DISPERAL IN PHYTOSEIULUS PERSIMILIS ATHIAS-HENRIOT
(ACARINA: PHYTOSEIIDAE)
AND ITS IMPORTANCE TO BIOLOGICAL CONTROL PROGRAMS
by
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B.Sc. (Hons.), McMaster University, Hamilton, 1978

A THESIS SUBMITTED IN PARTIAL FULFILLMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE
in
THE FACULTY OF GRADUATE STUDIES
(Department of Plant Science)

We accept this thesis as conforming to the
required standard

THE UNIVERSITY OF BRITISH COLUMBIA
April 1982

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ABSTRACT

The dispersal of *Phytoseiulus persimilis* Athias-Henriot, a predatory phytoseiid mite used in biological control of the phytophagous two-spotted spider mite, *Tetranychus urticae* Koch, has been largely ignored to the detriment of control programs. In this thesis, three aspects of behaviour were studied over the developmental period of the predator and related to dispersal. Two predictive indices for dispersal were derived.

Dispersive tendency was induced in adult female predators by confining them at high density (10 per capillary tube) and starving them for 24 hours. Dispersers were characterized behaviourally. Dispersers were typically geopositive and displayed an ability and strong tendency to distinguish edges and follow them. Dispersers moved at speeds three times greater than normal individuals, and were less efficient predators. Dispersers moved onto a novel substrate five times faster than normal individuals. Induced dispersal behaviour persisted for 40-46 hours after release, even when predators were provided with ample prey.

When released onto infested bean and cucumber plants, dispersive mites exercised poorer control on the pest population than non-dispersive predators. Prey numbers were greater and plant damage was more severe and less localized. On the young leaves of cucumber plants, predator egg placement was not harmonious with prey distribution.

The potentially disruptive affect of dispersal on control programs is discussed. A re-evaluation of predatory efficiency
in the light of this result is recommended. The need to assess the dispersive tendency of stock populations of the predator and eliminate those which are "too" prone to disperse is stressed. The impact of standard pre-release methods which apparently induce dispersal on greenhouse control programs is also discussed. The need to assess stocks which form the basis for organophosphate-resistance selection programs is also addressed. Cannibalism, inter-male aggression, substrate preference, and oviposition site selection in *P. persimilis* are also discussed.
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ACKNOWLEDGEMENTS

I am indebted to my supervisor, Dr. W.G. Wellington, for his many efforts throughout my entire Master's program to educate me, despite my schooling, in all aspects of Science. His fine exegesis of my early drafts and his seemingly inexhaustible patience have been greatly appreciated. I am also grateful for the consistent help and camaraderie provided by the staff of the UBC Plant Science greenhouse. Drs. E.S. Eveleigh, J.H. Myers, and H.A. Daubeny have all generously provided equipment necessary for this research. Dr. G.H. Gerber, many friends and relatives have been a constant source of encouragement--to you all, a very sincere "Thank you".

I am especially grateful to my summer assistants, P. Rueger, R. Smith and I. Wilkin for their faithful labour and light-hearted companionship. The cooperation of J.C. Thiele and Crane Memorial Library in allowing us access to their vast collection of "talking books" was enormously appreciated.
SECTION 1: INTRODUCTION

The first reference to the possible control of phytophagous mites by predatory phytoseiid mites was made in 1906 by Parrott, Hodgkiss and Schoene (McMurtry et al., 1970). It was not until many years later, however, that the phytoseiids received any appreciable scientific attention. Insect pests in agriculture were a more pressing problem. With the advent of potent new insecticides and acaricides in the late 1940's both insect and arthropod numbers were at first reduced. Pesticide-resistance has since been established in both groups but at apparently different rates. Moreover, insecticides seem likely to have reduced the numbers of native insects and arthropods preying upon phytophagous mites, while not harming the mites. As phytophagous mites have been perceived as a greater agricultural problem, phytoseiid predators have received more attention.

In 1960, with the report of Dosse that a population of phytophagous mites (Panonychus (=Metatetranychus) ulmi (Koch)) had been reduced and controlled by a predatory phytoseiid (Typhlodromus pyri (=tiliae Oudemans) Scheuten), interest in

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1 The taxonomy of the Family Phytoseiidae has undergone numerous revisions since the 1950's (see Chant, 1965 for review to that date) and is still a matter of some debate (Chant et al., 1978). Chaetotaxy is the major basis for taxonomic status, although the degree/nature of body sclerotizations and the shape of the spermatheca have also been used. The functional significance of these latter features remains unknown, and some authors are, therefore, conservative in their reliance on them (Chant, 1959; 1965; 1978). Thus, generic relationships within the Family Phytoseiidae vary widely with the author cited, and may or may not be illustrative of phylogeny within the family. For the purposes of this study the scheme of Pritchard and Baker (1962) modified by Schuster and Pritchard (1963) has been used. The most pertinent relationships are shown in Appendix 1.
phytoseiids increased. The prospect of controlling numbers of phytophagous mites while improving plant condition through the removal of pesticide-mediated phytotoxic effects (Gould, 1971) fueled new interest in biological control.

At approximately the same time, acarine predator-prey systems were recognized as useful study systems for more fundamental ecological research. The rapid generation time, small space requirements and ease of manipulating the components brought these systems to the attention of ecologists interested in studying population dynamics. Indirectly, these studies have provided some information pertinent to biological control. For instance, population studies have established the validity of using particular phytoseiid species based on the numerical analysis of several components of the predator-prey interaction (e.g., predator egg production, rate of development and feeding capacity).

Pest managers, on the other hand, have concentrated their efforts on discovering the right combination of release variables to ensure successful control (e.g., predator numbers needed, timing, compatibility with spraying regimes). Thus, behavioural studies of the predator and prey have been neglected although Huffaker (1958) and others have repeatedly stressed the importance of behavioural synchrony and environmental compatibility of predators and prey in biological control. Moreover, the difficulties encountered by pest managers suggest that these aspects of the predator-prey relationship are critical to successful control.
Way's comments summarize the problem:

"...at present too few research workers are able to bridge the gap between pest-control practitioners who are blinkered by short-term needs, and theoreticians or pure ecologists who have inadequate appreciation of practical realities."

(Way, 1973 in van Lenteren, 1980). This thesis is an attempt to bridge that gap.

The Phytoseiulus persimilis Athias-Henriot / Tetranychus urticae Koch predator-prey system has been the focus of considerable study, both by theoretical ecologists and pest managers. Yet the behavioural responses that define the synchrony of the system (in physiological time, in appropriate numbers and in physical space) have received little attention.

Under "some conditions" (Mori and Chant, 1966), the predator's rate of development is apparently sufficiently greater than that of the prey to allow a small initial predator population to increase and control a larger initial prey population, (Chant, 1961; Bravenboer and Dosse, 1962; Oatman, 1965; Laing and Huffaker, 1969; Takafuji and Chant, 1976). However, there has been great variability in results with P. persimilis on greenhouse cucumber and tomato (Stenseth, 1979). Thus, pest managers continue to seek a formula that will reliably duplicate successful programs within the constraints of allowable plant damage (Legowski, 1966; Oatman and McMurtry, 1966; Oatman et al., 1967; Oatman et al., 1968; Oatman et al.,

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1 The predator, P. persimilis is able to reproduce and develop when fed mites of the subfamily Tetranychinae (Ashihara et al., 1978), and has been used against a number of tetranychids other than T. urticae.
The functional response of the predator (number of prey eaten per unit time by each predator in relation to prey density) has received much attention. Mori and Chant (1966) claimed that P. persimilis took fewer prey at high prey densities than at lower densities. This anomalous result was apparently an artifact of conducting their experiments on an artificial substrate (Sandness and McMurtry, 1970; Laing and Osborn, 1974; Everson, 1979, 1980). It is now generally agreed that the predator, in fact, kills more prey and feeds less on each at high prey densities (Sandness and McMurtry, 1970; Sandness and McMurtry, 1972).

The response of the predator to low prey density is less well known. Phytoseiids are able to withstand and recover from prolonged periods of starvation (Blommers et al., 1977), but the effect this has on later predatory behaviour may be complex (Eveleigh and Chant, 1981a).

The translation of these aspects of the functional response into the numerical response (number of predators produced in the next generation in relation to prey consumption) has also been addressed. The five prey stages (egg [including prelarva], larva, protonymph, deutonymph, adult) have different motilities and body sizes. Qualitative differences in fluid content may also exist. When such prey types of different potential value (Ohnesorge, 1981) are sparsely distributed, the predator should attack all prey encountered, but abort the attempt if too much energy is required to justify the benefit (Hughes and Elner,
1979). Selection for a preferred stage should occur only at high prey densities (ibid). The stage of prey attacked by the predator will partially define the time lag before successful control is achieved and, therefore, the degree of host plant damage that will occur before the pest population is reduced (Huffaker, 1958).

Mori and Chant (1966) provided some evidence that eggs are the preferred prey stage at high prey density. McMurtry and Scriven (1975) confirmed that *P. persimilis* produces the greatest number of eggs when fed *Tetranychus pacificus* McGregor eggs and larvae, rather than equal weights of adult males and nymphs or adult females. The densities at which the predator prefers eggs to other stages, however, may be unrealistically high. Pest managers maintain that under the prey density conditions that exist in control situations phytoseiid predators feed mostly on active stages of the prey, not the eggs (Hussey et al., 1965). It is thought that the small size of eggs renders them difficult for the predator to find. Hence, a preference for this stage can only be expressed at high prey densities (Mori and Chant, 1966). Once detected, however, eggs offer no resistance to the easily-disturbed predator (ibid).

Ashihara et al. (1978) found that *P. persimilis* fed on all stages of most *Tetranychinae* but only on the adult females of *Oligonychus ununguis* (Jacobi). They, thereby, implied that prey species may interact with prey stage, in addition to prey density, in determining which prey are taken by the predator. McMurtry and Scriven (1964) also reported that greater numbers
of adult females of *O. punicae* Hirst were taken than was the case with *Panonychus citri* (McGregor). They suggested that this was due to the much smaller size of the former mite. Lee and Davis (1968) reported that immatures of *Metaseiulus* (=*Typhlodromus*) *occidentalis* (Nesbitt) were incapable of penetrating *T. urticae* eggs. Freshly laid eggs are often considered to be preferred over older eggs (Stenseth, 1979).

The availability of alternate food for the predator has also been considered. In biological control, the predator must prefer to feed on the prey rather than on other food items but the ability to withstand starvation or maintain itself on other foods is an advantage at low prey densities. This maintenance may be at a mere subsistence level (Huffaker and Kennett, 1956), or may involve limited reproduction (McMurtry and Scriven, 1964). *P. persimilis* is considered to be an obligatory predator on tetranychids but recent evidence has shown that cannibalism may sometimes occur (Laing, 1968). Ashihara et al. (1978) maintained *P. persimilis* in the absence of tetranychids on sucrose solutions and honey for over 40 days. Although reproduction did not occur while the mites were maintained on this diet, egg production resumed shortly after tetranychids were again made available, even after 35 days of feeding on only honey (ibid). Porres et al. (1975) listed seven phytoseiid species that have been shown to feed on plant juices, suggesting that this habit may be more widespread among phytoseiids than previously thought. Feeding on liquid water has been shown to have an important effect on the ability of another phytoseiid to
withstand prolonged starvation (Blommers et al., 1977).

Both the functional and numerical responses vary with temperature. It is thought that temperature affects the predator in two ways: metabolically (through determination of developmental and digestion rates) and physically (through the determination of motility rates and dispersal patterns). These factors interact, in turn, to define hunger levels (Sandness and McMurtry, 1972; Blommers et al., 1977; Everson, 1980). The importance of humidity to the fluid-feeding tetranychids has been much studied (Jeppson et al., 1975 for review), but the physiological and ecological demands of the predator are less well known.

The range of temperature and humidity within which P. persimilis is most efficient as a predator (with respect to prey consumption and egg production) is 25-30°C (Bravenboer and Dosse, 1962; Shinkaji et al., 1978) and 33-76% relative humidity (RH) (Hussey et al., 1965; Mori and Chant, 1966). At high temperatures and high RH, this predator tends to become inactive (Chant, 1961; Mori and Chant, 1966). Gould (1970) suggested that flare-ups of the prey population along the ridges of greenhouses in June may be a result of high temperatures (>30°C) where P. persimilis gives little control.

With decreasing temperature, the developmental period of P. persimilis lengthens (Hamamura et al., 1976) as does that of T. urticae. The relationship between the developmental periods of the two species, however, may not be maintained at low temperatures. The developmental rate of the predator is 2.4
times greater than that of the prey over fluctuating temperatures between 15 and 28.3°C (Laing, 1968, 1969). At constant temperatures of 17°C the advantage to the predator decreases since its rate of development is only 1.8 times greater than that of the prey (unpublished data of Gormican, 1980; Hamamura et al., 1976). Thus, although *P. persimilis* can control the pest over a wide range of temperatures and humidities (Hussey et al., 1965) control is less efficient (i.e., slower) at low temperatures and humidities (Stenseth, 1979).

Despite all this information on temperature- and humidity-related predatory performance, the synchrony of the predator and prey, in terms of microclimatic habitat preferences, has not been confirmed. Work with *Amblyseius* (=T.) *hibisci* (Chant) and *A. limonicus* Garman and McGregor has shown that these predators may not react passively to meteorological conditions, but may actively seek out alternate areas, if local conditions are not optimal. These species moved into the shade at high temperatures regardless of their feeding requirements, and re-emerged to hunt only after dark (Chant and Fleschner, 1960). Such movement away from non-preferred microclimates is an alternate explanation for Gould's control problems at high temperature.

The effect of various other environmental parameters, especially leaf surfaces, on the predator have been studied. Mori and Chant (1966) described *P. persimilis* as "ill suited to arboreal settings" since, on the basis of unpublished results, it was blown from the smooth leaves of "Prunus sp. and peach"
[sic] in airflows of 4.8-6.4 km/h. Johnson and Croft (1976) recorded the wind-blown dispersal of *A. fallacis* (Garman) in response to limited starvation, in airflows between 1.6 and 17.4 km/h. This suggests that Mori and Chant witnessed dispersal and not a basic unsuitability of *P. persimilis* to either these leaves or windy conditions.

Van de Vrie *et al.* (1972) reviewed the effect of natural leaf conditions ("texture, vestiture and contours") and the presence of inert residues on the suitability of leaves to tetranychid mites. Unfortunately, the work with phytoseiid mites has carried on in isolation from these findings. Thus, Sandness and McMurtry (1970) found the functional response curve of several phytoseiid predators increased on waterproof paper. Rasmy and El-Banhawy (1974) reported that *Phytoseius plumifer* (Canestrini and Fanzago) preferred and was less active on pilose fig leaves than on the glabrous leaves of sour orange. *Amblyseius gossipi* Elbrady, in contrast, preferred and was less active on sour orange than on fig (Rasmy, 1977). Blommers *et al.* (1977) found that *A. bibens* Blommers was more restive on pilose *Sida cordifolia* L. than on bean.

McMurtry *et al.* (1970) noted that *P. persimilis* is most closely associated with prey that form aggregations, such as *T. urticae* and *Eotetranychus sexmaculatus* (Riley). But work on another predatory phytoseiid (*T. pyri*) has suggested that genetic differences between populations may manifest themselves in different distribution patterns (Chant and Fleschner, 1960). Time of season may also be important in determining a predator's
distribution pattern (ibid).

In the *P. persimilis / T. urticae* predator-prey system, it is maintained that the distribution of the predator is generally well integrated with that of the prey (Chant, 1961). Yet it is also conceded that pockets of abundant prey may escape detection by the predator (Huffaker et al., 1963). The distributions of the two animals, therefore, are neither so congruent nor so harmonious as the generalizations lead one to expect. Takafuji and Chant (1976) have shown that the predaceous mite, *Iphiseius degenerans* (Berlese), avoids the webbed areas most suitable for its prey, *T. pacificus*, and thus often fails to control the prey population. Sandness and McMurtry (1972) also found that *A. largoensis* (Muma) was repelled by the webbing of *Oligonychus puniceae*. The degree to which a given predator's distribution is synchronized with that of its prey, under a variety of situations, obviously has an important bearing on control. Ohnesorge (1978) found that *P. persimilis* preferred old infested leaves to newly infested leaves even though adult prey had abandoned these surfaces. Since the adult female tetranychids spread the infestation, this preference behaviour lessens the predator's efficiency as a control agent (ibid).

Unfortunately, spatial synchrony has seldom been quantified. Nor are there extensive data referring to the frequency with which pockets of prey may escape predation under various circumstances. Huffaker (1958) suggested that the predator, *Metaseiulus (=T.) occidentalis*, would have the advantage over its prey, *Eotetranychus sexmaculatus*, in small
areas (ca. 1/2 room size [sic]) but that in large, more open settings, air currents would facilitate the dispersal of the prey on their silken threads, beyond the capacity of the predator to follow. Nevertheless, within a small area, M. (=T.) occidentalis is reported to be better able to overcome hazards to movement than its prey (Huffaker et al., 1963). This observation suggests that certain predator-prey pairs may be more suited to the confined conditions of the greenhouse than to open fields.

The experience of pest managers, however, suggests that it is very difficult to keep predaceous mites confined. Dixon (1973) cited instances of predators moving between greenhouses during his work in England. Oatman (1965) working in fields in California, stated in case after case that the predator spread very quickly across open ground between strawberry rows (a distance of just over 3 m), but moved along the rows much more slowly (ca. 15 m in 2 months). In some instances, the predators moved across as many as 4 rows (Oatman and McMurtry, 1966). Cochereau (1976) reported that P. persimilis travelled as far as 100 meters in one month, into neighbouring plots. Legowski (1966) failed to contain P. persimilis in release plots through the use of plastic screens. Oatman et al. (1968) also failed with their Stickem®-edged plastic barriers. Simmonds (1971) found the predator crossed all plots irrespective of the presence or absence of cloches.

Dispersal has also been noted in laboratory settings. Ball (1980) reported that 40% of the cohort of Galendromus longipilis
(Nesbitt) was lost in laboratory culture at 26.4°C, whereas only 36% was lost at 13.3°C. These losses included natural mortality but were mainly due to the predators dispersing off the cultures and into the surrounding water barrier. Ball (ibid) also reported that Proprioseiopsis temperellus (Muma and Denmark) was extremely restless when provided with T. urticae as prey in the laboratory. At 26.4°C, 77% of the cohort was lost by the adult stage as a result of dispersal. Chant (1959) reported a 20-50% escape rate of Typhlodromus finlandicus (Oudemans) in laboratory feeding experiments. There may also be differences in dispersal rates between populations of a single species. The Sicilian stock of P. persimilis seems to be more dispersive than the Chilean stock (Kennett and Caltagirone, 1968).

Although the numerical assessment of dispersive loss from cultures of predatory phytoseiids is infrequent, the mites' dispersive tendency is well recognized. It is considered a "nuisance" feature of the system, however, and results pertaining to mites which escape during experiments are routinely discarded (Mori and Chant, 1966; Eveleigh, 1979).

This dispersive tendency has been cited as a positive attribute of the predator P. persimilis (Oatman et al., 1976) since it would seem to enhance the spread of the predator over large infested areas. In smaller settings, however, dispersal may complicate control procedures. Dispersal out of a small area (e.g., a greenhouse or a single field) may be more significant as a means of depleting the predator population at the release site, than as a source for continually restocking the
surrounding larger area. Reduced predator numbers may adversely affect control at the release site, while supplemental releases of additional predators may not necessarily improve the situation, if the mechanisms that trigger dispersal (e.g., predator density, resource partitioning, food quality, etc.) cannot be countered. Consequently, control efforts dependent on a dispersive predator may prove less efficient and/or more costly (more predators necessary per unit area) in small settings, such as greenhouses, than in larger universes.

Takafuji (1977) maintained that immatures of Phytoseiulus persimilis have a lower dispersive tendency and capacity than adults. He also stated that the predator dispersed more as the number of prey available per predator dropped, and thus, that dispersal was a function of predator hunger. He did not explain why some predators dispersed even when sufficient prey were available. Overmeer and van Zon (1981) found that pesticide treatment increased the tendency of Amblyseius potentillae Garman to move off an infested leaf square. A. bibens was equally susceptible to pesticides but was less dispersive under these conditions and was recommended, therefore, for use in toxicity trials (ibid).

Environmental heterogeneity may influence dispersal. Huffaker (1958) increased the period of coexistence between M. (=T.) occidentalis and Eotetranychus sexmaculatus by increasing the number of patches in the environment. Using towers and

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1 This may be the reason Oatman has had such difficulty in specifying the optimal number of predators that should be released per acre (Oatman et al., 1967 et seq.).
barriers, he simultaneously curtailed predator dispersal and facilitated prey dispersal. Takafuji (1977), working with *P. persimilis* and *Tetranychus kanzawai* Kishida, showed that altering the spacing of the plants may prolong predator-prey interactions by partially limiting the dispersal of the predator. He also noted the potential importance of physical aspects of the cultivation system in hindering or enhancing dispersal. He reported that 95% of the predator population dispersed when there was interplant leaf contact. In the absence of such contact, predator dispersal between plants was greatly reduced. Dispersal was enhanced, however, by artificial connections between plants that did not touch. Thus, he suggested the use of strings between plants as a method of facilitating predator dispersal where more rapid control is required.

Takafuji (1977) stated that control of *T. kanzawai* by *P. persimilis* is inevitable once the predator is introduced into a patch containing the prey. He therefore discounted the influence of the predator's travelling time between patches. He stressed, instead, the rate of unsuccessful dispersal (i.e., the mortality of predators resulting from dispersal). This view, and that of Oatman, with respect to dispersal of the predator seem contrary to the evidence of other workers. It may be that some predatory mites are simply too prone to disperse to be useful in control situations. Laing and Huffaker (1969) reported that, overall, *Metaseiulus (=T.) occidentalis* had less tendency to disperse than *P. persimilis*. This observation may have been due to other
factors. For example, a reduced tendency of *M. occidentalis* to
overexploit the prey population or a greater facility for
cannibalism in *M. occidentalis* may have been responsible.

The paucity of information on the behavioural synchrony of
the predator and prey, particularly with respect to predator
dispersal, has been identified as a short-coming of the
extensive work on this predator-prey system (Burnett, 1977).
Without such basic work, enormous amounts of money may be
invested in sustaining programs that are doomed to be continuous
hide-and-seek games between a predator and prey that have only
limited possibilities of becoming synchronized in numbers, time
and space. To date, however, both pest managers and theoretical
ecologists have only referred to behaviour patterns when they
state their basic assumptions. The need for work in this area is
underlined by the fact that the assumptions of the two groups
are often unsubstantiated and sometimes contradictory (e.g., the
matter of preferred stages—see above; random vs. non-random

On the basis of the existing problems in pest control, a
study was initiated to assess the impact of terrestrial
dispersal by *P. persimilis* on its potential control of *T.
urticae*. Neither the predator nor the prey is known to disperse
on air currents, although other phytoseiids and tetranychids
apparently do (Johnson and Croft, 1976 for *A. fallacis*;
Fleschner et al., 1956 for tetranychids). *P. persimilis*
disperses simply by walking. *T. urticae* forms tight boluses of
webbing (and mites) at the apex of depleted host plants.
Eventually these become sufficiently weighty to cause the plant to droop onto adjacent plants, spreading the mites in the process.

Although, at one time, dispersal was viewed as an opportunistic behavioural reaction to adverse conditions (Nicholson, 1947 in Johnson, 1969), it is now viewed in a very different sense (Johnson, 1969). The various environmental influences (e.g., high density; low food quality; etc.) are still recognized as important "regulators" of dispersal but not as the "determinants" they were once seen to be. Instead, the ephemeral nature of the environment is viewed as a selective pressure which has led to the evolution of dispersive behaviours that are often manifest in the absence of environmental deterioration or transience. Thus, dispersal may be density-related without being density-dependent. Dispersal is now recognized as "a regular feature of many species" (Johnson, 1969) that is often expressed in pre-reproductive individuals and provides them with a means of transit between breeding places, whether such movement is apparently demanded by the circumstances or not.

The physiological determination of dispersal seems to vary greatly between species, and may involve very complicated interactions between such aspects as age, nutritional history, mating condition and hormonal state. Similarly, the termination of the process can be mediated by a variety of variables (e.g.,

\[\text{Staking the plants to prevent drooping thus hinders prey movement.}\]
weather patterns, waning hormonal levels, deteriorating physical condition, etc.). Hence, findings from one group may not necessarily be applicable to another group.

Work with *T. urticae* has revealed that dispersal in this mite generally occurs early in the life of adult females (often during the first day—Hussey and Parr, 1963b) when they weigh less than one half of their mature weight (Mitchell, 1973). Since mature weight is a consequence of pre-adult conditions, the ultimate time of dispersal is determined long before it is manifest (Mitchell, 1973). Males do not disperse (Hussey and Parr, 1963b).

Suski and Naegele (1963) found that lack of food and especially desiccation were the proximate causes of dispersal in *T. urticae*. They noted that Boulanger (1958 in Suski and Naegele, 1963) found a decrease in relative humidity at the leaf surface after heavy tetranychid feeding. McEnroe and Dronka (1971) noted that water-stressed females of *T. urticae* exhibited a shift in photobehaviour and geotaxis. They postulated that a drop in internal pressure was associated with water stress and was transmitted to the central nervous system via stretch receptors. Mites of sedentary and migratory phases (Suski and Naegele, 1968 in McEnroe and Dronka, 1971) were behaviourally characterized and found to differ in their responses to ultraviolet and green illumination, red illumination, skyshine and polarized light (McEnroe, 1969, 1971; McEnroe and Dronka, 1971). McEnroe and Dronka (1971) also noted a genetic component to dispersal. Sib-matings increased the expression of dispersal
whereas outcrosses decreased it. After selection for eight generations, however, they were unable to show heritability of responses associated with each phase. Thus, although dispersal seems to be at least partially genetically determined, the behaviours associated with it (but perhaps not the patterns) are basic to all individuals.

Johnson and Croft (1976) working with the phytoseiid, *Amblyseius fallacis*, tested all stages and both sexes but found only adults were prone to [aerial] dispersal. They were able to increase the proportion of ovipositing females which dispersed through limited starvation. Males and pre-ovipositing females took fewer prey under normal conditions and did not respond strongly to this stimulus, yet seemed to have a greater natural tendency to disperse than ovipositing females, as was evidenced by their constant activity (ibid). Croft and McMurtry (1972) also noted the restiveness of pre-ovipositional females and males of *M. (=T.) occidentalis*.

The effect of starvation (or low prey density) on motility and dispersal is not simple either (Sandness and McMurtry, 1970). Hamamura et al. (1980) reported "catastrophic dispersal" of female predators when the prey:predator ratio fell below one, although they noted that dispersal occurred at a lesser rate even when prey densities were high.

Although the *P. persimilis / T. urticae* predator-prey system has received considerable attention, the role of dispersal has been largely ignored. This thesis will investigate dispersal in the phytoseiid predator. When does dispersal occur
in *P. persimilis*? Can it be predicted? Can dispersal be induced? How intense and prolonged is dispersal? And, does dispersal influence the success of biological control programs? The study will focus on the qualitative differences between individuals in addressing these questions.
SECTION 2: GENERAL METHODS

Cultural Practices

Plants

All plants used in these studies were grown from seed in the UBC Plant Science greenhouse. The plants were not exposed to fumigation or pesticide treatment. Artificial lights were used over the seedlings and throughout the house. The light regime was 14L:10D. Temperatures ranged from 18 to 34°C.

Beans (*Phaseolus vulgaris* L., cv. Burpee's Improved Bush) and cucumbers (*Cucumis sativus* L., cv. Marketmore 76) were grown in pots containing a mixture of peat moss and top soil.

Mites

The two-spotted spider mite (*Tetranychus urticae*) was cultured on bean in two controlled environment chambers maintained at 25±2°C, 16L:8D and 65±10% RH. After three weeks in the prey culture, bean plants became chlorotic and were replaced by fresh plants. Infested plant material was moved between the chambers to encourage interbreeding between the two mite populations.

The stock culture of the predator, *Phytoseiulus persimilis*, was derived from individuals taken from a culture maintained by the BC Ministry of Agriculture at Cloverdale. The predator was cultured on excised prey-infested bean leaves, held in petri
dishes on water-soaked cotton pads. Fresh infested leaves were added to the cultures daily. Interbreeding between predator subcultures was facilitated by regularly subdividing, mixing, and re-establishing the cultures. Predator cultures were housed and all experiments were conducted in a controlled environment chamber at 25±2°C, 16L:8D and 65±5% RH.

**Experimental Practices**

The specific details of experimental practices (e.g., leaf area, mite numbers) are included in "Materials and Methods" of each section.

**Leaves**

Only fresh young leaves were used in the experiments. Squares cut from excised leaves were placed on water-soaked cotton in petri dishes. Squares kept in this manner remained turgid and green for several days when not exposed to prey. The petioles of whole leaves to be used in experiments were inserted into plastic drinking straws filled with water-soaked cotton. These leaves remained turgid for several hours when not in contact with an external water source, and for several days when the end of the drinking straw was put in contact with water.
Prey

In experiments where a specific known number of prey were required per unit area, it was necessary to place them on the appropriate substrate by hand. Prey were knocked off infested plants by soundly tapping the plants with a wooden ruler, and caught in a petri dish below. Prey of both sexes and all stages were thus removed from the culture at one time. The petri dish was then placed under a dissecting microscope where the desired individuals were selected with a size "0", sable-hair brush. After the necessary number of prey were transferred to the test substrate, they were re-counted and checked to ensure that all were unharmed.

Contrary to Everson's (1980) report that T. urticae is virtually immobile on all but the most unsuitable leaves, all the active stages moved quite freely between interconnected leaf squares so that the density relationships on the squares changed as the experiment progressed. The delicate nature of the egg, the only non-motile stage, prevented its use to overcome this problem. Similarly, the fragility of the larvae rendered them less suitable than the older stages for this work. Adult females were not used in the experiments because their constant egg production drastically changed established numbers of available prey. The protonymphs, however, were used extensively because of their ability to tolerate physical manipulation. In addition, their lack of sexual dimorphism (cf. deutonymph and adult stages) reduced individual differences in their food value for the predator.
Predators

Although there are several popular methods for measuring dispersal in various animal populations, the peculiar nature of mites renders most of them ineffectual. The small size of the predatory phytoseiids, and the inability to mark them, precludes tracking them except in very simple environments (preferably not far from a microscope). Yet, these mites are capable of travelling considerable distances. Any substrate of suitable dimension for their style of dispersal is far too large for tracking by inspection.

The only reliable "technique" for diagnosing dispersive individuals remains the death of apparently healthy individuals in the water barrier surrounding leaf arenas well supplied with food. In a sense, this might be thought of as a modified release-recapture method, the recaptured individuals making up 100% of the original population but being composed of dead (in the water barrier) and living members. While this "technique" is remarkably easy to "operate", it is riddled with numerous difficulties, notably that recaptured dispersers are, by definition, dead, and therefore not open to further experimental manipulation.

Since this method of classification does not differentiate behaviourally between individuals, observational data are needed to fill in the behavioural gaps. All mites on excised leaf squares surrounded by water barriers, eventually reach that barrier, apparently by random processes. Under normal conditions, the mites touch the water surface lightly with their
front legs, then turn away and move on. In some instances, during these exploratory manoeuvres, a mite becomes entrapped by the surface tension at the water's edge. In virtually all of these cases, the mite, after some struggling, manages to free itself and retreat to the leaf surface. This is distinctly different from the disperser's reaction to the water's edge. A dispersing individual typically moves ever more quickly along the leaf edge, probing the water surface. Eventually, the mite races headlong into the water, often travelling several centimeters before drowning. Apparently, both types of individuals are able to sense the same features of the water surface, and both would move off the leaf, by other paths, if allowed. The difference in dispersive tendency is one of degree, not kind. McEnroe (1971) used just such a difference in response to a Tanglefoot® barrier to identify qualitative differences between individuals of T. urticae.
SECTION 3: PREDATOR MOTILITIES

Introduction

Since any discussion of terrestrial dispersal must necessarily address the questions "how far?" and "how fast?", it was essential to assess the predator's motility. It has been suggested that substrate may affect motility (Blommers et al., 1977; Rasmy and El-Banhawy, 1974). Motility measurements have been made on predaceous mites on various types of leaves, glass and plastic (Everson, 1980 for *P. persimilis*; Blommers et al., 1977 for *Amblyseius bibens* Blommers). Preliminary attempts to use the established methods revealed several shortcomings. The method of Blommers et al. (1977) provided no criteria for selecting the test intervals, and there was as much difference between test intervals recorded for one individual, as there was between different individuals. The ink markings necessary for Everson's (1980) method interfered with mite movement. Moreover, the different motilities they reported for both phytoseiids on the test substrates were most likely artifacts of the inappropriate scales used when measuring surface areas covered by the mites on pubescent substrates.

An alternate method of describing predator movement was also considered. Suski and Naegele (1963), Penman and Cone (1972) and others have analysed photographic records of tetranychid tracks with the aid of a simplified statistic, CSL, the coefficient of a straight line. (CSL = shortest distance from start to finish of path / actual length of path standardized for...
time over each experiment.) This statistic provides a useful alternative from the traditional measurement, the sum of angular changes in the mite's course (as measured by the angle between the gnathosoma and the actual track) per total one-second distance. It is generally agreed that the angular measure is the most accurate representation of speed and direction, but it is so difficult to extract from experimental records that most workers tend to avoid it. There are, however, numerous objections to the CSL method. Firstly, it assumes a linear relation between the statistic and the corresponding angular measure which, because of outliers at both extremes of the scale is unfounded. Moreover, the CSL statistic itself breaks down under examination. A short convoluted path is rated by the CSL as straighter than a more linear path that turns back on itself. Additionally, a pathway which winds back and forth in open loops between the start and finish can receive different CSL scores, depending on the distance between consecutive loops. In ecological and behavioural terms at least, such tracks may not differ significantly. Thus, while purporting to be a relevant behavioural descriptor of animal movement, the CSL statistic can often obscure and confuse important aspects of a path.

Motility experiments are generally conducted on the upper surface of horizontal substrates (Everson, 1980; Blommers et al., 1977). *P. persimilis* and some other predatory phytoseiids, however, prefer and are less motile on substrates on which they may assume an inverted position (Sandness and McMurtry, 1970). Furthermore, the standard horizontal substrate does not allow
movement over both surfaces of the substrate as is normally possible.

For present purposes, therefore, it was necessary to design a method for measuring motility that would give easily reproducible results while allowing for possible differences in behaviour that might be related to the presence of different substrates. Two-sided vertical testing was adopted to improve the experimental design. At the outset of these experiments it seemed that this design would allow simultaneous measurements of geotaxis and motility. Veining patterns so influenced the predator's direction of movement, however, that geotaxis had to be tested separately on a more featureless substrate.

Motilities were not compared on a number of arbitrarily selected natural and man-made substrates. Instead, only two surfaces were used: uninfested and infested bean leaves. The former provided no potential for predator feeding. The latter was a well-stocked potential feeding area.

**Materials and Methods**

An adult female predator taken at random from the culture was allowed to roam freely for ten minutes on the abaxial surface of a vertically suspended, uninfested bean leaf. The mite's path was carefully sketched. At the end of the test period the individual was transferred to a vertically suspended infested bean leaf for an additional 20 minutes and a similar record of its path was made. A longer period was necessary on
infested leaves since feeding mites often did not move at all during the first ten minutes.

The length of the path travelled was measured from the diagrams with a piece of thread. These measurements were transformed to the real scale and standardized for a one-second interval. Adults of both sexes, protonymphs and larvae were tested.

Results

The average motilities of females, males, protonymphs and larvae are shown in Table 1. The average motility score for males was very close to that for females on both substrates. Protonymphs and larvae had much lower motilities than adults on both substrates.

Inspection of the tracings of mite pathways showed that females moved in broad sweeping patterns over both sides of uninfested leaves, so that they soon covered most of the leaf surface. One of the females followed leaf veins especially closely. On infested leaves these females moved more slowly (Table 1) and stopped on average two times during the 20-minute period to feed. Between feedings, however, they usually followed the same broad pattern of movement they had shown on the uninfested leaves.

Males travelled in the same broad sweeps as females on uninfested leaves. They often encountered the leaf edge, but they did not leave the side on which they were released. On infested leaves broad sweeps were again evident between bouts of
Table 1. Average motilities for various classes of individual predators measured on two substrates.

<table>
<thead>
<tr>
<th>Individuals Tested</th>
<th>Substrate</th>
<th>Uninfested Bean</th>
<th>Infested Bean</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adults: Females</td>
<td></td>
<td>0.94±.20</td>
<td>0.04±.02</td>
</tr>
<tr>
<td>Males</td>
<td></td>
<td>0.90±.10</td>
<td>0.06±.01</td>
</tr>
<tr>
<td>Protonymphs</td>
<td></td>
<td>0.37±.10</td>
<td>0.02±.01</td>
</tr>
<tr>
<td>Larvae</td>
<td></td>
<td>0.06±.02</td>
<td>0.02±.01</td>
</tr>
</tbody>
</table>

\(^1\) mean±S.E. (n=6).
feeding.

The protonymphs travelled along tightly convoluted paths on both uninfested and infested surfaces. Thus they covered much less surface area than their average motility might suggest. Larvae moved in tighter turns on uninfested than on the infested surfaces.

Discussion

The average motility of adult female *P. persimilis* on uninfested bean leaves was 1 mm/s. This agrees closely with the values obtained by Blommers *et al.* (1977) for female *A. bibens* on both bean and plastic at 25°C. Although Everson (1980) reported differences in activity of *P. persimilis* on bean and plastic (see problems with scale discussed earlier), he found that activity levels did not differ significantly between 15-30°C on either bean or plastic. Thus, a walking speed of 1 mm/s seems to be typical on "neutral substrates" over a range of temperatures.

All stages tested in this study were very sedentary on infested leaves. The low motilities were a result of feeding behaviour and not an artifact of the increase in surface area afforded by spider-mite webbing. There was some evidence of differences in searching style between males and females even though their motilities were very similar.

Everson (1980) reviewed the range of substrate-related motilities that have been reported for predatory phytoseiids, and concluded that no trend was evident. It is possible,
however, that with measurements taken on more appropriate scales
many of the apparent differences in motility would disappear.
Testing on leaf surfaces has also ignored the impact of plant
chemicals on motility. It may be more worthwhile to distinguish
between substrates with or without deterrent plant chemicals
(allomones) or potential food sources, than between those that
are glabrous or pilose. Thus, the different behaviour of various
phytoseiid species on the same plant surfaces (e.g., Rasmy and
El-Banhawy, 1974 cf. Rasmy, 1977) may represent different
responses to plant chemicals (or different microhabitat
preferences) rather than different inherent motilities.

Everson (1979, 1980) confirmed that differences in the
motility of the prey, not the predator, on artificial substrates
account for the anomalous results (dome-shaped functional
response curve) that opened the question of substrate-related
differences in predator motility (Mori and Chant, 1966).
Investigation of the role of plant chemicals is likely to remove
other apparent differences in predator motility from
consideration. Measurement of motilities on glabrous surfaces at
more appropriate scales may finally close the debate on
substrate-related differences in predator motility.
SECTION 4: DEVELOPMENT OF PREDATOR BEHAVIOUR

Introduction

A study of the predator's behaviour was undertaken to discover when and how dispersal in *P. persimilis* is initiated and what behavioural responses might be associated with it. Preliminary studies indicated that in predators of all ages, several degrees of response could be distinguished within three broad behavioural categories: geotaxis, reactions to small depressions, and reactions to an edge. There was no apparent correlation between response scores over the three tests, suggesting that the three behaviours were independent, and could be used to classify phases of dispersal during this study.

Preliminary tests also revealed that rough handling had a predictable effect on the mites' behaviour. Rough handling increased the frequency of certain scores that normally occurred infrequently. Thus, gentle handling was an important part of these tests. Individuals showing the behavioural responses known to be associated with rough handling were required to duplicate their scores at least three times before the values were recorded. Since the orientation of the mite at the time of release dictated its initial direction of movement throughout this study, each test had to be continued until it was evident that the mite's course was no longer reflecting its original placement.

During preliminary tests, the behavioural classes for the response to small depressions and the response to an edge were
categorized numerically (0-n), rather than descriptively. This classification avoided problems which might have arisen from assigning behavioural significance to the scores before the experiment was complete. The test referred to as "response to small depressions", for instance, might have reflected differences in thigmotaxis as much as or more than differences in predator motility.

Materials and Methods

Eggs were collected daily from a P. persimilis subculture and placed on uninfested bean leaves until the larvae hatched. Larvae were then transferred to individual infested bean-leaf squares (30 x 30 cm). Each day, from eclosion to death or dispersal, the predators were transferred from these squares to the experimental apparatus, and tested first for geotaxis, then for response to small depressions, and finally for response to an edge. After the behavioural tests were completed, the predators were returned to the infested leaf squares.

The apparatus was contained within a 14.5 cm diameter petri dish (Figure 1). A piece of plastic-coated wire was formed into an arch 4.5 cm high and 1.5 cm wide, and mounted on a platform of blue plasticine (a colour that facilitated observation of the pale white larvae and deutonymphs). A cross-bar of plasticine joined the two sides of the arch at midpoint in an "A" configuration. The platform also contained a triple ring of shallow circular depressions, 1 mm in diameter and approximately 1.5 mm deep, made with the tip of a capillary tube. Responses to
Figure 1. Behavioural apparatus. Geotaxis was tested on the arch of plastic-coated wire. Response to small depressions was tested on the triple ring of circular depressions made in the plasticine platform. A separate ridge of plasticine was used to test response to an edge.
Figure 2. Cross-section of platform of behavioural apparatus through triple ring of circular depressions.
edges were monitored along a ridge of plasticine (length: 7 cm; height: 1.5 cm; slope: 35-40°; width at crest: 1.5 mm) which formed the third test area. The scoring system for each behaviour is outlined in the following section.

**Scoring System**

**Geotaxis**

Each predator was first randomly released onto the upper half of the arch. Mites were grouped into three behavioural classes based on their final resting place. There was an apparent gradient of activity among the mites; those which settled rapidly could be distinguished from those that took longer to settle.

*Negative geotaxis*: Geonegative mites tended to position themselves on the upper and lower surfaces of the highest portion of the arch. Their movements most often involved repeated travel up one side and down the other. With each subsequent transit of the arch, the height of their turning point increased. Movements were typically rapid until the mite finally neared the top of the arch, where it slowed and began to settle. Some individuals, after reaching this highest point, began the entire sequence again, but they too eventually arrived at the same settling point. A few repeated the sequence a third time, after which observation ceased.
*Positive geotaxis:* Immediately following release, geopositive mites moved down the sides of the arch, down the edge of the plasticine platform, and across the petri dish. Since this behaviour was also associated with rough handling, for reasons noted above, a minimum of three downward trips was required before any mite could be scored as positively geotactic. When possible, a fourth test was added after the tests for responses to an edge and small depressions, to further confirm the validity of the geopositive score. Geopositive mites typically moved at exceptionally high speeds.

*Neutral Geotaxis:* Some mites did not fit either of the classes described above. They moved slowly, and often spiralled around the wire, but they did not consistently occupy a particular region of it.

**Response to Small Depressions**

Following the test for geotaxis, each mite was repositioned at the centre of the triple ring of circular depressions. As each individual moved across this ring, its response to the depressions was observed and scored from 0 to 3. The route taken and the time required to escape from the ring dictated the score class. All stages of the predator were physically able to cross over, as well as enter, the depressions.

*0* These mites did not respond to the depressions, but
moved rapidly over them along straight paths, traversing the 3 mm distance in less than 1 second.

*1* These mites moved less rapidly and hesitated to cross the depressions. Their pathways out of the ring, therefore, were not so straight as those mites scored as "0". The "1" mites displayed no interest in the depressions, but merely avoided them. They escaped from the ring in less than 3 seconds, after travelling approximately 5 mm.

*2* These mites moved very slowly over the ring of depressions. They often stopped at the edge of a depression (particularly where four abutting depressions met) and explored the pit before them with their first two pairs of legs and gnathosoma. They then moved on, but paused again to explore other holes they encountered. Consequently, these mites followed a convoluted path out of the ring. In some cases, individuals stayed within the ring for more than 10 minutes, describing a path several centimeters long.

*3* These mites moved slowly over the surface of the ring. Several depressions were entered and thoroughly explored. After a few such trials, type "3" mites settled into the bottom of a depression and stayed there. Preliminary observations revealed that such mites, if uninterrupted, would remain in the chosen depression for several hours.
Hence, they were gently prodded after a few moments and removed to the next test area.

Response to Edges

The final behavioural test was carried out on the ridge of plasticine. The mites were released along its crest. Responses were scored 0 to 3.

*0* These mites turned away from the crest, moving rapidly down the slope and across the petri dish. Since this behaviour was also associated with rough handling or directionally-biased release, such individuals were gently returned to the crest and re-released. The behavioural pattern had to be repeated three times before a mite was placed in this class.

*1* These mites moved along the crest for a distance of about 1 cm before moving down the slope. Their horizontal displacement while moving down-slope was approximately 0.5-1.5 cm.

*2* These mites covered a total distance of approximately 3 cm along the crest of the ridge. Their movements often included short distances (0.5-1.5 cm) along the slope in the upper half of the ridge.

*3* These mites moved along the crest of the ridge for
distances of 3-6 cm. They rarely moved off the crest and then only for very short distances (ca. 2 mm down the slope; ca. 5 mm along the ridge). On reaching the end of the ridge, some followed a less pronounced ridge down to the petri dish and proceeded across the dish. In a few cases, these individuals reached the rim of the dish and followed it until the test was ended. Other individuals, on reaching the end of the ridge, turned about and followed the crest back to its other end, before eventually moving off the test area.

Sixty-five mites were tested daily for geotaxis, response to small depressions and response to an edge.

Results

Behavioural scores on each test were independent of results on other tests although there were periods during the mites' lives when an association between behaviours was evident (see below). Of the 48 possible combinations of behavioural scores, only eight were not observed. Seven of these involved the score "1". Moreover, due to the low frequency of class "1" observations, for this analysis, it was possible to group data from the score "1" class with the "0" class. Assuming independence of behaviours, the expected probability of the eighth combination (positive geotaxis, response "2" to small depressions, and response "3" to edges) was 0.0049±0.0070. Since

\[ p \pm 1.96 \sqrt{\frac{p(1-p)}{n}} \]

1 95% confidence limits for a proportion (p±1.96 \sqrt{p(1-p)/n})
the range encompassed by the confidence limits included zero, the absence of this observation from the data was not significant.

All one-day-old mites were larvae. Day 2 results were taken mainly from protonymphs, and occasionally from deutonymphs. Deutonymphs, protonymphs, and adults of both sexes were included in the scores for day 3. By day 4, only deutonymphs and adults were evident. Only adults were present on Day 5. The longest series of observations spanned 30 days for one individual, but most individuals dispersed or died before the fifth day. Since it is difficult to determine the sex of mites less than five days old, the data from the 24 mites which could be identified to sex (10 females; 14 males) were used separately to check for any differences in behaviour between males and females, over their lifetimes, that might make it inappropriate to use data from mites of unknown sex.

The behavioural scores for both sexes are shown in Table 2. There was no significant difference between the male and female lifetime scores for geotaxis or response to an edge. There was, however, a significant difference in the male and female responses to small depressions. Although in both sexes the largest portion of responses fell in the "1,0" class (while the "2" class was next, and category "3" class had the fewest individuals), the females had almost 3/4 of their responses in the "1,0" class, with the other 1/4 divided between classes "2" and "3". Male responses were more evenly divided, with about 1/2 in the "1,0" class, while the rest were divided quite evenly
<table>
<thead>
<tr>
<th>Behavioural Test</th>
<th>Score</th>
<th>Females ±95% confidence intervals</th>
<th>Males ±95% confidence intervals</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geotaxis</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Negative</td>
<td>0.66±.09</td>
<td>0.72±.07</td>
<td></td>
</tr>
<tr>
<td>Positive</td>
<td>0.14±.06</td>
<td>0.09±.04</td>
<td></td>
</tr>
<tr>
<td>Confused</td>
<td>0.20±.07</td>
<td>0.19±.06</td>
<td></td>
</tr>
<tr>
<td>Response to Small</td>
<td>3</td>
<td>0.13±.06</td>
<td>0.21±.06</td>
</tr>
<tr>
<td>Depressions</td>
<td>2</td>
<td>0.16±.07 *</td>
<td>0.33±.07 *</td>
</tr>
<tr>
<td></td>
<td>0,1</td>
<td>0.71±.08 *</td>
<td>0.46±.08 *</td>
</tr>
<tr>
<td>Response to an Edge</td>
<td>3</td>
<td>0.22±.08</td>
<td>0.25±.07</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>0.26±.08</td>
<td>0.23±.06</td>
</tr>
<tr>
<td></td>
<td>0,1</td>
<td>0.51±.09</td>
<td>0.52±.08</td>
</tr>
</tbody>
</table>

* Significantly different response between males (n=14) and females (n=10).
between classes "2" and "3".

The data on responses to small depressions during days 1 to 5 were further analysed according to sex, but no apparent difference could be detected in the response pattern between the two sexes. The analysis of behaviours from days 1 to 5 was, therefore, based on data from both sexes (including those which escaped or died before they could be sexed on day 5).

Behaviour: Day 1 to Day 5

The modal behavioural scores (i.e., those occurring most frequently) for Days 1-5 are listed in Table 3.

On the first day following eclosion virtually all mites exhibited neutral geotaxis. The proportion displaying this response was lower on the following day and, by the third day, over half of the mites had begun to exhibit geonegative behaviour. The proportion of mites in this latter group increased over Days 4 and 5 until a new norm of negative geotaxis involving virtually all mites was established. Similarly, the class "3" response to small depressions which was displayed by most mites on Day 1 gave way over the following two days to the "0,1" response. By Day 4, over half of the mites scored a class "0,1" response to small depressions. The proportion of mites in this class increased further on Day 5. Over the five-day period, the proportion of individuals scoring "0,1" on an edge diminished steadily, with a corresponding

1 The complete listing of behavioural scores (with 95% confidence limits) is included in Appendix 2.
Table 3. Modal behavioural scores for individuals of both sexes, during the first five days after eclosion.

<table>
<thead>
<tr>
<th>Days After Eclosion</th>
<th>Geotaxis Response to Small Depressions</th>
<th>Response to an Edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Proportion of individuals in each modal class with 95% confidence limits)</td>
<td></td>
<td></td>
</tr>
<tr>
<td>1 (77%)</td>
<td>neutral</td>
<td>3 (0.94±0.06)</td>
</tr>
<tr>
<td>2 (20%)</td>
<td>neutral</td>
<td>3 (0.53±0.04)</td>
</tr>
<tr>
<td>3 (14%)</td>
<td>negative</td>
<td>3 (0.62±0.16)</td>
</tr>
<tr>
<td>4 (16%)</td>
<td>negative</td>
<td>0,1 (0.71±0.16)</td>
</tr>
<tr>
<td>5 (23%)</td>
<td>negative</td>
<td>0,1 (0.86±0.14)</td>
</tr>
</tbody>
</table>
increase in the proportion falling in class "3" response to an edge.

**Dispersal Behaviour**

The predators were well supplied with food and maintained individually on adequately large leaf squares throughout this study. Nevertheless, 40 of the 65 monitored individuals "dispersed" off the holding arenas into the surrounding water barrier. Although most died in the water or shortly after being returned to the leaf substrate, six individuals which were returned to their leaf squares survived to disperse a second time. Three of these six were found in the water again on the next day, illustrating the persistence of the dispersive drive. In total, 46 instances of dispersive behaviour were recorded.

All females in the study dispersed. Three of 14 males did not, but this difference was not significant (Fisher's Exact Test). Since, both sexes were equally likely to disperse, the data for males and females were analysed together.

Since the results cited above demonstrated a typical pattern of behaviour for one- to five-day-old predators (Table 3), analysis of dispersal behaviour was limited to behaviour on and after Day 5. During this latter period, virtually all individuals displayed bouts of positive or neutral geotactic behaviour, interspersed on a normally geonegative background (Table 4; items marked "G"). The first bout of positive or neutral geotaxis occurred on average on Day 8 (S.E.=0.88). In one instance, positive or neutral geotaxis was recorded on four
Table 4. Statistical description of the periodicity of recurrent positive or neutral geotactic scores (G) and class "0,1" responses to an edge (E). All numbers refer to calendar days.

<table>
<thead>
<tr>
<th></th>
<th>Mode (x/n)</th>
<th>Mean±S.E.</th>
<th>Range</th>
</tr>
</thead>
<tbody>
<tr>
<td>First instance of score</td>
<td>G 5 (3/11)</td>
<td>8.00±2.93 *</td>
<td>5-14</td>
</tr>
<tr>
<td></td>
<td>E 5 (11/19)</td>
<td>7.95±4.53</td>
<td>5-18</td>
</tr>
<tr>
<td>Duration of score</td>
<td>G 1 (20/27)</td>
<td>1.41±0.80 *</td>
<td>1-4</td>
</tr>
<tr>
<td></td>
<td>E 1 (11/28)</td>
<td>2.25±1.51 *</td>
<td>1-7</td>
</tr>
<tr>
<td>Interval between</td>
<td>G 2 (5/15)</td>
<td>3.53±3.50</td>
<td>1-11</td>
</tr>
<tr>
<td>consecutive scores</td>
<td>E 2 (16/42)</td>
<td>2.50±2.18</td>
<td>1-13</td>
</tr>
<tr>
<td>Number of scores (bouts)</td>
<td>G 1 (6/13)</td>
<td>2.08±1.50 *</td>
<td>1-6</td>
</tr>
<tr>
<td>to dispersal</td>
<td>E 1 (9/18)</td>
<td>2.50±1.86 *</td>
<td>1-6</td>
</tr>
<tr>
<td>Interval between</td>
<td>G 0 (5/13)</td>
<td>2.62±4.33</td>
<td>0-14</td>
</tr>
<tr>
<td>last score and dispersal</td>
<td>E 0 (15/20)</td>
<td>0.50±1.10 *</td>
<td>0-4</td>
</tr>
</tbody>
</table>

* The most reliable estimate of central tendency is indicated. When the standard deviation is large, the mode is a better estimate of central tendency than the mean especially if 50% or more of the observations are located there.
subsequent days, but most were scored on only one calendar day (mean=1.41±.15). Based on a 24-hour sampling interval, these bouts might last more than 24 hours, but on average were less than 48 hours long. Among individuals which displayed more than one bout of positive or neutral geotaxis, there were usually two calendar days between bouts. The average number of bouts occurring prior to dispersal was 2.08 (S.E.=0.42) in such individuals. Five of 13 individuals dispersed on the day immediately following their last bout of positive or neutral geotaxis.

Geotactic scores for one to four days prior to dispersal are shown in Table 5. There are significantly more individuals displaying positive or neutral geotaxis three days prior to dispersal. The data also suggest that individuals which have passed through this state of positive or neutral geotaxis are somewhat less likely than geonegative individuals to disperse on the first day after such a bout. Two days after the bout, their dispersive tendencies nearly equalled those of geonegative individuals. Three days after the bout of positive or neutral geotaxis, these mites displayed a higher tendency to disperse than did geonegative individuals. By the fourth day, the dispersive tendency had waned somewhat, but remained above the normal level.

There was also a relationship between dispersal and test scores for responses to an edge (Table 4; items marked "E"). The normal incidence of the "0,1" class was 0.42±.07, with the first bout occurring most frequently on Day 5. The "0,1" response to
Table 5. Pattern of positive or neutral geotaxis as related to dispersal.

<table>
<thead>
<tr>
<th>Individuals</th>
<th>Proportion Dispersing Daily (95% confidence interval)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal population (summed data from all individuals, Day 5-30)</td>
<td>0.19±.05</td>
</tr>
<tr>
<td>Scored unusual geotaxis, 1 day earlier</td>
<td>0.13±.13</td>
</tr>
<tr>
<td>2 days earlier</td>
<td>0.23±.18</td>
</tr>
<tr>
<td>3 days earlier</td>
<td>0.57±.21 *</td>
</tr>
<tr>
<td>4 days earlier</td>
<td>0.35±.21</td>
</tr>
</tbody>
</table>

* Significantly different from normal incidence of dispersal.
an edge was most often scored on two calendar days (mean=2.25±0.29). In 16 out of 42 cases, there were two calendar days between successive "0,1" responses. The average number of "0,1" scores occurring prior to dispersal was 2.50 (S.E.=0.44). Most individuals (15/20) dispersed on the day immediately following their last "0,1" score.

The incidence of the "0,1" response to an edge as it related to dispersal is shown in Table 6. Significantly more individuals scored "0,1" on the edge three days prior to dispersal. As was the case with positive or neutral geotactic behaviour, the tendency to disperse seemed to build over the first and second days after the "0,1" score was recorded, peak on the third and begin to fall off on the fourth day, although still remaining higher than normal.

The period of most active dispersal, thus, may last more than 24 hours; i.e., through Days 3 and 4. As described above, dispersal is persistent and, if unsuccessful the first time, may be repeated. Moreover, bouts of positive or neutral geotaxis, as well as "0,1" responses to an edge, may persist for as long as four or seven days, respectively. The recurrence of behaviour patterns associated with dispersal, at intervals during the adult stage, also suggests that this stage has more than one period of dispersive activity.
Table 6. Pattern of "0,1" class response to an edge as related to dispersal.

<table>
<thead>
<tr>
<th>Individuals</th>
<th>Proportion Dispersing Daily (95% confidence interval)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal population (summed data from all individuals, Day 5-30)</td>
<td>0.42±0.07</td>
</tr>
<tr>
<td>Scored &quot;0,1&quot; response to an edge, 1 day earlier</td>
<td>0.32±0.19</td>
</tr>
<tr>
<td>2 days earlier</td>
<td>0.36±0.20</td>
</tr>
<tr>
<td>3 days earlier</td>
<td>0.75±0.17 *</td>
</tr>
<tr>
<td>4 days earlier</td>
<td>0.55±0.22</td>
</tr>
</tbody>
</table>

* Significantly different from normal incidence of dispersal.
Effect of Mating on Behaviour

Males and females were tested before and after mating on the same day. The behavioural responses did not change in form, but were often less pronounced following mating, because recently mated mites moved at a generally slower pace. For instance, geotactic scores of mated adults were comparable to the scores of unmated adults, as were the responses to an edge, despite decreased motility in the mites. The score for response to small depressions either remained the same or "increased" one class, partly because the mites' slower pace affected the time component in this test. Comparison of an individual's behavioural scores over several days failed to show any difference in pattern between its mated and unmated states.

Discussion

Activity level varied between mites. Mites which had been handled roughly were extremely hyperactive, while larvae moved very little. Every effort was made to record behavioural scores and not activity levels by waiting patiently for each mite to traverse the various courses at its own pace. Yet within even one score class (e.g., negative geotaxis) it was sometimes possible to distinguish different activity levels. Each set of test responses could be ranked to indicate the order of scoring based on the predisposition provided by activity level (Table 7). Although activity levels predisposed mites to certain score classes, patient observation and careful handling revealed
Table 7. Relative activity of mites in each behavioural class.

<table>
<thead>
<tr>
<th>Highest Activity</th>
<th>Lowest Activity</th>
</tr>
</thead>
<tbody>
<tr>
<td>Geotaxis:</td>
<td></td>
</tr>
<tr>
<td>Positive</td>
<td>Negative</td>
</tr>
<tr>
<td>(3+ runs, 2 runs, 1 run to settle)</td>
<td>Neutral</td>
</tr>
<tr>
<td>Response to</td>
<td></td>
</tr>
<tr>
<td>Small</td>
<td></td>
</tr>
<tr>
<td>Depressions:</td>
<td></td>
</tr>
<tr>
<td>Response to</td>
<td></td>
</tr>
<tr>
<td>an Edge:</td>
<td></td>
</tr>
</tbody>
</table>

Scores in the same relative activity column should not be interpreted to indicate similar real activity levels in the mites so scoring.
underlying behavioural states independent of activity level. The 
geotactic test, while indicating that mites of different 
activity levels could be distinguished, also accurately assessed 
their geotactic tendencies. Similarly, the response to small 
depressions included a definite thigmotactic component in 
addition to its motility component. Highly motile females 
actively engaged in mating, often entered ever smaller 
depressions until, in the close quarters, they were able to 
extricate themselves from the males. When mites which scored "3" 
on the ridge apparatus were also tested on the edge of the petri 
dish, they showed that they were more capable than low scorers 
of following a physical marker, such as a 1-mm edge, 
irrespective of their activity level. This ability may reflect a 
predisposition to use such cues as much as or more than it 
reflects an innate difference in distinguishing them. 
Consequently, even though a minimal level of activity was 
necessary to perform these tests, with careful handling, the 
scoring pattern was largely independent of activity level.

The lack of association between the results of the 
geotactic test and the rate at which the mites descended from 
the ridge (response to an edge test) confirms that the tests 
were not interdependent. An association between positive 
geotaxis and the "0" response to an edge was noted earlier as a 
symptom of rough handling. The fact that this association was 
not evident following gentle handling (Appendix 2) indicates 
that these two tests actually could be used to monitor different 
behavioural states, provided the the mites were carefully
There was no significant difference between male and female lifetime scores with respect to geotaxis and response to an edge. Females, however, were apparently more prone to score "0,1" in response to small depressions, whereas males more often scored "2" or "3". The exceptional behaviour of mating females was mentioned above. Earlier experiments showed no essential difference in male and female motilities, so it seems that this difference in test scores reflects differences in male and female thigmotactic responses. The fact that males tolerate being pressed between the female and the substrate during mating confirms that they have a stronger thigmotactic response.

**Behaviour: Day 1 to Day 5**

This work provides a basis for describing the early part of the life history of these predators in terms of behavioural scores; e.g., with respect to geotaxis, responses to small depressions and responses to an edge. On the first day after eclosion, larvae exhibit neutral geotaxis, a class "3" response to small depressions and a class "0,1" response to an edge. These three scores are strongly associated in one-day-old mites. On the second and subsequent two days the association between behaviours breaks down (perhaps because of different individual development rates), and new norms are established for each behaviour. On Day 5, the adults typically score negative geotaxis, a class "0,1" response to small depressions, and a class "0,1" response to an edge.
Dispersal

As noted in Tables 5 and 6, the positive or neutral geotactic scores and the "0,1" class response to an edge can be used to forecast as much as three days in advance subsequent periods of higher than normal dispersive tendency. These predictive test scores may, in addition, indicate behaviours directly involved in dispersal or behaviours that precede it (on a 24-hour sampling system). For instance, neutral geotaxis may be a transition state between nondispersive geonegative and dispersive geopositive behaviour. Neutral geotaxis would then be a predictive precursor of dispersal whereas geopositive behaviour would be indicative of dispersal. The two predictors (geotaxis and response to an edge) appear to cycle nonsynchronously within the mites, as is evidenced by Table 4 and the low proportion of instances when both predictive scores were recorded simultaneously (20/202).

Information from Tables 4, 5 and 6 can be combined to produce a representation of changes in dispersive tendency, as measured by the two predictors, over time. The first adult instance of positive or neutral geotaxis, on Day 8, leads one to expect a higher than normal dispersive tendency on Days 11, 14 and so on (Figure 3). Similarly, the first adult instance of the "0,1" class response to an edge, on Day 5, foreshadows peaks in dispersive tendency on Days 8, 11, 14 and so on (Figure 4). The mean duration of the respective predictive scores is different however (geotaxis: 1.41 days; response to an edge: 2.25 days), suggesting that the resulting peaks in dispersive tendency
Figure 3. Daily pattern of dispersive tendency (=proportion dispersing) as predicted by recurring bouts of positive or neutral geotaxis. Normal range of dispersive tendency indicated by -----. Error bars indicate 95% confidence limits on a proportion (see Table 5).
Figure 4. Daily pattern of dispersive tendency (=proportion dispersing) as predicted by recurring bouts of class "0,1" response to an edge. Normal range of dispersive tendency indicated by ---. Error bars indicate 95% confidence limits on a proportion (see Table 6).
either should be "rounded off" to cover the appropriate
durations, or that some threshold value of dispersive tendency
is exceeded for 1.41 and 2.25 days, respectively, in Figures 3
and 4. If the peak shown in those graphs is actually the highest
possible dispersive value, the threshold value indicated by the
geotactic test would be 0.37; well above the normal level of
0.19±.05. Figure 4 gives a value of 0.46. Since this value is
well within the normal range of dispersive tendency that the
tests revealed, the figure of 0.75±.17 suggested by the edge
tests as the peak in dispersive tendency may actually be too
conservative.

Although these graphs, as drawn, indicate the superposition
of respective peaks and troughs, this is an artifact of the
discrete rather than continuous scale along the X-axis and the
sampling period's disregard for the duration of recurring bouts.
With 24-hour sampling, however, it is impossible to consider the
matter of superposition in finer detail. The duration of
predictive behaviours obscures any peaks after the first one.
The wide ranges covered by the actual periods and the large
standard deviations of the behaviours suggest a more complicated
interrelationship, particularly in later cycles. It is worth
noting, however, that the first peak in dispersive tendency, as
predicted by the "0,1" class response to an edge, falls on Day
8, which is also the first instance of the positive or neutral
dispersive trend.

That some predators do not display peaks in dispersive
tendency may be due to their individual physiological state.
Nutritional status and reproductive state may interact to define a level of responsiveness to dispersive stimuli. The recognizably distinct levels of activity in mites which were noted earlier may indicate just such different levels of responsiveness. It may be that mites which are readily responsive to increasing urges to disperse respond very quickly and strongly when only a few factors reinforce their dispersive drive. In contrast, mites which are less responsive to increases in their dispersive tendency may require cumulative pressure from many factors. For instance, such mites may need the stimulation that would be provided if two factors contributing to their dispersive drive peaked simultaneously. Thus, they may need the stimuli underlying both the predictive geotactic score and the predictive edge score to reinforce one another. If these were not synchronized, their independent effects might not be sufficient to elicit a dispersive response in these low-keyed individuals.

Further investigation of the impact of dispersing individuals on the population dynamics of predator-prey systems seemed to be warranted by the results of the study. According to the criterion of dispersal used here dispersing individuals were selectively killed and were not available for experimental manipulation. Based on the characteristic behavioural scores of dispersive individuals as found in the earlier experiment, it seemed that artificial means might be used to induce dispersive behaviour, as measured by those scores, in the predators. These "treated" predators might then be contrasted with "untreated"
predators under various regimes to assess their impact on pest populations.
SECTION 5: INDUCED DISPERSAL BEHAVIOUR

Introduction

Having established a pattern of recognizable behavioural scores associated with dispersal, the next step was to induce dispersive behaviour in adult mites.

Predaceous mites released to control greenhouse infestations of phytophagous mites almost invariably seem to scatter rapidly. Some aspect of the way these predators are treated immediately prior to release seems to be inducing dispersal. Although release methodology has differed between research groups, high-density confinement of adult females without food in small glass or gelatine vials or capsules is a common feature (see Burnett, 1977 for review). Mites packaged in this way are usually stored at low temperature for short periods until they are turned over to the growers for release. Although low temperature storage has been thought to minimize any adverse effect such high density confinement might have on the predators, the growers who receive the mites probably are not so careful with storage temperatures. Any extended period of storage at higher temperatures would certainly have adverse effects on these predators, if only by accentuating their tendency to disperse.

Preliminary experiments showed that dense populations of predators could not be confined on leaf surfaces, with or without prey. Very soon after their initial confinement large numbers of mites left the leaves, fell into the water and died.
Thus, confinement of dense populations had to be accomplished by methods similar to the encapsulation methods described above. These treated mites were then characterized behaviourally and compared to untreated individuals.

**Materials and Methods**

**Treatment**

One end of a capillary tube (length 7.5 cm; bore 1 mm) was closed with plasticine. The other end was appressed to the leaf surface of the *P. persimilis* culture to trap an individual of the desired sex. The predators readily climbed the glass, so the process could be repeated until the desired number of mites were in the tube. The open end was then sealed with plasticine.

Capillary tubes containing ten female or ten male predators were stored horizontally for 24 hours, at 25±2°C; 16L:8D. At the end of the 24-hour period, each capillary tube was broken open and the mites were allowed to crawl onto an uninfested bean leaf. Most individuals left the tube within 20 minutes and were tested immediately after their escape from the tube. Individuals which took longer than 20 minutes were discarded.

**Behavioural Characterization**

Ten crowded and starved individuals of each sex were tested on the behavioural apparatus (see Section 4). Ten individuals of each sex were taken randomly from the stock culture and run
through identical tests. The average motility of treated female mites was obtained by methods described in Section 3. Ten treated females were tested repeatedly (at first, every two hours; later, every six hours) on the behavioural apparatus to determine the persistence of tube-induced behaviour. These mites were held individually on infested bean leaf squares after their release from confinement and between behavioural testing sessions.

Results

Survival of confined female mites was approximately 90-95%. Females were extremely restive when first confined but settled as time progressed and even laid eggs in the tubes. Eggs were often clumped together in one region of the tube (especially near one end) and were sometimes attended by one or more females. These attendants were not so restive as the other females in the tube. In a few instances, where particularly large numbers of eggs were deposited within the tubes, the attendant females were very reluctant to leave the broken tubes at the end of the 24-hour confinement. Some remained with the eggs for several hours before finally escaping, and some died without ever leaving the tube.

Females may attack eggs, especially those not in clusters, but their attacks rarely succeed. Attacking females placed their

---

1 By this point in the experiment, males were no longer tested. Their survival was poor in the tubes making it difficult to acquire the required numbers of treated mites.
forelegs on top of the egg and attempted to pierce it with their mouthparts. Most frequently, the egg was not penetrated but only rolled away. Although no successful feeding attempt was witnessed, one female was seen sitting over a shrivelled egg, grooming her mouthparts. Several such shrivelled eggs were found in the tubes containing female predators. In most instances, these eggs were isolated from other eggs. In contrast, the carcasses of females which died within the tubes were never shrivelled (unlike some eggs, and male carcasses).

Male mites confined ten per tube had a much lower survival (ca. 50%) than the females. Males were exceptionally motile in the first half-hour of confinement. Inter-male encounters were extremely brief (<1 s) and terminated with the mites running off in opposite directions. Thus, the males generally avoided one another. After the first half-hour, the duration of inter-male encounters increased (up to several minutes) and often involved grappling with the forelegs and chelicerae. These aggressive displays were not limited to pairs of males; several males often became involved sequentially. After just six hours in the tubes, some deaths had occurred. Carcasses were generally badly shrivelled.

The treated predators which displayed positive geotaxis could be distinguished from the typically geopositive mites described earlier. Treated mites moved less rapidly over the behavioural apparatus than normally geopositive mites, and explored more of the apparatus before moving geopositively down the wire and off the platform. In fact, the suddenness of the
geopositive response of these treated individuals after their prolonged and apparently aimless exploration of the apparatus was very characteristic. When they were returned to the apparatus for second and third trials, they resumed their initial exploratory behaviour, but with diminished intensity, and for much briefer periods each time. The total time required to score these treated mites for geotaxis was approximately four times as long as that required to score normally geopositive mites among the untreated population.

The results of the behavioural tests are shown in Table 8. Since the probability of an observation in some classes was so low, the data were grouped further to give only two possible score classes per test (negative/positive or neutral; "0,1"/"2","3"). Fisher's Exact Test was then used to assess significance (Appendix 3). There was no significant difference between the scores of untreated males and females. Nor was there a significant difference between the scores of treated males and females. Hence, the results for both sexes were combined prior to further analysis (Table 9). There was a significant difference between the geotactic scores of treated and untreated predators (p<0.001). Most untreated predators were geonegative, whereas most treated predators displayed positive or neutral geotaxis. There was no significant difference between the responses of the two groups to small depressions. The majority of untreated predators scored "0,1" on the edge test. Treated predators showed the opposite trend scoring, for the most part, "2" or "3" on the edge (p=0.002).
Table 8. Behavioural scores for untreated and treated individuals of both sexes.

<table>
<thead>
<tr>
<th>Score</th>
<th>Number of Individuals in each Class (n=10)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Geotaxis</td>
</tr>
<tr>
<td></td>
<td></td>
</tr>
<tr>
<td>Untreated</td>
<td></td>
</tr>
<tr>
<td>Females</td>
<td>0,1/-</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
</tr>
<tr>
<td>Treated</td>
<td>0,1/-</td>
</tr>
<tr>
<td>Females</td>
<td>2 /+</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
</tr>
<tr>
<td>Untreated</td>
<td>0,1/-</td>
</tr>
<tr>
<td>Males</td>
<td>2 /+</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
</tr>
<tr>
<td>Treated</td>
<td>0,1/-</td>
</tr>
<tr>
<td>Males</td>
<td>2 /+</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
</tr>
</tbody>
</table>

"-" = negative, "+" = positive, "--" = neutral.
Table 9. Grouped behavioural scores for untreated and treated individuals of both sexes.

<table>
<thead>
<tr>
<th>Score</th>
<th>Number of Individuals in each Class (n=20)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Geotaxis</td>
</tr>
<tr>
<td>Untreated Mites</td>
<td>0,1/-</td>
</tr>
<tr>
<td>Treated Mites</td>
<td>2,3/+,-</td>
</tr>
<tr>
<td>Untreated Mites</td>
<td>0,1/-</td>
</tr>
<tr>
<td>Treated Mites</td>
<td>2,3/+,-</td>
</tr>
</tbody>
</table>

1 "-" = negative, "+" = positive, "--" = neutral.
The average motilities of treated and untreated adult predators are shown in Table 10. Treated female predators were three to five times more motile than their untreated counterparts on uninfested and infested substrates, respectively. Note, however, that both the treated and untreated predators displayed a greatly increased motility on uninfested bean leaves (23 times greater for untreated females; 14 times greater for treated females).

The tracings produced with treated females were markedly different from those of untreated females. Treated mites rarely left the side of the leaf on which they were released, although they had repeated contact with the leaf edge. The pathways described on subsequent sweeps across the leaf were closely appressed to one another indicating a more thorough exploration of a much smaller area than the sweeping paths of untreated females. Moreover, the areas traversed tended to be concentrated in the upper half of the leaf. Consequently, although these mites, with their greater motility, covered more leaf surface than untreated females, they actively explored only about one-third of the total leaf area. On infested leaves, treated females were more restive than untreated females. Searching took place along tightly convoluted paths, concentrated within a small area. Feeding stops were frequent (ca. four per 20-minute period) but of very short duration. Moreover, the prey often escaped, apparently because treated predators were frequently clumsy in their attacks.

No apparent change in behaviour occurred in the first 22
Table 10. Average motilities for various classes of individual predators measured on two substrates.

<table>
<thead>
<tr>
<th>Motilities' (mm/s)</th>
<th>Individuals Tested</th>
<th>Substrate</th>
<th>Uninfested Bean</th>
<th>Infested Bean</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Untreated Females</td>
<td>0.94±.20</td>
<td>0.04±.02</td>
<td></td>
</tr>
<tr>
<td></td>
<td>Treated Females</td>
<td>2.75±.32</td>
<td>0.20±.15</td>
<td></td>
</tr>
</tbody>
</table>

* mean±S.E.
hours after release from the tubes (positive geotaxis, "0,1" on small depressions and "3" on an edge). By the 28th hour most individuals showed a class "2" response to an edge. Geotaxis remained unchanged. Between 40 and 46 hours after release from confinement, the more typical adult responses (negative geotaxis and "0,1" response to an edge) once again became evident.

Discussion

Females attempted and, in a few cases, apparently proceeded to cannibalize eggs laid within tubes. Laing (1968) also reported cannibalism among starved *P. persimilis*, but indicated that this behaviour was rare, and that feeding on eggs and young larvae was far from vigourous. The few eggs cannibalized in this study could not have contributed much to the appeasement of the females' hunger.

Male mortality in the tubes seemed to be the result of inter-male aggression. Although inter-male aggression has not previously been reported for this species, Amano and Chant (1979) reported that *P. persimilis* males waited near or sometimes on female deutonymphs in their cultures (cf. Laing, 1968; observations on this culture) suggesting the presence of a sex-attractant in pre-adult females. This lurking behaviour of reproductive males is well known in *T. urticae*; the males of which claim and sometimes aggressively defend late female deutonymphs (Potter, 1981, Potter et al., 1976a, 1976b). Inter-male aggression was observed in the culture of *P. persimilis* used here although apparently not in relation to quiescent
deutonymphs. Thus, there seems to be a natural tendency for such aggressive behaviour, which the confined circumstances of the crowded tube seem to have accentuated. The condition of male carcasses (shrivelled) as opposed to female carcasses (not shrivelled) suggests that the males occasionally punctured one another's integument during aggression. Whether loss of body fluids occurred actively (through feeding activity of survivors) or passively (through evaporation), before or after the death of injured mites could not be determined here. However, the presence of water droplets in some tubes suggests that passive means may not have been sufficient to produce the observed results.

The predominantly positive or neutral geotactic scores of treated predators mimicked the scores of dispersers in the earlier behavioural experiment, and confirmed the value of this dispersive index. The geopositive tendency of dispersers is interesting; it suggests that terrestrial dispersal is, indeed, more typical of *P. persimilis*, than the aerial dispersal which has recently been cited among phytoseiids (Johnson and Croft, 1976).

The predominance of "2" and "3" scores on the edge test among treated predators suggests that the "0,1" class which seemed so important in the previous experiment is mainly a predictive tool. In fact, the predominance of the "2" and "3" scores among adults in the previous experiment, and their very brief "0,1"-type behaviour on an edge, suggests that the predictive value of the "0,1" response is mainly due to its
association with the brief refractory period which apparently occurs between longer bouts of highly dispersive behaviour.

An ability to distinguish and follow edges, veins or other physical landmarks during the dispersive phase would, in many cases, be as advantageous a path-straightening device for dispersers as the use of polarized sky-light has proven to be for insects (Wellington, 1955; 1976). Takafuji (1977) suggested that strings or supporting wires between plants might facilitate the dispersal of *P. persimilis* throughout a crop. The response to an edge described here, however, suggests that square- or beveled-edges connectors would be better than cylindrical connectors for encouraging predator dispersal. Experimental releases of predators in the UBC Plant Science greenhouse in fact confirmed that well-defined edges were better than round string or wire. Predators released onto horizontal metal wires laid around and through benches of carnations followed spiral paths along them and frequently reversed direction, so that they made little effective progress (0-10 cm). In contrast, predators released onto similarly-placed "L"-shaped metal bars travelled far greater distances (0.25-1 m before lost from view). The predators tended, however, to prefer the inner surface of the "L" perhaps because of its thigmotactic component. Once they were on the inner face, they did not encounter much plant foliage along their path. Mites on wires encountered foliage more frequently and so moved into the crop more readily than those on the bars.

It is easy to visualize both positive and negative
implications for pest control in some common greenhouse structures. Supports and substrates with directional components may increase distances travelled by dispersing mites, whereas more featureless surfaces should encourage more localized activity. How often a mite will encounter foliage while travelling on any kind of substrate will affect its chances of getting onto a plant. Thus, too much pruning along support structures may prevent these predatory mites from searching near their release point. Both extremes—too short or too long a dispersal distance—seem undesirable. Very localized movement cannot contribute to pest control farther out, whereas very long-distance travel which may take mites past the crop would be equally futile.

It would be interesting to test the impact of square or triangular wire on predator dispersal throughout a greenhouse. An encircling barrier, with a sharp edge to it around greenhouse plots might also be useful as a means of "containing" the predator and "reintroducing" it to the crop!

Treated females were much more motile than untreated predators on infested as well as uninfested substrates. On uninfested surfaces, treated females moved exceptionally rapidly (approximately 3 mm/s, three times the speed of untreated females). Moreover, they searched a smaller portion of the leaf, albeit more thoroughly, and rarely explored more than one side of the leaf during the experimental period. The high activity levels of treated predators may have been responsible for their apparent clumsiness when attacking the prey.
The remarkable persistence (40-46 h) of tube-induced behaviour underscores the potential importance of these responses in control programs. Mites could travel such long distances during such an extended period that the release stock could be greatly depleted. At the very least, typical predatory behaviour might not resume until almost two days after release; a time lag that could be critical.

It is appropriate to note that these results on the persistence of tube-induced dispersive behaviour were obtained from individuals which had ample food after they were released. So much locally available food is certainly not typical of release situations. Consequently, the above estimates concerning the amount of time required to revert to non-dispersive behaviour are likely to be optimistic. Indeed, continued starvation after release from high-density confinement may synergistically increase the likelihood of behaviours that work against "control", as defined by pest managers.
SECTION 6: BEHAVIOUR OF TREATED MITES

Introduction

The previous section revealed some of the peculiar behavioural characteristics of mites which were starved and crowded prior to release. The behaviours seemed consistent with those that were associated with normally-occurring dispersal in Section 4. Moreover, the experiences of pest managers indicated that this type of pre-release treatment seemed to increase the dispersive tendency of the predator, *P. persimilis*. As noted earlier, however, the behaviours displayed were not completely identical with those attributed to naturally-occurring dispersers (recall, the weaker intensity of positive geotaxis in treated individuals). Thus, further behavioural characterization of these treated mites was necessary.

Since terrestrial dispersal implies that the normally plant-dwelling mites must move onto and across other substrates, any hesitancy or tendency to move onto novel substrates could be critical to the dispersal process. Thus, mites were characterized for this behaviour. The mites were also tested for their response to a water barrier.
**Materials and Methods**

Treated female predators were obtained using the methods described earlier. Untreated females served as the controls. Two behavioural characterizations were made.

Mites were released individually onto a circular plastic arena (diameter: 2.5 cm; height above surroundings: 1 cm) placed in the middle of a tray (18 X 25 cm) filled with moist soil. The time taken to leave the arena and move across the soil was measured for each mite. Ten treated females and ten untreated females were tested in this manner.

Individuals were released individually onto moderately-sized leaf squares (2.5 X 2.5 cm) of either uninfested bean or cucumber. These squares were checked at 15 minute intervals for 2 hours. The number of individuals which had entered the surrounding water barriers during each period was recorded. A final observation was made 24 hours after initial release onto the leaf squares. Thirty-six treated and untreated individuals were tested on each substrate.

A further 15 treated and untreated individuals were released onto leaf squares (2.5 X 2.5 cm) of either infested bean or cucumber. These were surveyed 24 hours later and the number of dispersals was recorded.
Results

All mites encountered the soil surface soon after release on the arena. Preliminary explorations of the soil surface, however, ended with a return to the arena. Eventually, all mites left the arena and moved rapidly across the soil surface in an approximately linear path. On reaching the edge of the tray, all mites moved readily onto that surface and proceeded. Untreated female predators were slow to move off the arena and across the soil surface (mean=33±6 min). Treated individuals moved off across the soil surface much more readily (mean=6±1 min; 0.02>p>0.01).

The number of treated and untreated individuals remaining on uninfested bean and cucumber squares over time is shown in Figure 5. The difference between substrates was greater than the difference between predator treatments. Dispersal was apparently slower off cucumber than off bean.

On infested cucumber, there was no dispersal of individuals over the 24-hour period. There was no significant difference in the number of treated and untreated individuals dispersing off infested bean squares.
Figure 5. Number of treated and untreated predators remaining on uninfested leaf surfaces over time.

- untreated females on cucumber
- treated females on cucumber
- untreated females on bean
- treated females on bean
- initial number
Discussion

Treated predators were less hesitant to move onto a novel substrate than untreated predators. Once movement across the soil was initiated there was no difference between individuals.

The different responses of the predators to the two types of leaf substrate can be attributed to the increased effective surface area of the pilose cucumber leaves. There was no apparent difference in dispersive tendency, as measured by the response to a water barrier, between treated and untreated individuals. Based on the earlier results with regard to a novel non-aqueous substrate, this apparent similarity of response between treated and untreated individuals may reflect their response to water rather than their dispersive tendencies per se.
SECTION 7: CONTROL ATTEMPT USING TREATED MITES

Introduction

Earlier work revealed that starved and crowded (="treated") predators displayed a higher than normal dispersive tendency. Several aspects of their behaviour suggested that they might exercise weaker control on pest populations than untreated individuals. A small-scale release program was designed to provide information both on the success of each type of predator and processes involved in prey exploitation.

Materials and Methods

Ten cucumber plants bearing primary and five secondary leaves were selected for this experiment. These plants were 30-40 cm tall. Ten bean plants bearing the primary and five trifoliate leaves were similarly selected. These plants were 60-80 cm tall. The total surface area of secondary leaves was approximately 1600 sq. cm, for both plant types. The secondary leaves were numbered upward from the ground on each plant. A random number table was used to select one leaf (or one trifoliate leaf, on bean plants) for infestation. Approximately 150 prey, including all stages and both sexes, were released onto the upper surface of the randomly selected leaves. Plants were held for three days while the infestations became established.

One cucumber and one bean plant were placed on each of ten
glycerine-surrounded trays. In five of these trays, ten female predators which had been starved and crowded for 24 hours (referred to later as "treated"), were released onto one primary leaf of each plant. In the other five trays which served as a control, ten female predators taken randomly from the culture (referred to later as "untreated"), were similarly released. At one-day intervals, for the next four days, both surfaces of each leaf were examined for the presence of these predators. After the final survey, plants were dissected, leaf by leaf, and examined under the microscope. The outline of each leaf was traced and, on all but the originally infested leaf, the location and number of prey webbing, eggs, immatures, adults and carcasses were marked. Comparable data for the predator were also compiled. Only numerical data were collected from the originally infested leaves, since the high prey numbers and even distribution of mites on these leaves made it difficult to diagram specific mite locations.

Results

Predator and Prey Numbers

The number of untreated and treated predators remaining on the plants on each of the four days is recorded in Table 11 (raw data included in Appendix 4'). The results can be summarized in

1 Three-factor analysis of variance (ANOVA) was used to establish any interactions between factors. Since only two-way interactions existed, their specific nature could be identified using two-factor ANOVAs.
Table 11. The number of untreated or treated predators remaining on plants during the first four days after release.

<table>
<thead>
<tr>
<th>Days After Release</th>
<th>Untreated Predators</th>
<th>Treated Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cucumber</td>
<td>Bean</td>
</tr>
<tr>
<td>1</td>
<td>9.0±0.5</td>
<td>8.8±0.6</td>
</tr>
<tr>
<td>2</td>
<td>8.8±0.5</td>
<td>8.4±0.9</td>
</tr>
<tr>
<td>3</td>
<td>7.0±1.3</td>
<td>5.4±1.5</td>
</tr>
<tr>
<td>4</td>
<td>2.8±0.5</td>
<td>3.0±1.6</td>
</tr>
</tbody>
</table>

* mean±S.E.
the following manner. Host plant differences were never statistically significant. Treated and untreated predators disappeared from plants at essentially the same rate on each of the first three days after release. On the fourth and final day, however, there was a significant difference (0.05>p>0.025) in the number of untreated and treated predators remaining on both bean and cucumber plants. On average, 5.7 treated predators and only 2.9 untreated predators remained on the plants on the final day.

The counts of predator and prey numbers on the various plants after four days are shown in Table 12 and Appendix 5. There was no significant difference in mite numbers (either predator or prey) on bean and cucumber plants. Total predator numbers (all stages) were essentially the same on all plants. Total prey numbers (all stages), however, differed significantly on the plants (p<0.005). Fewer prey were found on plants receiving untreated predators (mean=37.2) than on plants exposed to treated predators (mean=183.7).

Most leaves on all plants receiving treated predators were visibly infested, by the end of the experimental period. Infestation on these leaves often occurred in several separate patches. Approximately one half of the infested patches on all plants were exploited by the predator. Infestations on lower leaf surfaces, however, were more frequently exploited than were those on upper leaf surfaces (exploitation rates 75% and 25%, respectively). The primary leaves of the plants receiving treated predators were involved in the infestation.
Table 12. Mite numbers after four days. Distribution of prey is indicated (I=originally infested leaves; U=originally uninfested leaves).

<table>
<thead>
<tr>
<th>Plants Exposed to Untreated Predators</th>
<th>Plants Exposed to Treated Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Cucumber</strong></td>
<td><strong>Bean</strong></td>
</tr>
<tr>
<td>Predator</td>
<td></td>
</tr>
<tr>
<td>83.6±5.7</td>
<td>90.6±24.5</td>
</tr>
<tr>
<td>Prey</td>
<td></td>
</tr>
<tr>
<td>37.6±14.5</td>
<td>36.8±28.1</td>
</tr>
<tr>
<td>I</td>
<td>21.8±7.7</td>
</tr>
<tr>
<td>U</td>
<td>15.8±7.4</td>
</tr>
</tbody>
</table>

*mean±S.E.*
There was, however, a difference in the response of the two plant types to infestation. Three out of five cucumber plants exposed to treated predators, bore wilted leaves. Bean plants with similar prey numbers did not show this response.

**Predator and Prey Distributions**

There was no significant difference between prey distributions on the two host plants. There were, however, differences in prey distribution associated with the predator treatment (Table 12). On plants receiving untreated predators 41% of the total prey population was found on the originally infested leaf at the end of the four days. In contrast, only 21% of the prey on plants receiving treated predators were found on the originally infested leaves, at the end of the experiment. Thus, the prey on plants exposed to untreated predators were much more localized than prey on plants receiving treated predators.

The presence of webbing¹ on most leaves of plants receiving untreated predators indicated that the prey had attempted to disperse throughout each plant. Predator eggs were found in most webbed areas and the close proximity of actively feeding adult

¹ Throughout this discussion webbing is used as an indicator of prey activity in an area. Where webbing occurred but no prey, carcasses usually indicated that predators had already exploited the area. On the other hand, the presence of prey without webbing indicated that dispersing prey had just recently arrived. Placement of predator eggs in webbed areas with no remaining prey was thus seen as distinct from egg placement in the absence of webbing although immatures would be without a food source in both cases.
female predators to previously unexploited areas illustrated that there was good synchrony in the distribution of predators and prey. In all cases, most predators were found on the underside of leaves, perhaps accounting for the slightly higher prey densities on the upper surface of the infested leaves. In most cases, predator eggs were found only within webbed areas. On the young leaves of cucumber plants, however, predator eggs were often found even when no prey webbing was evident. The primary leaves were never involved in infestation in plants exposed to untreated predators.

Discussion

For the first three days there was no difference in initial dispersal rates between treated and untreated predators. Only on the final day, was there a difference in dispersal between the two types of predator. Despite this apparent similarity in response with regard to dispersal per se many differences in control success were evident between the two groups by the end of the experiment.

Untreated predators were much more efficient at controlling prey numbers than were treated predators. Thus, the dispersal of untreated mites on the final day was probably a response to the low prey numbers remaining on these plants. The final prey distribution was also different for the two predator types. Untreated predators seemed to be more capable of limiting the spread of prey throughout a plant than were treated predators. Thus, on plants receiving untreated predators damage was mostly
restricted to single leaves; those originally infested. Plants exposed to treated predators, by contrast, were more likely to suffer damage at several sites. Cucumber plants seemed more susceptible to damage than bean plants.

Since mortality of released individuals over the experimental interval was the same for treated and untreated predators, it seems unlikely that reduced predator vigour was responsible for the different exploitation patterns. Even though treated predators didn't disperse off the plants any faster than untreated predators, the results of Section 5 suggest that these predators may have moved between leaves on the release plant more readily than untreated mites. Such high motility may have decreased their efficiency in the originally heavily infested areas. In addition, the general clumsiness of treated predators and the considerable duration of behavioural disruption in these mites (Section 5) may have contributed to their inefficiency in controlling the initial localized infestation. This reduced efficiency in turn may have provided time and opportunity for greater numbers of the prey to move throughout the plant (spurred by natural dispersive drives or destruction of the originally infested leaf).

As evidenced by the position of predator eggs, there was generally good synchrony between predator and prey distributions in both treated and untreated groups. This suggests that the final differences in prey distribution were the result of initial lack of control leading to increased prey dispersal, rather than some grosser disruption of predator synchrony.
The generally good synchrony of predators and prey broke down on the young leaves of cucumber plants. This suggests that features of the substrate may, indeed, be capable of disrupting normal egg placement behaviour. The precise components of the substrate which are involved are not known, but young cucumber leaves are much more pubescent than bean leaves, or older cucumber leaves. Daftari (1979) reported that *Amblyseius aberrans* Oudemans deposited most of its eggs on trichome tips, rather than on the leaf blades, on a number of different host plants, suggesting that the relevant component was physical rather than chemical. The placement of eggs on young cucumber leaves in the absence of webbing confirms that predators do not necessarily place eggs near potential food sources. Thus, immature stages may be forced to travel considerable distances to find food (if prey do not infest the area in the meantime) and starvation may result in the absence of alternate food sources. On cucumber plants with rapidly expanding infestations this egg-placement behaviour would seem to favour control on young leaves. At various points in the growing season this may have especially important consequences.

The treated predators had not exploited fifty percent of the infested patches by the end of the experiment. It seems unlikely that this was caused by some continuing behavioural response (e.g., an inability of the predators to find these patches, or some hesitancy to exploit webbed areas that were found) since treated predators lost their behavioural uniqueness after 40-46 hours in other tests (see Section 5). It seems more
probable that infested areas remained unexploited merely for lack of time—a repercussion of an initial lag in control by treated predators.
SECTION 8: GENERAL DISCUSSION

Few authors to date have considered the full importance of dispersal to the success of *Phytoseiulus persimilis* / *Tetranychus urticae* control systems. Dispersal of the prey has received modest attention (Hussey and Parr, 1963; McEnroe, 1969, 1971; McEnroe and Dronka, 1971) but many inaccuracies persist (e.g., the generally-held belief that prey are sedentary on all but the most unsuitable hosts—Everson, 1980). The predator's dispersive behaviour has alternately been assumed to be a positive attribute of the system (Oatman et al., 1976) or has been systematically excluded from investigation (Mori and Chant, 1966; Laing, 1968; Eveleigh, 1979). Yet without information on such a potentially important aspect of the predator's behaviour, it is difficult, if not impossible, to realistically confront the control problems that have arisen (Burnett, 1977).

The analysis of numerical data pertaining to survivorship, reproductive rate, and prey consumption has occupied much research time (Laing, 1968, 1969; Takafuji and Chant, 1976; Eveleigh, 1979; etc.). Based on these results, recommendations on the suitability of the predator, *P. persimilis*, as a control agent of the two-spotted spider mite have been overwhelmingly optimistic (ibid). The relevance of much of this laboratory-derived data, however, is open to question without at least some measure of the magnitude of dispersal effects.

In Section 4 of this thesis, it was shown that dispersal in *P. persimilis* is a natural aspect of the predator's behaviour. There may be large individual differences in the timing of
dispersal but the results of this work indicate that virtually all the mites tested eventually succumbed to the influences of dispersal and entered the water barrier.

Dispersal behaviour, both as defined for this study and as observed on a larger scale, occurs in immature stages even though the low motilities of these mites seems to preclude them from traversing appreciable distances (see also Eveleigh, 1981a). The egg-placement behaviour of adult female predators that allows them to oviposit in areas remote from prey may be the stimulus for dispersal among immatures. Thus, dispersal of immatures is likely to have no detrimental effect on control and may even serve to enhance the spread of the predator throughout a plant or small area.

Because of matters of scale and motility, the dispersal events with greatest impact on biological control seem to be those that occur in the adult stage. The results of Section 4 indicated that adult dispersal is both persistent and recurrent (on an apparently cyclic basis). The intensity of the predictive geotactic response (cf. Section 5) was particularly evident.

Dispersal behaviour induced by pre-release starvation and crowding, although quite similar in many respects, seems to be less intense than that associated with normal dispersal. The edge response of normal and induced dispersers was indistinguishable. Motilities of the two types of dispersers were also quite similar. The intensity of geopositive behaviour, however, was notably less among induced dispersers. Furthermore, the incidence of dispersal, as defined by the response to a
water barrier, among treated mites was not distinguishable from untreated adults. Yet recovery from induced dispersal took almost two full days even when the predators experienced "ideal conditions" of ample prey and webbing.

In Section 7, it was seen that plants receiving treated predators experienced higher prey numbers and greater plant damage than plants exposed to untreated mites. Oatman and McMurtry (1966) noted, however, that seasonal yields from badly damaged plants (which had experienced high prey numbers) may be indistinguishable from normal yields from healthy plants, since damaged plants may have increased later production. Although such resurgence may occur, seasonal yield as measured by weight (irrespective of numbers, quality and timing) may be a poor indicator of financial gain to the grower. In practice, then, the different level of immediate control on plants receiving treated predators is important, even though both types of predators may eventually control prey numbers.

The impact of normal dispersal (which is more intense than induced dispersal) on control attempts, if it occurred in any significant proportion of the population, thus would seem to be even more detrimental. Defining the size of a "significant proportion" may not be a simple matter. This is more a reflection of the difficulty in defining adequate control by

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1 Thus, the report that P. persimilis controls prey numbers over a wide range of temperatures (Hussey et al., 1965) may be misleading without a constraining time frame. Stenseth (1979) translated different temperature and humidity regimes into different initial predator:prey ratios required to produce control.
phytoseiids (with respect to prey density, distribution, microclimatic preferences, pesticide spraying regimes, acceptable plant damage, timing of release, etc.) than the difficulty in assessing the impact of dispersal. It would seem that, if the numbers of predators (and other variables) required to give control, and the incidence of dispersal in the population were known, it would be relatively easy to calculate the number of additional predators necessary to supplement the release population to counterbalance dispersive loss. Obviously, at some point, the adjusted numbers-of-predators-needed per release may be unrealistically expensive. Populations of such high dispersive tendency must then be recognized as being unsuitable sources of control agents, regardless of how well they do in "confined" settings.

Although this perspective has not been adopted in biological control with phytoseiids, there are some data to suggest that it is a very valid view. Laing's (1968) data, for instance, indicate that predator longevity may be as high as 50 days and that 35 days is a reasonable estimate of the half-life of a predator population. Since other workers have shown that feeding continues nearly until death (Takafuji and Chant, 1976), pest managers have extrapolated that release populations have a half-life of 35 days (minus age at release) with feeding occurring throughout that time. If, however, dispersal in addition to natural death is considered in survivorship estimates, a very different prediction arises.

Figure 6 shows the survivorship curves for P. persimilis in
confined (modified Munger cells) and unconfined circumstances based, respectively, on Laing's (1969) data and experiments conducted as part of this research (Section 4 and unpublished data). The loss of individuals through dispersal during the first four days is probably an overestimate. Although these immatures were able to disperse off moderately-sized leaf squares, their low motilities (Section 3) suggest that few would actually be able to disperse from a host plant (let alone out of a crop) in any but the most unusual situation. Results of this thesis, however, show the very real potential for dispersing adult predators to travel quite considerable distances. It is, thus, very important to control considerations that none of the population which was allowed to disperse remained after Day 30 (Figure 6); i.e., five days before the half-life projected from Laing's data. If the dispersal of the immatures is not considered, the half-life of predator populations where dispersal is allowed can be calculated to be a mere six and one half days.

Individual differences in the predators' dispersive tendencies are likely to result in different travel times and distances. Hence, even though 100% of the individuals disperse, not all will necessarily leave the release area. Within a greenhouse, however, it is clear that some—often a significant proportion—will actually escape. It is also evident that significant disruption of control can occur due to dispersal-related behavioural changes, even if the predators themselves do not leave. Thus, the effective half-life of a release population
Figure 6. Survivorship curves for *P. persimilis* including (▲) and excluding (●) dispersal, based on results of this thesis and Laing (1968).
could be expected to lie somewhere between the two predictions (6.5 and 35 days), probably closer to the lower value. In more open agricultural settings, dispersal may not have such detrimental effects.

The results of Section 7 reveal that induced dispersal may compound the problems of natural dispersal in control programs. The standard practice of confining mites with no food at high density prior to release apparently induces dispersal. Although, as discussed elsewhere, there are differences in the responsiveness of individuals to dispersive stimuli, and not all treated mites may manifest dispersal per se, a significant behavioural change is induced in virtually all treated individuals. Thus, predatory behaviour and control efforts are disrupted, one way or another, immediately after release.

The considerable efforts of pest managers to ascertain the optimal numbers and timing of releases has highlighted the important consequences of even relatively short delays in control efforts. Thus, the systematic release of predators whose effectiveness is virtually guaranteed to be delayed by one to two days seems ludicrous. In the light of such established methods, the recent publication of new release recommendations, although extremely labour-intensive, seem quite reasonable by

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1 It is noteworthy, however, that the results of control programs in field settings are much worse than those in greenhouses. Possibly, some structural features in greenhouses effectively confine and reintroduce predators into the crop (Section 5). Many other differences between the two cropping systems may also exert an influence (e.g., microclimate, competition with natural predators, presence of road dust on foliage, difficulty in noticing incipient infestations, etc.).
comparison. Burnett (1977) advocated daily releases of predators; an open admission that dispersive loss is continual and steady. Costello and Elliot (1981) essentially recommended that predators be placed, by hand, on each leaf of infested plants with additional mites being released on each uninfested plant. It is hard to imagine the economic system that could support such intensive pest control programs. At such a level of grower involvement, washing the leaves with insecticidal soap or water, or eliminating infested leaves by selective pruning seem equally feasible methods of control. The recent practice of storing predators at much lower densities on pieces of leaf, rather than in tubes is encouraging, but perfunctory cooling practices may simply result in predator dispersal off the leaves and out of the cooler rather than out of the vial and off the plants!

A more subtle, yet ultimately profound, effect of high density confinement may also be important to control. Release populations are generally composed of adults of approximately, though not exactly, the same age. Such a population will not be physiologically homogeneous and, therefore, inherent dispersal tendencies will probably vary within the bounds of some population norm. The dispersal event then, in each individual, will occur nonsynchronously (i.e., the half-life of the population is an underestimate for some individuals and an overestimate for others). The confinement and starvation of predators before release may break down this natural variability of response and physiology. Certainly this occurs over a brief
period (40-46 h). On a longer time scale, however, the recurrent pattern of natural dispersal may be reset on a more synchronous basis—perhaps in the subsequent generation rather than in the treated individuals themselves.

Precedents for an hypothesis of common past experiences setting common future responses exist. Eveleigh (1979), for instance, showed that the prey conditions experienced early in the adult life of _P. persimilis_, in addition to recent nutritional history, affected the predator's later response to prey density. This is almost certainly a physiological response, not an example of learning. Information on nutritional history can be "stored" through proprioreception of body expansion and extent of energy reserves. An interaction with predator density, via increased stimulation and motility, and thus with increasing depletion of energy reserves, could easily take place. The proximate cause of dispersal in starved and crowded mites therefore is more likely starvation than high predator density, _per se_ (see also Johnson and Croft, 1976).

Starvation alone, however, may not account for the entire process of dispersal inducement. It has long been recognized that the predator's feeding habits do not always match the published typical consumption rates. Many workers (Mori and Chant, 1966; Takafuji and Chant, 1976; Eveleigh, 1979) have routinely discarded the data pertaining to individuals which took "untypically" few prey or laid "untypically" few eggs over the experimental period. Ohnesorge (1981) admitted that "prey consumption is endogenously controlled" and does not necessarily
reflect prey availability. Thus it is evident that, no matter how well one carefully provisions a leaf square, the mite alone "decides" if it will eat or not; just as no optimal number of available prey can prevent a mite from entering a water barrier.

Accordingly, although a particular nutritional history (i.e., a period of starvation) may precede, and in some senses, "cause" dispersal, in the normal context there seems to be an earlier, more fundamental internal stimulus that effectively prescribes dispersal by limiting prey consumption. Because of our extremely limited knowledge of acarine anatomy and physiology, we can only speculate on the nature of this ultimate cause.
SECTION 9: CONCLUSIONS

Unlike dispersal in many insects (Johnson, 1969), dispersal in mites is not necessarily confined to a short period of life. Dispersal in P. persimilis may occur at any time during the adult stage and may recur throughout an adult's lifetime (Section 4). The intensity of dispersal differs between individuals and seems to indicate inherent differences in susceptibility to stimuli inducing dispersal. Part of the qualitative differences between individuals seems to result from differences in nutritional history, but other factors may also be involved.

Dispersal behaviour can be induced in P. persimilis by starving and crowding individuals for 24 hours, but is not so intense as normal dispersal behaviour (Sections 5 and 6). Yet even this relatively weak dispersal significantly disrupts biological control (Section 7). This result underlines the potential importance of normal dispersal in P. persimilis to the successful control of T. urticae.

Standard pre-release treatment of predators minimizes the chances of successful pest control by inducing dispersal when it is least desirable. Starvation seems to be more detrimental than crowding per se, although both factors may contribute to behaviour disruption. Thus, reduced pre-release predator densities may be an inadequate change in methodology (Costello and Elliot, 1981). Further investigation is needed to determine whether honey or sucrose solutions (Ashihara et al., 1978), rather than prey, might be suitable foods for pre-release
predators.

The potential importance of dispersal of *P. persimilis* to biological control programs warrants a systematic assessment of stock populations with respect to dispersal tendency. The Sicilian stock is apparently more prone to dispersal than the Chilean stock (Kennett and Caltagirone, 1968). The genetic bottlenecks that are often experienced in laboratory-reared populations, however, may mean that the dispersive tendency of a particular population cannot be predicted solely from its sources.

The necessity for such an assessment of laboratory-reared populations is particularly important, now that organophosphate-resistant predators are being bred (Hoy *et al.*, 1980; Roush and Hoy, 1980; Roush *et al.*, 1980; Hoy and Standow, 1981). Populations which form the basis of such selection programs should be assessed for the incidence of dispersal at the outset, and unsuitable populations should be eliminated. Obviously, a follow-up assessment at the end of the program would also be desirable.
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predatory mite Amblyseius gossipi (Acarina: Phytoseiidae)

of the predatory mite Phytoseius plumifer (Acarina:
Phytoseiidae) as affected by physical surface feature of


APPENDICES

Appendix 1.
Genera within the Family Phytoseiidae (Schuster and Pritchard, 1963).

Family Phytoseiidae

Tribe Typhlodromini Karg

Seiulus Berlese
Neoseiulus Hughes
Typhloseiopsis De Leon
Typhlodromus Scheuten
Metaseiulus Muma

Tribe Amblyseiini Muma

Amblyseius Berlese
Amblyseiella Muma
Kampimodromus Nesbitt
Proprioseius Chant
Phytoseiulus Evans
Asperoseius Chant
Ptenoseius Pritchard and Baker

Tribe Iphiseiini Berlese

Iphiseius Berlese

Tribe Chantiini Pritchard and Baker

Chantia Pritchard and Baker

Tribe Macroseiini Chant, Denmark and Baker

Macroseius Chant, Denmark and Baker

Some taxonomists, notably Chant, have considered the
Amblyseiids, *per se*, to be a subgroup within the Typhlodromids
and, therefore, distinct from the genus *Phytoseiulus*.
Tribe Phytoseiini Berlese

Pennaseius Pritchard and Baker
Phytoseius Ribaga
Appendix 2.

Behavioural scores for individuals of both sexes, during the first five days after eclosion.

Proportion of Individuals in each Class (with 95% confidence limits)

<table>
<thead>
<tr>
<th>Days After Eclosion</th>
<th>Score</th>
<th>Geotaxis</th>
<th>Response to Small Depressions</th>
<th>Response to an Edge</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0,1/-</td>
<td>0.02±0.03</td>
<td>0.03±0.04</td>
<td>0.94±0.06</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
<td>0.05±0.05</td>
<td>0.11±0.08</td>
<td>0.03±0.04</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
<td>0.94±0.06 *</td>
<td>0.86±0.08 *</td>
<td>0.03±0.04</td>
</tr>
<tr>
<td>2</td>
<td>0,1/-</td>
<td>0.33±0.13</td>
<td>0.17±0.10</td>
<td>0.81±0.11 *</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
<td>0.14±0.09</td>
<td>0.29±0.12</td>
<td>0.12±0.09</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
<td>0.53±0.14 *</td>
<td>0.54±0.14 *</td>
<td>0.08±0.07</td>
</tr>
<tr>
<td>3</td>
<td>0,1/-</td>
<td>0.62±0.16 *</td>
<td>0.35±0.15</td>
<td>0.65±0.15 *</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
<td>0.14±0.11</td>
<td>0.24±0.14</td>
<td>0.19±0.13</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
<td>0.24±0.14</td>
<td>0.41±0.19 *</td>
<td>0.16±0.12</td>
</tr>
<tr>
<td>4</td>
<td>0,1/-</td>
<td>0.71±0.16 *</td>
<td>0.52±0.18 *</td>
<td>0.55±0.18 *</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
<td>0.13±0.12</td>
<td>0.39±0.18</td>
<td>0.26±0.15</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
<td>0.16±0.13</td>
<td>0.10±0.11</td>
<td>0.19±0.14</td>
</tr>
<tr>
<td>5</td>
<td>0,1/-</td>
<td>0.86±0.14 *</td>
<td>0.70±0.19 *</td>
<td>0.43±0.20 *</td>
</tr>
<tr>
<td></td>
<td>2 /+</td>
<td>0.05±0.09</td>
<td>0.30±0.19</td>
<td>0.26±0.18</td>
</tr>
<tr>
<td></td>
<td>3 /--</td>
<td>0.09±0.12</td>
<td>0</td>
<td>0.30±0.19</td>
</tr>
</tbody>
</table>

¹ "-" =negative, "+" =positive, "--" =neutral.
* Indicates modal values.
Appendix 3.

Fisher's Exact Test.

Data were grouped to give a 2x2 contingency table for each test of significance. For example:

**Behavioural Test X: Observed results**

| Score A (successes) | Score B (failures) | n1 = k1 + l1
|---------------------|---------------------|------------------
| Treated             | k1                  | l1               |
| Untreated           | k2                  | l2               |
| K=k1+k2             | L=l1+l2             | N                |

Similarly all other fourfold tables having the same row and column totals (n1,n2,K,L) but smaller k1 values can be constructed.

**Behavioural Test X: More extreme cases**

<table>
<thead>
<tr>
<th>k1-1</th>
<th>l1+1</th>
<th>n1</th>
<th>k1-2</th>
<th>l1+2</th>
<th>n1</th>
<th>...</th>
<th>0</th>
<th>n1</th>
<th>n1</th>
</tr>
</thead>
<tbody>
<tr>
<td>k2+1</td>
<td>l2-1</td>
<td>n2</td>
<td>k2+2</td>
<td>l2-2</td>
<td>n2</td>
<td>...</td>
<td>K</td>
<td>n2-K</td>
<td>n2</td>
</tr>
<tr>
<td>K</td>
<td>L</td>
<td>N</td>
<td>K</td>
<td>L</td>
<td>N</td>
<td></td>
<td>N</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

The sum of the conditional probabilities described by all the tables, where each table's probability is calculated

\[
P(k1,k2) = \frac{n1! \times n2! \times K! \times L!}{k1! \times l1! \times k2! \times l2! \times N!}
\]

can then be used to test the hypothesis: \( p1 = p2 \). If \( P \leq \alpha \) (where \( \alpha \) is the desired level of significance) the hypothesis is rejected in favour of the alternative \( p1 \neq p2 \).

---

Appendix 4.

The number of untreated and treated predators remaining on plants on the first four days after release. Rows indicate replicates.

<table>
<thead>
<tr>
<th>Untreated Predators</th>
<th>Treated Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cucumber Plants</td>
<td>Bean Plants</td>
</tr>
<tr>
<td>Days After Release:</td>
<td></td>
</tr>
<tr>
<td>1</td>
<td>2</td>
</tr>
<tr>
<td>8 9 8 4</td>
<td>8 8 6 1</td>
</tr>
<tr>
<td>10 10 2 2</td>
<td>11 10 10 9</td>
</tr>
<tr>
<td>10 9 9 2</td>
<td>8 5 1 1</td>
</tr>
<tr>
<td>8 9 8 2</td>
<td>9 9 4 1</td>
</tr>
<tr>
<td>9 7 8 4</td>
<td>8 10 6 3</td>
</tr>
</tbody>
</table>
Appendix 5.

Mite numbers on the plants at the end of the four-day experiment. Rows indicates replicates.

<table>
<thead>
<tr>
<th></th>
<th>Untreated Predators</th>
<th>Treated Predators</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Cucumber Plants</td>
<td>Bean Plants</td>
</tr>
<tr>
<td>Mite:</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Prey</td>
<td>Predator</td>
<td>Prey</td>
</tr>
<tr>
<td>68</td>
<td>82</td>
<td>11</td>
</tr>
<tr>
<td>77</td>
<td>100</td>
<td>14</td>
</tr>
<tr>
<td>22</td>
<td>93</td>
<td>3</td>
</tr>
<tr>
<td>14</td>
<td>72</td>
<td>7</td>
</tr>
<tr>
<td>7</td>
<td>71</td>
<td>149</td>
</tr>
</tbody>
</table>