Chapter 6
The Pollen Feeders

Most, if not all, major classes of arthropod predators and parasitoids contain members that consume pollen in some fashion. Given the tremendous diversity of entomophagous arthropods, it is necessary to curtail the list of species treated in this chapter. To this end, the focus of this chapter is primarily on taxa for which the ecological function of the group is fairly well understood or where importance to biological control is demonstrated. While the scope of this review is intended to be comprehensive, the state of the literature on this topic prevents an entirely exhaustive treatment. Thus please view this as an attempt to point out the diversity of pollen feeding taxa, and the range of pollens that they are known to consume.

6.1 Predators

In addition to the families treated in detail below, other predatory taxa routinely consume pollen as part of their diet. As examples, Scoliodea: Myzininae, Pompilidae, Nyssonidae, Sphecidae, and Vespidae (subfamilies Eumeninae, Masarinae, Polistinae, Vespinae) (Hymenoptera) contain predaceous members that will accept pollen as food (Hunt et al., 1991). Also, some adults of Cleridae (Coleoptera) (*Enoclerus* spp. specifically) are pollinivorous (Balduf, 1935), and *Frankliniella occidentalis* (Thysanoptera: Thripidae) is a natural enemy of spider mites that actually experiences higher survival and reproduction on a diet of *Gossypium barbadense* pollen than on certain prey in the laboratory (Trichilo and Leigh, 1988). Many phalangiids also consume pollen under field conditions (Acosta and Machado, 2007). Suffice it to say that the instances reported here are intended to point out some of the specific relationships between entomophagous arthropods and pollen species, and to illustrate how groups of predators approach pollinivory.

6.1.1 Arachnida: Araneae

Spiders are traditionally regarded as strict carnivores, although investigations have revealed that pollen is of dietary importance for at least a handful of species.

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Exceptions to strict carnivory are accumulating in web-building and flower-dwelling spiders (Smith and Mommsen, 1984; Vogelei and Greissl, 1989) (Table 6.1). Immature spiders collect their webs periodically regardless of whether the webs contain prey (Lubin, 1978). A number of microorganisms, pollen, and spores are often adhered to the strands of silk, which can augment the nutrition of spiders, especially when prey is scarce (Agarwal, 1976; Bera et al., 2002; Linskins et al., 1993; Smith and Mommsen, 1984). Linskins et al. (1993) found that horizontal webs have more pollen than those arranged vertically, and that individual webs can contain thousands of pollen grains. This is confirmed by Ludy and Lang (2006b), who report 1,044 ± 1,193 pollen grains per web of *Araneus diadematus* near cornfields. The farther the webs are from the cornfield, the less corn pollen is found in the webs. Bera et al. (2002) report dozens of species of pollen in six spider webs.

There are some anatomical hurdles that spiders need to overcome in order to ingest pollen. Cuticular platelets covering the oral cavity prohibit spiders from ingesting materials larger than 1 µm. Yet, the fact that pollen is larger than 1 µm does not apparently prevent spiders from ingesting it, although it isn’t exactly clear how they accomplish this (Smith and Mommsen, 1984; Vogelei and Greissl, 1989). Linskins et al. (1993) suggest that when the pollen grains germinate in the sticky fluids on the web, their nutrients become accessible to spiders, which digest foods extra-orally.

Pollen feeding improves the fitness of spiders, especially with regard to adult longevity and survivorship of immatures. Ingesting webs that contain pollen from *Betula papyrifera* results in greater longevity, survivorship, and web-regeneration capacities in second and third instars of the orb-weaver, *Araneus diadematus*, compared to spiders that ingest webs containing no pollen (Smith and Mommsen, 1984). In another case, young *Thomisus onustus* subsist on pollen for more than 40 days in the laboratory, and this may be an important spring food for flower-inhabiting immatures that have not yet accumulated substantial fat reserves (Vogelei and Greissl, 1989). Thus, feeding on non-prey foods such as pollen may be important for the survival of some spider immatures when prey is unavailable. It should be noted that not all web-building spiders ingest pollen; offering the lyniphiid, *Frontinella communis* pollen from *Pinus elliottii* var. *densa* does not improve spider fitness over unfed individuals, nor are the spiders actually observed to feed on the pollen (Carrel et al., 2000).

6.1.2 Arachnida: Acari

Predatory mites in several families feed on pollen to varying degrees. McMurtry and Croft (1997) classify the feeding behavior of predatory Phytoseiidae into four groups, three of which feed on pollen. McMurtry & Croft’s Group IV is comprised of the genus *Euseius*, members of which can subsist on pollen in the absence of prey with minimal reductions in fitness. Indeed, pollen is as suitable for larval development and reproduction as prey for a number of entomophagous

Table 6.1 Predaceous families in Arachnida known to feed on plant pollen

Family	Species	Life stage	Pollen species	Reference
Class: Araneae				
Aranae	*Araneus diadematus*	Immature	*Betula papyrifera*; *Zea mays*	(Ludy and Lang, 2006b; Smith and Mommsen, 1984)
Argiopidae	*Meta segmentata*	Unknown	Pollen of numerous species found in webs (unknown whether this was ingested)	(Linskins et al., 1993)
Argiopidae	*Zygiella x-notata*	Unknown	Pollen of numerous species found in webs (unknown whether this was ingested)	(Linskins et al., 1993)
Thomisidae	*Misumenoides formosipes*	Adult males	*Daucus carota* (seen brushing grains into mouth)	(Vogelei and Greissl, 1989)
Thomisidae	*Thomisus onustus*	Immature	*Erigeron annuus, Bellis perennis*	(Pollard et al., 1995)
Class: Acari				
Cheyletidae	*Cheletogenes ornatus*	Immature/adult	*Phoenix dactylifera*, *Z. mays*	(Zaher et al., 1981)
Erythraeidae	*Balaustium florale*		*B. perennis*, *Ranunculus*, *Acer campestre*	(Childers and Rock, 1980; Grandjean, 1959)
Erythraeidae	*Balaustium putnami*	Immature	Unidentified yellow pollen, *Malus*	(Cadogan and Laing, 1977; Childers and Rock, 1980)
Phytoseiidae	*Amblyseius andersoni*	Immature/adult	*Mesembryanthemum criniflorum*	(Duso and Camporese, 1991)
Phytoseiidae	*Amblyseius largoensis*	Immature/adult	*Lysichiton camtschatcensis, Salix udensis*, *Betula platyphylla*, *Acer negundo*, *Plantago lanceolata*, *Sambucus sieboldiana* var. *miquelii*, *Pinus nigra*, *Heracleum dulce*, *Carpobrotus acinaciformis* (anthers), *Z. mays, Citrus limon* anthers, [completed development on a diet consisting solely of *Pyrus communis*, *Diospyros kaki*, *Camellia*, *Pinus*, *Tulipa*, *Castanea* (chestnut), *Portulaca grandiflora*, *Podocarpus macrophylla, Salix lucida lasiandra*, *Quercus argifolia*, an unidentified palm, *Ricinus communis*, *Quercus virginiana*, *Typha domingensis*, *Phoenix roebelenii*	(Kamburov, 1971; Kennett and Hamai, 1980; Mori, 1977; Yue and Tsai, 1996)

(continued)

Table 6.1 (continued)

Family	Species	Life stage	Pollen species	Reference
Phytoseiidae	*Amblyseius potentillae*	Immature/adult	*Vicia faba*, *M. criniflorum*	(Overmeer and van Zon, 1983)
Phytoseiidae	*Amblyseius similoides*	Adult	*Persea americana*	(Flechtmann and McMurtry, 1992b)
Phytoseiidae	*Euseius*	Adult/immature	Appear to be quite pollinivorous	(Kennett et al., 1979; McMurtry, 1985)
Phytoseiidae	*Eusius addoensis addoensis*	Immature	*Carpobrotus muirii*, *Casuarina cunninghamiana*	(Grout and Richards, 1992)
Phytoseiidae	*Euseius aleyrodis*	Immature/ adult	*Gossypium*, *Antirrhinum majus*	(Elbadry, 1968)
Phytoseiidae	*Euseius finlandicus*	Immature/ Adult	*Malus sylvestris*, *Prunus avium*, *Betula*, *Prunus persica*, *Prunus armeniaca*, *Juglans regia*, *Papaver rhoeas*, *P. communis*	(Broufas and Koveos, 2000; Schausberger, 1992)
Phytoseiidae	*Euseius gossipi*	Immature/adult	*Z. mays*, *P. dactylifera*, *Gossypium barbadense*	(Elbadry and Elbenhawy, 1968a, b)
Phytoseiidae	*Euseius mesembrinus*	Immature/adult	*Malephora crocea*	(Abou-Setta and Childers, 1989)
Phytoseiidae	*Euseius ovalis*	Immature	*Z. mays*	(Shih et al., 1993)
Phytoseiidae	*Euseius scutalis*	Adult	*R. communis*, *Z. mays*	(Allawi, 1991)
Phytoseiidae	*Euseius sojaensis*	Immature/adult	*Camellia sinensis*	(Osakabe, 1988; Osakabe et al., 1986)
Phytoseiidae	*Eusieus tipulatus*	Adult	*M. crocea*	(Flechtmann and McMurtry, 1992b)

Phytoseiidae	*Euseius tularensis*; = *Euseius hibisci*	Immature/adult	*Salix, S. l. lasiandra*, *Nicotiana glauca*, *Quercus agrifolia*, *Brassica nigra*, *Aesculus californica*, *Rubrus*, *Typha latifolia*, *Z. mays*, *Ligustrum japonicum*, *Ananas comosus*, *M. crocea*, *M. sylvestris*, *P. communis*, *Prunus dulcis*, *Olea europaea*, *Lolium multiflorum*, *Secale cereale* var. 'Merced', *Avena sativa* var. 'California red', *Hordeum vulgare* var. 'UC476', *Bromus mollis* var. 'Blando', *Bromus carinatus, Hordeum brachyantherum*, *Festuca rubra, Triticum aestivum, P. persica*, *Carpobrotus edulis, P. americana*, *R. communis*, *Capsicum annuum*, *Mesembryanthemum*, *Eucalyptus*, *J. regia*, *Citrus*, *G. barbadense*, *V. faba*, *Pisum sativum* var. '*arvense'*, *Trifolium repens*, *Vicia sativa*, *Vicia villosa* ssp. *dasycarpa* var. 'Lana', *Trifolium incarnatum* var. 'Flame', *Trifolium hirtum*, *Trifolium pratense*	(Grafton-Cardwell et al., 1999; Kennett et al., 1979; Kennett and Hamai, 1980; McMurtry and Scriven, 1964b; Ouyang et al., 1992; Swirski et al., 1970)
Phytoseiidae	*Euseius victoriensis*	Immature	*Typha orientalis*	(James, 1993)
Phytoseiidae	*Galendromus occidentalis*	Adult	*Prunus* (plum), *Z. mays*, *Carya* (pecan), *Pistacia* (pistachio), *Malus* (apple), *A. chinensis*, *P. dulcis*, *P. communis*	(Afifi et al., 1988)
Phytoseiidae	*Iphiseiodes quadripilis*	Adult/immature	*M. crocea*, *Quercus*	(Villanueva and Childers, 2007)
Phytoseiidae	*Iphiseius degenerans*	Adult/immature	>25 species of pollen	(Eveleigh and Chant, 1982; van Rijn and Tanigoshi, 1999b)
Phytoseiidae	*Kambimodromus aberrans*	Immature/adult	*Malus*, *Prunus* (cherry), *Betula*, *Corylus avellana*	(Chant, 1959; Schausberger, 1992)
Phytoseiidae	*Metaseiulus arboreus*	Immature/adult	*Q. argifolia*, *S. l. lasiandra*, unidentified palm	(Kennett and Hamai, 1980)
Phytoseiidae	*Neoseiulus chilenensis*	Immature/adult	*R. communis, Z. mays*, *C. edulis, Amygdalus communis*, *P. americana*	(Swirski et al., 1970)

(continued)

Table 6.1 (continued)

Family	Species	Life stage	Pollen species	Reference
Phytoseiidae	*Neoseiulus cucumeris*	Adult/immature	>25 species of pollen; *R. communis, Quercus*	(Skirvin et al., 2007; van Rijn and Tanigoshi, 1999b; Marisa and Sauro, 1990)
Phytoseiidae	*Neoseiulus fallacis*	Immature/adult	*Prunus*, *Z. mays*, *Carya*, *Pistacia*, *Malus*, *Actinidia chinensis*, *P. dulcis*, *P. communis*, *Malus*, *Campsis grandiflora*, *P. persica*	(Afifi et al., 1988; Zaher et al., 1969)
Phytoseiidae	*Neoseiulus idaeus*	Adult	*Manihot esculenta*, *Elaeis guineensis*, *R. communis*	(Tanigoshi et al., 1993)
Phytoseiidae	*Neoseiulus longispinosus*	Immature/adult	*S. udensis*, *A. negundo*, *Rosa rugosa*, *Z. mays*	(Mori, 1977)
Phytoseiidae	*Neoseiulus paraki*	Immature/adult	*L. camtschatcensis, S. udensis, A. negundo, P. lanceolata, Z. mays*	(Mori, 1977)
Phytoseiidae	*Neioseiulus umbraticus*	Not specified	*Rubus*, *C. avellana*	(Chant, 1959)
Phytoseiidae	*Phytoseiulus persimilis*	Adult	*Prunus* (plum), *Z. mays*, *Carya* (pecan), *Pistacia* (pistachio), *Malus* (apple), *A. chinensis*, *P. dulcis*, *P. communis*	(Zaher et al., 1969)
Phytoseiidae	*Phytoseius plumifer*	Immature/adult	*P. dactylifera*, *G. barbadense*, *Althaea rosea*	(Afifi et al., 1988)
Phytoseiidae	*Proprioseiopsis athiasae*	Immature/adult	*Gossypium* (can complete development and reproduce on)	(Swirski et al., 1967)
Phytoseiidae	*Proprioseiopsis rotundus*	Immature/adult	*M. crocea*, *Q. virginiana*, *T. latifolia*	(Abou-Setta et al., 1997)

Phytoseiidae	*Typhlodromus caudiglans*	Immature/adult	*Chenopodium album, Ambrosia artemisiifolia, Setaria pumila pumila*	(Putnam, 1962)
Phytoseiidae	*Typhlodromips deleoni*	Immature/adult	*R. communis*	(Shou-Jian and Fen-Wei, 1982)
Phytoseiidae	*Typhlodromus doreenae*	Immature	*T. orientalis*	(James, 1993)
Phytoseiidae	*Typhlodromus kerkirae*	Immature/adult	*V. faba*	(Koveos and Broufas, 1999)
Phytoseiidae	*Typhlodromalus limonicus*	Immature/adult	*Persea* (avocado), *C. annuum, R. communis, Mesembryanthemum*, *Citrus*	(McMurtry and Scriven, 1965)
Stigmaeidae	*Zetzellia mali*	Immature/adult	*Malus* (apple)	(White and Laing, 1977)
Phytoseiidae	*Typhlodromus pyri*	Immature/adult	*V. faba* (reared in culture for 6 months), *P. dactylifera*, *G. barbadense*, *A. rosea*, *Malus* (apple), *M. criniflorum, Alnus glutinosa*, *Salix*, *Citrus* (orange), *P. americana*	(Chant, 1959; Chant and Fleschner, 1960; Dicke, 1988b; Dosse, 1961; Duso and Camporese, 1991; Zaher and Shehata, 1971)
Phytoseiidae	*Typhlodromus rickeri*	Immature/adult	*P. americana* pollen and anthers	(Overmeer, 1981; Overmeer, 1985; McMurtry and Scriven, 1964a)
Phytoseiidae	*Typhlodromips swirskii*	Immature/adult	*Gossypium* (can complete development and reproduce), *R. communis*	(Abou-Awad and Elsawi, 1992; Swirski et al., 1967)
Phytoseiidae	*Typhlodromalus peregrinus*	Immature/adult	*M. crocea*, *Q. virginiana, T. latifolia*	(Fouly et al., 1995)

acarids (Elbadry and Elbenhawy, 1968a; Ouyang et al., 1992; Swirksi et al., 1970; Zaher and Shehata, 1971). Perhaps the best-studied member of this genus with regard to pollinivory is *Euseius tularensis*, which can develop and reproduce on dozens of species of pollen (Grafton-Cardwell et al., 1999; Kennett et al., 1979; McMurtry and Scriven, 1964b; Ouyang et al., 1992; Swirski et al., 1970). Natural peaks in pollen densities in California orchards are consistently followed by increases in the densities of *Euseius tularensis*, although their attractiveness and ability to induce reproduction varies among pollen species (Kennett et al., 1979). The ability of these highly pollinivorous predators to regulate pest populations has historically been questioned, but some examples suggest that pollen feeding may allow *Euseius* spp. and other polyphagous feeders to control pest mite populations before outbreaks occur (Elbadry, 1968; Wiedenmann and Smith, 1997) (see Chapter 16).

Pollen plays a different role in the life histories of entomophagous acarids that are relatively less reliant on pollen. In these taxa, pollen functions as a dietary supplement to prey of low quality or when prey is absent. The presence of pollen during spring before prey become abundant is important for several species of mites, which aggregate to spring flowering plants like the catkins of *Corylus avellana* and *Salix*, and flowers of *Malus* (Chant, 1959). For example, apple pollen was sufficient to sustain spring-collected *Typhlodromus pyri* and prompt egg production, whereas those fed only water soon died (Chant, 1959). But even for these more entomophagous mites, pollens can be equivalent to prey in terms of nutrition; two pollen species are equivalent to citrus rust mites for supporting development of *Iphiseiodes quadripilis* (Villanueva and Childers, 2007). Different pollens vary in their suitability for mites, and the importance of factors such as pollen nutrition and pollen grain structure are relatively well studied for acarid carnivores compared with other entomophages (see Chapter 7).

6.1.3 Coleoptera: Carabidae

The feeding behavior of carabids as a group is difficult to characterize, and while pollen is acceptable to a handful of species, the scope of pollinivory within this family requires more attention. Carabids range from nearly complete carnivory (as in most Carabini, Cicindelini), to nearly complete herbivory (as in some Harpalini, Zabrini). In actuality, most species are best described as omnivorous, feeding on fungal spores, sugar, seeds, plant tissue, and dead and living prey (Allen, 1979; Larochelle, 1990). Quantifying the dietary breadth of omnivorous carabids is difficult at best. Of the approximately 40,000 described species of Carabidae, feeding habits are only described for 1,054 (2.6%) of species (Larochelle, 1990). Of this minority, only 36 are recorded as feeding on pollen (Table 6.2). This proportion is undoubtedly a serious underestimate of pollinivory in carabids. For instance, in the laboratory, 14 carabid species never previously observed to consume pollen readily eat corn pollen under no-choice conditions (Ahmad et al., 2006; Mullin et al., 2005). Indeed, *Scarites quadriceps* (a predominantly entomophagous species) and

Table 6.2 Species in selected families of Insecta that are predaceous at some point during their lives (excluding parasitoids)

Family	Species	Life stage	Species of pollen consumed	Reference
Mantodea				
Mantidae	*Tenodera aridifolia sinensis*	Adult	Mixed species, bee-collected	(Beckman and Hurd, 2003)
Mantidae	*Tenodera aridifolia sinensis*	Nymph	Mixed species, bee-collected	(Beckman and Hurd, 2003)
Coleoptera				
Carabidae	*Agonum cupripenne*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Agonum decorum*	Adult	Leguminosae, Cruciferae, Caryophyllaceae, Umbelliferae, and Compositae	(Dawson, 1965)
Carabidae	*Agonum fuliginosum*	Adult	Leguminosae, Cruciferae, Caryophyllaceae, Umbelliferae, and Compositae	(Dawson, 1965)
Carabidae	*Agonum muelleri*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Agonum placidum*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Amara aulica*	Adult	pollen	(Forsythe, 1982a)
Carabidae	*Amara eurynota*	Adult	*Scabiosa*	(Jänner, 1905; Larochelle, 1990)
Carabidae	*Amara pennsylvanica*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Amphasia sericea*	Adult	Grass pollen	(Forbes, 1881)
Carabidae	*Anisodactylus sanctaecrucis*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Bembidion biguttatum*	Adult	Pollen	(Davies, 1953)
Carabidae	*Bembidion lampros*	Adult	Pollen	(Davies, 1953; Mitchell, 1963)
Carabidae	*Bembidion obtusum*	Adult	Pollen	(Davies, 1953)
Carabidae	*Bembidion quadrimaculatum oppositum*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Calathus gregarius*	Adult	Grass pollen	(Forbes, 1883)
Carabidae	*Carterus*	Adult	Anthers of Graminae and Umbelliferae	(Bonadona, 1971; Jeannel, 1941; Larochelle, 1990)
Carabidae	*Chlaenius tricolor tricolor*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Ditomus capito*	Adult	Graminaceous anthers	(Auber, 1965; Larochelle, 1990)
Carabidae	*Ditomus tricuspidatus*	Adult	*Ammi majus*	(Burmeister, 1939; Larochelle, 1990)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Carabidae	*Harpalus affinis*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Harpalus caliginosus*	Adult	Pollen (Compositae), *A. artemisiifolia*, *Z. mays* (mixed with dog food)	(Ahmad et al., 2006; Forbes, 1883; Mullin et al., 2005; Webster, 1881)
Carabidae	*Harpalus herbivagus*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Harpalus pensylvanicus*	Adult	*A. artemisiifolia*, *Koeleria macrantha*, *Z. mays* (mixed with dog food)	(Ahmad et al., 2006; Forbes, 1883)
Carabidae	*Harpalus rufipes*	Adult	Pollen	(Cornic, 1973; Larochelle, 1990)
Carabidae	*Lebia atriventris*	Adult	Pollen and anthers of grass, probably *Poa* (bluegrass)	(Forbes, 1883)
Carabidae	*Loricera pilicornis pilicornis*	Adult	Pollen	(Davies, 1953)
Carabidae	*Microlestes maurus*	Adult	Pollen	(Davies, 1953)
Carabidae	*Notiophilus biguttatus*	Adult	Pollen	(Davies, 1953)
Carabidae	*Notiophilus rufipes*	Adult	Pollen	(Davies, 1953)
Carabidae	*Patrobus longicornis*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Poecilus chalcites*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Poecilus lucublandus*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Pterostichus diligens*	Adult	Leguminosae, Cruciferae, Caryophyllaceae, Umbelliferae, and Compositae	(Dawson, 1965)
Carabidae	*Pterostichus melanarius*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Scarites quadriceps*	Adult	*Z. mays*	(Mullin et al., 2005)
Carabidae	*Stenolophus mixtus*	Adult	Pollen	(Gersdorf, 1937; Larochelle, 1990)
Coccinellidae	*Adalia bipunctata*	Larva	Bee pollen	(De Clercq et al., 2006)
Coccinellidae	*Adalia bipunctata*	Adult	Aceraceae, Amaryllidaceae, Berberidaceae, *Betula*, *Corylus*, Brassicaceae, Fagaceae, Grossulariaceae, Liliaceae, Pinaceae, Rosaceae, Salicaceae, bee pollen	(Hemptinne and Desprets, 1986; Putnam, 1964; De Clercq et al., 2006)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Coccinellidae	*Anatis ocellata*	Adult	*Pinus banksiana*	(Allen et al., 1970)
Coccinellidae	*Anisosticta novemdecim-punctata*	Adult	Pollen	(Goidanich, 1947; Hodek and Honěk, 1996)
Coccinellidae	*Apolinus lividi-gaster*	Adult	*Acacia, Bidens pilosa*	(Anderson, 1982)
Coccinellidae	*Bulaea*	Adults & larvae	Chenopodaceae	(Capra, 1947; Hodek and Honěk., 1996)
Coccinellidae	*Bulaea lichat-schovi*	Adults & larvae	*Euphorbia, Artemisia, Eurotia, Atriplex, Nitraria, Tamarix, Clematis*	(Hodek and Honěk., 1996; Savoiskaya, 1983)
Coccinellidae	*Chilocorus kuwa-nae*	Adult	*Euonymus*	(Nalepa et al., 1992)
Coccinellidae	*Coccinella*	Adult	Compositae	(Forbes, 1883)
Coccinellidae	*Coccinella reit-teri*	Adult	*Leontopodium alpinum*; exclusively pollinivorous	(Hodek and Honěk., 1996; Savoiskaya, 1970)
Coccinellidae	*Coccinella repanda*	Adult	pollen	(Smith, 1961)
Coccinellidae	*Coccinella sep-tempunctata*	Larva	pollen	(Triltsch, 1999)
Coccinellidae	*Coccinella sep-tempunctata*	Adult	*Ribes*, *Stellaria*, *Pinus*, *Solidago*, *Tanacetum vulgare*, *T. aestivum*, Graminae, *Helianthus anuus*, mixed pol-len, Umbelliferae, Compositae, *Laserpitium garganicum*, *Centaurea rupestris*, *Cachrys ferulacea*, also *Leucanthemum vulgare*, *Centaurea cyanus*, *Gentiana lutea*, *Cirsium eriophorum*, *Achillea collina*, *Heracleum sphondylium*	(Bozsik, 2006; Hodek and Honěk., 1996; Nedved et al., 2001; Ricci et al., 2005; Savoiskaya, 1970; Savoiskaya, 1983; Triltsch, 1997, 1999)
Coccinellidae	*Coccinella trans-versoguttata richardsoni*	Adult	Pollen	(Hodek and Honěk., 1996; Ibrahim, 1955)
Coccinellidae	*Coccinella trifa-ciata*	Larva	*Z. mays, Betula populifolia, T. latifolia, Carpinus caroliniana, Cannibas sativa, Tsuga canadensis, Carya ovata*, *Quercus rubra*, *Juglans cinerea*	(Anderson and Hale, 1986)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Coccinellidae	*Coccinella undecimpunctata aegyptiaca*		Pollen	(Hodek and Honěk., 1996; Ibrahim, 1955)
Coccinellidae	*Coccinula crotchi*	Adult	*Taraxacum officinale, Rumex acetosella*, *P. lanceolata*	(Hoshikawa, 1995)
Coccinellidae	*Coleomegilla maculata*	Larva	*Z. mays*, *B. populifolia*, *T. latifolia*, *C. caroliniana*, *C. sativa*, *T. canadensis*, *C. ovata*, *Q. rubra*, *J. cinerea*, *Pinus resinosa*, *A. artemisiifolia*, flowers of grass and Compositae, *Polygonum, M. crocea*, *Gossypium*, wildflower pollen, *Helianthus annus*, *Sorghum bicolor*, bee pollen	(Cottrell and Yeargan, 1998; Giroux et al., 1994; Harris, 1969; Lundgren et al., 2005; Lundgren et al., 2004; Lundgren and Wiedenmann, 2004; Michaud, 2000; Smith, 1960, 1961)
Coccinellidae	*Coleomegilla maculata*	Adult	*Z. mays, T. officinale*, *Populus deltoides*, *Caltha palustris*, wildflower pollen, *H. annus*, *S. bicolor*, bee pollen	(Benton and Crump, 1981; Forbes, 1881, 1883; Giroux et al., 1994; Harmon et al., 2000; Lundgren et al., 2005; Lundgren et al., 2004; Michaud and Grant, 2005; Putnam, 1964; Rondon et al., 2006; Solbreck, 1974; Webster, 1881)
Coccinellidae	*Cycloneda munda*	Adult	Pollen	(Putnam, 1964)
Coccinellidae	*Cycloneda sanguinea*	Larva	*Z. mays, B. populifolia, T. latifolia, C. caroliniana, C. sativa, T. canadensis*, *C. ovata, Q. rubra, J. cinerea*, other Compositae	(Forbes, 1883; Smith, 1961)
Coccinellidae	*Exochomus childreni childreni*	Adult	*A. artemisiifolia*	(Balduf, 1935)
Coccinellidae	*Exochomus flavipes*	Larva	Pollen	(Geyer, 1947)
Coccinellidae	*Exochomus flavipes*	Adult	Pollen	(Geyer, 1947)
Coccinellidae	*Harmonia axyridis*	Larva	*Z. mays, Spiraea douglasii*	(LaMana and Miller, 1996; Lundgren et al., 2004)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Coccinellidae	*Harmonia axyridis*	Adult	*Z. mays* (only 3% of adults had fed on corn pollen), *M. crocea*	(Lundgren et al., 2004; Michaud, 2000)
Coccinellidae	*Harmonia conformis*	Adult	*Serenoa repens*, *Crotalaria striata* (flowers and blossoms), *Erechtites hieracifolia* (blossoms, including pistils)	(Watson and Thompson, 1933)
Coccinellidae	*Hippodamia convergens*	Adult	*T. officinale*, Compositae, grass, bee pollen	(Forbes, 1883; Michaud and Qureshi, 2006)
Coccinellidae	*Hippodamia glacialis*	Adult	Compositae	(Forbes, 1883)
Coccinellidae	*Hippodamia notata*	Larvae	Umbelliferae, Graminaceae, Chenopodiaceae, other pollens	(Ricci and Ponti, 2005)
Coccinellidae	*Hippodamia notata*	Adult	*Carduus*, Graminaceae, *Z. mays*, Compositae, Umbelliferae, *Heracleum sphondylium*	(Ricci and Ponti, 2005)
Coccinellidae	*Hippodamia parenthesis*	Adult	Pollen	(Putnam, 1964)
Coccinellidae	*Hippodamia tredecimpunctata*	Adult	Pollen	(Goidanich, 1947; Hodek and Honěk., 1996)
Coccinellidae	*Hyperaspis notata*	Larva	*M. esculenta*; could not complete 1st instar	(Dreyer et al., 1997)
Coccinellidae	*Hyperaspis notata*	Adult	*M. esculenta*; doubtful whether it consumed pollen in the laboratory	(Dreyer et al., 1997)
Coccinellidae	*Ileis galbula*	Adult	*Ligustrum*, *Acacia*	(Anderson, 1982)
Coccinellidae	*Micraspis discolor*	Larva	*Z. mays*	(Omkar, 2006)
Coccinellidae	*Micraspis discolor*	Adult	*Z. mays*	(Omkar, 2006)
Coccinellidae	*Micraspis frenata*	Adult	*Chloris gayana*, *Chloris truncata*, *Paspalum urvillei*, *Setaria gracilis, S. bicolor* ssp. *bicolor, Themeda australis*	(Hawkeswood and Turner, 2002)
Coccinellidae	*Propylaea japonica*	Larva	*Oryza sativa*	(Bai et al., 2005)
Coccinellidae	*Propylaea japonica*	Adult	*O. sativa*	(Bai et al., 2005)
Coccinellidae	*Propylaea quatuordecimpunctata*	Adult	*Lamium album*, *Endymion nonscripta*	(Hemptinne et al., 1988; Hodek and Honěk., 1996)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Coccinellidae	*Rhyzobius litura*	Adult	Graminae, Asteraceae, Labiatae, Boraginaceae, Cruciphereae, Euphorbiaceae, Malvaceae, Ranunculaceae, Rubiaceae, Graminae, *Mercurialis annua*	(Ricci, 1986b)
Coccinellidae	*Spiladelpha barovskii kiritschenkoi*	Adult	*L. alpinum*; exclusively pollinivorous	(Hodek and Honěk., 1996; Savoiskaya, 1970)
Coccinellidae	*Tytthaspis sedec-impunctata*	Larvae	*Lolium perenne*, *Lolium multiflorum*	(Hodek and Honěk., 1996; Ricci, 1982)
Coccinellidae	*Tytthaspis sedec-impunctata*	Adult	*L. perenne, Alopecurus pratensis,* Gramineae, Compositae	(Hodek and Honěk., 1996; Ricci, 1986a; Ricci et al., 1983)
Coccinellidae	*Tytthaspis trilineata*	Larvae	*L. perenne*, *L. multiflorum*	(Hodek and Honěk., 1996; Ricci, 1982)
Coccinellidae	*Verania*	Larvae and adults	Exclusively pollinivorous	(Hodek and Honěk., 1996)
Neuroptera				
Chrysopidae	*Brinckochrysa scelestes*	Adult	*R. communis*	(Krishnamoorthy, 1984)
Chrysopidae	*Ceraeochrysa*	Adult	Pollen	(Albuquerque et al., 2001; Brooks and Barnard, 1990)
Chrysopidae	*Ceraeochrysa cubana*	Adult	Reared on pollen in aboratory	(Venzon and Carvalho, 1992)
Chrysopidae	*Chrysopa formosa*	Adult	Pollen	(Bozsik, 1992)
Chrysopidae	*Chrysopa nigricornis*	Adult	Pollen	(Sheldon and MacLeod, 1971)
Chrysopidae	*Chrysopa oculata*	Adult	Pollen	(Sheldon and MacLeod, 1971)
Chrysopidae	*Chrysopa pallens*	Adult	Pollen	(Bozsik, 1992)
Chrysopidae	*Chrysopa perla*	Adult	Pollen	(Bozsik, 1992)
Chrysopidae	*Chrysopa viridana*	Adult	Pollen	(Bozsik, 1992)
Chrysopidae	*Chrysoperla affinis*	Adult	Pollen from trees and herbaceous plants	(Villaneve et al., 2005)
Chrysopidae	*Chrysoperla carnea*	Larva	*Z. mays,* commercial bee pollen	(Patt et al., 2003; Pilcher et al., 1997)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Chrysopidae	*Chrysoperla carnea*	Adult	*Catalpa bignoniodes, Acer saccharum, Ulmus*, *Carya*, *Celtis occidentalis, Z. mays,* other grass pollen, *Phleum pratense*, up to 40 species of pollen found in guts	(Bozsik, 1992; Sheldon and MacLeod, 1971; Sundby, 1967; Villaneve et al., 2005)
Chrysopidae	*Chrysoperla externa externa*	Adult	Reared on pollen in laboratory; *Cajanus cajan*, *Crotalaria juncea*, *R. communis*	(Canedo and Lizarraga, 1988) (Venzon et al., 2006)
Chrysopidae	*Chrysoperla lucasina*	Adult	Ten species of pollen found in guts	(Villaneve et al., 2005)
Chrysopidae	*Chrysopodes nigripilosus*	Adult	Pollen	(Brooks and Barnard, 1990)
Chrysopidae	*Dichochrysa prasina*	Adult	Pollen	(Bozsik, 1992)
Chrysopidae	*Eremochrysa*	Adult	Exclusively pollinivorous	(Adams and Garland, 1981; Brooks and Barnard, 1990; Sheldon and MacLeod, 1971)
Chrysopidae	*Eremochrysa brevisetosa*	Adult	*Atriplex* (Chenopodiaceae)	(Adams and Garland, 1981)
Chrysopidae	*Eremochrysa fraterna*	Adult	Exclusively pollinivorous	(Sheldon and MacLeod, 1971)
Chrysopidae	*Eremochrysa sabulosa*	Adult	Pollen	(Brooks and Barnard, 1990)
Chrysopidae	*Hypochrysa*	Adult	Exclusively pollinivorous	(Brooks and Barnard, 1990; Canard, 2001; Tjeder, 1966)
Chrysopidae	*Hypochrysa elegans*	Adult	Pollen	(Canard, 2001)
Chrysopidae	*Kimochrysa*	Adult	Exclusively pollinivorous	(Brooks and Barnard, 1990; Canard, 2001; Tjeder, 1966)
Chrysopidae	*Pamochrysa stellata*	Adult	Exclusively pollinivorous; Dipsacacae, Compositae found in gut contents	(Brooks and Barnard, 1990; Canard, 2001; Tjeder, 1966)
Chrysopidae	*Parachrysopiella*	Adult	Pollen	(Brooks and Barnard, 1990)
Chrysopidae	*Pimachrysa*	Adult	Exclusively pollinivorous	(Brooks and Barnard, 1990; Canard, 2001)
Hemerobiidae	*Drepanepteryx phalaenoides*	Adult	Regularly feeds on pollen	(Canard, 2001; Stelzl, 1990, 1991)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Hemerobiidae	*Hemerobius lutescens*	Adult	Regularly feeds on pollen	(Canard, 2001; Stelzl, 1990, 1991)
Hemerobiidae	*Hemerobius nitidulus*	Adult	Regularly feeds on pollen	(Canard, 2001; Stelzl, 1990, 1991)
Hemerobiidae	*Micromus angulatus*	Adult	Reared on pollen in laboratory	(Stelzl and Hassan, 1992)
Hemerobiidae	*Micromus tasmaniae*	Adult	Buckwheat (*Fagopyrum esculentum*)	(Robinson et al., 2008)
Hemerobiidae	*Micromus lanosus*	Adult	Regularly feeds on pollen	(Canard, 2001; Stelzl, 1990, 1991)
Heteroptera				
Anthocoridae	*Anthocoris confusus*	Adult	Yellowish granules in the rectum of overwintering individuals	(Anderson, 1962b)
Anthocoridae	*Anthocoris nemoralis*	Adult	Aggregates to male catkins of *Salix*, and leaves when flowers senesce	(Anderson, 1962b)
Anthocoridae	*Anthocoris nemorum*	Adult	Yellowish Granules in the rectum of overwintering individuals	(Anderson, 1962b)
Anthocoridae	*Orius albidipennis*	Nymph	Bee-collected pollen, *C. annuum*	(Vacante et al., 1997)
Anthocoridae	*Orius albidipennis*	Adult	Bee-collected pollen, *C. annuum*	(Cocuzza et al., 1997)
Anthocoridae	*Orius insidiosus*	Nymph	*Glycine max*, *Z. mays, Acer*, *Verbascum thapsus*	(Corey et al., 1998; Elden and McCaslin, 1997; Kiman and Yeargan, 1985; McCaffrey and Horsburgh, 1986; Pilcher et al., 1997)
Anthocoridae	*Orius insidiosus*	Adult	*Z. mays, Acer*, *Abutilon theophrasti*, cotton	(Barber, 1936; Corey et al., 1998; Kiman and Yeargan, 1985; Richards and Schmidt, 1996) (Iglinsky, 1950, as cited by Chu, 1969)
Anthocoridae	*Orius laevigatus*	Nymph	Bee-collected pollen, *C. annuum*	(Vacante et al., 1997) J.G. Lundgren, unpublished data, 2007

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Anthocoridae	*Orius laevigatus*	Adult	Bee-collected pollen, *C. annuum*, *R. communis*	(Cocuzza et al., 1997; Hulshof and Jurchenko, 2000; Skirvin et al., 2007)
Anthocoridae	*Orius majusculus*	Nymph	*Z. mays*	(Obrist et al., 2006a)
Anthocoridae	*Orius majusculus*	Adult	*Z. mays*	(Obrist et al., 2006a)
Anthocoridae	*Orius minutus*	Nymph	*C. annuum*, *Corylus americana*, *Cucumis sativa*	(Carayon and Steffan, 1959; Fauvel, 1974; Lattin et al., 1989)
Anthocoridae	*Orius niger*	Nymph	*Z. mays*	(Baniameri et al., 2005)
Anthocoridae	*Orius pallidicornis*	Adult	*Ecballium elaterium*, exclusively; flower pollen	(Carayon et al., 1959, cited in Chu, 1969)
Anthocoridae	*Orius sauteri*	Nymph	*Momordica charantia*, *Luffa cylindrica*, *Dolichos lablab*, *Rosa chinensis*, *C. sativus*, *Z. mays*	(Funau and Yoshiyasu, 1995; Vacante et al., 1997; Zhou and Wang, 1989)
Anthocoridae	*Orius tristicolor*	Nymph	Bee-collected pollen	(Salas-Aguilar and Ehler, 1977)
Anthocoridae	*Orius tristicolor*	Adult	Bee-collected pollen	(Salas-Aguilar and Ehler, 1977)
Anthocoridae	*Orius vicinus*	Nymph	*V. fabae*, Rosaceae, bee-collected pollen, Cucurbita pepo, *V. thapsus*, *M. annua*, *Datura stramonium* (stamens), *P. persica*, *Prunus cerasus*, *Prunus domestica*/*P. cerasus* (cross), *Malus pumila* (all of these Rosaceae included stamens); *Z. mays*	(Fauvel, 1974; Heitmans et al., 1986)
Anthocoridae	*Orius vicinus*	Adult	*V. fabae*, Rosaceae, *V. thapsus*, *C. pepo*, *Cucurbita melo*	(Fauvel, 1974; Heitmans et al., 1986)
Anthocoridae	*Paratriphleps laeviusculus*	Adult	*Manilkara zapotilla*	(Bacheler and Baranowski, 1975; Lattin et al., 1989)
Geocoridae	*Geocoris punctipes*	Nymphs and adults	*T. officinale* (bee-collected)	(Stoner, 1970)
Nabidae	*Nabis alternatus*	Nymphs (first instars)	*T. officinale* (bee-collected)	(Stoner, 1972)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Nabidae	*Nabis americoferus*	Nymphs (first instars)	*T. officinale* (bee-collected)	(Stoner, 1972)
Nabidae	*Nabis capsiformis*	Nymphs (first instars)	*T. officinale* (bee-collected)	(Stoner, 1972)
Pentatomidae: Asopinae	*Tylospilus acutissimus*	Nymphs	*T. officinale* (bee-collected)	(Stoner et al., 1974)
Reduviidae	*Sinea complexa*	Nymphs	*T. officinale* (bee-collected)	(Stoner et al., 1975)
Reduviidae	*Sinea confusa*	Nymphs	*T.officinale* (bee-collected)	(Stoner et al., 1975)
Reduviidae	*Zelus renardii*	Nymphs	*T. officinale* (bee-collected)	(Stoner et al., 1975)
Reduviidae	*Zelus tetracanthus*	Nymphs	*T. officinale* (bee-collected	(Stoner et al., 1975)
Diptera				
Syrphidae	*Allograpta ropalus*	Adult	Compositae, *Taraxacum*, *Hebe*	(Holloway, 1976)
Syrphidae	*Cheilosia albitarsis*	Adult	*Ranunculus repens*	(Haslett, 1983)
Syrphidae	*Cheilosia splendida*	Adult	*Saxifraga hirculus, Galium uliginosum*	(Olesen and Warncke, 1989)
Syrphidae	*Chrysogaster hirtella*	Adult	*S. hirculus, Lychnus flos-cuculi, G. uliginosum, Ranunculus acris, Lotus uliginosus*	(Olesen and Warncke, 1989)
Syrphidae	*Chrysotoxum bicinctum*	Adult	*S. hirculus, L. flos-cuculi*	(Olesen and Warncke, 1989)
Syrphidae	*Episyrphus balteatus*	Adult	Almost exclusively pollinivorous, *Pulicaria dysenterica, Eupatorium cannabinum, Centaurea nigra, Echium vulgare, Crepis capillaris, Epilobium hirsutum, Rumex crispus, Achillea millefolium, Lythrum salicaria, Dipsacus fullonum, P. lanceolata, C. avellana*	(Gilbert, 1981; Goulson and Wright, 1998; Schneider, 1948, 1969)
Syrphidae	*Eriozona syrphoides*	Adult	*Bidens*, *Epilobium angustifolium*, *Succisa pratensis*, *Calluna vulgaris*, *Erica cinerea*, *Erica tetralix*, *Liguliflora*, *Serratula*	(Haslett and Entwistle, 1980b)
Syrphidae	*Eristalis abusivus*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, Cirsium palustre, Valeriana sambucifolia*	(Olesen and Warncke, 1989)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Syrphidae	*Eristalis tenax* NOT PREDACEOUS AS A LARVA	Adult	*Taraxacum*, *Matricaria*, *Metrosideros*, Rosaceae, Cruciferae, Leguminosae, *Achillea*, *Quintinia*, *Leptospermum*, *Ranunculus sardous*, *Raphanus maritimus*, *Raphanus sativus*	(Holloway, 1976)
Syrphidae	*Eupeodes corollae*	Adult	*Senecio jacobaea*, *Rubus*, *Artemisia*, *Hypericum*, *Epilobium*, *Scabiosa*, *Achillea*, *C. avellana*	(Barlow, 1961; Svensson and Janzon, 1984)
Syrphidae	*Helophilus campbellicus*	Adult	*Hebe elliptica*	(Holloway, 1976)
Syrphidae	*Helophilus hochstetteri*	Adult	*Taraxacum*, *Matricaria*, Cruciferae, Rosaceae, Umbelliferae, Ranunculaceae, Graminae,	(Holloway, 1976)
Syrphidae	*Helophilus hybridus*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre*	(Olesen and Warncke, 1989)
Syrphidae	*Helophilus montanus*	Adult	Compositae, *Ranunculus*	(Holloway, 1976)
Syrphidae	*Helophilus trilineatus*	Adult	*Leptospermum*, Compositae, *Taraxacum*, *Hebe*	(Holloway, 1976)
Syrphidae	*Lejogaster metallina*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre, L. uliginosus, V. sambucifolia*	(Olesen and Warncke, 1989)
Syrphidae	*Lejops contracta*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre, L. uliginosus*	(Olesen and Warncke, 1989)
Syrphidae	*Lejops lineatus*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, Epilobium palustre, C. palustre, L. uliginosus*	(Olesen and Warncke, 1989)
Syrphidae	*Melangyna novaezelandiae*	Adult	*Phacelia tanacetifolia tanacetifolia*, *Bulbinella*, *Ranunculus*, *Stellaria*, *Hebe*, Compositae	(Holloway, 1976; White et al., 1995)
Syrphidae	*Melanostoma fasciatum*	Adult	*P. t. tanacetifolia*, *P. lanceolata,* Graminae, *R. maritimus, R. sardous*, *Eschscholtzia californica*, *D. carota*, Malvaceae, Compositae: Liguliflorae	(Holloway, 1976; Leereveld, 1982; White et al., 1995)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Syrphidae	*Melanostoma mellinum*	Adult	*S. hirculus, L. flos-cuculi, C. palustre,* Graminae, *P. lanceolata,* Cyperaceae, Cruciferae, Compositae: Liguloflorae, Rosaceae, Ericaceae, Tiliaceae, Pteridophyta, Caryophyllaceae, *Pinus*, *Picea*, *Ranunculus*-type, Umbelliferae, *Convolvulus arvensis, Solanum nigrum*, *P. lanceolata, Anemone*-type, *Aster*-type, *Veronica*-type, *Stellaria*-type, *T. latifolia*	(Leereveld, 1982; Olesen and Warncke, 1989; van der Goot and Grabandt, 1970)
Syrphidae	*Melanostoma scalare*	Adult	Almost exclusively pollinivorous, Graminae, *P. lanceolata, Veronica*-type, Umbelliferae, Ranunculaceae, Roscaceae, Compositae: Liguloflorae	(Gilbert, 1981; Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Neoascia meticulosa*	Adult	*S. hirculus, R. acris*	(Olesen and Warncke, 1989)
Syrphidae	*Neoascia tenur*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre, L. uliginosus*	(Olesen and Warncke, 1989)
Syrphidae	*Paragus*	Adult	Compositae*, Forstera*, *Sebea*, *P. lanceolata, Hebe*, Cruciferae	(Holloway, 1976)
Syrphidae	*Parthelophilus frutetorum*	Adult	*S. hirculus, R. acris, E. palustre*	(Olesen and Warncke, 1989)
Syrphidae	*Platycheirus*	Adult	*Ranunculus gracilipes*, *Ranunculus*	(Holloway, 1976)
Syrphidae	*Platycheirus angustatus*	Adult	Graminae, *P. lanceolata, Pinus* Chenopodiaceae, Cruciferae	(Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus clypeatus*	Adult	Graminae, *P. lanceolata*, *Rumex*-like, *Melampyrum*	(Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus fulviventris*	Adult	Graminae, *P. lanceolata*, Caryophyllaceae	(Leereveld, 1982; van der Goot and Grabandt, 1970)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Syrphidae	*Platycheirus granditarsus*	Adult	Graminae, *P. lanceolata,* Cruciferae, *Aster*-type*,* Compositae: Liguliflorae, Rosaceae, *Stellaria*-type, *Ranunculus*-type, *Achillea*-type, Umbelliferae, *Hypericum*-type	(Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus immarginatus*	Adult	Grass, Cyperaceae	(Leereveld, 1982)
Syrphidae	*Platycheirus manicatus*	Adult	Chenopodiaceae, Cruciferae, *Aster*-type, Compositae: Liguliflorae, *Ranunculus*-type, *Cerastium*-type	(van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus peltatus*	Adult	*P. lanceolata*, Cyperaceae, Compositae: Liguliflorae, Liliaceae, Rosaceae, Caryophyllaceae, Rosaceae, *Ranunculus*-type, *Achillea*-type, *Cerastium*-type, *Allium*-type, *Rumex*-like, *Gladiolus*-type, *Urtica*, *T. latifolia*	(Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus scambus*	Adult	*P. lanceolata*, grass, Cyperaceae, *Rumex*, *Secale*, *Tilia*, *Pinus*, Pteridophyta	(Leereveld, 1982; van der Goot and Grabandt, 1970)
Syrphidae	*Platycheirus scutatus*	Adult	Chenopodiaceae, Cruciferae, *Aster*-type, Compositae: Liguliflorae, Rosaceae, Rosaceae-type, *Veronica*-type, *Stellaria*-type, *Ranunculus*-type, *Achillea*-type, *Allium*-type, Umbelliferae, *Cirsium*-type, *Melandrium*-type, *Polygonum*-type	(van der Goot and Grabandt, 1970)
Syrphidae	*Rhingia campestris*	Adult	*Stachys*, *Prunella*	(Haslett, 1983)
Syrphidae	*Sphaerophoria*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum*	(Olesen and Warncke, 1989)
Syrphidae	*Sphaerophoria abbreviata*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre*	(Olesen and Warncke, 1989)

(continued)

Table 6.2 (continued)

Family	Species	Life stage	Species of pollen consumed	Reference
Syrphidae	*Sphaerophoria menthastri*	Adult	*S. hirculus, L. flos-cuculi, G. uliginosum, R. acris, C. palustre*	(Olesen and Warncke, 1989)
Syrphidae	*Syrphus ribesii*	Adult	Almost exclusively pollinivorous, *P. dysenterica, E. cannabinum, C. nigra, C. capillaris, E. hirsutum, D. fullonum, S. jacobaea, Mentha aquatica, Lapsana communis, Lathyrus latifolius, R. repens*	(Gilbert, 1981; Goulson and Wright, 1998)

Harpalus pensylvanicus survive for up to 1 year on a diet of only corn pollen (Mullin et al., 2005). Few of the records presented in Larochelle (1990) are actual gut dissections of field-collected beetles, and many of the feeding reports result from experimental manipulations of feeding behavior such as providing factitious prey for rearing programs. Thus, the true dietary range of most carabids is still a mystery. Additional research is required to understand the role of pollinivory by carabids under field conditions, and the reader is diverted to Section III for a deeper discussion on the feeding ecology of this group.

6.1.4 Coleoptera: Coccinellidae

Coccinellidae as a family is primarily insectivorous, although many studies on the dietary breadth of ladybeetles under field conditions have revealed pollinivory (Ewing, 1913; Forbes, 1881, 1883; Hoogendoorn and Heimpel, 2004; Lundgren et al., 2004, 2005; Putnam, 1964; Ricci and Ponti, 2005; Ricci et al., 2005; Triltsch, 1999). Some species of coccinellids, i.e. *Coccinella reitteri* and *Spiladelpha barovskii kiritschenkoi*, are thought to be exclusively pollinivorous. Aphids do not occur within the high-altitude habitats of these ladybeetles, and they cope with the dearth of prey by feeding on pollen, especially that of *Leontopodium alpinum* (Hodek and Honěk, 1996; Savoiskaya, 1970). Comparatively few coccinellid species are exclusively phytophagous or mycophagous, and most species in this family are best described as omnivorous.

Of the entomophagous species of ladybeetles, beetles reared on a diet consisting solely of pollen seldom develop entirely or mature eggs without supplemental nutrition; thus pollen represents an “alternative food” (as defined by Hodek, 1967) for many species of ladybeetles. An important exception is *Coleomegilla maculata*, which can complete development on pollen from a number of plants (Lundgren and Wiedenmann, 2004; Michaud and Grant, 2005; Smith, 1961), and can produce

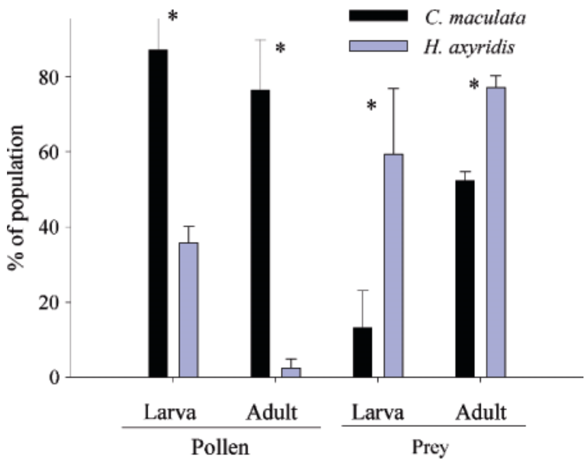

Fig. 6.1 Frequency that *Harmonia axyridis* and *Coleomegilla maculata* collected during anthesis from field corn had pollen and prey remains in their guts (Reproduced from Lundgren et al., 2004. With permission from the Entomological Society of America)

viable eggs on a diet consisting solely of *Zea mays* (Lundgren and Wiedenmann, 2004). Although pollen is an alternative food for most ladybeetles, it still serve a critical role in sustaining these natural enemies during periods of low prey availability (Ricci et al., 2005), or when prey is of low quality. Furthermore, pollen is important for building fat reserves used in diapause and migratory flights in some ladybeetles, and pollen engages sexual maturation of overwintered beetles. Most research has focused on pollinivory in adult ladybeetles, although some experiments suggest that larvae of ladybeetles can be quite pollinivorous (Hoogendoorn and Heimpel, 2004; Lundgren et al., 2004). For example, Lundgren et al. (2004) show that larvae of *C. maculata* and *H. axyridis* feed on *Zea mays* pollen more frequently than do adults, and that *C. maculata* larvae are more frequently pollinivorous than insectivorous during *Zea mays* anthesis (Fig. 6.1).

6.1.5 Neuroptera: Chrysopidae

The dietary breadth of lacewing adults is more extensively explored than for the larval stage. Most chrysopid adults are phytophagous to some degree, feeding on plant tissue (leaf-scraping; described by Sheldon and MacLeod, 1971), nectar, and pollen (Bozsik, 1992, 2000; Canard, 2001). The adults of some genera within Chrysopidae appear to be predominately pollinivorous (*Eremochrysa*, *Hypochrysa*, *Kimochrysa*, *Pamochrysa stellata*, and *Pimachrysa*). There is some evidence that adults of *Chrysoperla*, an important genus to biological control, are also predominately phytophagous. Up to 40 species of pollen (especially from the Brassicaceae, Chenopodiaceae, Rocaceae, and Graminae) are reported from the guts of field-collected *Chysoperla* spp. (Villaneve et al., 2005), and adults have been shown to aggregate to *Z. mays* tassels during anthesis (Sheldon and MacLeod, 1971), presumably to feed on pollen, although aphids are often found at high densities on *Z. mays* tassels. *Phleum pratense* pollen sustains low levels of oviposition in *C. carnea*, but egg production is lower on a pollen-only diet versus a more diversified one (Sundby, 1967). Exploring alternative pollen species may reveal pollens that could better promote reproduction in *Chrysoperla carnea* and other lacewing taxa.

Omnivory in lacewing larvae has gained attention due to several recent reports. In the past, lacewing larvae were thought to digest prey extra-orally and consume liquid foods exclusively. A series of experiments shows that larvae of *C. carnea* do not digest food extra-orally, nor do they possess the digestive physiology for extra-oral digestion (Yazlovetsky, 2001, and references therein). Because lacewing larvae were thought to be largely carnivorous, literature on pollinivory and glucophagy (see Chapter 2) by this life stage is scarce. Nevertheless, research is beginning to reveal phytophagy in *Chrysoperla* larvae. Larvae of *C. carnea* feed on *Z. mays* pollen in the laboratory (Pilcher et al., 1997), and even though this food on its own is suboptimal for larval survival, high quality non-prey foods such as *Z. mays* pollen may help to improve larval fitness when prey quality is poor (Patt et al., 2003).

6.1.6 Heteroptera

Many families of Heteroptera are described as omnivorous, and feeding behavior is best understood in the Anthocoridae, Nabidae, Reduviidae, Geocoridae, and Asopinae (Pentatomidae). Of these more carnivorous heteropterans, pollinivory research has focused almost exclusively on anthocorids. Many species of anthocorids (especially in the Anthocorinae) feed on pollen, although gut content analyses are scarce (one example is Corey et al., 1998). Anthocorids can often be captured in flowers, presumably feeding on nectar and pollen when prey is absent. Some species are quite herbivorous, preferring to feed on flowers or pollen even in the presence of prey (Bacheler and Baranowski, 1975; Carayon and Steffan, 1959; Corey et al., 1998; Dicke and Jarvis, 1962). Aggregations of *Orius insidiosus* shift between *Glycine max* (soybean) and *Z. mays* fields depending on the respective flowering periods of these crops (Dicke and Jarvis, 1962; Isenhour and Marston, 1981), and these bugs change their seasonal within-plant distribution in corn to best exploit available pollen during anthesis (Coll and Bottrell, 1991). Several species of *Anthocoris* aggregate on male *Salix* catkins during anthesis, and leave as the catkins senesce (Anderson, 1962a). Similarly, spring populations of *Orius vicinus* aggregate on flowers of Rosaceae, feeding on the flowers even in the presence of prey elsewhere on the plant (Fauvel, 1974). Some species of anthocorids can complete development on a diet consisting solely of *Z. mays* pollen (Kiman and Yeargan, 1985; Pilcher et al., 1997; Salas-Aguilar and Ehler, 1977), and nymphs have been observed to feed on corn pollen in the field (Dicke and Jarvis, 1962).

In the laboratory, *O. vicinus* completes development more quickly on the pollen of several rosaceous species than on some prey species, although resulting adults are smaller (by 10%), have more malformations, and lay fewer eggs than prey-fed individuals (Fauvel, 1974). But even "unsuitable" pollens (which do not permit pupation) such as that of *Mercurialis annua* are able to sustain *O. vicinus* nymphs for up to 40 days. Another laboratory experiment shows that nymphs and adults of *Orius majusculus* gain the most weight when fed on a diet of corn pollen and water; adults do even better on the pollen diet than when fed on prey (spider mites) alone (Obrist et al., 2006a).

Although nabids, pentatomids, reduviids and geocorids feed on plant tissues other than pollen, the only research on pollinivory by these insects was conducted in the 1970s by Stoner and colleagues (Stoner, 1970, 1972; Stoner et al., 1974, 1975). Pollen was invariably found to be the most suitable plant substance for survival in the absence of prey for these predatory heteropterans, and allowed nymphs to survive for up to 20 days with no other food.

6.1.7 Diptera: Syrphidae

All adults of Syrphidae are believed to use nectar and pollen as principle foods, but the degree to which they rely on pollen varies from species to species (Gilbert, 1981) (see also Chapter 2). For example, of eight common species of syrphids in the U. K., Gilbert found three that consume almost exclusively pollen, and the other five divide their diets fairly evenly between nectar and pollen. Care must be taken when describing a syrphid species as exclusively pollinivorous based on limited observations, because reproductive and physiological status predetermines what foods the flies will forage for (Haslett, 1989). The locale where pollen is consumed differs for syrphids; some consume pollen on the flowers, whereas others (*Xylota* spp.) feed on pollen from the phylloplane (Gilbert, 1986a; Holloway, 1976). Diurnal flight activity is strongly correlated with pollen availability for at least some species (Maier and Waldbauer, 1979), and syrphids sometimes display flower constancy, selectively visiting flowers of a single species (Goulson and Wright, 1998; Olesen and Warncke, 1989; van der Goot and Grabandt, 1970). Not all species have such fidelity to specific plants; *Scaeva pyrastri* visits flowers somewhat indiscriminately (Schneider, 1948; van der Goot and Grabandt, 1970).

Larvae of Syrphidae display a wide range of feeding habits, and are categorized as insectivorous, phytophagous, scavengers, or saprophytic (Gilbert, 1986b; Maier, 1978; Parmenter, 1953a; Schneider, 1969). All entomophagous syrphid larvae occur in the subfamily Syrphinae, and can be classified as strictly or factultatively insectivorous (Gilbert, 1986b). As an example of the latter, the genus *Platycheirus* feeds on both aphids and rotting plant material (Gilbert, 1986b). Although pollen-feeding has not been observed in entomophagous syrphid larvae, it is conceivable that some of the more polyphagous taxa will accept pollen if it were offered; more research on the dietary breadth of syrphid larvae is required.

6.1.8 Hymenoptera: Formicidae

If there was ever a scoundrel in the pollination drama, that role has been assigned to ants. (Faegri and van der Pijl, 1966)

Ants are key components of insect communities, and while they are known to consume pollen, it is surprising that this component of the ant diet does not receive more attention. Ants are frequent visitors to flowers and are commonly observed to be transporting pollen on their bodies (Peakall et al., 1991). Because adult ants consume primarily fluids, filtering all but the smallest particles from liquid meals, they must transport pollen grains to their larvae for digestion (see Chapter 10 for more discussion). Indeed pollen feeding by larvae is widespread in certain groups of ants, and may be a universal component in the diets of polyphagous species. For example, nearly all of the larvae of Pseudomyrminae ants feed on different pollens to various degrees (Wheeler and Bailey, 1920), but the dietary range of most species of ant larvae remains a mystery.

Given that ants are numerically abundant in nearly every terrestrial habitat worldwide, and that ants frequently visit flowers, it is surprising that plants have not come to rely on these insects as pollinators (Beattie and Hughes, 2002; Holldobler and Wilson, 1990). Peakall et al. (1991) present a compelling case that the reason that plants avoid ant pollinators is because the ants produce antibiotic substances that kill the pollen before it can be transferred to another flower. Nevertheless, some plant species that produce copious amounts of pollen and rely on general flying insects as pollinators may occasionally be pollinated by ants (Beattie and Hughes, 2002), and other plants actually specialize on ants through several adaptations outlined by Hickman (1974). How changes in the pollen grains alters their nutritional qualities for the ants is worthy of additional study.

6.1.9 Mantodea: Mantidae

Tenodera aridifolia sinensis can complete the first stadium on a diet consisting only of pollen collected by honeybees (Beckman and Hurd, 2003). Although mantids fed only pollen do not gain body mass as well as prey-fed individuals, adding pollen to the diet of prey-fed individuals results in significantly higher body mass accumulation (Beckman and Hurd, 2003). In the field, mantises that dwell on flowers produce more eggs and have a greater body mass relative to individuals collected from non-flowering plants (Hurd, 1989). Hurd hypothesizes that this may be a reflection of pollen feeding under field conditions.

6.2 Parasitoids

Flower-visiting is commonly recorded in parasitoids (Allen, 1929; Jervis et al., 1993; Leius, 1967), though it is not always clear whether parasitoids visit flowers for nectar, pollen, or other reasons. Direct feeding on pollen is apparently restricted

Table 6.3 The occurrence of pollinivory within selected parasitoid families of Insecta. Pollen feeding is observed only for the adult stages of parasitoid species

Family	Species	Pollen species consumed	Reference
Hymenoptera			
Braconidae	*Asobara*	*A. glutinosa*	(Eijs et al., 1998)
Eulophidae	*Edovum puttleri*	*Anethum graveolens*	(Jervis, 1998)
Ichneumonidae	Parasitoids of spruce web-worm sawfly (*Cephalcia abietis*)	Grass pollen	(Kanecka, 1993)
Ichneumonidae	*Itoplectis conquisitor*	*Pinus sylvestris*	(Leius, 1961a)
Ichneumonidae	*Liotryphon strobilellae*	*C. avellana*	(Györfi, 1945; Jervis et al., 1993)
Ichneumonidae	*Rhyssa persuasoria*	*Pinus*	(Hocking, 1967; Jervis et al., 1993)
Ichneumonidae	*Scambus buolinae*	*P. sylvestris*, *Papaver orientale, D. carota*, *Pastinaca sativa*, *A. artemisifolia*, *Solidago canadensis*, *A. majus*, *B. populifolia*, *P. resinosa*, *Tulipa*, *Z.mays*, *Malus*	(Leius, 1961b, 1963)
Ichneumonidae	*Tryphon signator*	Grass pollen	(Hassan, 1967; Jervis et al., 1993)
Mutillidae		Morphological adaptations to pollinivory	(Jervis, 1998)
Scoliidae		Morphological adaptations to pollinivory	(Jervis, 1998)
Tiphiidae		Pollen	(Quicke, 1997)
Trichogrammatidae	*Trichogramma bourarachae*	*Lycopersicon* (tomato)	(Rohi et al., 2002)
Trichogrammatidae	*Trichogramma brassicae*	*Z. mays*	(Zhang et al., 2004)
Trichogrammatidae	*Trichogramma chilonis*	*Gossypium hirsutum*	(Geng et al., 2006)

to medium-sized or large parasitoids, and is highly dependent on mouthpart structure (Jervis et al., 1996b). Pollen is one of the most nutritious non-prey food sources for parasitoids based on its protein levels (Jervis et al., 1996b); still, pollen-feeding by parasitoids has been studied much less frequently than sugar-feeding.

6.2.1 Diptera

Although tachinid adults visit flowers and some species are considered pollinators (Allen, 1929), actual pollinivory is not frequently documented (Herting, 1960; as reported by Jervis et al., 1996b). Sources of protein do not appear to be critical for many Nearctic species in this group, and adults survive for weeks in cages provided with only a sugar source (Wood, 1992). Mouthparts of tachinid adults are long and siphoniphorous or small and sponging (Allen, 1929; Wood, 1992). Thus, it does not appear that Tachinidae are capable of feeding on pollen grains directly because of their mouthpart morphology, although they may consume pollen indirectly if its contents are solubilized in fluid.

Pollinivory seems to be more important to parasitoid bombyliids than the Tachinidae. Initially believed to be exclusively glucophagous, direct observations proved that many (if not all) species of bee flies consume pollen in the field (Deyrup, 1988). In fact, these flies were observed to feed at plants in the Commelinaceae, which produce no nectar. Deyrup also describes several morphological adaptations that facilitate pollen collection and consumption in bombyliids.

6.2.2 Hymenoptera

Much of the literature suggests that pollen is either avoided by parasitoid Hymenoptera or is consumed only indirectly when it contaminates nectar, honeydew, and water sources (Jervis, 1998). This being said, few studies on pollinivory in parasitoid Hymenoptera have been published, and so making definitive conclusions regarding the importance of pollinivory to parasitic wasps is premature. Parasitoid wasps frequently visit flowers, and a number of studies support the notion that these insects are predominately feeding on nectar. Jervis et al. (1993) did not find pollen in the dissected guts of 42 ichneumonoid wasps (representing seven species) that were collected on flowers. Leius (1963) showed that *Scambus buolianae* did not ingest dry pollen in the laboratory. Microscopic examination has revealed that mouthpart structure in some families of parasitoid Hymenoptera does not allow them to feed on pollen, and some taxa actually have mechanisms for filtering pollen out of nectar. Instances of pollen-filtering were reported from Perilampidae and Eucharitidae, whose digitate labrum is used to filter pollen grains from liquid foods (Darling, 1988). Still, *Asobara* was able to increase fat reserves when reared on pollen, suggesting that some parasitoids may obtain nutrients directly from pollen (Eijs et al., 1998). Although Jervis et al. (1993) did not find pollen in the guts of parasitoids, they did observe what may amount to pollen feeding in the field, when parasitoid wasps would spend considerable time probing the sides of the corollas of flowers with open mouthparts.

Although indirect pollen feeding appears at first glance to be trivial to the nutrition of insects, there is evidence that this form of consumption can have important implications for the fitness of wasps and other natural enemies. In fact, pollen is naturally found contaminating nectar sources of many plant species (Todd and Vansell, 1942). Pollen loses amino acids and proteins within minutes of being placed into sucrose solution (Linskins and Schrauwen, 1969; Stanley and Linskins, 1965). Nectar contaminated with pollen absorbs proteins and amino acids from the grains, such that amino acid constituency and abundance of contaminated nectar are altered relative to clean nectar (Gilbert, 1972), and amino acid content of pollen-contaminated nectar increases over time (Erhardt and Baker, 1990) (these relationships are also discussed in Chapter 3). The quantity of pollen grains, and the species of pollen ultimately affect how many nutrients make their way into a nectar solution (Erhardt and Baker, 1990).

As non-prey foods go pollen is quite nutritious, and even as a nectar contaminant, pollen improves fecundity and longevity of other insects (Gilbert, 1972; Todd and Vansell, 1942) and possibly parasitoids. Leius (1961a, b, 1963, 1967) reports that sucrose solutions containing pollen significantly improve the longevity and fecundity of *Scambus buolianae* and *Itoplectis conquisitor* in the laboratory, but feeding on pollen without host-feeding is insufficient to produce eggs. *Trichogramma bourarachae* fed *Lycopersicon* sp. pollen had double the lifespan of unfed females, but the results in these treatments were not statistically different (Rohi et al., 2002). Fitness of other *Trichogramma* (*T. chilonis* and *T. brassicae*) species is promoted through the provision of pollen mixed in solution, but its suitability depends on what the pollen is mixed with. In one instance, mixing pollen with honey prolonged longevity of *T. chilonis* over honey alone, especially when host eggs accompany these non-prey foods (Geng et al., 2006). Mixing pollen with water improves longevity of *T. brassicae* over water alone, but for this species adding pollen to honey yields no measurable benefits (Zhang et al., 2004).

Given that most parasitic Hymenoptera appear to have mouthpart morphology that is suited to pollinivory, that closely related groups of carnivorous Hymenoptera are known to feed on pollen (Hunt et al., 1991), and that flower-visiting commonly exposes these wasps to pollen, it is surprising that pollinivory is not more prevalent within this group of entomophages. Two possible explanations for this phenomenon are (1) parasitoid wasps as a guild are not able to digest pollen, and therefore avoid feeding on pollen grains, or (2) parasitoid wasps are particularly susceptible to the defenses of pollen grains. The influences of pollen defenses and the structure and function of arthropods to pollinivory are discussed in subsequent chapters. Finally, it is possible that pollinivory is more prevalent in parasitoids than currently recognized, but glucocentric (to coin a term…) research on parasitoid nutrition has dominated the literature (Jervis and Kidd, 1996) and the importance of pollen feeding has been overlooked. Gut dissections of field-collected wasps are desperately needed, but are complicated by the fact that dissected specimens are difficult to identify (Jervis et al., 1993). Or if a pollen-specific molecular marker can be developed, then other forms of gut analysis (e.g., PCR, ELISA) may be employed to identify the importance of pollen feeding to this group.

6.3 Conclusions

An array of economically important natural enemies consumes pollen from a diversity of plants, including that of crop species. Furthermore, even fluid-feeding species not generally thought of as pollinivorous can benefit from pollen nutrition, which is readily released into sugar solutions. Recognizing the fact that many biological control agents consume pollen as part of their diet is the first step in designing effective biological control programs to conserve these natural enemies in our cropland. But pollen differs in its structure and nutrition from arthropod prey, and these natural enemies possess specialized adaptations that allow them to fully exploit pollen as food, a topic that will be discussed more in the next chapter.