Chapter 1

Review of the Literature

Introduction

Aphid pests of apple in the mid-Atlantic region.

Pest status and damage. Woolly apple aphid, *Eriosoma lanigerum* (Hausmann), spirea aphid, *Aphis spiraecola* Patch, and rosy apple aphid, *Dysaphis plantaginea* (Passerini), are the main aphid pests of apple, *Malus domestica* Borkhausen (Rosaceae), grown in the mid-Atlantic region of the United States (Pfeiffer et al. 1995). These species may be temporally synchronous during part of the growing season, although woolly apple aphid colonizes different parts of apple trees than spirea and rosy apple aphid. Feeding by *A. spiraecola* on the leaves of apple trees can reduce dry weight, lateral shoot growth, and the percentage of nonstructural carbohydrates in infested apple trees (Kaakeh et al. 1992). Rosy apple aphid feeding causes damage to apple trees through leaf curling and abscission, twisting of growing shoots, and systemic root damage and may induce direct damage by causing fruit to become stunted and deformed (Baker and Turner 1916, Varn and Pfeiffer 1989, Pfeiffer et al. 1995).

Indigenous to North America (Pescott 1935, Crane et al. 1936), woolly apple aphid (Fig. 1) colonizes various flora, including mountain ash (Venables 1929, Crane et al. 1936), hawthorn, pear and quince (Carnegie 1963), and is a pest of apple in many regions of the world, including North and South America, India, South Africa, Zimbabwe, New Zealand, Australia, Iraq, and the Netherlands (Baker 1915, Pescott 1935, Schoene and Underhill 1935, Lal and Singh 1946, Carnegie 1963, Eastop 1966, Holdsworth 1970, El-Haidari et al. 1978, Brown 1986, Alspach and Bus 1999, Nicholas 2000, Mols and Boers 2001). Trees can be infested simultaneously with arboreal and edaphic (root) colonies of woolly apple aphid (Walsh and Riley 1869, Baker 1915, Pescott 1935, Lal and Singh 1946). Arboreal colonies (Fig. 2) feed in leaf axils, wounds, scars, and pruning cuts on the trunk and branches of apple trees, while edaphic colonies feed below ground on roots (Pescott 1935, Schoene and Underhill 1935, Carnegie 1963, Brown and Schmitt 1990). Feeding by arboreal colonies may cause stem splitting and early defoliation (Brown et al. 1991) (Fig. 3) and trees with woolly apple aphid infestations are more prone to perennial canker (Childs 1929, Venables 1929, Crane et al. 1936). Serious injury to apple trees can result from feeding below ground, although the presence or severity of edaphic infestations cannot be extrapolated from an arboreal infestation (Brown and Schmitt 1990, 1994).

Fig. 1. Woolly apple aphid (10.2x)

Fig. 2. Arboreal colonies of woolly apple aphid

Fig. 3. Stem splitting and early defoliation

Woolly apple aphid feeding on roots causes abnormal growths or galls (Alfieri 1920, Venables 1929, Schoene and Underhill 1935) (Fig. 4) that can reduce the uptake of water and nutrients, impair the vigor of trees (Fluke 1930, Weber and Brown 1988), and can lead to tree death (Schoene and Underhill 1935, Klimstra and Rock 1985). There are conflicting reports concerning the effect of woolly apple aphid feeding on fruit yield. Brown et al. (1995) measured trunk diameter, branch linear growth, fruit weight, number of fruit, fruit drop, and fruit set on ‘Delicious’ trees for effects from woolly apple aphid root infestations. In the first year of their study, overall yield was not reduced but there was a reduction in trunk diameter, linear growth, fruit weight, fruit set, and an increase in fruit drop, while in the second year the number of fruit was negatively related to woolly apple aphid density. Woolly apple aphid induced root galls can inhibit water conduction by over five times that of ungalled roots (Brown et al. 1991). Inhibition of water conduction by portions of the roots limits the supply of water to the rest of the tree (Brown et al. 1991). Galls may also become a source for fungal growth (Pescott 1935, Klimstra and Rock 1985, Welty and Murphy 2000) and borer attack (Pescott 1935). Potted apple trees with edaphic and arboreal colonies of woolly apple aphid began forming root galls and stem splits after eight and four weeks, respectively (Weber and Brown 1988). Brown and Schmitt (1990) showed that feeding by edaphic colonies of woolly apple aphid on ‘Delicious’ trees reduced crown length after one year and trunk diameter and scion biomass after three years. Nitrogen concentration is higher in galled than ungalled portions of roots (Brown et al. 1991), causing a nitrogen sink that reduces the concentration in leaf and shoot tissue (Weber and Brown 1988). On seedlings in South Australia, Sen Gupta and Miles (1975) found that there were more galls per unit length on roots of four-millimeter diameter than on those twice as wide and that the roots were more heavily infested than shoots. Galls may be up to three inches in length and can occur both above and below ground (Venables 1929, Pescott 1935). If galls split, the tree produces new tissue around them, but aphids can still attack this area (Venables 1929).

Fig. 4. Apple roots with galls induced by woolly apple aphid feeding on a young tree

The percentage of trees with woolly apple aphid infested roots increases as orchards age. In eastern West Virginia orchards, 79-100 % of trees at least 25 years old had edaphic woolly apple aphid infestations, with 24-84 % of roots infested (Brown 1986). The severity of root infestation is not dependent upon orchard age, but on other factors including soil, rootstock, individual site, and apple variety (Brown 1986). The heaviest edaphic infestations occur in soils that crack, such as clay, allowing the aphid access to the roots (Dumbleton and Jeffreys 1938). Although woolly apple aphid is primarily an indirect pest, direct effects on fruit may occur from their infestation of fruit cores (Crane et al. 1936, Essig 1942, Carnegie 1963) or if honeydew promotes the growth of sooty mold on fruit (Carnegie 1963, Welty and Murphy 2000).

The level of infestation varies among years and orchards (Schoene and Underhill 1935), and while woolly apple aphid infests apple trees of all ages, young orchards and nursery trees are most susceptible to injury (Schoene and Underhill 1935, Crane et al. 1936). Pescott (1935) reported that the fruit-growing industry experienced significant economic loss in Victoria, England, solely from woolly apple aphid injury. Lohrenz (1911) examined young nursery trees in mid-June and noted that 20-25 % were infested with woolly apple aphid. From 1922 to 1930, Schoene and Underhilll (1935) reported that 81.7 % of apple trees in a Richmond, VA nursery were infested with arboreal colonies of woolly apple aphid. Sherbakoff and McClintock (1935) found that a greater percentage of nursery trees, planted with galls induced by woolly apple aphid feeding on roots, were dead within six years than those apparently healthy at planting.

Biology and life history. In the mid-Atlantic region of the United States, rosy apple aphid is most prevalent in orchards from May to early July, spirea aphid from June to mid-July (Pfeiffer et al. 1995), and the two species are commonly found feeding on the same leaves. Arboreal colonies of woolly apple aphid begin to appear in mid-April, peak in mid-June, then usually decline thereafter, but may resurge in early September (Brown and Schmitt 1994). In Kansas, USA (Lohrenz 1911) and India (Lal and Singh 1946), the same temporal cycle was noted for woolly apple aphid.

Historically, woolly apple aphid was reported to alternate between apple and American elm, *Ulmus americana* L., in most of North America (Patch 1912, Schoene and Underhill 1935, Eastop 1966). American elm was considered the primary host on which sexual reproduction occurred and where woolly apple aphid eggs overwintered. In Virginia, wingless viviparous aphids, or stem-mothers, hatched in March and moved to feeding sites at leaf scars, the bases of terminal buds, and leaves. This feeding resulted in the abnormal, curled leaf condition known as a rosette. The alate progeny, or spring migrants, of stem-mothers would fly to apple between the end of April and beginning of June (Schoene and Underhill 1935). After feeding on apple through summer, alate migrants were produced in aerial colonies that returned to elm (Schoene and Underhill 1935). The progeny of these viviparous fall migrants were wingless sex forms that did not secrete woolly material or feed (Lohrenz 1911), but laid overwintering eggs (Schoene and Underhill 1935).

With the decline of *U. americana*, due to diseases such as Dutch elm disease (Stipes and Campana 1981), woolly apple aphid is probably anholocyclic on apple in most of the mid-Atlantic region of the United States (M.W. Brown, USDA-ARS, Appalachian Fruit Research Station, Kearneysville, WV, personal communication), as it is around the world (Crane et al. 1936, Dumbleton and Jeffreys 1938, Hoyt and Madsen 1960, Eastop 1966, Mueller et al. 1992). Where the life cycle is solely on apple, two forms occur during the season. The most common form is the apterous viviparous female and the other is an alate viviparous female (Schoene and Underhill 1935). After overwintering as early instars (Dumbleton and Jeffreys 1938) on limbs or roots of apple (Hoyt and Madsen 1960), crawlers ascend the tree as early as green tip but primarily around petal fall (Brown 1993) and may be found commonly at wounds and woody tissue before moving to leaf axils (Brown and Schmitt 1994). First instars may search for more than two days before settling to feed (Hoyt and Madsen 1960) but remain stationary once feeding commences (Schoene and Underhill 1935).

Eriosoma lanigerum is distinguished in the field by its production of white, woolly masses, consisting of a wax covering secreted by epithelial cells. The wax coating serves multiple purposes for the aphid colony, including preventing the aphids from being coated in honeydew that may lead to fungal attack, defense against some natural enemies, and as a protectant against UV and solar radiation (Smith 1999). Some protection against contact pesticides may be afforded by the hydrophobic nature of the wax, although the degree to which this may occur is unknown.

Chemical Control. The systemic, neonicotinoid pesticides, imidacloprid, thiamethoxam, and acetamiprid are considered to provide excellent for control of spirea and rosy apple aphid (Virginia, West Virginia and Maryland Cooperative Extension Services 2003) (Table 1). Under the 1996 Food Quality Protection Act (FQPA), the organophosphate pesticides, methyl parathion and malathion, were removed from the list of commercial materials for apple pest management. These materials were considered most effective for managing arboreal populations of woolly apple aphid (Virginia, West Virginia and Maryland Cooperative Extension Services 1999) and it has been suggested that their loss may lead to more frequent outbreaks of this pest. An outbreak of woolly apple aphid was induced in New Zealand by the use of a pyrethroid, fenvalerate, when it was substituted for the commonly used azinphosmethyl (Penman and Chapman 1980). However, in Australia, use of azinphosmethyl, carbaryl, diazinon, and chlorpyrifos also increased woolly apple aphid infestations by killing natural enemies (Nicholas 2000). At present, no materials are considered excellent for control of arboreal woolly apple aphid populations (Virginia, West Virginia and Maryland Cooperative Extension Services 2003) (Table 1) and there are no registered products for controlling edaphic colonies.

Table 1. Relative effectiveness of chemicals for apple aphid control.[1]

Trade Name	Common Name	Efficacy Rating[2] Rosy Apple Aphid	Spirea Aphid	Woolly Apple Aphid
Actara	thiamethoxam	E	E	G
Ambush	permethrin	G-E	F-G	P
Asana XL	esfenvalerate	G-E	F-G	P
Assail	acetamiprid	E	E	ND
Aza-Direct	azadirachtin	G-E	F	ND
Cygon	dimethoate	G	G	F
Danitol	fenpropathrin	G-E	F-G	ND
Diazinon	diazinon	F-G	G	F
Esteem	pyriproxyfen	E	G	ND
Lannate	methomyl	F	G	P
Lorsban	chlorpyrifos	G-E	F-G	ND
M-pede	potassium salts	F	F	ND
Provado	imidacloprid	E	E	G
Sevin	carbaryl	P	F	F
Supracide	methidathion	G-E	E	ND
Thionex	endosulfan	F-G	E	G
Vydate	oxamyl	F-G	G	ND

[1] Virginia, West Virginia and Maryland Cooperative Extension Services 2003

[2] (E=excellent; G=good; F=fair; P=poor; ND=no data)

Cultural Control. Removal of water sprouts and limiting nitrogen fertilization to the level necessary for optimal tree growth may reduce spirea aphid populations (UMass Fruit Team 2003). An important horticultural consideration in the selection of an apple rootstock is its susceptibility to woolly apple aphid (Cummins 1971, Robinson 2003, Weibel and Häseli 2003).

The Malling-Merton series of rootstocks, parented by the apple variety, Northern Spy (Pescott 1935, Knight et al. 1962), were bred for their resistance to woolly apple aphid (Sen Gupta and Miles 1975) and are currently the only recommended control for edaphic populations. However, woolly apple aphid biotypes have been found infesting resistant rootstocks in North Carolina (Rock and Zeiger 1974, Young et al. 1982), Alabama (Dozier et al. 1974), South Africa (Giliomee et al. 1968), and South Australia (Sen Gupta and Miles 1975). Furthermore, a susceptible scion grafted onto a resistant rootstock does not preclude damage to the arboreal portion of the tree (Pescott 1935). Current breeding and selection programs emphasize rootstocks that reduce the size of trees, although these rootstocks are typically susceptible to woolly apple aphid attack (Palmer et al. 1995, Robinson 2003).

Biological Control.

***Aphelinus mali*.** Native to North America, *Aphelinus mali* (Haldeman) (Hymenoptera: Aphelinidae) is an arrhenotokous parasitoid of the woolly apple aphid (Howard 1929, Pescott 1935, Cohen et al. 1996) and other species in the genus *Eriosoma* (Bodenheimer 1947). *A. mali* is the main natural enemy of arboreal woolly apple aphid colonies in North and South America, Australia, Spain, Italy, Zimbabwe, Tadzhikistan, Israel, India, Iraq, New Zealand, and the Netherlands (Venables 1929, Pescott 1935, Dumbleton and Jeffreys 1938, Lal and Singh 1946, Bodenheimer 1947, Carnegie 1963, Boldyreva 1970, LeRoux 1971, El-Haidari et al. 1978, Mueller et al. 1992, Brown and Schmitt 1994, Cohen et al. 1996, Alspach and Bus 1999, Mols and Boers 2001) and has been successfully released for woolly apple aphid control around the world (Dumbleton and Jeffreys 1938, Carnegie 1963, Boldyreva 1970, Le Roux 1971, El-Haidari et al. 1978, Verma and Singh 1985, Mueller et al. 1992). Parasitism of woolly apple aphid by *A. mali* may be increased by the flora (Boldyreva 1970) and cultural practices in the surrounding area (El-Haidari et al. 1978). *A. mali* females usually deposit one egg per aphid host (Boldyreva 1970), although up to four have been observed (Bodenheimer 1947), and lay about 100 eggs during their lives (Dumbleton and Jeffreys 1938). Percentage parasitization is greater in long, narrow colonies, where more aphids are on the periphery, and decreases with increasing colony size (Mueller et al. 1992). Parasitized aphids continue to grow (Mueller et al. 1992), but will not reproduce (Pescott 1935). *A. mali* overwinters as a larva in aphid mummies (Dumbleton and Jeffreys 1938, Evenhuis 1960, Boldyreva 1970, Mueller et al. 1992). Boldyreva (1970) reported that *A. mali* was found overwintering in edaphic colonies of parasitized aphids in Tadzhikistan, although it is unlikely these aphids were parasitized below ground (M.W. Brown, personal communication).

Factors that can limit the potential efficacy of *A. mali* include cold temperatures (Asante et al. 1993, Nicholas 2000) and its susceptibility to many of the insecticides and fungicides commonly used in apple production (Pfluger and Schmuck 1991, Cohen et al. 1996, Nicholas 2000). Active at temperatures between 16 and 37ºC (Bodenheimer 1947), *A. mali* may not provide effective control of the woolly apple aphid at the cooler temperatures occurring in the Central Tablelands of New South Wales, Australia (Nicholas 2000) or north-western Europe (Mols and Boers 2001). The developmental rate and potential fecundity of *A. mali* is increased at higher temperatures (Boldyreva 1970), but is slower than that of the aphids (Dumbleton and Jeffreys 1938). Lal and Singh (1946) reported that parasitism by *A. mali* had little impact on reducing woolly apple aphid populations in caged trees in May and June when the aphid population was at its peak. In New Zealand (Dumbleton and Jeffreys 1938) and Palestine (Bodenheimer 1947), *A. mali* reduced populations of woolly apple aphid after mid-summer, but not earlier in the season. The peak occurrence of parasitized aphids in the mid-Atlantic region occurs in mid-July (Brown and Schmitt 1994) and only minimal activity is noted earlier in the season (M.W. Brown, personal communication).

Predators. Chamaemyiids (Sanders and Knight 1968), chrysopids (Bouchard et al. 1982, Wyss 1995), and coccinellids (Lakhanpal and Raj 1998, Michaud 1999, Solomon et al. 2000, Brown 2003, 2004) are valuable natural enemies of aphids in many crop systems, including apple. Syrphidae, Cecidomyiidae, Chrysopidae, and Coccinellidae have been shown to be effective predators of the spirea and rosy apple aphid (Pfeiffer et al. 1995, Wyss et al. 1999).

Aphidophagous syrphid flies. Adult Syrphidae, commonly known as flower flies or hover flies, are identified by the "false" or spurious vein that runs between the radius and medial veins, typically across the r-m cross-vein (Metcalf 1916). Active during sunny, warm weather, syrphid flies feed on the pollen and nectar of flowering plants (Metcalf 1916). Adult activity is reduced on cloudy, rainy days and starts earlier on hot days (Maier and Waldbauer 1979b). Yellow water pan traps (Disney et al. 1982, Finch 1992, White et al. 1995, Wratten et al. 1995, Soleyman-Nezhadiyan and Laughlin 1998, MacLeod 1999) and yellow sticky traps (Hickman and Wratten 1996) have been used in phenological surveys and were effective for monitoring and trapping syrphids.

In aphidozetic species, fecundity, egg maturation, and oviposition are influenced by the availability of pollen and aphids (Cornelius and Barlow 1980, Branquart and Hemptinne 2000). Upon emergence, females require pollen feeding for ovary maturation and normal egg production (Schneider 1969). Aphidophagous female syrphids select oviposition sites based on visual and olfactory cues (Schneider 1969), as well as the abundance and quality of prey for their offspring (Kan and Sasakawa 1986, Kan 1988, Hemptinne et al. 1993). Females tend to exhibit a 'buy-futures' approach to oviposition, such that colonies of aphids with younger nymphs are more attractive than older colonies (Kan and Sasakawa 1986, Kan 1988, Hemptinne et al. 1993, Sutherland et al. 2001). Female hover flies oviposit mostly in the morning (Rojo and Marcos-García 1997) and lay a single egg, or several in succession, within or near aphid colonies (Metcalf 1916, Dixon 1959, Tamaki et al. 1967, Chandler 1968, Rotheray and Dobson 1987) in response to oviposition stimuli (Niemczyk and Pruska 1986, Sadeghi and Gilbert 1999, 2000b,c, Branquart and Hemptinne 2000). *Episyrphus balteatus* (de Geer) females lay an average of 174 eggs per day during peak oviposition and over their lifetime lay about 3900 eggs (Cornelius and Barlow 1980). Syrphid flies will oviposit in low-density colonies (Chambers 1991) and are not deterred from ovipositing by the presence of conspecific larvae (Bargen et al. 1998), larval gut contents, or eggs (Chandler 1968).

Larvae of aphidophagous syrphid flies can be important biological control agents in agroecosystems (Sanders and Knight 1968, Sharma and Bhalla 1991, Tenhumberg 1995, Wratten et al. 1995, Rojo and Marcos-García 1997, Michaud 1999, Michaud and Belliure 2001), including apple (Walsh and Riley 1869, Curran 1920, Venables 1929, Evenhuis 1960, Holdsworth 1970, Brown and Schmitt 1994). Syrphid larvae, even when few in number, can be superior competitors (Valenti et al. 1996) and are capable of effectively reducing (Metcalf 1916, Niemczyk and Pruska 1986, Tenhumberg 1995) or eliminating aphid populations (Michaud and Belliure 2001). Michaud and Belliure (2001) reported that aphids surviving attack may produce fewer apterous migrants and produce alate aphids more slowly. Peak numbers of syrphid flies tend to coincide with peak aphid populations (Joshi et al. 1999).

Aphidophagous syrphid larvae search for prey by raising the anterior portion of their body and strike in all directions until contacting prey, a behavior known as casting, and then suck the contents from the captured aphid (Bhatia 1939). Syrphid larvae pass through three instars

(Metcalf 1916, Bhatia 1939), feeding on increasingly larger aphids as they age (Heeger 1858, Hågvar 1974). The rate of aphid consumption is positively correlated with temperature, whereas total aphid consumption is inversely related to temperature, due to a decreased developmental period at higher temperatures (Soleyman-Nezhadiyan and Laughlin 1998). As larvae feed, the midgut darkens (Mitchell and Maksymov 1977) and when feeding ceases the greasy, black gut contents are expelled (Rotheray and Dobson 1987). Puparial weight, survival, and duration of the larval stage vary with fly species, climate (Bhatia 1939, Lakhanpal and Raj 1998, Michaud and Belliure 2001), aphid species (Sadeghi and Gilbert 2000a), and the quantity, mobility, and nutritive value of the aphid prey (Rüzicka 1975).

Aphidophagous Syrphidae are either generalists or specialists. Generalist predators such as *E. balteatus* (Chambers 1988, Kan 1989, Sharma and Bhalla 1991, Budenberg and Powell 1992, Mizuno et al. 1997, Sadeghi and Gilbert 2000a), *Syrphus rectus* Osten Sacken, and *Eupeodes americanus* (Wiedemann) are polyphagous (Bergh and Louque 2000), whereas specialists, like many of the members of the Tribe Pipizini, are oligo- or monophagous (Heiss 1938, Mizuno et al. 1997).

In 2000, a severe and widespread outbreak of woolly apple aphid occurred in apple orchards in the mid-Atlantic region, and Bergh and Louque (2000) reported finding numerous hover fly eggs and larvae in colonies collected between 11 June and 6 July from commercial apple orchards near Winchester, VA. *E. americanus* and *S. rectus* were common, but a third species, *Heringia calcarata* (Loew) was most abundant. *H. calcarata* belongs to the hover fly Tribe Pipizini, members of which are known to specialize on hosts that cause leaf-curling, create galls (Rojo and Marcos-García 1997) and/or produce waxy, flocculent secretions (Heiss 1938, Delucchi et al. 1957, Evenhuis 1959, Evenhuis 1966). Pipizines overwinter as third instars

(Delucchi et al. 1957, Rojo and Marcos-García 1997) and may pupariate in the soil (Heeger 1858, Heiss 1938, Brown and Clark 1960, Mitchell and Maksymov 1977).

Pipizine syrphids have been collected from arboreal and edaphic colonies of woolly apple aphid in the United States. In Illinois, Walsh and Riley (1869) identified larvae collected from edaphic colonies of woolly apple aphid on apple as a new species, which they named *Pipiza radicum* (Williston). In Maine, Metcalf (1916) reported *Pipiza pisticoides* Williston preying on arboreal colonies of woolly apple aphid. Unfortunately, the original adult specimen described by Walsh and Riley was a female and is now lost. Also, voucher specimens from Metcalf's work in Maine have not been found. Hence, neither of these records can be verified. However, Dr. F. Christian Thompson (personal communication), USDA Systematic Entomology Laboratory, Smithsonian Institute, Washington, DC believes that both of these likely refer to *H. calcarata.* Holdsworth (1970) reported *P. pisticoides* larvae preying on woolly apple aphid colonies in Ohio. *Cnemodon vitripennis* (Meigen) and *Neocnemodon elongata* Curran were reported to be important natural enemies of the woolly apple aphid in the Netherlands and Nova Scotia, respectively (Evenhuis 1959, Evenhuis 1961). Table 2 summarizes the reports of other Pipizine syrphids and their aphid prey.

Table 2. Pipizine syrphids reported from aphid species.

Syrphid Species	Prey Species	Host Plant	Citation
Pipizella heringi Zetterstedt	*Eriosoma lanuginosum* Hartig	*Malus domestica* Borkhausen	Alfieri (1920)
Cnemodon dreyfusiae Ratzeburg	*Dreyfusia piceae* Ratzeburg	*Picea excelsa* L.	Delucchi et al. (1957)
Pipizella varipes (Meigen)	*Anuraphis subterranea* (Walker)	*Pastinaca sativa* L.	Dixon (1959)
Neocnemodon auripleura (Curran)	*Myzus persicae* (Sulzer)	*Prunus persica* (L.)	Tamaki et al. (1967)
Pipiza bimaculata Meigen	*Hyperomyzus lactucae* (L.)	*Ribes nigrum* L.	Wnuk (1972)
Pipiza bimaculata Meigen	*Myzus cerasi* (F.)	*Prunus avium* L.	Wnuk (1972)
Pipiza noctiluca L.	*Phorodon cannabis* (Passerini)	*Cannabis sativa* L.	Malinowska (1979)
Pipiza noctiluca L.	*Dysaphis devecta* Walker	*Malus domestica* Borkhausen	Visnyovszky (1983)
Pipiza luteitarsis Zetterstedt	*Schizoneura* sp.	*Ulmus glabra* L.	Rotheray (1986)
Heringia heringii (Zetterstedt)	*Dysaphis plantaginea* (Passerini)	*Malus domestica* Borkhausen	Rojo and Marcos-García (1997)
Heringia heringii (Zetterstedt)	*Aphis spiraecola* Patch	*Malus domestica* Borkhausen	Rojo and Marcos-García (1997)
Heringia heringii (Zetterstedt)	*Myzus persicae* (Sulzer)	*Prunus persica* L.	Rojo and Marcos-García (1997)
Pipiza festiva Meigen	*Dysaphis plantaginea* (Passerini)	*Malus domestica* Borkhausen	Rojo and Marcos-García (1997)

In summary, woolly apple aphid is a sporadic, but potentially serious pest of apple in the mid-Atlantic region, attacking both arboreal and edaphic portions of trees. Economic injury can result from infestations of the arboreal parts of apple trees, but the most serious injury results from feeding below ground. Control of edaphic populations has been limited to resistant rootstocks that have been shown in certain areas to be susceptible to attack. Under the FQPA, the most effective chemicals for controlling arboreal colonies of woolly apple aphid have been removed from commercial use. In a recent document commissioned by the Environmental Protection Agency (EPA), further research on biological control of the woolly apple aphid was recommended (Environmental Protection Agency Workshop 1999). Given that *H. calcarata* was the most abundant syrphid fly found in colonies of woolly apple aphid in apple orchards near Winchester, VA in 2000 (Bergh and Louque 2000), the research reported here addressed aspects of the life history and predator/prey association of this previously unstudied, aphidophagous syrphid fly. Specific objectives were to:

1. Describe all life stages of *H. calcarata*
2. Determine the duration of the developmental period of all life stages
3. Examine the seasonal phenology and relative abundance of *H. calcarata* in relation to woolly apple aphid
4. Determine the utility of traps for monitoring *H. calcarata*
5. Document prey specialization of *H. calcarata* on woolly apple aphid

Chapter 2

Life History of *Heringia calcarata* (Loew) (Diptera: Syrphidae)

Introduction

Pipizine syrphids have been noted preying on both arboreal and edaphic colonies of woolly apple aphid, *Eriosoma lanigerum* (Hausmann) in the United States and other countries (Walsh and Riley 1869, Metcalf 1916, Alfieri 1920, Evenhuis 1959, Holdsworth 1970). In 2000, a severe and widespread outbreak of woolly apple aphid occurred in apple orchards in the mid-Atlantic region, and Bergh and Louque (2000) reported finding numerous hover fly eggs and larvae in colonies collected from commercial apple orchards near Winchester, VA. Two generalist aphidophagous syrphids, *Eupeodes americanus* (Wiedemann) and *Syrphus rectus* Osten Sacken were common, but a Pipizine syrphid, *Heringia calcarata* (Loew) was most abundant. There are no published data on the biology or life history of this species. Given the report by Bergh and Louque (2000) and that larvae of aphidophagous syrphid flies can be important biocontrol agents of aphid pests of apple (Walsh and Riley 1869, Curran 1920, Venables 1929, Evenhuis 1960, Holdsworth 1970, Brown and Schmitt 1994), studies to elucidate aspects of the life history and relative abundance of *H. calcarata* were initiated. This chapter reports the results of laboratory studies on the duration of development of all life stages and the voracity of *H. calcarata*, descriptions of *H. calcarata* life stages, and field studies concerning its relative abundance and seasonal phenology.

Materials and Methods

Life history studies.

Egg morphology. In 2001, eggs collected from orchards at the Alson H. Smith, Jr. Agricultural Research and Extension Center (AHS AREC) and from commercial orchards near Winchester VA, were separated based on pronounced differences in the sculpting of the chorion. Larvae emerging from those eggs were reared in large, covered petri dishes (8.9 cm diameter x 1.4 cm deep) on a diet of woolly apple aphid. Adult flies generated by these rearings were identified to species by F.C. Thompson, USDA Systematic Entomology Laboratory, Smithsonian Institute, Washington, DC. Gross descriptions and measurements of five eggs of *H. calcarata*, *E. americanus*, and *S. rectus* were made using an ocular micrometer with an Olympus SZ-ST stereomicroscope (Olympus Optical Co. Ltd., Japan) at 15x magnification. Digital photographs were taken with a Nikon Coolpix 990 camera (Nikon Corp., Tokyo, Japan) with an Olympus SZ-CTV mount (Olympus Optical Co. Ltd., Japan) under the stereomicroscope described previously.

In 2003, *H. calcarata*, *E. americanus*, and *S. rectus* eggs were photographed with a scanning electron microscope (SEM) at the USDA-ARS, Appalachian Fruit Research Station, Kearneysville, WV USA. Preparation of eggs followed protocols recommended by J.M. Ehrman, Digital Microscopy Facility, Mount Allison University, Sackville, NB Canada. Eggs were fixed in a 2.5% glutaraldehyde and 0.1M phosphate buffer solution for 1 h at 4ºC and then rinsed in this solution three times for 10 min per rinse. Eggs were then dehydrated for 10 min each in 20, 50, 70, 85, and 95% ethanol, followed by four, 10 min rinses in 100% anhydrous ethanol. Eggs were placed in a Tousimis Samdri-780A critical point drier (Tousimis Research Corp., Rockville, MD) and then placed in a Hummer VI sputter coater (Anatech LTD., Springfield, VA).

Larval, puparial, and adult morphology. Five larvae, puparia, and adult *H. calcarata* were measured with a standard metric ruler. Only lengths of newly hatched and third instars were recorded. Digital photographs of larvae, puparia, and adults were taken with the camera and stereomicroscope described previously. Voucher specimens of adult *H. calcarata*, *E. americanus*, and *S. rectus* were submitted to the Virginia Tech Insect Collection, Price Hall, Department of Entomology.

Egg developmental period. A female *H. calcarata* observed in proximity to woolly apple aphid colonies was captured on 29 June 2002 and placed in a 1.4 L plastic container with screened top. A shoot infested with woolly apple aphids was placed in the cage as a stimulus for oviposition. The cage was held in a controlled environment chamber model I-36LL (Percival Scientific, Inc., Perry, IA) at 25 ±1ºC and a photoperiod of 15:9 (L:D), and the shoot was examined at 2-h intervals to determine if eggs had been laid. Within 12 h, 20 eggs were removed from colonies using a fine-tipped probe and placed individually in small, covered petri dishes (5 cm diameter x 0.8 cm deep). Eggs were observed at 12-h intervals for eclosion.

Larval and pupal developmental period. Between 10 and 13 July 2001, *H. calcarata* eggs were collected from arboreal woolly apple aphid colonies in a commercial orchard near Winchester, VA. Eggs were monitored daily for eclosion and 23 newly hatched larvae (< 12-h-old) were placed in small petri dishes with portions of shoots containing a woolly apple aphid colony. Petri dishes were held in an environmental chamber under conditions described previously. Larvae were checked daily for survival, by gentle probing with a fine-tipped brush, and the number of days to gut voidance and pupariation was recorded. New shoots with woolly apple aphid were provided to larvae as needed until gut voidance or death. Upon gut voidance, larvae were transferred to plastic diet cups (30 ml) with moistened tissue paper to increase humidity. Diet cups were held under the conditions described previously. Puparia were checked daily and the number of days to emergence was recorded.

Adult longevity. Potted 'Gala' and 'Idared' apple trees grown in screened, shaded field cages (1.83 m wide x 1.83 m high x 3.66 m long) (Fig. 5) and infested with woolly apple aphid were placed in an orchard at the AHS AREC. After several days, shoots and branches with woolly apple aphid colonies were pruned and the colonies searched for the presence of unhatched *H. calcarata* eggs. Colonies containing eggs were placed in large, covered petri dishes and emerging larvae were reared to adulthood. Between 19 June and 3 July 2002, 15 male and 15 female flies were held individually in screened-top, cylindrical plastic cages (16 cm high x 7.5 cm diameter) placed in a flowerpot (10.2 cm diameter) ¾ full of sand and provisioned with a source of sugar water, bee pollen, and a section of apple shoot as a perch. The sand was moistened with 50 ml of deionized water. Pollen and sugar water were replaced periodically. Cages were held in an environmental chamber under the conditions described previously (see Larval duration), with the exception of a 14:10 L:D photoperiod, and monitored daily for adult survival.

Fig. 5. Field cages used to grow potted apple trees infested with woolly apple aphid.

Mating. Preliminary attempts were made under laboratory conditions to mate *H. calcarata* adults. In 2001, twenty newly emerged males and females were paired in plastic containers and held in the controlled environment chamber, described previously (see Egg developmental period). Containers were provisioned with bee pollen, sugar, water, and a portion of a shoot infested with woolly apple aphid. Mortality of flies was recorded daily and the presence of eggs deposited on shoots was recorded after each female died.

Larval voracity. Eighteen neonate *H. calcarata* larvae (<12-h-old) were placed individually in small glass dishes (1.5 cm diameter x 0.5 cm deep) and given 50, 1st and 2nd instar woolly apple aphid. Arenas were sealed with Parafilm (American National Can, Chicago, IL) and held in a controlled environment chamber under conditions described previously. Larvae were placed in new arenas provisioned with 50 aphids daily. To accommodate the growth of larvae, larger arenas (2.2 cm diameter x 1.0 cm deep) were used after the fifth day. First instar *H. calcarata* were fed small (1st and 2nd instar) aphids, second instars were fed mid-sized (2nd and 3rd instar) aphids, and third instars were fed large (3rd instar and 4th instar) aphids. The number of aphids consumed by each larva was recorded at 24-h intervals until larvae voided their black gut contents, indicating that feeding had ceased.

Seasonal phenology. Between 2001 and 2003, several sampling methods were employed to determine the seasonal phenology, voltinism, and relative abundance of *H. calcarata* in apple orchards.

Water pan traps. On 13 April 2001, water pan traps, spray-painted ‘sun yellow’ (Rust-Oleum Corp., Vernon Hills, IL), were deployed at two commercial orchards, Middle Road (var. ‘York’ and ‘Rome Beauty’) and Barley Road (var. ‘Greening’), near Winchester, VA. Six water pan traps (25 cm diameter x 4.5 cm deep) (Fig. 6a) were placed at both orchards within tree rows. At the Middle Road orchard, traps were randomly distributed throughout and at Barley Road they were placed, two per block, in three blocks (7 trees long x 4 rows wide) sprayed only with *Bacillus thuringiensis*. Traps were filled with a 9:1 solution of water:ethylene glycol and a few drops of liquid soap. All flies caught in traps were removed weekly and placed in vials for identification later. The ethylene glycol solution was replaced as needed. Water pan traps were removed from both orchards on 1 June 2001, due primarily to peeling paint. On 25 May 2001, six yellow Solo bowls (Model PSB2Y, Solo Cup Co., Urbana, IL) (15.3 cm diameter x 4.5 cm deep) (Fig. 6b) and six yellow, plastic funnel traps (10.4 cm diameter x 6.0 cm deep) (Fig. 6c) were deployed at both orchards within tree rows. Traps were distributed at each orchard, as described previously. All traps were filled with the same solution and monitored weekly, except that a clear ethylene glycol was used. Traps were removed from both orchards on 27 July 2001.

Fig. 6. Yellow A. water pan, B. Solo, and C. funnel traps deployed in 2001.

Sticky traps. In 2002, sticky traps were employed, in lieu of the pan traps described previously. At heights of 0.5 and 2.0 m, sections of PVC pipe (5.1 cm diameter x 30.5 cm long) were affixed to a 2.44 m tall wooden stake (Fig. 7). Pieces of PVC pipe (4.5 cm diameter x 30.5 cm long) were driven into the ground and the wooden stakes were wedged inside, holding them in place and vertical. Tangle-Trap (Tanglefoot Co., Grand Rapids, MI) was applied to acetate sheets (30.5 cm^2) that were wrapped around the pipe and held in place with foldback binder clips or clothespins. Ten of these traps, with PVC pipes painted 'sun yellow', were deployed at each orchard at the AHS AREC, Barley Road, and Middle Road locations. Five traps were placed inside and outside the canopy of apple trees at each orchard. Traps were checked weekly from 19 April to 2 August 2002 at the AHS AREC and Barley Road orchards and until 14 June 2002 at the Middle Road orchard. Acetate sheets were replaced weekly and all syrphid flies captured were identified to species. Stakes with PVC pipes spray-painted 'flat white' (Rust-Oleum Corp., Vernon Hills, IL) were deployed on 21 June 2002 at the AHS AREC orchard and were monitored weekly until 2 August 2002.

Fig. 7. Sticky trap used in 2002.

Emergence traps. Traps were deployed to determine if *H. calcarata* pupariate and/or overwinter in the soil or duff beneath apple trees throughout the season. On 13 April 2001, pyramidal, wood framed, screened emergence traps (91 cm^2 base x 51 cm tall) were deployed at two commercial apple orchards (Middle Road and Barley Road) near Winchester, VA.

Emergence traps were designed to funnel insects upward into a sealed, plastic bowl atop the trap containing a 9:1 solution of water: ethylene glycol and a few drops of liquid soap. Six traps were entrenched in the ground 2.5-5.0 cm deep at the base of trees at each orchard. At Middle Road, traps were randomly distributed throughout the orchard block and at Barley Road they were placed two per block in three blocks sprayed only with *B. thuringiensis*. All flies caught in the trap top were removed weekly and placed in vials for identification later. The ethylene glycol solution was replaced as needed. Traps were removed from Barley Road on 22 June 2001 and Middle Road on 29 June 2001 due to leakage from the collection bowls and damage by animals. On 6 July 2001, four emergence traps were placed at the base of trees in an orchard block sprayed repeatedly with esfenvalerate and that contained a heavy arboreal infestation of woolly apple aphid. Monitoring was performed as described previously until 17 August 2001.

On 27 April 2002, six emergence traps were deployed in an orchard at the AHS AREC (var. ‘Nittany’) and in the commercial orchard at Barley Road. The traps had been modified from the previous season to prevent leakage and for increased protection against damage from animals (Fig. 8). Traps were randomly distributed in the AHS AREC orchard and placed two per block, in three blocks at the Barley Road orchard that were sprayed only with *B. thuringiensis*. These blocks at Barley Road had been sprayed repeatedly with esfenvalerate in 2001 and had heavy woolly apple aphid infestations that year. Traps were checked weekly until 2 August 2002.

Fig. 8. Emergence trap used in 2002.

Sentinel trees. In 2002, we found that eggs of *H. calcarata* could be very efficiently collected by placing young, potted apple trees infested with arboreal colonies of woolly apple aphid in an orchard for 2-d periods. In 2003, we employed sentinel trees (Fig. 9) to monitor the seasonal phenology and relative abundance of *H. calcarata*. Potted 'Gala' and 'Idared' trees infested with woolly apple aphid were kept in screened, field cages (Fig. 5) under shaded conditions. Trees were either naturally or artificially infested with woolly apple aphid. At weekly intervals from 17 April until 24 September 2003, two trees with five or more arboreal woolly apple aphid colonies were placed inside the canopy of unsprayed trees at an orchard at the AHS AREC (var. 'Rome Beauty'). After 2 d, five colonies were pruned from each sentinel tree and examined for unhatched syrphid eggs. General weather conditions and the number of eggs of each species were recorded. Periodically, woolly apple aphid colonies were collected from trees within the cages (1 colony per tree x 5 trees) and inspected for syrphid eggs as a check for contamination.

No data were collected on 11 July or 15 August 2003 due to the fact that there were no trees with at least five woolly apple aphid colonies.

Fig. 9. Sentinel tree used in 2003 (arrows point to woolly apple aphid colonies).

Syrphid egg and larval abundance in relation to woolly apple aphid density. On 19 April 2002, a single scaffold limb on each of 10 randomly selected trees was flagged and numbered in an orchard at the AHS AREC (var. 'Nittany'). Five limbs were flagged similarly in each of three blocks in the orchard at Barley Road (var. 'Greening'). At the AHS AREC orchard, the limbs were 2.0 ± 0.16 m long, 1.3 ± 0.08 m above ground, and 18.9 ± 1.36 cm in circumference at the base. At the Barley Road orchard, the limbs were 2.2 ± 0.12 m long, 1.3 ± 0.07 m above ground, and 14.5 ± 0.75 cm in circumference. At weekly intervals from 26 April until 16 August 2002, the number of woolly apple aphid colonies on the limbs, including all side branches and water sprouts, was recorded, and the mean number of woolly apple aphid colonies per branch was calculated. After 16 August 2002, woolly apple aphid colonies were sampled bi-weekly until 30 September 2002. From 14 May until 9 August, and on 13 September 2002, 25 woolly apple aphid colonies were pruned weekly from shoots and small branches on trees at each orchard. Colonies were inspected under a stereomicroscope and the number of hatched and unhatched *H. calcarata* eggs and larvae found in each colony was recorded.

Statistical analysis. Differences between male and female adult longevity were compared using a *t*-test. The relationship between the mean number of *H. calcarata* per colony and the mean number of woolly apple aphid colonies was compared using linear regression, with *H. calcarata* as the dependent variable (PROC REG, SAS Institute 1985).

Results

Life history studies.

Egg morphology. *H. calcarata* eggs were 0.65 ± 0.004 mm long x 0.24 ± 0.002 mm wide and possessed parallel, longitudinal rows of unbroken ridges (Fig. 10a,b).

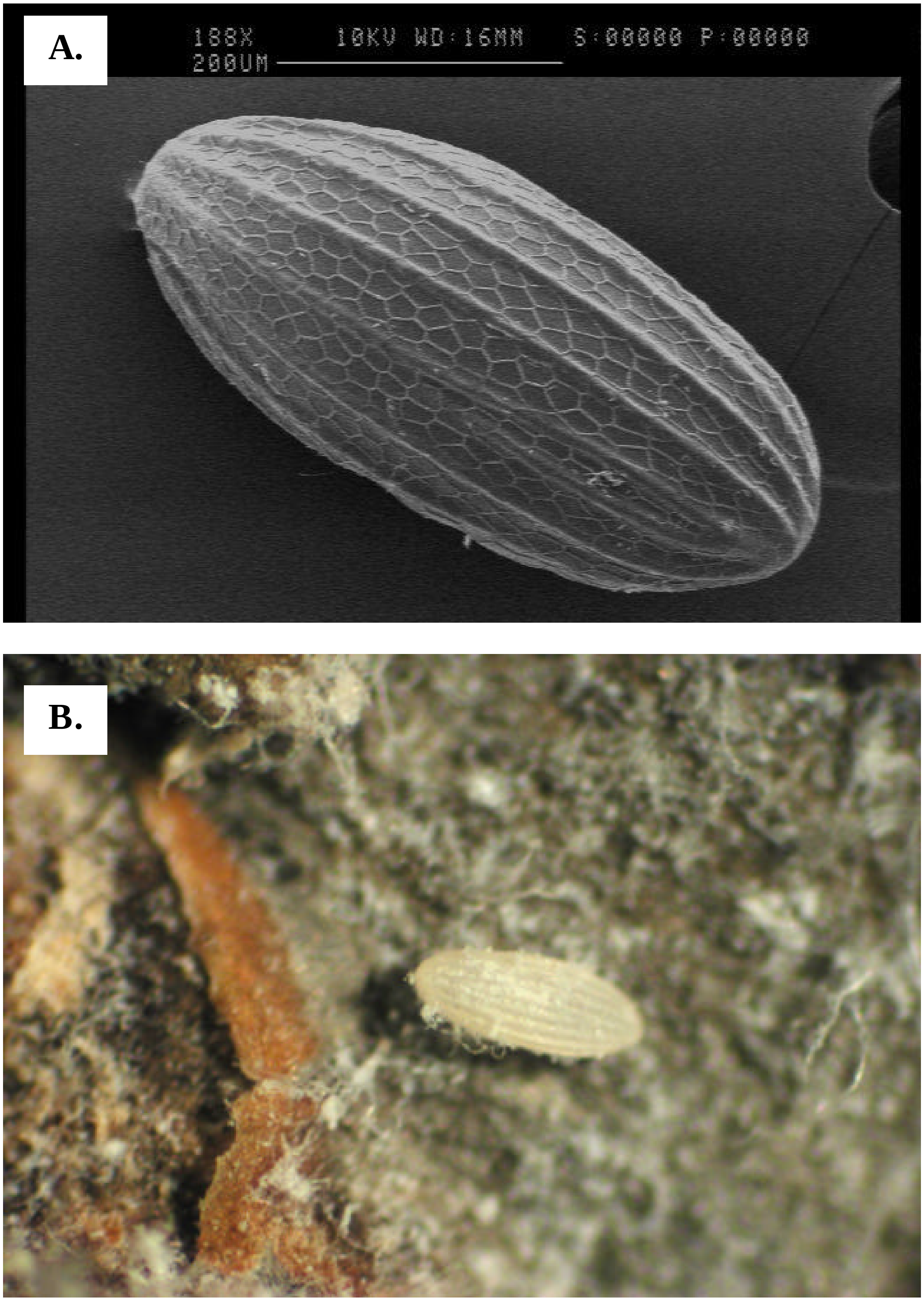

Fig. 10. A. Electron micrograph and B. digital photograph (3.5x) of *H. calcarata* eggs.

E. americanus eggs were 0.96 ± 0.002 mm long x 0.26 ± 0.002 mm wide and had longitudinal rows of short, broken ridges (Fig. 11a,b), while the surface of *S. rectus* eggs (1.19 ± 0.007 mm long x 0.45 ± 0.009 mm wide) and were covered with short protuberances (Fig. 12a,b).

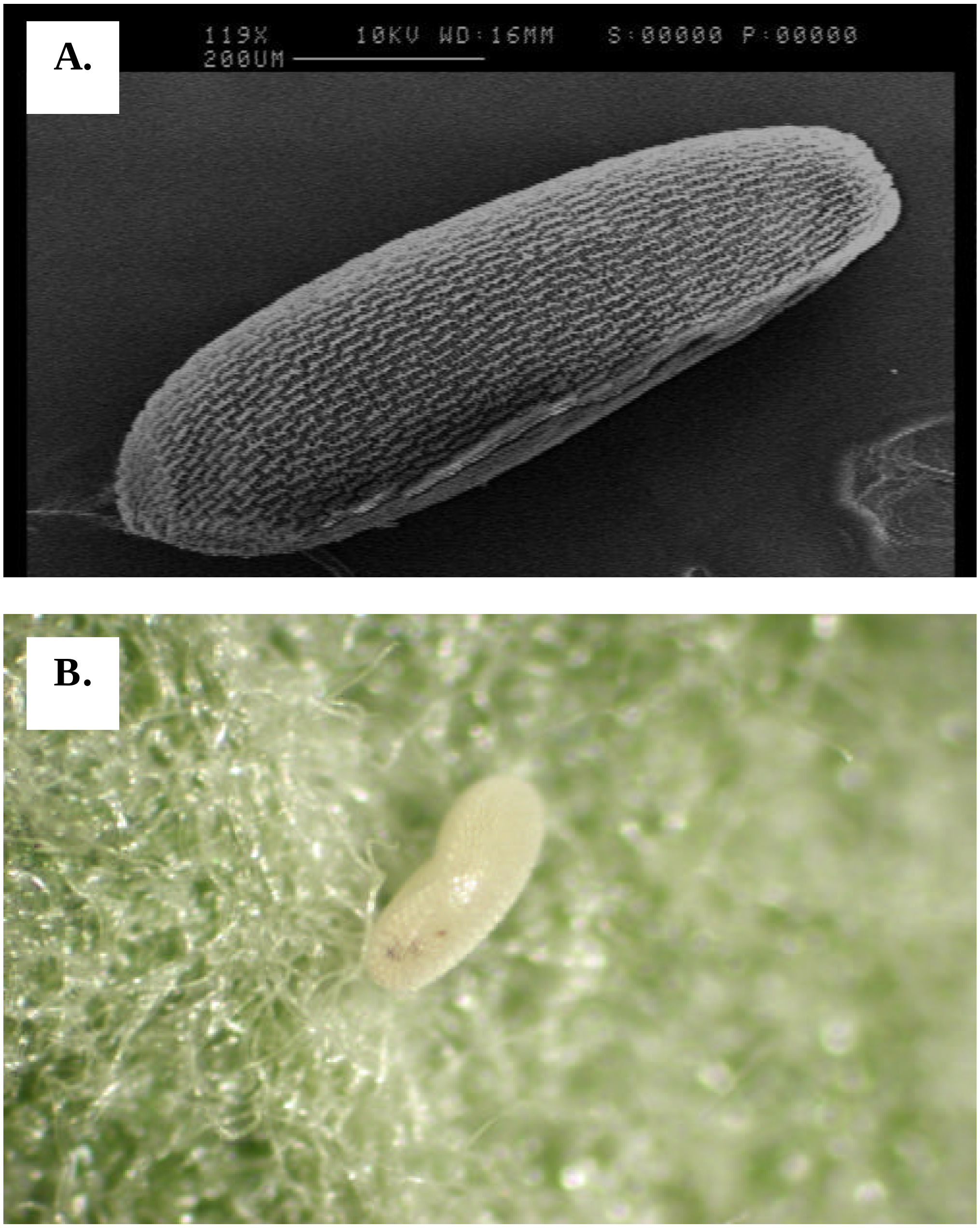

Fig. 11. A. Electron micrograph and B. digital photograph (3.5x) of *E. americanus* eggs.

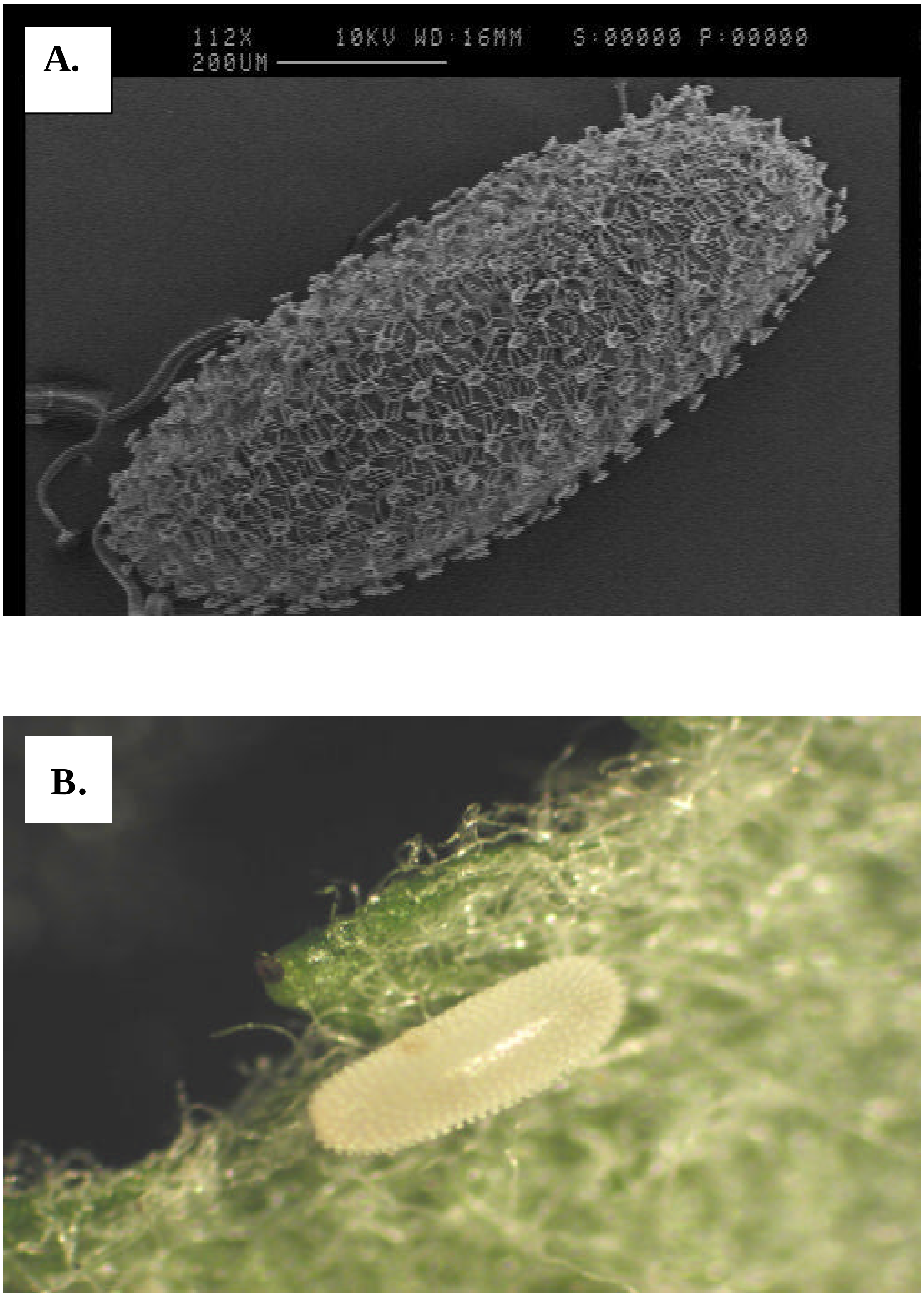

Fig. 12. A. Electron micrograph and B. digital photograph (4x) of *S. rectus* eggs.

Larval, puparial, and adult morphology. *H. calcarata* larvae were dorsoventrally flattened, changed in color from yellow/black (Fig. 13) to gray (Fig. 14) as they aged and fed, and ranged in length from 1.0 ± 0.2 mm (1st instar) to 6.5 ± 0.07 mm (3rd instar).

Fig. 13. *H. calcarata* 2nd instar (4.5x).

Fig. 14. *H. calcarata* 3rd instar before pupariation (5.9x).

Puparia were 5.0 ± 0.02 mm long x 2.0 ± 0.03 mm wide, light gray, teardrop-shaped, and became mottled closer to emergence (Fig. 15).

Fig. 15. *H. calcarata* puparium (5.9x).

H. calcarata adults are black and approximately 7.0 ± 0.05 mm from head to tip of abdomen, with a wingspan of 12.0 ± 0.03 mm. *H. calcarata* males (Fig. 16a) can be distinguished from females (Fig. 16b) by the presence of holoptic eyes and ventrally, by spurs that protrude from the hind trochanters (Fig. 17) and middle coxae.

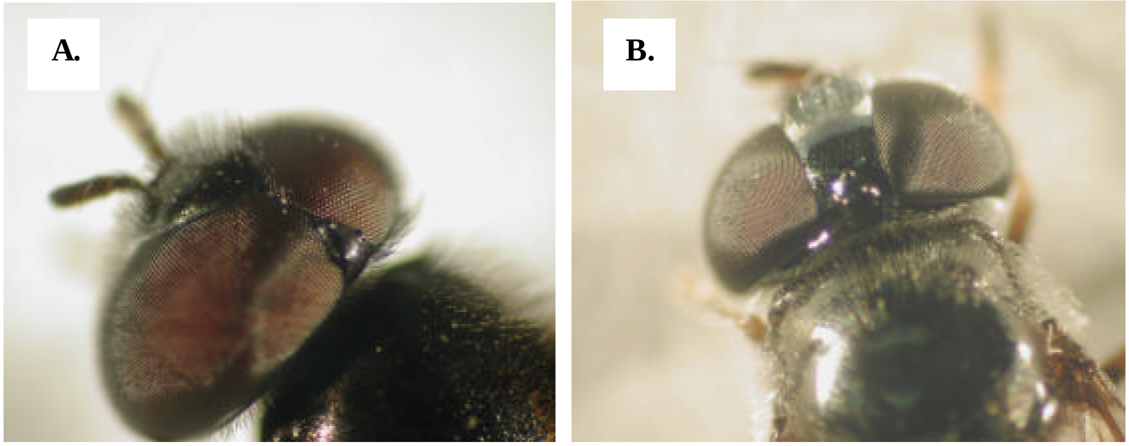

Fig. 16. A. Holoptic eyes of adult male *H. calcarata* (8.2x) and B. dichoptic eyes of adult female *H. calcarata* (8.2x).

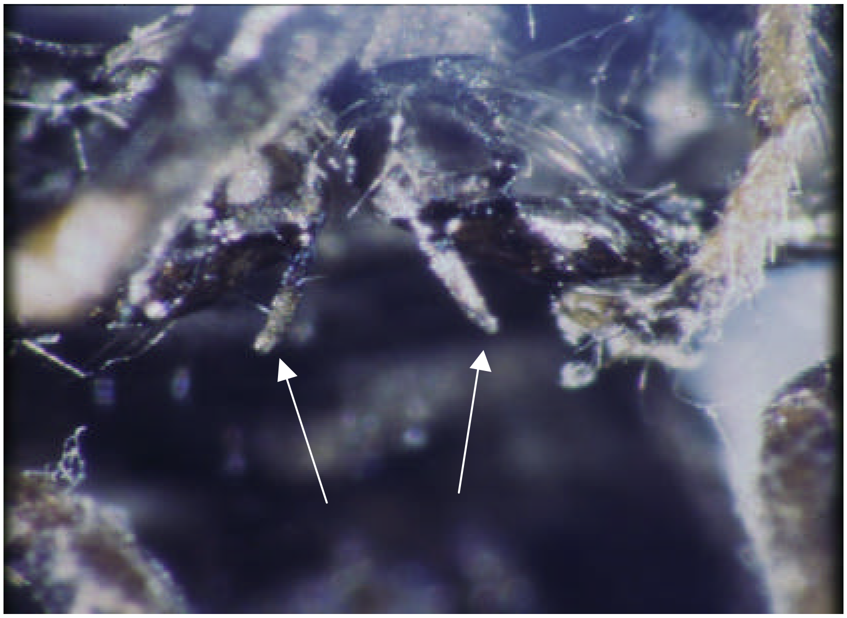

Fig. 17. Spurs on hind trochanter of adult male *H. calcarata* (64x) (arrow points to spur).

Egg, larval, pupal developmental duration, and adult longevity. The results of all measurements of the developmental periods of each life stage of *H. calcarata* are summarized in Table 3. The single gravid female captured on 29 June 2002 laid 24 eggs by 30 June 2002, all of which hatched on 3 July 2002. Under the laboratory conditions used, adult female *H. calcarata* longevity was greater than that of males ($t = 2.36$, $df = 28$, $P = 0.0254$) (Table 3).

Table 3. Developmental period of *H. calcarata* life stages.

Stage	*n*	Mean ± SEM (d)[1]
Egg	20	3.0 ± 0.08
Larva	16	7.63 ± 0.20[2]
	23	8.22 ± 0.16[3]
Pupa	23	8.74 ± 0.14
Adult	15 males	19.73 ± 2.57a
	15 females	27.80 ± 2.25b

[1] Mean values for adult longevity followed by different letters are significantly different according to a *t*-test at $P = 0.05$

[2] Time to feeding cessation based on presence of voided black gut contents

[3] Time to pupariation

Mating. No mating was observed under laboratory conditions. Adult male and female *H. calcarata* survived for 11.6 ± 1.39 and 13.6 ± 1.40 d, respectively. A total of 69 eggs were deposited on woolly apple aphid infested shoots by 11 of the 20 female *H. calcarata*, however none of the eggs were viable.

Larval voracity. Fourteen of 18 *H. calcarata* larvae reared on woolly apple aphid completed larval development and consumed 105.29 ± 1.95 SEM aphids before voiding their gut contents.

Eleven of 14 larvae voided their gut on day 7, while three did so on day 8 or 9. Figure 18 shows the mean daily aphid consumption.

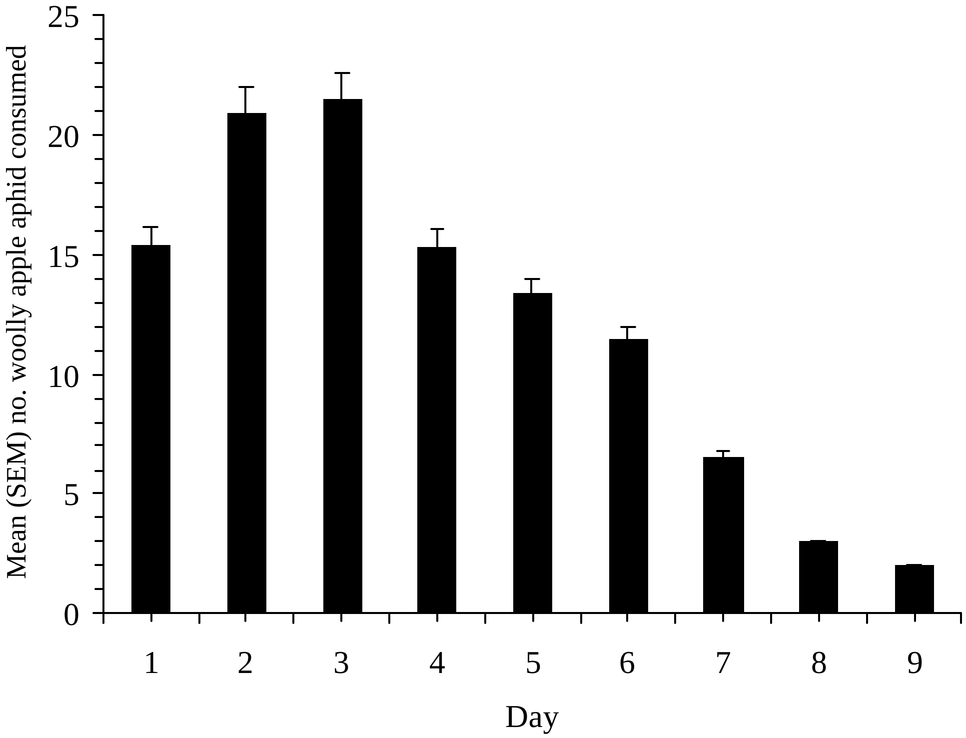

Fig. 18. Mean (SEM) number of woolly apple aphid consumed daily by *H. calcarata* larvae until gut voidance.

Seasonal phenology.

Water pan traps. Over 15 wk, yellow water pan traps at both orchards captured only 107 syrphid flies from eight species (Table 4). Due to the low number of syrphid flies in traps, no statistical analyses were performed.

Sticky traps. Yellow sticky traps captured 168 syrphid flies from six species at the three orchards, only 12 of which were *H. calcarata* (Table 4). Only eight individuals, from two species, were captured in white sticky traps, and none were *H. calcarata* (Table 4). Due to the small number of *H. calcarata* in traps, no statistical comparisons were made for the effects of trap height or location within the orchard.

Table 4. Total number of syrphid species captured in water pan traps at two orchards and yellow and white sticky traps at three orchards.

Water Pan Traps[1]	*n*	Yellow Sticky Traps[2]	*n*	White Sticky Traps[3]	*n*
Allograpta obliqua (Say)	1	*E. americanus*	39	*E. americanus*	1
E. americanus	2	*H. calcarata*	12	*Toxomerus marginatus* (Say)	7
H. calcarata	24	*Melanostoma mellinum* L.	12		
Melanostoma mellinum L.	2	*S. rectus*	4		
Platycheirus obscurus (Say)	3	*Toxomerus geminatus* (Say)	46		
S. rectus	2	*Toxomerus marginatus* (Say)	47		
Toxomerus geminatus (Say)	42	Unidentified	8		
Toxomerus marginatus (Say)	31				

[1] Water pan traps were deployed at the Barley Road and Middle Road orchards from 13 April until 27 July 2001.

[2] Yellow sticky traps were deployed at the AHS AREC and Barley Road orchard from 19 April to 2 August 2002 and Middle Road orchard from 19 April until 14 June 2002.

[3] White sticky traps were deployed at the AHS AREC orchard from 21 June to 2 August 2002.

Emergence traps. The first *H. calcarata* adult was captured in emergence traps on 25 May and 17 May in 2001 and 2002, respectively. In 2001, a total of 30 *H. calcarata* adults were captured over 17 wk. Twenty-six of those were caught between 13 July and 17 August in the block sprayed with esfenvalerate, where trees were heavily infested. In 2002, only three *H. calcarata* were caught between 27 April and 2 August at the two orchards.

Sentinel trees. No syrphid fly eggs were found from four samples of five woolly apple aphid colonies taken periodically from trees within the cages. Syrphids laid eggs very near or inside colonies of woolly apple aphid, and 52 percent (120 of 230) of all woolly apple aphid colonies contained at least one unhatched syrphid egg. A total of 163, 92, and 3, *H. calcarata*, *E. americanus*, and *S. rectus* eggs were collected from 230 woolly apple aphid colonies, respectively, between 19 April and 26 September 2003. From 19 April through 10 May 2003, *E. americanus* was the most abundant species in woolly apple aphid colonies (Fig. 19) but thereafter, when rosy apple aphid and spirea aphid colonies were abundant in orchards, few *E. americanus* eggs were found. Unhatched eggs of *H. calcarata* were first collected on 26 April and were most abundant in mid to late June and again in late August (Fig. 19). Fifty-eight percent (45 of 78) of colonies with *H. calcarata* eggs contained 2 or more eggs, with a maximum of eight in one colony. Over 10 percent (15 of 120) of colonies with syrphid eggs contained both *H. calcarata* and *E. americanus* eggs.

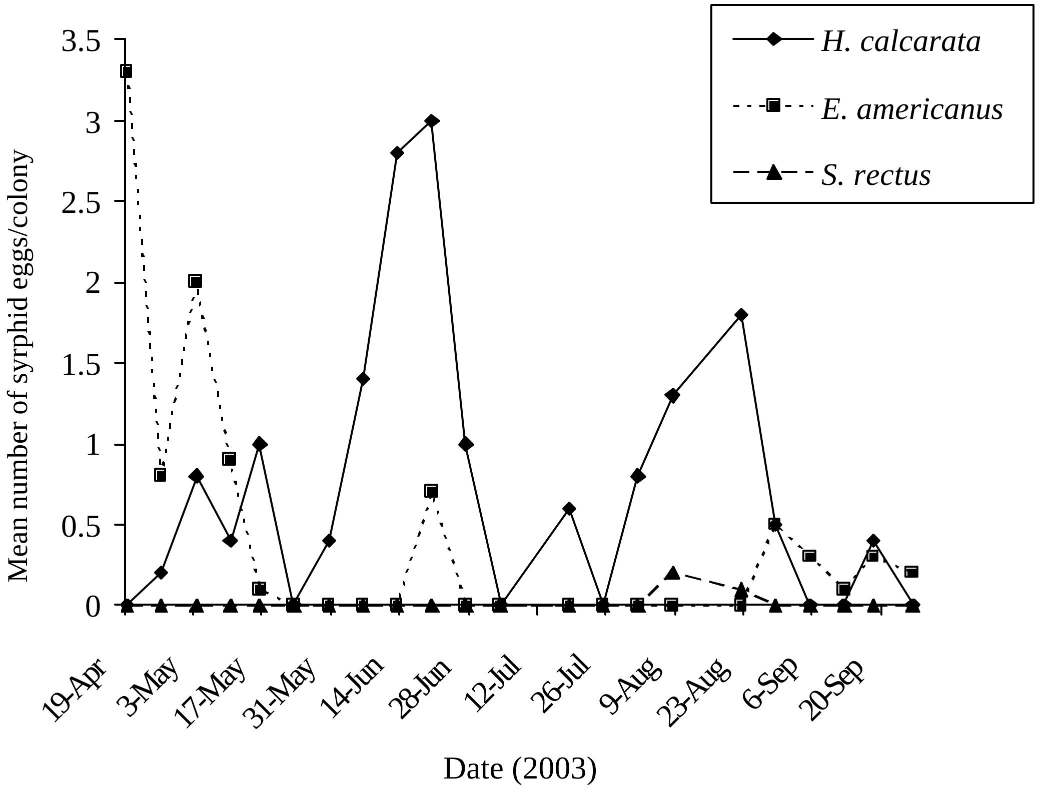

Fig. 19. *H. calcarata*, *E. americanus,* and *S. rectus* egg distribution from sentinel trees at the AHS AREC.

Syrphid egg and larval abundance in relation to woolly apple aphid density. At the AHS AREC, the number of colonies per branch began to rise during the last week of May 2002, and continued this trend until the beginning of August (Fig. 20b). At Barley Road, woolly apple aphid density was greatest in mid-June, late July, and mid-September (Fig. 20a). Colony density varied between 0 and 18 per branch and 0 and 14 per branch throughout the season at the AHS AREC and Barley Road orchard, respectively. At the AHS AREC orchard there was an inverse relationship ($P = 0.003$) between the mean number of *H. calcarata* per colony and the mean number of woolly apple aphid colonies per branch (Fig. 21a). There was no relationship ($P = 0.97$) between the mean number of *H. calcarata* per colony and the mean number of woolly apple aphid colonies per branch at the Barley Road orchard (Fig. 21b). In total, 207 *H. calcarata* eggs and 43 larvae were collected from both orchards. *H. calcarata* egg and larval abundance peaked on 24 May 2002 at both orchards (Fig. 20a,b).

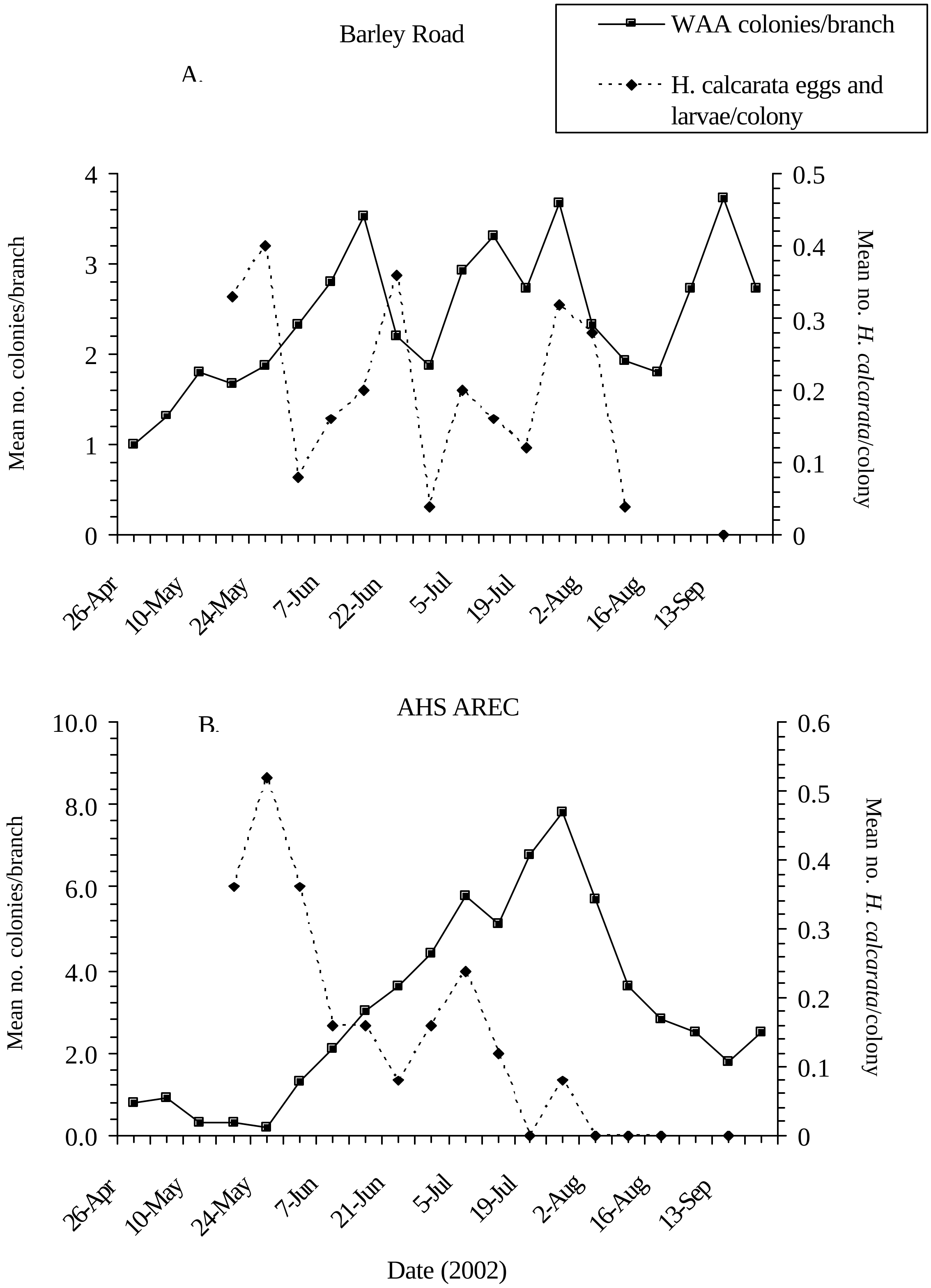

Fig. 20. Mean number of woolly apple aphid colonies per branch and *H. calcarata* per colony at the Barley Road (A.) and the AHS AREC orchards (B.).

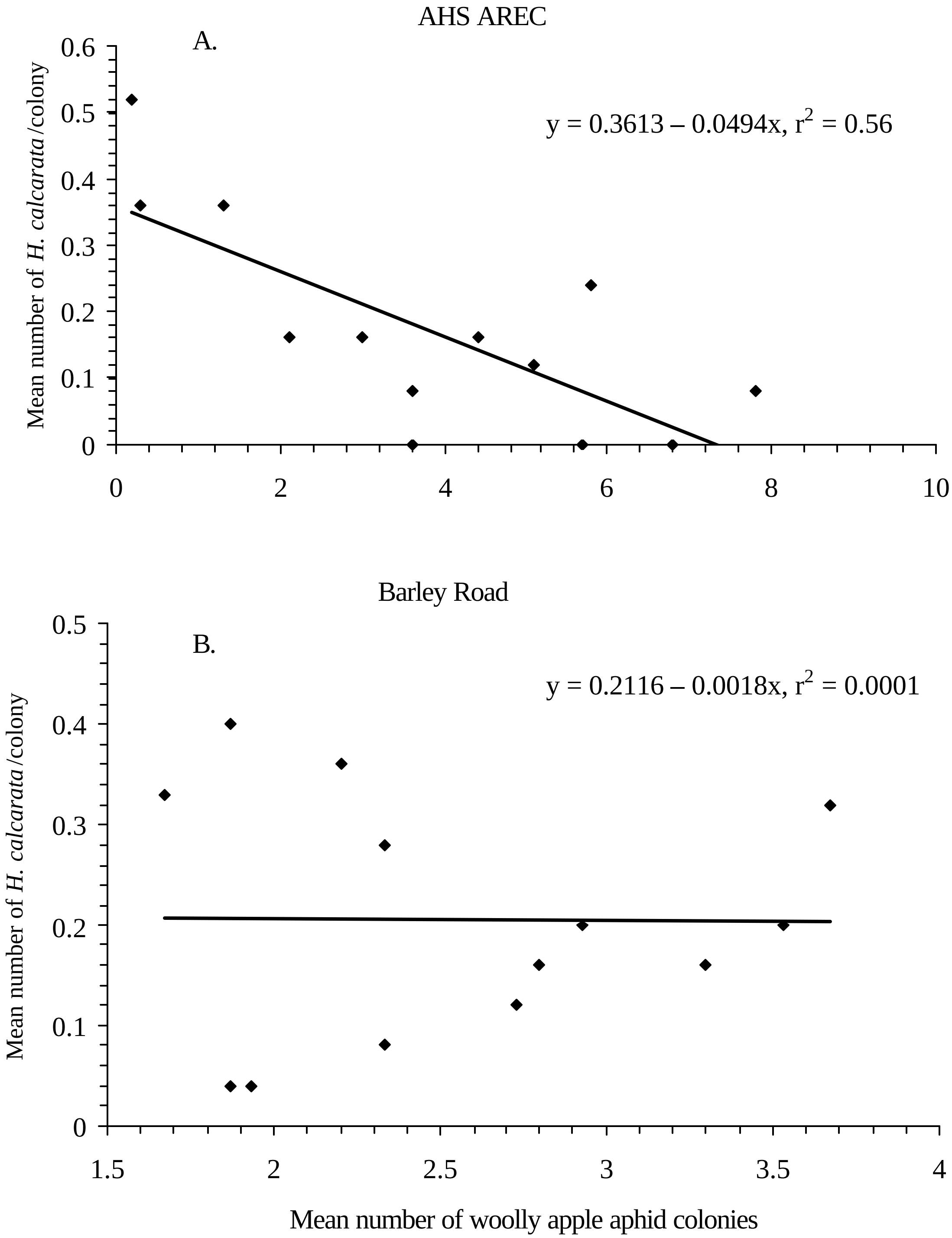

Fig. 21. Relationship between the number of *H. calcarata* per colony and the number of woolly apple aphid colonies per branch at the AHS AREC (A.) and Barley Road orchards (B.) in 2002.

Discussion

Marked differences in the chorionic sculpturing of eggs occur among *H. calcarata*, *S. rectus*, and *E. americanus*. This finding was fortuitous in that it afforded us a way by which to readily differentiate among these species. In the absence of an ability to mate *H. calcarata* in captivity, these morphological differences provided the means to collect and identify *H. calcarata* for laboratory-based life history studies. Furthermore, unhatched eggs were the most reliable sampling unit in field studies of seasonal phenology. However, since the chorionic sculpturing of eggs may be similar across hover fly species and genera (Chandler 1968, Kan 1988, Kula 1993), the morphological differences that we have documented only pertain, at this point, to eggs found in the Virginia apple ecosystem. Eggs of *H. calcarata* possess parallel rows of unbroken, longitudinal ridges. This description is similar to that for other Pipizine syrphids, including *P. heringi* (Alfieri 1920) and *C. dreyfusiae* (Delucchi et al. 1957), but in contrast to Valenti et al. (1996), who reported that eggs of a *Heringia* sp. possess no apparent ridges or chorionic sculpturing. Our measurements and general descriptions of the other stages of *H. calcarata* are similar to those reported by Brown and Clark (1960) for another Pipizine syrphid, *Neocnemodon coxalis* (Curran). They reported a mean larval length from 1.5 mm (1st instar) to 5.83 mm (3rd instar), with a maximum of 6.40 mm, and described the larva as dorsoventrally flattened and uniformly gray or reddish-brown in color. Puparia were 4.5 mm long x 1.9 mm wide, elongate-oval, and dull blackish in color. The adults ranged in length from 6 to 7 mm and were black in color.

The duration of the developmental period of *H. calcarata* eggs compared favorably with those of two other Pipizine syrphids (Rojo and Marcos-García 1997). At approximately 20ºC, both *H. heringii* and *P. festiva* remained in the egg stage for 2 to 3 d. At 25ºC, the period of *H.*

calcarata larval and pupal development was shorter than reported for other Pipizine syrphids. At 20ºC, the developmental period for *H. heringii* and *P. festiva* larvae was 15 to 20 d, and the pupal developmental period was 13 to 15 d and 15 to 20 d, respectively. Similarly, Heeger (1858) reported that the developmental periods of *Pipiza vitripennis* Meigen and *Pipiza varipes* Meigen were more than 15 d, although temperature was not reported. Differences in the duration of the developmental periods reported may be affected by fly species, climate (Bhatia 1939, Lakhanpal and Raj 1998, Soleyman-Nezhadiyan and Laughlin 1998, Michaud and Belliure 2001), aphid host (Sadeghi and Gilbert 2000a), and the quantity, mobility, and nutritive value of the prey species (Rüzicka 1975, Cornelius and Barlow 1980). Under the laboratory conditions used in these studies, the longevity of adult female *H. calcarata* was greater than that of males, but shorter than reported for other syrphids. Overwintered, gravid female *E. balteatus* lived for an average of 42.6 d at 18ºC (Kan 1988) and *Eristalis tenax* (L.) adults survive for up to four months under ambient conditions (Gladis 1994).

Total aphid consumption by *H. calcarata* was lower than has been reported for some syrphids studied, but comparable to others. In laboratory feeding studies in which 3rd instar *Acyrthosiphon pisum* (Harris) and *Megoura crassicauda* Mordvilko were offered simultaneously, an average of 85.5, 115.2, and 94.0 aphids were consumed by larvae of *E. balteatus, Metasyrphus frequens* Matsamura, and *Syrphus vitripennis* (Meigen), respectively (Kan 1989). Sharma and Bhalla (1991) fed first instars of *Scaeva pyrastri* L., *Metasyrphus confrater* (Wiedemann), and *E. balteatus* with first and second instar *Brevicoryne brassicae* L., *M. persicae*, and *Lipaphis erysimi* K. Second and third instar hover flies were fed third and fourth instar aphids. *S. pyrastri* consumed a total of 398, 521, and 431 of the preceding aphids, respectively. *M. confrater* consumed a total of 323, 527, and 381 and *E. balteatus* devoured 235, 269, and 285 aphids, respectively. Due to the sessile nature of the woolly apple aphid (Mueller et al. 1992) and the fact that female *H. calcarata* deposit eggs in close proximity to colonies, the aphid consumption we measured in the laboratory may be similar to that which occurs in the field. In contrast to many studies reporting that syrphid larvae consume most aphids in the 3rd instar (Kan 1989, Sharma and Bhalla 1991, Kumar et al. 1996, Debaraj and Singh 1998, Soleyman-Nezhadiyan and Laughlin 1998, Belliure and Michaud 2001, Hindayana et al. 2001), the majority of woolly apple aphid consumption by *H. calcarata* larvae, under the conditions of this study, occurred within the first 3 d of the larval developmental period.

In 2001, yellow water pan traps were deployed at two commercial orchards to examine the phenology and voltinism of *H. calcarata.* Syrphid flies were observed commonly in orchards and while these traps did catch adult syrphid flies, *H. calcarata* was captured too infrequently and in numbers too small to accurately represent abundance in the field. Furthermore, we experienced numerous difficulties with water pan traps including fading, peeling paint, animal damage, and leaks. Unlike other agricultural ecosystems (Disney et al. 1982, White et al. 1995, Wratten et al. 1995, Hickman and Wratten 1996, Soleyman-Nezhadiyan and Laughlin 1998, MacLeod 1999), we conclude that yellow water pan traps are not effective in this system, possibly due to their shaded position within the orchard, contamination by mud and dirt from rain, and/or lack of appropriate visual stimuli.

Similarly, yellow and white sticky traps caught very few syrphid flies in our orchards. Hickman and Wratten (1996) used yellow sticky traps to capture syrphid flies in cereal fields and, in one week, caught over 10x the number of flies captured in our traps over 15 wk. Differences may have occurred because our study used cylindrical sticky traps, while Hickman and Wratten (1996) used flat (25 cm^2) sticky cards. *H. calcarata* adult females likely use the white, flocculent wool produced by woolly apple aphids as one visual cue in host location. Therefore, we used cylindrical, white sticky traps as, perhaps, a supernormal stimulus, however these proved to be even more ineffective than the yellow sticky traps.

Emergence traps were deployed in orchards to determine if *H. calcarata* pupariated and/or overwintered beneath apple trees. *H. calcarata* adults were captured in emergence traps early in the season, although the majority (26 of 30) were captured in July and August beneath trees that supported heavy arboreal woolly apple aphid infestations. These data indicate that *H. calcarata* pupariated in the duff or soil beneath apple trees, although it is unclear as to whether these adults were from larvae that had preyed on arboreal or edaphic populations of woolly apple aphid. The data also suggest that some *H. calcarata* overwinter beneath apple trees.

The most promising method for phenological surveys of *H. calcarata* involved the use of sentinel trees. Since larvae of some hover fly species may move away from colonies during the day (Rotheray 1989, Hickman and Wratten 1996), pupariation may occur in the soil (Heeger 1858, Heiss 1938, Brown and Clark 1960, Mitchell and Maksymov 1977), and adult flies were not trapped reliably in our studies, unhatched eggs were the best sampling unit for the syrphid species we encountered most frequently. *E. americanus* was most abundant in woolly apple aphid colonies early in the season, when spirea and rosy apple aphid populations were at very low levels. During the period of peak abundance of spirea and rosy apple aphid, *E. americanus* eggs were rarely found in woolly apple aphid colonies and eggs of *H. calcarata* were most abundant. Future work on the seasonal phenology of syrphid flies, employing the use of sentinel trees, should begin earlier in the season than in this study, given that the greatest number of *E. americanus* eggs were found on the first sample date. In 2003, we experienced an unusually wet and cool spring. Given that hover flies are known to be most active during sunny, warm weather

(Metcalf 1916, Maier and Waldbauer 1979b), our data likely underestimate the relative abundance of syrphid flies. While our data do not allow an unequivocal interpretation of the voltinism of *H. calcarata*, it is undoubtedly multivoltine, given its presence early in the season and the rates of development that we have established. Since, the effectiveness of *A. mali* is limited by cooler temperatures, predation by *H. calcarata* and *E. americanus* larvae is likely extremely important for biological control of woolly apple aphid early in the season.

In 2002, *H. calcarata* abundance was greater at the more heavily infested commercial orchard (Barley Road) than at the AHS AREC, and there appeared to be some density dependence. In 2003, arboreal woolly apple aphid populations were, in general, very low in commercial orchards, and in the orchard at the AHS AREC where sentinel trees were deployed. Periodic evaluations of trees in that orchard made between 2 June and 13 August 2003 revealed mean numbers of woolly apple aphid colonies per 5-min count ranging from 0.25 to 2.25 colonies per tree. However, numerous *H. calcarata* eggs were collected from colonies on sentinel trees, suggesting that *H. calcarata* may have survived on edaphic colonies and/or on an unknown alternate host. The abundance of *H. calcarata* eggs found in arboreal colonies may also underestimate the population if eggs are also laid near roots of trees, as is seen in other Pipizine syrphids (Heeger 1858, Dixon 1959).

Since we were unable to successfully mate *H. calcarata* under laboratory conditions and did not observe mating in the field, we could not generate data regarding the fecundity of gravid females. Eggs were deposited by *H. calcarata* females paired with males, but were not viable.

The impact of *H. calcarata* as a biological control agent of woolly apple aphid in the field is not yet understood. We did not attempt to evaluate the impact that *H. calcarata* feeding would have on the growth or extinction of future colonies. If *H. calcarata* is a specialist predator of woolly apple aphid in the mid-Atlantic apple ecosystem, we might expect a negative numerical response representing the co-evolution of predator and prey, which was the case at the AHS AREC. This relationship may suggest that the number of woolly apple aphid colonies was reduced in the field when *H. calcarata* was most abundant.

Chapter 3

Specialization of *Heringia calcarata* (Loew) (Diptera: Syrphidae) on woolly apple aphid (Homoptera: Eriosomatidae)

Introduction

Aphidophagous syrphid larvae may be polyphagous (Metcalf 1916), oligophagous, or monophagous (Heiss 1938, Mizuno et al. 1997) in their feeding habits. In Virginia apple orchards, the most commonly encountered aphidophagous syrphids are the generalists, *Syrphus rectus* Osten Sacken and *Eupeodes americanus* (Wiedemann), and a putative specialist, *Heringia calcarata* (Loew) (Bergh and Louque 2000). *H. calcarata* belongs to the hover fly Tribe Pipizini, members of which are known to specialize on hosts that cause leaf-curling, create galls (Rojo and Marcos-García 1997) and/or produce waxy, flocculent secretions (Heiss 1938, Delucchi et al. 1957, Evenhuis 1959, Evenhuis 1966), as does woolly apple aphid. The predator/prey association between *H. calcarata* and woolly apple aphid, *Eriosoma lanigerum* (Hausmann), has not been studied previously. This chapter reports the results of laboratory feeding studies and field surveys that investigated the specialization of *H. calcarata* on woolly apple aphid. Laboratory experiments used no-choice feeding bioassays to examine the effect of pure diets of woolly apple aphid, spirea aphid, and rosy apple aphid on several measures of the performance of *H. calcarata* larvae. Choice-test feeding bioassays examined the prey preference exhibited by naïve, neonate *H. calcarata* larvae. Field surveys quantified the distribution of eggs of the three most common syrphid predators among colonies of woolly apple aphid, spirea aphid, *Aphis spiraecola* Patch, and rosy apple aphid, *Dysaphis plantaginea* (Passerini).

Materials and Methods

Insects. Potted 'Gala' and 'Idared' apple trees were grown in screened, shaded, field cages (1.83 m wide x 1.83 m high x 3.66 m long) (Fig. 5) and artificially infested with woolly apple aphid. Trees were positioned within the canopy of trees in an orchard at the Alson H. Smith, Jr. Agricultural Research and Extension Center (AHS AREC) that supported a resident population of woolly apple aphid. Trees were placed in the orchard for 2-d intervals in June, July, and August 2002, after which branch sections with individual woolly apple aphid colonies were pruned from the trees and inspected for unhatched *H. calcarata* eggs using a dissecting microscope at a magnification of 15x. Eggs of *H. calcarata* were distinguished by the sculpturing of the chorion (see Chapter 2). Eggs were removed from colonies using a fine-tipped probe, placed in small, covered petri dishes (5 cm diameter x 0.8 cm deep) and observed frequently for eclosed larvae. Unhatched eggs were stored in a refrigerator at 4ºC until the following day.

Woolly apple aphids used in feeding studies were collected from potted 'Gala' and 'Idared' apple trees grown in the field cages described previously. Spirea and rosy apple aphids used in feeding studies were collected from minimally sprayed orchards at the AHS AREC and from the Barley Road orchard (see Chapter 2).

No-choice feeding study. Sixty neonate larvae (<12-h-old) were placed individually in small, round glass dishes (1.5 cm diameter x 0.5 cm deep) and fed, *ad libitum,* pure diets of woolly apple aphid, rosy apple aphid, or spirea aphid (20 larvae per diet). Arenas were sealed with Parafilm (American National Can, Chicago, IL) and placed in a controlled environment chamber Model I-36LL (Percival Scientific, Inc., Perry, IA) at 25 ±1ºC and a photoperiod of 14:10 L:D.

Larval survival was recorded at 24-h intervals and surviving larvae were placed in new arenas provisioned with new aphids. To accommodate the growth of larvae, larger arenas (2.2 cm diameter x 1.0 cm deep) were used after the fifth day. The cessation of feeding was indicated when larvae voided their black gut contents. For those larvae completing development we recorded the duration of the period from the larval stage to pupariation, pupal developmental periods, and larval weight after feeding cessation. After emergence and sclerotization, adults were placed in a refrigerator at 4ºC, to slow movement, and then weighed with an analytical balance Model AB54-S (Mettler-Toledo International, Inc., Switzerland).

Choice-test feeding study. Forty-five neonate larvae (<12-h-old) were placed individually in the small glass dishes described above and assigned to one of three diets consisting of a pair of aphid species. Each dish contained 25 young aphids of each species (i.e. 50 aphids per pairing). Arenas were sealed with Parafilm and held in a controlled environment chamber under conditions described previously. At 24-h intervals for 48 h, larvae were placed in new dishes with aphids. After each 24-h interval we recorded the number of each aphid species consumed by each larva and the number of live and dead aphids (i.e. not consumed) of each species remaining in each dish.

Distribution of hover fly eggs. At weekly intervals from 14 May to 6 August 2002, 25 woolly apple aphid colonies were pruned from shoots and small branches from orchards (var. 'Nittany' and 'Rome Beauty') at the AHS AREC and from the Barley Road orchard (var. 'Greening'). Twenty-five leaf clusters with rosy apple aphid and 25 with spirea aphid colonies were also collected from orchards at the AHS AREC from 20 May to 2 July and at Barley Road between 10 June and 16 July. Colonies had at least five, and usually many more aphids. Each colony was examined under a dissecting microscope and the number of hatched and unhatched eggs of *H. calcarata*, *E. americanus* and *S. rectus* was recorded.

Statistical analysis. A 2 x 2 contingency table analysis was used to compare the number of larvae that completed development and emerged as adult flies on each pure diet of aphids (PROC FREQ, SAS Institute 1985). The duration of larval and pupal developmental periods and larval and adult weights were compared between diets of woolly and rosy apple aphid using a pooled t-test. For the choice test feeding study, the total number of aphids eaten was compared within each aphid diet using a log-linear model (PROC CATMOD, SAS Institute 1985). The number of hatched and unhatched eggs of each syrphid species collected from woolly apple aphid colonies was compared within sample locations using a log-linear model (PROC CATMOD, SAS Institute 1985). All statistical comparisons were considered significant at the 5% probability level.

Results

No-choice feeding study. Survival of *H. calcarata* larvae was greater ($c^2 = 8.120$, $df = 1$, $P = 0.004$) on a pure diet of woolly apple aphid (n=17) than on rosy apple aphid (n=9). No larvae survived on a pure diet of spirea aphid. The duration of larval development (days) was shorter ($t=2.149$, $df = 24$, $P = 0.04$) on a pure diet of woolly apple aphid (8.29 ± 0.19 SEM) than on rosy apple aphid (9.11 ± 0.39 SEM). The duration of the larval developmental period on woolly apple aphid was comparable to results from 2001 (Chapter 2, Table 3).

Mean weight (g) of third instars that had ceased feeding was greater ($t = 6.701$, $df = 2\ 3$, $P < 0.0001$) on a diet of woolly apple aphid (n = 16, 0.017 ± 0.0004 SEM) than on rosy apple aphid (n = 8, 0.013 ± 0.0005 SEM). There was no significant difference between the mean duration of pupal development (days) ($t = 0.575$, $df = 19$, $P = 0.572$) on a diet of woolly apple aphid (n =15, 8.33 ± 0.15 SEM) or rosy apple aphid (n = 6, 8.50 ± 0.20 SEM) or between adult weights (g) ($t = 1.138$, $df = 19$, $P = 0.269$) on woolly apple aphid (n = 15, 0.0083 ± 0.0002 SEM) or rosy apple aphid (n = 6, 0.0078 ± 0.0003 SEM).

Choice-test feeding study. Naïve *H. calcarata* larvae given a choice of aphid prey that included woolly apple aphid always consumed more woolly apple aphid than rosy apple aphid ($?^2 = 98.43$, $df = 1$, $P < 0.0001$) or spirea aphid ($?^2 = 95.67$, $df = 1$, $P < 0.0001$) (Table 5). When offered rosy apple aphid and spirea aphid, larvae consumed more rosy apple aphid ($?^2 = 40.47$, $df = 1$, $P < 0.0001$). Aphid mortality did not appear to influence the outcome of the tests. Over the 48-h test period, the mean ± SEM number of aphids remaining alive were as follows: woolly apple aphid/rosy apple aphid, 20.8 ± 1.3 and 27.6 ± 1.7, respectively; woolly apple aphid/spirea aphid, 20.6 ± 2.1 and 23.6 ± 2.0, respectively; rosy apple aphid/spirea aphid, 19.6 ± 1.8 and 25.4 ± 2.2, respectively.

Distribution of hover fly eggs. Weekly counts of the number of hatched and unhatched eggs on woolly apple aphid colonies showed that *H. calcarata* was the most abundant syrphid fly in both orchards ($?^2 = 80.23$, $df = 1$, $P < 0.0001$). *H. calcarata* eggs were not found in rosy apple aphid or spirea aphid colonies, whereas eggs of *E. americanus* and *S. rectus* were found in woolly apple aphid, rosy apple aphid, and spirea aphid colonies (Fig. 22).

Table 5. Aphid consumption by *H. calcarata* larvae in pairwise comparisons over 48 h

	Mean ± SEM number of aphids consumed[1]			
Aphid Pairing	Woolly apple aphid	Rosy apple aphid	Spirea aphid	n[2]
Woolly apple aphid/spirea aphid	15.7 ± 1.33a		3.0 ± 0.45b	11
Woolly apple aphid/rosy apple aphid	19.6 ± 1.30a	7.4 ± 0.54b		14
Rosy apple aphid/spirea aphid		12.3 ± 1.84a	4.5 ± 0.92b	10

[1] Means within rows followed by the same letter are not significantly different according to the log-linear model at the $P = 0.05$ level.

[2] n = number of larvae alive after 48 h.

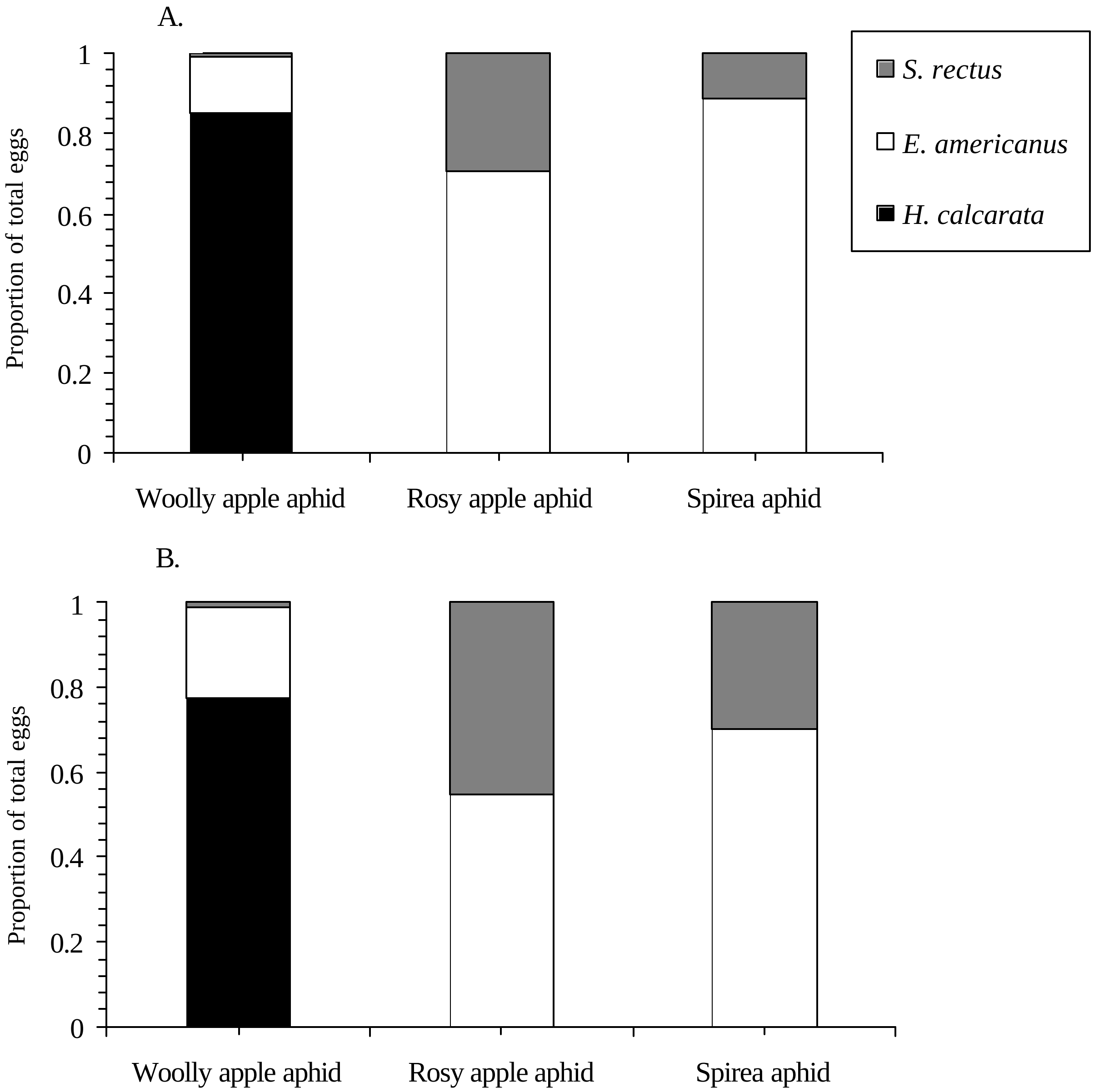

Fig. 22. Distribution of syrphid eggs collected weekly from 25 woolly apple aphid, rosy apple aphid, and spirea aphid colonies between 14 May and 6 August, 20 May and 2 July, and 10 June and 16 July 2002, respectively at the AHS AREC (A.) and Barley Road (B.) orchards. Percentages at the AHS AREC are based on 110, 108, and 27 syrphid eggs collected in woolly apple aphid, rosy apple aphid, and spirea aphid colonies, respectively. Percentages at the Barley Road orchard are based on 146, 62, and 27 syrphid eggs collected in woolly apple aphid, rosy apple aphid, and spirea aphid colonies, respectively.

Discussion

Our laboratory and field data strongly suggest that *H. calcarata* is a specialist predator of the woolly apple aphid in apple orchards in the mid-Atlantic region. While *H. calcarata* can complete development on a pure diet of rosy apple aphid, more larvae completed development on woolly apple aphid, the duration of their developmental period was shorter, and their weight was greater than when reared on a diet of rosy apple aphid. When offered a choice of aphid prey, naïve *H. calcarata* larvae always consumed more woolly apple aphid. No larvae completed development on a pure diet of spirea aphid and it was clearly a poor resource. Belliure and Michaud (2001) reported that survivorship of *Pseudodorus clavatus* (F.) larvae did not differ significantly between pure diets of *A. spiraecola* (24 %) and *Toxoptera citricida* (Kirkaldy) (36 %). However, larvae of *P. clavatus* were 50 % heavier and completed development sooner when reared on a pure diet of *T. citricida* than on a diet of *A. spiraecola*. *A. spiraecola* has also been shown to be a poor resource for larvae of *Coccinella septempunctata* L., *Coleomegilla maculata* (Mulsant), *Coelophora inaequalis* F., *Olla v-nigrum* Mulsant (Michaud 2000), and *Harmonia axyridis* (Pallas) (M.W. Brown, USDA-ARS, Appalachian Fruit Research Station, Kearneysville, WV, personal communication).

Pipizine syrphids have been reported from colonies of woolly apple aphid around the world. Evenhuis (1959) reported that *Cnemodon vitripennis* (Meigen) was an important natural enemy of the woolly apple aphid in the Netherlands and that it appeared to be restricted to aphids secreting flocculent wax (Evenhuis 1966). Holdsworth (1970) reported *Pipiza pisticoides* Williston larvae preying on woolly apple aphid colonies in Ohio. Reports of predation by Pipizine syrphids on other aphid species were summarized in Table 2 in Chapter 1.

Data reported by Rojo and Marcos-García (1997) provided an interesting contrast with our results. In south-eastern Spain, *Heringia heringii* Zetterstedt was noted preying on colonies of *D. plantaginea* and *A. spiraecola* on apple trees, which is in direct contrast with our observations that *H. calcarata* was not recorded from colonies other than woolly apple aphid. This may imply that the specialization of *H. calcarata* on woolly apple aphid in Virginia is a species-specific trait. The distribution of *H. calcarata* eggs implies that gravid female flies actively select woolly apple aphid colonies as oviposition sites. Given that naïve, neonate *H. calcarata* larvae preferred woolly apple aphid and that their performance was superior on a pure diet of woolly apple aphid in our studies, deposition of eggs by gravid, female *H. calcarata* in woolly apple aphid colonies clearly enhances larval fitness.

Chemosensory stimuli from aphid by-products (Dixon 1959, Schneider 1969, Budenberg and Powell 1992, Sutherland et al. 2001) and visual stimuli such as colony age (Kan 1988, Hemptinne et al. 1993) and size (Kan and Sasakawa 1986) mediate host recognition and elicit oviposition in other syrphid fly species. Speculation about the cues used by gravid, female *H. calcarata* to locate and identify arboreal woolly apple aphid colonies raise interesting questions about potential predation by *H. calcarata* on edaphic woolly apple aphid colonies. Pipizine syrphids have been reported preying on edaphic colonies of woolly apple aphid in apple orchards in the United States. Specifically, Walsh and Riley (1869) found larvae of *Pipiza radicum* (Williston), on edaphic colonies of the woolly apple aphid in Illinois. Heeger (1858) and Dixon (1959) reported eggs of *Pipiza varipes* Meigen and *Pipizella varipes* (Meigen), respectively, laid just above the soil level of *P. sativa* roots infested with aphids not visible from above. *Pipizella varipes* larvae were noted to feed on root colonies of *Anuraphis subterranean* (Del Guercio) (Chambers 1988) and various aphids inhabiting the roots of *Pastinaca sativa* L. and

Petroselinum sativum Hoffman (Heeger 1858). In the absence of arboreal wooly apple aphid colonies, can gravid female *H. calcarata* detect subterranean colonies of woolly apple aphid? If so, what are the cues used by females to find these colonies? In 2003, preliminary studies in our laboratory showed that *H. calcarata* eggs buried in soil, with a woolly apple aphid colony, hatched and fed for five days on the available aphids. Furthermore, when unhatched *H. calcarata* eggs were placed on the soil surface, separated by 5cc of soil from a woolly apple aphid colony, some larvae located and fed on the woolly apple aphid colony buried below. Similarly, some 3rd instar *H. calcarata* buried with a woolly apple aphid colony, fed for several days and then migrated to the soil surface to pupariate, where they emerged as adults. Anecdotal evidence reported in the literature, in combination with our preliminary laboratory data, generate many questions about the potential for predation of edaphic woolly apple aphid colonies by *H. calcarata* larvae.

Aside from syrphids and *Aphelinus mali* (Haldeman), other biological control agents are known to prey on *Eriosoma* sp., such as woolly apple aphid. Coccinellids in Italy, Palestine, and Australia (Alfieri 1920, Bodenheimer 1947, Nicholas 2000), chrysopids in Kansas, USA and Australia (Lohrenz 1911, Nicholas 2000), and forficulids in Australia (Nicholas 2000) are known to be important predators of woolly apple aphid. This predator complex is known to be a valuable part of biological control of other aphids on an array of flora, including aspen, apple, citrus, and rapeseed (Sanders and Knight 1968, Bouchard et al. 1982, Pfeiffer et al. 1995, Wyss 1995, Lakhanpal and Raj 1998, Brown 1999, Michaud 1999, Wyss et al. 1999, Solomon et al. 2000, Brown 2004). Unlike other reports, only syrphids and *A. mali* were observed in woolly apple aphid colonies in our study. *E. americanus* was predominant in woolly apple aphid colonies in April before spirea and rosy apple aphid colonies were abundant, but *H. calcarata* was most abundant throughout the season (see Chapter 2).

Given that *A. mali* population density may be low until later in the season (Dumbleton and Jeffreys 1938, Mueller et al. 1992, Mols and Boers 2001, M.W. Brown, personal communication), when woolly apple aphid populations can build to outbreak levels, early suppression of these aphids may be due solely to predation by syrphid larvae. More research is warranted on *E. americanus*, especially given its early appearance in arboreal woolly apple aphid colonies. However, the specialization by *H. calcarata* on woolly apple aphid, its predominance in colonies throughout the season, and its potential predation on edaphic colonies, clearly indicate its importance as a biological control agent of woolly apple aphid in the mid-Atlantic region.

Chapter 4

Summary Discussion

Apple production in the mid-Atlantic region of the United States is an especially challenging enterprise due to a much higher number of pests and diseases than in other important apple growing regions (e.g. the Pacific northwest). The recent loss of some important broad-spectrum pesticides, increasing restrictions on the use of others, and poor market conditions has created even more challenging conditions for farmers. Given these changes, management programs should continue to understand and accept integrated pest management tactics including monitoring, mating disruption, cultural practices, and biological control (Environmental Protection Agency Workshop 1999).

Our data indicate that *Heringia calcarata* (Loew) is an important specialist predator of woolly apple aphid, *Eriosoma lanigerum* (Hausmann). These studies revealed many aspects of the biology and life history of *H. calcarata*, including descriptions of morphological characteristics, the duration of developmental periods, voracity, prey preference, host suitability, and seasonal phenology. Furthermore, *H. calcarata* and other syrphid flies are present early in the growing season, when the efficacy of *Aphelinus mali* (Haldeman) may be limited by cooler temperatures and conventional spray programs. However, more research is needed to understand its impact on the population dynamics of woolly apple aphid.

Field studies should address the effect of feeding by *H. calcarata* larvae on the fate of woolly apple aphid colonies. It would be valuable to investigate the interactions between *H. calcarata*, *Eupeodes americanus* (Wiedemann), *Syrphus rectus* Osten Sacken, and *A. mali*, to determine if their effects on woolly apple aphid control are additive, synergistic, or antagonistic.

Choice tests with parasitized and unparasitized aphids should reveal whether syrphid larvae prey on both healthy aphids and those parasitized by *A. mali*. Furthermore, there may be differences in the feeding behavior of larvae of the three syrphid species. *E. americanus* larvae have been observed feeding on *H. calcarata* larvae and on conspecifics, while larvae of *H. calcarata* never exhibited cannibalism or attacks on other syrphid larvae. Given that over 10 % of woolly apple aphid colonies collected from our sentinel trees contained unhatched eggs of two syrphid species, differences in the feeding behavior of the generalists and *H. calcarata* should be examined for possible antagonistic effects. Other behavioral differences between the generalists and *H. calcarata* may influence their role as biological control agents of woolly apple aphid. Like many syrphids (Rotheray 1989), *E. americanus* and *S. rectus* larvae may move away from colonies when not feeding while, the specialist predator, *H. calcarata* may remain within the colony for the duration of larval development.

Perhaps the most intriguing and potentially valuable aspect of predation by *H. calcarata*, is its potential role as a predator of edaphic colonies of woolly apple aphid. Anecdotal evidence, our emergence trap data, and results from preliminary laboratory studies on predation of edaphic woolly apple aphid colonies suggest that *H. calcarata* is found beneath apple trees and may be capable of preying on woolly apple aphid colonies on roots of apple trees. More information is needed to confirm the presence of *H. calcarata* below ground in mid-Atlantic apple orchards and to determine its relative abundance and efficacy as a predator.

Two important aspects of *H. calcarata* life history that were not revealed in this research were adult mating and fecundity. The difficulty of mating syrphid flies under laboratory conditions has been reported in many studies (Schneider 1948, Bombosch 1956, 1957, Stürken 1964, Laska 1978, Gladis 1994) and success in mating appears to be dependent upon a great number of factors specific to an individual species (Bombosch 1956, 1957, Wilkening 1961, Asyakin 1973, Dai 1993). Only preliminary attempts were made to mate *H. calcarata* in laboratory and copulation was not observed in the field. Further studies should attempt to elucidate the appropriate laboratory and field conditions under which adult *H. calcarata* will mate, including nutritional requirements and the abundance of males needed to initiate copulation. Like many other syrphid flies (Maier and Waldbauer 1979a, Maier 1982, Waldbauer 1984), Pipizine syrphids are believed to be territorial (Mutin 1996), and further research could attempt to identify potential breeding sites.

More work is needed on flower preferences of *H. calcarata* in the field to determine suitable laboratory rearing conditions and the potential value of habitat manipulation to attract and retain syrphid flies in an area. Since adult hover flies require pollen and nectar for food (Metcalf 1916, Schneider 1948, 1969, Lovei et al. 1993) and breeding sites (Maier and Waldbauer 1979a), such information may support further work on mating, fecundity, and habitat manipulation. Habitat manipulation may (White et al. 1995) or may not increase the number of syrphid eggs or adults or decrease aphid populations in an area from year to year (Hickman and Wratten 1996). Furthermore, the preservation of certain flowers or weeds may provide a reservoir for pests, including stink bugs (Polk et al. 1995).

While our data indicate that *H. calcarata* is a specialist predator of woolly apple aphid in the apple ecosystem, its host range outside of this system is not known. In 2003, woolly apple aphid density was very low in apple orchards, yet *H. calcarata* eggs were relatively abundant in sentinel trees and it is unknown if *H. calcarata* is sustained below ground on edaphic colonies or is capable of feeding on other aphid species outside the apple ecosystem.

It will be important to understand the effects of orchard pesticide spray programs on populations of beneficial syrphid predators. This may be particularly true of pesticides used early in the season when syrphid larvae appear to be the predominant beneficial arthropods in woolly apple aphid colonies.

Finally, the underlying reasons for sporadic outbreaks of woolly apple aphid in certain seasons over large geographical areas remain unknown. Such outbreaks occurred in the mid-Atlantic region in 2000 and in Michigan in 2002. While outbreaks of woolly apple aphid have occurred in response to the use of pyrethroid pesticides (Penman and Chapman 1980), sporadic, region-wide outbreaks cannot be explained solely by pesticide use patterns. Commercial apple growers typically do not vary their pesticide programs significantly from year to year and different growers may use different combinations of products. Yet, in some seasons, woolly apple aphid heavily infests apple orchards, regardless of current or past pesticide programs. This phenomenon suggests that some combination of abiotic and/or biotic factors may disrupt biological control of woolly apple aphid early in the season. Studies designed to elucidate these factors could provide growers with valuable insight into the preservation of natural enemies and to reducing the likelihood of future outbreaks of woolly apple aphid.

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