Seeing nature alive, the bees and the flowers,
believing your own eyes' response and input
yield untold numbers and figures with power
to reveal mysteries of the world clearly put.
Beware the lifeless counts which theories abound
to prove, in shop, the world turns round.

G.J.R.

Dedicated to my generous and loving parents

Robert and Marie-Hélène

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ABSTRACT

Observations of the activity of native and domestic insect pollinators were carried out during the blossom period for three consecutive years (1978-1980) in a semi-dwarf apple orchard near Jordan Station, Ontario. Numbers and types of pollinators visiting blossoms were recorded as well as weather conditions and number of blossoms per tree. Of the 20 groups of insects used for field identification, the honeybee *Apis mellifera* L. was the most numerically significant pollinator for all years. The Anthomyiidae (Diptera) ranked second for 1978 and 1979. In 1980, the Andrenidae and Halictidae were of greater importance than the Diptera. Ranges of the activity of the various insect groups were studied from sunrise to sunset, throughout the blossom season and from one year to the next. The 1979 blossom period was the longest and had the greatest insect species diversity. Insect activity was correlated with apple cultivars located on the east and west slopes of the orchard, with the number of blossoms, with temperatures, humidity and light itensities. The physical factors, especially temperature, were mainly responsible for the variation of the numbers of honeybees. However, they were of little significance in the variation of the numbers of other Hymenoptera and Diptera. The other factors such as cultivar, east and west slopes, day and year were more significant for these native pollinators.

The efficiency of the various groups of pollinators was determined by analysis of the pollen carried on the bodies of the insects. Hymenoptera had significantly more pollen on their bodies than the Diptera. Among the Hymenoptera, the Andrenidae and the pollen-gathering Large Andrenidae had the greatest amount of fruit pollen on their bodies. Among the Diptera, the Syrphidae had the greatest amount of fruit pollen.

The effectiveness of the important pollinators was evaluated by measuring fruit set, seed set and the effective pollination period. Golden Delicious which had the least amount of insect visitors, had the greatest fruit and seed set. This indicates that when visited, more compatible pollen was transferred. There was no significant difference in fruit set between years. During a blossom season with adverse weather conditions such as 1979, the proportion of native pollinators to total insects was greater and seemed to compensate for the fewer honeybees, therefore resulting in equal fruit set.

The present work indicates that, although honeybees are the most important, native insects play a significant role in pollination and should therefore be taken into consideration when planning pesticide applications in an apple orchard ecosystem.

RESUME

L'activité des pollinisateurs sauvages et domestiques a été suivie durant la période de floraison pendant trois ans (1978-1980). Les nombres et les espèces de pollinisateurs visitant les fleurs ont été notés y compris le nombre de fleurs par arbre de même que les conditions météorologiques. Des 20 groupes d'insectes identifiés sur le terrain, l'abeille domestique *Apis mellifera* L. s'est révélée l'espèce la plus abondante à chaque année suivie des Anthomyiidae (Diptera) pour les années 1978 et 1979. En 1980, les Andrenidae et les Halictidae (Hymenoptera) étaient plus abondants que les Diptera. L'activité des divers groupes d'insectes a été étudiée de l'aube au crépuscule, pendant toute la période de floraison et pour chaque année. C'est en 1979, année où la période de floraison a été la plus longue, que la diversité des insectes observés a été la plus grande. De plus, l'activité des insectes a été corrélée avec le type de pommiers sur la pente est ou ouest, avec le nombre de fleurs, avec la température, l'humidité et l'intensité lumineuse. Les facteurs physiques, plus particulièrement la température, sont responsables pour la variation du nombre d'abeilles domestiques. Par contre, ces facteurs ont très peu d'importance dans la variation du nombre des autres Hymenoptera et Diptera. Les autres facteurs soit le type de pommiers, la pente (est ou ouest), la journée et l'année sont hautement significatifs pour expliquer la variation des pollinisateurs sauvages.

L'efficience des différents groupes de pollinisateurs a été déterminée en analysant le pollen provenant du corps des insectes. La quantité de pollen provenant des Hymenoptera était significativement plus élevée que celui des Diptera. Parmi les Hymenoptera, les Andrenidae possédaient le plus de pollen de fruits. Parmi les Diptera, les Syrphidae avaient la quantité de pollen de fruit la plus élevée.

L'efficacité des pollinisateurs importants a été évaluée en mesurant le nombre de fruits et de pépins, et la période effective de pollinisation. La variété Golden Delicious qui avait le moins d'insectes visiteurs, avait la plus grande quantité de fruits et de pépins par fruit. Donc lorsque visité, plus de pollen compatible a été transféré. Il n'y avait aucune différence significative entre la quantité de fruits de chaque année. Pendant une période de floraison avec des conditions météorologiques défavorables comme en 1979, la proportion de pollinisateurs sauvages par rapport au nombre total était plus élevée et semblait compenser pour la baisse en abeilles domestiques, résultant donc en un nombre de fruits équivalents.

Bien que les abeilles domestiques soient les plus importants, les insectes sauvages jouent un role significatif dans la pollinisation et devraient donc être considérés lors de la planification des applications de pesticide pour toute la saison.

INTRODUCTION

The importance and significance of insects in the pollination process has been established for a long time (Brittain, 1933; Free, 1960a; Kendall, 1971, 1973; Kendall and Solomon, 1973; Lewis and Smith, 1969; Martin and McGregor, 1973; Smith and Lewis, 1972; Williams, 1969).

Most fruit blossoms are self-incompatible and therefore require cross-pollination. The mechanism responsible for the inhibition of pollen-tube growth within the stigma is not fully understood (Heslop-Harrison, 1975) however, the necessity for pollen from another variety for fruit set has been well studied (Callan and Lombard, 1978; Faegri and van der Pijl, 1979; Free, 1960a, 1970a; Free and Smith, 1974; Jaycox, 1964; Kendall, 1973; Kendall and Smith, 1975a; Norse, 1977; Williams and Sims, 1977). Honeybees are mainly responsible for this pollen transfer (Free, 1960b; Jaycox, 1964; Kendall and Smith, 1975a; Langridge and Jenkins, 1970; Morse, 1976).

However, appreciable quantities of airborne pollen are present in orchards and this raises the possibility that pollination could occur in the absence of insects. Several workers enclosed limbs or trees with cages, some with insects, some without, and compared amounts of airborne pollen and fruit set (Brittain, 1933; Burchill, 1962; Free, 1964; Jaycox, 1964; Kaeser, 1976; Langridge, 1969; Langridge and Jenkins, 1970; Rom, 1970; Selimi, 1971; Solomon and Kendall, 1971). It was found that pollen was not carried for any great distance by the wind, barely between trees and therefore was ineffective for pollination. Also, the percentage of fruit set on a tree enclosed with insects was much higher than that on a tree from which insects had been excluded.

Honeybees form a high percentage of the insects visiting fruit flowers. But many others are frequent visitors. However, because of the intensive cultivation of land and thus the resulting decrease in nesting and overwintering sites, the numbers of these native pollinators have declined. To secure adequate pollination, hives are brought in on a rental basis for the blossom period (Free, 1960a; Kendall and Solomon, 1973; Martin and McGregor, 1973; NRCC, 1981). On the other hand, the activity and effectiveness in pollinating of honeybees is greatly dependent upon weather: strong winds (Lewis and Smith, 1969; Smith and Lewis, 1972; Teras, 1976), overcast skies, and temperature below a certain threshold (Bohart, 1952; Chansigaud, 1972; Free, 1960a; McLellan, 1976; Percival, 1947; Smith and Lewis, 1972; Synge, 1947; Taylor, 1963, Teras, 1976) will reduce their foraging which results in inadequate pollination. During these periods of unfavourable weather, a great many native or wild insects are more readily observed and are often seen on blossoms of fruit trees. These insects are present also while the hive bees are foraging but, since many are smaller in size, they are not as apparent upon field observation. Nevertheless, these wild insects seem to be less affected by weather than the hivebees and their role in pollination should not be ignored or underestimated (Bohart, 1952; Brittain, 1933; Chansigaud, 1972; Free, 1960a; Lewis and Smith, 1969).

An extensive use of pesticides is an acceptable practice in modern agriculture and many non-target, beneficial insects may suffer great losses. Even though nothing is sprayed in fruit orchards during the blossom period, bee poisonings have become increasingly important. These losses usually occur from indirect contact with pesticides such as drifts from sprayed neighbouring fields. The large foraging areas of honeybees increase the chance of contacting contaminated fields (Caine, 1977; Gary et al, 1975; Kevan, 1975; Todd and Reed, 1969; Weaver, 1951). Since fungicides can be applied even at the start of the blossom period, pollen, which is the main source of food for the young larvae, may be contaminated and its viability decreased thus causing major poisonings and declining fruit set (Church and Williams, 1977, 1978; Guirguis and Brindley, 1974; Johansen and Brown, 1972; Legge and Williams, 1975). The effect on native insects is even greater, because they forage under more adverse weather conditions thus increasing the time spent in the field and possibly their foraging area (NRCC, 1981). They are still present after the blossom season and after the hives are removed, and therefore in contact with all subsequent sprays.

The losses are considerable both monetarily and with regards to insect-pollinated crops. In crops that are dependent on wild bee pollinators, the latter may require three or more years to return to original population levels (Free, 1970a) or they may be eliminated from a locality indefinitely. Beekeepers have great difficulty supplying strong colonies of honeybees for pollination service after suffering chronic poisoning losses over a period of years. This presents an impending dilemma with reduction of profitable beekeeping and native pollinators on one hand and an increasing need for bees for crop pollination on the other (Johansen, 1977; Martin and McGregor, 1973). Anderson and Atkins (1968), Johansen (1977) and the National Research Council (1981) have presented elaborate reviews on the subject of bees (domestic and native) and their interactions with pesticides.

Native insects may not play as important a role as honeybees but, their presence, activity, and significance to the pollination process are worthy of investigation.

ORCHARD POLLINATION

The amount of cross-pollination in an orchard depends on the numbers of insect pollinators present (population density), their relative distribution on the various cultivars of trees (affected by flower attractiveness), the frequency with which they move and carry pollen between these cultivars (affected by constancy), the amount of pollen released by flowers and the amount and compatibility of the pollen carried by insects (Kendall and Smith, 1975). The effectiveness of cross-pollination can be seen by the fruit set, the size of fruit, and the number of seeds per fruit (Kendall and Smith, 1975a; Smith and Lewis, 1972). These steps are detailed below since they are essential in evaluating the importance of wild pollinators.

1. Population Composition:

The population density of flying insects in an orchard has often been determined using suction traps (Lewis and Smith, 1969; Smith and Lewis, 1972; Taylor, 1951, 1963). These suction traps were adopted because actual flower observations of the often small wild pollinators was thought to be inaccurate. Because the aerial population is not necessarily the pollinating population, the suction traps were placed near an abundance of blossoms, thus reducing the number of non-pollinating insects caught.

Most surveys have shown that honeybees form a high percentage of the insects visiting fruit flowers, from 60% to 90% (Bornus et al, 1977; Free, 1960a; Kendall, 1971). But there are many other insect visitors belonging mainly to the families Andrenidae, Halictidae, Megachilidae in the Hymenoptera; and the families Syrphidae, Calliphoridae and Muscidae in the Diptera (Brittain, 1933; Bohart, 1952, 1972; Chansigaud, 1972; Free, 1960a; Kendall, 1973). Most work has been done on honeybees, relating to all aspects of orchard pollination (Bornus et al, 1977; Erickson et al, 1973; Free, 1962b; Free and Smith, 1974; Langridge and Goodman, 1973; Langridge and Jenkins, 1972, 1975; Langridge et al, 1976, 1977; Morse, 1976; Waddington and Holden, 1979). More specific work has been conducted on the distribution of pollen and nectar gatherers, on the factors determining pollen collection, on the time spent foraging, on the size of the foraging area, on the movement between trees and on the general behaviour and efficiency of the honeybees visiting the flowers of fruit trees (Free, 1960b, 1966, 1967; Free and Spencer-Booth, 1964b; Jaycox, 1964; Kendall and Smith, 1975a; Langridge and Jenkins, 1970; Langridge et al, 1976; Percival, 1947, 1955; Synge, 1947).

Pollination has also been looked at for a variety of other crops such as alfalfa (Bohart, 1957; Gary et al, 1973); field and runner beans (Kendall and Smith, 1975b, 1977), blueberries (Finnamore and Neary, 1978; Kevan, 1975), strawberries (Pion et al, 1980), cotton (Moffett et al, 1975, 1976a, 1976b), honeydew melons (Gary et al, 1975), onions (Gary et al, 1977) and sunflowers (Rangarajan et al, 1974). Visits to flowers and behaviour have been studied for specific groups of native pollinators such as bumblebees (Bohart, 1972; Free, 1970b; Heinrich, 1976; Teras, 1976), *Osmia* (Bohart, 1972; Kitamura and Maeta, 1969; Torchio, 1976), *Andrena carantonica* Perez (Chansigaud, 1975); and Syrphid flies (Holloway, 1976; Solomon and Kendall, 1971).

Very little has been done to determine the importance of the various native populations as they relate to the entire pollination process. Chansigaud (1972) monitored the flights of wild bees in orchards and reported that the wild bees represented 5% to 10% of the total number of bees registered. However, observations were conducted for only one hour a day during the blossom season. Lewis and Smith (1969, 1972) investigated the effects of windbreaks on the distribution of the insect fauna in orchards. They used suction traps for collections and reported honeybees, Syrphidae, Bibionidae and Muscidae as the main groups present. These traps may give a good estimate of the aerial fauna, but the insects caught by this method are not necessarily actual pollinators.

A few other workers identified species present on fruit blossoms from general collections without monitoring actual numbers (Kendall, 1971, 1973; Kendall and Solomon, 1973; Williams, 1969).

2.0 Pollinator Activity:

The activity of pollinators is influenced by a number of biotic and physical factors.

2.1 Biotic Factors:

The numbers of blossoms present, flower morphology, pollen and nectar availability are responsible for the attractiveness of insect visitors to specific varieties.

Kendall and Smith (1975a) directed their attention towards the relative attractiveness of flowers to honeybees. Counts of bees visiting blossoms were made and compared with expected values based on the abundance of flowers. Equally attractive blossoms of main crop and pollinizer are desirable for adequate cross-pollination. The blossom period of the pollinizer should overlap or coincide with the variety to be pollinated (Free, 1960a; Nyeki, 1974; Nyeki and Soltesz, 1978; Rom, 1970; Williams and Sims, 1977). The numbers of blossoms per tree of both main crop and pollinizer, should also be similar, because trees with more blossoms attract more insect visitors (Brittain, 1933;

Free, 1966; Kendall and Smith, 1975a; Lewis and Smith, 1969; Silander and Primack, 1978).

Flower morphology may influence the behaviour of visitors and subsequent fruit set. Insects can approach nectaries from the side without touching the anthers or stigma. Some flowers have very short pistils so that even when a bee is collecting pollen the stigma is too far below the anthers to be touched resulting in poor setting (Free, 1960b; Roberts, 1945).

Nectar guides observed under ultra-violet light present great contrasts with the surrounding environment and readily attract visitors. The study of the ultra-violet spectrum of vision of insects as it relates to nectar guides and pollination is still relatively new, with most work carried out on weeds and vegetables (Brett and Sullivan, 1972; Grant, 1950; Kevan, 1972; Mosquin and Martin, 1967; Mulligan and Kevan, 1973; Silberglied, 1979).

Pollen and nectar availability are extremely important factors responsible for the distribution of insects on the main crop, on the pollinizer or on other competing blossoms. Pollen is of course the important component and its transport is essential for fruit set. From the insect's point of view, however, nectar is the main attraction (Percival, 1955).

The concentration of sugar in the nectar and the amount of nectar will determine which flowers will be visited. The concentration of nectar at the time of collection depends on species, ambient temperature, humidity and air movement, degree of protection, and standing of the flower (NRCC, 1981). Therefore, nectar concentrations vary greatly throughout one day as weather conditions change. Pollinators alter their foraging strategies with these hourly and daily fluctuations (Butler, 1945; Corbet et al, 1979; Heinrich, 1976; Norstog, 1981; Percival, 1947; Vansell, 1952). The availability of pollen due to anther dehiscence is also greatly dependent on changes in weather (McLellan, 1976; Percival, 1947, 1955; Synge, 1947). Apple blossoms, which are of particular interest in this study, display greater amounts of pollen and nectar from 11:00 to 16:00 hours (Butler, 1945; Free, 1960a; Langridge, 1969; Percival, 1955).

The amount of pollen and the concentration of nectar will make various flowering plants more or less attractive to insect visitors at different times of the day (Butler, 1945; Corbet et al, 1979; Free et al, 1960). This may increase competition both among plants and among pollinators.

Foraging between plants species is undesirable. However, movement between varieties is essential for adequate cross-pollination and fruit set. The foraging behaviour and constancy of honeybees have been well studied. These insects tend to forage in close proximity of their hive, particularly during unfavourable weather (Brittain, 1933; Free 1960a). Honeybees have been reported to remain constant to one species especially if it is the predominant one in bloom (Brittain and Newton, 1933; Free, 1960b, 1963; Kendall and Smith, 1975a). Apple blossoms have been found to be more attractive than other fruit blossoms (Free, 1960a; Langridge et al, 1976; Vansell, 1952). Free (1960a, 1960b, 1963) found that bees forage only on a few trees during one trip, and tend to move along a row and comparatively little between rows, especially when the adjacent rows are of a different variety.

The arrangement of the pollinizer and the main crop to be pollinated is very important and should be an integral part of orchard planning (Free, 1960a, 1960b, 1962a; Free and Spencer-Booth, 1964a; Kendall, 1973; Nyeki and Soltesz, 1978; Silander and Primack, 1978; Williams and Sims, 1977). When resources, nectar and pollen, become depleted towards the end of the day because of intense foraging, competition among insects causes an increase in the foraging area and pollinators will tend to move between rows and to more trees, thus increasing the amount of cross-pollination (Brittain, 1933; Brittain and Newton, 1933; Free, 1960a; Heinrich, 1979b; Heinrich and Raven, 1972; Jaycox, 1964; Silander and Primack, 1978). This decrease of resources may also cause some foragers to move to species that then become more attractive. In this way, dandelions can become a serious competitor to fruit blossoms (Butler, 1945; Free, 1968). If hives are to be taken to an orchard, they should not be installed until flowering has begun or until there are enough flowers for the bees to work, or else the foragers will visit other species and not concentrate in the orchard (Bornus et al, 1977; Free, 1960a, 1962b, 1963; Free et al, 1960; Gary et al, 1975; Martin and McGregor, 1973).

Bumblebees and solitary bees have been reported to work less methodically than honeybees, and fly more readily from tree to tree (Brittain, 1933; Brittain and Newton, 1933; Free, 1970b; Teras, 1976). They could therefore be more efficient cross-pollinators.

2.2 Physical Factors:

The effects of weather on flying activity are difficult to analyze, since weather in itself is complex. Activity can be affected by any one of temperature, light intensity, wind, rain, or their interaction, thus indirectly influencing the crop. Despite this, workers have tried to define what governs flight activities of bees. Williams and Sims (1977) suggested that temperature alone might dictate foraging activity of hive bees. Taylor (1963) concluded that the change from the inability to fly to the ability to fly occurs abruptly at some critical temperature. This threshold temperature has been reported to be 12°C to 14°C for honeybees, but some were observed flying at temperatures as low as 10°C (Eckert, 1955; Heinrich, 1979a; Langridge and Jenkins, 1970; Percival, 1955; Taylor, 1963; Teras, 1976; Williams and Sims, 1977). Brittain (1935) concluded that light had a greater influence on flight activity once the threshold temperature was attained. And according to Percival (1955), direct sunlight compensates for lower air temperature for insect flight. But a sunless day after a sunny one decreased foraging activity markedly (Percival, 1947).

Native insects were found to be much more tolerant of unfavourable weather conditions. They have been observed at lower temperatures and during stronger winds than honeybees, and could therefore be more efficient pollinators then (Bohart, 1952; Lewis and Smith, 1969; Heinrich, 1976; Smith and Lewis, 1972; Teras, 1976).

3. <u>Pollen Analysis and Fruit Set</u>:

The quantity and compatibility of pollen carried by the insects are of major importance for adequate cross-pollination.

Kendall and Solomon (1973) collected various species of insects from apple blossoms. The pollen grains were washed off the insects and counted. They concluded that the insects with the greatest amount of pollen grains would be the best pollinators. The larger solitary bees and bumblebees had the most pollen.

Transfer of viable pollen of the proper variety is essential since incompatible pollen reduces fertility and does not set fruit (Silander and Primack, 1978). Milutinovic and Milutinovic (1970) reported that pollen mixtures showed some advantage over individual pollen varieties on fertilization. Kendall (1971, 1973) pollinated unopened flower clusters with anaesthetized insects and concluded that subsequent initial fruit set and more particularly the number of fertilized ovules or seeds per fruit was related to the amount of viable and compatible pollen carried by the insects used to pollinate the blossoms. He found that most solitary bees tested carried larger quantities of compatible fruit pollen than honeybees. Wertheim (1973) explained that the more seeds there are per fruit the more sites of hormone production there are and the more resistant they are to abscission, thus increasing fruit set. Other workers also related pollination and seed content (Bornus et al, 1977; Callan and Lombard, 1978; Sharp, 1970). They concluded that the presence of a greater number of bees increased cross-pollination and also increased seed content, fruit-set, and size of fruit.

The timing for pollen transfer is critical. Not all flowers are receptive to pollen for equal periods of time. Generally, the stigma is receptive to pollen for the first four days following flower opening (Arnason, 1966; Ruiz, 1977; Stott, 1972; Williams, 1970). Varieties with longer receptive periods have a greater chance of being adequately pollinated (Stott, 1972; Williams, 1970). Consequently insect pollinators foraging during this critical period will be the only ones of value to pollination.

OBJECTIVES

The objective of the current thesis is to evaluate the role of native insects in the pollination of a cultivated apple orchard. This was carried out as follows: (1) establishing the pollinating population composition and density by field observations of the actual blossom visits and determining the most important groups; (2) monitoring the activity of the pollinators by characterizing types and numbers of insect visitors from sunrise to sundown and correlating with recorded weather conditions (temperature, humidity and light); (3) assessing the efficiency of the important pollinators by analysis of the pollen grains carried on the bodies of these insects; and (4) evaluating the effectiveness of the pollinators by measuring fruit set, seed set and the effective pollination period.

MATERIALS AND METHODS

Field work was carried out in an apple orchard of semi-dwarf trees at the Agriculture Canada Jordan Experimental Farm, Jordan Station, Ontario.

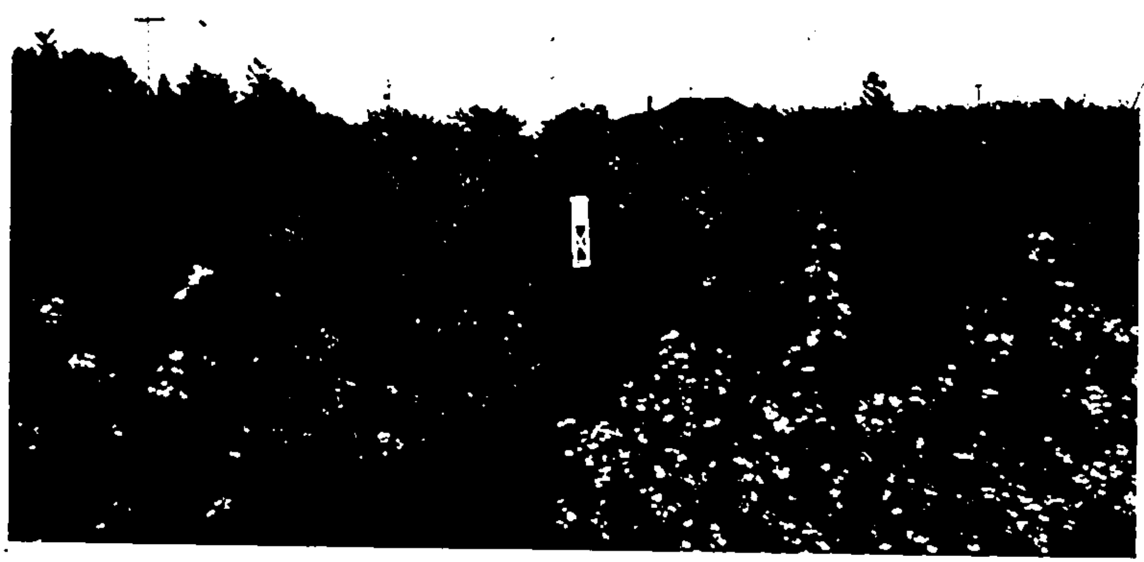
Research was conducted during three consecutive years: 1978, 1979, and 1980.

1. Description of Orchard and Monitoring Equipment:

The orchard, covering a 0.3 hectare area, was planted in May 1974 (Fig. 1). It resembled a small valley and had east and west facing slopes, with a stream running north-south. There were 240 trees in the orchard (12 rows of 20 trees). The trees were planted every 2.5 meters in rows 5 meters apart (Fig. 2).

Distributed evenly throughout the orchard, and within each row, were four cultivars: McIntosh, Empire, Red Delicious, and Golden Delicious. Both layout and cultivar distribution were highly appropriate for accurate field work. Honeybees have been reported to move readily along a row of trees and comparatively little between rows on a single foraging trip especially when trees within rows were closer than trees in adjacent rows (Free, 1960a). Cultivar distribution thus ensured proper cross-pollination.

Figure 1. General view of the orchard (looking east) with Red and Golden Delicious in full bloom to the far right.



COLOURED PICTURES

Figure 2. Layout of the Orchard.

0 represent sample trees.

<■ represent beehives, and
the arrow the entrance.

Apple Planting Jordan Pond (Plot 21)

Trailer

⊢2.5m⊣ ⊢6m⊣ ⊢6.6m⊣ ⊢5m⊣

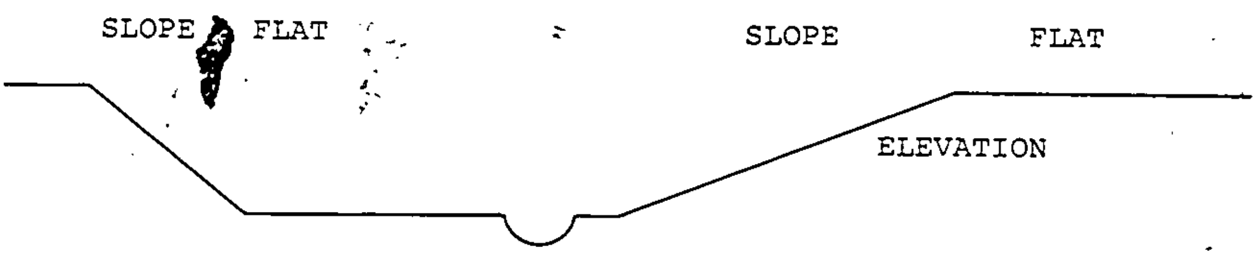
1	2*	3	4*	5
G	G	G	R	R
G	G	G	R	R
G	(G)	G	R	R
G	G	G	(R)	R
G	G	G	R	R
R	R	R	E	E
R	R	R	E	E
R	(R)	R	(E)	E
R	R	R	E	E
R	R	R	E	E
E	E	E	M	M
E	E	E	M	M
E	(E)	E	(M)	M
E	E	E	M	M
E	E	E	M	M
M	M	M	G	G
M	M	M	G	G
M	(M)	M	(G)	G
M	M	M	G	G
M	M	M	G	G

⊢5m⊣

STREAM

6	7	8*	9		10	11*	12
E	E	E	E	20	M	M	M
E	E	E	E	19	M	M	M
E	E	(E)	E	18	M	(M)	M
E	E	E	E	17	M	M	M
E	E	E	E	16	M	M	M
M	M	M	M	15	G	G	G
M	M	M	M	14	G	G	G
M	M	(M)	M	13	G	(G)	G
M	M	M	M	12	G	G	G
M	M	M	M	11	G	G	G
G	G	G	G	10	R	R	R
G	G	G	G	9	R	R	R
G	G	(G)	G	8	R	(R)	R
G	G	G	G	7	R	R	R
G	G	G	G	6	R	R	R
R	R	R	R	5	E	E	E
R	R	R	R	4	E	E	E
R	R	(R)	R	3	E	(E)	E
R	R	R	R	2	E	E	E
R	R	R	R	1	E	E	E

2.5m

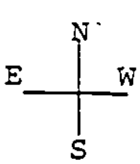


TREES: 240
SPACING: 2.5m X 5m
CULT: MAC (M) 60 trees
Gold-D (G) 60 "
RED-D (R) 60 "
EMP (E) 60 ".

ROOT STOCK: M.26

*Sample rows

Planted: May, 1974



Four trees of each cultivar were sampled and selected from rows 2, 4, 8, and 11. A few sample trees had to be changed from one year to the next because some appeared to blossom only every second year. When this occurred, the next flowering tree along the row was then chosen. Whenever changes were required, the trees were always selected so that the adjacent ones were of the same cultivar.

Tree size played an important role in this study. Height ranged from 1 to 3 meters making it possible to observe the entire tree without choosing a select few branches that visiting insects might seem to avoid. This also eliminated shading in the lower branches which had been reported to discourage foraging when compared with sunned areas (Free, 1960b). He also noted that during a single foraging trip, bees tended to move only to one or two large trees. Tree size, here being semi-dwarf, increased the chance of expanding their foraging area, and thus the diversity of pollen being carried by the insects which is imperative for proper cross-pollination.

In an attempt to reproduce cultivated orchard conditions but still maximize visitations by native populations, pesticides were not applied in the orchard unless during a major pest infestation when the lives of the trees were endangered. This situation occurred at most once a year late in the summer. The pesticide applications were kept to a minimum in adjacent plots. Absolutely no spraying was done during the blossom season because the Bees Act 1970 makes it illegal to do so in Ontario.

In the immediate vicinity, there were a few open fields, a small forest and pond, thus offering many possible over-wintering and nesting sites for native insects. In mono-cultures requiring cross-pollination, it is common practice to introduce domesticated species. If brought in too early the hivebees which are often constant to a single plant species, might forage elsewhere and continue to do so until the resources fail before coming back to the immediate area around the hive (Free, 1963). Therefore, two hives were introduced after the first blossoms appeared. Hives were placed in rows 4 and 7 between trees 19 and 20 with entrances facing the stream. Competition from other flowers, mainly dandelions (Free, 1968), was kept to a minimum by regular mowing of the lawn. There was little overlap in flowering times with other fruit trees as apple trees blossom last. Consequently, bees tended to remain in the orchard. The hives were removed at approximately 80% petal fall when most flowers had already set.

Temperature (°C), relative humidity (%) and light energy (Wm^{-2}) were recorded continuously. Thermocouples for temperature monitoring were placed on trees 10 or 11 of each of the sample rows. They were positioned at soil, trunk, canopy, leaf and blossom levels. The temperature readings used in this study were recorded at blossom level. The various thermocouples were connected to a Data Aquisition System and miniprocessor (Esterline Angus, PD 2064) which were located in a trailer just north of row 5. This apparatus had been programmed to print out temperatures every half-hour. The standard temperature ranges were -10°C to 40°C plus or minus 1.5% error. Relative humidity was recorded with a thermohygrograph (Lambrecht No. 252) which had been placed in a Stevenson Screen adjacent to tree 10, row 6. The humidity range was 5% to 100% relative humidity plus or minus 2.5% error. Total light energy was monitored using a meter master Solarimeter (Tip Zonen CM6) and a digital multimeter (Phillips PM 2421) placed adjacent to tree 10, row 5. This apparatus originally read in millivolts. It was calibrated in calories per centimeter squared per minute, then converted to Watt per meter squared according to the following equation (Latimer, 1974):

$$1 \text{ mv} = 0.119 \text{ cal cm}^{-2} \text{ min}^{-1} = 83.095 \text{ Wm}^{-2}$$

The accepted radiation term is Radiant Flux per unit area, but for simplicity will be referred to as light or light energy.

2. <u>Population Composition</u>:

As many insects as possible were collected from the blossoms for identification purposes and for pollen analysis. Each insect had to be collected individually to eliminate pollen contamination. Therefore, individual killing jars were made from small vials by inserting within the plastic caps a piece of foam which had been soaked with ethyl acetate as a killing agent. Once the insects were dead, a doubled up square of "kim wipe" held by an elastic band replaced the cap to allow insect and pollen to air dry. Date, time of day, and cultivar were recorded on each vial as the insects were caught and later correlated with previously monitored weather conditions.

Insects not being used in pollen analysis and insects which had been used for pollen studies were relaxed, mounted, pinned, and labelled according to Martin (1977). They were identified to family, then sent to the Biosystematics Research Institute, Agriculture Canada for identification to species. Insects caught in 1978 were used for identification only, those collected in 1979 and 1980 were used for both identification and pollen analysis.

3. Bloom Development:

Observations started when the first blossoms opened and ended when the last few fell. The number of opened blossoms on each sample tree was counted daily. A flower was considered open when an insect could actually enter, and was no longer counted when only two of the five petals were left.

4. Activity of Native Pollinators:

Daily observations of pollinators during the entire blossom period were carried out from sunrise to sunset. Since the general aerial fauna of an orchard is quite different from the pollinating insect fauna (Lewis and Smith, 1969), and since many insects just sit on the petals or approach the nectaries from the side without getting covered in pollen (Free, 1960a), observations and collections were made only of insects actually visiting and touching the reproductive parts (anthers and stigma) of the blossoms (Fig. 3).

Number and types of pollinators were recorded for each visit. A visit consisted of a 5-minute observation period of each tree, and a total of 16 trees was used for observations. Thus, each tree was visited approximately every 2½ hours throughout the day. Since identification of insects to species while in flight was impractical, the insects visiting the blossoms were subdivided into 20 easily recognizable groups (Table 1). Therefore for each visit, a record of the numbers and types of pollinators, the specific cultivar, and the weather conditions, was obtained from approximately 7:00 to 21:00 hours for each blossom day.

Figure 3. *Apis mellifera* L. nectar feeding but still touching the reproductive parts of the blossom. This behaviour is necessary for an insect to be considered as a visitor.

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Table 1. List of the 20 groups used to identify pollinating insects in the field

1.	*Apis mellifera*	Hymenoptera
2.	Bombinae	
3.	Andrenidae	
4.	Large Andrenidae	
5.	Halictidae	
6.	Green Halictidae	
7.	Formicidae	
8.	Others	
9.	Syrphidae	Diptera
10.	Scathophagidae	
11.	Bibionidae	
12.	Anthomyiidae	
13.	Chironomidae	
14.	Others Large	
15.	Others Small	
16.	Elateridae	Coleoptera
17.	Nitidulidae	
18.	Others	
19.	Lepidoptera	
20.	Hemiptera	

5. <u>Pollen Analysis</u>:

Insects caught at peak time (between 11:00 and 15:00 hours) and during peak days (from May 18 to May 28 in 1979, and from May 19 to May 25 in 1980) were used for pollen counts.

Many honeybees, bumblebees, and solitary bees when foraging collect pollen into "pollen baskets" on their hind legs. These loads are moistened with nectar and salivary secretions and adhere well during foraging. Therefore, when present, the hind legs of these insects were removed before washing because these "pollen baskets" are of little significance in pollination.

The method of washing and counting was adopted from Kendall and Solomon (1973). It consisted of washing each insect with a fine jet of 70% ethanol over a small glass dish approximately 3 centimeters in diameter. The insect was then placed in the liquid and brushed with a fine brush, removed and rinsed again. The pollen was allowed to settle. Because an even distribution was difficult to obtain, 1/10 of the surface area was counted as opposed to 1/30 as mentioned by Kendall and Solomon (1973). This was done by placing a grid with a blacked out area equal to 1/30 of the surface area under the glass dish and counting the pollen grains within three of these areas. The efficiency of recovery of pollen was checked for a few insects of each main group by repeating the washing and brushing procedure a total of three times. The third treatment yielded little or no more pollen. The first treatment was then compared with the total of the three considered as 100% recovery.

Under the light microscope, it was not possible to differentiate apple pollen grains from those of other Rosaceae which may have been visited by the insects. Rosaceous pollen is generally oblong when dry, but takes up moisture readily becoming flattened and angular in outline. The grains are tricolporate with long furrows extending almost to the polar axis. Given these characteristics, apple pollen grains were, however, easily distinguished from the usually rounder pollen grains with a much more textured exine of nearby flowering weeds or bushes. Consequently, not only was the total number of pollen grains recorded for each insect but also the number of fruit versus non-fruit pollen grains.

6. <u>Fruit Set</u>:

"Fruit Set" is an estimate of the yield of an orchard and is related to the amount of effective pollination. Fruit set was calculated from the ratio of fruitlets and fruit to the total number of potential blossoms.

Apple blossoms are arranged in clusters of six flowers, five laterals surrounding one blossom called the King Blossom (Fig. 4). The King Blossoms are first to open. It is rare that more than four of the laterals open.

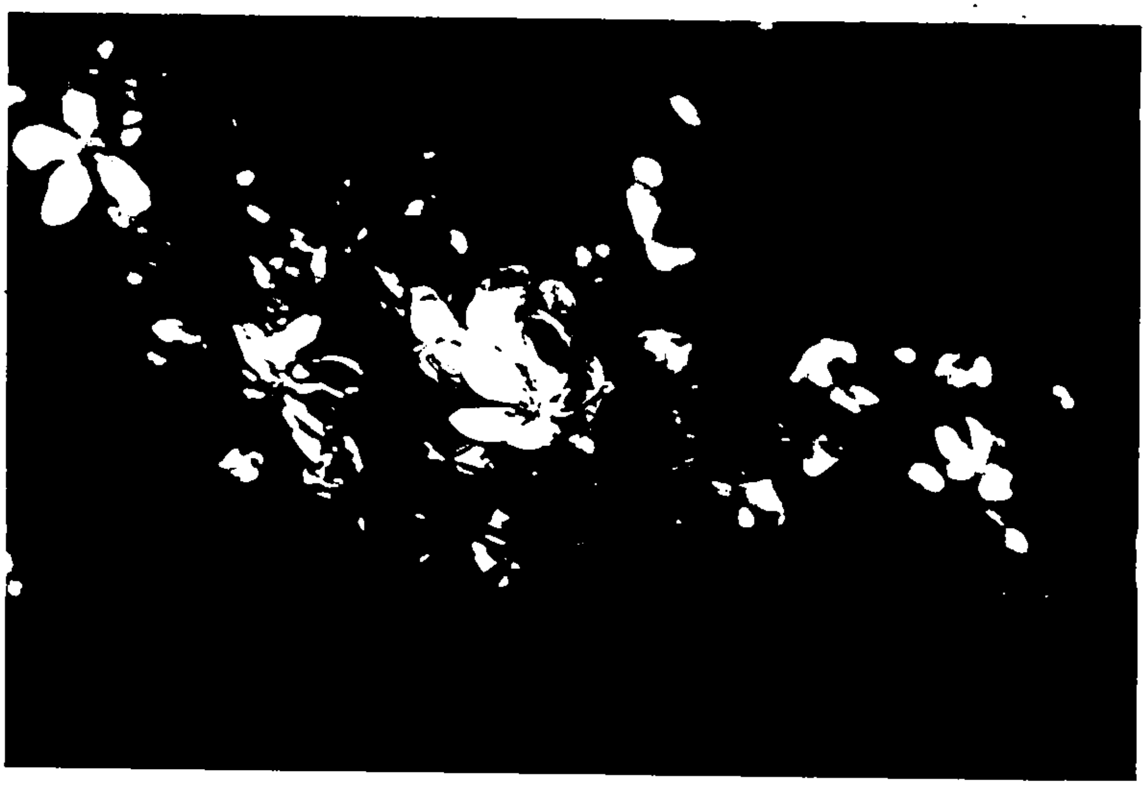
The total number of potential blossoms was therefore estimated by multiplying the total number of clusters by 5 (Williams, 1970). The total number of clusters was counted for each sample tree when the developing blossoms were well advanced at the "full pink stage" (Agriculture Ontario, 1980) and before the leaf-buds expanded. During peak blossom, the total number of blossoms that would open were counted on three trees to verify the ratio of clusters to potential blossoms. Fruitlets were counted from each sample tree 21 days after 80% petal fall (Williams, 1970). Just before full maturity, all apples from the observation trees were picked and counted.

In 1979 and 1980 a sample of 25 apples was randomly selected from each tree. The size of each one of these fruits was measured by water displacement and recorded as volume in milliliters. The apples were then cut in half and the number of seeds counted. When worms had eaten their way to the core, the apple was discarded for the purpose of seed counts.

7.. Effective Pollination Period:

The Effective Pollination Period (E.P.P.) is an estimate

Figure 4. Cluster showing the King Blossom in bloom surrounded by 5 laterals at the "full pink" stage.



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of the number of days the stigma is receptive to pollen after the flower opens. It was determined in 1980 only, in the following manner.

One tree from each of the four cultivars was selected. Five sleeve cages were installed on each tree. Each cage was placed over a branch to enclose four clusters (Fig. 5). The King Blossom and one lateral flower was pinched off before installing the cages, thus leaving each cluster with four uniform flowers. The sleeve cages made of transparent nylon mesh of $1mm^2$, were installed just before the blossoms opened to preclude pollination from outside sources.

Hand pollination was carried out in each cage using the appropriate pollen for each cultivar. A total of 15 flowers from each variety was collected daily. To obtain pollen, petals were removed and the anthers were left overnight to dehisce. Flowers in one cage were pollinated on day '0' which was the first day of opening, then those in one more were pollinated on each of days '2', '4', and '6' following flower opening. The four clusters left were available as a reserve. Each of the four flowers of each cluster was pollinated in turn by rubbing the stigma with the anthers of one flower prepared as above for pollen release; then using a second flower, each was pollinated again in reverse order. Following this hand pollination procedure, the clusters were

Figure 5. Sleeve cage made of 1 mm^2 transparent mesh enclosing clusters in full bloom to preclude pollination from outside sources.

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well marked, and initial and final fruit set were later recorded.

This procedure was followed for each of the four cultivars. McIntosh and Empire served as reciprocal pollinizers, so did Red and Golden Delicious. These were grouped because each pair blossomed at slightly different times.

RESULTS

1. Population Composition:

Observations and collections were made only of insects actually visiting and touching the reproductive parts of the blossoms. A total of 11,401 insects were observed throughout the three years. Altogether 106 different species belonging to 77 genera and to 40 different families were identified from the 758 insects caught. They are presented according to the 20 general groups used in field identifications (Table 2).

Apis mellifera L. were the most numerous of all visitors. The numbers observed increased greatly from one year to the next, with 162 in 1978, over three thousand in 1979 and more than four thousand in 1980. Five different species of Bombinae were identified, four *Bombus* and one *Xylocopa*. All were caught in 1979 and only the latter in 1980. There were also many more observed in 1979 than in the other years. The Andrenidae were the second most numerous group within the Hymenoptera (Fig. 6). Six different species were identified. *Andrena miserabilis* Cresson was the most important for all three years. Although 1979 had the greatest diversity of species, many more were observed in 1980 than in the previous years. No Large Andrenidae were caught or observed in 1978. Five species were

Table 2. Variation of the number of species caught for each year. They are presented according to their field identification into 20 general groups. The numbers following each species represents the numbers of individuals caught and identified.

HYMENOPTERA	1978	1979	1980
1. *Apis mellifera* L.	3	50	17
[a] Total number observed	162	3227	4479
2. Bombinae			
Bombus sp.		1	
Bombus bimaculatus Cresson		1	
Bombus impatiens Cresson		1	
Bombus sandersoni Franklin		2	
Anthophoridae			
Xylocopa virginica (L.)		1	1
Total number caught		6	1
Total number observed	2	30	7
3. Andrenidae			
Andrena sp.		12	37
Andrena imitatrix Cresson		3	
Andrena miserabilis Cresson	2	44	20
Andrena nasonii Robertson		14	4
Andrena sigmundi Cockerell		8	
Andrena wilkella Kirby			2
Megachilidae			
Osmia atriventris Cresson		1	
Total number caught	2	82	63
Total number observed	3	278	439
4. Large Andrenidae			
Andrena sp.		11	9
Andrena carlini Cockerell		4	6
Andrena crataegi Robertson		1	
Andrena dunningi Cockerell			2
Andrena milwaukeensis Graenicher		2	
Andrena vicina Smith		2	1
Total number caught		20	18
Total number observed		51	65

5. Halictidae	1978	1979	1980
Dialictus sp.		8	41
Dialictus admirandus Sandhouse		2	
Dialictus inconspicuus (Smith)		48	29
Dialictus pilosus (Smith)	1		
Evylaeus foxii Robertson		1	3
Evylaeus pectoralis Smith	1	1	
Halictus confusus Smith		1	
Lasioglossum coriaceum (Smith)		1	
Anthophoridae			
Ceratina calcarata Robertson			3
Total number caught	2	62	76
Total number observed		170	216
6. 'Green' Halictidae			
Augochlorella striata Provancher	3	17	10
Total number observed		31	28
7. Formicidae			
Camponotus sp.			1
Formica fusca group		11	
Formica glacialis Whlr.	2		
Lasius neoniger Emery	1		
Prenolepis imparis (Say)		13	2
Total number caught	3	24	3
Total number observed	24	264	50

8. Other Hymenoptera	1978	1979	1980
Anthophoridae			
Nomada sp.			1
Chalcidoidea			
Anacharis sp.		1	
Pholetesor ornigis Walsh		1	
Sympiesis marylandensis Girault		1	
Ichneumonidae			
Diplazon laetatorius Fabr.		1	
Pycnocryptus director (Thunberg)		2	
Syrphoctonus flavolineatus Gav.		1	
Tryphon (Symboëthus) seminiger (Cress.)		2	
Tymmophorus rufiventris Gravenhorst		1	
Tentredinidae			
Eutomostethus ephippium (Panzer)		1	
Vespidae			
Vespula (Dolichovespula) maculata (L.)		1	
Total number caught		12	1
Total number observed	12	16	3

DIPTERA

9. Syrphidae

	1978	1979	1980
Allograpta obliqua (Say)		2	
Eristalis sp.			1
Eristalis arbustorum (L.)	2	1	4
Eristalis dimidiata Wied.			3
Eristalis tenax (L.)		3	1
Helophilus fasciatus Walk.	1	6	2
Helophilus latifrons Lw.		1	
Melanostoma sp.			1
Metasyrphus sp.			1
Metasyrphus latifasciatus (Macq.)			1
Platycheirus quadratus (Say)		1	
Platycheirus scutatus (Mg.)			1
Sphaerophoria sp.		3	2
Sphaerophoria philanthus (Mg.)	1		1
Syrphus rectus O.S.			1
Syrphus torvus O.S.			1
Toxomerus geminatus (Say)		6	
Toxomerus marginatus (Say)		2	
Total number caught	4	25	21
Total number observed	24	46	114

10. Scathophagidae

	1978	1979	1980
Scathophaga furcata (Say)		2	
Scathophaga stercoraria (L.)		1	2
Total number caught		3	2
Total number observed		6	4

11. Bibionidae

	1978	1979	1980
Bibio sp.		5	
Bibio albipennis Say		8	
Total number caught		13	
Total number observed		35	2

12. Anthomyiidae	1978	1979	1980
Hylemya (Delia) sp.	2	9	1
Hylemya (Delia) brassicae (Wiedemann)			3
Hylemya (Delia) florilega (Zetterstedt)	1	12	1
Hylemya (Delia) platura (Meigen)		37	2
Hylemya (Pegohylemya) sp.		8	7
Hylemya (Pegohylemya) fugax (Meigen)	2	26	
Nupedia dissecta (Meigen)		1	
Total number caught	5	93	14
Total number observed	65	1070	198

13. Chironomidae	1978	1979	1980
Chironomini (genus unknown)		1	
Chironomus sp.		4	
Chironomus maturus Johannson		1	
Cricotopus sp.		1	
Endochironomus sp.		1	
Limnophyes (?) sp.	1		
Micropsectra sp.		2	
Orthocladiinae (genus unknown)	3	5	
Orthocladius sp.		11	
Procladius sp.		1	
Total number caught	4	27	
Total number observed	3	78	5

14. Large 'Other' Diptera

Calliphoridae	1978	1979	1980
Bufolucilia silvarum (Mg.)		2	1
Lucilia illustris (Mg.)		2	
Phormia regina (Mg.)		1	
Pollenia rudis (Fab.)		5	
Conopidae			
Myopa vesiculosa Say			1
Muscidae			
Fannia sp.		2	
Fannia coracina (Stein)		1	
Sarcophagidae			
Boettcheria sp.		4	
Ravinia (Chaetoravinia) latisetosa Park.		1	
Tachinidae			
Periscepsia helymus (Walker)		1	
Tachinomyia nigricans Webber		1	
Total number caught		20	2
Total number observed		44	5

15. Small 'Other' Diptera

Agromyzidae	1978	1979	1980
Japanagromyza viridula (Coq.)		1	
Ephydridae			
Hydrellia sp.		1	
Dolichopodidae			
Dolichopus sp.		1	
Total number caught		3	
Total number observed		33	6

COLEOPTERA

	1978	1979	1980
16. Elateridae			
Ctenicera lobata tarsalis (Melsh.)	4	4	
Total number observed		21	6
17. Nitidulidae			
Meligethes canadensis Easton	2		
Meligethes nigrescens Stephens		5	1
Total number caught	2	5	1
Total number observed		14	3
18. Other Coleoptera			
Cantharidae			
Cantharis bilineatus Say	1	3	
Coccinellidae			
Coccinella transversoguttata richardsoni Brown		2	
Scarabaeidae			
Phyllophaga sp.		2	
Phyllophaga rugosa (Melsh.)		2	
Pyrrhalta luteola (Müll.)		1	
Total number caught	1	10	
Total number observed	14	23	2

19. LEPIDOPTERA	1978	1979	1980
Gelechiidae (genus unknown)		1	
Geometridae			
Haematopis grataria (Fabr.)		1	
Gracilariidae			
Lithocolletis sp.		1	
Hesperiidae			
Erynnis juvenalis (Fab.)		2	
Noctuidae			
Anagrapha falcifera Kby.		1	
Apamea finitima Gn.		1	
Pseudaletia unipuncta Haw.		2	
Nymphalidae			
Vanessa (Vanessa) atalanta rubria (Frubstorfer)		1	
Olethreutidae			
Pseudeexentera sp.		1	
Total number caught		11	
Total number observed	1	12	

20. HEMIPTERA	1978	1979	1980
Anthocoridae			
Orius insidiosus (Say)		1	
Coreidae			
Kleidocerys resedae (Panzer)		1	
Miridae			
Lygus sp.		4	
Lygus lineolarius (Pal. de Beau.)	2		1
Total number caught	2	6	1
Total number observed	1	8	1

Figure 6. Andrenidae collecting pollen.

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identified; four different species were found in 1979 and three in 1980. As with the other Andrenidae, more individuals were observed in 1980 than in the other years. The pattern was similar for the Halictidae, with a greater variety in 1979, but greater numbers in 1980. Altogether eight species were identified, six different species in 1979 and three in 1980. *Dialictus inconspicuus* (Smith) was the most important for these two years. The 'Green' Halictidae consisted of only one species, *Augochlorella striata* Provancher. The numbers observed were more or less equal in 1979 and 1980. Five species of Formicidae were identified. The diversity was similar for each year, but many more were observed in 1979. There were very few 'Other' Hymenoptera caught. Of the 11 species identified, ten were present in 1979 and one in 1980. Few were observed, 1979 having the largest number.

Diptera were the second largest group. The Syrphidae were very diverse with 18 identified species (Fig. 7): three in 1978, nine in 1979 and 13 in 1980. The greatest diversity and the greatest numbers observed were in 1980. No Scathophagidae were observed or caught in 1978. Two species were identified in 1979 and one in 1980. Very few individuals were observed with more in 1979. Few Bibionidae were caught and only in 1979. None were observed in 1978 and only two in 1980. The Anthomyiidae were the second most numerous group of pollinators after the honeybees. Seven species were identified,

Figure 7. Syrphidae feeding on pollen.

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three different species were present in 1978, six in 1979 and five in 1980. The numbers observed were much greater in 1979 than in the other years. The Chironomidae were a very difficult group to identify. The diversity and the numbers observed were greater in 1979. The Large 'Other' Diptera consisted of 11 species belonging to five different families. None were caught or observed in 1978. In 1979, ten species were identified and in 1980 only two. The diversity and the numbers observed were much greater in 1979. The Small 'Other' Diptera consisted of three species belonging to three different families caught in 1979 only. A few were observed in 1980, but a much greater number was recorded for 1979.

The Coleoptera were mainly observed in 1979, they consisted of eight species belonging to five different families. They were considered chance pollinators because they were on the blossoms for other resources besides pollen and nectar. The Elateridae, the Cantharidae and the Scarabaeidae fed on plant tissue such as petals and anthers. The Nitidulidae were sap feeders, and the Coccinellidae were predators on other insects.

The Lepidoptera were nectar feeders. They were few in numbers and observed almost exclusively in 1979.

The Miridae were the main Hemipterans observed for the three years. However, the diversity and the numbers observed were much greater in 1979.

In 1979, additional observations were conducted during two nights at peak blossom. The three species of Noctuidae and the two species of Scarabaeidae were the only insects recorded during these nights.

Apis mellifera L. was by far the most important group for all years (Fig. 8). In 1978, the Anthomyiidae ranked second, followed by the Formicidae and the Syrphidae.

Species and group diversity was the greatest in 1979. The Anthomyiidae were again second in importance after the honeybees, followed by the Andrenidae, the Formicidae and the Halictidae. The total percentage of Diptera was however greater than the percentage of Hymenoptera (excluding the honeybees).

There was much less diversity in 1980 than in 1979. However both groups of Andrenidae and both groups of Halictidae were of greater importance than the Diptera. Among the Diptera, the Anthomyiidae and the Syrphidae were the main groups of significance.

Apis mellifera L. increased in relative importance from

Figure 8. The yearly distribution of the 20 groups of pollinators expressed as the percentage of the total number of insects observed, then summarized as the four main groups.

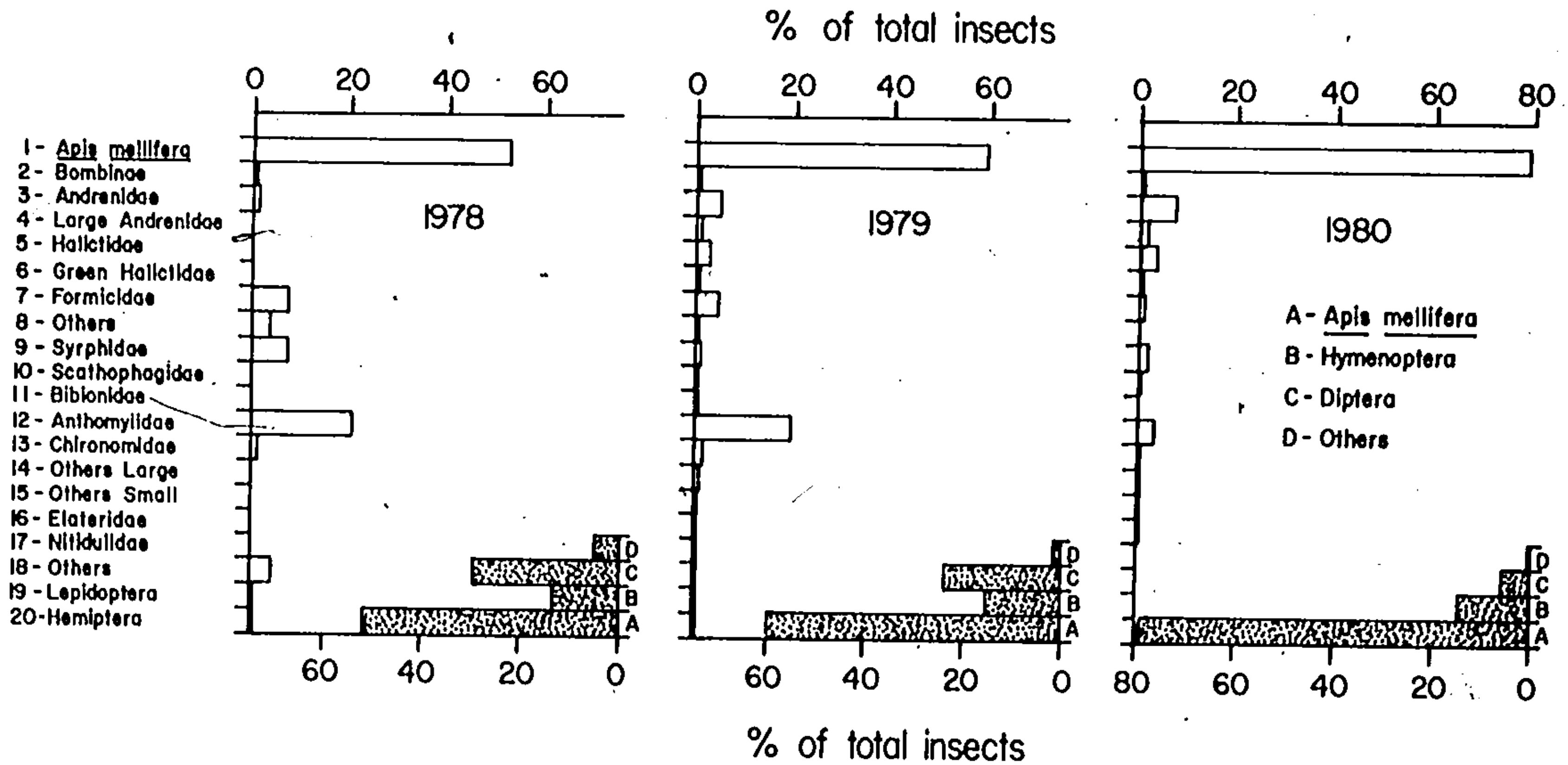
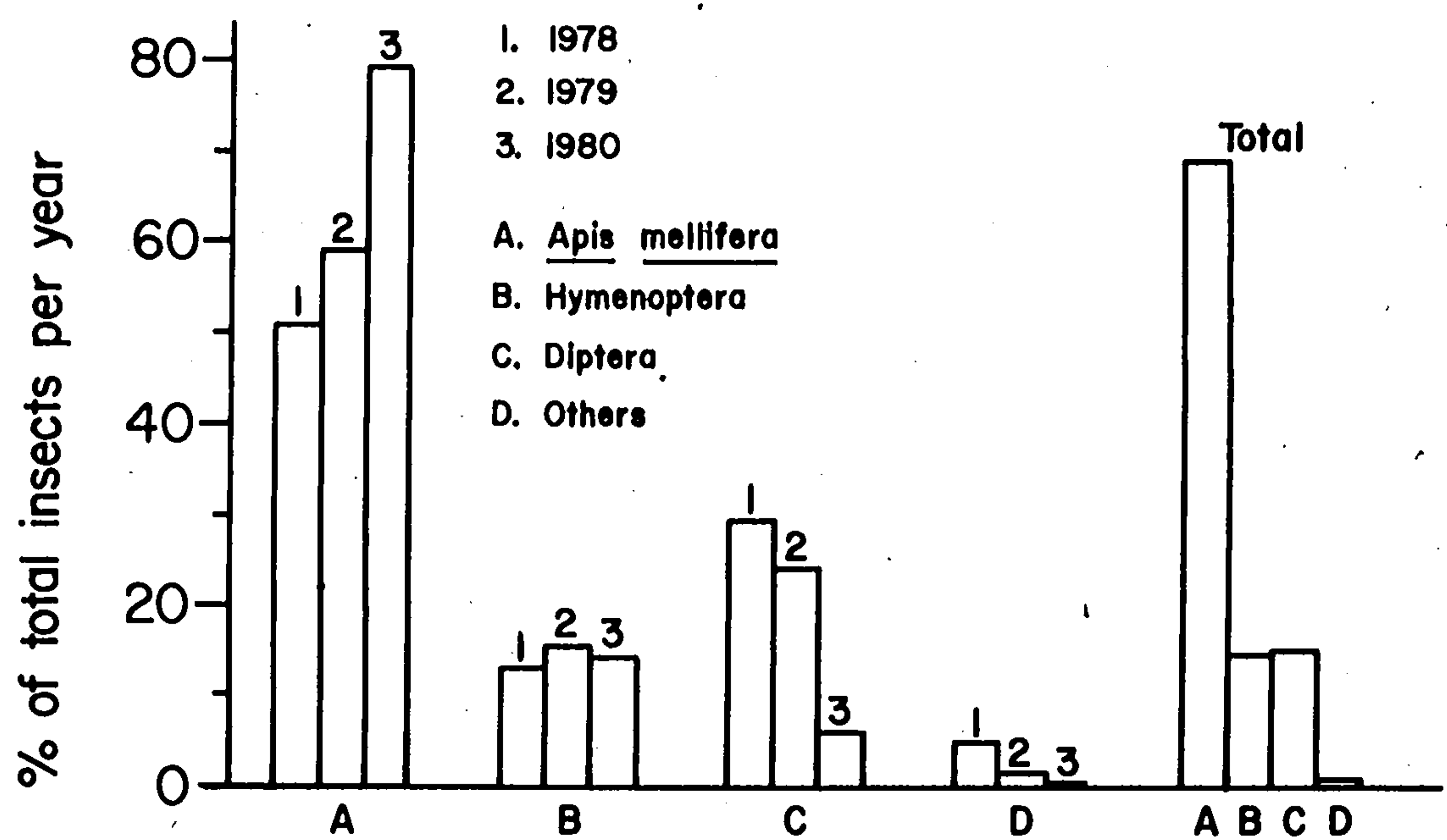

% of total insects
1978
1979
1980
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera
A - Apis mellifera
B - Hymenoptera
C - Diptera
D - Others
0
20
40
60
80
% of total insects

Figure 9. Comparison between years of the four main groups of pollinators and the relative importance of these groups for all years combined.


% of total insects per year
80
60
40
20
0
1. 1978
2. 1979
3. 1980
A. Apis mellifera
B. Hymenoptera
C. Diptera
D. Others
Total
1
2
3
A
B
C
D
A B C D

1978 to 1980 from 50% to 80% of the total pollinator population (Fig. 9). The other Hymenoptera were more or less equal for all three years around 15% of the total insects. The Diptera and the other insects decreased in relative importance from 1978 to 1980 with the Diptera ranging from 30% to 6% and the other pollinators from 16% to less than 1% of the total pollinator population. With all three years combined, *Apis mellifera* L. was of greater importance consisting of 69% of the total number of insects; the other Hymenoptera and the Diptera were of equal importance consisting each of 15% of the total and the others (Coleoptera, Lepidoptera and Hemiptera) were less than 1% of the total number of pollinating insects.

2. Bloom Development:

Each blossom season was very different as a result of tree growth and variable weather conditions. The M-16 rootstock gave a semi-dwarf appearance to the trees only if proper prunning was maintained. Despite this, the trees increased in size. Thus, the total number of clusters increased markedly from one year to the next for all four cultivars (Table 3). In 1978, McIntosh and Golden Delicious had the greatest number of clusters but in 1979 and 1980 Red Delicious replaced McIntosh in ranking. Both Delicious also developed into the largest trees with Empire remaining the smallest for all years.

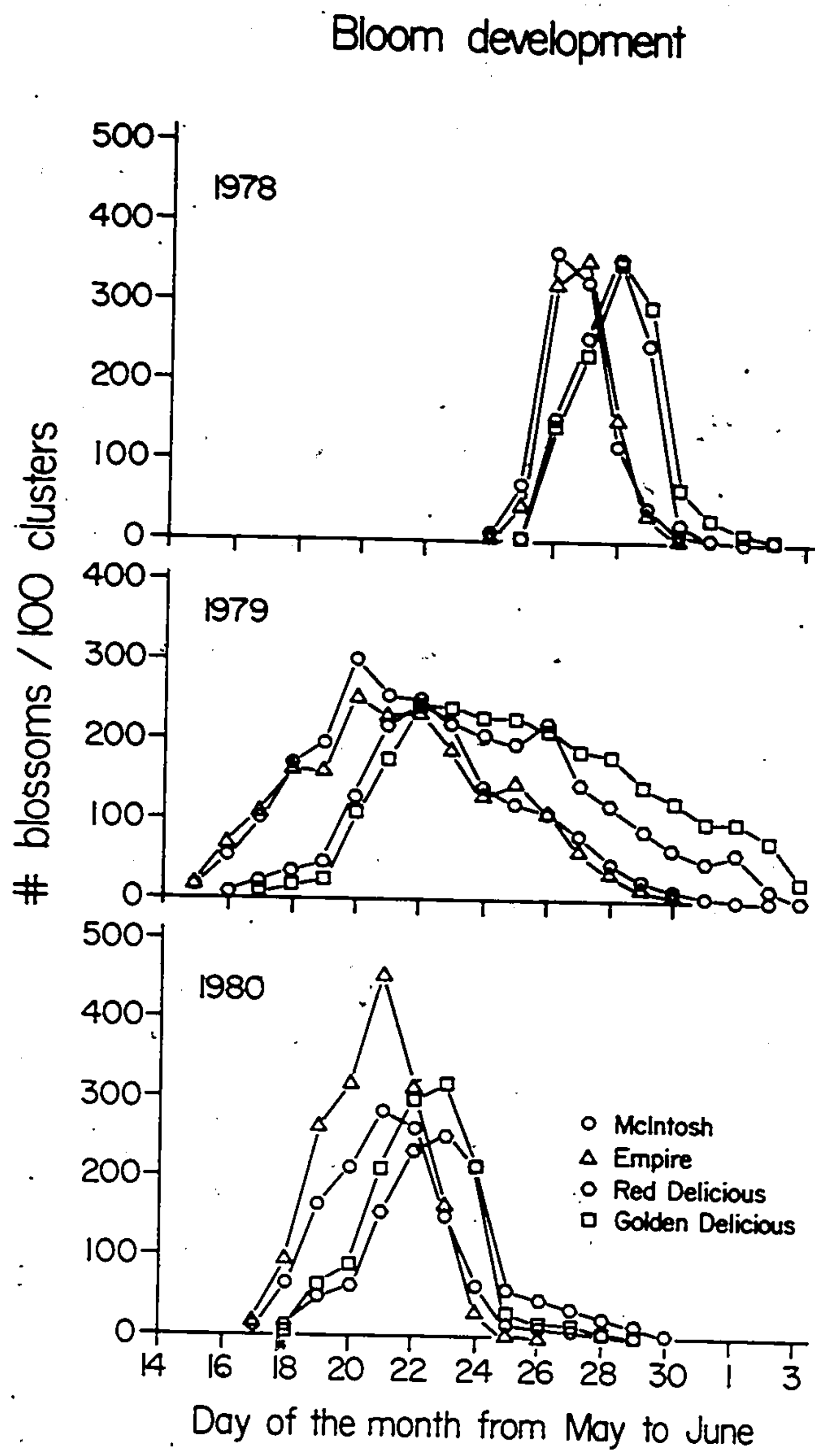
Table 3. Variation in the number of clusters for four sample trees of each cultivar for each year.

Tree	1978	1979	1980
McIntosh	307	521	1470
Empire	185	634	1048
Red Delicious	168	848	1723
Golden Delicious	318	1315	1671

For comparisons within each season and between cultivars, daily blossom counts were transformed to the number of blossoms open per 100 clusters as a mean of the four sample trees for each cultivar (Fig. 10).

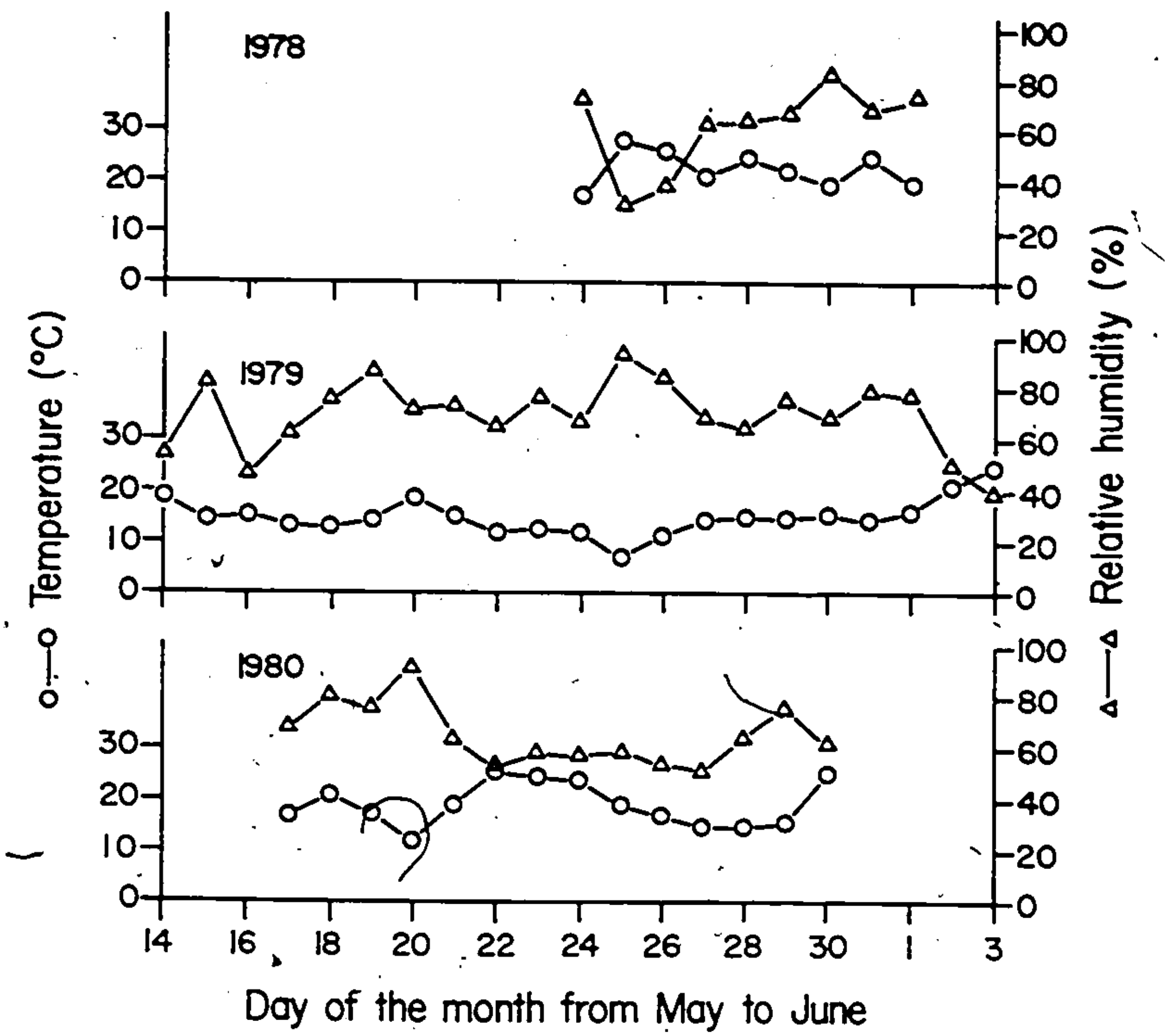
The shortest season lasting only ten days from May 24 to June 2, with peak blossom from May 26 to 28 was in 1978. Temperatures (Fig. 11) were above 20°C and relative humidity averaged 60%. The longest blossom period, lasting 21 days from May 14 to June 3, with a main peak from May 20 to 22 and a minor second peak extending until May 26 was in 1979. Temperatures during this year were very cool, usually below 15°C. They averaged 10°C or less from May 22 to 27 accounting for the extended peak in the number of blossoms. Higher relative humidity, over 70%, also coincided with this period, with continuous showers on May 25. The 1980 season was intermediate consisting of 14 days, from May 17 to 30 with peak blossom May 21 to 23. Weather conditions were humid and cool for the first few days but stayed warm and dry for most of the remaining season. For all three years, McIntosh and Empire peaked together and Red and Golden Delicious two days later. In addition, Red and Golden Delicious started blossoming one to two days after McIntosh and Empire, and also matured later in the fall.

Figure 10. Bloom development for the four cultivars for each year.



Bloom development
1978
1979
1980
500
400
300
200
100
0
blossoms / 100 clusters
McIntosh
Empire
Red Delicious
Golden Delicious
14
16
18
20
22
24
26
28
30
1
3
Day of the month from May to June

Figure 11. Average daily temperatures (°C) and the relative humidities (%) for each blossom season.


1978
1979
1980
Temperature (°C)
Relative humidity (%)
Day of the month from May to June
0
10
20
30
40
60
80
100
14
16
18
20
22
24
26
28
30
1
3

3.0 Activity of Native Pollinators:

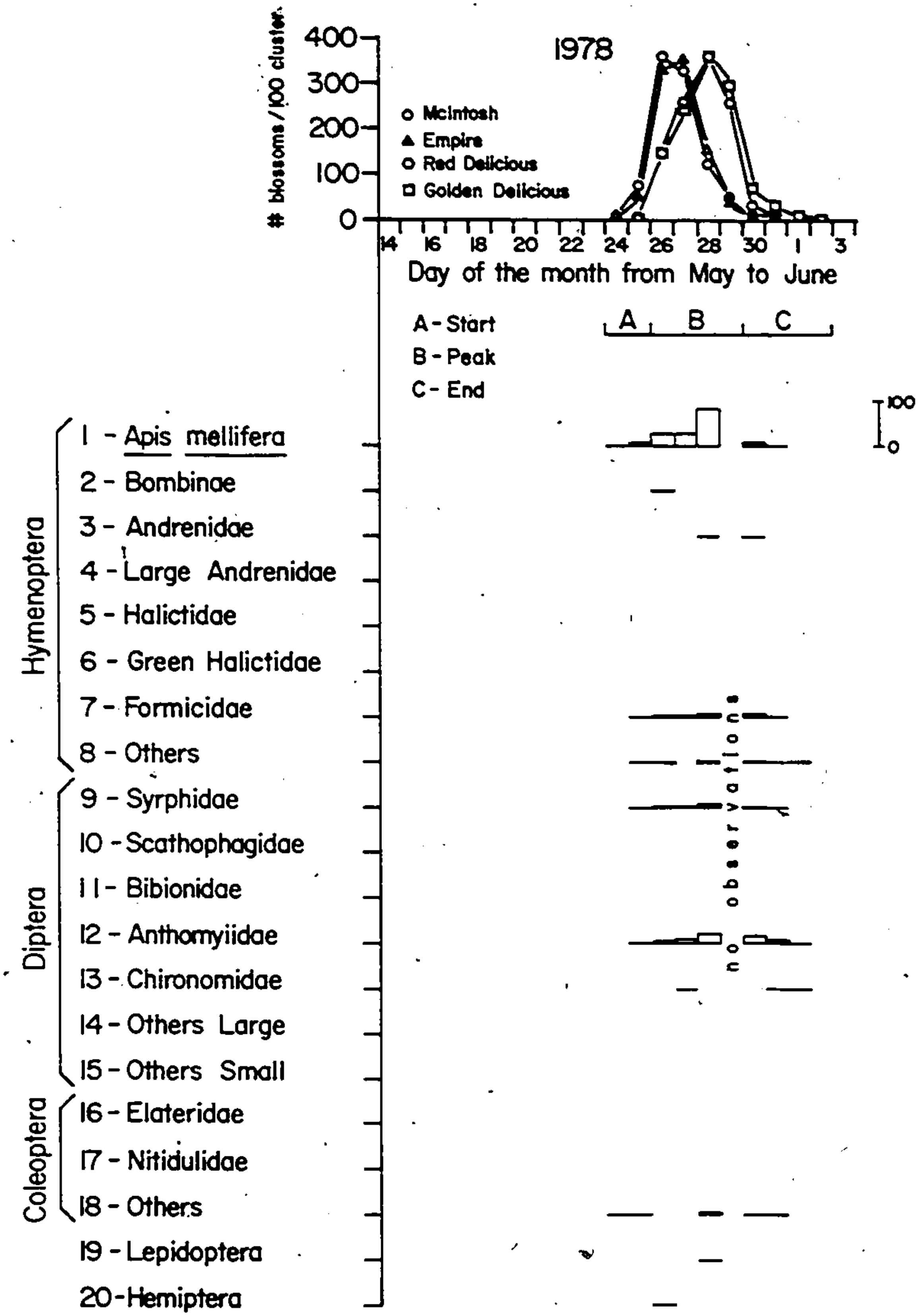
Activity in the context of this study refers to the presence or absence on the flowers of the various groups of pollinators. Over the three blossom seasons, a total of 2,736 five-minute observation periods monitoring the number and types of pollinators was conducted. The distribution of these various groups of insects with respect to the variables recorded is discussed.

3.1 Seasonal Distribution of Pollinators:

The numbers of insects present in each group throughout each blossom season are represented in Figs. 12, 13 and 14.

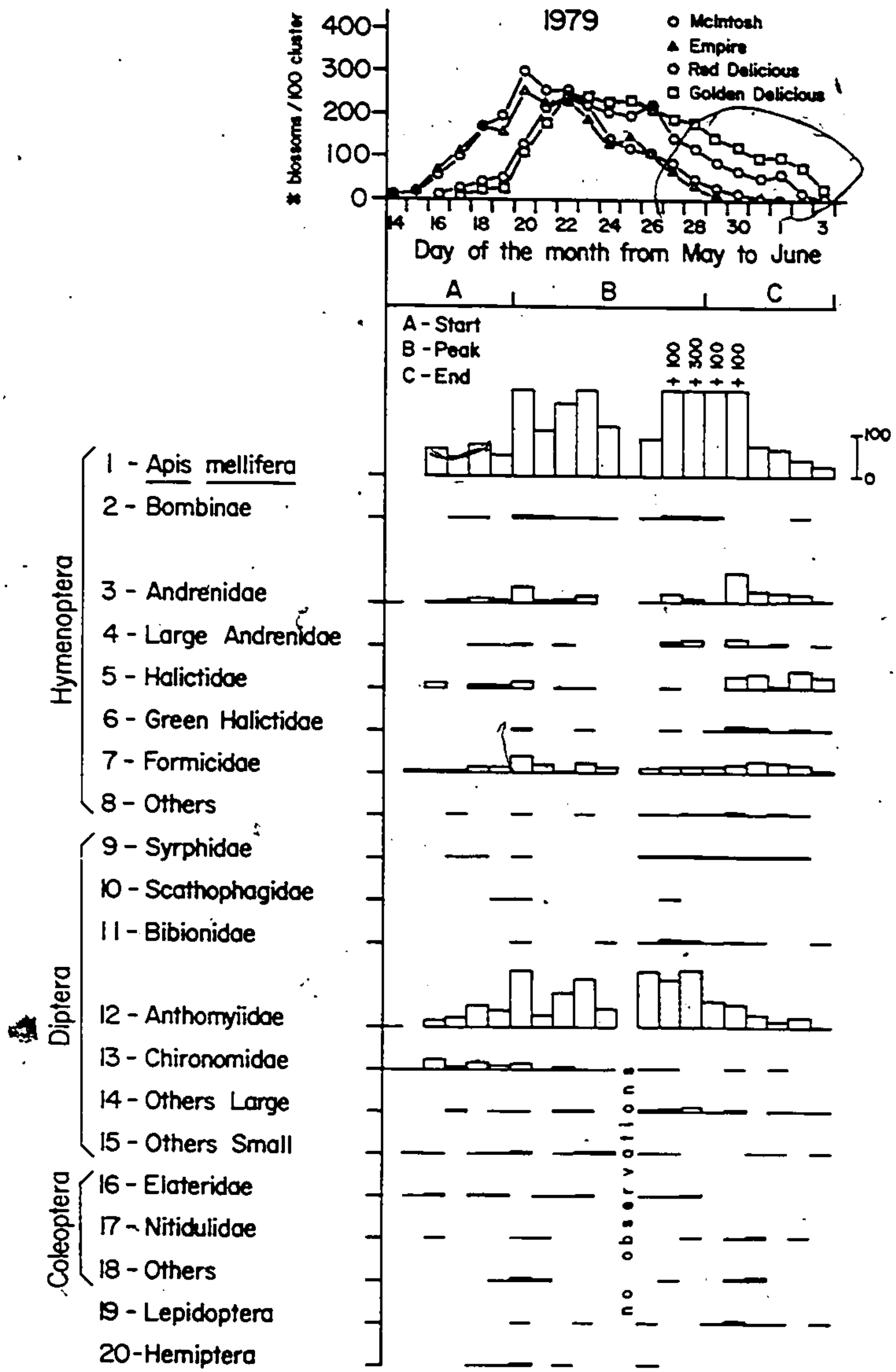
Apis mellifera L. was present throughout the blossom season and peaked with the peak blossom of Red and Golden Delicious in 1978 and 1980. In 1979, the bees were active only when Red and Golden Delicious started blossoming, they increased in number with the number of blossoms but peaked only towards the end of the season when weather conditions became favourable. The Bombinae were rare for all years. Only two were observed in 1978 at peak blossom for McIntosh and Empire. In 1979, they were present more or less throughout the season but only after McIntosh and Empire had over 100 blossoms per 100 cluster, and Red and Golden Delicious

Figure 12. Bloom development and seasonal distribution of the total number of insects of each group of pollinator observed each day for 1978.



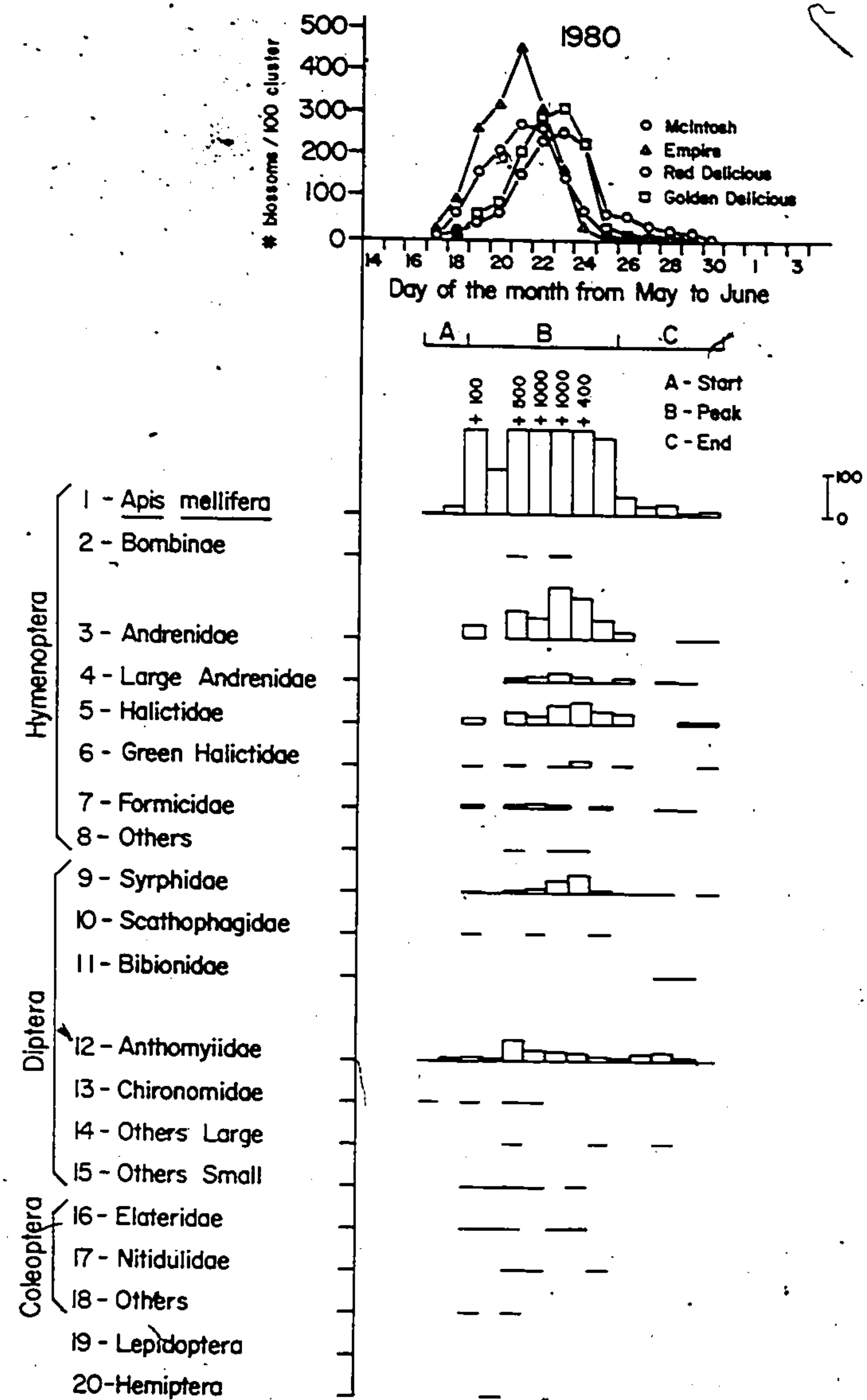
1978
blossoms / 100 cluster
400
300
200
100
0
○ McIntosh
▲ Empire
○ Red Delicious
□ Golden Delicious
14 16 18 20 22 24 26 28 30 1 3
Day of the month from May to June
A - Start
B - Peak
C - End
A B C
100
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera
no observations

Figure 13. Bloom development and seasonal distribution of the total number of insects of each group of pollinator observed each day for 1979.



1979
McIntosh
Empire
Red Delicious
Golden Delicious
blossoms / 100 cluster
400
300
200
100
0
14
16
18
20
22
24
26
28
30
1
3
Day of the month from May to June
A
B
C
A - Start
B - Peak
C - End
100
300
100
100
100
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera
no observations

Figure 14. Bloom development and seasonal distribution of the total number of insects of each group of pollinator observed each day for 1980.


1980
blossoms / 100 cluster
500
400
300
200
100
0
McIntosh
Empire
Red Delicious
Golden Delicious
14
16
18
20
22
24
26
28
30
1
3
Day of the month from May to June
A
B
C
A - Start
B - Peak
C - End
+100
+500
+1000
+1000
+400
100
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera

had started blossoming. They were present only at peak blossom of Red and Golden Delicious in 1980. In 1978, the Andrenidae were present only at the peak blossom of Red and Golden Delicious. They were present throughout the blossom period in 1979 and peaked towards the end of the season when weather conditions were favourable. In 1980, they were present once the blossoms were well established, and peaked with peak blossom of Red and Golden Delicious. The Large Andrenidae were not observed in 1978. In 1979 and 1980, they were observed a few days later than the other Andrenids when the McIntosh and Empire blossoms started peaking. They were present throughout both seasons and peaked, as the other Hymenoptera discussed so far, in 1979 towards the end of the season and, in 1980, with the peak blossom of Red and Golden Delicious. The Halictidae and 'Green' Halictidae were not observed in 1978. In 1979 and 1980, the Halictids followed the same pattern as the Andrenids and the 'Green' Halictids followed the Large Andrenids. The first pair were active a few days earlier than the second pair, with all peaking towards the end of the season in 1979, and, in 1980, with the peak blossom of Red and Golden Delicious. Both groups of Halictidae were fewer in number than the Andrenidae. The Formicidae were active more or less evenly throughout each of the three years. 'Other' Hymenoptera were present sparsely throughout 1978 and 1979, and only at peak blossom time in 1980.

The Syrphidae were present throughout each of the three seasons. In 1978 and 1980, they peaked with the peak blossom of Red and Golden Delicious. In 1979, they were evenly distributed throughout the blossom period except for their absence during three very cool and rainy days in the middle of the season. The Scathophagidae were not observed in 1978. In 1979, a few were present at the beginning and at the end of the season. In 1980, they were present at peak blossom time. The Bibionidae were not observed in 1978. They were present towards the end of the season in both 1979 and 1980. The Anthomyiidae were present throughout each of the three seasons especially at peak blossom time. The Chironomidae were present towards the end of the season in 1978. In 1979 and 1980, they were more active at the beginning. The 'Other' Diptera, Large or Small, were not observed in 1978. They were present sparsely throughout the season in 1979 and, in 1980, during peak blossom.

The other groups: Coleoptera, Lepidoptera, and Hemiptera, were very few in number and were present mainly at the beginning of the season for each year.

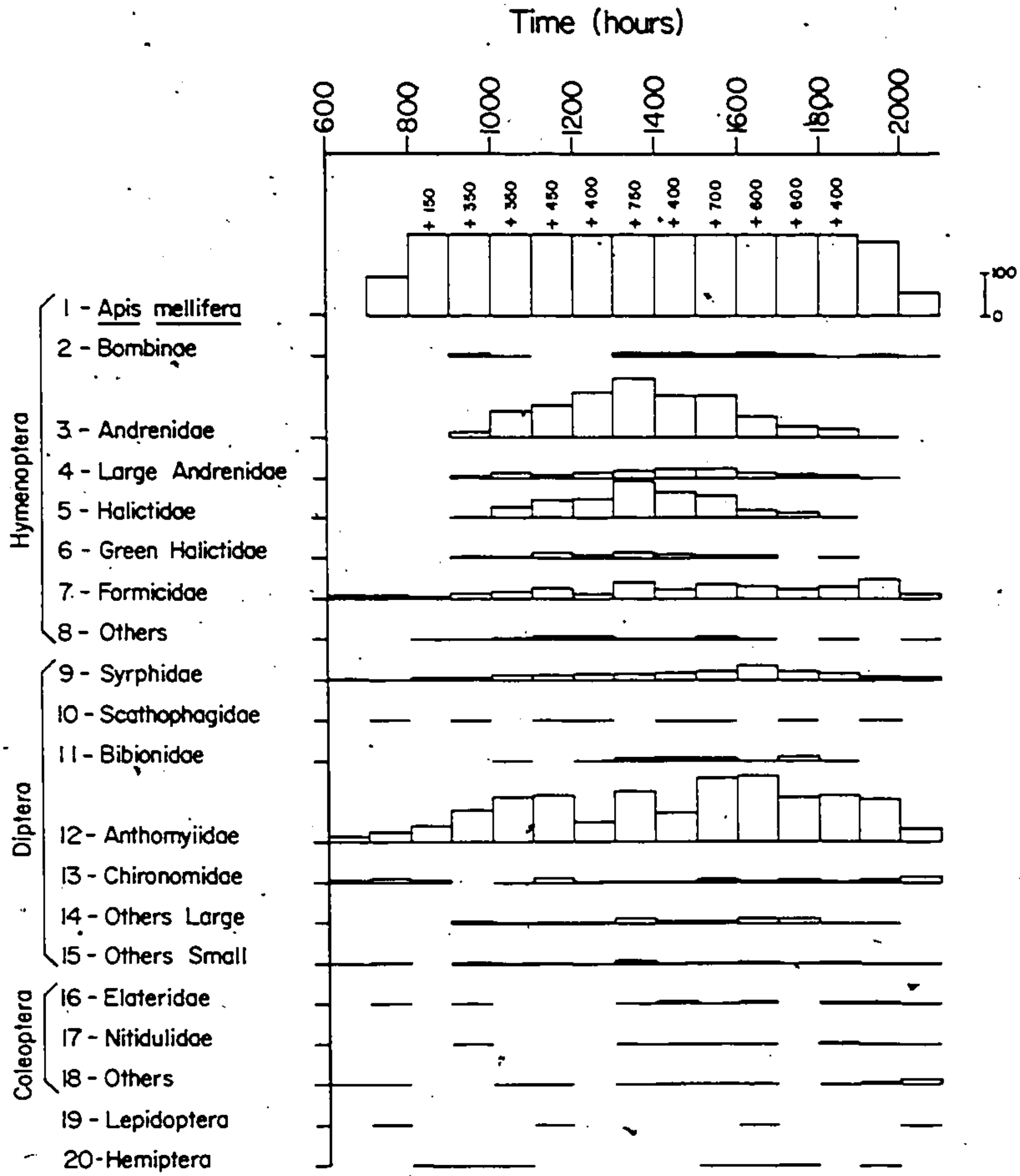
3.2 Daily Fluctuations in the Number of Insects for Each Group of Pollinators:

The distribution of the presence of each group of insects throughout the day was compiled on an hourly basis indicating the total number of insects for all years (Fig. 15).

Apis mellifera L. was present after 7:00 hours, peaking around 14:00 hours and slowly decreasing until sunset. The Bombinae were few and mainly active in the afternoon. The Andrenidae were active between 10:00 and 19:00 hours peaking around 14:00 hours. The Large Andrenidae had a similar range of activity but were much fewer peaking around 15:00 hours. The Halictidae were present between 10:00 and 18:00 hours, peaking around 14:00 hours. The 'Green' Halictidae showed a similar distribution but were much fewer in number. The Formicidae were present throughout the observation times, but were greater in number later in the day. The 'Other' Hymenoptera were present sparsely throughout the day after 8:00 hours.

Most Diptera were active throughout the observation times. The numbers of Syrphidae increased slowly, peaking around 17:00 hours, then decreased rapidly until sunset. The Scathophagidae were few and present sparsely between 7:00 and 20:00 hours. The Anthomyiidae were active throughout the day, peaking around 16:00 hours. The Chironomidae were most active early and late in the day. The Large 'Other' Diptera were present mainly in the afternoon. The Small 'Other' Diptera

Figure 15. Distribution of the total number of insects of each group of pollinator observed over the three years for each hour of the day from 6:00 to 21:00 hours.



Time (hours)
600
800
1000
1200
1400
1600
1800
2000
+ 150
+ 350
+ 350
+ 450
+ 400
+ 750
+ 400
+ 700
+ 600
+ 600
+ 400
100
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera

appeared sparsely throughout the observation times.

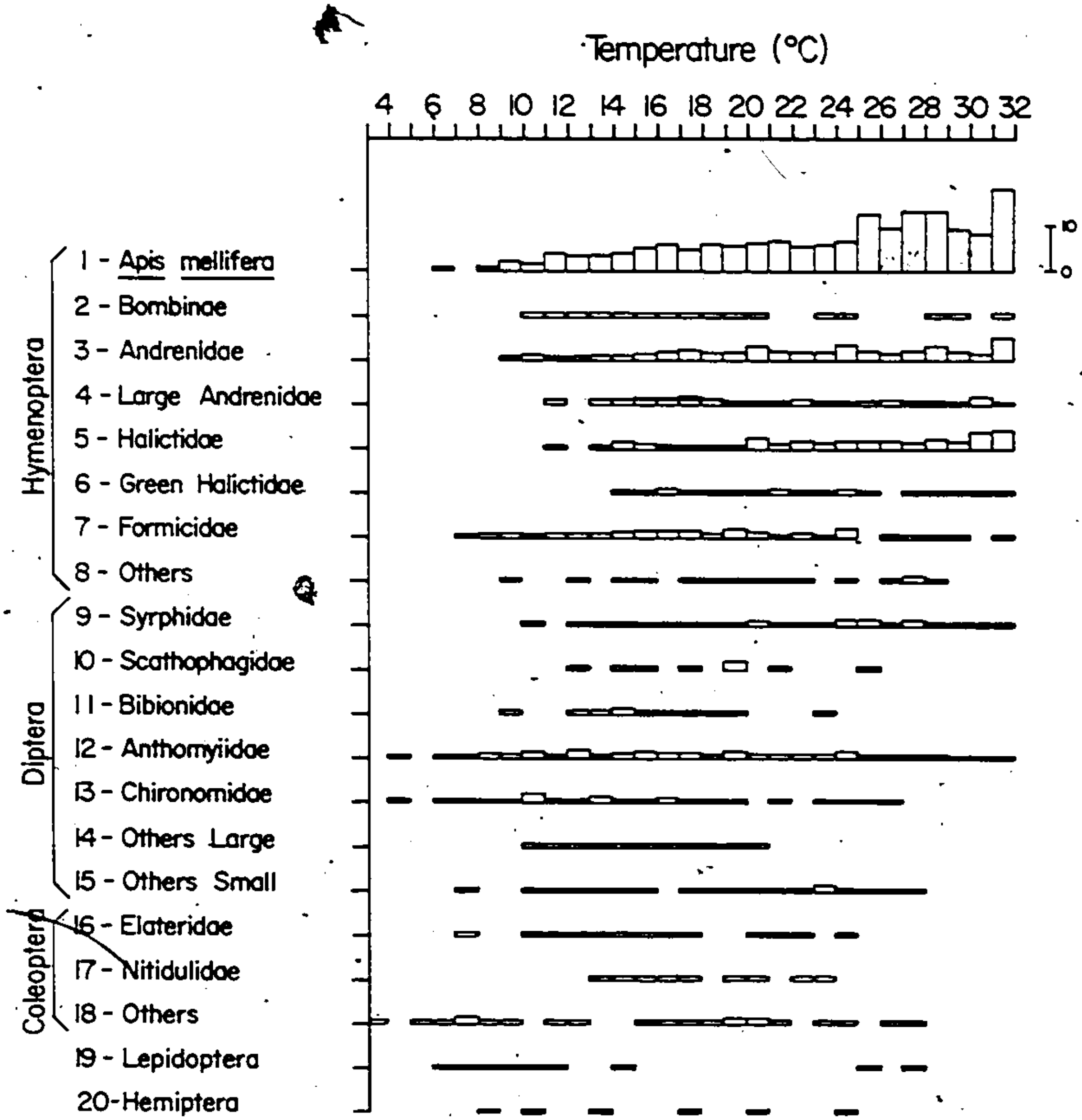
The other groups (Coleoptera, Lepidoptera and Hemiptera) were sparsely represented and were mainly active after 14:00 hours.

3.3 Distribution of Each Group of Pollinator with Respect to Weather Conditions:

Weather conditions have been reported to account for daily fluctuations in the number of pollinators (Free, 1960; Lewis and Smith, 1969, 1972). The range and distribution of the 20 different groups with respect to temperature, humidity, and light energy are presented in Figs. 16, 17 and 18.

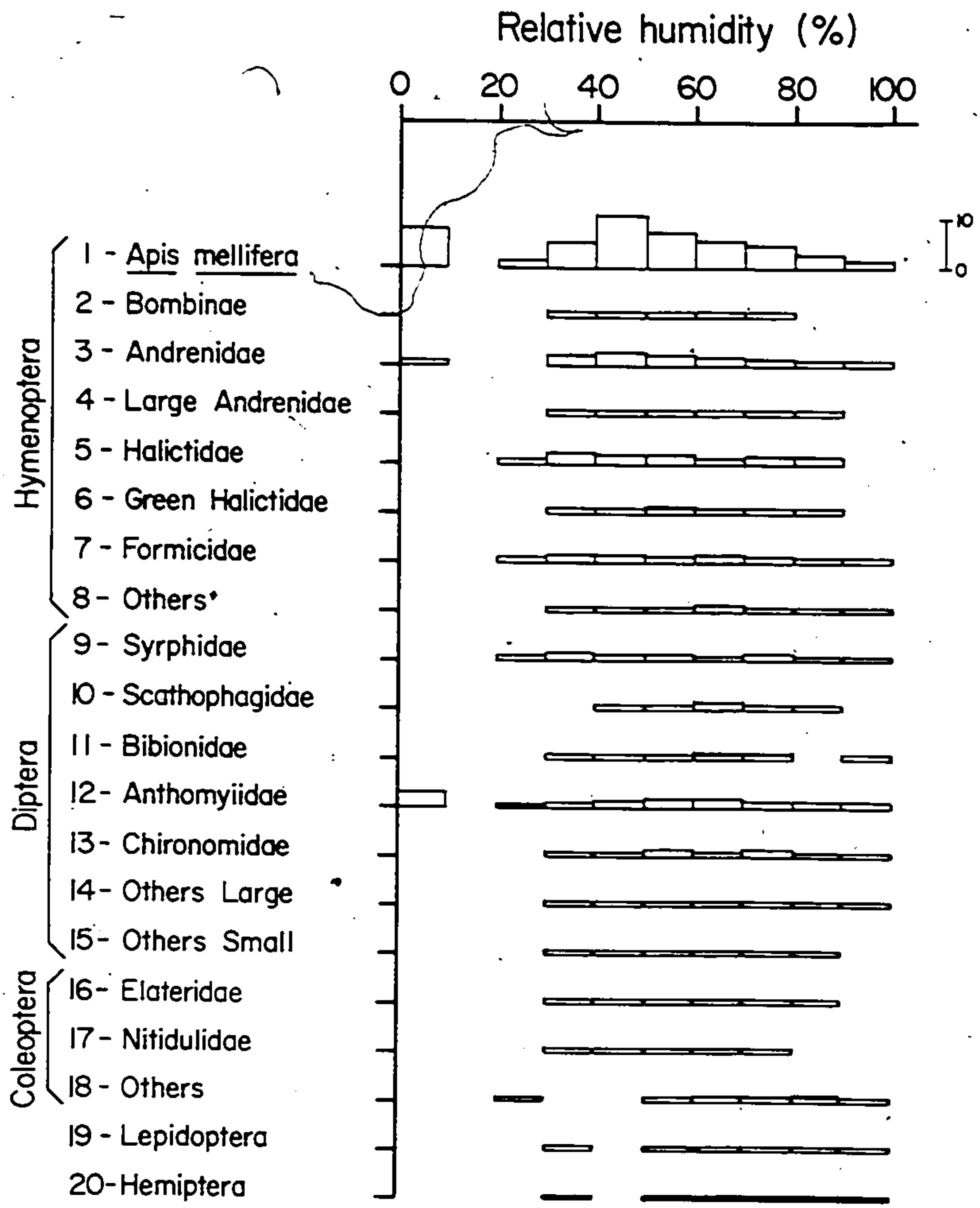
A few bees *(Apis mellifera* L.) were present when the temperature was as low as 7°C but their numbers increased with temperatures above 10°C. They were present throughout the range of humidity, but peaked around 50% relative humidity (R.H.). They were distributed over the entire range of light with their numbers increasing slightly at higher readings. Few Bombinae were present and only above 11°C and between 30% and 80% R.H. They were evenly distributed with respect to light from 0 to 900 Wm^{-2}. The Andrenidae were present above 10°C and increased in numbers with increasing temperatures. They were present throughout the range of humidity with a slight peak at 50% R.H. They were present between 0 and

Figure 16. Distribution of the mean number of insects of each group of pollinator observed per visit for the three years over the range of recorded temperatures (°C).



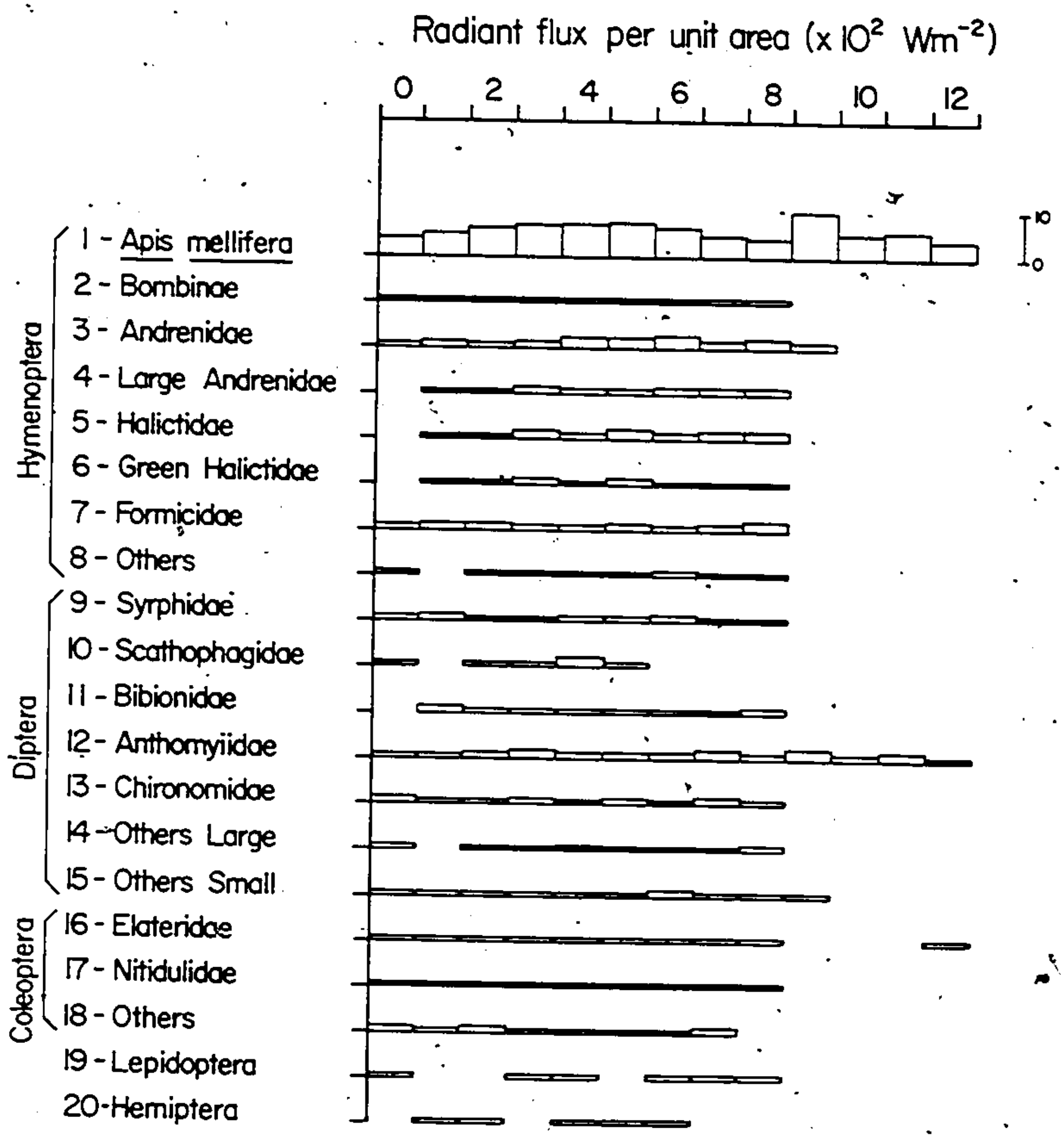
Temperature (°C)
4 6 8 10 12 14 16 18 20 22 24 26 28 30 32
10
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera

Figure 17. Distribution of the mean number of insects of each group of pollinator observed per visit for the three years over the range of recorded relative humidities (%).



Relative humidity (%)
0
20
40
60
80
100
10
0
Hymenoptera
Diptera
Coleoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others*
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera

Figure 18. Distribution of the mean number of insects of each group of pollinator observed per visit for the three years over the range of recorded radiant flux or light energy (Wm^{-2}).



Radiant flux per unit area (x 10² Wm⁻²)
0
2
4
6
8
10
12
10
0
Hymenoptera
1 - Apis mellifera
2 - Bombinae
3 - Andrenidae
4 - Large Andrenidae
5 - Halictidae
6 - Green Halictidae
7 - Formicidae
8 - Others
Diptera
9 - Syrphidae
10 - Scathophagidae
11 - Bibionidae
12 - Anthomyiidae
13 - Chironomidae
14 - Others Large
15 - Others Small
Coleoptera
16 - Elateridae
17 - Nitidulidae
18 - Others
19 - Lepidoptera
20 - Hemiptera

900 Wm^{-2} with their numbers increasing slightly at higher readings. The Large Andrenidae displayed a narrower range of activity. They preferred temperatures above 12°C, humidities between 30% and 90% R.H. and light intensities of 100 to 800 Wm^{-2}. The Formicidae were present whether temperatures were 8°C or the maximum temperature 32°C, but in greatest numbers below 26°C. They were present when humidity was 20% to 100% R.H., and light ranged from 0 to 900 Wm^{-2} with a slight preference for higher intensities. The numbers of 'Other' Hymenoptera were few and observed when temperatures were from 10°C to 29°C. They were present when humidities were between 30% and 100% R.H., and light ranged from 0 to 800 Wm^{-2}.

The Syrphidae were present above 11°C and increased in numbers with increasing temperatures. They preferred humidities between 20% and 100% R.H., and light intensities of 0 to 800 Wm^{-2}. The Scathophagidae were few and had a very narrow range of activity. They were present when temperatures were from 13°C to 26°C, when humidities were between 40% and 90% R.H., and when light ranged from 0 to 500 Wm^{-2}. The Bibionidae preferred temperatures between 10°C and 26°C, humidities between 30% and 100% R.H. and light intensities from 100 to 800 Wm^{-2}. The Anthomyiidae were the most widely distributed group. They were present throughout the entire recorded ranges of temperature, humidity, and light energy: from 5°C to 32°C, between 0% and 100% R.H., and from 0 to 1200 Wm^{-2}. The Chironomidae were present when temperatures were from 5°C to 27°C, when humidities were between 30% and 100% R.H., and when light ranged from 0 to 800 Wm^{-2}. The Large 'Other' Diptera preferred temperatures between 11°C and 21°C, humidities between 30% and 100% R.H., and light intensities from 0 to 800 Wm^{-2}. The Small 'Other' Diptera had a much wider range with temperatures ranging from 8°C to 28°C, humidities between 30% and 90% R.H., and light from 0 to 900 Wm^{-2}.

The Elateridae were present when temperatures were from 8°C to 25°C, when humidities were between 30% and 90% R.H., and when light ranged from 0 to 1200 Wm^{-2}. The Nitidulidae had a much narrower range of activity. They preferred temperatures from 14°C to 24°C, humidities between 30% and 80% R.H., and light intensities from 0 to 800 Wm^{-2}. The 'Other' Coleoptera had a wide range of activity since this group consisted mainly of Cantharidae which were diurnal, and of a few Scarabaeidae which were nocturnal. They were present when temperatures were from 4°C to 28°C, when humidities were between 20% and 100% R.H., and when light ranged from 0 to 700 Wm^{-2}.

The Lepidoptera also consisted of diurnal and nocturnal species. They preferred temperatures between 7°C and 15°C, with a few present at 27°C, humidities from 30% to 100% R.H., and light intensities between 0 and 800 Wm^{-2}.

The Hemiptera were present when temperatures were from 9°C to 25°C, when humidities were between 30% and 100% R.H., and when light ranged from 100 to 600 Wm^{-2}.

3.4.0 Significance of the Factors Responsible for the Fluctuations in the Numbers of Pollinators:

As seen in the previous sections, the numbers of insects present varied considerably. The factors responsible for these fluctuations were divided into two categories: discrete and continuous variables. The discrete variables were static, well delimited factors; these consisted of the number of blossoms per tree, the kind of cultivar, the different rows, the day, and the year. The continuous variables or covariates were time, temperature, humidity, and light energy. For statistical analysis, many of these variables were reorganized and recoded as follows.

Much unavoidable variation was introduced because of the differences in the number of blossoms present each year on each tree and cultivar. As expected and predicted, there were more insects present on a tree which had a greater number of blossoms. This was verified via a Stepwise Multiple Regression and 'F' test (Table 4) where the number of blossoms ranked among the first and was highly significant for the three main groups of pollinators. Therefore, for meaningful comparisons among the other variables, the number

Table 4. Significance of the discrete and continuous variables responsible for the fluctuations in the numbers of the three main groups of pollinators. A Stepwise Multiple Regression of the mean number of insects per visit was used.

Variables	B	Mult.R	R^2 change	F	Sign.F
Bees					
1. # Blossoms	0.0080	0.5727	0.3279	1406.566	0.000
2. Temperature	0.2515	0.6588	0.1062	139.457	0.000
3. Humidity	-0.0429	0.6649	0.0082	38.930	0.000
4. Light	0.1139	0.6674	0.0032	12.226	0.000
5. Day	0.2801	0.6687	0.0018	5.162	0.020
6. Tree	-0.1672	0.6695	0.0009	5.120	0.020
7. Row	0.3357	0.6700	0.0008	4.205	0.040
8. Time	-0.0893	0.6706	0.0008	3.751	0.070
(constant)	-1.7041				
Wild 1					
1. Temperature	0.0557	0.3358	0.1128	54.428	0.000
2. # Blossoms	0.0011	0.3971	0.0449	206.755	0.000
3. Light	0.1262	0.4387	0.0348	119.191	0.000
4. Day	0.1701	0.4445	0.0052	15.140	0.000
5. Tree	-0.0838	0.4479	0.0030	10.203	0.001
6. Humidity	-0.0059	0.4508	0.0026	5.919	0.020
7. Row	-0.1515	0.4528	0.0018	6.804	0.010
8. Time	-0.0289	0.4538	0.0009	3.133	0.070
(constant)	-0.8099				
Wild 2					
1. # Blossoms	0.0005	0.1718	0.0295	98.178	0.000
2. Humidity	-0.0071	0.2083	0.0139	17.598	0.000
3. Time	0.0604	0.2399	0.0092	28.808	0.000
4. Light	0.0471	0.2199	0.0049	34.989	0.000
5. Temperature	-0.0167	0.2473	0.0036	10.284	0.001
6. Row	-0.1126	0.2527	0.0027	7.932	0.005
7. Tree	-0.0058	0.2528	0.0000	0.104	0.25
8. Day	0.0085	0.2528	0.0000	0.081	0.25
(constant)	0.9457				

of insects present for each group per visit was transformed to the number of insects present per 100 blossoms.

The four different cultivars: McIntosh, Empire, Red Delicious, and Golden Delicious, were classified as 'Tree'. 'Row' was separated into east (rows 8 and 11) and west (rows 2 and 4) facing slopes. The three seasons, 1978, 1979, and 1980 were grouped as 'Year'. 'Day' was subdivided into three periods representing the beginning, the peak, and the end of the blossom season. The peak day started when 100 blossoms were present on each cultivar, and ended when about 100 blossoms or less were left (Figs. 12, 13 and 14). 'Time' was divided on a hourly basis from 6:00 to 21:00 hours. Temperature, humidity, and light energy remained as continuous variables.

For adequate testing, the logarithm to base 10 of the numbers of insects per 100 blossoms was used to approximate normal distribution. When means were tabulated, they were expressed as geometric means since they had to be retransformed from the logarithms.

To obtain adequate sample size, the 20 groups of insects were reclassified into the four groups as previously seen in Fig. 8. Group 1, *Apis mellifera* L. or Bees, remained unchanged. All other Hymenoptera were classified into a second group named Wild 1. The Diptera became Wild 2. The Coleoptera, the Lepidoptera, and the Hemiptera together constituted Wild 3. Since Wild 3 only consisted of 1% of the total pollinator population, it was excluded from statistical analysis.

All tests were done at the 5% significance level.

3.4.1 Static or Discrete Variables:

'Tree', 'Row', 'Day', and 'Year' are considered static or discrete variables (main effects) and were thus analyzed first using an analysis of variance (standard Anova), while still accounting for the covariates: temperature, humidity, light, and time. According to the 'F' test (Tables 5, 6 and 7), 'Tree', 'Day', and 'Year' were highly significant in explaining the number of Bees, other Hymenoptera (Wild 1), and Diptera (Wild 2) present. 'Row' (east and west facing slopes) was not significant for Bees, but was slightly significant for Wild 1 and Wild 2.

The larger the value of the Sum of Squares (SS), the greater is the contribution of the factors to the variation of the number of insects. For the Bees, the covariates had a much greater value of SS than the main effects. For Wild 1 and Wild 2, the main effects had a much greater value of SS

Table 5. Significance of the discrete variables (main effects) responsible for the fluctuations in the numbers of Bees, using a standard Anova accounting for the interactions of the covariates. This test was conducted on the logarithmic values of the number of Bees per 100 blossoms per visit.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Covariates	4	20.711	5.178	69.094	0.000
Temperature	1	2.661	2.661	35.506	0.000
Time	1	0.768	0.768	10.250	0.001
Humidity	1	3.920	3.920	52.309	0.000
Light	1	0.220	0.220	2.939	0.087
Main Effects	8	5.899	0.737	9.840	0.000
Tree	3	2.999	1.000	13.338	0.000
Row	1	0.004	0.004	0.050	0.823
Day	2	0.934	0.467	6.234	0.002
Year	2	2.323	1.161	15.499	0.000
Explained	12	26.61	2.218		
Residual	2723	210.844	0.077		
Total	2735	237.454	0.087		

(For detailed explanations of abbreviations and statistical tests refer to Snedecor and Cochran (1967); this applies to all subsequent tables.)

Table 6. Significance of the discrete variables (main effects) responsible for the fluctuations in the numbers of Wild 1, using a standard Anova accounting for the interactions of the covariates. This test was conducted on the logarithmic values of the number of Wild 1 per 100 blossoms per visit.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Covariates	4	3.492	0.873	12.432	0.000
Temperature	1	0.102	0.102	1.459	0.227
Time	1	0.255	0.255	3.628	0.057
Humidity	1	0.021	0.021	0.295	0.587
Light	1	2.190	2.190	31.186	0.000
Main Effects	8	18.558	2.320	33.035	0.000
Tree	3	1.285	0.428	6.101	0.000
Row	1	0.285	0.285	4.056	0.044
Day	2	15.015	7.507	106.908	0.000
Year	2	1.865	0.933	13.280	0.000
Explained	12	22.050	1.838		
Residual	2723	195.681	0.072		
Total	2735	217.731	0.080		

Table 7. Significance of the discrete variables (main effects) responsible for the fluctuations in the numbers of Wild 2, using a standard Anova accounting for the interactions of the covariates. This test was conducted on the logarithmic values of the number of Wild 2 per 100 blossoms per visit.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Covariates	4	1.440	0.360	4.329	0.002
Temperature	1	0.368	0.368	4.425	0.036
Time	1	0.091	0.091	1.098	0.295
Humidity	1	0.114	0.114	1.369	0.242
Light	1	0.372	0.372	4.468	0.035
Main Effects	8	29.720	3.715	44.679	0.000
Tree	3	4.769	1.590	19.119	0.000
Row	1	0.327	0.327	3.938	0.047
Day	2	18.807	9.404	113.093	0.000
Year	2	5.626	2.813	33.832	0.000
Explained	12	31.160	2.597		
Residual	2723	239.306	0.088		
Total	2735	270.466	0.099		

than the covariates. Therefore, weather conditions were responsible for the variation in the number of Bees; whereas the static factors, 'Tree', 'Row', 'Day', and 'Year' were more responsible for the variation in the numbers of Wild 1 and Wild 2.

Each of the main effects was then analyzed individually disregarding interactions from the other variables.

The Duncan Multiple Range Test for the numbers of insects present per 100 blossoms per visit, on the four cultivars, indicated that there were significantly more Bees on Empire and Red Delicious than on McIntosh and Golden Delicious, with Golden Delicious having the fewest Bees (Table 8). There were no significant differences in the numbers of other Hymenoptera (Wild 1) on McIntosh, Empire, and Red Delicious. But there were significantly less Wild 1 on Golden Delicious than on McIntosh and Red Delicious. There were no significant differences in the numbers of Diptera (Wild 2) on McIntosh, Empire, and Red Delicious, but significantly less on Golden Delicious. The numbers of insects present were significantly different according to the 'F' test, among the four different cultivars for all three groups of pollinators.

The Duncan Multiple Range Test for the numbers of insects

Table 8. DUNCAN MULTIPLE RANGE TEST for the number of insects per 100 blossoms per visit on the four cultivars. The test was conducted on the logarithmic values.

	Bees		Wild 1		Wild 2	
Tree	Geom.x	SSR	Geom.x	SSR	Geom.x	SSR
McIntosh	1.109	ab	0.994	a	0.891	a
Empire	1.187	bc	0.947	ab	0.880	a
Red Delicious	1.248	c	1.019	a	0.849	a
Golden Delicious	1.037	a	0.918	b	0.724	b

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Bees	3	2.628	0.876	10.192	0.000
Residuals	2732	234.829	0.086		
Total	2735	237.457			
Wild 1	3	0.887	0.296	3.724	0.011
Residuals	2732	216.847	0.079		
Total	2735	217.734			
Wild 2	3	3.579	1.193	12.211	0.000
Residuals	2732	266.900	0.098		
Total	2735	270.479			

present per 100 blossoms per visit, during the three periods of the blossom season, indicated that there was no significant difference in the number of Bees during the start and the peak of the blossom season, Day 1 and 2, but significantly more at the end of the season (Table 9). There were significantly less other Hymenoptera (Wild 1) during peak blossom, and significantly more towards the end of the season. The numbers of Diptera (Wild 2) showed no significant differences between the start and the end of the season, but were significantly less during peak blossom. The 'F' test for the numbers of insects present indicated that there were significant differences between days for each of the three groups of pollinators.

The Duncan Multiple Range Test for the numbers of insects present per 100 blossoms per visit, during the three years, indicated that there were significant differences in the number of Bees between 1978 and 1979 (Table 10). However, there was no significant difference in the number of Bees between 1978 and 1980, nor between 1979 and 1980. There were significantly fewer other Hymenoptera (Wild 1) and Diptera (Wild 2) in 1979 than in 1978, and significantly fewer in 1980 than in 1978 and 1979. The 'F' test for the numbers of insects indicated that there were no significant differences in the number of Bees between years, but there were significant differences among years for the numbers of Wild 1 and Wild 2.

Table 9. DUNCAN MULTIPLE RANGE TEST for the number of insects per 100 blossoms per visit for each blossom period or day. The test was conducted on the logarithmic values.

Day		Bees		Wild 1		Wild 2	
		Geom. $\bar{x}$	SSR	Geom. $\bar{x}$	SSR	Geom. $\bar{x}$	SSR
1.	Start	1.110	a	1.031	a	1.030	a
2.	Peak	1.113	a	0.842	b	0.704	b
3.	End	1.235	b	1.276	c	1.053	a

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Bees	2	1.096	0.548	6.337	0.002
Residuals	2733	236.360	0.087		
Total	2735	237.456			
Wild 1	2	16.372	8.186	111.105	0.000
Residuals	2733	201.362	0.074		
Total	2735	217.334			
Wild 2	2	19.643	9.821	107.007	0.000
Residuals	2733	250.837	0.092		
Total	2735	270.480			

Table 10. DUNCAN MULTIPLE RANGE TEST for the number of insects per 100 blossoms per visit for each of the three years. The test was conducted on the logarithmic values.

Year	Bees Geom. $\bar{x}$	Bees SSR	Wild 1 Geom. $\bar{x}$	Wild 1 SSR	Wild 2 Geom. $\bar{x}$	Wild 2 SSR
1978	1.269	a	1.219	a	1.199	a
1979	1.127	b	0.987	b	0.854	b
1980	1.150	ab	0.901	c	0.741	c

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Bees	2	0.412	0.206	2.377	0.093
Residuals	2733	237.043	0.087		
Total	2735	237.455			
Wild 1	2	2.678	1.339	17.015	0.000
Residuals	2733	215.053	0.079		
Total	2735	217.731			
Wild 2	2	6.759	3.379	35.026	0.000
Residuals	2733	263.719	0.097		
Total	2735	270.479			

Table 11. Significance of the east and west slopes (Row) on the variation of the number of insects per 100 blossoms per visit. The test was conducted on the logarithmic values.

Row	Bees Geom.x	Bees SSR	Wild 1 Geom.x	Wild 1 SSR	Wild 2 Geom.x	Wild 2 SSR
East	1.150	a	0.997	a	0.856	a
West	1.137	a	0.945	b	0.808	b

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Bees	1	0.018	0.018	0.209	0.647
Residuals	2734	237.435	0.087		
Total	2735	237.454			
Wild 1	1	0.357	0.357	4.495	0.034
Residuals	2734	217.374	0.079		
Total	2735	217.731			
Wild 2	1	0.436	0.436	4.415	0.036
Residuals	2734	270.042	0.099		
Total	2735	270.478			

The 'F' test for the numbers of insects present per 100 blossoms per visit, between rows indicated that there were no significant differences in the number of Bees between east and west facing slopes (Table 11). However, there were significantly more Wild 1 and Wild 2 on the east facing slope than on the west facing slope.

3.4.2 Covariates or Continuous Variables:

Temperature, humidity, light energy, and time are continuous variables, and were analyzed using a Stepwise Multiple Regression, which accounts for interactions among variables and ranks them to indicate which is responsible for the greatest variation in the numbers of insects.

Temperature, humidity, and time were highly significant in the variation of the number of Bees, with temperature ranking first (Table 12). For the other Hymenoptera (Wild 1), only light was significant. None of these variables was significant for the variation in the numbers of Diptera (Wild 2).

This analysis was conducted using all observations. Once the insects were present (excluding observations when the insects were absent or not recorded), humidity ranked first as a factor responsible for the variation in the

Table 12. Significance of the continuous variables responsible for the fluctuations in the numbers of the three main groups of pollinators. A Stepwise Multiple Regression was used on the logarithmic values of the mean number of insects per 100 blossoms per visit.

Variables	B	Mult.R	R^2 change	F	Sign.F
Bees					
1. Temperature	0.0080	0.2573	0.0662	33.528	0.000
2. Humidity	-0.0032	0.2850	0.0150	49.337	0.000
3. Time	-0.0044	0.2938	0.0051	9.671	0.002
4. Light	0.0036	0.2953	0.0009	2.783	0.150
(constant)	0.1651				
Wild 1					
1. Light	0.0113	0.1191	0.0142	27.946	0.000
2. Time	-0.0025	0.1248	0.0014	3.243	0.070
3. Temperature	-0.0016	0.1263	0.0004	1.310	0.250
4. Humidity	-0.0002	0.1267	0.0001	0.265	0.250
(constant)	0.0029				
Wild 2					
1. Temperature	-0.0029	0.0489	0.0024	3.746	0.060
2. Light	0.0047	0.0656	0.0019	3.775	0.062
3. Humidity	0.0005	0.0706	0.0007	1.152	0.25
4. Time	-0.0015	0.0730	0.0003	0.926	0.25
(constant)	-0.0746				

Table 13. Significance of the continuous variables responsible for the fluctuations in the number of the three main groups of pollinators, only when the insects were present. A Stepwise Multiple Regression was used on the logarithmic values of the number of insects different than zero per 100 blossoms per visit.

Variables	B	Mult.R	R^2 change	F	Sign.F
Bees					
1. Humidity	-0.0091	0.3249	0.1055	75.172	0.000
2. Time	-0.0200	0.3653	0.0279	27.920	0.000
3. Temperature	0.0107	0.3795	0.0105	13.967	0.000
4. Light	0.0165	0.3916	0.0094	13.709	0.000
(constant)	0.5791				
Wild 1					
1. Light	0.0521	0.3067	0.0941	37.070	0.000
2. Time	-0.0173	0.3136	0.0043	4.328	0.035
3. Humidity	-0.0022	0.3186	0.0032	1.261	0.25
4. Temperature	0.0009	0.3186	0.0000	0.027	0.25
(constant)	-0.0911				
Wild 2					
1. Light	0.0211	0.0934	0.0087	11.278	0.001
2. Temperature	-0.0065	0.1079	0.0029	2.861	0.15
3. Time	0.0052	0.1141	0.0014	1.119	0.25
4. Humidity	-0.0002	0.1143	0.0000	0.031	0.25
(constant)	-0.2369				

number of Bees (Table 13). Light energy remained the most significant for Wild 1, and became the only variable significant for Wild 2.

4.0 Pollen Analysis:

Pollen analysis consisted of washing the pollen grains off the bodies of a few insects from each group of Hymenoptera and Diptera. The pollen grains were counted and the numbers for each group of pollinator compared.

Since the counts varied over a considerable range, logarithmic transformation was required to give an approximation of the normal distribution for adequate statistical treatment. Therefore, the average amounts of pollen grains are presented as geometric means and the standard deviations are multiplicative.

4.1 Efficiency of the Washing Method:

The efficiency of recovery of pollen from the insects was checked for a few groups, by repeating the standard washing procedure a total of three times. The first washing was then compared with the total of three considered as 100% recovery. From the groups tested, the standard method yielded over 85% of the total pollen (Table 14). This was considered

Table 14. Estimates of efficiency of removal of pollen grains from insects by washing and brushing in 70% alcohol.

Group	# Insects	Geom. $\bar{X}$ pollen removed by standard method	Yield of pollen by standard method as % of total yield following 2 additional treatments	
			Arith. $\bar{X}$	S.D.±
Apis mellifera	7	10210	86.2	4.6
Andrenidae	11	9297	85.8	8.1
Large Andrenidae	5	39250	93.8	2.2
Halictidae	10	5388	97.8	3.1
Syrphidae	5	2674	91.8	3.9

adequate since it would be impossible to determine the percentage of pollen on an insect available to be brushed onto the stigma of a blossom.

4.2 Nectar Versus Pollen Gatherers:

Among the Hymenoptera collected, two categories can be distinguished, pollen gatherers and nectar gatherers. The pollen gatherers have pollen baskets on their hind legs, which were removed before washing. The nectar gatherers did not have such loads and were simply washed.

The differences in the numbers of pollen grains on the bodies of these insects were compared for six groups of Hymenoptera. Only the Large Andrenidae and the Halictidae displayed significant differences between their pollen and nectar gatherers for the numbers of fruit pollen and the numbers of total pollen grains (Tables 15 and 16). There were no significant differences in the numbers of pollen grains between nectar and pollen gatherers for the Bees (*Apis mellifera* L.), the Bombinae, the Andrenidae, and the 'Green' Halictidae. Therefore, the pollen and nectar gatherers were distinguished only in the case of the Large Andrenidae and the Halictidae.

Table 15: Comparison between the mean number of fruit pollen grains washed from the bodies of insects with and without pollen baskets for six groups of Hymenoptera.

Groups	Geom. $\bar{x}$ of fruit pollen washed from insects with pollen baskets	without pollen baskets
Apis mellifera	8480	7718
Bombinae	22589	2559
Andrenidae	8788	4016
Large Andrenidae*	36074	6747
Halictidae*	1488	186
'Green' Halictidae	2346	1686

* Insects with pollen baskets significantly different from those without, at the 5% level.

Table 16. Analysis of the significance of the mean number of fruit pollen grains washed from the bodies of insects with and without pollen baskets for six groups of Hymenoptera.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Bees	1	0.004	0.004	0.045	0.837
Residuals	9	0.737	0.082		
Total	10	0.741			
Bombinae	1	0.597	0.597	3.013	0.333
Residuals	1	0.198	0.198		
Total	2	0.795			
Andrenidae	1	0.222	0.222	1.137	0.292
Residuals	48	9.381	0.195		
Total	49	9.603			
Large Andrenidae	1	2.997	2.997	26.326	0.000
Residuals	21	3.390	0.114		
Total	22	5.387			
Halictidae	1	6.571	6.571	5.333	0.026
Residuals	39	48.058	1.232		
Total	40	54.629			
'Green' Halictidae	1	0.050	0.050	0.165	0.691
Residuals	14	4.246	0.303		
Total	15	4.296			

4.3 Amount of Pollen on the Bodies of the Various Groups of Hymenoptera and Diptera:

The differences in the numbers of fruit pollen grains for the various groups were tested using the Duncan Multiple Range Test at the 5% significance level (Table 17).

The Hymenoptera and the Diptera appear more or less as two distinct classes including a few overlapping groups, with the Hymenoptera having more fruit pollen grains than the Diptera.

The amount of fruit pollen was not significantly different for the Bees, the Bombinae, the Andrenidae and the Large Andrenidae (pollen and nectar gatherers). There were also no significant differences among the Bees, the Bombinae, the nectar gathering Large Andrenidae, and the 'Green' Halictidae. Similarly, there were no significant differences among the Bombinae, the pollen gathering Halictidae and the 'Green' Halictidae. The nectar gathering Halictidae, the Formicidae, and the 'Other' Hymenoptera had significantly less fruit pollen grains than the Hymenoptera previously mentioned, and had amounts similar to those found on the Diptera.

There were no significant differences in the amount of fruit pollen grains among nectar gathering Halictidae, the

Table 17. Quantity of pollen grains washed from the bodies of the various groups of Hymenoptera and Diptera (groups sharing a common letter do not differ significantly, at the 5% level, in the number of fruit pollen grains).

Group	Number Insects	Total pollen Geom. $\bar{X}$	Total pollen SD$\overset{\times}{\div}$	Fruit pollen Geom. $\bar{X}$	Fruit pollen SD$\overset{\times}{\div}$	SSR	%Fruit pollen	Insects with > 90% Fruit pollen
Apis mellifera	11	9020	1.9	8266	1.9	ab	92	7 (64%)
Bombinae	3	5617	4.3	5288	4.3	abc	94	3 (100%)
Andrenidae	50	9230	2.6	8517	2.8	a	93	41 (82%)
Large Andrenidae								
pollen gatherers	13	38610	2.1	36074	2.1	a	94	9 (69%)
nectar gatherers	10	7415	2.2	6747	2.3	ab	91	8 (80%)
Halictidae								
pollen gatherers	30	3558	2.3	1488	13.4	c	79	18 (60%)
nectar gatherers	11	388	6.1	186	11.6	de	75	6 (55%)
'Green' Halictidae	16	2640	3.2	2205	3.4	bc	78	4 (25%)
Formicidae	7	30	2.4	16	4.2	fg	86	6 (86%)
'Other' Hymenoptera	7	131	5.0	105	4.4	def	82	3 (43%)
Syrphidae	29	806	7.0	296	13.7	d	61	8 (28%)
Scathophagidae	3	168	2.1	130	2.4	def	79	1 (33%)
Bibionidae	5	41	11.1	41	11.1	ef	80	4 (80%)
Anthomyiidae	12	32	4.2	16	6.8	fg	68	7 (58%)
Chironomidae	2	0	0	0	0	g	0	0
Large 'Other' Diptera	10	108	6.8	73	5.5	def	64	3 (30%)
Small 'Other' Diptera	8	2	3.9	1	2.3	g	13	1 (13%)

'Other' Hymenoptera, the Syrphidae, the Scathophagidae, and the Large 'Other' Diptera. There were also no significant differences among the nectar gathering Halictidae, the 'Other' Hymenoptera, the Scathophagidae, the Bibionidae, and the Large 'Other' Diptera. There were no signficant differences among the Formicidae, the 'Other' Hymemoptera, the Scathophagidae, the Bibionidae, the Anthomyiidae, and the Large 'Other' Diptera. Similarly, there were no significant differences among the Formicidae, the Anthomyiidae, the Chironomidae, and the Small 'Other' Diptera.

4.4 Constancy of the Various Groups of Hymenoptera and Diptera:

Insects having greater percentage of fruit pollen in relation to total pollen were more constant to fruit blossoms than other insects.

The Bees, the Bombinae, the Andrenidae and the Large Andrenidae (both pollen and nectar gatherers) had the greatest percentage of fruit pollen (Table 17). The Halictidae (pollen and nectar gatherers, and 'Green' Halictidae) were the least constant among the Hymenoptera.

Besides the Chironomidae which had no pollen and the Small 'Other' Diptera which had very little, the Syrphidae, the Anthomyiidae, and the Large 'Other' Diptera were the least constant with more or less 64% fruit pollen.

5.0 Fruit Set:

Fruit set was calculated as a percentage of the ratio of fruit to the number of potential blossoms. According to Williams (1970), the total number of potential blossoms can be calculated by multiplying the number of clusters by five. This was verified by counting the total number of clusters and the total number of blossoms that would open on three trees each year. The ratio of clusters to potential blossoms was 5 in 1978 and 1979, as expected, but it was 4 in 1980 (Table 18). Consequently, the number of clusters on each of the sixteen sample trees was multiplied by the appropriate factor, and fruit set was calculated for each tree each year. For adequate statistical treatment, logarithmic transformation of the calculated fruit set was required to give an approximation of the normal distribution.

'Tree', 'Row', and 'Year' were the possible factors recorded responsible for the variation in fruit set. With interactions between the three variables taken into consideration, the 'F' test (Standard Anova) indicated that only 'Tree' was significant in explaining the variations in fruit set (Table 19).

Table 18. Comparison between the total number of clusters per tree and the total number of possible blossoms per tree for each year.

Year	Clusters	#Blossoms	Factor Blossoms/Clusters
1978	21	107	5.1
	58	302	5.2
	91	437	4.8
1979	98	524	5.3
	218	1089	4.9
	293	1563	5.3
1980	148	611	4.1
	344	1346	3.9
	546	2293	4.2

Table 19. Significance of the discrete variables (main effects) responsible for the fluctuations in the Fruit Set. The test was conducted on the logarithmic values of the percentage of the number of fruit per number of possible blossoms per tree.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Main Effects	6	1.532	0.255	5.575	0.001
Tree	3	1.319	0.440	9.601	0.000
Row	1	0.066	0.066	1.444	0.241
Year	2	0.147	0.073	1.601	0.222
Explained	6	1.532	0.255		
Residual	41	1.765	0.043		
Total	47	3.297	0.070		

Table 20. DUNCAN MULTIPLE RANGE TEST for the fruit set on each of the four cultivars. The test was conducted on the logarithmic values of the percentage of the number of fruit per number of possible blossoms per tree.

Tree	Geom. $\bar{x}$	SSR
McIntosh	8.5	ab
Empire	13.2	b
Red Delicious	10.4	a
Golden Delicious	23.5	c

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Tree	3	1.319	0.439	9.786	0.000
Residuals	44	1.977	0.045		
Total	47	3.297	0.070		

The Duncan Multiple Range Test for the percent of fruit that set on each of the four cultivars, indicated that there was no significant difference in the percent of fruit that set on McIntosh and Red Delicious, nor on McIntosh and Empire (Table 20). However, there was a significantly greater percentage of fruit that set on Golden Delicious than on any of the other cultivars.

5.1 Seed Set:

The number of seeds per fruit was determined for a sample of 25 apples from each observation tree, in 1979 and 1980. 'Tree', 'Row', and 'Year' were the possible factors recorded responsible for the variation in the number of seeds per apple. With interactions among the three variables taken into account, the 'F' test (Standard Anova) indicated that 'Tree' and to a lesser extent 'Year' was significant in explaining the variation in the number of seeds per apple (Table 21).

The Duncan Multiple Range Test for the number of seeds per apple of each of the four cultivars indicated that the number of seeds per apple was not significantly different for Empire and Red Delicious (Table 22). There were significantly more seeds per apple of McIntosh than of Empire and Red Delicious, and significantly more of Golden Delicious than of any of the other cultivars.

Table 21. Significance of the discrete variables (main effects) responsible for the fluctuations in the numbers of seeds per apple per tree. The test was conducted on the logarithmic values.

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Main Effects	5	1.431	0.286	14.970	0.000
Tree	3	1.329	0.443	23.171	0.000
Row	1	0.012	0.012	0.626	0.429
Year	1	0.080	0.080	4.203	0.041
Explained	5	1.431	0.286		
Residual	722	14.020	0.019		
Total	727	15.451	0.021		

Table 22. DUNCAN MULTIPLE RANGE TEST for the mean number of seeds per apple per tree for each of the four cultivars. The test was conducted on the logarithmic values.

Tree	Geom. $\bar{x}$	SSR
McIntosh	7.41	a
Empire	6.86	b
Red Delicious	5.98	b
Golden Delicious	7.74	c

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Tree	3	1.337	0.446	22.863	0.000
Residuals	724	14.114			
Total	727	15.451			

Table 23. Significance of the year on the variation of the number of seeds per apple per tree. The test was conducted on the logarithmic values.

Year	Geom. $\bar{x}$	SSR
1979	6.761	a
1980	7.122	b

Analysis of Variance

Source	df	S.S.	M.S.	F	Sign.F
Seeds	1	0.093	0.093	4.397	0.036
Residuals	726	15.358	0.021		
Total	727	15.451			

There were significantly more seeds per apple in 1980 than in 1979 (Table 23).

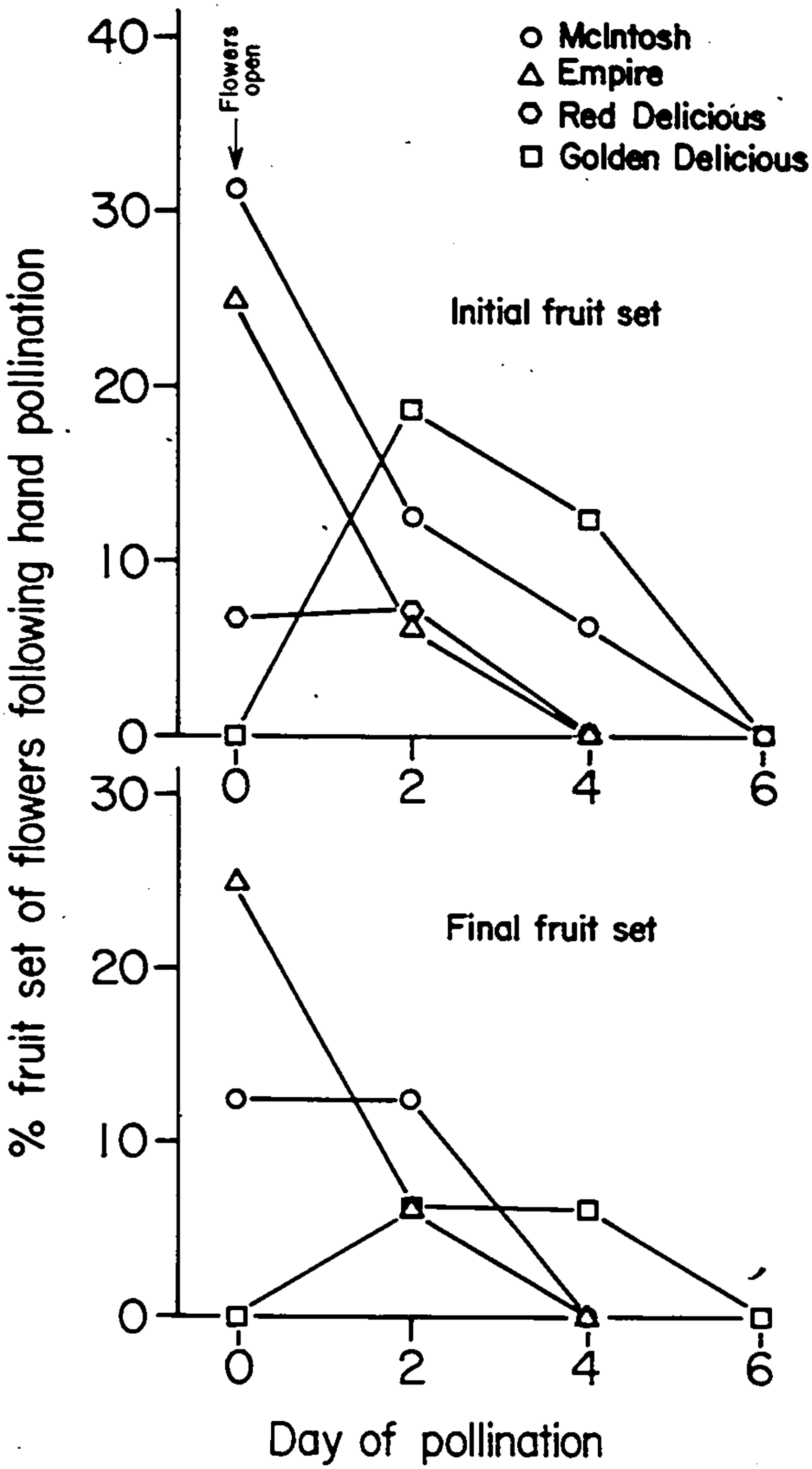
6. Effective Pollination Period:

The effective pollination period is an estimate of the length of time the stigma is receptive to pollen. Fruit set following hand pollination at various times was used for this estimate.

According to the Initial Fruit Set (Fig. 19), McIntosh and Red Delicious were receptive to pollen from day '0', the day of opening of the blossoms, until day '2', whereas Golden Delicious was receptive from days '2' to '4'. McIntosh was also receptive on the fourth day but did not set final fruit (Fig. 19). The Final Fruit Set followed the same trends as the Initial Fruit Set except for Red Delicious which did not produce any apples.

The number of seeds per fruit (Table 24) displayed similar results, with McIntosh and Empire having similar numbers of seeds for days '0' and '2', and Golden Delicious with similar numbers of seeds for days '2' and '4'.

Figure 19. Initial and Final Fruit Set following hand pollination for each of the four cultivars for 1980. Day of pollination represents the number of days after the blossoms opened when hand pollination occurred.



Flowers open
McIntosh
Empire
Red Delicious
Golden Delicious
Initial fruit set
Final fruit set
% fruit set of flowers following hand pollination
40
30
20
10
0
0
2
4
6
30
20
10
0
0
2
4
6
Day of pollination

Table 24. Mean number of seeds per apple per tree for each of the four cultivars. Day represents the number of days after the blossoms opened when hand pollination occurred. The number in ( ) represents the total number of apples.

Tree	Day			
	0	2	4	6
McIntosh	5 (2)	7 (2)	-	-
Empire	7 (4)	6 (1)	-	-
Red Delicious	-	-	-	-
Golden Delicious	-	9 (1)	8 (1)	-

DISCUSSION

The current work represents a significant contribution to our understanding of the various insect components of an orchard and their activity. The preceding results underline the significance of detailed observations on parameters as diverse as insect population composition, bloom development, attractiveness of the cultivars present and effective pollination period. It also reveals the impact weather conditions have on pollination success.

1. Population Composition and Seasonal Distribution

The first six groups of Hymenoptera, *Apis mellifera* L., Bombinae, Andrenidae, Large Andrenidae, Halictidae, and 'Green' Halictidae are true pollinators. They feed on pollen and nectar, and actively collect pollen to feed their brood. Except for the Syrphidae which actually eat pollen, all other groups are 'chance' pollinators. Many feed on nectar and may brush the anthers, thus accidentally carrying pollen between flowers.

Apis mellifera L. was the most numerous for all years. In 1978, the Anthomyiidae, the Formicidae and the Syrphidae followed in numbers. In 1979, the sequence was the Anthomyiidae, the Andrenidae, the Formicidae and the Halictidae. In 1980, the honeybee population was followed by the Andrenidae, the Halictidae, the Anthomyiidae and the Syrphidae.

The Bombinae, often thought to be more important pollinators than the honeybees, were extremely rare for all years. In accordance with Heinrich (1979b), *Apis* and *Bombus* seem to compete for similar resources, and thus, few *Bombus* are present when *Apis* are overly abundant.

The numbers of honeybees increased markedly from year to year over the three years. The numbers of Hymenoptera, excluding *Apis*, were more or less equal through the years, whereas, the Diptera and the other groups decreased from one year to the next.

General conclusions regarding the 1978 season would be very difficult since there were only 167 observation periods. In comparison, 1653 observation periods were conducted in 1979, and 916 in 1980.

The 1979 season was very long mainly because of adverse weather conditions. Towards the middle of the season, there were five days of very cool temperatures slowing down blossom development considerably. A much greater diversity of species was recorded because of this extended period. Discounting the honeybees, the various Diptera (except for the Syrphidae) were the main groups present. The Hymenoptera dominated in 1980 when the blossom period was short with excellent weather conditions.

In general, trees require a minimum number of blossoms for insect visits. The number of insects increased to a peak with the peak blossom of Red and Golden Delicious which was two days after the peak blossom of McIntosh and Empire. This increase in the number of insect visitors with the increase in the number of blossoms has been reported by many researchers (Brittain, 1933; Free, 1966; Kendall and Smith, 1975a; Lewis and Smith, 1969; Silander and Primack, 1978). In 1979, however, most insects had a greater peak towards the end of the blossom period because of unfavourable weather earlier.

Thus, flowers that open at different times are exposed to different insect pollinators (Lewis and Smith, 1969). Only the insects active during the critical receptive period (efficient pollination period or E.P.P.) of the flowers will contribute to their pollination. The E.P.P. was calculated and it was found that McIntosh and Empire were receptive to pollen for two days following flower opening. Red Delicious did not set final fruit but, from the initial fruit set, was also receptive for the first two days. Golden Delicious was receptive to pollen from day 2 to the fourth day following flower opening. Although these observations apply to 1980 only, it is reasonable to extrapolate that the insects present or peaking from the beginning to peak blossom are of greater significance in pollination than the insects present or peaking towards the end of the blossom season. The most numerous groups mentioned above correspond to the main pollinators present during this critical period. The Bibionidae are the only group active mostly at the end of the blossom period; therefore, they do not contribute significantly to pollination.

The amount of pollen on the body of an insect is a good indication of its efficiency in pollination (Kendall and Solomon, 1973). Thus, an insect with a greater amount of pollen will be a better pollinator. Hymenoptera, which possess morphological structures for pollen collection, had significantly more pollen on their bodies than the Diptera. For the first six groups of Hymenoptera (*Apis mellifera* L., Bombinae, Andrenidae, Large Andrenidae, Halictidae and 'Green' Halictidae), pollen and nectar gatherers were separated on the basis of the presence or absence of pollen loads on their hind legs. Hymenoptera with and without pollen baskets were compared; it was found that only the Large Andrenidae and the Halictidae had significantly less pollen on the nectar gatherers than the pollen gatherers. Therefore, nectar gathering Large Andrenidae and Halictidae would be less efficient in pollination.

Pollen gatherers have been reported more valuable as pollinators since they must necessarily touch the anthers and stigma, whereas many nectar-gatherers can approach the nectaries from the side without contracting pollen (Brittain, 1933; Free, 1960a, 1960b, 1967; Roberts, 1945). Of the Hymenoptera, the Andrenidae and the pollen-gathering Large Andrenidae had the greatest amount of fruit pollen on their bodies, followed in decreasing order by *Apis mellifera* L., the nectar-gathering Large Andrenidae, the Bombinae, the 'Green' Halictidae, the pollen and nectar-gathering Halictidae.

Kendall and Solomon (1973) reported that the larger solitary bees had the most pollen. They found that bumblebees also had great amounts. However in this study, because bumblebees were rare and only three were used for the pollen analysis, the discrepancies are likely due to a too small sample size. Following pollination of unopened flowers with anaesthetized insects, Kendall (1971, 1973) reported that most solitary bees tested carried larger quantities of fruit pollen than honeybees. This supports the idea that greater amounts of pollen on an insect corresponds to a better pollinator. Among the Diptera, the Syrphidae had the greatest amount of pollen.

The honeybees were the most numerous of all pollinators but were less efficient than the Andrenidae and their activity fluctuated greatly during adverse conditions. The Anthomyiidae, which ranked second numerically in 1978, and 1979 even during unfavourable conditions had however very few pollen grains, and therefore contributed very little to pollination. On the other hand, the Syrphidae, which had the greatest amount of pollen among the Diptera, were mainly active during seasons with better weather conditions. The Andrenidae and Halictidae compensated for the poor performance of the honeybees in 1979. The unfavourable weather during the 1979 season might have extended the receptive period of the flowers and thus increased the chance of better pollination. The percentage of fruit pollen was greater for the Andrenidae, and *Apis*. Therefore, these groups are more constant to fruit trees and thus appear to be better pollinators than the others.

2. Daily Fluctuations in Pollinator Activity:

All groups were mainly active in the afternoon corresponding to the greater availability of pollen and nectar (Butler, 1945; Free, 1960a; Langridge, 1969; Percival, 1955). All bees (hivebees and native bees) peaked between 12:00 and 16:00 hours. The Anthomyiidae, the Formicidae and the Syrphidae were active earlier in the morning and peaked later in the day corresponding to periods of reduced competition. Temperature, humidity and light seem to be mainly responsible for these daily fluctuations in activity.

Honeybees seem to be the only group affected by temperature changes. The numbers of honeybees increased markedly with higher temperatures. The other groups are constant throughout the ranges of temperature. However, all have a definite threshold below which they are not active. This critical temperature is higher for the native bees than for the honeybees.

The change from inability to fly to ability to fly occurs abruptly at the threshold temperature (Taylor, 1963) but, once attained, the other factors become important to the fluctuations in the numbers of active insects. The honeybees again seem to be the only group affected by changes in humidity as they peak at lower readings around 45% relative humidity. The other groups are constant throughout the ranges of humidity. The native bees however, are less tolerant of higher humidity readings than the other groups.

All groups are constant throughout the ranges of light readings. The Andrenidae and the Halictidae, though, are not active at low intensities.

The numbers of active honeybees fluctuate greatly with temperature and humidity. The native bees thought to be more tolerant to adverse conditions have definite threshold temperatures, humidities and light intensities for their activity.

3. Significance of the Factors Responsible for the Fluctuations in the Numbers of Pollinators:

According to the analysis of variance, the covariates: temperature, humidity, and light were the most important factors responsible for the variation in the numbers of honeybees. However, the main effects: tree, row, day, and year, were more important in explaining the variations in the numbers of other Hymenoptera and Diptera.

The analysis of the covariates (via a Stepwise Multiple Regression) supports the conclusions deduced qualitatively in the previous section. Temperature is the most significant factor for the honeybees followed by humidity. Only light is significant for the other Hymenoptera, and for the Diptera, none of the factors are significant. Once the insects are active, in other words once they have reached their threshold temperature, humidity is the most important for the honeybees. Light still remains the most significant factor for the other Hymenoptera and became the only significant one for the Diptera. In more concrete terms, the Diptera were active early and later in the day, and once the temperature was above 10°C (threshold temperature) the honeybees became active followed by the other Hymenoptera more towards midday at greater light intensities and higher temperatures.

The type of cultivar was significant for all pollinators. Empire and Red Delicious were more attractive to honeybees than the other cultivars. McIntosh and Red Delicious were more attractive to the other Hymenoptera; and McIntosh, Empire, and Red Delicious were equally attractive to the Diptera. There were significantly fewer insects per 100 blossoms on Golden Delicious than on the other cultivars for all three groups of pollinators. However, there were significantly more fruit that set on Golden Delicious than on any of the others. Golden Delicious also had singificantly more seeds per apple from the sample trees as well as when hand pollinated. Golden Delicious has been reported to be an extremely fertile cultivar (Milutinovic and Milutinovic, 1970), and therefore seems to require less pollinator visits. In addition, if the insects prefer the other cultivars, when they do visit Golden Delicious, they will transfer a greater amount of compatible pollen. The Effective Pollination Period for this cultivar was twice as long as for the others, therefore there was a better chance of being adequately pollinated (Stott, 1972; Williams, 1970). Red Delicious was very attractive to all pollinators, yet it had a low fruit set and the lowest seed count. Since there were more insect visitors on Red Delicious, little cross-pollination occurred particularly because Golden Delicious, whose flowering period is in phase with Red Delicious, was less attractive to pollinators. Red Delicious also was not very receptive to pollen because no fruit set following hand pollination. McIntosh and Empire were intermediate between these two extremes with adequate fruit and seed set, and a receptive period of two days following flower opening.

There was no significant difference in the number of honeybees on east and west slopes. There were, however, significantly more other Hymenoptera and Diptera on the east slope. This can be explained by the importance of light on the other Hymenoptera and Diptera as seen previously, because the east slope would be illuminated over a longer period towards the end of the day.

For the three main groups of pollinators, there were significantly less insects present during peak blossom and significantly more at the end. This can be related to the greater numbers of insects observed in 1979, when most insect groups peaked at the end of the season as weather conditions became more favorable. In 1978 and 1980, there were more insects during peak blossom, as expected.

Each blossom season was extremely different because of floral differences, bloom development, fluctuating weather conditions. The pollinator population was also very diverse. There were significantly fewer honeybees in 1979. There were significantly more other Hymenoptera and Diptera in 1978 than in 1979 and more in 1979 than in 1980. However, there was no significant difference in fruit set between years. The 1979 blossom season was the longest, with the most adverse weather conditions, and with the greatest insect species diversity. The proportion of native pollinators to total insects was greater. This seemed to compensate for the fewer honeybees and resulted in equal fruit set.

The greater proportion of honeybees in 1980 can explain the increase in the number of seeds between 1979 and 1980 (Bornus et al, 1977; Callan and Lombard, 1978; Sharp, 1970). There was also a greater proportion of other Hymenoptera than Diptera in 1980. A greater number of seeds per apple resulted from a greater number of bees (honeybees and native bees) and thus from more effective pollination.

4. <u>Conclusion:</u>

Although honeybees are by far the most important pollinator for commercial orchards, native insects play an important role, especially during seasons with unfavorable weather conditions, where they compensate for the reduced activity of the honeybees. More care should be taken during the pre and post-blossom periods in the timing of pesticide applications. This thesis revealed the important physical and biotic factors responsible for the fluctuations in the numbers of pollinators. These factors should be considered when planning the pesticide applications for the entire growing season. The natural breeding sites of these native insects should also be protected to ensure an ongoing supply of insects so far considered as rather insignificant in the general ecology and economy of the orchard.

SUMMARY

Experimental work performed in the field and in the laboratory on the pollinating populations in apple orchards showed that:

1- Field observations of insects actually visiting the blossoms are feasible and are much more accurate than suction traps for determining the pollinating population.

2- *Apis mellifera* L. are the most numerically significant pollinators for all years. Their relative importance, however, decreased with unfavourable weather conditions.

3- The Bombinae, thought to be the most important pollinators, are rare when honeybees dominate.

4- A much greater species diversity was recorded during a season with adverse weather conditions.

5- The Diptera, especially the Anthomyiidae, were second in numerical importance following the honeybees during a season of unfavourable weather conditions. They were less important during better seasons.

6- The Hymenoptera other than honeybees are equally important during all years.

7- Insects with greater amounts of pollen on their bodies are better pollinators. Hymenoptera have significantly more pollen on their bodies than the Diptera.

8- Only the Large Andrenidae and the Halictidae had significantly less pollen on the nectar-gatherers than the pollen-gatherers, the nectar-gatherers would thus be less effective pollinators.

9- Among the Hymenoptera, the Andrenidae and the pollen-gathering Large Andrenidae had the greatest amount of fruit pollen on their bodies.

10- Among the Diptera, the Syrphidae had the greatest amount of pollen.

11- The Hymenoptera other than honeybees therefore compensate for the decreased honeybee activity during unfavourable weather, because they are more efficient pollinators than the more abundant Diptera.

12- The Andrenidae and *Apis* are more constant to fruit trees than the other groups.

13- The numbers of active honeybees fluctuate greatly with temperature and humidity. The native bees thought to be more tolerant to adverse conditions have definite threshold temperatures, humidity and light intensities for their activity but, remain constant throughout their ranges once active.

14- The main effects: tree, row, day, and year, were more important in explaining the variations in the numbers of other Hymenoptera and Diptera than the covariates: temperature, humidity, and light.

15- Of the covariates, temperature is the most significant factor for the honeybees followed by humidity. Only light is significant for the other Hymenoptera and, for the Diptera, none of the factors are significant.

16- Golden Delicious had the least amount of insect visitors yet had the greatest fruit set, the greatest amount of seeds per apple and the longest effective pollination period. Therefore, when visited, more compatible pollen would be transfered.

17- There was no significant difference in the number of honeybees on east and west slopes. There were however significantly more other Hymenoptera and Diptera on the east slope; this can be explained by the importance of light on their activity because the east slope would be illuminated over a longer period towards the end of the day.

18- The number of insect visitors increased with an increase in the numbers of blossoms except when weather conditions were unfavourable.

19- There was no significant difference in fruit set between years.

20- During a blossom season with adverse weather conditions, insect species diversity increased. The proportion of native pollinators to total insects was greater and seemed to compensate for the fewer honeybees, thus resulting in equal fruit set.

21- A greater number of seeds per apple during a good season resulted from a greater number of bees (honeybees and native bees), and thus from more effective pollination.

22- Although honeybees are the most important, native insects play a significant role in pollination. Their behaviour and activity should therefore be considered when planning the pesticide schedule for the entire growing season.

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