THE UNIVERSITY OF MANITOBA

Predation by coccinellids of *Acyrthosiphon pisum* (Harris) on fababeans

by

Yueh Nan Chiang

A THESIS
SUBMITTED TO THE FACULTY OF GRADUATE STUDIES
IN PARTIAL FULFILMENT OF THE REQUIREMENTS FOR THE
DEGREE OF MASTER OF SCIENCE

DEPARTMENT OF ENTOMOLOGY

WINNIPEG, MANITOBA

October 1979

PREDATION BY COCCINELLIDS OF ACYRTHOSIPHON PISUM (HARRIS) ON FABABEANS

BY

YUEN NAN CHIANG

A dissertation submitted to the Faculty of Graduate Studies of
the University of Manitoba in partial fulfillment of the requirements
of the degree of

MASTER OF SCIENCE

results of field observations and laboratory predation trials, the conclusion can be made that adult *H. tredecimpunctata* is unlikely to regulate populations of pea aphids.

ACKNOWLEDGEMENTS

I wish to express my sincere appreciation to my supervisor, Dr. N. J. Holliday, Department of Entomology, University of Manitoba, for his guidance, patience and counsel during the course of my studies. I am grateful to Dr. A. G. Robinson, Head, Department of Entomology, University of Manitoba for his invaluable assistance and constructive advice.

I am indebted to Dr. F. M. Arscott, Department of Applied Mathematics, University of Manitoba, for his helpful suggestions and Dr. K. W. Clark, Department of Plant Science, University of Manitoa for criticism on the final draft of this thesis.

I wish to thank Mr. John Serger for his help with laboratory work and Mr. Jamie Richardson for his assistance with the photographs in the thesis, and Mrs. L. J. Hiebert for typing this thesis.

Special thanks to the following people for their assistance and friendship: Ms. Cathy O'Neill, Miss Kathryn McGinnis, Mr. Jack Harlos, Mr. Marius Kung, Mr. Patrick Lim, and Mr. Daniel Goh.

I am also grateful to my parents and the members of my family for their love and encouragement.

TABLE OF CONTENTS

CHAPTER Page

CHAPTER Page

LIST OF TABLES

LIST OF FIGURES

FIGURE Page

CHAPTER I

INTRODUCTION

"The use of insecticides largely destroyed the early attempts at biological control and interest remained low for as long as insecticides appeared quite successful. However, the problems of insecticides soon became apparent and in the last decade there have been tremendous developments in biological control, particularly in combination with other measures to form integrated control. In these developments aphids and mites, which perhaps include the most widespread crop pests, have received special attention and therefore there has been aroused great interest in coccinellids as potential control agents" (Hodek 1973).

There is abundant evidence that coccinellids are often a major cause of mortality of aphids. Despite the very considerable amount of work already done on aphidophagous coccinellids, much still needs to be done before they can be used to best advantage.

Solomon (1949) introduced the concept of "functional response to prey density" to describe the way in which the number of prey killed/individual predator changes, and "numerical response to prey density" to describe changes in the numbers of the predator brought about by changes in prey density. The effectiveness of coccinellids particularly

Hippodamia tredecimpunctata L. as predators of the pea aphid Acyrthosiphon pisum (Harris) on fababeans (Vicia faba L.) will be considered in relation to these responses.

Fababeans are small-seeded relatives of the garden broad bean, and are relatively new as a crop in Manitoba. Four cultivars of fababeans, Ackerperle, Diana, Herz Freya, and Erfordia are grown in Manitoba. Six thousand hectares were grown in the province in 1972, and in 1973. In 1974, the area of fababeans was approximately 1,200 ha (Hanec 1975). The area of fababeans planted in 1978 was 4,500 ha.

In the present study the population density of coccinellids and pea aphids in fababean fields at Glenlea, Manitoba was monitored in 1977 and 1978. This concerned the numerical response to prey density. A study of the influence of temperature and population density of pea aphids on the feeding rate of coccinellids on fababean was conducted in the laboratory. This concerned the functional response to prey density.

From the laboratory study, a response surface of predation can be constructed to predict the feeding rate of coccinellids on pea aphids under different temperature conditions and at different aphid densities. Incorporating the results of the field data and laboratory data, we can see whether coccinellids are likely to be effective in regulating pea aphid numbers on fababeans. This may give some idea of how coccinellids might be used in a biological control system for management of pea aphid populations on fababean.

CHAPTER II

REVIEW OF LITERATURE

Economic Importance and Biology of the Pea Aphid

A. Damage to Crop Plants

The pea aphid is a serious pest of peas, alfalfa, vetch, common clovers, and sweet clover. Pea aphids usually infest the terminal growth of the plant. Both adult and young aphids pierce the plant tissue and suck sap from leaves, stems, and blossoms. Heavily infested plants become stunted and wilted, and as a result the yield and quality of the crop may be greatly reduced (Cartier 1968).

Barlow (1977) fed pea aphids for 11 days on pea plants which were five days old at the beginning of the experiment. Two initial densities of aphids were used: 5 aphids/plant and 50 aphids/plant; the aphid density was allowed to increase unchecked throughout the duration of the experiment. Controls were run with 0 aphids/plant. He found that during the 11 days feeding by aphids decreased plant weight by 4.7 percent at an initial density of 5 aphids/plant and by 63.9 percent with an initial density of 50 aphids/plant.

In 1974, two fields of fababeans were heavily infested by the pea aphid in Manitoba. In the middle of August a field near Homewood had 100 pea aphids/plant;

another field near Darlingford was destroyed by pea aphids, the average number/plant was 2,200 pea aphids (Hanec 1975).

The pea aphid is an important vector of plant diseases. The principal viruses it transmits are alfalfa mosaic (Frosheiser 1969), bean yellow mosaic (Adlerz 1959), pea enation mosaic (Bath and Chapman 1964), pea seed-borne mosaic (Aapola and Mink 1973), pea streak (Hagedorn and Walker 1949) and red clover vein mosaic (Hagedorn and Hanson 1951). Fababeans are susceptible to bean yellow mosaic virus disease which can be transmitted by pea aphids (Evans and Zettler 1970).

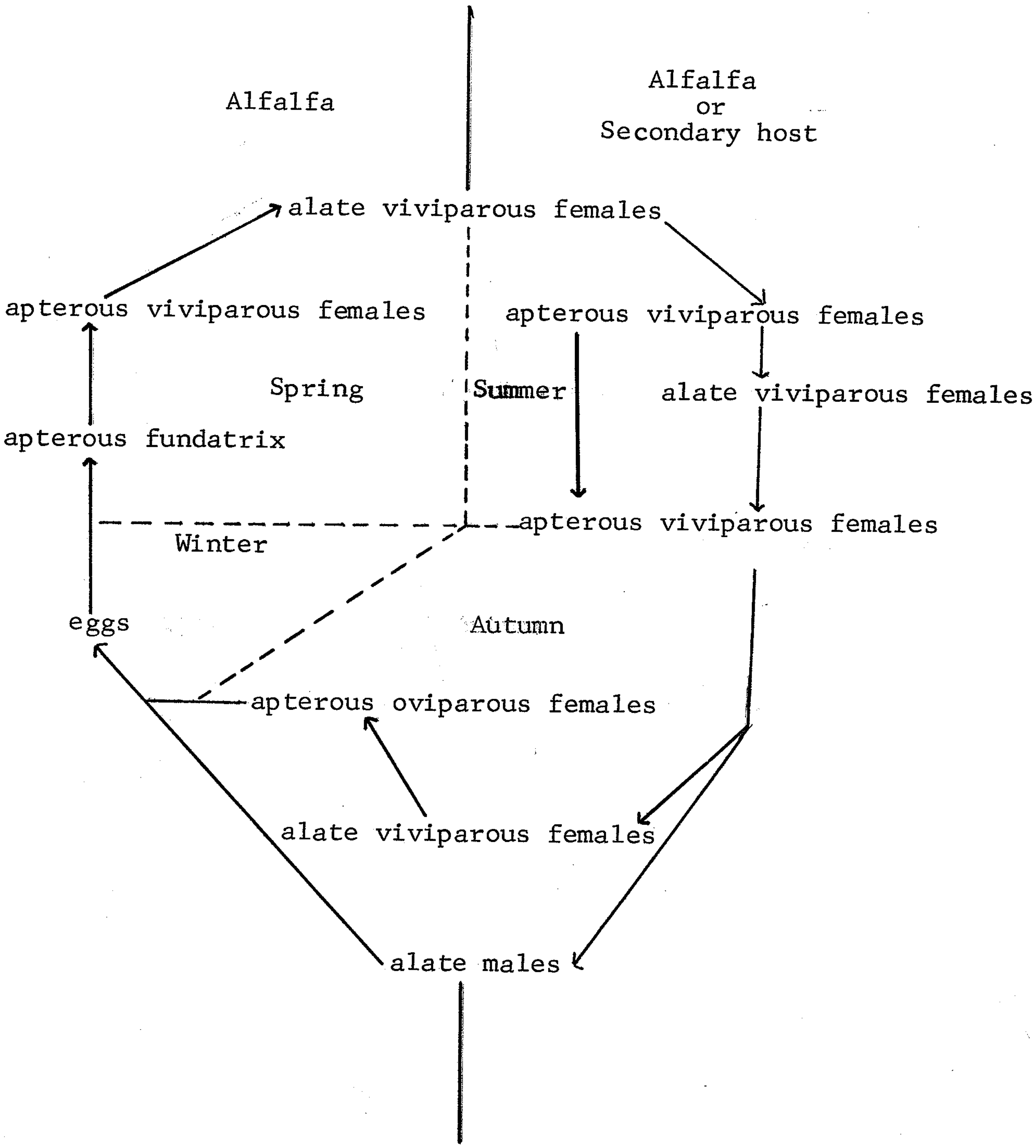
B. Life History

The pea aphid is an old-world species, occurring across the Palearctic and Oriental regions. It has invaded parts of Africa and the Nearctic region. Recently the pea aphid has become a serious pest of alfalfa in Argentina and Peru (Mackauer and Starý 1967).

Cooke (1963) made a detailed investigation of the ecology of the pea aphid in the Blue Mountain area of eastern Washington and Oregon. He found that pea aphids overwintered as fertilized eggs on leaves and stems of alfalfa. In March, apterous females hatch from eggs (Figure 1); these females are the fundatrix and begin oviparous, parthenogenetic reproduction. The resulting offspring are apterous and feed on alfalfa and give birth to other apterous and alate females. In late May, two or

FIGURE 1

Life cycle of the pea aphid


Alfalfa
Alfalfa or Secondary host
alate viviparous females
apterous viviparous females
apterous viviparous females
Spring
Summer
alate viviparous females
apterous fundatrix
apterous viviparous females
Winter
eggs
Autumn
apterous oviparous females
alate viviparous females
alate males

three generations of alate females are produced and migrate to secondary hosts (e.g., pea plants), and give birth to apterous females. Throughout the summer more parthenogenetic generations are produced. Before the secondary hosts stop growing, a few generations of alate females develop and migrate back to alfalfa. The aphids reproduce on these alfalfa plants until October. The last generation is composed of both males and females; they mate and the females lay the overwintering eggs.

In mild climates such as that of California the life history of the pea aphid is simple. Pea aphid continue to produce parthenogenetic aphids all year except in some of the inland or mountain regions where under the influence of cold weather the winter may be passed in the egg stage (Campbell 1926).

There are numerous biotypes or physiological races of pea aphids. Studies have shown that different biotypes reproduce at different rates on different hosts, and vary in their ability to transmit disease. In the field the rate of pea aphid development varies with weather. The average number of generations/year ranges from six to seven in Finland (Markkula 1963) and from 14 to 28 in California (Campbell 1926). The duration of development of pea aphids increased with a decrease in temperature (Kenten 1955; Siddiqui et al. 1973). The duration of apterous nymphal periods (from birth until the last imaginal moult) reported by Kenten (1955) was 4-5 days at 25-26°C, 8-9 days at

19-20°C, 21-24 days at 11-13°C, and 37-42 days at 5-9°C. Other reports on the speed of development of different pea aphid biotypes have been made by Kilian and Nielson (1971), Siddiqui et al. (1973), and Campbell and Mackauer (1975). The upper temperature limit for development of pea aphid was estimated to lie between 25° and 30°C, and the lower temperature limit was estimated to be 3.2°C (Siddiqui et al. 1973).

The fecundity of pea aphids decreased with increased constant temperature (Siddiqui et al. 1973), and differed with different biotypes and rearing conditions (Kilian and Nielson 1971; Frazer 1972). The greatest numbers of young parthenogenetic apterous aphids were produced at a constant temperature of 15°C when 5 pea aphids/plant were reared on *Pisum sativum* (L.) (Siddiqui et al. 1973). Kenten (1955) found that the total number of offspring was greatest at 19-20°C when pea aphids were reared on fababeans, at which temperature from 77 to 86 offspring per parent were produced. He also showed that a temperature of 20°C and photoperiod of L:D16:8 favours the rapid production of apterous virginoparous forms almost exclusively and inhibits the production of sexual forms completely. Kenten (1955) concluded that a long photoperiod and a high temperature favour the production of parthenogenetic forms and a short photoperiod and low temperature (20°C and below) favour the production of sexual forms. The production of alate forms of pea aphid was determined by many factors such as temperature, crowding, photoperiod, etc.

In the laboratory, Lowe (1971) found that concentrations of pea aphids on young fababean leaves formed colonies. Pea aphid colonies were normally compact, with most of the aphids on young leaves at the plant apex often densely crowded together. After birds had fed on uncaged field colonies of pea aphid, the remaining aphids were widely dispersed, so that the compact form of colony was only displayed on protected plants.

Over 70 species of predatory or parasitic arthropods attack the pea aphid in North America. The most important insect groups are Syrphidae (Diptera), Coccinellidae (Coleoptera), Chrysopidae (Neuroptera), and Aphidiidae (Hymenoptera). The parasite, _Aphidius smithi_ Sharma and Subba Rao was introduced from India and Pakistan into North America in 1958 (Sharma and Subba Rao 1958). _A. smithi_ was propagated and widely released in California and has become an important factor in the control of pea aphid in that area (Hagen and Schlinger 1960).

Biology of Coccinellids

A. Morphology

There is a tremendous number of papers discussing morphology of different species of coccinellid adults and larvae. Kovář (1973), Belicek (1976), and Savoĭskaya and Klausnitzer (1973) published general descriptions of the morphology of coccinellid adults and larvae.

Coccinellid eggs are usually oval or spindle-shaped and yellow or orange-yellow in colour. The eggs are laid mostly in clusters with each egg attached to the substrate by its narrow end (Hodek 1973).

Larvae of most coccinellids are elongate, campodeiform, and 2-18 mm in length (Belicek 1976). The head of the larva is frequently square with rounded corners and almost completely sclerotized. The frontal suture is well-developed; it is V-shaped or Y-shaped. The antennae are generally three-segmented, while the mandibles are triangular in shape. The maxillary palpi are three-segmented and the labial palps are one-or two-segmented. The legs are elongate or short with a group of setae and a claw situated at the apex of the tibiotarsus. In most larvae there is a tooth at the base of the claw. The abdomen of the larva is ten-segmented and is covered with setae and sclerotized plates with tubercles. The armature of both thorax and abdomen is rather variable and complex. In most species the pronotum has two or four sclerotized plates. The notum of both the mesothorax and metathorax has two plates. Usually third and fourth instar larvae possess a more well-developed body armature than the earlier instars (Savoĭskaya and Klausnitzer 1973).

The pronotum of H. tredecimpunctata (the most common species on fababeans in Manitoba) larvae has four closely adjacent plates. The larvae are black except for the fourth segment of the abdomen which is pale (Savoĭskaya and Klausnitzer 1973).

Different groups in the family Coccinellidae have different types of pupae, for example, *Chilocorini* and *Noviini* pupae are partially covered by the last larval skin, *Hyperaspini* and *Scymnini* pupae are completely covered by the larval skin; *Coccinellinae* and *Sticholotinae* pupae are not covered by the larval skin. The pupae are attached to the substrate by the caudal end (Hodek 1973).

Adult coccinellids are 0.8-18 mm in length. The body is most often oval, almost three times as long as wide with a convex dorsal surface and a flat ventral surface. The body surface is either bare or covered with short hairs, and is more or less shiny. Sculpturing is in the form of fine or coarse punctures, densely arranged. Four parts of the cranium (epicranium, frons, genae, and clypeus) are fused into the head. The antennae are 8-11 segmented, and are inserted at the inner front margin of the eyes. The labrum is short and transverse, the mandibles are sickle-shaped and acute at the apex, the maxillary palpi are four-segmented, and the labial palpi are three-segmented. The legs are well-developed. The construction of the coxae is regular; the front and larger hind coxae are transversely oval while the middle coxae are round. The femora are elongate and grooved. The tibiae are slender or with a spine-like projection on their outerside. The tarsal formula is 4-4-4 or 3-3-3. The abdomen is ten-segmented. The ventral side has only five or six visible sternites (Kovář 1973).

The head of adult *H. tredecimpunctata* is black. The pronotum is black except for the anterior and lateral margins which are yellowish-white. The elytra are reddish-orange, each with seven black spots. The legs are bicoloured: the tibiae and tarsi are light brownish-yellow, and the femora are black. The total length ranges from 5.2-6.2 mm; the width is from 3.1 to 3.5 mm (Belicek 1976).

B. Life History

In this section, the general features of the life history of coccinellids are discussed first, then the life history of *H. tredecimpunctata* will be described, since this is the most common coccinellid species found in the fababean fields studied.

Coccinellids are holometabolous, and they have the following stages: egg, four larval instars, prepupa, pupa, and adult. The first copulation in coccinellids usually takes place a few days after emergence, and is repeated several times during adult life; one copulation is sufficient for permanent fertility of the females. The male coccinellid uses its legs to hold on to the elytra of the female during mating (Hodek 1973). The females of *H. tredecimpunctata* produce fertile eggs for about three weeks after mating. Females will oviposit without having been fertilized, but the production of eggs is less than a quarter of the usual number. Infertile eggs generally collapse soon after they are deposited (Cutright 1924).

The speed of development of coccinellids is dependent upon food and ambient temperature. The developmental rate of all stages increases with temperature within the favourable range. The second instar is for the most part shorter in duration than the first, and the third is often passed in less time than the second. The fourth instar is the larval stage with the greatest duration (Hodek 1973). The duration in days of the developmental stage of *H. tredecimpunctata* is given in Table 1. Results from Cutright (1924) indicated that the mean duration of the larval stage of *H. tredecimpunctata* was 11 days, and that the mean total developmental time (egg to adult emergence) was 17 days. The duration of the larval stage was quite different when the larva of *H. tredecimpunctata* was fed on different species of aphids (Smith 1965). The mean duration of larval stages was 15.7 ± 1.4 days, 20.3 ± 0.7 days, and 29.6 ± 0.9 days when *H. tredecimpunctata* was fed on *A. pisum*, *Rhopalosiphum maidis* (Fitch), or *Aphis fabae* Scop., respectively.

The longevity of coccinellid adults is quite different for summer season and overwintering adults (Hodek 1973). Cutright (1924) reported that the life span of adult *H. tredecimpunctata* in summer was 30 days when adequate food was supplied. Hibernating adults of *H. tredecimpunctata* must live at least seven months.

TABLE 1

Duration in days of immature stages of *H. tredecimpunctata*[1]

Observer	Location	Temperature	Food species		Egg	Instar I	Instar II	Instar III	Instar IV	Pupa
Cutright (1924)	Ohio	Summer temperature	*Myzus persicae* (Sulzer)	Range	-	2-4	1-3	1-3	3-6	-
				Mean	3	3	1.5	2	4.5	3
Smith (1965)	Ontario	21.9 ± 0.7°C	*Acyrthosiphon pisum* (Harr.)	Mean ± S.E.	-	3.9±0.2	2.9±0.2	3.3±0.3	5.6±0.7	4.7±0.3
			Rhopalosiphum maidis (Fitch)	Mean ± S.E.	-	4.1±0.1	3.9±0.1	5.3±0.2	7.0±0.3	6.2±0.1
			Aphis fabae Scop.	Mean ± S.E.	-	7.1±0.3	6.1±0.2	6.1±0.1	10.3±0.3	5.6±0.1

---

[1] The prepupal period of *H. tredecimpunctata* is included with the fourth instar.

C. Distribution in Habitats

The adults of many coccinellids are not firmly restricted to a single habitat because of their great mobility (Hodek 1973). H. tredecimpunctata can be found in peach orchards, sorghum, cereals (corn, sweet corn, barley, and oats), potatoes (Hodek 1973), alfalfa, and in grassland and parkland (Belicek 1976). Putman (1964) considered that species of the genus Hippodamia are more adapted to low-growing plants which the larvae can easily reascend.

The presence of any species in a given habitat is mainly determined by the occurrence of essential prey and the physical conditions of the environment (Hodek 1973). Ewert and Chiang (1966a) investigated vertical stratification of three coccinellid species in four crops (corn, barley, sorghum, and alfalfa) in Minnesota. Vertical stratification in distribution was significant in corn and barley: H. convergens Guerin-Meneville and H. tredecimpunctata were normally found at higher levels on the plants than was Coleomegilla maculata DeGeer. The differential distribution was shown to be the result of differences in tactic reactions to light, humidity, and gravity, and in food preference. Information on food preference and survival of larvae indicated that Hippodamia species are specialized aphid feeders and C. maculata is a specialized pollen feeder. Examination of the microhabitat of these coccinellids in the field shows that aphids are usually on the upper part of the plant where the light is strong and humidity is low. The locations where plant pollen may be accumulated are lower on the plant, more shaded and humid. Smith (1971) found that C. maculata and H. tredecimpunctata were most abundant in corn plots with 3.2 plants/m^2 whereas Coccinella novemnotata Herbst and C. transversoguttata Faldermann were abundant in corn plots with 1.6 plants/m^2.

Ewert and Chiang (1966b) used two methods to investigate the dispersal of coccinellids in corn fields. Sticky traps were placed at different elevations to catch the beetles in flight, and a sucrose solution was sprayed on the upper or lower portions of plants to concentrate beetles. The sucrose was sprayed onto plants to simulate deposits of aphid honey dew in which sucrose is usually present. Since sucrose is non-volatile, it was considered that sucrose did not have an olfactory effect on flying coccinellids and did not attract beetles from any great distance. However, beetles do eat the sugar and stay near it when they encounter a deposit. Therefore, there would be a concentration of beetles on the sprayed plants. Since there was no attraction from a distance, the number concentrated on sprayed plants would reflect the number of beetles normally landing on those plants in the course of dispersal. The collection of beetles on the sticky traps suggested that H. convergens and H. tredecimpunctata move about more extensively than C. maculata. This conclusion is supported by changes in the populations of beetles in the sucrose spray study. The population of both species of Hippodamia increased throughout the study plot where sucrose solution was present, whereas the population of C. maculatata scarcely changed. They concluded that entomophagous coccinellids are more nomadic than their phytophagous relatives.

D. Dormancy

Coccinellids survive unfavourable environmental conditions mainly in the adult stage (Hagen 1962; Hodek 1973). The adults enter a diapause state of variable physiological arrest depending upon the species. A greatly enlarged fat body has been found in coccinellids before they diapause. The metabolic rate is reduced in diapausing coccinellids and the ovaries of diapausing females stop developing. These adaptations increase resistance to unfavourable physical conditions and enable coccinellids to survive over a long period without feeding (Hodek 1973).

Before diapause coccinellids may change their behaviour to a greater or lesser extent. Some species make lengthy migratory flights, some form large aggregations before entering a long period of dormancy, other species do both (Hagen 1962; Hodek 1973). Thomas (1932) described a hibernation site of H. tredecimpunctata in the trunk of a cedar tree near the laboratory at Chadbourn, North Carolina. H. tredecimpunctata aggregated on the southeastern side of the tree; cold winter winds in this area were from the northwest. Cutright (1924) found the overwintering adults of H. tredecimpunctata in grass dumps and under refuse near plants which had been aphid-infested. Storch and Vaundell (1972) found that diapause in _H. tredecimpunctata_ can be inhibited by exposing adult females to photoperiod regimes of L:D 16:8 or 14:10 hours at a constant temperature of 21 ± 2°C. Exposing adult females to a photoperiod of L:D 12:12 hours initiated diapause.

Definition of Density-Dependence

In natural insect populations extreme densities rarely occur in more than two or three successive generations. At high density the mortality and immigration rates ultimately exceed the reproductive and immigration rates. At low density it is just the reverse. Due to this effect populations in general show very restricted fluctuations, when compared with the theoretical possibilities of geometric increase. These fluctuations occur around a constant mean density level if the environment does not change. This phenomenon is referred to as regulation of population density (Klomp 1962).

The term density dependent first suggested by Smith (1935) is equivalent to Howard and Fiske's (1911) first category of mortality factor, i.e., "A natural balance can only be maintained through the operation of facultative agencies which effect the destruction of a greater proportionate number of individuals as the insect in question increases in abundance."

The importance of "density-dependent factors" is made clear in the following quotation from Elton (1949): "It is becoming increasingly understood by population ecologists that the control of populations, i.e., the ultimate upper and lower limits set to increase, is brought about by density-dependent factors, either within the species or between species. The chief density-dependent factors are intra-specific competition for resources, space or prestige, and inter-specific competition, predators or parasites."

The Principles of Predation

The behaviour of searching predators in relation to populations of their prey is very complex. Holling (1959, 1961) proposed that five main factors can affect predator-prey situations. These are: a) prey density, b) predator density, c) characteristics of the environment, d) characteristics of the prey, and e) characteristics of the predator. Solomon (1949) first introduced terms to describe the two fold nature of predation: the functional response, concerning the prey consumption by an individual predator, and the numerical response, concerning the density of predators. He stated that "...to be density dependent, the enemy must respond to changes in the numbers of the hosts (cf. Nicholson 1933; Varley 1947). The nature of this response is commonly twofold. First, there must be a functional response to (say) an increase in the host density, because of the increased availability of victims: as host density rises, each enemy will attack more host individuals, or it will attack a fixed number more rapidly. A frequent, but not invariable, result of this is an increase in the numbers of the enemy (a numerical response) due to an increased rate of survival or reproduction, or both; this may or may not be sufficient to produce an increase in proportion of enemies to the increasing hosts."

There are three possible components of the numerical response to prey density: 1) a relatively rapid response by concentration of the predator in areas of high prey density; 2) a reproductive response through the laying of more eggs by each female; 3) a relatively rapid numerical response through improved survival of immature predators (Huffaker *et al.* 1968). Since the numerical response is largely the outcome of the effects of food availability on reproduction, migration, and mortality; it often follows the trend of the functional responses, which are measured in terms of food consumption. Because of this, many authors have worked on analyzing the functional responses to prey and predator density to elucidate the predation process.

The first six components of the functional response that were identified by Holling (1961) are involved in prey density effects: 1) the time predator and prey are exposed (including the time spent in activities related or not related to feeding); 2) the discovery rate of the predator (including the speed of movement of the predator and prey, reactive distance of the predator for prey and capture efficiency); 3) the time spent chasing, killing and consuming prey; 4) hunger of the predator; 5) learning by the predator; and 6) inhibition by the prey. The first three are universally present (Holling 1961, 1965, 1966), since every predator has to have a particular rate of search which may not be constant, has to be exposed to prey, and has to spend time handling prey. Effects of the fourth component, hunger, were thought to be absent in some situations since some predators [e.g., belostomatid Lethocerus sp. (Hemiptera)] continue to attack and kill prey even though satiated (Holling 1961). The learning component has been variously labelled as "development of a specific searching image" (Tinbergen 1960) and as "stimulation of specific searching by prey discovery" (Holling 1961) since some predators, particularly vertebrates, learn to search specifically for those prey whose stimuli have become associated, through experience, with a palatable reward. The sixth component involved is the prey's unpalatability (Holling 1965), energetic defense (Morris 1963), or camouflage (de Ruiter 1952); these can inhibit attacks by the predator for a time after a contact.

The effects of predator density are involved in another four components: 7) exploitation, 8) interference between predators, 9) social facilitation, and 10) avoidance learning by prey. The exploitation component arises because predators compete for the same resource. Thus, as the density of predators increases, the chance that any predator will discover an unattacked prey decreases (Holling 1966). The interference component also becomes progressively more important as predator density rises and contacts become more frequent. Both these components of the functional response to predator density are probably universal, or basic; as a result they cause a regular decline in rate of attack as predator density increases. In some cases, contact with other animals of the same species can stimulate a predator to eat more, to search more rapidly (Holling 1961): this is the ninth component--social facilitation. The final component becomes important for those prey that can learn to avoid a specific predator they have encountered before. The greater the density of predators, the greater will be the chance for each prey to acquire an effective way to avoid attack.

The predation models developed by different authors all consider the first two components, i.e., 1) the time predator and prey are exposed, and 2) the discovery rate of the predator. The basically similar functional response models of Lotka (1923) and Volterra (1931) only discussed these two points so that the number of prey attacked per predator is simply a linear function of prey and predator density. Thompson (1924) and Nicholson and Bailey (1935) made a significant advance by including an exploitation component based on the assumption that predators search randomly. The Hassell and Varley (1969) model also includes an interference component in addition to those three components. Holling's (1959) disc equation includes the first three components, i.e., 1) the time predator and prey are exposed, 2) the discovery rate of the predator, and 3) the time spent chasing, killing and consuming prey.

Feeding Behaviour of Coccinellids

Coccinellids are predatory as larvae and adults, and the number of eggs laid is usually independent of prey density if sufficient food has been obtained for completed egg maturation. The searching efficiency of coccinellids depends not only on predator density, but also on the particular stage of development of the predator (Varley *et al*. 1973).

Thompson (1951) stated that coccidophagous Coccinellidae "have a full complement of sense organs and there is no doubt about that they can perceive their hosts at a distance." After Thompson wrote these words, a lot of papers on coccinellid searching behaviour were published. Detailed experiments with many species of both acarophagous and aphidophagous coccinellids have shown that neither optic nor olfactory orientation operates in prey searching behaviour (e.g., Fleschner 1950; Banks 1954, 1957; Kaddou 1960). Coccinellids respond to potential prey individuals only after touching them; this behaviour was first found by Fleschner (1950) when he investigated the searching capacity of three predators of the Citrus Red mite, *Panonychus* *citri* (McGregor), one of the predators being the coccinellid beetle *Stethorus picipes* Casey. He concluded from his laboratory studies that the photopositive and geonegative responses of this coccinellid larva corresponded very closely to those of the prey, that none of the species of predator was able to perceive the prey until actual physical contact had been made, and that the searching of larvae was random. Kenten (1969) found out that maxillary palps are important sensory organs by which both adults and larvae of *Anatis ocellata* (L.) recognize the prey. Storch (1976) considered that the prolegs and possibly the head and mouthparts are more important than the stemmata of the fourth instar larvae of *C. transversoguttata* in the detection of prey.

One of the qualities that determine the efficacy of a predator or a parasite as a natural enemy is its searching capacity. At high host density both a poor searcher and a more efficient one destroy hosts at their maximum potential, but searching capacity becomes of prime importance when host density is low. An efficiently-searching entomophagous insect can find and utilize its host at a low density level (Kaddou 1960). Other attributes which influence searching capacity are the mobility of the predator, its sensory powers, its power of survival, its aggressiveness and persistence, and its ability to coincide with the host geographically, phenologically, and ecologically. Environmental conditions such as light, temperature, and humidity also affect searching capacity (Balduf 1935; Smith 1939; Kaddou 1960).

A. The Searching Behaviour of Coccinellids

Some coccinellids lay their eggs singly near their prey and the larvae disperse from the oviposition site shortly after hatching. Other species, notably those that hatch from eggs laid in batches, postpone departure from the oviposition site and remain clustered together for a time on the empty egg batch before dispersing (Hagen 1962). This later type of behaviour favours sibling cannibalism while the larvae are clustered together on the egg batch. Sibling cannibalism is of wide occurrence in the predacious Coccinellidae but has also been recorded for some phytophagous forms (Balduf 1935). It is generally believed that cannibalism benefits survival of the remaining individuals enabling them to make a more prolonged search for aphid food (Kaddou 1960; Banks 1954; 1956; Dixon 1959; Brown 1972a). Cutright (1924) found that the eggs of *H. tredecimpunctata* are laid on the underside of leaves, usually in groups of ten to forty. Hence, cannibalism may play a very important role in the survival of the first instar larvae of *H. tredecimpunctata*.

Random searching behaviour evidently markedly increases the mortality of newly hatched first instar larvae when prey density is low. According to Banks (1957) the first instar larvae of *Propylaea quatuordecimpunctata* (L.)

The edges and prominent veins of leaves often determine the direction in which the insects move. When the larva is crawling on an isolated plant, the habit of crawling along the edges of leaves is of little consequence, for the larva eventually visits most parts of the plant. Although it may waste time and energy in moving over parts already visited, the larva will probably find any aphids present on an isolated plant. When the leaves of the plant touch adjacent plants, the larva may be led from the leaf of one plant to that of another, and it does not visit all the parts of one plant before going to the next plant. Its movements are unsystematic because they are determined by the chance arrangement of leaves; the larvae may be led back repeatedly to leaves it has already visited, thus wasting much time and energy.

Bänsch (1966) used a model tree to study the movements of A. bipunctata adults and larvae. The tree was 50 cm high and had four moveable branches with two twigs each. He observed that, when moving upward on the stem the coccinellid larvae stop moving at bifurcations but soon continue to follow the main axis. After an unsuccessful search at the top the larvae return down the stem, but their behaviour changes and they now follow each bifurcation. If also unsuccessful on a twig, the larvae change to positive geotaxis. But when reaching the stem this behaviour changes to negatively geotaxis and the larvae move to the top again. So the larvae are more or less confined between the apex and the tips of branches. When searching on the ground the larvae do not move to the top again until they have covered a certain distance. On the ground the larvae are positively phototactic until they meet another vertical surface. Coccinellid adults move quickly from the bottom of the model tree to the top and show the same search pattern as their larvae. However, after several changes from negative to positive geotaxis, the adults fly away. After they have encountered a prey, Bänsch found that beetles search intensively by making frequent turns. If this intensive search is unsuccessful, the movements soon change back to random ones.

B. Aphid Escape Reactions

Dixon (1958) has studied the escape responses of the nettle aphid, *Microlophium evansi* (Theobald) to the larvae and adults of *A. decempunctata* (L.). *M. evansi* avoids capture by *A. decempunctata* by kicking, by walking away, by daubing with siphunculi secretion, or by dropping off the plant. Each method of escape is most effective in different circumstances. While it is advantageous to an aphid to be able to repel a coccinellid and continue feeding, if it is unable to deter a young coccinellid by kicking and the latter continues to approach, the most effective means of escape is by withdrawing the stylets and walking away. As older and larger coccinellid larvae are capable of walking faster than even adult aphids, it is then most expedient to drop off the plant. If the coccinellid seizes an appendage of the aphid, the latter will attempt to kick the coccinellid away, or pull the appendage free. If pulling fails, the secretion from the siphunculi may be daubed on the predator's head, after which pulling is frequently effective, and the predator is temporarily paralysed. Wratten (1976) found that all instars of the lime aphid, _Eucallipterus tiliae_ L., can respond to the presence of a searching larva of _A. bipunctata_ by jumping, running or kicking. Nault _et al._ (1973) found that the aphids _Aphis coreopsidis_ (Thomas), _Acyrthosiphon pisum_, _Acyrthosiphon solani_ (Kaltenbach), and _Myzus persicae_ (Sulzer) can release alarm pheromones from their cornicles when attacked by coccinellids. When other nearby aphids perceive alarm pheromone, they escape from their feeding sites. Roitberg _et al_. (1978) made a further investigation on the adaptation of alarm pheromone responses of the pea aphid. Adult and fourth-instar pea aphids responded to alarm pheromone either by dropping, running, or backing up. Younger instars showed almost no response to pheromone but all instars responded to a pheromone-vibratory stimulus, usually by dropping. It was suggested that younger instars respond conservatively to alarm pheromone because they are less agile on the ground and are more likely to die there before finding a suitable food plant.

C. Efficiency of Capture

Dixon (1959) originally defined efficiency of capture as the proportion of prey captured in a series of encounters between predator and prey. An encounter was said to have occurred if the coccinellid touched the aphid or if the aphid moved out of the path of the searching coccinellid even though the prey might not have been touched.

The efficiency of a particular coccinellid species has been shown to vary with its stage of development as well as with that of its prey (Dixon 1958, 1959; Kaddou 1960; Brown 1972b; Wratten 1976). The first instar coccinellid was the least efficient at capturing prey. However, with each succeeding instar, efficiency improved until it attained its maximum in either the third or, more usually, the fourth instar. Adults of all coccinellid species were less efficient than their older larval instars.

The efficiency of a predator also depends upon the species of aphid attacked. According to Dixon (1958), the aphid M. evansi is a very difficult species to capture. Adults of the sycamore aphid, Drepanosiphum platanoides (Schrk.), were rarely captured by coccinellids (Dixon 1963); A. pisum and Megoura viciae Buckton also proved to be difficult prey species to capture (Blackman 1967). Capitophorus elaeagni (del Guercio) proved more difficult to capture than Schizaphis graminum (Rondani) Brown 1972b). Kaddou (1960) found that aphids with long appendages were more difficult for H. quinquesignata Kirby larvae to capture than the more compact and tenacious aphids with short appendages. Efficiency varies not only with the species of aphid but also with its stage of development, older aphids being more difficult to capture than the early instars. Apterous aphids are more difficult to capture because they are capable of putting up a violent struggle after capture (Dixon 1958; Brown 1972b).

Much of the variability in efficiency of capture can be ascribed to the different methods of attack employed by each coccinellid species and to the way their prey is overpowered. The predator may capture its prey by grasping part of the body (head, thorax or abdomen) or an appendage such as an antenna, leg or siphunculus. The method employed varies with the species of predator and was also influenced by its stage of development (Dixon 1958; Brown 1972b). Adults of Lioadalia flavomaculata (DeGeer), Cheilomenes lunata (F.) Scymnus morelleti Mulsant, and Exochomus concavus Fürsch, and larvae of L. flavomaculata and C. lunata used their prothoracic legs to seize and overpower their prey, the wheat aphid S. graminum. All four larval instars of S. morelleti and the first two instars of E. concavus rapidly immobilized S. graminum by injecting a toxic secretion. This secretion proved fatal to all instars of S. graminum and to several other aphid species (Brown 1972b).

Food Consumption by Coccinellids

A great deal of research has been done on the amount of food consumed by larvae and adults of individual coccinellid species. It is very difficult to compare all these data because of different species and developmental stages of prey and predators, and the data were obtained under a variety of physical conditions. Thus, for any one coccinellid species, figures quoted for the amount of food vary enormously. The smaller coccinellids take less food than larger ones, and the ovipositing females eat more than males (Hodek 1973). The feeding capacity increases progressively with the age of the larvae. Later instars are voracious, kill large number of aphids, and consume most of them, whereas younger larvae kill fewer aphids and consume them only partly (Kaddou 1960).

There are several different ways of measuring food consumption in predation trials. One method has been quite often used and will be described here. The base-line mortality of prey may be checked in cages identical to experimental ones, with the same amount of prey but without predators. The base-line value thus obtained is subtracted from the number of dead aphids in the experimental cages, using the formula (Hodek 1956)

$$f = n - (S_{24} + M_{24})$$

where: f is the daily feeding rate; n is the daily supply of prey, S_{24} is the number of prey surviving after 24 h, M_{24} is mortality of aphids within 24 h in the check cages (base-line mortality).

Hodek's equation cannot fully correct the results of the predation experiment, because it does not take into account that predators may eat prey which would have died as a result of base-line mortality.

Kaddou (1960) felt it possible to identify the aphids which have died from natural causes and eliminate them from calculations. Each prey killed is classified by the proportion of it which has been consumed, and these fractions are summed. Blackman (1967) expressed the quantity of prey consumed in terms of biomass. However, this approach requires the precaution that changes in dry weight by evaporation must be taken into account.

A. Feeding Behaviour

The type of feeding evidently depends on the comparative size of prey and predator. First and second instar larvae of coccinellids feed only on the body fluids of the aphid and discard the shrivelled skeleton. Later, instar larvae and adults may consume almost the entire aphid, leaving only parts of the appendages (Hagen 1962; Kaddou 1960).

Most coccinellids, particularly as larvae, show external digestion. During the course of feeding, the larva occasionally pumps some of the fluid from its own alimentary canal into the body of the host insect, then ingests it. It repeats this regurgitating and ingestion many times until all the body fluids of the aphid are imbibed by the larvae. This type of pre-digestion has been observed in larvae of many species of coccinellids *A. bipunctata*, *C. septempunctata* L., and *P. quatuordecimpunctata* (Banks 1957), *H. quinquesignata* (Kaddou 1960), *Stethorus* spp. (Fleschner 1950; Putman 1955; Hagen 1962), *Pullus impexus* (Mulsant) (Delucchi 1954), and *Scymnus* spp. (Davidson 1923; Smit 1917).

B. Effect of Physical Factors on Feeding Rate

The daily feeding rate of both larval and adult coccinellids increases with temperature through much of the favourable range (Hodek 1973). The range of this favourable temperature differed with each author's data. Under constant temperatures, the lowest feeding rate of the larvae of *H. quinquesignata* is at 15.6°C, and the rate increases up to 30.0°C, then drops at 32.2°C. Hodek (1957), Kaddou (1960) and Sundby (1966) found a slight increase of the total larval food consumption with increased temperature. Whereas Ellingsen (1969a), Gurney and Hussey (1970) reported the reverse. Kehat (1968) reported that the total feeding capacity of larvae of *Pharoscymnus numidicus* Pic was not affected by temperature.

Fluctuating temperatures have a stimulating effect on feeding rate (Hodek 1957; Kaddou 1960; Ellingsen 1969b). Frazer and Gilbert (1976) considered that coccinellids are much more effective predators at high temperatures than at low, and that predation and population studies must include temperature as an essential component. They found that most coccinellids are inactive in the field at low temperature. They did not investigate the relationship of temperature and feeding rate.

There are some indications (Hodek *et al*. 1965) which suggest that at lower relative humidities food intake may be increased. It seems quite possible that at lower humidities the coccinellids may consume more of a prey with a higher water content to make up for the decrease in water content they suffer from increased transpiration.

C. Response to Prey Density

Research demonstrating functional responses of various insect predators to prey density exists (DeBach and Smith 1941; Burnett 1951, 1954; Miller 1959, 1960; Watt 1959; Holling 1966; Messenger 1968; and Hull *et al*. 1977) but most of the published research on coccinellids deals primarily with the prey consumption capacity when a surplus of prey is present.

Coccinellids can act as a density-dependent mortality factor for aphids (Hodek 1973), although the application of the laboratory results to the field may not be fully justified. The proportion of *D. platanoides* killed by *A. bipunctata* on sycamore trees did not increase as the prey population density rose. Thus *A. bipunctata* does not regulate populations of *D. platanoides* (Dixon 1970). Frazer and Gilbert (1976) found that a study on predator-prey relationships revealed several sharp, qualitative, differences between the laboratory and field data. They believed that all laboratory studies must be suspect, until verified in the field.

Hodek (1973) considered that the increase in the number of aphids killed at high aphid density may be due to two different phenomena operating simultaneously. Firstly, the hungry coccinellids completely devour the first few prey they tackle but exploit subsequent prey with a gradually decreasing efficiency. Thus, with an increase in prey population density, an increasing proportion of partially consumed prey may be left. Secondly, when prey is abundant, the coccinellid larvae may consume considerably more than the minimum required for their development.

CHAPTER III

MATERIAL AND METHODS

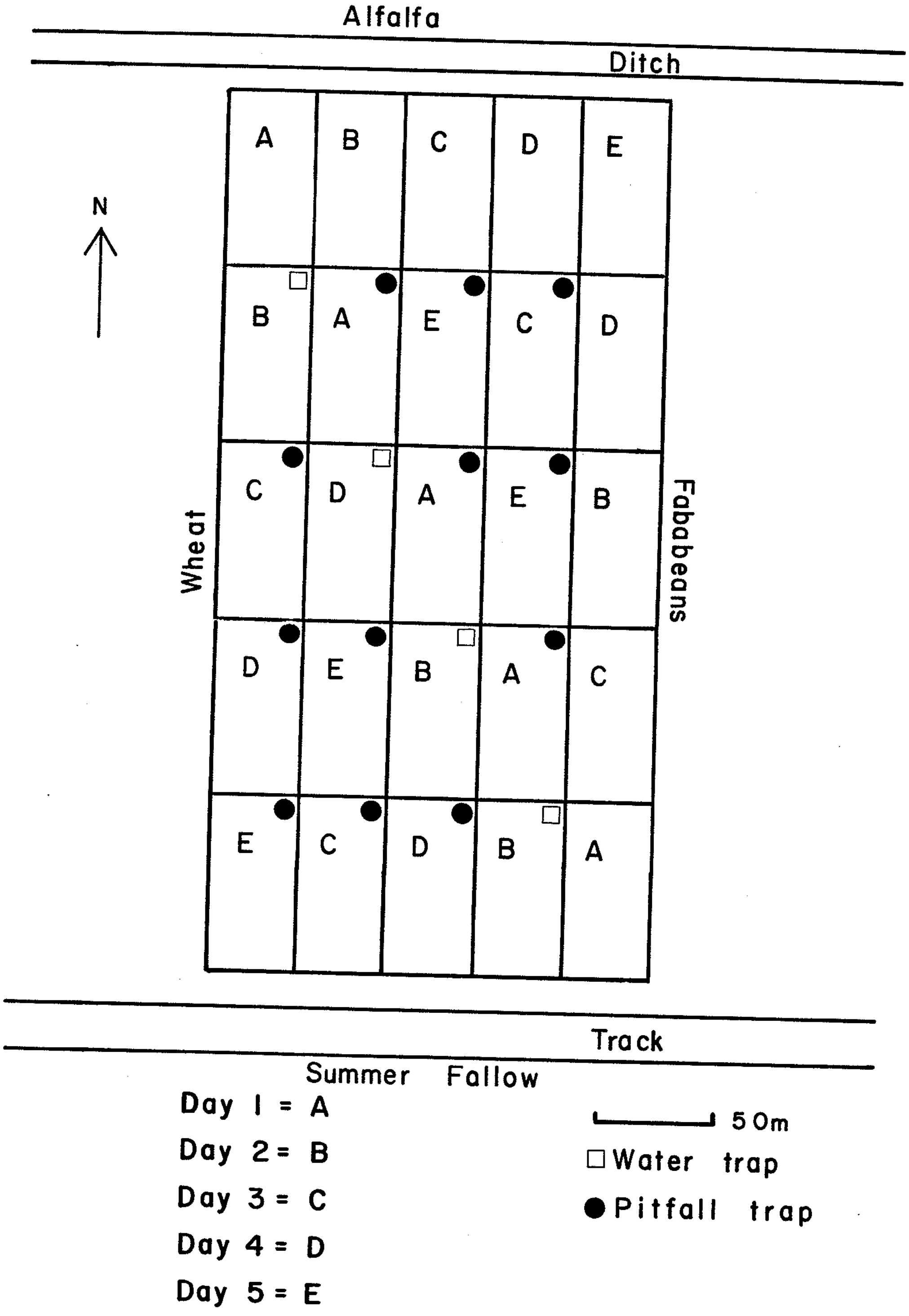
Field Observations

Field studies were carried out on fababean (cv. Ackerperle) crops at University of Manitoba Glenlea Research Station, south of Winnipeg, Manitoba. In 1977, a field of fababeans (approximately 7.1 ha) was partitioned into 25 plots (Figure 2). Five plots were selected on each sampling occasion by using a Latin square method (a standard 5 x 5 Latin square table). Figure 2 shows one example of the Latin square rotation for a sequence of 5 sampling dates. Different Latin squares would be used for each sequence of 5 sampling dates. Sampling was conducted twice each week throughout the growing season (May 26 - August 11). The use of the Latin square method avoids errors caused by gradients through the field.

Fifty plants from each plot (five rows of ten plants) were selected and searched. Each row of ten consecutive plants in a north-south row was selected for searching by the following method: the searcher stands at the south-west corner of the sampling plot (Figure 2) and walks from west to east for a certain number of paces, then

FIGURE 2

Map of the fababean field sampled in 1977 showing
Latin square arrangement for selecting
sample plots


Alfalfa
Ditch
N
A B C D E
B A E C D
C D A E B
D E B A C
E C D B A
Wheat
Fababeans
Track
Summer Fallow
Day 1 = A
Day 2 = B
Day 3 = C
Day 4 = D
Day 5 = E
50m
□ Water trap
● Pitfall trap

walks from south to north for a certain number of paces. The ten plants immediately north of the location reached by this method (i.e., ten consecutive plants in the north-south row) were searched. The number of paces walked in each direction was determined from random number tables. In this way fifty plants (five rows of ten plants) were selected from each plot and searched. The number of coccinellids, pea aphids and other insects on each searched plant was recorded. Pitfall traps (32 oz Mason jars) were used to monitor the epigeic fauna of the field. Yellow water-filled pails (water traps) were used to attract and capture flying insects. The number and the location of water traps and pitfall traps in the field are shown in Figure 2.

In 1978, the same sampling methods were used throughout the sampling periods (June 23 - September 1) except that the sample size of plants searched was reduced to thirty (three rows of ten plants) plants on each plot. The fababean field (approximately 2.3 ha) was almost 1 km south-east of the field sampled in 1977. In 1978 the nearest alfalfa field was 0.6 km west of the fababean field.

Laboratory Studies

Pea aphids and forty adult *H. tredecimpunctata* were collected from the fababean field in 1977. Adult pea aphids were reared on fababeans (cv. Ackerperle) in a growth chamber at 18-20°C, 18L:6D. Adult *H. tredecimpunctata* were confined in fours in petri dishes. The bottom of each petri dish was covered with moist filter paper; the dishes were maintained at room temperature (21°C) and a photoperiod of 18L:6D. The culture of *H. tredecimpunctata* was maintained from July 1977 to August 1978 and was fed on pea aphids.

A. The Hatching Rate of *H. tredecimpunctata* Eggs

Sixty batches of *H. tredecimpunctata* eggs were collected from the laboratory culture. Each batch of eggs was a product of a single female, and was placed in a petri dish having the bottom covered with moist filter paper. Then, twenty petri dishes were maintained at each of three constant temperatures 13, 18, and 23°C and photoperiod 18L:6D. The number of larvae hatching from eggs was recorded daily, and the newly hatched larvae were removed from the egg batch.

B. The duration of development of *H. tredecimpunctata*

Ten coccinellid eggs which were collected from one female were incubated in a petri dish having the bottom covered with moist filter paper. After the first instar larvae hatched from eggs, they were fed an excess of pea aphids each day. The pea aphids had been placed in the freezer for 5-10 minutes enabling the coccinellid larvae to catch their prey easily. When the coccinellid larvae reached third instar, they were reared individually in petri dishes to avoid cannibalism. The duration of development of *H. tredecimpunctata* in days was recorded for each of 20 successful replicates (where adults emerged) for three constant temperatures 13°, 18°, and 23°C. The light regime in all case was 18L:6D.

C. Predation Trials

One fababean plant aged 14 days (4-6 leaves, 12-17 cm height) (Figure 3) which had been planted in a clay pot (13 cm diameter, 13 cm height) was used in each predation trial. A known number of apterous adult aphids were randomly placed on the leaves of the fababean using a camel-hair brush. The fababean plant was covered with a plexiglass cage (Figure 4) 30.5 cm in height and 8 x 7.5 cm in horizontal cross section. The top of the cage was made of fine cloth (32 mesh/cm). Two holes (2.5 cm diameter) in the sides provided additional ventilation: each was covered with similar cloth to that of the top. The lower edge of the cage was pressed into the soil of the pot to prevent the aphids from escaping. One adult male *H. tredecimpunctata* or one adult female *H. tredecimpunctata* or no coccinellid was placed in each cage and the test was started. Predation trials were conducted at four aphid densities (5, 10, 15, and 20/cage), at three temperatures (13°, 18°, and 23°C) for each aphid density. Twenty replicates were carried out at each combination of aphid density, temperature and treatment type. The cages were examined every

FIGURE 3

Fababean plant, aged 14 days, as used in predation trials

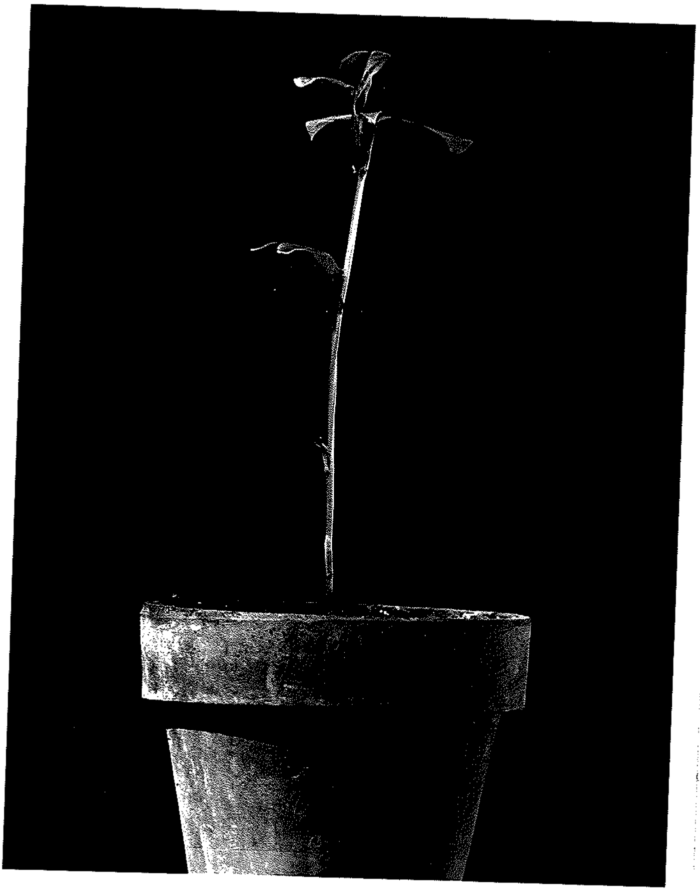
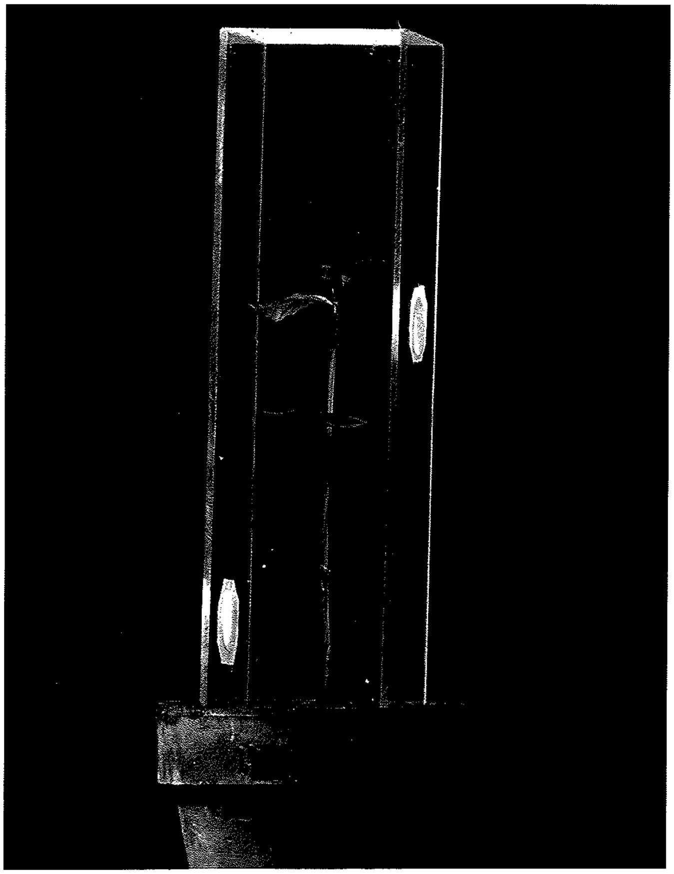


FIGURE 4

Fababean plant covered with a plexiglass cage
for predation trial



24 hours to record the number of adult aphids disappearing, remove any first instar aphids, and replenish the adult aphids to the original density. Each predation trial was run continuously for five days.

CHAPTER IV

RESULTS AND DISCUSSION

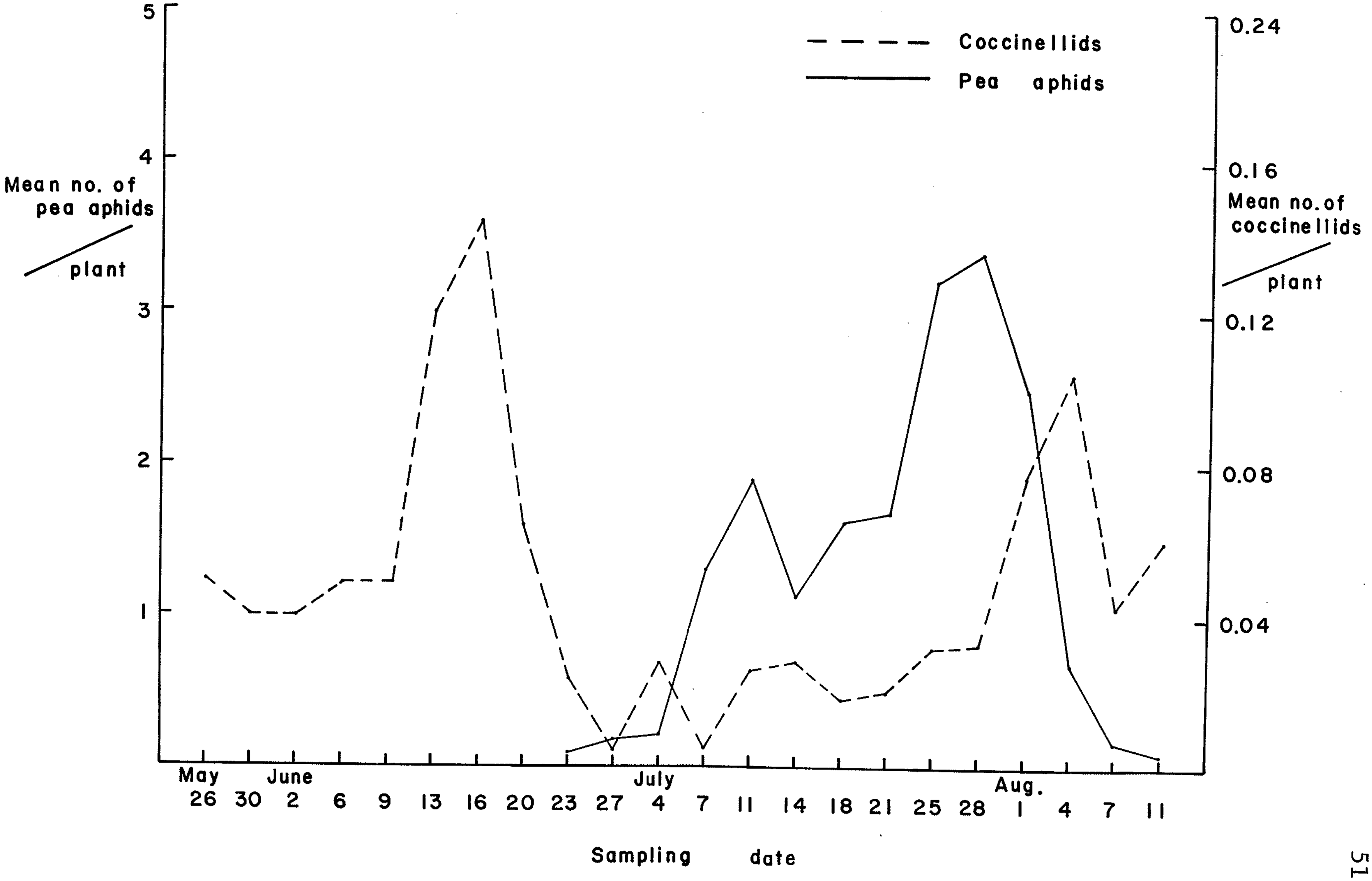
Field Observations

A. Results

The population trends of coccinellids and pea aphids in 1977 and 1978 are shown in Figures 5 and 6. Tables 2 and 6 show the mean number of pea aphids/fababean plant in 1977 and 1978. Tables 3 and 7 show the mean number of adult coccinellids/fababean plant in 1977 and 1978. The total number of coccinellid larvae observed in the fababean field during growing seasons of both 1977 and 1978 was less than 20. Figures 5 and 6 show that there was no obvious correlation between the phenology of population trends of coccinellids and pea aphids. Calculation of the correlation coefficient between the number of pea aphids and coccinellids on each date throughout the sampling period confirmed that the populations were not significantly synchronized ($p > 0.05$). Furthermore, when, for each date, density of aphids in a plot was compared with the density of coccinellids in the same plot, no significant correlation was found. Hence, coccinellid population density was not higher in areas of the field where there were high populations of aphids. Two x two contingency tables were used to determine whether coccinellids were

FIGURE 5

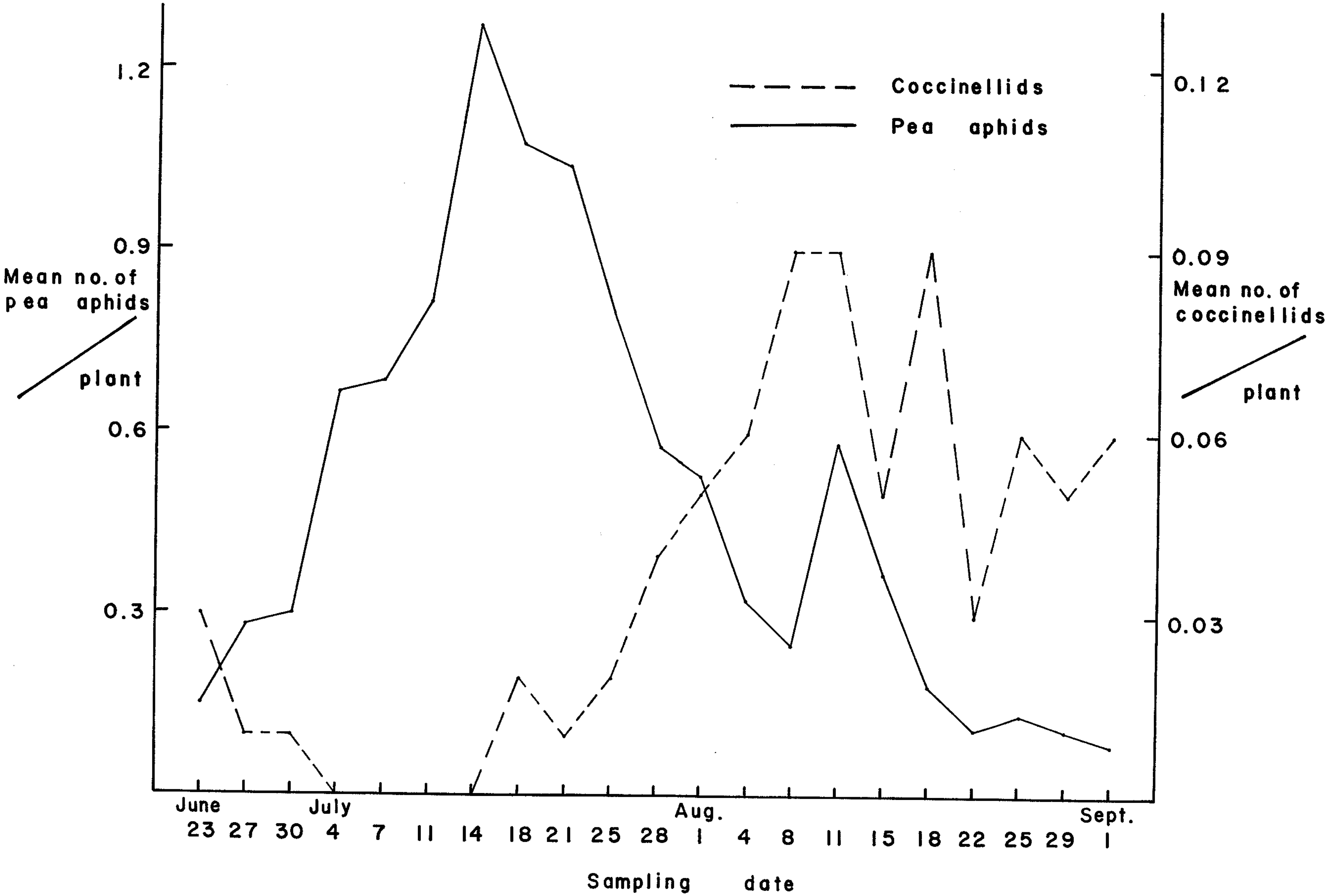
Mean number of coccinellids and pea aphids
in the sampling periods of 1977



Coccinellids
Pea aphids
Mean no. of pea aphids / plant
Mean no. of coccinellids / plant
5
4
3
2
1
0.24
0.16
0.12
0.08
0.04
May
26
30
June
2
6
9
13
16
20
23
27
July
4
7
11
14
18
21
25
28
Aug.
1
4
7
11
Sampling date

FIGURE 6

Mean number of coccinellids and pea aphids in the sampling periods of 1978


Coccinellids
Pea aphids
Mean no. of pea aphids / plant
1.2
0.9
0.6
0.3
Mean no. of coccinellids / plant
0.12
0.09
0.06
0.03
June 23
27
30
July 4
7
11
14
18
21
25
28
Aug. 1
4
8
11
15
18
22
25
29
Sept. 1
Sampling date

more frequently found on plants with aphids: on all dates of both years coccinellids were distributed independent of the presence or absence of aphids on individual plants.

The common species of coccinellids found in the fababean field in 1977 were *H. tredecimpunctata* (60.5 percent), *H. convergens* (22.2 percent), *H. parenthesis* (8.7 percent) and *C. transversoguttata* (8.7 percent). In 1978 only three coccinellid species were found in the fababean field: *H. tredecimpunctata* (52.1 percent), *H. convergens* (37.6 percent) and *C. transversoguttata* (10.3 percent).

The numbers of insects captured in the field are shown in Tables 4, 5, 8 and 9. The black blister beetle, *Epicauta pennsylvanica* (De Geer) was found on plants and in water traps. This beetle was present mainly around the periphery of the field, and the population densities were very low. Slight damage from blister beetles to the leaves of fababean plants near the field margins was noted. Grasshoppers caused severe damage to an area of about 2 ha of fababeans in the centre of the field in 1977. No severe damage was observed in 1978. Although cutworms occasionally damage fababeans, no damage was observed in 1977 and 1978 studies, and only one cutworm was collected in plant searches. Leafhoppers and thrips were very common on fababean plants and could cause some damage to flowers and leaves. However, no damage attributable to these insects was observed in 1977 and 1978 studies.

TABLE 2

Mean number of pea aphids/fababean plant in 1977

(Sample size: 250 plants for each sampling date)

Sampling date	Mean no. of aphids/plant	S.E.	Range
May 26	0.00	0.00	0
30	0.00	0.00	0
June 2	0.00	0.00	0
6	0.00	0.00	0
9	0.00	0.00	0
13	0.00	0.00	0
16	0.00	0.00	0
20	0.00	0.00	0
23	0.05	0.01	0 - 1
27	0.12	0.04	0 - 10
July 4	0.20	0.06	0 - 8
7	1.28	0.15	0 - 13
11	1.90	0.20	0 - 17
14	1.18	0.15	0 - 18
18	1.62	0.20	0 - 18
21	1.76	0.21	0 - 21
25	3.20	0.31	0 - 29
28	3.46	0.26	0 - 25
Aug. 1	2.48	0.20	0 - 16
4	0.76	0.10	0 - 11
7	0.17	0.03	0 - 3
11	0.05	0.02	0 - 2

TABLE 3

Mean number of adult coccinellids/fababean plant in 1977

(Sample size: 250 plants for each sampling date)

Sampling Date		Mean no. of coccinellids/plant	S.E.	Range
May	26	0.05	0.02	0 - 3
	30	0.04	0.01	0 - 1
June	2	0.04	0.01	0 - 1
	6	0.05	0.01	0 - 2
	9	0.05	0.01	0 - 2
	13	0.12	0.02	0 - 2
	16	0.14	0.03	0 - 2
	20	0.06	0.02	0 - 1
	23	0.02	0.01	0 - 1
	27	0.00	0.00	0 - 1
July	4	0.03	0.01	0 - 1
	7	0.00	0.00	0 - 1
	11	0.02	0.01	0 - 3
	14	0.03	0.01	0 - 2
	18	0.02	0.01	0 - 1
	21	0.02	0.01	0 - 1
	25	0.03	0.01	0 - 1
	28	0.03	0.01	0 - 1
Aug.	1	0.08	0.02	0 - 2
	4	0.10	0.02	0 - 2
	7	0.04	0.01	0 - 2
	11	0.06	0.02	0 - 1

TABLE 4

Total numbers of insects caught in four water traps in 1977

	May 26 to June 9	June 10 to June 27	June 28 to July 18	July 19 to August 11
Pea aphids	0	5	131	249
Blister beetles	0	0	2	1
Grasshoppers	2	11	12	12
Leafhoppers	32	25	30	238
Flea beetles	48	19	28	167
Coccinellidae	10	3	0	7
Staphylinidae	6	31	16	14
Syrphidae	81	48	85	8

TABLE 5

Total numbers of insects caught in twelve pitfall traps in 1977

	May 26 to June 9	June 10 to June 27	June 28 to July 12	July 19 to August 11
Elateridae	7	15	6	10
Carabidae	36	10	24	47
Staphylinidae	0	13	7	10
Gryllidae	0	0	7	0
Araneida	2	4	6	8

TABLE 6

Mean number of pea aphids/fababean plant in 1978

(Sample size: 150 plants for each sampling date)

Sampling date	Mean no. of aphids/plant	S.E.	Range
June 23	0.15	0.03	0 - 3
27	0.29	0.05	0 - 3
30	0.30	0.05	0 - 5
July 4	0.66	0.11	0 - 8
7	0.67	0.09	0 - 6
11	0.83	0.09	0 - 5
14	1.28	0.14	0 - 10
18	1.13	0.13	0 - 11
21	1.10	0.15	0 - 16
25	0.80	0.10	0 - 8
28	0.59	0.09	0 - 6
Aug. 1	0.51	0.09	0 - 7
4	0.31	0.06	0 - 4
8	0.25	0.05	0 - 4
11	0.58	0.10	0 - 7
15	0.37	0.08	0 - 6
18	0.19	0.05	0 - 4
22	0.11	0.04	0 - 3
25	0.14	0.03	0 - 2
29	0.13	0.03	0 - 3
Sept. 1	0.09	0.03	0 - 2

TABLE 7

Mean number of adult coccinellids/fababean plant in 1978

(Sample size: 150 plants for each sampling date)

Sampling date		Mean no. of coccinellids/plant	S.E.	Range
June	23	0.03	0.01	0 - 1
	27	0.01	0.01	0 - 1
	30	0.01	0.01	0 - 1
July	4	0.00	0.00	0
	7	0.00	0.00	0
	11	0.00	0.00	0
	14	0.00	0.00	0
	18	0.02	0.01	0 - 2
	21	0.01	0.01	0 - 1
	25	0.02	0.01	0 - 1
	28	0.04	0.02	0 - 2
Aug.	1	0.05	0.02	0 - 1
	4	0.06	0.02	0 - 1
	8	0.09	0.02	0 - 1
	11	0.09	0.02	0 - 1
	15	0.05	0.02	0 - 1
	18	0.09	0.02	0 - 1
	22	0.03	0.01	0 - 1
	25	0.06	0.02	0 - 1
	29	0.05	0.02	0 - 2
Sept.	1	0.06	0.02	0 - 1

TABLE 8

Total numbers of insects caught in four water traps in 1978

	June 23 to July 7	July 8 to July 25	July 26 to August 11	August 12 to September 1
Pea aphids	27	57	34	15
Blister beetles	0	1	0	0
Grasshoppers	13	10	5	7
Leafhoppers	21	18	53	29
Flea beetles	30	28	47	50
Coccinellidae	0	0	8	10
Staphylinidae	2	12	9	16
Syrphidae	32	40	18	15

TABLE 9

Total numbers of insects caught in twelve pitfall traps in 1978

	June 23 to July 7	July 8 to July 25	July 26 to August 11	August 12 to September 1
Elateridae	6	0	3	7
Carabidae	41	18	17	21
Staphylinidae	10	13	8	11
Gryllidae	0	5	2	1
Araneida	6	6	9	12

Syrphid flies were frequently caught in water traps; the larvae of these flies are aphidophagous predators.

B. Discussion

Economic losses to fababeans in Manitoba in 1974 have been reported as a result of infestations by the pea aphid (Hanec 1975). 1977 and 1978 were years in which pea aphid densities on fababeans were generally low. The low numbers of pea aphids may be due to the high rainfall in July of both 1977 and 1978 (Table 10). Heavy rainfall may wash aphids off plants, causing high mortality. The predation by potential predators of the pea aphid may be an important factor contributing to the low densities of pea aphid. There was no synchronization between coccinellids and pea aphids, since the time of reaching maximum densities and that of the beginning of the rates of decline of adult coccinellid populations was not significantly synchronized with pea aphid populations. There was no apparent aggregative numerical response of coccinellids to pea aphids; it seems likely that adult coccinellids may not regulate pea aphid numbers well.

The Eggs Hatching Rate and Developmental Duration of *H. tredecimpunctata*

A. Results

Data of the average percentage of eggs hatching rate of H. tredecimpunctata at 13°, 18°, and 23°C are shown in Table 11. Overall the average number of eggs in one

TABLE 10

Weather data for Glenlea Research Station

Year	Month	Mean Temperature (°C)	Total Precipitation (mm)
1977	June	16.8	97.8
	July	19.5	121.4
	August	13.5	73.6
1978	June	13.9	31.0
	July	18.8	130.1
	August	23.0	40.1

		Long term average mean temperature (°C)	Mean total Precipitation (mm)
1967-1976	June	16.7	100.8
	July	19.1	70.0
	August	18.3	50.9

batch was 23.4, all these eggs were laid at the same temperature (21°C). Table 11 shows that the egg batch size used for measuring duration of development at 13°C was larger than that used at 18° and 23°C: this was a sampling artifact which probably did not affect the speed of development. The percentage of hatching eggs has been angularly transformed for analysis of variance. Table 12 shows that there was no significant difference of the egg hatching rate among these three temperatures, i.e., the eggs hatching rate is not significantly influenced by these three temperatures.

Table 13 shows the mean total developmental time of H. tredecimpunctata (from egg to adult emergence) are 37.2 and 23.9 days at 18° and 23°C respectively. The larval stages of H. tredecimpunctata lasted an average of 30.3 and 19.5 days at 18° and 23°C respectively. At 13°C, only seven replicates completed the prepupal stage, twelve replicates completed the fourth instar stage, and twenty replicates completed the third instar stage. Data of Table 13 were analyzed using one-way analysis of variance. The results show that temperature has a significant effect on the development of immature stages of H. tredecimpunctata (Table 14-20): within the range tested, increased temperature results in increased developmental rate. The data for the prepupal stage were not analyzed because the variance was zero at 23°C.

TABLE 11

Egg batch size and average percentage hatch of *H. tredecimpunctata* eggs at three temperatures

Temperature	No. of replicates	Mean no. of eggs/batch	S.E.	Mean percentage of eggs hatching	S.E.	Range
13°C	20	28.3	1.68	87.0	2.2	71 - 100
18°C	20	20.4	1.86	81.0	4.3	40 - 100
23°C	20	21.4	1.97	81.5	5.6	23 - 100

TABLE 12

Analysis of variance of percentage of the egg hatch data in Table 11

Source of variation	d.f.	S.S.	M.S.	F
Total	59	14,447.93	244.88	
Temperature	2	66.83	33.41	0.13 (n.s.)
Error	57	14,381.10	252.30	

TABLE 13

Mean duration (± Standard Error) in days of immature stages of *H. tredecimpunctata* at three temperatures

Temperature	No. of replicates	Egg	1st	2nd	3rd	4th	Prepupa	Pupa	Total
13° C	20	13.2±0.2	8.7±0.3	7.8±0.2	9.6±0.2	17.7±0.8*	4.4±0.2*	-	-
18° C	20	6.9±0.4	5.8±0.4	3.7±0.1	4.0±0.1	6.9±0.2	1.7±0.1	8.8±0.2	37.2±0.4
23° C	20	4.4±0.1	3.5±0.1	2.3±0.1	2.9±0.2	3.6±0.2	1.0±0.0	6.2±0.1	23.9±0.3

*Only 12 replicates survived to complete the fourth instar and seven of these completed the prepupal stage. None of them successfully completed pupation.

TABLE 14

Analysis of variance of the data for the duration of the egg stage (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	59	822.98	13.95	
Temperature	2	802.53	401.27	1,114.64*
Error	57	20.45	0.36	

*P<<0.001

TABLE 15

Analysis of variance of the data for the duration of the first instar (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	59	334.33	5.67	
Temperature	2	282.63	141.32	155.30*
Error	57	51.70	0.91	

*$P \ll 0.001$

TABLE 16

Analysis of variance of the data for the duration of the second instar (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	59	356.73	6.05	
Temperature	2	322.23	161.12	264.13*
Error	57	34.50	0.61	

*$P << 0.001$

TABLE 17

Analysis of variance of the data for the duration of the third instar (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	59	544.93	9.24	
Temperature	2	511.23	255.62	433.25*
Error	57	33.70	0.59	

*P<<0.001

TABLE 18

Analysis of variance of the data for the duration of the fourth instar (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	51	1,634.52	32.05	
Temperature	2	1,534.50	767.25	376.10*
Error	49	100.02	2.04	

*P<<0.001

TABLE 19

Analysis of variance of the data for the duration of the pupal stage (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	39	82.00	2.10	
Temperature	1	67.60	67.60	177.90*
Error	38	0.38	0.38	

$^*P \ll 0.001$

TABLE 20

Analysis of variance of the data for the total duration of the immature stages (from Table 13)

Source of Variation	d.f.	S.S.	M.S.	F
Total	39	1,861.90	47.74	
Temperature	1	1,768.90	1,768.90	722.00*
Error	38	93.00	2.45	

$^*P \ll 0.001$

B. Discussion

The size of egg batches in coccinellids is different with species and also associated with food species. The number of eggs per batch in Propylea 14-punctata (L.) is usually 6 or 7. In A. bipunctata the average number per batch is between 12 and 17. In Coccinella 7-punctata the number of eggs is also variable, the average being between 20 and 30 (Banks 1956). The eggs of H. tredecimpunctata reported by Cutright (1924) are usually in groups from 10 to 40. The egg hatch size of H. tredecimpunctata is quite high, so this species may be able to survive at low aphid densities by cannibalism on unhatched eggs. The results show that the egg hatching rates of H. tredecimpunctata are fairly high at three experimental temperatures, and the temperatures ranging from 13° to 23°C are favourable to the egg hatching of H. tredecimpunctata.

The developmental rate of coccinellids is different with environmental situations (Hodek 1973) and food species as well (Smith 1965a). The duration of the larval stage of H. tredecimpunctata recorded by Smith (1965) was 15.7 days when fed on powdered freeze-dried pea aphids at 21.9°C. Since, in the present study whole, fresh-frozen aphids were used, this may account for the slower rate of development found. The duration of developmental stage of H. tredecimpunctata increases with decreasing temperatures from 23° to 18°C. In other words, the developmental rate is increasing with increasing temperatures. From the results

TABLE 21

Mean number of pea aphids disappearing or dying in predation trials in the presence of female predators

Temperature (° C)	Initial Density (ρ_0)	Mean	S.E.
13	5	0.95	0.12
	10	1.46	0.17
	15	2.26	0.33
	20	3.24	0.60
18	5	2.64	0.18
	10	2.68	0.38
	15	6.05	0.74
	20	3.95	0.84
23	5	2.41	0.18
	10	5.43	0.91
	15	6.40	0.67
	20	9.38	1.72

TABLE 22

Mean number of pea aphids disappearing or dying in predation trials in the presence of male predators

Temperature (°C)	Initial Density (ρ_0)	Mean	S.E.
13	5	0.79	0.09
	10	1.36	0.15
	15	2.08	0.33
	20	2.28	0.31
18	5	1.36	0.13
	10	2.69	0.29
	15	3.94	0.58
	20	6.05	0.89
23	5	1.40	0.14
	10	2.05	0.38
	15	4.96	0.92
	20	8.16	1.03

TABLE 23

Mean number of pea aphids disappearing or dying in predation trials in the absence of predators

Temperature (° C)	Initial Density (ρ_o)	Mean	S.E.
13	5	0.54	0.07
	10	0.73	0.08
	15	1.89	0.17
	20	2.25	2.32
18	5	0.54	0.07
	10	0.96	0.17
	15	2.83	0.38
	20	4.31	0.88
23	5	0.74	0.08
	10	2.20	0.39
	15	5.04	0.86
	20	6.84	1.17

it can be concluded that 13°C is not a favourable temperature for the larval development of *H. tredecimpunctata*.

Predation trials

A. Results

Figures 7, 8, and 9 show the mean proportion of pea aphids disappearing or dying in predation trials. Tables 21, 22 and 23 show the mean number of pea aphids disappearing or dying in predation trials. All aphids which were not present and alive were grouped in the same category, irrespective of whether they had escaped or died. In the control trials, less than 0.5 percent of aphids escaped from cages, most aphids which were not feeding had not escaped but were dead. For statistical analysis, the number dying or disappearing in each predation trial was transformed logarithmically $[\log (x + 1)]$. Factorial analysis of variance was used to determine significant effects. It was found that the first of the five consecutive 24 h test periods was significantly different from the others (Table 24), but that days 2-5 were not significantly different. This was assumed to be a "settling down" effect and the data were re-analyzed using only test periods 2-5.

The $\log_{10} (x + 1)$ of the number disappearing/test period for days 2-5 was subjected to analysis of variance (Table 25). There were 30 significant effects accounting for 96 percent of the variation due to treatments

FIGURE 7

Mean proportion of pea aphids disappearing or dying in predation trials at 13°C (Each point represents 80 trials)

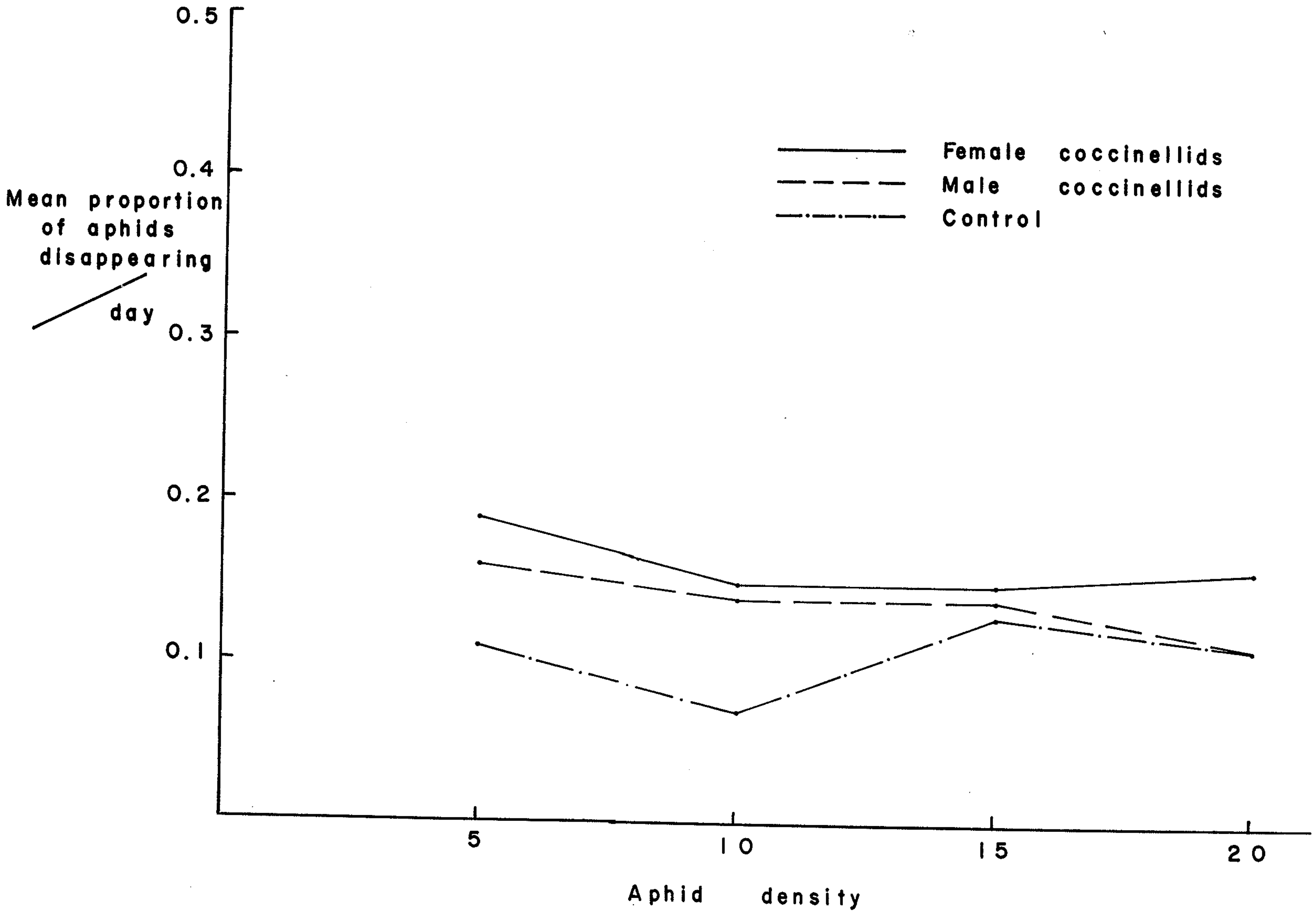

0.5
0.4
0.3
0.2
0.1
Mean proportion of aphids disappearing / day
Female coccinellids
Male coccinellids
Control
5
10
15
20
Aphid density

FIGURE 8

Mean proportion of pea aphids disappearing or dying in predation trials at 18°C

(Each point represents 80 trials)

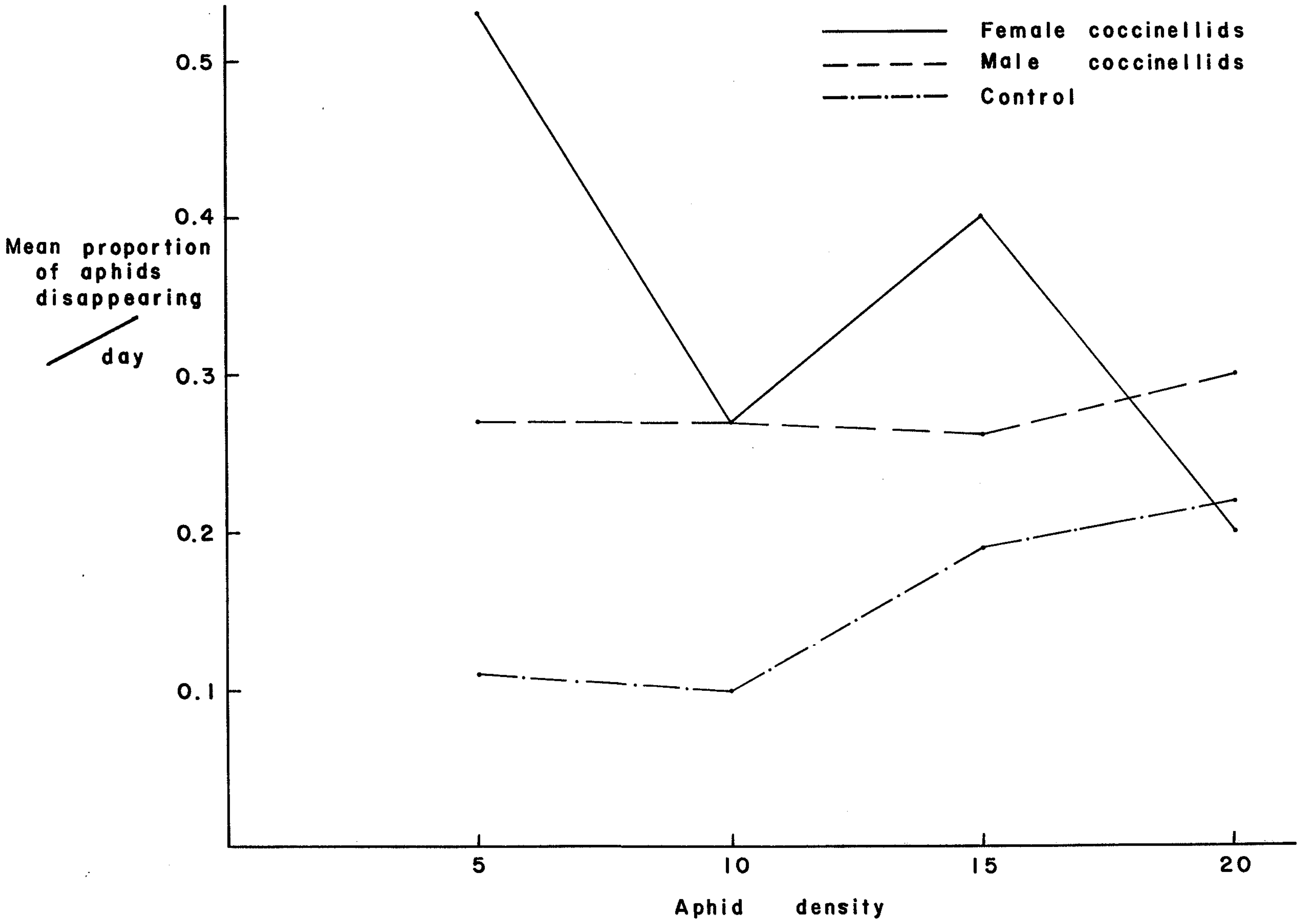

Female coccinellids
Male coccinellids
Control
Mean proportion of aphids disappearing / day
0.5
0.4
0.3
0.2
0.1
5
10
15
20
Aphid density

FIGURE 9

Mean proportion of pea aphids disappearing or dying in predation trials at 23°C

(Each point represents 80 trials)

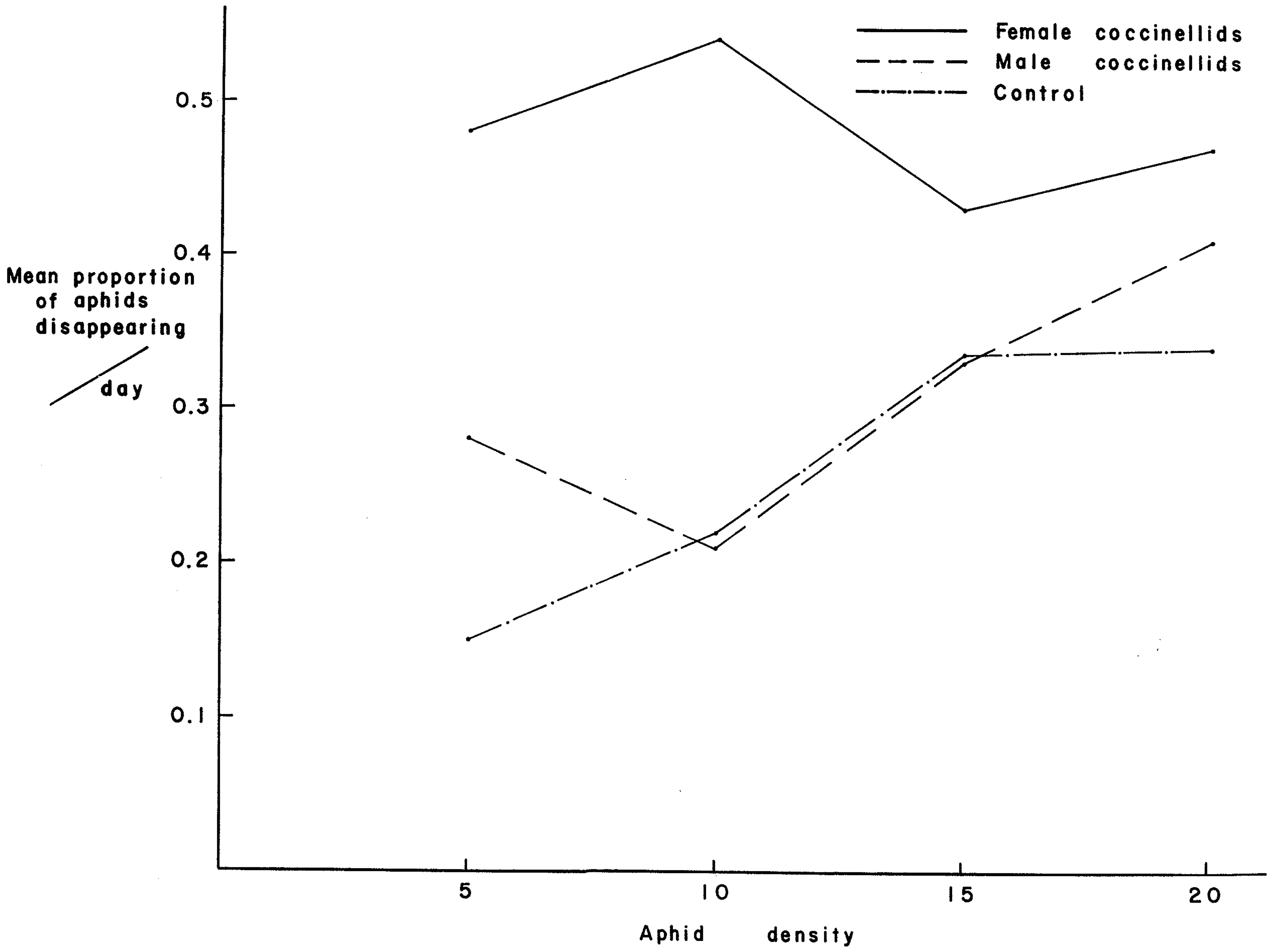

Female coccinellids
Male coccinellids
Control
Mean proportion of aphids disappearing / day
0.5
0.4
0.3
0.2
0.1
5
10
15
20
Aphid density

TABLE 24

Analysis of variance of coccinellid predation on pea aphids for five days

Source of variation	d.f.	S.S.	M.S.	F	Sig.
Total	3,599	370.65	-	-	-
Replications	19	4.55	0.24	4.67	<0.001
Treatments	179	191.78	1.07	20.90	<0.001
Error	3,401	174.32	0.05	-	-
Factors:					
Temperature	2	46.06	23.03	449.30	<0.001
Coccinellid presence	2	20.68	10.34	201.69	<0.001
Aphid density	3	89.10	29.70	579.48	<0.001
Days	4	0.94	0.58	4.59	<0.01
Day 1 vs rest	1	0.58	0.58	11.36	<0.001
Residual	3	0.36	0.12	2.34	N.S.
Interactions	168	34.99	0.21	4.10	<0.001

TABLE 25

Analysis of variance of coccinellid predation
on pea aphids for four days
(2-5 inclusive)

(For abbreviations see footnote)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
Total	2,879	301.33	-	-	-
Replications	19	3.99	0.21	4.19	<0.001
Treatments	143	160.97	1.13	22.43	<0.001
Error	2,717	136.37	0.05	-	-
FACTORS					
1. Temperature	2	41.90	20.95	417.42	<0.001
Linear effect	1	41.25	41.25	821.86	<0.001
Quadratic	1	0.65	0.65	12.98	<0.001
2. Coccinellid presence	2	15.70	7.85	156.36	<0.001
Absence vs. presence	1	12.07	12.07	240.53	<0.001
Coccinellid sex	1	3.62	3.62	72.19	<0.001
3. Initial density of aphids	3	76.75	25.58	509.72	<0.001
Linear effect	1	75.01	75.01	1,494.51	<0.001
Quadratic	1	0.25	0.25	5.15	<0.05
Cubic	1	1.48	1.48	29.48	<0.001
4. Days (2-5 inclusive)	3	0.36	0.12	2.39	N.S.

(Continued)

TABLE 25 (continued)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
INTERACTIONS					
1 x 2	4	3.95	0.99	19.65	<0.001
1_L2	2	1.76	0.88	17.48	<0.001
1_L2 A/P	1	0.38	0.38	7.60	<0.01
1_L2 ♀/♂	1	1.37	1.37	27.37	<0.001
1_Q2	2	2.19	1.10	21.82	<0.01
1_Q2 A/P	1	1.79	1.79	34.03	<0.001
1_Q2 ♀/♂	1	0.48	0.48	9.60	<0.01
1 x 3	6	6.23	1.04	20.69	<0.001
1_L3	3	5.45	1.82	36.18	<0.001
1_L3_L	1	5.43	5.43	108.26	<0.001
1_L3_Q	1	0.00	0.00	0.00	N.S.
1_L3_c	1	0.01	0.01	0.28	N.S.
1_Q3	3	0.78	0.26	5.20	<0.01
1_Q3_L	1	0.23	0.23	4.68	<0.05
1_Q3_Q	1	0.01	0.01	0.23	N.S.
1_Q3_c	1	0.54	0.54	10.70	<0.001

(Continued)

TABLE 25 (Continued)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
1 x 4	6	0.20	0.03	0.67	N.S.
$^{1}L^{4}$	3	0.16	0.05	1.04	N.S.
2 x 3	6	3.60	0.60	11.95	<0.001
$^{2}A/P^{3}$	3	1.98	0.66	13.12	<0.001
$^{2}A/P^{3}L$	1	1.73	1.73	34.42	<0.001
$^{2}A/P^{3}Q$	1	0.01	0.01	0.14	N.S.
$^{2}A/P^{3}c$	1	0.24	0.24	4.79	<0.05
^{2}♀/♂^{3}	3	1.62	0.54	10.79	<0.001
^{2}♀/♂^{3}L	1	1.16	1.16	23.11	<0.001
^{2}♀/♂^{3}Q	1	0.33	0.33	6.66	<0.01
^{2}♀/♂^{3}c	1	0.13	0.13	2.59	N.S.
2 x 4	6	0.75	0.12	2.48	<0.05
$^{2}A/P^{4}$	3	0.27	0.09	1.76	N.S.
^{2}♀/♂^{4}	3	0.48	0.16	3.20	<0.05
^{2}♀/♂^{4}L	1	0.31	0.31	6.11	<0.05
^{2}♀/♂^{4}Q	1	0.00	0.00	0.00	N.S.
^{2}♀/♂^{4}c	1	0.17	0.17	3.42	N.S.

(Continued)

TABLE 25 (Continued)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
3 x 4	9	0.81	0.09	1.80	N.S.
123	12	5.39	0.45	8.95	<0.001
$^{1}{}_{L}{}^{23}$	6	1.77	0.30	5.88	<0.001
$^{1}{}_{L}{}^{2}\text{A/P}{}^{3}\text{L}$	1	0.07	0.07	1.48	N.S.
$^{1}{}_{L}{}^{2}\text{A/P}{}^{3}\text{Q}$	1	0.18	0.18	3.59	N.S.
$^{1}{}_{L}{}^{2}\text{A/P}{}^{3}\text{c}$	1	0.03	0.03	0.57	N.S.
$^{1}{}_{L}{}^{2}\text{♀/♂}{}^{3}\text{L}$	1	0.62	0.62	12.40	<0.001
$^{1}{}_{L}{}^{2}\text{♀/♂}{}^{3}\text{Q}$	1	0.63	0.63	12.61	<0.001
$^{1}{}_{L}{}^{2}\text{♀/♂}{}^{3}\text{c}$	1	0.24	0.24	4.71	<0.05
$^{1}{}_{Q}{}^{23}$	6	3.62	0.60	12.03	<0.001
$^{1}{}_{Q}{}^{2}\text{A/P}{}^{3}\text{L}$	1	0.34	0.34	6.75	<0.01
$^{1}{}_{Q}{}^{2}\text{A/P}{}^{3}\text{Q}$	1	0.36	0.36	7.18	<0.01
$^{1}{}_{Q}{}^{2}\text{A/P}{}^{3}\text{c}$	1	0.11	0.11	2.26	N.S.
$^{1}{}_{Q}{}^{2}\text{♀/♂}{}^{3}\text{L}$	1	0.88	0.88	17.54	<0.001
$^{1}{}_{Q}{}^{2}\text{♀/♂}{}^{3}\text{Q}$	1	0.02	0.02	0.39	N.S.
$^{1}{}_{Q}{}^{2}\text{♀/♂}{}^{3}\text{c}$	1	1.91	1.91	38.08	<0.001

(Continued)

TABLE 25 (Continued)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
124	12	1.17	0.10	1.94	<0.05
$1_{L}24$	6	0.10	0.02	0.32	N.S.
$1_{Q}24$	6	1.07	0.18	3.57	<0.01
$1_{Q}2_{A/P}4_{L}$	1	0.60	0.60	11.90	<0.001
$1_{Q}2_{A/P}4_{Q}$	1	0.09	0.09	1.78	N.S.
$1_{Q}2_{A/P}4_{c}$	1	0.08	0.08	1.67	N.S.
$1_{Q}2_{\text{♀/♂}}4_{L}$	1	0.07	0.07	1.43	N.S.
$1_{Q}2_{\text{♀/♂}}4_{Q}$	1	0.00	0.00	0.00	N.S.
$1_{Q}2_{\text{♀/♂}}4_{c}$	1	0.23	0.23	4.56	<0.05
134	18	1.16	0.06	1.28	N.S.
234	18	1.92	0.11	2.12	<0.01
$2_{A/P}34$	9	1.45	0.16	3.20	<0.001
$2_{A/P}3_{L}4_{L}$	1	0.16	0.16	3.24	N.S.
$2_{A/P}3_{L}4_{Q}$	1	0.44	0.44	8.80	<0.01
$2_{A/P}3_{L}4_{c}$	1	0.10	0.09	1.83	N.S.
$2_{A/P}3_{Q}4_{L}$	1	0.03	0.03	0.64	N.S.
$2_{A/P}3_{Q}4_{Q}$	1	0.00	0.00	0.00	N.S.

(Continued)

TABLE 25 (Continued)

Source of variation	d.f.	S.S.	M.S.	F	Sig.
234 (continued)					
^{2}A/P^{3}Q^{4}c	1	0.01	0.01	0.12	N.S.
^{2}A/P^{3}c^{4}L	1	0.31	0.31	6.22	<0.05
^{2}A/P^{3}c^{4}Q	1	0.14	0.14	2.85	N.S.
^{2}A/P^{3}c^{4}c	1	0.26	0.26	5.13	<0.05
^{2}♀/♂^{34}	9	0.47	0.05	1.05	N.S.
^{2}♀/♂^{3}L^{4}L	1	0.01	0.01	0.10	N.S.
^{2}♀/♂^{3}L^{4}Q	1	0.06	0.06	1.14	N.S.
^{2}♀/♂^{3}L^{4}c	1	0.01	0.01	0.23	N.S.
^{2}♀/♂^{3}Q^{4}L	1	0.00	0.00	0.00	N.S.
^{2}♀/♂^{3}Q^{4}Q	1	0.10	0.10	1.99	N.S.
^{2}♀/♂^{3}Q^{4}c	1	0.04	0.04	0.88	N.S.
^{2}♀/♂^{3}c^{4}L	1	0.12	0.12	2.36	N.S.
^{2}♀/♂^{3}c^{4}Q	1	0.11	0.11	2.21	N.S.
^{2}♀/♂^{3}c^{4}c	1	0.02	0.02	0.39	N.S.
1234	36	1.08	0.03	0.60	N.S.

(Continued)

TABLE 25 (Continued)

Abbreviations:

1	Temperature
2	Coccinellid absence or presence and effect of coccinellid sex
3	Initial density of aphids
4	Days
L	Linear effect
Q	Quadratic effect
c	Cubic effect
A	Absence
P	Presence

(50 percent of the total variation). The five most important effects (Table 25A) accounted for 85 percent of the treatment variation and were used to construct a response surface (an equation linking the value of the dependent variable to the values of the independent variables).

The logarithmic transformation renders the data suitable for factorial analysis and allows the significant factors to be identified reliably. However, once these factors have been identified, arithmetic equations incorporating them are far more easy to use in further analysis. Hence, the response surface was constructed from the untransformed data. The response surface constructed is represented by the following three equations:

Controls:

$$\hat{Y} = 1.6940 - 0.1357\,T - 0.2634\,\rho_o + 0.0297\,\rho_o T$$

Proportion of variation in treatment means explained by this equation ($r^2 = 0.971$).

Female Predators:

$$\hat{Y}_{\text{♀}} = 0.1581 - 0.2656\,\rho_o + 0.0375\,T + 0.0284\,\rho_o T$$

$$(r^2 = 0.883)$$

Male Predators:

$$\hat{Y}_{\text{♂}} = 4.5404 - 0.3577\,\rho_o - 0.2827\,T + 0.0360\,\rho_o T$$

$$(r^2 = 0.943)$$

TABLE 25 A

Summary table of major effects

Source of variation	d.f.	S.S.	M.S.	F	Sig.
Total	2,879	301.33	-	-	-
Replications	19	3.99	0.21	4.19	< 0.001
Treatments:	143	160.97	1.13	22.43	< 0.001
Linear temperature	1	41.25	41.25	821.86	< 0.001
Coccinellid presence/absence	1	12.07	12.07	240.53	< 0.001
Coccinellid sex	1	3.62	3.62	72.19	< 0.001
Linear initial density of aphids	1	75.01	75.01	1,494.51	< 0.001
Linear temp. x Linear density	1	5.43	5.43	108.26	< 0.001
Residual treatments	138	23.57	0.17	3.40	< 0.001
Error	2,717	136.37	0.05	-	-

When:

$\hat{Y}$ = predicted number of aphids disappearing/test period

ρo = initial density of aphids/plant

T = temperature (°C)

Table 26 shows the predictions from the above equations compared with the observed results.

B. Discussion

To make calculations easier, the linear equations at constant temperature may be expressed as

$$\hat{Y} = a + b\rho o \qquad (1)$$

where:

a = constant containing non-ρo terms

b = coefficient of ρo terms.

Both a and b consist of a temperature dependent term and a temperature independent term. From this it can be seen that at time t = 1 density

$$\rho_t = \rho o - (a + b\rho o) \qquad (2)$$

Since in this equation, t = 1, the general form of the equation could be one of several types. To determine what the general form is, let us examine what is expected to happen at various values of t.

TABLE 26

Mean number of aphids disappearing or dying at the end of 24 h test

Temperature (°C)	Initial Density (ρ_o)	Controls		♀ Predators		♂ Predators	
		Observed	Predicted*	Observed	Predicted*	Observed	Predicted*
13	5	0.54	0.54	0.95	1.16	0.79	1.42
	10	0.73	1.16	1.46	1.68	1.36	1.97
	15	1.89	1.77	2.26	2.20	2.07	2.52
	20	2.25	2.38	3.24	2.72	2.28	3.07
18	5	0.54	0.61	2.64	2.06	1.36	0.90
	10	0.96	1.96	2.67	3.29	2.69	2.35
	15	2.82	3.32	6.05	4.52	3.94	3.81
	20	4.31	4.68	3.95	5.75	6.05	5.26
23	5	0.74	0.67	2.41	2.96	1.40	0.39
	10	2.20	2.77	5.42	4.90	2.05	2.74
	15	5.04	4.87	6.40	6.83	4.96	5.09
	20	6.84	6.97	9.38	8.77	8.16	7.44

* Predicted numbers from response surface equations.

$$
\begin{aligned}
t &= 0 \qquad \rho_t = \rho o \\
t &= 1 \qquad \rho_t = \rho o - (a + b\rho o) \\
t &= 2 \qquad \rho_t = \rho o - (a + b\rho o) - \left[a + b\,(\rho o - (a + b\rho o))\right] \\
t &= 3 \qquad \rho_t = \rho o - (a + b\rho o) - \left[a + b\,(\rho o - (a + b\rho o))\right] \\
&\qquad\qquad - \left[a + b\,(\rho o - (a + b\,(\rho o - (a + b\rho o))))\right]
\end{aligned}
$$

These may be simplified as:

$$\rho_t = (1 - b)^t \rho o - a \sum_{n = 0}^{n = t - 1} (1 - b)^n \qquad (3)$$

The second part of equation (3) is the sum of a geometric progression in which the t^{th} term is added at time t. The formula for the summation of a geometric progression to the t^{th} term is

$$\frac{a\,(1 - r^t)}{(1 - r)}$$

where, in this case, $r = (1 - b)$. Hence, equation (3) may be written as

$$\rho_t = (1 - b)^t \rho o - \frac{a\left[1 - (1 - b)^t\right]}{\left[1 - (1 - b)\right]}$$

$$\text{or} \quad \rho_t = (1 - b)^t \rho o - \frac{a}{b} + \frac{a}{b}\,(1 - b)^t \qquad (4)$$

The differential of equation (4) with respect to time gives the rate of change of aphid density at any time t, and is

$$\frac{d\rho}{d_t} = (1 - b)^t \,\log_e (1 - b)\,(\rho o + \frac{a}{b}) \qquad (5)$$

In order to determine the rate of change of aphid density at any density we can use equations (4) and (5). Rewriting equation (4) we find that

$$\rho_o = - \frac{a}{b} + \frac{a}{b(1 - b)^t} + \frac{\rho_t}{(1 - b)^t}$$

substituting this in equation (5) we have

$$\frac{d\rho}{d_t} = (1 - b)^t \log_e (1 - b) \left\{ \frac{a}{b(1 - b)^t} + \frac{\rho_t}{(1 - b)^t} - \frac{a}{b} + \frac{a}{b} \right\}$$

which simplifies to

$$\frac{d\rho}{d_t} = (\frac{a}{b} + \rho) \log_e (1 - b) \qquad (6)$$

This relates directly to the equations obtained from the construction of the response surface.

In addition, the natural mortality in a treatment with a predator can be determined and, as a result the mortality due to predation. Let a, b = values in equation for tests with a predator and α, β the corresponding values for controls (without predator). Then, in tests with a predator equation (4) gives the density at any time and equation (6) gives the rate of change of density at any density. Substituting α and β in equation (6) we obtain the rate of change of density due to control processes $\left(\frac{d\rho}{d_t}\right)_c$ at any density

$$\left(\frac{d\ell}{d_t}\right)_c = \frac{\alpha}{\beta} + \rho_t \quad \log_e (1 - \beta) \qquad (7)$$

From equation (4) ρ_t at time t can be determined. Hence

$$\left(\frac{d\ell}{d_t}\right)_c = \left[\frac{\alpha}{\beta} + (1 - b)^t \rho_o - \frac{a}{b} + \frac{a}{b}(1 - b)^t\right] \log_e (1 - \beta) \quad (8)$$

and since the overall rate of change is given in equation (5), loss due to predation is

$$\left(\frac{d\rho}{d_t}\right)_p = \frac{d\rho}{d_t} - \left(\frac{d\ell}{d_t}\right)_c = (1 - b)^t \log_e (1 - b) \left(\rho_o + \frac{a}{b}\right)$$

$$- \left[\frac{\alpha}{\beta} + (1 - b)^t \rho_o - \frac{a}{b} + \frac{a}{b}(1 - b)^t\right] \log_e (1 - \beta)$$

or

$$\left(\frac{d\ell}{d_t}\right)_p = (1 - b)^t \left(\rho_o + \frac{a}{b}\right)\left(\log_e \frac{(1 - b)}{(1 - \beta)}\right) - \log_e (1 - \beta)$$

$$\left(\frac{\alpha}{\beta} - \frac{a}{b}\right) \qquad (9)$$

Integrating equation (9) from t = 0 to t = 1 will give the number predated in a test

$$\int_{t=0}^{t=1} \left(\frac{d\ell}{d_t}\right)_p dt = \left[\frac{(1 - b)^t \left(\rho_o + \frac{a}{b}\right)}{\log_e (1 - b)} \left(\log_e \frac{(1 - b)}{(1 - \beta)}\right.\right.$$

$$\left. - \log_e (1 - \beta) \left(\frac{\alpha}{\beta} - \frac{a}{b}\right) t\right]_{t=0}^{t=1}$$

(Continued)

$$= \left[(1 - b - 1) \left(\rho_o + \frac{a}{b} \right) \left(1 - \frac{\log_e (1 - \beta)}{\log_e (1 - b)} \right) - \log_e (1 - \beta) \left(\frac{\alpha}{\beta} - \frac{a}{b} \right) \right]$$

$$= - b \left(\rho_o + \frac{a}{b} \right) \left(1 - \frac{\log_e (1 - \beta)}{\log_e (1 - b)} \right) - \log_e (1 - \beta) \left(\frac{\alpha}{\beta} - \frac{a}{b} \right) \qquad (10)$$

Substituting for ρ_o in equation (9) we obtain the rate of predation at any density

$$\left(\frac{d\rho}{d_t} \right)_p = (1 - b)^t \left(- \frac{a}{b} + \frac{a}{b\,(1 - b)^t} + \frac{\rho_t}{(1 - b)^t} + \frac{a}{b} \right) \left(\log_e \frac{(1 - b)}{(1 - \beta)} \right) - \log_e (1 - \beta) \left(\frac{\alpha}{\beta} - \frac{a}{b} \right)$$

$$\left(\frac{d\rho}{d_t} \right)_p = \left(\frac{a}{b} + \rho \right) \left(\log_e \frac{(1 - b)}{(1 - \beta)} \right) - \log_e (1 - \beta) \left(\frac{\alpha}{\beta} - \frac{a}{b} \right) \qquad (11)$$

For controls

$\alpha = 1.6940 - 0.1357\ T$

$\beta = 0.0297\ T - 0.2634$

For females

$a = 0.1581 + 0.0375\ T$

$b = 0.0284\ T - 0.2656$

For males

$a = 4.5404 - 0.2827\ T$

$b = 0.0360\ T - 0.3577$

Tables 27 and 28 show the predicted number of pea aphids predated by female (or male) predators in predation trials, and the instantaneous rate of predation. Table 29 shows the instantaneous rate of mortality of aphids in the absence of predators. Table 30 shows the mean density of pea aphids at the end of the 24 h test.

It is important to know whether predation operates in a superproportional density dependent manner, i.e., an increasing proportion of the prey population is killed as the prey population density increases. Since, if it does, regulation of the prey population may result. From equation (11) we see that the only term containing ρ is a constant at constant temperature and ρ is to the power 1. Hence, number predated will directly proportional, rather than superproportional to density.

As mentioned earlier, Hodek's equation does not consider that predators may eat prey which would have died as a result of base-line mortality. This shortcoming can be overcome by using the equations discussed in this section, which have been separated into two components: the overall mortality equation and the natural mortality equation. The reasons for separating components mathematically are:

TABLE 27

Predicted number of aphids predated by females in trials ($\int_{t=0}^{t=1} (\frac{d\rho}{dt})_P \, dt$) , and instantaneous rate of predation by females $((\frac{d\rho}{dt})_P)$

Temperature (°C)	Initial Density (ρ_0)	$\int_{t=0}^{t=1} (\frac{d\rho}{dt})_P \, dt$	$(\frac{d\rho}{dt})_P$
13	5	-0.61	-0.65
	10	-0.56	-0.54
	15	-0.46	-0.43
	20	-0.36	-0.33
18	5	-1.70	-1.66
	10	-1.54	-1.48
	15	-1.39	-1.31
	20	-1.24	-1.14
23	5	-2.96	-2.87
	10	-2.75	-2.60
	15	-2.53	-2.33
	20	-2.32	-2.06

TABLE 28

Predicted number of aphids predated by males in trials ($\int_{t=0}^{t=1} (\frac{d\rho}{dt})_P \, dt$) , and instantaneous rate of predation by males $((\frac{d\rho}{dt})_P)$

Temperature (° C)	Initial Density (ρ_0)	$\int_{t=0}^{t=1} (\frac{d\rho}{dt})_P \, dt$	$(\frac{d\rho}{dt})_P$
13	5	-0.93	-0.92
	10	-0.87	-0.85
	15	-0.80	-0.78
	20	-0.73	-0.71
18	5	-0.35	-0.36
	10	-0.46	-0.49
	15	-0.57	-0.62
	20	-0.68	-0.76
23	5	-0.36	-0.34
	10	-0.03	-0.11
	15	-0.31	-0.57
	20	-0.65	-1.02

TABLE 29

Instantaneous rate of mortality of aphids in the absence of predators

Temperature (° C)	Initial density (ρ_0)	$(\frac{d\rho}{dt})_c$
13	5	-0.58
	10	-1.23
	15	-1.89
	20	-2.54
18	5	-0.71
	10	-2.29
	15	-3.87
	20	-5.45
23	5	-0.87
	10	-3.59
	15	-6.31
	20	-9.03

TABLE 30

Mean density of aphids at the end of 24 h test

Temperature (° C)	Initial Density (ρ_0)	Controls		Predators		Predators	
		Observed	Predicted*	Observed	Predicted*	Observed	Predicted*
13	5	4.46	4.46	4.05	3.84	4.21	3.58
	10	9.27	8.84	8.54	8.32	8.64	8.03
	15	13.11	13.62	12.74	12.80	12.93	12.48
	20	17.75	17.62	16.76	17.28	17.73	16.93
18	5	4.46	4.39	2.36	2.94	3.64	4.10
	10	9.04	8.04	7.33	6.71	7.31	7.65
	15	12.18	11.68	8.95	10.48	11.06	11.19
	20	15.69	15.32	16.05	14.25	13.95	14.74
23	5	4.26	4.33	2.59	2.04	3.60	4.61
	10	7.80	7.23	4.58	5.10	7.95	7.26
	15	9.96	10.13	8.60	8.17	10.04	9.91
	20	13.16	13.03	10.63	11.23	11.84	12.56

* $\rho_1 = \rho_0 - (a + b\rho_0)$

1. A mathematical expression for predation, enables the determination of how predation is affected by changing conditions.
2. A mathematical method will take into account that, if natural mortality is density-related, the rate of natural mortality in controls will be different from that in treatments with predators, since the densities are different. Hodek's equation does not do this.

This mathematical approach is only justified because, in this study, large quantities of reliable data have been collected.

CHAPTER V

SUMMARY AND CONCLUSIONS

The results of two years (1977 and 1978) field observations on population trends of pea aphids and coccinellids show that coccinellids are not found at greater densities in areas of the field where aphid densities are high. Also, coccinellids are not found more frequently on aphid-infested plants. Hence, there was no apparent aggregative numerical response of coccinellids to pea aphids.

The egg hatching rate of H. tredecimpunctata was very high at 13°, 18°, and 23°C. There is no significant difference in egg hatching rate of H. tredecimpunctata among these three temperatures. The duration of developmental stage of H. tredecimpunctata is significantly influenced by temperature, i.e., increases with decreasing temperature from 23° to 18°C. The results show that 13°C is not a favourable temperature for the larval development of H. tredecimpunctata.

The response surface constructed from the untransformed data from laboratory predation trials indicates that the functional response of adult H. tredecimpunctata was directly proportional to aphid density. This means that functional responses of adult H. tredecimpunctata do not regulate aphid density. Hence, it appears that adult H. tredecimpunctata may not regulate pea aphid populations on fababean during the course of a single season. No conclusion can be drawn regarding the influence of adult H. tredecimpunctata on aphid populations from one season to the next.

The conditions observed in the field differ from those in the laboratory. All laboratory studies must therefore be suspect, until verified in the field (Frazer and Gilbert 1976). In the laboratory the single fababean plant aged 14 days was put inside a cage, fallen aphids and coccinellids were easily able to find the plant to reascend, and the aphids and the coccinellids were always confined on the same plant. In the field, the sizes of fababean plants are generally larger than those in the laboratory, neighbouring plants touch, and so both aphids and beetles walked or flew freely between plants or between fields or parts of a field. In the laboratory only adult insects were used, whereas in the field, five instars of pea aphid and five predatory stages of coccinellid are present.

Hodek (1973) stated that the feeding rate of adult coccinellids increases with temperature through much of the favourable range. Frazer and Gilbert (1976) considered that coccinellids are much more effective predators at high temperatures than at low, and that predation and population studies must include temperature as an essential component. In the present study female coccinellids ate more at higher temperatures, but the effect of temperature on the predation rate of male coccinellids was negligible. Hodek (1973) considered that coccinellids can act as a density-dependent mortality factor for aphids, i.e., increase in the number of aphids killed at high aphid density. Frazer and Gilbert (1976) had a different opinion, i.e., "The coccinellid-aphid relationship permits no equilibrium, or steady state,.... The coccinellid's functional response is inherently unstable." In the present study the results of field observations and predation trials are in accordance with the findings of Frazer and Gilbert (1976).

There is a complex relationship between the number of aphids predated in laboratory trials and these factors: coccinellid sex, temperature, and density of aphids. The main features of this relationship are: 1) Female coccinellids eat more aphids than male coccinellids; 2) the number of aphids eaten by females increases as the temperature increases, whereas there is a slight tendency for males to eat more aphids at lower temperature; 3) the number of aphids eaten increases as the density of aphids increases. All experiments were conducted at constant temperature; however, in field conditions diurnal variations occur, and frequently the fluctuating temperatures have a stimulating effect on feeding rate (Hodek 1957; Kaddou 1960; Ellingsen 1969b), but these effects were not taken into account in our predation trials. The results of predation trials also show that adult _H. tredecimpunctata_ cannot act as a superproportional density-dependent mortality agent.

Since this coccinellid-aphid relationship is unstable, we cannot expect _H. tredecimpunctata_ to keep aphid numbers low for any length of time. However, _H. tredecimpunctata_ may still in conjunction with other members of the predator complex be an important mortality factor acting on aphids. Coccinellids that prey on aphids are relatively unspecific, and this characteristic, together with the aphids' ephemeral occurrence on particular host-plants makes it possible that coccinellids could be an important component of the predator complex. To use coccinellids as effective and permanent agents for biological control, much more behavioural and ecological work is required for building population models in which the quantitative effects of the different natural enemies are determined separately and together.

BIBLIOGRAPHY

Aapola, A.I.E. and G. I. Mink. 1973. Potential aphid vectors of pea seed-borne mosaic virus in Washington. Plant Dis. Rep. 57:552.

Adlerz, W. C. 1959. Factors affecting transmission of bean yellow mosaic virus. J. econ Ent. 52:260-262.

Balduf, W. V. 1935. The bionomics of entomophagous Coleoptera. John S. Swift. Co., St. Louis.

Banks, C. J. 1954. Random and non-random distribution of Coccinellidae. J. Soc. Br. Ent. 4:211-215.

________. 1956. A second record of a tachinid (Dipt.) parasite bred from one of the Coccinellidae (Coleoptera: Coccinellidae). Ent. mon. Mag. 92:188.

________. 1957. The behaviour of individual coccinellid larvae on plants. Br. J. Anim. Behav. 5:12-24.

Bänsch, R. 1966. On prey-seeking behaviour of aphidophagous insects, pp. 123-128. *In* I. Hodek (Ed.), Ecology of aphidophagous insects. W. Junk, The Hague.

Barlow, C. A. 1977. Effects of pea aphids, *Acyrthosiphon pisum* (Homoptera: Aphididae), on growth and productivity of pea plants, *Pisum sativum*. Can. Ent. 109:1491-1502.

Bath, J. E. and R. K. Chapman. 1964. Transmission of pea enation mosaic virus by pea aphid adults and nymphs. Proc. N. Centr. Br. ent. Soc. Am. 19:100-101.

Belicek, J. 1976. Coccinellidae of western Canada and Alaska with analyses of the transmontane zoogeographic relationships between the fauna of British Columbia and Alberta (Insecta: Coleoptera: Coccinellidae). Quaest. Ent. 12:283-409.

Blackman, R. L. 1967. The effects of different aphid foods on *Adalia bipunctata* L. and *Coccinella 7-punctata* L. Ann. appl. Biol. 59:207-219.

Brown, H. D. 1972a. The behaviour of newly hatched coccinellid larvae (Coleoptera: Coccinellidae). J. ent. Soc. sth. Afr. 35:149-157.

Brown, H. D. 1972b. Predacious behaviour of four species of Coccinellidae (Coleoptera) associated with the wheat aphid, *Schizaphis graminum*, in South Africa. Trans. R. ent. Soc. Lond. 124:21-36.

Burnett, T. 1951. Effects of temperature and host density on the rate of increase of an insect parasite. Am. Nat. 85:337-352.

________. 1954. Influence of natural temperatures and controlled host densities on oviposition of an insect parasite. Physiol. Zool. 27:239-248.

Campbell, R. E. 1926. The pea aphis in California. J. Agric. Res. 32:861-881

Campbell, A. and M. Mackauer. 1975. Thermal constants for development of the pea aphid (Homoptera: Aphididae) and some of its parasites. Can. Ent. 107:419-423.

Cartier, J. J. 1968. The pea aphid. Can. Dep. agric. Publ. No. 1146.

Cooke, W. C. 1963. Ecology of the pea aphid in the Blue Mountain area of eastern Washington and Oregon. U.S. Dep. Agric. Tech. Bull. 1287:48.

Cutright, C. R. 1924. Bionomics of *Hippodamia tredecimpunctata* L. Ann. ent. Soc. Am. 17:188-192.

Davidson, W. M. 1923. Biology of *Scymnus nubes* Casey (Coleoptera: Coccinellidae). Trans. Am. ent. Soc. 49:155-163.

DeBach, P. and H. S. Smith. 1941. The effect of host density on the rate of reproduction of entomophagous parasites. J. econ. Ent. 34:741-745.

Delucchi, V. 1954. *Pullus impexus*, a predator of *Adelges piceae*. (Hemiptera: Adelgidae) with notes on its parasites. Bull. ent. Res. 45:243-278.

Dixon, A. F. G. 1958. The escape responses shown by certain aphids to the presence of the coccinellid *Adalia decempunctata* (L.). Trans. R. ent. Soc. Lond. 110: 319-334.

________. 1959. An experimental study of searching behaviour of the predatory coccinellid beetle *Adalia bipunctata* (L.). J. Anim. biol. 28:259-281.

Dixon, A. F. G. 1963. Reproductive activity of the sycamore aphid, *Drepanosiphum platanoides* (Schr.) (Hemiptera Aphididae). J. Anim. Ecol. 32:33-48.

________. 1970. Factors limiting the effectiveness of the coccinellid beetle, *Adalia bipunctata* (L.), as a predator of the sycamore aphid, *Drepanosiphum platanoides* (Schr.). J. Anim. Ecol. 39:739-751.

Ellingsen, I. J. 1969a. Fecundity, aphid consumption and survival of the aphid predator *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Norsk. ent. Tidsskr. 16:91-95.

________. 1969b. Effect of constant and varying temperature on development, feeding, and survival of *Adalia bipunctata* L. (Coleoptera: Coccinellidae). Norsk. ent. Tidsskr. 16:121-125.

Elton, C. 1949. Population interspersion: an essay on animal community pattern. Ecology 37:1-23.

Evans, I. R. and F. W. Zettler. 1970. Aphid and mechanical transmission properties of bean yellow mosaic isolates. Phytopathology 60:1170-1174.

Ewert, M. A. and H. C. Chiang. 1966a. Dispersal of three species of coccinellids in corn fields. Can. Ent. 98:999-1003.

________. 1966b. Effects of some environmental factors on the distribution of three species of Coccinellidae in their microhabitat, pp. 194-219. *In* I. Hodek (Ed.) Ecology of aphidophagous insects. Junk, The Hague.

Fleschner, C. A. 1950. Studies on searching capacity of the larvae of three predators of the citrus red mite. Hilgardia 20:233-265.

Frazer, B. D. 1972. Population dynamics and recognition of biotypes in the pea aphid (Homoptera: Aphididae). Can. Ent. 104:1729-1733.

Frazer, B. D. and N. Gilbert. 1976. Coccinellids and aphids: A quantitative study of the impact of adult ladybirds (Coleoptera: Coccinellidae) preying on field populations of pea aphids (Homoptera: Aphididae). J. ent. Soc. Br. Columb. 73:33-56.

Frosheiser, F. I. 1969. Variable influence of alfalfa mosaic virus strains on growth and survival of alfalfa and on mechanical and aphid transmission. Phytopathology. 59:857-862.

Gurney, B. and N. W. Hussey. 1970. Evaluation of some coccinellid species for the biological control of aphids in protected cropping. Ann. appl. Biol. 65:451-458.

Hagedorn, D. J. and J. C. Walker. 1949. Wisconsin pea streak. Phytopathology 39:837-847.

Hagedorn, D. J. and E. W. Hanson. 1951. A comparative study of the virus causing Wisconsin pea stunt and red clover vein mosaic. Phytopathology 41:813-819.

Hagen, K. S. 1962. Biology and ecology of predaceous Coccinellidae. A.Rev. Ent. 7:289-326.

Hagen, K. S. and E. I. Schlinger. 1960. Imported Indian parasite of pea aphid established in California. Calif. Agric. 14:5-6.

Hanec, W. M. 1975. The susceptibility of fababeans to insect pests in Manitoba in 1973 and 1974. The Manitoba Entomologist 9:35-38.

Hassell, M. P. and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. Nature 223:1133-1137.

Hodek, I. 1956. The influence of *Aphis sambuci* L. as prey of the ladybird beetle *Coccinella septempunctata* L. Věst. Čs spol. zool. 20:62-74.

________. 1957. The larval food consumption of *Coccinella 7-punctata* L. Zool. Listy. 6:3-11.

________. 1973. Biology of Coccinellidae. W. Junk, The Hague.

Hodek, I., K. Novan, V. Skuhravy, and J. Holman. 1965. The predation of *Coccinella septempunctata* L. on *Aphis fabae* Scop. on sugar beet. Acta. ent. bohemoslov. 62:241-253.

Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. Can. Ent. 91:385-398.

________. 1961. Principles of insect predation. Ann. Rev. Ent. 6:163-182.

________. 1965. The functional response of predators to prey density and its role in mimicry and population regulation. Mem. ent. Soc. Can. 45:1-60.

________. 1966. The functional response of invertebrate predators to prey density. Mem. ent. Soc. Can. 48: 1-86.

Howard, L. O. and W. F. Fiske. 1911. The importation into the United States of the parasites of the gipsy moth and the brown-tail moth. U.S. Dep. Agric. Bur. Ent. Bull. 91:1-312.

Huffaker, C. B., C. E. Kennet, B. Matsumoto, and E. G. White. 1968. Some parameters in the role of enemies in the natural control of insect abundance. Symp. R. ent. Soc. Lond. 4:59-75.

Hull, L. A., D. Asquith, and P. D. Mowery. 1977. The functional responses of *Stethorus punctum* to densities of the European red mite. Environ. Ent. 6:85-90.

Kaddou, I. K. 1960. The feeding behaviour of *Hippodamia 5-signata* (Kirby) larvae. Univ. Calif. Publs. Ent. 16:181-230.

Kehat, M. 1968. The feeding behaviour of *Pharoscymnus numidicus* (Coccinellidae), predator of the date palm scale *Parlatoria blanchardi*. Ent. exp. appl. 11:30-42.

Kenten, J. 1955. The effect of photoperiod and temperature on reproduction in *Acyrthosiphon pisum* (Harris) and on the forms produced. Bull. ent. Res. 46:599-624.

________. 1969. Zur Morphologie und Biologie von *Anatis ocellata* (L.) (Coleoptera: Coccinellidae). Z. angew. Ent. 63:412-445.

Kilian, L. and M. V. Nielson. 1971. Differential effects of temperature on the biological activity of four biotypes of the pea aphid. J. econ. Ent. 64:153-155.

Klomp, H. 1962. The influence of climate and weather on the mean density level, the fluctuations and the regulation of animal populations. Arch. néerl. Zool. 15:68-109.

Kovář, I. 1973. Taxonomy and morphology of adults, pp. 15-35. *In* I. Hodek (Ed.), Biology of Coccinellidae. W. Junk, The Hague.

Lotka, A. J. 1923. Contribution to quantitative parasitology. J. Wash. Acad. Sci. 13:152-158.

Lowe, H. J. B. 1971. Relationship of the movements of aphids over the host-plant to their spatial distribution. Bull ent. Res. 60:599-605.

Mackauer, M. and P. Starý. 1967. "Hym. Ichneumonoidea: World Aphidiidae. Index of Entomophagous Insects." LeFrancois, Paris, p. 195.

Markkula, M. 1963. Studies on the pea aphid, Acyrthosiphon pisum Harris (Homoptera: Aphididae) with special reference to the differences in the biology of the green and red forms. Ann. agric. fenn. 2:3-29.

Messenger, P. S. 1968. Bioclimatic studies of the aphid parasite Praon exsoletum. I. Effects of temperature on the functional response of females to varying host densities. Can. Ent. 100:728-741.

Miller, C. A. 1959. The interaction of the spruce budworm, Choristoneura fumiferana (Clem.), and the parasite Apanteles fumiferanae Vier . Can. Ent. 91:457-477.

________. 1960. The interaction of the spruce budworm, Choristoneura fumiferana (Clem.), and the parasite Glypta fumiferanae (Vier). Can. Ent. 92:839-850.

Morris, R. F. 1963. The effect of predator age and prey defence on the functional response of Podisus maculiventris Say to the density of Hyphantria cunea Drury. Can. Ent. 95:1009-1020.

Nault, L. R., L. J. Edwards, and W. E. Styer. 1973. Aphid alarm pheromones: secretion and reception. Environ. Ent. 2:101-105.

Nicholson, A. J. 1933. The balance of animal populations. J. Anim. Ecol. 2:132-178.

Nicholson, A. J. and V. A. Bailey. 1935. The balance of animal populations, Part I. Proc. zool. Soc. Lond. 1:551-598.

Putman, W. L. 1955. Bionomics of Stethorus punctillum Weise in Ontario. Can. Ent. 87:9-33.

________. 1964. Occurrence and food of some coccinellids (Coleoptera) in Ontario peach orchards. Can. Ent. 96:1149-1155.

Roitberg, B. D. and J. H. Myers. 1978. Adaptation of alarm pheromone responses of the pea aphid Acyrthosiphon pisum (Harris). Can. J. Zool. 56:103-108.

de Ruiter, L. 1952. Some experiments on the camouflage of stick caterpillars. Behaviour 4:222-232.

Savoĭskaya, G. I. and B. Klausnitzer. 1973. Morphology and taxonomy of the larvae with keys for their identification, pp. 36-53. In I. Hodek (Ed.), Biology of Coccinellidae. W. Junk, The Hague.

Sharma, A. K. and B. R. Subba Rao. 1958. Description of two new parasites of an aphid from North India (Aphididae: Ichneumonidae and Pteromalidae: Chalcidoidea). India J. Ent. 20:181-188.

Siddiqui, W. H., C. A. Barlow, and P. A. Randolph. 1973. Effects of some constant and alternating temperatures on population growth of the pea aphid, Acyrthosiphon pisum (Homoptera: Aphididae). Can. Ent. 105:145-156.

Smit, W. H. 1917. Note on the feeding habits of a ladybird larva. South Afr. Jour. Sci. 13:202-305.

Smith, B. C. 1965. Growth and development of coccinellid larvae on dry foods (Coleoptera: Coccinellidae). Can. Ent. 97:760-768.

________. 1971. Effects of various factors on the local distribution and density of coccinellid adults on corn (Coleoptera: Coccinellidae). Can. Ent. 103:1115-1120.

Smith, H. S. 1935. The role of biotic factors in the determination of population densities. J. econ. Ent. 28:873-898.

________. 1939. Insect populations in relation to biological control. Ecol. Monogr. 9:311-320.

Solomon, M. E. 1949. The natural control of animal populations. J. Anim. Ecol. 18:1-35.

Storch, R. H. 1976. Prey detection by fourth stage Coccinella transversoguttata larvae (Coleoptera: Coccinellidae) Anim. Behav. 24:690-693.

Storch, R. H. and W. L. Vaundell. 1972. The effect of photoperiod on diapause induction and inhibition in Hippodamia tredecimpunctata L. (Coleoptera: Coccinellidae). Can. Ent. 104:285-288.

Sundby, R. 1966. A comparative study of the efficiency of the predatory insects--Coccinella septempunctata L. (Coleoptera: Coccinellidae), Chrysopa carnea St. (Neuroptera: Chrysopidae) and Syrphus ribesii L. (Diptera: Syrphidae) at two different temperatures. Entomophaga 11:395-404.

Thomas, W. A. 1932. Hibernation of the 13-spotted lady-beetle. J. econ. Ent. 25:136.

Thompson, W. R. 1924. Theorie mathematique de l'action des parasites entomophages et le facteur du hasard. Ann. Fac. Sci. Marseille 2:69-89.

________. 1951. The specificity of host relations in predaceous insects. Can. Ent. 83:262-269.

Tinbergen, L. 1960. The dynamics of insect and bird populations in pine woods. Arch. néerl Zool. 13:259-472.

Varley, G. C. 1947. The natural control of population balance in the knapweed gall-fly (Urophora jaceana Hering). J. Anim. Ecol. 16:139-187.

Varley, G. C., G. R. Gradwell, and M. P. Hassell. 1973. Insect population ecology. Blackwell Scientific Publ., Oxford.

Volterra, V. 1931. Variations and fluctuations of the number of individuals in animal species living together. In: Animal ecology, by R. N. Chapman. pp. 409-448.

Watt, K. E. F. 1959. A mathematical model for the effect of densities of attacked and attacking species on the number attacked. Can. Ent. 91:129-144.

Wratten, S. D. 1976. Searching by Adalia bipunctata (L.) (Coleoptera: Coccinellidae) and escape behaviour of its aphid and cicadellid prey on lime (Tilia x vulgaris Hayne). Ecol. Ent. 1:139-142.