



## Durham E-Theses

---

### *Plant - insect interactions in a riparian grassland: a community approach to pollination*

Hamley, Sarah

#### How to cite:

---

Hamley, Sarah (1993) *Plant - insect interactions in a riparian grassland: a community approach to pollination*, Durham theses, Durham University. Available at Durham E-Theses Online:  
<http://etheses.dur.ac.uk/5587/>

#### Use policy

---

The full-text may be used and/or reproduced, and given to third parties in any format or medium, without prior permission or charge, for personal research or study, educational, or not-for-profit purposes provided that:

- a full bibliographic reference is made to the original source
- a [link](#) is made to the metadata record in Durham E-Theses
- the full-text is not changed in any way

The full-text must not be sold in any format or medium without the formal permission of the copyright holders.

Please consult the [full Durham E-Theses policy](#) for further details.

---

Academic Support Office, Durham University, University Office, Old Elvet, Durham DH1 3HP  
e-mail: [e-theses.admin@dur.ac.uk](mailto:e-theses.admin@dur.ac.uk) Tel: +44 0191 334 6107  
<http://etheses.dur.ac.uk>

The copyright of this thesis rests with the author.  
No quotation from it should be published without  
his prior written consent and information derived  
from it should be acknowledged.

**PLANT - INSECT INTERACTIONS IN A RIPARIAN GRASSLAND: A  
COMMUNITY APPROACH TO POLLINATION.**

by

**Sarah Hamley**

A Dissertation Submitted In Part Fulfilment Of The Requirements For The Degree Of  
Master Of Science In Advanced Ecology

Biological Sciences

The University Of Durham

1993



18 MAR 1994

### **ACKNOWLEDGEMENTS.**

I would like to thank Dr. P. Hulme for his advice and support throughout the period of this study. I would also like to thank all the other members of the M. Sc. Advanced Ecology Course. I would like to especially thank Dave, for his help and support during the whole year as well as throughout study period.

## **LIST OF FIGURES.**

<b>Figure 1</b>	The Total Percentage Of Flowering Stems In May.	13
<b>Figure 2</b>	The Total Percentage Of Flowering Stems In June.	13
<b>Figure 3</b>	The Total Percentage Of Flowering Stems In July.	14
<b>Figure 4a</b>	The Diurnal Variation In The Percentage Abundance Of Insects During May.	15
<b>Figure 4b</b>	The Diurnal Abundance Of Insects During May.	15
<b>Figure 5a</b>	The Diurnal Variation In The Percentage Abundance Of Insects During June.	17
<b>Figure 5b</b>	The Diurnal Abundance Of Insects During June.	17
<b>Figure 6a</b>	The Diurnal Variation In The Percentage Abundance Of Insects During July.	18
<b>Figure 6b</b>	The Diurnal Abundance Of Insects During July.	18
<b>Figures 7a - 7e</b>	The Diurnal Variation In Activity Within Each Insect Order Throughout The Study Period.	19
<b>Figure 8a</b>	The Diurnal Variation In The Percentage Abundance Of Pollinators During May.	23
<b>Figure 8b.</b>	The Diurnal Abundance Of Pollinators During May.	23
<b>Figure 9a</b>	The Diurnal Variation In The Percentage Abundance Of Pollinators During June.	24
<b>Figure 9b</b>	The Diurnal Abundance Of Pollinators During June.	24
<b>Figure 10a</b>	The Diurnal Variation In The Percentage Abundance Of Pollinators During July.	25

<b>Figure 10b</b>	The Diurnal Abundance Of Pollinators During July.	25
<b>Figure 11</b>	The Seasonal Variation In Insect Abundance.	27
<b>Figure 12</b>	The Seasonal Variation In Pollinator Abundance.	27
<b>Figure 13</b>	Relationship Between The Ranked Number Of Flowers And Pollinators Per Quadrat During May.	29
<b>Figure 14</b>	Relationship Between The Ranked Number Of Flowering Stems And Pollinators During May.	29
<b>Figure 15</b>	Relationship Between The Ranked Number Of Flowers And Pollinators Per Quadrat During June.	30
<b>Figure 16</b>	Relationship Between The Ranked Number Of Flowers And Pollinators Per Quadrat During July.	30
<b>Figure 17</b>	Comparison Between The Percentage Visits To Open And Tubular Flowers In June.	32
<b>Figure 18</b>	Comparison Between The Percentage Visits To Open And Tubular Flowers In July.	32
<b>Figure 19</b>	Comparison Between The Total Number Of Pollinator Visits To White, Yellow And Purple - Pink Flowers In May.	33
<b>Figure 20</b>	Comparison Between The Total Number Of Pollinator Visits To White, Yellow And Purple - Pink Flowers In June.	33
<b>Figure 21</b>	Comparison Between The Total Number Of Pollinator Visits To White, Yellow And Purple - Pink Flowers In July.	34

## **LIST OF TABLES.**

<b>Table 1</b>	The Monthly Median Domin Scores And Constancy Values Of Herbaceous Plants.	11
<b>Table 2</b>	The Results After Using $\chi^2$ Contingency Tables To Identify Any Significant Differences In Diurnal Abundance / Activity Throughout The Season Within Each Insect Order.	19
<b>Table 3</b>	Results After Performing A Fisher's Exact Probability Test To Determine Significant Differences In Pollinators Preferences For Open Or Tubular Flowers.	35

## CONTENTS.

<b>ABSTRACT</b>	
<b>INTRODUCTION.</b>	
<b>1.1 The Community Approach To Pollination</b>	1
<b>1.2 Project Aims</b>	4
<b>2.0 MATERIALS AND METHODS</b>	
<b>2.1 Study Site</b>	5
<b>2.2 Vegetation Surveys</b>	5
<b>2.3 Insect Observations</b>	6
<b>2.4 Methods of Analysis</b>	6
2.4.1 Vegetation Data	6
2.4.2 Insect Data	7
2.4.2.1 Diurnal Activity	7
2.4.2.2 Seasonal Variation	7
2.4.3 Plant And Insect Interactions	7
<b>3.0 RESULTS</b>	
<b>3.1 Plant Assemblages</b>	10
3.1.1 Vegetation Survey	10
3.1.2 Floral Characteristics	12
<b>3.2 Insect Assemblage</b>	12
3.2.1 Diurnal Activity And Abundance Of Insects	12
3.2.2 Diurnal Activity And Abundance Of Pollinators	22
<b>3.3 Seasonal Variation</b>	26
3.3.1 Insect Abundance	26
3.3.2 Pollinator Abundance	26
<b>3.4 Plant And Insect Interactions</b>	28
3.4.1 Floral Abundance And Insect Interactions	28
3.4.2 Flower Morphology And Insect Interactions	28
3.4.3 Flower Colour And Insect Interactions	31
<b>3.5 Specific Plant - Pollinator Interactions</b>	36
<b>3.6 Pollinator Observations</b>	37
<b>4.0 DISCUSSION</b>	
<b>4.1 Methodology</b>	39
4.1.1 Validity Of Vegetation Survey Technique	39
4.1.2 Validity Of Insect Observation Technique	39
<b>4.2 Plant Assemblage</b>	40
4.2.1 Seasonality	40
4.2.2 Floral Characteristics	40
<b>4.3 Diurnal Variation</b>	41
4.3.1 Diurnal Activity Of Insects	41
4.3.2 Diurnal Activity Of Pollinators	42
<b>4.4 Seasonal Variation</b>	42
4.4.1 Insect Abundance	42
4.4.2 Pollinator Abundance	43



<b>4.5</b>	<b>Plant And Insect Interactions</b>	44
4.5.1	Floral Abundance And Pollinator Abundance	44
4.5.2	Flower Morphology And Insect Interactions	46
4.5.3	Flower Colour And Pollinator Activity	48
<b>4.6</b>	<b>Specific Plant - Pollinator Interactions</b>	49
<b>4.7</b>	<b>Pollinator Observations</b>	50
<b>4.8</b>	<b>Consequences Of The Plant - Pollinator Interaction</b>	51
 <b>REFERENCES</b>		 54
 <b>APPENDIX</b>		 I

## ABSTRACT.

This investigation into plant and insect interactions was carried out at a riparian grassland site in Shincliffe, Durham and commenced during the month of May and ended in early July. Vegetation surveys were carried out throughout the growing season to establish the species composition, plant and flower density, dominant plant species and various plant characteristics of the community as a whole. The plant found most frequently in flower during May was *Stellaria holostea*, whilst in June the plants most frequently in flower included *S. holostea*, *Cruciata laevipes* and *Aegopodium podagraria*. In July *A. podagraria* was once more the most frequently flowering plant. There was also a progressive increase in plant diversity, morphology and flower colour throughout the study period.

Observation periods throughout the investigation enabled the overall insect and pollinator assemblage of the community to be identified. Insect abundance was found to be diurnally heterogeneous throughout the study period. The only 'within' differences in ranked activity were identified for Diptera in June and 'others' in July. There were also significant differences in the absolute diurnal activity within the orders of Diptera, Coleoptera, Hymenoptera and 'others'. There were also quite striking and significant seasonal variations in the insect assemblage. Pollinator abundance was also found to be diurnally heterogeneous in June and July, whilst being homogeneous throughout May. In addition the dominant pollinators varied seasonally. There were no significant 'within' pollinator differences in ranked or absolute activity during any of the months.

During all three months plant - pollinator interactions were looked at in some detail. Significant relationships were found to exist between the ranked number of flowers and the ranked number of pollinators per quadrat. In May there were also significant relationships between the ranked number of Diptera, Coleoptera and flowers per quadrat. In June there was a significant correlation between the ranked number of Hymenoptera and flowers per quadrat. There were no such findings for the month of July. Finally, during May there was a significant correlation between the ranked number of flowering stems and the ranked number of pollinator visits per quadrat.

The preference and avoidance of certain plant characteristics such as colour and flower morphology were identified for some groups of pollinators. However, although some of these interactions were analysed, the precise nature of pollinator behaviour was difficult to prove.

A closer look at individual plant species and their associated pollinator assemblages enabled generalisations to be made, but these associations were not apparent when the community was studied as a whole.

## 1.0 INTRODUCTION.

### 1.1 The Community Approach To Pollination.

Pollination studies have been popular for many years and they are becoming increasingly so as they give a valuable insight into plant breeding systems, floral and animal evolution, foraging behaviour and the outcome of competition between plant species for pollinators. The majority of pollination studies have traditionally concentrated on specific interactions between plants or on a few closely related plant species and their pollinator assemblages. However community pollination studies are relatively sparse in number even though they give a valuable insight into the relationships between plants and their visitors in a more complex and ecologically realistic context (Motten, 1986). Community studies can also be used to identify inter specific relationships within groups of plants and pollinators. Other studies have been carried out to illustrate the connection between flower visitors and flower characteristics such as shape and colour (Grant, 1949; Weevers, 1952; Vögel, 1954; Van der Pijl, 1961; Faegri & Van der Pijl, 1979). Previous community studies have examined the energetic relationships between plant assemblages and their animal pollinators (Hocking, 1968; Heinrich & Raven, 1972; Heinrich, 1973; 1975a), whilst others have examined the specialisation of plants and their pollen vectors in relation to the plant community structure (Heithaus, 1974; Moldenke 1975; Heinrich, 1976b; Pleasants, 1977). The majority of studies have also tended to concentrate on the pollinators which are the most discernible, numerically dominant and / or continuously resident throughout the season (O'Brien, 1980). As a consequence bees are by far the most well studied group of pollinators, especially in terms of their flower constancy and foraging behaviour, although other studies have concentrated on the pollinator assemblage as a whole (O'Brien, 1980; McCall & Primack, 1992).

There also appears to be a general lack of community pollination studies which deal with the effects of time of day, season, weather or light levels. Although the latter two variables were not monitored in this particular study, time of day was found to have a noticeable effect on the diurnal abundance and in some cases activity of pollinators and insects. Reasons for this are discussed in detail later. However, McCall & Primack (1992) investigated the effect of time of day, weather, light levels and seasonality on the rate of insect visitation rates to flowers in three plant communities. Another parameter known to affect pollinator assemblages is altitude. For example Arroyo *et al* (1982) discovered that high altitudes of melittophilous species (i.e. bee pollinated) with broad altitudinal ranges, were perpetually visited by fewer bee species compared to plant

populations at lower altitudes. There also appears to have been few community studies carried out in the British Isles.

In order to appreciate the many variables which influence pollination within a community, it is perhaps useful to examine the major interactions between plants and insects within a community. A major factor influencing the act of pollination is the competition between plants for pollinators, an area which has been little studied. However, Kevan & Baker (1984) have described 'weeds' such as dandelions (*Taraxacum officinale* agg.) as being successful competitors as they have the ability to attract pollinators away from other plants by producing copious amounts of nectar. Goyder (1983) observed that competition with blossoms of certain species growing in a limestone community adversely affected pollination in some plants whilst enhancing it in others. Pojar (1974) concluded that competition for pollinators is increased in communities with short growing seasons and a large number of entomophilous plants. Work carried out by Levin & Anderson (1970) identified that pollinators became less specialised in their feeding patterns as blossom diversity declined and they eventually fed with very little discrimination. It has been suggested that unsuccessful competitors become more specialised and reduce their spectrum of pollinators but guarantee rewards to those that visit them (Kevan & Baker, 1984). Alternative strategies adopted by plants includes shifting or altering their period of flowering (Kevan & Baker, 1984). Pojar (1974) points out that inter specific competition may be an important factor in the timing and length of a species blooming period. The longevity of individual flowers will largely depend upon the energy constraints of the individual because long lived flowers may represent a major drain on the water and energy budget of the plant (Southwick, 1984; Nobel, 1977). For example Kerner von Marilaun (1895) observed that the flower longevity of orchids are relatively long with few flowers produced but require insect visits for seed production. Conversely, species with short lived flowers produce many inflorescences but in the absence of pollinators are capable of self pollination. It also worth noting that the longevity of flowers shows great variation at many levels, for instance differences amongst species in the same habitat, amongst habitats and seasons and within and amongst Families. One argument which has been proposed to explain this variation is based on the overall abundance of pollinators (Primack, 1985). However Kevan & Baker (1984) point out that whilst such observations are interesting, they have not been established as fact and although phenological trends may have evolutionary significance they are not proven. They also point out that plant competition for pollinators may only be a weak force in the evolution and ecology of pollination systems. Work carried out by Motten (1986) on the pollination ecology of a spring wildflower community of a temperate deciduous forest, suggested that although

inter specific competition for pollination occurred, the effect was not sufficiently strong to decrease total seed or fruit production, except in some of the queen bumblebee pollinated species. Other factors such as resource limitation and the quality of pollinators was found to affect the total fecundity of the wildflowers.

Another important component of the community is the competition between flower visitors for available flowers. Inter specific rankings carried out by Kikuchi (1962; 1964) placed bumblebees as the dominant insects, followed by syrphids and butterflies. However this is rather general and unlikely to be true for every community. For example McAlpine (1965) observed that flies were the most important pollinators amongst arctic plants, whilst in the Andean zone in central Chile bees were the most important. There are also likely to be differences within pollinator groups, such as bees. For example the proboscis length can vary quite markedly between species of bees. Queens of the species *Bombus terrestris* have tongue lengths of 9 - 11mm whilst queen species of *Bombus hortorum* have tongue lengths of between 19 and 21mm. This will influence whether or not nectar is accessible and will ultimately effect pollination.

The idea that pollination syndromes exist, as proposed by Faegri & Van der Pijl (1979) is useful as a general guide to the types of visitors expected to visit flowers. However, in pollination studies involving the community such tight interactions are difficult to prove, as illustrated by this particular study. Heithaus (1979) concluded that in tropical forests of Costa Rica there did not appear to be a high degree of specialised relationships, and such interactions were community specific. Research carried out by Proctor (1978; cited in Kevan & Baker 1984) in Ireland, established that in more stable and species rich communities the incidence of entomophily increased over anemophily, and entomophily was more specialised. An important point to remember is that factors favouring specialist or generalist pollinators are not necessarily those which favour specialist or generalist plants within a community (Kevan & Baker, 1984).

The overall pollination process within a community will be affected by the equilibrium of plants and pollinators, with respect to the competition interactions of plants for pollinators and flower visitors for plants. The entire community of plant and pollinator assemblages are dynamic and there will always be variations in the degree of competition and mutualism.

## 1.2 Project Aims.

For this particular study it was decided that the community as a whole would be examined to try and quantitatively identify the overall insect assemblage in addition to dominant guilds of pollinating insects. It was hoped that once the floral composition of the site had been established, the interactions of pollinators and insects with plant characteristics such as flower and plant density, morphology and colour could be closely examined. Subsequently it was hoped that the presence or absence of specific plant - pollinator interactions / syndromes would be apparent, as postulated by Faegri & Van der Pijl (1979). The effect of time of day and seasonality were also quantitatively investigated for plant, insect and pollinator assemblages within the community, although due to time constraints the study only covered part of the growing season.

## **2.0 MATERIALS AND METHOD.**

### **2.1 Study Site.**

The study area is a riparian habitat of rank grassland and was situated at Shincliffe (Grid Reference NZ285403) adjacent to the River Wear in County Durham, England (see map for location of study site). The entire length of the site also lay adjacent to large fields of arable crops which were separated from the study site by a wire fence. This area was chosen since it was not grazed or mown and so allowed permanent quadrats to be put in place. The site also showed little evidence of trampling even though there were several footpaths leading through it.

### **2.2 Vegetation Surveys**

Prior to the vegetation surveys a total of 30 permanent 1m<sup>2</sup> quadrats were marked out at approximately 20m intervals along a transect. Each quadrat was placed alternately on either marginal river bank vegetation or on grassland situated further away from the river bank, and its position was marked by a wooden stake (this always marked the bottom left hand corner of the quadrat when facing away from the river). The first vegetation survey commenced on May 13th and terminated on May 19th 1993. The second and third surveys commenced on June 6th and July 6th and terminated on June 11th and July 7th respectively. For each quadrat the total number of flowering stems were recorded (a flowering stem was defined as one bearing either buds, open flowers or both), the total number of flowers and the total number of inflorescences post flowering were also noted for each plant species. In addition plant species were identified using keys by Fitter *et al* (1989), Rose (1981) and Hubbard (1984) enabling percentage ground cover to be estimated for each species occurring in the quadrat, using the Domin Scale of cover. The collection of this data every month enabled seasonal variations to be noted.

Floral traits of each flowering plant including depth, diameter, symmetry and colour of at least 5 flowers per species were recorded (provided that there were 5 flowers for a particular species). Vegetation surveys were always carried out prior to the insect observation period.



### **2.3 Insect Observations.**

At each of the permanent quadrats insect observations were carried out at three different time periods. These periods covered the following times of day, 9.30 - 12.30, 12.30 - 3.30 and 3.30 - 6.30 for May, June and July. At each quadrat the observation period lasted for 10 minutes during which time the number and type of invertebrates visiting the quadrat were identified to order. Where possible insects were collected using a pooter, if this was inappropriate a specimen jar was used instead. All of these specimens were taken back to the lab for further identification. In addition, the number and type of flower visitors were noted for each 10 minute observation period as well as the species of flower visited. An insect was classed as a flower visitor if it touched either the anthers or stigma of an open flower. These observation periods enabled possible pollinators to be identified for the whole of the study period. Invertebrates were identified using keys by Chinery (1986a; 1986b), Roberts (1985a; 1985b; 1987), Unwin (1981; 1984), Richards (1977) and Stubbs and Falk (1983). Observations were not carried out in the rain or in very windy weather.

In order to obtain a more accurate estimate of pollinator activity, a fixed transect running through the site was walked for a duration of 10 minutes, for each month. This enabled fast moving flower visitors such as bees, (which made relatively few flower visits to each quadrat) to be observed. Such visitors were not collected but were identified as being either Lepidoptera, *Bombus* sp., *Psithyrus* sp. or 'others'. For each flower species visited, its morphology and colour were noted. This was repeated for every time period to identify diurnal differences. This data could also be compared to the information collected from the 'sit and wait' approach.

### **2.4 Methods Of Analysis.**

#### **2.4.1 Vegetation Data.**

The median domin scores and constancy values for each plant species for May, June and July were calculated to identify differences in species dominance and frequency, respectively. For each month the data from each quadrat was pooled so that the total number of flowering stems, buds, flowers and flowers in the post flowering state could be calculated.

#### 2.4.2 Insect Data.

Due to insufficient observations, visitors to flowers and quadrat vegetation could not be analysed when classified into families and therefore orders were used (see Appendices 1 - 6 for family data).

##### 2.4.2.1 Diurnal Activity.

For the months May, June and July in order to identify any significant differences in insect and pollinator abundance between the three time periods, the data were analysed using chi - square contingency tables. In order to ascertain any significant differences in activity within each insect group a ranked one way analysis of variance was used for all three months. Chi - square contingency tables were also used to identify significant differences in activity within each insect order throughout the season.

A ranked one way analysis of variance was used once more to identify any significant differences in pollinator activity for May, June and July within each insect group. Chi - square contingency tables were also used to establish significant differences in pollinator activity for all three months. In certain cases Yate's correction was applied if there were expected values less than 5.

##### 2.4.2.2. Seasonal Variation.

To identify any seasonal differences in the total number of insects and pollinators visiting quadrat vegetation and flowers respectively (i.e. insect / pollinator abundance), chi - square contingency tables were used.

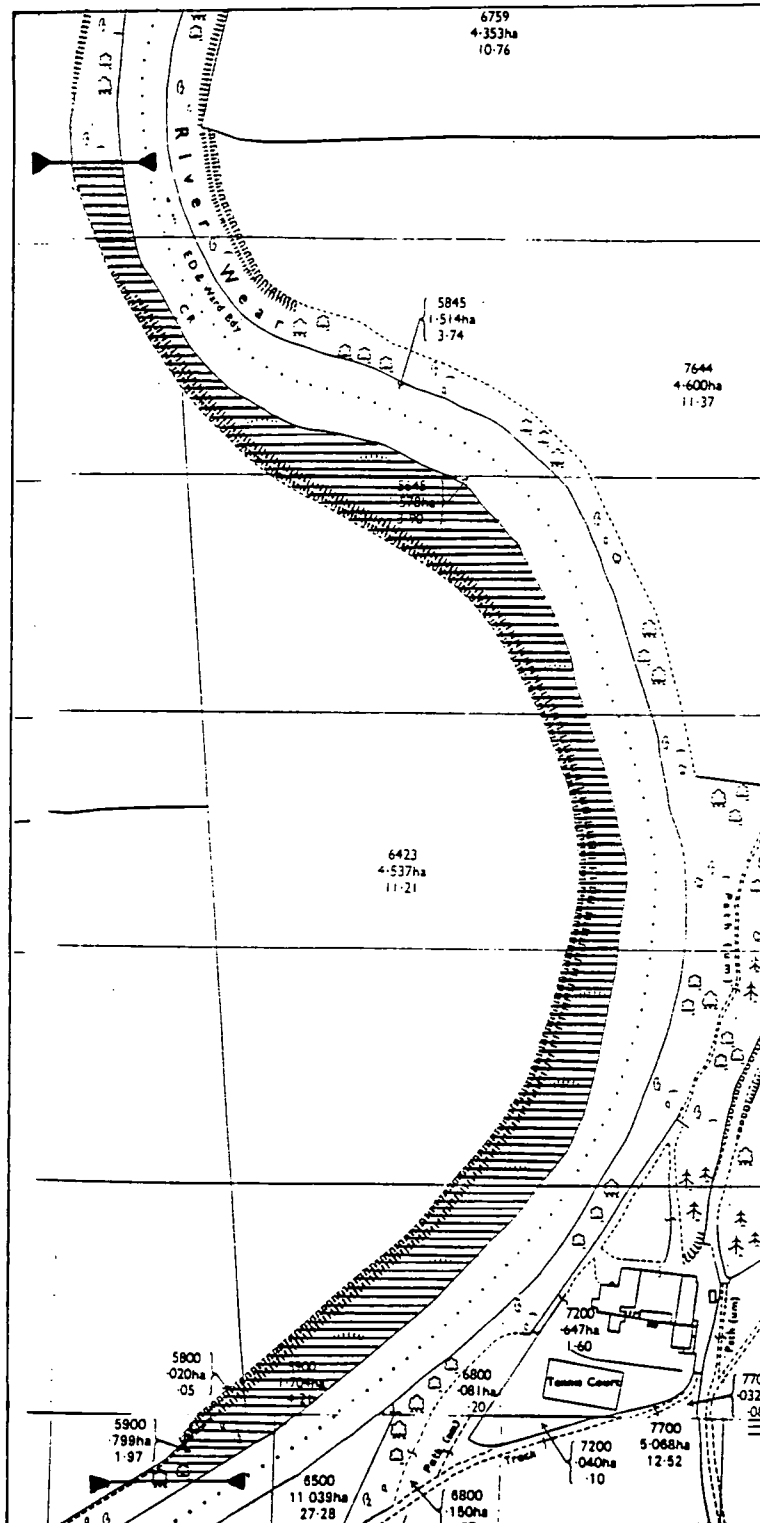
#### 2.4.3 Plant And Insect Interactions.

Spearman's rank correlation coefficients were calculated to identify relationships between pollinator and insect activity, and flower and plant density. This analysis was required since the data did not fit a normal distribution, even when log transformed and so would have given spurious results.

Fishers' Exact tests were carried out to detect if pollinators displayed a preference for or an avoidance of different flower types. Flowers were classed as being either 'open' or 'tubular' as described by Proctor & Yeo (1973). This classification relies on the

position of the nectaries for each individual flower as well as the shape of the corolla. Nectaries of tubular flowers tend to be concealed whilst they are more obvious in open flowers. Fishers' Exact tests were also used to compare the types and colours of flowers visited by pollinators (as chi - square contingency tables were inappropriate due to the low number of observations).

**Map Showing The Location Of The Study Site At Shincliffe, County Durham.**



 Study Site

### 3.0 RESULTS.

#### 3.1 Plant Assemblage.

##### 3.1.1 Vegetation Survey.

There were 43 species of flowering plants identified during the course of the survey. The median domin scores (m.d.s.) and the constancy values (c.v) calculated for each herbaceous plant species are presented in table 1, together with the time periods during which they flower. From these values it is obvious that *Aegopodium podagraria* (m.d.s. 5 and c.v. IV) and *Stellaria holostea* (m.d.s. 4 and c.v. IV) were the most abundant and frequent species during May. Although *Epilobium angustifolium*, *Myrrhis odorata* and *Symphytum uplandicum* were very abundant when found (m.d.s. of 5, 6 & 8, respectively) they were very infrequent overall. *Galium aparine*, whilst not as abundant was observed repeatedly throughout the site (m.d.s. 2 and c.v. V). During June *A. podagraria* was again the most abundant and frequently occurring dicotyledon (m.d.s 5 and c.v IV), whilst *Vicia cracca*, *S. holostea*, *Lamium album* and *G. aparine* (m.d.s. 2, 3, 2 & 3 and c.v IV, III, III & III respectively) were less abundant they occurred frequently within the community. Finally, in July the most frequently occurring species were found to be *A. podagraria*, *G. aparine*, *Rubus idaeus*, *S. holostea* and *V. cracca* (m.d.s. 4, 2, 4, 2 & 3 and c.v. IV, IV, III, III, III respectively) although their abundances' were relatively low compared to that of the infrequent *E. angustifolium*, *M. odorata*, *Saponaria officinalis* and *S. uplandicum* (m.d.s 8, 7, 6, & 7 respectively all had c.v of I).

The seasonal changes in the percentages of flowering stems are shown in figures 1 - 3. In May *S. holostea* accounted for 76.4% of all flowering stems and was therefore the plant most frequently in flower in addition to being the most abundant and frequent species with regards to its vegetative characteristics. In June the plants most frequently in flower included *S. holostea*, *Cruciata laevipes* and *A. podagraria* (with values of 26.34%, 25.2% and 25.85% respectively). Finally, in July the most frequent plant in flower was *A. podagraria* which accounted for 31.5% of all flowering stems. There were also a greater number of plant species in flower during July than for either of the two previous months.

**Table 1. The Monthly Median Domin Scores And Constancy Values Of Herbaceous Plants**

Species	Median Domin Score.			Constancy Value			Period of Flowering
	May	June	July	May	June	July	
<i>Achillea millefolium</i>	3	1	2	I	I	I	June-Aug.
<i>Aegopodium podagraria</i>	5	5	4	V	IV	IV	June-Aug.
<i>Artemisia vulgaris</i>	1.5	3	4	I	I	I	July-Sept.
<i>Centurea nigra</i>	3	3	3	I	I	I	July-Aug.
<i>Cerastium fontanum</i>	1	1	1	I	I	I	April-Sept.
<i>Chaerophyllum temulentum</i>	1.5	2.5	3	I	I	I	June-July
<i>Cirsium arvense</i>	2.5	4	4	I	I	I	July-Sept
<i>Cirsium vulgare</i>	4	4	4	II	II	II	July-Oct.
<i>Cruciata laevipes</i>	4	4.5	3.5	I	I	I	May-June
<i>Epilobium angustifolium</i>	5	6	8	I	I	I	July-Sept
<i>Equisetum arvense</i>	2	2	1	I	I	I	-
<i>Galium aparine</i>	2	3	2	V	III	IV	June-Aug.
<i>Geranium pratense</i>	4	4	4	I	II	II	June-Sept.
<i>Heracleum sphondylium</i>	1	2	3	II	II	I	June-July
<i>Hesperis matronalis</i>	4	2	3	I	I	I	May-July
<i>Hieracium sp.</i>	1	3	0	I	I	0	-
<i>Lamium album</i>	2	2	2	II	III	II	March-Oct.
<i>Lamium purpureum</i>	0	0	2	0	0	I	March-Oct.
<i>Lathyrus pratensis</i>	2.5	3	4	I	I	I	May-Aug.
<i>Linaria vulgaris</i>	3	2	3	I	I	I	July-Oct
<i>Myrrhis odorata</i>	6	7	7	I	I	I	May-June
<i>Petasites hybridus</i>	2	3.5	4	I	II	II	March-May
<i>Plantago lanceolata</i>	2	1	1	I	I	I	April-Oct.
<i>Ranunculus acris</i>	2	0	0	I	I	0	May-Aug.
<i>Ranunculus repens</i>	2	4	3	I	I	I	May-Aug.
<i>Rubus idaeus</i>	2	3	4	II	II	III	June-Aug.
<i>Rumex acetosa</i>	2	2.5	1	I	I	I	May-June
<i>Rumex obtusifolius</i>	3	1.5	1.5	I	I	I	July
<i>Saponaria officinalis</i>	4	5	6	I	I	I	July-Sept.
<i>Senecio jacobaea</i>	1.5	2	1	I	I	I	June-Oct.
<i>Silene dioica</i>	0	2	3	0	I	I	March-Oct
<i>Silene vulgaris</i>	0	0	2	0	0	I	June-Aug.
<i>Stellaria graminea</i>	0	0	3	0	0	I	May-Aug.
<i>Stellaria holostea</i>	4	3	2	IV	III	III	April-June
<i>Symphytum uplandicum</i>	8	9	8	0	I	I	May-June
<i>Tanacetum parthenium</i>	2	0	0	I	0	0	June-Sept.
<i>Taraxacum officinale agg.</i>	3	2	1.5	I	I	I	March-Oct.
<i>Torilis japonica</i>	3	2	0	I	I	I	July-Aug.
<i>Trifolium repens</i>	2	0	0	I	0	0	June-Sept
<i>Trifolium pratense</i>	2	3	3	II	II	II	May-Sept
<i>Urtica dioica</i>	2	2	2	II	I	II	June-Aug.
<i>Veronica chamaedrys</i>	4	4	3.5	I	I	I	March-July
<i>Vicia cracca</i>	2	2	3	III	IV	III	June-Aug.

### 3.1.2 Floral Characteristics.

Seasonal variations in floral traits such as morphology and flower colour were quite striking throughout the study period. For instance in May 71.43% of all plants in flower were classed as being open and simple whilst only 28.57% were tubular, compared to 55.56% open and 44.44% tubular in July. In this study 'open' flowers included *Stellaria holostea*, *S. graminea*, *Cruciata laevipes*, *Taraxacum officinale*, *Myrrhis odorata*, *Veronica chamaedrys*, *A. podagraria*, *G. aparine*, *Torilis japonica*, *Rubus idaeus*, *Geranium pratense*, *Hesperis matronalis*, *Heracleum sphondylium*, *Trifolium pratense*, and *Epilobium angustifolium*. Tubular plants included *Lamium album*, *L. purpureum*, *Silene dioica*, *S. vulgaris*, *Cirsium vulgare*, *Symphytum uplandicum*, *Lathyrus pratensis*, and *Vicia cracca*.

There also seemed to be a general trend in the colour of the plant species in flower from May to July. For example in May 28.56% of plants in flower were pink-purple or blue whilst in July this increased to 44.44%. However the increase in the number of plants with white flowers was not as striking, increasing from 42.86% in May to only 44.44% in July. Finally, the percentage of plants with yellow flowers was 28.57% in May which decreased to 11.11% in July. There seems to be a general increase in the complexity of flower types throughout the season with a gradual progression from white and yellow flowers through to blue and pink-purple flowers.

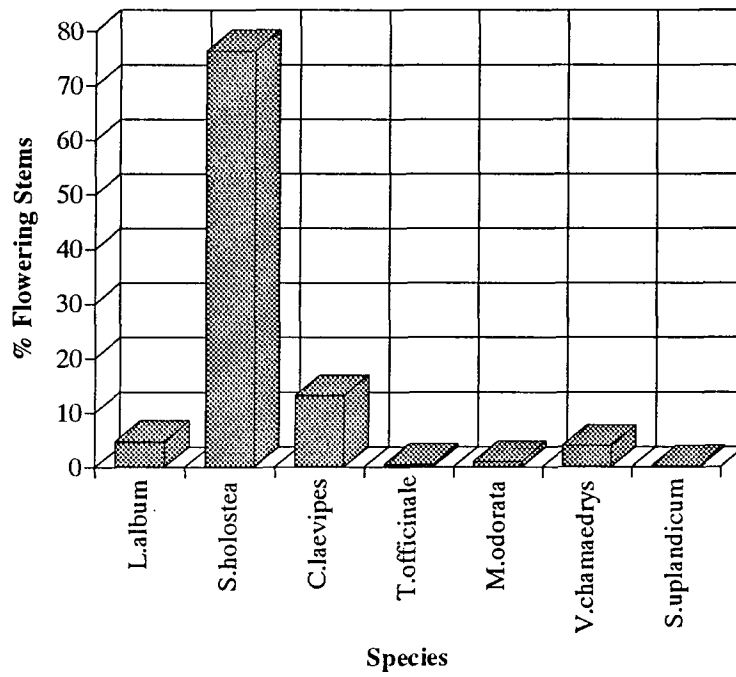
## 3.2 Insect Assemblage.

### 3.2.1 Diurnal Activity And Abundance Of Insects.

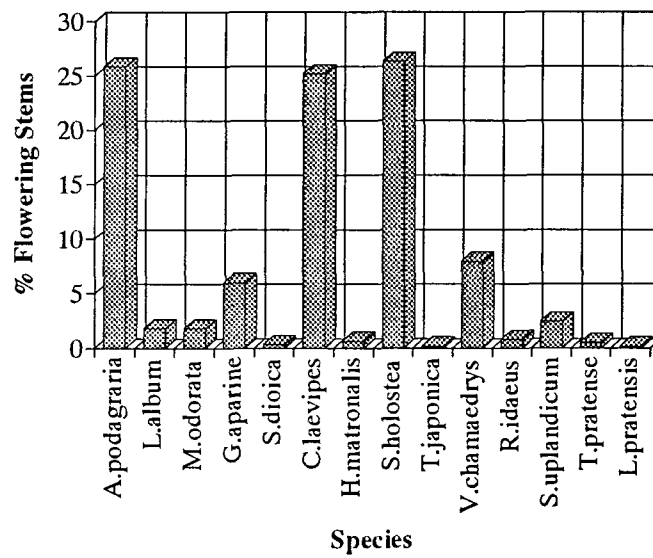
Significant differences in insect abundance were identified for May ( $\chi^2 = 16.008$ , df 6,  $p < 0.02$ ) June ( $\chi^2 = 67.484$ , df 8,  $p < 0.001$ ) and July ( $\chi^2 = 313.657$ , df 10,  $p < 0.001$ ). Insect abundance was therefore diurnally heterogeneous throughout the study period.

In May the insects compared included Diptera, Hymenoptera, Coleoptera and Hemiptera. With the most abundant order being Coleoptera, observed on 619 occasions in total (see figure 4a). Figure 4b illustrates how insect abundance increased as the day progressed, the most abundant time period being 3.30 - 6.30 when a total of 308 insects were observed (accounting for 39.18% of all observations, compared to 28.80% and 32.01% during 9.30-12.30 and 12.30 - 3.30, respectively).

**Figure 1. The Total Percentage Of Flowering Stems In May.**

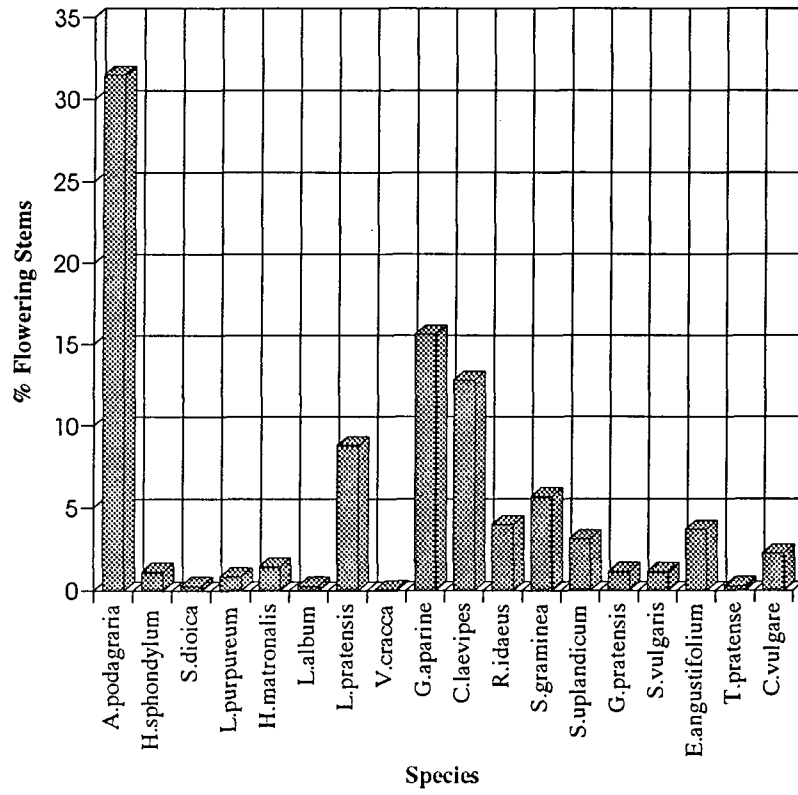


**Figure 2. The Total Percentage Of Flowering Stems In June.**

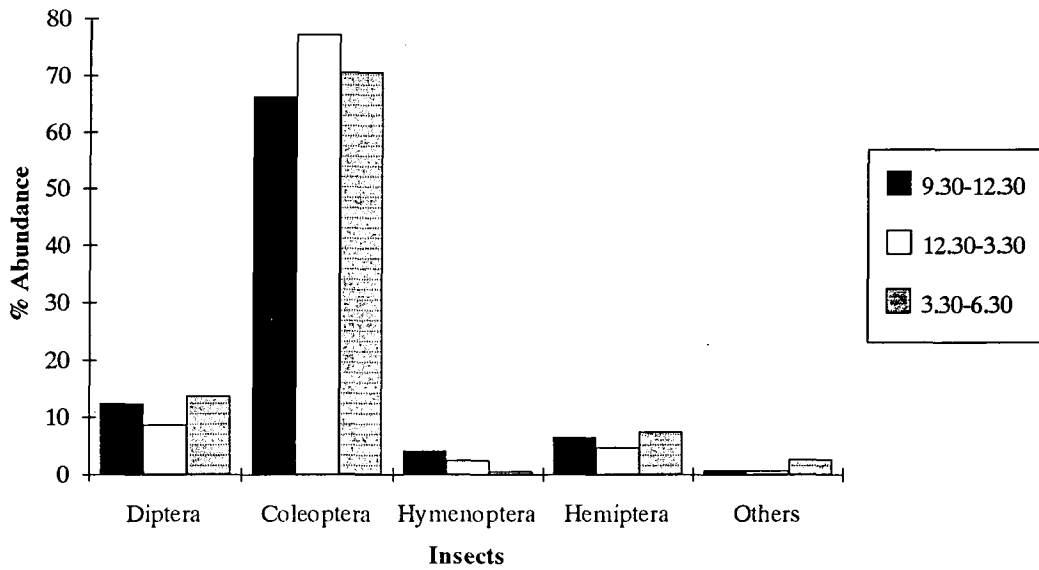




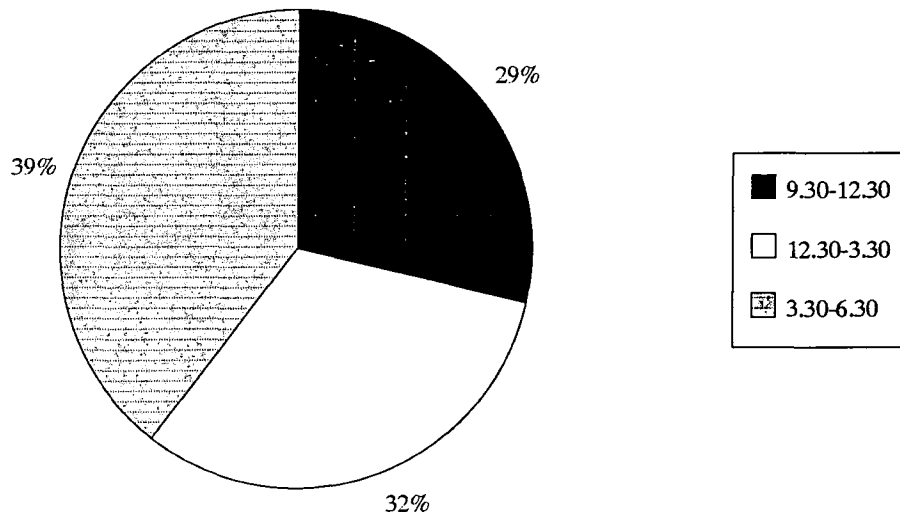
**Figure 3. The Total Percentage Of Flowering Stems In July.**



**Figure 4a. The Diurnal Variation In The Percentage Abundance Of Insects During May.**



**Figure 4b. The Diurnal Abundance of Insects During May.**



After performing a ranked one way analysis of variance it was obvious that during May, there were no significant differences in the activity of Diptera, Coleoptera, Hymenoptera or Hemiptera throughout the day.

In June the insects compared were the same as for May except there was an additional category of 'others' (this included the orders Trichoptera, Odonata, Mecoptera, Ephemoptera, Thysanoptera, Lepidoptera and Neuroptera). In this particular month the most abundant insect order was Diptera, observed on 607 occasions (see figure 5a for diurnal variations). Insect abundance tended to drop during 12.30 - 3.30 whilst remaining relatively high in the morning and late afternoon, as shown in figure 5b.

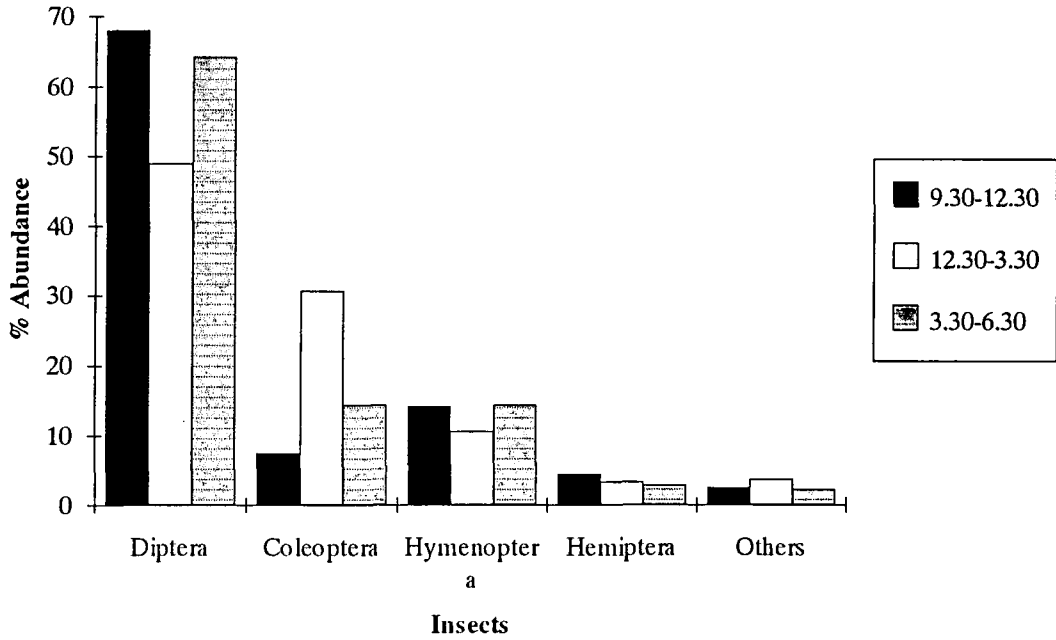
In June, after performing a ranked one way analysis of variance, the only significant difference was in the activity of Diptera ( $F(2, 87) = 5.32, p < 0.0066$ ). The median values of the ranks indicated that abundance peaked in the morning and late afternoon, whilst falling from 12.30 - 3.30. This trend is also apparent from the recorded observations used in the chi - square analysis.

The insects compared in July were the same as for June with the exception of the category 'others' (this included Lepidoptera, Plecoptera, Ephemoptera, Thysanoptera, Mecoptera and Pscoptera). Once again Diptera were the most abundant insect order, observed on 535 occasions (see figure 6a). The abundance of insects tended to peak in the morning from 9.30 - 12.30 after which there was a gradual decline, as illustrated in figure 6b.

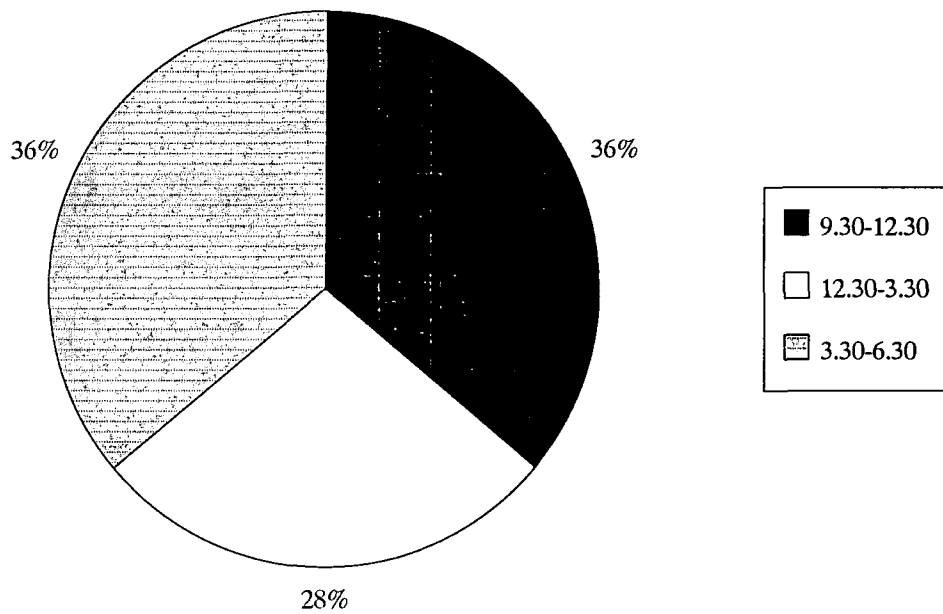
After calculating a ranked one way analysis of variance the only significant difference in the activity was for 'others' ( $F(2, 87) = 5.69, p < 0.004$ ). The median values of the ranks indicated that activity was greatest from 12.30 - 6.30 whilst being lower from 9.30 - 12.30, the complete reverse to the general trend.

Statistical analyses identified heterogeneity in diurnal activity within insect orders, throughout the season, with significant differences being found for Diptera, Coleoptera, Hymenoptera, Hemiptera and 'others' (see Table 2). These trends in activity are illustrated in figures 7a - 7e as a percentage of the total number of observations for each time period. Diptera tended to be more active / abundant in the early morning and late afternoon in May and June, whilst in July the activity remained more or less constant from 9.30 - 3.30 with a gradual decline thereafter. It is difficult to identify trends in abundance for Hymenoptera in May since they were only observed on 8 occasions, however during all three months they were most abundant in the early morning.

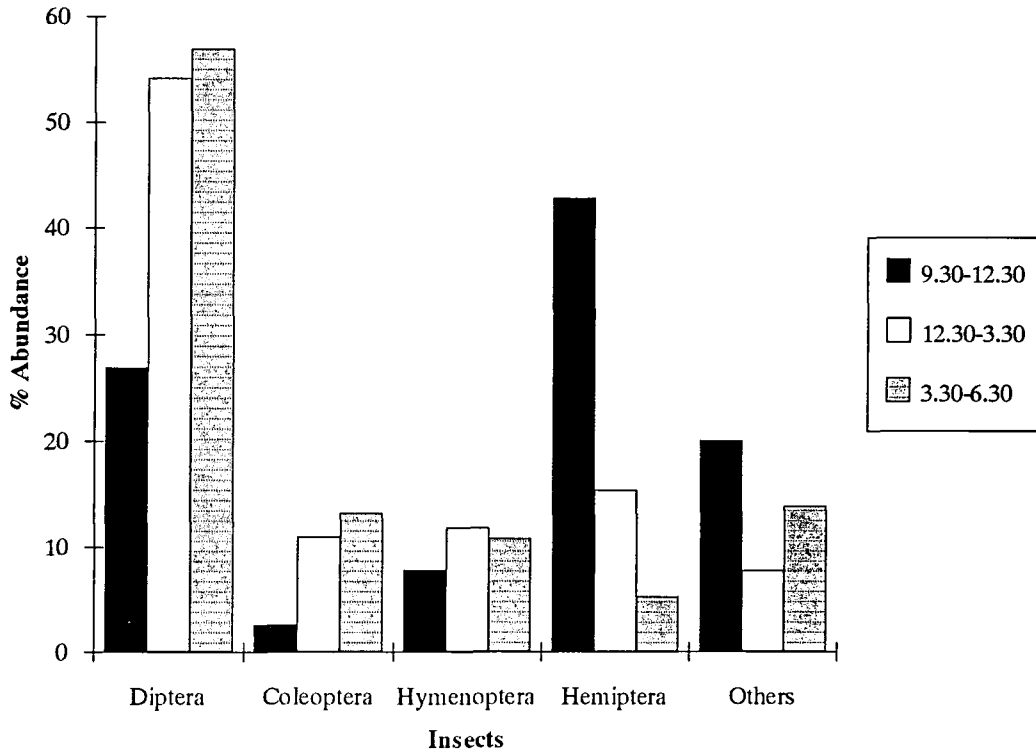
**Figure 5a. The Diurnal Variation In The Percentage Abundance Of Insects During June.**



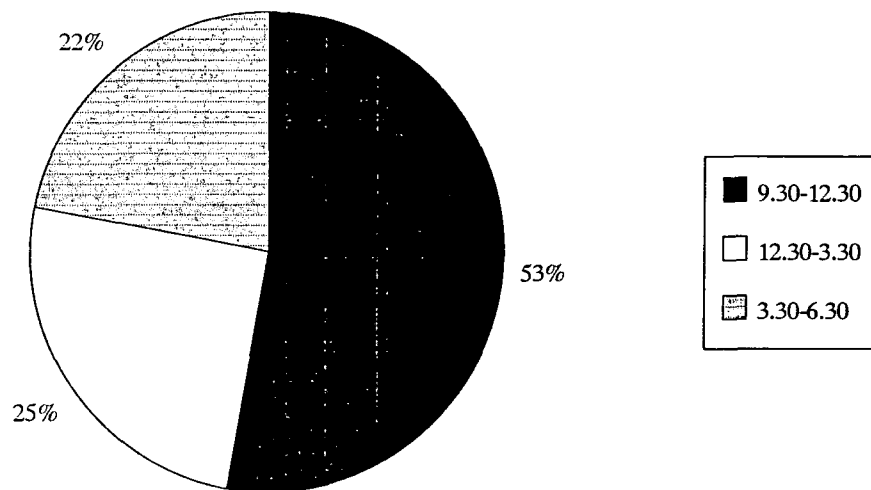
**Figure 5b. The Diurnal Abundance of Insects During June.**



**Figure 6a. The Diurnal Variation In The Percentage Abundance Of Insects During July.**



**Figure 6b. The Diurnal Abundance Of Insects During July.**



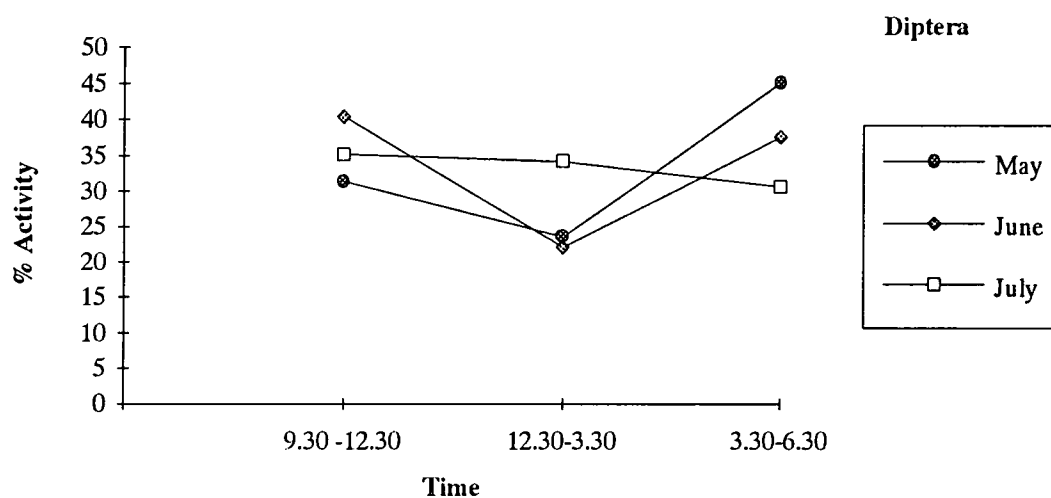
**Table 2. The Results After Using  $\chi^2$  Contingency Tables To Identify Any Significant Differences In Diurnal Abundance / Activity Throughout The Season Within Each Insect Order**

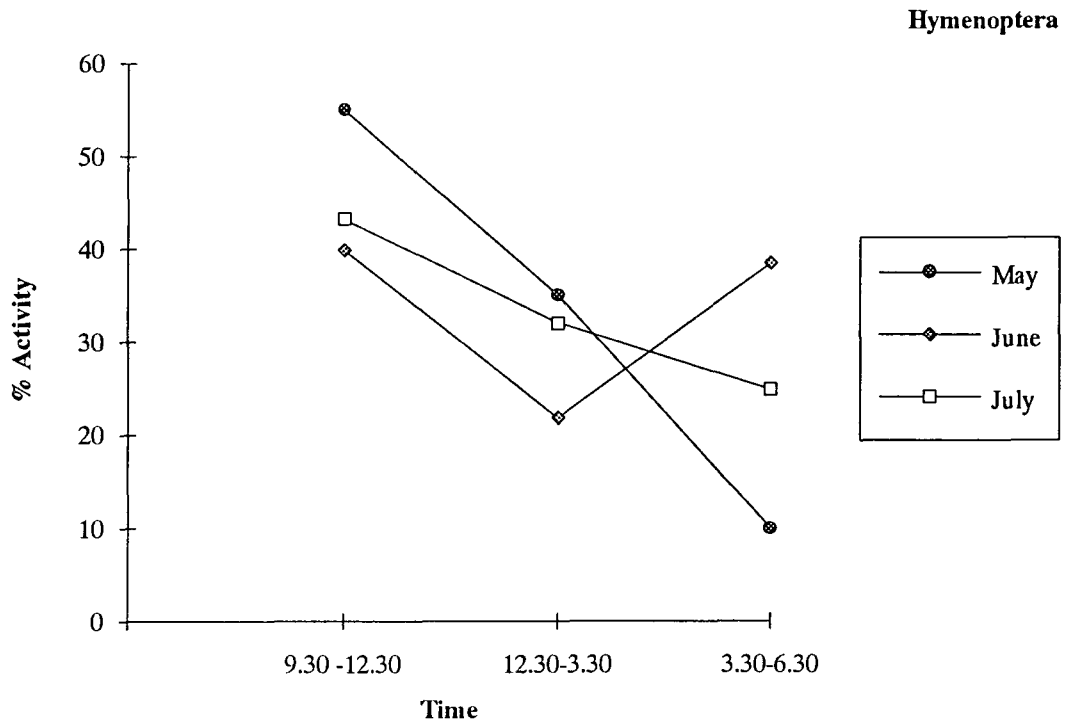
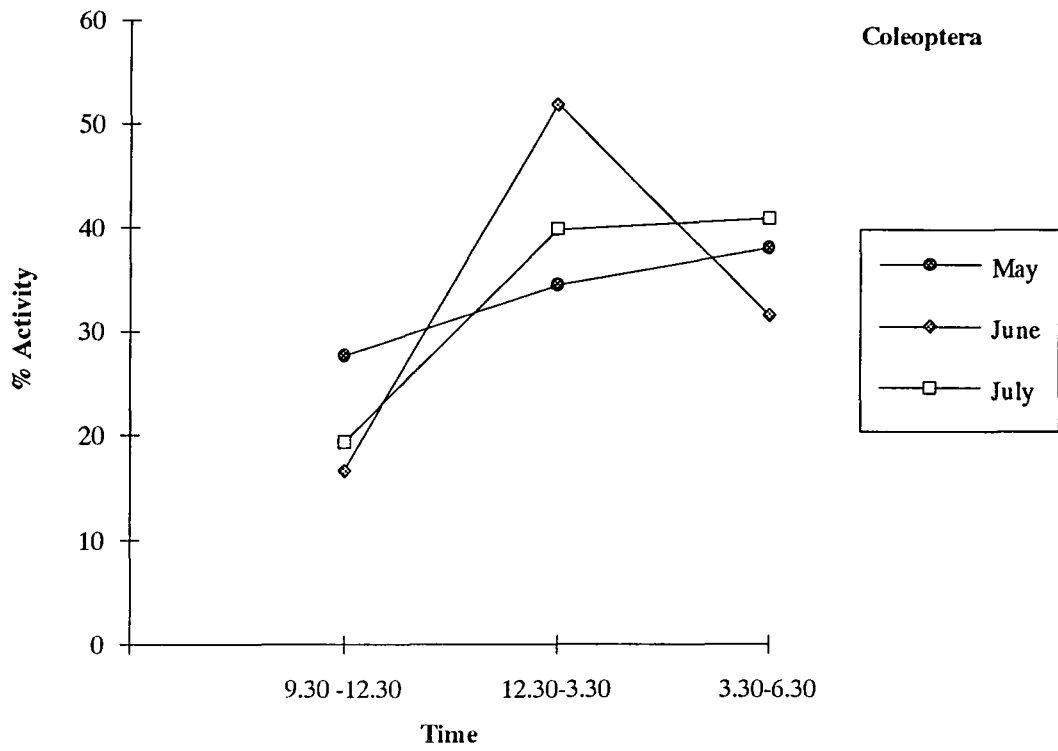
Order	$\chi^2$ Value	D.F	Significance
Diptera	25.961	4	<b>p &lt; 0.001</b>
Hymenoptera	10.711	4	<b>p &lt; 0.05</b>
Coleoptera	19.595	4	<b>p &lt; 0.001</b>
Hemiptera	110.781	4	<b>p &lt; 0.001</b>
Others	32.736 ( Y.C. )	4	<b>p &lt; 0.001</b>

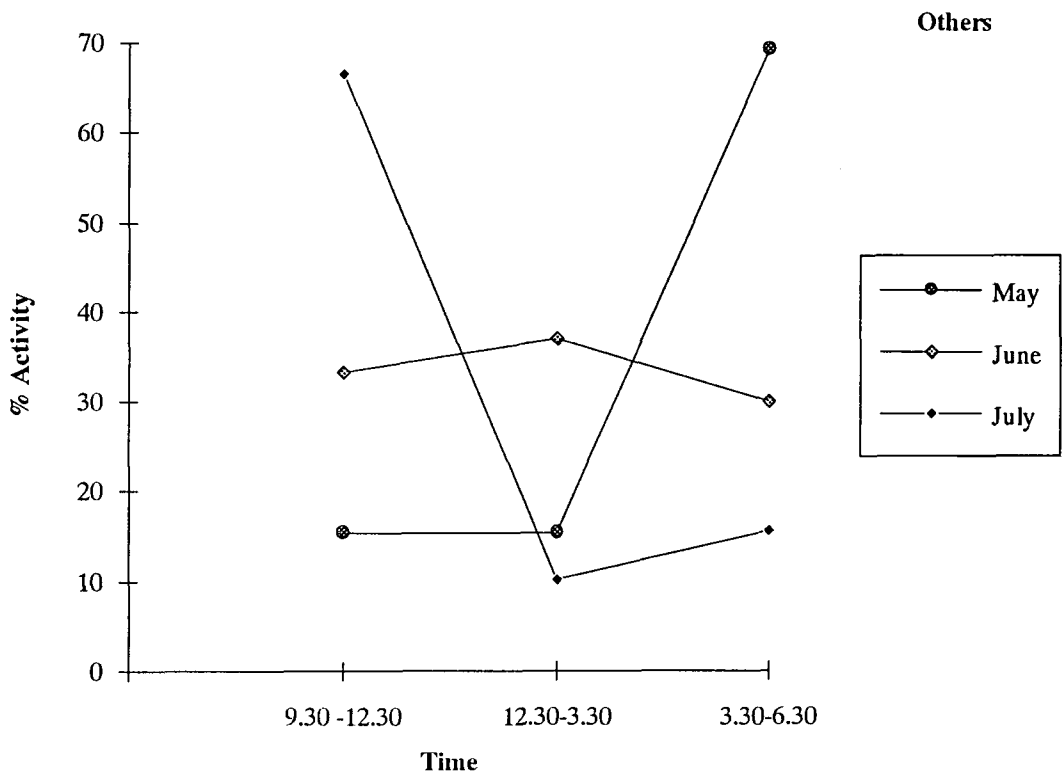
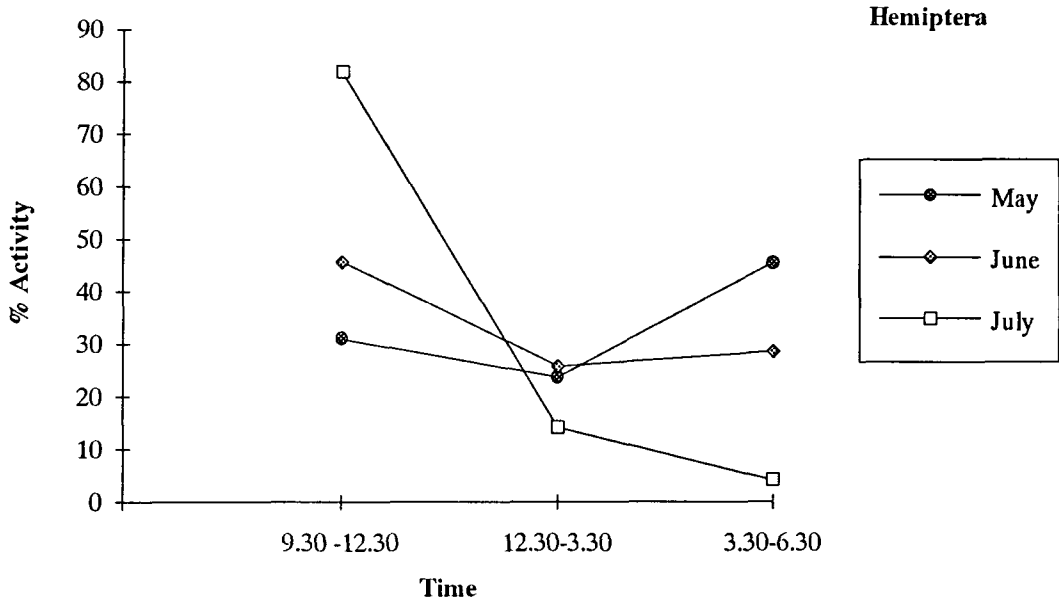
**Key**

Y.C. = Yate's Correction

**Figures 7a-7e. The Diurnal Variation In Activity Within Each Insect Order Throughout The Study Period.**









Coleoptera were less active from 9.30 - 12.30 throughout the season. In June and July their activity peaked at midday, whilst in May they were more active in the late afternoon. Hemiptera tended to show great heterogeneity throughout the study period, being the least active during 12.30 - 3.30 in May and June but in July they were less active during 3.30 - 6.30. Finally the category 'others' tended to be scarce in May making trends difficult to identify. However they had a relatively constant abundance during June, whilst in July they were most abundant during the early morning becoming less so at mid - day with a final increase in late evening.

In terms of diurnal activity Diptera, Hymenoptera and others were always more abundant in the early morning, becoming less so during the early afternoon, with a final increase in activity towards late afternoon. Coleoptera tended to peak in abundance at 12.30 - 3.30, and declined thereafter. Hemiptera were most abundant in the early morning their frequency falling later in the day.

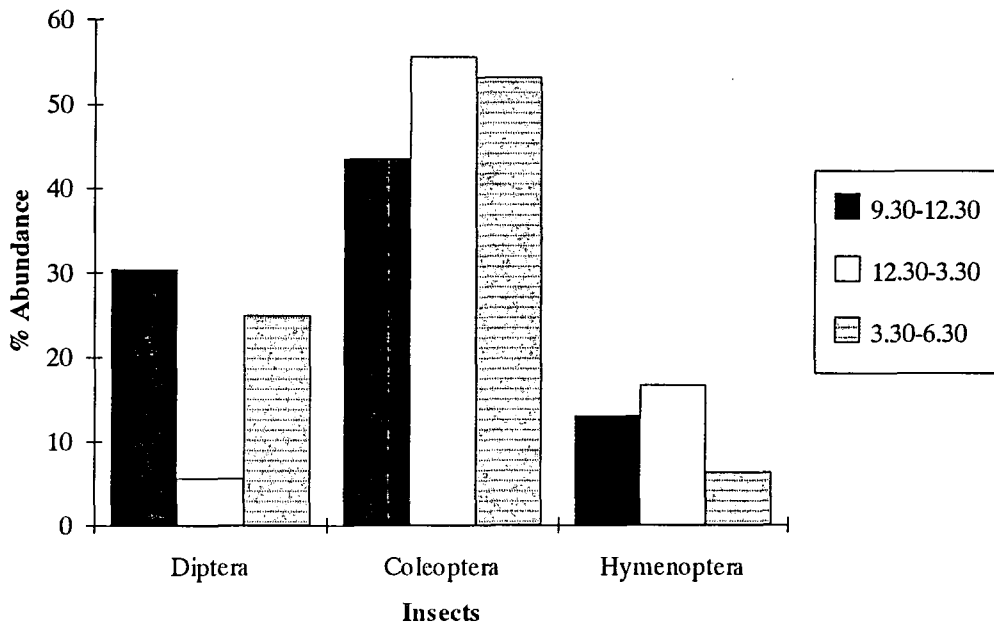
### 3.2.2. Diurnal Activity And Abundance Of Pollinators.

In May there was no significant difference in the types of pollinators present with respect to time. However significant differences were found for June ( $\chi^2 = 18.253$ , df 4,  $p < 0.001$ ) and July ( $\chi^2 = 13.732$ , df 4,  $p < 0.01$ ). Pollinator abundance was therefore diurnally heterogeneous for the final 2 months, whilst being homogenous throughout May (see figure 8a and 8b). The orders compared for all three months included Diptera, Hymenoptera and Coleoptera.

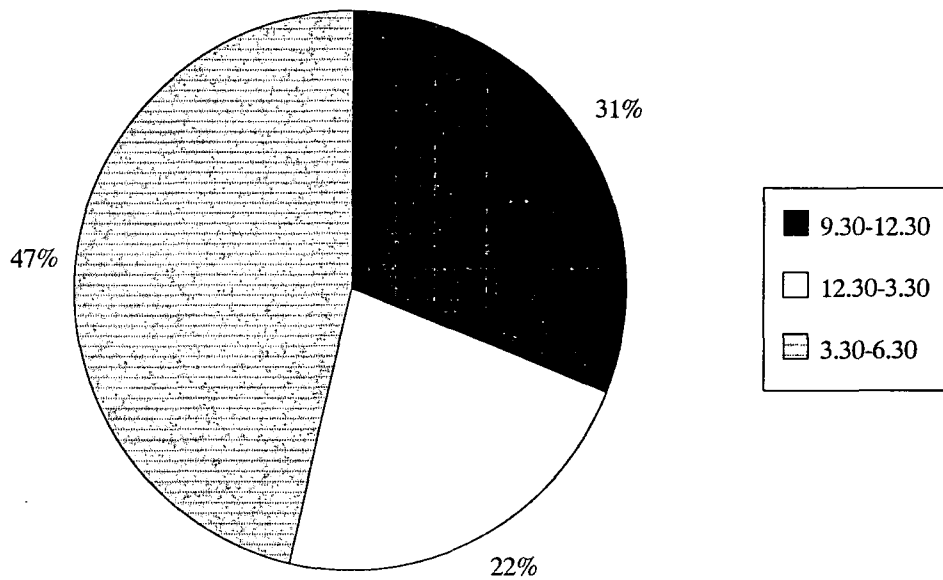
In June the most abundant pollinator was Diptera, accounting for 216 pollinator visits, and figure 9a shows the diurnal variation in pollinator abundance. Pollinator abundance was at its greatest from 9.30 - 12.30 (accounting for 47.34% of all observations), declining thereafter to a constant level (see figure 9b).

In July, Hymenoptera were the most abundant pollinators, observed on 80 occasions (see figure 10a). The most abundant time period was also 9.30 - 12.30 (accounting for 40.57% of all observations), however pollinator abundance tended to decrease steadily as the day progressed, this is illustrated in figure 10b.

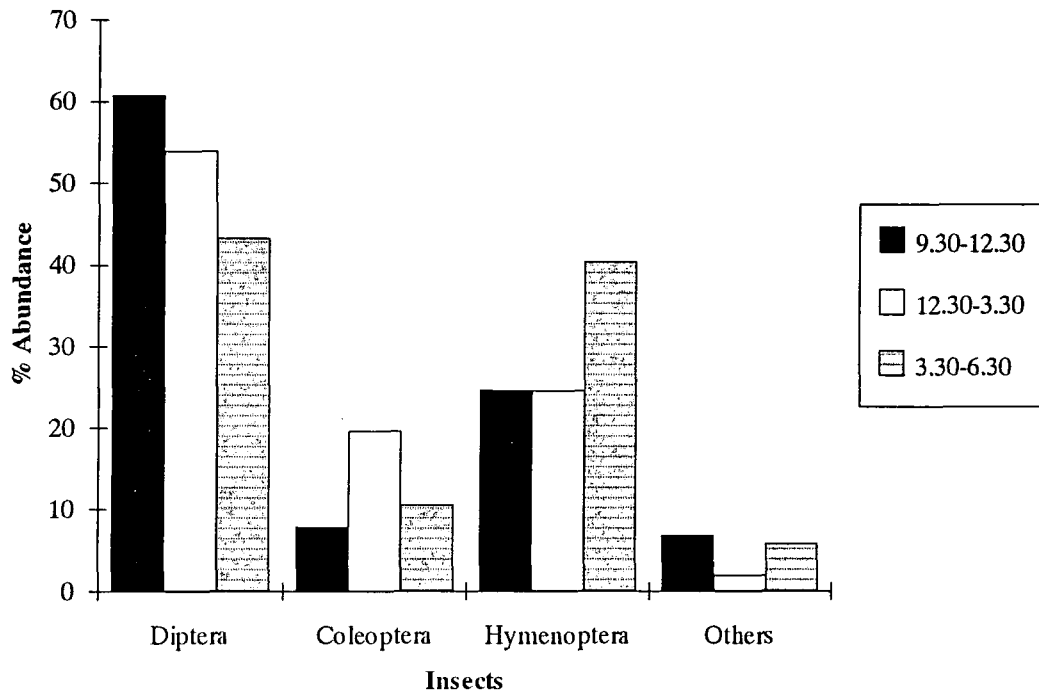
**Figure 8a. The Diurnal Variation In The Percentage Abundance Of Pollinators During May.**



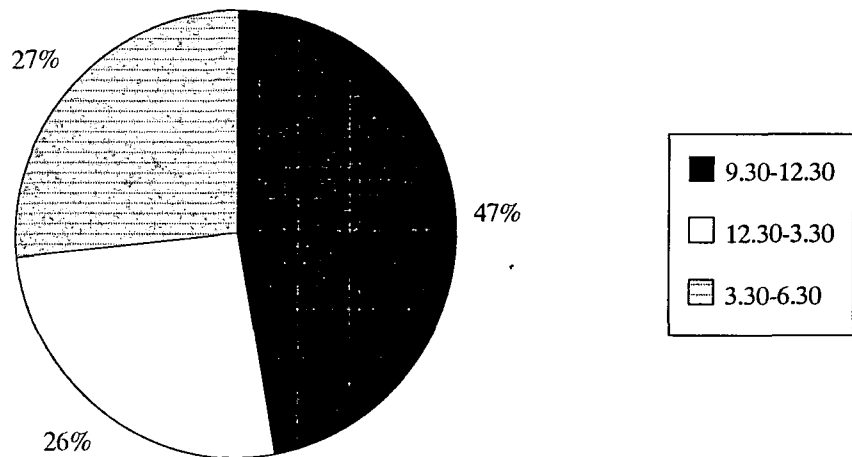
**Figure 8b. The Diurnal Abundance Of Pollinators During May.**



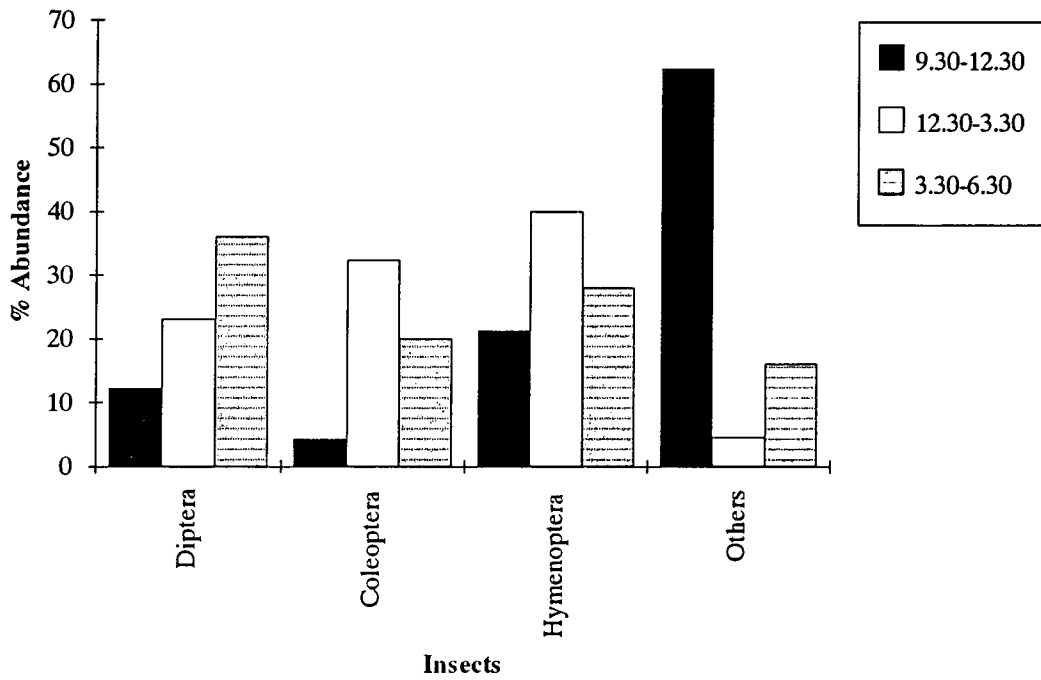
**Figure 9a. The Diurnal Variation In The Percent Abundance Of Pollinators During June.**



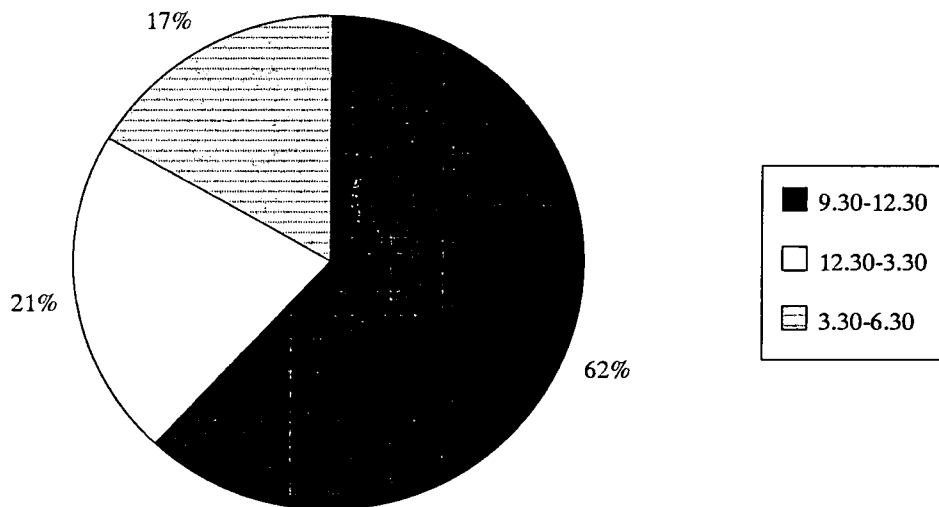
**Figure 9b. The Diurnal Abundance Of Pollinators During June.**



**Figure 10a. The Diurnal Variation In The Percent Abundance Of Pollinators During July.**



**Figure 10b. The Diurnal Abundance Of Pollinators During July**



After performing a ranked one way analysis of variance for each month, there were no significant differences in the diurnal activity for Diptera, Hymenoptera or Coleoptera. Chi - square calculations (Yate's correction was used for Diptera and Hymenoptera) also confirmed that there were no significant differences in absolute diurnal activity within the three insect orders throughout the study period.

### **3.3. Seasonal Variation.**

#### **3.3.1 Insect Abundance.**

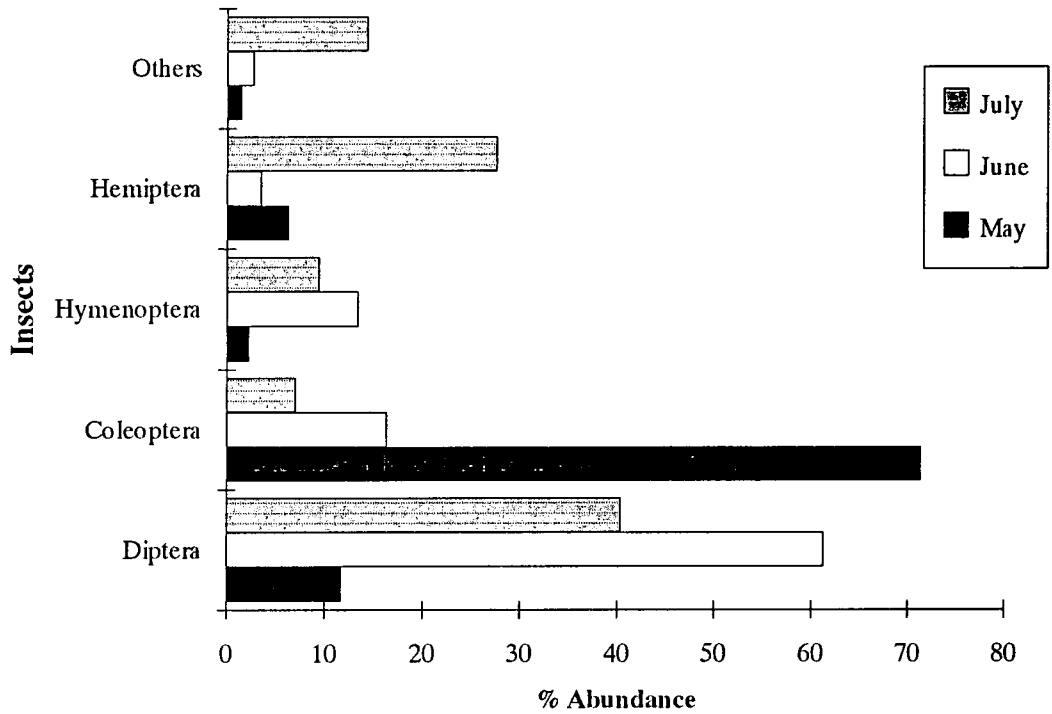
The seasonal variation in insect abundance was obvious after calculating a chi - square contingency table and is clearly illustrated in figure 11 ( $\chi^2 = 1677.194$ , df 8,  $p < 0.001$ ). The insect orders compared included Diptera, Coleoptera, Hymenoptera, Hemiptera and 'others' (including Lepidoptera, Plecoptera, Ephemoptera, Thysanoptera, Mecoptera, Pscoptera, Odonata, Trichoptera, Neuroptera, Isopoda, Collembola and Dermaptera).

The most abundant order overall was Diptera (accounting for 40.36% of all observations), whilst others was the least abundant (accounting for only 7.46% of the total observations). July was the most abundant month in terms of the greatest number of insects observed, although this is probably due to the large number of Aphididae (Hemiptera) and Thysanoptera detected in two separate quadrats. In May Coleoptera were the most abundant whilst Diptera and Hymenoptera were most abundant in June.

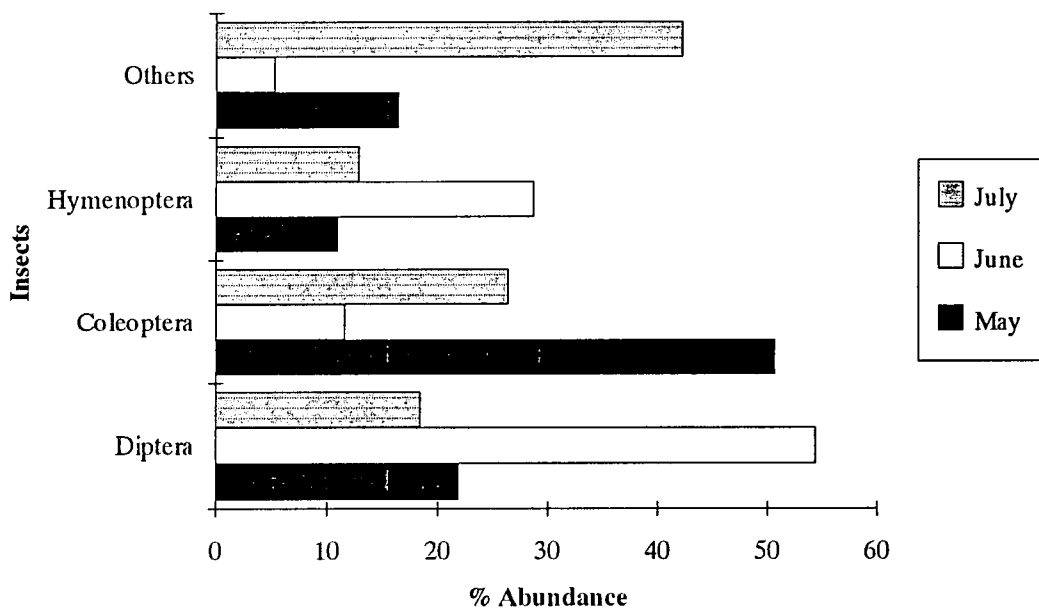
#### **3.3.2 Pollinator Abundance.**

Seasonal variations in pollinator abundance were quite striking, which can be seen from the large chi - square value ( $\chi^2 = 270.228$ , df 6,  $p < 0.001$ ) as well as from figure 12. In terms of absolute numbers, pollinators were most abundant in June, whilst being quite scarce during May. Pollinators from the orders Diptera, Coleoptera and Hymenoptera were always more abundant in June, however others were more abundant in July. This was mainly due to the large number of recorded Thysanoptera.

**Figure 11. The Seasonal Variation In Insect Abundance.**



**Figure 12. The Seasonal Variation In Pollinator Abundance.**



### 3.4 Plant And Insect Interactions.

#### 3.4.1 Floral Abundance And Insect Interactions.

During May, after calculating a Spearman's rank correlation coefficient there was a significant correlation between the ranked number of flowers and ranked number of pollinators ( $r_s = 0.6554$ ,  $df = 28$ ,  $p < 0.001$ ). There was also a significant positive correlation between the ranked number of flowering stems and the ranked number of pollinators ( $r_s = 0.3755$ ,  $df = 28$ ,  $p < 0.05$ ). Therefore as the number of flowers and flowering stems increased so did the number of flower visitors. Figures 13 - 14 illustrates this. There was no significant correlation between the number of ranked flowers or flowering stems and the total number of ranked insect visits.

In June and July the only significant positive correlation was between the ranked number of flowers and pollinators ( $r_s = 0.3723$ ,  $r_s = 0.3630$ ,  $df = 28$ , respectively and  $p < 0.05$ ). Figures 15 -16 illustrate these relationships.

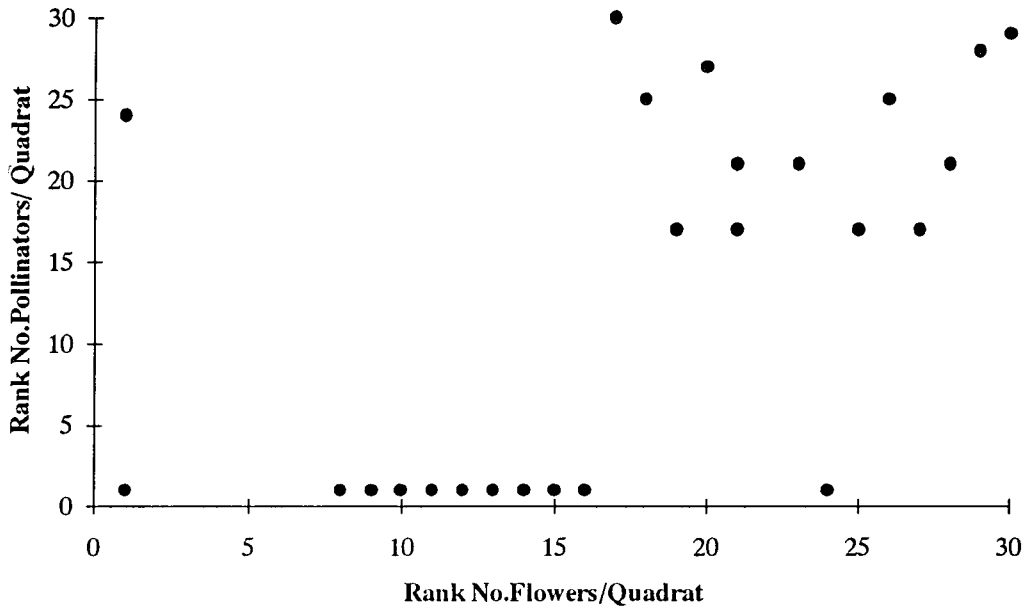
To examine these plant - pollinator relationships further a Spearman's correlation coefficient was calculated for individual pollinating insect orders for each month. In May a significant negative correlation existed between the rank number of pollinating Diptera, and the ranked number of flowers per quadrat ( $r_s = -0.5346$ ,  $df = 28$ ,  $p < 0.001$ ). This was also the case for the ranked number of pollinating Coleoptera and flowers per quadrat ( $r_s = -0.4229$ ,  $df = 28$ ,  $p < 0.05$ ). There was no such relationship for the Hymenoptera.

In June and July there were no such correlations, with the exception of pollinating Hymenoptera in June where there was a positive correlation ( $r_s = 0.3701$ ,  $df = 28$ ,  $p < 0.05$ ).

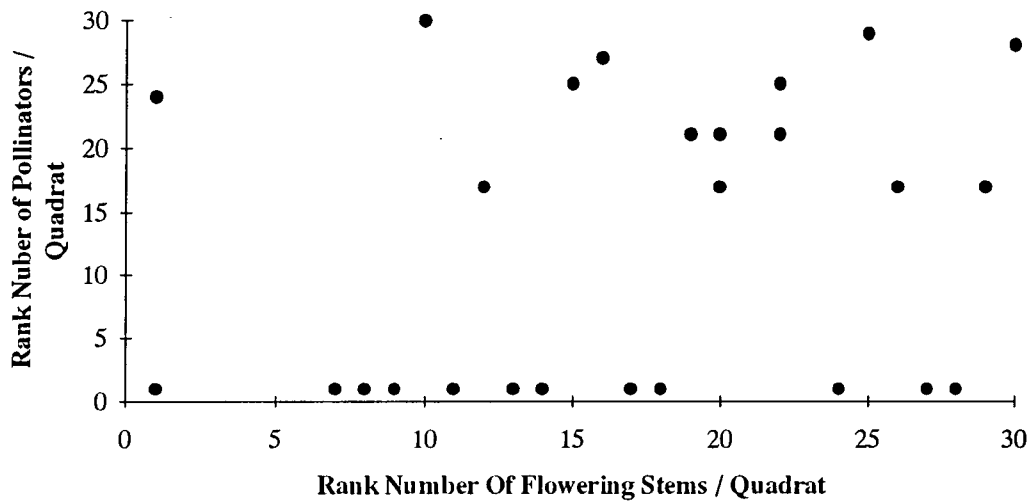
#### 3.4.2 Flower Morphology And Insect Interactions.

After performing Fishers' Exact tests for the months of May and July the insects Diptera, Coleoptera, Hymenoptera, bees and others were found to neither prefer or avoid open or tubular flowers. In May open flowers included *S. holostea*, *C. laevipes*, *Taraxacum officinale* agg, *M. odorata* and *Veronica chamaedrys* and the only tubular flower was *S. uplandicum*. In July open flowers included *A. podagraria*, *Hesperis*

**Figure 13. Relationship Between The Ranked Number Of Flowers And Pollinators Per Quadrat During May.**

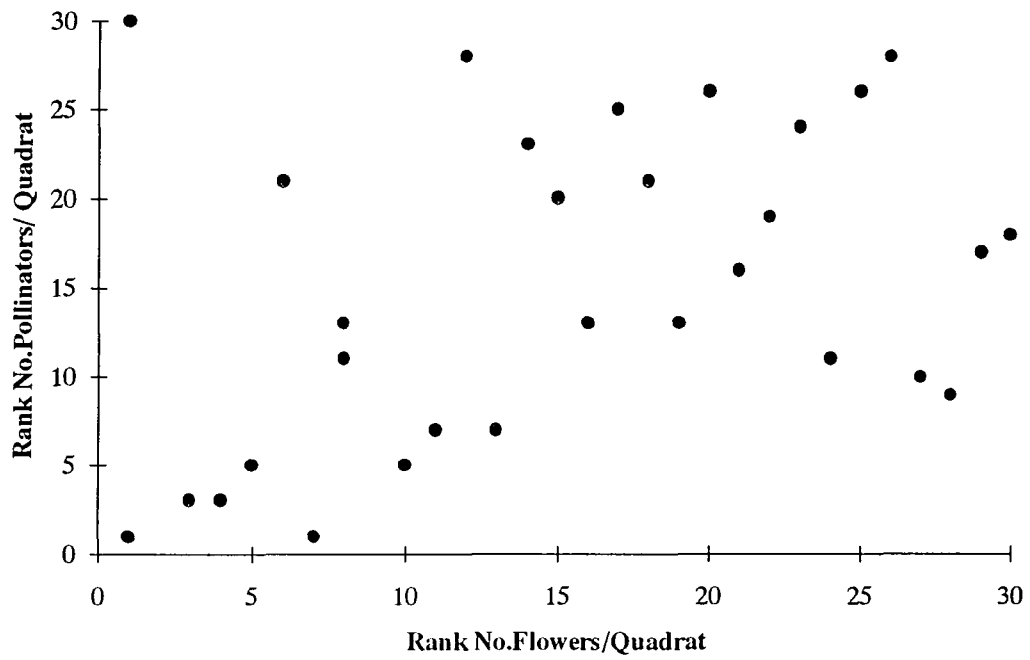


**Figure 14. Relationship Between The Ranked Number Of Flowering Stems And Pollinators During May.**

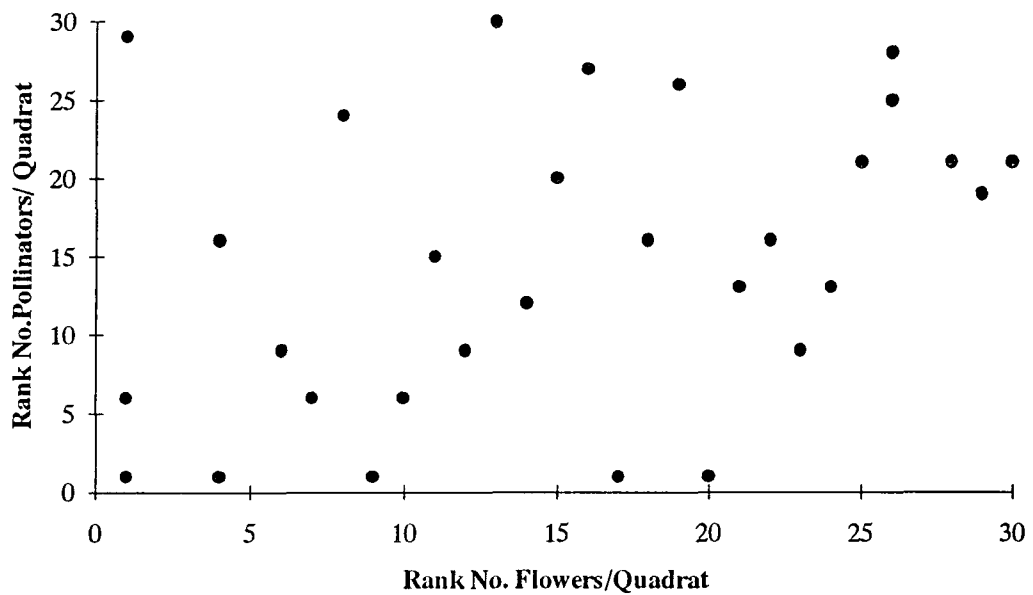




**Figure 15. Relationship Between The Rank Number Of Flowers And Pollinators Per Quadrat During June.**



**Figure 16. Relationship Between The Ranked Number Of Flowers And Pollinators Per Quadrat During July.**



*matronalis*, *G. aparine*, *C. laevipes*, *R. idaeus*, *S. graminea*, *Geranium pratensis*, *Epilobium angustifolium*, *H. sphondylium* and *Trifolium pratense*. Tubular flowers included *Cirsium vulgare*, *Silene dioica*, *Lamium purpureum*, *Lathyrus pratensis*, *Vicia cracca*, *Silene vulgaris* and *S. uplandicum*. Although the outcome of the analysis was not significant it is worth mentioning that in May Diptera, Coleoptera, Hymenoptera and others were never found visiting tubular flowers, whilst bees only visited tubular flowers. In July bees visited tubular flowers on 69.57% and open flowers on 30.43% of occasions, whilst conversely, Diptera and Coleoptera were found more frequently on open rather than tubular flowers (see figure 18).

In June, the same analysis revealed that Hymenoptera were the only insect group to distinguish between the two flower classes. From the data collected Hymenoptera appear to show an avoidance of open flowers but a preference for tubular flowers. Open flowers included *A. podagraria*, *G. aparine*, *H. matronalis*, *C. laevipes*, *S. holostea*, *Torilis japonica*, *V. chamaedrys*, *Rubus idaeus* and *M. odorata*. Tubular flowers included *Lamium album*, *S. dioica*, *S. uplandicum* and *L. pratensis* (see figure 17).

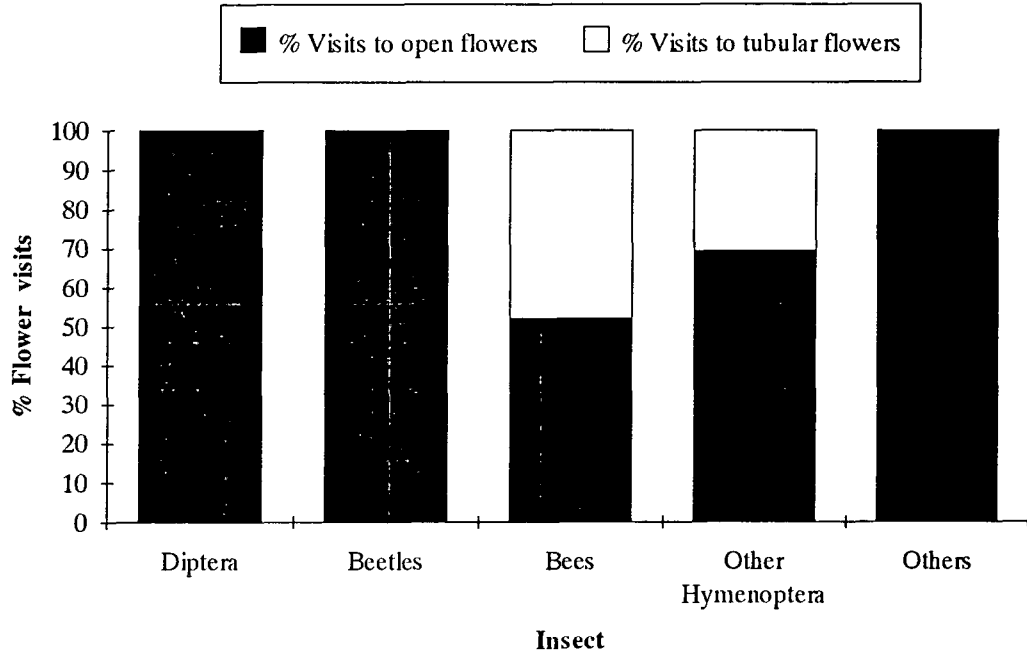
Table 3 shows that there is a significant difference in the types of flowers visited by Hymenoptera and 'others' ('others' includes all pollinators except Hymenoptera) during all three months. This is also true when comparing the flower types visited by bees and 'others' (which includes all pollinators except bees). There appears to be a general trend whereby bees and Hymenoptera visit tubular flowers and avoid open flowers whilst the reverse is true for the category of others. During May, Hymenoptera were found to differ significantly from bees, with respect to the types of flowers they visited. However no such avoidance or preference was shown for the previous two months.

### 3.4.3. Flower Colour And Insect Interactions

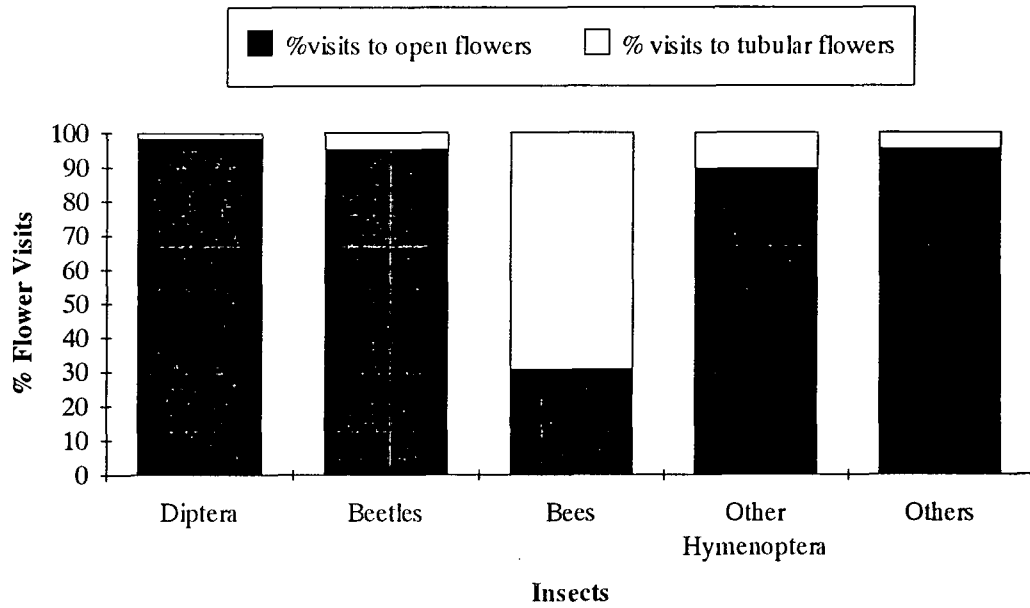
Due to a lack of data the statistical analysis used to distinguish preference or avoidance of flower colour was a Fisher Exact Test (see figures 19 - 21 for percentage flower visits). In May pollinators were unable to distinguish between white and non - white flowers. The insects compared included bees and 'others' (see above) and Hymenoptera and 'others' (as above). In June and July the test proved significant for both comparisons.

It is also worth noting that bees were never observed visiting yellow flowers in June or May and only visited yellow flowers on 16.67% of occasions in July. Bees visited pink,

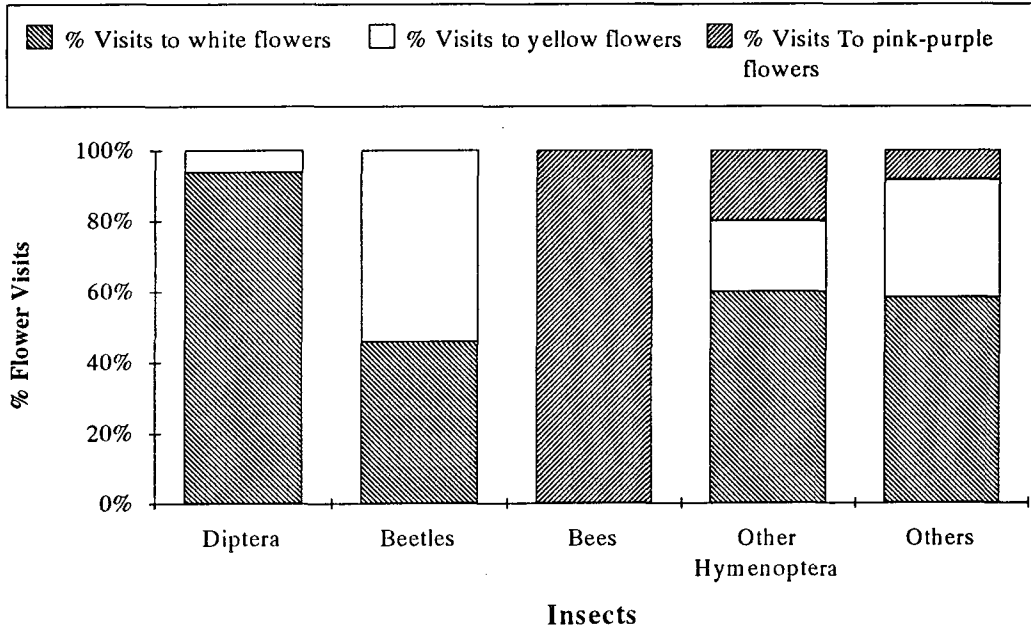
**Figure 17. Comparison Between The Percentage Visits To Open And Tubular Flowers In June.**



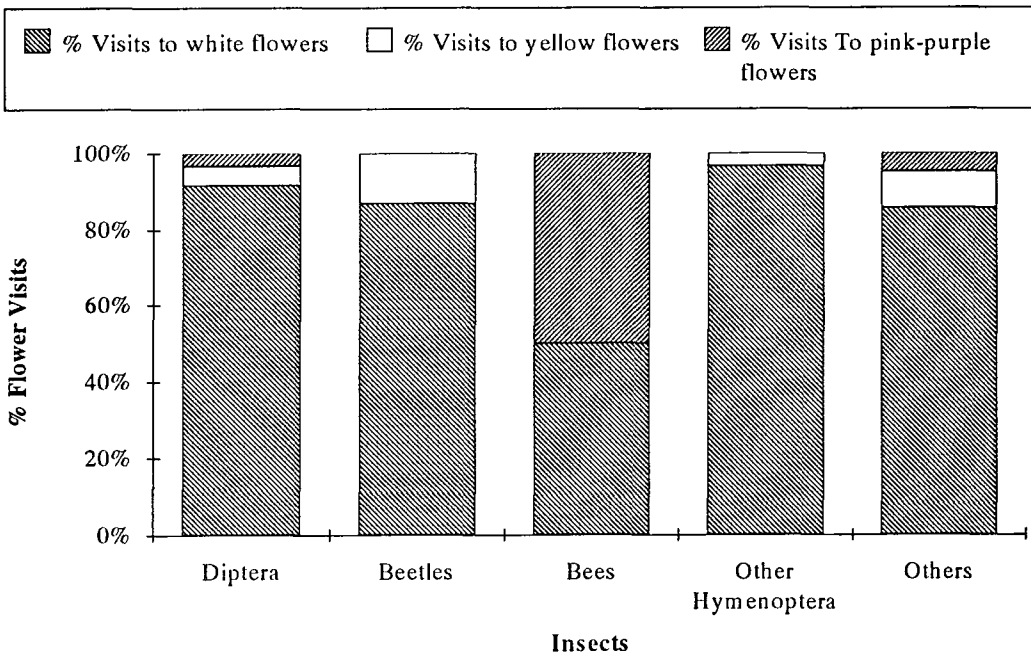
**Figure 18. Comparison Between Visits To Open And Tubular Flowers In July.**



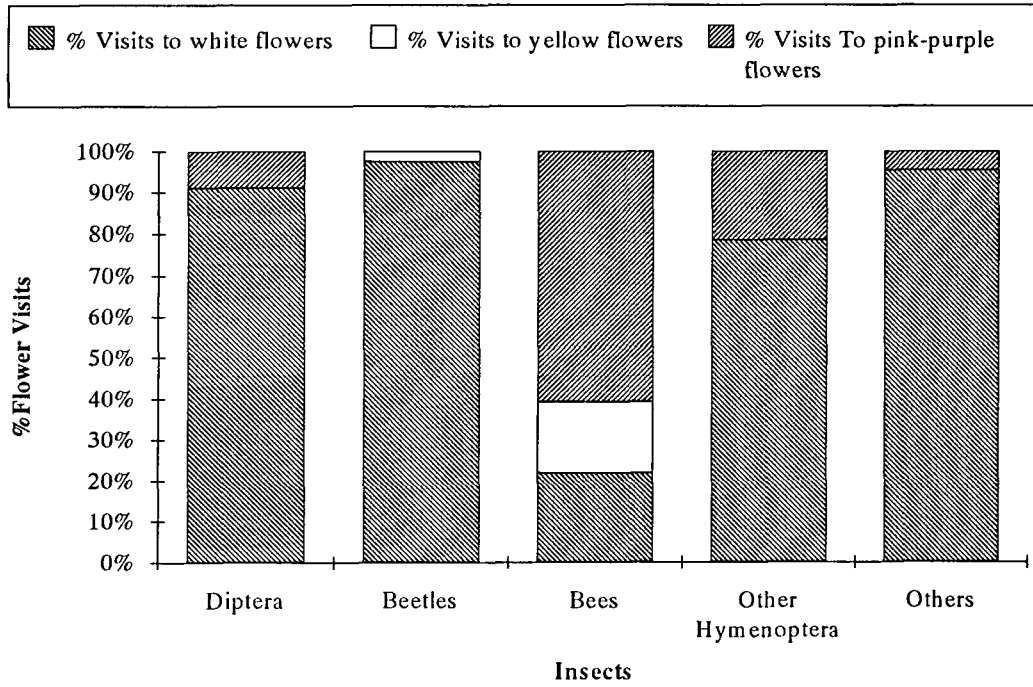
**Figure 19. Comparison Between The Total Number Of Pollinator Visits To white ,Yellow And Purple-Pink Flowers In May.**



**Figure 20. Comparison Between The Total Number of Pollinator visits To White, Yellow And Purple-Pink Flowers In June.**



**Figure 21. Comparison Between The Total Number of  
Pollinator Visits To White, Yellow And Purple-Pink Flowers  
In July.**



**Table 3. Results After Performing Fisher's Exact Probability Tests To Determine Significant Differences In Pollinators' Preferences For Open Or Tubular Flowers.**

<b>Comparisons</b>	<b>Calculated Probability Value</b>	<b>Significance</b>
<b>May</b>		
All Hymenoptera Vs A.N.B	0.00653	<b>Significant</b>
Bees Vs A.N.B.	0.00047	<b>Significant</b>
Bees Vs Hymenoptera	0.23704	<b>Not Significant</b>
<b>June</b>		
All Hymenoptera Vs A.N.H.	0.0000	<b>Significant</b>
Bees Vs A.N.B.	0.0000	<b>Significant</b>
Bees Vs Hymenoptera	0.08698	<b>Not Significant</b>
<b>July</b>		
All Hymenoptera Vs A.N.H.	0.0000	<b>Significant</b>
Bees Vs A.N.B.	0.0000	<b>Significant</b>
Bees Vs Hymenoptera	0.0000	<b>Significant</b>

**Key**

1) A.N.H. = All Non - Hymenopteran Pollinators (includes bees).

2) A.N.B. = All Non - Bee pollinators (includes all other Hymenoptera)

(see Appendices 2, 4 and 6 for details of pollinating insects during each month)

purple and blue flowers on more occasions than any other insect group (i.e. 100%, 50% and 58.33% of occasions for May, June and July, respectively).

Beetles were never observed visiting pink, purple or blue flowers in June or July but visited white flowers more often than any other flower colour (i.e. 86.96% and 97.5% of occasions, respectively). In May, however they visited yellow and white flowers on approximately the same number of occasions.

Diptera never visited pink, purple or blue flowers in May and were observed infrequently visiting these flower colours during June and July (3.24 & 8.93% respectively). Diptera were found visiting white flowers more often than any other coloured flower throughout the study period.

### **3.5. Specific Plant - Pollinator Interactions.**

During May *Cruciata laevipes* (Rubiaceae) was the most frequently visited plant. Its flowers had an average diameter of 2.6mm and there were an average number of 4.533 flowering stems per quadrat. The pollinator assemblage associated with this plant was relatively sparse. Coleoptera were the order of insects observed most frequently visiting this plant, whilst neither Diptera or bees were observed pollinating. Below is a list of the families of Coleopterans observed as pollinators.

#### **Coleoptera.**

Cantharidae    Curculionidae  
Elateridae    Dermestidae

The plant which was most frequently visited by pollinators in June was *Aegopodium podagraria*, a white open Umbelliferae. The umbels were relatively large and conspicuous having a mean diameter of 6.73cm, and there were an average of 5.3 flowering stems per quadrat. It was visited by a wide range of pollinators, including Diptera, Hymenoptera, Coleoptera and occasionally Hemiptera and others. The families (and types of bees) observed pollinating this plant are listed below.

#### **Diptera.**

Anthomyiidae	Chironomidae	Lestremiinae	Sepsidae
Calliphoridae	Chloropidae	Muscidae	Syrphidae
Ceratopogonidae	Empididae	Opomyzidae	

### Hymenoptera.

<i>Apis</i>	Chalcidoidea	Ichneumonoidea	Tenthredinidae
<i>Bombus</i>	<i>Eucera</i>	Formicoidea	

### Coleoptera.

Cantharidae	Staphylinidae
Elateridae	Curculionidae

Although not statistically analysed the most abundant Dipteran family were the Anthomyiidae, the Elateridae were the most abundant Coleopterans whilst *Eucera* were the most abundant Hymenopteran pollinator.

Although the most frequently visited flowering plant in July was *A. podagraria*, *S. uplandicum* (Boraginaceae) was the most frequently visited tubular plant. This particular plant species had tubular to bell shaped, purple - pink corollas and was relatively infrequent. However it was dominant when it did occur. This particular plant received a very low diversity of pollinators, which included *Bombus* and *Colletes*, *Bombus* being the most frequently observed pollinator.

#### **3.6.0. Pollinator Observations.**

After carrying out the walks it was noted that in May the hover fly *Rhingia campestris* visited *L. album* on a number of occasions, even though it was not observed visiting this plant species during the observation periods. Although not observed visiting *L. album* during the sit and wait approach *Bombus* sp. was found visiting this plant species on more occasions than either *S. uplandicum* or *T. officinale* (agg).

In June, *Bombus* sp. were observed frequently visiting *A. podagraria* and *S. uplandicum*. The visits to *S. uplandicum* were more frequent than those observed from the sit and wait approach because although this plant species was frequently distributed throughout the site it was only present in one quadrat. Wasps were also observed visiting *A. podagraria*.

In July there was a greater diversity of plants in flower than for any other month. *Bombus* sp. were observed frequently visiting *Geranium pratense*, *Knautia arvensis*



and *Centurea nigra* and were also found visiting *Cirsium vulgare* and *S. uplandicum* on fewer occasions. *Bombus* sp. were also observed visiting *E. angustifolium*, *Trifolium pratensis* and *V. cracca*. Skipper butterflies were also observed visiting flowers, the most frequently visited flower being *K. arvensis*. Fewer visits were made to *C. vulgare* and *G. pratense*.

## 4.0 DISCUSSION.

### 4.1 Methodology.

#### 4.1.1 Validity Of Vegetation Survey Technique.

The sampling technique was standardised and was based on the National Vegetation Classification methodology used by English Nature. This method proved to be accurate since 86% of all flowering plant species were sampled within the permanent quadrats. The techniques applied to record floral traits were also standardised and similar to those used in other pollinator studies (McCall & Primack, 1992; Arroyo *et al*, 1985).

The only drawback was that because the numbers of flowers and buds were estimated prior to the insect observations, certain plant species may have been over or underestimated with respect to the actual number of flowers available to potential pollinators. In retrospect it may have been useful to estimate how successful pollination had been by recording seed set. However since all of the plants within the community were studied time constraints would have made this unrealistic.

#### 4.1.2. Validity Of Insect Observation Technique.

The methodology applied to estimate insect and pollinator activity and abundance was also standardised and was again similar to previous studies. For instance, the observation period of 10 minutes per quadrat was identical to that used by McCall and Primack (1992) who were concerned with the effects of weather, time of day and flower morphology on pollinator activity within a community. The distance between each quadrat (i.e. 20m) was identical to that of Thomson (1981), who investigated the spatial and temporal components of a flower feeding insect assemblage. This methodology also demonstrated quantitatively, how rare the event of pollination actually is. The information collected from the ten minute walks along fixed transects, gave data of a more qualitative type which illustrated the overall diversity of pollinator activity throughout the site.

The main criticism was that due to lack of time environmental variables such as light levels and temperature were not recorded. This would have given a more complete picture of the components effecting pollinators within a community. It would also have been useful to record the time a particular flower visitor spent foraging on

individual flowers, however due to time constraints and the fact that there was only one recorder in the field this would have been impractical.

## 4.2. Plant Assemblage.

### 4.2.1 Seasonality.

The vegetation survey illustrated the seasonal variation in both numbers and types of flowering plants. In May for instance there were only 7 species of plant in flower, compared to 18 in July, 3 of which flowered throughout the study period. Not surprisingly, as the growing season progressed so did the diversity of plants in flower. In terms of flower diversity the study site was temporally heterogeneous, however the distribution of the dominant plant species indicates that the site was spatially homogeneous.

### 4.2.2 Floral Characteristics.

Throughout the study period open flowers were more abundant than tubular flowers, as indicated by the large percentage of flowering stems. However, floral complexity tended to increase as the season progressed, despite the fact that white open flowers were the dominant flower type throughout the season. This was mainly due to the presence of *A. podagraria*, especially during June and July. The predominance of white flowers has been noted in other communities, for instance Motten (1986) noted that in a spring wildflower community of a temperate deciduous forest, white flowers predominated, even in the height of the blooming season. Similar results were found by Schemske *et al* (1978) whilst studying the flowering ecology of spring woodland herbs. This apparent trend in flower morphology may be related to the reproductive strategies of individual plant species. For example tubular flowers may rely on more specialist pollinators which are not present until later in the season. Conversely open flowers may rely on generalists, which may lead to a greater frequency of self rather than cross pollination. This will be discussed in more detail later.

### 4.3 Diurnal Variation.

#### 4.3.1 Diurnal Activity of Insects.

Insect abundance was identified as being diurnally heterogeneous throughout the study period. This diurnal variation may however, be related to weather conditions such as wind speed, humidity temperature or light intensity, rather than being directly related to the time of day. Weather has been considered an important variable in determining insect abundance (McCall & Primack, 1992). For instance, exceptionally high temperatures have been found to reduce insect abundance (Hagerup, 1932; Kevan & Baker, 1983; Arroyo *et al*, 1985) as does cool, cloudy or windy weather (Müller, 1881; Hagerup, 1951; Mani, 1962; Primack, 1983). Light intensity is also known to affect insect activity, for instance increased light intensities were found to increase the level of insect activity in 3 communities of deciduous woodland meadow, alpine tundra and fynbos when investigated by McCall & Primack (1992). Conversely, long periods of cloudiness are known to depress insect activity, especially certain flies and bees (Kevan & Baker, 1983).

In this particular study the most abundant time period in May was during 3.30 - 6.30. It may be that during this time period environmental variables such as temperature, light intensity or humidity reached an optimum level for insects, whilst in June this period was between 9.30 -12.30 and once again during 3.30 - 6.30. Similarly in July environmental variables may have favoured insects during 9.30 - 12.30. The fact that the most abundant time period varied seasonally may indicate that different environmental variables were more important for different months and the overall impact of such variables will depend on the insect assemblage at that particular time. Since these variables are dynamic and unpredictable it is not unusual to find that insect abundance alters seasonally as well as diurnally. The fact that the insect assemblage was found to be diurnally heterogeneous may indicate that competition between insect orders was reduced somewhat, especially if they were able to differentially exploit temporal niches. However since environmental parameters were not recorded in this study, explanations must remain speculative.

The only insects found to have a heterogeneous ranked activity were the Diptera in June and others in July. However Diptera, Coleoptera, Hymenoptera, Hemiptera and others were all found to differ in diurnal activity throughout the season. This may imply that families within each order occupied separate temporal niches, thus reducing 'within' competition for essential resources such as food and shelter *etc.*

#### 4.3.2 Diurnal Activity Of Pollinators.

During May the diurnal abundance of pollinators was homogeneous, whilst in June and July it was heterogeneous. This diurnal variation may once more be attributed to environmental variables such as weather and light intensity rather than being directly related to the time of day. Weather is known to effect the foraging rates of pollinators indirectly, by causing direct changes in the rate of anthesis, nectar flow and flower duration (Arroyo *et al*, 1985). In June the majority of pollinators were observed during 9.30 - 12.30, which was also one of the most abundant periods in terms of insect abundance. A similar trend is seen in July when pollinator activity was greatest during 9.30 - 12.30 which was also the most abundant time period with respect to insect abundance. This diurnal variation between populations of pollinators is not surprising since such findings have invariably been found whenever plant and pollinator interactions have been studied in both temperate and tropical habitats (Herrera, 1988).

The fact that Diptera were the most abundant pollinator in June may be related to its ability to exploit flowers as a resource when environmental variables were acting as a constraint on other potential pollinators. Alternatively it may be related to the simple fact that they were the most abundant insect during July and so were observed on a greater number of occasions. In July, however, Hymenoptera were the most abundant pollinator overall, whilst the most abundant insect order was Diptera. In this particular month it is possible that the combination of optimal environmental conditions and preferential flower characteristics within the plant assemblage enabled Hymenoptera to exploit flowers on more occasions compared to any other types of pollinating insects.

Although in this particular study the activity within each insect order remained constant (since there were no significant differences identified), small scale differences have been inferred by Beattie (1971), who investigated the effect of micro climate on localised pollinator activity.

### 4.4 Seasonal Variation.

#### 4.4.1 Insect Abundance

There were significant differences in insect abundance throughout the whole study period. The most abundant species changed from Coleoptera in May to Diptera in June and July. The most abundant family of Coleopterans in May were the

Curculionidae, whilst in June and July the most abundant Dipteran families were the Anthomyiidae and Muscidae respectively. There was also an increase in the diversity of families as the season progressed. In addition the total number of observations increased also from May through to July.

#### 4.4.2. Pollinator Abundance.

Similarly, significant differences were found in the abundance and types of pollinators throughout the study period. There was a dramatic increase in the numbers observed in May (only 73 pollinator visits) compared to June and July (397 & 303 visits, respectively). This quantitative increase is in accordance to the theory that visitation rates by pollinators in the early spring are generally thought to be lower than those which occur later in the growing season (Robertson, 1895). In this particular study Dipteran, Coleopteran and Hymenopteran pollinators all peaked in abundance during June, decreasing in abundance thereafter. In May the most abundant pollinator was the Coleoptera, whilst in June it was the Diptera and in July the Thysanoptera. Although the Thysanoptera were the most abundant pollinators in terms of absolute numbers, they were only observed on one occasion in very large numbers, which biased the overall result. It is probably more accurate to consider Hymenoptera the most abundant pollinator in July as it was observed on a greater number of separate occasions and was also the second most abundant pollinator after the Thysanoptera.

In conclusion seasonal variation in pollinator assemblages are not rare, in fact it is quite the contrary as such variation has been documented frequently (Montalvo & Ackerman, 1986; Acker, 1982). For example McCall & Primack (1992) discovered that in a meadow - woodland community as the season progressed from spring to late summer the probability of flower visitation increased. Seasonal differences in pollinator activity may also be due to overall differences in insect abundance levels (Arroyo *et al*, 1985). It is likely that if this study was repeated over more than one season that annual variations would have been quite apparent. For instance, Herrera (1988) discovered significant differences in the pollinator assemblage of *Lavandula latifolia* over a five year period, whilst Beattie *et al* (1973) discovered annual variations in the pollinator assemblage of *Frasera speciosa*. Other annual variations have also been well researched (Aker, 1982; Boyle & Philogène, 1983; Calder *et al*, 1983).

## 4.5 Plant And Insect Interactions.

### 4.5.1 Floral Abundance And Pollinator Interactions.

During all three months there was a positive correlation between the ranked number of flowers and the ranked number of pollinators. There appears therefore to be a relationship between flower density and the frequency of visits to each permanent quadrat. If this is true then the proportion of pollinators to plants in a particular patch should be affected by energetic constraints (Pleasants, 1981) and therefore higher levels of pollinator visitation would be expected in patches yielding a higher rate of energy gain. In addition to this a pollinator may be differentially attracted to plants with a greater number of flowers (Schmitt, 1983). The majority of studies concerned with plant density and pollinator activity have concentrated on individual plant species rather than the overall densities of plants within a community. It is therefore difficult to draw parallels with this particular piece of research. Despite this fact these findings do lend themselves to the theory of optimal foraging which predicts that pollinators 'decide' when to forage within a patch and when to leave a patch / inflorescence, depending upon it's maximum net rate of energy intake (Pyke *et al*, 1977). It has been suggested that plant and flower density will effect energy intake rate because the time spent moving between flowers will increase with plant spacing (Levin & Kester, 1969; Heinrich & Raven, 1972).

An experiment to support this hypothesis along with the findings of this study was carried out by Thomson (1981) who discovered correlation's between flower density and visitation rates for *Potentilla gracilus* and *Senecio crassulus* in meadows of the Colorado Rocky Mountains. His study illustrated the variation in overall levels of pollinator activity in response to the natural variation in density of plants throughout his study site, rather than artificially manipulating stands of plants to identify pollinator preferences.

In pollination studies concentrating on one or a few plant species, the presence of 'other' plant species can have detrimental or favourable effects on the pollinator visits and hence successful pollination, as shown by Goyder (1983) who studied the pollination ecology of 5 plant species in a limestone community. For instance competition with blossoms of 'other' species was found to adversely affect pollination in *Campanula rotundifolia*, but enhance it in *Geranium robertianum*. The fact that in May there was a significant negative correlation between the ranked number of flowers and the ranked number of Diptera and Coleoptera illustrates that as flower density

increased the number of pollinator visits decreased (the inverse of that found when pollinator visits were pooled). A possible explanation for this apparent anomaly is that flower density was relatively unimportant, and plant characteristics such as inflorescence / flower size, were more important in 'attracting' pollinators. These more conspicuous blossoms could monopolise insect visitors (Beattie, 1969) and prevent pollinators from visiting flowers within the permanent quadrats. In May for instance, *S. holostea* was the most frequent flowering plant and was also relatively dense in terms of the number of flowering stems. However this plant was visited on fewer occasions by Diptera and Coleoptera than *C. laevipes* which was less dense and had fewer flowering stems per quadrat. *Cruciata laevipes* had a plethora of flowers arranged in dense clusters around the plant stem, forming a larger and more conspicuous inflorescence than *S. holostea*. Inflorescence size may have therefore been the most important contributing factor in attracting pollinators in this particular instance. An example of similar research to support this finding was carried out by Schmid - Hempel & Speiser (1988), who discovered how inflorescence size influenced the number of individual bee visits. *Epilobium angustifolium* flowers were artificially manipulated to form large and small floral displays. Large inflorescences were visited by a greater number of individually different bees than plants with smaller inflorescences. Other factors such as flower colour, flower shape, odour or abundance of nectar as a reward were more important in 'attracting' potential pollinators. Therefore although plants may occur in relatively dense stands, other plant characteristics may be the dominant factor determining pollinator visitation. It is also possible that in plots adjacent to the permanent quadrats blossoms were more conspicuous and eye catching, which tended to draw pollinators away from the observation plots.

In June there was a positive correlation between the ranked number of Hymenoptera visiting flowers and the ranked number of flowers (i.e. as ranked flower density increased so did the number of ranked pollinator visits). Such a finding may be explained by the theory of optimal foraging. If this is the case then at high flower densities, the distance between each flower (i.e. the inter flight distance) will be short. This in turn will influence the behaviour of the Hymenoptera, as in theory they should forage within such a favourable patch on a greater number of occasions (Kevan & Baker, 1984). In other words they will forage to overcome energetic constraints. Finally in July there was no relationship whatsoever between the ranked number of Diptera, Coleoptera, Hymenoptera and flower density. This lack of association has been true for a number of other studies, for instance Heinrich (1979) discovered that the rate of bumblebee visitation to white clover florets was unaffected by a ten fold



increase in flowering density. It may be that in this particular month the rate of nectar reward per flower was more important than flower spacing in attracting potential pollinators. Alternatively pollinators could have foraged for longer at each flower as well as being more selective at higher plant densities. For instance Schmidt (1983) illustrated that if stands of *Senecio integerrimus* were artificially thinned, pollinators were more selective in the dense plots compared to the thinned plots. Again inflorescence size or flower colour may have been more important in attracting pollinators at high densities. For example, the same study by Schmidt (1983) found that *Bombus* sp. and *Psithyrus* sp. visited a greater number of *Senecio integerrimus* heads per plant as the inflorescence size increased, whilst butterflies typically visited only one flowering head per plant regardless of size.

In May there was a significant positive correlation between the ranked number of stems and the ranked number of pollinator visits but there was no such relationship during June and July. In the early part of the growing season plant density appears to be more important than later on in the season. The low diversity of flowering plants in May could account for this association since insects would have had to travel greater distances to find plants in flower and there would have also been a limited choice in available flowers. It would therefore be energetically favourable for them to forage within dense patches once they had been located. In June and July the relative number of plants in flower increased and hence insects would have had a greater choice in where they foraged for food and the distance between flowers would also have decreased. Once more other factors such as flower colour *etc.* may have been more important in attracting pollinators.

Flower and plant density are therefore only two of many possible variables which may affect the possibility of potential pollinators visiting flowers. In this particular study, flower density was important with respect to the overall trends of pollinators as well as for several insect orders during specific months. However a combination of flower morphology, colour, inflorescence size and flower density are likely to influence the foraging behaviour of pollinators rather than one particular plant attribute.

#### 4.5.2. Flower Morphology And Insect Interactions.

Hymenoptera, Coleoptera others and Hymenoptera were unable to distinguish between open and tubular flowers in May and July. During May there was a very low diversity of floral shapes since only one tubular plant was in flower (*Symphytum uplandicum*), in addition to which pollinator visits were also very scarce. This lack of overall

morphological choice combined with the low pollinator abundance may account for the apparent inability of pollinators to distinguish between flower types. The fact that pollinators were unable to distinguish between flower types in July is more difficult to explain since pollinators were relatively more abundant and morphological diversity of flowers was at its greatest. In June although Hymenoptera were able to distinguish between open and tubular flowers the test did not allow identification of whether they were avoiding one flower type or preferentially foraging in another. However Hymenoptera and others, and bees and others were found to distinguish between the two flower classes but by pooling the data the individual trends were masked. It is also interesting to note that for May and June Hymenoptera and bees were found to be unable to distinguish between flower morphology, whilst in June this was not the case. A possible explanation for this could be that certain Hymenoptera, whilst appearing to be pollinators, were actually exploiting available nectar produced by the more complex plants during May and June. This is especially true for ants which are wingless and so often reach flowers by crawling up stems and are unlikely to affect cross pollination (Proctor & Yeo, 1973). In this particular study many ants were observed in the complex *L. album* during June and although they appeared to behave as pollinators were probably acting as nectar thieves.

Flower shape has often been considered of key importance in limiting the types of visitors able to pollinate specific flowers (McCall & Primack 1992). Flower morphology has been described as an inter specific mechanism used by plants within a community to partition visitor resources and thus reduce competition for pollination (Heithaus 1974; Macior 1970a). Although not statistically proven in this particular study Diptera, Coleoptera, Other Hymenoptera and others were always found more frequently on open compared to tubular flowers throughout the study period (see figures 16 & 17). Bees, mainly the relatively long tongued *Bombus*, were found on tubular flowers more frequently in July, whilst in June were observed on open and tubular flowers on approximately an equal number of occasions. However the study by McCall & Primack (1992) discovered that although open flowers received a higher rate of pollinator visits than open flowers (as in this study) the pollinator spectra were similar. This was not the case for this research since Diptera, Coleoptera and Others were never observed pollinating tubular flowers in June and only very rarely in July. Therefore there appears to be a general trend whereby unspecialised insects visit open flowers on a greater number of occasions compared to tubular flowers, whilst the more specialised *Bombus* can exploit the more complex flowers, when they are available. This agrees with Faegri & Van der Pijl (1979) who postulated that tubular flowers were pollinated by a more specialised fauna.

Therefore in this instance, although not proven statistically, bees were observed as being the most abundant visitor of tubular flowers and could therefore be the most effective pollinators for these particular plants. It is documented that generally Hymenoptera are the most effective and abundant pollinators of flowers compared to other insects (Proctor, 1973; Faegri & Van der Pijl, 1978; Kevan & Baker, 1983) and bees are considered to be the most significant pollinator within this order (Proctor & Yeo, 1973). It is also possible that for these particular tubular flowers bees would contribute the strongest selective force compared to any other pollinator group. Conversely it is unlikely that open flowers will have the same selective force, since they are more efficient in attracting sufficient numbers of generalist pollinators to allow successful pollination.

The identification of specific relationships between pollinators and plants was not within the limits of this project and since data was pooled the patterns of pollinator activity became masked. There were also great variations within and between families of pollinators which would have made more specific relationships difficult to analyse.

#### 4.5.3 Flower Colour And Pollinator Activity.

In the latter months Hymenoptera and Others and bees and Others were able to distinguish between white and non white flowers, but unfortunately the ability of individual families / orders of pollinating insects to distinguish between colour was difficult to prove statistically due to lack of data. However the fact that different insect pollinators were observed visiting certain coloured plants more frequently than others was not really surprising. It is in the pollinators interest to be able to discriminate between flowers if they are to increase their foraging efficiency, which will in turn improve their overall fitness (i.e. ability to maximise their number of offspring) as explained by Pyke *et al* (1977). Since flowers tend to be an unreliable and scattered food resource insects must be able to distinguish between profitable and unprofitable flowers. The perception of colour will allow insects to optimise their discrimination for different plant species (Chittka & Menzel, 1992). The strategies adopted by insects to overcome this problem is to restrict foraging to one or a few rewarding plant species rather than trying to forage amongst all flowers within a habitat / community (Heinrich, 1979 ; Waser, 1986).

In this study bees visited pink - purple and blue flowers on more occasions than any other pollinator group, whilst Coleoptera were never found on purple - pink flowers

and Diptera visited these flower colours very rarely. It is difficult to draw comparisons to other studies as flower colour preferences are likely to be community specific (McCall & Primack, 1992). Evidence for this theory is given by Kevan (1972), who concluded that alpine pollinators tended to prefer yellow flowers whilst bees, the major pollinators within a fynbos community, comprised a larger proportion of the visits to pink - red flowers (McCall & Primack, 1992). It is not only important from the pollinators' point of view to visit the correct flower, but the plant must attract the correct pollinator and colouration is one strategy employed by plants to ensure that pollination is successful. In order to ensure this occurs it is the flower constancy of the potential pollinator which is of vital importance (Chittka & Menzel, 1992). In this study it is important for the purple - pink flowers to accumulate visits from bees and to prevent them from making 'mistakes', whereby they visit similar flowers. If this were to occur such plants would lose precious pollen to foreign plant species, gain foreign pollen from previously visited plants and lose valuable foraging time to a foreign plant species. Chittka & Menzel (1992) argue that colour vision and flower colour are the two most important mechanisms used by pollinators to locate flowers at greater distances. They argue that odours would not travel sufficient distances and given the poor resolution of the insect eye, floral shapes would not be distinguished from afar. Although O'Brien (1980) points out that there may be cases when the combination of colour and morphology has the additive effect of attracting or deterring pollinators from visiting a particular plant.

#### **4.6 Specific Plant - Pollinator Interactions.**

In May *C. laevipes* (Rubiaceae) was the most frequently visited plant species but there was a relative lack in the diversity of pollinators visiting it even though it is an entomophilous plant. This was probably due to the overall low abundance of pollinators during this particular month. The dominant order of pollinators were the Coleoptera, classed as generalists, and *C. laevipes* is a yellow open flower. According to Knuth (1906 - 1909), flowers with exposed nectar may be yellow, amongst other colours, and are usually visited by generalist pollinators. This particular example is illustrated quite well by Knuth's generalisations. However the family of Coleopterans observed visiting this plant on the greatest number of occasions were the Elateridae, a family known to feed destructively on flowers (Proctor & Yeo, 1973). The overall value of this particular pollinator to *C. laevipes* is likely to be offset by its destructive feeding behaviour.

In June the most frequently visited plant was *A. podagraria*, a white, open Umbelliferae. This plant has umbels in bloom more or less simultaneously, producing a large floral display which attracts many insects (Proctor & Yeo, 1973). Diptera were the dominant order in the pollinator assemblage for this particular plant species, the dominant family being the Anthomyiidae. This family are well known pollinators, since some have quite long mouth parts and are known to feed on nectar and pollen which is thought to be the protein staple for adult nutrition (Kevan & Baker, 1984). These observations also tend to agree with Knuth's generalisations as *A. podagraria* is white with exposed nectar and is likely to be visited by generalist pollinators.

Finally in July, *S. uplandicum* (Boraginaceae) was the most frequently visited tubular plant, with the dominant pollinator in its assemblage being *Bombus*. The Boraginaceae are documented by Kevan & Baker (1984) as being bee pollinated. Other literature has described *S. uplandicum* as being an outstanding bumblebee flower since it is long tubed and zygomorphic (Kugler, 1943). The nectar is very difficult to find and physical barriers must be pushed aside for pollinators to find it (Proctor & Yeo, 1974). The ultimate factor which will influence the types of bees visiting this plant will be tongue length, perhaps the most important anatomical feature which partitions different species of flowers with corresponding corolla tube lengths (Iouyne, 1978). This particular plant - pollinator interaction seems to agree with the generalisation whereby complex flowers are visited by a specialist pollinator assemblage.

#### 4.7 Pollinator Observations.

In May, the hover fly *Rhingia campestris* was observed visiting *Lamium album* (Labiatae) which has deep seated and well hidden nectar. Similar observations have been described for this particular insect species by Proctor & Yeo (1974). *Bombus* were also observed visiting this plant species, these long tongued bees are known to pollinate this plant species as described by James & Clapham (1935). In June *Bombus* were observed visiting *A. podagraria* and *S. uplandicum*, however these interactions have already been discussed.

Finally in July *Bombus* were once more observed visiting *Geranium pratense* (Geraniaceae) which has concealed nectar and is chiefly visited by long tongued bees (Proctor & Yeo, 1974). *Bombus* also visited several Compositae, including *Centurea nigra* and *Circium vulgare*. Compositae are known to be visited by a wide variety of insects. For instance Harper & Wood (1957) list 178 insect visits to *Senecio jacobea*.

The 'attractiveness' of this particular family to insects was observed by Goyder (1983) who discovered pollen on many more pollinators compared to other plant families.

#### **4.8 Consequences Of The Plant - Pollinator Interaction.**

In this particular study the majority of the plants, in terms of absolute numbers and dominant species, were unspecialised. The diversity of plants was also relatively low. The majority of the pollinators were generalists and by definition are not known for their flower constancy. However these insects may still serve as efficient pollinators in the same way that specialists are thought to interact with complex plants. A similar conclusion was reached by O' Brien (1980) who studied the pollination biology of 20 plant species of a treeless pavement plain in the San Bernardino Mountains of southern Carolina. She found that the plants with open, generalised flower morphologies received the heaviest pollinator visitation rates, whilst the more specialised plants received little. The conclusion was that in a community where few species were blooming at any one time generalist pollinators were as effective for open flowers as specialist pollinators were for more complex plants.

In this particular study there was insufficient evidence to prove statistically that specialised pollinators, such as bumblebees, forage on one plant type as they were observed on both open and tubular flowers in July. However this apparent lack of constancy has been documented in previous studies. For example Free (1970) confirmed that single foraging trips of bumblebees were not very constant as was the day to day constancy of ten *Bombus agrorum*. It has been shown that bumblebees are much more constant where one plant species predominates than when several species are flowering together (Brittain & Newton, 1933; Brian, 1954; Spencer - Booth, 1965). This tends to support the findings of this study as there were always more than a single plant species in flower at one particular time. The absolute constancy cannot be accurately quantified since the flight paths or pollen loads of individual pollinators were not recorded. Such measurements are vital to clearly identify constancy as Mulligan (1972) noted that although nearly all of the pollinating insects within a weed community were found on at least 7 plant species, 90 - 100% of the pollen load of any one individual was identical to that of the plant on which it was collected. Schemske *et al* (1978) discovered by closely monitoring the sequence and variety of flowers visited by individual insects that Syrphid flies, *Apis mellifera* and *Adrena* bees foraged constantly amongst spring woodland herbs. It is also important to note that the constancy of pollinating insects, especially bees, is not only dependant upon the flora

but also upon the colony of bees present (Free, 1970). Several workers (Free & Butler, 1959) have concluded that certain bumblebees cannot communicate a source of food directly to other members of their colony which they argue explains the lack of constancy within a colony of bees which may all forage within the same community. Unfortunately very little is known about the constancy in non - Hymenopteran pollinators.

There does not appear to be significant relationships between the plants and pollinators in this community, whereby the pollinator assemblage contributes a great deal to the plant's overall fitness. Studies which agree with this were carried out by McCall & Primack (1992) and Herrera (1988) who concluded that communities were characterised by relatively unspecialised relationships between plants and the animals that visited them. Perhaps if a community was dominated completely by morphological complex flowers, the relationship between plant and insect would be more specialised. Since seed set was not recorded in this particular study it is impossible to draw any accurate conclusions on the overall efficiency of the pollinator assemblage within this community, and whether or not insufficient pollination was a cause of unsuccessful reproduction. In certain studies unreliable pollination has been found to exert a strong selective force on the reproductive strategies adopted by plants. For example, unreliable pollination has been described as being responsible for high percentages of autogamous species in habitats with frequently inclement weather (Hagerup, 1951; Kevan, 1972; Moldenke, 1975). Other studies have upheld the idea that self pollination is promoted when there is a paucity of pollinators (Schemeske, 1978).

From examining the specific interactions of *A. podagraria*, *C. laevipes* and *S. uplandicum* and their associated pollinator assemblages generalisations, according to Faegri & Van der Pijl (1979), the types of pollinators expected were identified. However, tight plant - insect interactions are not evident when the pollination biology of the overall community is considered. This is probably because factors such as weather, season and light intensity also influence insect activity and abundance. From this study the abundance of the insect and pollinator assemblages varied markedly with time of day and seasonal differences were even more striking. These variables were seen to influence the pollinator assemblage to a greater extent than flower characteristics such as colour or morphology.

Since communities are spatially and temporally dynamic a multidimensional approach will enable us to gain a better understanding of the complex relationships which exist between plants, insects and their physical environment.



## REFERENCES.

- Aker, C.L. (1982). Spatial and temporal dispersion patterns of pollinators and their relationship to the flowering strategy of *Yucca whipplei* (Agavaceae). *Oecologia*, **54**:243-252.
- Arroyo, M.T.K.J., Armesto, J. and Primack, R. (1982). Community studies in pollination ecology in the high temperate Andes of central Chile. I. Pollination mechanisms and altitudinal variation. *American Journal Of Botany*, **69**: 82-97.
- Arroyo, M.T.K.J., Armesto, J. and Primack, R. (1985). Community studies in pollination ecology in the high Andes of central Chile. II. Effect of temperature on visitation rates and pollination possibilities. *Plant Systematics and Evolution*, **149**: 187-203.
- Beattie, A.J. (1969). Studies in the pollination ecology of *Viola*, 1. The pollen content of stigmatic cavities. *Watsonia*, **7**: 142-156.
- Beattie, A.J. (1971). Itinerant pollinators in a Forest. *Madroño*, **21**: 120-124.
- Beattie, A.J., Breedlove, D.E. and Ehrlich, P.R. (1973). The ecology of the pollinators and predators of *Frasera speciosa*. *Ecology*, **54**: 81-91.
- Boyle, R.M.D. and Philogène, B.J.R. (1983). The native pollinators of an apple orchard: variations and significance. *Journal of Horticultural Science*, **58**: 355-363.
- Brian, A.D. (1954). The foraging of bumblebees. *Bee World*, **35**: 61-67, 81-91.
- Brittain, W.H. and Newton, D.E. (1933). A study in the relative constancy of hive bees and wild bees in pollen gathering. *Can.J.Res.*, **9**: 334-349.
- Calder, W.A., Waser, N.M., Hiebert, S.M., Inouye, D.W. and Miller, S. (1983). Site fidelity, longevity and population dynamics of broad tailed hummingbirds: a ten year study. *Oecologia*, **56**: 359-364.
- Chinery, M. (1986a). *A field guide to the insects of Britain and Northern Europe*. Collins, London. pp 1-352.

Chinery, M. (1986b). *A field guide to the insects of Britain and Western Europe*. Collins, London. pp 1-320.

Chittka, L. and Menzel, R. (1992). The evolutionary adaptation of flower colours and the insect pollinators' colour vision. *Journal of Comparative Physiology A.*, **171** (No.2): 171-181.

Faegri, K. and Van der Pijl, L. (1979). *The principles of pollination ecology*. 3rd ed. Peramon Press, New York.

Fitter, F., Fitter, A. and Blamey, M. (1989). *The wild flowers of Britain and Northern Europe*. Collins, London. pp 1-336.

Free, J.B. (1970). The flower constancy of bumblebees. *Journal of Animal Ecology*, **39**: 395-402.

Free, J.B. and Butler, C.G. (1959). *Bumblebees*. London.

Goyder, D.J. (1983). Pollination ecology of five species in a limestone community. *Watsonia*, **14**: 397-405.

Grant, V. (1949). Pollination systems as isolating mechanisms in flowering plants. *Evolution*, **3**: 82-97.

Hagerup, O. (1932). On pollination in the extremely hot air in Timbuctu. *Danske Botaniske Archiv*, **8**: 1-20.

Hagerup, O. (1951). Pollination in the Faroes - in spite of rain and poverty of insects. *Biologiske Meddelelser Kongelige Danske Videnskabernes Selskab*, **18**: 1-48.

Harper, J.L. and Wood, W.A. (1957). Biological flora of the British Isles. *Senecio jacobea*. *Journal of Ecology*, **45**: 617-37.

Heinrich, B. (1973). The energetics of bumblebees. *Scientific American*, **228**: 96-102.

Heinrich, B. (1975a). Bee flowers: A hypothesis on flower variety and blooming times. *Evolution*, **29**: 325-334.

Heinrich, B. (1976b), Foraging specialisations of individual bumblebees. *Ecological Monographs*, **46**: 105-128.

Heinrich, B. (1979). "Majoring" and "minoring" by foraging bumblebees, *Bombus vagans*: an experimental analysis. *Ecology*, **60**: 245-255.

Heinrich, B. and Raven, P.H. (1972). Energetics and pollination ecology. *Science*, **176**: 597-602.

Heithaus, E.R. (1974). The role of plant-pollinator interactions in determining community structure. *Annals of the Missouri Botanical Garden*, **61**: 657-691.

Heithaus, E.R. (1979). Community structure of neotropical visiting bees and wasps: diversity and phenology. *Ecology*, **60**: 190-202.

Herrera, C.M. (1988). Variation in mutualisms: the spatio-temporal mosaic of a pollinator assemblage. *Biological Journal of The Linnean Society*, **35**: 95-125.

Herrera, J. (1988). Pollination relationships in southern Spanish Mediterranean shrublands. *Journal of Ecology*, **76**: 274-289.

Hocking, B. (1968). Insect-flower associations in the high Arctic with special reference to nectar. *Oikos*, **19**: 359-388.

Hubbard, C.E. (1984). Grasses. *A guide to their structure, identification, uses and distribution in the British Isles*. Penguin, London. pp 1-476.

Inouyne, D.W. (1978). Resource partitioning in bumblebees : Experimental studies of foraging behaviour. *Ecology*, **59**: 672-678.

James, W.O. and Clapham, A.R. (1935). *The biology of flowers*. Dept of Botany, Oxford. pp 1-115.

Kerner von Marilaun, A. (1895). The natural history of plants, their forms, growth, reproduction and distribution. New York: Henry Holt. pp 777-983.

Kevan, P.G. (1972). Insect pollination of high arctic flowers. *Journal of Ecology*, **60**: 831-847.

Kevan, P. and Baker, H. (1983). Insects as flower visitors and pollinators. *Annual Review of Entomology*, **28**: 407-453.

Kevan, P and Baker, H. (1984). Insects on Flowers. In C.B. Huffaker and R.L.Rabb[eds]. *Ecological entomology*. John wiley and Sons, New York.pp 607-632.

Kikuchi, T. (1962-1964). *Sci. Rep. Tohoku. Univ.*, sec 4, Biol, **28**: 17-22, 47-51; **29**: 1-8, 9-14, 107-115; **30**: 143-149.

Knuth, P. (1906-1909). Handbook of flower pollination. *Trans.J.R.Ainsworth Davis*. (3 vols; **I**, 1906; **II**, 1908; **III**, 1909). Oxford

Kügler, H. (1943). Hummeln als blütenbesuchen. *Ergebn.Biol*, **19**: 143-323.

Levin, D.A. and Kerster, H.W. (1969). The dependence of bee-mediated pollen dispersal on plant density. *Evolution*, **23**: 560-571

Levin, D.A. and Anderson, W.W. (1970). Competition for pollinators between simultaneously flowering species. *American Naturalist*, **104**: 455-467.

Macior, L.W. (1970a). The pollination of Pedicularis in Colorado. *American Journal of Botany*, **57**: 6-11.

Mani, M.S. (1962). *High altitude entomology : insect life above the timberline in the northwestern Himalaya*. Methuen, London.

McAlpine, J.F. (1965). Observations on anthophilous Diptera at Lake Hazen, Ellesmere Island. *Canadian Field Naturalist*, **79**: 247-252.

McCall, C. and Primack, R.B. (1992). Influence of flower characteristics, weather, time of day and season on insect visitation rates in three plant communities. *American Journal of Botany*, **79**(4): 434-442.

Moldenke, A. (1975). Niche specialisation and species diversity along a California transect. *Oecologia*, **21**: 219-242.

Montalvo, A.M. and Ackerman, J.D. (1986). Relative pollinator effectiveness and evolution of floral traits in *Spathyllum friedrichsthali* (Araceae). *American Journal of Botany*, **73**: 1665-1676.

Motten, A.F. (1986). Pollination ecology of the spring wildflower community of a temperate deciduous forest. *Ecological Monographs*, **56**(1): 21-42.

Muller, H. (1881). Die alpenblumen, ihre befruchtun durch insekten und ihre anpassung an dieselbe. Verlag von Wilhelm Elgelmann, Lepzig, Germany.

Mulligan, G.A. (1972). Autogamy, allogamy, and pollination in some Canadian weeds. *Canadian Journal of Botany*, **50**: 1767-1771.

Nobel, P.S. (1977). Water relations of flowering of *Agavem deserti*. *Botanical. Gaz*, **138**: 1-6.

O'Brien, M.H. (1980). The pollination ecology of a pavement plain: Pollinator visitation patterns. *Oecologia*, **47**: 213-218.

Pleasants, J.M. (1977). Competition in plant- pollinator systems: an analysis of meadow communities in the Colorado Rocky Mountains. Ph D Thesis Univ. of Calif. Los Angeles.

Pleasants, J.M. (1981). Bumblebee response to variation in nectar availability. *Ecology*, **60**: 1648-1661.

Pojar, J. (1974). Reproductive dynamics of four plant communities of southwestern British Columbia. *Canadian Journal of Botany*, **52**: 1819-1834.

Primack, R. (1983). Insect pollination in the New Zealand mountain flora. *New Zealand Journal of Botany*, **21**: 317-333.

Primack, R. (1985). Longevity of individual flowers. *Annual Review of Ecology and Systematics*, **16**: 15-37.

Proctor, M. (1973). *The pollination of flowers*. Collins, London.

- Proctor, M. and Yeo, P. (1973). *The pollination of flowers*. Collins, London. pp 1-418.
- Pyke, G.H., Pulliam, H.R. and Charnov, E.L. (1977). Optimal foraging: a selective review of theory and tests. *Quart.Rev. Biol.*, **52**: 137-154.
- Richards, O.W. (1977). Hymenoptera. Introduction and key to families. *Royal Entomological Society of London VI*, Part 1: 1-100.
- Roberts, M.J. (1985a). *The spiders of Great Britain and Ireland. Atypidae to Theridiosomatidae. Volume 1*. Harley Books, Great Horkesley. pp 1-229.
- Roberts, M.J. (1985b). *The spiders of Great Britain and Ireland. The colour plates: Atypidae to Linyphiidae. Volume 3*. Harley Books, Great Horkesley. pp 1-204.
- Roberts, M.J. (1987). *The spiders of Great Britain and Ireland. Linyphiidae and check list. Volume 2*. Harley Books, Great Horkesley. pp 1-204.
- Robertson, C.R. (1895). The philosophy of flower seasons. *American Naturalist*, **29**: 97-117.
- Rose, F. (1981). *The wild flower key*. Penguin, London. pp 1-480.
- Schemske, D.W., Willson, M.F., Melampy, M.N., Miller, L.J., Verner, L., Schemske, K.M., and Best, L.B. (1978). Flowering ecology of some spring woodland herbs. *Ecology*, **59**: 351-366.
- Schmid - Hemel, P. and Speiser, B. (1988). Effects of inflorescence size on pollination in *Epilobium angustifolium*. *Oikos*, **53**: 98-104
- Schmitt, J. (1983). Flowering plant density and pollinator visitation in *Senecio*. *Oecologia*, **60**: 97-102.
- Southwick, A.K. (1984). Photosynthate allocation to floral nectar: A neglected energy investment. *Ecology*, **65**: 1715-1719.
- Spencer - Booth, Y. (1965). The collection of pollen by bumblebees and its transport in the corbiculae and the proboscidal fossa. *Jornal of Apic.Res.*, **4**: 185-90.

- Stubbs, A.E. and Falk, S.J. (1983). British Hoverflies. An illustrated identification guide. *British Entomological & Natural History Society*. pp 1-253.
- Thomson, J.D. (1981). Spatial and temporal components of resource assessment by flower feeding insects. *Journal of Animal Ecology*, **50**: 49-59.
- Unwin, D.M. (1981). A key to the families of British Diptera. *Field Studies* **5**: 513-553.
- Unwin, D.M. (1984). A key to the families of British Coleoptera. *Field Studies* **6** : 149-197.
- Van der Pijl, L. (1961). Ecological aspects of flower evolution. II. Zoophilous flower classes. *Evolution*, **15**: 44-59.
- Vogel, S. (1954). Blütenbiologische typen als elemente der sippengliederung. *Botanische Studien*, **1**: 1-338.
- Waser, N.M. (1986). Flower constancy: definition, cause and measurement. *American Naturalist*, **127**: 593-603.
- Weevers, T. (1952). Flower colour and their frequency. *Acta Botanica Neelandica*, **1**: 81-92.

**Appendix 1. Total Number Of Invertebrates (Orders, Families & Species)  
Observed Visiting Quadrats Or Vegetation During May.**

Invertebrates.	9.30-12.30	12.30-3.30	3.30-6.30
<b>Diptera</b>	4	6	14
Anthomyiidae	0	0	1
Bibionidae	6	7	2
Cecidomyiidae	0	0	0
Chironomidae	0	1	2
Dolichopodidae	0	1	0
Empididae	0	0	2
Gasteruptiidae	0	0	0
Lestremiinae	1	0	0
Lonchopteridae	3	2	0
Mycetophilidae	1	1	0
Odiniidae	0	0	1
Phoridae	0	0	1
Rhagionidae	1	0	3
<i>Rhingia campestris</i>	8	3	8
Sepsidae	0	0	3
Syrphidae	1	0	0
Thaumaleidae	0	2	0
Trichoceridae	0	0	1
<b>Arachnids</b>			
Araneidae	2	1	7
Clubionidae	1	0	0
Lynxiphiidae	10	7	2
Tetragnathidae	8	4	4
Araneae	2	2	1
Opilones	1	0	0
<b>Coleoptera</b>	0	0	1
Cantharidae	2	0	1
Carabidae	2	0	0
Coccinellidae	1	0	0
Coleoptera larvae	2	0	0
Curculionidae	145	199	207
Dermestidae	0	0	4
Elateridae	9	3	3
Nitidulidae	0	1	0
Sphaeritidae	0	0	0
Staphylinidae	0	0	2
<b>Hymenoptera</b>			
Anthocoridae	0	1	0
Argidae	1	0	0
<i>Bombus sp</i>	2	0	0
Formicoidea	4	3	0
Orussidae	1	0	0
Pteromalidae	0	0	0



<b>Hemiptera</b>			
Anthocoridae	0	0	2
Apididae	0	1	1
Homoptera	14	12	22
Reduviidae	2	0	0
<b>Neuroptera</b>	2	0	1
<b>Pscoptera</b>			
Psyllipsocidae	0	1	0
<b>Lepidoptera</b>	0	0	2
<b>Isopoda</b>	0	0	1
<b>Collembola</b>			
Entomobryoidea	0	0	1
<b>Others</b>			
Caterpillar	0	0	3

**Appendix 2. The Total Number Of Invertebrates (Orders, Families & Species)  
Observed Pollinating Flowers During May.**

Invertebrates	9.30-12.30	12.30-3.30	3.30-6.30
<b>Diptera</b>	0	0	1CF
Bibionidae	0	0	2SCF, 1SF
Cecidomyiidae	3SF	0	0
Empididae	0	0	1SCF
Gasteruptionidae	1SF	0	0
Lonchopteridae	0	0	1SF
Rhingia campestris	1SCF, 1SF	1SF	1SCF, 1SF
Syrphidae	1SF	0	0
<b>Arachnids</b>			
Araneidae	1SCF	0	0
Lynphyiidae	1SCF	2SF, 1CF	1CF
<b>Coleoptera</b>	0	0	5SCF
Cantharidae	1SF, 3CF	0	0
Curculionidae	3CF	4SF,	
Dermestidae	0	0	5SCF, 1CF
Elateridae	2SCF, 1CF	6CF	6CF
<b>Hymenoptera</b>			
<i>Bombus</i> sp	0	0	2RCF
Formicoidea	1VCF	0	0
<i>Psithyrus</i> sp.	0	1RCF	0
Pteromalidae	2SF	0	0
Trichogrammatidae		1CF, 1SF	0
<b>Hemiptera</b>			
Homoptera	1CF	0	0
<b>Neuroptera</b>	0	0	1CF
<b>Lepidoptera</b>	0	1VCF	0
<b>Thysanoptera</b>			
Thripidae	0	0	2SF
<b>Dermoptera</b>			
<i>Forficula auricularia</i>	0	0	1SCF

**KEY**

1) SC = Sweet Cicily Flower (*Myrrhis odorata*)

2) SF = Stitchwort Flower (*Stellaria holostea*)

3) VC = Speedwell Flower (*Veronica chamaedrys*)

4) CF = Crosswort Flower (*Cruciata laevipes*)

**Appendix 3. The Total Number Of Invertebrates (Orders, Families & Species)  
Observed Visiting Quadrats Or Vegetation During June.**

Invertebrates	9.30-12.30	12.30-3.30	3.30-6.30
<b>Diptera</b>	4	28	36
Anthomyiidae	56	37	112
Asteiidae	0	2	0
Calliphoridae	13	0	1
Cecidomyiidae	1	0	0
Ceratopogonidae	1	0	0
Chironomidae	2	1	3
Chloropidae	3	0	2
Dryomyzidae	0	0	1
Empididae	1	6	0
Fanniidae	0	0	1
Lonchaeidae	2	2	0
Lonchopteridae	0	0	1
Muscidae	4	0	5
Opomyzidae	1	0	2
Sepsidae	41	1	17
Syrphidae	0	0	1
Syrphini (tribe)	0	2	0
Tipulidae	0	0	1
<b>Arachnids</b>			
Araneidae	1	3	6
Linyphiidae	1	0	0
Tetragnathidae	2	5	1
<b>Hymenoptera</b>			
<i>Bombus sp</i>	0	1	1
<i>Bombus terrestris</i>	1	0	0
Cephidae	0	0	1
Chalcidoidea	1	1	0
Elasmidae	0	0	2
Formicoidea	3	1	4
Ichneumonoidea	1	1	0
<b>Coleoptera</b>	2	2	0
Cantharidae	0	3	2
Coccinellidae	4	1	2
Curculionidae	3	47	27
Elateridae	2	10	8
Staphylinidae	0	0	1
Larvae	1	0	0
<b>Hemiptera</b>	6	0	0
Delphacidae	0	1	5
Homoptera	7	4	4
Nabiidae	1	1	0
Reduviidae	0	2	1

<b>Odonata</b>			
Platycnemididae	0	0	1
<b>Mecoptera</b>			
Panorpidae	2	0	1
<b>Ephemoptera</b>	0	1	0
Baetidae	0	1	0
<b>Neuroptera</b>	0	2	0
<b>Lepidoptera</b>	2	5	0

**Appendix 4. The Total Number Of Invertebrates (Orders, Families & Species)  
Observed Pollinating Flowers During June.**

Species	9.30-12.30	12.30-3.30	3.30-12.30
<b>Diptera</b>	2GEF	1GEF	1GEF
Anthomyiidae	49GEF, 5CWF, 3SCF	32GEF, 2DVF	35GEF, 1CWF
Calliphoridae	5GEF	0	0
Ceratopogonidae	3GEF	0	0
Chironomidae	7GEF, 1CWF	2GEF	0
Chloropidae	0	4VCF	1GEF
Empididae	30GEF, 1DVF, 4CWF	6GEF	1GEF
Muscidae	2GEF	0	1GEF
Sepsidae	1GEF	1GEF	3GEF
Syrphidae	0	1GEF	0
Syrphini (tribe)	3GEF	2GEF	0
<b>Arachnids</b>			
Araneidae	2GEF, 2CWF	0	0
Linyphiidae	2GEF	0	0
<b>Hymenoptera</b>			
<i>Apis</i> sp	0	3GEF	0
Apoidea	1GEF	0	0
<i>Bombus</i> sp	1GEF, 7RCF, 2RIF	3RCF	6GEF
<i>Bombus terrestris</i>	1GEF	1RCF	6RCF, 1DVF
Cephidae	0	1CWF	1LAF
Chalcidoidea	2GEF	0	0
Eucera (genus)	10GEF	0	2GEF
Formicoidea	10GEF, 9WDF	8GEF, 9WDF	18GEF
Ichneumonoidea	2GEF	0	0
<i>Psithyrus</i> sp	0	0	1RCF
Tenthredinidae	1GEF	0	0
<b>Coleoptera</b>			
Cantharidae	2GEF	5GEF, 1CWF	0
Curculionidae	2CWF, 1GEF, 1RIF	0	0
Elateridae	8GEF	12GEF, 2CWF	10GEF, 1CWF
Staphylinidae	1GEF	0	0
<b>Hemiptera</b>			
Miridae	1GEF	0	0
Nabiidae	1GEF	0	0
Reduviidae	0	1GEF	0
<b>Trichoptera</b>		1GEF	0
Sericostomatidae	1VCF	0	0
<b>Mecoptera</b>			
Panorpidae	1GEF	0	0

<b>Thysanoptera</b>			
Phlaeothripidae	0	0	1SHF
Thripidae	3SHF	0	5SHF

**Key.**

- 1) GEF = Ground Elder Flower (*Aegopodium podagraria*).
- 2) CWF = Crosswort Flower (*Cruciata laevipes*).
- 3) RCF = Russian Comfrey Flower (*Symphytum uplandicum*).
- 4) DVF = Dames Violet Flower (*Hesperis matronalis*).
- 5) LAF / WDF = White Dead Nettle Flower (*Lamium album*).
- 6) SHF = Stitchwort Flower (*Stellaria holostea*).
- 7) RIF = Raspberry Flower (*Rubus idaeus*).
- 8) VCF = Speedwell flower (*Veronica chamaedrys*).

**Appendix 5. The Total Number Of Invertebrates (Orders, Families & Species)**  
**Observed Visiting Quadrats Or Vegetation During July.**

<b>Invertebrates</b>	<b>9.30-12.30</b>	<b>12.30-3.30</b>	<b>3.30-6.30</b>
<b>Diptera</b>	38	58	36
Anthomyiidae	20	21	25
Calliphoridae	1	0	0
Carniidae	0	1	0
Cecidomyiidae	0	1	0
Ceratopogonidae	5	0	1
Chironomidae	16	9	12
Chloropidae	1	1	4
Dolichopodidae	0	1	0
Empididae	3	1	6
Fanniidae	0	0	1
Lestremiinae	1	0	0
Lonchaeidae	3	0	5
Muscidae	42	38	31
Opomyzidae	2	1	0
Scatopsidae	1	0	0
Sepsidae	26	28	13
Sphaeroeridae	1	2	2
Stratiomyidae	2	0	0
Syrphidae	1	3	3
Tephritidae	1	2	5
Therevidae	0	0	1
Tipulidae	1	0	1
<b>Hymenoptera</b>			
Apoidea	1	0	0
<i>Bombus sp</i>	0	5	3
<i>Bombus terrestris</i>	0	0	1
Braconidae	1	0	0
Chalcididae	0	4	0
<i>Colletes sp</i>	0	0	0
Elasmidae	6	1	9
<i>Eucera sp</i>	1	0	1
Formicoidea	4	0	1
Ichneumonidae	1	0	0
Mymaridae	0	1	0
Pteromalidae	0	1	1
Vespoidea	0	2	1
<b>Coleoptera</b>			
Cantharidae	3	8	18
Chrysomelidae	0	1	0
Coccinellidae	0	1	0
Curculionidae	4	2	5
Dermestidae	0	0	0
Elateridae	3	4	5
Nitidulidae	0	0	0

<b>Hemiptera</b>			
Aphididae	281	38	4
Aradidae	0	0	1
Cercopidae	1	0	0
Delphacidae	1	1	2
Heteroptera	1	2	0
Homoptera	4	5	5
Miridae	1	1	0
Nabiidae	3	4	2
Reduviidae	0	0	0
<b>Arachnida</b>			
Araneidae	1	2	3
Linyphiidae	0	2	4
Tetragnathidae	1	0	1
Opiliones	0	1	0
<b>Lepidoptera</b>	3	4	6
<b>Plecoptera</b>	1	0	0
<b>Ephemeroptera</b>	1	0	
Baetidae	0	0	4
Ephemeridae	4	5	1
Leptophlebiidae	7	9	9
<b>Thysanoptera</b>			
Phlaeothripidae	10	0	0
<b>Pscoptera</b>			
Psyllipsocidae	0	2	4
<b>Mecoptera</b>			
Panorpidae	1	0	1



**Appendix 6. The Total Number Of Invertebrates (Orders, Families & Species)  
Observed Pollinating Flowers During July.**

<b>Invertebrates</b>	<b>9.30-12.30</b>	<b>12.30-3.30</b>	<b>3.30-6.30</b>
<b>Diptera</b>	2GEF, 1HWF	3GEF	7GEF, 1HWF
Anthomyiidae	0	2GEF	8GEF
Cecidomyiidae	1CVF	0	0
Chironomidae	3GEF	4GEF	1GEF, 1HWF
Chloropidae	0	1GEF	0
Empididae	3GEF	0	0
Faniidae	1GEF, 1HWF		0
Muscidae	1HWF	1GEF	0
Scatopsidae	1GEF	2GEF	0
Sepsidae	3GEF, 3GPF	1GEF	0
Syrphidae	1GEF, 1RIF	1GPF	0
<b>Hymenoptera</b>			
Apoidea	1GEF	0	0
<i>Bombus sp</i>	2RCF, 1LPF	1GEF, 1RNF, 3LPF, 1GPF, 5RCF1WNF, 1WHF	1HWF, 1GPF
<i>Bombus terrestris</i>	0	0	2RCF, 1WHF
Chalcididae	2GEF, 1CVF	7GEF, 1CVF	0
<i>Colletes sp</i>	1RCF	0	0
Elasmidae	23GEF, 2CVF	2HWF	2GEF, 1WHF, 3HWF
<i>Eucera sp</i>	0	0	1GEF
Formicoidea	1GEF	0	0
Mymaridae	3VCF, 1SGF	3CVF	0
Pteromalidae	1GEF	0	0
Tenthredinidae	1GEF	0	2GEF
<b>Coleoptera</b>			
Cantharidae	5GEF	19GEF	9GEF
Chrysomelidae	0	1GEF	1LPF
Dermestidae	1GEF	1GEF	0
Elateridae	1GEF	0	0
Nitidulidae	1WNF	0	0
<b>Hemiptera</b>			
Aphididae	0	0	1HWF
Nabiidae	5VCF	0	0
Reduviidae	1GEF	0	0
			0
<b>Arachnida</b>			
Linyphiidae	0	1HWF	0
Tetragnathidae	1RIF	0	0
<b>Ephemeroptera</b>			
Leptophlebiidae	0	1GEF	0
<b>Thysanoptera</b>			
Phlaeothripidae	110HWF	0	3SGF, 1VCF

<b>Pscoptera</b>			
Psyllipsocidae	0	0	3SGF

**KEY.**

- 1) GEF = Ground Elder Flower (*Aegopodium podagraria*).
- 2) HWF = Hogweed Flower (*Heracleum sphondylium*),
- 3) SGF = Stitchwort Flower (*Stellaria graminea*).
- 4) GPF = Cranesbill Flower (*Geranium pratense*).
- 5) RCF = Russian Comfrey Flower (*Symphytum uplandicum*).
- 6) WHF = Willowherb Flower (*Epilobium angustifolium*).
- 7) LPF = Vetch Flower (*Lathyrus pratensis*).
- 8) VCF = Vicia Flower (*Vicia cracca*).
- 8) CVF = Nettle flower (*Cirsium vulgare*).
- 9) WNF = White Dead Nettle Flower (*Lamium album*).
- 10) RNF.= Red Dead Nettle Flower (*Lamium purpureum*).

