more numerous than the specialized ones. The low overall abundances of the 1981 season reflect a poor year for predatory species in which no species managed to stage anything approaching a population outbreak, whether from local or migratory origins. *Episyrphus balteatus* and *Meliscaeva cinctella* dominated the large catches obtained in 1982, accounting for 25.5% and 17.7% of the whole catch respectively in this year.

The three years saw a successive increase in the numbers of hoverflies associated with decaying organic matter. *Helophilus pendulus* is the most common species in this trophic category and ranks third in the 1982 abundance list, with almost eight times as many individuals caught as in the first year of sampling. *Eristalis pertinax* is rather less common than *H. pendulus* but shows the same trend in abundance over the three years whereas *Rhingia campestris*, which is almost as common as *H. pendulus* over the combined three years, declines in abundance over the three years, although not so dramatically as the increase in *Helophilus*. *Ferdinandea cuprea*, which is by far the most common of the wood-associated species, maintains steady numbers over the three years, although *Criorhina berberina*, *Xylota segnis* and *X. sylvarum* are much more common in 1982 than in either of the previous two years.

The populations of individual species of hoverflies behave in an unstable manner when comparing annual totals for yearly catches but even this masks violent population explosions that can occur in a single week. The trophic categories provide a measure of stability in the organisation of the hoverfly community, although this must be due in part to the lower resolution of taxonomy. Thus Bahr (1982) proposes that classical taxonomy may actually hinder the development of ecosystem theory through an over-reliance upon the species as the basic fundamental unit of the ecosystem and he puts forward a functional system of classification defined by the trophic categories of the organisms in that ecosystem.

This approach imposes considerable stability on the Bernwood hoverfly samples. Each site is recognisable by its overall trophic components (Figs. 10.1 and 10.2) with the possible exception of the two deciduous sites, which share a similar trophic structure. This site individuality is maintained in the comparison of the early and late samples, with similar changes occurring in each year at a particular site. These patterns of the relative abundance of the trophic groups again produce consistent site groupings, with S1 and S2 showing similar changes as S5 and S3 and S4 showing consistent trends in at least the first two sampling seasons.

The stability of the trophic structure of the hoverfly communities over the three years implies stability in the flow of energy through these woodland syrphid taxocenes. The individual species is relatively unimportant because the overall potential for each species is only rarely fulfilled; it is the assemblage of the community that is ecologically important, with many species being able to fulfill the role of 'key' species in the assemblage. The instability of the numbers of many individual syrphid species is thus seen to nevertheless form a trophically stable community, but this still leaves unresolved the causes of vast population fluctuations among a group of ecologically apparently similar hoverfly species.

CHAPTER ELEVEN

DISCUSSION

11.1 Introduction

The project has been successful in that the Malaise traps have proved to be efficient tools for sampling the aerial insect fauna of the five sites. The traps obtained consistent samples from each site within the bounds of the considerable annual fluctuations to which insect populations are subject. Each site has a characteristic fauna, which not only validates the sampling technique but also confirms that the selection of sites was representative of different ecological systems within the Forest.

The choice of the Syrphidae as the representative family of the insect community in the Malaise trap fauna has been a good one. Over twenty thousand syrphids were captured at the five sites over the three years, including several rare species of national interest. The family is distinctive and easy to recognize, which allows efficient and reliable extraction of specimens from the weekly trap samples. Identification to the species level is taxonomically feasible and allows a beginner to understand the family within a few months. Only three of the genera encountered at Bernwood evaded identification to the species level, it not currently being possible to identify the females of *Neocnemodon*, *Paragus* and *Sphaerophoria*;

none of these genera is common at Bernwood and together they account for only 161 individuals in the total catch. The Syrphidae are sufficiently well-known to allow ecological interpretation of the samples but despite this, and their abundance, little is known of their community organization in the woodland ecosystem.

11.2 Seasonality

The bimodal distribution of the Bernwood hoverflies appears to be unique to woodland syrphid communities. J. Owen's Malaise trap records of garden hoverflies from Leicester show a single peak of abundance in August (Owen J. 1981) and Bombosch (1966) records single-peaked distributions in a variety of situations, none of them true woodland. Banks' (1959) Rothamsted collections are strongly concentrated in August whilst collections of the Hymenoptera-mimic syrphids from Hafren Forest in mid-Wales show bimodal seasonality (Entwistle 1979).

Why should the forest hoverflies be conspicuously bimodal in abundance while those in other situations are apparently largely unimodal? Virtually all those syrphids with strong bimodality are the aphidophagous species; the Eristalini, and presumably the other larger filth-inhabiting syrphids such as *Rhingia*, are most probably univoltine and their presence early on in the year is due to over-wintering adults. The most simple explanation of the bimodality of the Syrphinae must therefore rest with the source of larval food: the aphids. The bimodality of good-quality aphid food sources within the forest has already been introduced as a possible factor governing the seasonality of hoverfly populations and I believe it to be the major contributing factor to the bimodality of these woodland syrphids. Gardens, fields and roadside edges are recent additions to the landscape in comparison with woodland habitats and it is to changes in the quality of food sources within the latter that woodland syrphids are synchronized. The lack of the early abundance peak outside forest ecosystems is probably further enhanced by the disturbance of overwintering sites through cultural practices: apparently the Syrphinae overwinter as larvae or pupae and many do so in the topsoil, disturbance of which could lead to high mortality prior to emergence.

The May peak is richer than the late period of syrphid abundance, containing in most cases more species but fewer individuals at all sites except S3. The low catches at this site after the end of May are probably due to the shading of the trap by the clump of *Sorbus torminalis*, which came into full leaf by the week ending 20 May each year. The higher abundances at the other sites in the later season must be due largely to generally better weather conditions later in the year, with more sunshine and higher temperatures leading to greater insect activity.

The greater species richness of the early season is attributable largely to more aphidophagous species in that period. The primary consumers are also strongly biassed towards the early season at the three sites where they are common. The wood-associated hoverflies are represented by different species in each of the two sampling seasons, with slightly more species, and many more individuals, present in the early season. But the main difference in species richness is attributable to the aphidophagous syrphids, with more rare species in the early season. This probably reflects a better and more reliable larval food source later in the season, because the early-season adults are imagines of late-season larvae that have overwintered locally. Later early-peak catches also contain adults reared from both the early and the late flushes of aphid abundance, further enhancing the richness of these samples.

The low species richness and abundance at most sites in the early season of 1981 compared with the other two early seasons coincides with much heavier rainfall during May 1981 than in the other two years. The early season samples from S2 are similar in abundance and species richness in all three years but this can be explained by the vegetation structure at S2. Because the herb layers are more complex at this site in comparison with the others, more sites are provided within the vertical trapping zone for sheltering insects, thus increasing flight activity around the trap of insects seeking, and moving from, shelter during periods of rain.

The higher diversity of the early season Malaise trap samples might also be influenced by the behaviour of the insects. Spring insects in general fly closer to the ground than they do later in the year, taking advantage of the warmer band of air close to the ground (Townes 1962). This could increase the catches of the Malaise trap, which does not catch insects flying higher than 1.3 m. above the ground: a greater proportion of the aerial fauna will be compressed into the vertical stratum which represents the potential trapping zone in the early season than in the late one, when the warmer weather allows a wider utilization of the vertical component of habitat structure.

11.3 Species Diversity

Studies of ecological diversity are focussed on the most basic problem of the ecology of a particular community: namely, are there any discoverable laws governing the composition and structure of the species assemblage? (Pielou 1975). All species diversity indices measure, in different ways, the amount of each species in the community. Some species diversity indices focus on the more stable species within the community, or on an assumed distribution of individuals amongst the component species, and these indices are the most suited to understanding and investigating why particular communities have a particular species richness. Other indices focus on more variable parts of the species distribution curve, for example the common species, and provide information on the changing species diversity and stability of the communities. Thus Q and α, and the Hill's diversity Numbers, can respectively be used to address these different questions concerning the Bernwood hoverfly communities.

The Hill's diversities demonstrate that the fluctuating species populations of the Bernwood hoverflies do not fit within a community framework of species abundance that remains relatively stable from year to year. The values of Hill's diversity, the number of common and moderately common species in the community, changes markedly at each site and in each year and thus there appear to be no general rules governing the assembly of adult hoverfly communities. Community equitability also fluctuates dramatically between the three years at any given site and there is no simple relation connecting diversity changes with changes in equitability. Because of the unstable nature of the species populations involved, apparent trends in Hill's diversity from only three years' data have no long term ecological significance.

One stable community property does, however, emerge from the Hill's diversity Numbers. Whilst the actual number of common and moderately common species present at a site changes from year to year, the relative abundance of these two categories of species remains stable over the three years at all sites, with one notable exception, at S2 in 1981, when the number of common species, N_2, rose dramatically in relation to the number of moderately common species. The richer communities have relatively more moderately common species than do the poor ones and this can thus be used in defining rich communities: they possess relatively more moderately common species than do poor communities.

In comparison with Hill's diversity, both α and Q give stable estimations of hoverfly diversity at each site over the three years. The intersite variation in calculated diversity is much larger than intrasite fluctuations in diversity between the three years' samples and this clear site separation, with a consistent ranking of the five sites in each year, makes these indices suitable both as site discriminators and as estimators of absolute species diversity at a site. The consistent ordering of the sites by these two diversity indices can be interpreted as an ordering of the sites in terms of ecological quality: quality is, in conservation terms, most often equated with high abundance and species richness and thus defined, species diversity is the most-used criterion used in the selection of nature reserves. The consistent ranking of the sites in terms of their ecological quality also potentially allows the identification of features of the sites which are concomitant with the gradient of diversity across the sites.

Hoverfly species diversity at Bernwood Forest does not appear to be related to the transition of the Forest from deciduous to coniferous woodland. The best of the five sites is dominated by *Picea abies* plantations and the second-best site is in a mixed plantation in which deciduous trees predominate. The deciduous, old coppice site ranks only third in hoverfly richness and abundance, with the old *Pinus* plantation supporting the fewest hoverflies, both in number of species and individuals. The coniferization of the Forest thus has had a mixed influence on the resident syrphid communities: some of the conifer plantations continue to support rich hoverfly assemblages whereas others harbour only few species.

The ordination of the plant abundance data from the five sites by principal components analysis (PCA) results in site groupings which reflect hoverfly abundance and diversity. S1 and S2 are closest to each other, both in terms of their plant and syrphid communities, but they also share similar, if slightly lower, syrphid diversity with S4. This latter site is less polarized by the PCA due to the presence of floral features of both the deciduous and coniferous sites. This greater floral diversity is reflected in the species composition of the hoverflies at S4, although the overall syrphid diversity is not conspicuously greater than at S1 and S2. The floral isolation of S5 is reproduced in the low-diversity and distinct syrphid fauna at this site whereas the low-diversity hoverfly samples from S3 bear a closer resemblance to the richer sites, particularly to S4, as befits the plant abundance ordination.

The principal latent vectors of the PCA identify the plant species which account for the majority of the variation between the sites and these can be implied as indicators of syrphid diversity. S1, S2 and S4 are separated from S3 and S5 by *Quercus robur*, *Lonicera periclymenum* and *Festuca rubra*, although the presence of *Picea abies* displaces S4 slightly away from the group and towards S3. S5 is identified by *Pinus sylvestris* and isolated from the other four sites, whereas S3, although isolated along the second principal component by *Sorbus torminalis*, falls mid-way along the first principal component.

The ordinations of the plant abundance data, rather than simply species presence or absence, provide a broad indication of the abundance and diversity of the hoverflies found at the five sites. Floristically distinct sites can be expected to support characteristic and distinct syrphid faunas. The *Quercus* sites harbour a rich syrphid fauna compared with the *Picea* and *Pinus* sites which are well shaded, but the richest hoverfly communities are found at the sites with both *Quercus* and *Picea* present.

Various measures of habitat diversity have been correlated to the species diversity of animal communities since MacArthur and MacArthur (1961) used foliage height diversity to predict and explain bird species diversity. The relationship between the diversity of habitat and associated fauna has been demonstrated for flatland lizards (Pianka 1966, 1967), insects in general (Murdoch *et al.* 1972, Southwood *et al.* 1979), marine invertebrates (Abele 1973), spiders (Uetz 1975, Hatley and MacMahon 1980) and beetles (Bach 1980). Habitat may not be a rigid, causal template for ecological strategy and species diversity (Southwood 1977) but it clearly exerts influence on the community organization of its associated fauna. How does habitat diversity in Bernwood Forest affect hoverfly species diversity?

The structural characteristics of the five sites were assessed by the distribution of the six vegetation height classes over the 400 m^2 surrounding each of the Malaise traps. Overall Shannon diversity of these height classes neither provides a clear separation of the sites by structural diversity nor gives any association with hoverfly species diversity. S1, S2 and S3 all have identical Shannon structural diversities, but the hoverfly samples from S3 are very much poorer, both in abundance and species richness, than at either of the two deciduous sites. Shannon structural diversity at S4 is slightly lower than at these three sites but S4 supports the richest hoverfly communities, whilst S5 does have both the lowest structural diversity and the poorest syrphid communities. Overall site structural diversity thus does not correlate with hoverfly species diversity.

Nor do the overall relative abundances of the six vegetation height classes bear a relation to hoverfly diversity across the five sites. S1 and S2 share similar distributions of vegetation among the height classes and also similar hoverfly communities, but whilst S3 and S4 are both characterized by half the site area consisting of dense vegetation from forest floor to canopy, the syrphid communities at these two sites are vastly different in species richness and abundance. S5 has both a distinct site structure and a distinct syrphid fauna, in terms both of species composition and abundance.

One component of the vegetation structure does appear to be associated with the distribution of hoverflies at the five sites. The ranking of the sites by decreasing amounts of overhead canopy gives the same ranking of sites as does increasing hoverfly abundance, species richness and diversity with the exception of the 1980 abundance data, which is, however, significantly correlated (Spearman's Rank Correlation, $p = 0.05$). Hoverfly activity is largely dependent upon ambient temperature and although syrphids are able to maintain thoracic temperatures 10°C above the ambient temperature, this is only achieved at great energetic loss to the hoverfly (Heinrich and Pantle 1975). Syrphids are therefore highly heliotropic and tend to avoid shade to maximize flight activity and energetic conservation. The negative correlation between hoverfly abundance and overhead canopy is thus not remarkable but nevertheless is an important factor governing the richness and abundance of syrphid communities.

The summarization of habitat structure into the relative abundance of six vertical height classes gives no account of the spatial arrangement of the habitat structure on the ground. This is an important factor in governing insect distribution and can have a profound effect on the catching efficiency of the Malaise trap. What structural features of the vegetation at the five sites might influence hoverfly abundance and diversity?

Both S1 and S2 have little clear spatial ordering of the vegetation layers and both sites have high-quality syrphid faunas. There are no dense, impenetrable blocks of trees and both sites have an overgrown bramble patch covering about 20% of the area around the trap. The site at S2 borders one of the 'Elton' glades, originally cut in 1956 and which must further enhance the heterogeneity of this site: three more species of *Cheilosia*, whose larvae are grass-feeders, have been caught at S2 and the genus is almost four times as common at this site than at S1. The presence of coniferous trees further increases the heterogeneity at S2 and must be responsible for the capture of *Megasyrphus annulipes*, a species of the Caledonian pine forests. The overall vegetation structure of these two sites can be described as diffuse, with no prominent features to channel syrphid movements, although both Malaise traps were positioned to catch insects moving between a clearing and the surrounding trees.

S3 and S4 both have similar relative abundances of the height classes of vegetation structure, but have very different syrphid communities, with over twice as many hoverflies, and almost twice as many species, captured at S4 over the three years than at S3. S4 has a much greater proportion of coniferous woodland than S3, which has roughly equal proportions of coniferous and deciduous trees. The spatial structure of the two sites is also markedly different and this must account for at least some of the variation in syrphid abundance and diversity between the two sites.

The trap at S3 was located in a small glade largely surrounded by plantations of mixed and coniferous woodland. The mixed woodland is not particularly dense and there are several grassy corridors into the clearing. The trap was located across the biggest of these corridors, backed up against a dense *Picea* plantation. The trap was thus apparently placed to catch insects moving through the glade, but the shading provided by a clump of *Sorbus torminalis* from the end of May, when the leaves of this tree become fully open, appears to have had a profound effect on the numbers of syrphids in the clearing. The site never showed even early-season potential as a rich syrphid area before the trees became effective shade. This could be taken as evidence that the early-season adults are the imagines of the late-aphid flush larvae, because adults would have been scarce in the late season of the previous year when the eggs were laid. It also demonstrates that hoverflies caught in Malaise traps are essentially local in origin, although some migrations from outside the area, such as the influx of *Syrphus ribesii* in May 1980, can from time to time occur.

The high syrphid species diversity and abundance at S4 is linked with the clear spatial arrangement of dense plantations of *Picea* alternating with grassy and overgrown avenues. These avenues not only support a wide variety of flowering plants upon which the adult hoverflies feed, but also concentrate insect movement along these channels or flyways. For this reason, the Malaise trap at S4 was carefully located out of the main flyway so as to minimize the capture of purely migratory individuals. Placing the trap in the centre of this Forestry compartment also ensured that most of the trapped individuals were local in origin, because they would not have penetrated far into an area intrinsically hostile to them. The high diversity and abundance of hoverflies captured at S4 is thus an indication of the overall entomological quality of this forest habitat and not simply a reflection of the number of migratory insects that pass through it.

Three features of the vegetation architecture at S5 conspire to make this the site of the poorest hoverfly samples. The continuous overhead canopy of *Pinus sylvestris* casts the whole of the Forestry compartment in shade and makes the area unattractive to heliotropic aerial insects, and although patches of the forest floor are rich in flowering plants throughout the spring and summer, the lack of vegetation above 0.5 m. from the forest floor offers limited sites for oviposition. The lack of tall herb and shrub layers provides no physical features that might guide insects into flyways and thus the catching efficiency of the Malaise trap will be lower than at the other sites, where the traps were located across flyways. These features are reflected in the hoverfly catches from S5, which consistently contain the lowest number of both species and individuals of all the five sites.

The precise effect of vegetation structure upon the species richness and abundance of hoverfly communities is thus difficult to ascertain from the five Bernwood sites. Of the three sites with the highest structural diversity, two have rich syrphid communities but one has a poor associated fauna. The most important component of habitat structure in terms of hoverfly diversity is the overhead canopy, the presence of which is negatively correlated with syrphid abundance, richness and diversity. The two spatially-diffuse sites, with no outstanding features to the vegetation architecture, both support a high-diversity fauna, as does a predominately coniferous site arranged into dense conifer plantations and grassy avenues.

Poor syrphid collections were obtained from a glade surrounded by both dense conifer plantations and more open mixed plantings of trees, although the glade is connected to the main rides by overgrown, grassy corridors. The inferences from this site are, however, complicated by the overshadowing of a clump of *Sorbus torminalis*. Finally, the old conifer plantation of *Pinus*, which possesses extremely poor structural diversity and continuous canopy cover, produced the poorest syrphid samples fromm all of the five sites.

11.4 Principal Components Analysis of the Hoverfly Samples

Unlike the diversity statistics, the principal components analysis (PCA) employed uses standardized species data as the basis for the computation. This is of particular importance in communities where the abundance of many species can change dramatically from year to year and in samples prone to the influx of large numbers of migrant individuals, both of which are features of the Bernwood hoverfly community.

The most consistent feature of the PCA ordinations is the separation of the early and late season catches in all the samples. This seasonal identity of the catches is an important feature of hoverfly community organisation and the richest and most diverse sites show this seasonal difference of species more strikingly than do the low-diversity sites, which tend to fall in a cluster around the seasonal interface. No overlap between the two seasons is observed in the three years' analysis, despite this clustering, which is particularly astonishing in view of the fact that most hoverflies are bimodally distributed and appear in both seasons' abundance data.

The strong seasonal identity of the syrphid samples from the rich sites in comparison with the poor seasonal identity from the sites of low species diversity appears to be a function of species diversity and not of the species assemblage at a particular site. This is demonstrated by the poor seasonal separation of the two samples from S1 in 1981, when this site produced poor samples in comparison with the other two years, when the ordinations widely separate the two within-year communities. The distinction between the high-diversity sites at S1, S2 and S4 compared with the much lower richness and diversity found at both S3 and S5 is thus attributable to each season possessing a distinct fauna at the former sites but not at the latter.

The 1980 and 1981 ordinations follow a common pattern, with seasonality split largely across the first principal component and species diversity by the second. The horseshoe effect in the ordinations is an artefact and should not be emphasized. There is a small degree of 'site wandering' in the 1981 ordination but this can be attributed to the poor nature of the catches in that year, particularly at S1, which is the most-changed site as it forms part of the cluster in both seasons' ordinations with S3 and S5. This is in keeping with the low α and Q species diversities obtained from the samples from S1 in 1981.

The 1982 ordination does not give a clean split across each axis in turn for the two parameters of season and species diversity although the sites are split by the former and do follow the correct sequence for the latter. The ordination is different compared with those of 1980 and 1981 and this shows that the increased abundance of certain species in 1982, notably *Episyrphus balteatus*, *Meliscaeva cinctella* and *Helophilus pendulus*, and the decline in others, for example *Platycheirus albimanus*, have more effect on the community structure of hoverfly populations than do poor years such as 1981 when the general level of diversity is reduced.

The principal components analysis gives a good fit of the sequencing of the sites with the species diversity gradient and combines this with a further refinement because it identifies the different species that are important in each site's community. The principal latent vectors that define the communities do however show little constancy between the years with regard to the actual species that they represent and the ordinations are the product of many important species, unlike the ordinations of the plant abundance data which are attributable to three or four species for each axis. The PCA therefore reveals that none of the hoverfly species can be regarded as indicator species with which to rank the five sites from Bernwood, let alone assess syrphid quality in sites which have not been thoroughly investigated. Whilst the family taken as a whole can be a useful indicator group to ecological diversity and quality, individual species, unless they be rarities in their own right, cannot be used with any confidence in the assessment of woodland site quality.

The ordinations of the Bernwood syrphids show considerable stability, particularly in view of the fundamentally dynamic nature of multi-species insect communities, which Kempton (1981) has demonstrated with the ordinations of 14 sites from the Rothamsted Insect Survey over 15 years. This is in common with the site diversity indices, which also show an essentially stable pattern of inter-site diversity in keeping with overall abundance and species richness. And yet this stability has its foundations in the turbulent sea of shifting species populations, which rise and fall violently in an apparently unpredictable manner. The Hill diversity numbers and the equitability indices demonstrate that the fluctuating nature of the species' populations is not bound within a strict framework of population structure within the community but that this also contains considerable plasticity. There is thus something of a paradox within hoverfly community structure that is not explicable simply by different levels of resolution within the analytical techniques, but rather is of the nature of the communities themselves.

11.5 Woodland Hoverfly Communities

May (1981) points to many examples "where the world appears chaotic and vagarious at the level of individual species, but nonetheless constant and predictable at the level of community organization". May suggests the analysis of numbers of individuals in species and trophic levels, of biomass and of energy flow as increasingly fundamental aspects of community organization and that patterns of ecological function are of more immediate appeal than the relatively abstract quantities such as energy flow. Bahr (1982) puts forward a strong case for elevating functional taxonomy to at least the status of classical species taxonomy in ecological investigations of communities, and suggests that an over-reliance on the species concept has hindered the understanding of ecological communities. Can the "chaotic and vagarious" Bernwood hoverflies be fitted into a relatively stable framework derived from their ecological niches?

Functional organization can be examined from the identified guilds present within the community, which ought to remain constant as the population fluctuations of individual species within a guild are balanced by other species in that guild (Root 1973). The assignment of the Bernwood syrphids into the five recognised guilds, or trophic categories, is seen to impose a considerable measure of stability within the sites that is not merely the consequence of the lower taxonomic resolution. The sites each maintain their characteristic guild composition over the three years, with the possible exception of the two deciduous sites, which bear a close resemblance to each other. Detailed accounts of the life histories of most hoverfly species are not available and further breakdown of the trophic categories into smaller guilds would probably reveal that much of the instability arises from localised guilds. For example, the aphidophagous syrphids employ a wide range of strategies, from those that feed only upon specific species of aphid, through those species which favour particular sites for oviposition regardless of the aphid species that live there, to syrphids which are able to exploit the majority if not all of sources rich in aphid colonies. This latter, generalist group, appears to contain the species which are the most prone to population outbreaks.

Further division of the guilds is more likely to reveal a pattern of syrphid abundance that more accurately reflects the flow of energy through the habitat in which the collections are made. Guild values,no matter how narrowly defined the guild may be, should not be expected to remain static. The 'ecological opportunities' within a community change through the seasons and in each and every year as the biotic community is subject to ever-changing environmental and climatic conditions. It is particularly variable in young ecosystems that have not reached a climax state, but even then reflects the steady change of ecosystem development rather than the dramatic changes in the annual fortunes of individual species populations.

The Bernwood hoverfly communities appear to be organized by a characteristic set of functions which determine community structure. These functions are manifested in the guild structure of the communities and remain constant from year to year within the bounds of climatic and ecological change. However, this identification of community stability exacerbates the problem of the presence, and often dominance, in the community of so many individual species whose numbers, and indeed actual presence in the community, fluctuate so violently and dramatically over the course of years. How does the Bernwood hoverfly fauna include so many species with such a variation in abundance?

Within a taxocene, there are often many different species that can fulfil a common ecological role; this is certainly true of the Syrphidae, in which only five broad trophic categories are commonly recognised (Colyer and Hammond 1968, Owen J. 1981). The community present at any point in time may thus be the result of many successful species additions and subsequent population growths and extinctions (Fager 1968, Whittaker and Woodwell 1972). Alternatively, this duplication of functional fulfilment could cause redundancy in the community, which buffers the effects of change and disturbance and thus maintains both community structure and function (MacMahon 1976). Within the context of the Bernwood hoverflies I do not believe that there is a future for species which pass through many generations of 'ecological redundancy' whilst awaiting the availability of some particular ecological niche; such species would fall to extinction from the community. Neither can an equilibrium model contain the essential dynamism inherent in these communities, particularly in view of the growing body of literature that supports non-equilibrium mechanisms of the maintenance of species diversity of apparently stable populations (Abele 1976, Connell 1978, Sousa 1979, Paine and Levin 1981, Abugov 1982, Miller 1982 and Spence 1983). Vandemeer (1982) identifies chaos as an intrinsic feature of rare species' strategies, with long periods of chaos resulting in long periods of rarity, but nevertheless with population flushes expected now and again. Such an approach provides more of an understanding of hoverfly populations than do equilibrium models, and might also explain the co-existence of competitors.

The populations of individual syrphid species certainly appear to be chaotic, both in abundance and in some cases presence in the community. This chaotic phasing of the species populations through time could however be a mechanism maintaining the species richness in a family where there is considerable 'duplication' of ecological roles. Each guild might possess several potentially competitive species, but the chaotic phasing of their abundance is usually such that they are rarely present in the community at the same time. Competition is thus reduced to a minimum, preventing competitive displacement and maintaining diversity within the family.

The phasing of species' abundances is most likely to be under climatic control, although some species, for example the wood-decomposing hoverflies, show a pattern of seasonal abundance that separates species in time. Each year's climatic conditions will affect each species slightly differently, some synchronizing with the climate and thus producing large populations of adult hoverflies, others being less favoured by the prevailing conditions. There must be sufficient variation in the yearly weather patterns to provide the heterogeneity required to support this mechanism of 'chaotic' population phasing and the adult populations captured will further be modified by other factors, including parasitism[1], disease and weather conditions during the flight period. Niche exploitation is nevertheless maximized because there are always some abundant species in each guild, although many may have only poor breeding success for a period of years.

High species diversity is thus maintained in woodland hoverfly communities by a non-equilibrium mechanism of population control. Such a mechanism is in keeping both with the unstable nature of the populations themselves and with current community theory, which refutes the traditional view (Elton 1927, 1958) that diverse communities are the product of inherent stability and that the two properties are causally linked. The diversity - stability relationship was first questioned through modelling techniques (Gardner and Ashby 1970, May 1972, 1973) and has since been further supported by many studies, both theoretical and biological (de Angelis 1975, Lawlor 1978, 1980, Nunney 1980, Zaret 1982; for a review see Goodman 1975).

High diversity in the Bernwood hoverflies may be further enhanced by the environmental instability caused by the Forestry operations. S4 is the most diverse of the Bernwood sites and it represents a medium-term disturbance phasing in comparison with S1 and S5, which ought to produce the most diverse assemblages (Abele 1976, Connell 1978 and Abugov 1982). S3, however, was planted only three years later than S4 and is host to a much

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[1] The Ichneumonidae parasitic on Syrphidae have been identified and are given in Appendix 3.

poorer fauna: the habitat features discussed clearly play a more important role in determining insect diversity at a site than a simple reference to disturbance patterns.

11.6 Conservation of Hoverflies at Bernwood Forest

If disturbance of the habitat helps to maintain insect communities of high diversity, the freedom of the Forest from disturbance until the main felling operations begin early in the 21st century will cause a reduction in hoverfly diversity. This factor is most likely to have the greatest effect on the communities at S4 and S2, but it is impossible to identify those species which will be most affected. The rich hoverfly samples from S1 suggest that habitat disturbance is not a major factor affecting the diversity of hoverflies.

The major threat facing the diverse hoverfly assemblages at Bernwood is the growing up of the Forest to cover the woodlands with much more shade than at present. Shade appears to be the major habitat feature that prevents high diversity assemblages of hoverflies, as is witnessed by the samples from S3 and S5. As the conifers grow taller they will cast greater shade over the rides and glades that appear to be so important for adult hoverflies, with the result of reducing the diversity of the syrphid communities. The hoverfly samples obtained from S3 and S5 demonstrate the paucity of both species and individuals in heavily shaded habitats and these faunas would probably be typical of most of the forest if it becomes subject to heavy overshading. The aphidophagous syrphids would dominate the community and account for 90% or more of all the individuals present, with the associated decline of all the other trophic groups, particularly the primary consumers and hymenopteran commensals. Some species are relatively more abundant at these shaded sites, for example *Baccha elongata*, *Melangyna lasiophthalma*, *Dasysyrphus albostriatus* and *Meliscaeva auricollis*, but of these, only *Baccha* is at all common in the overall sample. At worst, the shading might produce a two to three fold decrease in the number of hoverflies the woods would support, with the loss of probably half of the species which make up the present collection.

Such a decline in the abundance and diversity of the Bernwood hoverflies is unlikely to occur. The most recent Forest Nature Reserve Agreement reached between the Forestry Commission and the Nature Conservancy Council makes the provision for the maintenance of a good ride structure on all the main rides within the forest and the creation of intersection glades. The openness of the rides, with a saucer-shaped profile to include herbaceous plant and shrub layers, will serve to increase habitat diversity and create a food resource for hoverflies as well as for the butterflies, which were the principal concern of the conservation plan. The Forest still maintains an excellent mosaic of habitat diversity and, with the most recent plantings as late as 1973, this is likely to persist until the first fellings create new areas of open space in the first decade of the next century, with the rides and area of old coppice providing further refuges.

The Malaise trap at S4 has convincingly shown that commercial softwood forestry plantations need not be the biological deserts that they so easily can become, as witnessed at S3 and S5. The wide, grassy and overgrown avenues between the dense stands of *Picea* and *Quercus* provide an excellent habitat for syrphids, with a huge increase in the amount of woodland edge over a dense block of conifers without these avenues. Although the trees bordering the avenues do not provide a good ride edge structure, the avenues nevertheless achieve the habitat diversity essential for flourishing insect communities through being largely unmanaged and thus (to the gardening eye) untidy. This kind of management should be encouraged as an active conservation measure, particularly in view of the frequent mowing of the main rides. It was unfortunately impossible to compare the insect faunas of these avenues with those of the main rides, because of problems of interference from the public, but I would imagine that the two areas harbour a similar diversity of hoverflies, with seclusion and freedom from disturbance of the avenues possibly allowing a richer fauna.

The species likely to suffer from the Forestry operations are associated with old woodlands, and it is these syrphids that are the most threatened nationwide. Many of these species are associated with rotting wood and sap runs, for example *Criorhina* and *Ferdinandea*, and it is these resources that are most endangered with the 'clean and tidy' approach to land management. The retention of old conifer stands beyond normal felling age has been proposed to increase the numbers of breeding birds (Currie and Bamford 1982) and such measures can only benefit insect populations as well.

The advent of large areas of conifer plantations across Britain has been of benefit to several hoverfly species. *Dasysyrphus friuliensis* is a species new to Britain that has been found only in coniferous and mixed woodlands, but it appears to have become established since it was first recognized in 1975. *Parasyrphus malinellus* has increased its abundance considerably with the advent of large conifer plantations as have *Megasyrphus annulipes*, *Parasyrphus lineolus*, *Scaeva selenitica*, *Metasyrphus lapponicus* and *Eriozona syrphoides* (Entwistle 1978). These latter two species have not yet been found in Bernwood but I would expect them to turn up in the near future. Increasing geographical range is witnessed among the Bernwood records. *Megasyrphus annulipes* is recently described (Stubbs and Chandler 1978) as a species of the Scottish pinewoods and the captures of *Metasyrphus neilseni* and *Parasyrphus nigritarsis* are amongst the first outside of the Scottish highlands (Stubbs, *in litt.*): the expansion of conifer woodland in Britain is clearly of benefit to certain species.

The image of foresters has changes from one of consumption to one of conservation (Schoenfeld *et al.* 1980) and the need for positive conservation is at least recognized by foresters (Holmes 1980, Zehetmayr 1981). Bernwood Forest is fortunate in that it is being used as something of a showpiece by the Foresty Commission, but the majority of plantations do not enjoy this priviledge, despite the fact that the need is more acute now than ever before. How long rare old woodland hoverflies such as *Ferdinandea ruficornis* manage to persist in Bernwood remains to be seen but I would be surprised if they survive until the first fellings. Let us hope that the syrphids prove to be as resilient to change in the woodlands as Bernwood's famous butterfly community.

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APPENDIX 1

BERNWOOD SITE DATE : PERCENTAGE FREQUENCY OF FLOWERING PLANTS 1980

½M. QUADRATS, 40 THROWN RANDOMLY AT EACH SITE, 18-19.8.80

		---------- % Frequency ----------				
		S1	S2	S3	S4	S5
Acer campestre L.	field maple	2.5				
Bellis perennis L.	daisy		15.0			
Betonica officinalus L.	betony		5.0			
Betula pendula Roth.	silver birch	27.5	22.5	5.0		
Bromus ramosus Huds.	wood brome			17.5	20.0	5.0
Carduus acanthoides L.	welted thistle				5.0	
Carex nigra Reich	common sedge	7.5	5.0		7.5	
Cirsium acaula Scop.	dwarf thistle		2.5		2.5	
Coryles avellana L.	hazel	22.5	25.0	12.5		
Crataegus monogyna Jacq.	hawthorn	17.5	10.0	2.5	12.5	
Deschampsia caespitosa L.	tufted hair grass	65.0	30.0	57.5	42.5	
D. flexuosa L.	wavy hairgrass		5.0			
Euphorbia amygdaloides L.	wood spurge		10.0		2.5	
Festuca rubra L.	creeping fescue	70.0	72.5	15.0	65.0	
Holcus lanatus L.	Yorkshire fog	20.0	5.0			
Hypericum hirsutum L.	hairy St. John's wort				15.0	
H. pulchrum L.	slender St. John's wort	2.5	2.5			
Juncus effusus L.	soft rush	2.5	5.0	2.5	5.0	
Lonicera periclymenum L.	honeysuckle	62.5	47.5	32.5	72.5	
Melampyrum pratense L.	common cow-wheat		2.5		2.5	
Picea abies L.	Norway spruce		10.0	47.5	40.0	

APPENDIX 1 CONTINUED

			--------- % Frequency ----------				
			S1	S2	S3	S4	S5
Pinus sylvestris L.	scots pine						100.0
Populus tremula L.	aspen		2.5	22.5			
Potentilla erecta L.	tormentil		7.5	42.5	5.0	50.0	
Prunus avium	wild cherry			20.0		2.5	
Ranunculus sp.			2.5				
Quercus robur L.	English oak		82.5	65.0		15.0	
Rosa canina L.	dog rose		15.0	35.0		15.0	
Rubus fruticosus agg.	bramble		97.5	65.0	67.5	57.5	60.0
Rumex sanguinea L.	wood dock			20.0			2.5
Senecio jacobaea L.	ragwort				2.5		
Sorbus torminalis L.	wild service tree				97.5		
Taraxicum officinale Weber	dandelion		2.5		2.5	2.5	
Urtica dioica L.	stinging nettle						27.5
Viola riviniana Reich	common violet		45.0	35.0	25.0	20.0	2.5
"ferns"					2.5		
"mosses"			45.0	57.5	75.0	72.5	10.0
	excluding "mosses"	N	555.0	580.0	392.5	447.5	200.0
	and "ferns"	S	19	25	15	21	7

APPENDIX 1 CONTINUED.

BERNWOOD SITE DATA : PERCENTAGE FREQUENCY OF FLOWERING PLANTS 1981

½M. QUADRATS, 40 THROWN RANDOMLY AT EACH SITE, 21-24.8.81

Species		% Frequency				
		S1	S2	S3	S4	S5
Acer campestre L.	field maple	2.5				
A. pseudoplatanus L.	sycamore	2.5				
Ajuga reptans L.	bugle		20.0			
Angelica sylvestris	angelica		5.0		12.5	
Anthoxantham odoratum L.	scented vernal grass	7.5	27.5	25.0	50.0	
Arrhenathemum elatus L.	oat grass				10.0	
Betonica officinalis L.	betony	5.0	45.0	5.0		
Betula pendula Roth.	silver birch	20.0	72.5	12.5	2.5	
Brachypodium sylvaticum Huds	wood false brome		12.5	30.0		45.0
Calamogrostis epigejos L.	wood small reed			2.5	2.5	
Carex flacca Schrebb.	glaucous sedge			2.5	57.5	
Carex sylvatica Huds.	wood sedge	22.5				
Carex sp. 1				2.5	5.0	
Carex sp. 2			10.0	25.0		
Circaea lutetiana L.	enchanter's nightshade					7.5
Cirsium palustre L.	marsh thistle	2.5	2.5		27.5	
Cornus sanguinea L.	dogwood		2.5			
Corylus avellana L.	hazel	30.0	15.0	22.5		7.5
Cratagusmonogyna Jacq.	hawthorn	37.5	17.5	30.0	20.0	7.5
Dactylus glomerata L.	cocksfoot			2.5		

APPENDIX 1 CONTINUED

Species		% Frequency				
		S1	S2	S3	S4	S5
Deschampsia caespitosa L.	tufted hair grass	82.5	62.5	47.5	67.5	12.5
Endymion non-scriptus L.	bluebell					10.0
Epilobium angustifolium L.	rosebay willowherb				10.0	
Euphorbia amygdaloides L.	wood spurge		20.0			
Festuca rubra L.	creeping fescue	65.0	62.5	20.0	77.5	5.0
Fragaria vesca L.	wild strawberry			22.5		
Fraximus excelsior L.	ash	5.0				
Galium sp.			5.0			2.5
Geranium robertianum L.	herb robert					20.0
Glechoma hederacea L.	ground ivy					5.0
Holcus lanatus L.	Yorkshire fog	5.0	7.5	10.0	2.5	
Hypericum hirsutum L.	hairy St. John's wort		2.5			
H. pulchrum L.	slender St. John's wort	7.5	7.5	7.5	25.0	
Juncus conglomeratus L.	common rush	5.0	2.5		20.5	
J. effusus L.	soft rush		2.5	12.5	2.5	
Lamiastrum galeobdolon Huds.	yellow archangel					17.5
Lapsana communis L.	nipplewort					15.0
Lonicera periclymenum L.	honeysuckle	65.0	92.5	72.5	85.0	
Lotus corniculatus L.	bird's foot trefoil	2.5				
Luzula campestris L.	field wood rush		22.5		7.5	
Malus sylvestris Mill.	crab apple	5.0				
Mercuralis perennis L.	dog's mercury		2.5			5.0
Picea abies L.	Norway spruce		17.5	77.5	60.0	

APPENDIX 1 CONTINUED

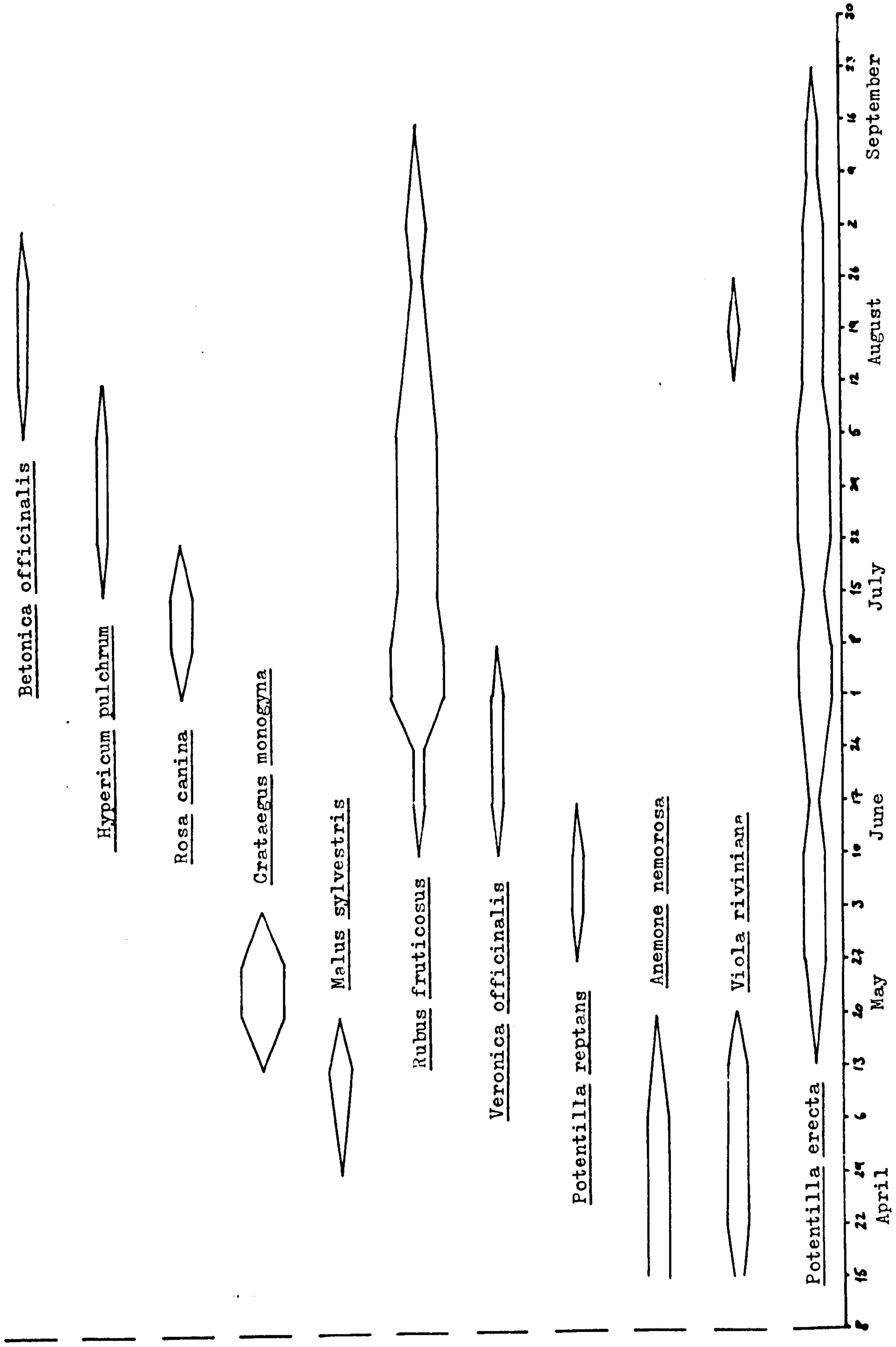
Species			% Frequency				
			S1	S2	S3	S4	S5
Pinus sylvestris L.	Scot's pine						100.0
Potentilla erecta L.	tormentil		10.0	35.0		65.0	
Primula vulgaris Huds.	primrose						5.0
Prunus spinosa L.	blackthorn			67.5	2.5	12.5	2.5
Quercus robur L.	English oak		82.5	77.5	7.5	35.0	
Rosa canina L.	dog rose		12.5	25.0	2.5	2.5	
Rubus fruticosus agg.	bramble		100.0	92.5	90.0	87.5	95.0
Rumex sanguineus L.	wood dock						20.0
Sorbus torminalis L.	wild service tree				95.0		
Stachys sylvatica L.	hedge woundwort						5.0
Stellaria holostea L.	greater stitchwort			15.0			
S. media L.	common chickweed						2.5
Succisa pratense Moench.	devilsbit scabious					12.5	
Urtica dioica L.	stinging nettle						15.0
Viola riviniana Reichb.	common violet		35.0	47.5	45.0	30.0	20.0
"ferns"				2.5	5.0		2.5
"moss"			62.5	62.5	65.0	70.0	10.0
"lichen"				7.5	2.5	12.5	
	excluding "mosses"	N	245.0	359.0	268.0	316.0	170.0
	and "ferns"	S	23	31	24	26	22

APPENDIX 1 (CONTINUED)

FLOWERING PHENOLOGY AT THE FIVE SITES

BERNWOOD FOREST 1980 - 1982

The following kite diagrams are the result of weekly visual estimates of flowering abundance on a five - point scale at each of the five sites in Bernwood Forest.


Betonica officinalis
Hypericum pulchrum
Rosa canina
Crataegus monogyna
Malus sylvestris
Rubus fruticosus
Veronica officinalis
Potentilla reptans
Anemone nemorosa
Viola riviniana
Potentilla erecta
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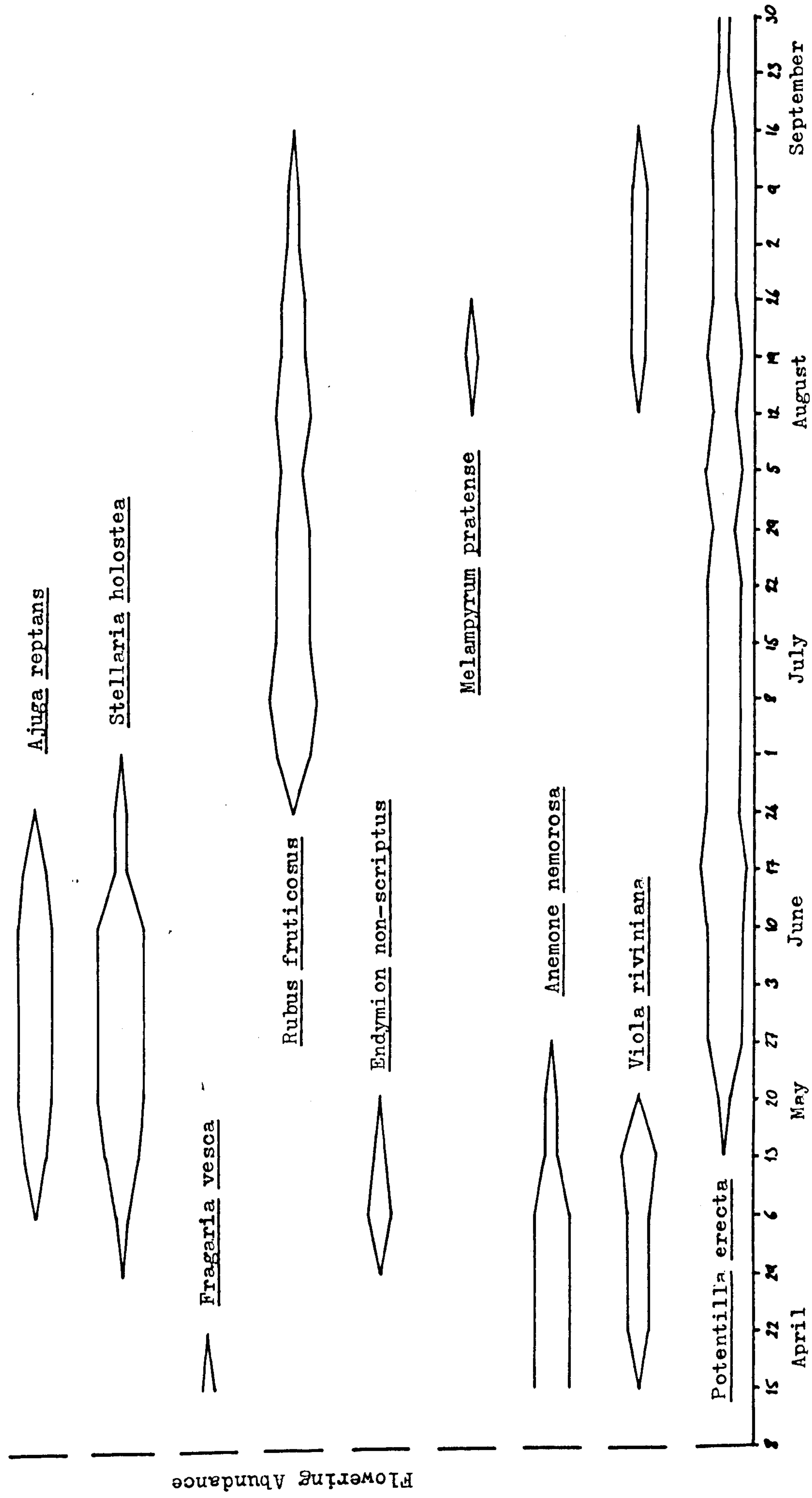
S1/80


Ajuga reptans
Stellaria holostea
Fragaria vesca
Rubus fruticosus
Endymion non-scriptus
Melampyrum pratense
Anemone nemorosa
Viola riviniana
Potentilla erecta
Flowering Abundance
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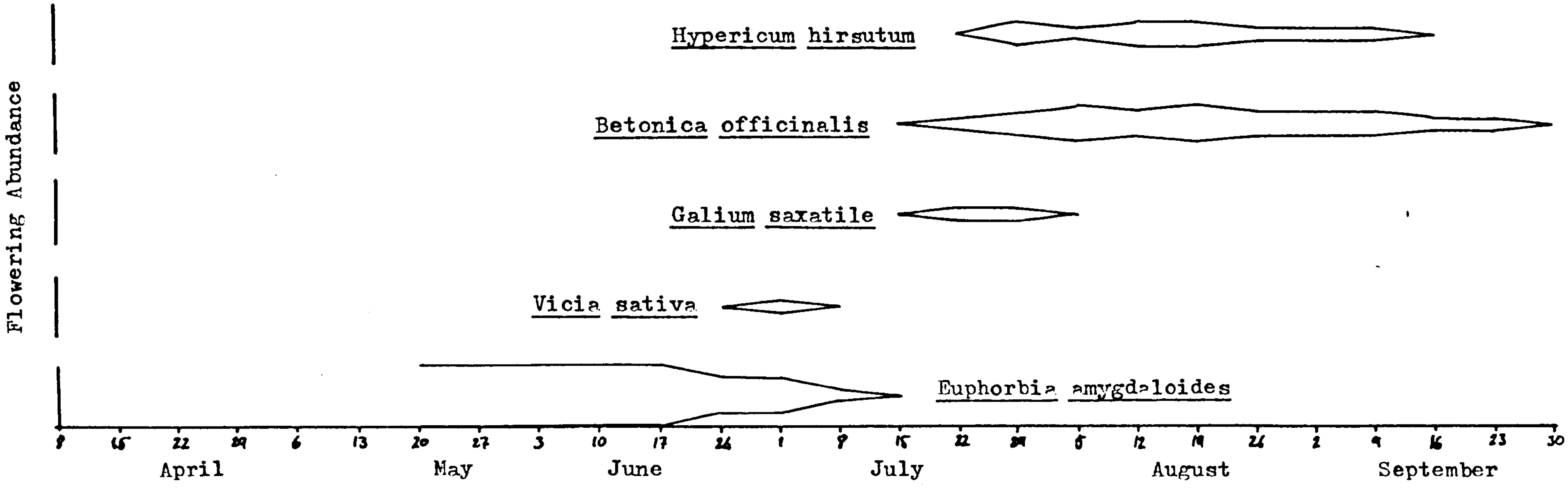
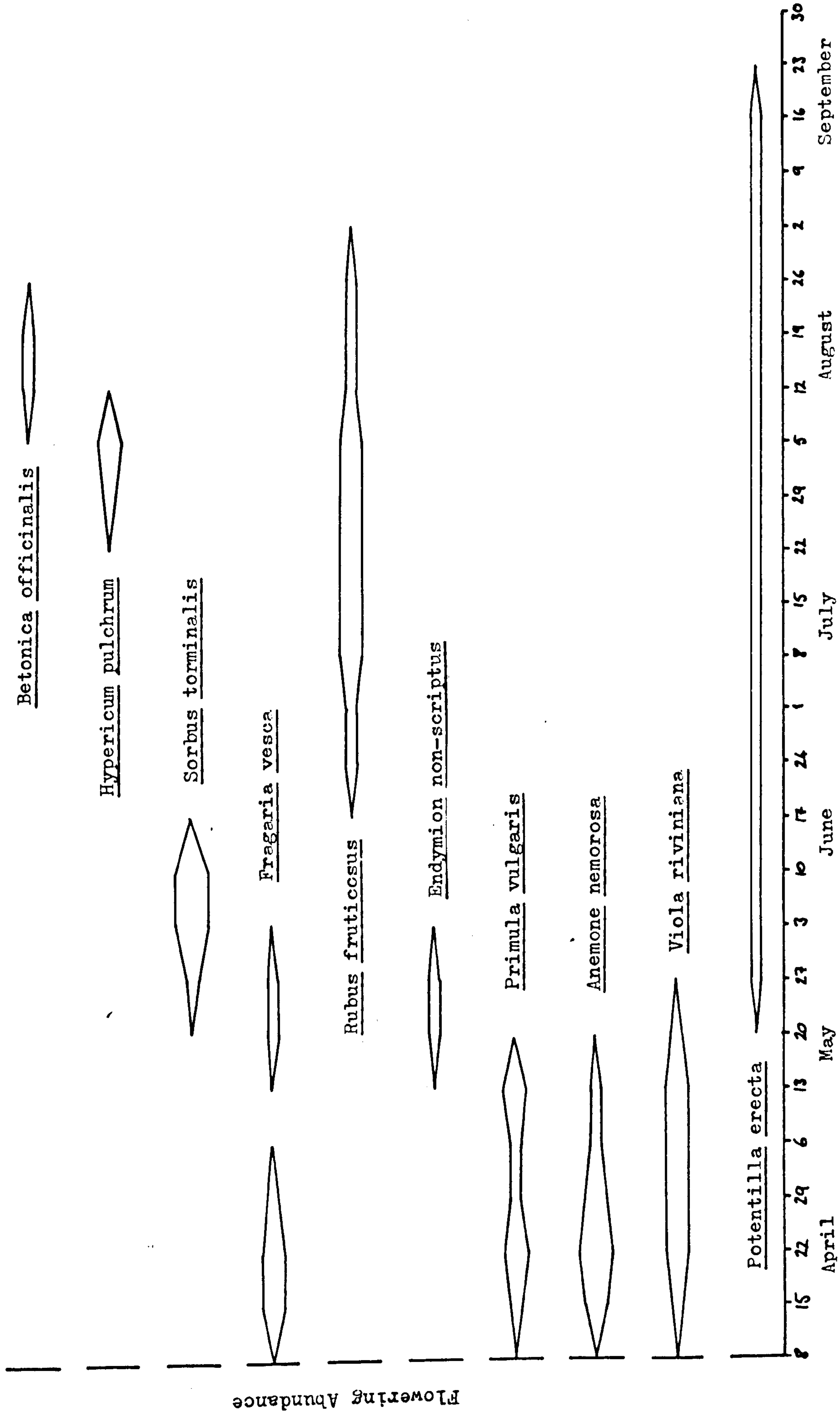
S2/80



S2/80 (Continued)

Betonica officinalis
Hypericum pulchrum
Sorbus torminalis
Fragaria vesca
Rubus fruticosus
Endymion non-scriptus
Primula vulgaris
Anemone nemorosa
Viola riviniana
Potentilla erecta
Flowering Abundance
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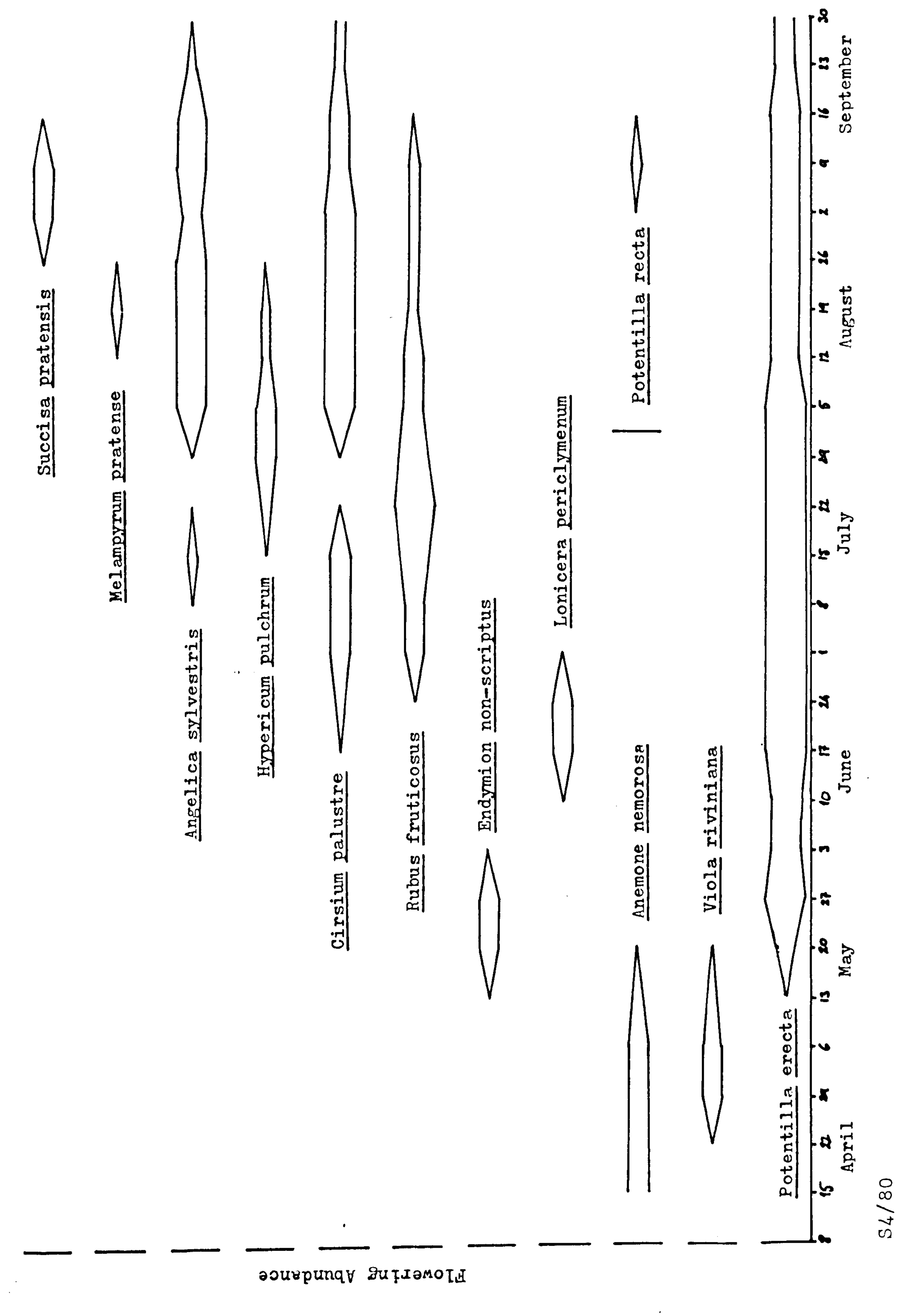
Succisa pratensis
Melampyrum pratense
Angelica sylvestris
Hypericum pulchrum
Cirsium palustre
Rubus fruticosus
Endymion non-scriptus
Lonicera periclymenum
Anemone nemorosa
Potentilla recta
Viola riviniana
Potentilla erecta
Flowering Abundance
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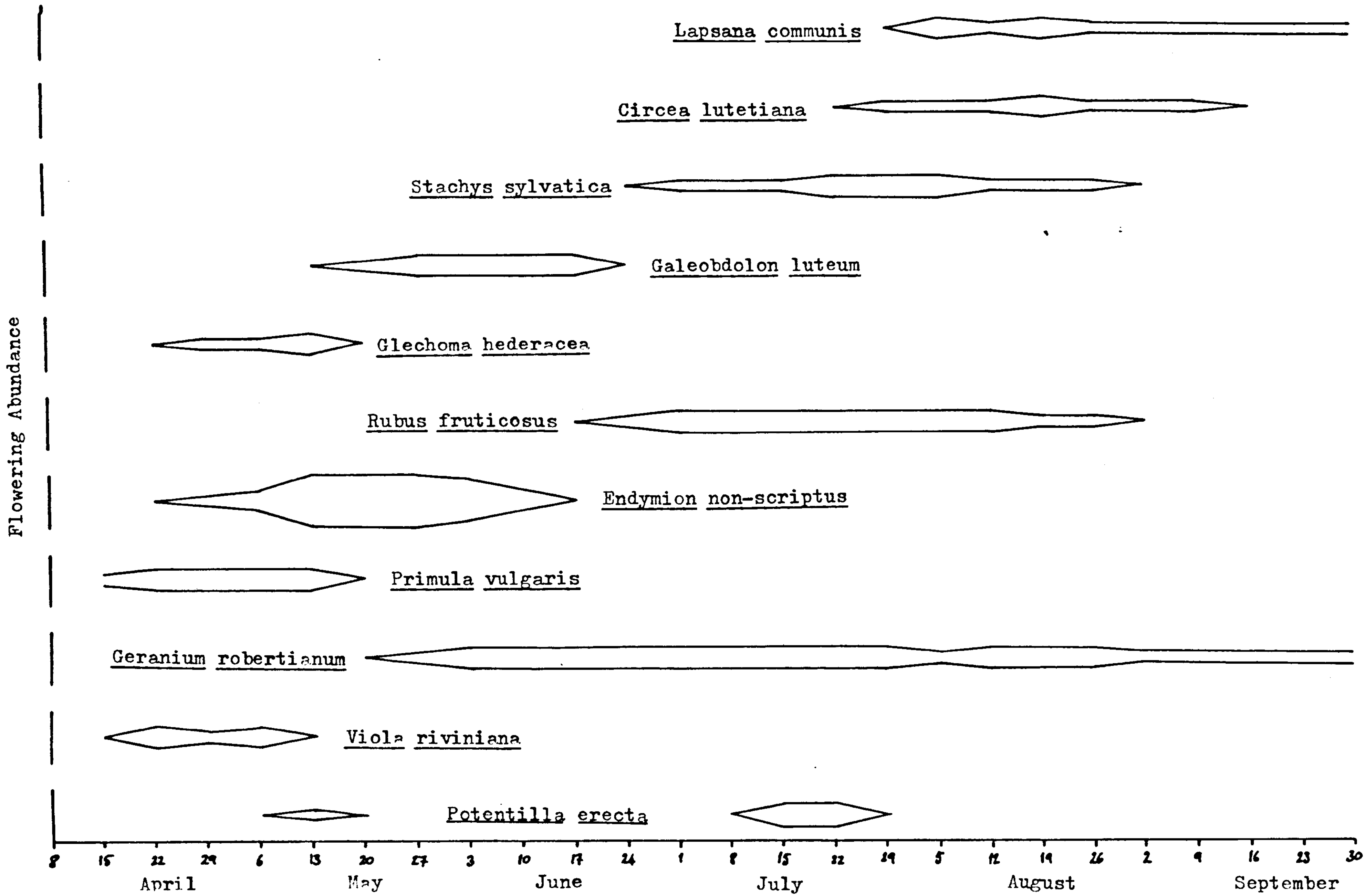
S4/80


Flowering Abundance
Lapsana communis
Circea lutetiana
Stachys sylvatica
Galeobdolon luteum
Glechoma hederacea
Rubus fruticosus
Endymion non-scriptus
Primula vulgaris
Geranium robertianum
Viola riviniana
Potentilla erecta
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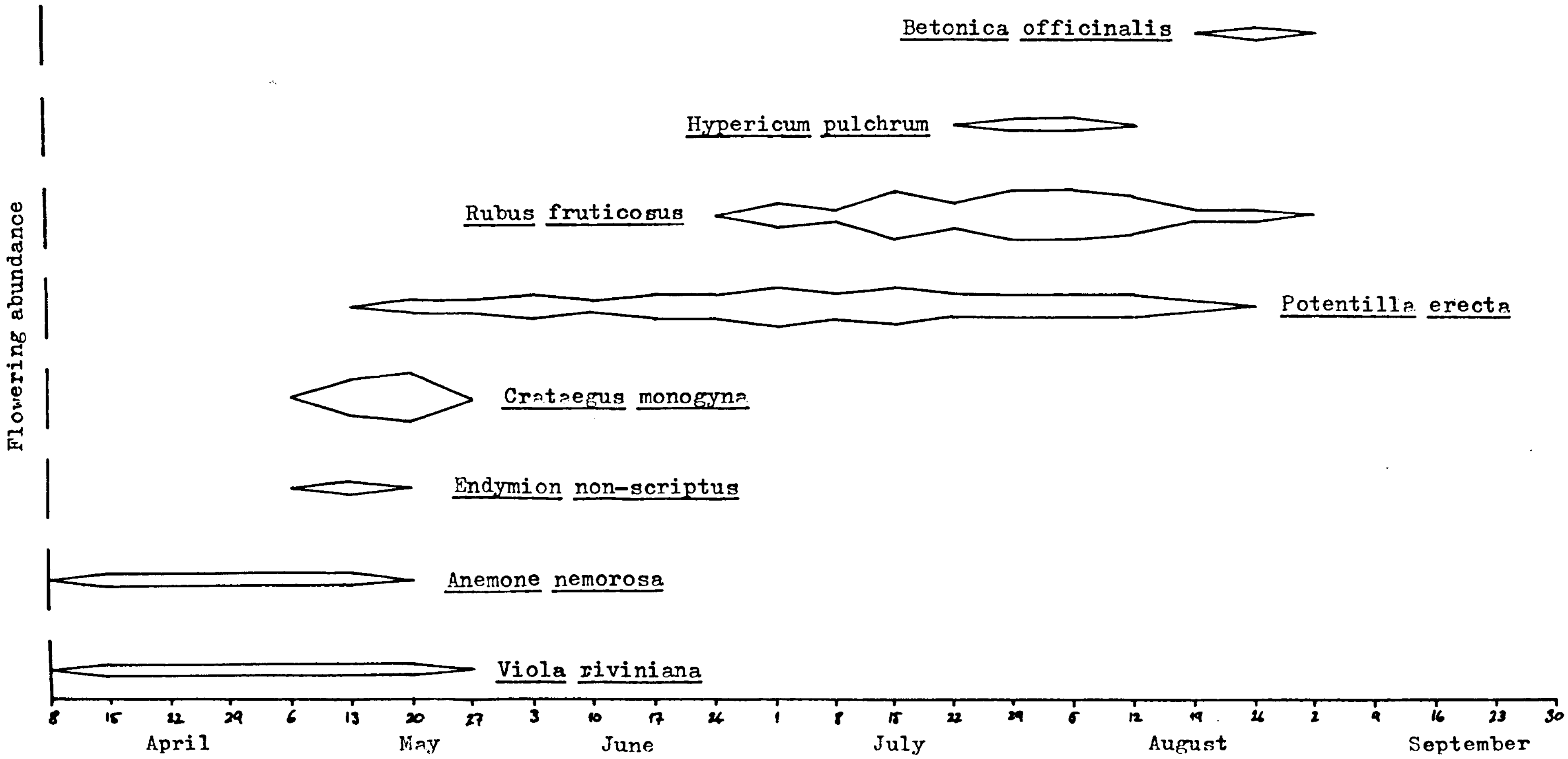
S5/80


Betonica officinalis
Hyypericum pulchrum
Rubus fruticosus
Potentilla erecta
Crataegus monogyna
Endymion non-scriptus
Anemone nemorosa
Viola riviniana
Flowering abundance
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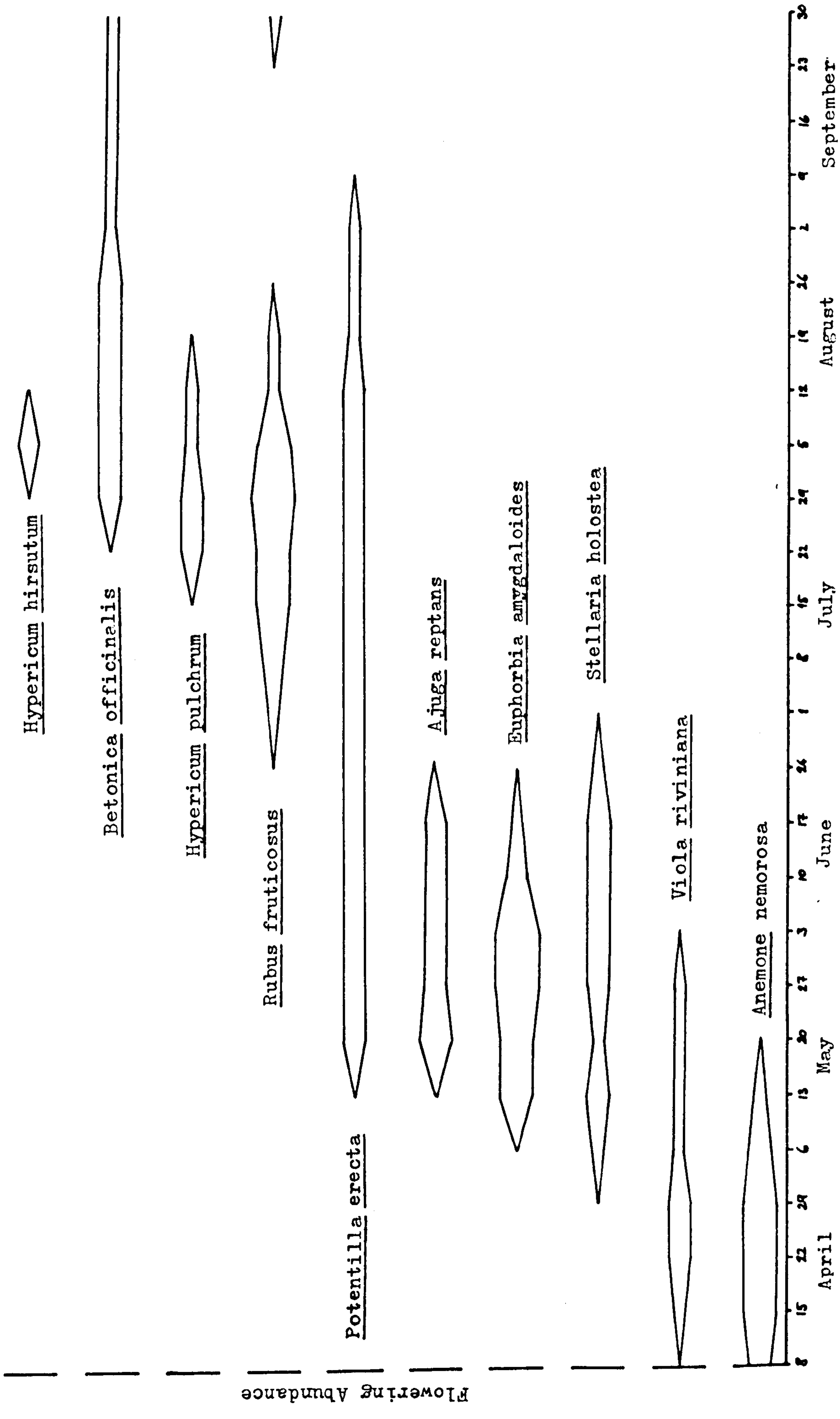
S1/81


Flowering Abundance
Hypericum hirsutum
Betonica officinalis
Hypericum pulchrum
Rubus fruticosus
Potentilla erecta
Ajuga reptans
Euphorbia amygdaloides
Stellaria holostea
Viola riviniana
Anemone nemorosa
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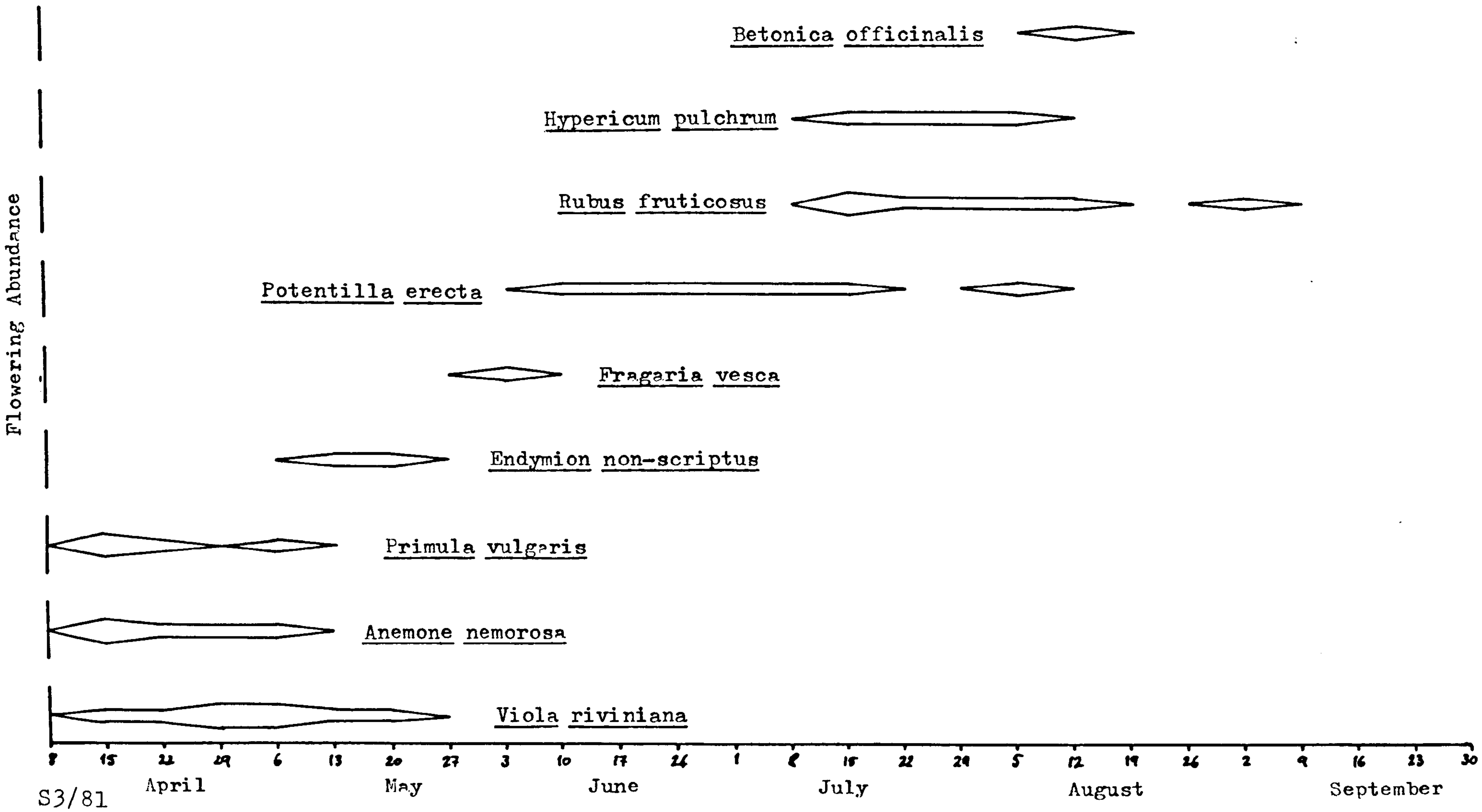
S2/81


Betonica officinalis
Hypericum pulchrum
Rubus fruticosus
Potentilla erecta
Fragaria vesca
Endymion non-scriptus
Primula vulgaris
Anemone nemorosa
Viola riviniana
Flowering Abundance
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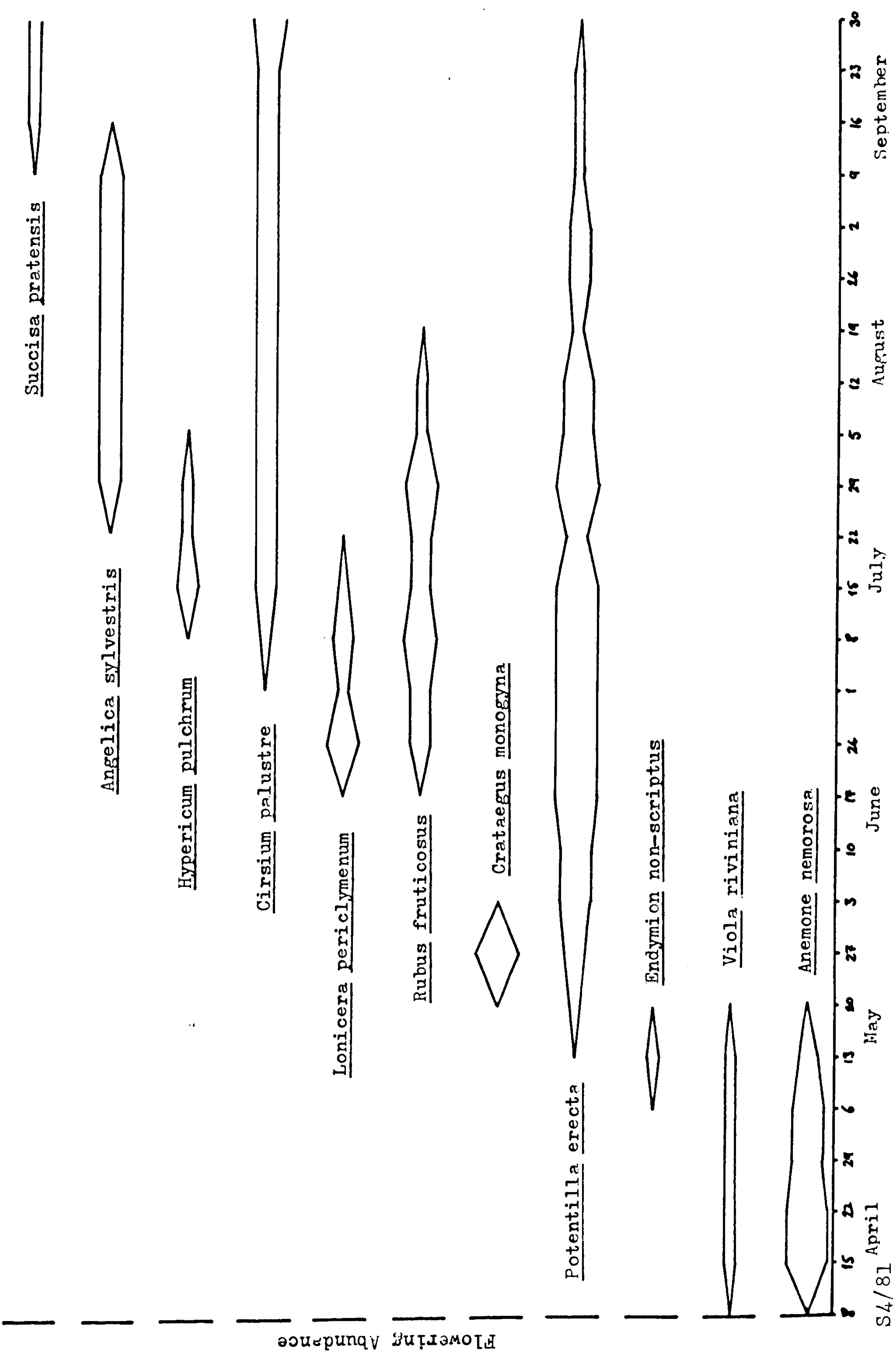
S3/81


Succisa pratensis
Angelica sylvestris
Hypericum pulchrum
Cirsium palustre
Lonicera periclymenum
Rubus fruticosus
Crataegus monogyna
Potentilla erecta
Endymion non-scriptus
Viola riviniana
Anemone nemorosa
Flowering Abundance
S4/81
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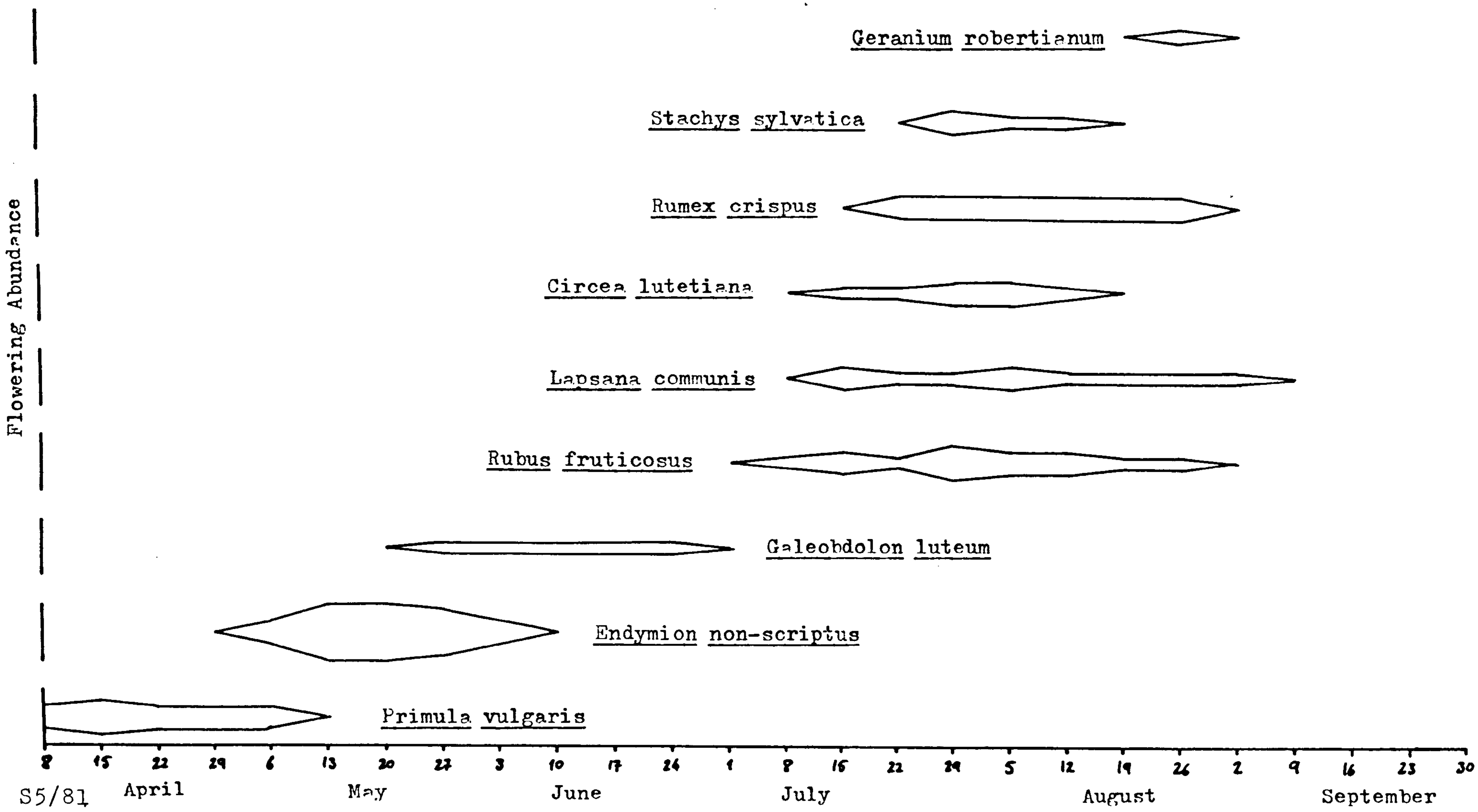
Geranium robertianum
Stachys sylvatica
Rumex crispus
Circea lutetiana
Lapsana communis
Rubus fruticosus
Galeobdolon luteum
Endymion non-scriptus
Primula vulgaris
Flowering Abundance
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S5/81
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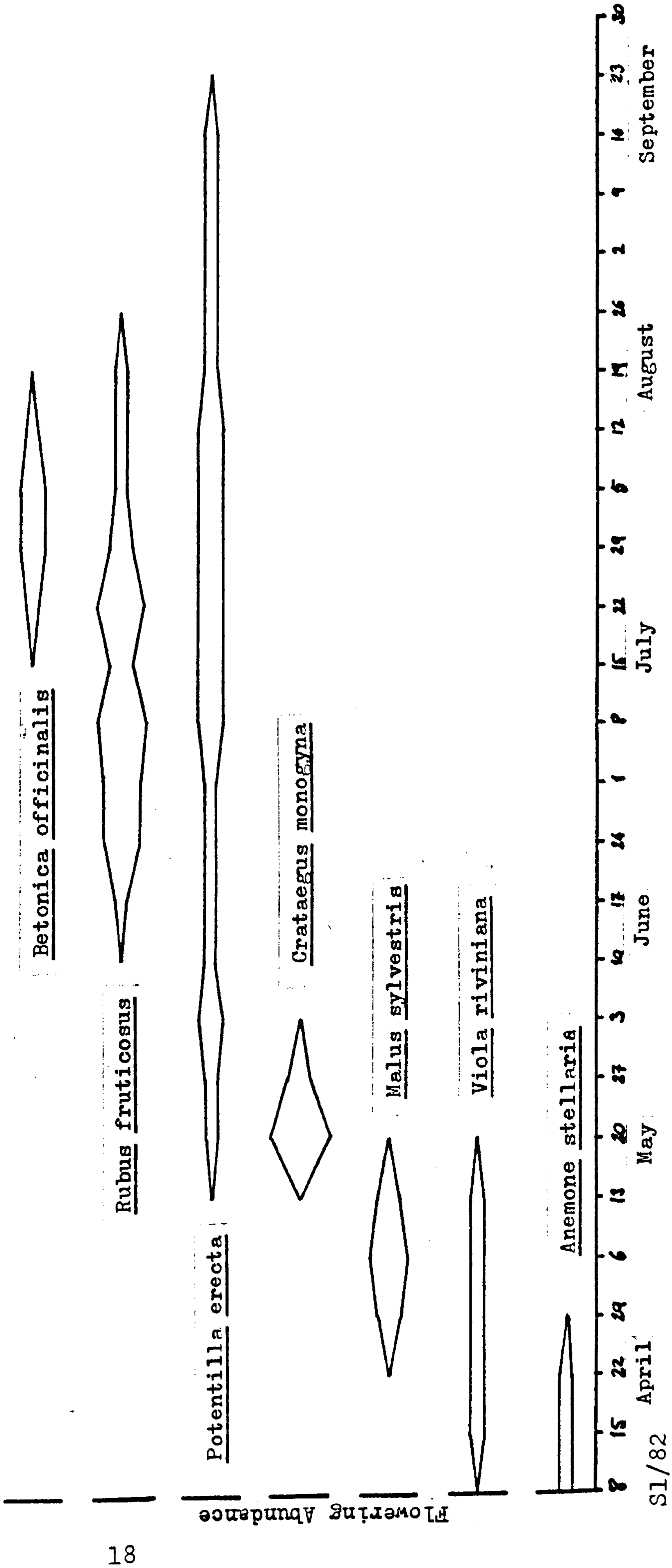Betonica officinalis
Rubus fruticosus
Potentilla erecta
Crataegus monogyna
Malus sylvestris
Viola riviniana
Anemone stellaria
Flowering Abundance
S1/82
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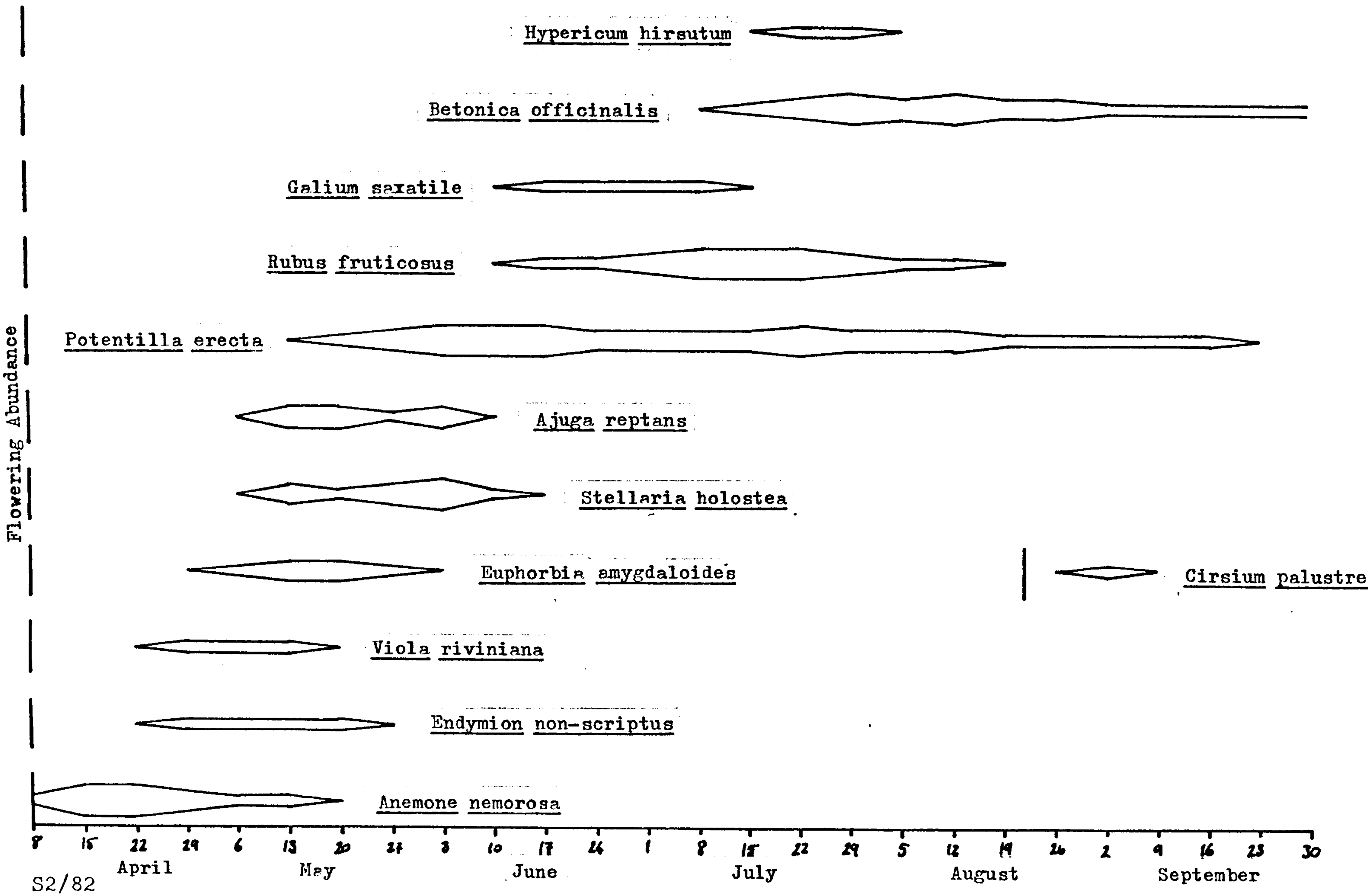
Hypericum hirsutum
Betonica officinalis
Galium saxatile
Rubus fruticosus
Potentilla erecta
Ajuga reptans
Stellaria holostea
Euphorbia amygdaloides
Cirsium palustre
Viola riviniana
Endymion non-scriptus
Anemone nemorosa
Flowering Abundance
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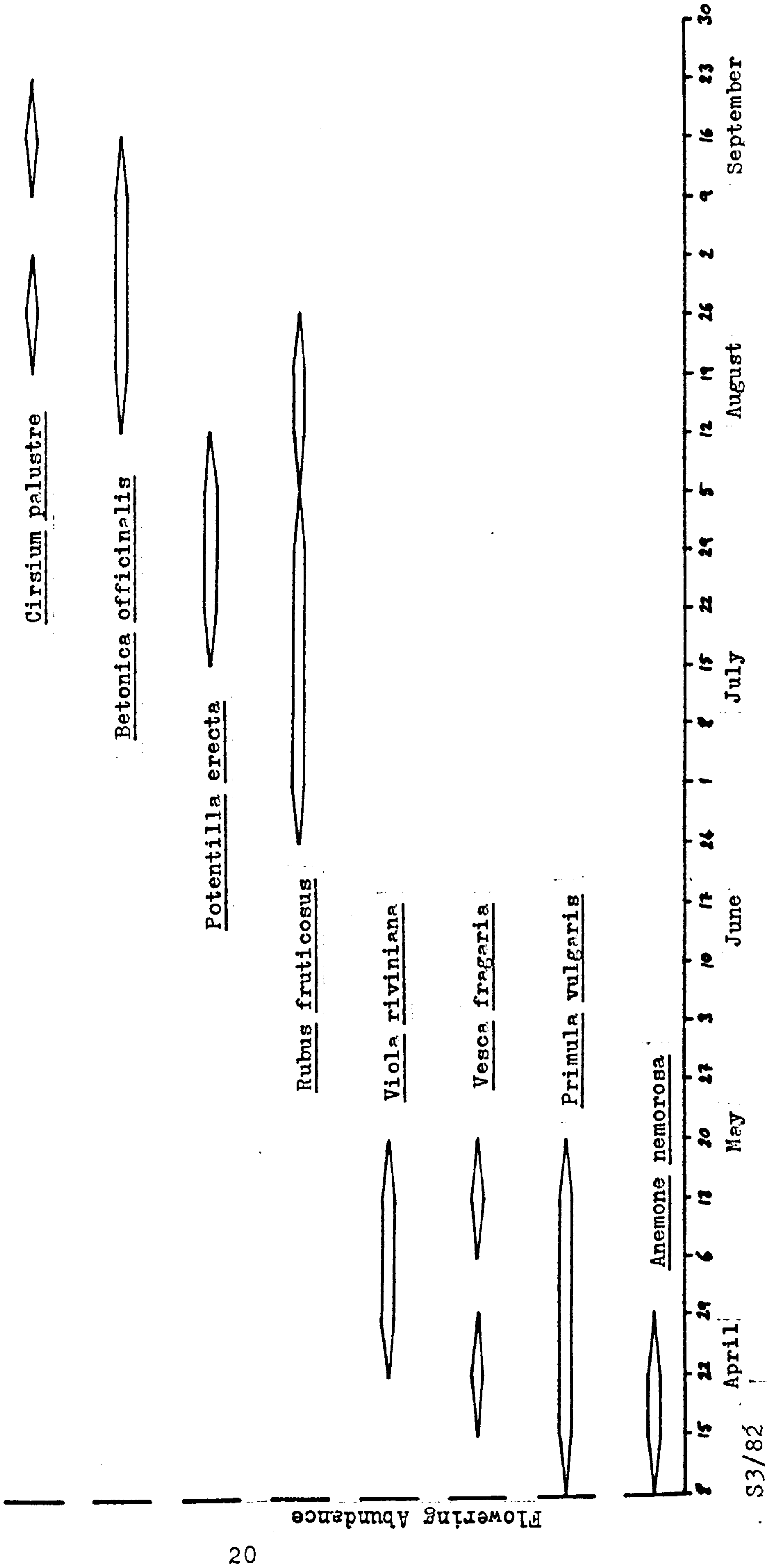
S2/82


Flowering Abundance
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Primula vulgaris
Vesca fragaria
Viola riviniana
Rubus fruticosus
Potentilla erecta
Betonica officinalis
Cirsium palustre
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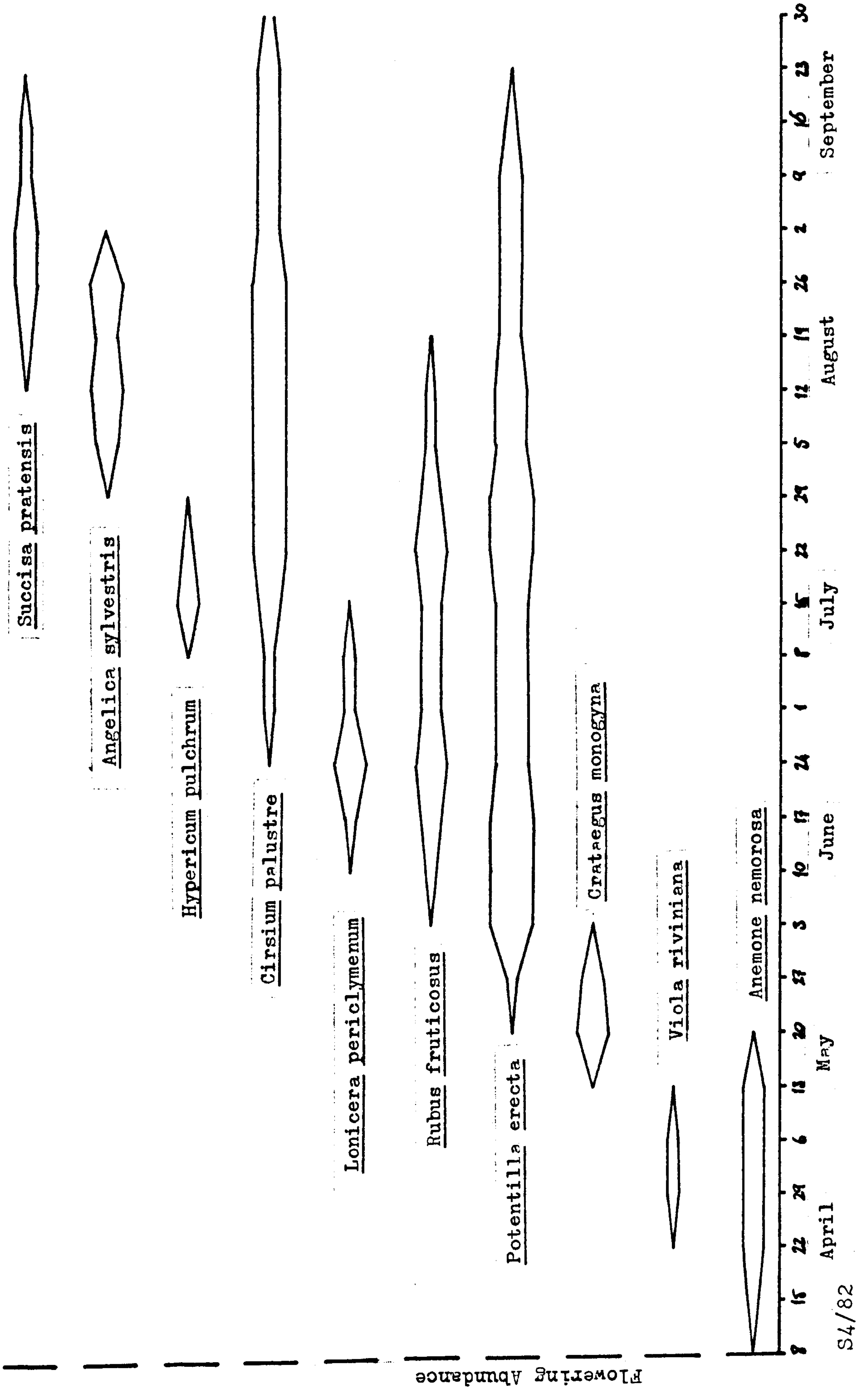
S3/82


S4/82
Flowering Abundance
Anemone nemorosa
Viola riviniana
Crataegus monogyna
Potentilla erecta
Rubus fruticosus
Lonicera periclymenum
Cirsium palustre
Hypericum pulchrum
Angelica sylvestris
Succisa pratensis
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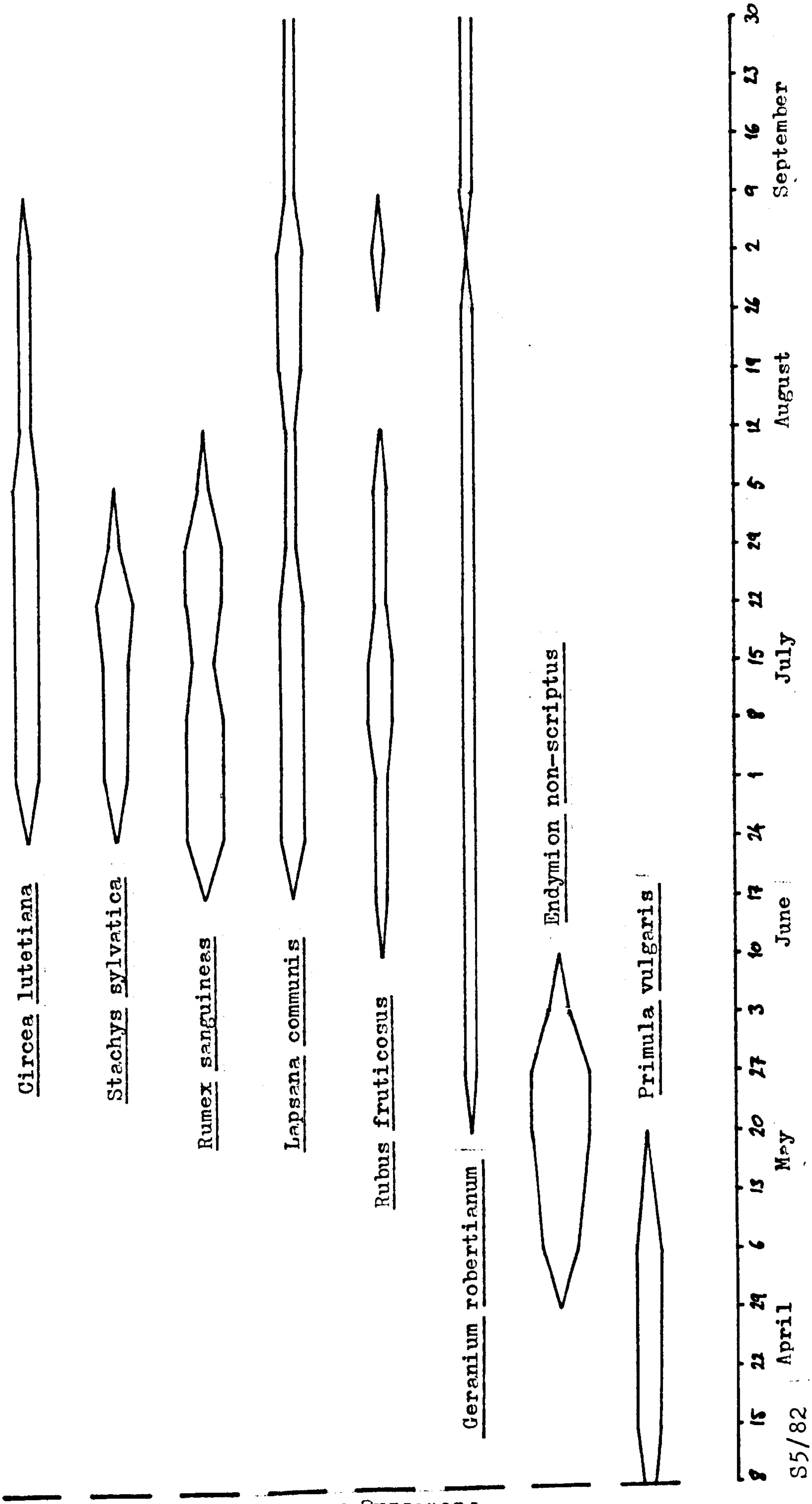
Circea lutetiana
Stachys sylvatica
Rumex sanguineas
Lapsana communis
Rubus fruticosus
Geranium robertianum
Endymion non-scriptus
Primula vulgaris
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S5/82
Flowering Abundance

APPENDIX 2

TOTAL HOVERFLY LIST FROM BERNWOOD FOREST, 1980-1982
FROM FIVE MALAISE TRAPS AT SITES 1-5

	1980	1981	1982	N
Baccha elongata (Fabricius)	168	153	70	391
Chrysotoxum bicinctum (Linnaeus)	31	90	64	185
C. verralli (Collin)	3	1	1	5
Dasysyrphus albostriatus (Fallen)	29	7	22	58
D. friuliensis (Van der Goot)	1			1
D. lunulatus (Meigen)	5	6	8	19
D. tricinctus (Fallen)	17	16	12	45
D. venustus (Meigen)	268	79	128	475
Didea fasciata (Macquart)	17	15	110	142
Epistrophe diaphana (Zetterstedt)	2			2
E. eligans (Harris)	38	13	44	95
E. grossulariae (Meigen)		6	4	10
E. nitidicollis (Meigen)	7	4	2	13
Epistrophella euchroma (Kowark)	9	4	3	16
Episyrphus balteatus (Degeer)	483	170	2200	2853
Leucozona lucorum (Linnaeus)	27	25	57	109
Megasyrphus annulipes (Zetterstedt)		2	7	9
Melangyna arctica (Zetterstedt)	3	1		4
M. barbifrons (Fallen)			1	1
M. cincta (Fallen)	4	4	4	12
M. ericarum (Collin)	1		1	2
M. labiatarum (Verrall)	1			1
M. lasiophthalma (Zetterstedt)	99	192	119	410
M. quadrimaculata (Verrall)	1	1		2
M. triangulifera (Zetterstedt)	40	17	9	66
M. umbellatarum (Fabricius)	1	5	4	10
Melanostoma mellinum (Linnaeus)	533	366	332	1231
M. scalare (Fabricius)	791	839	680	2310
Meliscaeva auricollis (Meigen)	16	22	2	40
M. cinctella (Zetterstedt)	407	613	1523	2543
Metasyrphus corollae (Fabricius)	35	32	64	131
M. latifasciatus (Macquart)	25	27	5	57
M. luniger (Meigen)	6	5		11
M. nielseni (Dusek and Laska)	1		3	4
M. nitens (Zetterstedt)	1	1		2
Paragus (Latreille)		1	1	2
Parasyrphus annulatus (Zetterstedt)	10		3	13

APPENDIX 2 CONTINUED

	1980	1981	1982	N
Parasyrphus lineolus (Zetterstedt)	160	60	286	506
P. malinellus (Collin)	91	54	32	177
P. punctulatus (Verrall)	23	71	54	148
P. vittiger (Zetterstedt)	4	6		10
Platycheirus albimanus (Fabricius)	310	413	82	805
P. angustatus (Zetterstedt)		1	3	4
P. clypeatus (Meigen)	9	27	28	64
P. discimanus (Loew)	2			2
P. manicatus (Meigen)	19	5	4	28
P. melanopsis (Loew)	1			1
P. peltatus (Meigen)	230	25	34	289
P. podagratus (Zetterstedt)	1			1
P. scambus (Staeger)		1	7	8
P. scutatus (Meigen)	154	49	17	220
P. tarsalis (Schummel)	73	18	15	106
Pyrophaena granditarsa (Forster)			1	1
Scaeva pyrastri (Linnaeus)	1			1
S. selenetica (Meigen)	9	2		11
Sphaerophoria menthastri (Linnaeus))	65	5	16	86
S. scripta (Linnaeus))				
Syrphus ribesii (Linnaeus)	868	157	137	1162
S. torvus (Osten-Sacken)	42	5	14	61
S. vitripennis (Meigen)	26	12	4	42
Xanthandrus comtus (Harris)			1	1
Xanthogramma pedissequum (Harris)	13	7	6	26
Cheilosia albipila (Meigen)	6	3	11	20
C. albitarsis (Meigen)	3	7	26	36
C. antiqua (Meigen)	5			5
C. bergenstammi (Becker)	1		1	2
C. chrysocoma (Meigen)	4	5	6	15
C. fraterna (Meigen)	6	23	16	45
C. illustrata (Harris)	2		2	4
C. impressa (Loew)	1		4	5
C. intonsa (Loew)		1		1
C. nebulosa (Verrall)	8	2	2	12
C. paganus (Meigen)	48	74	89	211
C. praecox (Zetterstedt)			1	1
C. proxima (Zetterstedt)	12	2	3	17
C. scutellata(Fallen)		2	3	5
C. soror (Zetterstedt)		1		1

APPENDIX 2 CONTINUED

	1980	1981	1982	N
Cheilosia variabilis (Panzer)	4	4	4	12
Criorhina asilica (Fallen)	2		10	12
C. berberina (Fabricius)	50	44	81	175
Eristalis arbustorum (Linnaeus)	1			1
E. horticola (Degeer)		1	2	3
E. intricarius (Linnaeus)		6	1	7
E. nemorum (Linnaeus)	3	60	20	83
E. pertinax (Scopoh)	46	153	238	437
E. tenax (Linnaeus)	8			8
Eumerus ornatus (Meigen)	4	3	9	16
Ferdinandea cuprea (Scopoh)	208	176	233	617
F. ruficornis ((Fabricius)	1	2	10	13
Helophilus hybridus (Loew)		3	1	4
H. pendulus (Linnaeus)	124	321	987	1432
Heringia heringi (Zetterstedt)			2	2
Merodon equestris (Fabricius)	1			1
Microdon eggeri (Mik)	11	6	6	23
Myathropa florea (Linnaeus)	6	6	10	22
Neoascia podagrica (Fabricius)	16	59	34	109
Neocnemodon pubescens (Delucchi & Pschom-Walcher)	41	18	14	73
N. vitripennis (Meigen)				
Pipiza austriaca (Meigen)		6	11	17
P. bimaculata (Meigen)	4	6	18	28
P. fenestrata (Meigen)	1	2	3	6
P. noctiluca (Linnaeus)	29		1	30
Pipizella varipes (Meigen)		6		6
P. virens (Fabricius)	2	5		7
Rhingia campestris (Meigen)	567	347	214	1128
Syritta pipiens (Linnaeus)	8		15	23
Volucella bombylans (Linnaeus)	8	1	5	14
V. inflata (Fabricius)		1	9	10
V. pellucens (Linnaeus)	15	13	40	68
Xylota florum (Fabricius)			1	1
X. segnis (Linnaeus)	9	20	133	162
X. sylvarum (Linnaeus)	49	59	91	199
X. tarda (Meigen)	2		2	4
Xylotomima lenta (Meigen)	8	18	20	46
X. nemorum (Fabricius)	6	6	3	15
	6511	5107	8616	20,234
	95	87	92	115

APPENDIX 3

LIST OF ICHNEUMONIDAE PARASITIC ON SYRPHIDAE FROM THE MALAISE TRAP SAMPLES FROM BERNWOOD FOREST, 1 APRIL - 30 SEPTEMBER, 1980 - 1982

Subfamily Diplazontinae	1980	1981
Bioblapsis polita Snellen	1	
Campocraspedon caudatus Thom.	4	1
Diplazon laetatorius Fab.	11	21
D. pectatorius Thbg.	15	8
D. tetragonus Thbg.	14	81
Diplazon sp. 1	6	
Diplazon sp. 2	1	
Diplazon sp. 3	2	8
Diplazon sp. 4	1	
Enizemum ornatum Grav.	1	7
Promethes bridgmanni Fitton	2	1
P. punctiventris Thom.		4
P. sulcator Grav.	1	4
Sussaba cognata Hgn.	51	322
S. festiva Fab.		1
S. pulchella Hgn.	1	39
S. punctiventris Thom.	2	
Syrphoctonus pallipes Grav.	10	97
S. pictus Grav.	45	83
S. pulcher Hgn.	1	4
S. reflexus Morl.	5	
S. signatus Grav.		7
S. tarsatorius Panz.	9	7
Syrphoctonus sp. 3	1	
Syrphoctonus sp. 5		2
Syrphoctonus sp. 6		1
Syrphoctonus sp. 7		6
Syrphophilus tricinctorius Thbg.	28	31
Tymmophorus graculus Grav.	2	2
Woldsteditius abdominator Bridge.	10	67
W. biguttatus Grav.	4	5
W. flavolineatus Grav.	2	3
W. holarcticus Diller	1	27
Woldstedtius n. sp.		6

APPENDIX 3 CONTINUED

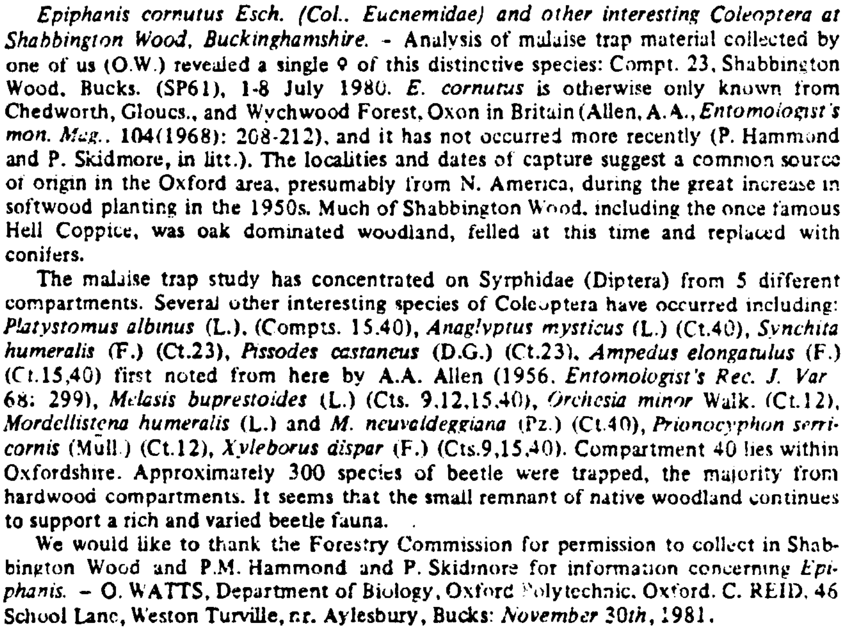
	1980	1981
Subfamily Gelinae		
Genera *Ethelurgus* and *Rhembobius* parasitic on Syrphidae; one species of *Bathythrix* also parasitic on Syrphidae		
Bathythrix pellucidator Grav.	154	77
Ethelurgus vulnerator Grav.	36	7
Rhembobius perscrutator Thbg.	2	
	425	929

Acknowledgement

All of the above species determinations were made by Henry Townes of the American Entomological Institute, Ann Arbor, Michigan.

APPENDIX 4

Note to the Entomologists' Monthly Magazine on Rare Coleoptera Captured in Malaise Traps at Bernwood Forest (Ent. Mon. Mag. 118: 78).



Epiphanis cornutus Esch. (Col.. Eucnemidae) and other interesting Coleoptera at Shabbington Wood, Buckinghamshire. - Analysis of malaise trap material collected by one of us (O.W.) revealed a single ♀ of this distinctive species: Compt. 23, Shabbington Wood, Bucks. (SP61), 1-8 July 1980. *E. cornutus* is otherwise only known from Chedworth, Gloucs., and Wychwood Forest, Oxon in Britain (Allen, A.A., *Entomologist's mon. Mag.*. 104(1968): 208-212), and it has not occurred more recently (P. Hammond and P. Skidmore, in litt.). The localities and dates of capture suggest a common source of origin in the Oxford area, presumably from N. America, during the great increase in softwood planting in the 1950s. Much of Shabbington Wood, including the once famous Hell Coppice, was oak dominated woodland, felled at this time and replaced with conifers.

The malaise trap study has concentrated on Syrphidae (Diptera) from 5 different compartments. Several other interesting species of Coleoptera have occurred including: *Platystomus albinus* (L.), (Compts. 15.40), *Anaglyptus mysticus* (L.) (Ct.40), *Synchita humeralis* (F.) (Ct.23), *Pissodes castaneus* (D.G.) (Ct.23), *Ampedus elongatulus* (F.) (Ct.15,40) first noted from here by A.A. Allen (1956. *Entomologist's Rec. J. Var* 68: 299), *Melasis buprestoides* (L.) (Cts. 9,12,15,40), *Orchesia minor* Walk. (Ct.12), *Mordellistena humeralis* (L.) and *M. neuvaldeggiana* (Pz.) (Ct.40), *Prionocyphon serricornis* (Müll.) (Ct.12), *Xyleborus dispar* (F.) (Cts.9,15,40). Compartment 40 lies within Oxfordshire. Approximately 300 species of beetle were trapped, the majority from hardwood compartments. It seems that the small remnant of native woodland continues to support a rich and varied beetle fauna.

We would like to thank the Forestry Commission for permission to collect in Shabbington Wood and P.M. Hammond and P. Skidmore for information concerning *Epiphanis*. - O. WATTS, Department of Biology, Oxford Polytechnic, Oxford. C. REID, 46 School Lane, Weston Turville, nr. Aylesbury, Bucks: *November 30th*, 1981.