The Influence of Microclimate on The Spatial Distribution of Flying Insects

by

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The candidate confirms that the work submitted is his own and that appropriate credit has been given where reference has been made to the work of others

To my mother

ABSTRACT

The spatial distribution of flying dipterans and the effect of microclimate on their abundances and spatial distributions in the vicinity of single trees, both free standing and in a hedgerow in Yorkshire, England, have been studied using nine inch suction traps and a YETI micro-meteorological system.

Although the abundance of flying dipterans varied with time, the patterns of spatial abundance were quite reproducible in similar wind conditions. It is suggested that biological effects control the distribution of the insects in calm conditions, but physical effects are more important in exposed and in artificial sheltered conditions, while both biological and physical effects are significant in the sheltered conditions created by living vegetation.

The effects of microclimate on the daily abundances of families of flying dipterans is in accord with Johnson's 'flight activity' hypothesis.

Common species of Scatopsidae all respond very similarly to light intensity, temperature and relative humidity.

The vertical profiles are consistent with the existence of discontinuities for almost all of the common families. The predicted mean flight speed of the common species of Scatopsidae matched the mean wind speed very well at the discontinuities in agreement with Taylor's concept of an "insect boundary layer".

Weak or small-bodied insects are more sensitive to wind speed than are strong or big-bodied ones.

The spatial distribution of flying dipterans within their boundary layers are more likely to be determined by biological and mechanical effects than by the microclimatic factors measured.

The importance of wind in determining the vertical distributions of insects in lowland Britain is in marked contrast to the reported lack of significance of wind in tropical rain forests.

Temporal patterns of the dusk- and night-flying dipterans are discussed in relation to the reported foraging patterns of insectivorous bats. It is suggested that the effects of wind speed and temperature on the abundance of the insects may be an important factor influencing foraging activities of bats.

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CONTENTS

CHAPTER 6 EFFECT OF SHELTER ON DISTRIBUTION OF FLYING DIPTERA.. 90

SUMMARY OF NOTATION

Microclimatic variables

Av-light	Average light intensity during the trapping period.
Av-temp.	Average temperature during the trapping period.
Av-RH	Average relative humidity during the trapping period.
Av-wind	Average wind speed during the trapping period.
Max-day-temp.	Maximum temperature during the 24 hours.
Max-light	Maximum light intensity during the trapping period.
Max-temp.	Maximum temperature during the trapping period.
Max-RH	Maximum relative humidity during the trapping period.
Max-wind	Maximum wind speed during the trapping period.
Min-day-temp.	Minimum temperature during the 24 hours.
Min-light	Minimum light intensity during the trapping period.
Min-temp.	Minimum temperature during the trapping period.
Min-RH	Minimum relative humidity during the trapping period.
Min-wind	Minimum wind speed during the trapping period.
NE	North easterly wind.
Prec-temp.	Average temperature during one previous trapping period.
Prec-wind	Average wind speed during one previous trapping period.
Prec-rain	Rainfall during one previous trapping period.
Pre-win-dire.	Wind direction during one previous trapping period.
Rain	Rainfall during the trapping period.
SE	South easterly wind.
SW	South westerly wind.
Std-wind	Variability of mean wind speed during the trapping period.
Time	Average trapping time, increasing with trapping period.
Win-dire.	Wind direction during the trapping period.

Family of Diptera

Anis. = Anisopodidae
Anth. = Anthomyiidae
Call. = Calliphoridae
Culi. = Culicidae
Empi. = Empididae
Musc. = Muscidae
Myce. = Mycetophilidae
Phor. = Phoridae
Sarc. = Sarcophagidae
Scia. = Sciaridae
Scth. = Scathophagidae
Stra. = Stratiomyidae

Ceci. = Cecidomyiidae
Cera. = Ceratopogonidae
Chir. = Chironomidae
Doli. = Dolichopodidae
Pipu. = Pipunculidae
Plat. = Platypezidae
Psyc. = Psychodidae
Scat. = Scatopsidae
Syrp. = Syrphidae
Tach. = Tachinidae
Tipu. = Tipulidae

Species of Diptera

acut = *Swammerdamella acuta* Cook
albi = *Cookella albitarsis* Zetterstedt
brev = *Swammerdamella brevicornis* Meigen
clav = *Ectaetia clavipes* Loew
cook = *Rhegmoclema cooki* Hutson
coxe = *R. coxendix* Verrall
sp = *R. sp.*
fusc = *Coboldia fuscipes* Meigen
nota = *Scatopse notata* Linnaeus
solu = *Anapausis soluta* Loew

Statistics

ANOVA	Analysis of variance
DIF	Difference between group means
F	F value
NS	Not significant
P	Probability
PR	Proportion of explained variance
SPRC	Standard partial regression coefficients
S.E.	Standard error of SPRC value
SIG	Significance

Others

AC	After cutting the hedge
AN	After netting the hedge
AF	Afternoon (1220 - 1800 GMT)/afternoon-flying family
B	Bottom level (1.2m)
BC	Before cutting the hedge
BN	Before netting the hedge

DU	Dusk (1820 - 2200 GMT)/dusk-flying family
F	4.5m away from trees
M	Middle level (5.0m)
MO	Morning (0520 - 1200 GMT)
N	Near trees
NI	Night (2220 - 0500 GMT)/night-flying family
Outstation	Micro-meteorological outstation
S1	Trapping site 1
S2	Trapping site 2
T	Top level (8.8m/8.5m)
m	Metre
mph	Miles per hour
n	Numbers of Sample
r	Revolutions of anemometer cup
--	Too few insects to analyse

TABLES AND FIGURES

Chapter 1
GENERAL INTRODUCTION

This study concentrates on the distribution of flying Diptera in relation to single trees, both free standing and in a hedgerow, at a site in northern England. It is also concerned with the influence of microclimate on distribution patterns. Previous work in relation to the local distributions of flying insects has centred mainly in two areas. The first concerns the spatial distribution of flying insects in tropical rain forest (Sutton 1989), the second is the distribution of flying Diptera in relation to agricultural crops in Great Britain.

1.1 Distributions of flying insects in tropical rain forests

As early as in 19th century, the naturalists A. R. Wallace and H. W. Bates commented on the relative richness of insect life in the upper canopy of lowland rain forest of the tropics (*vide* Bates 1863). Pioneering work carried out at Moraballi Creek in Guyana was summarised by Hingston (1932). He suggested that many groups of insects showed considerable activity in the canopy. Since then it has been generally accepted that much of the insect life of the lowland rain forest is centred in the upper canopy, where flowers, fruits and leaves are most abundant.

Studies on insects in the forest canopy (Davis 1944; Haddow & Dick 1948) and investigations of mosquitoes at a number of levels up to upper canopy level in East Africa (Garnham *et al*. 1946; Haddow 1945; Haddow *et al*. 1947; Haddow & Mahaffy 1950) have shown that certain species bite mainly in the canopy, others in the understorey and yet others at ground level. Similar work carried out in Colombia (Bugher *et al*. 1944; Bates 1944; Galindo *et al*. 1950, 1951) showed similar results to those obtained in Africa. From these studies, it is clear that there is a correlation between the vertical distribution of mosquitoes and their feeding preferences.

Extensive research on the behaviour of insects of medical importance in East Africa in the 1950's led to the building of a tower in Uganda which provided the foundation for the quantitative approach to vertical distribution of flying insects in tropical forests (Haddow et al. 1961). The steel tower was 36.6m high; the canopy was from 15.2m to 21.3m. Detailed data obtained in this study suggested that several species of mosquitoes exhibited a non-random vertical distribution of larval occurrence; a few species were common at ground level and one above the canopy. Most biting insects showed supra-canopy swarming behaviour as adults. The tower itself was found to act in part as a swarming marker. It also showed that species of butterflies showed a concentration in and just below the main canopy with some considerable movement above the canopy. More Sphingidae (Lepidoptera) were caught above the canopy upper limit than below it. The study also demonstrated that most Coleoptera were caught in or above the canopy, while some other groups of flying insects (including Diptera) did not show a strong preference for the canopy (Haddow et al. 1961). Taking flying insects as a whole, This study seems to suggest that there is a tendency for diversity and abundance to be greater in the canopy than below it.

The studies on biting insects of medical importance carried out by Snow (1955, 1975, 1979), Snow & Wilkes (1977) and Gillies & Wilkes (1976, 1978) produced similar results to those obtained by Haddow et al. (1961), in particular confirming that each species has its own flying height.

Wolda (1979), who studied the seasonality of insects in the Panamanian forest, and Penny & Arias (1982), who investigated the life and diversity of forest insects near Manaus in Brazil, using light traps at 1 and 15m, established that many, but by no means all, flying insects were much more abundant at the upper level, including such major groups as staphylinid beetles and cicadellids (Homoptera). A study on the abundance and diversity of psocids at two sites in rain forest in Panama suggested that the relationship between abundance, diversity and height varied from the wet to the dry season (Broadhead 1983, Broadhead & Wolda 1985).

Rees (1983), using light and suction traps to study the flying hemipteran fauna of a primary lowland rain forest in Sulawesi, showed that bugs were caught in far greater numbers in the canopy than below it. A series of studies on the vertical distribution of flying insects, at various sites in tropical rain forests between 1974 and 1982, carried out by Sutton and his associates (including Rees as above) using UV light (actinic) traps, suction and sticky traps hung at four levels from floor to upper canopy, established a generality for most groups of insects for most localities studied. This was that the gradient in abundance between floor and canopy was greatest where the ecological inversion surface (Richards 1983) was relatively smooth; where irregular topography was or other factors caused this surface to be rough the gradient was less marked (Sutton 1979, 1983, 1989; Sutton & Hudson 1980; Sutton _et al_. 1983). Their findings provide a very good summary of the results obtained by earlier observers.

Little is known about the influence of physical factors on the vertical distribution of flying insects in tropical rain forests. Pittendrigh (1950), in an intensive study of two species of _Anopheles_ (Culicidae) inhabiting bromeliads in Trinidad, demonstrated that each oviposited at its own preferred level, which was correlated with the humidity requirement of the adult. Cachan (1964), working from a 45m tower in the forest of Banco, Abidjan, Ivory Coast on populations of scolytid beetles, attempted to relate insect distribution to microclimate. He proposed that preferences for certain evaporation rates determined the species vertical pattern. A similar analysis, but on a much broader scale, was that of Rees (1983). He found that the vertical distribution of Hemiptera differed on rainy and dry nights; when it was wet relatively more bugs flew in the upper canopy as compared to the level below. He suggested that this might be a response to predators (bats). The data obtained by Rees also suggested that on dry nights moonlight depressed the number of bugs caught in the upper level, but not below. Data from this and other insects trapped during the same study (Sutton 1989) showed a variety of related responses. Rees and Sutton found that _Apis dorsata_ was only active on dry light nights, and suggested that the insect probably used the moonlight for visual navigation. They also demonstrated that moonlit/dry nights depressed the number of individuals of Homoptera, Diptera, Ephemeroptera and Hymenoptera, and changed the gradients of Homoptera, Diptera and Coleoptera.

From the tropical study on vertical distribution of flying insects, the question arises as to how insects are distributed in relation to the unlayered vegetation and living architecture typical of much of the north temperate region. A second question concerns differences in the influence of microclimate in the temperate and tropical environments. It was felt that the techniques and equipment developed for tropical forest research could be used effectively in the very different environment of the long deforested English lowlands. Perhaps, in future years as the tropics become deforested, insights gained from such a temperate study may prove useful in helping to understand the factors which influence flying insects in the deforested and unlayered tropical landscape.

1.2 Vertical distribution of flying insects in temperate habitats

The second line of enquiry leading to this study concerns the distribution of flying Diptera in areas of cultivation and managed woodland in lowland Britain. There has been a fairly large volume of work, not all of it in agreement.

In woodland, vertical and temporal distributions of biting flies of Culicidae and Culicoides have received the most attention. Kettle (1951), using sticky traps, studied Culicoides impunctatus at three levels and suggested that the vertical distribution of the insect was related to the height of the leaf canopy. Bennett (1960) studied seven species of ornithophilic blood-sucking ceratopogonids and found that this group of insects were likely to fly in the tree canopy. Bidlingmayer (1961) also used sticky traps to study Culicoides dispersal at four levels from 0.3 to 4.3m, and suggested that the majority of males were active at higher levels (2.4 - 4.3m, which was the main leaf layer of trees) than the females (0.3 - 0.6m, which was grass height). Love & Smith (1958) made a study of the distribution patterns of mosquitoes at six levels and found four different patterns, some species flying higher and some lower. Service (1971a, 1971b), using suction traps to study stratification patterns of mosquitoes and Culicoides at 8 levels from 0.23 to 5.5m in a wood where the tree canopy was 10m high above the ground, showed that aerial densities of most species declined with increasing height and suggested that most species preferred the bush level. More unfed Culex pipiens and females of C. morsitans were caught in the highest traps. Somewhat similar results were also obtained by Service (1973) on aerial populations of woodland tipulids.

Extensive studies on vertical distributions of various flying insects of agricultural importance, other than flies, have been carried out by many researchers in crop fields. Broadbent (1948), for example, using sticky traps at three levels up to 1.8m above soil level in a potato field, found that as the foliage increased in density the proportion of aphids caught in the lower traps decreased. Lewis (1959) used three different types of trap to study vertical distributions of thrips, and found that most species were active at crop level. Lewis & Macaulay (1976), setting traps at 4 levels (ground, mid-crop, crop and twice the height of the crop), found that pea moths were most abundant at the crop level.

The vertical distributions of some important flies in crop fields have also been studied. Calnaido et al. (1965), used suction traps at 5 levels up to 7.6m in 1961 and at 14 levels up to 32m in 1962 to study Oscinella frit, suggested that over grass at all times, over oats in the tiller generation and possibly over fallow ground in the wintering generation, the insects were most abundant from the top of the vegetation up to 0.5m above. Bardner et al. (1977) used suction traps at four levels (ground, mid-crop, crop and 2m above the crop) to study the wheat bulb fly, and found that most flies flew at middle and crop levels.

In a grass field Reuben (1963) used suction traps at three levels (0.2, 0.9, and 1.8m) to study the behaviour of Culicoides impunctatus, and found that the trap at 0.2m caught significantly fewer insects than the other two. On grassland with vegetation Korting (1931) who set traps at 7 levels for frit fly, thrips and other insects from 0.2 to 5.4m, suggested that 1.3m seemed to be the preferred height for all insects. Using coloured water traps to study vertical distributions of bibionids on grassland, D'arcy-Burt et al. (1987) demonstrated that different species have different stratification patterns and suggested that the spatial distribution of these species was likely to be a compromise between passive agreggation, mainly due to wind, and behavioural differences.

Johnson and Taylor (1955a), using suction traps to study aphids at 5 levels (3.0, 6.4, 17.1, 76.2 and 304.8m), suggested that around 7.6m height was a discontinuity point. Taylor (1974), also used suction traps. He studied many groups of insects over a closely mown grass sward at 15 levels up to 32m. He found a density discontinuity at 30cm, at about the height of the grass, for all insects.

Studies on the vertical distribution of flying insects were also carried out in many other habitats, such as pasture (Johnson 1957), cow-dung in a field (Downes 1955), fallow land (Bardner et al. 1977, Taylor 1974), fields with scrub (Reader et al. 1984; Snow 1975; Willard 1974), fields with artificial windbreaks (Gillies & Wilkes 1978; Lewis 1967), gardens (El-Ziady 1954), sewage bacteria beds (Khalsa 1948), moorland (Kettle 1951), and marsh (Bidlingmayer 1961; Henrry & Adkins 1975). All showed that different species or different groups of insects distributed themselves differently, in ways which are, in general, related to their biological and physical requirements.

From this brief review, it can be seen that the study on the vertical ditributions in temperate region has been spread widely over many types of habitat. It also shows that no matter which habitat is under study, the distribution patterns of flying insects are all related to their biological and physical needs, and this leads to patterns of distribution characteristic in time and space for different taxa. However no work has been reported about the distribution in relation to emergent hedgerow trees or even to isolated ones, which are very typical of the living architecture of much of lowland Britain. Do such objects have a significant influence on the patterns of distributions of flying insects, or insect predators like birds and bats in a similar way as in other habitats? From the conservation point of view, I believe it is crucial to have quantitative evidence for the importance of such trees in the lives of animals in modern world, rather than just qualitative descriptions or speculation by extrapolation.

1.3 Distribution of flying insects in the upper air

Studies on this subject began in the late 1920s and early 1930s, stimulated especially by work in the United States of America on the dispersal of the Cotton Bollworm Moth (Coad 1929) and the Gipsy Moth (Collins & Baker 1934). Coad (1931) used sticky traps on an aircraft in Louisiana to sample insects up to 4207m, and found that insect density was less by half for every 305m up to 914m, changed little up to 1524m, but was much lessend above 1829m. Berland (1935) published more detail about insects caught in nets on an aircraft near Paris in France at heights up to 2300m. His conclusions were much like Coad's. After a large scale study of insect populations at high levels in the air up to 4572m over Tallulah, Louisiana, Glick (1939, 1942) stated:

"The numbers of insects taken in the air at any given time is dependent directly on the condition of the weather preceding and on combinations of one or more meteorological factors". He concluded that the numbers in the air increased rapidly to a maximum as temperatures increased from 1.7 to 25°C, after which they diminish as temperatures increase towards 38°C. His data also showed a vertical characteristic distribution pattern of diminishing density with height. Similar work carried out by Hardy & Milne (1938) and Freeman (1945) up to 610m in Yorkshire, England, also suggested that the density of flying insects decreased with height, and that high temperature, low relative humidity and wind velocities of 12 mph. coincided with maximum numbers of most groups caught in the air. Johnson (1957), using tow-nets to study aerial populations of aphids at 6 levels from 15.2 to 609.6m high, found that density declined continuously with height.

From this review, two points can be seen clearly: 1) the aerial density of flying insects reduced gradually with the increase in height; 2) physical factors dominate the aerial density of flying insects.

It is known that physical factors correlate with altitude, especially wind and temperature. This relationship leads some researchers to produce formulae to fit the existing data to express the dispersal process of flying insects in the upper air. Wolfenbarger (1946) produced an empirical semi-logrithmic formula to fit both Hardy & Milne's (1938) and Freeman's (1945) data for catches up to 610m; he was, however, unable to find a satisfactory expression for Glick's (1939) figures. Later Johnson & Penman (1951) found that log density of aphids was linearly related to log height only beyond a certain height above the ground.

After detailed study, Johnson (1957) gave a general empirical formula that fitted most of the published data for profiles of density of a variety of insects, showing that insect density diminishes continuously and regularly as height increase, and suggesting that vertical distribution at high levels is determined by factors outside the immediate control of the insect. The ranges of height he dealt with were: 61 to 1524m (data from Glick 1939); 24.4 to 457.2m (data from Hardy & Milne 1938); 3.1, 53.9 and 84.4m (data from Freeman 1945); 15.2 to 610m and a small amount of material at 3.1, 15.2, 152.4, and 304.8m (data of Johnson 1957).

1.4 Insect boundary layers

Below the minimum level mentioned above, the distribution of flying insects is influenced in different way. Taylor (1960) found the evidence that the distribution of insect density in relation to height up to about 9m is different from that at higher levels, through comparing published vertical distribution data at low level (Korting 1931; Profft 1939; Shands et al. 1956; Riggert 1931) with those at high levels (Glick 1939; Freeman 1945; Johnson 1957; Johnson & Taylor 1955). He established that there are maximum densities of insects at particular heights specific to individual species. He used this to propose the existence of "insect boundary layer" (Taylor 1958). He concluded that insect activity is mainly restricted to a layer in which the insect is able to control its movement relative to the ground; that is where its flight speed exceeds the wind speed. This he called the insect boundary layer. This is distinct from the planetary boundary layer which extends from the surface to about one km where a transition from turbulent air flow to the smooth flow of the upper atmosphere occurs (Sutton, 1953 and Oke, 1987). Subsequently the concept of an insect boundary layer was supported by Duelli (1980), Lewis (1967) and further developed by Taylor (1974). Since its description it has helped interpretation of experimental work (Lewis 1967) and has also provided a basis for classifying migratory flights of aphids (Taylor & Palmer 1972). However, Snow (1979, 1982), using suction traps to study vertical distributions of flying mosquitoes in Gambia and in West African savanna, was not able to confirm that observed discontinuities (see also Taylor 1974) in vertical profiles did match the forecast position of the insect boundary layer. It therefore seemed worthwhile to carry out a further study to test the concept of the boundary layer as described in the Chapters 4.

The question of the relative importance of physical and biological factors in determining flight positions within the insect boundary layer is examined in Chapter 4 and 5. Although insect species behave very differently, in general, it is to be expected that biological effects such as food, mating, swarming, egg-laying and responses to olfaction, and visual mechanical stimuli will be more important than physical or microclimatic factors, since they can control their track within their boundary layers (Taylor 1958, 1960; Pedgley 1982). This problem I believe is a great challenge for insect ecologists and much of this thesis is concerned with it.

1.5 Dispute about the effect of shelter

Little has been reported about the effect of wind on the vertical distribution of flying insects in the tropics. This is probably because of the stability of the air within the forest; even above the canopy, light winds or calm air are the norm (Haddow et al. 1961; Sutton 1989). This stability of the air in tropical rain forest is almost completely absent in temperate habitats, especially in oceanic climates like the British Isles. Instead the wind has come to be regarded as one of the most important physical factors determining the dispersal of flying insects (Johnson 1950; Taylor & Johnson 1954; Wegorek 1959; Van Eimern 1964; Lewis 1965b, c). Correspondently, the significance of shelter to flying insects has been much studied.

Key work in this area is that of Lewis (1965 a, b, c; 1966 a, b; 1967; 1969 a, b, c; 1970), Lewis & Dibley (1970), Lewis & Smith (1969), Lewis & Stephenson (1966) and Smith & Lewis (1972). These papers showed that flying insects accumulate in the lee of obstacles to the wind, and that patterns of distribution of flying insects in the air and around sheltered crops depend largely on the height and permeability of windbreaks and their orientation to prevailing winds. These generalizations apply to many kinds of artificial windbreaks, including barriers made of laths, coir and plastic netting (Lewis 1965 a, b; 1966 a, b; 1967; Lewis & Stephenson 1966; Smith & Lewis 1972), and to living hedgerows (Lewis 1969b) and windbreaks of tall trees (Lewis 1970).

However, similar work carried out by Bowden & Dean (1977) on the distribution of flying insects in and near a tall hedgerow suggested that insects were most numerous on one side of the hedgerow irrespective of speed and direction of wind, and concluded that the pattern of distribution appeared to be determined primarily by the comparative richness of the vegetation surrounding the trapping sites, the western side of the hedgerow having the most varied flora. Similarly studies in and near a wheat crop (Dean 1974) showed that distributions of some hymenopterous parasitoids and predators of aphids, notably Chrysopidae and Syrphidae (Diptera) on either side of a boundary hedgerow were independent of both direction and speed of wind. These pieces work stand in isolation to the larger and more comprehensive body of work associated with Lewis and his co-workers.

In his review of the subject, Pasek (1988) concluded that flying insects tend to accumulate in areas of reduced windspeed where they have most control of flight; however, distribution patterns can be modified by directed movements in response to olfactory and visual stimuli. Pasek also suggested that the pattern of distribution of flying insects may be affected by wind speed, wind direction, permeability of the windbreak, turbulence and vegetation composition. He was unable to resolve the conflict in the conclusions of Lewis & Dibley (1970) on the one hand, and Bowden & Dean (1977) on the other. It therefore seemed worthwhile to investigate further of the distribution of flying insects in relation to shelter.

1.6 Rationale of this study

There are three approaches to the study of insect ecology; laboratory experiments, field observations and manipulative field experiments. All have their own strengths and shortcomings. The best method will depend on the question being asked. For the questions raised above field observations and manipulative field experiments are believed to be the most suitable methods. The technique used was that developed by Sutton (1983) and Rees (1983), working together, for research on the spatial distribution of flying insects in the tropical forest environment.

In this thesis observed distribution patterns are compared with those published in literature and with predictions made according to the "insect boundary layer" concept, further evidence is examined in an attempt to resolve the conflict over shelter effects obtained by means of field observations and manipulative field experiments, and the importance of trees in the life of flying insects is examined. Chapter 3 documents the temporal and spatial distribution patterns of common families of flying Diptera in relation to an emergent hedgerow tree, suggesting possible causal processes of the patterns and the importance of such trees on lives of flying insects. Chapter 4 concerns the temporal and spatial distributions of common species of the commonest family (Scatopsidae) in the collection, focusing on testing the "insect boundary layer" concept and looking at the behaviour of the insects within their boundary layer. The fifth Chapter deals with the effect of microclimate on the daily abundance of flying Diptera, testing consistency with Johnson's "flight activity" hypothesis and testing the hypothesis that the insects distributions are determined by physical and biological factors within the "insect boundary layer". Chapter 6 records experiments undertaken to obtain further evidence on the effects of shelter, in the hope of resolving the conflicting views of the effects of shelter mentioned. Again the influence of physical factors on flying Diptera are suggested and general spatial patterns found in the third Chapter are confirmed. Chapter 7 looks at the importance of isolated trees on flying insects, testing predicted patterns in relation to a real tree and an artificial one to try to separate responses to biological factors from the purely physical shelter provided by both.

Chapter 2
GENERAL METHODS

The study was carried out over a four year period at Bond Ing, 10km north-east of Leeds city centre at 150m altitude. Field work was undertaken during four field seasons; May to August 1986, May to September 1987, May to August 1988 and June to August 1989.

2.1 Study site

The study site (fig. 2.1) is a one hectare meadow. It is bounded by well grown hedges, the one on its southern border consisting of hawthorn (Crataegus monogyna Jacq.) 3m high, with several emergent trees along its 90m length. The most prominent are three common limes (Tilia sp.), between 9 and 11.5m high (see map, fig. 2.1). Also forming small trees or prominent bushes are: elder (Sambucus nigra L.), pear (Pyrus communis L.), ash (Fraxinus excelsior L.), sloe (Prunus sp.), white willow (Salix alba L.), great sallow (Salix caprea L.) and birch (Betula pubescens Ehrh.). The southern side of the hedge is bounded by a deep ditch, with a 10m strip of rough grass, bramble (Rubus fruticosus Agg.), stinging nettle (Urtica dioica L.) and young norway spruce (Picea abies (L.) Karst). Beyond that is a re-sown grass meadow, cut for hay, which rises to the south-west, forming the boundary between the lower reaches of Airedale and Wharfedale.

On the eastern border of Bond Ing is another hawthorn hedge, while on the western edge thick scrub forms a mosaic with well established gardens. To the north, the meadow is bounded by a thick hedge of holly, hawthorn and other hedgerow species. The central half hectare of Bond Ing is mown for hay every year, and is best described as an unimproved species-rich neutral grassland (S. Clark, pers. comm.). The periphery is managed as scrub and unmown grassland, with extensive nettle beds and with a diversity of plant species typical of temperate marginal habitats. The site slopes gently to the south-west. The well grown hedges, tall scrub and trees create a sheltered environment, with much lower wind speeds and higher temperatures than in the surrounding fields.

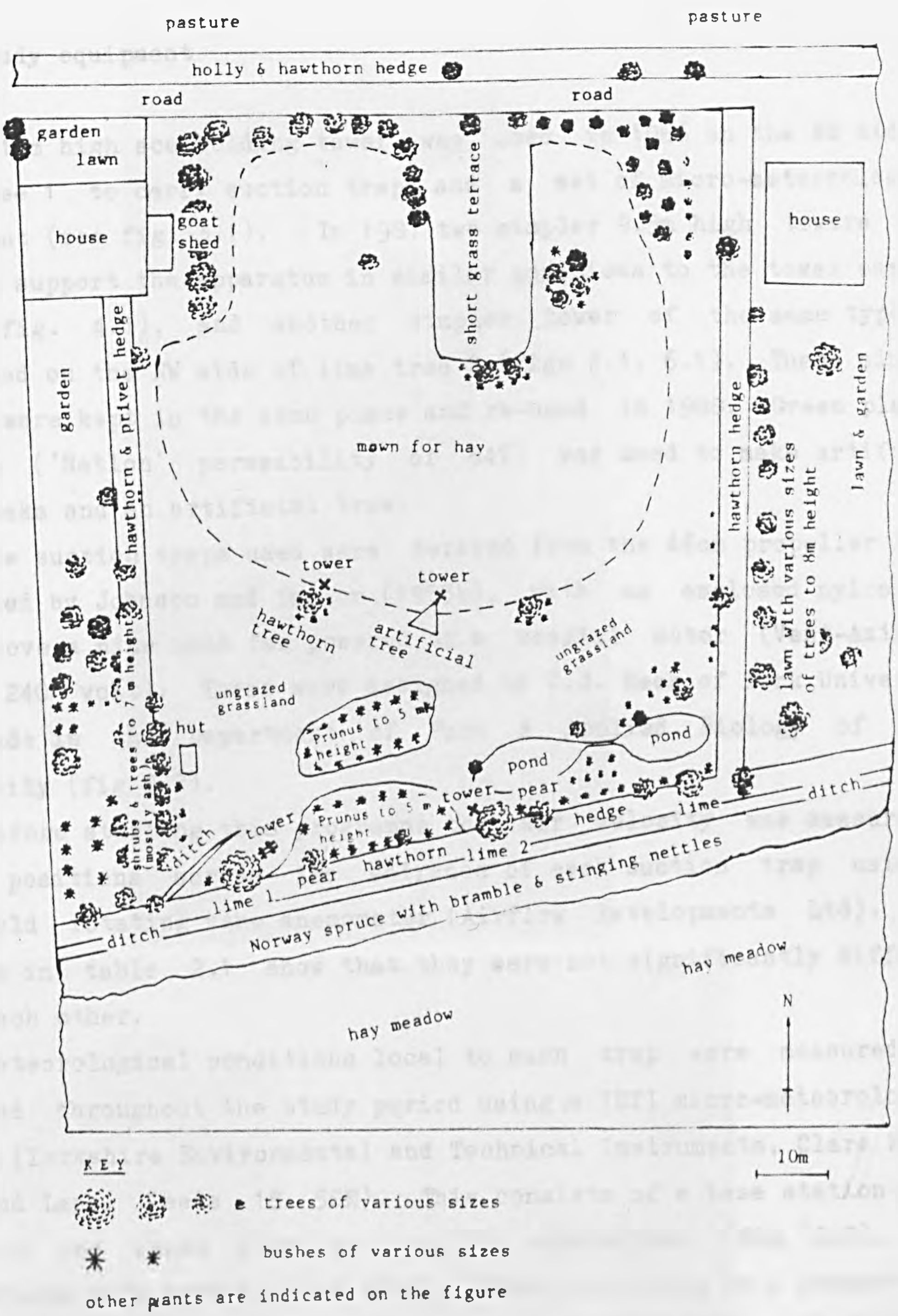

Figure 2.1. Study site. Bond Ing, Leeds, England.

2.2 Study equipment

A 10m high scaffolding tower was used in 1986 on the NE side of lime tree 1 to carry suction traps and a set of micro-meteorological equipment (see fig. 3.1). In 1987 two simpler 9.5m high towers were used to support the apparatus in similar positions to the tower used in 1986 (fig. 4.1), and another simpler tower of the same type was installed on the NW side of lime tree 2 (figs 2.1, 6.1). These simpler towers were kept in the same place and re-used in 1988. Green plastic netting ('Netlon' permeability of 54%) was used to make artificial windbreaks and an artificial tree.

The suction traps used were derived from the 46cm propeller traps described by Johnson and Taylor (1955b), with an enclosed nylon mesh cone above a nine inch fan powered by a coaxial motor (Vent-Axia, 75 watt, 240 volt). These were designed by C.J. Rees of York University and made in the Department of Pure & Applied Biology of Leeds University (fig 2.2).

Before starting this programme the air velocity was measured at seven positions across the entrance of each suction trap using a hand-held rotating vane anemometer (Airflow Developments Ltd). The results in table 2.1 show that they were not significantly different from each other.

Meteorological conditions local to each trap were measured and recorded throughout the study period using a YETI micro-meteorological system (Yorkshire Environmental and Technical Instruments, Clare House, Scotland Lane, Leeds 18 5SE). This consists of a base station which controls and reads from up to 15 outstations (fig 2.2). Six outstations were used in this study. Each outstation is a compact unit containing an aspirated psychrometer, an air-temperature thermometer, photometers, a rotating cup anemometer and electrical circuitry to average or integrate readings from these (fig 2.2). The values were automatically read out by the base station at twenty minute intervals and recorded with the time on magnetic tape, for later analysis by computer.

Prior to use the six micro-meteorological outstations were hung in close proximity and the data from them compared for consistency. The temperature and light intensity readings differed by small but significant amounts and corrections were applied accordingly. Later

Figure 2.2. Apparatus used for this study. A. a nine-inch suction trap; B. a YETI micro-meteorological system: (1), outstation, (2), base station. See text for further information.

Table 2.1. Comparison of the performance of suction traps and of the micro-meteorological outstations (outstation) under test conditions. For the suction traps measurements are in m sec^{-1}. T = average temperature in Celsius, L = average light intensity in lux, W = calibration factor in wind tunnel tests and H = wet bulb depression in Celsius. 'Sig' indicates the significance level, NS not significant and ** P < 0.01.

		1	2	3	4	5	6	Sig	Sample	Test method
Suction Trap		2.914	2.971	2.992	2.907	2.893	2.929	NS	n=42	ANOVA
Outstation	T	12.36	12.91	12.17	12.49	12.74	12.47	**	n=282	ANOVA
	L	4657.4	4454.3	4798.6	4675.1	4862.3	4619.2	**	n=282	ANOVA
	W	2.23	2.20	2.15	2.07	2.13	2.13	NS	n=60	GLM
	H	1.34	3.81	3.13	3.28	1.61	3.67	**	n=156	ANOVA

checks showed that neither the temperature sensors nor the silicon photocells drifted appreciably but the psychrometer readings differed substantially (table 2.1) and the performance of the psychrometers remained a problem throughout the work due to leakage of water into the wet bulb sensors, degredation of the wet-bulb wicks, impaction of moths and beetles in the airways and on the fan. Psychrometer giving low readings were standardized ~~overhandled~~ between experiments but final corrections were performed by comparison with readings of a standard Assman psychrometer. Relative humidity was calculated from the wet bulb depression and temperature using standard tables (Meteorological Office 1964). The psychrometer was made by Delta-t Devices Ltd. 128 Low Road, Burwell, Cambridge CB5 OEJ, England.

A weather vane and a standard rain gauge were used to measure wind directions and rainfall. These readings were taken four times each day manually during each observation period.

2.3 Techniques of sampling

Two individuals of the same species of lime tree (*Tilia* sp.) and a hawthorn tree (*Crataegus monogyna* Jacq.) were concerned in this study. Lime trees 1 and 2 were growing out of a 3m high thick hawthorn hedgerow (fig. 2.1). The former was 11.5m tall with a narrow canopy and without foliage below 2m. The latter was 10m in height with a relatively broad canopy compared with the tree 1 and no foliage below 1.5m. The hawthorn tree was in the middle of the grassland (fig. 2.1). It was 6m high and grew out of a thick patch of bramble with dogwood, creeping thistle and stinging nettle. The tree and bramble together made a substantial obstacle. In order to compare the effect of isolated trees on the distributions of flying insects, an artificial tree of similar height to the hawthorn tree was constructed. It was made of fine mesh plastic 'Netlon' mounted on scaffolding in the shape of a triangle to provide a similar profile (from the direction of the prevailing wind) as the hawthorn tree (figs 2.1, 7.1).

Samples were taken in the vicinity of these trees at different levels. Insects were collected in 60ml of 70% ethanol in each trap. Catch bottles were emptied at the end of each collecting run. The catch was examined and sorted into Orders, and then preserved in 70% ethanol. As the Diptera constituted from 91% to 95.5% of the total catches in the observations, they were chosen for this study. They were later identified to families, genera and, in some cases, to species.

2.4 Identification

As British species of Diptera have been extensively studied, the procedures used for identifying Diptera collected in this study are those described in the following keys based on external facies and genital features. The keys used for the identification of flying Diptera are Oldroyd (1970) and Unwin (1981) for identification at family level, Freeman (1950) for Anisopodidae, Edwards (1926) for Ceratopogonidae, Harris (1966) and Edwards (1938) for Cecidomyiidae, Coe *et al.* (1950) and Pinder (1978) for Chironomidae, Fonseca (1978) for Dolichopodidae, Collin (1961) for Empididae, Fonseca (1968) for Muscidae, Hutson *et al.* (1980) for Mycetophilidae, Disney (1983) for Phoridae, Freeman (1950) for Psychodidae, Freeman & Lane (1985) for Scatopsidae and Bibionidae, Freeman (1983) for Sciaridae, Coe *et al.* (1950) for Tipulidae and Cranston *et al.* (1987) for Culicidae. During trapping the flying Diptera within a radius of 10m of the trapping place were closely observed and occasional samples taken by hand net, and using a beating tray.

The constitution of 14 common families caught in 1986 and 1987 and the habits for genera and species are shown in Appendix 1. The following points emerge:

1) each family contained just a few genera, and each genus consisted of three or less species except for *Psychoda* (Psychodidae) and *Tachydromia* (Empididae);

2) only one or two species were abundant within each family in each of the two years. These species have a dominant influence on the family distribution pattern;

3) the activity periods for the majority of species contained in each family are similar;

4) according to the literature, both species and genera within each family have similar habits and live in similar habitats.

It is believed that the spatial distribution patterns to be seen at family level are the appropriate approach in this study. For the biggest family (Scatopsidae), which composes 65.8% of the total catch in 1986 and 26.7% in 1987, the analysis for the spatial distribution and microclimatic effect on them is carried out at species level.

It is worth pointing out that Rhegmoclema cooki Hutson was found to be the most abundant species of Scatopsidae in Leeds area during this study, although it was named quite recently by Hutson (1970). It can be easily recognized by the highly characteristic male 7th sternite and by the female genital capsule (Freeman & Lane 1985). The unexpected dominance of this species is probably related to the fact that it is very rare in collections from southern England. However Hutson (1973) stated: "specimens of Rhegmoclema cooki were found swarming with R. coxendix on a blue tent at Yorkshire: East Riding, Spaldington". By contrast, Ectaetia clavipes Loew is very common in southern England (Freeman & Lane 1985), but only three specimens obtained in 1986 and 1987 in this study,

2.5 Data treatment

The Friedman two-way analysis of variance by ranks and the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) were employed to test the significance of differences between trapping periods and heights, and distances from trees respectively. These two tests are the most useful ones for behavioral data and for the data in an ordinal scale (Siegel 1956). Statistical analysis was performed using the SAS statistical package (SAS, 1985). In the analyses of the relationship between microclimate and the abundances of flying Diptera, the data sets of families or species were transformed to base 10 logarithms. No transformation was carried out on microclimatic factors and the units used in this study were degrees Celsius for temperature, lux for light intensity, anemometer revolutions/minute for wind speed, percentage for relative humidity and mm for rainfall.

The use of suction traps with unprotected cones can lead to significant reductions in the catch in cross-winds of more than 6.25m sec^{-1} (Taylor 1955). Below 4.47m sec^{-1} the effect is minimal. The suction traps used for this study had a conical hat 23cm above the orifice of the netting cone (fig 2.2), which reduces the effect of cross-winds. Average wind speeds during the observations varied from 0.3 to 2.2m sec^{-1} at a height of 8.8m from the ground in afternoons when the wind speeds were almost always stronger than during the other trapping periods (morning, dusk and night). Consequently, it is not considered that under these conditions any appreciable loss of catching efficiency arose. The exception was that the average winds in late September of 1988 (during the 'cutting' experiment), were 4.1m sec^{-1}. Accordingly the loss of efficiency of suction traps was taken into account in the analysis (Southwood 1978; Taylor 1962). This study was concerned with the relative densities of flying Diptera at different heights and at different distances, and it was not considered necessary normally to convert these data to absolute densities.

Chapter 3

SPATIAL AND TEMPORAL DISTRIBUTION PATTERNS OF FLYING DIPTERA

3.1 Introduction

The distribution of flying insects in time and space has been the subject of much study in the past, but some aspects have hardly been considered. There has been an understandable tendency to concentrate on uniform agricultural systems in temperate situations (see General Introduction for detail). Little has been done in the tropics (see Sutton, 1989 for a review of work in tropical forest) and little has been done on 'architecturally' complex sites in the temperate zone. Using technology developed for the tropical work (Sutton, 1983, Rees, 1983) it seemed interesting to study the influence of an emergent hedgerow tree on the distribution of flying Diptera in a temperate habitat. There are many anecdotal reports and casual observations of the effect of such a tree (eg. Elton 1966), but no thorough quantitative study of which I am aware. The matter is important not only for the understanding of how insects behave and distribute themselves in the field, but also to understand foraging behaviour of predators such as bats and birds (especially hirundines and flycatchers). Declining populations of these predators is a matter of great concern in conservation circles, and a knowledge of their prey is an obvious way into the problem.

The principal sources of reference have been Haddow et al. 1961; Lewis & Taylor (1964), Lewis (1969b, 1970), Service (1971a, 1971b, 1973), Taylor (1974), Bowden & Dean (1977) and Sutton et al. (1983). In this Chapter I look at the effect of a hedgerow tree in the context of these and other findings of flying insect distribution in architecturally simpler situations.

3.2 Materials and methods

3.2.1 Trapping site

The study site has been described in detail in General Methods (fig. 2.1, Chapter 2). The 11.5m tall lime tree (lime 1 in fig. 2.1) that has been used in this study is in the south-west corner of Bond Ing. It has a rather narrow canopy with no foliage below 2m. It was in full flower at the time of trapping. 10m from it is a 7 m high pear tree, surrounded by an extensive patch of Prunus sp. suckers. The area of scrub to the west of the lime tree is up to 7m high. The rest of the area close to the tree is grass, unmown to the north-east, mown to the south. Further detail is shown in fig. 2.1. No substantial changes in the management of the meadow or the surrounding fields has occurred in the last ten years.

3.2.2 The arrangement of study equipment

A 10m high scaffolding tower was erected in 1986 close to the lime tree to carry six suction traps and a set of micro-meteorological equipment (fig. 3.1). Trapping was between 18 July - 1 August inclusive. In 1987 two simpler towers were used to support traps in similar positions to the single tower used in 1986, and trapping was from 22 July to 1 August inclusive.

The suction traps (see General Methods, Chapter 2) were suspended each side of the single tower at three different levels, the top two traps with their intakes at 8.8 meters from the ground (no.1 and no.4) (figs 3.1, 4.1), the middle two at 5 meters (no.2 & no.5) and bottom two at 1.2 meters (no.3 & no.6). The vertical distance between any two traps was sufficient to prevent the down-draft of the upper one affecting the efficiency of the lower. Traps 1, 2 and 3 were almost brushing the leaves of the tree canopy. Traps 4, 5 and 6 were 4.5m further away. In 1987 the two simpler towers provided the same spatial array.

3.2.3 Trapping programme

Initial observation showed that flight activity of flying Diptera appeared to vary with time of day. Four separate trapping periods were set up to reflect differences in light intensity, temperature and relative humidity. Asymmetry of the periods reflects the need for the observer to sleep.

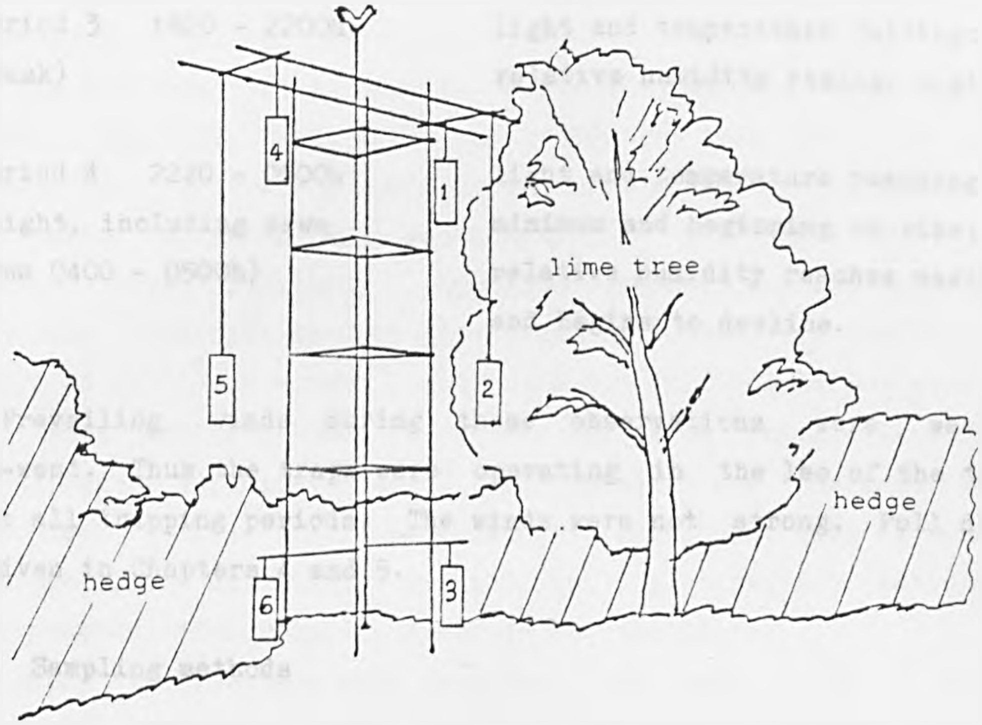

Figure 3.1. The position of suction traps in relation to the lime tree and the hedge. Rectangles = suction traps. Traps 1, 2 and 3 were almost touching the foliage of the tree and traps 4, 5, and 6 were 4.5 m away from traps 1, 2, and 3 respectively. Bond Ing, Leeds; 1986.

Period 1 0520 - 1200h GMT. (morning)	Light and temperature rising; relative humidity declining.
Period 2 1220 - 1800h (afternoon)	light and temperature at maximum; relative humidity reaches minimum and begins to rise.
Period 3 1820 - 2200h (dusk)	light and temperature falling; relative humidity rising; nightfall.
Period 4 2220 - 0500h (night, including dawn from 0400 - 0500h)	light and temperature reaching minimum and beginning to rise; relative humidity reaches maximum and begins to decline.

Prevailing winds during these observations were west or south-west. Thus the traps were operating in the lee of the tree in almost all trapping periods. The winds were not strong. Full details are given in Chapters 4 and 5.

3.2.4 Sampling methods

Flies were collected in 60ml of 70% alcohol in each trap. Catch bottles were emptied four times each day at the end of each run. The catch was examined and sorted into Orders, and then preserved in 70% alcohol. Later the Diptera were identified to families, and some to genera and species (Appendix 1). During trapping the flying Diptera within a radius of 10m of the tree were closely observed and occasional samples taken by hand net, and using a beating tray during short breaks of trapping periods.

3.2.5 Data treatment

The Friedman two-way analysis of variance by ranks and the Wilcoxon matched-pairs signed-ranks test (Siegel 1956) were employed to test the significance of differences between trapping periods and heights, and distances from the tree respectively. Statistical analysis was performed using the SAS statistical package (SAS 1985).

3.3 Results

3.3.1 Distribution patterns by year

A total of 84,132 individuals of flying Diptera were trapped, 28,601 in 336 samples in 1986 and 55,531 in 246 samples in 1987. Twenty three families were represented. The whole catch is summarised by family in fig. 3.2 and table 3.1.

The following points emerge: Most of families were much more abundant in 1987 than those in 1986. In 1986 only three families exceeded two individuals per hour in their most activity period of day (scatopsids, sciarids and cecidomyiids). In 1987 a further five families were similarly plentiful (ceratopogonids, chironomids, psychodids, anisopodids and tipulids). A further six families may be classified as "less common", exceeding 0.5 individuals per hour during their most activity time in either or both years (anthomyiids, dolichopodids, empidids, muscids, mycetophilids and phorids). The rest of the twenty three families found were relatively rare in both years (calliphorids, culicids, pipunculids, platypezids, sarcophagids, scathophagids, stratiomyids, syrphids and tachinids).

Among the fourteen main families, six were 2 to 5 times as abundant in 1987 as in 1986 (fig 3.2), two families (mycetophilids and psychodids) were 8.8 and 11 times more abundant in 1987 respectively and four families (ceratopogonids, chironomids, anisopodids and anthomyiids) reached even higher ratios, with a peak value of 33. The most abundant family in 1986, the scatopsids, was also the most abundant in 1987, but with an only slightly increased total. Clearly the stability of management of the surrounding countryside is not reflected in stability in numbers of individuals from year to year.

3.3.2 Temporal patterns

Most families with total catches above 100 individuals showed distinctly greater abundance at some times of the day than others (table 3.1, 3.3). There were more families flying by day than by night. The activity period of mycetophilids extended from afternoon through

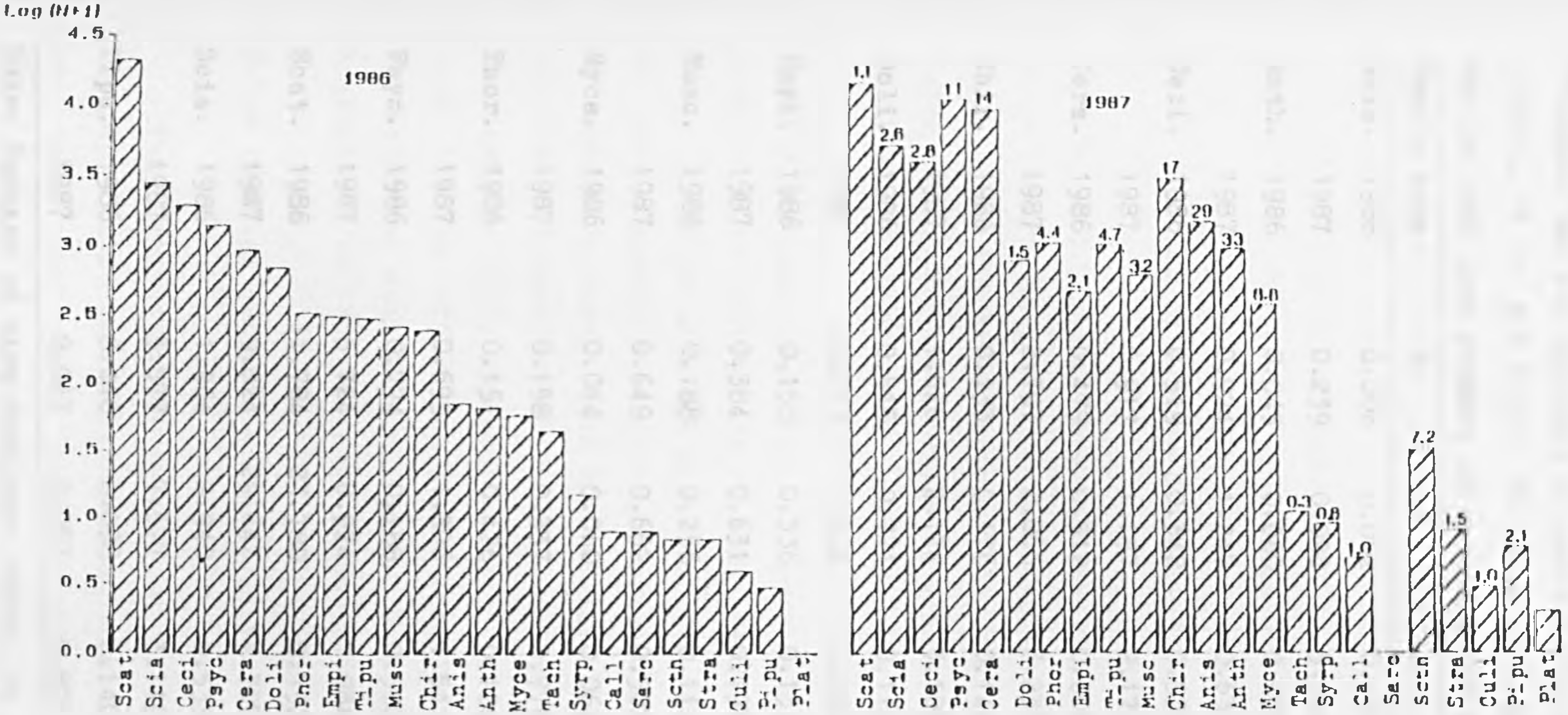

Figure 3.2. Total catch each year in all traps. The numbers above the 1987 columns are the ratios of abundance of 1987 to 1986.

Acal. = acalypterates
Anis. = Anisopodidae
Anth. = Anthomyiidae
Call. = Calliphoridae
Culi. = Culicidae
Ceci. = Cecidomyiidae
Cera. = Ceratopogonidae
Chir. = Chironomidae

Doli. = Dolichopodidae
Empi. = Empididae
Musc. = Muscidae
Myce. = Mycetophilidae
Phor. = Phoridae
Pipu. = Pipunculidae
Plat. = Platypezidae
Psyc. = Psychodidae

Scat. = Scatopsidae
Sarc. = Sarcophagidae
Scia. = Sciaridae
Scth. = Scathophagidae
Stra. = Stratiomyidae
Syrp. = Syrphidae
Tach. = Tachinidae
Tipu. = Tipulidae

Table 3.1. Numbers per hour by trapping periods. Significance of departure from uniform numbers in the different periods determined by Friedman two way analysis of variance by ranks: *** = $p < 0.001$, ** = $p < 0.01$, * = $p < 0.05$, NS means not significant. n = 336 in 1986 and 246 in 1987 (see summary of notation for abbreviations).

Family	year	MO	AF	DU	NI	Sig.
Anis.	1986	0.006	0.002	0.158	0.043	*
	1987	0.239	0.098	5.041	0.867	***
Anth.	1986	0.045	0.060	0.039	0.002	*
	1987	0.924	1.247	0.631	0.028	***
Ceci.	1986	0.519	0.342	0.530	2.476	***
	1987	0.917	1.187	2.179	6.959	**
Cera.	1986	0.479	0.512	0.606	0.469	NS
	1987	2.797	2.065	13.236	12.374	**
Chir.	1986	0.133	0.176	0.144	0.088	NS
	1987	1.626	2.174	3.106	2.423	NS
Doli.	1986	0.515	0.771	0.119	0.007	***
	1987	0.740	1.192	0.286	0.013	***
Empi.	1986	0.158	0.336	0.137	0.039	***
	1987	0.384	0.631	0.197	0.133	*
Musc.	1986	0.188	0.256	0.112	0.006	***
	1987	0.649	0.662	0.502	0.049	***
Myce.	1986	0.014	0.060	0.062	0.007	*
	1987	0.158	0.337	0.779	0.089	**
Phor.	1986	0.151	0.426	0.126	0.006	***
	1987	0.699	1.306	1.541	0.005	***
Psyc.	1986	0.774	0.188	0.508	1.393	***
	1987	5.724	0.924	7.984	17.561	***
Scat.	1986	11.784	23.780	0.750	0.388	***
	1987	9.024	29.642	1.707	0.187	***
Scia.	1986	1.964	2.940	0.533	0.150	***
	1987	3.577	7.577	3.119	1.106	***
Tipu.	1986	0.010	0.008	0.140	0.468	***
	1987	0.047	0.057	0.808	2.098	***

Note: Numbers of rare families taken in 1986 are as follows: 7(4) in Call.; 3(2) in Culi.; 0(1) in Plat.; 2(5) in Pipu.; 7(0) in Sarc.; 6(32) in Scth.; 6(7) in Stra.; 14(8) in Syrp. and 45(10) in Tach.. Numbers in brackets are those caught in 1987.

dusk whilst anisopodids were most active at dusk and in the night. Tipulids and cecidomyiids were mostly night flyers. Psychodids were most active at night but were also well represented in morning catches. Chironomids were roughly equally common at any time of day. This was also true for ceratopogonids in 1986, but in 1987 they were distinctly more common at night.

Altogether eight kinds of diel distribution patterns have been subjectively determined from table 3.1 and are displayed in fig. 3.3.

3.3.3 Spatial patterns - distance from the tree

Table 3.2 shows the percentage of the catch taken in the three traps near the tree for each family in each trapping period. For example, of the total anisopodids taken in the six traps, 81% were taken near the tree during the morning period in 1987. In the 14 families for which good numbers were trapped, it can be seen that despite the strong differences in abundances in the two years the results for most families are remarkably similar, that is, the greater proportion of individuals of most families were caught close to the tree. Likewise although most families were much more abundant in one or two trapping periods the preferences for distance from the tree do not appear to change with time of day. These generalisations break down for the cecidomyiids which were markedly scarcer close to the tree at the dusks in 1986, psychodids which were less localised close to the tree in the afternoons, and scatopsids which showed a strong concentration away from the tree. Dolichopodids and sciarids showed no aggregation in 1986 but were concentrated near the tree in 1987.

3.3.4 Spatial patterns - height above ground

The distribution of catches by height is given in table 3.3, and the representative distribution patterns are shown in fig. 3.4. It can be seen that each family displays a characteristic vertical distribution. Most of the families previously noted as occurring close to the tree are most frequently caught in the mid-level traps. However some like dolichopodids are also common in the lower traps, others like

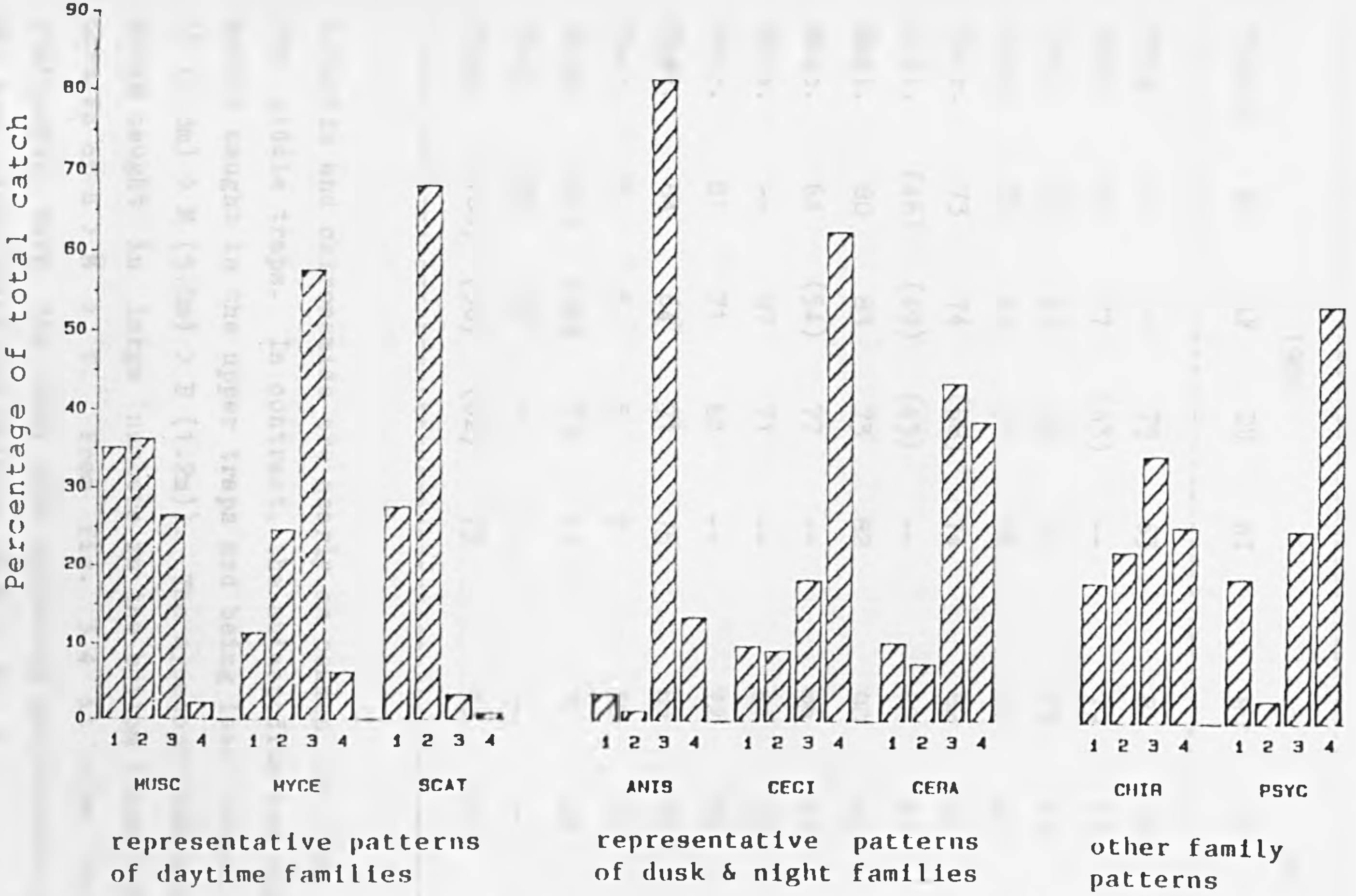

Figure 3.3. Diel distribution patterns of selected families, pooling the results of 1986 and 1987. Trapping period 1 = morning, 2 = afternoon, 3 = dusk and 4 = night. Myce. pattern also represents that of Phoridae; Scat. pattern also represents those of Sciaridae, Empididae, Dolichopodidae and Anthomyiidae; Ceci. pattern represents that of Tipulidae as well.

Table 3.2. Percentage of each family trapped close to the tree in each trapping period. Figures in brackets show no significance from the tree (P > 0.05 using the Wilcoxon matched-pairs signed-ranks test (Siegel 1956)).

	1986				1987			
Family	MO	AF	DU	NI	MO	AF	DU	NI
Anis.	--	--	75	63	81	89	78	73
Anth.	80	77	(63)	--	79	63	73	--
Ceci.	65	67	24	73	75	69	64	86
Cera.	76	82	71	73	77	82	87	90
Chir.	73	74	(58)	74	82	80	82	86
Doli.	(46)	(49)	(43)	--	62	64	66	--
Empi.	80	83	73	82	90	89	83	83
Musc.	64	(54)	77	--	86	73	70	95
Myce.	--	87	71	--	84	79	86	83
Phor.	81	71	66	--	72	72	72	--
Psyc.	84	64	71	75	85	59	82	86
Scat.	8	6	5	9	30	27	14	15
Scia.	(54)	(54)	73	71	71	68	75	88
Tach.	80	85	--	--	--	--	--	--
Tipu.	(100)	(50)	(62)	73	90	(52)	72	80

sciarids and chironomids are nearly as common in the top traps as in the middle traps. In contrast, the anisopodids are high flyers, being mainly caught in the upper traps and being least common at ground level (T (8.8m) > M (5.0m) > B (1.2m)). The mycetophilids are ground flyers, being caught in large numbers in the bottom traps and displaying the pattern of B > M > T. From fig. 3.4 it also can be seen that scatopsids were the only ones appearing preponderantly far away from the tree, displaying the pattern of M >> T > B.

Table 3.3. Numbers of individuals trapped at two distances, far away from the tree (F) and near to it (N) and three heights. Significant dependence of numbers caught upon height is indicated: *** = P < 0.001, ** = P < 0.01, * = P < 0.05 and ~~Z 8 xyc fboxbficant~~ NS = not significant (Friedman two way analysis of variance by ranks).

		Chir.		Cera.		Musc.		Anth.		Empi.	
Year	Height	F	N	F	N	F	N	F	N	F	N
	8.8m	26	40	54	101	41	44	0	8	6	17
1986	5.0m	26	113	150	574	42	93	10	37	28	172
	1.2m	17	30	28	44	23	24	6	6	27	67
	Sig.	NS	**	***	***	NS	**	*	**	NS	***
	8.8m	164	1060	331	2450	42	197	69	224	11	80
1987	5.0m	209	1114	635	5541	67	265	165	390	19	232
	1.2m	163	413	268	386	25	33	51	75	28	113
	Sig.	NS	**	**	**	NS	**	**	***	NS	**

		Tipu.		Ceci.		Phor.		Psyc.		Anis.	
Year	Height	F	N	F	N	F	N	F	N	F	N
	8.8m	8	33	32	70	9	34	31	156	11	41
1986	5.0m	9	96	104	701	32	142	144	824	7	8
	1.2m	70	91	471	601	50	70	166	118	3	2
	Sig.	**	**	***	***	**	***	***	***	NS	*
	8.8m	25	201	100	399	38	147	263	1516	191	681
1987	5.0m	45	408	168	1745	161	518	543	6173	120	440
	1.2m	106	217	525	1141	89	128	1008	1911	41	54
	Sig.	***	*	***	***	***	**	**	*	*	***

		Myce.		Scat.		Doli.		Scia.	
Year	Height	F	N	F	N	F	N	F	N
	8.8m	0	1	2786	545	10	30	534	654
1986	5.0m	1	2	12953	559	174	189	586	783
	1.2m	8	47	2006	92	189	120	138	116
	Sig.	NS	***	***	***	***	***	***	***
	8.8m	0	13	3014	2134	30	63	655	1066
1987	5.0m	3	109	6946	1788	148	280	553	2226
	1.2m	61	196	926	222	114	168	313	512
	Sig.	***	**	***	**	**	***	**	***

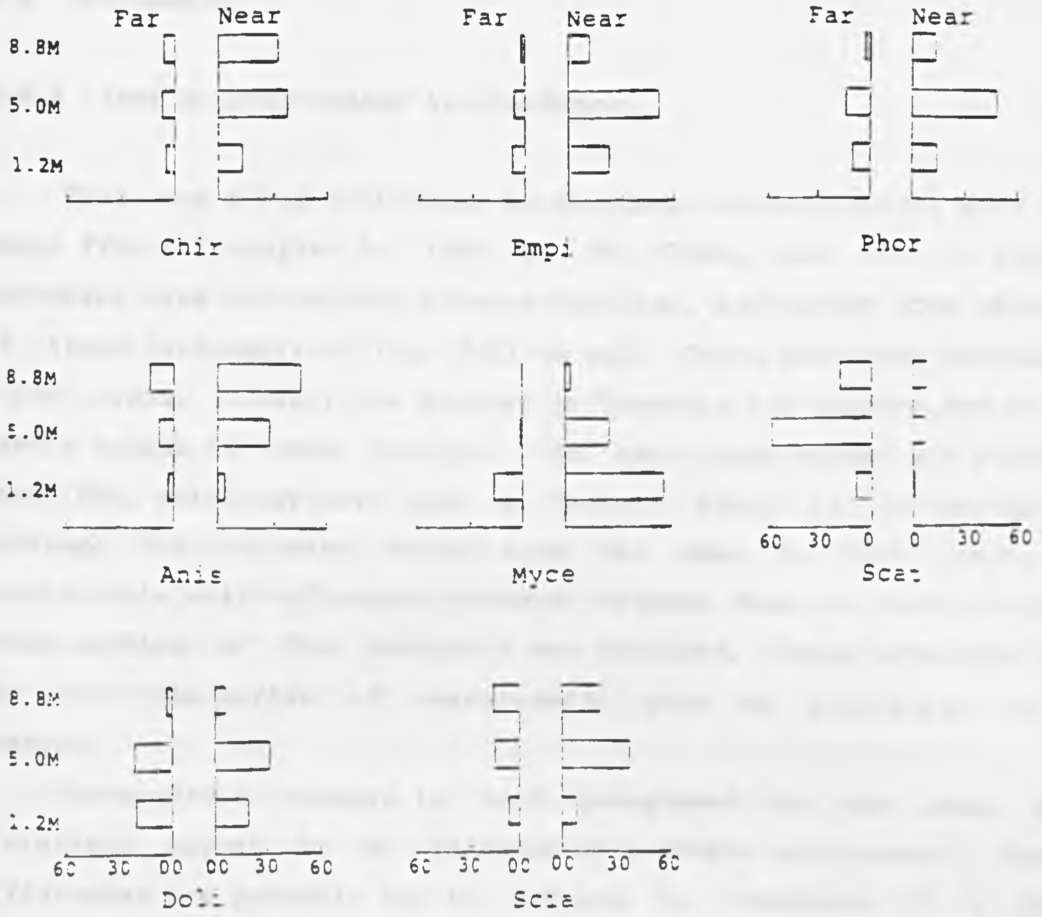

Figure 3.4 Spatial distribution patterns of selected families, pooling results of 1986 and 1987. Abscissa values are the percentage of the total catch for each family. The total catch is taken from 6 traps, 3 in the ´Near´ profile, 3 in the ´Far´ profile, Near and Far being 0 and 4.5 m respectively from the tree canopy edge. Also, Phor. pattern represents that of Psychodidae; Chir. pattern represents those of Anthomyiidae, Muscidae and Ceratopogonidae; and Empi. pattern represents those of Tipulidae and Cecidomyiidae.

3.4 Discussion

3.4.1 Year on year change in abundance

There was a big difference in abundance between years, with a mean value from all samples in 1986 of 85 flies, and 226 in 1987. The increases were not uniform between families, but varied from as much as 33 times (anthomyiids, fig. 3.2) to nil. There were even decreases in a few cases. Clearly the factors influencing the numbers are at least partly unique to each family. 1987 was a much warmer and drier year than 1986, which may have been a factor. Also, it is possible that although the calendar dates were the same in both years, some considerable shift of season occurred between them, so that a different cross-section of the community was obtained. Other work done before and after this series of measurements gave no indication of this, however.

There were no changes in land management in the area, so the variations appear to be features of a stable environment. Such big differences are probably due to changes in abundance of a few key species in each family. For example, Anisopus punctatus Fabricius, a dominant species of anisopodids, increased greatly in 1987 (Appendix 1).

3.4.2 Diel patterns

Strong diel flight patterns are evident in table 3.1. They are very much in agreement with the literature (Glick, 1939; Hawkes, 1951, 1961; Lewis & Taylor, 1964; Service, 1973). The constancy in pattern from year to year, in contrast to the variation in abundance, is notable. It might be expected that flies of weak flight would be active at night, when wind speeds are, in general, lower. This is true for some families, e.g. psychodids, tipulids and cecidomyiids, but the peak flight for chironomids at least in 1986 was in the afternoon, when wind speeds are strongest. At this time of year nights are short, with only 5 hours of real darkness, which limits the potential for flight activity for nocturnal species. It would be interesting to know if the proportion of nocturnal families is greater in spring and autumn.

The overall picture is of stable patterns of flight activity at the family level, with a strong predominance of day flyers and much variation in the precise detail of pattern between families. In some cases the flight times are very precise. The case of anisopodids (fig. 3.3) is a good example. Such precision may be connected with the fact that the catch of this family consisted very largely of one species (see Appendix 1). In contrast, the relatively even spread of chironomids across the trapping periods may be due to the presence of a variety of species with different flight times (Appendix 1). Body lengths and colour of chironomids caught both varied considerably, indicating a wide range of species. Nevertheless, this result is surprising, as previous work (e.g. Lewis & Taylor, 1964) has indicated that the family is mainly crepuscular.

Ceratopogonids showed different patterns in the two years (table 3.1). This seems to be due to a shift in the relative proportions of the genus *Culicoides* and the species *Forcipomyia bipunctata* Linnaeus. The former are more active at lower light intensities (Kettle, 1962), and were more abundant in 1987, tipping the advantage heavily towards the evening and night trapping periods.

3.4.3 Spatial distribution

The two sets of traps, close to and away from the tree, have demonstrated dramatic differences in the distribution of families, with all except one being commoner close to the tree (table 3.2). The one exception, the scatopsids, was represented by 10 species, of which 67% were *Rhegmoclema cooki* Hutson, 27% *Anapausis soluta* Loew and 4% *R. coxendix* Verrall (see table 4.1 in Chapter 4). All three species were often found crammed into crevices in the suction traps on sunny afternoons, with a concentration in trap 5 (fig. 3.1). These species are well known for swarming over artefacts such as fences and tents (Colyer & Hammond, 1968; Hutson, 1973). The bright metallic finish of the suction traps may have attracted them (see Chapter 4 for detail). From mid-day for several hours the outer traps would be in the sun, while those close to the tree would be in shadow, and this may explain the distribution. The scatopsids were among the minority of families which were found to be uncommon around and on the tree using sweep nets and beating trays. They appear to have flown in from some distance, and to have little association with the tree. This spatial distribution is quite related to that of wind eddy behind the tree (see Chapter 4 for detail).

For the rest of the families, the tree appeared to act as a centre of attraction (fig. 3.4). The literature makes it clear that for all these families the tree would provide a likely food source, or mating station, or both. Willmer (1983) investigated the activity of nectar-feeding insects on a lime tree. She found that Muscidae visited the flowers early and late in the day. Fig. 3.3 shows that on the lime tree they were equally active both morning and afternoon, but were also present in the dusk sample. The only anomaly is the cecidomyiids at dusk in 1986 (table 3.2), which were most abundant further away from the tree. This is currently unexplained.

The eight different patterns of vertical profile which could be identified (fig. 3.4) indicate that flies of different families have clearly different patterns of spatial distribution close to the tree, even at this rather limited level of resolution. The chironomid pattern is quite general, being shared by anthomyiids, muscids and ceratopogonids. The chironomids themselves were observed to swarm. They did this at different times of day, close to the foliage and at a fairly high level, showing the same distribution as was evident in the trap catches. Swarming is a notable feature of this family (Colyer & Hammond, 1968, Kidd & Brindle, 1959). However, they are also known to feed on flowers, and this could be a factor in their presence (see above). Whether the ceratopogonids which share this same spatial pattern were swarming or feeding is unclear. Downes (1955) found that swarming behaviour was well developed in the genera Culicoides and Forcipomyia. As the ceratopogonids caught in this study were mainly consisted of these two genera (Appendix 1), it appears that swarming behaviour might explain some variation of the distribution of the family. Also Edwards (1926, 1939) found that sap-sucking of adults in Culicoides was developed and larvae of Forcipomyia were found to develop under tree bark and rotting vegetation. This seems that they may be attracted by the lime tree for food and breeding site. It also notes that the wind has significantly negative effect on their activity (see Chapter 5); therefore the shelter provided by the tree may be important for this family.

The empidids, tipulids, cecidomyiids, phorids and psychodids have very similar patterns, except that the first three are more common at ground level close to the tree. The common factor is the prevalence of individuals at the mid-level near the tree. All families were common in the surrounding vegetation, and were probably using the tree for a variety of purposes. Kidd and Brindle (1959) record several species of cecidomyiids forming galls on lime foliage. This lime tree had no foliage below 2m, and good development at 5m, the height of the second tier of traps. At this time of year, with full leaf development, flowers and honeydew, the canopy of the tree could be expected to provide a food source for a great variety of organisms. For weak flyers such as tipulids the prevalence at 5m rather than ground level is surprising, but this distribution is related to the shelter of the tree (see Chapter 5).

Service (1973), trapping in a wood, found tipulids to be concentrated at his lowest trapping level (23cm), although Glick (1939) reported a few at high levels. Psychodidae are also weak flyers and lovers of sheltered damp places near the ground, so their prevalence at 5m is another surprise. Investigation made by sweeping nets and beating trays showed that Psychoda albipennis Zett. was common. However, the collection from the suction traps suggested that Psychoda phalaenoides Linn., P. setigera Tonn. and P. severini Tonn. were abundant (Appendix 1), and these three species were mainly dung-breeding ones (Satchell 1948). there was no dung in this study site. The majority of psychodids were probably blown in from grazed pasture nearby (100m) by wind. Hence it seems likely that the shelter provided by the tree is the reason. Phoridae are certainly known to swarm, but are also flower feeders (Disney, 1980, 1983).

Dolichopodidae are another family which peak at mid-level, but they occur more frequently away from the tree than groups mentioned above (fig. 3.4). They were found commonly in the area, on the trunk of the tree and on foliage. They prey on many of the smaller flies and other insects (Dyte, 1959; Laurence, 1951 and Fonseca, 1978). This does not explain their presence away from the tree, unless good dispersal powers are associated with their predatory habits, as is often the case.

The anisopodids were unique among the families in having a marked concentration at the top level. It will be recalled that 85% of individuals belonged to the species Anisopus punctatus Fab. (Appendix 1). This was common in the area close to the tree in hand net samples.

It is well known for its swarming behaviour (Kidd & Brindle, 1959 and Colyer & Hammond 1968). Anisopodids are not noted as particularly strong flyers and yet so near the top of the tree they would be exposed to the prevailing south west winds. The very strong preference for evening flight (fig. 3.3) suggests that they avoided strong winds by flying late. The relationship between flight pattern and weather conditions in this and other taxa is explored in Chapter 5.

The mycetophilids are much in contrast to the anisopodids, with a strong preference for flying low. Using sweep nets they were found commonly at ground level in shaded areas around the tree. Hutson *et al.*, (1980) and other authors regard them as shade and moisture loving, with weak, low flight.

3.4.4 Boundary layer considerations

For a given insect, place and time there may be a height above which wind speed is greater than insect flight speed. Below that height there is a layer in which the insect can reach any goal; this layer is known as the "insect boundary layer" (Taylor 1958, 1960, 1974). The evidence for a boundary layer (*sensu* Taylor) was found by the discontinuity in vertical profiles of flying insect catches (Taylor, 1960 and 1974).

In this study, discontinuities in the two vertical profiles, away from and close to the tree, are easily seen by inspection of fig. 3.4. For strong flyers of the day active group (scatopsids, sciarids, anthomyiids and muscids), for example, the height of the discontinuity is between 5m and 8.8m for both the profile near the tree and that away from it. This suggests that the height of the boundary layer for these insects does not change appreciably with distance from the tree. This agrees with the result obtained by Lewis (1967). He suggests that the presence or absence of a windbreak would make little difference to the vertical distributions of two families of strong-flying insects, Staphylinidae (Coleoptera) and Bibionidae (Diptera). For less strong flyers, e.g. empidids, phorids and dolichopodids, the results show that the discontinuity is at 5m level near the tree and from 1.2m to 5m in height away from the tree. This suggests a deeper boundary layer close to the tree. This holds true for dusk flyers as well (fig. 3.4). From the spatial distribution patterns in table 3.3 and fig. 3.4, it can be seen that most families (except for scatopsids) prefer to congregate near the tree. This is compatible with the suggestion that the boundary layer there is deeper, because of the shelter offered by the tree.

The diversity of pattern described in this Chapter precludes any simple, entirely weather induced explanation of distribution of these flying Diptera. A number of influences must be at work, and the tree clearly plays a highly significant role in the life of these insects, whether as a landmark, a source of food or shelter. Hedgerow trees, I suggest, make a significant contribution to the spatial diversity of the landscape and to the dipterous fauna associated with it.

3.5 Summary

1. The distribution of flying Diptera around an emergent hedgerow tree have been studied using six suction traps hung at three levels and two distances from the tree. Collections were made four times each day from the middle of July to the start of August in 1986 and 1987. All Diptera were identified to family level and some to genera and species.

2. Although most families were far more abundant in 1987 than in 1986, patterns of spatial and temporal abundance were basically the same.

3. There was a marked concentration close to the tree for almost all families. The main exception was the Scatopsidae which accumulated 4.5 metres away from the tree in large numbers.

4. Most families were concentrated at the middle level, the main leaf layer, the exceptions being the Anisopodidae and Mycetophilidae, which were most numerous at the top and bottom levels respectively.

5. Vertical distributions are consistent with the existence of discontinuities for almost all common families. Dependence of shelter in flying height on distance from the tree was most marked in weak flyers.

6. It is suggested that the emergent hedgerow tree in the field/hedgerow environment plays a very important part in the life of flying insects.

Chapter 4

DISTRIBUTION OF SOME SPECIES OF SCATOPOSIDAE (DIPTERA) AND THE EFFECT OF MICROCLIMATE ON THEIR FLIGHT PATTERNS

4.1 Introduction

Much of the information on the biology of scatopsids comes from two sources. The first consists of laboratory studies on rearing larvae for classification (Edwards, 1925; Cook, 1956 and Freeman & Lane, 1985) and recordings of food sources for the adults (Dula, 1928; Colyer & Hammond, 1968 and Hutson, 1973). The second (Lewis (1965a, 1967, 1969b and 1970) concerns the effect of artificial and natural windbreaks on the aerial distributions of flying insects using the family of Scatopsidae as one of the indicators. The present Chapter is concerned with the temporal and spatial distribution of common species of Scatopsidae and the effect of microclimate on their flight activity in relation to an emergent hedgerow tree (Tilia sp.).

Taylor hypothesised that insect flight activity was largely confined to a region close to the ground, where the insect is able to control its movement relative to the ground; that is where its flight speed exceeds the wind speed. This region he named the 'boundary layer' for the insect (Taylor 1958, 1960). Note that the height of the boundary layer thus defined varies from insect to insect and from time to time, as it will depend on the overall wind speed clear of the ground, and the powers of flight of the insect species concerned. To avoid confusion with other uses of the term 'boundary layer' (see Oke 1987; Sutton 1953; and Chapter 1), Taylor's term is referred to in this thesis as the 'insect boundary layer' except where otherwise stated.

The same author then reported the existence of 'discontinuities' in the vertical profiles of insect distribution, at heights at which insect flight speed in general matches the local wind speed (Taylor 1974). This was interpreted as support for the insect boundary layer hypothesis. Such discontinuities in vertical profiles of flying insects have also been obtained by Lewis (1967) and Duelli (1980).

However, Snow (1979, 1982) was unable to confirm that observed discontinuities in vertical profiles did match the boundary layer interface.

This chapter analyses observations on the vertical distribution of several common species of scatopsids and microclimatic information determined at the same time, with the object of exploring the boundary layer concept. Another purpose is to understand how important the physical and biological effects are in determining the distribution of the scatopsids within their boundary layer, if such a layer exists.

4.2 Materials and methods

The trapping site, arrangement of the equipment, trapping programme and sampling methods have been all described in Chapters 3 in detail. The Scatopsidae from each trap were separated and stored in 75% ethanol. They were sorted into species following the key provided by Freeman & Lane (1985). During the observation period, the species composition of the family was also investigated by visual search, beating trays and hand nets.

4.2.1 Meteorological data

The wind force, temperature, light intensity and relative humidity were automatically recorded once every twenty minutes at each suction trap position by a YETI micro-meteorological system (see General Methods of Chapter 2 for detail). Six outstations were used, one paired with each suction trap, being at the same level and one metre away (fig. 4.1). The wind direction was visually recorded four times daily from a windvane fixed on a 10m scaffolding pole in the open meadow. Rainfall was also measured four times daily using a standard rain gauge. The changes of the weather within each run were also logged in detail.

4.2.2 Data Treatment

4.2.2.1 Temporal and spatial distributions

Since both sexes of each main species were almost equally distributed and similar in their body size, except for Rhegmoclema sp. which were all females, it was not considered necessary to analyse them separately.

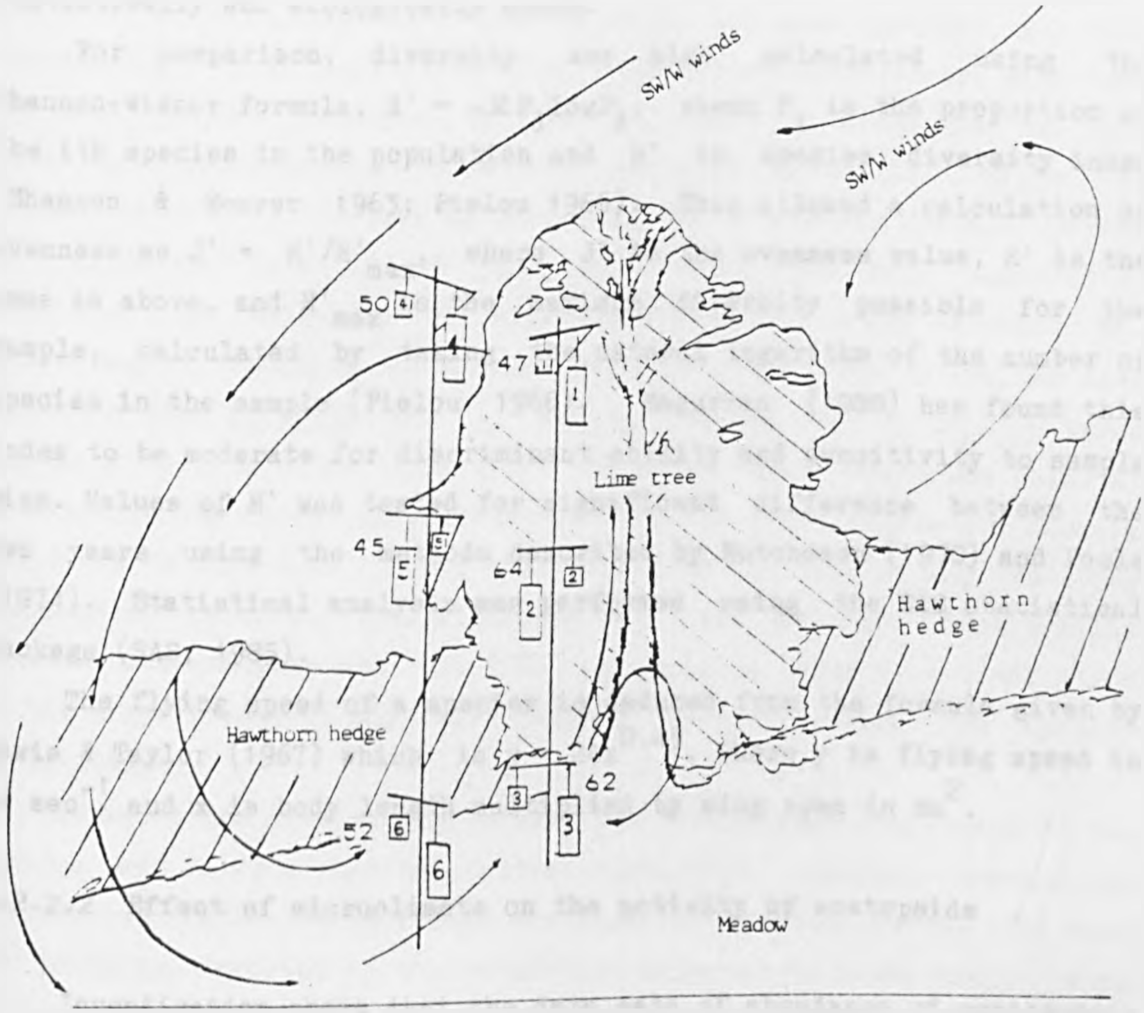

Figure. 4.1. Position of suction traps (▯) and minimets (□) in relation to the lime tree and a hedgerow. Numbers in squares and rectangles represent the number of micro-meteorological outstations and of suction traps respectively. ——→ wind direction. The number adjacent to each trap is the wind eddy value (R).

The diversity of species was calculated using the log series model (Fisher et al. 1943); $S = \alpha \ln(1 + N/\alpha)$, S = the total number of species, N = the total number of individuals, and α = the log series index. Taylor (1978) found this index to have good discriminant ability and not to be unduly influenced by the sample size. Magurran (1988) states that this index appears to combine quite satisfactorily the advantages of being simple to calculate, easy to interpret and statistically and ecologically sound.

For comparison, diversity was also calculated using the Shannon-Wiener formula, $H' = -\Sigma P_i \log P_i$, where P_i is the proportion of the ith species in the population and H' is species diversity index (Shannon & Weaver 1963; Pielou 1966). This allowed a calculation of evenness as $J' = H'/H'_{max}$, where J' is the evenness value, H' is the same as above, and H'_{max} is the maximum diversity possible for the sample, calculated by taking the natural logarithm of the number of species in the sample (Pielou 1966). Magurran (1988) has found this index to be moderate for discriminant ability and sensitivity to sample size. Values of H' was tested for significant difference between the two years using the methods described by Hutcheson (1970) and Poole (1974). Statistical analysis was performed using the SAS statistical package (SAS, 1985).

The flying speed of a species is deduced from the formula given by Lewis & Taylor (1967) which is $y = 24x^{0.45}$, where y is flying speed in cm sec^{-1} and x is body length multiplied by wing span in mm^2.

4.2.2.2 Effect of microclimate on the activity of scatopsids

Investigation shows that the data sets of abundance of scatopsids, which were selected from their most active period (the afternoon), tend to be distributed non-normally whereas they become almost normal after transformation to base 10 logarithms. No transformation was used on the microclimatic data. The units used in this chapter are degree Celsius for temperature, lux for light intensity, revolutions/minute for wind speed, percentage for relative humidity and mm for rainfall.

The use of the compass measure of degrees for wind direction in correlation with abundances is justified principally by the incidence of two main wind directions (NE and SW) so the values correspond to traps exposed or in the lee of the tree respectively.

The relative variability or gustiness of the wind (R) was calculated by the ratio of the standard deviation of average wind speed to the mean wind speed expressed as a percentage (this method is similar to that of Lewis (1966a)), and the average value at each outstation throughout the observation period is shown beside each trap in fig 4.1.

The data was analysed in two ways; firstly by selecting the trap and time of day producing highest catches of each species, and then correlating these logarithmically transformed abundances with the physical factors measured by the adjacent outstation and manually determined measurements of rainfall and wind direction. Since the largest catches by far were in trap 5 in the afternoons for all species with sufficient data it is this data which has been analysed to determine the influence of microclimate on day to day catches. The second way of analysing the effects of microclimate was to include data from five (for R. cooki and A. soluta) or six (for S. notata) traps deemed to be within the space where the mean wind speed was below or similar to the flight speed determined by the above regression formula and shown on fig. 4.4. Again only data from the time of day producing the highest catches, viz. afternoon data, was analysed. Similarities between this analysis and the first one will be taken as an indication of the significance of physical factors in influencing the spatial distribution.

Correlations were sought between the transformed abundances of the species and various physical factors including average, maximum and minimum temperature, wind forces and light intensities during the time of trapping, recorded by the outstation adjacent to each trap. Wind direction and rainfall values recorded manually were assumed to apply similarly to all traps. In addition correlations were sought with the average temperature, rainfall, wind speed and wind direction for the previous trapping period since it was thought that the conditions immediately before might predispose an insect to flight or otherwise. The maximum and minimum temperature for the day of 24 hours were also included in the analysis and the variablity of the wind, expressed as the standard deviation of the readings during the trapping period. The abbreviations for these physical variables and their detail are given in the Summary of Notation.

Statistical analysis was performed using the SAS Statistical

Packages (SAS 1985); the procedure "CORR" was used to calculate Pearson correlation coefficients between the transformed abundances and all of the above physical factors. Multiple regression analysis using the STEPWISE procedures (SAS, 1985 and Dreper & Smith, 1981) for one-trap data analysis was used to examine the data, as was the technique of partial regression improvement and of polynomial curve fitting. Multiple regression analysis was also done. The procedure "GLM" was used, with the selection of CLASSES for multiple-trap data analysis. This allowed creation of a dummy variable to determine the importance of the trap positions within the 'slow air' area as distinct from the local meteorological conditions factored out first.

4.3 Results

During the periods of observation the wind came mostly from the southwest or west. On only 3 out of 52 collection runs in 1986 and 9 out of 40 in 1987 did it come from different directions, viz. NE, E and NW, and the catches were smaller.

4.3.1 Distribution by year

The total catch for each species of scatopsid in the two years is summarised in table 4.1. A total of 33959 scatopsids were caught, 18941 in 318 samples in 1986 and 15018 in 246 samples in 1987. Ten species were represented each year (fig. 4.2). They were classified into three groups based on the proportion of each species to the total catch (table 4.1), ie. a common group of more than 25% (Rhegmoclema cooki Hutson and Anapausis soluta Loew), a less common group of between 0.5% and 5% (Rhegmoclema coxedix Verrall, Rhegmoclema sp. (which is an unidentified species) and Scatopse notata Linnaeus), and a rare group of species, each averaging less than 0.5 % (Swammerdamella brevicornis Meigen, S. acuta Cook, Coboldia fuscipes Meigen, Cookella albitarsis Zett. and Ectaetia clavipes Leow). From the figures over the bars of 1987 (fig. 4.2), it can be seen that although some species within each group were more abundant than in 1986 or vice versa, their abundances, generally, did not vary dramatically except for R. coxedix and S. notata in which the former decreased by 5 times and the latter increased by 4.7 times in 1987. The rank orders of species in two years

Table 4.1. Total numbers caught for each species in two years. Proportion of each species to the total is used to classify the abundance of each species. n = 564 in two years.

Species	Total	Proportion of total (%)	Class
R. cooki	22755	67.01	common
A. soluta	9013	26.53	common
R. coxedix	1319	3.88	less common
S. notata	368	1.08	less common
R. sp.	286	0.84	less common
S. brevicornis	143	0.42	rare
C. albitarsis	29	0.09	rare
S. acuta	28	0.08	rare
C. fuscipes	15	0.04	rare
E. clavipes	3	0.01	rare

were similar, the only change being the elevation of S. notata (fig. 4.2). There was no significant differences of diversity index (H') between the two years. Log series and species evenness of scatopsid community were very similar in the two years (table 4.2).

Table 4.2. Species richness, diversity and evenness of Scatopsidae. n = 318 in 1986 and n = 246 in 1987. S = number of species.

Year	Richness (S)	Total individuals	Log series (α)	Diversity (H')	Evenness (J')
1986	10	18941	1.017	0.848	0.368
1987	10	15018	1.045	0.856	0.372

4.3.2 Temporal distributions

The number of individuals of each species caught over the four daily trapping periods (for detail see Chapter 3) is shown in table 4.3. Common and less common species are also summarized in fig. 4.3.

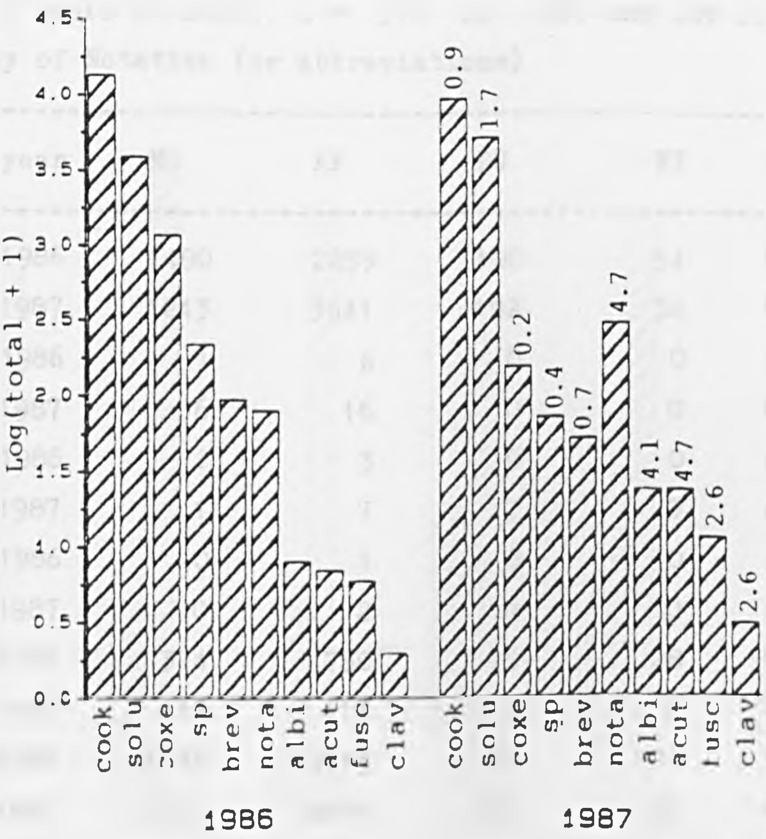

Fig. 4.2. Total catch each year in all traps. cook = *Rhegmoclema cooki*, coxe = *R. coxendix*, sp = *R. sp.*,solu = *Anapausis soluta*, brev = *Swammerdamella brevicornis*, nota = *Scatopse notata*, albi = *Cookella albitarsis*, acut = *Swammerdamella acuta*, fusc = *Coboldia fuscipes* and clav = *Ectaetia clavipes*. The ratio of the 1987 catch to the 1986 catch for each species is shown by the numbers over the bars for 1987.

Table 4.3. Total numbers of scatopsid species trapped at different times of day. Significance of departure from uniform numbers caught per hour in the different periods determined by Friedman two way analysis by ranks: *** $p < 0.001$, ** $p < 0.01$, * $p < 0.05$. NS: not significant, -- indicates that the numbers are too few to be analysed. The trapping periods were 6.6 hours in the morning, 6.0 hours in the afternoon, 3.3 hours at dusk and 6.6 hours at night. n = 318 in 1986 and 246 in 1987. (See Summary of Notation for abbreviations)

Species	year	MO	AF	DU	NI	sig.
A. solu.	1986	1490	2255	100	54	***
	1987	1243	3641	192	38	***
C. albi.	1986	1	6	0	0	--
	1987	6	16	0	0	*
C. fusc.	1986	2	3	0	0	--
	1987	1	7	2	0	--
E. clav.	1986	0	1	0	0	--
	1987	0	2	0	0	--
R. coxe.	1986	374	750	15	28	***
	1987	32	114	4	2	**
R. cook.	1986	4555	8713	79	121	***
	1987	2252	6873	130	32	***
R. sp.	1986	57	143	8	8	**
	1987	6	63	0	1	*
S. acut.	1986	3	3	0	0	--
	1987	11	11	0	0	*
S. brev.	1986	11	80	1	1	**
	1987	4	45	1	0	*
S. nota.	1986	40	31	5	3	*
	1987	106	164	17	2	**

Both undoubtedly indicate that all species of scatopsids were day flyers. During daylight, almost all species were much more active in afternoons than in mornings except for S. acuta (in both years) and S. notata (in 1986) which did not show any significant difference in their

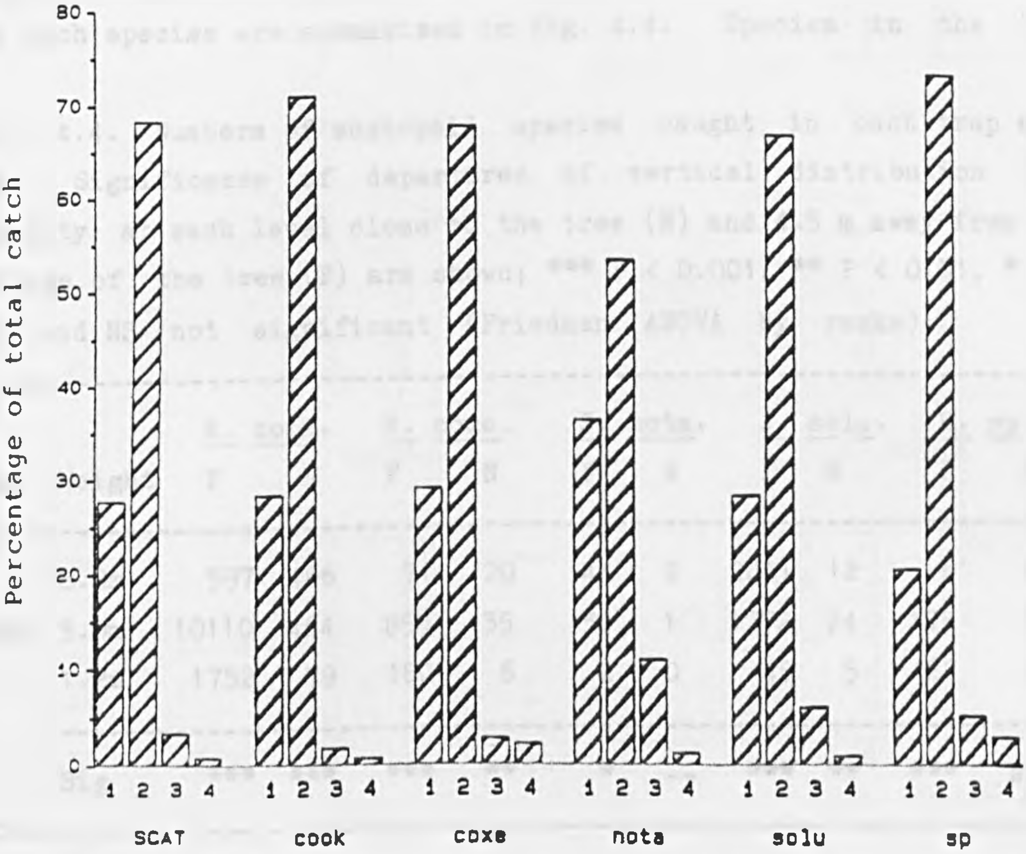

Fig. 4.3. Trapping period distribution patterns of common and less common species through the day compared with the diel pattern of the whole family (SCAT), pooling the results for 1986 and 1987. 1 = morning, 2 = afternoon, 3 = dusk and 4 = night.

abundance between morning and afternoon. The five most important species shared the same diel pattern (afternoon > morning > dusk > night), which also represents the pattern for the whole family (fig. 4.3).

4.3.3 Spatial distributions

Total catches of each "common" or "less common" species in each trap for both years are given in table 4.4. The distribution patterns for each species are summarized in fig. 4.4. Species in the "rare" group were too few in numbers to be analysed spatially. Some general points were drawn from these:

Table 4.4. Numbers of scatopsid species caught in each trap each year. Significance of departures of vertical distribution from equality at each level close to the tree (N) and 4.5 m away from the foliage of the tree (F) are shown; *** P < 0.001, ** P < 0.01, * P < 0.05 and NS not significant (Friedman ANOVA by ranks).

		R. cook.		R. coxe.		S. nota.		A. solu.		R. sp.	
Year	Height	F	N	F	N	F	N	F	N	F	N
	8.8m	597	466	71	20	44	2	2041	12	6	4
1986	5.0m	10110	464	855	35	30	1	1772	24	175	8
	1.2m	1752	79	180	6	2	0	45	5	22	1
	Sig	***	***	***	**	*	--	***	**	***	NS
	8.8m	1487	1999	28	35	111	19	1366	37	12	15
1987	5.0m	3171	1661	38	21	140	6	3527	46	29	7
	1.2m	790	179	8	4	12	1	108	30	3	4
	Sig	***	***	*	*	**	*	***	*	*	*

1) All species were very highly concentrated in the vertical profile away from the tree except for *R. coxedix* which showed nearly equal distribution in 1987 (table 4.4);

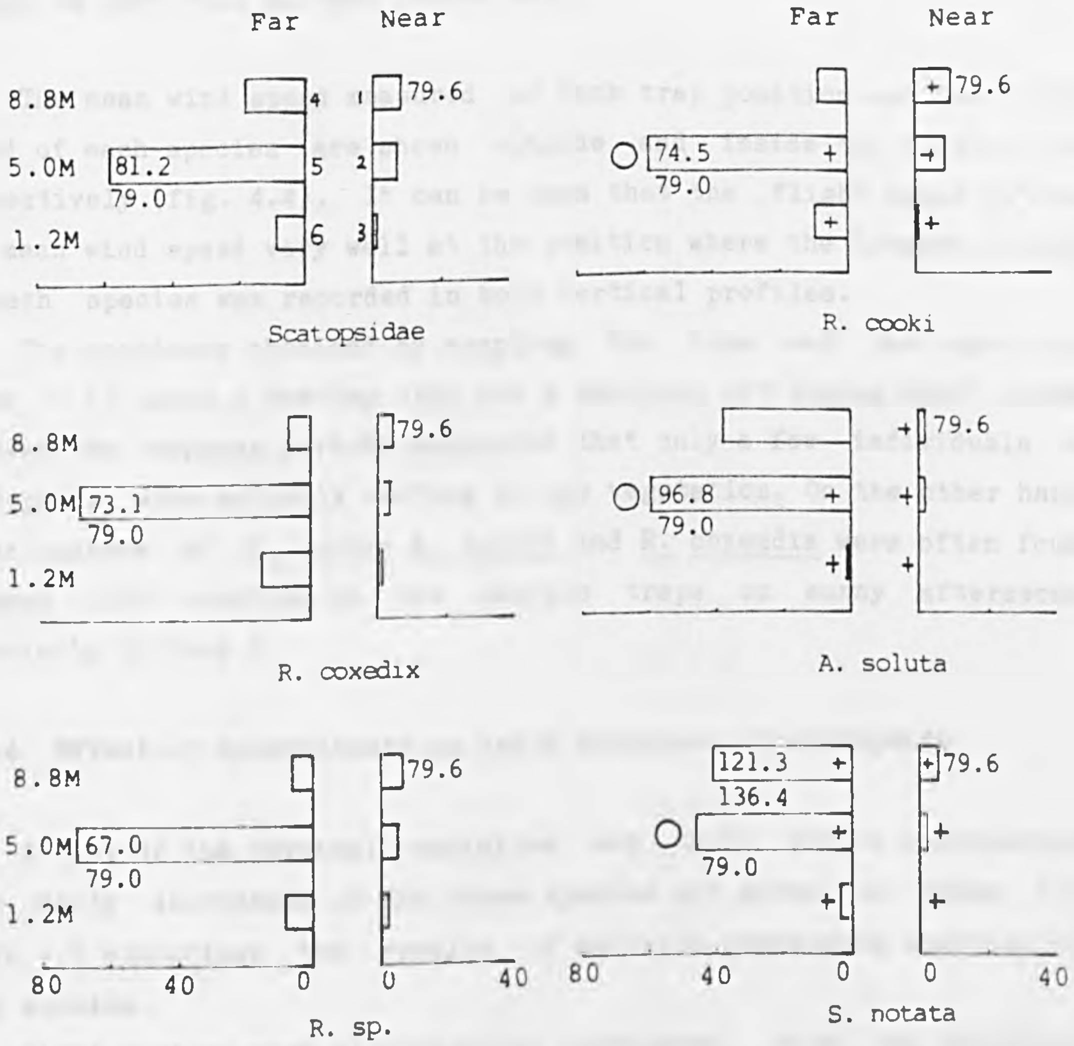

Fig. 4.4. Spatial distribution patterns of commoner species of scatopsids compared with the spatial pattern of the family. The data for 1986 and 1987 have been pooled. The numbers along abscissa are the percentage of the total catch of the species in each trap. 'Near' means the profile near the tree and 'Far' indicates the profile further away from the tree. Numbers in rectangles are flight speed for each species and those outside of them are wind speeds at each position (both in cm/sec.). Numbers along vertical axes of Scatopsidae indicates the trap number related to fig. 4.1. Rectangles with + inside or near them indicate those trap positions to be within 'slow air' area, and with ○ means that trap data is used for daily abundance analysis.

2) the height producing the largest catches was the 5 m level, except for A. soluta and S. notata, which were more common at 8.8m in 1986;
3) the numbers of each species was more evenly distributed among the traps in 1987 than in 1986 (table 4.4);

The mean wind speed measured at each trap position and the flight speed of each species are shown outside and inside the highest bars respectively (fig. 4.4). It can be seen that the flight speed matched the mean wind speed very well at the position where the largest catches of each species was recorded in both vertical profiles.

The specimens obtained by sampling the tree and the vegetation close to it using a beating tray and a sweeping net during short breaks between the trapping periods suggested that only a few individuals of scatopsids were actually resting on the vegetation. On the other hand, large numbers of R. cooki, A. soluta and R. coxendix were often found crammed into crevices in the suction traps on sunny afternoons, especially in trap 5.

4.3.4 Effect of microclimate on daily abundance of scatopsids

A list of the physical variables and their simple correlations with daily abundances of the three species are given in table 4.5. Table 4.6 summarises the results of multiple regression analyses for each species.

Eight factors were significantly correlated with the abundances of R. cooki (table 4.5), the relative humidity negatively and rest positively. These eight variables were all strongly correlated with each other (fig 4.5); periods with a high average temperature had high maxima and minima, and were typically bright sunny days with low relative humidity. Therefore the variables cannot be regarded as independent and whilst they were combined in multiple regression models to produce quite accurate fits to abundance data, these models were sensitive to the order in which factors were entered and hence cannot be regarded as more than descriptive. The best fit model is given in table 4.6, and shows abundance of R. cooki increasing with temperature but depressed slightly by high wind, and declining overall during the

Table 4.5. Physical variables and their correlation coefficients with daily abundance of species. Numbers in the table are Pearson correlation coefficients, *** P < 0.001; ** P < 0.01; * P < 0.05. N = 10 in each case. (see Summary of Notation for abbreviations)

Variable	_R. cooki_	_A. soluta_	_S. notata_
Av-temp.	0.912 ***	0.785 **	0.607 *
Min-temp.	0.643 *	0.515	0.350
Max-temp.	0.826 **	0.687 *	0.467
Max-day-temp.	0.399	0.064	-0.196
Min-day-temp.	0.060	-0.356	-0.454
Prec-temp.	0.133	-0.095	-0.276
Av-light	0.826 **	0.886 ***	0.845 **
Min-light	0.688 *	0.657 *	0.658 *
Max-light	0.840 **	0.822 **	0.701 *
Av-wind	-0.477	-0.559	-0.472
Min-wind	-0.416	-0.420	-0.309
Max-wind	-0.422	-0.568	-0.517
Std-wind	-0.294	-0.535	-0.532
Prec-wind	-0.346	-0.346	-0.186
Win-dire.	0.513	0.493	0.299
Pre-win-dire.	-0.270	-0.321	-0.376
Rain	0.167	0.029	-0.131
Prec-rain	-0.447	-0.540	-0.333
Av-RH	-0.687 *	-0.811 **	-0.814 **
Min-RH	-0.711 *	-0.788 **	-0.668 *
Max-RH	-0.425	-0.534	-0.629 *
Time	0.138	0.079	-0.170

observation period. The relationships are illustrated diagrammatically in fig 4.5.

A. soluta abundances were significantly correlated with seven physical variables, all correlated with each other. The strongest correlation was with average light intensity (table 4.5), and this was the only significant variable in the best fit regression model (table

4.6, fig. 4.5).

Table 4.6. Regressions of daily activity of scatopsid species with the independent variables listed in table 4.5. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$. Partial explained variance (PR) and standard partial regression coefficients (SPRC) are shown for each species.

Species	Variable	SPRC	F	p	PR(%)
R. cooki	intercept	1028.995			
	Average temp.	0.306	24.26	**	77.61
	Time	-0.120×10^{-5}	23.83	**	17.89
	Maximum wind	-0.005	23.06	**	3.70
A. soluta	intercept	-0.946			
	Average light	3.220×10^{-4}	26.95	**	79.4
S. notata	intercept	-6.372			
	Average light	4.794×10^{-4}	14.95	***	68.11
	Minimum RH	-0.039	9.88	*	19.84

Abundances of *S. notata*, were best correlated with light intensity, and secondarily negatively with the relative humidity (table 4.5). These factors provided the best fit regression model (table 4.6, fig. 4.5), but again almost as good a fit were obtained with other combinations including temperature. Therefore the conclusion is that *S. notata* prefers warm bright conditions with lower relative humidity.

4.3.5 Response within the 'slow air' area

The large analysis included five or six traps (see fig. 4.4) since the average wind speeds recorded in the vicinity of these were deemed to be within the 'slow air' area for these insects (see also fig 4.4). The simple correlations of abundances with the physical variables are given in table 4.7. In the analysis for *R. cooki* the same correlations are present as in the previous analysis but at lower values. The large data set reinforces statistical significances and allows a correlation with wind direction, and negative correlations with minimum wind and

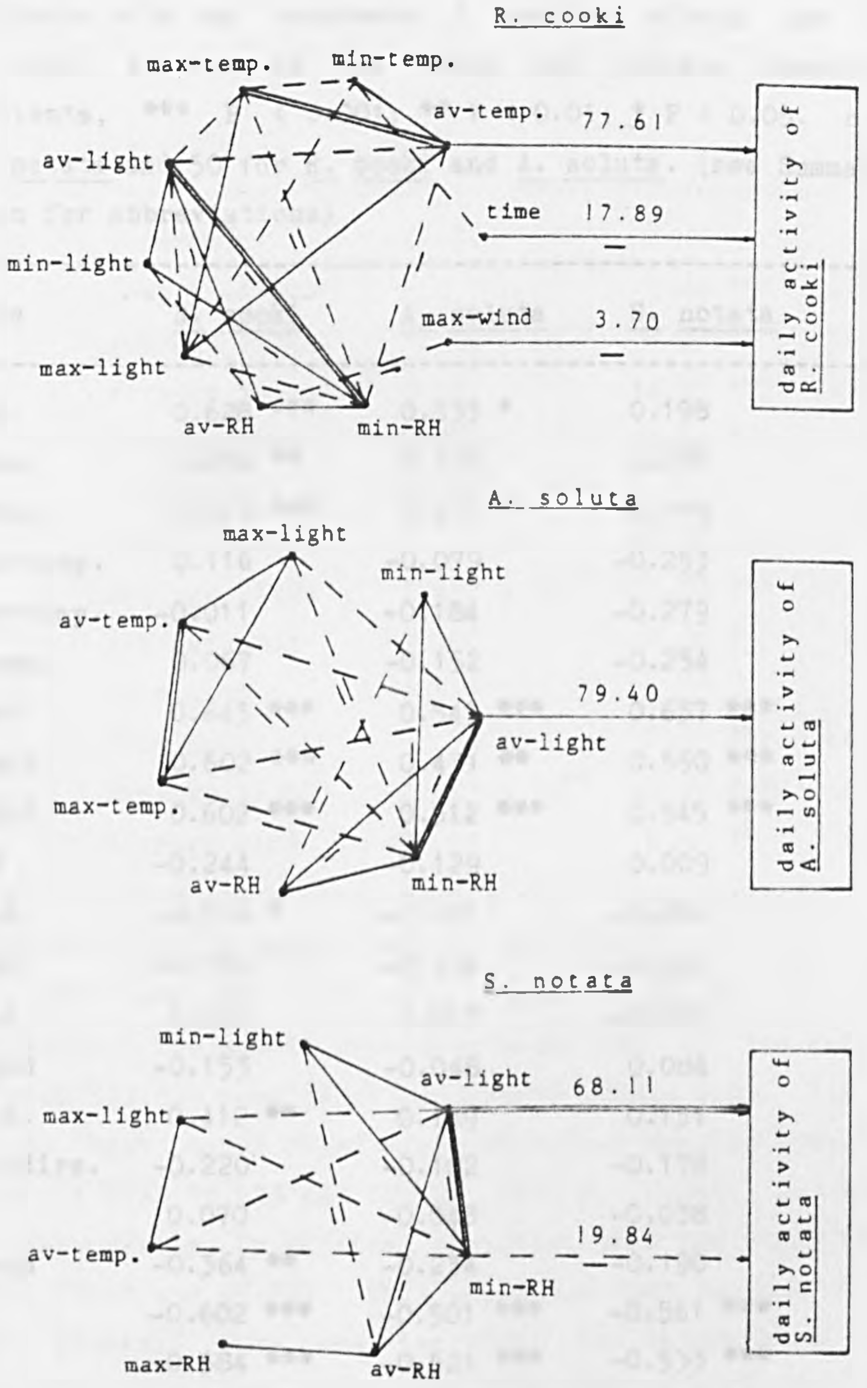

Fig. 4.5. The inter-correlations among the microclimatic factors, which were significantly related to the abundance of the species, and their influences on insect daily activities. ══⇒ indicates significance at $P < 0.001$, ——— at $P < 0.01$, – – – – at $P < 0.05$. Minus signs with the correlation lines indicate that the two variables are negatively related to each other. The number represents the partial explained variance in percentage by the physical factor adjacent to it.

rain in the preceding period to reach statistical significance. Again

Table 4.7. Physical variables and their correlation coefficients with the abundance of species within the 'slow air' area. Numbers in the table are Pearson correlation coefficients, *** P < 0.001; ** P < 0.01; * P < 0.05. n = 60 for S. notata and 50 for R. cooki and A. soluta. (see Summary of Notation for abbreviations)

Variable	R. cooki	A. soluta	S. notata
Av-temp.	0.628 ***	0.333 *	0.198
Min-temp.	0.432 **	0.176	0.035
Max-temp.	0.513 ***	0.273 *	0.149
Max-day-temp.	0.116	-0.079	-0.253
Min-day-temp.	-0.011	-0.184	-0.279
Prec-temp.	0.067	-0.152	-0.254
Av-light	0.643 ***	0.545 ***	0.637 ***
Min-light	0.602 ***	0.431 **	0.550 ***
Max-light	0.602 ***	0.512 ***	0.545 ***
Av-wind	-0.244	-0.129	0.009
Min-wind	-0.316 *	-0.181	-0.002
Max-wind	-0.191	-0.114	-0.006
Std-wind	0.042	0.017	-0.003
Prec-wind	-0.153	-0.048	0.084
Win-dire.	0.412 **	0.149	0.131
Pre-win-dire.	-0.220	-0.182	-0.178
Rain	0.070	-0.043	-0.038
Prec-rain	-0.364 **	-0.234	-0.190
Av-RH	-0.602 ***	-0.501 ***	-0.561 ***
Min-RH	-0.584 ***	-0.521 ***	-0.533 ***
Max-RH	-0.381 **	-0.340 **	-0.414 **
Time	0.100	-0.073	-0.094

a range of models provided adequate fits to the data, the best includes light intensity, temperature and wind (table 4.8).

Table 4.8. Multiple regression analysis of scatopsid species with the physical variables listed in table 4.7 within the 'slow air' area using GLM procedure of SAS. * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Species	Variable	SPRC	F	PR(%)
R. cooki	intercept	-2.151		
	Trap position		7.28 ***	21.48
	Average light	1.306×10^{-4}	8.67 **	34.75
	Average temp.	0.137	13.85 ***	12.28
	Average wind	-0.007	6.54 *	4.24
A. soluta	intercept	-0.537		
	Trap position		23.36 ***	61.85
	Average light	1.453×10^{-4}	21.73 ***	12.91
	Average wind	-0.006	6.28 *	3.22
S. notata	intercept	-0.502		
	Trap position		6.81 ***	44.00
	Average light	8.003×10^{-4}	20.18 ***	15.80
	Average wind	-0.003	6.44 **	4.40

Likewise all the major correlations with the other two species are reduced in magnitude, and with minor changes in statistical significances. The models providing best fit to the data show small differences but the same major components (table 4.8). In all these cases the best model found explains a much smaller proportion of the variance (51.27%, 16.13% and 20.2% for R. cooki, A. soluta and S. notata respectively) by physical variables than the study based on trap 5 (99.2%, 79.4% and 87.5%). This indicates that factors other than the measured physical ones are important in determining the spatial distribution; the insects are not just seeking high light intensities or low wind speed. This is seen in the part of the variance explained by the different trap positions, viz. 21.4%, 61.85% and 44.00% for R. cooki, A. soluta and S. notata respectively. This is presumably because the insects tend to occur at certain positions, especially at trap 5 for R. cooki and A. soluta and at traps 5 and 4 for S. notata (fig 4.4).

4.4 Discussion

Although some species were a little more abundant in one year than the other, the community stucture of scatopsids was relatively stable between the two years (fig. 4.3, table 4.2). As the observations were carried out at similar times in the two years, this stability may be related to similar food availability, to similar conditions at breeding sites and to similar relationships between scatopsids and the other organisms, such as predators and parasites, in the two years.

The diel patterns of common and less common species all share the same pattern (afternoon > morning > dusk > night) in the two years (table 4.3 and fig. 4.3), and emphasize that they are most likely to be active on during afternoons, which confirms the description given by Colyer & Hammond (1968) for A. soluta and by Hutson (1973) for R. cocki and R. coxedix. Lewis & Taylor (1964) reported similar results for this family. This pattern also coincides with the diel patterns of light intensity and temperature, in agreement with the generalisation that the flight activity of scatopsids is enhanced by brighter light with higher temperature.

By examining the two vertical profiles for each species and for the family, discontinuities are clearly defined at 5m high in the profile away from the tree, and up to 8.8m for A. notata (fig. 4.4). For the profile close to the tree, the discontinuities seem to be around 8.8m or higher. The flight speed of each species and of the family matched the wind speed at the discontinuities very well. This result appears to agree with Taylor's hypothesis of the 'insect boundary layer' (Taylor 1958, 1960, 1974), and thus the 'slow air' area can be regarded as the same as the 'insect boundary layer'. In short, the scatopsids do seem to concentrate their flight within this layer. However the vertical profiles obtained consisted only of three points and the flight speed of the species are deduced from the existing regression formula, therefore further work is needed before reaching a firm conclusion.

Many fewer scatopsids were caught close to the tree than further away, and this is true of each species with sufficient numbers to test statistically, indicating an actual avoidance of the environs of the tree. This agrees with the very small numbers found on the foliage.

Scatopsids have been reported to breed in dung and decaying organic matter and to take food in the form of nectar or sugar-water (Edwards 1925; Freeman & Lane 1985), and possibly to seek honeydew (Hutson 1973). The lime tree was in flower and heavily infested by aphids at the time, but was not obviously attractive to the scatopsids. It seems likely that the insects caught probably had flown from some distance with the help of the wind and accumulated at around 5m for most species, but up to 8.8m or more for A. soluta and S. notata. Since for most of the time the wind was south-west to west the traps were in the lee of the tree, and it may be hypothesised that the scatopsids were collecting in the wind eddy to be expected there. This would explain why the considerable proportion of the variability for common scatopsid species are explained by the trap position (table 4.8).

The presence of the wind eddy can be expressed by R values shown in fig. 4.1. They are larger at traps 2, 3 and 6 than at 1, 4 and 5. The value at trap 5 is the smallest of all. The bigger the R is, the more gusty the wind is at that position. As the traps 2, 3 and 6 were heavily sheltered from SW or W winds, the big values at these traps indicate that the wind probably came from the opposite direction rather than from SW or W directions directly. Therefore air movement behind the tree may be hypothesised to be as indicated by the arrows shown in fig. 4.1, resulting in wind circulation. Hence scatopsids could be circulated in the eddy and the large numbers caught in trap 5 would be because of its position closer to the centre of the eddy.

This would be enhanced if scatopsids carried by circulating air actively sought areas of high light intensity, as indicated in their flight activity in relation to light intensity (table 4.5 - 4.8). From mid-day for a few hours the outer traps would be in the sun, while those close to the tree would be in shaddow, so scatopsids carried close to the tree by the eddy would be flying towards the outer traps possibly because of attraction by the shininess of the metal, which was used to make the suction traps, so into the centre of the eddy.

The only significant correlation with wind direction is in the multiple-trap data set (table 4.7) for the most abundant small body-sized species, R. cooki. This evidently shows the importance of shelter for this species. There is no such significant correlation for the large bodied A. soluta and S. notata. It could well be that big body-sized species have a stronger ability to control their flight track than do small body-sized ones and hence show similar activity between sheltered and exposed conditions, which indicates that Lewis & Taylor's regression of flying speed on the body size is an applicable method to use here (Lewis & Taylor 1967). This result is in agreement with the results of Lewis (1967) that for strong flyers vertical profiles in sheltered and exposed positions were indistinguishable.

The difference between the spatial distributions in 1986 and 1987 has been noted and is best described as more even in 1987 than in 1986 (table 4.4). This discrepancy could have been caused by the different structure of scaffolding towers used in the two years. In 1986, the scaffolding tower had four wooden platforms evenly distributed in the middle of the tower (fig. 3.1). These platforms may have changed the pattern of air movement appreciably and reduced the effect of wind eddy. In 1987 two simpler scaffoldings were used (fig. 4.1). The wind circulation is likely to be less affected by them and the wind eddy was probably more marked. Hence it could be that small body-sized *R. cooki*, *R. coxedix* and *R. sp* were more affected by the disturbed patterns of airflow in 1986, and that 1987 is the more natural distribution. The big body-sized *S. notata* and *A. soluta* would also be affected in the same way although they are probably more able to control their flight track, and hence less affected.

As a preliminary approach to assessing the importance of the physical effects on common species of adult scatopsids, the evidence obtained in this work clearly shows that the day-to-day abundances are highest when there are strong light intensities with relatively high temperatures and low relative humidities. Their distributions within their boundary layers seem to be largely determined by factors other than these, and it is suggested that wind eddy may be important. The unexplained variance (20% to 35%) for the distribution in the boundary layer (table 4.8) may due to unknown biological attractiveness, such as, swarming and mating, olfactory and visual stimuli (eg. attraction to shiny objects) and slight behaviour difference of individuals of each species.

4.5 Summary

1. Temporal and spatial distribution patterns of common species of Scatopsidae and the effect of microclimate on the activity of these insects have been studied using six suction traps and six computer-linked micrometeorological stations hung at three heights vertically and two distances from an emergent hedgerow tree (*Tilia sp.*). All Scatopsidae were identified to species.

2. Although some species were a little more abundant in one year than the other, the patterns of spatial and temporal abundance were basically the same, and the species diversity between two years was stable.

3. There was a marked concentration at 5 m height 4.5 m away from the tree for all common species of scatopsids.

4. Almost all species showed more flight activity in the afternoons than at other times.

5. Mean flight speed of the common species matched mean wind speed very well at discontinuities in vertical profiles, which agrees with Taylor's concept of an "insect boundary layer".

6. Three species, *R. cooki*, *A. soluta* and *S. notata*, all showed very similar response to the light intensity, temperature and relative humidity in their daily activities.

7. The distributions of common species within their boundary layers are more likely to be determined by wind eddy and some other unknown biological attractiveness rather than the physical factors concerned.

Chapter 5

THE EFFECT OF MICROCLIMATE ON FLYING DIPTERA

5.1 Introduction

In chapter 4 of this thesis, scatopsid species were shown to increase in abundance with height to a maximum, and then decrease above this, forming a discontinuity of slope. There is close similarity between the mean wind speed at this discontinuity and the estimated flight speed for the species in agreement with Taylor's "insect boundary layer" hypothesis. Discontinuities in the vertical profiles have also been obtained for 13 other common families of flying Diptera (Chapter 3).

Although insect species behave very differently, in general it is to be expected that biological stimuli, such as food and mates, would be important to them since they can more or less control their track within their boundary layers (Taylor 1958, 1960). Above the boundary layer they are dominated by physical factors related to height, (Johnson 1957; Taylor 1974). So far, the behaviour of flying insects within the boundary layer is not well known except for the results reported in Chapter 4, where it is concluded that the spatial distributions of several species of scatopsids within their boundary layers are not determined by the physical factors measured, but probably by the wind eddy and possibly by some other unknown biological attraction.

The most important climatic factors to small terrestrial animals are thought to be the temperature and moisture content of the air (Willmer, 1982a). Also significant are solar radiation and wind. Insects are considered to be particularly vulnerable to both of these physical variables because of their small size and proportionally large surface area, but this is offset by their mobility, enabling them to escape from harsh ambient conditions into more favourable microniches (Cloudsley-Thompson, 1962). In his review of this field, Johnson (1969) suggested that much flight, being unrelated to recognizable migratory displacements, can be described as 'trivial', that is local in range and very dependent on vagaries of the weather. Johnson developed the 'flight activity' hypothesis which envisages that changes in aerial densities of insects are caused mainly by changes in weather-induced flight as the insects land, fly, and take off again more or less locally. It would be interesting to know whether the daily abundance of flying Diptera is in accord with this hypothesis.

To test these two ideas of the behaviour of insects within the boundary layer and the 'flight activity' hypothesis, a study was carried out in 1987. Insects were caught at different times of day by six suction traps at different heights and distances in relation to an emergent hedgerow tree. The numbers were related to meteorological conditions monitored at the position of each trap. Spatial distribution patterns for 14 families of flying Diptera at the study site are described in Chapter 3. Twelve of them have been chosen for further study according to the availability of adequate numbers. They are classified into three groups, afternoon-flying (Anthomyiidae, Dolichopodidae, Muscidae, Scatopsidae and Sciaridae), dusk-flying (Phoridae, Anisopodidae, Ceratopogonidae and Chironomidae) and night-flying (Cecidomyiidae, Psychodidae and Tipulidae), on the basis of numbers caught at different times of day (table 3.1 Chapter 3). Their spatial distributions are shown in fig. 5.1. There are no morning flying families in this analysis.

5.2 Materials and methods

5.2.1 Arrangement of study equipment

The trapping site was at Bond Ing, about 7 miles NE of Leeds, England. A detailed description of the site has been given in the General Methods (Chapter 2). Two 9.5m high scaffoldings were used to carry suction traps and the micro-meteorological stations. One was installed near the foliage of a 11.5m high lime tree in the SW corner of the meadow and the other one was 4.5m further away from the tree (fig 4.1). Observations were made from the 22nd July to the first of August 1987 inclusive.

5.2.2 Insect trapping

Flying Diptera were caught using six 9-inch diameter enclosed nylon mesh cone suction traps (see General Methods of Chapter 2). They

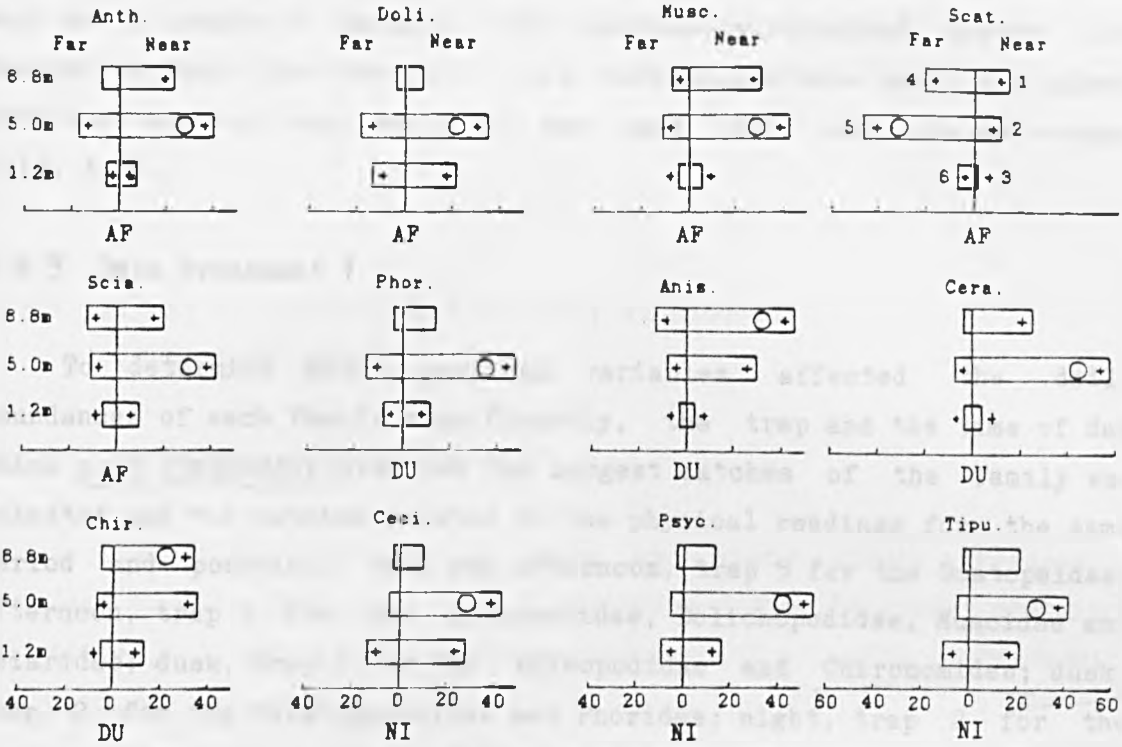

Figure 5.1. Spatial distribution patterns of twelve families. Abscissa values are the percentage of the total catch for each family. The total catch is taken from six traps, 3 in the 'Near' profile, 3 in the 'Far' profile. 'Near' and 'Far' being 0 and 4.5m respectively from the tree canopy edge. AF = afternoon-flying family, DU = dusk-flying family and NI = night-flying family. Numbers close to bars on the figure for Scat. indicate the position of the suction trap as shown in fig 4.1. + indicates traps deemed to be within the insect boundary layer, and ○ indecates the traps selected for daily abundance analysis for the family (see text, P.64).

were suspended from the scaffoldings as in fig. 4.1 (Chapter 4), and identified by numbers; 1, 2 and 3 were close to the tree whilst 4, 5 and 6 were 4.5m further away to the NE. The intake of 1 and 4 were 8.8m above the ground, 2 and 5 were 5m, and 3 and 6 were 1.2m (fig. 4.1).

Meteorological data local to each trap were obtained in the same way as in chapter 4, using a YETI micro-meteorological system (see General Methods for detail). Six outstations were used, one paired with each suction trap, being at the same level and one metre away (fig. 4.1).

5.2.3 Data treatment 1

To determine which physical variables affected the daily abundances of each family significantly, the trap and the time of day which most frequently produced the largest catches of the family was selected and the catches related to the physical readings for the same period and position. This was afternoon, trap 5 for the Scatopsidae; afternoon, trap 2 for the Anthomyiidae, Dolichopodidae, Muscidae and Sciaridae; dusk, trap 1 for the Anisopodidae and Chironomidae; dusk, trap 2 for the Ceratopogonidae and Phoridae; night, trap 2 for the Cecidomyiidae, Psychodidae and Tipulidae (fig. 5.1 and table 3.1).

5.2.4 Data treatment 2

To study the relationship between the response of the insects and the physical factors within their boundary layer, data from three or more traps deemed to be within the "insect boundary layer" sensu Taylor (1958, 1960, 1974) were used (those under or equal to the discontinuities of the vertical profiles), but again only data from the time of day producing the highest catches, viz. afternoon data for afternoon-flying families, dusk data for dusk-flying ones and night data for night-flying ones was analysed (see fig. 5.1 for detail). As the large variation in depth of the boundary layer with size of insects, this is only valid if members of the family are uniform in size. Similarities between this analysis and the former were taken as an indication of the significance of physical factors in affecting the daily abundances and the spatial distribution of each family.

Investigation shows that the data sets of above families, which were selected from the most active period, tend to be distributed non-normally whereas they become almost normal after transformation to base 10 logarithms. No transformation was carried out on any of the microclimatic factors. The units used in this chapter were the same as in chapter 4. The same 22 physical variables used in chapter 4 were considered with the transformed abundances of 12 families. Single and multiple-trap data analyses were performed using the technique as in chapter 4.

5.3 Results

5.3.1 Effect of microclimate on daily abundances (data treatment 1)

5.3.1.1 Afternoon-flying families

A list of the physical variables and their simple correlations with day to day abundances of five afternoon-flying families are given in table 5.1. Table 5.2 summarises the results of multiple regression analysis for each family.

Seven factors were significantly correlated with the daily abundances of Scatopsidae, relative humidity negatively and the rest positively. These seven variables were almost all strongly correlated with each other (fig. 5.2); periods with a high average temperature had high maxima, and were typically bright sunny days with lower relative humidity. Therefore the variables cannot be regarded as independent and whilst they are combined in multiple regression models to produce quite accurate fits to the abundance data, these model are sensitive to the order in which factors were entered, and hence cannot be regarded as more than descriptive. The strongest correlation was with average light intensity and this was the only significant variable in the best fit regression model found by adding regressors (table 5.2), and shows abundances of Scatopsidae increasing with average light intensity. Models have also been found which provide even lower residual variance. Such models include temperature in combination with other factors. Hence the conclusion is that scatopsids prefer bright warm dry weather, which confirms the overall results obtained in Chapter 4. The relationships are illustrated diagrammatically in fig 5.2.

Table 5.1. Physical variables and their correlation coefficients with daily abundance of afternoon-flying Diptera. Numbers in the table are Pearson correlation coefficients, *** means significant at $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. $n = 10$ in each case. (see Summary of Notation for abbreviations).

Variable	Anth.	Doli.	Musc.	Scat.	Scia.
Av-temp.	0.700 *	0.726 *	0.780 **	0.860 **	0.506
Max-temp.	0.659 *	0.557	0.748 *	0.774 **	0.292
Min-temp.	0.446	0.692 *	0.574	0.580	0.402
Max-day-temp.	0.124	0.294	0.161	0.238	-0.314
Min-day-temp.	-0.204	-0.070	0.036	-0.166	-0.517
Prec-temp.	0.130	0.351	0.412	0.027	-0.045
Av-light	0.721 *	0.357	0.543	0.881 ***	0.597
Max-light	0.743 *	0.245	0.541	0.848 **	0.434
Min-light	0.672 *	0.381	0.580	0.685 *	0.663 *
Av-wind	-0.527	-0.785 **	-0.732 *	-0.535	-0.702 *
Max-wind	-0.404	-0.792 **	-0.616	-0.507	-0.767 **
Min-wind	-0.621	-0.700 *	-0.773 **	-0.444	-0.581
Std-wind	0.104	-0.429	0.053	-0.414	-0.519
Prec-wind	-0.378	-0.564	-0.609	-0.367	-0.278
Win-dire.	0.482	0.757 **	0.550	0.523	0.551
Pre-win-dire.	-0.287	0.071	0.048	-0.290	-0.095
Rain	0.195	-0.128	0.314	0.125	-0.268
Prec-rain	-0.590	-0.361	-0.591	-0.506	-0.430
Av-RH	-0.768 **	-0.453	-0.559	-0.771 **	-0.837 **
Max-RH	-0.473	-0.317	-0.266	-0.486	-0.701 *
Min-RH	-0.740 *	-0.335	-0.543	-0.779 **	-0.588
Time	0.118	0.719 *	0.311	0.107	0.222

Abundances of Anthomyiidae and Dolichopodidae were also significantly correlated with seven environmental factors (table 5.1). These seven variables can be roughly separated into two groups in terms of their intercorrelations (fig 5.3), viz. a group of relative humidity with light and a group of temperature for the anthomyiids, and a wind group and a temperature group for the dolichopodids. As no direct correlations occurred between the groups, each group of physical factors may be regarded as independent as far as they affect the daily abundances of these families. Again the variables from each group were combined in several ways to form multiple regression models with quite good fits to the abundance data. The best for each family is given in table 5.2, and suggest day to day abundances of the anthomyiids decreasing with high relative humidity and increasing with temperature, dolichopodid abundances increasing with temperature but depressed by

Table 5.2. Regressions of daily abundance of afternoon-flying Diptera with the independent variables listed in table 5.1. * means significant at $P < 0.05$; ** at $P < 0.01$; *** at $P < 0.001$. Partial explained variance (PR) and standard partial regression coefficients (SPRC) are shown for each family. The probability (P) shown is for the null hypothesis that the parameter = 0.

Family	Variable	SPRC	P	PR (%)
Anthomyiidae	intercept	1.549		
	Average RH	-0.018	*	55.84
	Average temp.	0.068	*	22.59
Dolichopodidae	intercept	-0.476		
	Maximum wind	-0.007	**	62.76
	Average temp.	0.113	*	20.22
Muscidae	intercept	-0.115		
	Average temp.	0.051	**	60.88
	Minimum wind	-0.004	*	16.42
	Minimum light	1.029×10^{-4}	*	13.05
Scatopsidae	intercept	-0.472		
	Average light	3.057×10^{-4}	**	78.22
Sciaridae	intercept	4.374		
	Average RH	-0.026	**	66.24
	Maximum wind	-0.006	**	23.98
	Prec-rain	-0.896	*	6.10

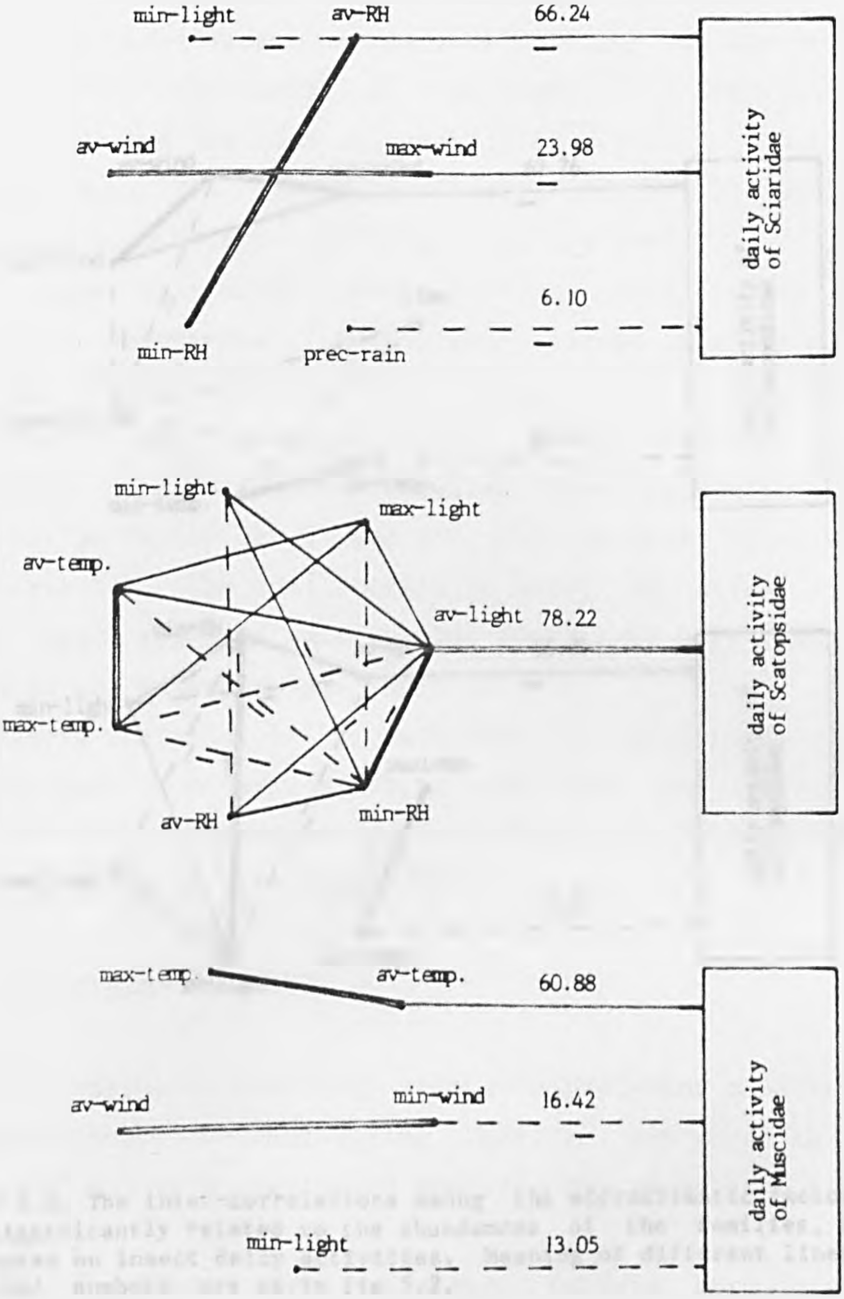

Figure 5.2. The inter-correlations among the microclimatic factors, which were significantly related to the abundances of the families, and their influences on insect daily activities. ═══ indicates signifcant at $P < 0.001$, ——— at $P < 0.01$, - - - - -at $P < 0.05$. Minus sign with the correlation lines indicates that the two variables are negatively related to each other, otherwise positively. The number represents the partial explained variance in percentage by the physical factor adjacent to it. (see Summary of Notation for abbreviations).

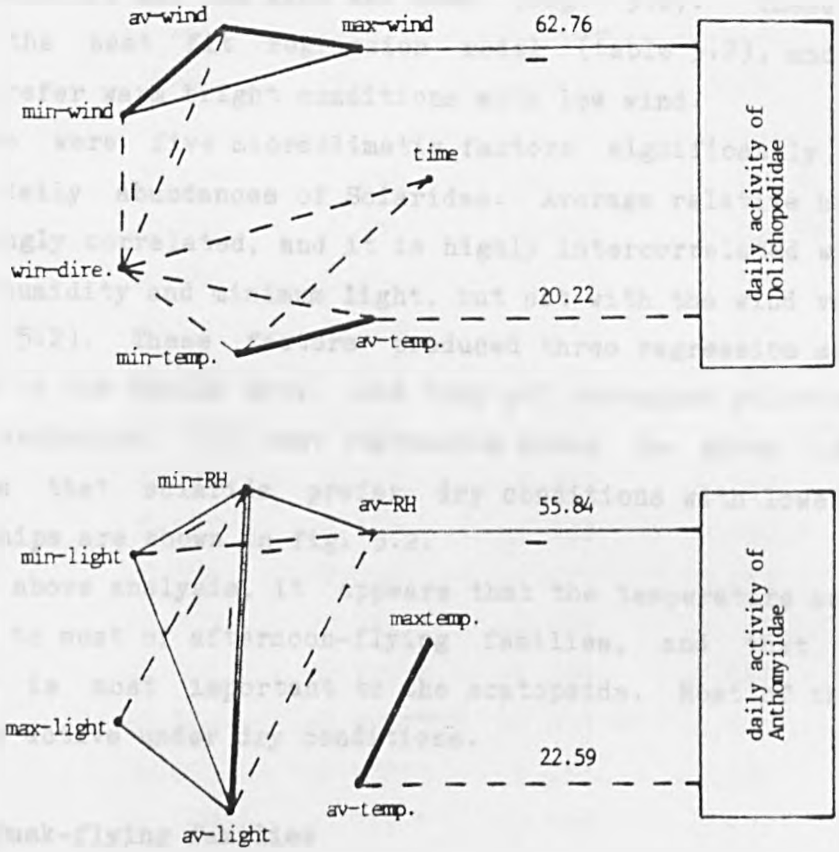

Figure 5.3. The inter-correlations among the microclimatic factors, which were significantly related to the abundances of the families, and their influences on insect daily activities. Meaning of different lines, minus signs and numbers are as in fig 5.2.

high wind. These relationships are displayed in fig 5.3.

Muscidae abundances were positively correlated with temperature and negatively with wind (table 5.1). The two temperature variables providing significant correlations were strongly intercorrelated each other, as were the wind variables. No significant correlation between the temperature and the wind was seen (fig. 5.2). These variables provided the best fit regression model (table 5.2), and shows that muscids prefer warm bright conditions with low wind.

There were five microclimatic factors significantly correlated with the daily abundances of Sciaridae. Average relative humidity was most strongly correlated, and it is highly intercorrelated with minimum relative humidity and minimum light, but not with the wind variables at all (fig. 5.2). These factors produced three regression models with good fits to the family data, and they all contained relative humidity and wind variables. The best regression model is given in table 5.2 and shows that sciarids prefer dry conditions with lower wind. The relationships are shown in fig. 5.2.

From above analysis, it appears that the temperature and wind are important to most of afternoon-flying families, and that the light intensity is most important to the scatopsids. Most of the families like to be active under dry conditions.

5.3.1.2 Dusk-flying families

Physical variables and their simple correlation coefficients with day to day abundances of dusk-flying families are given in table 5.3. The results of multiple regression analysis are summarised in table 5.4 for each family.

In the Phoridae, seven physical factors were significantly correlated with daily abundances of the family (table 5.3). The temperature in the preceding trapping period, ie. afternoon temperature, was the strongest one and strongly correlated with the other six (fig. 5.4), and this was the only significant variable in the best fit regression model (table 5.4). This suggests that phorids prefer stable warm weather. The relationships are shown diagrammatically in fig. 5.4.

Daily abundances of Ceratopogonidae were highly correlated with wind speed, and secondarily with wind direction in the afternoon

Table 5.3. Physical variables and their correlation coefficients with daily abundance of dusk-flying Diptera. Numbers in the table are Pearson correlation coefficients, *** means significant at $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. $n = 10$ in each case.

Variable	Anis.	Cera.	Chir.	Phor.
Av-temp.	-0.133	0.458	0.476	0.758 *
Max-temp.	-0.016	0.532	0.554	0.806 **
Min-temp.	-0.256	0.256	0.271	0.565
Max-day-temp.	-0.580	-0.639	-0.256	0.671
Min-day-temp.	-0.728 *	-0.313	-0.449	0.686
Prec-temp.	-0.519	0.395	0.371	0.902 ***
Av-light	0.170	0.311	0.393	0.542
Max-light	0.079	0.173	0.491	0.680 *
Min-light	-0.368	-0.032	-0.071	0.339
Av-wind	-0.307	-0.782 *	-0.508	-0.546
Max-wind	-0.303	-0.735 *	-0.289	-0.562
Min-wind	-0.324	-0.898 ***	-0.853 **	-0.511
Std-wind	-0.055	-0.122	0.339	-0.360
Prec-wind	-0.105	-0.745 *	-0.503	-0.524
Win-dire.	-0.655 *	0.289	0.135	0.832 **
Pre-win-dire.	-0.613	0.283	0.060	0.745 *
Rain	0.222	0.037	0.040	-0.462
Prec-rain	-0.143	-0.015	-0.047	-0.027
Av-RH	-0.156	-0.483	-0.527	-0.432
Max-RH	-0.118	-0.353	-0.479	-0.481
Min-RH	-0.293	-0.553	-0.562	-0.305
Time	-0.747 *	0.195	0.172	0.855 **

preceding trapping (table 5.3). These significant variables were strongly correlated with each other (fig. 5.4). Only minimum wind speed was found to be significantly correlated with Chironomidae (table 5.3). Multiple regression analyses show that both families have very similar response to the minimum wind speed and minimum relative humidity (table 5.4). This seems that ceratopogonids and chironomids prefer drier and calm dusks.

Table 5.4. Regressions of daily abundance of dusk-flying Diptera with the independent variables listed in table 5.3. * means significant at $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Family	Variable	SPRC	P	PR (%)
Anisopodidae	intercept	1957.426		
	Time	-0.225×10^{-5}	***	55.81
	Minimum wind	-0.019	***	30.92
	Prec-rain	-0.067	*	6.91
Ceratopogonidae	intercept	3.628		
	Minimum wind	-0.022	***	80.72
	Minimum RH	-0.018	*	12.43
Chironomidae	intercept	2.468		
	Minimum wind	-0.018	***	72.53
	Minimum RH	-0.012	*	14.50
Phoridae	intercept	-3.168		
	Prec-temp.	0.248	***	81.39

Through the collecting period the daily abundance of the Anisopodidae was gradually decreasing, and thus time is the variable most strongly correlated with their abundance. The best fit regression model is given in table 5.4, and indicates that abundances of the insects were declining overall during the observational period and were depressed by high wind and rain level in the preceding period. If the effect of time was allowed for, then the minimum wind speed would explain 70% of the remaining variance. Hence the conclusion is that anisopodids prefer to fly in calm dry conditions at dusk. The relationships are shown in fig. 5.4.

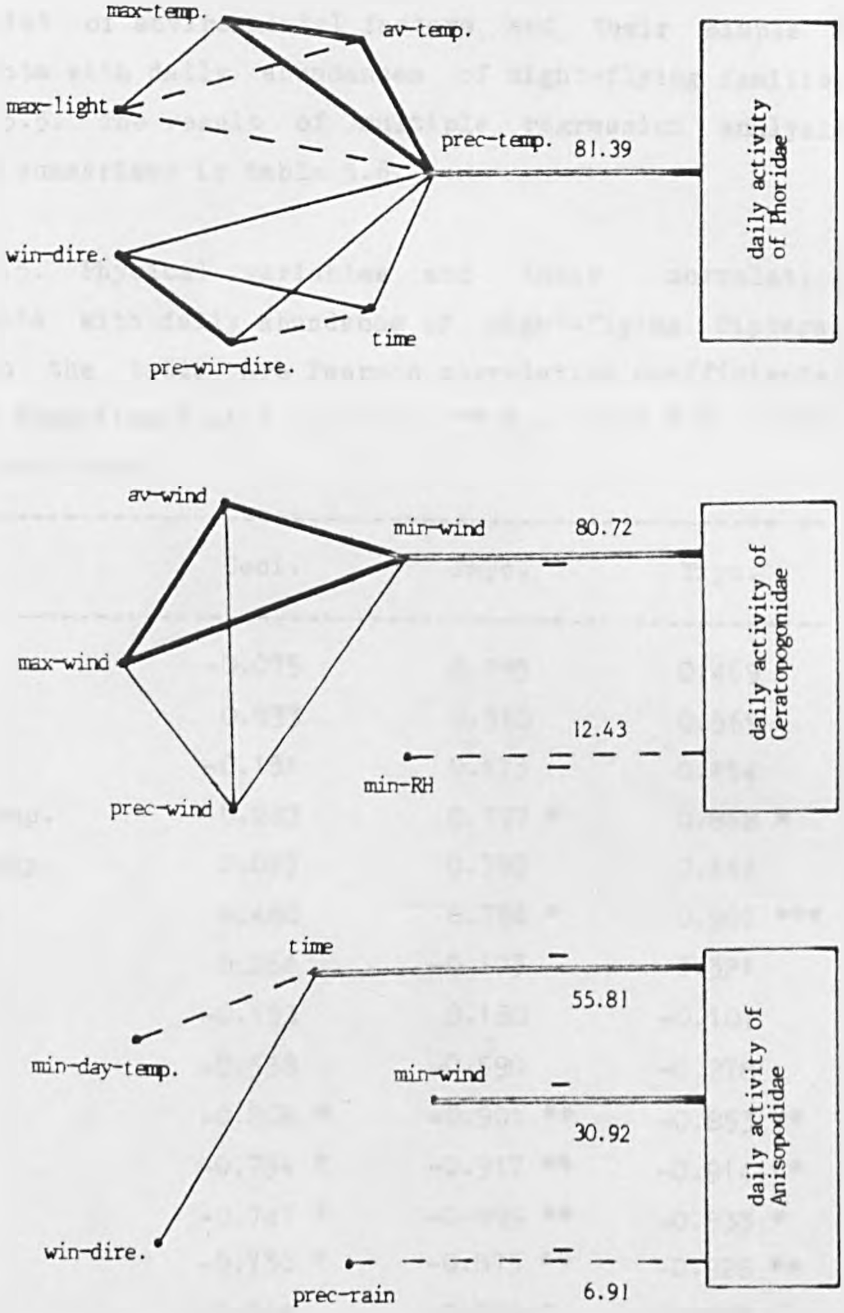

Figure 5.4. The inter-correlations among the microclimatic factors, which were significantly related to the abundances of the families, and their influences on insect daily activities. Meaning of different lines, minus signs and numbers as in fig 5.2.

5.3.1.3 Night-flying families

A list of environmental factors and their simple correlation coefficients with daily abundances of night-flying families are given in table 5.5. The result of multiple regression analysis for each family is summarised in table 5.6.

Table 5.5. Physical variables and their correlation coefficients with daily abundance of night-flying Diptera. Numbers in the table are Pearson correlation coefficients, *** means significant at $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. $n = 9$ in each case.

Variable	Ceci.	Psyc.	Tipu.
Av-temp.	-0.075	0.195	0.469
Max-temp.	0.033	0.310	0.569
Min-temp.	-0.151	0.173	0.454
Max-day-temp.	0.283	0.797 *	0.818 *
Min-day-temp.	0.023	0.399	0.442
Prec-temp.	0.480	0.784 *	0.902 ***
Av-light	0.064	-0.103	-0.321
Max-light	-0.193	0.180	-0.101
Min-light	-0.558	-0.590	-0.278
Av-wind	-0.808 *	-0.901 **	-0.853 **
Max-wind	-0.794 *	-0.917 **	-0.914 **
Min-wind	-0.747 *	-0.899 **	-0.833 *
Std-wind	-0.730 *	-0.875 **	-0.928 **
Prec-wind	-0.544	-0.708 *	-0.619
Win-dire.	0.762 *	0.687 *	0.679 *
Pre-win-dire.	-0.011	0.594	0.646 *
Rain	-0.418	-0.301	-0.128
Prec-rain	-0.368	-0.319	-0.329
Av-RH	-0.100	-0.654	-0.450
Max-RH	-0.240	-0.711 *	-0.455
Min-RH	-0.130	-0.637	-0.499
Time	-0.049	0.615	0.557

Table 5.6. Regressions of daily abundance of night-flying Diptera with the independent variables listed in table 5.5. * means significant at $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

Family	Variable	SPRC	P	PR (%)
Cecidomyiidae	intercept	1290.045		
	Average wind	-0.029	***	65.33
	Time	-1.48×10^{-6}	*	18.76
	Rain	-0.170	*	11.79
Psychodidae	intercept	7.538		
	Maximum wind	-0.013	**	84.07
	Maximum RH	-0.051	*	10.37
Tipulidae	intercept	-0.704		
	Prec-temp.	0.157	***	83.53
	Maximum wind	-0.011	***	15.23

Eight physical factors were significantly correlated with abundances of Tipulidae, wind speed negatively and the rest positively (table 5.5). These eight variables were all strongly intercorrelated with each other, except for the temperature in one preceding period (Fig. 5.5); nights with a high average wind had high maximum and minimum wind speeds and high wind variability. Again these factors cannot be regarded as independent. The best regression model is given in table 5.6, but other quite accurately fitting models were also obtained with the other combinations including wind variability. Thereby, it appears that the flying activity of tipulids is enhanced by high temperature at dusk and suppressed by high wind.

Likewise, Psychodidae and Cecidomyiidae require very similar environmental conditions to tipulids. This is shown in table 5.5. The best regression models and the relationships between physical variables and these two families are shown in table 5.6 and fig. 5.5. Both families have very similar weather preferences, ie. low wind and dry conditions. The abundances of cecidomyiids also declined overall during the observation period.

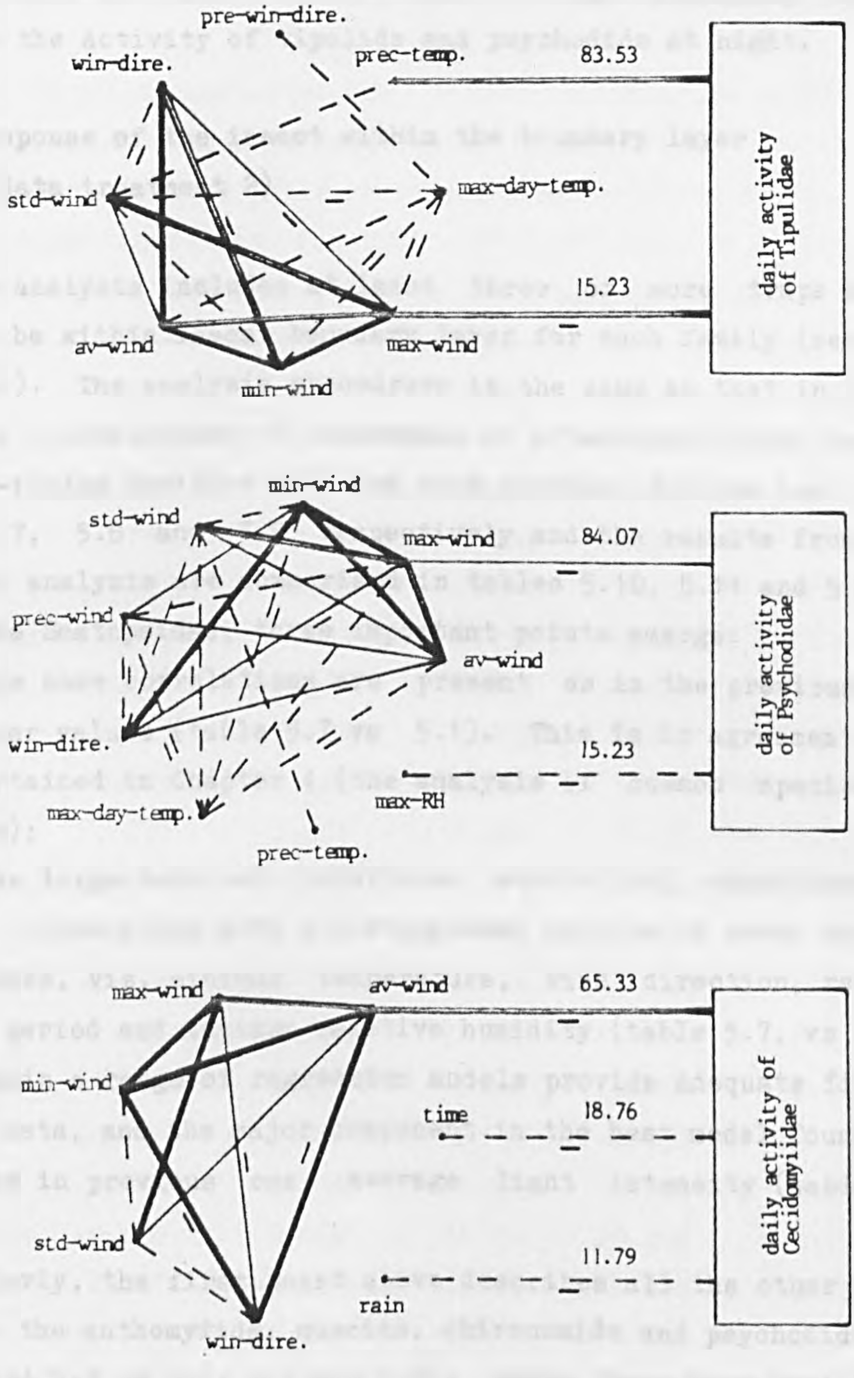

Figure 5.5. The inter-correlations among the microclimatic factors, which were significantly related to the abundances of the families, and their influences on insect daily activities. Meaning of different lines, minus signs and numbers as in fig 5.2.

In conclusion, night-flying families all prefer to fly under calm dry conditions in the lee of the tree. High preceding temperature increases the activity of tipulids and psychodids at night.

5.3.2 Response of the insect within the boundary layer (data treatment 2)

This analysis includes at least three or more traps which were deemed to be within insect boundary layer for each family (see fig. 5.1 for detail). The analysis procedrure is the same as that in Chapter 4. The simple correlations of abundances of afternoon-flying, dusk-flying and night-flying families with the same physical factors are given in tables 5.7, 5.8 and 5.9 respectively and the results from multiple regression analysis are summarised in tables 5.10, 5.11 and 5.12.

In the Scatopsidae, three important points emerge:

1) the same correlations are present as in the previous analysis but at lower values (table 5.7 vs 5.1). This is in agreement with the results obtained in Chapter 4 (the analysis of common species of the scatopsids);

2) the large data set reinforces statistical significances and allows a correlation with other physical factors to reach statistical significances, viz. minimum temperature, wind direction, rain in the preceding period and maximum relative humidity (table 5.7, vs 5.1);

3) again a range of regression models provide adequate fits to the abundance data, and the major component in the best model found here is the same as in previous one, average light intensity (table 5.10 vs 5.2).

Similarly, the first point above describes all the other families, except for the anthomyiids, muscids, chironomids and psychodids (tables 5.7, 5.8 and 5.9 vs 5.1, 5.3 and 5.5). Among these four families, some previously statistically significant correlations lose significance, especially for the chironomids. The second point derived from the scatopsids applies to all the other families very well. A feature seen here is that relative humidity variables become more statistically significant than they are in the previous analyses (tables 5.7, 5.8 and 5.9 vs 5.1, 5.3 and 5.5). The third point noted in relation to the scatopsids is also true of the other families, except for chironomids, phorids and psychodids. The weight given to the two components of the models for chiromonids are reversed (table 5.4, 5.11). The main component for phorids is still temperature, but maximum temperature in the collection period accounts for more of the variance than the average for the preceding period (table 5.4, 5.11). For the psychodids

Table 5.7. Physical variables and their correlation coefficients with the abundance of afternoon-flying family within the boundary layer. Numbers in the table are Pearson correlation coefficients. *** means significant at P < 0.001; ** P < 0.01; * P < 0.05. n = 60 for Musc. Scat. and Scia., 50 for Anth. and 40 for Doli..

Variable	Anth.	Doli.	Musc.	Scat.	Scia.
Av-temp.	0.165	0.372 *	0.286 *	0.574 ***	0.239
Max-temp.	0.059	0.217	0.200	0.474 ***	0.085
Min-temp.	0.059	0.399 **	0.184	0.366 **	0.158
Max-day-temp.	-0.265	-0.062	-0.050	0.029	-0.345 *
Min-day-temp.	-0.111	-0.012	0.003	-0.094	-0.284 *
Prec-temp.	-0.114	0.137	0.015	-0.017	-0.174
Av-light	0.312	0.060	0.140	0.650 ***	0.280 *
Max-light	0.207	0.015	0.084	0.633 ***	0.139
Min-light	0.354	0.197	0.171	0.562 ***	0.353 **
Av-wind	-0.136	-0.497 **	-0.207	-0.153	-0.313 *
Max-wind	-0.100	-0.456 **	-0.186	-0.123	-0.329 *
Min-wind	-0.185	-0.460 **	-0.206	-0.201	-0.265 *
Std-wind	0.028	-0.315 *	-0.083	0.036	-0.244
Prec-wind	-0.081	-0.384 *	-0.145	-0.092	-0.114
Win-dire.	0.054	0.450 **	0.139	0.381 **	0.253 *
Pre-win-dire.	-0.196	-0.058	-0.182	-0.218	-0.173
Rain	0.051	-0.116	0.026	0.056	-0.133
Prec-rain	-0.368 **	-0.234	-0.275 *	-0.352 **	-0.325 *
Av-RH	-0.477 ***	-0.374 *	-0.308 *	-0.610 ***	-0.641 ***
Max-RH	-0.398 **	-0.355 *	-0.231	-0.387 **	-0.601 ***
Min-RH	-0.370 **	-0.207	-0.255 *	-0.601 ***	-0.446 ***
Time	-0.171	0.396 *	-0.008	0.054	-0.101

Table 5.8. Physical variables and their correlation coefficients with the abundance of dusk-flying family within the boundary layer. Numbers in the table are Pearson correlation coefficients. *** means significant at $P < 0.001$; ** $P < 0.01$; * $P < 0.05$. n = 60 for Anis., 50 for Cera. and Chir. and 40 for Phor..

Variable	Anis.	Cera.	Chir.	Phor.
Av-temp.	0.041	0.388 **	0.124	0.664 ***
Max-temp.	0.127	0.446 **	0.214	0.688 ***
Min-temp.	-0.107	0.195	-0.052	0.441 **
Max-day-temp.	-0.352 *	-0.425 **	-0.397 *	0.142
Min-day-temp.	-0.346 *	0.021	-0.103	0.306
Prec-temp.	-0.252	0.155	-0.062	0.563 ***
Av-light	0.190	0.391 **	0.214	0.347 *
Max-light	0.163	0.396 **	0.330 *	0.412 **
Min-light	-0.205	0.020	-0.105	0.279
Av-wind	-0.166	-0.235	-0.026	-0.162
Max-wind	-0.102	-0.135	0.065	-0.085
Min-wind	-0.331 *	-0.452 **	-0.262	-0.323 *
Std-wind	0.265	0.268	0.304 *	0.220
Prec-wind	0.034	-0.110	0.100	-0.041
Win-dire.	-0.403 **	0.104	-0.078	0.455 **
Pre-win-dire.	-0.404 **	0.066	-0.137	0.355 *
Rain	0.110	-0.140	-0.051	-0.341 *
Prec-rain	-0.085	-0.110	-0.170	0.013
Av-RH	-0.317 *	-0.513 ***	-0.437 **	-0.447 **
Max-RH	-0.273 *	-0.554 ***	-0.458 ***	-0.486 **
Min-RH	-0.388 **	-0.482 ***	-0.402 **	-0.360 *
Time	-0.453 ***	0.037	-0.068	0.397 *

the main physical factor is different but maximum relative humidity is present in both models (table 5.6, 5.12).

Compared with the proportions of variability accounted for by physical factors in the one-trap data analysis, in all cases the best models found in the multiple-trap data analysis explain much smaller

Table 5.9. Physical variables and their correlation coefficients with the abundance of night-flying family within the boundary layer. Numbers in the table are Pearson correlation coefficients. *** means significant at P < 0.001; ** P < 0.01; * P < 0.05. n = 27 in each case.

Variable	Ceci.	Psyc.	Tipu.
Av-temp.	-0.019	0.181	0.402 *
Max-temp.	0.049	0.224	0.434 *
Min-temp.	-0.040	0.211	0.435 *
Max-day-temp.	0.126	0.104	0.428 *
Min-day-temp.	0.138	0.336	0.424 *
Prec-temp.	0.549 **	0.228	0.781 ***
Av-light	-0.114	-0.138	-0.437 *
Max-light	-0.146	0.272	-0.064
Min-light	-0.472 *	-0.336	-0.157
Av-wind	-0.676 ***	-0.163	-0.569 **
Max-wind	-0.612 ***	-0.056	-0.551 **
Min-wind	-0.636 ***	-0.248	-0.584 **
Std-wind	-0.484 *	0.048	-0.511 **
Prec-wind	-0.345	-0.052	-0.275
Win-dire.	0.647 ***	0.064	0.402 *
Pre-win-dire.	0.062	0.226	0.372 *
Rain	-0.386 *	-0.070	-0.140
Prec-rain	-0.369 *	-0.001	-0.263
Av-RH	-0.244	-0.671 ***	-0.456 *
Max-RH	-0.361	-0.711 ***	-0.415 *
Min-RH	-0.268	-0.583 **	-0.503 **
Time	0.055	0.388 *	0.416 *

proportions of the variance than in single trap analysis, viz. 15-52% for afternoon-flying families in multiple, while 78-96% in single; 20-58% for dusk-flying families in multiple, while 81-93% in single; 15-69% for night-flying families in multiple, while 94-98% in single (tables 5.10 vs 5.2; 5.11 vs 5.4; 5.12 vs 5.6). This indicates that

Table 5.10. Multiple regression analysis of afternoon-flying Diptera with the physical variables listed in table 5.7 within the boundary layer using GLM procedure of SAS. * at $P < 0.05$; ** at $P < 0.01$; *** at $P < 0.001$. The probability shown is for the null hypothesis that the parameter of SPRC = 0.

Family	Variable	SPRC	F value	P	PR (%)
Anthomyiidae	intercept	1.951			
	Trap position		8.31	***	29.38
	Average RH	-0.019	27.38	***	26.63
Dolichopodidae	intercept	-0.129			
	Trap position		4.28	*	7.22
	Maximum wind	-0.006	14.25	***	29.48
	Average temp.	0.056	7.00	*	10.81
Muscidae	intercept	0.150			
	Trap position		9.44	***	38.47
	Average temp.	0.040	4.78	*	10.90
	Average RH	-0.008	4.99	*	4.44
Scatopsidae	intercept	-1.946			
	trap position		8.01	***	26.48
	Average light	1.202×10^{-4}	10.15	**	30.27
	Average temp.	0.135	17.15	***	12.05
	Average wind	-0.007	10.13	**	5.17
Sciaridae	intercept	3.118			
	Trap position		12.16	***	20.92
	Average RH	-0.026	52.47	***	47.79
	Maximum wind	-0.004	8.70	**	4.49

factors other than the measured physical ones are important in determining the spatial distribution within their boundary layer; the insects are not just seeking the positions with high temperature, high light, low wind or low humidity. This is shown by the part of the variance explained by the different trap positions, viz. 7-38%, 17-47% and 8-41% for afternoon, dusk and night-flying families respectively (tables 5.10 - 5.12). This is because the insects tend to occur at certain positions, especially more at trap 5 for scatopsids, at trap 1 for anisopodids, at trap 1 or 2 for chironomids and at trap 2 for the other families (fig 5.1). Although tipulids do not show significant preference to trap positions (table 5.12), more individuals still tend to appear at trap 2 (fig 5.1). This result is, overall, in agreement with that obtained in Chapter 4.

Table 5.11. Multiple regression analysis of dusk-flying Diptera with the physical variables listed in table 5.8 within the boundary layer using GLM procedure of SAS. * at $P < 0.05$; ** at $P < 0.01$; *** at $P < 0.001$.

Family	Variable	SPRC	F value	P	PR(%)
Anisopodidae	intercept	1126.204			
	Trap position		19.73	***	29.62
	Time	-1.294×10^{-6}	62.60	***	20.48
	Minimum wind	-0.016	71.42	***	25.94
	Prec-rain	-0.046	8.42	**	3.46
Ceratopogonidae	intercept	2.095			
	Trap position		42.56	***	47.11
	Minimum wind	-0.019	73.90	***	30.11
	Minimum RH	-0.016	33.61	***	10.13
Chironomidae	intercept	2.076			
	Trap position		10.98	***	41.58
	Average RH	-0.017	10.64	**	13.21
	Minimum wind	-0.007	8.09	**	7.30
Phoridae	intercept	-1.684			
	Trap position		4.79	**	17.35
	Maximum temp.	0.130	43.58	***	45.63

Table 5.12. Multiple regression analysis of night-flying Diptera with the physical variables listed in table 5.9 within the boundary layer using GLM procedure of SAS. * at $P < 0.05$; ** at $P < 0.01$; *** at $P < 0.001$.

Family	Variable	SPRC	F value	P	PR(%)
Cecidomyiidae	intercept	0.901			
	Trap position		7.12	**	11.32
	Average wind	-0.014	7.39	**	57.00
	Wind direction	0.003	8.58	**	7.91
	Rain	-0.106	6.62	*	4.00
Psychodidae	intercept	10.218			
	Trap position		8.53	**	40.99
	Maximum RH	-0.087	11.19	**	15.23
Tipulidae	intercept	-0.948			
	Trap position		3.31		8.81
	Prec-temp.	0.143	23.99	***	57.85
	Average wind	-0.009	7.26	*	8.82

5.4 Discussion

Williams (1940) showed that the number of insects caught in a light trap in one day depends on the activity of the insects and on the total population from which the day's sample is drawn. Changes in activity can best be estimated from differences between catches on successive days. In this present study, samples were obtained by suction traps which can distinguish insect flight activity from population changes (Johnson, 1969). Taylor (1962) showed that suction traps themselves do not in general have significant attractiveness to flying insects. The bright metal used to construct these suction traps (fig. 2.1) might have effects on the behaviour of the insect, but all traps should be equally attractive. The one exception would be when some were in the sun and other were not. For example, possible attraction by the shiny metal could increase the catches of scatopsids (see also Chapter 4).

5.4.1 Daily abundances

In the afternoon-flying group, the significant correlation with wind direction occurred either in the one-trap or in the multiple-trap data analysis for small body-sized families, such as dolichopodids, scatopsids and sciarids (table 5.1, 5.7). This indicates that more of these tend to be trapped in SW or W wind conditions in which the traps were sheltered, and shows the importance of shelter for these insects. In contrast, no such significant correlation can be detected for the larger bodied-flies, viz. anthomyiids and muscids (table 5.1, 5.7). It could be that big body-sized families have a stronger ability to control their flight track than do small bodied ones, and so show similar activity in both sheltered and exposed conditions. This phenomenon applies to night-flying families very well (table 5.5, 5.9), when wind speeds tend to be lower in any case. Although tipulids are big in body size they are usually poor flyers (Service, 1973). In the dusk-flying group, the activity of small body-sized phorids was enhanced in the sheltered condition, while big bodied anisopodids even showed more activity in the more exposed conditions (table 5.3). However, this does not apply to small bodied chironomids and ceratopogonids (table 5.3, 5.8). This may be due to the fact that wind speed at dusk was weaker than in the afternoon whatever the wind direction was, and could be ignored by the ceratopogonids and chironomids which have strongly developed swarming behaviour (Colyer & Hammond, 1968; Dowes, 1955). Lewis (1967) states that for strong flyers vertical profiles in sheltered and exposed positions were indistinguishable, but not for weak flyers.

Nine out of twelve families show significant negative correlations with the wind speed. The anthomyiids, scatopsids and phorids do not show such a correlation (tables 5.1 - 5.6). This suggests that the wind speed has an important effect upon the daily abundance of many flying Diptera. This provides quantitative support to the idea that most families tend to fly under sheltered conditions, in agreement with the demonstration by Lewis & Stephenson (1966) that the zones of maximum density of flying insects and maximum shelter usually coincide.

Temperature is found to be more important to anthomyiids, dolichopodids, muscids, scatopsids and phorids than to the other families concerned here (tables 5.1 - 5.6). The obvious feature for these five families is that they all prefer to fly in daytime (table 3.2), and are generally darker in their body colour than the others. These insects probably need high temperature to warm them up for flying, and the darker colour may be helpful to them to gain the required temperature quickly. Lewis & Taylor (1964) noted that there is an association between the light intensity when species or genera of Nematocera fly and their body colour. Graham-Smith (1916) suggested that temperature influenced the activity of flies more than any other meteorological condition.

The relationships between the microclimate factors and the daily abundances of scatopsids suggest that these insects prefer warm bright dry weather (fig 5.2). This tallies with the general description given by Colyer & Hammond (1968) and Kidd & Brindle (1959) that adults of scatopsids have been recorded as swarming in large numbers in hot sun.

Daily abundances of dolichopodids are largely dependent on wind speed and temperature (fig. 5.2). This is partly consistent with the results obtained by Willmer (1982b) that air temperature is significantly correlated with the mean number of dolichopodids.

85% of anisopodids are Anisopus punctatus Fabricius, and 13% are A. fenestralis Scop. (Appendix 1). The day to day abundances of anisopodids gradually reduced during the trapping sequence (22nd July to first August, 1987), hence a large proportion of variability of the insects is temporal (Table 5.5). It seems that the observation period was after the peak emergence of these two species. Khalsa (1948) showed that A. fenestralis in the Leeds area was at its maximum abundance from about the middle of May to the about the middle of July, after which its number gradually decreased. After allowing for the effect of time on anisopodid abundances the minimum wind speed contributes most to the variability; day to day abundances of the insects were depressed by high winds. This is in agreement with the results obtained by Khalsa (1948) and Hawkes (1961). The negative correlations with the 24 hour minimum temperature and wind direction (table 5.3) are likely to be due to the decline in numbers through time occurring simultaneously with rising temperatures and with the change of wind condition from the exposed (NE) to the sheltered (SW) during the observation period as the weather became more mild. This relation appears to be stochastic without causality.

Night to night abundances of tipulids are strongly correlated with high maximum temperatures in the day and the dusk (preceding period) temperature in the one-trap data analysis and with all the temperature-related variables in the multiple-trap data analysis. In both cases the correlation with the dusk temperature is the strongest. The observation here of closest correlation with average temperature in the preceding trapping period, the dusk, is interesting. It suggests that high dusk temperatures predispose tipulids to fly, possibly by raising the metabolic rate in preparation for flight. This is concordant with the suggestion of Barnes (1925) that there is a correlation between temperature and the number of species of tipulids on the wing. Pinchin & Anderson (1936) and Roberston (1939) found that activity of Tipulinae is very definitely favoured by a high minimum temperature. The wind speed is significantly negatively correlated with daily abundances of tipulids (tables 5.5, 5.6, 5.9 and 5.12), and the wind direction is seen to be positively significant. This suggests that tipulids tend to be active in calm sheltered conditions. However, this result does not agree with the comment given by Barnes (1925) that "there is not any direct correlation between wind and the number of adults of tipulids occurring, and the chief influence of wind on crane-flies is to drive them into shelter where they are not easily found (no adequate data are available)". He did not, however, have the advantage of quantitative data.

Average wind and minimum wind, minimum wind and all the wind-related variables are highly correlated with abundances of the muscids, chironomids and psychodids respectively in the one-trap data analysis (tables 5.1 - 5.6), but these effects are not significant in the multiple-trap data analysis (tables 5.7 - 5.12), especially in muscids and psychodids. This indicates that wind effects on these insects are not consistent from one trap to another. The reason for this is not clear and further work is needed before reaching a conclusion. Lewis (1966a) failed to show any relationship between catches of Psychodidae and wind speed or wind direction.

Wind speed and direction appear to be important physical factors affecting the abundance of cecidomyiids (tables 5.5, 5.6, 5.9, 5.12). This may be related to their delicate body construction. Perhaps, in order to avoid desiccation, they tend to avoid high wind conditions by seeking shelter. Lewis (1966a) suggested that catches of Cecidomyiidae were more closely related to the mean angle of the incident wind than to the wind speed though wind speed had some effect. The slight difference between this study and Lewis's results could be due to different species composition of the family. The dominant species of cecidomyiids in this study was Clinodiplosis leguminicola Milne (Appendix 1), which is very small and delicate.

Both ceratopogonids and chironomids show a very strong negative relation with minimum wind speed in simple correlation analysis (table 5.3), and with minimum wind speed and minimum relative humidity in multiple regression analysis (table 5.4). This particular requirement could be related to their notable swarming behaviour at dusk (Colyer & Hammond, 1968; Kidd & Brindle, 1959; Dowes, 1955).

Anthomyiids, muscids and phorids are more active when the temperature is high (table 5.1, 5.3). Insects of these families are known to have flower-feeding and honeydew-seeking behaviour (Willmer, 1983; Skidmore, 1985; Stubbs & Chadler, 1978 and Disney, 1980). Warmth will result in increased nectar production in flowers of the lime tree (Willmer 1983) and also stimulate aphids to feed more and so to produce more honeydew (Peng 1986). Both processes will attract these insects. Also high temperature could be needed to raise their body temperature for them to fly. This may be related to their darker body. Willmer (1983) showed that numbers of Anthomyiidae are positively correlated with air temperature.

From the results it may be seen that climatic conditions affect the numbers of flying Diptera and that all of the variables measured are involved in correlations, rain least often, wind and temperature most frequently. These relationships between day to day abundances of the flying Diptera and the environmental conditions confirm Johnson's 'flight activity' hypothesis (1969) that changes in aerial densities of insects are caused mainly by changes in weather-induced flight as the insects land, fly and take off again more or less locally. At least this hypothesis is true for the flying Diptera concerned here.

The problem encountered here of interaction of the physical variables is likely to apply to any such study conducted over a short period in the British climate. However extending it over a longer period would make it more sensitive to emergence patterns. That insect families are responding differently is however apparent. The close correlation of scatopsids with light are much stronger than those seen in any other family, and the sciarids are sensitive to humid conditions (table 5.1). It is also notable that the only family that seems to be significantly affected by light level at dusk and night is the Phoridae (tables 5.3, 5.5)

5.4.2 Response within the boundary layer

In the analyses including all of the traps deemed to be within the boundary layer the trap position accounts for a significant proportion of the variance (Tables 5.10 - 5.12). This is to be expected in view of what is reported about spatial distributions in Chapter 3. However when trap positions and physical variables are both included the unexplained variation in the abundance data is still higher in the large data set for all of the families than in the single trap data set (tables 5.10 - 5.12 vs 5.2, 5.4, 5.6).

These unexplained variances are at least as important as the effect of trap positions. It could be that this variance is due to the behavioural diversity of species contained in each family, but an analysis of the individual species of scatopsids within their boundary layer still shows the same features (see chapter 4 for detail). One hypothesis tested was that climate affects the behaviour differently at different traps, but no statistically significantly interaction was found between trap position and any average microclimatic factors affecting the abundance of any family. Therefore the reason for this is not at present clear but it could be that different individuals of each family behave slightly differently.

According to the results obtained in the multiple-trap data analysis of the distributions of the flying Diptera within their boundary layer, in general, the hypothesis put forward at the beginning of this chapter that biological effects and mechanical stimuli would be more important to flying insects within their boundary layer than do physical ones is confirmed, in the flying Diptera concerned here.

5.5 Summary

1) The relationship between microclimate and daily abundances of flying Diptera and the response of the insects within their boundary layer have been assessed using six suction traps and six computer linked micro-meteorological stations. Collections were made from four

periods each day and from different positions in relation to an emergent hedgrow tree. Sampling was from 22 July - 1 August 1987.

2) Daily abundances of each family are very dependent upon the vagaries of the weather, and different families respond to the measured conditions differently.

3) Temperature is found to be the most important factor influencing afternoon-flying families, while low wind speed is important for dusk and night-flying families.

4) Weak flyers and small-bodied insects are more sensitive to wind than are strong flyers and big-bodied sized insects.

5) The major physical components of the multiple regression models are similar whether the analysis is performed on the trap catching most of the family or on all the traps within the boundary layer for the family.

6) It is concluded that factors other than the measured physical ones are important in determining the response of flying Diptera within their boundary layer, but precisely what these are is yet to be established.

Chapter 6

EFFECT OF SHELTER ON DISTRIBUTION OF FLYING DIPTERA

6.1 Introduction

A series of studies on the distribution of insects in relation to shelter carried out by Lewis (1965 a, b, c; 1966 a, b; 1967; 1969 a, b, c), Lewis & Smith (1969) and Lewis & Stephenson (1966), showed that flying insects accumulate in the lee of obstacles to the wind (see General Introduction, Chapter 1). This extensive work led to the hypothesis that insects accumulate in re-circulating air to the leeward of barriers to wind flow (Lewis 1970; Lewis & Dibley 1970). The shelter effect caused by an emergent hedgerow tree has been shown by the spatial distribution of common species of Scatopsidae (Chapter 4) and by the relationship between the wind direction and the daily abundance of common families (Chapter 5) in this study.

However, similar work carried out by Bowden & Dean (1977) and Dean (1974) on the distribution of flying insects in and near a tall hedgerow suggested that the pattern of distribution appeared to be determined primarily by the comparative richness of the vegetation irrespective of speed and direction of wind (see General Introduction, Chapter 1). Hawkes (1973), using yellow water traps to study distributions of cabbage root fly, suggested that the distribution of males and females of the flies were not correlated with the shelter effects of a windbreak.

In his review of the subject, Pasek (1988) was unable to resolve the conflict in the conclusions of Lewis and Dibley on the one hand, and Bowden and Dean on the other (see General Introduction, Chapter 1). It therefore appeared worthwhile to re-examine the distribution of flying insects in relation to shelter.

The site chosen consisted of simple emergent trees growing out of a tall hedgerow, this being very typical of the living architecture of much of lowland Britain. Although there is plenty of qualitative evidence for the importance of such trees in the lives of insects, birds, bats and other animals that feed on them (Elton, 1966), no quantitative data on the distribution of flying insects around them is available.

Developing from this general aim, an effort has been made in this study to distinguish biological influences from physical ones in flying Diptera. It was expected that the similar plant flora and similar plant architecture would produce similar diversity of flying insects (Bowden & Dean 1977). Therefore two lime trees of the same species (Tilia sp.) were chosen. They were both growing out of the 3m high thick hawthorn hedgerow and 30m apart from each other (fig. 6.1a). Suction traps and outstations (see General Methods, Chapter 2) were installed close to each of the trees at three levels, but in two different compass directions from them. The observations were carried out in two phases.

In phase 1, the first half (phase 1a) was carried out without disturbing the natural vegetation, in order to provide base line data. According to the shelter effect principle found by Lewis (1970), Lewis & Stephenson (1966) and Lewis & Dibley (1970), the hypothesis here was that the two vertical distribution patterns of flying insects in relation to the trees should be different since the traps are in different shelter conditions relative to the prevailing SW winds (fig. 6.1a) and these patterns should be reversed when the wind was from the south east due to reversal of the exposure conditions, and became similar due to similar lack of shelter with winds from a northerly direction. The second half of phase 1 (phase 1b) involved the cutting of the hedgerow near lime tree 2 (fig. 6.1a), while maintaining the undisturbed nature of the surroundings of tree 1 as a control. The hypothesis in phase 1b was that the difference between the two vertical patterns in phase 1a should be accentuated because of reduced shelter due to the cutting at tree 2.

Phase 2 was also divided into halves. In the first half (phase 2a) the design was as in phase 1b, but 9 months later. The repetition was necessary to check that the patterns had not changed between years. The experiment ended with phase 2b in which the gap in the hedgerow by tree 2 was reinstated with an artificial windbreak. The hypothesis here was that the distribution patterns obtained in this period should be similar to those in phase 1a, if the artificial windbreak plays the same role as does the hawthorn hedge, ie. if physical effects (shelter from the elements) predominate over biological effects (attraction to food, shelter from enemies).

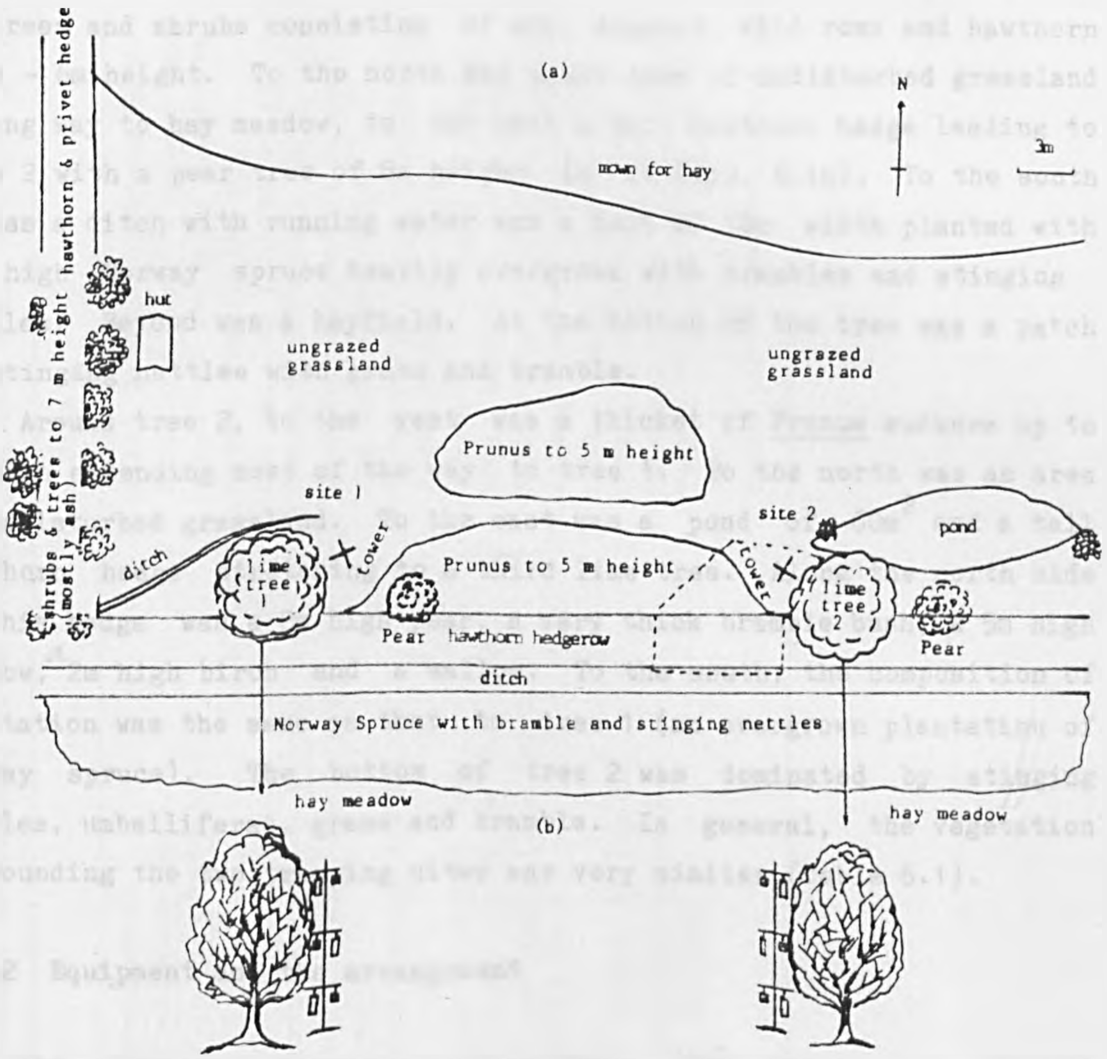

Figure 6.1. (a) Diagrammatic representation of two trapping sites. The vegetation enclosed in the dotted line in site 2 was cut down in the middle of phase 1. (b) profiles of lime trees and arrangement of suction traps (▯) and outstations (▨) in relation to trees.

6.2 Materials and methods

6.2.1 Trapping sites

Detailed information about the study site has been given in General Methods (Chapter 2). There are two aspects to this study (control and test). Each of them concerns two lime trees, tree 1 (trapping site 1, control) was 11.5m high and tree 2 (trapping site 2, test) was 10m in height. Around tree 1, to the west, there was a bank of trees and shrubs consisting of ash, dogwood, wild rose and hawthorn of 4 - 6m height. To the north was small area of undisturbed grassland giving way to hay meadow, to the east a tall hawthorn hedge leading to tree 2 with a pear tree of 8m height in it (fig. 6.1a). To the south across a ditch with running water was a belt of 10m width planted with 2m high Norway spruce heavily overgrown with brambles and stinging nettles. Beyond was a hayfield. At the bottom of the tree was a patch of stinging nettles with grass and bramble.

Around tree 2, to the west was a thicket of Prunus suckers up to 4m high extending most of the way to tree 1. To the north was an area of undisturbed grassland. To the east was a pond of $60m^2$ and a tall hawthorn hedge stretching to a third lime tree. Along the north side of this hedge was a 8m high pear, a very thick bramble bush, a 5m high willow, a 2m high birch and a sallow. To the south, the composition of vegetation was the same as that to tree 1 (an overgrown plantation of Norway spruce). The bottom of tree 2 was dominated by stinging nettles, umbelliferae, grass and bramble. In general, the vegetation surrounding the two trapping sites was very similar (table 6.1).

6.2.2 Equipment and the arrangement

Six nine-inch diameter suction traps (for detail see General Methods, Chapter 2) were suspended on two scaffolding towers at three different levels, the top two traps with their intakes at 8.5 metres from the ground, the middle two at 5 metres and the bottom two at 1.2 metres. The vertical distance between any two traps was sufficient to prevent the down-draft of the upper one affecting the efficiency of the lower (fig. 6.1b). Top and middle traps were almost brushing the leaves of the trees. Six outstations (see General Methods for detail)

Table 6.1. Vegetation of trapping sites around lime tree 1 and 2 within a radius of 10m.

Site 1	Site 2
Ash *Fraxinus excelsior* L.	Birch *Betula pubescens* Ehrh.
Bramble *Rubus fruticosus* Agg.	Bramble *Rubus fruticosus* Agg.
Cocksfoot *Dactylis glomerata* L.	Cocksfoot *Dactylis glomerata* L.
Common lime *Tilia spp.*	Common lime *Tilia spp.*
Cow parsley *Anthriscus sylvestris* (L.) Hoffm.	Cow parsley *Anthriscus sylvestris* (L.) Hoffm.
Creeping Buttercup *Ranunculus repens* L.	Creeping Buttercup *Ranunculus repens* L.
Creeping Cinquefoil *Potentilla reptans* L.	Creeping Cinquefoil *Potentilla reptans* L.
Dog rose *Rosa canina* L.	Dog rose *Rosa canina* L.
Dogwood *Thelycrania sanguinea* L.	Dogwood *Thelycrania sanguinea* L.
Elder *Sambucus nigra* L.	Elder *Sambucus nigra* L.
Hawthorn *Crataegus monogyna* Jacq.	Hawthorn *Crataegus monogyna* Jacq.
Marsh Thistle *Cirsium palustre* (L.) Scop.	Great sallow *Salix caprea* L.
Norway spruce *Picea abies* (L.) Karst.	Marsh Thistle *Cirsium palustre* (L.) Scop.
Pear *Pyrus communis* L.	Norway spruce *Picea abies* (L.) Karst.
Sloe *Prunus spp.*	Pear *Pyrus communis* L.
Stinging nettle *Urtica dioica* L.	Sloe *Prunus spp.*
Sycamore *Acer pseudoplatanus* L.	Stinging nettle *Urtica dioica* L.
Teasel *Dipsacus fullonum* L.	Teasel *Dipsacus fullonum* L.
Various grasses	Various grasses
	Water plants in/around the pond

were also hung on the two scaffoldings. Each of them was kept at the same level as a suction trap, and one metre from it (fig. 6.1b). The towers were on the ~~NW~~ NE side of tree ~~2~~ 1 and the NW side of tree 2, which were 3m away from a hawthorn hedgerow perpendicularly (fig. 6.1a). The reason for this arrangement was to put the traps in positions of similar flora but different exposure which should vary with wind direction and which could be manipulated experimentally at one site whilst keeping the other as control, thus enabling the relative importance of biological and physical effects to be determined.

6.2.3 Trapping programme and sampling methods

6.2.3.1 Phase 1

Phase 1a was from 15 September to 20 September, 1987. Collections were made from the traps without disturbing any vegetation around the trapping sites. In phase 1b, 22 -27 September, a channel aligned NE - SW was cut adjacent to tree 2. This involved removing branches on the NW side from tree 2 to a height of 5m, cutting down to one metre a 7m section of hawthorn hedgerow next to tree 2 and cutting the vegetation along a 7 metre transect to reach the hedge (fig. 6.1a). This allowed prevailing SW winds to blow through freely. Site 1 was left as a control with no disturbance.

During phase 1 the traps were run for two periods each day: that is, 09:00 - 18:00 (daytime) and 19:00 - 06:00 (night) GMT. The collecting jars, filled with 70 ml of 70% ethanol, were emptied at the end of each run. The Diptera were separated from the catch and sorted to families.

6.2.3.2 Phase 2

Phase 2a was a re-run of phase 1b, but carried out the following year. It lasted from 23 June to 11 July 1988. The site was unchanged except for some regrowth of the hedge. Ground vegetation was cut back a little. In phase 2b, an artificial hedge was put up to block the 7m gap in the hawthorn hedge at trapping site 2 to reduce the wind force from the SW direction (fig. 6.1a). The windbreak was 3m high, made of green plastic netting (see General Methods) in double layers. Trapping site 1 was again kept as a control and nothing was changed around it. The phase 2b was from 11 July to 27 July 1988.

The collection regime for phase 2 was the same as previously except that times were 09:30 - 19:00 and 21:00 - 07:00 GMT.

6.2.4 Meteorological data

The wind force, temperature, light intensity and relative humidity were automatically recorded once every twenty minutes at each suction trap position by the outstations. The wind direction was visually recorded four times daily from a wind vane fixed on a 10m scaffolding pole in the open meadow. Rainfall were measured twice a day using a standard rain gauge. The changes of the weather within each run were also logged in detail.

6.2.5 Data treatment

A total of 22 collection runs were obtained in phase 1 and 48 in phase 2. 18 runs were selected for the analysis in phase 1 and 24 in phase 2 according to the consistency of the wind direction within each collection run. Runs with variable wind direction were discarded.

The numbers of flying Diptera in each trap for each sampling period were transformed to base 10 logarithms and analysed against physical variables. Vertical stratification of flying Diptera were tested on the basis of the null hypothesis using Chi-square test of analysis of frequencies, within which combined tests of homogeneity and heterogeneity were considered (Sokal & Rohlf 1981). Statistical analyses were performed using the SAS statistical package (SAS 1985), within which the PROC ANOVA was used to test for significant differences both in physical variables between two trapping periods and in wind vertical distributions between heights in each observation, while the PROC CORR and PROC STEPWISE were used to determine how much of the variability of the activity of Diptera can be attributed to physical variables.

6.3 Results

6.3.1 Phase 1

6.3.1.1 SW winds

During phase 1a and 1b, wind direction was SW (taken as 210° - 240°) for 64% of the trapping periods (runs). With the wind from this direction, the three traps in site 1 were sheltered by tree 1. In site 2 the top trap was exposed to the wind, the middle one was semi-exposed before cutting and wholly exposed after cutting and the bottom one was sheltered before cutting and exposed after that (fig. 6.2). A total of 14 runs were made, 6 runs in daytime and 8 runs at night under this wind conditions. The significance of changes induced by cutting were tested by calculating Chi-square in 2 x 2 contingency tables for each height. The results under SW wind conditions for daytime and night are analysed separately below:

6.3.1.1.1 Distribution patterns by day

Total catch for each family from the 6 daytime runs, 3 before cutting and 3 after, are shown in table 6.2. It can be seen that before cutting the richness (as number of families) of flying Diptera was the same in both sites and the number of individuals contained in each family was also generally similar. Comparing the catch size of each family after cutting with that before cutting, most families in site 1 (the control) decreased in numbers except for the Chironomidae. A much larger decrease in site 2, where the vegetation had been cut, was evident in all families.

As there is a common trend of decrease for almost all families, the data has been lumped in table 6.3 to allow an analysis of the extent of decrease by level. Key features are summarised in fig. 6.2. Three points emerge:

1) more insects occurred at the top and the middle levels at site 1 than at site 2, because tree 1 gave better shelter from the SW wind at these levels (fig. 6.2);

2) in phase 1b, numbers at both sites were decreased, but most flying insects still flew around the middle and top levels in sheltered site 1. In site 2 numbers at these levels were sharply decreased.

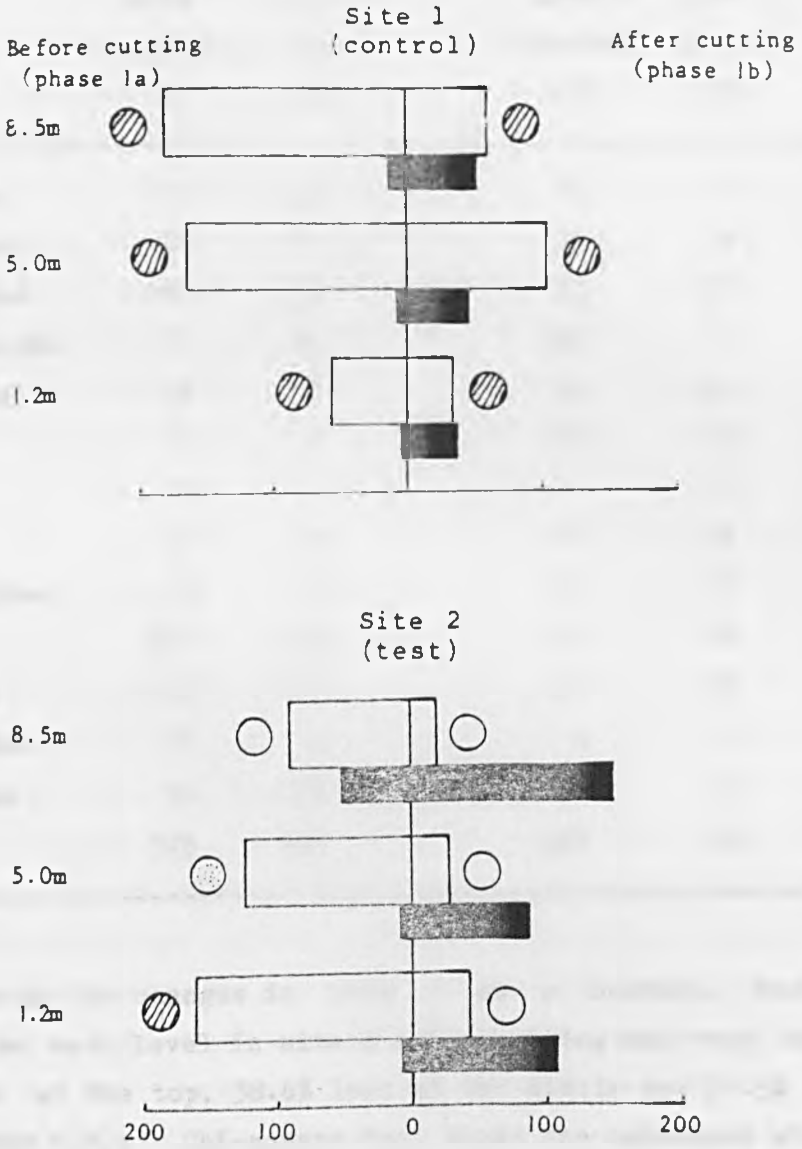

Figure 6.2. Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps in daytime under SW wind conditions. Abscissa values are a) the mean number of individuals (open rectangles); b) the mean wind force in revolutions per minute (black bars). ▨, ◌ or ○ indicate that the trap at that positon was sheltered, semi-sheltered or exposed.

Table 6.2. Diptera caught during daytime under south-westerly wind conditions. Numbers in the table are number of individuals (pooling the three levels) and those in brackets are sample size.

	Before cutting (phase 1a)		After cutting (phase 1b)	
	site 1 (control) (3)	site 2 (test) (3)	site 1 (control) (3)	site 2 (test) (3)
Chloropidae	12	22	8	11
Anthomyiidae	24	17	20	9
Cecidomyiidae	158	163	41	57
Ceratopogonidae	71	45	49	11
Chironomidae	43	76	92	62
Empididae	17	7	12	2
Fanniidae	18	6	1	1
Muscidae	41	23	17	2
Mycetophilidae	28	16	14	3
Phoridae	231	144	40	18
Psychodidae	153	299	52	26
Sarcophagidae	11	8	4	1
Scatoposidae	36	16	10	2
Sciaridae	375	281	227	70

3) taking the changes in site 1 as a control, the additional depression at each level in site 2 after cutting was very marked with 10.5% less at the top, 38.6% less at the middle and 31.3% less at the bottom (table 6.3); Chi-square test shows the decreases at middle and bottom levels to be highly significant (table 6.3).

6.3.1.1.2 Effect of microclimate on the distribution by day

Four microclimatic factors were available for this analysis, viz. wind force, temperature, light intensity and relative humidity. There

Table 6.3. Individual Diptera caught in daytime under SW wind conditions. Numbers in the first two columns are mean numbers ± S.D. at each level. T = top trap (8.5m from the ground), M = middle trap (5.0m) and B = bottom trap (1.2m). Sample size is given in brackets. Chi-square is calculated for the effect of cutting using the total numbers caught in 2 x 2 contingency tables, independently for each level.

		Before cutting (3)	After cutting (3)	change %	additional change in site 2 %	value of Chi-squ.	P
Site 1	T	182 ± 36	60 ± 19	-67.0			
	M	165 ± 31	101 ± 38	-38.8			
	B	58 ± 12	34 ± 4	-41.4			
Site 2	T	89 ± 31	20 ± 6	-77.5	-10.5	4.96	<0.05
	M	124 ± 48	28 ± 14	-77.4	-38.6	51.12	<0.001
	B	161 ± 46	44 ± 11	-72.7	-31.3	22.82	<0.001

was no rainfall with the SW winds. Comparisons of these physical variables between sites at each level and within sites before and after cutting at each level are summarised in table 6.4. It can be seen that the cutting in site 2 had a strong effect on mean wind force at all levels, a significant effect on mean light intensity at the top and bottom levels and no effect on mean temperature and mean relative humidity at all levels. It is noted that the mean temperature decreased at each level by 2°C, which was not mainly due to the cutting but to the cooler weather because the decreases at the two sites were similar. According to this analysis, the mean wind force was the most important variable, therefore details are given in table 6.5 and also shown in fig. 6.2. From table 6.5, it can be seen that the mean wind force after cutting was much stronger than before in both sites. At site 2, the wind force at the top trap, which was exposed before and after cutting, was increased up to 3 times. Unexpectedly, the wind at site 1 was increased more than 3 times. This is probably due to the early loss of leaves from the exposed crown of the tree around the time

Table 6.4. The effect of cutting on physical factors. Comparison of physical variables at three levels (T = top, M = middle and B = Bottom) in two trapping sites (S1 = site 1 and S2 = site 2) between BC (before cutting) and AC (after cutting) during the daytime under SW wind conditions. Numbers in the table are the difference between means (DIF). * = significant at $P < 0.05$ and NS = not significant using paired T test where appropriate and unpaired otherwise. r = revolutions of anemometer cups.

	Comparison		Mean wind force r min^{-1}		Mean temperat. °C		Mean light intensity Lux		Mean RH %	
			DIF	SIG	DIF	SIG	DIF	SIG	DIF	SIG
T	BC	S2 - S1	40.92	*	-1.19	NS	706.8	NS	5.43	NS
	AC	S2 - S1	98.64	*	-0.30	NS	2489.7	*	1.17	NS
	S1	AC - BC	40.61	NS	-2.92	NS	-1147.6	NS	-7.78	NS
	S2	AC - BC	98.34	*	-2.02	NS	635.3	NS	-12.04	NS
M	BC	S2 - S1	0.14	NS	0.35	NS	7.6	NS	-6.14	*
	AC	S2 - S1	40.36	*	-0.33	NS	1212.9	NS	-1.25	*
	S1	AC - BC	38.95	NS	-2.20	NS	-158.6	NS	-3.25	NS
	S2	AC - BC	79.18	*	-2.88	NS	1046.8	NS	-8.36	NS
B	BC	S2 - S1	0.47	NS	0.22	NS	-866.8	NS	-1.26	NS
	AC	S2 - S1	69.21	*	-0.69	NS	1013.0	NS	3.78	NS
	S1	AC - BC	32.55	NS	-1.99	NS	-147.2	NS	-4.35	NS
	S2	AC - BC	102.93	*	-2.89	NS	1732.6	*	0.69	NS

cutting, resulting in the crown of the tree being more permeable in phase 1b. At this altitude (150m) and latitude, lime trees are at the edge of their range and do lose leaves from the more exposed area in September. On the other hand, the wind at middle and bottom levels at site 2 were dramatically increased by 9 and 30 times respectively. This is obviously due to the effect of cutting.

Table 6.6 shows strong correlations between the activity of the insects and the mean wind force and standard deviation of the wind at

Table 6.5. Mean wind force in the daytime under SW wind conditions. Numbers in the first two columns are mean wind force ± standard deviation of the mean. Sample size is shown in brackets. Change of wind speed at top level at site 2 is regarded as a reference because of the same exposed condition before and after cutting.

		Before cutting (3)	After cutting (3)	change %	Change related to top trap at site 2 (%)
Site 1	T	10.7 ± 2.7	51.3 ± 1.8	+379.4	+188.7
	M	7.8 ± 6.0	46.7 ± 26.3	+498.7	+308.0
	B	3.8 ± 4.1	36.4 ± 26.6	+857.9	+667.2
Site 2	T	51.6 ± 15.3	150.0 ± 31.5	+190.7	----
	M	7.9 ± 4.0	87.1 ± 30.1	+1002.5	+811.8
	B	3.3 ± 3.3	105.6 ± 50.0	+3100.0	+2909.3

site 2, but not, generally, with the other three physical variables. These figures suggest that the increased wind force due to cutting was a key element in the reduction of Diptera trapped at each level in site 2. Multiple regression analysis shows that 84.3%, 91.5% and 81% of total variability of the abundance of Diptera are accounted for only by the mean wind force at the top, the middle and the bottom levels respectively. Also it is apparent that the wind increased and the Diptera decreased at site 1 (fig. 6.2). This result evidently suggests that the physical shelter effect is more important on the abundance of the insects than any biological factor.

6.3.1.1.3 Distribution patterns by night

The total catch for each family from 8 runs, 5 before cutting and 3 after that, are given in table 6.7. The results are very similar to those for daytime samples. This suggests that the composition of the insects was very similar in two sites before cutting, although the number of individuals in most families was a little less at site 2 than site 1. This probably reflects the similarity in the habitat structure

Table 6.6. Independent microclimatic variables used in stepwise multiple regressions against the daytime abundance of flying Diptera during phase 1 at site 2. Pearson correlation coefficients are given above, and regression values below. n = 6.

	Top	Middle	Bottom
Mean wind force	-0.918 **	-0.956 **	-0.900 **
Mean temperature	0.460	0.442	0.646
Mean light Intensity	-0.161	-0.697	-0.668
Mean relative humidity	0.814 *	0.666	-0.098
Standard deviation of mean wind force	-0.267	-0.930 **	-0.839 *

* $P < 0.05$; ** $P < 0.01$.

		SPRC	S.E.	F	P	PR(%)
Top	Intercept	2.2132				
	mean wind	-0.0059	0.0013	21.51	0.0097	84.3
Middle	Intercept	2.8372				
	mean wind	-0.0070	0.0004	42.91	0.0028	91.5
Bottom	Intercept	2.1927				
	mean wind	-0.0048	0.0012	17.03	0.0145	81.0

and vegetation of the two sites which were only 30m apart. The catches for almost all families in both sites after cutting were smaller than before cutting, especially in site 2.

Table 6.7. Diptera caught at night under south-westerly wind conditions. Numbers in the table are number of individuals (pooling the three levels) and those in brackets are sample size.

	Before cutting (phase 1a)		After cutting (phase 1b)	
	site 1 (control) (5)	site 2 (test) (5)	site 1 (control) (3)	site 2 (test) (3)
Anisopodidae	311	178	77	11
Cecidomyiidae	496	768	131	59
Ceratopogonidae	787	525	383	69
Chironomidae	299	222	167	89
Culicidae	8	27	4	0
Mycetophilidae	53	32	10	1
Phoridae	20	10	0	0
Psychodidae	2260	2019	836	309
Sciaridae	279	140	42	5
Tipulidae	244	204	57	34

Table 6.8. Individual Diptera caught at night under SW wind conditions. Numbers in the first two columns are mean numbers ± S.D. at each level. Chi-square test is given in table 6.3. Sample size is in brackets.

		Before cutting (5)	After cutting (3)	change %	additional change in site 2 %	value of Chi-squ.	P
Site 1	T	223 ± 71	93 ± 46	-58.3			
	M	584 ± 189	342 ± 91	-41.4			
	B	144 ± 29	134 ± 27	-6.9			
Site 2	T	113 ± 62	37 ± 26	-67.3	-9.0	3.61	>0.05
	M	334 ± 175	67 ± 31	-79.9	-38.5	176.62	<0.0001
	B	379 ± 90	88 ± 9	-76.8	-69.9	252.74	<0.0001

Table 6.9. The effect of cutting on physical factors. Comparison of physical variables at three levels in two trapping sites before and after cutting at night under SW wind conditions. Numbers in the table are the difference between group means (DIF). * = significant at $P < 0.05$ and NS = not significant. Testing method are as in table 6.4.

	Comparison		Mean wind force $r\ min^{-1}$		Mean temperat. °C		Mean light intensity Lux		Mean RH %	
			DIF	SIG	DIF	SIG	DIF	SIG	DIF	SIG
	BC	S2 - S1	39.51	*	-0.09	NS	2.72	NS	0.55	NS
T	AC	S2 - S1	53.04	*	-0.34	NS	2.36	NS	0.49	NS
	S1	AC - BC	4.49	NS	-2.20	NS	-6.18	NS	-4.09	NS
	S2	AC - BC	18.02	NS	-2.45	NS	-6.54	NS	-4.41	NS
	BC	S2 - S1	-0.99	NS	0.35	NS	1.78	NS	-2.92	NS
M	AC	S2 - S1	16.55	NS	0.15	NS	2.93	NS	-9.14	*
	S1	AC - BC	7.16	NS	-1.97	NS	-3.90	NS	1.95	NS
	S2	AC - BC	24.69	NS	-2.17	NS	-2.74	NS	-4.27	NS
	BC	S2 - S1	3.04	NS	0.09	NS	0.16	NS	0.23	NS
B	AC	S2 - S1	39.61	*	0.09	NS	1.37	NS	0.11	NS
	S1	AC - BC	1.29	NS	-1.83	NS	-3.80	NS	0.58	NS
	S2	AC - BC	37.90	*	-1.83	NS	-2.59	NS	0.46	NS

The mean frequency of Diptera at the three levels in the two sites is given in table 6.8 and also shown in fig 6.3. The pattern is very much the same as for daytime catches except that significant changes in abundance due to cutting are only seen at the bottom and middle traps.

6.3.1.1.4 Effect of microclimate on the distribution by night

The microclimatic results are summarised in table 6.9. It can be seen that the cutting at site 2 had a generally significant effect on mean wind force at the bottom level, a little effect on mean relative

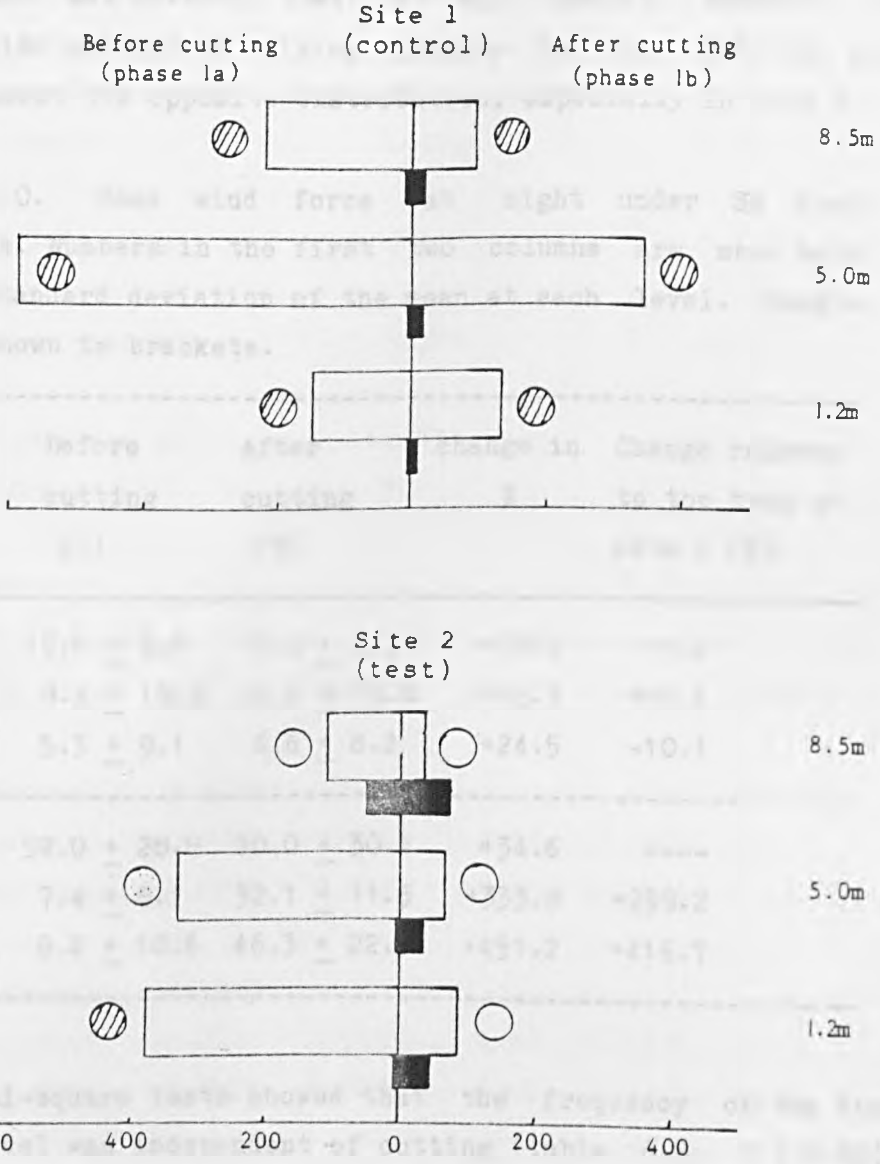

Figure 6.3. Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps at night under SW wind conditions. The meaning of symbols, numbers and abbreviations as in figure 6.2.

humidity at middle level, and no significant effect on the other factors at all. The mean temperature decreased at each level by about 2°C between two trapping sites and it was not due to the cutting but to the cold weather. The mean wind force is tabulated in detail in table 6.10, and also shown graphically in fig. 6.3. Its distribution pattern was very consistent with that shown in the daytime except that wind force was markedly lower at all levels. Compared with the distribution pattern of flying insects in fig. 6.3, the wind force showed almost the opposite distribution, especially in site 2.

Table 6.10. Mean wind force at night under SW wind conditions. Numbers in the first two columns are mean wind force ± standard deviation of the mean at each level. Sample size is shown in brackets.

		Before cutting (5)	After cutting (3)	change in %	Change related to top trap at site 2 (%)
Site 1	T	12.5 ± 9.3	17.0 ± 5.5	+36.0	+1.4
	M	8.4 ± 10.9	15.6 ± 13.0	+85.7	+51.1
	B	5.3 ± 9.1	6.6 ± 8.2	+24.5	-10.1
Site 2	T	52.0 ± 28.8	70.0 ± 30.4	+34.6	----
	M	7.4 ± 8.1	32.1 ± 11.5	+333.8	+299.2
	B	8.4 ± 10.6	46.3 ± 22.5	+451.2	+416.7

As Chi-square tests showed that the frequency of the insects at the top level was independent of cutting (table 6.8, $P > 0.05$), it is unnecessary to do any analysis for this level. Therefore, only the data for insects and physical variables from two sites at middle and bottom levels were analysed. The results are summarised in table 6.11. The Pearson correlation coefficient shows that only wind force and standard deviation of the wind are significantly correlated with the activity of flying Diptera. Multiple regression analysis shows that around 80% of the variability of the abundance of Diptera at the middle and the bottom levels at site 2 were accounted for by the wind force

Table 6.11. Independent microclimatic variables used in stepwise multiple regressions against night abundance of flying Diptera during phase 1 at site 2. Pearson correlation coefficients are given above, and regression values below. n = 8.

	Middle	Bottom
Mean wind force	-0.723 *	-0.737 *
Mean temperature	0.575	0.454
Mean light Intensity	0.397	0.421
Mean relative humidity	0.368	-0.177
Standard deviation of mean wind force	-0.714 *	-0.685

* P < 0.05.

		SPRC	S.E.	F	P	PR(%)
Middle	Intercept	1.5974				
	mean wind	-0.0362	0.0090	6.23	0.0468	50.9
	mean tempe.	0.0911	0.0282	10.40	0.0233	33.1
Bottom	Intercept	1.9219				
	mean wind	-0.0105	0.0029	7.12	0.0371	54.3
	mean tempe.	0.0586	0.0238	6.06	0.0500	25.1

and temperature, especially the wind. So, this result suggests that the significant differences of frequency of Diptera before and after cutting at middle and bottom levels (table 6.8) are mainly due to the physical influence by reducing shelter by cutting at site 2.

It is noted that the explained proportion of the variability of the insect by wind force at night is much lower than by day (table 6.11 vs 6.6). Instead the temperature explained a considerable part of the variability at night (table 6.11). These differences are probably due to the insect source and their flying threshold. Concerning the former, most daytime flying Diptera were found not to be residents of the trapping sites, but in fact transients moving on the wind. Hence the speed and direction of wind is very important to them. In contrast, most Diptera caught at night originated in this site and had a close relation with the surroundings. Therefore, their abundance was affected jointly by the change of wind force through cutting, by decreased temperature and by the environmental change. Also the wind force is, in general, much stronger in daytime than at night (tables 6.5, 6.10), therefore the shelter acts as a more effective accumulator of insects in daytime (see also Lewis 1966a). As to the latter (the flight threshold), in terms of the results obtained by Taylor (1963) that temperature acts as a threshold above which flight is uninhibited, the average temperature was 17 - 18.6 °C before cutting and 14.3 - 17.3 °C after, which probably exceeded the flight threshold for most daytime Diptera. In contrast, at night it was 9.8 - 14.3 °C before cutting and 8.2 - 12.3 °C after. Perhaps the upper temperature exceeded the flight threshold for most night Diptera but the lower ones did not.

6.3.1.2 SE winds

When the wind was from the SE, the three traps at site 2 were all sheltered, while at site 1 the top trap was exposed, the middle one semi-exposed and the bottom one sheltered by the hedge (fig. 6.4). This is also indicated by the average wind force at each trap position in fig. 6.4. Only one daytime catch was obtained before cutting with this wind direction. In order to make within-site comparisons, the data obtained under SW wind conditions in daytime before cutting was re-used.

The distribution patterns under these two wind conditions are shown in fig. 6.4 (before cutting). Some general points are summarised as follows:

1) the vertical distribution pattern of catches under SE winds in site 1 was almost opposite to the SW wind pattern, and the mean numbers trapped in the SE wind conditions were less than in the SW winds;

2) In site 2, although the stratification pattern did not differ much with wind direction, the mean numbers of the insects caught in the

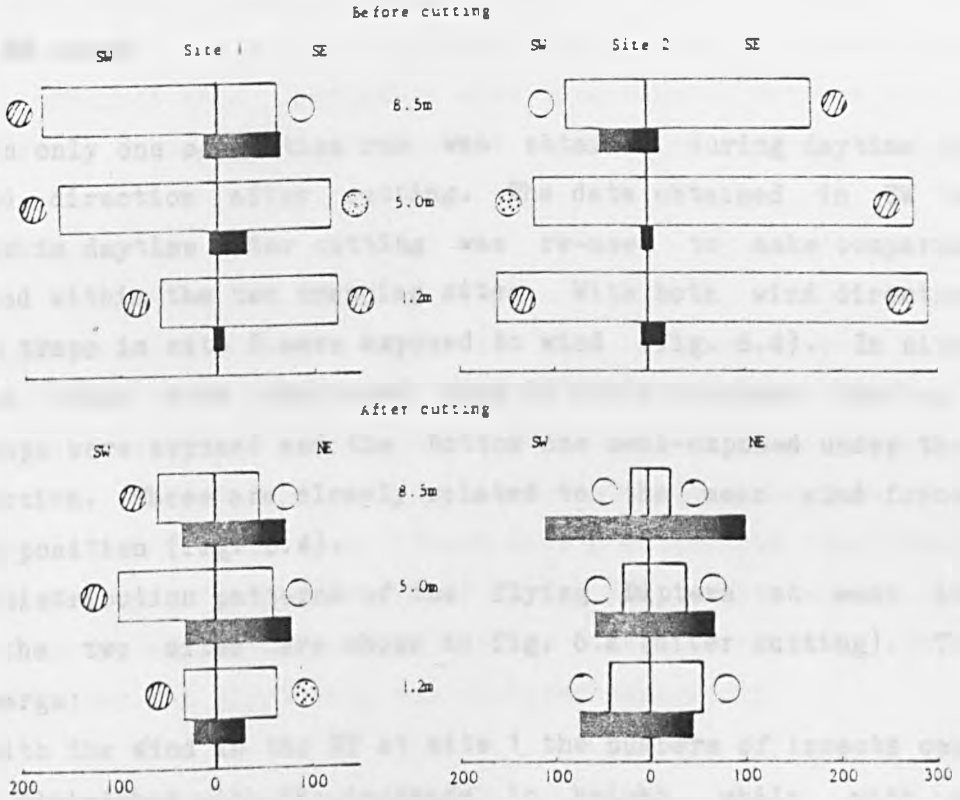

Figure 6.4. Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps in daytime under south-westerly winds (SW), south-easterly winds (SE) and north-easterly winds (NE). The meaning of symbols and numbers as in figure 6.2.

SE winds were much greater than with the SW wind, which exposed the traps;

3) although the distribution patterns under SE winds between the two sites were similar to each other, the total numbers trapped at each level in site 2 were much more than in site 1.

These suggest that the more exposed the traps were, the stronger the wind force and the less frequently the insects occurred.

6.3.1.3 NE winds

Again only one collection run was obtained during daytime under this wind direction after cutting. The data obtained in SW wind conditions in daytime after cutting was re-used to make comparisons between and within the two trapping sites. With both wind directions, all three traps in site 2 were exposed to wind (fig. 6.4). In site 1, the three traps were sheltered from SW winds, whereas the top and middle traps were exposed and the bottom one semi-exposed under the NE wind direction. These are closely related to the mean wind force at each trap position (fig. 6.4).

The distribution patterns of the flying Diptera at each level between the two sites are shown in fig. 6.4 (after cutting). Three points emerge:

1) with the wind in the NE at site 1 the numbers of insects caught generally diminished with the increase in height, while with more insects occurring at middle and top levels when the traps were sheltered from SW winds;

2) at site 2 vertical distribution patterns were much similar, the numbers trapped decreased gradually with height, because the traps at this site were always exposed to both wind directions (fig. 6.4);

3) Compared with the slight increase in average numbers of the insects under the NE wind conditions at each level at site 2, at site 1 the total catch at the top level was smaller, that at the middle level much smaller and that at the bottom level bigger under the NE than under the SW.

Generally speaking, this result agrees with that obtained in the SE winds and the shelter effect is clearly seen.

6.3.2 Phase 2

In 1988, the year after phase 1, the trapping programme was continued, first with the gap in the hedge at site 2 as it was in phase 1b, and then with an artificial hedge of netting erected to a height of the original hedge (3m). In this phase, these were 20 runs under SW wind conditions (11 runs in phase 2a and 9 in phase 2b), 2 runs under SE wind conditions (in phase 2a) and 2 runs with the wind from the NE (in phase 2a). The rest of the collection runs were discarded because they were obtained under changeable wind directions. Between phase 2a and 2b there is a gap of a week when the winds were not from the SW.

6.3.2.1 SW winds

With SW winds, all three traps in site 2 were exposed to wind before netting. After netting the bottom trap was well sheltered, the other two still exposed. In site 1, the three traps were sheltered (fig. 6.5, 6.6). A total of 14 runs were obtained in daytime, 7 runs before netting and 7 after that. There were 6 collection runs obtained at night, 4 before netting, and only 2 after that within which one run was made immediately after netting and the other one obtained in two weeks later. Day and night data was analysed separately.

6.3.2.1.1 Distribution patterns by day

The total number of individuals for each family caught before and after netting in daytime are given in table 6.12. It can be seen that family richness between the two sites was the same, while the total number of individuals for most families was less in site 2 than in site 1. It is also noted that the catch size for most families in both trapping sites were bigger after netting than before netting.

As scatopsids were abundant, and extremely abundant in phase 2b (table 6.12), they have a very big influence on the overall results of this phase. Table 6.13 shows a typical characteristic of this family. They are flying higher than other families, with huge numbers occurring at the top levels in both sites, but especially in site 1 (see also chapter 4 for detail). Table 6.13 also shows that the majority of Scatopsidae appeared after netting. This seems to be due to a change in species composition, with the most abundant species (*Rhegmoclema cooki* Hutson) only reaching maximum abundance after netting. The

Table 6.12. Diptera caught in the daytime before and after netting under SW wind conditions. Numbers in the table are number of individuals (pooling the three levels) and sample size is indicated in brackets.

	Before netting (phase 2a)		After netting (phase 2b)	
	site 1 (control) (7)	site 2 (test) (7)	site 1 (control) (7)	site 2 (test) (7)
Chloropidae	54	90	113	61
Anthomyiidae	37	24	55	20
Cecidomyiidae	300	76	272	214
Ceratopogonidae	299	133	599	118
Chironomidae	144	128	671	402
Dolichopodidae	178	67	164	70
Empididae	80	32	188	33
Fanniidae	13	9	25	3
Muscidae	78	20	138	37
Mycetophilidae	135	17	66	13
Phoridae	75	43	87	32
Psychodidae	118	108	116	201
Scatopsidae	1276	757	11655	1596
Sciaridae	234	109	437	213
Scathophagidae	9	4	11	5
Syrphidae	6	4	48	10
Tachinidae	28	11	11	3

important species before netting were *Scatopse notata* Linn. and *Anapausis soluta* Loew. Whilst the number of scatopsids caught at site 1 increases by nearly tenfold between phase 2a and 2b, it just about doubles at site 2. Since scatopsids are high flyers freqently to be caught in the wind eddy behind a tree (chapter 4), and the high traps

Table 6.13. Number of individuals of Scatopsidae caught in daytime under SW wind conditions. Numbers in the first two columns are mean numbers ± S.D. at each level. Sample size is given in brackets.

		Before netting (7)	After netting (7)	change in %
Site 1	T	158 ± 166	1481 ± 1180	+838.7
	M	21 ± 34	166 ± 137	+702.9
	B	3 ± 6	18 ± 15	+454.5
Site 2	T	92 ± 129	198 ± 191	+115.4
	M	14 ± 19	27 ± 24	+92.1
	B	1.4 ± 1.7	2.8 ± 2.4	+100.0

at site 2 were not sheltered at all in south-westerly winds with or without netting, this result is not surprising. Scatopsids are treated as a special case and therefore are excluded from the following analysis of other dipterans.

The average numbers of the Diptera caught at each level between the two sites are given in table 6.14, and the key features are shown in fig 6.5. Two points emerge:

1) the vertical distribution at site 1 is even in phase 2a but becomes high in phase 2b;

2) the vertical distribution at site 2 is similar between phase 2a and 2b and changes little with addition of the netting.

The principle change is an overall increase in numbers seen also at the control site. This lack of substantial change in vertical distribution doubtless reflects the modest change in vertical wind profile seen on placing the netting (table 6.16, fig. 6.5).

Considering the difference of height between the artificial windbreaks (3m) and the traps at middle (5m) and the top (8.5m) levels, the result seems that the increase in numbers at the bottom is due to the effect of netting (table 6.14).

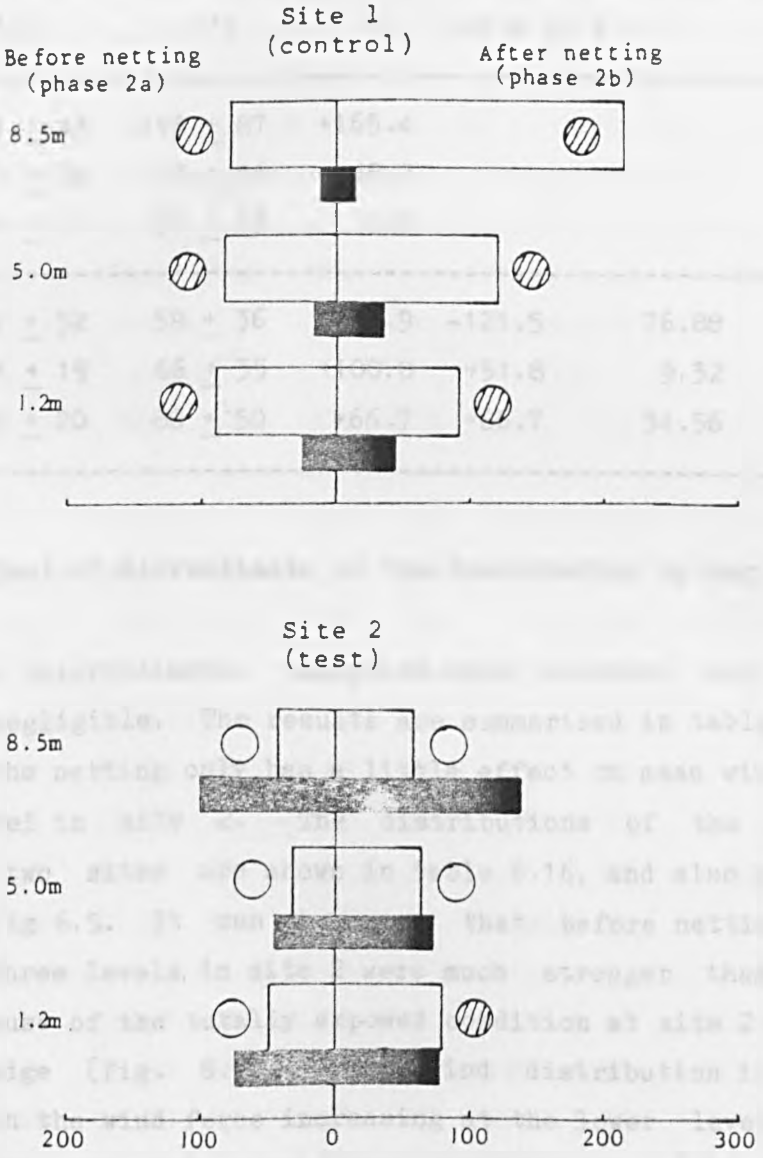

Figure 6.5. Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps in daytime in phase 2 under SW wind conditions. The meaning of symbols, numbers and abbreviations as in figure 6.2.

Table 6.14. Individual Diptera caught in the daytime under SW wind conditions in phase 2 (Scatopsidae was excluded). Numbers in the first two columns are mean numbers ± S.D. at each level. Sample size is given in brackets.

		Before netting (7)	After netting (7)	change %	additional change in site 2 %	value of Chi-squ.	P
Site 1	T	81 ± 43	215 ± 87	+165.4			
	M	83 ± 36	123 ± 56	+48.2			
	B	91 ± 11	91 ± 23	0.0			
Site 2	T	41 ± 52	59 ± 36	+43.9	-121.5	76.88	<0.001
	M	33 ± 19	66 ± 35	+100.0	+51.8	9.32	<0.01
	B	49 ± 20	80 ± 50	+66.7	+66.7	34.56	<0.001

6.3.2.1.2 Effect of microclimate on the distribution by day

The same microclimatic variables were measured and analysed. Rainfall was negligible. The results are summarised in table 6.15. It appears that the netting only has a little effect on mean wind force at the bottom level in site 2. The distributions of the wind force between the two sites are shown in table 6.16, and also graphically presented in fig 6.5. It can be seen that before netting the wind force at all three levels in site 2 were much stronger than those in site 1, because of the totally exposed condition at site 2 due to the gap in the hedge (fig. 6.5). The wind distribution in site 1 is unexpected with the wind force increasing at the lower levels although the differences are not significant statisticaly (fig. 6.5). The reason for this is not clear, but might be due to the thick leaf layer in the growing season preventing SW winds penetrating the main leaf layer (top and middle levels). The same wind distribution was seen at the same site at night (table 6.20) and with the wind from the SE at site 2 (fig 6.7).

The final phase after netting was windier than the phase 2a, and average winds were higher at all locations. The increase is lowest at the lowest trap at site 2, which should be sheltered by the netting, and various between 25 and 107% elsewhere (table 6.16). The variability is thought to reflect minor differences in wind direction and consequent changes in eddy patterns, but the lowest position at site 2, supposedly sheltered by the netting is still slightly windier than it was before netting the hedge (table 6.16). This might be due to the wind eddy caused by the netting itself.

Table 6.15. The effect of netting on physical factors in the daytime. Comparison of physical variables at three levels (T = top, M = middle and B = Bottom) in two trapping sites (S1 = site 1 and S2 = site 2) between before netting (BN) and after netting (AN) under SW wind conditions. Numbers in the table are the difference between group means (DIF). * = significant at $P < 0.05$ and NS = not significant. Statistical methods used are as in table 6.4.

	Comparison	Mean wind force r min^{-1}		Mean temperat. °C		Mean light intensity Lux		Mean RH %	
		DIF	SIG	DIF	SIG	DIF	SIG	DIF	SIG
	BN S2 - S1	89.74	*	-1.49	NS	901.6	NS	-0.28	NS
T	AN S2 - S1	115.91	*	-1.51	NS	-0.2	NS	-0.27	NS
	S1 AN - BN	3.00	NS	0.81	NS	2.1	NS	0.48	NS
	S2 AN - BN	29.17	NS	0.79	NS	-899.7	NS	0.49	NS
	BN S2 - S1	28.53	NS	-0.43	NS	2.7	NS	-0.32	NS
M	AN S2 - S1	37.82	NS	-0.73	NS	711.2	NS	-0.21	NS
	S1 AN - BN	18.16	NS	0.54	NS	-611.8	NS	0.43	NS
	S2 AN - BN	27.45	NS	0.23	NS	96.6	NS	0.54	NS
	BN S2 - S1	50.33	*	-0.01	NS	811.5	NS	-0.21	NS
B	AN S2 - S1	30.88	NS	0.33	NS	1150.6	NS	0.17	NS
	S1 AN - BN	21.70	NS	0.41	NS	-962.3	NS	0.40	NS
	S2 AN - BN	2.25	NS	0.75	NS	-623.2	NS	0.78	NS

The data on flying Diptera and physical variables at site 2 are treated in the same way as in phase 1. Only the mean wind force is significantly correlated with the abundance of the insects at top and bottom levels (table 6.17). Multiple regression included both wind and the variability of the wind at the bottom level; wind explained 44% of the variability of the catches at both top and bottom levels (table 6.17). Though the abundance of the flying Diptera increased at the middle level after netting (table 6.14) no relationship between the insects and the physical factors can be found (table 6.17). In addition table 6.15 and 6.16 show no significant changes of the physical factors at the middle and the top levels after netting. Thus it seems that the abundance of the insects at top and middle levels are independent of the netting, although 43.6% of the variance is accounted for by the wind at top level (table 6.17).

Table 6.16. Wind force in daytime under SW wind conditions in phase 2. Numbers in the first two columns are mean anemometer revolutions ± S.D. at each level. Sample size is shown in brackets.

		Before netting (7)	After netting (7)	change in %	Change related to top trap at site 2 (%)
Site 1	T	11.9 ± 14.4	14.9 ± 11.9	+25.2	-3.5
	M	16.9 ± 11.7	35.1 ± 32.1	+107.7	+79.0
	B	24.4 ± 17.9	46.1 ± 38.3	+88.9	+60.2
Site 2	T	101.6 ± 51.2	130.8 ± 75.8	+28.7	----
	M	45.5 ± 19.6	72.9 ± 48 7	+60.2	+31.5
	B	74.3 ± 30.2	77.1 ± 43.3	+3.6	-25.1

6.3.2.1.3 Distribution patterns by night

Table 6.18. shows similarities to the daytime results of table 6.12; most families were more numerous in the shelter at site 1 than at exposed site 2. It is also shows that most families were less abundant in the second period after netting, at both sites. Chironomids and

Table 6.17. Independent microclimatic variables used in stepwise multiple regressions against daytime abundance of flying Diptera during phase 2 at site 2. Pearson correlation coefficients are given above, and regression values below. Stdwind = standard deviation of mean wind force. n = 14.

	Top	Middle	Bottom
Mean wind force	-0.660 **	-0.271	-0.490 *
Mean temperature	0.180	0.095	0.398
Mean light Intensity	-0.152	-0.180	-0.021
Mean relative humidity	-0.213	-0.253	-0.027
Stdwind	-0.218	-0.117	-0.439

* P < 0.05; ** P < 0.01.

		SPRC	S.E.	F	P	PR(%)
Top	Intercept	2.0113				
	mean wind	-0.0039	0.0013	9.27	0.0102	43.6
Bottom	Intercept	2.4137				
	mean wind	-0.0029	0.0013	5.09	0.0453	23.9
	stdwind	-0.0177	0.0087	4.47	0.0479	20.9

ceratopogonids were more abundant in the final phase. The average numbers of all flying Diptera at three levels at each site is presented in table 6.19, and also shown in fig. 6.6. It can be seen that there are lower numbers in the final phase at all levels, and may be reasonably described as due to smaller populations or conditions generally less favourable to flight. The decline is least marked at the bottom trap at site 2, where the decline is not significant. So

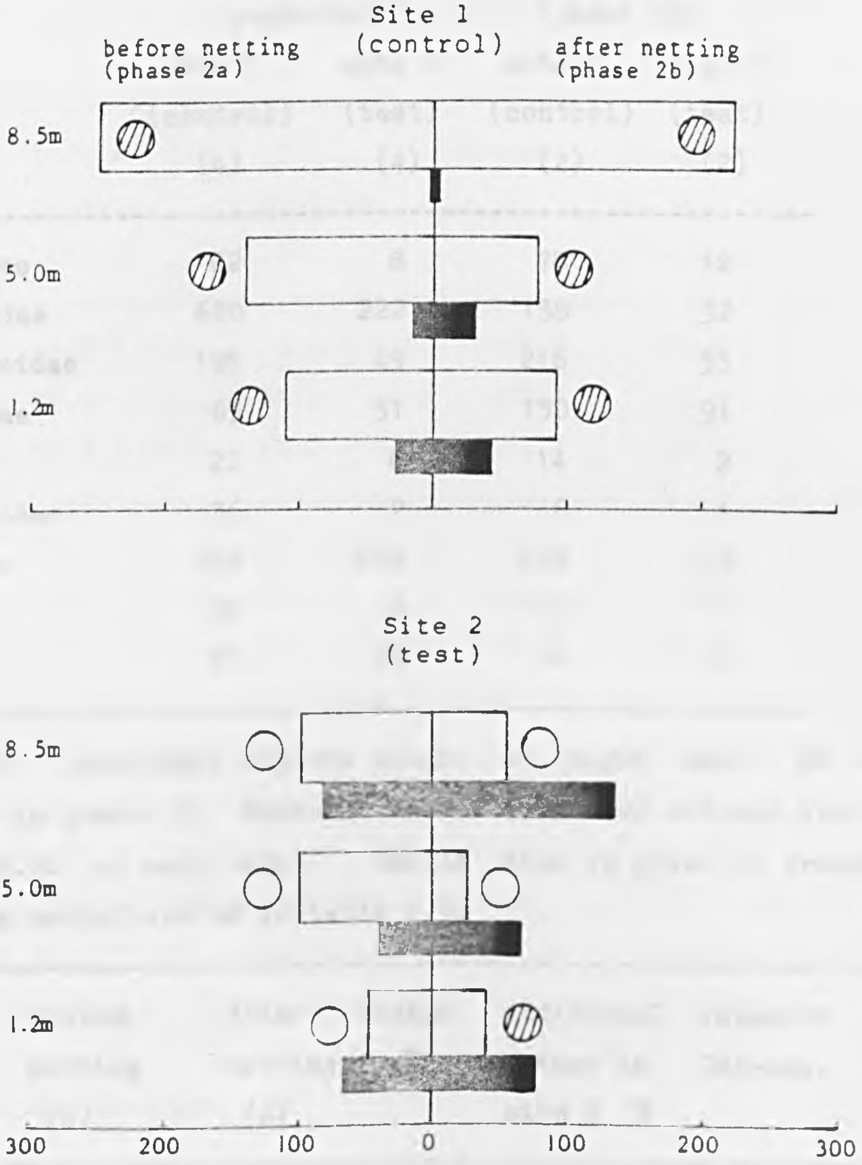

Figure 6.6. Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps at night in phase 2 under SW wind conditions. The meaning of symbols, numbers and abbreviations as in figure 6.2.

Table 6.18. Diptera caught at night before and after netting under SW wind conditions. Numbers in the table are number of individuals (pooling the three levels) and sample size is indicated in brackets.

	Before netting (phase 2a)		After netting (phase 2b)	
	site 1 (control) (4)	site 2 (test) (4)	site 1 (control) (2)	site 2 (test) (2)
Anisopodidae	62	8	78	12
Cecidomyiidae	620	222	138	32
Ceratopogonidae	195	49	216	33
Chironomidae	65	51	130	91
Empididae	22	6	14	2
Mycetophilidae	36	2	6	1
Psychodidae	903	604	163	73
Sciaridae	20	8	10	1
Tipulidae	95	33	34	2

Table 6.19. Individual Diptera caught at night under SW wind conditions in phase 2. Numbers in the first two columns are mean numbers ± S.D. at each level. Sample size is given in brackets. Calculating method are as in table 6.3.

		Before netting (4)	After netting (2)	change %	additional change in site 2 %	value of Chi-squ.	P
Site 1	T	250 ± 184	224 ± 83	-10.5			
	M	142 ± 135	78 ± 33	-45.2			
	B	113 ± 38	94 ± 54	-17.5			
Site 2	T	99 ± 96	57 ± 29	-42.8	-32.3	13.41	<0.001
	M	100 ± 101	28 ± 12	-72.4	-27.2	15.95	<0.001
	B	48 ± 46	40 ± 11	-16.8	+0.7	0.003	>0.90

there is an indication of a weak effect of the netting on insect catches, but it is not conclusive. Reference to table 6.20 shows that

Table 6.20. Mean wind force at night under SW wind conditions in phase 2. Numbers in the first two columns are mean anemometer revolutions ± S.D. at each level. Sample size is shown in brackets.

		Before netting (4)	After netting (2)	change %	Change related to top trap at site 2 (%)
Site 1	T	2.0 ± 1.8	3.9 ± 4.8	+95.0	+29.0
	M	15.3 ± 15.1	30.2 ± 40.0	+97.4	+31.4
	B	22.9 ± 22.5	44.0 ± 56.6	+92.1	+26.1
Site 2	T	81.5 ± 55.5	135.3 ± 74.4	+66.0	----
	M	40.4 ± 22.3	66.9 ± 57.5	+65.4	-0.6
	B	67.2 ± 38.2	88.5 ± 50.2	+31.7	-34.3

the netting has given rather little shelter to the bottom trap at site 2, so the lack of effect on the Diptera fauna could be due to the inefficiency of the windbreak used. As only two runs were obtained in phase 2b at site 2, it is not possible to do any statistical analysis of the distributions of the insect with the physical factors.

6.3.2.2 SE and NE winds

Under these two wind conditions, the degree of shelter of each trap corresponded to similar wind conditions in phase 1 (fig 6.4). This is indicated in fig. 6.7 with the mean wind force at each trap position. Two collections were made with the wind from the SE before netting, one in the daytime and the other at night. In both winds were light (wind < 70 revolutions/min). For comparison, data from six runs in light SW winds before netting were used, three runs in the daytime and the other three at night.

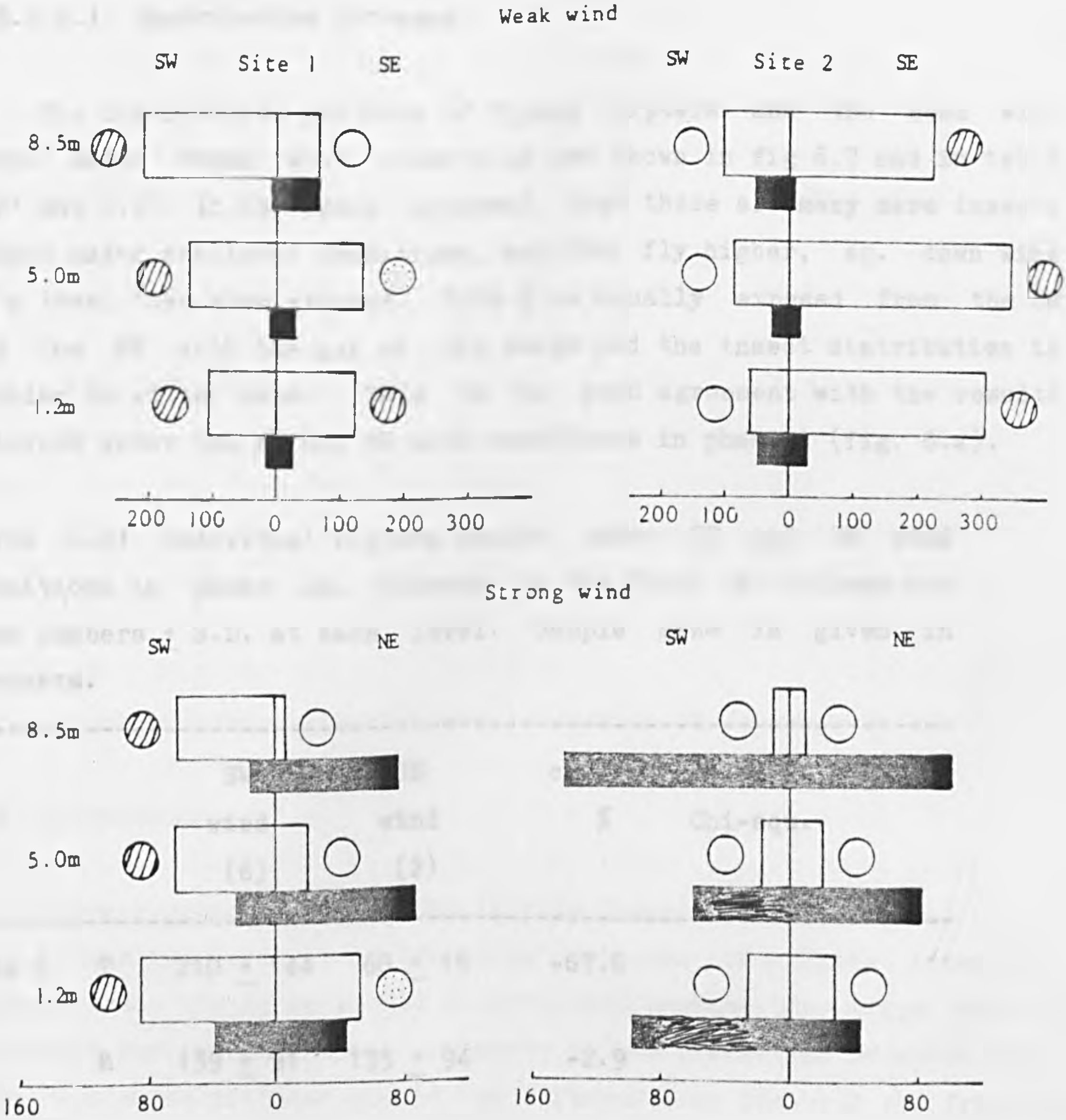

Figure 6.7.Distribution patterns of Diptera and wind force, and the degree of shelter of suction traps before netting under south-westerly winds (SW), south-easterly winds (SE) and north-easterly winds (NE). The meaning of symbols and numbers as in figure 6.2.

Two collections were obtained with the wind from the NE in the daytime in strong wind condition (wind > 100 revolutions/min) before netting. For comparison, data from 5 daytime runs with SW winds of similar strength before netting were selected.

6.3.2.2.1 Distribution patterns

The distribution patterns of flying Diptera and the mean wind force under these wind conditions are shown in fig 6.7 and in table 6.21 and 6.22. It is again apparent that there are many more insects caught under sheltered conditions, and they fly higher, eg. down wind of a tree, than when exposed. Site 2 is equally exposed from the SW and the NE with the gap of the hedge and the insect distribution is similar in either case. This is in good agreement with the results obtained under the NE and SE wind conditions in phase 1 (fig. 6.4).

Table 6.21. Individual Diptera caught under SE and SW wind conditions in phase 2a. Numbers in the first two columns are mean numbers ± S.D. at each level. Sample size is given in brackets.

		SW wind (6)	SE wind (2)	change %	Value of Chi-squ.	P
Site 1	T	210 ± 144	68 ± 15	-67.6		
	M	139 ± 91	135 ± 94	-2.9		
	B	110 ± 23	123 ± 48	+11.8		
Site 2	T	105 ± 68	224 ± 116	+112.9	338.65	<0.0001
	M	90 ± 71	346 ± 171	+284.4	240.43	<0.0001
	B	65 ± 28	304 ± 167	+367.7	217.58	<0.0001

Table 6.22. Individual Diptera caught in daytime under NE and SW wind conditions in phase 2a. Numbers in the first two columns are mean numbers ± S.D. at each level. Sample size is given in brackets.

		SW wind (5)	NE wind (2)	change %	additional change in site 2 %	value of Chi-squ.	P
Site 1 test	T	62 ± 17	7 ± 2	-88.7	-75.1	33.42	<0.001
	M	63 ± 34	21 ± 0	-66.7	-80.6	24.54	<0.001
	B	85 ± 16	54 ± 8	-36.5	-36.5	5.2	<0.05
Site 2 control	T	11 ± 6	10 ± 8	-13.6			
	M	18 ± 9	21 ± 11	+13.9			
	B	28 ± 11	28 ± 5	0.0			

6.4 Discussion

Three hypotheses are tested in this Chapter:

1) the two vertical distribution patterns of flying insects in relation to the trees should be different because the traps are in different shelter conditions relative to the prevailing SW winds (fig. 6.1a) and these patterns should be reversed when the wind was from the south east due to reversal of the exposure conditions, and became similar due to similar lack of shelter with winds from a northerly direction.

2) cutting a channel through the vegetation would reduce the wind shadow and accentuate the difference in the vertical distributions in SW winds;

3) replacing the vegetation removed in phase 1 by an artificial windbreak should restore the vertical distribution at the experimental site to that observed before cutting the hedge, if the physical effect

was more than the biological effect.

Depending upon wind direction more dipterans were caught at one site or the other, but both sites provided similar diversity of families. Clearly this reflects to the similar plant constitution of two trapping sites (table 6.1). With SW wind conditions (figs 6.2, 6.3) both during daytime and night, most individuals tended to occur at the top and the middle levels at sheltered site 1, but flew lower at exposed site 2. Patterns like these but in reverse are also seen in SE wind conditions (fig 6.4, before cutting; fig. 6.7). In addition, with the wind from the NE, when both sites were exposed to wind, few insects were caught and tended to fly lower (figs 6.4 and 6.7), and similar vertical distribution patterns were found at the two sites. The suggested explanation is that the insects were avoiding exposure to the wind, and the traps were in different degrees of exposure (figs 6.2, 6.3, 6.4 and 6.7). From these figures the catches are obviously larger where the measured wind is lower at both sites. Therefore it is suggested that the different distribution patterns found in phase 1a are mainly due to the effect of shelter, in agreement with the first hypothesis.

In phase 1b, the control patterns at site 1 both during the day and at night are shifted downwards compared with the patterns in phase 1a, but most Diptera were still caught at the middle level (fig 6.2 and 6.3). The numbers were reduced at all levels, and both of these effects are in agreement with the sensitivity of dipteran catches to wind and temperature (see chapter 5), the wind being higher on average in the second phase and the temperature lower (tables 6.4, 6.9). The numbers at each level at the experimental site all decreased substantially in phase 1b (tables 6.3 and 6.8). These reductions are much stronger than those at the control site.

This shift of the stratification pattern of the insects in site 1 (fig. 6.2) can be mostly explained by the higher wind force experienced in the second phase discouraging flight at all levels, particularly the top level. Also, this shift could be related to a loss of efficiency of the top suction trap in high wind (Taylor 1962). Using the information provided by this author the daytime insect catches (table 6.3) have been used to calculate the absolute insect densities, assuming average wind speeds as in table 6.5 and average insect size (based upon table 6.2 and the sizes of common specimments caught). The results, in numbers of insects per 10^4 cu.ft. of air, are shown in table 6.23, whilst the wind speed effect is substantial, reducing trap efficiency by up to 60% at the windiest position, the effect of cutting is still clear. It must be noted that the 9-in suction trap used in this study, being a little different from the one Taylor used for this correction, was with a conical hat 23cm above the orifice of the netting cone (fig 2.2) which can reduce the effect of cross-winds. Therefore reduced trap efficiency at the windiest position must be less than 60%. Since other situations and times are less windy the effects of reduced efficiency will be smaller and whilst undoubtedly contributing to the observations it is not principal cause, but the changes must be explained largely by the effect of wind upon abundance. Over 80% of the variability of the abundance of Diptera was accounted for by the wind (table 6.6 and 6.11), which also supports the second hypothesis.

Table 6.23. Individual Diptera per 10^4 cu.ft. of air caught in daytime under SW wind conditions. Original data are shown in table 6.3.

		Before cutting (3)	After cutting (3)
Site 1	T	204.2	86.7
(control)	M	184.9	113.2
	B	65.0	38.0
Site 2	T	128.5	64.2
(test)	M	139.0	53.3
	B	180.7	83.8

The cutting removes physical shelter. It directly lowers the boundary layer, and might be expected also to decrease the temperature because of increased evaporation. However the latter is not apparent in the data here; the reduced temperature at both sites are mainly due to cooler weather (table 6.4 and 6.9). These factors will affect the flight activity of the insects, and these are particularly reflected to the night Diptera (table 6.11). Taylor's "insect boundary layer" (Taylor 1958, 1960, 1974) is useful to explain the pattern changes in relation to different wind conditions. Each species has its own boundary layer depending on its performance characteristics, and changes in distribution can be seen as resulting from boundary layer changes due to shift in wind direction, wind force or management of the environment. At site 1 which was well sheltered from SW winds between phase 1a and 1b, the wind was light, this layer was deeper and most insects flew freely towards the middle and the top levels of tree 1 where the biological attractiveness is probably of importance (fig 6.2 and 6.3). In contrast, in semi-exposed site 2 before cutting where the wind moved faster, this layer for most species was shallow, and they tended to fly lower (fig 6.2 and 6.3). This phenomenon can be seen even more clearly after cutting, when all the traps are exposed to wind,in both day and night collections (fig 6.2 and 6.3). Also this general rule applies to all the patterns obtained in SE and NE wind conditions very well (fig 6.4 and 6.7).

It is worthwhile looking at the other possible effects of the cutting. The cutting will have lowered the biological attractiveness of site 2 for some species, by removing food and reproduction sites (courtship, oviposition for example). Pollard (1968) reported that a reduction in total numbers and biomass of the associated fauna in the second and third years after removal of the bottom flora in a hawthorn hedgerow. To cut the hawthorn hedge at site 2 it was necessary to clear some of the ground vegetation near tree 2 to gain access to it, but this management is thought not to be the main cause of such sharp changes since the cleared area was only 21 m^2. Another way of seeing the effect of this clearance is to examine the fauna before and after cutting when the wind from the NW and both of traps were subject to similar degree of shelter. Only two such collections were obtained, both in the daytime, one before cutting and one after. These are shown in table 6.24. It can be seen that the same families are represented and the number of individuals in most families before and after cutting is similar. The sciarids and bibionids and chloropids are less frequent after cutting, but this might be due to the drop in temperature (table 6.24).

Table 6.24. Diptera caught in phase 1a and 1b at site 2 in daytime under NW wind conditions. Numbers in the table are number of individuales caught at three levels.

	Before cutting (phase 1a)	After cutting (phase 1b)
Chloropidae	11	5
Anisopodidae	1	4
Anthomyiidae	1	2
Bibionidae	16	7
Cecidomyiidae	21	21
Ceratopogonidae	19	16
Chironomidae	37	40
Muscidae	3	4
Mycetophilidae	7	5
Phoridae	30	21
Psychodidae	31	47
Scatoposidae	4	5
Sciaridae	231	148
Scathophagidae	0	1
Average wind (R min^{-1})	45.3 ± 29.4	44.1 ± 22.8
Average tempe. (°C)	14.6 ± 0.2	12.6 ± 0.2
Average light (Lux)	6887.9 ± 2116.4	6801.3 ± 1727.4
Average RH (%)	84.0 ± 4.6	84.7 ± 3.5

The cutting may also affect the architecture of the site, and therefore the behaviour of flies which swarm on 'landmarks' (Colyer and Hammond 1968). A few branches of tree 2 were removed up to 5m high and the 7 metre long gap in the hedge might be seen as changing such landmarks. However, the most prominent features of this micro-landscape were not altered , and these are likely to be the most important in swarming behaviour.

At the control site in phase 2a, both the vertical wind profile and the insect distribution differ to that observed in phase 1b both during day and night (fig 6.5 vs 6.2; 6.6 vs 6.3). This difference of wind pattern between phase 1b and 2a at the control site are most likely to be due to differences of the developing stages of the crown of the tree and of wind conditions. In the late September of phase 1b, the leaves had just begun to fall, and the crown was thinning out. This would allow an increase in permeability. In contrast, in phase 2a of June-July 1988 the tree crown was at its maximum density and formed a relative impermeable barrier blocking the air flow through it. Also the wind was only moderate during phase 2a (2m/sec, table 6.16), and therefore was less capable of passing through the tree crown in any case. These factors may account for the inversion of the wind profile seen in phase 2a compared to phase 1b.

The differences of vertical stratification of insects at the control site between phase 1b (Scatopsidae was included since they occurred in very small numbers (table 6.2)) and phase 2a (Scatopsidae was excluded, see text for reason) could be caused by several things. Differences in the wind profile (as above) is one such factor. Another is that phase 1b was in late September when the leaves of the vegetation such as were left became old and tough, and the flowers had gone, resulting in little biological attraction for the insects. In contrast, phase 2a was in June and July the next year when new leaves and new shoots were present, honeydew was available due to aphid colonization on the lime tree and many plants of the undergrowth were in flower. In the autumn the pattern would be influenced mostly by physical factors, especially the wind, with most insects caught in shelter, whereas in the spring the biological effects would have been stronger, as a result the flies were almost equally distributed between three levels. Also the species constitution of the flying Diptera community between phase 1b and 2a may have differed enough to cause this difference in control tree patterns. Because of this clear discrepancy occurred between the phase 1b and 2a in control site 1, the discussion is not pursued further in experimental site 2.

The attempt to fill the gap in the hedge using an artificial windbreak did not proved very satisfactory. With the wind in the SW the proportion of permeability of the middle and bottom levels of site 2 before cutting was 15% and 6% respectively to that at the top level (table 6.5). After cutting the proportion were 58% and 70% (table 6.5). With the gap filled with the artificial windbreak the proportion were 56% and 59% (table 6.16) showing that the plastic netting was much less effective a windbreak than the hedgerow and Prunus suckers. Against this background and the changes in abundance of dipterans and their vertical distribution at the control site between phases 2a and 2b, the modest change in abundance and distribution at site 2 must be regarded as inconclusive, and it cannot be said from these results to what extent the effects of the hedge are purely physical, providing shelter from the wind, and to what extent they are biological, providing some attractive resource.

Clearly the results, involving the changes of distribution in phase 1 and 2 under different wind conditions (fig 6.2 - 6.7), cannot be explained in terms of the result obtained by Bowden and Dean (1977) that the pattern of distribution of flying insects appeared to be determined primarily by the comparative richness of the vegetation surrounding trapping sites irrespective of the speed and direction of the wind.

The trapping sites used here are floristically very similar (fig 6.1 and table 6.1), and this is reflected in the very similar family diversity of flying Diptera (tables 6.2, 6.7). If the richness of the vegetation had a primary influence on the distribution of the insects, it would have been expected that the distribution patterns between site 1 and 2 in different wind conditions would be similar since the three traps at each site were all at the same distance to the same species of tree. But they are not. Instead these patterns varied in great deal with the wind direction, so that there were always more insects caught at sheltered traps (fig 6.2 - 6.7). Even if the scatopsid pattern is independent of the netting, the abundance of the family between two trapping sites is still dependent on shelter (table 6.13). The difference between these results and those of Bowden & Dean (1977) might be caused by the different insect indicators used; all Diptera caught (which comprised 91.5% of the suction trap catch) were used in this study, while Neuroptera, large Diptera, Syrphidae and others were used in Bowden & Dean's study. Another possible significant difference are the locations of the study sites with consequent difference of habitats between this study and that carried out by Bowden and Dean.

On the other hand, the change in the vertical distribution patterns of Diptera in SW, SE and NE wind conditions in phase 1 and 2 (figs 6.2 - 6.7) evidently suggest that the more sheltered the traps were, the weaker the wind force and the more abundant the insects were.

Although this result cannot be directly compared with those obtained by Lewis (1969b, 1970) since the traps used here were placed vertically in relation to emergent hedgerow trees, while the traps he used were arranged horizontally behind a hedgerow, it supports the hypothesis that the accumulation of small airborne insects in sheltered places, is probably caused when the insects wonder into the recirculating air behind barriers (Lewis 1970; Lewis & Dibley 1970).

6.5 Summary

1) Effect of shelter on the distributions of flying Diptera in different wind conditions is amply demonstrated.

2) The effect of wind speed is apparently correlated with effect of shelter. Changes of vertical distribution patterns of flying Diptera are dependent on the degree of shelter.

3) Cutting the hedgerow increased exposure at experimental site 2 to SW wind; the numbers of Diptera are much reduced compared to the control site 1, although all were reduced by cold and windier conditions.

4) The netting experiment is essentially inconclusive; possible reasons for this are discussed.

Chapter 7

DISTRIBUTION PATTERNS OF FLYING DIPTERA CLOSE TO A REAL AND AN ARTIFICIAL TREE IN DIFFERENT WIND CONDITIONS

7.1 Introduction

In the chapters on "Spatial and temporal distribution patterns of flying Diptera" (Chapter 3) and "The effect of microclimate on flying Diptera" (Chapter 4 and 5), it was shown that the majority of taxa were most numerous in the lee of the tree and at the height of the main leaf layer. In Chapter 6 on "Effect of shelter on distribution of flying Diptera", it suggested that changes of vertical distribution patterns of the flying insects were dependent on the degree of shelter offered by emergent hedgerow trees. Therefore the conclusion was reached that such trees have a significant influence in the life of flying Diptera, not merely as physical objects, but as biological entities. However, it remains to be seen whether isolated trees are similarly influential. So far little has been reported about the distribution of flying insects around isolated trees, although there is plenty of qualitative evidence for the importance of such trees in the lives of animals (e.g. Elton, 1966).

Predictions in the literature suggest that flying insects will be more abundant around a real tree than an artificial one in sheltered or in low wind conditions, because of biological attraction (Bowden & Dean 1977; Hawkes, 1973) and that this preference for the real tree will break down in exposed conditions, because of the effect of wind (Lewis & Stephenson, 1966). To test these predictions an artificial 'tree', made of green plastic netting, was erected near to small isolated hawthorn tree in Bond Ing meadow, to enable a comparison to be made between distributions of flying insects about each of these.

7.2 Materials and methods

The observations were carried out in the hay meadow area of Bond Ing (see General Methods of Chapter 2). An isolated six metre high hawthorn (Crataegus monogyna Jacq.) was chosen as the 'real tree'. An artificial tree of similar height was constructed, occupying the area of 15.6 M^2 of the meadow. The hawthorn tree was also in the hay meadow area, in an isolated position about 20m away from hawthorn hedgerows, a high Prunus bush and hedgerow trees (fig. 2.1). It is important to note that the tree grew out of a thick patch of bramble (Rubus fruticosus Agg.) with dogwood (Thelycrania sanguinea L.), creeping thistle (Cirsium arvense (L.) Scop.) and stinging nettle (Urtica dioica L.). The area of this patch was 16 M^2. The tree and brambles together made a substantial obstacle. The artificial tree was made of fine mesh plastic (Netlon) mounted on scaffolding in the shape of a triangle to provide a similar profile from the direction of the prevailing wind as the hawthorn tree (figs 2.1, 7.1). It was erected 10m to the east side of the hawthorn tree in the mown area. The grass at the base of the artificial tree was cut and removed to reduce potential biological attraction.

7.2.1 Arrangement of study equipment

Two scaffoldings were used to carry experimental equipment. One was erected one metre away from the foliage of the real tree on the NE side. and the other one was one metre from the same side of the artificial tree. Both were six metres high (figs 2.1, 7.1).

Four nine-inch diameter suction traps were suspended on the scaffoldings, the top two traps with their intakes at 5.0m and the bottom two at 1.2m from the ground. They were all one metre away from the foliage or the netting of the trees. Four outstations (see General Methods, Chapter 2) were hung on the scaffoldings at the same level and one metre apart from each of the correspondent suction traps (fig. 7.1)

7.2.2 Trapping programme and sampling methods

Observations were made from 5 - 25 August in 1988. Two collection runs were made each day: 09:00 - 18:00 (daytime) and 19:00 - 06:00 (night) GMT, following the regime reported previously in this study. The collecting jars, filled with 70 ml of 70% alcohol, were emptied twice daily at the end of each run. All the Diptera from each jar were separated out; most of them were sorted to families, genera and some to

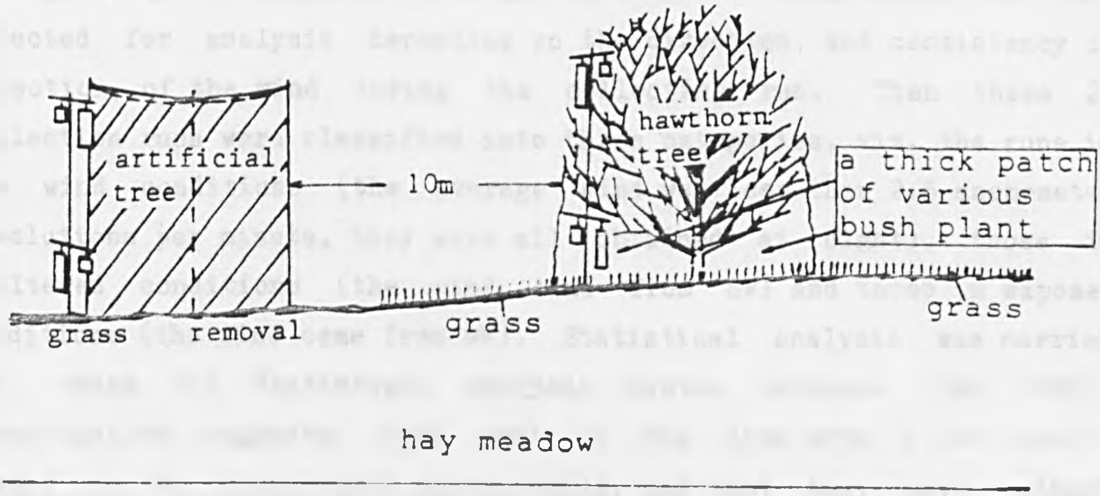

Figure 7.1. The position of suction traps in relation to the real and artificial trees. ▯ = suction trap and □ = micro-meteorological outstation. They were all one metre away from the SE side of the foliage of the trees.

species. Meteorological data was recorded in the same way as those described in previous chapters.

7.2.3 Data treatment

A total of 36 collection runs were made, from which 25 were selected for analysis depending on the direction, and consistency of direction, of the wind during the collecting run. Then these 25 collection runs were classified into three categories, viz. the runs in low wind conditions (the average wind was less than 2.5 anemometer revolutions per minute, they were all obtained at night), those in sheltered conditions (the wind came from SW) and those in exposed conditions (the wind came from NW). Statistical analysis was carried out using the Statistical Analysis System packages (SAS 1985). Investigation suggested that most of the data sets of the insects tended to be distributed non-normally, but that they were almost normalized by transformation to base 10 logarithms. Such transformation was therefore applied to all insect data before analysing with physical variables. Multiple regression has been used to determine which of a set of selected physical factors were most important in affecting the distributions of the insects. Spatial distribution was included in the analysis by creating a dummy variable for it using the CLASS statement in the GLM procedure of SAS, under which the variables selected for the model were incorporated in order of their contribution to R^2. To test the significance of differences of the insect abundances at different levels or between trees the data was first ranked (SAS PROC RANKS) and then analysed by ANOVA. This corresponds to Friedman's two way ranking method (Conover, 1980; SAS 1985).

7.3 Results

7.3.1 Low wind condition

Six collection runs of insects along with six runs of measurements of microclimatic factors were made under low wind conditions. They were all in night periods (winds are generally stronger in the daytime, and calm conditions were seldom recorded by day during August 1988).

7.3.1.1 Distributions of flying Diptera under low wind conditions

The total catches of each taxon made from the real tree and the artificial one at two levels are given in table 7.1. A total of 16 taxa with 3189 individuals were trapped, with 11 taxa (871 individuals) occurring at the top of the real tree and 10 (1124) at the bottom. 13 taxa (405 individuals) were caught at the top of the artificial tree and 10 (789) at the bottom. The family Cecidomyiidae and the genus Psychoda were found to be the most abundant, and occupied 59.9% and 24% of the total respectively. These two groups were therefore chosen for further analysis. After taking them out, it can be seen that the

Table 7.1. Flying Diptera caught from the real and artificial trees at night in calm conditions. Numbers in brackets are sample size and those in the table are number of individuals.

	Real tree		Artificial tree	
	5.0m (6)	1.2m (6)	5.0m (6)	1.2m (6)
Cecidomyiidae	275	904	184	548
Ceratopogonidae	42	13	17	11
Chironomidae	15	4	8	9
Mycetophilinae	1	12	0	0
Tipulidae	73	11	67	10
Bradysia (Sciaridae)	13	1	4	4
Psychoda (Psychodidae)	280	164	105	193
Anisopus punctatus Fab. (85% of female)	25	3	8	5
Culex territans Walker (male)	145	10	7	6

Note: Numbers of rare families are as follows: Agromyzidae 1(0), Anthomyiidae 1(1), Chloropidae 0(3), Drosophilidae 2(1), Muscidae 0(1), Scatopsidae 0(1) and Sphaeroceridae 0(1). Numbers in brackets are those caught near the artificial tree.

majority of individuals in most of the other common groups (see table 7.1 for detail) tended to be caught at the top of the real tree than elsewhere.

The distribution patterns of Cecidomyiidae and *Psychoda* in relation to the two kinds of the trees are shown in fig. 7.2. The analyses of variance for these two taxa between levels and trees are given in table 7.2. In Cecidomyiidae, from fig. 7.2, it is clear that

Table 7.2. Analysis of variance of total numbers of the Cecidomyiidae and *Psychoda* caught in low wind conditions. n = 24.

	Component	F	P
	Levels	110.77	0.0001
Cecidomyiidae	Trees	6.92	0.0160
	Interaction of level & tree	0.77	0.3909
	Levels	0.74	0.3996
Psychoda	Trees	0.74	0.3996
	Interaction of level & tree	11.85	0.0026

most members of the family were trapped near the real tree ($P < 0.016$ in table 7.2), and at the bottom level ($P < 0.0001$). Further investigation as to the species composition of the family showed that *Clinodiplosis leguminicola* Milne constituted 78% of the total catch of the family at night. So, it has overwhelming influence on the distribution of the group. The *Psychoda* mainly consisted of *Psychoda phalaenoides* Linn., *P. setigera* Tonn. and *P. albipennis* Zett., *P. phalaenoides* being dominant. No significant difference in the catch of *Psychoda* between levels and trees was detected (table 7.2 and fig 7.2). However, from the significance of the interaction of tree and level ($P < 0.0026$ in table 7.2), it seems that the *Psychoda* were more abundant close to the top of the real tree than in the vicinity of the artificial one, as can be seen in fig. 7.2. It also shows that the occurrence of these two taxa was lowest at the top near the artificial

Calm conditions

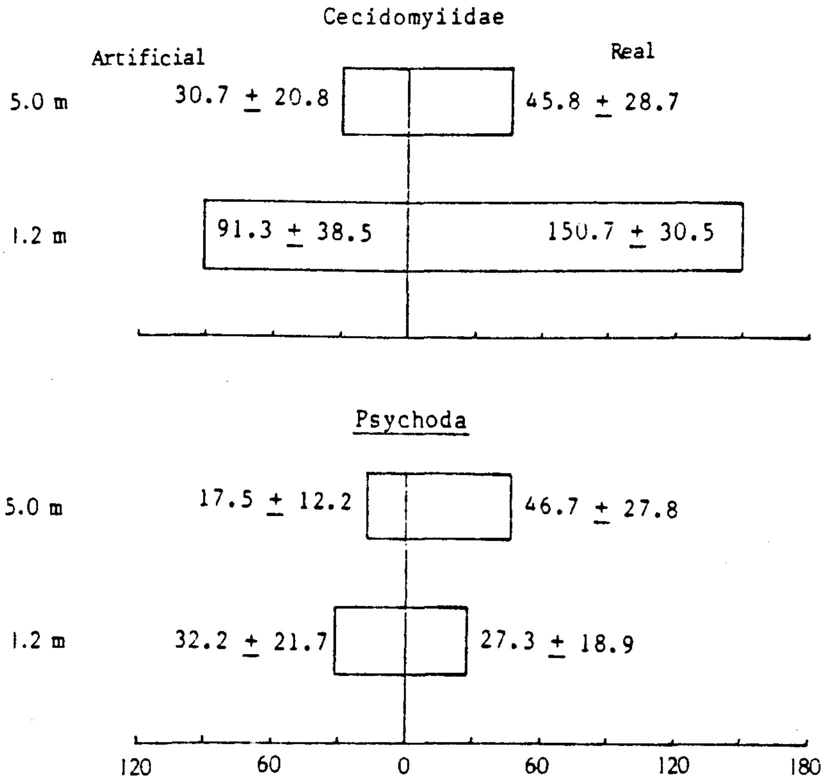

Figure 7.2. Spatial distribution patterns of Cecidomyiidae and Psychoda close to the real and artificial trees. Abscissa values are the mean number of individuals. Numbers by bars are mean ± standard deviation. n = 6.

tree.

7.3.1.2 Physical factors and their effects: low wind conditions

Having established a tendency for association with the real tree in the two most numerous taxa, it is necessary to distinguish whether these differences relate to differences in microclimatic parameters between the two trees or to differences in the biological attractiveness of the trees themselves.

Firstly, four microclimatic factors were taken into consideration, e.g. average wind force, average temperature, average light intensity and average relative humidity. Rainfall was ignored because it was recorded from one standard rain gauge. The

Table 7.3. Measurements of microclimatic factors taken from the real and artificial trees in low wind conditions. Numbers in brackets are the number of observations and those in the table are mean and standard deviation.

		Real tree (6)	Artificial tree (6)
Average wind speed r/min.	5.0m	2.4 ± 1.7	2.0 ± 1.5
	1.2m	0.7 ± 0.4	1.1 ± 0.5
Average temperature °C	5.0m	12.4 ± 2.2	12.4 ± 2.3
	1.2m	11.9 ± 2.4	11.9 ± 2.5
Average light lux	5.0m	119.4 ± 147.4	152.4 ± 202.8
	1.2m	111.9 ± 163.5	152.1 ± 233.2
Average relative % humidity	5.0m	93.3 ± 3.9	93.3 ± 3.8
	1.2m	96.3 ± 4.3	96.3 ± 5.2

distributions of the four microclimatic factors between levels and trees is shown in table 7.3. The only factor differing with statistical significance by ANOVA is wind speed with height. However, there are no differences of the wind speed between the two trees here.

Secondly, the position of traps was considered to see if the occurrence of the insects is related to certain positions. At this stage, four trap positions were included in multiple regression analyses of abundances of the two taxa together with the 4 microclimatic factors. The results from this analysis are tabulated in table 7.4. In the distribution of Cecidomyiidae, 62.4% of the total variability is accounted for by the position of the traps and no other physical variable is found to be significantly related to the distribution of the family. In the *Psychoda*, besides 17.5% of the total variability being accounted for by the mean light intensity, 41.3% of the total variance of the distribution is accounted for by the position of the traps. This suggests that both groups of the insects tend to occur at certain positions consistently, especially most *Psychoda* appearing at the top of the real tree and most cecidomyiids at the bottom of it.

Table 7.4. Multiple regression analysis of Cecidomyiidae and *Psychoda* with physical factors at night under low wind conditions. The analysis included a dummy variable for trap position. Only significant components are shown. n = 24.

	Source of variance	SPRC	F	P	PR(%)
Cecidomyiidae	Position of traps		11.07	0.0002	62.4
Psychoda	Position of traps		6.18	0.0213	41.3
	Mean light	+0.0018	4.67	0.0418	17.5

In low wind conditions, it is concluded that the real tree has significant attraction to Cecidomyiidae, especially the bottom flora of the tree, and has some slight attraction to the second most abundant taxon, the genus Psychoda. It also has obvious attraction to the other common groups, particularly to the males of Culex territans Walker, Anisopus punctatus Fab. and Bradysia (Sciaridae) (table 7.1).

7.3.2 Sheltered condition

When the winds came from the south-west (225° ± 20°) all traps were totally sheltered either by the real tree or by the artificial one. A total of 12 collection runs together with corresponding microclimatic measurements were obtained, of which 7 were in daytime and 5 at night.

7.3.2.1 Distributions of flying Diptera: sheltered conditions by day

The number of individuals caught in each taxon at the two levels by the two trees is shown in table 7.5. A total of 27 taxa with 1828 individuals were obtained, with 19 (688 individuals) occurring at the top of the real tree and 18 (395) at the bottom. 18 (with 317 individuals) appearing at the top of the artificial tree and 23 (428) at the bottom. Bradysia (Sciaridae) and Cecidomyiidae are most abundant, and constitute 37% and 20.6% of the total respectively. Hence much more attention will be given to them. In daytime Campylomyza flavipes Meigen is the dominant species of cecidomyiid and comprises the majority of the catch overall. Only one species in the genus Bradysia is dominant. In addition to these two main taxa, table 7.5 also shows that more individuals of each of the other common taxa were caught near the real tree than by the artificial one except for the males of Dilophus febrilis (Lin.). Also all common taxa except one were more numerous at the top of the real tree than at the bottom. The exception was the Psychoda. This appears mainly due to the biological attractiveness of the leaf layer of the tree. In contrast, most taxa were more often caught low down near the artificial tree. The exception were Dilophus febrilis and Scatopsidae (table 7.5). This distribution seems to represent the effect of shelter provided by the artificial tree.

Table 7.5. Flying Diptera caught from the real and artificial trees during daytime in sheltered conditions. Numbers in brackets are sample size and those in the table are number of individuals.

	Real tree		Artificial tree	
	5.0 m (7)	1.2 m (7)	5.0 m (7)	1.2 m (7)
Agromyzidae	6	2	3	1
Anthomyiidae	2	5	1	5
Cecidomyiidae	42	209	16	109
Ceratopogonidae	62	12	11	46
Chironomidae	37	22	15	30
Phoridae	23	17	9	25
Scatopsidae	109	5	36	14
Bradysia(Sciaridae)	337	62	139	139
Psychoda	21	32	7	22
Dilophus febrilis (Lin.) male	32	0	59	5

Note: Numbers of rare families are as follows: Asteiidae 5(2), Chloropidae 4(4), Dolichopodidae 6(6), Drosophilidae 1(2), Empididae 3(4), Ephydridae 1(2), Fanniidae 1(2), Lonchopteridae 3(3), Micropezidae 1(1), Muscidae 4(10), Mycetophilinae 5(4), Pipunculidae 0(1), Sciomyzidae 0(1), Simuliidae 0(2), Sphaeroceridae 6(5), Syrphidae 4(2) and Tipulidae 2(2). Numbers in brackets are those caught near the artificial tree.

The distribution patterns of the *Bradysia* and Cecidomyiidae are shown in fig. 7.3 (a), and the analyses of variance for the two groups are summarised in table 7.6. It can be seen that most members of the taxa are significantly attracted by the real tree ($P < 0.0001$ for the cecidomyiids and $P < 0.0429$ for *Bradysia*), and that most cecidomyiids concentrate at the bottom levels ($P < 0.0001$), in contrast, the *Bradysia* are more often caught at the top level ($P < 0.0003$), especially in the real tree, which is also emphasized by the interaction of level and tree ($P < 0.0001$), indicating that they fly

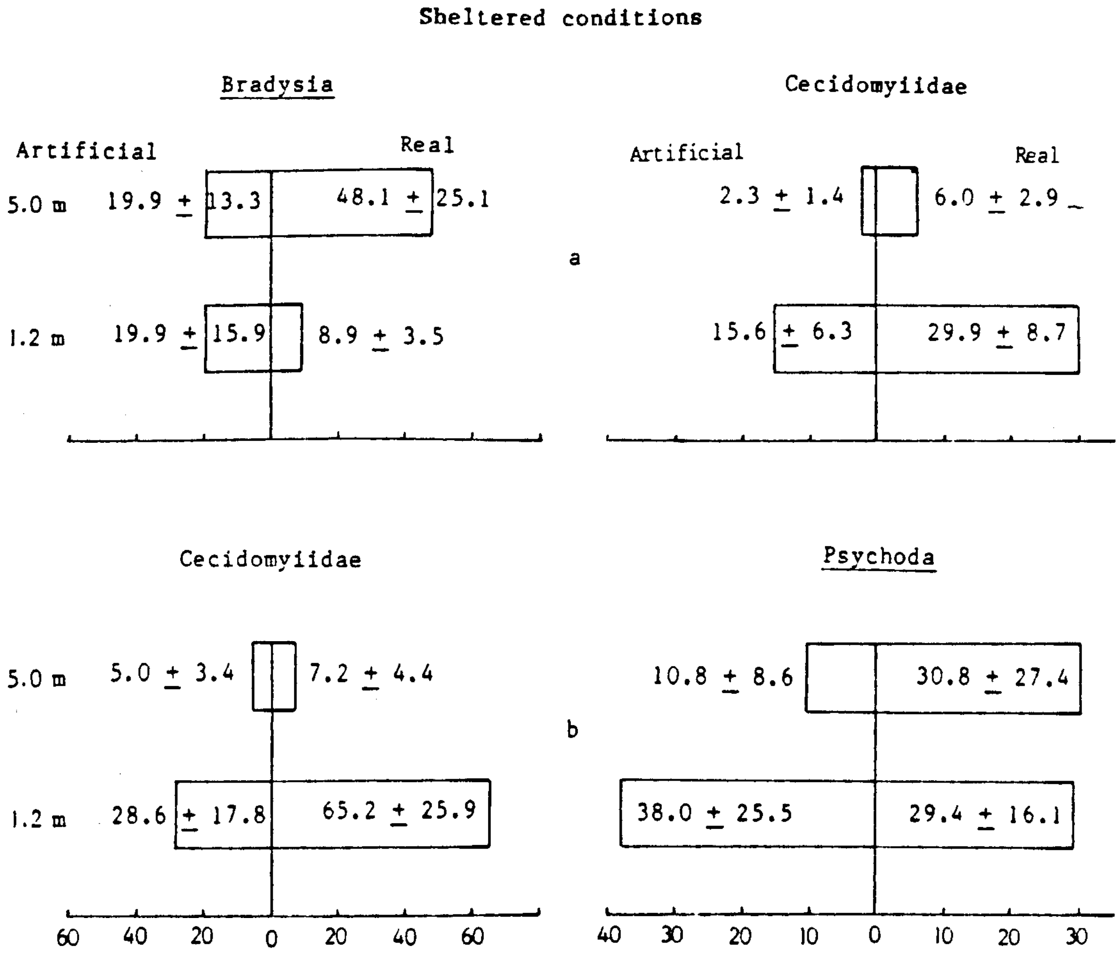

Figure 7.3. Spatial distribution patterns of Cecidomyiidae and Bradysia in daytime (a) and Cecidomyiidae and Psychoda at night (b) in relation to the real and artificial trees. Abscissa values are the mean number of individuals. Numbers by bars are mean ± standard deviation. n = 7 in daytime and 5 at night.

significantly higher in the vicinity of the real tree. The day-flying cecidomyiids are low flyers, while most Bradysia are high ones. Both are attracted by the real tree.

Table 7.6. Analysis of variance of total numbers of Cecidomyiidae and Bradysia caught during daytime in sheltered conditions. n = 28.

	Component	F	P
	Levels	196.00	0.0001
Cecidomyiidae	Trees	25.00	0.0001
	Interaction of level & tree	0.00	1.0000
	Levels	18.29	0.0003
Bradysia	Trees	4.57	0.0429
	Interaction of level & tree	23.14	0.0001

7.3.2.2 Physical factors and their effects: sheltered conditions by day

As before, four microclimatic factors between the two types of trees are used (table 7.7). ANOVA shows that the mean wind force varied significantly between levels ($P = 0.02$) and trees ($P = 0.04$). This shows that the artificial tree was more permeable than the real tree. Mean light intensity was significant only between levels ($P < 0.0001$), because of the bottom traps being given better shelter by the trees during sunny afternoons. No significant difference can be detected for mean temperature and mean relative humidity or mean light intensity between trees.

The next step is to take the position of the traps into consideration together with the four microclimatic variables and to analyse these with the distributions of the cecidomyiids and Bradysia. The results are summarised in table 7.8. In the cecidomyiids, 83.3% of the total variability of the distribution is significantly accounted

Table 7.7. Measurements of microclimatic factors taken from the real and artificial trees in daytime in sheltered conditions. Numbers in brackets are the number of observations and those in the table are mean and standard deviation.

		Real tree (7)	Artificial tree (7)
Average wind speed r/min.	5.0m	47.9 ± 26.8	66.0 ± 30.2
	1.2m	26.3 ± 12.9	45.0 ± 16.6
Average temperature °C	5.0m	17.9 ± 2.8	17.6 ± 2.4
	1.2m	18.5 ± 2.6	18.4 ± 2.9
Average light lux	5.0m	9913.4 ± 1197.4	9912.3 ± 849.3
	1.2m	8108.6 ± 1004.7	8236.8 ± 952.3
Average relative % humidity	5.0m	74.9 ± 8.9	76.0 ± 7.6
	1.2m	72.1 ± 8.2	73.1 ± 9.1

for only by the position of the traps. This suggests that the real tree and the bottom flora of it have high potential to attract cecidomyiids. As to the Bradysia, the position of the traps was most important and accounts for 46.5% of the variability, while the explained proportion for the mean wind force and mean relative humidity was only 5.5% and 9.5% respectively (table 7.8). This suggests that the spatial distribution pattern of the genus is not determined largely by the physical variables measured but really is related to the presence of the "tree".

7.3.2.3 Distribution of flying Diptera: sheltered conditions by night

A total of 17 taxa (with 1560 individuals) were presented at night runs under sheltered conditions (table 7.9), with 13 taxa (408 individuals) occurred at the top of the real tree and 13 (547) at the bottom. 11 taxa (140 individuals) appeared at the top of the artificial tree and 12 (445) at the bottom. Again Cecidomyiidae and Psychoda were the most abundant taxa, and composed 34% and 34.9% of the total catch of the Diptera respectively. The total numbers of the other common taxa (table 7.9) show a majority at the top of the real tree, but Ceratopogonidae and Chironomidae are exceptions. Most ceratopogonids tended to fly higher by the real tree, and lower by the artificial one. More chironomids occurred at the bottom of both trees than at the top.

Table 7.8. Multiple regression analyses of Cecidomyiidae and Bradysia with physical factors in daytime under sheltered conditions. The analysis includs a dummy variable for trap position. Only significant components are shown. n = 28.

	Source of variance	SPRC	F	P	PR(%)
Cecidomyiidae	Position of traps		39.94	0.0001	83.3
Bradysia	Position of traps		7.72	0.0011	46.5
	Mean RH	-0.0146	5.41	0.0296	9.5
	Mean wind	-0.0058	6.14	0.0214	5.5

The distributions of the two most abundant taxa, the cecidomyiids and Psychoda, are shown in fig 7.3 (b), and the analysis of variance between levels and trees are summarised in table 7.10. In the cecidomyiids, significant difference of the distribution is not only found by levels and trees, but also by the interaction of level and tree ($P < 0.0001$, $P < 0.0001$ and $P = 0.0499$ respectively in table

Table 7.9. Flying Diptera caught from the real and artificial trees at night in sheltered conditions. Numbers in brackets are sample size and those in the table are number of individuals.

	Real tree		Artificial tree	
	5.0 m (5)	1.2 m (5)	5.0 m (5)	1.2 m (5)
Cecidomyiidae	36	326	25	143
Ceratopogonidae	47	24	20	53
Chironomidae	4	10	2	24
Tipulidae	55	17	22	16
Bradysia	17	5	5	5
Psychoda	154	147	54	190
C. territans(male)	79	2	22	6

Note: Numbers of rare taxa are as follows: Agromyzidae 7(0), *Anisopus punctatus* 6(5), *Anapausis soluta* 2(0), Anthomyiidae 0(3), *D. febrilis* 3(4), Drosophilidae 3(2), Empididae 3(0), Muscidae 1(1), Mycetophilinae 6(3), and Syrphidae 1(0). Numbers in brackets are those caught near the artificial tree.

Table 7.10. Analysis of variance of total numbers of Cecidomyiinae and *Psychoda* caught at night in sheltered conditions. n= 20.

	Component	F	P
Cecidomyiidae	Levels	200.00	0.0001
	Trees	24.50	0.0001
	Interaction of level & tree	4.50	0.0499
Psychoda	Levels	1.76	0.2037
	Trees	1.76	0.2037
	Interaction of level & tree	4.88	0.0421

7.10). This agrees with the results obtained at night in low wind conditions. The members of Psychoda were almost equally distributed between the top and the bottom of the real tree, but heavily concentrated at the bottom level by the artificial one (fig. 7.3 (b)). Although the analysis of variance for Psychoda does not show any significant difference between levels and trees (table 7.10), the interaction of level and tree is significant (P = 0.0421). This suggests that the Psychoda do not like to fly at the top level of the artificial tree (fig. 7.3 (b)).

Table 7.11. Measurements of microclimatic factors taken from the real and artificial trees at night in sheltered conditions. Numbers in brackets are the number of observations and those in the table are mean and standard deviation.

	Height	Real tree (5)	Artificial tree (5)
Average wind speed r/min.	5.0m	27.5 ± 23.2	41.2 ± 24.1
	1.2m	13.4 ± 12.0	26.3 ± 14.4
Average temperature °C	5.0m	12.8 ± 1.4	13.0 ± 1.4
	1.2m	12.9 ± 1.4	13.0 ± 1.5
Average light lux	5.0m	79.3 ± 63.8	96.9 ± 82.2
	1.2m	63.0 ± 56.5	71.3 ± 59.7
Average relative % humidity	5.0m	93.6 ± 5.2	93.2 ± 5.6
	1.2m	93.5 ± 5.5	93.0 ± 4.8

7.3.2.4 Physical factors and their effects: sheltered conditions by night

Table 7.11 shows significant differences between level (P = 0.042) and the trees (P = 0.038) for the wind speed. No significant differences between level and trees for the other physical factors.

Table 7.12 shows that 77.9% of total variability of the distribution of cecidomyiids is accounted for by the position of the traps. This is similar to the result found in low wind conditions (table 7.4). In the Psychoda, 44.1% of the variability of the distribution is accounted for by the position of the traps and 25.3% by mean light intensity. This is also in agreement with the result obtained at night (table 7.4); in addition it may be noted that the mean light intensity has a negative effect here, but positive under low wind conditions at night (table 7.12 vs 7.4) (see discussion for detail).

The above results may suggest that in the sheltered conditions

Table 7.12. Multiple regression analysis of Cecidomyiidae and Psychoda with physical factors at night under sheltered conditions. The analysis includs a dummy variable for trap position. Only significant components are shown. n = 20.

	Source of variance	SPRC	F	P	PR(%)
Cecidomyiidae	Position of traps		18.75	0.0001	77.9
Psychoda	Position of traps		8.63	0.0102	44.1
	Mean light	-0.0033	4.44	0.0202	25.3

both by day and by night, the real tree and the bottom flora are more attractive to the most abundant taxa, Bradysia, cecidomyiids and Psychoda, than are the physical factors. This generalization appears to apply to the other common taxa except for D. febrilis.

7.3.3 Exposed condition

When the winds came from the NW (315° ± 15°), all traps were exposed to the wind. Seven collection runs were obtained, five in daytime and only two at night.

7.3.3.1 Distributions of flying Diptera: exposed conditions by day

Table 7.13 shows that a total of 26 taxa were represented in the 929 individuals caught, with 16 taxa (239 individuals) caught at the

Table 7.13. Flying Diptera caught from the real and artificial trees during daytime in exposed conditions. Numbers in brackets are sample size and those in the table are number of individuals.

	Real tree		Artificial tree	
	5.0 m (5)	1.2 m (5)	5.0 m (5)	1.2 m (5)
Cecidomyiidae	26	154	15	72
Ceratopogonidae	14	4	3	15
Chironomidae	17	28	16	9
Phoridae	12	9	5	15
Scatopsidae	37	5	17	5
Bradysia	91	37	69	56
Psychoda	3	11	1	10
D. febrilis	26	5	64	6

Note: Numbers of rare families are as follows: Agromyzidae 3(2), Anthomyiidae 3(4), Calliphoridae 2(4), Chloropidae 1(5), Dolichopodidae 2(6), Drosophilidae 2(1), Empididae 2(4), Fanniidae 1(2), Muscidae 1(4), Mycetophilidae 2(4), Sarcophagidae 0(1), Sphaeroceridae 7(6), Syrphidae 1(1) and Tipulidae 1(0). Numbers in brackets are those caught near the artificial tree.

top of the real tree and 19 (268) at the bottom. 17 taxa (212 individuals) were trapped at the top of the artificial tree and 20 (210) at the bottom. Cecidomyiidae and Bradysia were the most abundant groups, and made up 28.7% and 27.2% of the total respectively. The other common taxa were almost equally distributed between the two trees except for D. febrilis and the Scatopsidae. Most individuals of the D. febrilis appeared at the top of the artificial tree, while more scatopsids were caught at the top level of the real tree, which agree with those of the same taxa under sheltered conditions in daytime (table 7.5).

The distribution of Cecidomyiidae and Bradysia at two levels close to the two trees are shown in fig. 7.4(a). The results of the analyses of variance are tabulated in table 7.14. Most individuals of the cecidomyiids tended to fly at the bottom level of the real tree ($P < 0.0002$, $P < 0.0055$). This seems to agree with the result of the same family in daytime under sheltered conditions (table 7.6). No significant differences of the catches of the Bradysia at the two levels between the trees are detected, and the interaction of tree and level is also not significant ($P = 0.0686$ in table 7.14). This suggests

Table 7.14. Analysis of variance of total numbers of Cecidomyiidae and Bradysia caught during daytime in exposed conditions. n = 20.

	Component	F	P
Cecidomyiidae	Levels	23.08	0.0002
	Trees	10.26	0.0055
	Interaction of level & tree	0.92	0.3510
Bradysia	Levels	2.31	0.1484
	Trees	0.92	0.3510
	Interaction of level & tree	3.81	0.0686

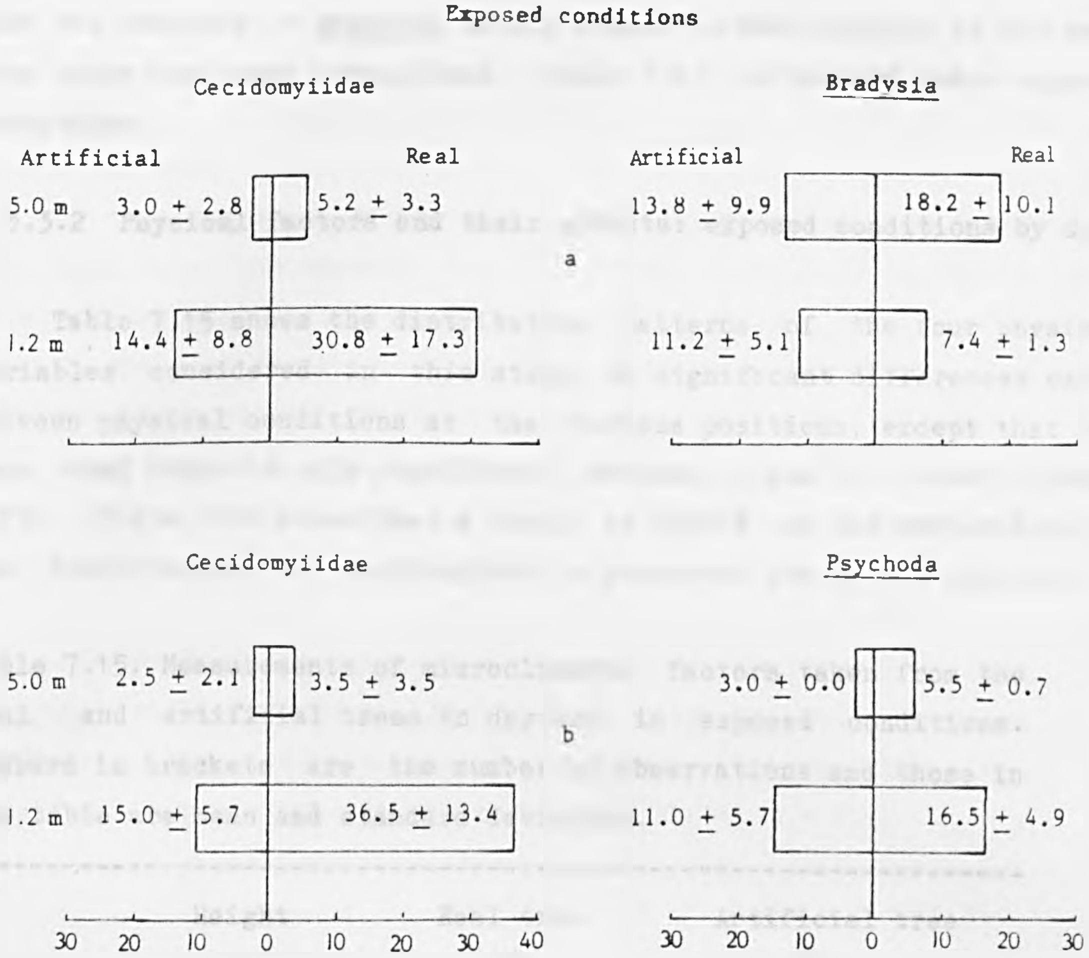

Figure 7.4. Spatial distribution patterns of Cecidomyiidae and *Bradysia* in daytime (a) and Cecidomyiidae and *Psychoda* at night (b) in relation to the real and artificial trees. Abscissa values are the mean number of individuales. Numbers by bars are mean ± standard deviation. n = 5 in daytime and 2 at night.

that the tendency of Bradysia to fly higher in the vicinity of the real tree under sheltered conditions (table 7.6), is reduced under exposed conditions.

7.3.3.2 Physical factors and their effects: exposed conditions by day

Table 7.15 shows the distribution patterns of the four physical variables considered in this study. No significant differences exist between physical conditions at the various positions, except that the mean wind force is only significant between levels (P = 0.047) (table 7.15). Table 7.16 shows that a total of 62.4% of the variability of the distribution of cecidomyiids is accounted for by the position of

Table 7.15. Measurements of microclimatic factors taken from the real and artificial trees in daytime in exposed conditions. Numbers in brackets are the number of observations and those in the table are mean and standard deviation.

	Height	Real tree (5)	Artificial tree (5)
Average wind speed r/min.	5.0m	56.8 ± 38.0	50.3 ± 34.8
	1.2m	27.3 ± 18.4	34.1 ± 23.0
Average temperature °C	5.0m	16.2 ± 1.8	16.3 ± 1.6
	1.2m	16.5 ± 1.5	17.2 ± 1.8
Average light lux	5.0m	9804.0 ± 2077.4	9784.7 ± 2012.9
	1.2m	8262.4 ± 1840.5	8239.7 ± 2009.2
Average relative % humidity	5.0m	71.1 ± 12.2	70.2 ± 11.3
	1.2m	69.2 ± 10.7	66.4 ± 11.1

the traps and the mean wind speed, of which the former (44.4%) is more important than the latter (18.2%). Compared with the result of the same family in daytime under sheltered conditions (table 7.8), two points emerge:

1) the proportion of the variability explained by the position of the traps under the exposed conditions is only half as big as it is under the sheltered conditions;

2) the wind force contributes a considerable part of the explained variance under exposed conditions, but none under the sheltered.

These facts suggest that the biological attractiveness of the bottom flora to the cecidomyiids is less effective under the exposed than under the sheltered conditions.

Table 7.16. Multiple regression analysis of Cecidomyiidae and Bradysia with physical factors in daytime under exposed conditions. The analysis includs a dummy variable for trap position. Only significant components are shown. n = 20.

	Source of variance	SPRC	F	P	PR(%)
Cecidomyiidae	Position of traps		5.93	0.0071	44.4
	Mean wind	-0.0076	7.26	0.0166	18.2
Bradysia	Position of traps		7.71	0.0033	20.2
	Mean wind	-0.0098	31.67	0.0001	35.1
	Mean light	5.297×10^{-5}	6.66	0.0228	11.4
	Mean RH	0.0165	11.73	0.0045	10.8

In the Bradysia, table 7.16 shows 57.3% of the variability is accounted for by physical factors, within which the mean wind speed is most important (35.1%). This provides a striking contrast to the results obtained under the sheltered condition for the same genus (table 7.8). The microclimatic factors play a main role here, whereas they contribute little (15%) under sheltered conditions. In addition only 20.2% of the variability is explained by the position of the traps when exposed to the wind, compared with 46.5% under sheltered conditions. The insects show a reduced tendency to fly towards the top of the real tree. This suggests that under exposed conditions the real tree is less effective in attracting Bradysia than under sheltered conditions. This effect is evident for most of the other common taxa, such as Ceratopogonidae, Chironomidae, Phoridae and Psychoda. Scatopsids are exceptional and still show as strong an association with the real tree as under sheltered conditions.

7.3.3.3 Distribution of flying Diptera: exposed conditions by night

Cecidomyiidae and Psychoda were still dominant and constituted 48% and 35.9% of the total respectively (table 7.17). Only a few members appeared in the other taxa. Compared with the insects caught at night under sheltered and low wind conditions (table 7.1 and 7.9), both the number of individuals in each taxon and the number of taxa are reduced, beyond what would be expected from the small number of windy nights experienced.

Table 7.17. Flying Diptera caught from the real and artificial trees at night in exposed conditions. Numbers in brackets are sample size and those in the table are number of individuals.

	Real tree		Artificial tree	
	5.0 m (2)	1.2 m (2)	5.0 m (2)	1.2 m (2)
Cecidomyiidae	7	73	5	22
Psychoda	11	33	6	30

Note: Numbers of rare taxa are as follows: D. febrilis 1(0), Ceratopogonidae 1(1), Chironomidae 6(2), Drosophilidae 1(0), Mycetophilinae 1(0), Bradysia 7(0), Sphaeroceridae 0(1) and Tipulidae 6(9). Numbers in brackets are those caught near the artificial tree.

The distributions of Cecidomyiidae and Psychoda at two levels between two types of trees are shown in fig. 7.4(b). Although the cecidomyiids show a similar pattern to that observed in other conditions (fig. 7.2 and 7.3b), the number of individuals caught at each position are much less. This probably simply reflects a reduced probability of , or time spent in flight than under the sheltered or low wind conditions. A sharp change of the pattern of the Psychoda is apparent compared with the patterns found under the other conditions (fig. 7.2, 7.3); the majority of the insects tended to fly at the bottom level in windy conditions (fig. 7.4 (b)), and distributed almost equally between the two trees. As only two collection runs were obtained it is impossible to do statistical analysis with the physical factors on the patterns, but table 7.18 shows that only the wind speed is obviously different between levels.

Table 7.18. Measurements of microclimatic factors taken from the real and artificial trees at night in exposed conditions. Numbers in brackets are the number of observations and those in the table are mean and standard deviation.

	Height	Real tree (2)	Artificial tree (2)
Average wind speed r/min.	5.0m	44.2 ± 14.8	43.4 ± 12.2
	1.2m	19.0 ± 7.1	23.6 ± 7.8
Average temperature °C	5.0m	11.0 ± 1.6	11.2 ± 1.6
	1.2m	11.1 ± 1.8	11.3 ± 1.9
Average light lux	5.0m	43.3 ± 3.3	54.0 ± 0.8
	1.2m	31.3 ± 2.9	43.9 ± 1.7
Average relative % humidity	5.0m	95.1 ± 0.5	94.3 ± 0.6
	1.2m	94.5 ± 2.0	93.8 ± 2.6

7.4 Discussion

It must be mentioned that the collection runs chosen under the different wind conditions were randomly distributed throughout this set of observations, depending on when the appropriate winds occurred.

On some occasions a few more groups were caught by the real tree, but in others a few less (table 7.19). This may be due to the environmental conditions around the trapping site. The trapping site was surrounded by high hedgerow trees, and high Prunus bushes about 20 or 30 metres away in the S, SW, W and NW directions from the trapping site (fig. 2.1). This high vegetation would create a relatively deep "insect boundary layer" and allow most flying Diptera to fly around the site freely (Taylor, 1974; Lewis, 1967; Pedgley 1982). Some taxa, particularly the common ones, showed a preference for the real tree, possibly because of a biological connection with it, while the others which were present in very small numbers, such as Pipunculidae, Sciomyzidae, Simulidae, Lonchopteridae, Asteiidae, Ephydridae, Drosophilidae and Sphaeroceridae (tables 7.1, 7.5, 7.9, 7.13, 7.17) did not show any detectable preference for either the real tree or the artificial one, possibly because they have no direct connections to the hawthorn tree or the flora at the base of it (Colyer & Hammond, 1968), and were caught by chance, therefore 'balancing out' the family

Table 7.19. Number of groups trapped at two levels close to the real and artificial trees. Numbers outside and inside brackets are the number of groups and the total individuals in them.

Wind condition	Real tree 5.0m	Real tree 1.2m	Artificial tree 5.0m	Artificial tree 1.2m
Low (night)	11 (871)	10 (1124)	13 (405)	10 (789)
Sheltered (day)	19 (688)	18 (395)	18 (317)	23 (428)
Sheltered (night)	13 (408)	13 (547)	11 (160)	12 (445)
Exposed (day)	16 (239)	19 (268)	17 (212)	20 (210)
Exposed (night)	8 (29)	6 (118)	6 (20)	4 (56)

diversity of flying Diptera.

The spatial distribution patterns of both day-flying and night-flying Cecidomyiidae are very consistent in all of the conditions described here. The numbers of individuals are always distributed in the following series: real tree (bottom) > artificial tree (bottom) > real tree (top) > artificial tree (top) (figs 7.2 - 7.4). This suggests that they have poor flight performance which may reflect their small and delicate body, and that they may have particular biological affinity to the region around the bottom of the real tree. In the suction trap collections, Clinodiplosis leguminicola (Cecidomyiidae) and Campylomyza flavipes (Cecidomyiidae) were both common and the former constituted the greater part of the night time catch whilst the latter formed most catch of the daytime. Hand net collections made around the real tree and in the meadow also consisted mainly of the same two species. The studies made by Milne (1960) and by Harris (1966) suggest that Clinodiplosis leguminicola feeds on clovers, which are abundant in this meadow. Edwards (1938) suggested that the majority of species of the genus Campylomyza live in dead wood and can be very often found along hedgerows and in dead vegetation. Hence, the shrubby vegetation at the base of the real tree would meet one requirement of Campylomyza flavipes. Therefore in each of the conditions, the majority of cecidomyiids always occurred at the bottom of the real tree, but not of the artificial one probably because of the effect of the absence of a bottom flora around the artificial tree.

The number of cecidomyiids caught at night declines from low wind to sheltered to exposed conditions (figs 7.2, 7.3b, 7.4b), and whilst this is not seen in the daytime data, and in exposed condition numbers decreases significantly as the mean wind speed increases (table 7.16). In each case however the numbers around the artificial tree are about half of those around the real one. This may suggest that biological factors dominate over the distribution and abundance of cecidomyiids under low wind conditions, both biological and physical factors under sheltered conditions, and physical factors under exposed conditions.

The distribution of the Psychoda also varied with the conditions. In the sheltered and low wind conditions, it was found that close to the real tree most individuals were caught either at the top or spread equally between the top and the bottom levels, while near the artificial tree they were always concentrated at the bottom level in all conditions (fig. 7.2 and 7.3b). One possible explanation is that this would be caused by different permeability of the two kinds of trees. Lewis and Stephenson (1966) suggested that insects accumulated in the air nearer to dense windbreaks than to more permeable ones, and the position of maximum aerial density of insects coincided with that of maximum shelter. In low wind conditions and in exposed conditions the mean wind force seen by the outstations was similar between the real and the artificial trees (tables 7.3, 7.18). In sheltered conditions the wind seen behind the artificial tree was stronger (tables 7.7, 7.11), suggesting a difference in permeability. As the wind speed progresses from low wind to sheltered to exposed the numbers caught are reduced more strongly at the top, and if the artificial tree is more permeable this would account for some of the difference between it and the real tree in sheltered condition (fig. 7.3b). However such explanations cannot apply in low wind conditions (fig. 7.2) when no difference in wind speed is seen (table 7.3). These observations suggest that the biological attraction of the real tree under low wind conditions is more important to the distributions of Psychoda than the physical factors, and that both biological and shelter effects dominate under the sheltered conditions.

In exposed conditions, the vertical distributions of the Psychoda between the two trees agree with each other with the majority caught at the bottom levels (fig 7.4(b)) in both cases. Compared with the patterns in the other conditions (fig 7.2 and 7.3(b)), the attraction of the real tree is much less evident, especially at the top level. Clearly, these suggest that physical factors under exposed conditions are the dominant influence, especially the wind.

Further examination of the collection of the Psychoda shows that Psychoda phalaenoides Linn. P. setigera Tonn. and P. albipennis Zett. were the common species. They are all very similar in body size and constitute the majority of the total in all three wind conditions. P. phalaenoides was the most abundant of all. P. albipennis was frequently caught in hand-netting but the other two were much less frequently found on the tree, suggesting that P. albipennis is probably more of resident here. Satchell (1948) showed that P. albipennis can breed in dung, but mainly breeds in decaying vegetation. Colyer & Hammond (1968) noted that large numbers of Psychoda were often found on the tree trunks when the atmosphere is humid; another typical habitat is the undersurface of leaves in damp places. P. phalaenoides and P. setigera are dung-breeding species (Satchell 1948) and there was little or no dung in Bond Ing. Therefore the large numbers of P. phalaenoides and P. setigera caught by the suction traps were probably carried in from grazing pastures nearby by wind. From fig 7.2 and 7.3(b), it seems clear that in the real tree the leaves are having a significant influence on them, either by providing food, olfaction or visual cues for mating, shelter or some other resources. In the artificial tree, nothing is provided but shelter, and so most individuals stay at the bottom, where the shelter is found (Lewis 1970; Lewis & Dibley 1970).

The genus Bradysia (Sciaridae) shows a marked abundance for the top of the real tree, particularly under sheltered conditions (fig 7.3a, 7.4a). This suggests that they are largely attracted by the biological attractiveness of the tree, and that this attraction can be altered by physical factors under exposed conditions. The pattern seen for Psychoda is also seen in other taxa including Chironomidae, Tipulidae and the day-flying Phoridae and Ceratopogonidae. The high-flying pattern of the Bradysia is also seen in Scatopsidae, Anisopus punctatus, Culex territans and night-flying Ceratopogonidae (tables 7.1, 7.5, 7.9, 7.13 and 7.17).

In all circumstances, the bottom flora of the real tree appears to show a very strong attraction to the most important day-flying and night-flying cecidomyiids, especially under sheltered and low wind conditions. Under sheltered and low wind conditions, the real tree and bottom flora seem to have a clear attraction to Psychoda, and the real tree, especially the leaf layer, to Bradysia . This generalization can be applied to most of the other common taxa. In the exposed conditions, on the other hand, this attraction is reduced for the cecidomyiids and Bradysia, and not apparent in the case of the Psychoda and of the most other common taxa as well. Instead the effect of physical factors, especially the wind, appears to dominate. Generally speaking, these results confirm the hypothesis proposed at the beginning of this chapter, which predicted that more flying insects would be caught close to the real tree than in association with the artificial one in sheltered or in low wind conditions, and that this distribution would be break down under exposed conditions.

In marked contrast to other common taxa, most members of Dilophus febrilis (Bibionidae) were caught at the top level of the artificial tree under both exposed and sheltered conditions (table 7.6 and 7.16). By looking at the relationship between the abundances of the family and the four physical variables (table 7.20), it can be seen that in both

Table 7.20. Multiple regression analysis of D. febrilis with physical factors in daytime under exposed and sheltered conditions. The analysis includs a dummy variable for trap position. Only significant components are shown. Numbers in brackets are sample size.

Wind condition	Source of variance	SPRC	F	P	PR(%)
Sheltered (28)	Position of traps		5.81	0.0032	38.4
Exposed (20)	Position of traps		10.65	0.0007	53.2
	Mean RH	-0.0301	10.66	0.0056	10.0
	Mean temp.	0.2109	9.69	0.0076	9.0

sets of conditions, the position of the traps explained a considerable proportion of the total variability of occurrence of this taxon, while the microclimatic factors only explained a small part ($R^2 = 0.19$) under exposed conditions and none otherwise. This means that the tendency to fly towards the top level of the artificial tree is mainly due to the attraction of the artificial tree *per se* rather than the measured physical factors found there. The reason for this might be the behaviour of newly emerged flies. The artificial tree could form a swarming focus since swarming behaviour is developed in this species (Freeman & Lane, 1985). Colyer & Hammond (1968) and D'arcy-Burt & Blackshaw (1987) found that the males of D. febrilis hover in the air and fly high. Another possible reason could be the colour of the artificial tree. The colour of the netting was between blue and green, which was easily distinguishable from the colour of the vegetation nearby. D'arcy-Burt & Blackshaw (1987) showed that the colour of water traps affected the catches of grassland Bibionidae, and green has some attraction to the males of D. febrilis.

It is noted that the mean light intensity is positively correlated with the abundances of the Psychoda under low wind conditions (table 7.5), but negatively under sheltered conditions (table 7.15). This is anomalous and the reason is not known. The observations reported in chapter 5 does not show that light intensity has any influence on the abundances of Psychodidae at all; hence this correlation might be spurious, or it may be that these insects response differently to light according to wind speed. This could cause the observed move downwards in windier conditions, but no significant interaction between wind and light was found in the analysis (table 7.4, 7.12).

By looking at the patterns of strong flyers, eg. the scatopsids of which Anapausis soluta Loew, which is big-bodied species of the family (see Chapter 4), was the most abundant, or big-bodied species with strong flight ability, eg. D. febrilis (Bibionidae), it can be seen that the distributions are not obviously different between sheltered and exposed conditions (tables 7.6, 7.16). This phenomenon may also be seen more or less in fairly strong flyers, eg. Bradysia and the phorids, (tables 7.6, 7.16). For weak flyers like Psychoda, in contrast, both the distribution patterns and the number of individuals varied dramatically with wind conditions (fig. 7.3(b), 7.4(b)). This was also true of the ceratopogonids and chironomids which are also weak flyers. This suggests that strong flyers have a higher ability to cope with vagaries of the weather and show less response to changes of wind conditions than do weak flyers. This agrees with the result obtained in chapters 4 and 5, and confirms the findings of Lewis (1967) that vertical profiles of weak-flying insects differed in sheltered and exposed positions but that this is not true for strong flyers.

The biological attraction of the real tree and the plants growing around the base of it for the common taxa of flying Diptera has been indicated even at this rather limited level of resolution. From this result, it is suggested that an isolated tree makes a significant contribution both as a biological entities and as physical shelter to the life of flying Diptera as do single emergent hedgerow trees. From this study, it seems likely that isolated trees generally play an important part in the life of flying insects. In essence, a real tree is a habitat which can also act as a shelter; an artificial tree is not a habitat and only has a shelter effect and cannot act as a real tree.

7.5 Summary

1) The distributions of flying Diptera in relation to a real and an artificial tree under sheltered, exposed and low wind conditions have been studied.

2) The four most abundant taxa of flying Diptera, day-flying and night-flying Cecidomyiidae, Psychoda and Bradysia, were examined in detail. Together they comprised from 55.9% to 84% of the total flies caught.

3) The biological attraction of an isolated real tree and its base flora seems to be a major influence on almost all the common taxa in low wind conditions, both biological and physical effects appears to determine the distribution under sheltered conditions, while the effect of physical factors, especially the wind, seems to be most important in exposed conditions.

4) It is suggested that isolated trees make a significant contribution to the life of flying Diptera.

5) Most males of Dilophus febrilis were attracted by the artificial tree, which is perhaps explained by the colour of the netting used to construct it and by their swarming behaviour.

6) Day-flying and night-flying Cecidomyiidae showed very consistent patterns in relation to the real and the artificial trees, which is probably explained by the dominance of certain species in each case.

7) Strong flyers have a greater ability to cope with the changes of wind conditions than do weak flyers.

Chapter 8

GENERAL DISCUSSION

Most work on flying insect distribution has concentrated on intensive agricultural systems. A series of studies on distributions of flying insects in relation to artificial windbreaks and hedgerows carried out by Lewis and his associates showed that flying insects accumulated in the lee of barriers to the wind, and that patterns of distribution of insects in the air and in sheltered crops are closely related to the height and permeability of barriers (see General Introduction for references). Attention has paid to the consequences of uniformity in the landscape rather than on the impact of diversity of landscape form. The distribution in time and space of insects flying around a single tree, including both emergent hedgerow trees and isolated ones, has not been quantitatively studied, although such trees are increasingly common features of many areas (see General Introduction of Chapter 1). To approach this, two questions have been addressed in this study:

1) is variation in spatial distribution of flying insects in relation to such trees mostly caused by the physical shelter provided by the trees as it is by hedgerows or artificial windbreaks (Lewis 1970; Lewis & Dibley 1970) or it is only caused by the biological attraction of the trees as might be predicted from the results obtained by Bowden & Dean (1977)?

2) how important are such trees to the life of flying insects?

As similar techniques have been carried out in tropical rain forests, what is the difference in biological and physical effects on insect vertical distributions between long deforested lowland Britain and closed canopy forest of the tropics (see General Introduction for references)?

Taylor's (1958, 1960) hypothesis of the "insect boundary layer", has helped interpretation of experimental work and has also provided a basic reference for classifying migratory flight of insects. However, a dispute about the usefulness of this concept has occurred. The problem was that discontinuities (intercept) did occur in vertical profiles of flying insects, but at that intercept the wind speed did not match the insect flight speed (see General Introduction of Chapter

1). Therefore, two questions are concerned with this dispute in this study:

1) if a discontinuity point (Taylor 1960, 1974) exists in a vertical profile of flying Diptera, does the flight speed match the wind speed at this height?

2) how an insects distributes itself within its boundary layer if such exists?

Flying insects are known to be prey to many kinds of animals, such as birds and bats. Do the spatial and temporal distribution patterns obtained in this study suggest any relationships with the feeding patterns of bats and swallows? This is a question of increasing concern in relation to the conservation of such insectivores which hunt on the wing, in many part of the world.

A knowledge of the factors influencing flying insect distribution and abundance can be used to predict what types of conservation management could be most effective. Such knowledge would also help to predict when and where pest problems may develop. This work can therefore provide information useful to the management of insect pests of agricultural importance.

8.1 Relative importance of physical and biological factors under different wind conditions

Different factors dominate in different situations.

8.1.1 Calm condition

Under calm conditions, in the comparative experiment of a real and an artificial tree in Chapter 7, if the effect of the real tree was equivalent to that of the artificial one, the distributions in relation to these two kinds of trees would be similar. But they are not (fig. 7.2). All common taxa are significantly more abundant near the real tree (table 7.1 - 2); most taxa prefer the top, with a few at the bottom. This can be mostly explained by food source, swarming focus and other biological factors provided by the hawthorn tree (see Chapter 7). Physical factors measured in this experiment seem to have no significant effects on the distribution pattern at all (table 7.4). This suggests the importance of biological effects due to the real tree under calm conditions.

8.1.2 Non-calm condition

The position in non-calm conditions is different. When advection occurs (when a breeze is blowing) the uniform character of the air around the tree becomes disturbed. There is an exposed side and a sheltered side.

8.1.2.1 Exposed side

On the exposed side, if the biological factors still dominate as they do in calm conditions, the distribution patterns in relation to the two kinds of trees (real and artificial) will be different. But they are not. The patterns between two trees, when the traps are exposed, are not significantly different for most common taxa (tables 7.13, 7.14, 7.17; fig. 7.4). This suggests the importance of physical factors, especially the wind, in exposed conditions. Such a conclusion also holds true in the experiment of cutting the hedge (Chapter 6). By comparing distribution patterns in relation to the two lime trees between exposed and sheltered conditions (Chapter 6), it can be seen that the abundance of the insects diminishes with increase in height under exposed conditions while almost the opposite is true in sheltered conditions (tables 6.2 - 7). It would be expected that these vertical distributions would be similar if the shelter did not have an effect on the distribution of the insects, since the plant diversity and structure at both trapping sites were very similar (Table 6.1, see also Chapter 6). But they are not. On the one hand, this suggests that physical factors dominate the vertical distribution under exposed conditions, particularly the wind (tables 6.6, 6.11). On the other hand under sheltered conditions the distribution pattern is affected jointly by the re-circulating air and by biological stimuli of the tree (tables 6.3, 6.8; figs 6.2 - 4, 6.7).

8.1.2.2 Sheltered side

On the sheltered side, the distribution patterns of flying insects are different behind the artificial tree and the real one. Hence two aspects need to be considered. Firstly, on sheltered side of the artificial tree, as shown in Chapters 6 and 7 most members of most taxa concentrated on the top and middle levels near the real tree (figs 6.2 - 7, 7.3; tables 7.5, 7.9), if the artificial tree played the same role as that of the real one, most taxa would be more abundant at the top level, and the numbers of individual caught between two trees would be similar. But they are not. Most common taxa are more abundant at the bottom of the artificial tree and a few almost equally abundant at both levels (table 7.5, 7.9). Thus it appears that the shelter offered by the artificial tree is mainly responsible for accumulating the insects. It is also interesting to note that the formation of this pattern is more or less a similar process to the way in which snow accumulates in sheltered places if the wind is blowing as it falls (Van Eimern et al. 1964), which is largely due to the effects of slowing of air and wind eddy behind barriers. This limits the air's ability to carry particles. Insects behave partly as passive particles, and partly as self-propelled entities.

On the sheltered side of the real tree the distribution shows some similarities to the vertical distribution on the sheltered side of the artificial one, and some similarities to the distribution by the real tree in calm conditions. A few taxa distribute themselves at the bottom level or almost equally between the top and the bottom; this is like their distribution in the lee of the artificial tree (tables 7.5, 7.9; also see above). Others are caught more often at the top; like the pattern obtained in calm conditions (tables 7.1, 7.5, 7.9). Table 7.5 and 7.9 also show that under sheltered conditions individuals of most taxa are caught significantly more frequently near the real tree than near the artificial one. which is also in agreement with the result obtained in calm conditions (table 7.1). From these comparisons, it is suggested that on sheltered side of the real tree the insect distribution is determined jointly by biological effects and by physical influence (shelter). This suggestion is supported also by the results obtained under sheltered conditions in the cutting experiment (Chapter 6), which shows that the flying Diptera are either more abundant at the top and the middle levels (figs 6.2 - 7) or almost equally abundant between levels (figs 6.4, 6.5, 6.7), rather than just concentrating at the bottom and the middle levels. This generalization is also applied to the spatial distributions of 14 common families of the insects (Chapter 3), which show that most members of most families are caught at the middle level near the lime tree, with the tendency to spread upwards to the top level for most families and downwards to the bottom for the others. However, anisopodids are much more abundant at the top level, mycetophilids at the bottom, and scatopsids further away from the tree (table 3.3, fig. 3.4).

The biological and physical effects on the distribution patterns of the insects are difficult to separate quantitatively from each other. However, from the above comparison it can be said that biological effects seem to dominate in calm conditions, physical effects both in exposed conditions and in artificial sheltered conditions, while both biological and physical effects have a strong influence in the sheltered conditions created by living vegetation.

These results, in general, support the shelter hypothesis of Lewis (1970) and Lewis & Dibley (1970) that insects accumulate in re-circulating air to the leeward of barriers to wind flow. These results provide more support for the importance of biological influences on distribution patterns of flying insects than is indicated in Lewis' work (Lewis 1969b, 1970). To that extent they provide limited support for the conclusions of Bowden & Dean's study (1977), who regarded biological factors of being of over-riding importance. It is clear that strength and direction of wind in relation to trap sites can radically affect conclusions drawn from this type of study. This is, quite possibly, the solution to the contradiction between the results of Lewis & Dibley on the one hand, and Bowden & Dean on the other.

8.2 Importance of trees in the life of flying insects

From the records of the literature and investigations made in this study on the adult behaviour and habitat for 14 common families, it is showed that there exist a number of connections between the insects and the lime tree (Chapter 3). The tree not only provides food, a swarming focus and a reproduction site for most of the taxa concerned here, but also produces appreciable shelter to harbour insects being blown past the tree that might not otherwise be present, Scatopsidae for example. Again, the manipulation experiment of cutting and netting (Chapter 6) suggests that such trees significantly influence the spatial distribution of the insects under sheltered conditions, particularly by increasing abundance near the canopy (figs 6.2 - 7). This significant contribution of emergent hedgerow trees to the life of the insects has also been suggested by the comparative experiment of real and artificial trees (Chapter 7). From agricultural pest control point of view, these trees can increase habitat diversity to provide natural enemies with alternate host and prey, pollen and nectar source, protected sites for mating, resting and overwintering. They may be regarded as a reservoir for natural enemies, for example Sryphidae, Empididae, Phoridae and Dolichopodidae. But they can also aid agronomic pests, such as Cecidomyiidae and Anthomyiidae.

In conclusion, trees, whether isolated or emergent from a hedgerow, play an important part both in the life of flying insects and in the management of insect pests. It seems reasonable to extend this conclusion more broadly and to predict that such trees are also important to many other groups of animals, such as birds and bats, which are associated with them directly or indirectly because of the flying insects which accumulate around such trees due to both biological and physical factors.

8.3 A model of flying insects around trees

According to relative importance of physical and biological effects in different conditions and the relationship between flying insects and trees, it is possible to provide a picture to demonstrate such correlations among each other. Insects remain inactive at cool temperatures, and a minimum temperature threshold, which varies with insects, is required before active take-off begins (Lewis & Taylor 1964; Pedgley 1982; Taylor 1963). When a temperature meets the requirement of an insect for flight, active take-off may be triggered by specific wind speed preference. This differs among insect species (sexes). Passive take-off may also occur when a gust of wind or a raindrop knocks the insect into the air, especially in an open or exposed area. Most insects initiate flight more readily in the sheltered zone of trees, where wind speeds are reduced and flight is more easily controlled (Lewis 1967; Taylor 1974). Under windy conditions evaporative cooling may lower an insect's body temperature sufficiently to prevent take-off (Digby 1955). In this case, if the ambient air temperature on both sides of a tree is at threshold level, active take-off would be expected to be greater for most insects on the sheltered side where evaporative cooling is less. This expectation applies to the vertical distributions obtained in calm, exposed and sheltered conditions very well in this study. Therefore, a model could be constructed as in fig. 8.1. Note that in other than calm conditions temperatures and humidities near each side of a tree (sheltered or exposed) have been found to differ little between trap locations (tables 7.7, 7.11, 7.15, 7.18), but about 0.5 °C differ between the exposed and sheltered sides (tables 6.4, 6.15). In calm conditions differentials and gradients are seen, the lower levels generally being warmer and drier in the daytime and conversely at night (Table 7.3).

8.4 Comparison of factors affecting the distribution of flying insects between the tropics and lowland Britain

This work developed from the tropical rain forest studies (see General Introduction), and it is appropriate to make comparison. The detail of these comparisons is inevitablely limited. From a series of studies carried out in the tropics on the vertical distribution of flying insects (see General Introduction of Chapter 1), the general vertical profile of flying insects is summarized by Sutton (1989) that the gradient in abundance between floor and canopy was greatest where the ecological inversion surface was relatively smooth (Richards 1983), and irregular topography or other factor causing this surface to be rough, make the gradient less marked.

The work on the insects of medical importance suggests that there are correlations between the vertical distribution of biting insects and their preferred targets (see General Introduction for references). The biological effect is also apparently indicated by the work carried out by Sutton and his co-workers. However, little has been reported about the influence of physical factors on the vertical distributions in the tropics, except that relative humidity (Cachan 1964; Pittendrigh 1950) and moonlight with dry and wet conditions (Rees 1983; Sutton 1989) are important (see General Introduction). But no analysis has been done on the relationship between winds and the vertical distribution of flying insects in the tropics. This is probably

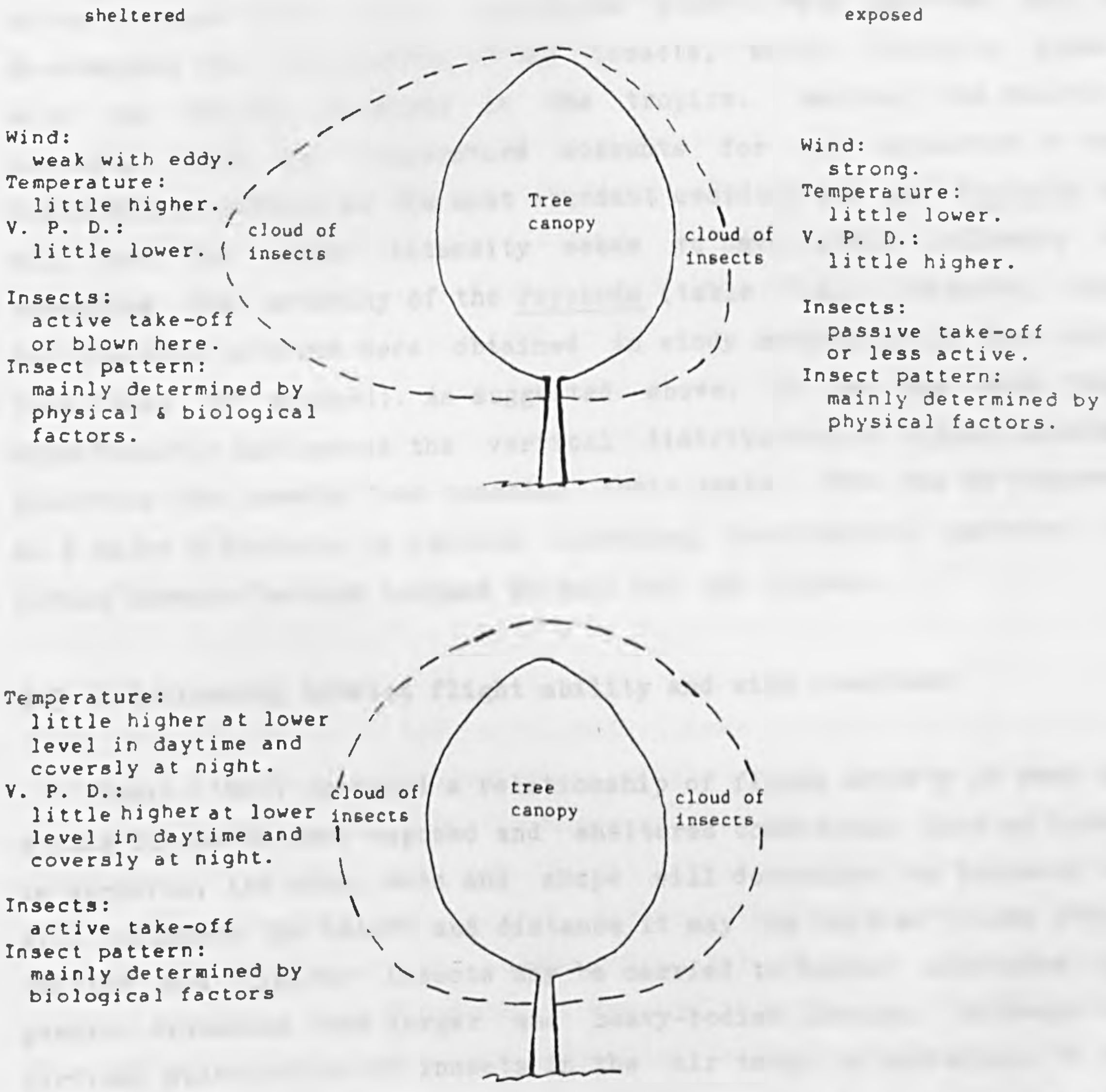

Figure 8.1. Distribution of flying insects around trees when the air temperature is high enough for flight. V. P. D. = vapour pressure deficit.

because of the stability of the air within the tropical forests (Allee 1926; Haddow et al. 1961; Sutton 1989), which allows flying insects to reach their goals more easily.

The species composition of Diptera and spatial structure of flora in this study may be completely different from those in the tropics under most conditions. Hence it may be impossible to make a direct comparison of the distribution pattern between these two regions. However, the distribution pattern obtained in calm conditions may be considered. As discussed above, in this study the biological attractiveness under these conditions plays a very important part in determining the distribution of the insects, which obviously agrees with the results obtained in the tropics. Neither the relative humidity, wind nor temperature accounts for any variation of the distribution pattern of the most abundant cecidomyiids and Psychoda at all, and the light intensity seems to have little influence in enhancing the activity of the Psychoda (table 7.4). However, most distribution patterns were obtained in windy conditions in this study (sheltered or exposed). As suggested above, it is the wind that significantly influences the vertical distribution of flying insects, hindering the insects from reaching their goals. This can be regarded as a major difference of factors affecting distribution patterns of flying insects between lowland Britain and the tropics.

8.5 Relationship between flight ability and wind condition

Lewis (1967) produced a relationship of flying ability of weak and strong flyers between exposed and sheltered conditions. Once an insect is airborne, its size, mass and shape will determine its buoyancy and will influence the height and distance it may be carried (Glick 1939). Smaller and lighter insects may be carried to higher altitudes and greater distances than larger and heavy-bodied insects. Although the vertical distribution of insects in the air tends to correspond to the buoyancy relationship, winged insects are capable of modifying the height at which they fly when wind speeds are low (Johnson 1969, Taylor et al. 1979; Pasek 1988). Therefore it is to be predicted that strong or big-bodied flyers will have a greater ability to fly in different wind conditions (even in exposed) than do weak or small-bodied insects. This would explain why, in Chapter 4, no correlations can be found between wind directions and the big-bodied species, Anapausis soluta and Scatopse notata. In contrast, there is a significant correlation between the wind direction (determining whether the traps are sheltered or exposed) and a small-bodied species, Rhegmoclema cooki, (Table 4.8). Similarly, this result can also be found in Chapter 5 (Tables 5.1, 5.3, 5.5, 5.7 - 9) and in Chapter 7 (tables 7.6, 7.16; figs 7.3b 7.4b). Clearly these results are in agreement with the above expectation.

8.6 Distribution within the insect boundary layer

8.6.1 Confirmation of the insect boundary layer

Taylor (1958, 1960, 1974) defined the insect boundary layer as the air layer in which an insect can control its movement relative to the ground because its flight speed exceeds the wind speed. Above the insect boundary layer, an insect will always be blown downwind. A density discontinuity (Taylor 1960, 1974) was, in this present study, apparent at 8.8m near the lime tree and 5m further away from it for the small-bodied species, Rhegmoclema cooki, R. coxendix and R. sp., where the mean wind speeds were 79 cm/sec. and 79.6 cm/sec. respectively (fig.4.4). The mean deduced flight speed of the species were 74.5, 73.1 and 67.0 cm/sec. respectively (fig. 4.4). The discontinuity of the vertical profile for Anapausis soluta was apparent more than 8.8m near the tree and between 5m and 8.8m away from it, where the wind speed was 107cm/sec. and estimated flight speed was 96.8cm/sec. (fig.4.4). Moreover, the density discontinuity for big-bodied species, Scatopse notata, was 8.8m further away from the tree, where the wind speed was 136.4cm/sec. and the flight speed was 121.3cm/sec. (fig. 4.4). This appears to support Taylor's hypothesis of the "insect boundary layer" (Taylor 1958, 1960, 1974), but further work is needed before reaching a firm conclusion because the vertical profiles only consisted of three points and the flight speeds are deduced from the regression formula of Lewis & Taylor (1967).

8.6.2 Response within the insect boundary layer

Boiteau et al. (1979) showed that bean leaf beetles, Ceratoma trifurcata (Forster), are usually able to control their flight within a boundary layer of 2.4m, and disperse equally upwind and downwind in soya bean and corn field. In a wind tunnel experiment, Brantjes (1981) showed that the hawkmoth, Deilephila elpenor, is able to reach flowers by means of their scent plumes when the wind speed was less than the moth's air speed of 5m/sec.. It is generally to be expected that when the temperature allows the insects to fly within the boundary layer, biological factors, such as food, mating, egg-laying, swarming, olfaction and visual cue, and stimuli, e.g. mechanical effects (effects from the apparatus and facilities used for catching insects), will play a major role in determining the spatial distribution of flying insects, rather than microclimatic ones, since the insects can control their flight track within this layer (Taylor 1958, 1960, 1974; Pedgley 1982). To test this, a uniform vegetation area is desirable. As the distribution of flying insects obtained in this work is closely related to single trees, the wind eddy behind the trees must have some potential effect on the insect distribution tested. Preliminary approaches to this subject suggest that among 22 physical variables concerned in this study, none of them is found to be a major element to determine the distributions of three commonest species of Scatopsidae (Chapter 4) and 12 common families (Chapter 5), except for the wind eddy. Instead, these distributions are significantly correlated with suction trap positions; and most insects tend to appear near the tree canopy (which are explained mainly by biological influences and by the shelter), and scatopsids prefer to fly at middle level further away from the tree (which is explained in part by the wind eddy behind the tree) (Chapter 4). Similar results are also obtained in the experiment of a real and an artificial tree in Chapter 7, showing that the distribution patterns of the most abundant taxa, Cecidomyiidae, Psychoda (Psychodidae) and Bradysia (Sciaridae) are closely related to certain positions in relation to two types of trees, rather than to physical factors measured (Tables 7.4, 7.8, 7.12). These results, in general, agree with the above hypothesis of the response of flying insects within their boundary layer, although whichever biological factor being important to which group of insect has not been quantitatively determined in this study.

8.7 Temporal pattern of insects in relation to feeding behaviour of birds and bats

From the conservation point of view, it is interesting to know whether or not the temporal distribution patterns of flying insects is related to the feeding activity of insectivorous bats in the evening. Pipistrellus pipistrellus Schreber, is the commonest British bat, and is widely distributed in Europe (Stebbings 1977). The average nightly foraging period of the bat in late July and the beginning of August is bimodal in pattern; the number of the bats outside the roost shows peaks after dusk and immediately before dawn (Church 1957; Stebbings 1968; Swift 1980). Such a pattern of bat activity has also been widely reported in some other areas (Barclay 1991; Fenton 1970; Kunz 1973, 1974; Herreid & Davis 1965; Funakoshi & Uchida 1975, 1978).

The temporal distribution patterns of dusk- and night-flying insects (table 3.1) show that some families had a peak at dusk with sub-peak at night (Anisopodidae, Ceratopogonidae and Chironomidae), others a peak at dusk (Mycetophilidae and Phoridae) and others a peak at night and sub-peak at dusk (Cecidomyiidae, Psychodidae and Tipulidae). These insect activity patterns in this study show similar peaks as do bats. During the course of trapping in summer, some bats were found to live in a goat's shed adjacent to Bond Ing (fig. 2.1), and to come out at dusk visiting the trapping sites. Literature makes it claer that bats take insects of more than 2mm in body length (Barclay 1991; Anthony & Kunz 1977); most groups of the insects caught here are considered to be suitable prey of bats. It might be suggested that bats, which require low light intensity, forage in the hours of maximum insect abundance to compensate for a dearth of nocturnal food. Table 3.1 shows clear that at this time of year day-flying dipterous prey is plentiful, fully nocturnal prey is not. As hirundines seem to require fairly high light levels before they can hunt successfully, flying at dawn and dusk by some flying insects may avoid the inroads they can make. Therefore these insects become targets of bats. This might even be one reason why crepuscular flight is common among flies.

Wind speed and temperature are determined to be the most important physical factors to influence the abundance and distribution of dusk- and night-flying Diptera (tables 5.3 - 5.6; figs 6.3, 6.6, 6.7, 7.2 - 7.4), presumably, the interaction between ambient wind condition and temperature and insect abundance may be an important factor influencing the foraging pattern of insectivorous bats in time and space.

8.8 Information for agriculture

Effective and ecologically sound management of insect pests depends on a knowledge of the distribution and abundance of the pests and their natural enemies (Pasek 1988). A knowledge of the factors affecting insect distribution and abundance can be used to forecast when and where pest problems may develop. Also, development of pest management strategies requires such information.

The results obtained in this study show that many factors affect the daily abundances and distributions of flying insects, particularly the wind and temperature (Chapters 4, 5, 6, 7). This has meant that in the temperate region, where the wind is a pervasive element of the environment, study of the influence of wind on insect distribution is particularly important.

Artificial windbreaks constructed to ameliorate the adverse effects of the wind will affect the movement and local distribution of insects (Van Eimern *et al*. 1964). Spatial and temporal distribution patterns of many groups of Diptera observed in this work may prove useful when designing sampling programme for Diptera and to design field and high vegetation windbreaks to minimize the influence of important pest species and to maximize the effectiveness of natural enemies. However, according to the experimental results of netting the hedge (Chapter 6), it is not suggested that plastic netting is the best material for constructing artificial windbreaks for gardeners and farmers, because of lack of biological attractiveness.

REFERENCES

Allee, W.C. (1926) Measurement of environmental factors in the tropical rain-forest of Panama. Ecology, 7, 273-302.

Anthony, E.L.P. and Kunz, T.H. (1977) Feeding strategies of the little brown bat, Myotis lucifugus, in southern New Hampshire. Ecology, 58, 775-786.

Barclay, R.M.R. (1991) Population structure of temperate zone insectivorous bats in relation to foraging behaviour and energy demand. Journal of Animal Ecology, 60, 165-178.

Bardner, R., Fletcher, K.E. & Margaret, G.J. (1977) The activity and distribution of wheat bulb fly (Delia coaretata) (Diptera: Anthomyiidae) in cereal crops and over fallow land. Annals of Applied Biology, 86, 329-337.

Barnes, H.F. (1925) The ecological distribution of adult crane-flies in Carnarvonshire. Journal of Ecology, 13, 138-148.

Bates, H.W. (1863) The Naturalist on the River Amazons. Murray, London.

Bates, M. (1944) Observations on the distribution of diurnal mosquitoes in a tropical forest. Ecology, 25, 159-170.

Bennett, G.F. (1960) On some ornithophilic blood-sucking Diptera in Algonquin Park, Ont., Canada. Canadian Journal of Zoology, 38, 377-389.

Berland, L. (1935) Premiers resultats de mes recherches en avion sur la faune et la flore atmospheriques. Annales de la Societe entomologique de France, 104, 73-96.

Bidlingmayer, W.L. (1961) Field activity studies of adult Culicoides furens. Annals of the Entomological Society of America, 54, 149-156.

Boiteau, G., Bradley, Jr., J.R. and Van Duyn, J.W. (1979) Bean leaf beetle: flight and dispersal behaviour. Annals of the Entomological Society of America, 72: 298-302.

Bowden, J. & Dean, G.J.W. (1977) The distribution of flying insects in and near a tall hedgerow. Journal of Applied Ecology, 14, 343-354.

Brantjes, N.B.M. (1981) Wind as a factor influencing flower-visiting by Hadena bicruris and Deilephila elpenor. Ecological Entomology, 6, 361-363.

Broadbent, L. (1948) Aphids migration and the efficiency of the trapping method. Annals of Applied Biology, 35, 379-394.

Broadhead, E. (1983) The assessment of faunal diversity and guild size in tropical forest with particular reference to the Psocoptera. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Editors), Tropical rain forest: Ecology and Management. Blackwell, Oxford, pp. 107-119.

Broadhead, E. and Wolda H. (1985) Diversity of Psocoptera in the two tropical forests of Panama. Journal of Animal Ecology, 54(3), 739-854.

Bugher, J.C., Boshell-Manrique, J., Roca-Garcia, M. and Osorno-Mesa, E. (1944) Epidemiology of jungle yellow fever in eastern Colombia. American Journal of Hygiene, 39, 16-51.

Cachan, P. (1964) Analyse statistique des pullulations de Scolytoidae mycetophages en foret Sempervirente de cote d'Ivorie. Annales de la Faculte des Sciences, Universite de Dakar, 14, 5-70.

Calnaido, D., French, R.A. & Taylor, L.R. (1965) Low altitude flight of Oseinella frit L. (Chloropidae). Journal of Animal Ecology, 34, 45.

Church, H.F. (1957) The times of emergence of the Pipistrelle. Proceedings of the Zoological Society of London, 128, 600-602.

Cloudsley-Thompson, J.L. (1962) Microclimates and the distribution of terrestrial arthropods. Annual Review of Entomology, 7, 199-222.

Coad, B.R. (1929) Organization and progress of Pink Bollworm research inverstigations. Journal of Economical Entomology, 22, 743-750.

Coad, B.R. (1931) Insects captured by airplane are found at surprising heights. United States Department of Agriculture, Yearbook 1931: 320-323.

Coe R.L., Freeman, P. & Mattingly, P.F. (1950) Handbooks for the identification of British insects. Diptera, Nematocera families, Tipulidae to Chironomidae. Volume IX, Part 2, Royal Entomological Society of London.

Collin J.E. (1961) British flies "Empididae". Cambridge University Press, Volume VI, Part I-III, Cambridge.

Collins, C.W. and Baker, W.L. (1934) Exploring the upper air for wind-borne Gipsy-moth larvae. Journal of Economical Entomology, 27, 320-327.

Colyer, C.N. and Hammond, C.O. (1951) Flies of the British Isles. Warne, London & New York.

Colyer, C.N. (1954) "Swarming" of Phoridae (Diptera). Journal of the Society of British Entomology, 5, 22-27.

Colyer, C.N. & Hammond, C.O. (1968) Flies of the British Isles. Frederick Warne and Co. Ltd. London & New York.

Conover, W.J. (1980) Practical nonparametric statistics. Second Edition, New York, John Wiley and Sons, Inc.

Cook, E.F. (1956) A contribution towards a monograph of the Scatopsidae (Diptera). Part VI, Annals of the Entomological Society of America, 49, 593-611.

Cranston, P.S., Ramsdale, C.d., Snow, K.R. and White G.B. (1987) Adults, larvae and pupae of British Mosquitoes (Culicidae). Freshwater Biological Association Scientific Publication.

Crisp, G. and Lloyd, Ll. (1954) The community of insects in a patch of woodland mud. Transactions of the Royal Entomological Society of London, 105(13), 269-314.

D'arcy-Burt & Blackshaw, R.P. (1987) Effects of trap design on catches of grassland Bibionidae. Bulletin of Entomological Research, 77, 309-315.

Davis, D.E. (1944) A comparison of mosquitoes captured with an avian bait at different vegetational levels. Revista de entomologia, Rio de Janeiro. 15, 209-215.

Dean, G.J.W. (1974) Effects of parasites and predators on the cereal aphids Metopolophium dirhodum (Walk.) and Macrosiphum avenae (F.) (Hem., Aphididae). Bulletin of Entomological Research, 63, 411-422.

Digby, P.S.B. (1955) Factors affecting the temperature excess of insects in sunshine. Journal of Experimental Biology, 32, 279-298.

Disney, R.H.L. (1980) Records of flower-visiting by scuttle flies (Diptera, Phoridae) in the British Isles. Naturalist, Hull, 105, 45-50.

Disney, R.H.L. (1983) Handbooks for the identification of British insects. Volume 10, Part 6. Scuttle flies (Diptera, Phoridae). Royal Entomological Society of London.

Downes, J.A. (1955) Observations on the Swarming flight and mating of Culicoides (Diptera, Ceratopogonidae). Transactions of the Royal Entomological Society of London, 106, 213-235.

Draper, N.R. and Smith, H. (1981) Applied Regression Analysis. Second Edition, New York, John Wiley and Sons, Inc.

Dula, O. (1928) Scatopsidae, Fleigen palaearkt Reg., 2(1), fascicle 5, 1-62.

Duelli, P. (1980) Adaptive dispersal and appetitive flight in the green lacewing, Chysopa Cornea. Ecological Entomology, 5, 213-220.

Dyte, C.E. (1959) Some interesting habitats of larval Dolichopodidae. Entomologist's Monthly Magazine, 95, 139-143.

Edwards, F.W. (1925) A synopsis of British Bibionidae and Scatopsidae. Annals of Applied Biology, 12, 263-275.

Edwards, F.W. (1926) On the British biting midges. Transactions of the Royal Entomological Society of London, 74, 389-426.

Edwards, F.W. (1938) On the British Lestremiinae, with notes on exotic species. Proceedings of Royal Entomological Society of London (B) 7. Part 1: 18-24. Part 2: 25-32. Part 5: 102-108. Part 9: 173-182.

Edwards, F.W. (1939) In Edwards, F.W. Oldroyd, H. and Smart, J. (1939) British Blood-Sucking Flies. 25-50, 129-148. British Museum, London.

Elton, C.S. (1966) the pattern of Animal Communities. Methuen & Co Ltd. London.

El-Ziady, S.A.E. (1954) Field studies in flight activity of insects in relation to their physical environment. Ph.D. Thesis, London University.

Fenton, M.B. (1970) A technique for monitoring bat activity with results obtained from different environments in southern Ontario. Canadian Journal of Zoology, 48, 847-851.

Fisher, R.A., Corbet, A.S. and Williams, C.B. (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. Journal of Animal Ecology, 12, 42-58.

Fonseca, E.C.M. (1968) Handbooks for the Identification of British Insects. Vol. 10, Part 4(B), Calypterata Muscidae. Royal Entomological Society of London.

Fonseca, E.C.M. (1978) Handbooks for the identification of British insects. Volume IX, Part 5, Diptera Orthorrhapha Brachycera, Dolichopodidae. Royal Entomological Society of London.

Freeman, J.A. (1945) Studies in the distribution of insects by aerial currents. The insect population of the air from ground level to 300 feet. Journal of Animal Ecology, 4, 128-154.

Freeman, P. (1950) Handbooks for the identification of British insects. Volume IX, Part 2, Psychodidae and Anisopodidae. Royal Entomological Society of London.

Freeman, P. (1983) Handbooks for the identification of British insects. Sciaridae (Diptera). Royal Entomological Society of London.

Freeman, P. & Lane, R.P. (1985) Handbooks for the identification of British insects. Bibionid and Scatopsid flies. Volume 9, Part 7. Royal Entomological Society of London.

Funakoshi, K. and Uchida, T.A. (1975) Studies on the physiological and ecological adaptation of temperate insectivorous bats: 1. Feeding activities in the Japanese longfingered bats Miniopterus Schreibersi fulignosus. Japanese Journal of Ecology, 25, 217-234.

Funakoshi, K. and Uchida, T.A. (1978) Studies on the physiological and ecological adaptation of temperate insectivorous bats: III Annual activity of the Japanese house-dwelling bat, Pipistrellus abramus. Journal of the Faculty of Agriculture, Kyushu University, 23, 95-115.

Garnham, P.C.C., J.O. Harper and R.B. Highton (1946) The mosquitoes of the Kaimosi forest, Kenya Colony, with special reference to yellow fever. Bulletin of Entomological Research, 36, 473-494.

Galindo, P., H. Trapido and S.J. Carpenter (1950) Observations on diurnal forest mosquitoes in relation to sylvan yellow fever in Panama. American Journal of Tropical Medicine, 30, 533-574.

Galindo, P., S.J. Carpenter and H. Trapido (1951) Ecological observations on forest mosquitoes of an endemic yellow fever area in Panama. American Journal of Tropical Medicine, 31, 98-137.

Gillies, M.T. & Wilkes, T.J. (1976) The vertical distribution of some West African mosquitoes over open farmland in the fresh water area of the Gambia. Bulletin of Entomological Research, 66, 5-15.

Gillies, M.T. & Wilkes, T.J. (1978) The effect of high fences on the dispersal of some West African mosquitoes (Diptera, Culicidae). Bulletin of Entomological Research, 68, 401-408.

Glick, P.A. (1939) The distribution of insects, spiders, and mites in the air. United States Department of Agriculture, Technical Bulletin No. 673. 1-150.

Glick, P.A. (in Moulton, F.R.) (1942) Insect population and migration in the air. In Aerobiology. American Association for the Advancement of Science, Washington, D. C. 17, 88-98.

Graham-Smith, G.S. (1916) Observations on the habitats and parasites of common flies. Parasitology, 8, 440-543.

Grensted, L.W. (1947) Diptera in the patches of Arum maculatum L. Entomologist's monthly Magazine, 83, 1-3.

Haddow, A.J. (1945) the mosquitoes of Bwamba County, Uganda. III. The vertical distribution of mosquitoes in a banana plantation and the biting cycle of Aedes (Stegomyia) simpsoni Theo. Bulletin of Entomological Research, 36, 297-304.

Haddow, A.J. and G.W.A. Dick (1948) Catches of biting Diptera in Uganda with anaesthetized monkeys as bait. Annals of Tropical Medicine and Parasitology, 42, 271-277.

Haddow, A.J. and A.F. Mahaffy (1950) The mosquitoes of Bwamba County, Uganda. VII. Intensive catching on tree-platforms, with further observations on Aedes (Stegomyia) africanus Theobald. Bulletin of Entomological Research, 40, 169-178.

Haddow, A.J., J.D. Gillett and and R.B. Highton (1947) The mosquitoes of Bwamba County, Uganda. V. The vertical distribution and the biting cycle of mosquitoes in rain-forest, with further observations on microclimate. Bulletin of Entomological Research, 37: 301-330.

Haddow, A.J., Corbet, P.S. and Gillett, J.D. (1961) Entomological studies from a high tower in Mpanga forest, Uganda. Transactions of the Royal Entomological Society of London, 113, 249-368.

Hardy, A.C. & Milne, P.S. (1938) Studies in the distribution of insect by aerial currents, Experiments in aerial tow-netting from kites. Journal of Animal Ecology, 7, 199-229.

Harris, K.M. (1966) Gall midge genera of economic importance (Diptera: Cecidomyiidi). Part 1. Introduction and subfamily Cecidomyiinae, Supertribe Cecidomyiidi. Transactions of the Royal Entomological Society of London, 118, 313-358.

Hawkes, C. (1973) Factors affecting the aggregation of the adult cabbage root fly at hedges. Journal of Applied Ecology, 10, 695-703.

Hawkes, H.A. (1951) A study of the biology and control of *Aniscopus fenestralis* (Scopoli, 1963), A fly associated with sewage *filters.* Annals of Applies Biology, 38, 592-605.

Hawkes, H.A. (1961) Fluctuations in the aerial density of *Anisopus fenestralis* Scop. (Diptera) above sewage bacteria beds. *Annals of Applies Biology*, 49, 66-76.

Henrry, L.G. & Adkins, J.R. (1975) Vertical distribution of biting midges in coastal South Carolina. Annals of the Entomological Society of America, 68, 321-324.

Herreid, C.F.II and Davis, R.B. (1966) flight patterns of bats. Journal of Mammalogy, 47, 78-86.

Hingston, R.W.G. (1932) A Naturalist in the Guiana Forest. Arnold, London.

Hutcheson, K. (1970) A test for comparing diversity based on the Shannon formula. Journal of Theoretical Biology, 29, 151-154.

Hutson, A.M. (1970) corrections and additions to the life of British Nematocera (Diptera) since Kloet and Hincks' "A check list of British insects" (1945). Part 2. Scatopsidae. Entomologist's Gazette, 21, 117-123.

Hutson, A.M. (1973) *Scatopse lapponica* Duda, new to Britain, with notes and records of other British species of Scatopsidae (Diptera). Entomologist's Monthly Magazine, 108, 200-201.

Hutson, A.M., Ackland, D.M. & Kidd, L.N. (1980) Handbooks for the identification of British insects, Mycetophilidae (Diptera, Nematocera). Volume IX, Part 3, Royal Entomological Society of London.

Johnson, C.G. (1950) A suction trap for small airborne insects which automatically segregates the catch into successive hourly samples. Annals of Applied Biology, 37, 80-91.

Johnson, C.G. (1957) The distribution of insects in the air and the empirical relation of density to height. Journal of Animal Ecology, 26, 479-494.

Johnson, C.G. (1969) Migration and Dispersal of Insects by Flight. Methuen & Co Ltd. London.

Johnson, C.G. and Penman, H.L. (1951) Relationship of aphid density to altitude. Nature, London. 168, 337-338.

Johnson, C.G. & Taylor, L.R. (1955a) The measurement of insect density in the air. Part II, Laboratory Practice, 4, 187-192.

Johnson, C.G. & Taylor, L.R. (1955b) The development of large suction traps for airborne insects. Annals of Applied Biology, 43, 51-61.

Kettle, D.S. (1951) The spatial distribution of *Culicoides impunctatus* Geot. under woodland and moorland conditions and its flight range through woodland. Bulletin of Entomological Research, 42, 239-291.

Kettle, D.S. (1962) The bionomics and control of *Culicoides* and *Leptoconops* (Diptera, Ceratopogonidae: Heleidae). Annual Review of Entomology, 7, 401-418.

Kettle, D.S. and Lawson, J.W.H. (1952) The early stages of British biting midges *Culicoides* Latreille (Diptera, Ceratopogonidae) and allied genera. Bulletin of Entomological Research, 43, 421-467.

Khalsa, H.G. (1948) Biology of *Anisopus fenestralis* Scop., a new invader of sewage filter beds at Knostrop, Leeds. Thesis, Leeds University.

Kidd, L.N. & Brindle, A. (1959) The Diptera of Lancashire and Cheshire. T. Buncle & Co Ltd, Cheshire.

Korting, A. (1931) Beobachtungen uber die fluggewohnheiten der fritfliege und einiger getreidethysanopteren. Zeitschrift Fur Angewandte Entomologie, 18, 154-160.

Kunz, T.H. (1973) Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy, 54, 14-32.

Kunz, T.H. (1974) Feeding ecology of a temperate insectivorous bat (*Myotis velifer*). Ecology, 55, 693-711.

Laurence, B.R. (1951) The prey of some tree trunk frequenting Empididae and Dolichopodidae (Diptera). Entomologist's Monthly Magazine, 87, 166-169.

Lewis, T. (1959) A comparison of water traps, cylindrical sticky traps and suction traps for sampling Thysanoptera population at different levels. Entomologia experimentalis applicata, 2, 204-215.

Lewis, T. (1965a) The effects of an artificial windbreaks on the aerial distribution of flying insects. Annals of Applied Biology, 55, 503-512.

Lewis, T. (1965b) The effect of an artificial windbreaks on the distribution of aphids in a lettuce crop. Annals of Applied Biology, 55, 513-518.

Lewis, T. (1965c) The effects of shelter on the distribution of insect pests. Scientific Horticulture, 17, 74-84.

Lewis, T. (1966a) An analysis of components of wind affecting the accumulation of flying insects near artificial windbreaks. Annals of Applied Biology, 58, 365-370.

Lewis, T. (1966b) Artificial windbreaks and the distribution of turnip mild yellow virus and Scaptomyze apicalis (Diptera) in a turnip crop. Annals of Applied Biology, 58, 371-376.

Lewis, T. (1967) The horizontal and vertical distribution of flying insects near artificial windbreaks. Annals of Applied Biology, 60, 23-31.

Lewis, T. (1969a) Factors affecting primary patterns of infestation. Annals of Applied Biology, 63, 315-317.

Lewis, T. (1969b) The distribution of flying insects near a low hedgerow. Journal of Applied Ecology, 6, 443-452.

Lewis, T. (1969c) The diversity of the insect fauna in a hedgerow and neighboring fields. Journal of Applied Ecology, 6, 453-454.

Lewis, T. (1970) Patterns of distribution of insects near a windbreak of tall tree. Annals of Applied Biology, 65, 213-220.

Lewis, T. & Dibley, G.C. (1970) Air movement near windbreaks and a hypothesis of the mechanism of the accumulation of airborne insects. Annals of Applied Biology, 66, 477-484.

Lewis, T. & Macaulay, E.D.M. (1976) Design and elevation of sex-attractant traps for pea moth and the effect of plume shape on catches. Ecological Entomology, 1, 175-185.

Lewis, T. & Smith, B.D. (1969) The insect faunas of pear and apple orchards and the effect of windbreaks on their distribution. Annals of Applied Biology, 64, 11-20.

Lewis, T. & Stephenson, J.W. (1966) The permeability of artificial windbreaks and the distribution of flying insects in the leeward sheltered zone. Annals of Applied Biology, 58, 355-363.

Lewis, T. & Taylor, L.R. (1964) Diurnal periodicity of flight by insects. Transactions of Royal Entomological Society of London, 116, 393-476.

Lewis, T. & Taylor, L.R. (1967) Introduction to Experimental Ecology. Academic Press, London.

Love, G.J. & Smith, W.W. (1958) The stratification of mosquitoes. Mosquito News, 18, 279-283.

Lundbeck, W. (1922) Diptera Danica. Vol. VI Wm. Wesley & Son, London.

Magurran, A.E. (1988) Ecological Diversity and its measurement. London, Sydney.

Meteorological Office (1964) Hygrometric Tables. Part III Second Edition, Aspirated Psychrometer Readings Degrees Celsius, Her Majesty's Stationery Office, London.

Milne, D.C. (1960) the gall midges (Diptera: Cecidomyiidae) of clover flower heads. Transactions of the Royal Entomological Society of London, 112, 73-108.

Niblett, M. (1941) Notes on some gall-causing Cecidomyiidae: I. Entomologist. 74, 221-224.

Oke, T.R. (1987) Boundary Layer Climates. Second edition, Methuen. London and New York.

Oldroyd, H. (1970) Diptera: Introduction and Key to Families. Handbooks for the Identification of British Insects, Vol IX Part 1, Royal Entomological Society of London.

Pasek, J.E. (1988) Influence of wind and windbreaks on local dispersal of insects. Agriculture, Ecosystems and Environment, 22/23, 539-554.

Pedgley, D. (1982) Windborne pests and diseases: Meteorology of airborne organisms. Ellis Horwood Ltd., Chichester, U.K..

Penny, N.D. and Arias, A.R. (1982) Insects of an Amazon forest. Columbia University Press. New York, New York.

Peng, R.K. (1986) Biology and control strategies of tea aphid (Toxoptera aurantii Boyer). Tea Journal, 3. In Chinese.

Pielou, E.C. (1966) The measurement of diversity in different types of biological collections. Journal of Theoretical Biology, 13, 131-144.

Pinchin, R.D. & Anderson, J. (1936) On the nocturnal activity of Tipulidae (Diptera) as measured by a light trap, (1) The time of flight and proportion of sexes. Proceedings of Royal Entomological Society of London, 11, 69-75.

Pinder, L.C.V. (1978) A key to the adult males of the British Chironomidae. Vol. 1 & 2. Freshwater Biological Association Scientific Publication.

Pittendrigh, C.S.(1950) The ecoclimatic divergence of Anopheles bellator and A. homunculus. Evolution, 4, 43-63.

Pollard, E. (1968) Hedges. The effect of removal of the bottom flora of a hawthorn hedgerow on the fauna of the hawthorn. Journal of applied Ecology, 5, 109-23.

Poole, R.W. (1974) An Introduction to Quantitative Ecology, McGraw-Hill Book Company, New York.London.

Profft, J. (1939) Uber fluggewohnheiten der blallause im zusammenhang mit der verbreitung von kartoffelviosen. Arbeiten uber Physiologische und Agewandte Entomologie aus Berlin-Dahlem, 6, 119-145.

Reader, P.M. & Southwood, T.R.E. (1984) Studies on the flight activity of the Uiburnum whitefly, a reluctant flyer. Entomologia experimentalis et applicata. 36, 185-191.

Rees, C.J.C. (1983) Microclimate and flying Hemiptera fauna of a primary lowland rain forest in Sulawesi. In: S.L. Sutton, T.C. Whitmore and A.C. Chadwick (Editors), Tropical Rain Forest: Ecology and Management. Blackwell, Oxford, pp. 121-136.

Reuben, R. (1963) A comparison of trap catches of Culicoides impunctatus Go. (Diptera, Ceratopogonidae) with meteorological data. Proceedings of Royal Entomological Society of London, Serials A, General Entomology, 38, 181-193.

Richards, P.W. (1983) The three dimentional structure of tropical rain forest. In: S.L.Sutton, T.C. Whitmore and A.C. Chadwick (Editors), Tropical Rain Forest: Ecology and Management. Blackwell, Oxford, pp. 3-10.

Riggert, E. (1931) Uber die flughohe der fritfliege. Nachrichtenblatt fur den Deutschen Pflanzenschutzdienst. Berlin, 2, 26-27.

Robertson, A.G. (1939) The nocturnal activity of crane-flies (Tipulidae) as indicated by captures in a light trap at Rothamsted. Journal of Animal Ecology, 8, 300-322.

Satchell, G.H. (1948) The ecology of the British species of Psychoda (Diptera, Psychodidae). Annals of Applied Biology, 34, 611-621.

SAS Institute Incorporated. (1985) SAS User's Guide, Statistics, Version 5 Edition. Cary, North Carolina.

Service, M.W. (1971a) Fight periodicities and vertical distribution of Aedes cantans, Ae. geniculatus (Ol.), Anopheles plumbeus and Culex pipiens L. (Diptera, Culicoides) in southern England. Bulletin of Entomological Research, 60, 639-651.

Service, M.W. (1971b) Adult flight activity of some British Culicoides species. Journal of Medical Entomology, 8, 605-609.

Service, M.W. (1973) Spatial and temporal distribution of aerial populations of woodland tipulids (Diptera). Journal of Animal Ecology, 42, 295-303.

Shands, W.A., Simpson, G.W. & Dudley, J.E. (1956) Low-elevation movement of some species of aphid. Journal of Ecological Entomology, 49, 771-776.

Shannon, C.E. and Weaver, W. (1963) The Mathematical Theory of Communication. Urbana: University of Illinois Press.

Siegel, S. (1956) Nonparametric statistics for the behavioral science. McGRAW-Hill, Book Company, New York.Toronto.London.

Skidmore, P. (1985) The biology of the Muscidae of the world. Dr. W. Junk Publishers, Dordrecht.

Smith, B.D. & Lewis, T. (1972) The effects of windbreaks on the blossom-visiting fauna of apple orchards and on yield. Annals of Applied Biology. 72, 229-238.

Snow, W.E. (1955) Feeding activities of some blood-sucking Diptera with reference to vertical distribution in the bottomland forest. Annals of the Entomological Society of America, 48, 512-521.

Snow, W.F. (1975) The vertical distribution of flying Mosquitoes (Diptera, Culicidae) in West African Savanna. Bulletin of Entomological Research, 65, 269-277.

Snow, W.F. (1979) The vertical distribution of flying mosquitoes (Diptera, Culicidae) near an area of rice-fields in the Gambia. Bulletin of Entomological Research, 69, 561-571.

Snow, W.F. (1982) Further observations on the vertical distribution of flying mosquitoes (Diptera, Culicidae) in West African Savanna. Bulletin of Entomological Research, 72, 695-708.

Snow, W.F. and Wilkes, T.J. (1977) Age composition and vertical distribution of mosquitoe populations in the Gambia, West Africa. Journal of Medical Entomology, 13, 507-513.

Sokal, R.R. and Rohlf, F.J. (1981) Biometry. Second eddition, Freeman & Co., New York.

Southwood, T.R.E. (1978) Ecological Methods. Second edition. Chaman & Hall, London.

Stebbings, R.E. (1968) Measurements, composition and behaviour of a large colony of the bat Pipistrellus pipistrellus. Journal of Zoology. London, 156, 15-33.

Stebbings, R.E. (1977) Order Chiroptera; Bats. In Handbook of British Mammals: 68-128, Second edition. Corbet, G.B. & Southern, H.N. (Editors) London, Blackwell.

Stubbs, A. & Chandler, P. (1978) A Dipterist's Handbook. Kingprint Ltd, Richmond, Surrey.

Sutton, S.L. (1979) The vertical distribution of flying insects in the lowland rain forest of Brunei: preliminary report. Brunei Museum Journal, 4(3), 161-173.

Sutton, S.L. (1983). The spatial distribution of flying insects in tropical rain forests. In: S.L. Sutton, T.C. Whitemore and A.C. Chadwick (Editors), Tropical Rain Forest: Ecology and Management. Blackwell, Oxford, pp. 77-79.

Sutton, S.L. & Hudson, P.J. (1980) The vertical distribution of small flying insects in the lowland rain forest of Zaire. Zoological Journal of the Linnean Society, 68, 111-123.

Sutton, S.L. (1989) The spatial distribution of flying insects. In Lieth, H. and Werger, M.J.A. (Editors), Tropical Rain Forest Ecosystems. Elsevier Science Publishers B.V., Amsterdam, pp. 427-436.

Sutton, S.L., Ash, C.P. & Grundy, H. (1983). The vertical Distribution of flying insects in the lowland rain forests of Panama, Papua New Guinea and Brunei. Zoological Journal of the Linnean Society, 78(3), 287-297.

Sutton, O.G. (1953) Micrometeorology. Mcgraw-Hill, New York.

Swanton, E.W. (1912) British plant-galls. Methuen & Co. Ltd., London.

Swift S.M. (1980) Activity patterns of Pipistrelle bats (Pipistrellus pipistrellus in north-east Scotland. Journal of Zoology, London, 190, 285-295.

Taylor, L.R. (1955) The standardization of air-flow in insect suction traps. Annals of Applied Biology, 43, 390-408.

Taylor, L.R. (1958) Aphid dispersal and diurnal periodicity. Proceedings of the Linnean Society of London, 169, 67-73.

Taylor, L.R. (1960) The distribution of insects at low level in the air. Journal of Animal Ecology, 29, 45-63.

Taylor, L.R. (1962) The absolute efficiency of insect suction traps. Annals of Applied Biology, 50, 405-421.

Taylor, L.R. (1963) Analysis of the effect of temperature on insects in flight. Journal of Animal Ecology, 32, 99-117.

Taylor, L.R. (1974) Insects migration, flight periodicity and the boundary layer. Journal of Animal Ecology, 43, 225-238.

Taylor, L.R. (1978) Bates, Williams, Hutchinson - a variety of diversities. In Diversity of Insect Fauna: 9th Syposium of the Royal Entomological Society (Eds L.A. Mound and N. Warloff), Blackwell, Oxford, pp. 1-18.

Taylor, L.R., Brown, E.S. and Littlewood, S.C. (1979) The effect of size on the height of flight of migrant moths. Bulletin of Entomological Research, 69, 605-609.

Taylor, L.R. and Johnson C.G. (1954) Wind direction and infestation of bean fields by Aphis fabae Scop. Annals of Applied Biology, 41, 107-116.

Taylor, L.R. and Palmer, J.M.P. (1972) Aerial sampling. In Van Emden, H.F. (editor), Aphid Technology. pp.189-234. Academic Press, London.

Unwin, D.M. (1981) A key to the families of British Diptera. Field Studies, 5, 513-533.

Van Eimern, J., Karschon, R. Razumova, L.A. and Robertson, G.W. (1964) Windbreaks and shelterbelts. W.M.O. Tech. note no. 59.

Wegorek, W. (1959) The Colorado Potato beetle (Leptinotarsa decemlineata Say) Pr. nauk. Inst. Ochr. Rosl. I (2), 105 pp. [English translation published by Centralny Instytut Informacji Naukowo-Techniczneji Ekonomicznej, Warsawa, 1964].

Willard, J.R. (1974) Horizontal and vertical dispersal of California red scale in the field. Australia Journal of Zoology, 22, 531-548.

Williams, C.B. (1940) An analysis of four years captures of insects in a light trap. Part II. The effect of weather conditions on insect activity; and the estimation and forecasting of changes in the insect population. Transactions of the Royal Entomological Society of London, 90, 227-306.

Willmer, P.G. (1982a) Microclimate and the environmental physiology of insects. Advances in Insect Physiology, 16, 1-57.

Willmer, P.G. (1982b) Hygrothermal determinants of insect activity patterns: the Diptera of water lily leaves. Ecological Entomology, 7, 221-231.

Willmer, P.G. (1983) Thermal constraints on activity patterns in nectar-feeding insects. Ecological Entomology, 8, 455-469.

Wolda, H. (1979) Abundance and diversity of Homoptera in the canopy of a tropical forest. Ecological Entomology. 4(2), 181-190.

Wolfenbarger, D.O. (1946) Dispersion of small organisms. Distance dispersion rates of bacteria, spores, seeds, pollen, and insects; incidence rates of diseases and injuries. American Midland Naturalist, 35, 1-152.

APPENDIX 1

Constitution of common family, relative abundance of species and their life history traits

Table A.1 Constitution of each common family, relative abundance of species and their life history traits. Species or genera with ++++, +++, ++ and + indicate the most abundant, abundant, common and rare respectively. Their main activity period (AP) is indicated by MO (morning), AF (afternoon), DU (dusk) and NI (night).

Name	86	87	AP	Habit
Anisopodidae:				
Anisopus cinctus Fabricius		+	DU	Larvae: feeding in wet decaying organic matter, dung, manure heaps and fermenting sap (Freeman 1950). Adult: swarming in slight breezes, resting on tree trunks (Khalsa 1948; Colyer & Hammond 1968; Hawkes 1951).
A. fenestralis Scopoli	+	++	DU	
A. punctatus Fabricius	++	++++	DU	
Anthomyiidae:				
six species included			AF	Adult: flower-feeding (Stubbs & Chandler 1978) and honeydew-seeking.
four of them were common	++	+++	AF	
no proper key to follow so far				
Ceratopogonidae:				
Culicoides vexans Staeger	++	++++	DU NI	Larvae: breeding in damp earth round bushes and under big tree (Kidd & Brindle 1959), mud-lined shallow pools and woodland mud (Kettle & Lawson 1952; Crisp & Lloyd 1954) Adult: biting, blood and sap-sucking (Edwards 1926, 1939) and probable swarming (Downes 1955)
C. chiopterus Meigen	++	+++	DU	
C. sp.	+	+	DU	
Forcipomyia bipunctata Linnaeus	++	+++	AF DU	Larvae: under bark and rotting vegetation (Edwards 1926). Adult: probable swarming (Downes 1955).
Serromyia morio Fabricius	+	+	AF,DU	

Table A.2

Name	86	87	AP	Habit
Cecidomyiidae:				
Cecidomyiinae:				
Asphondyliidi (one sp.)	+	+	DU,NI	Probable gall-making (Swanton 1912; Niblett 1941).
Cecidomyiidi (one sp.)	++	++	NI	
Clinodiplosis leguminicola Milne	++++	++++	NI	Feeding on clovers & many flowering plants (Harris 1966).
C. sp.	+	++	DU,NI	Probable gall-making.
Oligotrophidi (one sp.)		+	DU,NI	
Lestreminae:				
Anarete sp.	+	+	MO,AF	Many species live in dead wood, ground fungi and active along hedgerow (Edwards 1938)
Campylomyza flavipes Meigen	++	++	AF	
Lestremiini (one sp.)	+	++	MO,AF	
Porricondylinae (one sp.)	+	+	AF,DU	
Chironomidae:				
Hydrobaenus sp.	+++	++	AF	
Metriocnemus atratulus Zetterstedt	+++	++++	AF,DU	Male > female (numbers), swarming high in sheltered place near trees & bushes (Colyer & Hammond 1968; Coe *et al.* 1950).
M. atriclavus Kieffer	++	+++	DU,NI	
M. sp.	+	++	DU,NI	
Micropsectra spp.	++	++	DU,NI	Breeding in ditches of stagnant water and swarming high at dusk (Coe *et al.* 1950; Coyler & Hammond 1968).
Lundstromia sp.	++	+	DU	
Tanytarsus spp.	+	++	DU	
Dolichopodidae:				
Dolichopus sp.	++	+++	AF	Feeding on aphid excretions and exuviae (Kidd & Brindle 1959).
Medetera sp.1	+++	++++	AF	Preying on small insects on tree trunks or foliage (Laurence 1951; Colyer & Hammond 1951).
M. sp.2	+++	++++	MO,AF	
Sciapus sp.	++	++	AF	

Table A.3

Name	86	87	AP	Habit
Empididae:				Larvae: carnivorous, living in decaying vegetation and moss (Kidd & Brindle 1959).
Symballophthalmus pollinosus C.	++	++	AF	Adult: active in wood (Collin 1961).
Tachydromia subtilis C.	+++	++++	AF	Adult: preying small insects and active in hedgerow (Collin 1961; Colyer & Hammond 1968).
T. parvicauda Colin	+++	+++	AF	
T. rapida Meigen	++	+	AF	
T. sp.	+	++	MO,AF	
Muscidae:				Larvae: feeding on decaying matter or excrement.
Alloeostylus diaphanus Wi.	+++	++++	MO,AF	Adult: preferring sweet substances, active in sheltered spot under tree and visiting lime tree flowers (Colyer & Hamm. 1968; Willmer 1983). flower- and honeydew-feeding Skidmore 1985; Stubbs & Chandler 1978).
Dasyphora cyanicolor Zett.	+++	+++	MO,AF	
Fannia sp.1	+++	++	AF	
Fannia sp.2	++	+	AF	
Lispe spp.	++	++	MO,AF	
Lispocephala sp.		+	MO,AF	
Mycetophilidae:				Larvae: feeding on fungi and decaying matter.
Mycetophilinae sp.1	+++	++++	DU	Adult: preferring moist dark places, swarming beneath bushes and flower-feeding (Kidd & Brindle 1959; Colyer & Hamm. 1968; Hutson et al. 1980).
M. sp.2	++	++	DU	
M. sp.3		++	DU	
Phoridae:				Larvae: developing in fungi, decaying vegetation and animals, preying on other insects & the eggs of spiders and slugs (Disney 1983).
Megaselia scutellaris Wood	+++	++++	AF,DU	Adult: swarming, visiting flowers and preying on animals (Lundbeck 1922; Colyer 1954; Kidd & Brindle 1959; Disney 1983)
M. sp.	+++	+++	AF,DU	
Phora spp.	++	+++	AF	
Triphleba sp.	+	+	AF,DU	Breeding in fungua (Colyer 1954)

Table A.4

Name	86	87	AP	Habit
Psychodidae:				Larvae: feeding in dung, decaying vegetation matter, fungi and manure. Adult: Occurring in large numbers near their breeding places, limited ability for dispersal, preferring damp dark places, resting low on tree trunks in daytime, flower visiting (Satchell 1947, Grensted 1947; Kidd & Brindle 1959; Colyer & Hammond 1968)
Pericoma pilularia Tonnoir	+	+	AF,DU	
P. cognata Eaton	+	++	AF,DU	
Psychoda albipennis Zetterstedt	++	++	DU,NI	
P. brevicornis Tonnoir	++	+	DU	
P. crassipenis Tonnoir	+	++	DU	
P. grisescens Tonnoir	++	++	DU	
P. erminea Eaton		+	DU,NI	
P. phalaenoides Linnaeus	++++	++++	NI	
P. setigera Tonnoir	++	+++	NI	
P. severini Tonnoir	++	+++	DU,NI	
P. trinodulosa Tonnoir	+	+	DU,NI	
Scatopsidae:				Larvae: feeding on dung and various decaying organic matter. Adult: occurring in large numbers, swarming on leaves, crowded together in confined places, active in hot sun, flower-feeding and honeydew-seeking (Kidd & Brindle 1959; Hutson 1973; Colyer & Hamm. 1968; Freeman & Lane 1985). Sexes distributed almost equally except for R. sp.
Anapausis soluta Loew	+++	+++	AF	
Coboldia fuscipes Meigen	+	+	AF	
Cookella albitarsis Zetterstedt	+	+	AF	
Ectaetia clavipes Loew	+	+	AF	
Rhegmoclema cooki Hutson	++++	++++	AF	
R. coxendix Verrall	++	++	AF	
R. sp.	++	++	AF	
Scatopse notata Linnaeus	++	++	MO,AF	
Swammerdamella brevicornis M.	++	+	AF	
S. acuta Cook	+	+	MO,AF	

Table A.5

Name	86	87	AP	Habit
Sciaridae:				Larvae: feeding on dead leaves, moss, fungi, animal excrement and decaying material; damaging various plants. Adult: flower-feeding and often occurring near or in woodland (Freeman 1983; Kidd & Brindle 1959). They often appeared together (observed in this study).
Bradysia sp.1	+++	++++	AF	
B. sp.2	++	+++	MO,AF	
Sciara sp.	+	++	AF,DU	
Tipulidae:				Larvae: feeding on grass and decaying wood of deciduous trees. Adult: breeding in meadow or in decaying wood; *Nephrotoma* can breed from trees, including lime tree. *Limoniini sp.* swarm at dusk or dawn (Coe *et al.* 1950; Colyer & Hammond 1968).
Hexatomini (one sp.)	++	++	NI	
Limoniini (one sp.)	+++	++++	NI	
Nephrotoma sp.	++	+++	DU,NI	