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**Plant-Pollinator Interactions of the Ground Flora of a Deciduous
Woodland**

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A thesis submitted as part requirement for MSc in Ecology by Advanced Course

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ABSTRACT

The relationship between plants and pollinators were investigated in Shincliffe Woods, Durham, using 35 fixed quadrats. For three months, May, June and July, flowering phenology of the ground flora, general insect abundance and pollinator abundance were examined.

Most of the plant species present at the site flowered during May. This was also the month during which overall insect and pollinator abundance were greatest. General insect abundance fell during the next two months, while the number of plant species in flower and pollinator numbers fell in June but recovered in July. After May the majority of plants in flower were found at the site margins.

Most pollinators were generalists in nature and found on a number of plant species. This agrees with the findings of previous studies conducted in deciduous woodland. Few groups appeared to show a preference for any particular floral morphology, except Apidae which were found almost entirely on tubular flowers. These findings tend to support recent studies which suggest that plant-pollination relations are very general.

Coleoptera and Diptera were the most numerous pollinator classes. The array of pollinators seen changed with season, both in composition and abundance.

The majority of flowers had an open morphology and were white in colour. This may have been an adaptation to conditions where pollinators are scarce or erratic.

Fruit-set in most species was generally quite high. This was probably because of the widespread occurrence of autogamy and self-compatibility in the species studied. Because of the abundance of small, immobile pollinators such as Coleoptera and Diptera it is unlikely that the amount of outcrossing experienced by most plant species was high. Plants which relied on outcrossing for their reproductive success generally showed low fruit-set.

1.INTRODUCTION

The basic principles of biotic pollination are well known and have been widely reviewed (Baker and Hurd, 1968; Proctor and Yeo, 1973; Faegri and van der Pijl, 1979; Kevan and Baker, 1983; 1984). Most animal pollinated flowers offer pollen and/or nectar as rewards to their visitors. In return, the pollinator transfers pollen from the anther of one plant to the stigma of the same or another plant.

Many plant species are normally self pollinated, but outcrossing, the transfer of pollen from one plant to another, has positive selection value for plants by producing greater genetic variability (Faegri and van der Pijl, 1979). In addition, the amount of seed produced by outcrossed plants is often greater than that produced by self fertilised plants of the same species (Motten, 1986).

Pollination Communities

Pollination communities are competitively interacting systems, with plants competing for the services of pollinators and pollinators competing for plants (Faegri and van der Pijl, 1979; Kevan and Baker, 1983; 1984). Plants which utilise the same pollinators can come into competition with each other. Such competition can arise either by differential attraction to pollinators between competing species or by interspecific pollinator movements (Kordic-Brown and Brown, 1979; Motten, 1986). Differential attraction can lead to a reduced number of visits to poorer competitors, while interspecific pollinator movement acts by blocking the stigma with foreign pollen grains or by the loss of pollen to flowers of other species. Insufficient movement of compatible pollen to plant stigmas may limit the fecundity of a plant species and can therefore be a potent selective force on plant populations (Bierzuchudek, 1981). Plants should therefore act in such a way as to reduce this competition. Kevan and Baker (1984) listed several ways in which they could do this. The most common is thought to be staggering their flowering times so that species occupy different time niches. This can either be done seasonally or diurnally. This increases the likelihood that insect will concentrate their activity on one species of flower. However, if cross pollination is to be achieved, then insects must move between plants while foraging for food. Flowers must therefore maintain a balance in the reward they offer. It must be sufficient to attract the interest of pollinators but it must not be so great that they become satiated and do not visit conspecific flowers (Heinrich and Raven, 1972).

Competition may also be avoided by becoming more specialised and so reducing the spectrum of pollinators visiting flowers. Plant species which offer rich rewards may develop specialised

morphologies so to exclude insects with low energetic demands (Heinrich, 1979). Restricting pollinators also means that they are more likely to move between plants of the same species, so promoting outcrossing and minimising the wastage of pollen on the stigmas of unrelated species. A third possible means of reducing competition is by becoming autogamous (self fertilising).

However, Kevan and Baker (1983) have written that it is not established fact that the primary function of most of these mechanisms is to avoid competition. Brown and Kodric Brown (1979) have suggested that plant competition for pollinators may be only a weak force in the evolution and ecology of pollinator systems.

Studies at the Community Level

Most pollination studies have concentrated on one or a few closely related plants or pollinators. Few investigations have been undertaken at the community level. Those which have been made have concentrated on how plant species partition themselves to avoid competition for pollinators (e.g., del Moral and Standley, 1979; Thomson, 1980), while others have concentration on the relative contributions of different insects which act as pollinators within a community (e.g., O'Brien, 1980; Herrera, 1988b), or on how dependent plants within a community are on animal pollen vectors (e.g. Mulligan, 1972), or on the factors effecting insect visitation rates to flowers (McCall and Primack, 1992).

Recent community studies have thrown doubt on the ability of classical pollination syndromes to accurately describe the relationship between floral characteristics and patterns of insect visits (e.g. Herrera, 1988b; McCall and Primack, 1992). For example, It is widely believed that flowers with open morphologies should have a wider, less specialised range of pollinators than tubular flowers. McCall and Primack (1992) found that there was no difference in the proportions of each insect group which were found on flowers with either morphology, although the visitation rate to open flowers was higher. Similarly, Herrera (1988b) found that flowers in bloom at the same time tended to attract the types of insect, regardless of their morphology. However, Herrera (1988a) found that the tubular specialised flowers of the Mediterranean shrub *Lavandula latifolia* (Labiatae) attracted as diverse a range of pollinators as found visiting some open flowers, the difference being that the pollinators it attracted tended to be more efficient. These authors concluded that the relationship between insects and flowers is generally non-specific and might well vary between different communities.

Studies in Woodland

Pollination studies in woodland have tended to concentrate on the factors limiting fecundity in individual plant species (e.g., McCall and Primack, 1987; Horowitz and Schemske, 1988; Bertin and Shales, 1993). Few studies have been made at the community level and those which do exist have tended to concentrate on spring flowering woodland herbs. Schemske *et al.* (1978) studied flowering phenology and pollination of such herbs, while Motten (1986) made an extensive study of spring flowering woodland herbs, their pollinators and the factors which influenced their reproductive success.

There is a strong selection pressure on woodland herbs to flower early. Low light intensities after canopy closure are generally unsuitable for plant growth and can mean that plants cannot mature seeds even if they are sufficiently pollinated (Schemske *et al.*, 1978; Bertin and Shales, 1993). It appears that flowering in spring herbs takes place during the first prolonged period of warm weather suitable for pollinator activity (Schemske *et al.*, 1978). Early flowering means that plants risk exposure to weather conditions which are unsuitable for plant growth and pollinator activity. However, early flowering also means that light levels are relatively high since canopy closure has not yet occurred.

Spring flowering woodland herbs are unable to segregate themselves by blooming time to avoid competition because of the short period before canopy closure in which flowering is possible and because weather conditions early in the year often lead to unreliable pollinator activity (Motten, 1986). For these reasons, and because there was extensive sharing of generalist pollinators among plant species, it was hypothesised by Motten (1986) that insufficient pollination would limit fruit- and seed-set among early flowering herbs.

A surprising finding of Motten's study was that most of the plant species he studied did not suffer from pollen limited fecundity. The exception was for species which relied extensively on queen bumblebees for pollination. It was suggested that several characteristics of the plants helped to promote successful pollination despite these influences. Foremost among these was the accessibility of the flowers to different kinds of floral visitors which act as efficient pollinators, but also important were autogamy and self compatibility and the extended lifespan and receptivity shown by the flowers of most species.

Several characteristics of spring wildflowers promote pollination by generalist visitors. Foremost among these was the small number of visits required for full seed- or fruit-set. A second trait was self

compatibility since visitors need not move between separate, compatible plants. Motten (1986) speculated that it was competition between plants for pollinators was acting as a selective force to maintain these characteristics.

Aims of the Investigation

The aims of this investigation were to answer the following questions:

- i) What invertebrate groups formed the guild of flower visitors within the study site, and which were particularly dominant?
- ii) Did the array of flower visitors seen change with season?
- iii) What range of floral characteristics were found among the plant assemblages at the site, and did these change with season?
- iv) How did different plant species vary in the range and diversity of their pollinators?
- v) How did different insect groups vary in the range and number of the plants they visited?

The study did not limit its self to spring flowering herbs but also looked at later flowering species.

2. MATERIALS AND METHODS

2.1 The Study Site

The study site was an area of Shincliffe Woods, Durham. This is a mixed deciduous woodland with a canopy consisting mainly of Sycamore (*Acer pseudoplatanus*), Beech (*Fagus sylvatica*) and Oak (*Quercus robur*) and an understory of Holly (*Ilex aquifolium*) and Elder (*Sambucus nigra*). The area was bordered by a public footpath at one of its ends and an arable field at the other. A map of the area is shown in figure 1.

Originally, thirty 1m² fixed quadrats were arranged in a 5 parallel rows of 6 quadrats, each placed approximately 20m from the other. The rows transected the wood from near the footpath to the hedge marking the boundary of the arable fields and ran approximately North-east South-west. These quadrats were set approximately 10m in from the path to avoid trampling by the public. An extra 5 quadrats were later added near to the footpath to increase the number of blossoms being observed. In total 35 quadrats were laid down (figure 2).

Figure 2: Diagram of the study site. Quadrats were laid out in a grid system each approximately 20m apart. The shaded area shows quadrats that were added at the end of May.

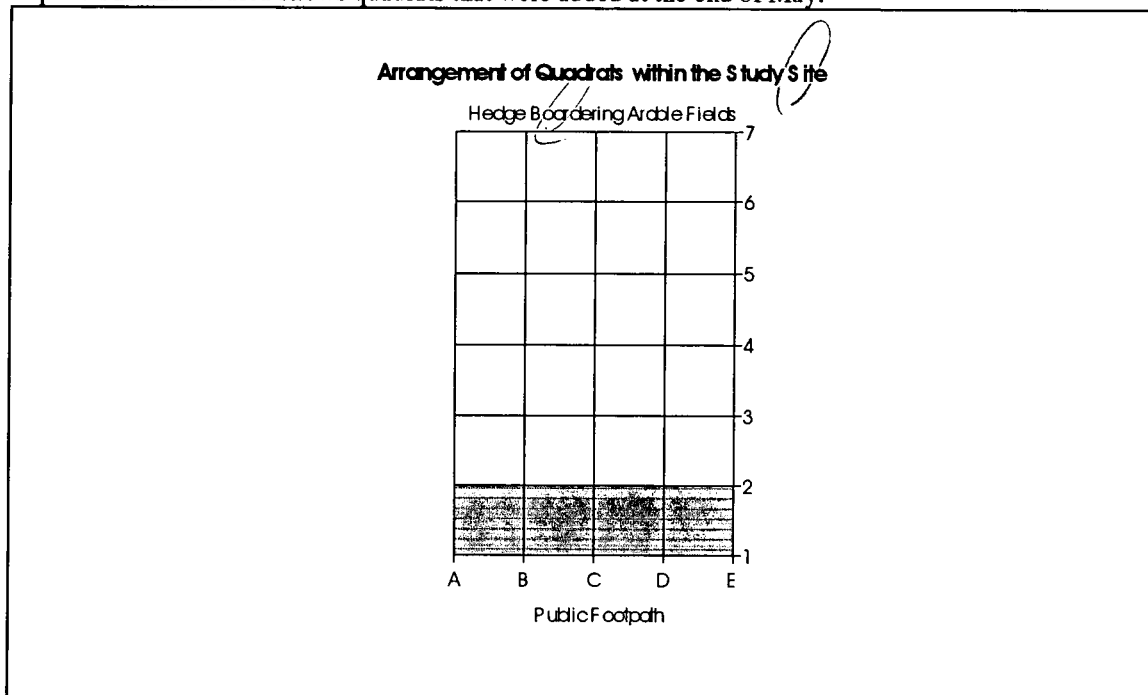

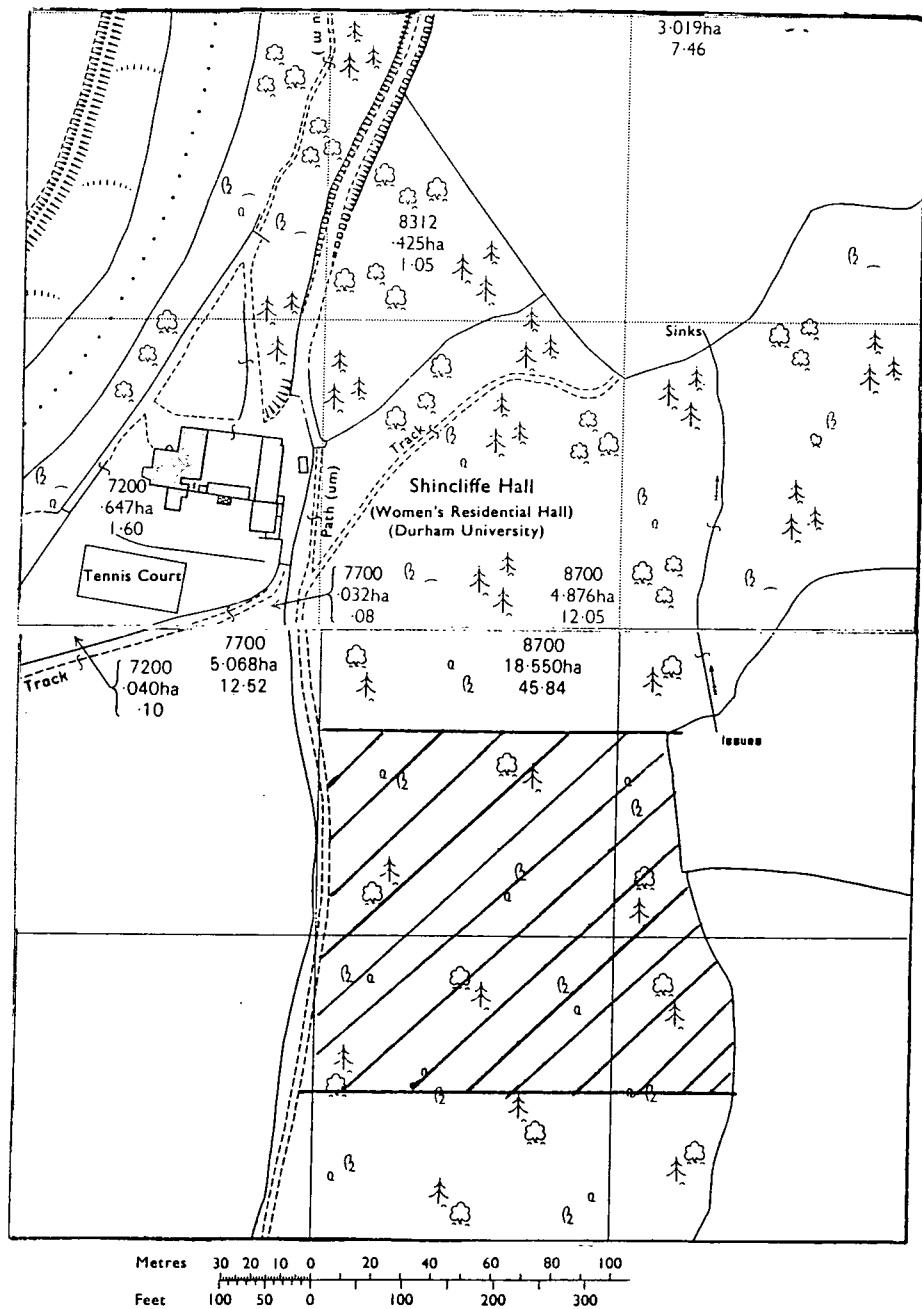


Figure 1: Map showing location of the study site.

Approximate location of study site 



2.2 Observation Periods

Observations were made in three different seasons. These three periods were:

- (1) **May** (mid-May to mid-June)
- (2) **June** (mid-June to early July)
- (3) **July** (early July to late July)

2.3 The Ground Flora

In each of the three seasons the following information was collected about the ground flora in each of the quadrats:

- (1) The percentage cover (Domin Scale) of each of the species.
- (2) The total number of the flowering stems present.
- (3) The number of flower buds, flowers and post flowering flowers present.

For the most common flowering plants a record of floral traits of the species was taken. These include flower size, colour, depth, morphology, symmetry and scent. This was done for at least five flowers per species. A note was taken of any invertebrates found within flowers.

2.4 Tree Density

The canopy density around each of the quadrats was calculated using the Point-Centred Quarter Method. An estimate of understory density was taken by counting the numbers and species of all the shrubs within 10m² of the centre of each quadrat.

2.5 Light Meter Readings

The light levels at the centre of each quadrat were measured using a standard light meter. This was done between 12.00 and 13.00 Hours on a uniformly overcast day in July. A measure of outside light levels was taken in an open field near the study site for comparison.

2.6 Insect Observations

Each of the quadrats was observed for a 10 minute period. The details recorded were:

- (1) The total numbers of flying insects entering the quadrat.
- (2) The numbers of flying insects making pollinator visits to flowers.
- (3) For pollinating insects, the number of flowers of each plant species visited.

Where possible the insects which entered the quadrats were captured using an aspirator.

The 10 minute observations were made twice each season during each of three time intervals. These time intervals were:

- (1) 09.00-12.00 Hours
- (2) 12.00-15.00 Hours
- (3) 15.00-18.00 Hours

2.7 Identification of Insects

Collected insects were identified down to the lowest possible taxonomic level using standard keys. This was mostly down to the level of family. Where possible flower visitors were identified down to species.

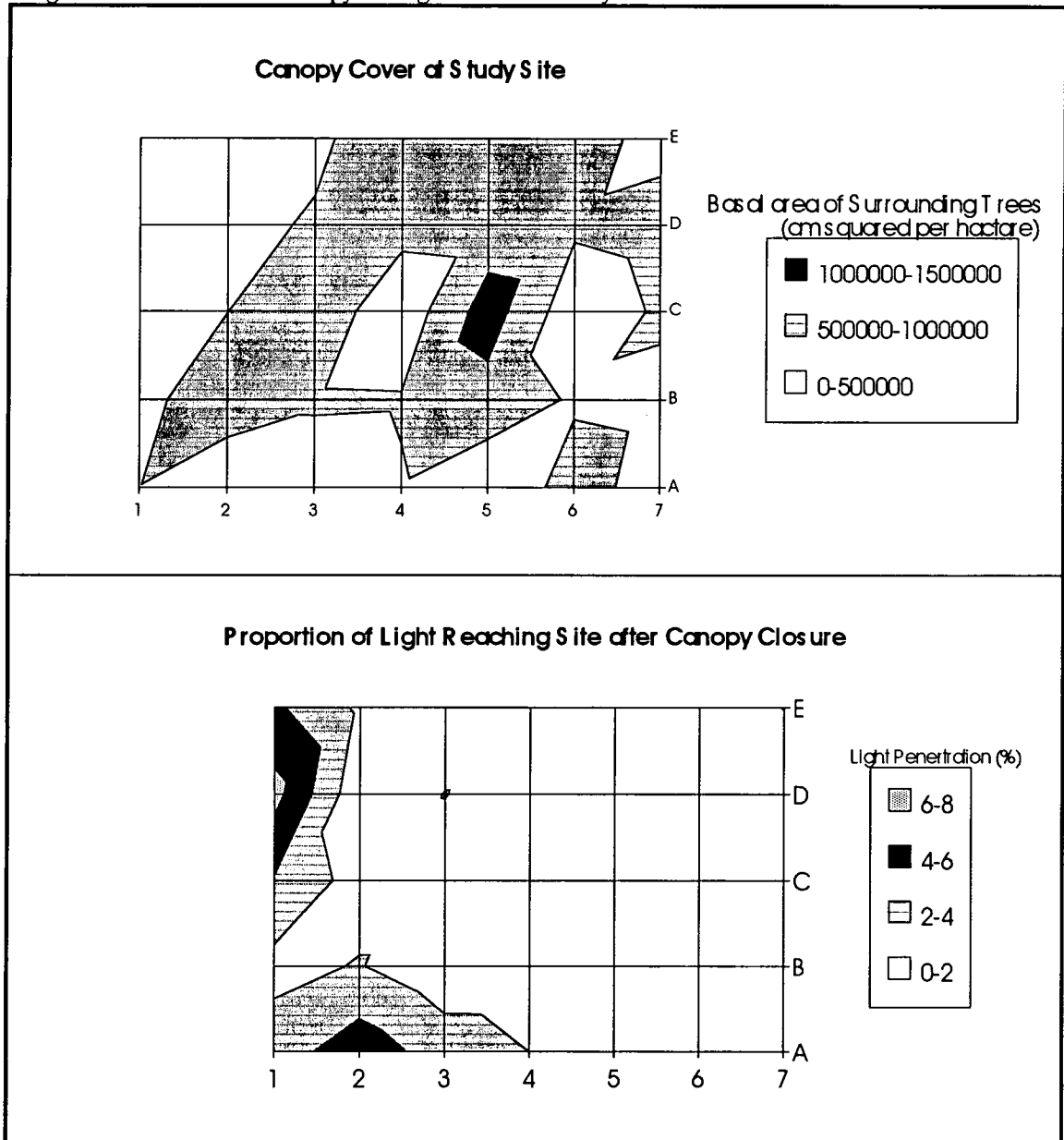
3. RESULTS

3.1 The Site

3.1.1 Environmental Factors

Figure 3 shows how canopy density (expressed as basal area) and the amount of available light after canopy closure, varied within the study area.

Figure 3: Distribution of canopy and light within the study site.



Canopy cover was greatest within the interior of the study site, while available light was greatest at its edge, particularly by the path. These two factors are probably related, although linear regression shows that there is no significant relationship between canopy density and the reduction in light levels. The amount of available light after canopy cover was very low.

3.1.2 Composition of Ground Flora

The complete list of plant species found within the quadrats is given in Appendix 1. Overall, 41 plant species were found of which 21 produced insect pollinated flowers. Table 1 shows the total number of species and the numbers of species in flower within each of the quadrats .

The numbers of plant species in the ground flora was highest in May. This was also the season in which most of the flowering species bloomed. Flowering plants were rare within the site interior after May. There was no relationship between either canopy cover or the amount of light penetration with either the total number of species in the ground flora or with the number of flowering species present (data log transformed).

Table 1 : Numbers of plant species within quadrats

QUADRAT	Number of Plant Species			Number of Plant Species in Flower		
	MAY	JUNE	JULY	MAY	JUNE	JULY
A1	11	10	10	6	4	3
A2	6	6	6	2	0	1
A3	6	6	6	1	0	1
A4	6	6	6	1	0	0
A5	7	7	7	1	0	0
A6	5	5	5	2	0	0
A7	6	5	5	2	2	2
B1	7	7	7	5	5	5
B2	7	7	7	2	0	1
B3	2	2	2	0	0	0
B4	3	3	3	0	0	0
B5	2	2	2	0	0	0
B6	7	6	6	3	0	1
B7	11	7	7	4	2	2
C1	10	10	11	4	3	3
C2	6	5	5	3	0	1
C3	2	2	2	0	0	0
C4	5	3	3	2	0	0
C5	12	7	5	6	0	0
C6	7	7	7	1	2	2
C7	9	8	8	4	3	3
D1	12	12	12	4	4	4
D2	6	4	4	4	0	0
D3	13	12	12	3	2	0
D4	7	7	7	1	1	0
D5	6	6	6	2	0	0
D6	8	8	8	2	0	0
D7	9	9	9	2	0	0
E1	8	8	9	4	3	5
E2	5	5	5	2	0	1
E3	5	5	5	1	0	0
E4	5	5	5	1	0	1
E5	6	6	6	3	0	0
E6	6	5	4	3	0	0
E7	5	4	4	2	0	1

3.1.3 Floral Characteristics

A list of the floral characteristics of the flowering species found is given in table 2.

Table 2: Floral characteristics of the plant species found during the study. Wind pollinated species excluded.

Species	Flower Type	No. Potential Flowers	Location within Site	Flowering Period
<i>Arum maculatum</i>	Trap	6	Interior+Margin	M
<i>Ranunculus ficaria</i>	Actinomorphic Open: Yellow	78	Interior+Margin	- M
<i>Oxalis acetosella</i>	Actinomorphic Open: White	16	Interior+Margin	- M
<i>Stellaria holostea</i>	Actinomorphic Open: White	410	Margin	- M
<i>Allium ursinum</i>	Actinomorphic Open: White	954	Interior+Margin	M
<i>Endymion non-scriptus</i>	Bell: Blue	4756	Interior+Margin	- M
<i>Adoxa moschatellina</i>	Green: Inconspicuous	190	Interior+Margin	- M
<i>Allaria petiolata</i>	Actinomorphic Open: White	32	Margin	- M
<i>Moehringia trinervia</i>	Actinomorphic Open: White	145	Margin	M J Jul +
<i>Veronica montana</i>	Actinomorphic Open: Blue	44	Margin	M
<i>Silene dioica</i>	Tubular: Red	348	Margin	M J Jul +
<i>Geranium robertianum</i>	Tubular Red	1973	Margin	M J Jul +
<i>Geum urbanum</i>	Actinomorphic Open: Yellow	121	Margin	M J Jul
<i>Galium aparine</i>	Actinomorphic Open: White	237*	Interior+Margin	J Jul
<i>Rubus fruticosus</i>	Actinomorphic Open: White		Interior+Margin	Jul +
<i>Lapsana communis</i>	Actinomorphic Open: Yellow	85	Margin	Jul +
<i>Heracleum sphondylium</i>	Actinomorphic Open: White	52 (Umbels)	Margin	Jul
<i>Stachys sylvatica</i>	Zygomorphic Purple	190*	Margin	J Jul +
<i>Impatiens glandulifera</i>	Zygomorphic : Pink. Scented	25	Margin	Jul +

+ Continued to flower beyond end of July season

- Already in Flower at the start of the May season

* Probably underestimated

The majority of the plant species which were in bloom during May had flowers of the open-bowl type. Many of these had flowered before the start of the May vegetation survey and one species not included on the list, wood anemone (*Anemone nemorosa*), had finished flowering altogether. Almost half of the plants which flowered in July had tubular flowers and continued to bloom after the investigation had ended. Most of the flowering species at the site were in bloom during May.

Few plants flowered in June. For most of this month only four species flowered. Three of these, herb robert (*Geranium robertianum*), herb bennet (*Geum urbanum*) and red campion (*Silene dioica*) were only found at the wood margins, with only common cleavers (*Galium aparine*) being found within the interior of the study site. Towards the very end of June some hedge woundwort (*Stachys sylvatica*) plants produced flowers.

During July the majority of species were still only to be found at the wood margins, with only bramble (*Rubus fruticosus*) being found in the interior. Species which produced complex zygomorphic flowers, such as *S.sylvatica* and himalayan balsam (*Impatiens glandulifera*) bloomed extensively during this month.

The majority of plant species found at the site had flowers of the open-bowl type. Most of these types of flower were white in colour. Tubular flowers were mostly red or pink in colour.

The number of flowers produced by *G.aparine* and *S.sylvatica* at the site were probably underestimated. For *G.aparine* this was because the stems tended to stick together and make counting difficult, while for *S.sylvatica* it was because not all the individual plants had produced flowering stems at the time of the July vegetation survey.

3.1.4 Insect Abundance

For each of the monthly observation periods there was a significant difference in the mean numbers of insects with both quadrat position, while in June and July there was also a significant differences with time of day. The effects of time of day and quadrat position showed a significant interaction in May and July, but not in June (table 3).

Table 3: Results of two way ANOVA conducted on insect observations from May, June and July

	MAY		JUNE		JULY	
Source of Variation	F value	P	F value	P	F value	P
Time of Day (df=2)	2.614	>0.05	15.678	<0.001	8.08	<0.001
Quadrat Position (df=30)	6.259	<0.001	6.533	<0.001	15.67	<0.001
Interaction (df=60)	1.609	>0.01	0.848	>0.05	2.186	<0.001

The combined results for each month show that there were significant differences in the mean numbers of insects seen between months ($F(2,270)=6.247$ $P<0.01$) and with time of day ($F(2,270)=6.112$ $P<0.01$). There was no apparent interaction between these two factors ($F(4,270)=1.082$ $P>0.05$). Table 4 shows that the number of insects seen was highest in May then fell steadily in June and July. The abundance of insects also changed with time of day, with overall numbers being highest at around midday, although in May they were higher in the afternoon.

Table 4: Total number of insects seen during May, June and July.

Month	Time of Observations			TOTAL
	0.900-12.00	12.00-15.00	15.00-18.00	
MAY	1246	1364	1422	4032
JUNE	926	1449	1233	3608
JULY	922	1151	1055	3128
TOTAL	3094	3964	3710	10768

Figure 4 shows the numbers of insects observed within each quadrat during the three seasonal observation periods.

Insect abundance was greatest at the edges of the site, but lower in the centre. This would seem to relate to canopy density and the amount of light penetration, which show the reverse of this pattern (figure 3), although there is no significant linear relationship between either of these two factors and insect abundance.

Diptera made up the largest proportion of insects seen during each month, bees and 'others' made up the smallest proportion (figure 5).

Figure 4: Total numbers of insects seen within the study site during each of the monthly observation periods. No observations were made of the quadrats corresponding to B3, B4, B5 and C3 because of the absence of any flowering plant species.

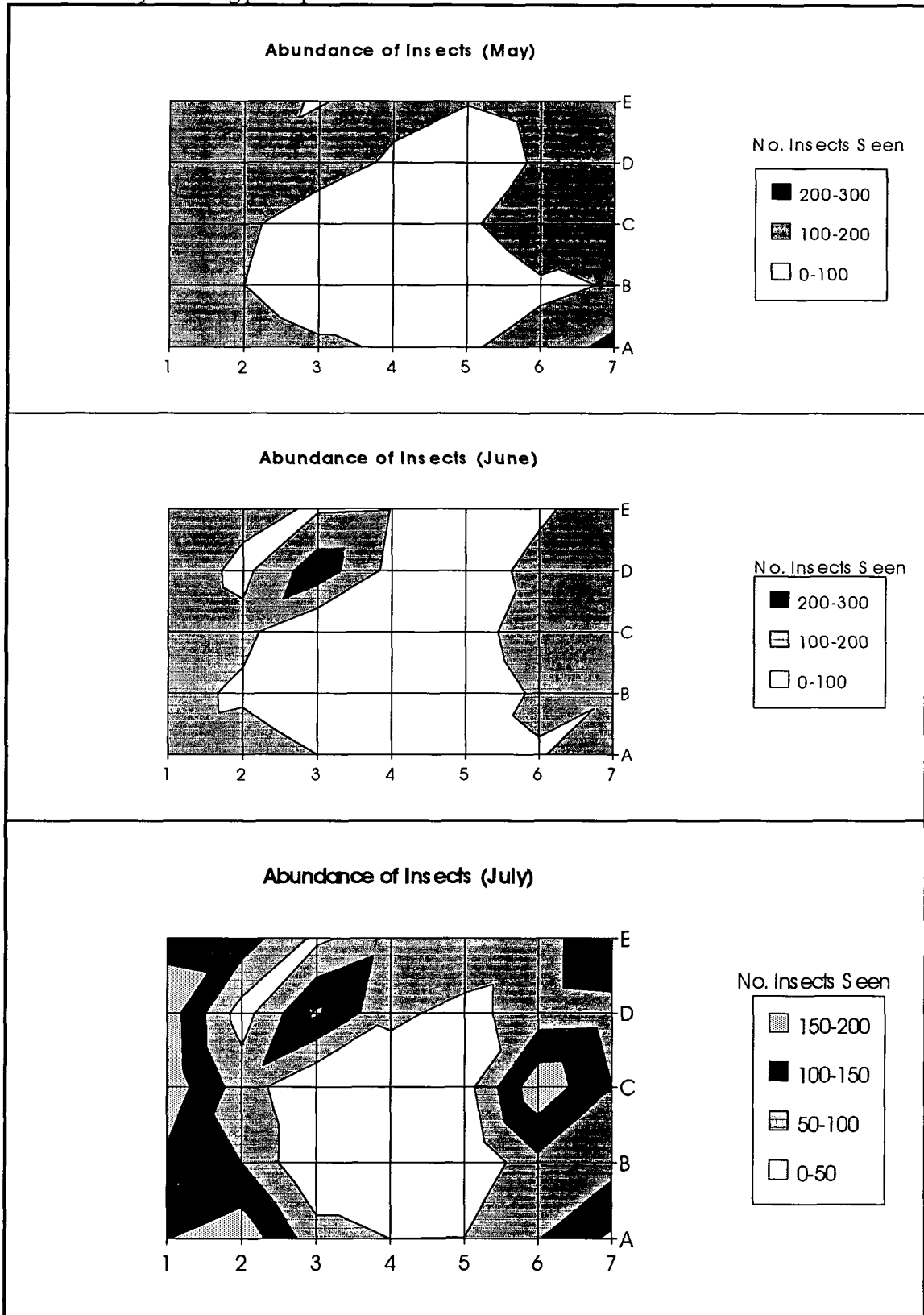
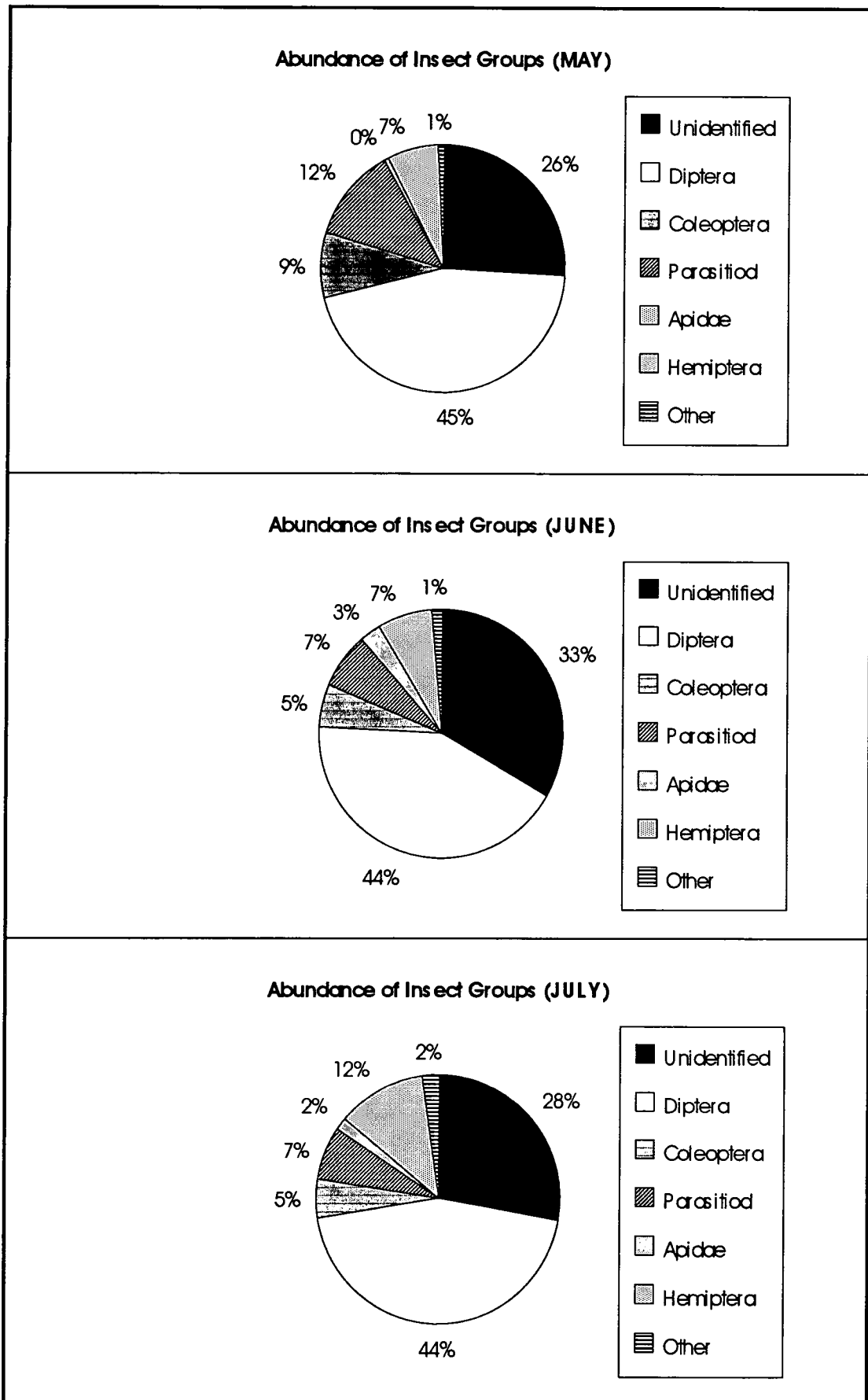


Figure 5: Relative abundance of insect groups during May, June and July



3.2. Flower Visitors

Pollinators were classified into 5 groups: Syrphidae (Hoverflies), other Diptera, Coleoptera (Beetles), Apidae (Bees), Hemiptera (Bugs) and other (miscellaneous flower visitors such as hymenopteran parasitoids or thrips). No lepidopteran pollinators were seen. The term pollinator is used for all insects found on or in flowers even though the presence of some of these may not have resulted in the transfer of pollen from anther to stigma. Table 5 shows the numbers of pollinator seen during the investigation and the number of flowers they visited.

Table 5: Summary of pollinators seen during the study and the number of flowers they visited.

a) Numbers of Pollinators

	MAY	JUNE	JULY	TOTAL
Syrphidae	4	2	16	22
Other Diptera	71	6	20	97
Coleoptera	69	33	38	140
Apidae	9	9	19	37
Hemiptera	9	0	19	28
Other	11	0	2	13
TOTAL	173	50	114	337

b) Numbers of Flowers Visited by Pollinators

	MAY	JUNE	JULY	TOTAL
Syrphidae	9	6	29	45
Other Diptera	94	10	23	127
Coleoptera	69	33	38	140
Apidae	28	25	70	123
Hemiptera	9	0	19	28
Other	11	0	2	13
TOTAL	220	74	181	475

By far the most numerous of the pollinator groups were the Coleoptera and the Diptera. The greatest number of flowers visits (almost 36% of total flowers visited) were made by Diptera (syrphids plus other), although Coleoptera and Apidae also made a substantial contribution to the number of flowers receiving pollinator visits (29% and 26% of total flower visits respectively).

There was significant variation across seasons in the numbers of Diptera (Syrphidae plus other Diptera), Coleoptera and Apidae pollinators ($\chi^2=26.213$; $df=2$, $P<0.001$) and in the numbers of flowers they visited ($\chi^2=51.386$; $df=2$, $P<0.001$). There was insufficient data on Hemiptera and others to include them in the

analysis but table 5 shows that they were also very variable between seasons. Diptera (Syrphidae and other Diptera combined) were the most variable group both in number ($\chi^2=57.09$) and number of flowers they visited ($\chi^2=67.053$) (df=2, $P<0.001$ in both cases).

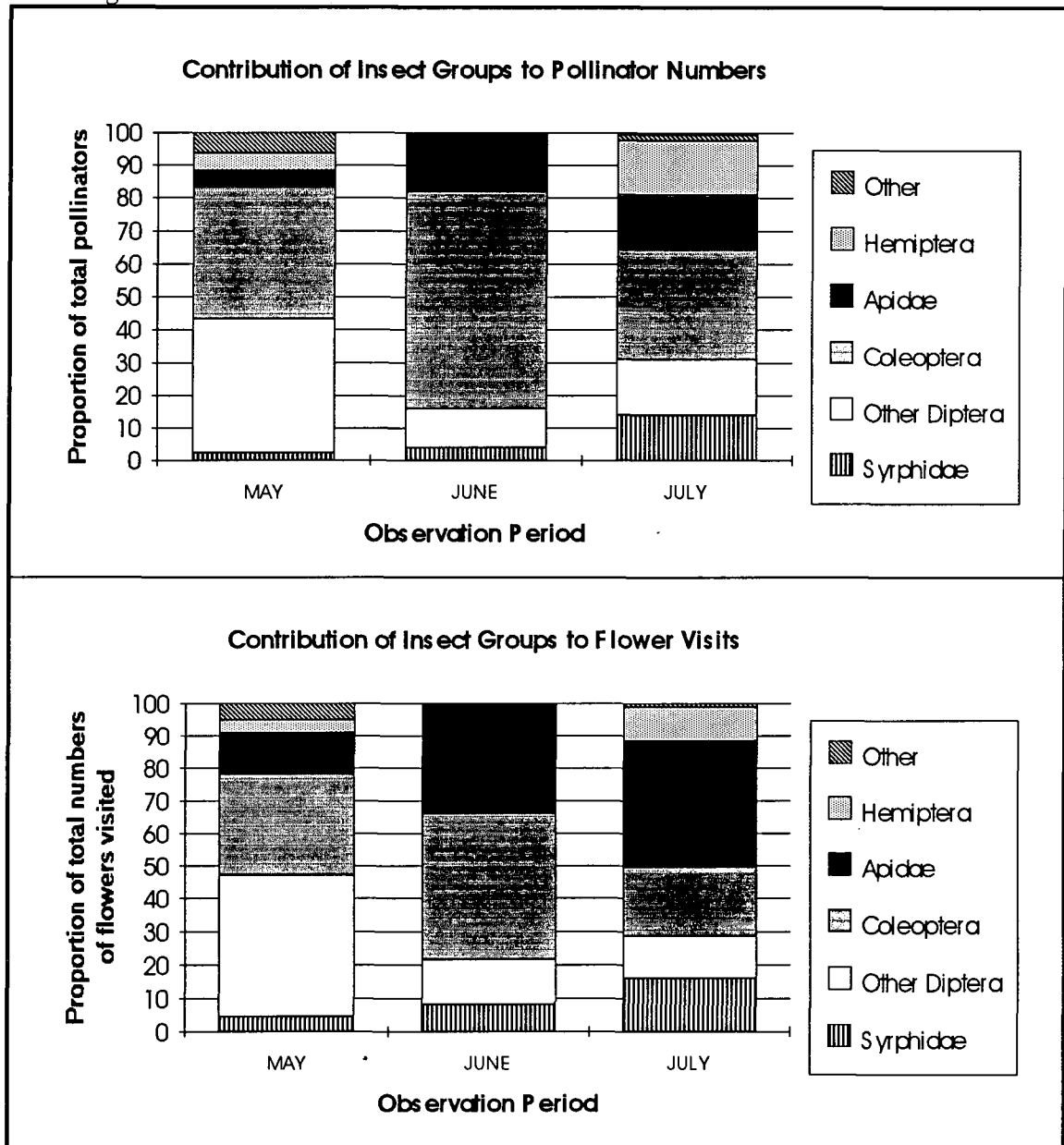
Numbers of Diptera and Coleoptera were greatest during May and then showed a fall. With Diptera there was a steep decline in numbers during June and then a slight recovery in July. Coleoptera numbers almost halved in June but stayed roughly constant in July. The number of flowers visited by syrphids and Apidae were greatest during July. The number of Apidae pollinators remained constant in the two months before this, while the number syrphid pollinators were very low in June. The number of pollinators seen during June was lower than in either of the other two months. Pollinators were most numerous during May.

Syrphids, Diptera and Apidae were mobile pollinators and were often seen visiting more than one flower whereas Coleoptera and Hemiptera seemed to remain within the same flowers.

Figure 6 shows the contribution of each visitor class to total pollinator numbers and to total number of flowers visited.

Diptera and Coleoptera made up the greatest proportion of the pollinators seen during May, with Diptera (syrphids plus others) being responsible for almost half of the visits to flowers during this month. Coleoptera accounted for a bigger proportion of visits to flowers in June than in May, although their numbers were lower in June. Bees were responsible for the biggest proportion of flowers visited during July although they did not account for a particularly large proportion of the pollinators seen during that month. In all months the contribution of bees and syrphids to the number of flowers which received pollinator visits was greater than their contribution to total pollinator numbers.

Figure 6: Contribution of insect groups to total pollinator numbers and to the total number of flowers receiving visits



3.2.1. Syrphidae

The numbers of hoverflies observed entering the quadrats showed significant variation between months ($\chi^2=15.5$; $df=2$, $P>0.001$). This was probably because of a sharp dip in the numbers seen in June, since the numbers seen in May and July are almost identical (figure 6).

Between months there was no significant difference in the ratio between the numbers of pollinators seen and number of flowers they visited ($\chi^2=0.388$. $P>0.5$). Figure 6 suggests that the proportion of the observed hoverflies which acted as pollinators was greater than in May than in July.

Figure 6: A summary of the observations made of Syrphidae during the study

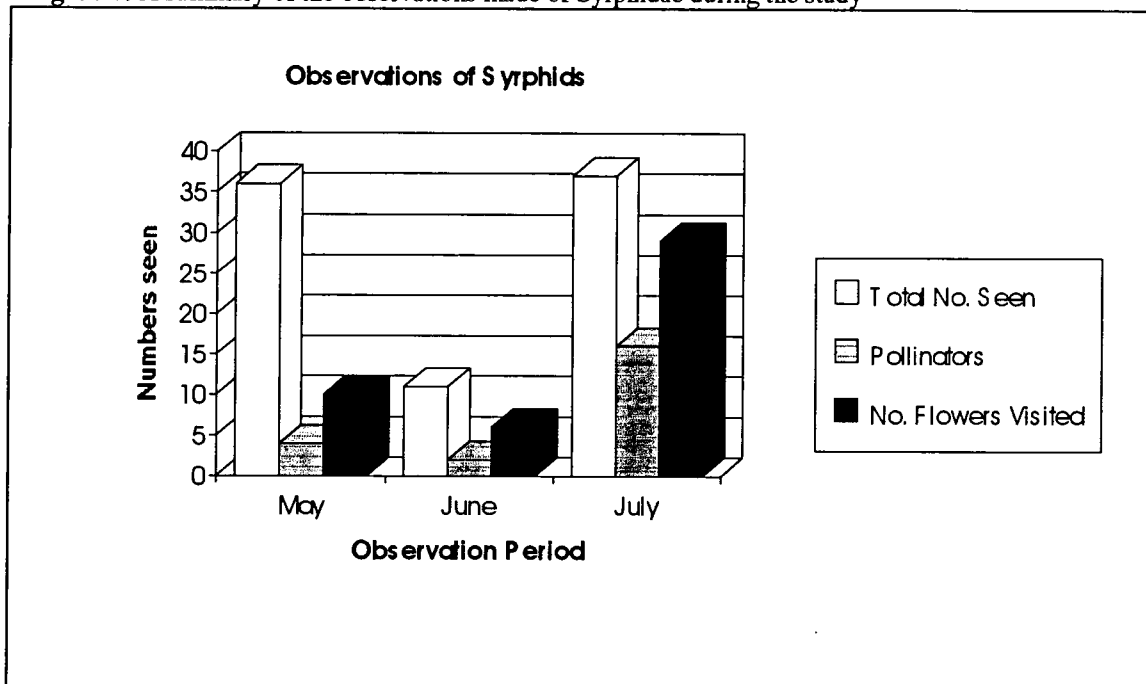


Table 6 summarises the flower visits made by hoverflies .

Table 6: Flower visits by Syrphidae

Species	No. Pollinators	% of Total Syrphid Pollinators	No. Flowers Visited	% of Total Flowers Visited by Syrphids	Flowers Visited per Pollinator	Proportion of Available Flowers Visited
<i>Geranium robertianum</i>	10	45.45	21	47.72	2.2±0.35	0.0117
<i>Silene dioica</i>	4	18.18	11	25.0	2.75±0.85	0.0316
<i>Rubus fruticosus</i>	6	27.27	8	18.18	1.66±0.21	0.32
<i>Heracleum sphondylium</i>	1	4.54	1	2.27	1	0.2*
<i>Lapsana communis</i>	1	4.54	3	6.62	3	0.428

* Based on 5 inflorescences

The plant species with the greatest number of flowers receiving visits by syrphids was *G.robertianum*, although when flower density is taken into account it can be seen that only about 1% of available flowers received visits. A high proportion of the available flowers of *L.communis* and *R.fruticosus* were visited.

There was no significant difference in the mean number of *G.robertianum*, *S.dioica* and *R.fruticosus* flowers visited by syrphids ($F_{(2,17)}=2.032$, $P>0.05$).

3.2.2. Other Diptera

Overall abundance of Diptera fell in each of the monthly observation periods (figure 8). Only a very small proportion of Diptera acted as pollinators. As can be seen from table 7, this is probably because a narrow range of dipteran families visited flowers.

Figure 8: A summary of the observations made of 'other Diptera' during the study

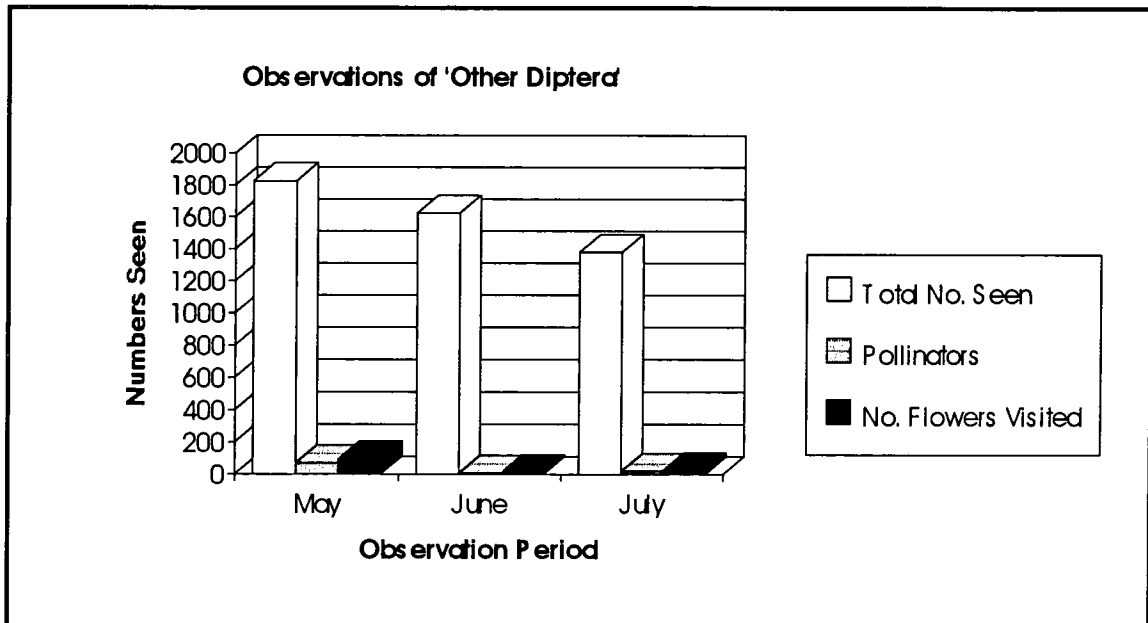


Table 7 gives a summary of Diptera which acted as pollinators.

Table 7: Dipteran Pollinators.

	Empidae	Schizophora	Other	TOTAL
May	59	5	7	71
June	4	1	1	6
July	6	13	1	20
TOTAL	69	19	9	97

Empidae were the most numerous in May but then showed a steep decline. Numbers of Schizophora were greatest in July, mostly due to pollinating visits by Muscidae to *R. fruticosus*. The rise in the number of Schizophora explains most of the rise in the total number of dipteran pollinators during July.

Table 8 summarises flower visits by Diptera.

Table 8: Flower Visits by Diptera

	No. Pollinators	% Total Dipteran Pollinators	No. Flowers Visited	% of Total Flowers Visited by Diptera	Proportion of Available Flowers Visited
<i>Endymion non-scriptus</i>	2	2.083	2	1.63	0.00042
<i>Allium ursinum</i>	17	17.71	17	13.82	0.1156
<i>Stellaria holostea</i>	23	23.96	23	18.7	0.0437
<i>Geranium robertianum</i>	34	35.42	61	49.59	0.0339
<i>Geum urbanum</i>	1	1.04	1	0.81	0.0096
<i>Silene dioica</i>	2	2.08	2	1.626	0.0057
<i>Galium aparine</i>	1	1.04	1	0.81	0.00422
<i>Lapsana communis</i>	1	1.04	1	0.81	0.1428
<i>Rubus fruticosus</i>	8	8.33	8	6.504	0.32
<i>Heracleum sphondylium</i>	7	7.29	7	5.69	3.5*

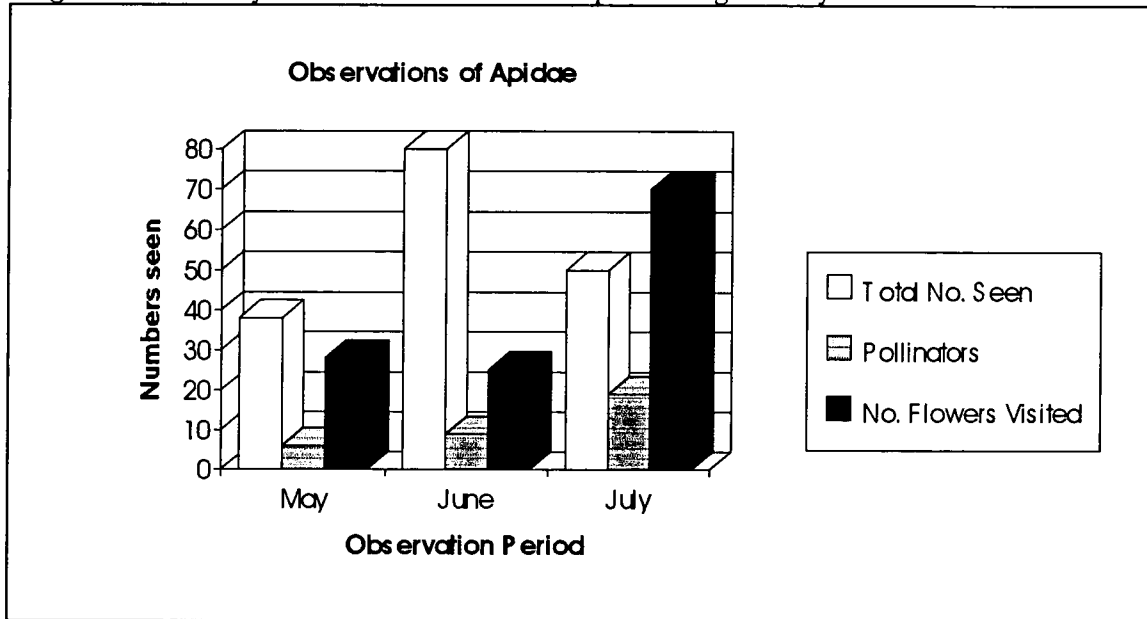
* Based on 5 inflorescences

The plants whose flowers received the most visits in proportion to their abundance were *Lapsana communis*, *R.fruticosus* and *H.sphondylium*. Once again *G.robertianum* was relatively unpopular despite attracting a large number of pollinators.

3.2.3 Apidae

Figure 9 summarises the observations of bees .

Figure 9: A summary of the observations made of Apidae during the study



There was an increase in the numbers of Apidae observed entering quadrats between May and June/July.

The very high number of bees in June resulted from one 10 minute observation in which 25 bees were seen. There was a significant difference in the numbers of pollinating bees ($\chi^2=8.176$) and the number of flowers they visited ($\chi^2=30.878$) between months (df=2, $P<0.001$ in both cases).

The ratio between the numbers of bees acting as pollinators and the numbers of flowers they visited appears to be greater in July than in the two previous seasons, although the difference was not significant ($\chi^2=0.402$ on 2 df, $P>0.5$).

The number of Apidae pollinators seen did not show a drop in June, whereas the number of pollinators of every other group did.

Table 9 summarises the flower visits made by bees.

Table 9: Flower visits by Apidae

Species	No. Pollinators	% of Total Apidae Pollinators	No. flowers visited	% of Total Flowers Visited by Apidae	Flowers Visited per Pollinator	Proportion of Available Flowers Visited
<i>Geranium robertianum</i>	19	55.88	66	55.46	3.58±0.61	0.0367
<i>Silene dioica</i>	3	8.82	7	5.88	2.33±0.33	0.0201
<i>Stachys sylvatica</i>	7	20.58	37	31.09	5.28±1.24	0.195
<i>Impatiens glandulifera</i>	1	2.94	3	2.52	3	0.6
<i>Rubus fruticosus</i>	4	11.76	6	5.04	1.5±0.21	0.24

G.robertianum received the greatest number of visits from pollinating Apidae. When correction is made for the numbers of flowers present it can be seen that only about 3% of the available *G.robertianum* flowers actually received visits and that only *Silene dioica* had a lower proportion of visits.

One way ANOVA showed that there was no significant difference in the mean number of *G.robertianum* flowers visited by syrphids and Apidae ($F_{(1,27)}=2.77, P>0.1$).

Table 10 gives a monthly breakdown of flower visits by bees.

Table 10: Pollination visits by Apidae during May, June and July

Species	MAY		JUNE		JULY	
	No. Pollinators	No. Flowers Visited	No. Pollinators	No. Flowers Visited	No. Pollinators	No. Flowers Visited
<i>Geranium robertianum</i>	5	24	8	24	6	20
<i>Silene dioica</i>	2	4	0	0	1	3
<i>Stachys sylvatica</i>	-	-	1	1	6	36
<i>Impatiens glandulifera</i>	-	-	-	-	1	3
<i>Rubus fruticosus</i>	-	-	-	-	6	8

One way ANOVA shows that there is no significant difference in the mean number of *G.robertianum* flowers visited by bees between months ($F_{(2,16)}=0.7109, P>0.05$). However, the proportion of pollinators

visiting *G.robertianum* shows a sharp decrease in July when visits to other plant species become more frequent. The rise in the number of flowers visited during July seems to have occurred because more bees were visiting plants such as *S.sylvatica* and *R.fruticosus*. There was no significant difference in the mean number of flowers visited by bees between months (one way ANOVA : $F_{(2,31)}=0.906$, $P>0.05$), or in the mean number of flowers of different plant species visited ($F_{(3,31)}=2.87$, $P>0.05$).

3.2.4. Coleoptera

The majority of pollinators in this class were *Meligethes* or *Byturus*. Their relative numbers are shown in table 11.

Table 11: Abundance of Coleopteran pollinators during May, June and July

	<i>Meligethes</i> Sp.	<i>Byturus</i> Sp.	Other	TOTAL
May	31	35	4	70
June	0	31	1	32
July	15	20	3	38
TOTAL	46	86	8	140

There is a big difference between seasons in the numbers of *Meligethes*, while *Byturus* numbers are more constant. *Byturus* seems to be more abundant than *Meligethes* in all seasons. The cause of the fall in the number of Coleopteran pollinators between May and June seems to have been caused by the loss of *Meligethes*.

Table 12 summarises pollination visits by beetles.

Table 12: Pollination visits by Coleoptera

Plant Species	No. Pollinators	% of Coleopteran Pollinators	Proportion of Available Flowers Visited
<i>Endymion nonscriptus</i>	12	8.57	0.0025
<i>Allium ursinum</i>	10	7.14	0.068
<i>Stellaria holostea</i>	4	2.86	0.0076
<i>Geranium robertianum</i>	58	41.43	0.0322
<i>Geum urbanum</i>	20	14.28	0.192
<i>Silene dioica</i>	4	2.86	0.0115
<i>Lapsana communis</i>	13	9.28	1.857
<i>Rubus fruticosus</i>	12	8.57	0.48
<i>Heracleum sphondylium</i>	7	5.00	3.5*

* Based on 5 Inflorescences

Compared to syrphids and Apidae, Coleoptera were found on a wide range of plant species. This perhaps reflects their abundance during each month. Beetles are not very mobile flower visitors and were not seen to move between individual flowers, although some were observed coming from outside quadrats to make flower visits. Once again *G.robertianum* had the greatest number of flowers visited by pollinators although only a small proportion of the available flowers received visits. The flowers of many species had more than one beetle within them and this accounts for the high proportion of *H.sphondylium* and *L.communis* which were visited.

3.2.5 Hemiptera

The Hemiptera found on flowers in May mostly belonged to the family Aphidae. Those found in July were either Miridae or predatory Reduviidae.

3.3 Visits to Particular Plant Species

3.3.1 Pollinators on Plants

Table 13 gives a full list of the pollinators found on different plant species.

Table 13: Pollinators observed visiting different plant species

PLANT	Pollinator	Numbers	Number of flowers visited	Proportion of total flower visits
<i>Geranium robertianum</i>	Empidae	15	16	7.84
	<i>Polyblepharis opaca</i>	6	14	6.86
	Tabanid	7	23	11.27
	Syrphidae	10	22	10.78
	Other Diptera	6	8	3.92
	<i>Byturus</i> Sp.	45	45	22.06
	<i>Meligethes</i> Sp.	5	5	2.45
	Elateridae	3	3	1.47
	Apidae	19	68	33.33
<i>Silene dioica</i>	Empidae	1	1	3.45
	Syrphidae	4	11	37.93
	Muscidae	1	1	3.45
	<i>Byturus</i> Sp.	1	1	3.45
	<i>Meligethes</i> Sp.	3	3	10.34
	Aphidae	4	4	13.79
	Miridae	1	1	3.45
	Apidae	3	7	24.14
<i>Geum urbanum</i>	<i>Byturus</i> Sp.	20	20	90.9
	Schizophora	1	1	4.95
	Parasitoid	1	1	4.95
<i>Stellaria holostea</i>	Emptidae	23	23	60.52
	<i>Meligethes</i> Sp.	3	3	7.89
	Elateridae	1	1	2.63
	Parasitoid	1	1	2.63
	<i>Anthocoris nemorum</i>	1	1	2.63
	Thysanoptera	9	9	23.68
<i>Allium ursinum</i>	Empidae	17	17	62.96
	<i>Meligethes</i> Sp.	9	9	33.33
	Elateridae	1	1	3.7

<i>Endymion non-scriptus</i>	Empidae	2	2	14.2
	<i>Meligethes</i> Sp.	12	1	85.71
<i>Lapsana communis</i>	Empidae	1	1	4.54
	Syrphidae	1	3	13.64
	<i>Byturus</i> Sp.	3	3	13.64
	<i>Meligethes</i> Sp.	10	10	45.45
	Curculionidae	1	1	4.54
	Miridae	2	2	9.1
	Reduviidae	2	2	9.1
<i>Galium aparine</i>	Mycetophilidae	1	1	100
<i>Stachys sylvatica</i>	Apidae	7	37	100
<i>Impatiens glandulifera</i>	Apidae	1	3	100
<i>Heracleum sphondylium</i>	Empidae	2	2	7.69
	<i>Scatophaga stercoraria</i>	2	2	7.69
	Scatopsidae	1	1	3.85
	Fannidae	1	1	3.85
	Muscidae	2	2	7.69
	Syrphid	1	1	3.85
	<i>Meligethes</i> Sp.	6	6	23.08
	Curculionidae	1	1	3.85
	Miridae	4	4	15.38
	Reduviidae	2	2	7.69
	Parasitoid	4	4	15.38
<i>Rubus fruticosus</i>	Empidae	2	2	5.13
	Syrphidae	6	8	20.51
	Muscid	6	6	15.38
	<i>Meligethes</i> Sp.	5	5	12.82
	<i>Byturus</i> Sp.	7	7	17.95
	Miridae	8	8	20.51
	Reduviidae	1	1	2.56
Apidae	4	6	15.38	

Because of the scarcity of pollinators the relative importance of some insects as flower visitors is overvalued (e.g. Aphidae on *S.dioica*). There did not appear to be much specialisation among pollinators. Insects were frequently found on several different plant species. For mobile pollinators such as bees there seemed to be a high degree of fidelity within individual foraging trips. Only on two occasions was a bee seen to move between two different plant species. Most plant species had a range of pollinators, not all of which are likely to be equally efficient. The exception to this was with complex zygomorphic flowers, which were visited entirely by bees.

Some of the plant species with open-bowl type flowers seemed to receive pollinating visits from a remarkably few different types of insect (e.g. *G.urbanum*) compared to some more complex flowers.

The list only includes pollinator visits which were observed within the quadrats. From general observations at the site it could be seen that: *Endymion non-scriptus* was also visited by *Bombus terrestris* and *Ranunculus ficaria* growing by the footpath received visits from *Byturus*. A biblionid fly and a specimen of the predatory bug *Anthocoris nemorum* were collected from *Anemone nemorosa* before it ceased flowering.

The common honeybee (*Apis mellifera*) was not observed at any time at the site during the period of field work but could be seen visiting *G.robertianum* and *I.glanduifera* during August.

3.3.2 Pollination of *Geranium robertianum*

Because of the large number of pollinators which made visits to *Geranium robertianum* and its extended flowering period, it was possible to compare insect visits between the three seasons (Table 10).

Table 10: Pollinators of *Geranium robertianum*

a) Numbers and Type of Pollinators

Visitor	MAY	JUNE	JULY	Total
Syrphidae	3	1	7	11
Other Dipper	26	5	3	34
Coleopteran	29	23	6	58
Aped	6	8	6	20
Hemiptera	3	0	0	3
Total	67	37	22	126

b) Number of Flowers Visited by Pollinators

Visitor	MAY	JUNE	JULY	TOTAL	Proportion of Available flowers Visited
Syrphidae	5	1	16	22	0.0122
Other Diptera	49	9	3	61	0.0339
Coleoptera	29	23	6	58	0.0322
Apidae	27	24	20	71	0.0395
Hemiptera	3	0	0	3	0.0016
TOTAL	113	57	45	215	

The numbers of Coleoptera and Diptera decreased between May and July. Coleoptera numbers were fairly constant in May and June but fell in July. The same could be seen with overall coleopteran pollinators (Table 5), although this is not surprising since a large proportion of coleopteran pollinators (40%) were found on *G.robertianum* (Table 9). The number of flowers visited by syrphids increased in July compared to June and May.

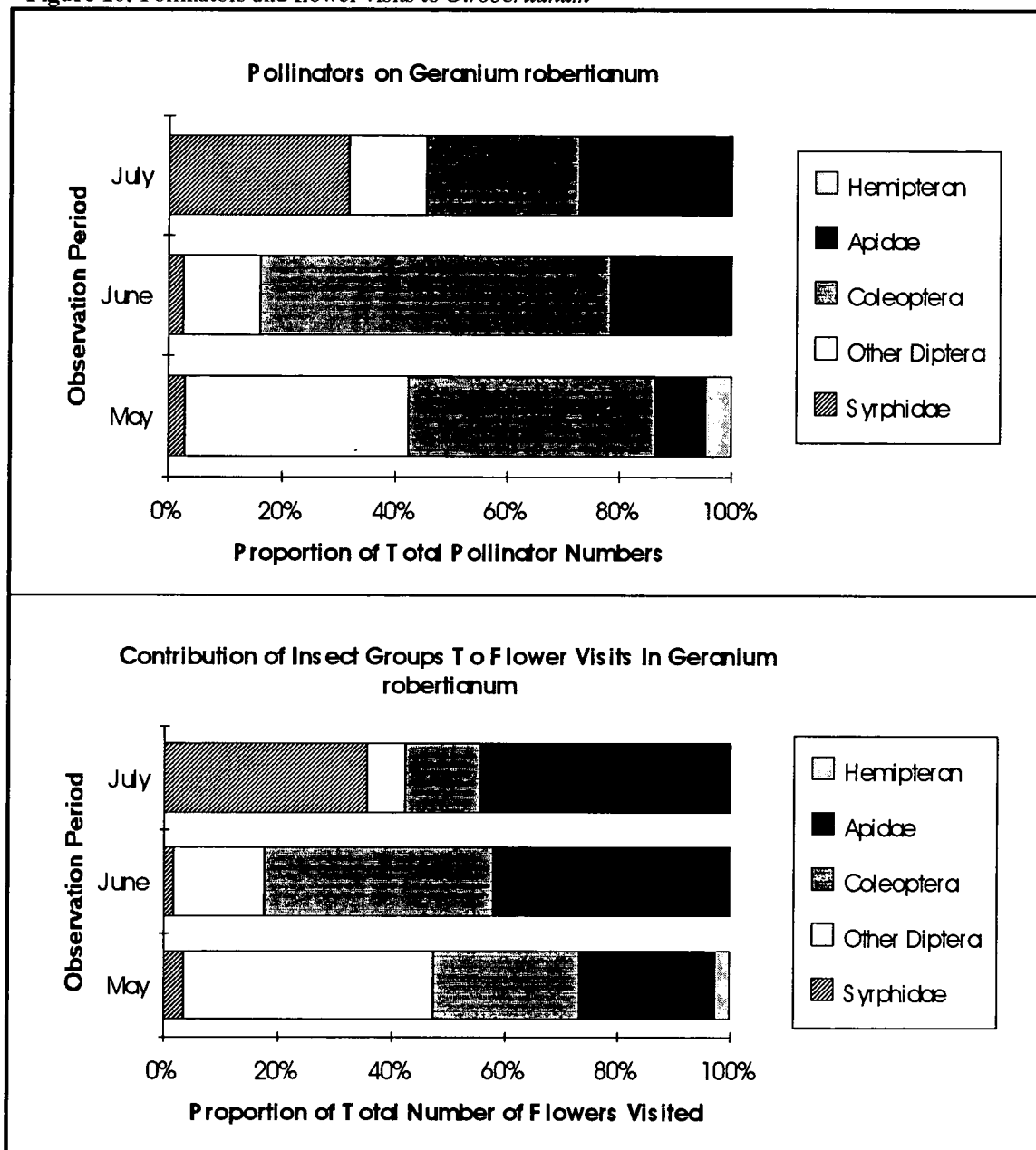
Total number of pollinators were highest in May and decrease in June and July. It is interesting that the number of visitors are greater in June than in July. This goes against the overall trend for pollinators (table 5), and is probably the result of *G. robertianum* being the dominant plant species during that month. The fall in July may be the result of more attractive plant species becoming available.

There is no significant difference in the distribution of pollinating bees between the three seasonal periods ($\chi^2=0.737$; $df=2$, $P<0.05$). This tends to confirm that the increase in bee pollinators which was seen in July was caused by visits to more specialised flowers such as *S.sylvatica* .

No pollinator visited more than about 4% of the available *G.robertianum* flowers.

Figure 10 shows the proportional contribution of each insect group in visits to *G. robertianum*.

Figure 10: Pollinators and flower visits to *G. robertianum*



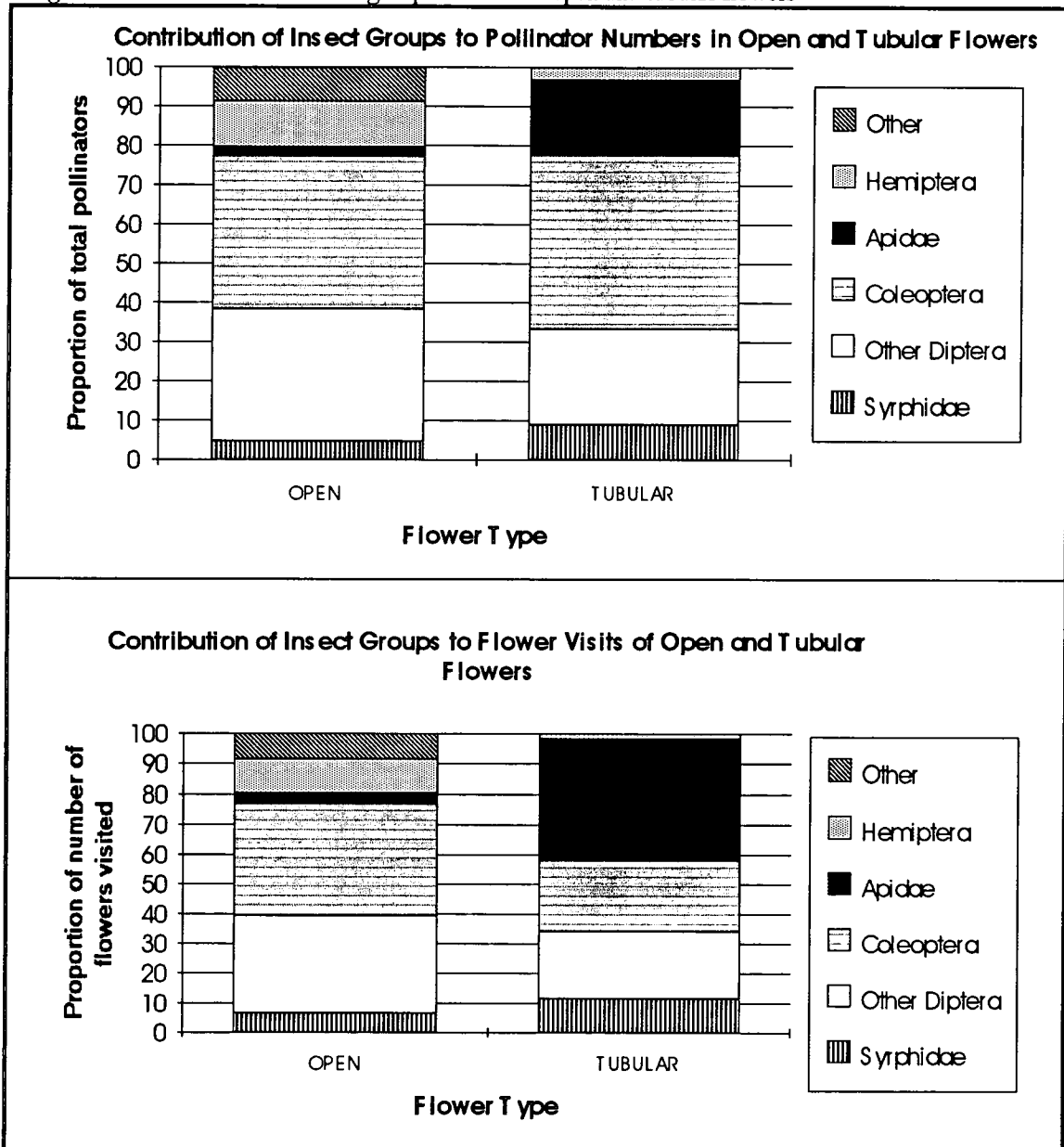
Coleoptera and Diptera made up the greatest proportion of flower visitors during May. Coleoptera make up the greatest proportion of pollinators in June but a smaller proportion in July. Syrphids and Apidae together make account for a larger proportion of the flowers visited in July (around 80%) but a small proportion of pollinator numbers (around 40%). This is a greater proportional contribution than was made

to overall flower visits (figure 5). The importance of bees increases over each month with a decrease in the numbers of other pollinators.

3.4. Flower Preferences

Figure 11 shows the contribution made by each insect group to the total number of pollinators visiting open and tubular flowers and the contribution made to total flower visits.

Figure 11: Contribution of insect groups to visits of open and tubular flowers



There does not appear to be much difference in the proportion of coleopteran pollinators which were found on tubular and open flowers, although their contribution to the number of open flowers visited is greater. A slightly larger proportion of dipteran pollinators were found on open than tubular flowers although again they contributed a larger proportion to the number of open flowers visited.

The majority of fly and beetle visits to tubular flowers consisted of visits to *G.robertianum*.

Hoverflies account for a slightly greater proportion of the pollinators on tubular than open flowers. Bees account for around 40% of tubular flowers visited, but only 20% of the pollinators on tubular flowers. All the open flowers visited by bees were of one species, *R.fruticosus*.

Fisher's Exact Test was used to examine whether there was any preference among insect groups for open and tubular flowers. For each insect group a 2x2 Contingency table was drawn up comparing the numbers of plant species with open flowers and the number of plant species with tubular flowers which did or did not receive visits from that group. The only significant result was for Apidae (Fisher Exact Probability of 0.01963). Figure 9 would suggest that bees have a distinct preference for tubular flowers.

3.5. Successful Fruit Set by Plant Species

3.5.1 Failures and species not examined

There was no observed fruit-set in *Oxalis acetosella*, although this species later produced cleistogamous flowers. All the *Arum maculatum* within the quadrats was grazed before flowering. *Anemone nemorosa* had ceased to flower at the time of the first vegetation survey but there was no evidence that it had successfully set seed. *Adoxa mochatellina* had died before there was a chance to assess its success.

3.5.2 *Ranunculus ficaria*

Most of the remaining plants of this were washed away by bad weather in late May so it was not possible to achieve a full measure of their success. In most cases there were only a few scattered flowering stems, but in all the quadrats at which this species occurred had at least one successful flower and comparatively dense patches the proportion of flowers reaching maturity was as great as 70%.

3.5.3. *Endymion non-scriptus* and *Allium ursinum*

For these two species there was no data available on the numbers of flowers on each individual stem so it was not possible to compare samples using ANOVA. The coefficient of variation (CV) was used instead. CV is equal to standard deviation / mean x 100 (Snedicore and Cochran, 1967). As a rule of thumb CV values of over 50% are usually taken to indicating extreme variation within a sample, while those under 10% signify extreme uniformity; intermediate CV values are considered to represent no more than the normal variation expected in most samples (P.E.Hulme, *Pers.Comm.*).

CV for the number of flowers per stem of *E.non-scriptus* was about 25%, and for the proportion of successfully matured flowers per stem was 62.07%. Therefore it appears that there was significant variation in fruit-set within the site. The proportion of *E.non-scriptus* flowers which successfully matured was extremely variable and ranged from 80% to 2.35% between quadrats. No relationship between flower success and either canopy cover or light levels could be found using linear regression.

For *A.ursinum* CV for the proportion of successful flowers was 14% and for numbers of flowers produced per stem 91.5%. In this case there appears to be significant variation in the number of flowers produced by *A.ursinum* plants within the site. Fruit set was usually very high with the proportion of flowers matured being greater than 80% in all except one case. The lowest proportion of matured flowers was 64%.

3.5.5. *Geranium robertianum* and *Geum urbanum*

One Way ANOVA showed that there was significant variation in the mean numbers of flowers per stem of these two species in between quadrats ($F_{(6,146)}=8.31$ $P<0.001$ for *Geranium robertianum*; $F_{(5,32)}=5.69$ $P<0.001$ for *Geum urbanum*), but not in the mean proportion of successful flowers ($F_{(6,146)}=0.89$ $P>0.5$ for *Geranium robertianum*; $F_{(5,32)}=1.357$ $P>0.05$ for *Geum urbanum*). No relationship could be found between either canopy cover or light levels and the number of flowers per stem.

Although neither species had completely finished flowering at the time of the last vegetation survey, percentage fruit set was high with a mean of 75.839% \pm 1.18% for *G.robertianum* and 92.12% \pm 2.38% for *G.urbanum*.

3.5.6. *Silene dioica*

One way ANOVA showed that there was no significant difference between quadrats in the mean number of flowers per plant for either male or female plants ($F_{(4,20)}=0.663$ $P>0.05$ for male plants; $F_{(3,18)}=0.743$ $P>0.05$ for female plants), or in the proportion of flowers which had successfully matured at the time of the last vegetation survey ($F=1.738_{(3,18)}$ $P>0.05$). Mean fruit-set was generally quite low, $47.58\% \pm 4.9\%$

Contingency table analysis showed that there was no overall difference in the numbers of male to female plants ($\chi^2=2.552$, $df=3$ $P<0.01$)

4.DISCUSSION

4.1 Site Characteristics

There was great heterogeneity in the density of canopy within the site and the amount of light reaching the site floor. In general canopy density was greatest, and light penetration lowest, within the interior of the study site. Canopy density and light levels at the site are obviously related, although linear regression showed no significant relationship between these two factors. The reason for this is not clear.

There was no significant relationships found between either canopy density or light penetration and any other factor which was measured.

There was very little light reaching the floor of the study site after canopy closure. Both Schemske *et al.* (1978) and Motten (1986) found that light levels fell markedly after canopy closure, from 50% to less than 10%.

4.2 Flower Characteristics

The biggest proportion of flowering species found at the site bloomed, or were in flower at the beginning of, May. This presumably is related to increased canopy cover, with conditions being unfavourable for plant growth after levels of available light had fallen. Several authors have found that the reproductive output and receipt of pollen by woodland plants decreases after canopy closure (e.g., Agren and Willson, 1992; Bertin and Sholes, 1993). After canopy closure the majority of flowering species were found at the site margins, where presumably the light environment was more suitable for plant growth.

The majority of plant species found had open-bowl type flowers. This was particularly true of the early flowering species. Open flowers are generally regarded as being non-exclusive to all pollinator types (Faegri and van der Pijl, 1979). This is obviously valuable where pollinator activity is low or erratic. There was a comparative lack of more specialised flowers, and these tended to appear later in the season when 'specialist' pollinators such as bees were more common.

Most open flowers were white in colour. This was also the finding of Schemske *et al.* (1978) and Motten (1986). Schemske *et al.* (1978) speculated that this was because the colour white is very conspicuous against the brown and green background of leaf litter and foliage. High visibility can lead to rapid location, which may be important if pollinators numbers are low or if suitable flight

conditions are sporadic, as they would tend to be early in the year (Heinrich, 1979). However, some late flowering species also had white flowers. Baker and Hurd (1968) reported that the majority of flowers in North American dark redwood and douglas fir forests were white or pink in colour, although O'Brien (1980) also found that most of the open flowers in the Californian pavement plane which she studied were also white in colour. Pale colours seem to be generally associated with syndromes attracting generalist pollinators (Faegri and van der Pijl, 1979) and this might explain the predominance of white.

Motten (1986) found that autogamy and self compatibility was common among spring flowering wildflowers. This trait was also found extensively among the flowers in this study and some, such as *S.holostea*, *A.ursinum* and *G.aparine* have mechanisms to pollinate themselves in the absence of insect visitors (Grime, Hodgson and Hunt, 1988).

4.3 Insect Abundance

There was a consistent fall in the total numbers of insects observed between the three months. Numbers were highest in May, lowest in July. This probably relates to increased canopy cover and the associated decrease in light levels at the site. The fall in temperature and reduction in radiant heat which followed may well have reduced the activity of small insects.

The numbers of insects seen also seemed to be effected by time of day, with abundance being highest around midday and dropping off slightly in the afternoon. This presumably results from increased temperatures at midday leading to an increase in insect activity. In two out of the three months the position of quadrats within the site and time of day interacted to effect the mean abundance of insects seen. This is not surprising since different parts of the site were exposed to the sun at different times, and this will have effected the time of day at which insect abundance reached its peak.

Insect activity seemed to be reduced at sites where there was dense canopy cover or low light levels. However, no relationship could be found between either canopy density or light penetration and insect abundance.

The changes in numbers of insects seen are probably reflected in a changes in the numbers of pollinators seen. Unfortunately, not enough pollinators were observed to test this. Willmer (1983) found that nectar feeding insects show diurnal activity patterns which were related to weather, in particular their need to thermoregulate and avoid overheating. The only group not effected by this were

Bombus whose activity was thought to be influenced by the times at which the plants they were foraging on produced most nectar.

4.5 Seasonal Changes in Pollinator Numbers

The number of pollinators seen showed a strong dip in June compared to the other two months. Interestingly, this trend was not shown by the pollinators which visited *G.robertianum*. Instead there was a consistent fall in the number of pollinators seen between May, June and July, with pollinator numbers in July being about a third of what they were in May. This gradual fall is probably related to the general number of insects seen at the site, which also fell in each of the three months. The number of species in flower also dropped during July. This together with the failure of pollinator numbers on *G.robertianum* to show a sharp fall would suggest that the low overall number of pollinators seen during June was the result of the low number of species in flower during this month. Thus, general pollinator numbers fell during June because of a lack of flowers to visit, while the number of pollinators on *G.robertianum* held because the species was constantly in bloom. *G.robertianum* was one of the dominant plant species at the study site and one of the few that flowered in June; 74% of the pollinators seen during that month were found on *G.robertianum*. In July, when a number of other species bloomed, there were more flowers available to be visited and so the number of insects that were found on flowers increased.

This theory can provide a possible explanation possible of why numbers of bee pollinators did not fall during June along with most other insect groups. Bees foraged almost exclusively on *G.robertianum* during May and June and so were not effected by the absence of other plant species. However, this theory does not explain why the number of syrphids which also foraged on *G.robertianum* were different in each month.

4.6 Pollinators

The most abundant pollinator groups found in this study were Coleoptera and Diptera. Diptera tended to dominate during May and then showed a fall while Coleoptera were numerous in each of the three months. Apidae were not particularly abundant until the end of the study period, although they visited a large number of flowers in each month.

It was not possible to compare the abundance of empids at the site with their abundance as pollinators since too few of the insects which entered quadrats could be captured to get a reasonable estimate of

their numbers. The same problem did not apply to other pollinator groups. Apidae and syrphids were easy to identify, while *Meligethes* and *Byturus* beetles were fairly immobile and mostly found on flowers.

The overall abundance of different insect types at the site did not appear to give any indication of the abundance of the different pollinator types which were found, with only a small subset of each group visiting flowers. The most abundant insect group at the site in all months were the Diptera, but these were only the most abundant pollinator group in one of the three months.

There was little evidence of specialisation by the pollinators. Insects found on one plant species were usually found on several others. This agrees with the results of Schemske *et al.* (1978) and Motten (1986) who also found there was extensive sharing of generalist pollinators by woodland plants. The only possible specialists on one plant species which were seen were the empid, *Polyblepharis opaca*, and a tabanid fly, which were only seen to forage on *G.robertianum*. This specialisation was probably of necessity rather than preference for that plant species since at the time these two pollinators were in flight, *G.robertianum* was the dominant flower species at the site and probably the most common and readily available source of nectar. However, the numbers of these insects were probably too small and they were present for too short a time to have much effect on the pollination of *G.robertianum*.

This finding tends to agree with Herrera (1988b) and McCall and Primack (1992) who found that the interactions shown between plants and their pollinators are often very general and unspecialised, with species currently in bloom attracting insects which are currently available. For example, Herrera (1988b) found that in a Mediterranean scrub community which he studied, plants which flowered at about the same time of year tend to have their flowers visited by the same types of insects, irrespective of floral characteristics. However, he also discovered that some plants consistently attracted some kinds of pollinators more than others. The evidence from *G.robertianum* and from *S.dioica* would suggest that the range of insects found on tubular flowers is no less diverse than those on open ones, although plants with very specialised zygomorphic flowers were only seen to be visited by bees. The general findings of this study do not contradict this conclusion. Most pollinators were found on a variety of plant species although some preference did seem to be shown, for example *G.urbanum* was almost exclusively visited by *Byturus*.

Few pollinator visits were observed during this study and the flowers of some species were not seen to receive any pollinator visits. This probably reflects the low insect activity and the paucity of flowers present at the site. The range of pollinators found seems surprisingly small. They were representatives of many different families found entering quadrats (see Appendix 2), many of which have been reported as being pollinators (e.g. Knuth, 1906-1909; Proctor and Yeo, 1973) but were not seen to visit any flowers. *Meligethes* was a common visitor to flowers was quite abundant at the site during the May period, but only 31 individuals were ever discovered visiting flowers within the quadrats where observations were made during this month. It is therefore possible that other less common or infrequent pollinating insects could have been missed because of the generally low pollinator activity at the site.

4.7 Seasonal Changes in Pollinator Groups

There was significant variation between months in the abundance of the different pollinator groups. The group that showed the greatest variation was the Diptera. During May, when Empididae were common visitors to flowers they formed the biggest proportion of the pollinators seen. Numbers dropped considerably in June when empids ceased to be common but increased again in July with a rise in the numbers of syrphids and muscids. Coleoptera numbers showed a gradual decline throughout each month, while Hemiptera and syrphids showed a through in abundance during June. Numbers of Apidae were steady in May and June but rose in July.

All groups of pollinators increased in abundance in July compared with June, probably because of an increase in the numbers of flowers available. Syrphids, Apidae and Hemiptera pollinators were seen in greater numbers during July than in either of the two previous months.

The groups which accounted for the biggest number of flowers visits were Diptera and Coleoptera in May, Coleoptera and Apidae in June and Coleoptera, Apidae and Syrphidae in July. Coleoptera and Diptera (excluding syrphids) were responsible for a large number of visits to flowers because they were so numerous while syrphids and Apidae were responsible for a large number of flower visits because they were very mobile. Syrphids and Apidae were therefore potentially more important as pollinators than their abundance might have suggested.

Most insect populations show seasonal cycles in abundance and so it is not surprising that the array of pollinators found at the study site changed between months. Several authors have found that plant

species experience changes in the number and type of pollinators within their flowering season (e.g. Herrera, 1988a). It is also usually found that the pollinators of a plant species or within a plant community show marked changes in abundance and composition between years. This is not surprising because insect populations in general often show annual variation in population sizes (e.g. Pollard, 1984). Plants therefore meet with an array of possible pollinators throughout their flowering season and between years. This has implications for the evolution of mutualistic relationships between plants and their pollinators. Under the 'most effective pollinator' principle of Stebbins (1970) natural selection should favour traits that attract and maintain only those flower visitors that provide the best pollination services. It is obvious that the unpredictability pollinator composition found in this and other studies will hinder such specialisation.

There seemed to be distinctive characteristics in the interactions between plants and pollinators in each month. In May most of the pollinators seen were Empididae or *Meligethes* found on early blooming species with open-bowl shaped flowers. Tubular flowers were comparatively rare during this period; pollinators were most numerous during this period although only a small proportion of the available flowers received visits. In June most pollinator activity was concentrated on *G.robertianum*, while in July there was an increase in the numbers of plants species in flower and the appearance of plants such as *S.sylvatica* with specialised zygomorphic flowers. A high proportion of the available flowers during July were visited by pollinators. By the end of July a high proportion of the plant species in flower had tubular flowers.

4.8 Efficiency of Generalist Pollinators

Not all pollinators are equally effective in pollinating a plant species. An efficient pollinator is one that transfers pollen to con specific plants without wasting it on other plant species. Factors which influence the effectiveness and importance of pollinators include the pollen loads they are capable of carrying, the efficiency of pollen transfer between flowers and the amount of outcrossing they achieve. Pollinators which restrict their visits to one plant species will ensure that no pollen is wasted on non-conspecifics but may not be efficient if they are uncommon or do not carry much pollen (Primack and Silander, 1975; Kearns, 1992). Where a plant species is pollinated by a range of insects, abundance is not necessarily a guide to which is the most efficient. This was shown by Primack and Silander (1975) in their investigation of the relative importance of *Apis mellifera* and the soldier beetle,

Chauliognathus mariginatus to pollination of the evening primrose, *Oenothera fruticosa*. It was found that although soldier beetles were more abundant as pollinators, *A.mellifera* transferred more pollen grains per unit time and more efficiently than beetles.

Bees and syrphids showed a high degree of floral constancy within foraging trips despite being found to visit the flowers of several different species. This was probably aided by the clumped distribution of many of the plant species at the site and by the generally low number of plant species. If the distribution of flowers is clumped, floral movements are more likely to be intraspecific rather than interspecific. This is one of the factors Motten (1986) considered to be important in ensuring adequate pollination within spring wildflower communities. This could have disadvantaged some of the plant species with fairly heterogeneous distributions, such as *O.acetosella*. However, a mathematical model developed by Straw (1972) suggests that such any disadvantage 'minority' species might experience because of their low numbers could be overcome if pollinators show a high degree of constancy. Because of the lack of pollinators on plant species such as *O.acetosella* it is not possible to comment on how constant its pollinators might have been.

A limited number of plant species with flowers in bloom will reduce the chance of insects moving to non-conspecific flowers (Heinrich and Raven, 1972; Kevan, 1972). This could also have been a factor contributing to floral constancy at the study site.

It appears to be common for generalist pollinator which are found on several different species of plant to show a high degree of floral constancy (O'Brien, 1980). For example, Mulligan (1972) studying the insect pollinators of a Canadian weed community discovered that although nearly every insect he studied was found on at least seven weed species, 90-100% of the pollen load of any one individual was identical to that of the plant on which it was collected.

If outcrossing is to be achieved, pollinators must not confine their visits to a single flower. Flowers therefore limit the rewards they provided so that pollinators will go on to visit other plants of the same species (Heinrich and Raven, 1972). Flies and beetles have low energetic demands (Heinrich, 1975) and so may have been limited in their amount of interfloral movement. During the course of observations, Coleoptera were never observed to move between flowers, while flies did on a few occasions. Flies were considered by Faegri and van der Pijl (1979) to be indiscriminate flower visitors which are unlikely to transfer pollen between conspecific plants. However, Kevan (1972) found a high

degree of floral constancy by Dipteran pollinators in the high arctic, largely due to the low number of species in flower at any one time. In the few cases where Diptera were observed to move between flowers they visited flowers of the same species, probably because of the clumped distribution of many of the plant species. Kearns (1992) found that fly species fed at many plant species but analysis of gut contents revealed that many fed predominantly on a single plant species. Without examining the pollen loads of the pollinators found at the site no conclusion can be reached about their floral constancy.

Insects differ in the pollen loads they carry. O'Brien (1980) found that in the community she studied that frequent flower visitors, bees, wasps and syrphids, carried quite large pollen loads, while flies generally carried much smaller loads. Kearns (1992) has reported that muscid flies carry pollen loads comparable to that of some solitary bees.

The importance of Coleoptera as pollinators is likely to be less than their abundance at the study site would suggest. They generally show very little movement between flowers and are usually less active than flies and so less able to cause outcrossing (Proctor and Yeo, 1973), although this may not be an important consideration at this site were most species are self compatible. Many beetles also feed destructively on the flowers they visit and this has to be weighed against the pollination service they may provide. In particular, the effectiveness *Meligethes* as a pollinator seems to have been doubted by Proctor and Yeo (1973) who say that this species 'sometimes probably cause pollination'.

Another group of pollinating insects whose abundance at the site might not be reflected in their importance as pollinators are the Empididae. These are predatory insects which visit flowers to feed on nectar using their long proboscis (Baker and Hurd, 1968). Proctor and Yeo (1973) write that these insects can reach the rewards offered by open flowers without touching the stigmas and may therefore be inefficient pollinators as they might not transfer pollen.

Even if many of the pollinators present at the site are limited in their effectiveness it should be remembered that when flower visitors are rare even inefficient pollinators may be valuable in maintaining some degree of outcrossing within a plant population (Kearns, 1992)

4.9 Apidae Pollinators

Bee are usually considered to be the insect group that is most highly adapted to visiting flowers and therefore to be among the most important of pollinators (Faegri and van der Pijl, 1979; Kevan and Baker, 1983; 1984). However, for most of the period which observations of insects were made, bees

were rare. This contrasts previous studies of pollination in woodland communities (e.g. Schemske *et al.*, 1978; Motten, 1986) which found bees to be among the most common pollinators especially of spring flowering species. This difference is probably accounted for by the different types of bees which were found in these studies. The pollinators observed by Schemske *et al.* and Motten found were mostly solitary bees such as andrenidae, halictids and anthophorids or honey bees (*Apis mellifera*), while the majority of bees in this study were bumblebees (*Bombus* sp.). It is known that bumblebees show a negative association with woodland (Fussell and Corbet, 1992) and this could probably account for their low numbers.

The number of bees active within the site was lowest in May. This can probably be explained by considering the life cycle of bees. Bumblebees sharply increase in number during early June when workers emerge. This is followed in most species by the appearance of males from late June onward (Fussell and Corbet, 1992). Therefore, for some of the May period the only bees present will have been queens. The May observation period extended well into the time when workers emerged so the numbers given are likely to be an overestimate of bee numbers during the actual month of May. During the May period almost all bee pollinators were found on *G. robertianum*. This did not flower until almost the end of the month of May, so during that month there were no pollination visits by bees observed within quadrats, although outside of the quadrats in which observations were made, a few scattered *Bombus terrestris* were seen foraging on *E. non-scriptus*. This lack of pollination by bees probably reflects their low numbers during May, when the early flowering species were in bloom and the negative association between bumblebees and woodland. Lack of suitable floral rewards could also play a part, but bees have been reported as foraging on some of the early flowering plant species found, e.g. *S. holostea* and *A. ursinum* (Knuth, 1906-1909; Proctor and Yeo, 1973).

The number of bees seen during June was particularly high because of one observation in which 25 bees were observed in one quadrat. The results might therefore give a misleading impression that the number of bees at the study site fell in July compared with June.

In May there was a rise in both the number of bees which acted as pollinators and in the number of flowers visited by pollinators. The rise in the number of flowers visited per pollinator can probably be explained by the presence of *S. sylvatica* during July. Bees were commonly found foraging on this plant and a large number of flowers were visited per foraging trip

The increase in the number of pollinators seems to have occurred because of the increased number of plant species in flower during July. For May and June periods bees foraged almost exclusively on *G. robertianum*. This probably explains why bee numbers did not fall in June. The numbers of pollinators seen foraging on *G. robertianum* did not increase along with the general increase in pollinator numbers. It might be possible that the number of bees seen on this species during May and June were the maximum number that could forage efficiently on the species and that a greater number of pollinators could not be economically sustained. Of the two major plant species which bees also foraged on in July, *R. fruticosus* is known to have high nectar secretion (Proctor and Yeo, 1973), while zygomorphic flowers such as possessed by *S. sylvatica* are generally rich in nectar (Heinrich, 1979).

Fussell and Corbet (1992) report that bumblebees tend to forage on perennials and biennials in preference to annuals because of the greater amounts of nectar they contain. There did not seem to be much evidence of this at the study site but this may reflect the lack of bees and the generally low numbers of plant species.

4.10 Syrphid Pollinators

The numbers of Syrphidae seen during May and July seem to have been about equal, but there was a dramatic fall in their numbers during June. The reason for this is not certain, although syrphid activity is known to be affected by light levels, being particularly low during cloudy periods (Kevan and Baker, 1984), and this could have played a part. The proportion of total syrphids numbers which acted as pollinators was different in each month, although the number of flowers visited per pollinator seemed to remain constant.

During July there was a general increase in the number of syrphid pollinators. This may be partially explained by an increase in the number of plants species producing flowers during that month. A large proportion of all the syrphid pollinators seen were observed during July, often on plant species which did not flower in other months, for example, almost a third of all syrphid pollinators seen were foraging on *R. fruticosus*. However, there was also an increase in the number of syrphids which foraged on *G. robertianum*, which had been present throughout most of the study period. An increased number of plant species would therefore not seem to explain everything. Perhaps the weather was more favourable for pollinator activity during July.

There was no significant difference in the mean number of flowers visited in a foraging trip between plant species. This explains why the number of flowers visited per pollinator appeared to be the same in each month.

4.11 Flower Preferences

McCall and Primack (1992) studied in their study of pollinators in three contrasting plant communities found that most pollinator groups visited open and tubular flowers in the same proportion. The only exception to this was the group they described as 'other' group which were found mostly on open flowers. They also found that the rate at which pollinators visited open flowers was much higher than for tubular ones.

The results of this study differ from those of McCall and Primack in that bees were seen to comprise a much greater proportion of visits to tubular than to open flowers. The results of Fishers Exact Test showed that bees were significantly more common on plant species with tubular flowers than those with open flowers. This may have been because a number of the open type flowers found at the site were of small size and offered low rewards to flower visitors (e.g. *G. aparine* or *M. trinervia*). The high energetic demands of bees (Heinrich, 1979) might therefore have made foraging on these species uneconomic. Another contributing factor to the lack of bees on open flowers could be that most were in bloom early in the season when bees numbers were low. However, it should not be forgotten that tubular flowers are generally considered to be pollinated by specialised pollinators such as bees (Faegri and van der Pijl, 1979) and that from these results, bees do appear to be more important on tubular flowers than on open ones. In particular, plants with specialised flowers, such as *S. sylvatica*, were only seen to be visited by bees. This would agree with the belief that specialised flower morphologies are intended to exclude animals with low energy expenditure, which would probably restrict their visits to one flower (Heinrich, 1979)

Syrphids seem to have made up a slightly greater proportion of the pollinators on tubular than on open flowers but the numbers found on either flower type were low and so it is not possible to say with certainty whether the difference is statistically significant. Beetles and 'other Diptera' were pollinators of open and tubular flowers in about the same proportions, but because bee pollinators were usually seen to visit many flowers, they consequently accounted for a much lower proportion of visits to tubular flowers than to open flowers.

It was not possible to compare the pollinator visitation rates of the flower species within this study, since a record was not taken of how many flowers within a quadrat were open before observations were made. However, it is likely that tubular flowers may have been visited at a higher rate than open flowers because a large proportion of the visitors to tubular flowers were mobile groups such as bees, while the insects found on open flowers were usually rather immobile pollinators such as Coleopterans. Late flowering species with open flowers, for example *R.fruticosus*, were visited by mobile pollinators such as bees and syrphids while early flowering species were not. It would be interesting to compare the visitation rates of tubular flowers with some of the late flowering open flowers to see if they were different.

There was no evidence of colour preference between pollinators. This was probably because there was not a diverse enough range of colour types for any pattern to become clear. Most open flowers were white while most tubular flowers were red or pink, so it was not possible to separate the effects of colour and morphology. Flower morphology is usually thought to act to limit the numbers of potential pollinators, with open type flowers being regarded as unexclusive to generalist pollinators (O'Brien, 1980). However, many of the open type flowers found during this study were visited by a narrow range of pollinators, for example, *G.urbanum* was visited almost exclusively by *Byturus*, or were not seen to be visited by any pollinators at all, e.g. *R.ficaria*. Only with late blooming open flowers such as *H.sphondylium* or *R.fruticosus* were a range of pollinating insects found. This could reflect the low pollinator activity at the site, with only the most common flower visitors being seen and the rarer ones missed.

It was difficult to examine possible flower preferences since both the number of pollinators and the number of plants at the site was so low. The result of this was that the pollinators found on one plant species could significantly effect the overall trend. For example, most pollinators in the 'other' class were found on open flowers, but this is almost entirely due to the presence of 9 thrips (60% of the 'other' group) on one plant species, *S.holostea*. It is obvious that if any meaningful conclusions are to be draw about the flower preferences shown by insects a much larger number of observations are needed.

4.12. Pollinators of *Geranium robertianum*

G.robertianum was one of the most dominant plant species at the study site during each of the three months during which observations were made. It was therefore possible to study how the pollinators of this species changed with season. In general the pollinators groups found on *G.robertianum* showed the same changes in abundance over the observation period as did pollinators in general. This is perhaps not surprising since a large proportion of the total pollinators seen were found on *G.robertianum*. However, the total number of pollinators found on *G.robertianum* fell consistently between May, June and July while total pollinator numbers at the site showed a fall during June and a recovery in July. The probable reasons for this have already been discussed.

Bees visited much the same number of flowers during each of the three months but made up a greater proportion of total flower visits in June and July when numbers of other insect groups began to fall. During July most of the flower visits were either from syrphids or bees. The contribution of these two groups to total flower visits for *G.robertianum* was therefore greater there contribution to total flower visits to all species.

The proportion of available *G.robertianum* flowers which received pollinator visits was never more than 4%. This is surprising low considering that *G.robertianum* was the dominant flower species during most of the study period. It is possible that the number of visits by pollinators such as syrphids and bees were underestimated because of their mobility, since they could visit many flowers in a short period of time.

4.13 Pollination of *Silene dioica*

S.dioica was the only dioecious plant species at the study site and therefore outcrossing had to take place if it was to set seed. The great majority of insects found on the flowers of this species were probably opportunists looking for nectar and pollen and therefore unlikely to carry pollen between different plants. The only insects found on this plant that were likely to cause pollination were mobile pollinators such as syrphids and bees. These were only ever seen visiting *S.dioica* in low numbers, although they made up a large percentage of the flowers which received pollinator visits. The reason for the low numbers of visits to *S.dioica* is uncertain. Numbers of the plant were generally low and this could have effected its attractiveness to potential pollinators, as visitation rates and attractiveness to

potential pollinators are greater in conspicuous floral displays (Heinrich, 1979; Schmitt, 1983). Kay *et al.* (1984) found that seed set in widely spaced populations of *S.dioica* could be effected by discrimination between sexes leading to reduced visits to female flowers.

4.14 Flower Success

Despite the low number of pollinators seen, the proportion of flowers which successfully produced fruit seemed high in most of the species studied. There was no evidence that any flowers of *O.acetosella* had successfully developed fruit, but this would agree with reports that *O.acetosella* is not often successfully pollinated by insects (Grime, Hogdson and Hunt, 1988). *A.nemorosa* had ceased flowering at the time of the first vegetation survey but there was no evidence that it had successfully flowered. This would not be unexpected as the species is an obligate outcrosser (Proctor and Yeo, 1973).

Flower success in *E.non-scriptus* was very variable but generally low. Extremely few insects were found to visit its flowers. Bell shaped flowers, such as are found on this species, are primarily adapted for pollination by bees (Faegri and van der Pijl, 1979) The pollinator found most often on this species was being *Meglilithes*, which is unlikely to have been particularly effective as a pollinator since they are unlikely to have transferred pollen between plants and *E. non-scriptus* is only slightly self compatible (Grime, Hodgson and Hunt, 1988). *E.non-scriptus* was seen also to be visited by *B.terrestris*. This is likely to have been a much more effective and efficient pollinator than *Meligethes*. Motten (1986) discovered that some of the plant species in his spring flowering community relied for pollinated entirely on queen bumblebees and these generally had low seed set. Proctor and Yeo (1973) report that *E.non-scriptus* is also visited by long tongued syrphids so it is not entirely dependent on queen bumblebees for its pollination. However, bumblebees are the insects which were most likely to cause outcrossing at the site during May and seed-set was probably limited to some degree by their low numbers.

One curious result was the apparently high flower success of *R.ficaria*. Knuth (1906-1909) reports that this species rarely sets seed although it is commonly visited by insects. No insects were seen to visit this species and the impression was gained that a high proportion of flowers were successful. However, this could not be investigated fully since most individuals of the species were washed away by heavy rain before a full count of the number of seed heads was made. This merits further investigation.

The flower success seen probably reflects the widespread occurrence of autogamy among the plant species studied. This varied in degree and in importance for the different species. This may well be an adaptation to low incidence of pollinators (Motten, 1986). The obligate outcrosser among the plants studied was *S.dioica*, where seed set was much less than 100%. This probably reflects the low incidence of suitable pollinators for that species.

It is not possible to say for many of the plant species whether or not pollination was the result of insect pollination or of self pollination. Many of the species investigated were autogamous and so had mechanisms which allow them to be pollinated in the absence of insect pollinators. Mulligan (1972) came to the conclusion that most of the seed set found in the weed community which studied came from self pollination.

Interestingly, fruit set in some species which are known to be self pollinating, such as *A.ursinum*, was less than 100%. This is a common phenomenon and can be caused by many factors, including the selective abortion of damaged fruits or a lack of resources to mature all possible fruits. Stephenson (1981) has reviewed this subject fully.

4.15 Conclusions

There were a lack of pollinators at the study site. Few species were observed to be visited by insects in any number. This was probably due to the low insect activity paucity of flowers at the study site. The pollinator assemblage met during the three months was very variable. This is to be expected from previous studies.

Most of the plants species studied were autogamous and self compatible. This probably help to ensure adequate seed-set in the absence of pollinators. In these species a similar proportion of flowers were successful. In contrast, species which relied on some degree of outcrossing, such as *S.dioica* or *E.non-scriptus* did not appear to have a very high proportion of successful flowers. The amount of outcrossing which occurred at the site was probably very low.

Plant-insect interactions were usually very general with little specialisation, however, without analysis of pollen loads it was not possible to comment on how constant particular insects were to a particular plant species.


The study was hampered throughout by the low numbers of pollinators seen. This was probably the result of the short time during which observations were made and the small numbers of flowers in the

study quadrats. To come to any satisfactory conclusion about plant-pollinator interactions in woodland a much longer and more detailed study is need.

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APPENDIX 1

The Ground Flora of The Study Site

A list of the plant species found at the study site is given below together with the median Domin scores for each month.

	Median Domin Scale Values		
	May	June	July
<i>Acer pseudoplatanus</i>	1	1	1
<i>Adoxa moschatellina</i>	3	2	0
<i>Agrostis capilaris</i>	1	1	1
<i>Alliaria petiolata</i>	2.5	2.5	2.5
<i>Allium ursinum</i>	4	4	3.5
<i>Anemone nemorosa</i>	4	0	0
<i>Arum maculatum</i>	4.5	0	0
<i>Dactylis glomerata</i>	3.5	4	4
<i>Deschampsia cespitosa</i>	3	3	3
<i>Deschampsia flexuosa</i>	4	4	4
<i>Dryopteris dilata</i>	1	5	5
<i>Dryopteris filix-mas</i>	1	1	1
<i>Endymion non-scriptus</i>	4	3	3
<i>Fagus sylvatica</i>	1	1	1
<i>Fraxinus excelsior</i>	1	1	1
<i>Galium aparine</i>	3	3	3
<i>Geranium robertianum</i>	7	7	7
<i>Geum urbanum</i>	4	4	4
<i>Hedera helix</i>	9	9	9
<i>Heracleum sphondylium</i>	3	3	3
<i>Holcus lanatus</i>	3	3	3
<i>Ilex aquifolium</i>	1	1	1
<i>Impatiens glandulifera</i>	6	6	6
<i>Lapsana communis</i>	2	2	2
<i>Lonicera periclymenum</i>	5	5	5
<i>Luzula sylvatica</i>	7	7	7
<i>Mercurialis perennis</i>	6	6	6
<i>Millium effusum</i>	3	3	3
<i>Moehringia trinervia</i>	3.5	3	3
<i>Oxalis acetosella</i>	4	4	4
<i>Rumex obtusifolium</i>	3	3	3
<i>Ranunculus ficaria</i>	4	0	0
<i>Rubus fruticosus</i>	3	4	4
<i>Sambucus nigra</i>	4	5	5
<i>Silene dioica</i>	5	5	5
<i>Stellaria holostea</i>	4	4	4
<i>Stachys sylvatica</i>	7	7	7
<i>Urtica dioica</i>	7	7	7
<i>Veronica montana</i>	3	3	3
moss	3	3	3

Appendix 2

Miscellaneous Insect Data

Representatives of the following families were found within the study quadrats.

Diptera

Sub-order Nematocera

Bibionidae
Cecidomyiidae
Chironomidae
Culcidae
Mycetophilidae
Psychopteridae
Scatopsidae
Simuliidae
Tipulidae

Sub-order Brachycera

Empididae
Stratiomyidae
Tabanidae

Sub-order Cyclorrhapha

Agromyzidae
Anthomyiidae
Calliphoridae
Clusiidae
Fannidae
Helcomyzidae
Lauxaniidae
Lonchopteridae
Micropezidae
Muscidae
Otitidae
Phoridae
Scathophagidae
Sepsidae
Sphaeroceridae
Syrphidae

Coleoptera

sub-Order Adephaga

Carabidae

sub-Order Polyphaga

Byturidae
Curculionidae
Elateridae
Nitidulidae
Staphylinodae

Hemiptera

sub-Order Homoptera

Aphidae

sub-Order Heteroptera

Cimicidae
Miridae
Reduviidae

Members of the following orders and sub-orders were also found:

Apocrita
Ephemeroptera
Thysanoptera
Neuroptera
Mecoptera
Lepidoptera
Symphyta

The following syrphid species were seen visiting flowers:

Episyrphus balteatus
Epistrophe grossulariae
Platycheirus albimanus
Melanstoma scalare
Meliscaeva cictella
Syrphus torvus

The following Apidae species were seen visiting flowers:

Bombus lapidarius
Bombus pascuorum
Bombus terrestris

