FEEDING AND EGG LAYING BEHAVIOUR IN *CAMPYLOMMA VERBASCI* MEYER (HEMIPTERA: MIRIDAE)

by

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Feeding and egg laying behaviour in *Campylomma verbasci*

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FEEDING AND EGG-LAYING BEHAVIOUR IN *CAMPYLOMMA VERBASCI* (MEYER) (HEMIPTERA: MIRIDAE)

Abstract

The feeding requirements of *Campylomma verbasci* nymphs, their predatory and plant feeding behaviour, the timing of diapause-egg laying, and the effect of prey presence on adult residence time, were investigated.

First- and second-instar *C. verbasci* did not survive to adulthood on apple leaves alone. The proportion of nymphs surviving to adulthood and the number of eggs found in 5-day-old adult females reared on a nymphal diets of leaves plus pollen were not different than that of nymphs reared on leaves plus spider mites *ad libitum*. Adult *C. verbasci* reared on leaves plus pollen were larger than those reared on leaves plus mites. These results did not support the previous assumption that *C. verbasci* nymphs require arthropod prey to develop to adulthood.

To test the importance of prey in orchards, where pollen is not available throughout the entire development of first-generation *C. verbasci*, nymphs were reared from first- or second-instar on leaves, flowers and fruitlets, on which pollen was only available during the first three nymphal instars. A higher proportion of nymphs survived to adulthood with access to spider mites than with no prey, suggesting that there is some advantage for a nymph to be located where prey is abundant, and thus some advantage for females to lay eggs near prey.

The abundance of prey and recent prey-feeding experience of first and second instar *C. verbasci* nymphs did not have a significant effect on the number of bouts or the duration of time spent feeding on fruit. Plant feeding by *C. verbasci* nymphs occurred frequently and was not precluded by encounter with prey or by feeding on prey. *C. verbasci* nymphs apparently did not locate prey by sight and often responded to direct contact with prey by moving away from the prey.

Nymphs fed on all three arthropods tested, *Panonychus ulmi* (Koch), *Aphis pomi* (DeG.) and *Aculus schlechtendali* (Nalepa), but fed most readily on *P. ulmi*. Adult females had longer residence time on apple branches infested with *P. ulmi* than on branches with no prey. A longer residence time for ovipositing females may have biological significance in terms of the distribution of *C. verbasci* in the following year. Oviposition of winter-diapausing eggs occurred from mid-summer through fall, and corresponded to the flight of second- and third-generation adults.

Dedication

to my parents Shirley and d'Arcy Bartlett

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Table of Contents

List of Tables

List of Figures

Chapter I

Introduction

The mullein bug, *Campylomma verbasci* (Meyer) (Heteroptera:Miridae), is a bi- or trivoltine, generalist feeder. It spends the summer principally on a herbaceous host, mullein, *Verbascum thapsus* L., and overwinters as eggs laid on woody hosts such as apple and pear trees. The nymphs emerge in the early spring, around the time of bloom in apple trees. At this time they feed on arthropod prey such as mites as well as on small fruitlets, often causing deformation to some of the major apple varieties grown in Canada, Washington State (Caesar and Ross1920; Picket 1938; Hoyt 1973: Boivin and Stewart 1982; Thistlewood *et al.* 1989; Reding and Beers 1993), and more recently in Europe, *C. verbasci*'s place of origin (Jesus Avilla, pers. comm., 1995; Gary Judd, pers. comm., 1995). By early June,the nymphs develop into adults, most of which migrate to mullein plants where they establish the first of usually two summer generations (Thistlewood *et al.* 1990).

Campylomma verbasci nymphs are susceptible to organophosphate insecticides. However, the first-generation nymphs emerge shortly before and during the blossom period of apples, at which time organophosphates are not applied because such treatments kill pollinating insects. Therefore, orchardists apply organophosphates shortly before or after bloom or both, but are often unable to avoid economic damage from *C. verbasci*.

In addition to the direct costs of pesticide application, hand thinning of damaged fruit, and the downgrading of harvested fruit, there are also indirect losses attributable to *C. verbasci*: monitoring to determine if populations warrant spraying; risks to the environment and health of farmers due to exposure to insecticides; losses to apiarists as bees fly into sprayed orchards; and losses of natural enemies that help to control other pests in orchards.

There is evidence in the work of Bartlett and Edwards (1993) and McBrien *et al.* (1994) that amount and type of pesticide use were correlated with densities of *C. verbasci* and damage. They reported that organic orchards in which organophosphate pesticides and Sulfur were not used had very low densities of *C. verbasci* nymphs in the spring and no economic damage due to their feeding. If the reasons for the low density of *C. verbasci* were understood, it might be possible to induce such conditions in other orchards through management tactics.

Bartlett and Edwards (1993) hypothesized that the low density of European red mite, *Panonychus ulmi* (Koch), a major prey of *C. verbasci* (McMullen and Jong 1970; Lord 1971; Niemczyk 1978;) may lead to the low density of *C. verbasci* in organic orchards. In a survey of over 50 orchards varying in pesticide management, weak but consistently positive correlations were found between densities of *P. ulmi* in the summer and of *C. verbasci* nymphs the following spring. Within trees, Thistlewood and McMullen (1989) found correlations between the occurrence of *P. ulmi* and *C. verbasci*. The number of *C. verbasci* in orchards was also correlated with the average number of branches infested with green apple aphids, *Aphis pomi* (DeG.) (Acquafresca and Newton 1986).

My central hypothesis is that the availability of arthropod prey in apple orchards during the summer and fall influences the density of *C. verbasci* nymphs in the following spring. To test this hypothesis it is important to understand *C. verbasci*'s degree of dependence on prey, which species it can prey on, and whether the behaviour of adult *C. verbasci* is influenced by prey availability. It is also important to know when adults lay overwintering eggs, and whether they are influenced by the availability of prey at that time.

Little is known about the feeding and oviposition habits of *C. verbasci*. McMullen and Jong (1970) and Niemczyk (1978), concluded that arthropod prey are necessary for nymphs to develop to adulthood. If this is true there would be strong selective pressure for females to lay diapausing eggs on branches on which prey will be present the following spring. However, McMullen and Jong (1970) and Niemczyk (1978) used leaves as the only food for their control groups, without considering the availability of flower parts and young fruit in the early spring. Thus, more information is needed on *C. verbasci*'s degree of dependence on prey in the field.

The diet breadth and requirements of other generalist hemipterans are reviewed in Chapter 2 to provide a background of knowledge from which hypotheses, experiments and discussions about *C. verbasci* could be built. Chapter 3 investigates the assumption that *C. verbasci* nymphs require arthropod prey in order to develop to adulthood. Percentage survival, body size and reproductive development are compared for individuals reared on nymphal diets of apple leaves only, apple leaves plus mites, and apple leaves plus pollen. This chapter also investigates survival and body size of *C. verbasci* reared under field-like conditions on blossoms and fruitlets on which pollen is available only during the first three instars.

It is also important to know which prey species *C. verbasci* can exploit. Previous authors have determined that it can prey upon *P. ulmi*, two spotted spider mite, *Tetranychus urticae (Koch), A. pomi* (DeG.), apple sucker, *Psylla mali* (Schm.), and pear psylla *Cacopsylla pyricola* (Foerster) (Niemczyk 1978; and McMullen and Jong 1970; Lord 1971; Acquafresca and Newton 1986; Arnoldi *et al.* 1992). However, the relative ability of young nymphs to catch and eat these prey has not been observed. Chapter 4 explores the feeding behaviour of individual nymphs observed under the microscope. The relative abilities of nymphs to feed on three arthropod species available on apple in early spring are compared. The assumption that nymphs feed less on fruit when mites are available is investigated by observing individual nymphs on mite infested and uninfested fruitlets.

It is possible that prey-feeding increases fecundity or quality of eggs in the adult female. If this is the case, females probably reside longer and lay more eggs in orchards where prey is available. No work has been done previously to determine if prey influences the behaviour of adults. In Chapter 5, the effect of prey presence on the residence time of adult *C. verbasci* on apple branches with and without prey is investigated.

Although there has been no direct research on diapause-egg laying, temporal data on migration of adults from summer hosts to orchard trees suggests that it occurs only in the late summer and fall (McMullen and Jong 1970; Thistlewood *et al.* 1990; Smith 1991; McBrien *et al.* 1994). To determine the time period when diapause eggs are laid, apple branches were exposed to wild females in the field during different two-week periods in two growing seasons (Chapter 6).

Chapter II

Review of plant-feeding by generalist, predatory Hemiptera

Introduction:

Hemipterans exploit a broad range of food types. Sweet (1979), Cobben (1979), and Cohen (1996) discuss predation and phytophagy among the Hemiptera from phylogenetic and evolutionary perspectives. Evidence for the origins of feeding habits based on morphology, biochemistry, nutritional requirements, the presence of symbiotes and the production of stylet flanges and other adaptations, are reviewed by Cohen (1990, 1996). Cohen (1996) and Coll (1996b) also discuss switching between plant and prey-feeding by Hemipterans. Coll (1996a,b) explores direct and indirect effects of different plant species on the fitness of omnivorous Hemipterans, and examines the consequences of supplementing and substituting plant diets with prey and *vice versa*. The following is a review of the advantages, in terms of survival, development, fecundity and longevity, that plant-feeding provides to generalist predatory Hemiptera. The literature review is summarized in Table 2.1.

Orius (Anthocoridae)

The majority of insects in the family *Anthocoridae* are exclusively predaceous with the exception of the subfamily Anthocorinae, many of which are occasionally phytophagous (Carayon 1961; Couturier 1972) including the genus *Orius* (Miller 1956). Several *Orius spp.* were found to be associated with flower blossoms (Carayon and Steffan 1956; Dicke and Jarvis 1962; Fauvel 1974; Salas-Aguilar and Ehler 1977). This suggests that they may feed on pollen or other parts of the flower.

Orius pallidicornis (Reuter) survived to adulthood on a diet of pollen alone (Carayon and Steffan 1959). Survival and development were not compared with that of nymphs fed any other diet. Longevities of adult *O. pallidicornis* fed diets of pollen and of water plus fresh plant cuttings were 2 - 3 months, and 5 - 15 days, respectively. Adults punctured the pollen grains with their proboscis and apparently fed on the contents. Fecundity was not reported.

Orius tristicolor (White) survived to adulthood on a diet of either pollen or green bean pods (Salas-Aguilar and Ehler 1977). Mean development times on the various diets were significantly different. A diet of thrips plus pollen resulted in the fastest development (9.33 days), followed by thrips alone (10.44), bean pods plus thrips (11.30), pollen alone (12.96), and bean alone (15.71). Percent mortality followed the same trend: 10.0, 10.0, 17.5, 37.5 and 57.5%, respectively. Adults which survived the nymphal feeding experiment were used in fecundity experiments but the method of assigning them to treatments was not reported. Adults fed green bean pods plus pollen produced eggs at the same daily rate as those fed bean plus thrips or bean plus pollen plus thrips, but longevity differed (6.84, 11.55 and 15.36 days respectively), so lifetime egg production was higher for females fed prey than for those with no prey. Viability of the eggs was not reported.

Dicke and Jarvis (1962) concluded that pollen is an important food for both nymphs and adults of *O. insidiosus* (Say). Nymphs occurred in large numbers among the sheath hairs of corn and were observed probing and inserting their extended beaks into pollen grains and removing the contents. The buildup of the *O. insidiosus* populations and the decline in predation by *O insidiosus* coincided with pollen shedding stages of the corn.

Kiman and Yeargan (1985) also observed *O. insidiosus* feeding on pollen grains. Nymphs did not reach adulthood on a diet of bean pods only, but 91.2% of pollen-fed individuals survived to adulthood. This was not different from survival of nymphs fed on various prey (94.1 - 96.9%). However, the pollen fed nymphs had a significantly longer development time (18.9 days), than those fed prey (13.4 - 15.8 days). Average longevity of adults fed only pollen throughout their lives was not different from that of adults fed the best prey diets. Pollen-fed adults laid significantly fewer eggs per day than adults on the best four out of nine prey diets. The percentage egg hatch was not reported.

Coll (1996a) compared the growth and longevity of *O. insidiosus* nymphs and the longevity and fecundity of adults on corn, bean, pepper and tomato, in a vegetative state, without pollen or prey. Nymphs had the best growth and longevity, and adults the best longevity and fecundity on bean plants. Of the nymphs, only a few of the fourth instars which had previously been fed prey, survived to adulthood on the vegetative diets.

Fauvel (1971, 1972) showed that *O. vicinus* (Ribaut) nymphs took the same time to develop to adulthood on pollen as on prey diets. However, new adults from the pollen-fed group were 10% smaller than those from the prey-fed group. Pollen fed individuals often had abnormalities of antennae, eyes and pigmentation (Fauvel 1971, 1974).

Even though adult *O. vicinus* were attracted to flowers in olfactometer experiments Fauvel (1972) concluded that pollen is a much less important food than prey. Females fed pollen or prey through both nymphal and adult stages produced means of 11 and 90.3 eggs per lifetime, respectively (Fauvel 1974). However when adults which were fed pollen as nymphs were fed prey during adulthood (*Anagasta kuehniella* Z.), average lifetime fecundity was the same as for individuals fed only on prey throughout their lives. Thus, it was the diet in early adulthood that determined fecundity.

Heitmans *et al.* (1986) found no significant difference in development rate of *O. vicinus* nymphs reared on pollen *vs.* any of seven prey species. Fecundity of pollen fed individuals ranked 6th out of the eight diet treatments. There were no data on egg hatch and it is not clear if individuals were reared continuously on the same diet or if the adult and nymphal feeding experiments represents different sets of individuals.

Campylomma (Miridae)

C. verbasci has been reported as phytophagous (Pickett 1938), predaceous (Acquafresca and Newton 1986), and omnivorous (Collyer 1953; McMullen and Jong 1970; Lord 1971; Niemczyk 1978; Boivin and Stewart 1982; Jonsson 1985; Smith 1991; Arnoldi *et al.* 1992; Beers 1992). Niemczyk (1978) reported that newly hatched nymphs fed only apple leaves died while those fed arthropod prey survived, but older nymphs and adults could develop and survive several days on a diet of apple leave alone. Similarly, first- and second-instar nymphs died when caged on pear leaves with no prey but third and fourth instar nymphs fed prey prior to being caged with pear leaves completed their development, although markedly slower than nymphs fed pear psylla, *Psylla pyricola*. (McMullen and Jong 1970).

C. livida Reuter did not survive to adulthood on vegetative parts of cotton without prey but survived significantly longer than nymphs provided with water only (Chinajariyawong and Walter 1990). A significantly higher proportion of nymphs survived to adulthood on a diet of cotton plus prey than on prey alone. Adults fed cotton in addition to prey lived significantly longer and produced more eggs than those fed prey only. Females that were not fed prey did not produce any eggs and did not live as long as those provided with prey.

Macrolophus (Miridae)

Carayon (1986) concluded that *M. caliginosus* Wagner is partially or temporarily phytophagous on some plant species. The proportion of *M. caliginosus* nymphs which survived to adulthood was higher when geranium leaves were provided in addition to insect eggs or prey-based artificial diets (Grenier *et al.* 1989). Survival of *M. caliginosus* nymphs on leaf disks increased and development time decreased as the number of prey provided each day increased (Fauvel *et al.* 1987). The fecundity of females on leaf disks increased as the number of prey provided per day increased.

Other Miridae

D. signatus (Distant) did not survive to adulthood on vegetative parts of cotton without prey but survived significantly longer than nymphs provided with water only (Chinajariyawong and Harris 1987). A higher proportion of nymphs survived to adulthood and the development time was shorter for those reared on a diet of cotton in addition to prey than for those reared on prey alone. Adults fed cotton in addition to prey lived significantly longer and produced more eggs than those fed prey only. Females that were not fed prey did not produce any eggs and did not live as long as those provided with prey.

Three other species of predaceous mirids, *Deraeocoris olivaceus* (F), *D. lutescens* (Sch.), and *Miris striatus* (L.), were unable to survive without prey on plants on which they normally reside (Couturier 1972). Collyer (1953) reviewed and described the life histories and feeding behaviour of predatory insects associated with the red spider mite, *Metatetranychus (Panonychus) ulmi* (Koch), in England. *Camptobrochis lutescens* (Schilling) was partially phytophagous but also fed on relatively sedentary prey such as *P. ulmi* and aphids. *Campyloneura virgula* (H.-S.) preyed on small insects and mites but could adapt to plant food "when necessary". *Orthotylus marginalis* (Reuter) fed on apple leaves and fruit in the absence of prey but caused no visible damage. Kullenberg (1944) also found this insect to be partially phytophagous though it preferred prey. *Capsus* (*Heterotoma*) *meriopteras* (Scop.) was primarily predaceous but sometimes fed on foliage and apples. *Atractotomus mali* (Mey -Dur.) preferred to feed on small insects and mites but could survive in the absence of prey. Likewise, *Malacocoris chlorizans* (Panz.) fed primarily on *P. ulmi* but could survive entirely on plant material. In contrast, *Psallus ambiguus* (Fall.) and *Plagiognathus arbustorum* (F.) were partially phytophagous but unable to survive on plant tissue alone. Kullenberg (1944) on the other hand found that *P. arbustorum* was wholly phytophagous in Sweden. Female *P. ambiguus* provided only with plant material produced no eggs (Niemczyk 1968).

Geocoris (Lygaeidae)

Two members of this genus feed on nectar: *G. pallens* Stal (Yokoyama 1978; Crocker and Whitcomb 1980; De Lima 1980); and *G. punctipes* (Say) (De Lima and Leigh 1984; Thead *et al.* 1985). *Geocoris punctipes* were more abundant and lived longer on knotweed (*Polygonum aviculare* L.), than on other plants (Bugg *et al.* 1987), possibly because of copious nectar or abundant prey on knotweed. Supplementing a diet of arthropod prey with extrafloral nectar of cotton maximized longevity, fecundity and prey consumption rates of *G. pallens* (DeLima 1980). For *G. pallens* and *G. bullatus* (Say), longevity, fecundity and rate of development were improved by the addition of certain plant materials to arthropod diets (Tamaki and Weeks 1972).

Naranjo and Stimac (1985) compared development times, survival to adulthood, and fecundity of *G. punctipes* on diets of prey alone, 12 different plant foods, or prey plus one of the plant foods. No nymphs developed to adulthood on any of the plants alone. Seven of the twelve plant diets significantly increased longevity over water only, but development did not progress past the second instar. Average longevity and development were superior on green bean pods than on any of the foliage diets. When combined with prey, six of the twelve plant foods significantly increased survival of nymphs over that of nymphs on prey-only diets. None of the plant foods significantly decreased overall development time but there were differences in development of some instars. Three of the 12 plant foods had a significant positive effect on weight of adult females when added as a supplement to a nymphal diet of prey. However, the average weight of adult females was significantly higher for the group provided with prey during the immature adult stage than for those provided with plant food (5.4 and 4.6 mg respectively).

Supplemental plant-feeding did not influence adult fecundity of *G. punctipes* as much as it did nymphal survival (Naranjo and Stimac 1985). There was no difference between the fecundity of females fed only prey during adulthood and those fed plant and prey. Only two out of ten females, fed during adulthood on a diet of plant and water without prey, laid eggs and only one eggs was fertile. Dissection revealed that all other females had no ovarian or egg development, resembling newly emerged (immature), adult females. Individuals fed prey during their immature adult stage (up to five days old), and water and plant thereafter laid more eggs than those fed only plant and water throughout adulthood, but laid fewer eggs for a shorter duration than adults fed prey throughout adulthood. The total number of eggs laid was significantly influenced by the type of plant food provided.

Naranjo and Stimac (1985) also identified a difference between the effects of bean pods and plant foliage on adult longevity of *G. punctipes*. Adults fed only plant foliage had an average longevity not significantly different from that of adults provided water only (6.0 ± 0.3 days). Longevity of adults fed green bean pods, however, was significantly higher (30.6 ± 6.5 days). Allowing immature adults to feed on prey prior to a plant-food diet significantly increased the longevity of the foliage diet group but not that of the bean diet group.

Geocoris punctipes can develop and reproduce on animal food alone but the addition of plant food was beneficial (Dunbar and Bacon 1972). No nymphs survived to adulthood on a diet of pea aphids, *Acrythosiphon pisum* (Harris), alone, but when green bean pods where provided in addition to pea aphids, 52% of nymphs survived to adulthood. Development time and survival of nymphs fed bean in addition to tuber moth eggs, *Phthorimaea operculella* (Zeller), was not significantly different from that of nymphs fed eggs only. Individuals reared on green bean pods plus eggs of tuber moth produced significantly more eggs over their lifetimes, and with a higher percent hatch, than those fed tuber moth eggs alone (263.8 ± 32.6 and 124.9 ± 22.2 eggs produced respectively).

Stoner (1970) found that prey was essential for both development and reproduction in *G. punctipes*. Only one out of 46 survived from hatch to adulthood on each of only two of the twenty-six plant foods tested (barley and green bean pods). This proportion was not compared to the survival of prey-fed nymphs. Nymphs could not survive past the second instar when fed dandelion pollen plus water only, but they did live 9 days longer on average than those provided with water only. They concluded that prey was important for male fertility because no fertile eggs were laid by females reared on a prey-based diet and mated with males that were fed a sunflower seed diet plus prey only once in their lives. Females fed prey only once in their lives laid no eggs and on dissection had ovaries which contained no eggs and which were smaller than ovaries of females fed prey diets. Mating pairs fed prey during the nymphal stages but only sunflower seeds during adulthood produced 82.2% fewer eggs, and of those 30.6% fewer hatched, than pairs fed prey through their entire lives. Prey-fed adults lived longer than those fed only sunflower seeds but the statistical significance of this difference was not reported.

Cohen and DeBolt (1983) reared over ninety generations of *G. punctipes* on an arthropod based diet with water supplement, indicating that water, but not plant material, was necessary for this insect's survival. Similarly, York (1944) found that adult *G. pallens* and *G. punctipes* could not survive on animal food alone without plants or water, but adults provided with beet leaves or with water had the same longevity. York (1944) concluded that *Geocoris* spp. probably feed on plants as a source of water but not of nutrients. However, Ridgway and Jones (1968) showed that adult *G. pallens* lived longer when fed on cotton cotyledons than when fed water alone.

Nabis (Nabidae)

Ridgway and Jones (1968) determined with radiolabeling that adult *N. americoferus* Carayon fed on cotton plants, and that adults lived longer when provided with cotton cotyledons than with water alone. Nymphs of *N. alternatus* Parshley, *N. americoferus* and *N. capsiformis* Germar provided with plant foods survived longer than those provided with water only (Stoner 1972). Of the eight plant foods tested, dandelion pollen resulted in the highest longevity, e.g. *N. americoferus* lived 15.7 ± 2.3 days on pollen and 2.1 ±

0.3 days on water only. Nymphs did not develop past the first instar on any plant foods, but on suitable arthropod prey, the first instar was completed in three days.

Podisus (Pentatomidae)

Stoner *et al.* (1974) found that *P. acutissimus* Stal nymphs survived 21.8 ± 9.0 days on dandelion pollen, 32.0 ± 16.7 days on safflower seed, 39.0 ± 11.7 days on prey and only 4.2 ± 0.8 days when only water was provided. Nymphs survived only to the second instar when fed pollen or water alone. Most nymphs provided with safflower seeds survived only to the second instar but a minority developed to the third, fourth or fifth instars, and no nymphs reached adulthood on plant food diets.

Podisus maculiventris (Say) fed on potato foliage in the presence of abundant prey (Ruberson *et al.* 1986). Nymphs provided with potato foliage in addition to prey had significantly higher percent survival to adulthood, larger adult size, and shorter preoviposition times than nymphs fed prey alone (percents surviving were 92.5 and 65% respectively; preovipostion times were 8.8 ±1.08 days and 9.43 ±1.4 days respectively).

Nymphs of *P. maculiventris* have been observed feeding on the stems of evening primrose and celery (Olsen 1910; Stoner 1930) and on the mid-veins of apple leaves in the presence of prey (Morris 1963). Nymphs < 10 days old were not observed feeding on prey (Stoner 1930). Adults ranging from 20 - 40 days of age spent 9 - 16 % of their time feeding on plant material (Morris 1963).

Valicente (1992) observed *P. maculiventris* nymphs feeding on tomato and potato plants for 2- to 30-minute periods. Nymphs provided with no food or water, water only, potato plants and tomato plants survived for 9.1 ± 0.28, 27 ± 3.53, 31.9 ± 1.86, and 28.8 ±2.47 days respectively but none reached adulthood. Although the difference in duration of survival between plant-fed and the water-only groups was not statistically significant, the former weighed more, suggesting that plants provided more nutrition than water.

Nymphs of *P. maculiventris* maintained on green bean pods and provided prey *ad libitum* developed significantly faster than those fed prey at 3- or 9-day intervals (Legaspi and O'Neil 1994). None of the nymphs fed prey at 9-day intervals survived past the fourth instar. The duration of the second instar was significantly shorter for nymphs from mothers that were fed prey more frequently. However, the total duration of nymphal development did not vary with maternal diet. In adult feeding experiments (Legaspi and O'Neil 1993), the shorter the interval between prey, the higher the lifetime egg production, resulting from larger clutch size, shorter time to first oviposition and more frequent oviposition. The percent hatch of eggs did not vary with the interval between prey items. Adult females could survive on a diet of only bean pods four times longer than females with no food or water (38.5 ± 7.92 days and 10.3 ± 0.63 days respectively), but neither group laid eggs.

O'Neil and Wiedenmann (1990) and Wiedenmann and O'Neil (1990) fed *P. maculiventris* nymphs on green bean pods plus prey and then varied the adult diet. Adults fed only green bean survived longer than those provided with water only. The bean-fed individuals produced no eggs and had lower average body weight than adults fed prey. Adults lost weight but could survive 1- to 16-day intervals between prey if beans were provided. Those with no food or water died in 8.3 days (Wiedenmann and O'Neil 1990). The more frequently prey was provided, the more eggs were laid. As the interval between prey increased, weight loss was reduced by decreasing the clutch size and frequency of oviposition (Wiedenmann and O'Neil 1990).

Discussion

The contribution of plant-feeding to the diet of predaceous Hemiptera varies between genera and species. All species tested received some benefit from feeding on plant material, but in a few cases plant materials appeared to provide more than a source of water. There was only one report of experimental evidence that predator nymphs

(*Orius tristicolor*) could survive to adulthood on a diet of plant tissue other than pollen (green bean pods in this case) (Salas-Aguilar and Ehler 1977). In two unsubstantiated reports, *Atractatomus mali* and *Malacocoris chlorizans* apparently matured without prey or pollen (Collyer 1953).

When prey was not provided, plant materials, particularly some pollens and seeds, were shown to sustain individuals of the genera *Orius, Nabis, Podisus*, and *Geocoris* longer than water alone, indicating that these predators have some ability to obtain nutrients from plants. This ability could be adaptive when prey is scarce. As a supplement to arthropod prey, plant food had a positive effect on survival and fecundity in all the genera tested (*Podisus, Macrolophus,* and *Geocoris* for survival and *Podisus* and *Geocoris* for fecundity).

Fecundities of adults fed diets of plant tissue other than pollen were tested for only three species (*Psallus ambiguus, Geocoris punctipes* and *Podisus maculiventris*), all of which had either no or very low levels of reproduction on such diets.

Evidence of pollen feeding was found in the genera *Orius, Nabis* and *Podisus* but was directly observed only in *Orius* spp. which could survive, develop and reproduce on diets of pollen alone. Nymphs of the genera *Geocoris, Nabis* and *Podisus* did not survive to adulthood on diets of pollen alone. For *Orius* spp., development times were longer, percent survival lower and longevity, size and fecundity of adults lower for pollen fed *vs.* arthropod-fed individuals. However, one paper reported that when all females were fed arthropod prey during adulthood, there was no difference in fecundity between individuals fed nymphal diets of pollen or prey (Fauvel 1974). *Campylomma verbasci* may be similar to *Orius* spp. in its ability to develop to adulthood and possibly reproduce on a diet of pollen.

Growth of plant-feeding insects is generally believed to be limited by nitrogen rather than energy (Karowe and Martin 1989). The protein content of food (percent of dry weight), ranges from 0.6 - 6.9 %, 2 - 4%, and 6.6 - 12% for tree foliage, pollen and arthropod prey respectively, but the water content of pollen is much lower (11 - 12% of wet weight) than that of foliage (36 - 87%), or prey (60 - 89%) (Slansky and Scriber 1985). Therefore pollen provides a concentrated source of protein. The lack of evidence for survival of predaceous hemipterans on foliage diets suggests that unlike herbivores they are not adapted to process and assimilate the dilute protein source provided by foliage. Foliage feeders may have digestive and metabolic adaptations specific to the amino acid profile of their host plants and may be able to enhance absorption and conservation of the amino acids available in the most limiting amounts (Karowe and Martin 1989). Unavailability of protein due to conjugation with plant phenolics may also reduce the availability of plant proteins to insects that are mostly predaceous (Felton *et al.* 1992).

Table 2.1 Summary of literature on plant feeding in generalist, predatory Hemiptera. Asterisks indicate that well documented evidence was not provided.

Criteria investigated or results obtained	References and species
Evidence of pollen feeding	
Yes	Carayon and Steffan (1956), *O. pallidicornis* Dicke and Jarvis (1962), *O. insidiosus* Kiman and Yeargan (1985), *O. insidiosus* Salas-Aguilar and Ehler (1977), *O. tristicolor* Fauvel (1971, 1972, 1974), O. *vicinus* Heitmans *et al.* (1986), O. *vincinus* Stoner (1972), *N. alternatus, N. americoferus* and *N. capsiformis* Stoner *et al.* (1974), *P. acutissimus*
Pollen feeding seen	
Yes	Carayon and Steffan (1956), *O. pallidicornis* (adults) Dicke and Jarvis (1962), *O. insidiosus* (nymphs) Kiman and Yeargan (1985), *O. insidiosus*, (stage not reported)
Survival to adulthood on pollen only	
Yes	Carayon and Steffan (1956), *O. pallidicornis* Kiman and Yeargan (1985), *O. insidiosus* Salas-Aguilar and Elher (1977), *O. tristicolor* Fauvel (1971, 1972, 1974), *O. vicinus* Heitmans *et al.* (1986), *O. vicinus*
No	Stoner (1970), *G. punctipes* Stoner (1972), *N. alternatus, N. americoferus* and *N. capsiformis* Stoner (1974), *P. acutissimus*
Survival to adulthood on plant tissue other than pollen	
Yes	Salas-Aguilar and Elher (1977), *O. tristicolor*, green bean pods Collyer (1953), *M. chlorizens, A. mali*, plant tissue not specified*

Table 2.1 continued

Criteria investigated or results obtained	References and species
Survival to adulthood on plant tissue other than pollen	
No	Kiman & Yeargan (1985), *O. insidiosus* Coll (1996a), *O. insidiosus* Niemczyk (1978); McMullen and Jong (1970), *C. verbasci* Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Couturier (1961), *D. olivaceus, D. lutescens* and *M. striatus** Collyer (1953), *P. ambigus, P. arbustorum** Naranjo and Stimac (1985), *G. punctipes* Stoner (1970), *G. punctipes* Stoner (1972), *N. alternatus, N. americoferus* and *N. capsiformis* Stoner *et al.* (1974), *P. acutissimus* Ruberson *et al.* (1986), *P. maculiventris* Valicente (1992), *P. maculiventris* Legaspi and O'Neil (1994), *P. maculiventris*
Reproduction on pollen only	
Yes	Kiman and Yeargan (1985), *O. insidiosus* Fauvel (1974), *O. vicinus** Heitman *et al.* (1986), *O. vicinus* Salas-Aguilar and Ehler (1971), *O. tristicolor*
Reproduction on plant tissue other than pollen	
Yes and No	Niemczyk (1968), *P. ambiguus* Coll (1996a), *O. insidiosus* Naranjo and Stimac (1985), *G. punctipes* Stoner (1970), *G. punctipes* Wiedenman and O'Neil (1990), *P. maculiventris*
Comparative survival on different diets	Salas-Aguilar and Ehler (1971), *O. tristicolor* Kiman and Yeargan (1985), *O. insidiosus* Coll (1996a), *O. insidiosus* Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Fauvel *et al.* (1987), *M. caliginosus*

Table 2.1 continued

Criteria investigated or results obtained	References and species
Comparative development time on different diets	Salas-Aguilar and Ehler (1971), *O. tristicolor* Kiman and Yeargan (1985), *O. insidiosus* Fauvel (1971, 1972, 1974), *O. vicinius** Heitmans *et al.* (1986), *O. vicinus* McMullen and Jong (1970), *C. verbasci* Chinajariyawong and Harris (1987), *D. signatus* Fauvel *et al.* (1987), *M. caliginosus* Legaspi and O'Neil (1994), *P. maculiventris*
Comparative reproduction on different diets	Salas-Aguilar and Ehler (1971), *O. tristicolor* Kiman and Yeargan (1985), *O. insidiosus* Fauvel (1974), *O. vicinius* Heitmans *et al.* (1986), *O. vicinus* Coll (1996a), *O. insidiosus* Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Fauvel *et al.* (1987), *M. caliginosus* Naranjo and Stimac (1985), *G. punctipes* Stoner (1970), *G. punctipes* Legaspi and O'Neil (1994), *P. maculiventris* Wiedenman and O'Neil (1990), *P. maculiventris*
Comparative longevity on different diets	Salas-Aguilar and Ehler (1971), *O. tristicolor* Kiman and Yeargan (1985), *O. insidiosus* Coll (1996a), *O. insidiosus* Carayon and Steffan (1956), *O. pallidicornis* Kiman and Yeargan (1985), *O. insidiosus* Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Stoner (1972), *N. alternatus*, *N. americoferus* and *N. capsiformis* Naranjo and Stimac (1985), *G. punctipes* Stoner (1970), *G. punctipes* Stoner *et al.*(1974), *P. acutissimus*
Comparative adult size on different diets	Fauvel (1974), *O. vicinius** Coll (1996a), *O. insidiosus* Naranjo and Stimac (1985), *G. punctipes* Wiedenman and O'Neil (1990), *P. maculiventris*

Table 2.1 continued

Criteria investigated or results obtained	References and species
Plant food an improvement over a diet of water only	
Yes and No	Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Naranjo and Stimac (1985), *G. punctipes* Stoner (1970), *G. punctipes* York (1994), *G. pallens, G. punctipes* Ridgway and Jones (1968), *G. pallens* and *N. americoferus* Stoner (1972), *N. alternatus, N. americoferus* and *N. capsiformis* Stoner *et al.* (1974), *P. acutissimus* Ruberson *et al.* (1986), *P. maculiventris* Valicente (1992), *P. maculiventris* Wiedenman and O'Neil (1990), *P. maculiventris*
Plant food as a supplement to prey: effect on survival and development time	Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* Naranjo and Stimac (1985), *G. punctipes* Dunbar and Bacon (1972), *G. punctipes* Grenier (1989), *M. caliginosus* York (1944), *G. pallens* and *G. punctipes* Tamaki and Weeks (1972), *G. pallens* and *G. bullatus* Ruberson *et al.* (1986), *P. maculiventris*
Plant food as a supplement to prey: effect on adult longevity	Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* De Lima (1980), *G. pallens*
Plant food as a supplement to prey: effect on reproduction	Chinajariyawong and Walter (1990), *C. livida* Chinajariyawong and Harris (1987), *D. signatus* De Lima (1980), *G. pallens* Tamaki and Weeks (1972), *G. punctipes* and *G. bullatus* Naranjo and Stimac (1985), *G. punctipes* Dunbar and Bacon (1972), *G. punctipes* Ruberson *et al.* (1986), *P. maculiventris*
Plant food as a supplement to prey: effect on adult size	Naranjo and Stimac (1985), *G. punctipes* Ruberson *et al.* (1986), *P. maculiventris*

Chapter III

Requirements of *C. verbasci* nymphs for arthropod prey

Introduction

The potential for omnivorous hemipterans to survive on plant tissue without arthropod prey (Chapter 2) is an important consideration in understanding and predicting their distribution and their persistence when prey are scarce or have a patchy temporal or spatial distribution.

Investigations into the survival of *C. verbasci* in the absence of arthropod prey have shown that first- and second-instar nymphs died when fed only apple or pear leaves but that some older nymphs, which were fed prey in their early instars, survived to adulthood without prey (McMullen and Jong 1970; Niemczyk 1978). These findings lead to the initial assumption that arthropod prey are necessary for *C. verbasci* nymphs to survive to adulthood and thus to the hypothesis that females could enhance their offsprings' survival by choosing to lay overwintering eggs on trees where prey is abundant. However, neither McMullen and Jong (1970) nor Niemczyk (1978) explored the possibility that *C. verbasci* could feed on pollen, which is high in protein content (Stanley and Linskens 1974, Slansky and Scriber 1985) and abundantly available in cultivated apple orchards at blossom time when winter diapausing eggs of *C. verbasci* hatch. Therefore, the hypothesis that prey are necessary for survival was tested, initially in a small experiment, spring, 1994. The results showed no significant difference in the percent survival or in development time of nymphs fed on blossom clusters with and with out prey (N = 13 and 19, respectively). Observations of nymphs under the microscope revealed that they pierced pollen grains with their proboscis and appeared to be feeding. These preliminary results led to three experiments (Exp.) which tested the following hypotheses:

Exp. 1: The proportion of *C. verbasci* nymphs that survive from first- or second-instar to adulthood is expected to be higher for those reared on apple leaves plus mites provided *ad libitum* than for nymphs reared on leaves alone, leaves plus pollen provided *ad libitum*, leaves plus mites provided in limited numbers, or on apple flowers without pollen or prey.

Exp. 2: *Campylomma verbasci* nymphs reared from first- or second-instar to adulthood on apple leaves plus *T. urticae* provided *ad libitum* are expected to have (1) a higher chance of survival to adulthood, (2) a shorter duration of development from first- or second-instar to adulthood, (3) larger adult body size, and (4) higher potential fecundity, than *C. verbasci* reared on apple leaves plus pollen provided *ad libitum*.

Exp. 3: *C. verbasci* nymphs reared from first- or second-instar on apple blossoms and fruitlets as they occur in the field (i.e. pollen is available during the early instars only), are expected to have (1) a higher chance of survival to adulthood, and (2) larger adult body size, if they have access to *T. urticae* provided *ad libitum* than if they have no access to prey.

Methods

Leaves, blossoms (with petals removed), and fruitlets were collected from unsprayed Golden Delicious apple seedlings, and examined with a dissecting microscope for the presence of prey. Those devoid of prey were inserted into wet Oasis™ florist foam and each one was placed in an individual petri dish (100 x 25 mm). Leaves were also examined for the presence of pollen and only those without pollen were used in the Exp. 1 and 2. The florist foam was kept moist throughout the trials and the leaves, blossoms and fruitlets were replaced every second day.

First- or second-instar *C. verbasci* (identified according to Leonard (1915)) were collected from apple branches which were cut from orchards and incubated at ca. 20°C. One nymph was placed in each petri dish. Only nymphs that had cream- or clear-coloured guts, indicating that they had not fed on *P. ulmi* within approximately two days (Appendix 1), were used.

Nymphs in all treatments were provided with water *ad libitum* in wet florist foam, in addition to the following food sources: (1) leaf only, (2) leaf plus apple pollen every day, (3) leaf plus 20 - 25 *T. urticae* every day (there were live mites left uneaten from the previous day, indicating that prey was provided *ad libitum),* (4) leaf plus mites provided in limited numbers (4 to 12 *T. urticae* or *P. ulmi,* provided every second day to first- and second-instar of *C. verbasci*, and then 10 *T. urticae* provided every day to third to fifth instars; rarely were any prey left on the leaf the following day indicating the mites were not provided *ad libitum*), (5) leaf plus pollen plus *T. urticae ad libitum*; (6) apple flower (including an unfertilized fruitlet), with pollen removed, (7) leaf plus blossom or fruitlet without prey, (8) leaf plus blossom or fruitlet with *T. urticae ad libitum*. Exp. 1 included treatments 1 - 6; Exp. 2 included treatments 2 and 3; Exp. 3 included treatments 7 and 8.

Exp. 1 and 2 were carried out from February to April, 1995 at 22° to 27°C and at 16° to 28° C, respectively. Exp. 3 was carried out at the same time that eggs were hatching in the field (May, 1995), and was performed outside, under a roof for shelter, so that nymphs would be exposed to temperatures similar to those in the orchard. As Exp. 3 proceeded, the phenological stage of the blossoms in the field changed so that by the time most nymphs in the experiment and in the orchard were in the fourth instar, they were being provided with fertilized apple fruitlets with no pollen (Figure 3.1).

Nymphs were checked every morning before 1000 h, and their instar was recorded. When individuals reached adulthood in Exp. 2 and 3 they were mildly anaesthetized with CO_2 and their pronota were measured with an ocular micrometer at 40 X power, to the nearest 0.025 mm. In Exp. 3 the female adults were then preserved in FAA (Ethanol, Acetic acid and Formaldehyde, 18:1:1) and later dissected to record the condition of ovaries and the number of eggs.

After measurement, each adult female in Exp. 2 was placed on a potted eggplant which was covered with a plastic and screen cloth lid (Figure 3.2). Smith and Borden (1991) also used potted eggplants in fecundity trials with *C. verbasci*. Females from both nymphal diet groups were provided with *T. urticae ad libitum* during their adulthood, in order to separate the effects of adult and nymphal diets on fecundity. The feeding requirements of adults are irrelevant to the immediate hypothesis because adults are able to fly to find prey even if the tree on which they hatched and developed to adulthood was devoid of prey. Two males, one from the pollen-fed group, the other from the mite-fed group (in order to avoid the possible effects of nymphal diet on male reproductive capacity), were placed with each female for five days. The pollen-fed males were marked with a small white paint dot on their pronotum. If a male died before day 5, another male from the same treatment was placed in the cage. If a female died before day 5, the replicate was discarded. If the plant wilted before day 5 it was kept but the adults were transferred to another plant for the remainder of the five days. When each adult female reached five days of age she was anesthetized with CO_2 , removed from the eggplant and preserved in FAA solution for later dissection to record the condition of ovaries and the number of eggs (Figure 3.3). For two months after the adults were removed, the eggplants were checked every second day for the emergence of nymphs.

Statistical Analysis

For each experiment, the proportions of nymphs surviving to adulthood in each treatment were compared using a log-likelihood G test, $\alpha = 0.05$, with William's correction to better approximate the chi^2 distribution (Sokal and Rolf 1981). In Exp. 1 some of the proportions were zero so the natural logs of the raw proportions plus 1 were used. Also in Exp. 1, the non-significant subsets and their G_W values were determined by the log-likelihood simultaneous test procedure.

The duration of development for the two treatments in Exp. 2, and the pronotal widths in Exp. 2 and 3, were compared for the two diets using two-way analysis of variance (General Linear Model Procedure, SAS, 1995) with sex and treatment as factors. Survivorship curves for the two treatments in Exp. 3 were compared using the Log Rank method, Kaplan-Meier Survival Analysis (SPSS for Windows, 6.1, 1994). The numbers of eggs found in the females in Exp. 2 were compared between treatments using a two-sample t-test (SAS General Linear Model Procedure). The proportions of females with developed ovaries in Exp. 2 were compared between the two treatments using the log-likelihood G test, $\alpha = 0.05$, with William's correction (Sokal and Rolf 1981).

Results

None of the nymphs provided with a diet of apple leaves alone in Exp. 1 survived > 2 days. There was a significant difference between proportions surviving to adulthood on the six diets (Table 3.1). The survival of nymphs provided with a leaf plus pollen, mites or both *ad libitum* (treatments 2, 4 and 5) was very high and not significantly different. No nymphs survived to adulthood in treatments in which they were provided with a leaf only (treatment 1), or with a leaf plus mites non-*ad libitum* (treatment 3). These two treatments were significantly different from all others except for treatment 6, in which the proportion surviving was 0.38 on a diet of apple blossoms without mites or pollen.

In Exp. 2, 87% of 46 nymphs survived to adulthood on the leaf plus pollen diet (treatment 2) and 95% of 40 nymphs survived to adulthood on leaf plus *T. urticae* provided *ad libitum* (treatment 4). These proportions were not significantly different from each other ($G_W = 1.622$, $P > 0.05$). Sex had a significant effect on development time, with males developing faster, but the diet treatment had no effect and there was no interaction (Table 3.2). Both sex and diet had a significant effect on pronotal width and there was no significant interaction effect between sex and diet (Table 3.3). Adults which were reared on nymphal diets of pollen were significantly wider than those which were reared on mites, and females were significantly wider than males.

No nymphs hatched from the eggplants on which adults were confined in Exp. 2. Developed ovaries and eggs were found in most five-day-old females from both diet groups, and there was no significant difference in either the proportion of females with developed ovaries or in the number of eggs per female (Table 3.4).

In Exp. 3, the proportion of nymphs which survived to adulthood on a diet of leaf plus fruitlet without prey (treatment 7), was significantly lower (46% of 22 nymphs), than for nymphs that had access to *T. urticae* (treatment 8) (77% of 26 nymphs) ($G_W = 4.934$, $P < 0.05$). Survivorship of nymphs on the two diets was similar up to and including the fourth instar, after which pollen was no longer available and nymphs with no access to prey had significantly higher mortality than those provided with prey (Figure 3.4). Neither sex nor diet had a significant effect on the pronotal widths of surviving adults in Exp. 3 (Table 3.5).

Due to the small sample size, it was not possible to statistically analyze the results of the dissections in Exp. 3. All three adult females from the fruitlet-only diet, and three of the eight adult females from the fruitlet-plus-mite diet, had developed ovaries. None of the adults from either group had eggs.

Discussion

In agreement with Niemczyk (1978) and McMullen and Jong (1970), Exp. 1 showed that leaves alone could not provide a sufficient diet for nymphal development. However, all three experiments provided strong evidence that when pollen is available, *C. verbasci* nymphs do not require arthropod prey in order to develop to adulthood.

Exp. 1 and 2 indicated that nymphs fed a diet of leaves plus pollen had an equal chance of survival to adulthood, similar development rate and similar adult size as those fed leaves plus mites. Pollen may have a very important role in providing a source of protein for nymphs, particularly first and second instars which appear to be poor predators (Chapter 4). Several hemipteran species, considered to be mainly predaceous, are known to feed on pollen (Chapter 2, Table 2.1), and diets of prey provided advantages over diets of pollen in some aspects of fitness but not others (Salas-Aguilar and Ehler 1977; Fauvel 1971, 1972, 1974; Stoner 1972; Stoner *et al.* 1974; Kiman and Yeargan 1985; and Heitmans *et al.* 1986). It is possible that *C. verbasci* use other sources of protein, such as fungal spores, available in apple orchards.

Females reared on leaves plus pollen (Exp. 2) had larger pronotal widths than females reared on leaves plus mites provided *ad libitum* (Exp. 2) and than wild females (Appendix 2), suggesting that pollen may be superior to mites as a food for *C. verbasci*. However, the small difference in pronotal size (3.6%), between individuals reared on the two diets (Exp. 2) may not be biologically significant in terms of fitness.

When pollen is not available throughout nymphal development (i.e. after the fourth instar in spring 1995), *C. verbasci* nymphs provided with mites had a higher chance of survival than those with only fruitlets (Exp. 3). The survivorship curve of the two diet groups in Exp. 3 shows that the higher mortality of nymphs in the no-prey diet group occurred during the fourth and fifth instar and the first day of adulthood (Figure 3.4). A possible explanation for this is that after pollen was no longer available, mortality due to starvation occurred among the nymphs with no access to prey (treatment 7), but not in the group provided with mites. These results suggest that, while it is available, pollen can provide an adequate source of food for developing *C. verbasci* nymphs; however, when pollen is no longer available, nymphs become more dependent on prey for survival. The survival of 45% of the nymphs on fruitlets without prey is in agreement with the results of McMullen and Jong (1970) and Niemczyk (1978), who reported that some older nymphs reared on prey during their early instars were able to survive to adulthood without prey but that their chance of survival was lower than that of nymphs which had access to prey throughout development.

In one orchard observed closely in 1995, pollen was generally unavailable by May 19 when most *C. verbasci* were fourth instars. The "petal fall" stage, when pollen availability begins to decline, usually occurs during mid to late May for most varieties of apples, and in most years in the Okanagan and Similkameen Valleys (B.C. Ministry of Agriculture, Fisheries and Foods, records for 1982-1984 and 1992-1993, and data from B.C. Fruit Packers Cooperative, 1976 to 1995). *C. verbasci* nymphs began hatching in late April or early May and fifth instars have been recorded in orchards the Okanagan and Similkameen Valleys as late as early June (Integrated Crop Management Inc., unpublished field data), or late June (1982) (Thistlewood *et al.* 1990). Based on this information apple pollen is probably not available throughout the development of first-generation nymphs in the Okanagan and Similkameen Valleys.

It is very unlikely that branches in the field will be completely free of suitable prey between the time pollen is no longer available and the completion of *C. verbasci* development. However, if the density of prey is low, late instar *C. verbasci* nymphs may have a lower chance of survival, slower development rate and smaller adult size than if prey is abundant. Therefore, a female laying winter diapausing eggs in the summer or fall may be able to increase her offsprings' survival by ovipositing where prey is abundant.

Exp. 2 failed to obtain a direct measure of fecundity for adults reared on different nymphal diets because no offspring were produced. However, ovaries and eggs were found in five-day-old females from both nymphal diet groups in Exp. 2, indicating that reproductive development in females may proceed on a nymphal diet of leaves plus pollen without prey. There was no significant difference in the numbers of eggs found in the females reared on leaves plus *T. urticae* or leaves plus pollen, but the trend was towards higher egg numbers in the latter group. However, the power of this test was low ($0.25 < \beta < 0.10$ to detect a difference of at least 8 eggs), so I am unable to make any quantitative comparisons between the fecundities of females reared on the two diets.

In Exp. 3, two-day-old adult females that received no prey during development and no pollen after the fourth instar (treatment 7) had developed ovaries, suggesting they were capable of reproduction. These results suggest that reproductive development can occur in an orchard environment in the absence of prey. In contrast to the results of Exp. 2, none of the females from the prey or the no-prey treatments in Exp. 3 contained any eggs. Females in Exp. 2 had opportunities to mate and to feed on mites during the five days prior to being killed, whereas the females in Exp. 3 were killed at only one to two days of age and had been caged separately from males and had no access to prey. Either age, mating, or adult diet differences could be responsible for the difference in egg development between the two experiments.

Although the data on egg production are not sufficient to draw concrete conclusions, they suggest that, for *C. verbasci*, pollen can replace arthropod prey in providing a nymphal diet capable of producing reproductive adults. *C. verbasci*, like some anthocorids (Salas-Aguilar and Ehler 1977; Fauvel 1971, 1974; Kiman and Yeargan 1985; Heitman *et al.* 1986), may be able to reproduce on a diet of pollen without prey. For these anthocorids, the average fecundity was lower for adults which were fed pollen than for those fed prey diets, with the exception of *O. vicinus.* Fauvel (1974) found that female *O. vicinus* reared on nymphal diets of pollen and adult diets of prey had fecundities equal to those of females reared on prey throughout both stages, suggesting that the adult diet alone determined fecundity. An alternative hypothesis as to why a female *C. verbasci* may lay eggs near prey is that prey may be required by an ovipositing female to maintain her fecundity, and therefore females remain longest and lay the most eggs on trees with sufficient prey. Chapter 5 explores this hypothesis.

It is possible that during the evolution of *C. verbasci*, pollen was not as reliably available in the spring on *C. verbasci*'s woody hosts as it is in cultivated apple orchards today. Under these condition, arthropod prey would have been extremely important to the survival of first-generation nymphs. Therefore, there may have been substantial selection pressure on females to lay overwintering eggs where prey were abundant. The patchy distribution of pollen or prey may have contributed to the evolution of the ability to feed on both plants and arthropods.

Figure 3.1 Arena in which *C. verbasci* nymphs were reared with *T. urticae* provided *ad libitum* or with no prey (Exp. 3). The arena consisted of a apple blossom plus a leaf supplied fresh every second day until blossoms were no longer available in the field, after which small apple fruitlets, as shown in this photo, were provided.

Figure 3.2 Potted eggplants (cv. Black Beauty), on which one adult female and two adult male *C. verbasci* were placed for mating and oviposition (Exp. 2).

Figure 3.3 Eggs in the abdomen of an adult, female *C. verbasci* dissected at five days of age (35X actual size) (Exp. 2).

Table 3.1 Proportion of *C. verbasci* nymphs surviving to adulthood, reared in petri dishes on five diets (Exp. 1).

Treatment	Nymphal diet	N	Proportion surviving to adulthood [a]
1	apple leaf only	14	0.00 a
2	apple leaf plus pollen *ad libitum*	20	0.95 b
3	apple leaf plus mites non *ad libitum*	9	0.00 a
4	apple leaf plus mites *ad libitum*	8	0.88 bc
5	apple leaf plus pollen and mites *ad libitum*	9	1.00 bc
6	apple blossom and fruitlet alone (no pollen)	8	0.38 ac

[a] Significant difference between the proportions surviving to adulthood on different diets, $G_W = 64.94$, $P < 0.05$, log-likelihood test (Sokal and Rolf 1981). Proportions followed by the same letter are not significantly different from each other, $P > 0.05$, log-likelihood simultaneous test procedure.

Table 3.2 Development time for *C. verbasci* nymphs to reach adulthood when reared in petri dishes in the lab on two diets (Exp. 2).

Treatment	Nymphal diet	Sex	N	Development time (days) ($\bar{x}$ ± SE)[a]
2	apple leaf plus pollen *ad libitum*	female	18	16.8 ± 0.2
4	apple leaf plus mites *ad libitum*		16	16.7 ± 0.3
2	apple leaf plus pollen *ad libitum*	male	22	15.9 ± 0.2
4	apple leaf plus mites *ad libitum*		22	16.4 ± 0.2

[a] No difference in development time within each sex between treatments, $P = 0.4134$. Development times between sexes significantly different, $P = 0.0088$. No significant interaction between sex and treatment, $P = 0.2225$, two-way analysis of variance (General Linear Model Procedure, SAS, 1995)

Table 3.3 Pronotal widths of adult *C. verbasci* reared in petri dishes in the lab on two nymphal diets (Exp. 2). Measurements were made using an ocular micrometer and a dissecting microscope at 40X magnification.

Treatment	Nymphal diet	Sex	N	Pronotal width (mm) ($\bar{x}$ ± SE) [a]
2	apple leaf plus pollen *ad libitum*	male	20	0.994 ± 0.011
4	apple leaf plus mites *ad libitum*		22	0.986 ± 0.006
2	apple leaf plus pollen *ad libitum*	female	16	1.033 ± 0.005
4	apple leaf plus mites *ad libitum*		16	0.997 ± 0.008

[a] Pronotal widths significantly different between diets, $P = 0.0129$, and between sexes, $P = 0.0045$, but no interaction between sex and diet, $P = 0.1035$, two-way analysis of variance (General Linear Model Procedure, SAS, 1995).

Table 3.4 Occurrence of developed ovaries and eggs in five-day-old adult female *C. verbasci* reared on two nymphal diets (Exp. 2). Females preserved in FAA, and dissected under a microscope at 40X magnification.

Treatment	Nymphal diet	N	Proportion with developed ovaries [a]	Number of eggs per female ($\bar{x}$ ± SE) [b]
2	apple leaf plus pollen *ad libitum*	14	0.716	5.3 ± 1.7
4	apple leaf plus mites *ad libitum*	11	0.727	3.4 ± 1.4

[a] No significant difference between proportions with developed ovaries for females reared on the two diets, $G_W = 0.004774$, $P < 0.05$, log-likelihood test (Sokal and Rolf 1981)

[b] All females, with and without developed ovaries included. No significant difference between the numbers of eggs in females reared on the two diets, $P = 0.4107$, two-tailed t-test (General Linear Model Procedure, SAS, 1995).

Figure 3.4 Survivorship distributions of *C. verbasci* reared in petri dishes outdoors on apple blossoms and fruitlets with *T. urticae* provided *ad libitum* (N = 26), and on apple blossoms and fruitlets with no prey (N = 22) (Exp. 3). Stadia 1 to 5 are the nymphal instars.. Survivorship distributions for the two treatments are significantly different, *P* = 0.0055, Kaplan-Meier Survival Analysis, Log Rank method (SPSS for Windows, version 6.1, 1994).

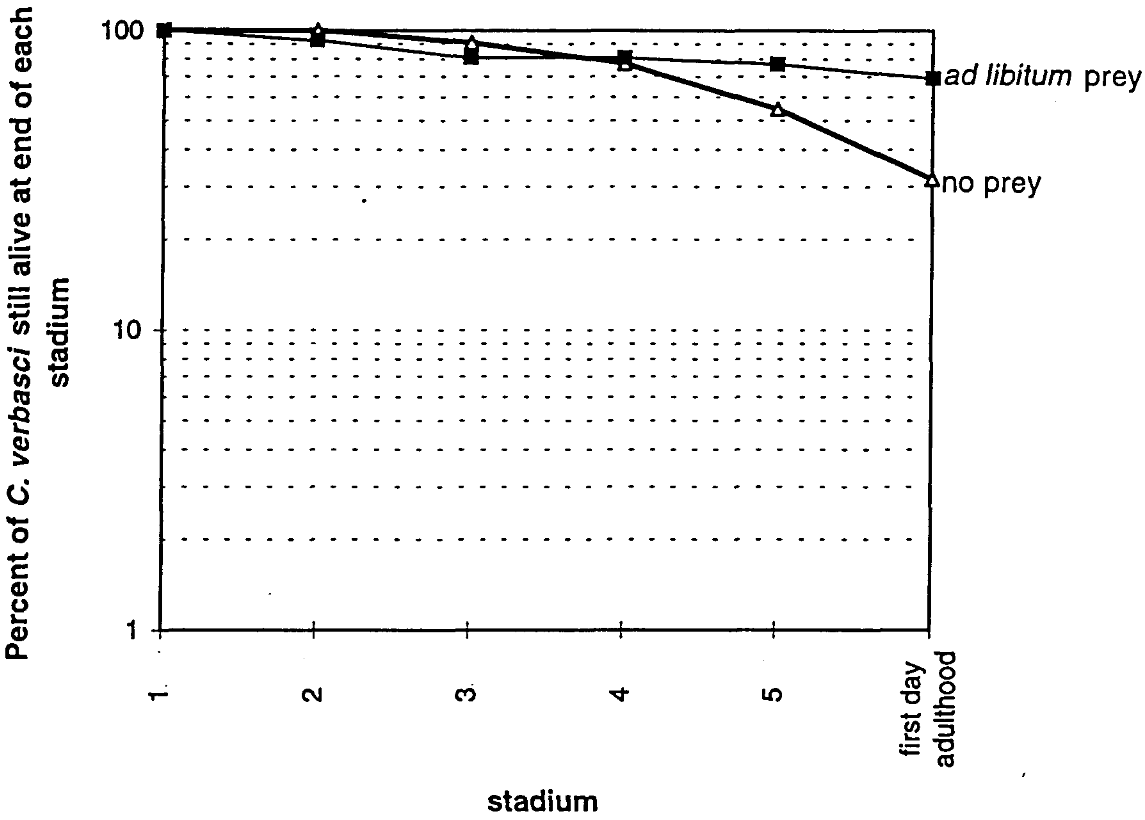
Percent of *C. verbasci* still alive at end of each stadium
100
10
1
ad libitum prey
no prey
1
2
3
4
5
first day adulthood
stadium

Table 3.5 Pronotal widths of adults *C. verbasci* reared in petri dishes outdoors on apple blossoms and fruitlets with *T. urticae* provided *ad libitum,* and on apple blossoms and fruitlets with no prey (Exp. 3). Measurements were made using an ocular micrometer and a dissecting microscope at 40X magnification.

Treatment	Nymphal diet	Sex	N	Pronotal width (mm) (x ± SE) [a]
7	apple leaf plus blossom or fruit	male	5	0.940 ± 0.018
8	apple leaf plus blossom or fruit plus mites *ad libitum*		8	0.987 ± 0.003
7	apple leaf plus blossom or fruit	female	5	0.995 ± 0.012
8	apple leaf plus blossom or fruit plus mites *ad libitum*		9	0.997 ± 0.016

[a] Pronotal widths not significantly different between diets, $P = 0.223$, or between sexes, $P = 0.1161$, and no interaction between sex and diet, $P = 0.2651$, two-way analysis of variance (General Linear Model Procedure, SAS, 1995).

Chapter IV

Feeding behaviour of *C. verbasci* nymphs

Introduction

C. verbasci feeds on both plant materials and on other arthropods, and therefore has potential both as a predator and as an economically important pest (Smith 1991). Other hemipterans that may play these dual roles in agricultural systems include *Actractotomus mali* (Collyer 1953; Sanford 1964*b*; Lord 1971; Jonsson 1985); *Plagiognathus politus* Uhler and *P. obscurus* Uhler (Braimah *et al.* 1982); and *Psallus ambiguus* (Jonsson 1985). So little of their predaceous behaviour is understood that these insects tend to be treated as pests at all times on susceptible crops. Similarly, several species of hemipterans considered to be primarily beneficial predators are also known to feed on plant materials. These include: *Geocoris spp., Orius spp., Nabis spp., Podisis spp., Deraeocoris spp., Miris striatus, Macrolopus caliginosus*, and others (Chapter 2). Because their feeding habits and preferences are not well understood, their reliability and persistence in controlling pest species is not known.

The initial assumption behind this research was that arthropod prey is essential for the development of *C. verbasci* nymphs. The results of the nymphal feeding experiments (Chapter 3), suggest that *C. verbasci* is a facultative feeder on pollen or prey. However, because pollen is generally not available throughout the entire development period of first-generation nymphs, they have a higher chance of survival if prey is available to them. The rationale for Exp. 4 was that, if arthropod prey are important in the survival of *C. verbasci* nymphs, it is necessary to know which species are potential prey. If a prey species can not be located, recognized, handled or fed on by nymphs there would be no advantage, in terms of offspring survival, for an adult female to lay more eggs where this species is abundant.

C. verbasci nymphs feed on European red mite, *Panonychus ulmi;* two-spotted spider mite, *Tetranychus urticae*; pear psylla, *Cacopsylla pyricola;* green apple aphid *Aphis pomi;* angoumois grain moth eggs, *Sitotrogo cerealella;* and pear rust mites *Epitrimerus pyri* (Nalepa) (McMullen and Jong 1970; Lord 1971; Niemczyk 1978; Acquafresca and Newton 1986; Arnoldi *et al.* 1992). Some of the previous research has quantified the daily or life-time consumption of prey (McMullen and Jong, 1970; Lord, 1971; Niemczyk 1978; Arnoldi et al, 1992), but no direct observations of foraging and feeding behaviour have been reported. Therefore, Exp. 4, below, was designed to observe directly if and how first- and second-instar nymphs feed on each of three prey species, commonly found in apple orchards in the early spring: *P. ulmi, A. pomi,* and the apple rust mite, *Aculus schlechtendali* (Nalepa).

It has been speculated that *C. verbasci* nymphs cause less damage to fruit in orchards with abundant *P. ulmi* than in orchards with low densities of prey. However, a survey of >50 orchards did not show a correlation between the percentage of fruit damage in the orchard and the ratio of *C. verbasci* to prey (Bartlett and Edwards 1993). Field data can be influenced by many uncontrolled factors which could confound such a correlation if it existed. Therefore, a controlled design (Exp. 5) was needed to determine if the availability of mites, and the previous feeding experience of *C. verbasci* nymphs affect the amount of fruit-feeding. Damage to apples due to insects such as *C. verbasci* probably results from the mechanical damage of piercing and by components of the insects' saliva secreted during feeding (Strong 1970; Boivin and Stewart 1982; Ecale and Backus 1995) which could be indexed by the number of feeding bouts and the duration of feeding, respectively.

Because *C. verbasci* is considered to be a pest in apple orchards, there was no immediate, practical reason to study its relative preference for different species of prey. On pear trees, where *C. verbasci* is considered to be a beneficial predator, nymphs showed no preference between eggs of *C. pyricola* and *P. ulmi,* but did prefer eggs of *C. pyricola* over nymphs. They did not show any preference between eggs and active stages of *P. ulmi* (McMullen and Jong 1970). *C. verbasci* preferred both *T. urticae* and *P. ulmi* over *A. pomi* but did not discriminate between the two mite species (Arnoldi *et al.* 1992).

Exp. 4 and 5 were designed to test the following hypotheses.

Exp. 4: The following statistics are expected to be different for the three prey species tested: (1) the proportion of *C. verbasci* nymphs that feed on prey when prey are encountered at least once during a 1 hour period; (2) the average number of encounters with prey before a *C. verbasci* nymph feed on the prey; (3) the average time elapsed before first predation occurs.

Exp. 5: I expect that: (4) *C. verbasci* nymphs will feed less on fruitlets on which *P. ulmi* are abundantly available, than on fruitlets with no prey; (5) *C. verbasci* nymphs will feed less on fruitlets if they have recent experience feeding on prey than if they do not; and (6) *C. verbasci* nymphs will feed more on *P. ulmi* if the nymphs have recent experience feeding on prey than if they do not.

Methods

For Exp. 4, apple branches were collected from orchards in early April 1994 and incubated at ca. 22° C. Newly emerged first-instar *C. verbasci* nymphs were collected daily and placed on 5 - 10 cm tall, arthropod-free apple seedlings caged in the same room. From 12 - 36 hours elapsed prior to observation so that arthropod food would be cleared from the nymph's gut (Appendix 1), while allowing the nymph to feed on the apple seedling. By this time, some of the nymphs were identified as second instars (Leonard 1915). Each nymph was removed from the seedling and starved in a petri dish with a wet cotton ball, for 1 h prior to observation in Exp. 4.

The observation arena in Exp. 4 consisted of a young apple leaf, 8 - 10 mm long, cut from an unsprayed Golden Delicious apple tree an hour before each trial. Leaves were examined under a dissecting microscope at 40X magnification, and only leaves without prey or pollen were used. The leaf petiole was inserted in wet florist foam and a thin band of petroleum jelly, was applied around the base of the petiole to prevent nymphs from leaving the leaf.

Adult and nymphal stages of the prey were collected on leaves of unsprayed apple trees and transferred one at a time with an insect pin from the infested leaf to the arena leaf according to the following treatments in Exp. 4: (1) 10 P. *ulmi*; (2) 5 *A. pomi*; or (3) 20 *A. schlechtendali*. The number of prey was adjusted according to the size of the prey species so that approximately the same leaf surface area would be covered by prey in all three treatments.

The leaf, held in the florist foam was set on a small, angled mirror on the stage of a dissecting microscope and secured with modelling clay (Figure 4.1). By focusing the microscope on the upper side of the leaf or on the mirror image of its under side, a nymph could be observed on either side of the leaf. Temperature was kept below 30°C by positioning the light as far as possible from the arena and keeping the light intensity low. A thermometer (Smart2™, InterTAN Texas Inc.), was attached to the mirror, adjacent to the leaf.

Nymphs used in Exp. 5 were collected as first- and second-instars from blossom clusters on unsprayed Golden Delicious apple trees in April, 1995. Both red- and cream-coloured nymphs were used for observations. It was assumed that cream-coloured nymphs had not fed on prey for at least one day prior to the trial, while red-coloured nymphs probably fed on prey within the last three days (Appendix 1). It is unlikely that the nymphs had fed on rust mites or thrips which do not cause red colouration of the gut, because rust mites were not found on the trees from which the nymphs were collected, and thrips were larger than second-instar *C. verbasci*, and therefore unlikely to be preyed upon by them. The nymphs were placed in a petri dish for 1 h before observations, as in Exp. 4, but in addition to the wet cotton ball, nymphs in Exp. 5 were provided with an unsprayed, prey-free apple leaf. This difference in method was to avoid the possibility that a nymph which had been deprived of all plant material prior to the trial, would feed immediately on the fruitlet before exploring the arena and having a chance to encounter prey.

Blossoms were cut from unsprayed Golden Delicious apple trees. For the arena used in Exp. 5 petals, sepals, stamens and pistils were removed leaving only the unfertilized fruitlet and a short stem. Stickum™ was applied to the inflorescence end of the fruitlet and to the base of the stem to prevent the nymph from leaving the stem and fruitlet and from moving out of view. The stem was inserted into a piece of wet florist foam and was placed on a V-shaped trough made of two pieces of mirror (Figure 4.2). The arena was placed inside a 100 x 25 mm petri dish floating in a tray of ice-water on the stage of a dissecting microscope . The nymph could be seen anywhere on the stem and fruitlet, by focusing on the fruitlet itself or on one of its images in the mirrors. The ice water helped to keep the temperature of the arena between 22° and 30°C, as measured by a thermometer attached to the petri dish adjacent to the fruitlet. There were two arena treatments in Exp. 5: (1) a fruitlet with no arthropod prey; and (2) a fruitlet with five live *P. ulmi,* transferred from leaves of unsprayed apple trees.

In Exps. 4 and 5, one *C. verbasci* nymph was removed from a petri dish and placed on the arena leaf (Exp. 4), or fruitlet (Exp. 5). Each nymph was observed continuously at 10 - 40X magnification for 1 h (Exp. 4) or 40 min. (Exp. 5). In Exp. 4, observations were terminated after the nymph finished eating its first prey. It was assumed that the nymph's nutritional state would have changed by feeding on high protein food, and that this change in state could influence subsequent behaviour. In Exp. 5, however, I was interested in the effect that prey feeding may have on subsequent fruit feeding, so behaviour occurring after predation was recorded. When a prey item was consumed it was not replaced as this disturbance could have influenced behaviour of the *C. verbasci* nymph.

Behaviour was recorded directly into a computer program (written in Quick Basic). Continuous activities recorded were: resting, walking, grooming, feeding on the leaf or fruitlet, and feeding on prey. The latter observation included only the time when the proboscis was directly in the prey item. Instantaneous events recorded were: contacting prey directly (with antennae or proboscis), or indirectly (with another part of the body), flinching or darting away.

Statistical Analysis

The proportions of nymphs which fed on the three different prey in Exp. 4 were compared using a log-likelihood G test, $\alpha = 0.05$, with William's correction to better approximate the chi^2 distribution (Sokal and Rolf 1981).

The data from Exp. 4 on the number of direct encounters before nymphs fed on each of the three prey species were transformed by square root and compared using 1-way analysis of variance (General Linear Model Procedure, SAS, 1995), followed by a multiple comparison test (Duncan's multiple range test, SAS, 1995). Analysis of variance is not ideal for these data because it does not consider the censored data (i.e. individuals for which the 'event', predation in this experiment, did not occur before the end of the observation period). Therefore, the mean duration of time before feeding on prey was analyzed using Kaplan Meier survival analysis, with a log rank test to evaluate the null hypothesis that the "survival" functions were equal (SPSS for Windows, version 6.1, 1994). Kaplan Meier analysis is designed for use with factors which occur at regular intervals, such as time, and therefore could not be used to analyze the number of encounters with prey occurring before predation.

For Exp. 5 the number of fruit-feeding bouts > 5 seconds long, and the total duration of fruit-feeding by nymphs with and without recent prey-feeding experience, on fruit with and without prey were compared using a 2-way analysis of variance (General Linear Model Procedure, SAS, 1995). Prior to analysis the data for number of fruit-feeding bouts were transformed by natural $\log(x + 1)$ and, for duration of fruit-feeding, by square-root $(x + 1)$.

For nymphs in Exp. 5, treatment 2, the difference in the total duration of time spent feeding on prey by *C. verbasci* nymphs with and without recent predation experience was compared using a two-tailed t-test (General Linear Model Procedure, SAS, 1995). The durations of time spent feeding on prey and fruit by the same individual were compared using a paired t-test (SPSS for Windows, version 6.1, 1994).

Results

Of the 60 *C. verbasci* nymphs in Exp. 4, two failed to feed, one never contacted the prey directly, and one moulted during the observation period. These four nymphs were excluded from the data analysis. Nymphs were able to feed on all three species of prey, but the proportion of nymphs which fed on *P. ulmi* was greater than on either of the other species. (Table 4.1). *A. pomi* used in the trial were the same size or slightly larger than the first- and second-instar *C. verbasci,* and kicked defensively when touched by nymphs. Encounters with aphids were often followed by the *C. verbasci* nymph running away from the aphid even if the aphid did not display defensive behaviour. In three of the seven cases in which nymphs fed on aphids, they did so by piercing and feeding from the aphid's leg. Aphids thus attacked did not respond by kicking or walking away. *A. schlechtendali* usually lay lower than the tops of the leaf hairs, and *C. verbasci* nymphs often walked over them apparently with no direct contanct or response. Nymphs readily fed on rust mites when they were encountered directly with their proboscis, as indicated by the relatively low number of encounters prior to predation (Table 4.2). Attempts by *P. ulmi* to escape after attack by *C. verbasci* nymphs were rarely successful.

There were significantly more direct encounters with prey prior to predation when the prey species available was *A. pomi* than when it was *P. ulmi,* or *A. schlechtendali* (Table 4.2). The time prior to predation was significantly shorter when the prey species was *P. ulmi* than when it was *A. schlechtendali* or *A. pomi* (Figure 4.3). It must be noted that time prior to predation was not independent of the rate of prey encounter.

Of 50 nymphs observed in Exp. 5, five walked into the stickum™ and the observations were terminated, and four did not feed and were excluded from the analysis. In all 21 replicates of treatment 2 the *C. verbasci* nymph encountered at least one mite by direct contact with the nymph's proboscis. In only 10 of these replicates did the nymph feed on a mite. In 19 of the 21 replicates the nymph either fed on mites or encountered mites with its proboscis before at least one of its fruit-feeding bouts. In four of these cases the *C. verbasci* fed on fruit after feeding on a mite. In the remaining 2 out of 21 replicates, the *C. verbasci* did not feed on the plant tissue after a mite feeding bout or after directly encountering a mite with its proboscis.

Neither prior prey-feeding experience nor the availability of prey was associated with a significant difference in the total duration of fruit feeding or in the number of fruit-feeding bouts (Table 4.3). However, there was a non-significant trend toward less time spent feeding on fruit when prey were present and nymphs had recent prey-feeding experience (Figure 4.4). Prior prey-feeding experience had no significant effect on the duration of time spent feeding on prey, and nymphs with prey available to them spent more time feeding on fruit than on prey (Table 4.3).

Discussion:

Panonychus ulmi, *A. schlechtendali*, and *A. pomi* were all preyed upon by first- and second-instar *C. verbasci,* but *P. ulmi* appeared to be the most acceptable of the three prey species, as suggested by the higher proportion of nymphs feeding on *P. ulmi*. This was probably a result of two factors: (1) *P. ulmi* was smaller and less defensive than *A. pomi*; (2) and *P. ulmi* was easier to encounter than *A. schechtendali,* due to the latter's flatter shape allowing it to lay beneath the leaf hairs. The lack of difference in the number of encounters prior to predation on *A. schlechtendali* compared to *P. ulmi,* suggests that low encounter rate rather than failure to recognize or capture *A. schlechtendali* lead to differences in the time prior to predation and the proportion of nymphs feeding on the two prey.

The higher proportion of *C. verbasci* nymphs feeding on *P. ulmi* than on *A. schlechtendali* and *A. pomi* may have been influenced by the test nymphs having previous experience feeding on *P. ulmi* on the branches from which they were collected (as indicated by the red abdomens of most of the nymphs at the time of collection). Preference for different prey based on prior experience occurs in some cases but not others (Holmberg and Turnbull 1982; Bergelson 1985). Nymphs were held on apple seedlings with no prey for 12 - 24 h before observations in Exp. 4. Therefore, the influence of prior experience with *P. ulmi* on apple branches would probably have been weak.

Older nymphs may have fed differently on prey than the first- and second-instars tested. For example, larger nymphs may have been more aggressive towards aphids and not been deterred by their size and defensive behaviour. It is also possible that rust mites are too small to be fed on by the larger *C. verbasci* nymphs. In light of the results of Chapter 3, which showed that pollen was an important food source for young nymphs, observations of the feeding behaviour of fourth and fifth instars and adults would have been more useful in elucidating the importance of different prey species to *C. verbasci*'s distribution.

Based on observations of first- and second-instar *C. verbasci*, it can be concluded that they are not particularly aggressive predators. Encounters with *P. ulmi, A. schlechtendali,* and particularly with *A. pomi* were often followed by *C. verbasci* moving away from rather than attacking the prey, possibly as a strategy to reduce the risk of reciprocal predation.

There was no evidence that *C. verbasci* nymphs were able to locate prey by sight. They often walked, probing the leaf, within a body length of a stationary prey, without reacting to it. Occasionally *P. ulmi* escaped initial attack by a *C. verbasci* nymph, which probed quickly in all directions with its proboscis, and moved its antennae up and down and in an arc in front of its head, apparently in an unsuccessful attempt to relocate its prey. Stationary *C. verbasci* often appeared to respond to *P. ulmi* and *A. pomi* passing in front of them by turning their antennae to follow the movement of the prey. Similar behaviour was reported in two Reduviidae species (Parker 1969), but unlike the reduvids, *C. verbasci* nymphs did not noticeably walk in the direction of, or attack, the prey to which their antennae appeared to respond.

Although the experiments were not designed to test for food preference, *C. verbasci* nymphs did not appear to prefer prey over plants for food. A preference for prey would have been suggested by the failure to feed on the plant after prey was encountered. However, *C. verbasci* spent more time feeding on plant tissue than on prey, even when prey were abundant, and there was no statistical difference in the amount of feeding by *C. verbasci* on fruit with abundant mites *vs.* fruit with none (Exp. 5). Nymphs often fed on a leaf or fruit within a few seconds of encountering or feeding on prey, suggesting that direct encounter with or feeding on prey do not preclude feeding on plant material.

C. verbasci has been described as having a "Jekyll-and-Hyde" behaviour (Beers 1992), suggesting that they switch from beneficial predation to damaging fruit-feeding. Switching theory is based on the tendency of a predator or parasite to prefer the most abundant host species (Murdoch 1969). Experiments on preference and switching behaviour typically involve manipulating the relative proportions of two or more types of foods and comparing them to the proportions preyed upon (Cock 1978). This is straightforward if both foods are arthropod prey which are fairly equal in size, but not if one of the foods is the plant over which the prey are distributed. Generalist hemipterans present an interesting problem to the concepts of preference and switching because their food is in different trophic levels (Cobben 1979; Sweet 1979; Cohen 1996; Coll 1996b). Shifts from predaceous to phytophagous behaviour in two *Orius* spp. were associated with pollen becoming available (Schoenig and Wilson 1992; Dicke and Jarvis 1962), but there is no evidence that the availability of fruit may have the same effect. Pollen contains high proportions of protein (Stanley and Linskens 1974) and probably provides nutrients equivalent to arthropod prey for nymphal development in some hemipterans (Chapter 2 and 3).

The role of foliage and fruit in the diet of *C. verbasci* is not known. They may be important only as sources of water, as was suggested for some generalist hemipterans (York 1944; Ruberson *et al.* 1986), but not for others (Ridgway and Jones 1968; Stoner 1972; Stoner *et al.* 1974; Naranjo and Stimac 1985; Wiedenmann and O'Neil 1990). If prey do not provide sufficient water, as was the case for laboratory-reared *G. punctipes* (Dunbar and Bacon 1972; Cohen and Debolt 1983), feeding on foliage or fruit may be vital to survival. The importance of foliage and fruit in the diet of *C. verbasci* could be elucidated by comparing survival and longevity between diets of prey or pollen with and without foliage or fruit, and between water alone and foliage or fruit alone.

The mechanisms controlling thirst in insects are unclear. Dethier (1976) suggested that hunger and thirst had separate behavioural responses by showing that starvation alone did not induce drinking of water by flies. The laboratory conditions in Exp. 4 and 5 may have increased the insects' need for moisture. Humidity was not recorded but the temperature was often above what would be expected in the field in the early spring. Therefore the potential moisture loss was probably higher in the lab than in the field and may have resulted in a bias toward a higher ratio of plant feeding to prey feeding in the experiment.

Wiedenmann and O'Neil (1991) suggested that feeding on plants allowed *P. maculiventris* to sustain itself between prey. Similarly, Bell (1991) suggested that fitness of an animal may be higher if it expands its consumption to less suitable but more easily located foods. It is possible that while feeding on foliage or fruit, *C. verbasci* nymphs usually encounter sufficient numbers of prey. In Exp. 5, the apparent, but non-significant trend toward less plant feeding when prey were available (Figure 4.4), may have resulted from random foraging by nymphs over the surface of the fruit. Because some of the surface area was covered with mites in treatment 2, nymphs foraging randomly would necessarily feed less on the fruit than in treatment 1 in which no prey were present.

Although there are several alternative experimental designs which may have lead to interesting information on foraging and feeding behaviour of *C. verbasci,* the two experiments in this chapter allowed me to make the following important conclusions. First- and second-instar *C. verbasci* were able to feed on all three prey species tested, but fed most readily on *P. ulmi*. This was probably due to the small size and cryptic location of *A. schlechtendali,* and to the large size and defensive behaviour *A. pomi*. The reaction of *C. verbasci* to encounters with mobile prey, particularly *A. pomi,* suggested that they are not aggressive predators. Fruit-feeding was frequent and not significantly reduced by the presence of prey, or recent predation experience of *C. verbasci.* Therefore, it can be recommended that neither abundance of prey nor colour of *C. verbasci* can be reliably considered in the estimation of the risk of fruit damage.

Figure 4.1 Arena for observations of feeding behaviour of *C. verbasci* nymphs on apple leaves with three different prey species: *A. pomi, P. ulmi* and *A. schlechtendali* (Exp. 4). The arena consisted of small apple leaf, held in florist foam and held in place with modelling clay on an angled mirror on the stage of a dissecting microscope.

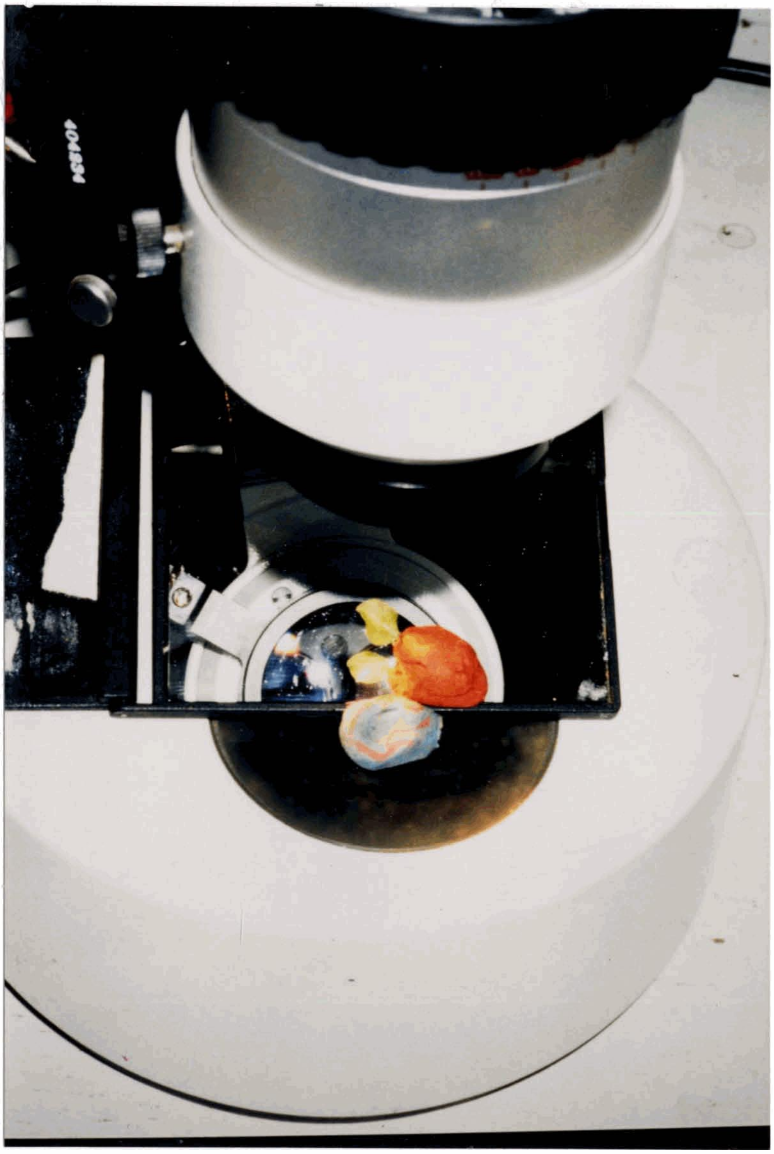

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Figure 4.2 Arena for observations of feeding behaviour of *C. verbasci* nymphs on fruitlets with five *P. ulmi* or with no prey (Exp. 5). The arena consisted of a small apple fruitlet, held in florist foam and set on a V-shaped trough made of two angled pieces of mirror on the stage of a dissecting microscope.

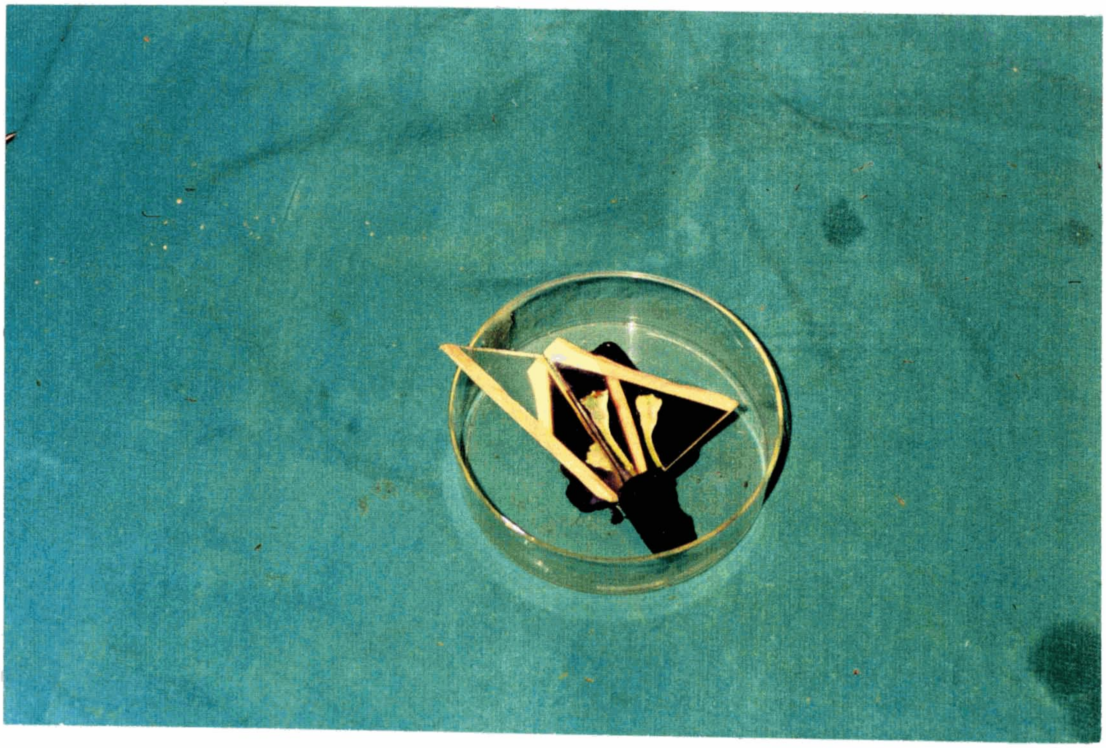


Table 4.1 Proportion of first- or second-instar *C. verbasci* nymphs which fed on prey when mobile stages of one of three species of prey were available on an apple leaf. The data include only nymphs which encountered at least one prey during the 1-h observation period (Exp. 4).

Treatment	Prey	N	Proportion of nymphs which fed on prey [a]
1	*P. ulmi*	19	0.84 a
2	*A. pomi*	19	0.37 b
3	*A. schechtendali*	18	0.50 b

[a] Significant difference between the proportions which fed on different prey, $G_W = 9.598$, $P < 0.05$, log-likelihood test (Sokal and Rolf 1981). Proportions followed by the same letter are not significantly different, $G_W = 0.6276$, $P > 0.05$, log-likelihood test (Sokal and Rolf 1981).

Table 4.2 Number of encounters with prey before *C. verbasci* nymphs fed on prey when one of each of three species of prey were available on an apple leaf (Exp. 4).

Treatment	Prey	N	Number of encounters with prey prior to feeding on first prey ($\bar{x}$ ± SE) [a]
1	*P. ulmi*	16	3.7 ± 0.6 a
2	*A. pomi*	7	10.5 ± 2.6 b
3	*A. schlechtendali*	9	2.3 ± 0.7 a

[a] Significant difference between number of encounters, $P = 0.0001$, one-way analysis of variance on the square-root transformed data (General linear Model, SAS, 1995). Numbers followed by the same letter were not significantly different, $P > 0.05$, Duncan's multiple range test (SAS, 1995).

Figure 4.3 Percent of *C. verbasci* nymphs which had not yet fed on prey at the start of each 2-min. period, over the course of 1-h observations on apple leaves with one of three prey species: *A. pomi, P. ulmi* and *A. schlechtendali* (sample sizes were 19, 19 and 18, respectively) (Exp. 4). The distribution of times before first feedings on *P. ulmi* was different than distributions for *A. pomi* and *A. schechtendali*, *P* = 0.0002, but the latter two were not different from each other, *P* = 0.4936, Kaplan Meier Survival Analysis, log rank method (SPSS for Windows, version 6.1, 1994).

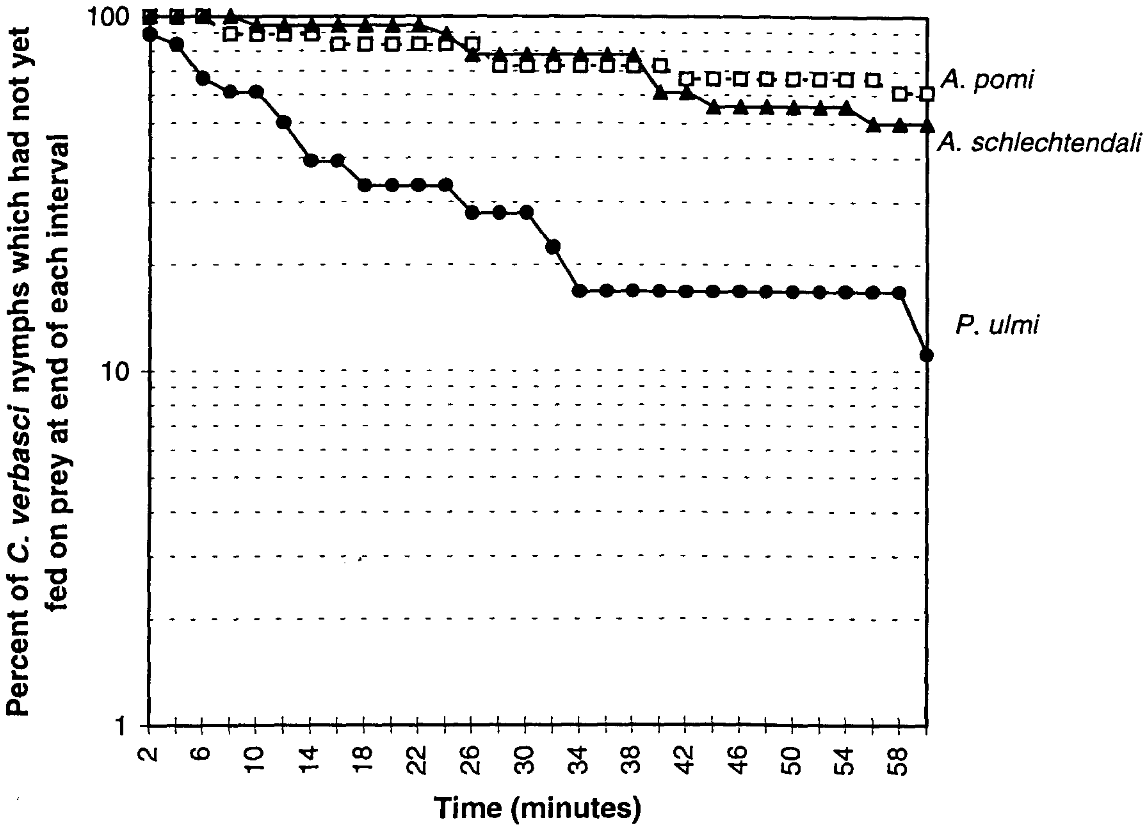

Percent of C. verbasci nymphs which had not yet fed on prey at end of each interval
100
10
1
2
6
10
14
18
22
26
30
34
38
42
46
50
54
58
Time (minutes)
A. pomi
A. schlechtendali
P. ulmi

Table 4.3 Mean number of feeding bouts and duration of time spent feeding on prey (*P. ulmi*), and on apple fruit by *C. verbasci* nymphs with different prey feeding experience (indicated by colour), when observed for 40 min on fruitlets with and without *P. ulmi* (Exp.5).

Nymph colour	Prey	N	Number of direct encounters with prey ($\bar{x} \pm$ SE)	Number of prey feeding bouts ($\bar{x} \pm$ SE)	Total duration of time (min) spent feeding on prey ($\bar{x} \pm$ SE) [a, b]	Number of fruit feeding bouts ($\bar{x} \pm$ SE) [c]	Total duration of time (min) spent feeding on fruit ($\bar{x} \pm$ SE) [b,d]
cream	no prey	10				4.80 ± 1.08	11.0 ± 2.8
red		10				7.50 ± 1.20	7.8 ± 1.9
cream	*P. ulmi*	11	3.73 ± 0.80	0.82 ± 0.23	2.7 ± 1.4	8.64 ± 1.75	6.3 ± 1.7
red		10	3.40 ± 0.96	0.50 ± 0.31	1.2 ± 0.8	5.20 ± 0.86	5.38 ± 1.2

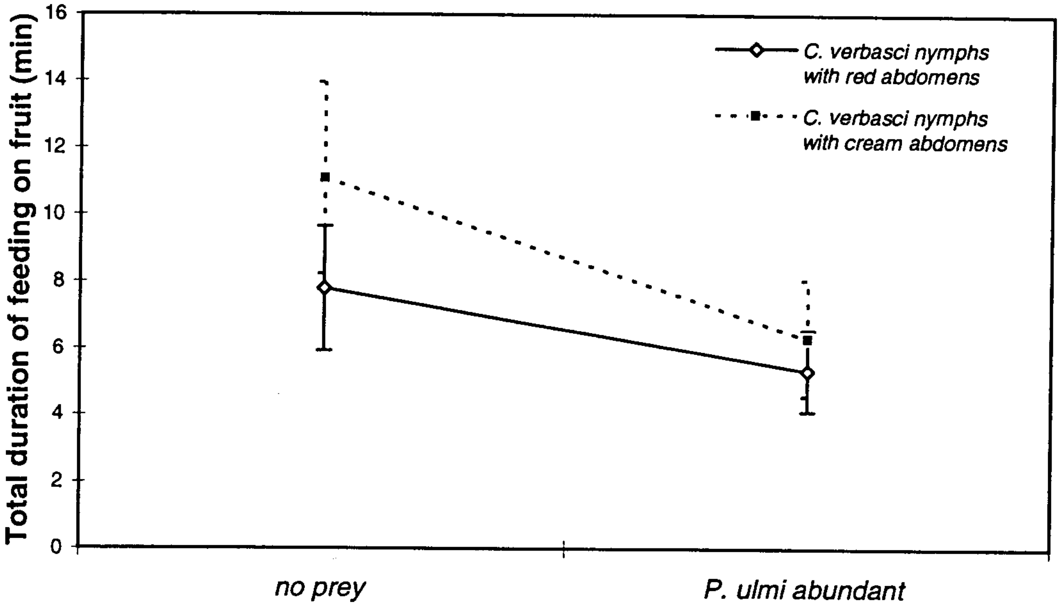
[a] No differerence in the total duration of time spent feeding on prey between red and cream coloured nymphs, $P = 0.3629$, two tailed t-test (General Linear Model Procedure, SAS, 1995)

[b] Nymphs with prey available to them spent more time feeding on fruit than feeding on prey, $P = 0.0018$, one tailed, paired T-test (SPSS for Windows, version 6.1, 1994).

[c] No differerence in the number of fruit feeding bouts, transformed by natural log (number of bouts + 1), between red and cream coloured nymphs $P = 0.5994$, or between fruit with and without prey, $P = 0.5365$, and no significant interaction, $P = 0.0653$, two way analysis of variance on ln transformed data, (General Linear Model Procedure, SAS, 1995)

[d] No differerence in the total duration of fruit feeding, transformed by square root (duration + 1) between red and cream coloured nymphs $P = 0.5572$, or between fruit with and without prey, $P = 0.1604$, and no significant interaction $P = 0.6879$, two-way analysis of variance on square root transformed data (General Linear Model Procedure, SAS, 1995).

Figure 4.4 The mean and standard errors of the duration of fruit-feeding when five *P. ulmi* were present and when no prey was provided, for nymphs with and without recent prior predation experience (as indicated by nymph colour) (Exp. 5). Sample sizes were 10, 10, 11, and 10 for cream-coloured nymphs with no prey, red-coloured nymphs with no prey, cream-coloured nymphs with mites, and red-coloured nymphs with mites, respectively.


Total duration of feeding on fruit (min)
16
14
12
10
8
6
4
2
0
C. verbasci nymphs with red abdomens
C. verbasci nymphs with cream abdomens
no prey
P. ulmi abundant

Chapter V

The influence of the presence of *P. ulmi* on the residence time of adult, female *C. verbasci* on branches

Introduction

Little is known about the factors that make an orchard or a branch a suitable site for oviposition of winter diapausing eggs, but some orchards have high densities of *C. verbasci* in the spring, while adjacent, similar orchards have none. The patterns of search for resources such as food, mates, or oviposition sites have been studied for many animals (Bell 1991) to better understand their behaviour and distribution. Environmental cues can influence search patterns by attracting animals towards or arresting them near a resource (Kennedy 1978). For arthropod predators and parasitoids, these cues may include stimuli associated with the presence of their hosts or prey (Powell 1986; Honek 1980), as well as semiochemicals emitted by plants infested by their hosts or prey (Dicke and Sabelis 1992; Drukker *et al.* 1995).

One might hypothesize that *C. verbasci* can perceive stimuli associated with their prey, and perhaps respond by remaining longer and laying more eggs where prey is abundant. In support of this hypothesis, there were positive correlations between the density of *P. ulmi* in the summer and density of *C. verbasci* nymphs the following spring in a survey of > 50 apple orchards (Bartlett and Edwards 1993). In addition, more *C. verbasci* nymphs were present in the spring on branches naturally infested with *A. pomi* the previous summer, than on branches on adjacent, uninfested trees (Bartlett and Edwards 1993). Similarly, the number of *C. verbasci* was correlated with the number of aphid colonies per tree (Acquafresca and Newton 1986).

The following experiment (Exp. 6), tested the hypothesis that adult female *C. verbasci* remain longer on branches infested with *P. ulmi* than on branches with no arthropod prey.

Methods

The experiment was conducted on unsprayed, two year old, Golden Delicious apple trees in Okanagan Centre, B.C. Paired branches on adjacent trees were matched by size, height above ground and aspect. One of the branches in each pair was randomly selected to be a control and the other to be infested with *P. ulmi.* Leaves on the distal 5 - 9 cm were infested by transferring *P. ulmi* adults and nymphs from infested leaves collected in other orchards. This process was repeated several times over 2 - 3 week to ensure that populations of *P. ulmi* were established. All arthropods visible with a 10X magnifying lens, including *P. ulmi* eggs, were removed from the control branches with an insect pin. On both branches of each pair, leaves were removed from the 10 cm section of branch below the distal 5 - 9 cm, and a thin band of Stickum™ was applied around this section to prevent *P. ulmi* from migrating from or onto the branch.

Wettable Sulfur was applied to all trial branches at least one week prior to observations to kill apple rust mites, *A. schlechtendali*. Sulfur is not known to affect *C. verbasci* but it may benefit *P. ulmi* indirectly by killing predator mites.

C. verbasci were collected as fourth and fifth instars from unsprayed mullein plants. They were reared to adulthood in petri dishes (100 x 25 mm) with *P. ulmi* infested apple leaves in a sheltered, outdoor cage. Females were used in observations after one or two days of adulthood. Twelve hours before use they were mildly anesthetized with CO_2, marked with a small spot of white enamel paint on their pronotum in order to identify them from wild *C. verbasci,* and placed individually in petri dishes with wet florist foam but no food.

Twenty-nine replicates were run between July 14 and August 9, 1995. One mildly CO_2 anesthetized *C. verbasci* was placed on each of the paired branches between 0730 and 0830. If necessary, a large, clear cup was used to shield the branch from breezes for up to a minute until the insect was clinging firmly to the leaf.

Each branch was checked at 30-min intervals for the presence of the adult until it left the branch or until it became too dark to see. Immediately following a trial, one leaf was randomly selected and removed from each branch and *P. ulmi* and *A. schlechtendali* were counted directly on the leaf using a dissecting microscope.

The durations of time that adults remained on *P. ulmi* infested and uninfested branches were compared using a one-tailed, paired t-test (SPSS for Window, Version 6.1, 1994). The number of *P. ulmi* eggs and motile stages, and the number of *A. schlechtendali* on *P. ulmi* infested and uninfested branches were compared using the nonparametric Wilcoxon matched-pairs signed ranks test (SPSS for Windows, Version 6.1.2, 1995).

Results and Discussion

The numbers of eggs and motile *P. ulmi* per leaf on the infested branches were significantly higher than on the control branches. The number of *A. schlechtendali* per leaf was very low and not different between the control and the *P. ulmi* infested branches. Adult female *C. verbasci* remained significantly longer on branches infested with *P. ulmi* than on control branches from which mites had been removed (Table 5.1). Because *C. verbasci* can oviposit throughout their lives (Smith and Borden, 1991), remaining near prey that could provide nutrients to help sustain fecundity (Dethier 1976) would be a distinct advantage to a female. Her emerging offspring may also benefit because they too feed on *P. ulmi*. It would be difficult to determine whether the behaviour of adult females to remain longer where prey are available, had evolved as a result of benefits to their own lifetime fecundity, or if it was also due to increases in their offspring's survival. It is not known if the females were responding to olfactory, visual or tactile cues from the prey or from the plant.

The 3-h difference in average residence time may not have been long enough to lead to a significant difference between the number of eggs laid on infested and non-infested branches. Little is known about the number of eggs laid by *C. verbasci* because their oviposition into plant tissue makes the eggs very difficult to find (Collyer 1953; Sanford 1964*a*; Smith and Borden 1991). However only 6.7 ± 0.6 (range 0 - 36) nymphs emerged per 48-h oviposition period for *C. verbasci* reared in the laboratory (Smith and Borden 1991). Therefore if ovipositions are uniformly distributed throughout the day, an average of 0.42 offspring would be produced during the 3-h difference in residence time. The difference in the median residence times was 7 h (Table 5.1) and may be more relevant to the question of how prey presence influences *C. verbasci* distribution.

The results of this experiment demonstrate that the presence of *P. ulmi* on branches had a significant, positive effect on the residence time of adult female *C. verbasci*. This is consistent, albeit on a small scale, with the hypothesis that the number of *C. verbasci* in an orchard is positively influenced by the availability of prey. Further work is needed to clarify the mechanisms of this influence on residence time and its implications for *C. verbasci* distribution.

Table 5.1 Residence duration of adult, female *C. verbasci* placed on paired, 5 - 9 cm long apple-branch tips (N = 29) with all visible prey removed or infested with *P. ulmi*. *C. verbasci* were placed on the branches between 0730 and 0830, and were checked every 30 min until the insect left the branch or until it became too dark to see. .

	Number of mites found post-experiment on one sample leaf from each branch (x ± SE)			Duration (h) that *C. verbasci* remained on branch	
		P. ulmi [b]			
Treatment	*A. schlechtendali* [a]	Eggs	Adults or nymphs	(x̄ ± SE)[c]	median
All visible mites removed	2.3 ± 1.7	1.3 ± 0.4	1.1 ± 0.3	5.8 ± 0.8	5.5
P. ulmi population established on branch	0.8 ± 0.4	52.7 ± 8.3	8.6 ± 2.1	8.9 ± 0.9	12.5

[a] No difference between number of *A. schlechtendali* per leaf, $P = 0.7489$, Wilcoxon matched-pairs test (SPSS for Windows, Version 6.1.2, 1995)

[b] Significant differences between the number of *P. ulmi* eggs per leaf, $P < 0.0001$, and the number of *P. ulmi* nymphs or adults per leaf $P = 0.0010$, Wilcoxon matched-pairs test (SPSS for Windows, Version 6.1.2, 1995)

[c] Significant difference in the duration of time adult female *C. verbasci* remained on branches, $P = 0.0010$, one-tailed paired t-test (SPSS for Windows, Version 6.1, 1994)

Chapter VI

Determination of the oviposition period for winter-diapausing eggs in *C. verbasci*

Introduction:

Campylomma verbasci spend the winter as diapausing eggs imbedded in the bark of apple and pear trees (Sanford 1964*a*; McMullen and Jong 1970; Smith 1989, 1991; Thistlewood *et al.* 1990). The oviposition period for winter-diapausing eggs has been estimated from observations of the migration of adults from their summer host mullein, *V. thapsus*, to orchards. This migration period has been described as occurring in the latter half of September to mid-October (McMullen and Jong 1970), beginning in late summer (Smith 1991), and beginning in late August (Thistlewood *et al.* 1990; McBrien *et al.* 1994). However, a residual population of *C. verbasci* often remains in orchards throughout the summer (Thistlewood *et al.* 1990; McBrien *et al.* 1994; Bartlett and Edwards 1993), which may also lay winter-diapausing eggs.

Diapause can be induced by the responses of the insect to cues in the environment, possibly strengthened or weakened by endogenous rhythms, internal timers, or the influence of the mothers' age and experience. Environmental cues could include: photoperiod, rate and direction of change in photoperiod; light intensity and wavelength; food quality and quantity; and temperature. Sensitivity to temperature for diapause induction could be very complex, possibly involving maximum, minimum or average daily temperatures, duration of time below a threshold temperature (thermoperiod), number of successive days below a threshold temperature, and rate of warming and cooling. An insect's response to any of the above factors could be integrated to induce diapause (Danks 1987).

Diapause occurs in all life stages and all periods within stages among different insect species. The lack of patterns within insect orders suggests that diapause probably evolved independently numerous times (Tauber *et al.* 1986). Eggs are often the most winter hardy life stage in freezing intolerant species (which comprise the majority of insects in cool climates) (Leather *et al.* 1993). The sensitive life stages for the induction of diapause in eggs can be any stage of the parental generation, or in the current generation, the embryo itself, or in both generations (Walker 1980; Danks 1987).

If the presence of prey influences the number of *C. verbasci* eggs laid in an orchard (Chapters 3 and 5), then it is important to know when winter-diapausing eggs are laid so that efforts can be made to reduce prey during that period to numbers that do not encourage females to remain and oviposit. Pheromone-mediated mating disruption is also being developed as a method of controlling *C. verbasci* (McBrien *et al.* 1996). The relationship between when mating occurs and when eggs are laid is not known. However, the identification of the earliest period during which significant numbers of diapausing eggs are laid could be used as a guideline for when mating disruption should be implemented. Exp. 7 and 8 were conducted to determine the period or periods during which *C. verbasci* lay winter diapausing eggs in apple orchards in the north-central Okanagan Valley.

Methods

Summer 1993 to Spring 1994 (Exp. 7)

Two unsprayed blocks (sites 1 and 2), of mature Red Delicious apple trees were selected. Forty branches at site 1 and 56 at site 2 were chosen for their similarity of size and wood age. Some of these branches were on the same trees. All fruit and insects were removed and sleeve cages (75 cm long and 30 cm diameter) were placed over each branch on July 6 to exclude *C. verbasci*. The cages were made of tightly woven, polyester-voile fabric with plastic boning for support (Figure 6.1)

Randomly selected sets of five or eight branches (for sites 1 and 2, respectively), had their cages removed for different two-week periods throughout the summer (seven periods at site 1, six periods at site 2). This allowed wild *C. verbasci* adults to land and oviposit on a branch only during the two-week period of exposure. The first two-week period of cage removal was from July 20 - August 3. Cages on randomly selected control branches (five and eight branches at sites 1 and 2 respectively), were not removed at any time during the summer except during weekly checks of all branches for *C. verbasci*. The number of *C. verbasci* nymphs and adults in the orchards were monitored by limb-tap samples (Thistlewood and McMullen 1989) of 25 non-caged branches chosen randomly at each site every week. The sex of *C. verbasci* was not recorded. In January and February, 1994, all caged branches were removed and incubated at ca. 22°C. Newly emerged nymphs were counted and removed daily.

Degree-day accumulation over 10°C (DD_{10}) and under 31°C (obtained from B.C. Fruit Products), was calculated using a formula which closely approximated (within 10 DD_{10} over 600 DD_{10}), the models of Brunner *et al.* (1982) and Reidl and Croft (1978). The temperatures used in the calculations were from Environment Canada weather stations at Winfield, 3 km from site 1, and East Kelowna, 2 km from site 2. DD_{10} is based roughly on the lower development threshold for *C. verbasci* eggs (Smith and Borden 1991; Judd and McBrien 1994) not on the development or activity of nymphs and adults. It also does not take into consideration the slower development which occurs at temperatures less than 10°C (Judd and McBrien 1994) or the reduction in feeding activity and therefore development which may occur in wet or windy weather. However, because DD_{10} values are available to orchardists and pest managers throughout the growing season, and because DD_{10} was used in research on seasonal flight patterns of *C. verbasci* (McBrien *et al.* 1994), I chose to compare the occurrence of diapause-egg laying with DD_{10} as well as with calendar date.

Summer 1994 to Spring 1995 (Exp. 8)

The same methods were used as for Exp. 7, except that Exp. 8 was started six weeks earlier, before the first-generation of *C. verbasci* had matured to adulthood, and there were 10 periods of branch exposure rather than six or seven. Site 1 was used again and a third site, an organic orchard in Winfield, replaced site 2 which was to be sprayed in 1994. There were five replicate branches at each orchard for the control and for each of 10 two-week periods, beginning June 7 - 12.

DD_{10} data were obtained as in Exp. 7 and were calculated using temperature data from the Environment Canada weather station at Winfield, 3 km and 0.5 km from sites 1 and 3 respectively..

Results

In both years, diapause-egg laying began in mid- to late-July (at around 697 and 783 DD_{10} in 1993 and 1994, respectively), and continued into the fall, as evidenced by nymphs that emerged from branches exposed during these periods (Fig 6.2). In Exp. 7, the largest number of nymphs emerged from branches exposed between August 18 to September 1 for which the mid point DD_{10} were 952 and 975 at the two sites, respectively (average = 963)(Figure 6.3). In Exp. 8 the largest number of nymphs emerged from branches exposed approximately two-weeks earlier, between August 2 to 16 but with a similar mid-point DD_{10} of 954.

There were residual populations of *C. verbasci* in the orchards throughout the summer, as evidenced by nymphs recorded in limb-tap samples (Figure 6.2). These samples did not discriminate between adults from the residual orchard population and those that migrated from mullein to the apple trees.

Discussion

Exp. 7 and 8 showed that winter-diapausing eggs can be laid beginning around July 26 (the mid point of period 4), which is approximately 2 - 6 weeks earlier than they were previously believed to be laid (McMullen and Jong 1970; Thistlewood *et al.* 1990; McBrien *et al.* 1994). The single nymphs which emerged from one control branch and from one branch exposed between June 21 and July 5, 1994, may have resulted from oviposition through the cage material, but probably do not indicate that diapausing eggs were laid prior to July 5.

As would be expected, the peaks in oviposition corresponded roughly to peaks in the adult population. The results suggested that a significant number of winter-diapausing eggs were laid by adults of the second- and third-generations of *C. verbasci* which are usually present from mid-July to late October (Thistlewood *et al.* 1990, McBrien *et al.* 1994).

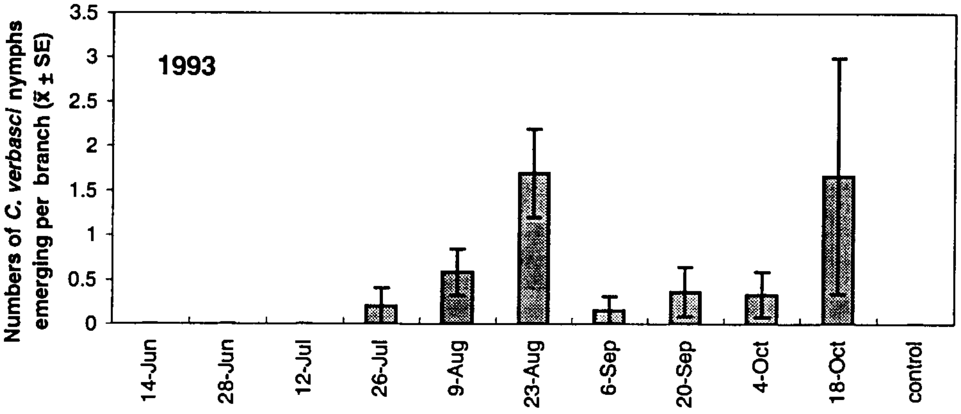
The nymphs recorded in limb-tap samples late in the summer (Figure 6.2) were probably also produced by second-generation females, suggesting that this generation can lay both diapausing and non-diapausing eggs. It is not known whether individual female *C. verbasci* can lay both types of eggs or whether the different types are laid during the same period by different females within the same generations. It is not unusual for there to be enough variation in the environment or in individuals' responses to it, to result in variation in the type of egg laid by a given generation, or even by an individual female (Korboot 1961; Walker 1980; Hokey *et al.* 1983; Ingrisch 1987; Sternberg 1994). Likewise, diapausing eggs can be laid over a long period of time varying in temperature and photo-periodic regime, and by more than one generation of adults (Walker 1980; Hokey *et al.* 1983; Golden and Meinke 1991; Morales 1993; Sternberg 1994).

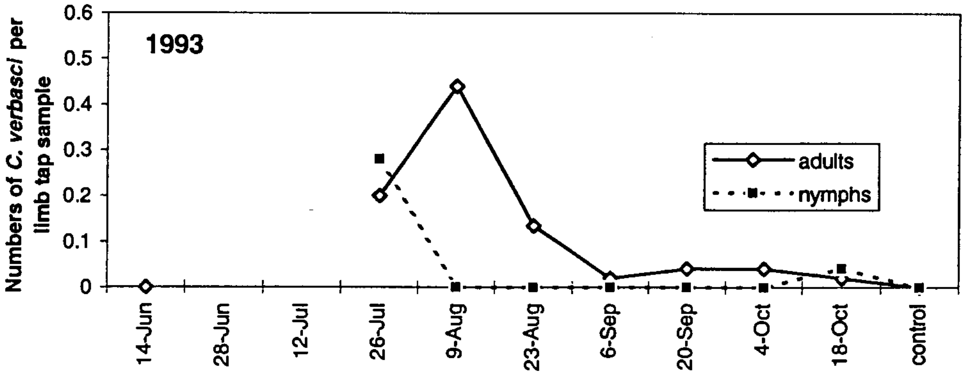
The presence of adult *C. verbasci* in an orchard could be used as an indication of the beginning of the flight of second-generation adults and thus the beginning of diapause-egg laying. In Exp. 7 and 8, adult *C. verbasci* numbers in the orchards were recorded only on a weekly basis, by the limb-tap method which is subject to error due to weather on the day of sampling. This method is not practical after June because it dislodges apples from the branches. Pheromone traps (Phero Tech Inc.), placed within the orchard, may be used to estimate the beginning of the flight of second-generation adults. DD_{10} accumulation could also be used to make this estimate, however, DD_{10} does not indicate whether *C. verbasci* are actually present in the orchard and therefore could be misleading.

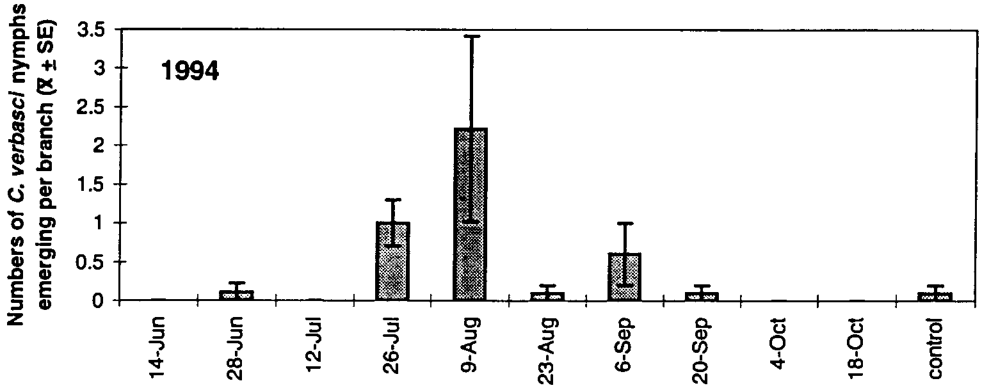
The high summer populations of *C. verbasci* in the test orchards may be unusual and an artifact of conducting the experiments in unsprayed orchards. In conventional orchards the use of organophosphate insecticides may reduce the summer population of *C. verbasci*. In such orchards, the adults returning to the orchard in the fall from mullein may be the major contributors to diapause-egg laying and thus to the population of nymphs in the following spring.

Figure 6.1 Sleeve cages (75 x 30 cm), made of woven polyester-voile fabric and plastic boning, placed over branches in an apple orchard to exclude *C. verbasci.*

Figure 6.2 Number of first generation *C. verbasci* nymphs emerged from branches exposed to wild adults during two-week periods in 1993 (site 1 and 2 combined) and 1994 (site 1 and 3 combined), and the number of *C. verbasci* adults and nymphs counted in limb-tap samples at the mid-point of the two-week periods. Sample sizes for the control and for each period in 1993, beginning with July 26 were 12, 5, 12, 13, 13, 11, 12, and 12, respectively. Sample sizes for the control and for each period in 1994, beginning with June 14, were 10, 8, 9, 9, 10, 9, 10, 10, 10, 10, and 9 respectively.


Numbers of C. verbasci nymphs emerging per branch (x̄ ± SE)
1993
0
0.5
1
1.5
2
2.5
3
3.5
14-Jun
28-Jun
12-Jul
26-Jul
9-Aug
23-Aug
6-Sep
20-Sep
4-Oct
18-Oct
control


Numbers of C. verbasci per limb tap sample
1993
0
0.1
0.2
0.3
0.4
0.5
0.6
adults
nymphs
14-Jun
28-Jun
12-Jul
26-Jul
9-Aug
23-Aug
6-Sep
20-Sep
4-Oct
18-Oct
control


Numbers of C. verbasci nymphs emerging per branch (x̄ ± SE)
1994
0
0.5
1
1.5
2
2.5
3
3.5
14-Jun
28-Jun
12-Jul
26-Jul
9-Aug
23-Aug
6-Sep
20-Sep
4-Oct
18-Oct
control

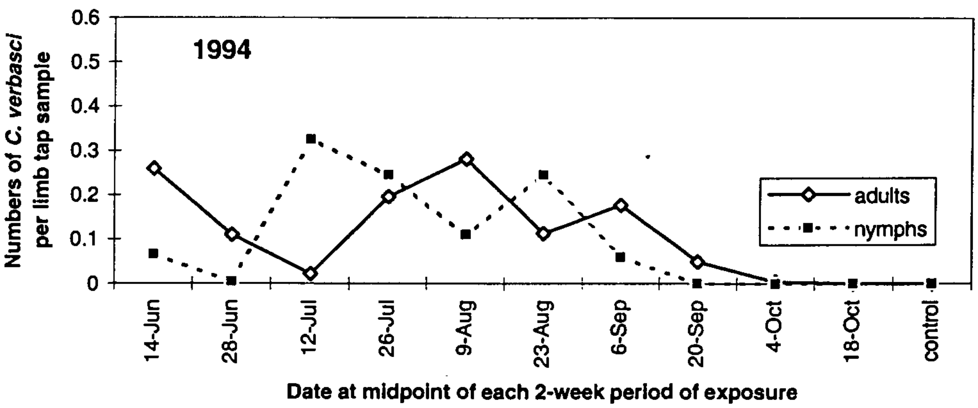
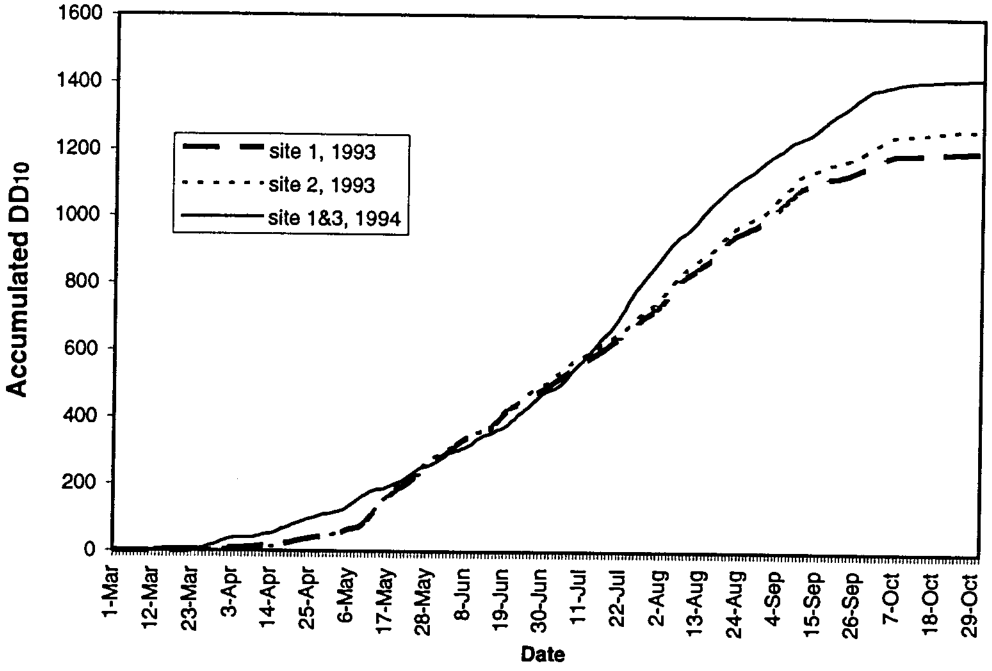

Numbers of C. verbasci per limb tap sample
1994
0
0.1
0.2
0.3
0.4
0.5
0.6
adults
nymphs
14-Jun
28-Jun
12-Jul
26-Jul
9-Aug
23-Aug
6-Sep
20-Sep
4-Oct
18-Oct
control
Date at midpoint of each 2-week period of exposure

Figure 6.3 DD_{10} accumulation through 1993 (site 1,Winfield and 2, East Kelowna) and 1994 (site 1 and 3, Winfield), calculated according to Brunner *et al.* (1982) and Reidl and Croft (1978) from Environment Canada weather data.


1600
1400
1200
1000
800
600
400
200
0
Accumulated DD10
site 1, 1993
site 2, 1993
site 1&3, 1994
1-Mar
12-Mar
23-Mar
3-Apr
14-Apr
25-Apr
6-May
17-May
28-May
8-Jun
19-Jun
30-Jun
11-Jul
22-Jul
2-Aug
13-Aug
24-Aug
4-Sep
15-Sep
26-Sep
7-Oct
18-Oct
29-Oct
Date

Chapter VII

Conclusions

This thesis demonstrates that *C. verbasci* nymphs are not entirely dependent on arthropod prey for survival to adulthood. This result is contrary to past assumptions, probably because pollen was not previously considered as a possible high-protein food for *C. verbasci*. The suitability of pollen as a food source is demonstrated by the result that a high proportion of first- and second-instar nymphs reared on apple leaves plus pollen survived to adulthood, and that this proportion and the rate of development were similar to that of nymphs reared on apple leaves plus mites provided *ad libitum*. In addition, adult female *C. verbasci* reared on nymphal diets of leaves plus pollen were 3.6 % larger and had reproductive development similar to those reared on leaves plus mites. Pollen may play a very important role as a source of protein for nymphs, particularly first and second instars which appear to be poor predators.

Pollen is not available throughout the entire development of first-generation nymphs in apple orchards. In 1995, nymphs were mainly in their fourth instar when pollen became unavailable. In experiments in which these field conditions were simulated, nymphs reared with access to spider mites had a higher chance of surviving to adulthood than those with no prey. These results suggest that there is some advantage to a nymph of being located where prey are abundant, and from this it follows that there may be a corresponding fitness advantage to females which lay their winter-diapausing eggs near prey. The patchy distribution of pollen or prey in non-cultivated habitats may have contributed to the evolution of omnivorous feeding in *C. verbasci* and other species.

Feeding on plants has been reported in other generalist, predatory Hemipterans but the role of plants in their diet is unclear. *C. verbasci* nymphs were observed to feed on leaves and fruit even when prey were present and had been encountered or fed on, suggesting that plants are a necessary part of the nymphal diet. The presence or absence of prey, and the colour of *C. verbasci* nymphs (as an indicator of recent prey-feeding) did not have a significant effect on the amount of fruit-feeding. Based on these results, neither prey abundance nor colour of *C. verbasci* nymphs should be used to help predict the amount of damage that may occur to fruit.

Among three arthropods tested as prey, *P. ulmi*, *A. schlechtendali*, and *A. pomi*, the former were the most readily fed on by young *C. verbasci* nymphs. *P. ulmi* is very common and subject to large fluctuations in density in conventional apple orchards in the Okanagan Valley of B.C. The hypothesis that the presence of *P. ulmi* is an important factor in the distribution of *C. verbasci* is supported by the fact that adult females were found to remain longer on branches infested with this mite than on branches with no prey. It is not known whether the adults stayed simply to feed or if they also remained to oviposit on what they perceived to be a productive site for the survival of their offspring. To determine this, more research would be needed on the foraging and oviposition behaviour of adult females, the effect of different diets on their fecundity, and the correlation between prey abundance in the summer and in the following spring.

If the abundance of *P. ulmi* influences the distribution of *C. verbasci* in the following year, it may do so throughout the summer and fall. Oviposition of winter diapausing eggs was found to occur from late July to late October and corresponded to the flight of second- and third-generation adults. The results suggest that the second-generation lays both diapausing and non-diapausing eggs. In conventional orchards however, insecticide use may reduce the summer population of adults so that only those returning to the orchard in the fall from mullein may contribute to the numbers of diapausing eggs.

C. verbasci is currently managed by pesticide sprays targeting first-generation nymphs that emerge around the time of bloom in apple orchards. To conserve pollinators, organophosphate sprays are not applied during bloom, and thus economic damage can occur from *C. verbasci* feeding, making the current control strategy unsatisfactory. It seems logical to try to improve *C. verbasci* management by discouraging high densities of prey in the summer and fall, which in turn may discourage oviposition of overwintering eggs. This tactic could be used in conjunction with a pheromone-based mating disruption program that should begin before the end of July in the Okanagan Valley of B.C., or when second- and third-generation adults are present in the orchard.

Appendix 1 - Duration of time abdomens of *C. verbasci* remain red after feeding on *P. ulmi*

When *C. verbasci* nymphs feed on colour-intense food such *P. ulmi*, the red colour of the mites can be easily seen through the nearly transparent integument of the nymphs' abdomens (Figure A1.1) Therefore, gut colour could be used as an indicator of recent prey-feeding experience, which could have important implications for experiments on feeding requirements and behaviour (Chapters 3 and 4). The following experiment was carried out to determine how long the guts of *C. verbasci* nymphs remain red after feeding on *P. ulmi*.

Methods:

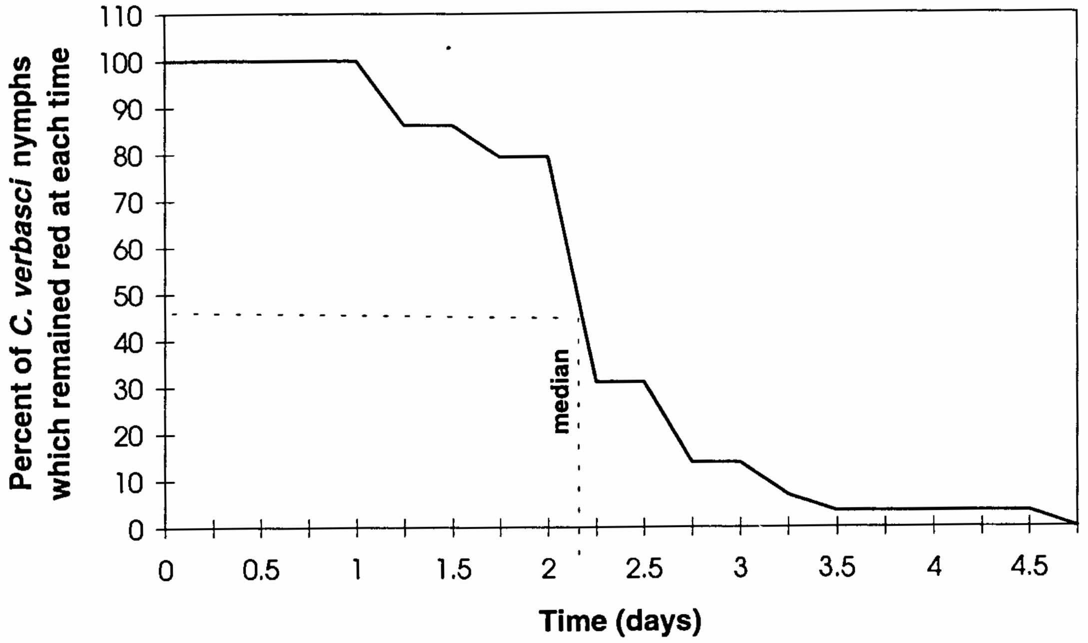
Thirty-four second-instar *C. verbasci* were collected from unsprayed mullein plants and placed individually in petri dishes for 1 - 2 days during which they were provided with apple leaves infested with *P. ulmi*. Nymphs with red abdomens were then removed and each was placed in an individual petri dish (100 x 25mm), and provided with a piece of mullein flower stalk, with pollen but no prey. The nymphs were examined under 10X magnification every 6 - 12 hours and the presence or absence of red colour in their guts was recorded.

Results:

Five of the original 34 nymphs in the trial were missing or dead before the red colour could no longer be seen in their guts. For the remaining nymphs, the median time for the red colour to completely disappear from the gut was 2.25 days (Figure A1.2).

Figure A1.1 First-instar *C. verbasci* with red- and green-coloured guts resulting from feeding on *P. ulmi* and young apple leaves, respectively. Nymphs are 0.8 mm in length.

Figure A1.2 The percent of nymphs which still had some red coloration in their guts at each time after *P. ulmi* had been removed and mullein flower stalks provided.


Percent of *C. verbasci* nymphs which remained red at each time
110
100
90
80
70
60
50
40
30
20
10
0
median
0
0.5
1
1.5
2
2.5
3
3.5
4
4.5
Time (days)

Appendix 2 - Comparison of the sizes of wild and experimentally reared *C. verbasci* adults

This experiment was conducted to determine if *C. verbasci* adults reared in Exp. 2 and 3 (Chapter 3) were different in size than wild *C. verbasci*.

Method:

First-generation adults of unknown age and previous diet were collected from mullein plants in early June, 1995. Each was mildly anesthetized with CO_2 and the width of their pronotum measured as in Exp. 2. The widths were compared with those of adults reared in Exp. 2 and 3, using a two-way analysis of variance (General Linear Model Procedure, SAS, 1995) and pairwise comparisons (eight pre-planned comparisons). The acceptable *P*-value for eight comparisons is 0.0062 using the Bonferroni adjustment.

Results and Discussion

Both treatment and sex had a significant impact on the pronotal size and there was no interaction between sex and treatment (Table A2.1). Only females reared in Exp. 2, treatment 2 (apple leaves plus pollen *ad libitum*) had wider pronota. Pronota of wild *C. verbasci* were not wider than those of females reared in any of the experimental treatments. In general, laboratory rearing did not result in deviations in adult size from the wild population.

Table A2.1 Pronotal widths of first-generation *C. verbasci* adults collected from mullein in the field, compared with *C. verbasci* reared in Exp. 1 and 2, Chapter 3. Measurements were made using an ocular micrometer and dissecting microscope at 40X magnification.

Treatment	Nymphal diet	Males		Females	
		N	Pronotal width (mm) ($\bar{x} \pm$ SE)[a]	N	Pronotal width (mm) ($\bar{x} \pm$ SE)[b]
Wild	unknown: collected on mullein	24	0.971 ± 0.002	31	0.994 ± 0.001
Exp. 2, #2	apple leaf plus pollen *ad libitum*	20	0.994 ± 0.011	16	1.033 ± 0.005
Exp. 2, #4	apple leaf plus mites *ad libitum*	22	0.986 ± 0.006	16	0.997 ± 0.008
Exp. 3, #7	apple leaf plus blossom or fruit	5	0.940 ± 0.018	5	0.995 ± 0.012
Exp. 3, #8	apple leaf plus blossom or fruit plus mites *ad libitum*	8	0.987 ± 0.003	9	0.997 ± 0.016

[a] No difference between pronotal widths of wild, adult males and laboratory-reared adult males, $P > 0.05$, pair-wise comparisons after two-way analysis of variance (General Linear Model Procedure, SAS, 1995).

[b] Pronotal widths of adult females reared in Exp. 2, treatment 2, on leaf plus pollen *ad libitum*, were significantly larger than pronotal widths of wild adult females, $P = 0.0042$ (for $\alpha < 0.05$ with Bonferroni correction for 8 pre-planned comparisons, the acceptable P-value is 0.0062), in pair-wise comparisons after two-way analysis of variance (General Linear Model Procedure, SAS, 1995).

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