STUDIES ON THE DISPERAL BEHAVIOUR OF APTEROUS PEA
APHIDS Acyrthosiphon pisum (Harris)

by

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DEPARTMENT OF PLANT SCIENCE

We accept this thesis as conforming
to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA
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The dispersal behaviour of apterous pea aphids, *Acyrthosipon pisum* (Harris) was studied in the laboratory and field. In the laboratory, aphids exhibited two types of behaviour while on the ground, after dropping from plants in response to predators. Most aphids showed a high frequency of turning and tended to return to the plant they left, while a smaller proportion walked in straight lines and did not return to the plant they left. Adults and older nymphs had the highest proportion of individuals which showed the second type of behaviour and adults showed the greatest tendency to disperse to plants more distant than the nearest available plants. Young instar aphids were less successful at locating a host than older nymphs and adults.

Aphids were placed on the central bean seedlings within plots, inside large field cages. Adult coccinellids were released into two of the cages while the other cage remained predator-free. Aphids in the cages with predators frequently moved between plants, while aphids in the predator-free cage did not. Adult aphids colonized more plants and had a lower mortality while on the ground than all other instars. Aphids did not show a preferred dispersal direction and the distance dispersed by aphid nymphs was proportional to the density of aphids on the plant they left. The importance of emigrating apterae in the exploitation of new resources and the regulation of aphid populations is discussed.

Bean plants infected with an aphid transmitted virus were transplanted into the central position of bean plots in the field cages.
Aphids were placed on the central infected plants and adult coccinellids were released into two of the three cages for three days. Aphids frequently moved to other plants from the centre infected plant in the two cages with predators but not in the predator-free cage. When plants were examined two weeks later, significantly more plants were infected with virus in the cages with predators than in the predator-free cage. New virus infections were correlated with plants that were visited or colonized by aphids from the central infected plant. The influence of predators in the spread of aphid transmitted diseases is discussed.

In laboratory experiments, pea aphids from Vancouver were presented with alarm pheromone from irritated conspecifics. Adult and fourth instar aphids responded to the pheromone by either dropping, running or backing up. Instars one, two and three responded to the pheromone only when a vibratory stimulus accompanied it. A high proportion of all instars responded to the double stimulus by dropping. When adult aphids from Vancouver and Kamloops were presented with alarm pheromone, the Kamloops adults exhibited a more conservative reaction to alarm pheromone. Kamloops adults also were more conservative about leaving their plant when confronted by a coccinellid predator.

A hypothesis is presented, which accounts for the differences in escape reactions between instars and biotypes. The hypothesis takes into consideration predation risk, escape behaviour repertoire and survival on the ground.

Pea aphid adults resisted heat paralysis longer than first instars when subjected to high temperature treatments. All aphids succumbed to paralysis sooner at 42°C than at 37.5°C, but there appeared to be no
difference in aphid survival in dry compared to moist conditions at high temperatures. Kamloops aphids were not more resistant to high temperatures.
Many people have contributed to the work contained in this thesis and I appreciate their help. My supervisor, Dr. Judy Myers, has provided a great deal of assistance financially, intellectually, and physically throughout this project. Dr. Bryan Frazer has been a constant source of ideas and help. Mr. Dave Rollo, Dr. Bob Elliott, and Dr. Mitch Trimble all read earlier drafts of papers contained herein, and provided useful suggestions. Dr. Ron Forbes and Dr. Richard Hamilton of Agriculture Canada helped me by suggesting ideas pertaining to aphid stylets and for providing a suitable plant virus, respectively. Ms. Rosemarie Iyer, Ms. Carol Hubbard, and Ms. Maggie Chang gave much needed assistance in both the laboratory and field. Mr. Don Pearce and his crew maintained excellent field conditions at the Vancouver study site, as did the crew at Agriculture Canada, Kamloops. Many other people have contributed as well and I thank all of them, particularly my committee, Drs. Myers, Wellington, Frazer and Runeckles for their help.
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INTRODUCTION

The pea aphid *Acrythosiphon pisum* (Harris) is preyed upon by a large number of natural enemies. These include Syrphids (Diptera), Chrysopids (Neuroptera), Anthocorids (Hemiptera), Coccinellids (Coleoptera), Hymenopteran parasites, and many other more general predators. The pea aphid has evolved a repertoire of escape behaviours to prevent capture. The aphid may kick at natural enemies which are similar in size (Evans, 1976), but in the presence of larger predators, they either run from the predator or drop from the plant (Dixon, 1958). The dropping behaviour is the major topic of this thesis.

The fact that pea aphids readily drop from their plant suggests that they are able to either return to their original host plant or locate a new plant. Host finding behaviour has been extensively studied in alate aphids (Kring, 1972) but relatively little research has been conducted on the apterous morphs. Ferrar (1969) has demonstrated that *Myzus persicae* (Sulzer) do not utilize olfactory cues when searching for a plant and Niku (1973) reported that *A. pisum* responds to vertical objects when on the ground after dropping from a plant.

The actions of natural enemies may enhance the spread of pea aphids throughout a crop. In the laboratory, the presence of predators (Niku, 1972) and parasites (Tamaki et al., 1970) was correlated with the spread of apterous pea aphids. Blanchard (1934) reported that springtail harrowing can reduce pea aphid spread and Cooke (1970) showed that rill irrigation reduces the spread of pea aphids more effectively than sprinkler irrigation.
Both rill irrigation and harrowing reduced the movement of apterous aphids between rows, suggesting that cultural practices may reduce aphid outbreaks.

Niku (1975) has shown that within a group of pea aphids, some apterae run in a straight line after dropping to the ground while others turn frequently, and respond positively to verticle stripes. He suggested that those moving in a straight line are active dispersers while those showing high turning rates are non-dispersers.

This thesis is composed of four separate studies, all dealing with dispersal in apterous pea aphids. The overall aim of the thesis is to elucidate the factors involved in the dispersal of apterous pea aphids, and the response of aphids to changes in these factors. In the first section of the thesis, I examine the behaviour of individual aphids while off their plants, and make predictions about how pea aphids will respond to predators in the field, and how environmental factors can modify dispersal behaviour. Since aphids are the most important vectors of plant viruses (Eastop, 1977), the role of predators as an agent increasing the dispersal of infectious aphids and therefore the spread of plant disease is of major importance. In chapter II, I examine the influence of adult coccinellids on the spread of a plant virus by apterous pea aphids in the field.

Dispersal is an activity which can benefit the entire population, because it allows for exploitation of new plant resources and can relieve population pressure on the colonized food plant. But it can have its costs through the mortality of dispersers and reduction of time and energy for other activities. When costs exceed benefits in any activity, we should expect the activity to be modified or eliminated through natural selection. Pea aphids exist in both the hot dry interior of British
Columbia and the milder coastal zone. Because of the hot, dry weather in the interior region, conditions on the ground should be more detrimental to aphid dispersers than would be the case on the coast. I show that conditions in the interior can result in higher mortality of dispersing apterae than on the coast. In the final two chapters of this thesis I test the hypothesis that aphids that live in situations where risks of mortality when leaving plants is high, should be more reluctant to leave their plants than aphids that live in situations where dispersal success is high, viz., the pea aphids in the interior compared to those on the coast. By examining the dispersal behaviour of pea aphids under different environmental situations, I hope to gain some insight as to how aphids exploit their food plants. Figure 1 shows a pea aphid behavioural model, upon which much of the work contained herein is based.
Fig. 1. A conceptual model of a predator-pea aphid interaction.
A flowchart illustrating the predator-prey interaction between aphids and predators. The process begins with a predator on the plant. The aphid can escape, run, or be missed by the predator. If escaped, it can either run or be captured. If captured, the aphid resists by kicking, which can lead to escape or capture. If kicked, it can either run or stay. If run, it can either find a host or be captured. If stay, it can either search or die. The flowchart also includes decision points for searching and running, with conditions for speed and time. If none of these conditions are met, the aphid is captured or dies.
Chapter I

DISPERSAL DYNAMICS
Introduction

Apterous pea aphids, *Acyrthosiphon pisum* (Harris), readily drop from plants when disturbed by natural enemies (Dixon, 1958). Pea aphid clones have individuals which immediately search for a plant after dropping, as well as individuals which leave the area before searching for a host (Niku, 1975). In laboratory exercises, when natural enemies were present, pea aphids readily dispersed from a colonized host to non-colonized plants (Tamaki et al., 1970; Niku, 1972). Therefore, the presence of predators can have a strong influence on the dispersal dynamics of pea aphids.

Dispersal movements of pea aphids were quantified under laboratory and field conditions both in the presence and absence of predators. The aim was to identify the factors influencing the movement of pea aphids among plants in field populations and to assess the cost of dispersal of different instars.

Materials and Methods

A colony of pea aphids was started from many individuals collected from alfalfa on the University of British Columbia campus, Vancouver. Aphids were reared on broad bean *Vicia faba* cv Exhibition Long Pod, under a light regime of 16L:8D at 20°C ± 1.5°C using the method of Harrison and Barlow (1972) to provide groups of aphids of known age. Maternal age was kept constant and all tests were conducted between 1100 and 1400 hr. First, second, third and fourth instar nymphs as well as three day adults
were tested. The number of aphids on a plant varied between 4 and 8.

When a group of aphids reached testing age, the host plant on which they were feeding, was placed in the centre of a 0.9 x 0.9 m cardboard arena divided into 8,100 numbered 1 cm square blocks. The grid also contained 48 vertically positioned green plastic straws in a 7 x 7 matrix with the host plant occupying the central position. Each straw was 14 cm from its nearest neighbour. Pea aphids orient to vertical stripes when searching for a host plant (Niku, 1974). Preliminary tests showed that straws were treated as if they were potential hosts by the pea aphids.

An adult coccinellid *Coccinella californica* Mannerheim which was starved for 24 hours, was released onto the central bean plant and allowed to search for aphids, until an aphid dropped from the plant. I recorded whether the coccinellid contacted the aphid before it dropped and the height from which it dropped. Pea aphids go through a period of thanotosis (death feigning) after dropping from a plant (Niku, 1975). The duration of this behaviour was recorded. Once the aphid began moving, I recorded its position on the arena grid at five second intervals, until the aphid either returned to the original plant, settled on a straw, or ceased moving for more than three minutes. The grid data were analyzed with a computer program which graphically displayed the dispersal path and computed the rate of movement, total distance moved, and the distance from the host at the end of the trial. Searching aphids exhibit rapid antennal movements and high turning rates compared to those showing running behaviour, which run in straight lines and hold their antennae rigid over their back. By observing these behavioural traits and examining the dispersal paths, it was possible to separate the two behaviour types (Fig. 2).
Results and Discussion

Statistical significance was tested with the Dixon and Massey (1969) proportions test unless otherwise indicated. Data are presented as means, percents or proportions ± one standard error.

All instars exhibited thanotosis after dropping, which increased in average duration with age although not significantly so in all cases. First instars either moved almost immediately after hitting the surface or did not move for over three minutes and were therefore disqualified from the tests.

Neither height of fall or physical contact by coccinellids had any effect on the length of the thanotosis period. This differs from Niku's (1975) observation that the duration of thanotosis is negatively correlated with the height of fall. Niku purposely varied the height of fall between 10 and 100 cm whereas my differences of between 10 and 25 cm were due to chance.

Characteristics of running and searching behaviour are given in Table 2. Searching aphids show a higher turning rate than runners, and also move at a slower rate. The aphid movement rates I observed are similar to those shown by Phelan et al. (1976) for aphids dropping after alarm pheromone stimulation. Whether an aphid shows running or searching behaviour, influences which host it settles upon. Searching aphids more frequently returned to the original plant than aphids exhibiting running behaviour (Table 2). Adult pea aphids ran more often (Table 1) and returned to the original host plant less often (p < 0.05) than all other instars (Fig. 6). Adults moved onto straws more distant than the nearest straw.
more often than all other instars (Table 1).

Generally, aphids either searched or ran although in a few cases, mostly in the adults, aphids showed both behaviours separated by resting periods of 5 seconds to a minute.

Most adults which were searching, found new host plants (94%) but first and second instars were less successful with only 55% of first and 78% of second instars finding new hosts while searching. When the first two instars fell within 3 cm of a host, they walked directly to it, but beyond that distance they usually showed a high frequency of small turns in their search paths. From these results it appears that older instars are more capable of locating host plants at greater distances than young instars.

The results from the grid studies allowed me to make some predictions regarding the aphid-predator interactions in the field:

(1) The presence of actively searching coccinellids should result in the dispersal of some individuals of all instar classes to new host plants.

(2) Adults, which more frequently adopt running behaviour, should disperse more widely in field plots and should be found beyond the nearest available plants more frequently than the other instars.

(3) Because the younger instars are less successful in locating plants they are expected to suffer higher mortality.
Fig. 2. Comparison of search and run behaviour paths by adult pea aphids (drawn to scale). The points indicate the position of the aphid at five second intervals. P = Host plant. S = Position of aphid after it drops from plant.
Table 1. Behaviour of each instar of the pea aphid after dropping from a plant in the laboratory.

<table>
<thead>
<tr>
<th>Instar</th>
<th>N</th>
<th>Thanotosis Duration (sec. ± SE)</th>
<th>Proportion Running ± SE</th>
<th>Proportion of successful host finders going to a new host ± SE</th>
<th>Proportion of successful host finders going beyond nearest host ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>46</td>
<td>13.31 ± 2.15</td>
<td>.23 ± .07</td>
<td>.54 ± .07</td>
<td>.26 ± .06</td>
</tr>
<tr>
<td>4'th</td>
<td>40</td>
<td>12.58 ± 2.53</td>
<td>.15 ± .06</td>
<td>.33 ± .07</td>
<td>.13 ± .05</td>
</tr>
<tr>
<td>3'rd</td>
<td>22</td>
<td>6.20 ± 2.04</td>
<td>.05 ± .05</td>
<td>.32 ± .10</td>
<td>.14 ± .07</td>
</tr>
<tr>
<td>2'nd</td>
<td>28</td>
<td>2.80 ± 0.90</td>
<td>.03 ± .03</td>
<td>.29 ± .09</td>
<td>0</td>
</tr>
<tr>
<td>1'st</td>
<td>12</td>
<td>0.46 ± 0.16</td>
<td>.08 ± .08</td>
<td>.33 ± .14</td>
<td>.08 ± .08</td>
</tr>
</tbody>
</table>
Table 2. Comparison of pea aphids showing running and searching behaviour.

<table>
<thead>
<tr>
<th>Behaviour Type</th>
<th>N</th>
<th>Speed cm/sec</th>
<th>Turns/5 sec</th>
<th># aphids that return to their original host</th>
<th># aphids that went to hosts beyond the nearest host</th>
<th>Distance (cm) from original host that aphid settled</th>
</tr>
</thead>
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<tr>
<td>Running</td>
<td>11</td>
<td>0.67 ± .03</td>
<td>0.18 ± .06</td>
<td>0</td>
<td>8</td>
<td>31.3 ± 4.8</td>
</tr>
<tr>
<td>Searching</td>
<td>35</td>
<td>0.27 ± .01*</td>
<td>0.75 ± .04*</td>
<td>21**</td>
<td>3**</td>
<td>5.8 ± 1.8*</td>
</tr>
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* Significantly different (p < 0.05) using Dixon and Massey's proportion test.

** Significantly different (p < 0.01) Chi Square.
Field Studies

Materials and Methods

Field experiments were conducted in cages measuring 3 x 3 x 1.85 m high, modified from the design of Woodford (1973) and Farrar (1963). The walls were nylon screen mesh size 7 threads/cm. The cage environment was similar to that outside, although day temperatures were 1° to 2°C cooler and night temperatures were 1° to 2°C warmer inside. Solar insolation was reduced by the screen but did not visibly affect plant growth.

Each cage contained 4 plots each 0.85 x 0.85 m in size, with approximately 0.65 m of bare soil between plots and 0.3 m between plots and cage walls. The distance between plots was such that aphids rarely moved between plots, although coccinellids could freely do so.

Within each plot, I transplanted a 7 x 7 array of broad bean seedlings. Each plant was 14 cm from its nearest neighbour. The cages were kept weed free.

Pea aphids were collected from alfalfa on the University of British Columbia campus, and placed on broad beans in a screen house for three days to acclimatize them. After four days the aphids were separated into age classes. Because of the difficulties of rapidly identifying instars in the field, we considered only three age classes: young nymphs of first and second instars; old nymphs consisting of third and fourth instars, and apterous adults.

I placed 15 aphids (5 from each class) on the centre plant in each plot. A plastic ring coated with Fluon® (a plastic coating too smooth for aphids to walk on) was placed around the centre plant for one day to ensure
that the aphids settled on their host. At the end of twenty-four hours, the ring was removed and twenty-five male coccinellids, *C. californica*, were released into the two experimental cages while the control cage remained predator free.

Aphids and beetles were counted on every plant in each plot at 900, 1100, 1300, 1500 and 1700 hr (PDT) each day with the aid of dental mirrors (Tamaki et al., 1970). In addition, casual observations were made on the activity of beetles between counts, and I recorded whether they were actively moving about and whether beetles entered any plots.

Aphid movements were calculated from the changes in occupation patterns on plants within a plot from one observation to the next. With the density of aphids and coccinellids that were used, the counts and estimates were accurate over the five days of each experiment.

From laboratory observations it was estimated that 70% of the aphids dropped from a plant when a predator entered an aggregation of between 5 and 15 aphids. Therefore, if a beetle interacted with an aggregation of ten aphids, I would assume that seven dropped and three remained. If the original plant now held two aphids and I found three on other plants, I would estimate that one was killed on the plant and five died on the ground. The return of aphids was estimated in three ways: (1) by direct observation of a beetle-aphid group interaction; (2) by the return of an aphid which was missing during one census and showed up on the next; (3) by the presence of more aphids than I would have estimated if 70% left the plant. In all cases it was obvious if a beetle had interacted with a group of aphids because the remaining and returning aphids were scattered over the plant instead of aggregated.
When possible, I calculated the fecundity of dispersing aphids on the day of dispersal and on the following three days. Fecundity was measured as the number of offspring per day-degree, above a threshold of 4°C (Campbell et al., 1974). Temperatures fluctuated during the day and aphid birth rate increases with temperature. The fecundity of some aphids was measured over six hours and others over eight hours. The use of the physiological time scale allowed all measurements to be rendered to the same base.

Results

Aphids frequently moved between plants in the experimental cages, but rarely in the predator free cages. The few movements observed in the control cages were found to be associated with the presence of coccinellid larvae that had managed to enter the cage. In all other cases, aphids in the predator free cage were tightly packed, indicating an undisturbed state (Phelan et al., 1976). Aphids were rarely found clumped in cages when predators were present and never for the duration of a trial.

The relationship of coccinellid position and aphid movement is shown in Table 3. For all three age classes of aphids, coccinellids were found in the vicinity of the aphid infested plant, when aphid movements were recorded.

Direction of aphid dispersal

The direction of aphid movement was calculated by measuring the angle
between the plant the aphid left and the new host. The path taken was considered to be a straight line. The angular measurements were pooled into sixteen, 22.5 degree arcs. The data were analyzed using the method of Batschelet (1965) to determine if the aphids had a preferred direction of movement. \( R \) refers to the tendency for movement to occur in one direction. \( R \) equals 1 when all movement is in one direction, whereas \( R \) equals 0 when dispersal is equal in all directions. In this study, \( R \) was between 0.074 and 0.2 for all instars.

Aphid density and dispersal distance

Dispersal distances were calculated and compared with the density of aphids on the plant from which the aphids left. Aphid density was positively correlated with the dispersal distance in the immature aphids (Figs. 3 and 4). The relationship was not significant for the adults.

Effects of dispersal on fecundity

The fecundity of aphids was significantly \((p < 0.05)\) lower on the day after dispersal than at all other times (Fig. 5). Fecundity was slightly lower on the day of dispersal, measured after the aphid reached a new plant, than on the second and third day after dispersal but the difference was not significant at the 5% level. The fecundity of aphids in the control cage was the same as non-dispersing aphids in the experimental cages.

Mortality factors

Of the aphids that left their plants, significantly more \((p < 0.05)\)
young nymphs were never found in later counts (Table 4). Of the aphids which remained on plants during a coccinellid encounter, young nymphs had higher mortalities than adults ($p < 0.001$) or older nymphs ($p < 0.05$). Similarly, the mortality of old nymphs after encounters with predators was twice that of adults (N.S.).

**Distribution of dispersers**

The distances moved by aphids of the three age groups differed significantly ($p < 0.001$ Chi Square) (Fig. 6). Almost twice as many adults and old nymphs went to new plants after leaving their original host, as did young nymphs (Table 5). Almost three times as many adults and twice as many old nymphs moved beyond the nearest available plant than was the case for the younger nymphs (Table 5).

**Discussion**

Niku (1972) released *Syrphus corollae* (Fab.) larvae into small greenhouse plots in which the centre plants were colonized by pea aphids. Four days later, aphids were found throughout the plots, while the spread of aphids in the predator-free plots was minimal. Tamaki et al. (1970) obtained similar results by releasing *Aphidius smithi* Sharma and Subba Rao into pea aphid colonies. These studies suggest that natural enemies are important in the dispersal of apterous pea aphids and the present experiments have confirmed this.

Laboratory experiments can rarely duplicate nature; however, these
Table 3. Aphid movements in relation to the location of coccinellids.

<table>
<thead>
<tr>
<th>Coccinellid Position</th>
<th>Adults</th>
<th>Old nymphs</th>
<th>Young nymphs</th>
</tr>
</thead>
<tbody>
<tr>
<td>On host plant</td>
<td>.39 ± .06</td>
<td>.28 ± .06</td>
<td>.36 ± .04</td>
</tr>
<tr>
<td>On adjacent plant</td>
<td>.29 ± 0.6</td>
<td>.22 ± .06</td>
<td>.39 ± .04</td>
</tr>
<tr>
<td>In plot</td>
<td>.21 ± .05</td>
<td>.29 ± .07</td>
<td>.16 ± .03</td>
</tr>
<tr>
<td>None active</td>
<td>.11 ± .04</td>
<td>.17 ± .05</td>
<td>.10 ± .03</td>
</tr>
</tbody>
</table>

Total number observed  
62  46  132
Fig. 3. The relationship between the distance a young nymph dispersed and the density of aphids on the plant from which the aphid left. The number beside each point indicates the sample size.
\[ y = 2.35 + 0.14x \]

\[ r = 0.29 \quad p < 0.01 \]
Fig. 4. The relationship between the distance an old nymph dispersed and the density of aphids on the plant from which the aphid left.
\[ y = 2.87 + 0.17x \]

\[ r = 0.47 \quad p < 0.05 \]
Fig. 5. The relationship between fecundity and dispersal in pea aphids.

The number beside each point indicates the sample size.

ND = non-dispersers; C = aphids in predator-free cage.
Table 4. Direct and indirect pea aphid mortalities from coccinellid-aphid interactions.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Killed on plant ± SE</th>
<th>Died on ground ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult</td>
<td>100</td>
<td>.09 ± .03</td>
</tr>
<tr>
<td>Old nymphs</td>
<td>49</td>
<td>.16 ± .05</td>
</tr>
<tr>
<td>Young nymphs</td>
<td>315</td>
<td>.18 ± .02*</td>
</tr>
</tbody>
</table>

* Significantly different from adults and old nymphs (p < 0.05)
** Significantly different from adults (p < 0.001) and old nymphs (p < 0.05)
Table 5. Comparison of success of three age classes of the pea aphid in finding new host plants, after leaving their host.

<table>
<thead>
<tr>
<th>Age class</th>
<th>N</th>
<th>Proportion returning to host ± SE</th>
<th>Proportion finding new plant ± SE</th>
<th>Proportion finding new plant beyond nearest plant ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults</td>
<td>91</td>
<td>.27 ± .05</td>
<td>.67 ± .05</td>
<td>.31 ± .05</td>
</tr>
<tr>
<td>Old nymphs</td>
<td>41</td>
<td>.22 ± .06</td>
<td>.61 ± .08</td>
<td>.22 ± .06</td>
</tr>
<tr>
<td>Young nymphs</td>
<td>257</td>
<td>.28 ± .03</td>
<td>.34 ± .03*</td>
<td>.11 ± .02**</td>
</tr>
</tbody>
</table>

* Significantly different from adults and old nymphs (p < 0.001)

** Significantly different from adults (p < 0.001) and old nymphs (p < 0.05).
Fig. 6. The frequency distributions of dispersal distance in three age classes of the pea aphid in the laboratory and field. 1 = Adults; 2 = Old nymphs; 3 = Young nymphs.
Proportion of dispersed aphids ± S.E.

Returns
Distance dispersed in cm
15
30
45
65

Field
Lab
studies point out important aspects of a behavioural process. I found two behaviour types, runners and searchers, in the laboratory studies. Niku (1975) made similar observations on a different biotype of the pea aphid. An important feature of these differences in behaviour is that one type allows the aphid to return to the plant from which it dropped. The behaviour of the other type reduces the probability of its returning to the original plant.

More aphids returned to their original host plants in the laboratory studies than in the field. This is probably due to differences in terrain between the two studies. In the laboratory, all instars easily moved in the paper arena. Natural terrain is never as flat as that in the laboratory, and from the aphid's perspective, it is a rough plain strewn with very large masses. I often observed an aphid to change course after encountering difficulty moving over the ground. This was especially true for the younger instars when the ground was dry and soil particles loose. It appears that, even though the laboratory experiments allowed for an estimation of the proportions of aphids that are motivated to return to a plant, physical effects can modify the actual numbers that do so.

The proportion of aphids which were unsuccessful in finding plants while on the ground, was highest in the young instars. Since the cages excluded predators which are normally present on the ground, I assume that those aphids died before finding a host plant. In the laboratory, many young instars did not move after dropping to the ground, and a high proportion of those that did, did not find a plant in the time allotted. Aphids which spend more time on the ground are exposed longer to the detrimental conditions found there. On warm sunny days, coccinellids are most active
Temperatures were measured within the bean plant foliage and on the ground with a Yellow Springs Instruments thermometer. When the average temperature within the foliage was $18^\circ C \pm 1.0^\circ C$, the ground temperatures were $25.4^\circ C \pm 2.1^\circ C$. Although aphids can withstand temperatures as high as $41^\circ C$ for twenty-five minutes (Harrison and Barlow, 1973), experiments in chapter IV show that they are unable to walk after a short time when exposed to high temperatures (6.2 minutes for adults $N=90$ and 2.8 minutes for first instars $N=80$, both at $42^\circ C$). That means that survival on the ground is dependent upon the length of time the aphid can continue to walk in search of a new plant. Young instars are in double jeopardy if they leave a plant because they are less successful at finding new plants and are more susceptible to the high ground temperatures than adults. I suggest, therefore, that young instars should require a stronger stimulus to elicit drop behaviour, compared to older instars. First, second and third instar pea aphids only respond to alarm pheromone when it is accompanied by a vibratory stimulus, while adults and fourth instars respond to alarm pheromone alone (chapter III). If risks are higher for young instars, and the data indicate they are, one would expect young instars to return to their host plant as quickly as possible. This does occur, because thanotosis duration is shortest in the younger instars and only two of forty young instars exhibited running behaviour in the laboratory. Young nymphs rarely dispersed beyond the nearest host.

Young instars are also under greater pressure from predation while on their host plant. The proportion of aphids that were estimated to have been taken by predators was significantly higher for young instars than
adults. Frazer and Gilbert (1976) reported similar differential predation mortalities between pea aphid instars on alfalfa.

Pea aphid fecundity is less the day after dispersal, which may be due to two causes. First, the aphid is unable to feed but continues to use energy reserves while on the ground. Fecundity is not affected on the day of dispersal, probably because the embryos to be born that day are already formed (Ulchanco, 1921; 1924). However, the inability to feed and the energy used for dispersal may affect the development rate of the embryos to be born the following day. Randolph et al. (1975) showed that as much as 91% of the energy required for the production of young comes from the food an aphid ingests. Roff (1977) found that a reduction in fecundity related to the energy costs of dispersal in Drosophila, and Burns (1971) showed that flight in the vetch aphid Megoura vicia Buckton, reduces the number of young produced. High ground temperatures may also harm developing embryos when the aphid is dispersing (Muride, 1969a).

Thus far I have focused on the process of dispersal in the apterous pea aphid. The costs and benefits of that process will now be examined, not only for the pea aphid, but as it may relate to other species of aphids. Van Valen (1971) and Lidicker (1962) have discussed the importance of emigration in population regulation and the colonization of new resources. In populations composed of solitary individuals, the advantages of emigrating (new resources, higher chance of finding a mate, etc.), must be weighed against the costs (greater potential mortality, lower fecundity) for that individual. When a family group occupies a single resource unit, the costs and benefits of dispersal can be analyzed from the group's standpoint as well as the individual's (Myers and Campbell,
1976). If we view aphid clones as one "individual" made up of many parts (cf Jansen, 1977), then the risks can be spread between the total number of aphids of that "individual". Emigration of some of the aphids relieves population pressure on those which remain on the known resource while possibly extending the clone to new resources. Overall fitness of the clone will be maximized by a balance of the number of aphids which emigrate, to those that stay. In this way, there is competition between clones to most effectively balance their proportions of different behaviour types to suit different environments.

When the host plant is declining, two tactics might be employed. First, aphids may immigrate to new plants by developing winged forms. A second ploy is to reduce competition on the plant through a reduction in size and fecundity of the adults which remain (Murdie, 1969b). When plant quality is good and is expected to remain so, then selection should favour high numbers of apterous non-dispersers, since these produce more young than alates (MacKay and Wellington, 1975) and they avoid the risk of dispersal mortality.

Predator influenced dispersal of apterous aphids is an extension of the principles discussed above, but with one major advantage over alate dispersal. The production of alates in response to declining resource quality has a lag time of up to one generation. Apterous dispersers eliminate this lag. Niku (1975) suggests that running behaviour increases in frequency in aphids dropping from plants, as plant quality decreases. Way (1973) noted that migratory urge in apterae may increase with increasing crowding. Both of these suggestions are consistent with the argument I have developed for aphid emigration in general.
The presence of a predator in the vicinity of an aphid decreases the survival value of its staying on the plant and therefore makes dispersal a more favourable option. Selection pressure from predators will reduce the probability of over crowding of aphids on a plant. Therefore, if aphids have evolved with predation as a regulating force either by dispersing the population or through predator induced mortality, then those aphids are likely to lack mechanisms to prevent overcrowding in an environment without predators. For example, the alfalfa aphid *Theroioaphis maculata* (Buct.), like the pea aphid, readily leaves the host plant when disturbed. In the absence of predators, this species continues to multiply at high rates until the host plant collapses (Messenger and Force, 1963).

Not all species of aphids readily drop from host plants when disturbed and so we should expect to find differences in lifestyles between the two if both can avoid depleting their food resources. We can view the production of alate emigrators and readily dispersive apterae as intrinsic mechanisms which allow populations to lower their numbers below carrying capacity. Extrinsic factors such as predator or other physical disturbance can also be important in emigration, much more so in some species than others.

In many species of aphids, apterae seldom leave a plant. The cabbage aphid *Brevicoryne brassicae* (L.) is a sedentary aphid and is found tightly packed on plants. Apterae rarely leave their plants and when they do it is across plant bridges (Hughes, 1963). We suggest that *B. brassicae* should be very sensitive to plant conditions which stimulate alate production. In fact, young aggregates of *B. brassicae* contain alates.
(Way and Cammell, 1971), but they do not necessarily emigrate (Way, 1973). In contrast, the pea aphid, at least the Vancouver biotype, does not produce alates at low densities. A test for the hypothesis that aphids which are reticent to leave the host plant as apterates should have a lower threshold for alate production, comes from observations on the Kamloops biotype pea aphids. Summer weather in Kamloops is hotter than in Vancouver. Higher mortality on the ground associated with hotter ground temperatures may have lead to the observed reduced dispersal by apterae of the Kamloops biotype in comparison to the Vancouver biotype (chapter III). The Kamloops biotype produces alates in the laboratory even at low densities while the Vancouver biotype does not. Sutherland (1969) has shown that different strains of the pea aphid can have different sensitivities to stimuli that promote alate production.

The black bean aphid *Aphis fabae* Scopoli, is often found in dense aggregations and it does not drop in response to predators, although apterae will leave their plants when food quality is poor. *A. fabae* clones contain alates which vary quantitatively. Some alates fly long distances, others colonize nearby plants and still others do not emigrate at all. The proportion of alates showing the migratory urge is affected by crowding (Shaw, 1970). This is similar to my observations on the distance dispersed by apterous pea aphids, in that crowded nymphs disperse farther (Figs. 3 and 4). Wolfenbarger *et al.* (1975) made similar observations on *Myzus persicae* (Sulz.) under highly artificial conditions. It is curious that adult pea aphids did not show a relationship between distance dispersed and aphid density. The reason may be related to the manner in which the different instars are aggregated on a plant. Young
instars are tightly aggregated, and adults, especially those that have been disturbed, may be in loosely aggregated groups or isolated on a plant. My data considered only aphid density per plant and not the degree of packing of that group of aphids on the plant. Because of the way in which they are aggregated on plants, total population numbers are likely to be more realistic estimates of the size of the group the aphid left, for a young instar, than an adult. Future experiments on this phenomena should centre on aggregate size (cf Way, 1968).

Aphids whose apterae readily disperse from their plants, probably are distributed differently in the field than species that rarely disperse as apterae. The pea aphid, for example, should be more evenly dispersed around a central colonization point than the black bean or cabbage aphid. Way (1968) showed that even at low total population densities, A. fabae can be distributed so that most of the aphids are crowded beyond an optimal level on a few plants, while many of the available plants are not colonized. The pea aphid on alfalfa is much more evenly distributed in the field and group sizes tend to be small.

The activities of predators can effect the distribution of aphids within a field in two ways. In species whose apterae do not disperse, predators could keep populations sufficiently low that alates are rarely produced. The distribution of clones in the field would remain nearly constant. In contrast, species whose apterae readily leave the plant could be spread throughout a field without alates being produced. If predators are adapted to search for groups of prey, a more uniformly dispersed aphid population would be perceived as a lower density population. Therefore, predator activity could spread the aphids to the extent that the predator would leave even though the number of aphids in the area was still
relatively high (cf Murdoch and Oaten, 1975).

Population studies rarely take into account, movements within a system because of the difficulties involved in measuring them (cf Gilbert et al., 1977). The large staff required to follow aphid movements and the difficulties in marking aphids (Petterson, 1969), make large scale studies of aphid movements impractical. Because of these difficulties, ecologists often ignore movement even though it is known to be an important process in many species of insects, e.g. cherry bug (Fujisaki, 1975), cinnabar moth (Myers and Campbell, 1976), cabbage butterfly (Jones, 1976).

The present studies provide information on between plant movements of pea aphids when food plants are discrete and separated by short distances (14 cm). Future studies should evaluate this process when plant and other environmental characteristics are varied. It may be possible to gain further insight into how aphids exploit food plants under different circumstances by comparing a variety of aphid species and of different biotypes within a species: those that readily disperse as apterae as well as those, whose apterae rarely leave plants in response to predators. Earlier I alluded to the importance selection might play in adjusting the ratio of runners and searchers in pea aphid clones under different circumstances. Pea aphids which colonize plants that exist as large continuous mats should be more prone to drop from plants and show running behaviour, than aphids which live on discrete plants separated by long distances since their apterae would largely be unsuccessful in finding new plants. Myers and Campbell (1976) found an association between plant spacing and the tendency of cinnabar moth larvae to drop from plants when disturbed. It may be possible to compare the apterae of readily dispersing species and
species whose apterae do not readily disperse, in terms of MacArthur and Wilson's (1967) r and K model. For example, the pea aphid readily disperses, has a relatively high fecundity (Frazer, 1972), and its populations on a plant are often brought below carrying capacity by external forces (i.e. predator induced dispersal from clones). The cabbage aphid is a sedentary species, has a relatively low fecundity (Way, 1968) and maintains its population below carrying capacity through intraspecific mechanisms.
Chapter II

THE SPREAD OF A PLANT VIRUS
Introduction

Aphids are the most important vectors of plant virus diseases. Of the 620 known plant viruses, 164 are aphid transmitted (Eastop, 1977). Control of virus spread by the use of chemical aphicides has met with mixed success (cf Adams et al., 1976). Reflective soil mulches reduce the ability of virus carrying aphids to locate host plants (Smith and Webb, 1969), and non-toxic chemicals can be used to reduce transmission success (Bradley et al., 1966). Natural enemies may eventually control aphid numbers, but do not necessarily lower virus incidence (Grylls, 1972).

Aphid predators are not always successful in capturing their prey (Dixon, 1958), and their searching behaviour dislodges prey from the host plant. This interaction disperses aphids to new host plants (Tamaki et al., 1970; Niku, 1972) which can have serious implications for the spread of virus disease. Frazer (1977) suggested that the spread of Alfalfa Mosaic virus by pea aphids may be increased by the presence of their coccinellid predators. In this chapter, I examine the influence of adult coccinellids on the spread of a strain of Bean Yellow Mosaic virus (BYMV) by the pea aphid Acyrthosiphon pisum (Harris) to broad beans.

Materials and Methods

The BYMV isolate was obtained from Dr. R. Hamilton, Agriculture Canada, Vancouver. The virus had been maintained by mechanical transmissions to broad bean Vicia faba cv Exhibition Long Pod in the greenhouse for 1 year.
BYMV is transmitted in a non-persistent manner (i.e. readily picked up on and lost from the mouthparts of the vector) by pea aphids. Obvious symptoms of chlorotic mottling, often with leaf margins rolled down, show in broad beans ten days after inoculation when grown in the greenhouse.

Fifteen bean seedlings were mechanically inoculated and after ten days, eight plants showing definite symptoms were transplanted to the central position of a 7 x 7 array of healthy bean seedlings in 0.85 x 0.85 meter plots. Each plant was 14 cm from its closest neighbour. All experiments were conducted in the large field cages 3 x 3 x 1.85 meters with walls of nylon screen, 7 threads/cm used earlier. Conditions in the cage were similar to those outside, although air temperatures in the cage were generally 1° to 2°C cooler during the day and 1° to 2°C warmer at night. Three plots were planted in each of the two experimental cages and two plots in the control cage.

Pea aphids were collected from alfalfa growing near the field cages on the University of British Columbia campus, Vancouver. The aphids were placed on bean plants in a screen house to acclimatize them. In order to rapidly identify individuals in the field, we separated the aphids into three major classes:

(1) apterous adults
(2) third and fourth instars
(3) first and second instars

Fifteen apterous aphids, five from each class, were placed on each of the central plants in each plot and allowed to settle for twenty-four hours.

Twenty adult coccinellids, Coccinella californica Mannerheim were released into each of the experimental cages. Beetle and aphid censuses
were 900, 1100, 1300, 1500 and 1700 hr. (PDT) each day. I was able to ascertain numbers and positions of all of the aphids without disturbing them by using dental mirrors (Tamaki et al., 1970). Through frequent censuses, the identity of individual aphids in each plot was known.

Three days after the release of the coccinellids, the central plant in each of the experimental plots harboured few or no aphids. The experiment was terminated after three days and all of the aphids from all plants in each of the eight plots were removed. The cages were kept closed for twelve days and then the plants were examined for virus symptoms.

Twenty-five field collected aphids were placed individually onto bean plants for 1 day. None of these plants showed any signs of virus infection after fourteen days, so it was assumed that all infected plants in the experiment were produced by aphids having acquired the virus from the diseased central plant.

Results

Aphids in the cages with coccinellids frequently moved between plants but only 4 of the 64 aphids in the two control plots left their host plant. The aphids on the control plants were in dense colonies while those in the experimental plots were far less aggregated. At the end of three days, the aphid populations were larger in the control plots than the experimental plots (Table 6). In 89.5% ± SE 7.0 cases of observed aphid movements, active coccinellids were present in that plot.

In the experimental plots, an average of 11.33 (range 9 to 15) new
plants were colonized by aphids from the central plant compared to an average of only 2 (range 1 to 3) in the control plot (Table 6). Because the virus was non-persistent, only movements of aphids from the infected plant to new plants were considered as potential inoculations. In actuality, an average of 16.66 (range 10 to 24) plants per plot were visited by aphids in the cages with coccinellids compared to a mean of 2 (range 1 to 3) in the control cage. New virus infections were significantly higher ($p < 0.001$) in the experimental plots. Figure 7 shows the distribution of infected plants in each of the eight plots.

The infection front was calculated by measuring the most distant infected plant from the central plant. Sixty cm was the maximum distance the infection could spread in any plot, and this was reached in four of the six experimental plots (Table 6). The average distance was 55.40 cm ± 3.10 in the experimental plots and only 14 cm in both of the control plots.

All except five of the newly infected plants were known to have received aphids from the central plant. Adjacent plants to the five exceptions had received colonizers from the central plant. It is highly likely those aphids visited one of those five plants before settling on the adjacent plant.

**Discussion**

Apterous pea aphids frequently drop from the plant and move to new hosts when disturbed by predators (Niku, 1972). Ferrar (1969) has suggested
that apterous aphids may be important in the spread of plant viruses. Considerable controversy exists as to whether apterous or alate aphids are the more important field vectors of plant virus diseases (Broadbent, 1965; Ribbands, 1965). Watson and Healy (1953) showed that *Myzus persicae* (Sulz.) apterae can be important vectors when infection sources are randomly distributed within a crop. Ribbands (1962) reported heavy coccinellid predation of apterates coincident with the spread of beet yellows. In another study on groundnuts, Booker (1962) noted the correspondence between heavy predation on aphid populations and the short time that an aphid population persisted on any one plant. As in the present study, plant disease was more closely related to the number of plants infested by aphids rather than to total aphid numbers.

Where timing of virus inoculation is crucial to the existence of high virus incidence, the activity of aphid predators may actually enhance the probability of vector spread. We might envision the following scenario: a number of infectious alates alight in different sections of an agroecosystem, creating a number of point source infections. Barley yellow dwarf virus is only economically damaging for a short part of the early growing season (Doodson and Saunders, 1970). The aphid populations build up, but not to such extremes that alates are produced. In the presence of predators, the apterous aphids disperse, creating patches of infected plants as opposed to point source infections. A short delay of an influx of predators until after the infectious period has passed might still allow for reduction of aphid numbers without affecting the virus spread.

In this study, the virus spread ca 4 times as far in the plots with coccinellids compared to the controls. This is probably a conservative
estimate because:

(1) In four of the six experimental plots the virus spread the maximum distance possible with the experimental design. I do not know how far the virus may have spread over the three days given unlimited space.

(2) I used a non-persistent virus so that transmission success will be small after the first plant is visited (Kennedy et al., 1962). A persistent virus could be carried on with further dispersal movements.

(3) The experiment covered only three days. Over a longer period, symptoms could develop in newly inoculated plants, and aphids from these could further inoculate non-infected plants.

These experiments have shown that the importance of predators in reducing aphid populations may be overridden by their effect on the spread of virus by dislodged aphids. Even though populations were lower in the experimental cages than in the control, virus incidence was higher. Therefore, the abundance and degree of activity of aphid predators is an important aspect of the epidemiology of aphid-borne plant viruses.
Table 6. Spread of Bean Yellow Mosaic virus by pea aphids in predator-containing and predator-free cages.

<table>
<thead>
<tr>
<th>Plot</th>
<th>Total no. aphids in plot after 3 days</th>
<th>Total plants colonized by aphids from infected plant</th>
<th>No. of infected plants after 12 days</th>
<th>Infection spread (cm)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>12</td>
<td>11</td>
<td>7</td>
<td>60</td>
</tr>
<tr>
<td>2</td>
<td>9</td>
<td>11</td>
<td>9</td>
<td>60</td>
</tr>
<tr>
<td>3</td>
<td>10</td>
<td>12</td>
<td>12</td>
<td>50</td>
</tr>
<tr>
<td>4</td>
<td>9</td>
<td>12</td>
<td>10</td>
<td>60</td>
</tr>
<tr>
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<tr>
<td>6</td>
<td>16</td>
<td>9</td>
<td>4</td>
<td>42</td>
</tr>
<tr>
<td>Control</td>
<td>47</td>
<td>3</td>
<td>1</td>
<td>14</td>
</tr>
<tr>
<td>1</td>
<td>27</td>
<td>1</td>
<td>1</td>
<td>14</td>
</tr>
</tbody>
</table>
Fig. 7. The spread of BYMV by pea aphids in cages with and without coccinellid predators.
Plots with Predators

- Infection source
- New infection

Control
Chapter III

ADAPTATION OF ALARM PHEROMONE RESPONSES OF THE PEA APHID
Introduction

When attacked by natural enemies, many aphids release a cornicle secretion. Although this secretion may be employed in a defensive manner (Edwards, 1966), an active alarm pheromone often present in the secretion warns other nearby aphids of imminent danger. Alarm pheromones are present in many species of aphids (Kislow and Edwards, 1972; Nault et al., 1973; Wientjens et al., 1973; Nault and Bowers, 1974; Bowers et al., 1977). Aphids respond to the pheromone by leaving the area of pheromone reception. This escape response is considered to be an adaptation for avoiding predators (Nault, 1973). The survival value of this will vary, however, depending upon the circumstances. For example, an individual which leaves the host plant reduces the probability of being captured by a predator on that plant, but now must face the adversities of being on the ground.

I used the pea aphid Acyrthosiphon pisum (Harris) to test the hypothesis that the response of aphids to alarm pheromone has been adjusted by their agility in avoiding predators on the plant and by the probability of their successfully finding another host plant after leaving the original plant. This suggests two hypotheses: first, variation in mobility and host plant finding ability among instars (see chapter 1) leads to the prediction that young instars should be more conservative than adults in responding to alarm pheromone. Second, aphids living in hot, dry climates are exposed to more severe stress on the ground than those living in more salubrious surroundings. I predict, therefore, that aphids from the hot, dry interior of British Columbia should respond more
conservatively to alarm pheromone than those from Coastal British Columbia, because the risks of leaving the plant are higher in the hot, dry region.

Materials and Methods

Age Class Responses

A colony of pea aphids was started from many individuals collected from alfalfa on the University of British Columbia campus, Vancouver. Aphids were reared on broad bean *Vicia faba* cv Exhibition Long Pod, under a light regime of 16L:8D at 20°C ± 1.5°C. The aphids were reared using the methods of Harrison and Barlow (1972) to provide groups of apterous aphids of known age. The groups I used, ranged in size from three to eleven individuals with one or two groups per plant. Maternal age was kept constant and all tests were conducted between 1100 hr and 1400 hr.

Cornicle secretions generally indicate pheromone release. In over 73% of the times that aphids released cornicle secretions, there was response by aphids indicating presence of biologically active levels of alarm pheromone. This is consistent with the estimate for adult pea aphids by Nault et al. (1973). Cornicle secretions will be called alarm pheromone throughout this paper since it is this active component which is of interest here.

One of three stimuli were presented to each of the groups of aphids:

1. Pheromone - A fourth instar aphid was removed from the main colony and brought within 0.5 to 1.0 cm of the group being tested. The aphid's thorax was gently squeezed with microforceps to cause the release of alarm pheromone.
(2) Vibratory stimulus - The plant was gently prodded with micro-forceps near the group being tested. This was done to simulate the presence of a natural enemy. This stimulus did not differ in its effect from that of a struggling aphid (Dixon and Stewart, 1975).

(3) Pheromone-vibratory stimulus - This is the presentation of the two stimuli described above, applied simultaneously.

The aphids were allowed three seconds to respond in each test. A group was tested only once, with one of the three stimuli. The responses recorded were:

(1) Run - The aphid removes its stylet from the plant and runs from the area where it was feeding.

(2) Drop - The aphid drops from the plant.

(3) Back up - The aphid removes its stylet from the plant and, in so doing, moves its body backwards and then remains rigid.

(4) No visible response.

Another group of adult aphids were tested to determine if the behavioural response to alarm pheromone was constant for an individual or if it varied. Environmental and rearing conditions were the same as in the previous test. Adults were exposed to alarm pheromone from a squeezed aphid. Those that dropped in response were placed on a new plant with two others that responded similarly. The aphids were again exposed to alarm pheromone twenty-four hours later and their responses recorded. Aphids that did not drop on the first day were also exposed to alarm pheromone on the following day.
Behaviour of Kamloops aphids

Pea aphids were collected from alfalfa in the interior region of British Columbia, near Kamloops. The aphids were brought to Vancouver and reared under the same conditions as the Vancouver pea aphids. Fourth instar Kamloops aphids were exposed to alarm pheromone and adult Kamloops aphids were exposed to alarm pheromone or pheromone-vibratory stimuli. Methods employed were the same as in the age class experiments.

Results

All significance tests employed either the Chi-square test or Dixon and Massey's (1969) proportions test. Results of tests are followed with * or ** respectively to indicate which test was used.

Less than 20% of any instar showed a visible response to the vibratory stimulus alone (Fig. 8). Older instars tended to respond more frequently.

A greater proportion of fourth instar and adult aphids (p < 0.01**) responded to the pheromone than the younger instars. Figure 9 shows the proportion of each type of response with back up behaviour being the most prevalent response by the oldest instars. The proportions of the different responses by instars two and three (not shown) was similar to instar one.

At least 78% of all instars responded to the pheromone-vibratory stimulus. More than 80% of the responses were the dropping type in the first four instars (Figure 10).

The dropping behaviour demonstrated by some individuals was repeatable.
Individuals which left the plant in response to pheromone on day one, dropped more frequently on day two ($p < 0.01^{**}$) (Table 7). Day one non-droppers responded significantly less on day two ($p < 0.05^{**}$) than did the total group of the first day. Data of day one were not significantly different from the data collected for adults in the age class experiments.

Fourth instar nymphs and adult aphids from Kamloops responded less than their counterparts from Vancouver ($p < 0.05^*$) (Figure 11). Aphids from the hotter, drier interior region showed a lower frequency of back up behaviour and were more reluctant to leave the host plant when stimulated by pheromone alone. However, both groups reacted similarly when exposed to the pheromone-vibratory stimulus.

Discussion

If an animal is to survive when the environment is frequently changing, it must be able to alter its behaviour and/or physiological state. The pea aphid displays plasticity in the response to alarm pheromone between instars and biotypes. Adult and fourth instar pea aphids are about three times larger than first instar pea aphids. Adults collected from the field were 3.175 mm in length ($SE=0.025, N=105$) from antennal tubercle to anal plate while first instar aphids were only 1.041 mm long ($SE=0.014, N=94$).

Related to size differences are the risks of predation associated with each instar. For example, all stages of the pirate bug Anthocoris
Fig. 8. Responses of different age classes of the pea aphid to a vibratory stimulus. The number beside each point indicates the number of aphids tested.
Fig. 9. Types of responses to pheromone stimulus by pea aphids. Second and third instar aphids respond similarly to first instar aphids.
Fig. 10. Types of responses to a pheromone-vibratory stimulus by pea aphids. Second and third instar aphids respond similarly to first instar aphids.
Instar 1 N = 64

Instar 4 N = 55

Adult N = 50

Type of response to stimulus

Proportion responding ± S.E.
Table 7. The repeatability of pea aphid responses when exposed to alarm pheromone on consecutive days.

<table>
<thead>
<tr>
<th>Day</th>
<th>Group</th>
<th>N</th>
<th>Proportion Run ± SE</th>
<th>Proportion Drop ± SE</th>
<th>Proportion Back up ± SE</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>All aphids</td>
<td>71</td>
<td>.07 ± .03</td>
<td>.18 ± .05*</td>
<td>.44 ± .06</td>
</tr>
<tr>
<td>2</td>
<td>First day droppers</td>
<td>18</td>
<td>.05 ± .05</td>
<td>.28 ± .11**</td>
<td>.33 ± .11</td>
</tr>
<tr>
<td>2</td>
<td>First day non-droppers</td>
<td>45</td>
<td>0</td>
<td>.07 ± .04</td>
<td>.22 ± .06</td>
</tr>
</tbody>
</table>

* Significantly different from day 1 non-droppers (p < 0.05)

**Significantly different from day 1 non-droppers (p < 0.01)
Fig. 11. Comparative responses of Vancouver and Kamloops aphids to pheromone and pheromone-vibratory stimuli.
nemorum (L.) (Heteroptera: Anthocoridae) are more efficient at capturing first instar than fourth instar pea aphids (Evans, 1976). In the laboratory, Frazer and Gilbert (1976) found that when a coccinellid was present on an aphid infested, the probability of a first instar pea aphid being captured and eaten was 3.5 times greater than for an adult. In the field, they found that most of the aphids captured by the beetles were the younger instars. These observations are to be expected if one examines the probable success of each escape option available to the different instars.

When predator:aphid size ratio is large, the probability of avoiding capture by running is low (Evans, 1976). First and second instars are generally unsuccessful at escaping predators whereas the older instars may be successful, especially if the predator is small (e.g. young coccinellid larvae).

Back up behaviour requires the removal of the stylet from the feeding site. The stylet lengths of earlier instars of aphids are disproportionately large. For example, first instar green peach aphid *Myzus persicae* (Sulzer) nymphs possess stylets only slightly smaller than the adults (Forbes, 1969). Presumably, the first instar needs a disproportionately longer stylet in order to reach the same feeding sites as the adults. Stylet removal may be more awkward and energetically costly to the younger instars, which appear to have difficulty doing this. For a once only response, this expenditure may appear insignificant, however, with numerous exposures to alarm pheromone, constant removal of the stylet may be detrimental to the young instars. The younger instars are reluctant to move about on the plant compared to the fourth instars and adults. Unprovoked
movements in the former tend to occur only around moulting time when
the stylets must be removed.

Dropping behaviour ensures the success of escaping predation on the
plant but this response may be costly. Aphid survival on the ground in
warm weather can be very low. Greenbugs, Schizaphis graminum (Rondani),
pushed off their host plants on a hot sunny day were unable to survive
high ground temperatures for more than four seconds (Ruth et al., 1975).
Frazer and Gilbert (1976) reported that young instars of A. pisum have a
more difficult time finding a host plant when knocked off a plant.
Young instars suffer a significantly higher mortality ($p < 0.01$) on the
ground than adults (see chapter 1), in dispersal experiments in field
cages. The mortality rates are probably even higher in the field, since
the cages shade the ground, thereby reducing ground temperatures and
potential dessication rates.

When exposed to alarm pheromone only, the younger instars may drop
or stay. Other options such as running do not significantly reduce the
probability of capture and can entail even greater risks once off the plant.
Pheromone alone signals a disturbed aphid nearby, but the signal is not
definite enough to warrant drastic action. Nearby tactile stimulus
accompanying the pheromone probably does indicate more imminent danger,
requiring an immediate response. Aphid predators show a much higher
turning frequency once an aphid has been contacted (Dixon, 1959). In
this situation, the probability of mortality from predation may be higher
than the probability of death on the ground. The dual stimulus of pheromone
and vibration caused over 90% of the first instar aphids to leave the plant.

The older instars improve their chances of survival with a larger
repertoire of escape responses. Dropping has the highest potential cost and is the least utilized. Pheromone-vibratory stimulation elicits a high probability of dropping and this complies with the argument presented for the smaller instars: when all indications are that a predator is near, it is time to leave. But, other avoidance behaviours are also successful for these instars and they occur with a relatively high frequency.

Aphids in Kamloops are exposed to a harsher environment than those in Vancouver. In a survey of maximum monthly temperatures in the summer months for the years of 1968 to 1974, the Kamloops region average maxima were 37.8°C ± 3.6°C compared to Vancouver's average maxima of 25.4°C ± 2.5°C. These differences are even greater at ground level where temperatures are much higher than ambient air temperatures. For example, I recorded ground temperatures of 40°C and 33°C when air temperatures were 31°C and 28°C respectively.

In the summer of 1977, I ran aphid dispersal tests in field cages in Kamloops, similar to those conducted in Vancouver in 1976. On-ground mortality was much higher for the Kamloops adults and first instars than it was for their Vancouver counterparts (p < 0.001*).

The Kamloops adults tend to act more like the young nymphs in Vancouver with regard to dropping. Selection would favour those individuals that utilize non-dropping escape options because of the harsh on-ground environment in Kamloops. Other physiological and behavioural differences are known to occur between different biotypes of the pea aphid. Frazer (1972) has shown difference in population dynamics between the Vancouver and Kamloops biotypes. The Kamloops adult pea aphid is more reluctant to drop in a direct confrontation with a coccinellid than the Vancouver type (see
Some individuals show a repeatable tendency to drop in response to alarm pheromone. The offspring of one female consists of droppers and non-droppers, so it appears that the trait is not characteristic of the whole clone. This mixed strategy is similar to the production of both alates and apterae by one female which allows her offspring to better exploit available resources (McKay, 1974). Those offspring which drop from the host plant may possibly find new resources. Those that stay and are not captured by predators, ensure the survival of the group of a known resource. Way and Cammell (1971) have reasoned similarly for aphid populations in which differential reproductive effort under varying circumstances ensures the maximum number of individuals of the group will reach adulthood.
Chapter IV
ESCAPE REACTIONS AND POSSIBLE EFFECTS OF HIGH TEMPERATURE ON DISPERSAL SUCCESS
Introduction

The pea aphid *Acyrthosiphon pisum* (Harris) drops from a plant when disturbed by natural enemies (Klingauf, 1967) and the micro-environment on the ground is often very different from that on the plant. Conditions on the ground may be hot and dry or wet and muddy. An aphid that leaves a plant must be able to move on the ground for long enough to find a host plant if it is to survive.

In British Columbia, pea aphids occur in many areas where alfalfa is grown. Two such areas are Vancouver and Kamloops. Aphids living in these two areas are considered to be two different biotypes and differences between the two have been shown for population dynamics (Frazer, 1972) and behaviour (chapter III).

In Kamloops, ground temperatures and evaporation rates at ground level are much higher than those in Vancouver, and this would be a greater stress on dispersing apterae in Kamloops than in Vancouver. Aphids in Kamloops could cope with this problem in two ways: (1) through reduced tendency to drop in response to predator activity, (2) through greater physiological resistance to heat and desiccation.

Pea aphids release alarm pheromone when disturbed by natural enemies (Nault et al., 1973). Alarm pheromone can elicit either run, drop, or back up escape responses from aphids which are near the aphid that releases the pheromone. Kamloops aphids of all instars and Vancouver aphids in the first three instars do not readily drop when exposed to alarm pheromone, whereas adult Vancouver aphids do. Higher mortalities on the ground in the former groups was suggested as the force selecting against dropping
in response to reception of an alarm pheromone. Relative responses to alarm pheromone provide an indirect measure of willingness to disperse. In this chapter I examine the predator-escape responses of adult aphids from Vancouver and Kamloops, to test the hypothesis that Kamloops aphids are conservative about leaving the host plant. This is done by observing the behaviour of the two biotypes when directly confronted by a predator.

Secondly, I test the physiological tolerance of the two aphid biotypes to heat and desiccation. If aphids from hotter regions are more resistant to heat and desiccation, then the conditions that they face on the ground might not be perceived as more stressful.

Harrison and Barlow (1973) showed that first instar pea aphids can survive temperatures of 41°C at near 100% relative humidity for up to 25.5 minutes. Harrison and Barlow's (1973) data cannot be used to test the hypothesis of temperature effects on pea aphid dispersal success because they did not indicate what effects the high temperatures had on behaviour. Ruth et al. (1975) showed that greenbugs, *Schizaphis graminum* (Rondani), ceased moving within four seconds of dropping to the ground on a sunny day when ground temperatures ranged from 45°C to 54°C. We also do not know what effects high evaporation rates might have on aphid survival at high temperatures. On hot, sunny days, evaporation rates at ground level would be much higher than in the closed tubes used by Harrison and Barlow (1973).
Materials and Methods

A colony of pea aphids was started from many individuals collected from alfalfa on the University of British Columbia campus, Vancouver, in the mild, moist coastal region of British Columbia. A second colony was collected from alfalfa at the Agriculture Canada Research Station, Kamloops which is situated in the hot, dry interior region of the province. The two colonies were reared separately on broad bean *Vicia faba* cv Exhibition Long Pod, under a light regime of 16L:8D at 20°C ± 1.5. The aphids were reared using the method of Harrison and Barlow (1972) to provide three-day-old adult aphids for the escape-reaction experiments and one-day-old first instars and three-day-old adults for the temperature treatment tests. All tests were conducted between 1100 and 1400 hr. The colonies were 8 generations old when the experiments began.

Escape Response Experiments

One adult coccinellid *Coccinella californica* Mannerheim (starved for twenty-four hours) was released onto a plant holding a group of three-day-old adult aphids. The beetle was allowed to search until it confronted and elicited a reaction from an aphid. Three aphid reactions were recorded:

(1) run - the aphid removes its stylet from the plant and runs to another part of the plant;

(2) drop - the aphid drops from the plant;

(3) back up - the aphid removes its stylet from the plant and, in so doing, moves its body backwards and then remains rigid.

If the aphid ran or dropped within one second of exhibiting a back
up reaction, then the reaction was not recorded as the back up type. Only results from direct confrontations were recorded. Reactions of aphids that were approached from the back or side were not recorded. In all, 61 Kamloops adults and 62 Vancouver adult aphids were tested.

High Temperature Experiments

Ground temperatures were measured with a Yellow Springs Instruments thermistor surface probe in field plots containing bean seedlings separated by 14 cm. Measurements were taken at 0900, 1100, 1300, 1500 and 1700 hr (PDT) over 2 five-day periods in Kamloops and 6 five-day periods in Vancouver. At the same time, evaporation was measured using a 1 mm bore glass capillary tube described by Wellington (1949) over a three-minute period.

The locomotory response and orientation of insects can be affected by high temperatures (Barlow and Kerr, 1969; Wellington, 1960). Adult aphids were placed in the centre of an arena with a 25 x 25 cm cardboard floor and 5 cm plastic walls which were coated with Fluon\textsuperscript{R} (a smooth plastic coating which aphids are unable to walk on) to prevent the aphids from escaping. The arena contained four bean plants which were evenly spaced 10 cm from the middle of the floor. The arena was kept in a Hot-pack temperature-controlled growth chamber at 40\degree C. Aphids were released into the centre of the arena and allowed to search for plants. Of the 20 aphids tested (in groups of 5), 14 were able to find plants before exhibiting signs of heat stupor. This showed that aphids are able to locate plants until they are paralyzed by the heat.
Temperature Chamber Experiments

Aphids were removed from their plants and immediately placed into open glass Petri dishes whose walls were coated with Fluon™. The dishes were placed into a sealed plastic box (33 x 22 x 7.75 cm high) which was kept in an incubator for testing at two temperatures, 42°C and 37.5°C.

Twenty-four hours before a group of aphids was tested, 50 gm of dehydrated silica gel was placed into the incubator and 30 gm into the plastic box. The following morning, three hours before the experiment began, the silica was renewed. In a further set of treatments, similar procedures were used but water was used instead of silica, to provide a moist atmosphere.

Aphids were tested in groups of five, two groups at one time. The plastic box had a clear cover that allowed me to observe the aphids without disturbing them. Observations were made every 5 minutes at 37.5°C and every 2 minutes at 42°C. A replicate was terminated when all aphids exhibited signs of paralysis (i.e. heat stupor); aphids that remained motionless after having fallen on their backs or sides with their legs curled inwards were considered paralyzed. Aphids in this condition usually remained that way until death. On a few occasions, an aphid would recover temporarily. I did not record such an aphid as having been paralyzed until the condition was permanent.

Each of the four aphid groups, adult and first instar Kamloops and Vancouver aphids, were tested with the following four treatments:

(1) 42°C + silica
(2) 42°C + water
(3) 37.5°C + silica
(4) 37.5°C + water

Control aphids were kept at room temperature and humidity in the
same manner as the heat-treated aphids.

Probit analysis (Busvine, 1971) was applied to the data to calculate the $\text{PT}_{50}$ (the time at which 50% of the aphids were paralyzed) and the 95% confidence limits for $\text{PT}_{50}$. A non-parametric test (Mann Witney U Test) was used to compare group mean paralysis times because the experimental design was such that paralysis times were not independent within any one group tested.

Results and Discussion

Kamloops adult aphids exhibited back up behaviour more frequently ($p > 0.001$) than Vancouver adult aphids (Figure 12). Back up behaviour is a response to predators which allows an aphid to prepare itself for immediate dropping, should it become necessary. However, the aphid does not commit itself to leaving the plant, and if the threat of predation diminishes, the aphid can reinsert its stylet and continue feeding. Coc-cinellids do not usually recognize the presence of an aphid until they contact it (Dixon, 1959). Therefore, an aphid which faces high mortality risks on the ground, should wait until the last possible moment before dropping because an approaching predator may not contact it. An aphid should only drop in response to the approach of a predator if it is able to cope with the environment on the ground of if the potential mortality on the ground is less than if the aphid were to remain on the plant. Adult aphids in Kamloops suffer higher mortality on the ground than the adult pea aphids in Vancouver ($0.33 \pm 0.08$ compared to $0.06 \pm 0.02$) ($p > 0.01$).
Therefore, the probability of capture by an approaching predator should exceed .33 before a Kamloops adult aphid drops, whereas the probability of capture need not be very high before an adult pea aphid in Vancouver should drop to improve its chances of survival. Whereas dropping behaviour eliminates the possibility of the aphid being captured while on the plant, an aphid may occasionally be captured while exhibiting back up behaviour. However, the potential mortality during back up behaviour is much lower than that on the ground in Kamloops and so the Kamloops aphid's best strategy is to exhibit back up behaviour as a preliminary step for dropping and then only drop when necessary.

Ground temperatures in Vancouver were not as high as those measured in Kamloops. The highest ground temperature recorded in Vancouver was 33°C and the mean temperature was 25.4°C (SE 2.1, N = 35). By contrast, I recorded temperatures exceeding 40°C on five different occasions on three different days during July 1977 at Kamloops; the highest temperature recorded was 44°C and the mean temperature was 31.3°C (SE 1.6, N = 30). Evaporation rates at ground level were significantly higher (p > 0.001) at Kamloops (2.9 mm/min SE 0.2, N = 30) than at Vancouver (2.0 mm/min SE 0.2, N = 35).

Adults and first instar aphids from Kamloops and Vancouver exhibited signs of paralysis far sooner (p > 0.001) at 42°C than at 37.5°C (Table 8). First instar aphids always succumbed to heat paralysis sooner than the adults. In the 42°C treatments, aphids resisted paralysis longer in the moist treatments but the differences were not significant at the 5% level. At 37.5°C, Kamloops adults became paralyzed sooner (p > 0.02) in the dry atmosphere than in moist conditions. None of the other three
classes of aphids tested became paralyzed sooner in the dry atmosphere. In fact, Vancouver adults resisted paralysis longer \((p > 0.04)\) in the dry than the moist treatment at \(37.5^\circ C\). I am unable to explain this unexpected result, although there is some evaporative cooling of the aphids in the dry atmosphere for a short time.

There was no clear pattern of a greater inherent resistance to heat paralysis by Kamloops aphids compared with Vancouver aphids. Kamloops adults resisted paralysis longer \((p > 0.003)\) than Vancouver adults at \(37.5^\circ C\) but at \(42^\circ C\) the biotypes are not significantly different. I suspect that the treatment temperatures are so high that physiological resistance at these extreme temperatures cannot be selected for without high costs to other physiological or enzymatic functions which normally occur at lower temperatures.

Since Kamloops adult aphids do not appear to be any more resistant to high temperatures, I conclude that the high ground temperatures observed in Kamloops would be stressful to their dispersing apterae. Field conditions in the dispersal experiments were similar for both biotypes, except for temperature and evaporation rates. Therefore, high ground temperatures should be considered as a factor in the higher mortality rates of Kamloops aphids since paralysis times are relatively short at high temperatures.

Kamloops aphids appear to have adjusted their escape behaviour in order to cope with higher risks on the ground rather than to adjust physiologically. First instars are not only more susceptible to high temperatures but they also tend to be exposed longer on the ground because they have difficulty locating plants and walking over the terrain in the field (chapter I). First instars appear to have made a similar behavioural
adjustment as the Kamloops adult aphids. However, first instar aphids and Kamloops adult aphids will drop from the plant when the dropping stimuli is strong enough, e.g. contact with a coccinellid. There is consistent with the argument developed earlier for dropping response in high risk situations for Kamloops adult aphids.

I consider paralysis times a more realistic indicator of potential mortality for aphids on the ground than lethal times at a given temperature. A paralyzed aphid will probably die while lying exposed on the ground unless microenvironmental conditions change radically, and even then it is not known how quickly an aphid can recover from heat stupor. Therefore, paralysis can be viewed as an indication of imminent death (Darby and Kapp, 1933).

CONCLUSIONS

These studies provide the first definitive evidence that natural enemies are an important factor in the dispersal of apterous pea aphids in the field. This is especially important from an agricultural point of view, since the actions of predators may increase the spread of plant diseases by inducing infectious aphids to disperse to virus free plants.

Pea aphids show a plasticity in behaviour not only between populations but also within individual clones. This means that the clone as an "individual" can react to a variety of situations by containing a number of behaviourally-different aphids, some of which will react
Table 8. Paralysis times of first instar and adult pea aphids from Vancouver and Kamloops at 2 temperatures and 2 humidity treatments.

<table>
<thead>
<tr>
<th></th>
<th>MOIST</th>
<th>DRY</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Temp.</td>
<td>N</td>
</tr>
<tr>
<td>ADULTS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Van.</td>
<td>42</td>
<td>60</td>
</tr>
<tr>
<td>Kam.</td>
<td>42</td>
<td>60</td>
</tr>
<tr>
<td>Van.</td>
<td>37.5</td>
<td>60</td>
</tr>
<tr>
<td>Kam.</td>
<td>37.5</td>
<td>60</td>
</tr>
<tr>
<td>FIRST INSTARS</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Van.</td>
<td>42</td>
<td>90</td>
</tr>
<tr>
<td>Kam.</td>
<td>42</td>
<td>100</td>
</tr>
<tr>
<td>Van.</td>
<td>37.5</td>
<td>60</td>
</tr>
<tr>
<td>Kam.</td>
<td>37.5</td>
<td>90</td>
</tr>
</tbody>
</table>

Paralysis times are in minutes.
Figure 12. Responses of adult Kamloops and Vancouver pea aphids in a direct confrontation with an adult coccinellid.
optimally to a given situation. If we imagine two clones of aphids living in two consistently different environments, we can expect natural selection to act upon the clones to promote greater numbers of those individuals whose behaviour best suits the environment they are in. Dixon (1971) stated that it would be surprising if different morphs of the bird cherry-oat aphid *Rhopalosiphum padi* L. exhibited similar reproductive strategies since they are exposed to different environments. The same can be said for the same morphs of the pea aphid living in different environments. If aphid clones are able to alter the proportion of behavioural and physiological types contained within, to best suit environmental situations, they may be able to track their environment. However, it is important that they maintain enough variation within the clone so that all responses are available for a given situation.

Janzen (1977) stated that we know almost nothing of aphid population dynamics because what we view as an entire field population of aphids, may in reality be a few individual clones spread wide and thin over a large area. I support this consensus and suggest that it is very difficult to determine fitness values of a particular behavioural or physiological reaction in the field because the real value can only be measured by the number of genes an "individual" contributes to the gene pool and individuals are difficult to recognize in the field. These very important problems should not discourage further research into population processes and the effects of natural enemies on aphids, but instead should provide direction for future inquiries.

The past decade has seen a resurgence in the use of natural enemies
for the control of insect pests (cf Debach, 1974). Although there have been some dramatic successes in biological control, I feel that introduction of natural enemies to control pests must be done in a cautious and well-developed manner. The results of the virus spread experiments described in this thesis point to the fact that the actions of predators may not always be economically beneficial in the final analysis.
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