

# Chapter 2

## The Sugar Feeders

Because feeding on sugary fluids does not require considerable specialized morphology or physiology, most (if not all) of the arthropods that are commonly designated as entomophagous will readily feed on nectar and honeydew. In addition to taxonomic groups treated in detail in this chapter, several other groups of natural enemies consume sugar, predatory wasps being one of the more conspicuous cases in point (Beggs, 2001; Cuautle and Rico-Gray, 2003; Opler, 1983). Indeed, Krombein (1951) found 93 species of wasps (more than half of those found locally) fed on honeydew of the tulip tree scale, *Toumeyella liriodendri*. Even epigeal predators like Carabidae and Staphylinidae will readily consume sugar sources when offered (Lundgren, personal observations), and when one considers that 35% of native grass plants have root sternorrhynchans in some habitats (Tennant and Porter, 1991), the potential importance of sugar-feeding to this understudied guild of predators may be much greater than is currently appreciated. Although many entomophagous arthropods accept sugar sources as food, these foods are typically insufficient as a sole source of nutrition for all life processes. In short, nectar is great for supporting short-term metabolic requirements and survival. But nectar and honeydew seldom possesses the nutritional wherewithal to support development and reproduction in natural enemies. This notwithstanding, the taxonomic breadth of natural enemies known to consume sugar is testament to the importance of this non-prey food to natural enemy populations.

### 2.1 Predators

#### 2.1.1 Arachnida: Araneae

*All spiders are carnivorous. Their prey consists chiefly of insects; but they will feed on other spiders that they can overcome, even on weaker members of their own species.* (J. H. Comstock, 1913)

This historical view of spider feeding behavior is only recently being challenged, and now it is widely understood that many spiders include nectar and honeydew in their diets, and that sugar promotes longevity in spiders under some conditions (Pollard et al., 1995; Taylor and Foster, 1996; Vogelei and Greissl, 1989). Spiders have infrequently been observed feeding on honeydew; one instance, (the only example of this phenomenon I could find), involves the ant-mimicking salticid, *Myrmarachne foenisex*, which consumes coccid honeydew (as cited in Taylor and Foster, 1996). Some of the best studied examples of glucophagy in spiders relate to foliar- and flower-dwelling species feeding on nectar.

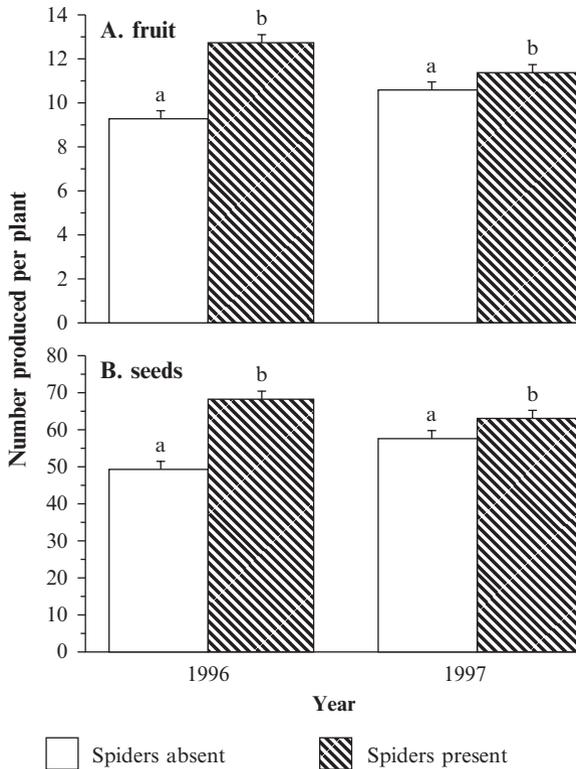
Spiders frequently hunt on flowers, and at least some of these flower-hunting species benefit from floral food sources. Because spiders have short mouthparts, nectar sources buried deep within the flower are difficult to access. But hungry spiders are resourceful, and have devised ways of getting at concealed nectar when in a pinch (Vogelei and Greissl, 1989). ‘Wandering spiders’ have been observed to visit the flowers of *Terminalia catappa*, *Eupatorium serotinum*, and *Hibiscus tiliaceus*, where they bury their faces in the flowers to ingest nectar meals (Taylor and Foster, 1996). To feed on the nectar of *Daucus carota*, males of *Misumenoides formosipes* pull the flower close to their mouthparts using their first pair of legs. Then they squeeze the nectary with their fangs, presumably to ‘milk’ the nectar from the flower (Pollard et al., 1995). The spiders will visit several nectaries from the same inflorescence, spending about 40 s at each one.

The size and nectar-status of inflorescences affect spider residence decisions, and while these floral characteristics also influence visitation by prey, spider residence time may be related in part to their use of these nectar resources (Schmalhofer, 2001). Crab spiders are frequently reported to be more attracted to large inflorescences as hunting sites. They also preferred umbels that produced the most nectar, and were likely to leave umbels that did not contain nectar-producing flowers (Morse and Fritz, 1982). Nectar-bearing umbels were more attractive to prey insects, but Morse (1986) was unable to detect differences in predation frequency on umbels of large and medium sizes, even though fewer prey insects arrived at the medium-sized umbels. Whether consuming nectar may have contributed to the satiation of the crab spiders was not determined, but the causation bears investigation.

Extrafloral nectaries (EFNs) are accessible to and frequently consumed by spiders (Edmunds, 1978; Hespeneide, 1985; Lanza, 1988; Taylor and Foster, 1996). Both immature and adult spiders feed on EFN e.g., both life stages of *Hibana tiliaceus* feed on the EFNs of *Ricinus communis* (Taylor and Foster, 1996). Taylor and Pfannenstiel (in press) show that *Cheiracanthium inclusum* hatchlings fed EFN from *Terminalia catappa* have markedly higher fitness when they are prey limited than those not provided sugar. Spider nymphs offered only low quantities of prey (three *Helicoverpa zea* eggs per week) molt only once. When this same dietary treatment is supplemented with nectar, the nymphs molt up to nine times and survive for 505 days. When the spiders are provided with an intermediate quantity of prey (15 eggs per week), none mature to adulthood; nectar allows this treatment to fully mature and produce eggs in 50% of the emerged adults. Finally, nectar provision allows spiderlings fed 75 eggs per week to grow to a size equivalent to those

fed 375 eggs per week in the absence of nectar. Clearly, this sugar source dramatically improves the fitness of developing spiders.

Two studies to date show that glucophagy in spiders benefits plants that produce extrafloral nectaries. Spider abundance is positively associated with plants that produce extrafloral nectar. Jumping spiders, *Eris* sp. and *Metaphidippus* sp., are six times more attracted to *Chamaecrista nictitans* that have extrafloral nectaries than those without (Rurhen and Handel, 1999). Similarly, *Phryganoporus candidus* colonies are an order of magnitude larger on *Acacia ligulata* plants with extrafloral nectaries than on those without (Whitney, 2004). On *A. ligulata*, seed set is higher on plants with spiders and nectaries. Whitney showed that this was likely because fruit protected by web colonies are less damaged by predispersal seed predators (although it is worth noting that stable isotope analysis could not verify that the spiders were actually consuming the nectar in this case). Excluding the jumping spiders from *C. nictitans* results in lower seed set and fruit production under field conditions (Rurhen and Handel, 1999) (Fig. 2.1).



**Fig. 2.1** Mean production (plus SE) of fruit and seeds by *Chamaecrista nictitans* as a function of jumping spider (*Eris* sp. and *Metaphidippus* sp.) presence in field patches of varying sizes in 1996 and 1997. Years were analyzed separately. Bars marked with different letters are significantly different (Reproduced from Ruhren and Handel, 1999. With permission by Springer)

### 2.1.2 *Arachnida: Acari*

Predaceous mites frequently consume sugars, and although the strength of the interactions varies both by the sugar source and the mite species in question, it is generally safe to say that glucophagy is largely used as a fuel for the short-term metabolic needs of the mites. van Rijn and Tanigoshi (1999a) present a list of studies involving sugar feeding in predaceous mites and how the mites have put the sugar to use. Trends from this literature search reveal that sugar feeding in mites drastically improves survival over starved or water-fed individuals, although nectar and honeydew is not sufficient to support reproduction on its own. However, a number of studies show that sugar sources can improve reproduction over a prey-only diet for many species. The two most commonly studied sources of sugar for predaceous mites are sternorrhynchan honeydew and nectar from extrafloral sources.

Honeydews from aphids, coccids, and whiteflies have all been evaluated as food for different predaceous mite species. It appears that mites vary in their ability to use these sugary secretions as a food, and the quality of honeydew from different sources varies in its nutritional suitability (as will be discussed at length in Chapter 5). For instance, nymphs of *Typhlodromips swirskii* could not complete development on the honeydews from three non-whitefly sternorrhynchans (Ragusa and Swirski, 1977), nor could nymphs of *Euseius victoriensis* complete development on honeydew from *Orchamoplatus citri* (James, 1989), although the sugar improved mite survival over a water-only diet. Still, other studies show that some predatory mites can complete development on honeydew-only diets, though survival is invariably less than 31% (Bruce-Oliver et al., 1996; Ferragut et al., 1987; Nomikou et al., 2003b).

The effects of honeydew consumption on reproduction have also been studied extensively for predaceous mites. Similar to nymphal development, some honeydews support reproduction on their own in certain predaceous mites (Nomikou et al., 2003b), but this is far from always being the case (Bruce-Oliver et al., 1996; Ferragut et al., 1987; James, 1989; McMurtry and Scriven, 1964a; Ragusa and Swirski, 1977). More often, it has been reported that honeydews in addition to prey support higher levels of reproduction than when these mites are fed on prey alone (McMurtry and Scriven, 1964b; Ragusa and Swirski, 1977; Zhimo and McMurtry, 1990). Another common observation is that honeydews are able to improve survivorship of adults over unfed individuals (Bruce-Oliver et al., 1996; McMurtry and Scriven, 1964a, 1965; Nomikou et al., 2003b), which may improve lifetime fecundity rates. Honeydew may also serve to shorten the duration of the pre-oviposition period in predaceous mites (Ragusa and Swirski, 1977).

The nutritional suitability of EFN for predatory mites is the focus of several studies, and results are in line with those seen for honeydew. In the field, *Anystis* sp. were seen to feed from the EFNs of *Prunus sargentii* and *Populus tomentiglandulosa*, and *Czenspinkia* sp. was seen feeding from the cup-like EFNs of *Paulownia tomentosa* (Pemberton, 1993). In the latter case, the *Czenspinkia* mites stand on their hind legs to reach the nectar contained in cup-like nectaries on the plant.

In the laboratory, EFN from lima beans improves the survivorship of *Phytoseiulus persimilis* over water alone (Choh et al., 2006), and nectar from various organs on *Ricinus communis* is better able to sustain *Ipheseius degenerans* adults compared to water alone (van Rijn and Tanigoshi, 1999a). Bakker and Klein (1992) found that cassava exudates arrests adult foraging behavior and sustains nymphal development in *Typhlodromalus limonicus*. Thirty-one percent of *Euseius fustis* can complete development on these cassava exudates (Bruce-Oliver et al., 1996). Although *R. communis* nectar supports little reproduction by *I. degenerans* on its own, adding nectar to a pollen diet increases fecundity by 25% over pollen alone (van Rijn and Tanigoshi, 1999a). The importance of EFN to predatory mites can be seen in their numerical response to these nectaries. After 10 days in the laboratory, leaves of *Viburnum tinus* possessing EFNs contain seven times as many phytoseiids and eight times as many total predatory mites than a plant with nectaries excised (Walter and O'Dowd, 1995).

### 2.1.3 Heteroptera

Many members of predaceous families of Heteroptera are phytophagous to varying degrees, and members of the Anthocoridae, Nabidae, Pentatomidae (Asopinae), Geocoridae, Reduviidae, and Phymatidae all feed on sugar, mainly nectar. For anthocorids, *Orius tristicolor* feeds at EFNs of cotton (Yokoyama, 1978) and at floral nectaries of *Quillaja saponaria* (Bugg, 1987), and *Anthocoris gallarumulmi* feeds on aphid honeydew (Miller, 1971). *Geocoris pallens* also feeds at the EFNs of cotton, and both this species and *O. tristicolor* lay their eggs in close proximity to these nectaries (Yokoyama, 1978). Anthocorids generally have substantially greater longevity when provided with sugar over water alone (Anderson, 1962b; Chu, 1969). Indeed, nectar is essential for development of *G. pallens* raised on different cotton varieties in the absence of prey (De Lima and Leigh, 1984). Up to 17% of this species completes development to the 5th instar on a diet of only nectar and leaf tissue; 55% of insects develop to 4th instars. Adult longevity is four times greater in nectar-fed *G. pallens* than those fed only leaf tissue. Another geocorid that feeds on nectar is *G. uliginosus*, who defends foliar nectaries of *Senna obtusifolia* from visiting *Dorymyrmex* ant (Crocker and Whitcomb, 1980). Finally, observers of EFNs frequently record predatory heteropterans (e.g., Reduviidae, Pentatomidae, and Miridae) as visiting and consuming the nectar (Hespenheide, 1985; Keeler, 1978).

Some indirect evidence of the importance of nectar-feeding in predaceous Heteroptera is summarized by Naranjo and Gibson (1996). In reviewing the literature on population densities of *Orius*, *Geocoris*, and *Nabis* species in nectaried versus nectariless cotton, they found that the vast majority of studies show reduced predator densities in nectariless cotton. Obviously, the presence of nectar is not the only difference between these systems, but the results are at least in line with the hypothesis that nectar-feeding occurs and is important for these heteropterans.

Members of the Phymatidae (ambush bugs) frequently hunt on flowers, where in addition to consuming flower-visiting prey, they appear to also drink nectar. *Phymata pensylvanica* was observed by Balduf (1939b) to insert their mouthparts into the nectar-bearing regions of *Helianthus tuberosus* and *Symphiotrichum ericoides* flowers. He observed this behavior on a windy day when prey were not actively visiting flowers, and he concluded that the ambush bugs were drinking nectar to compensate for poor hunting conditions. Nearly 60 years later, Yong (2003) revisited this system to find that nectar feeding is important to the survival of these normally predaceous bugs. In the laboratory, *P. pensylvanica* adults prefer to drink from sugar water over plain water under choice conditions, indicating their ability to perceive nectar. Although bugs do not attain adulthood on a diet of sugar water alone, *P. pensylvanica* survives for around two months on this non-prey food; on average, sugar-fed individuals survived three times longer than on water alone, although they lose weight over this period. In the field, *P. pensylvanica* moves to inflorescences during and after the 4th stadium. Through the use of cages, the survival of *P. pensylvanica* adults was monitored on inflorescences and leaves in the absence of prey. Nectar provided by the wildflowers is able to sustain the ambush bugs substantially longer than those held on vegetative material. Thus, phymatids provide one more example of predators which hunt on flowers taking advantage of floral resources.

### 2.1.4 Coleoptera: Coccinellidae

*Such common aphidophagous coccinellids as Coccinella spp., Adalia bipunctata (L.), and Cycloneda sanguinea (L.) are often conspicuous as they feed on the leaf nectar of young peach trees in midsummer when aphids are scarce. (Putnam, 1963)*

Floral and extrafloral nectar, as well as honeydew, are a significant food source for many of the Coccinellidae (Hagen, 1962). Indeed, sugar feeding in coccinellids has been going on for a long time; coccinellids found in association with fossilized EFNs of *Populus* date back 35 million years (Pemberton, 1992). From a sensory standpoint, coccinellids are able to distinguish sugar foods from water in choice tests (Koch et al., 2004), indicating their ability to perceive sugar solutions. In addition to prolonging their lives in the absence of prey, glucophagy can promote reproduction when only suboptimal prey is available, and honeydew may be of wide importance in arresting coccinellid foraging behavior.

In addition to frequently feeding on floral nectar sources (Bugg, 1987; Nalepa et al., 1992; Spellman et al., 2006), coccinellid adults are often some of the most frequent visitors to EFNs (Banks, 1957; Keeler, 1978; Ricci et al., 2005; Stephenson, 1982b). In an extensive literature review, Pemberton and Vandenberg (1993) document 41 coccinellid species (representing 19 genera) that are known to consume EFN. These coccinellids do not show strong fidelity to the nectaries

of any given plant species or group; in sum 32 plant species, representing 23 genera and 15 families, are visited by the ladybeetles. Springtime is often when ladybeetles are found on EFNs (Ewing, 1913; Rockwood, 1952; Watson and Thompson, 1933), presumably because prey is scarce. One study showed that *Stethorus punctillum*, which normally dies within 4–5 days on water alone, can survive for 43.2 days on a diet of nectar from peach tree secretory glands (Putnam, 1955). Another instance of this is *Exochomus flavipes*, for whom sugar water and honey are able to prolong their lives tenfold in the laboratory (Geyer, 1947). Surprisingly, only two instances of coccinellid larvae consuming nectar sources have been documented, *E. flavipes* larvae feeding on EFNs (Geyer, 1947), and *Harmonia axyridis* larvae feeding at the EFNs of *Prunus*, *Populus*, and *Sambucus* (Pemberton and Vandenberg, 1993). This is in spite of the importance of pollinivory to this life stage in several coccinellid species (see Chapter 6).

In addition to providing fuel for normal metabolic processes, honeydew can improve reproduction and is used as a cue for locating the sternorrhynchan prey of ladybeetles. Larvae of *Chilocorus bipustulatus* can be maintained for ‘a long time’ on the honeydew of scale insects in the laboratory (Yinon, 1969). *Stethorus punctillum* feeds the honeydew of *Coloradoa rufomaculata* on chrysanthemum leaves in the laboratory (Putnam, 1955). Evans (2000) reports that *Coccinella transversalis* does not lay eggs on *Helicoverpa armigera* larvae, nor on a diet of sucrose (nutritionally equivalent to honeydew from *Acyrtosiphon pisum* for this coccinellid), when these foods are offered on their own. However, when these two suboptimal foods are offered together, females produce small numbers of eggs (10–15% of fecundity realized on the preferred food of aphids) (Table 2.1). In addition to providing direct nutrition, sternorrhynchan honeydew also functions as a cue for locating sternorrhynchan prey. Carter and Dixon (1984) showed that honeydew of the cereal aphid, *Sitobion avenae*, arrests the movement of *Coccinella septempunctata* larvae. Corn ears coated in honeydew have greater numbers of ladybeetle larvae, and they spent more time searching these sugary ears. Increased residence

**Table 2.1** Number of eggs laid per day [mean (s.e.)] by female *Coccinella transversalis* that were maintained on different diets (n = 6 females per treatment). Honeydew was produced by *Acyrtosiphon pisum*. Within a column, values followed by different letters are significantly different (Data is from Evans, 2000. With permission by Blackwell)

Diet	Days 4–10 of experiment
Aphids	20.0 (3.8) A
<i>Helicoverpa armigera</i> (2nd stadium)	0.4 (0.2) C
Sucrose solution only (150 g l <sup>-1</sup> )	0.0 (–) C
<i>Helicoverpa</i> + sucrose	2.7 (1.3) B
<i>Helicoverpa</i> + honeydew	2.0 (1.2) B

time by the larvae is ultimately associated with fewer aphids. Thus in this case, glucophagy by ladybeetles leads to increased pest suppression.

### 2.1.5 Neuroptera: Chrysopidae

*all green lacewings were for a long time considered predaceous, essentially aphidophagous. Further studies showed that most of them have, at least partially, non-live food, mainly honeydew and other sweet juices* (Canard, 2001)

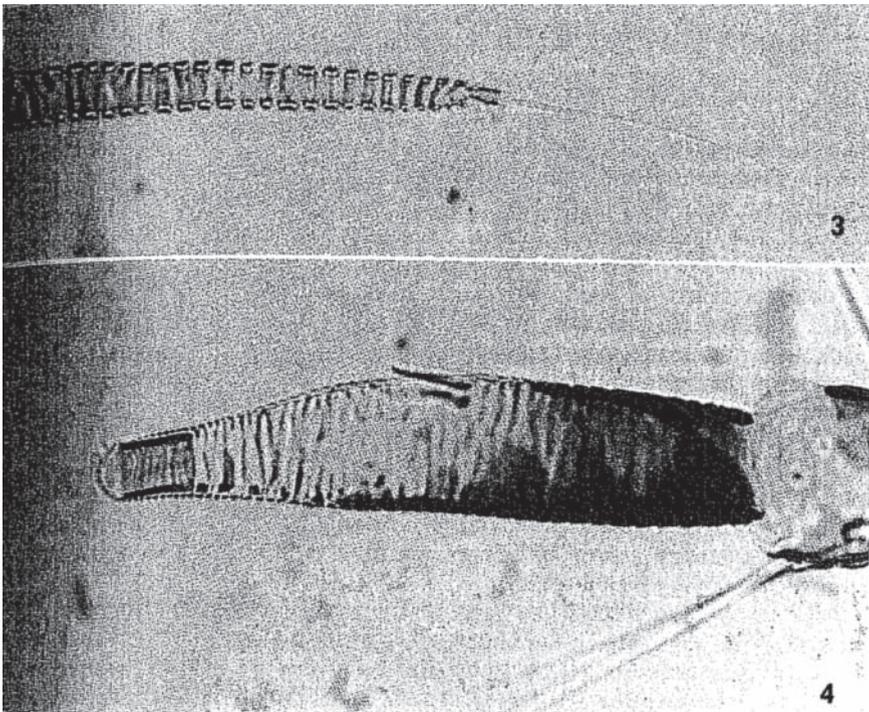
Adults of the Chrysopidae, Hemerobiidae (Bugg, 1987), and Mantispidae (Keeler, 1978) feed at sugar sources of various classes under field conditions. Some hemerobiids feed on honeydew in the field (Stelzl, 1990, 1991 as cited in Canard, 2001), and sugar feeding improves their longevity significantly over water alone (Neuenschwander and Hagen, 1980). Still, the most studied taxa within this order are the chrysopids, and most adult green lacewings are glucophagous to some degree. They consume nectar and various plant exudates, as well as honeydew. In addition to maintaining metabolic processes in the adult stage of chrysopids, a growing body of literature indicates that the larval stage may also rely on sugar meals as an important source of non-prey food.

Many chrysopids are well adapted to a non-carnivorous lifestyle during the adult stage (Canard, 2001; Duelli, 1987; Hagen et al., 1976). Only three genera of Chrysopini are considered to be insectivorous as adults (*Anomalochrysa*, *Atlantochrysa*, and *Chrysopa*) (Canard, 2001), and of these half the species of *Chrysopa* are believed to be non-predaceous (Hagen et al., 1976). The mouthparts of many green lacewings are adapted for sugar feeding. They have symmetrical mandibles without any incisor, and spoon-like laciniae that allow them to scrape dried honeydew from substrates (Canard, 2001). Also, patterns in the digestive systems suggest that there are microbial symbioses that support a glucophagous lifestyle. The trunk diameter of the trachea that leads to the diverticulum (and aerobic gut microorganisms), and its ratio to forewing length is a good predictor of diet in various chrysopid species, with greater tracheation to the gut associated with glucophagy and plant-feeding (Canard, 2001). This potential symbiotic relationship will be discussed more at length in Chapter 15, but suffice it to say that adaptations to a glucophagous lifestyle in chrysopid adults are evident.

Sugar feeding promotes longevity, fecundity, and intrinsic growth rates in green lacewing adults, and these functions are reinforced through observations of sugar feeding by these insects in the field. Sugar feeding is particularly prevalent in *Chrysoperla carnea*; which consumes honeydew (Schuster and Calderon, 1986; Sheldon and MacLeod, 1971), and possibly other sugar sources (Bozsik, 1992) in the field. Sheldon and MacCleod (1971) found that 89% of adults (n = 28) consume honeydew on a single sample date during the early spring when other food sources were scarce, and adults scrape the leaf surfaces with their mandibles to gather dried honeydew. In fact, *Chrysoperla plorabunda* adults can be maintained on a sole diet

of *Pseudococcus citri* honeydew, which allows full reproduction of 150 eggs daily per female (Finney, 1948). Research has not shown sugar-only diets to be capable of supporting reproduction in other lacewing species, although sugars can improve egg production when combined with other foods (Sundby, 1967; Venzon et al., 2006). Under field conditions, research suggests that more eggs and larvae are typically found in fields where honeydew and nectar is relatively more available compared with fields where sugar availability is reduced (Adjei-Mafo and Wilson, 1983; McEwen et al., 1994).

Sugar feeding by lacewing larvae is best studied in *Chrysoperla* spp., which will accept sugar from a variety of sources. *Chrysoperla* larvae visit the EFNs of several plant species in the lab and field (Keeler, 1978; Limburg and Rosenheim, 2001; Schuster and Calderon, 1986). In cotton fields, 21% of *Chrysoperla plorabunda* larvae consume nectar from cotton EFNs, and they are found even more frequently at the EFNs of almond (Limburg and Rosenheim, 2001). Downes (1974) observed *Chrysopa* larvae probing the florets of *Cirsium vulgare* searching for and drinking nectar droplets. In the laboratory, these larvae recognize a sucrose solution when it comes in contact with the tips of their palps (Fig. 2.2). Another unspecified chrysopid species does not recognize dried honeydew, but will readily consume a sucrose solution.



**Fig. 2.2** The apex of antenna (top) and labial palp of *Chrysopa* sp. larva to show terminal sensillae, presumably used in contact chemoreception of sugars (Reproduced from Downes, 1974)

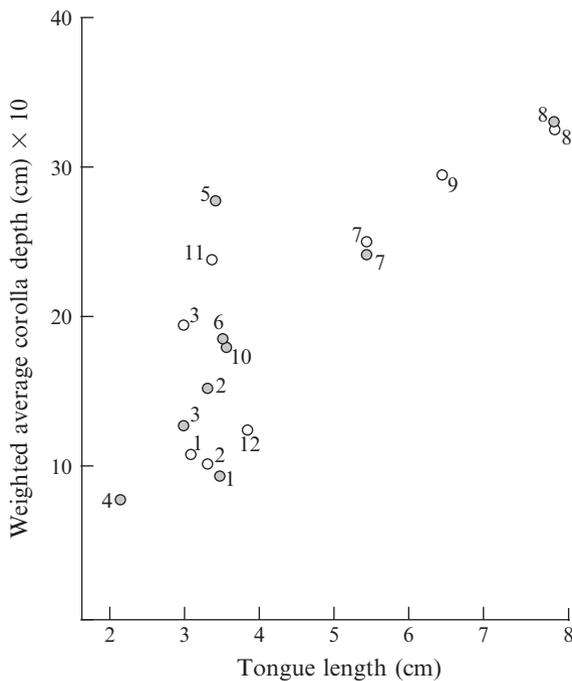
The physiological function of carbohydrates appears to be in sustaining the larvae during periods of prey scarcity, and as a result sugar feeding may lead to higher levels of predation by lacewing larvae. Patt et al. (2003) found that *Chrysoperla carnea* larvae are able to metabolize sucrose more efficiently than bee pollen in the laboratory, and suggest that these larvae are better adapted to sugar feeding than pollen consumption. *Chrysoperla plorabunda* larvae fed sucrose do not lose weight as quickly as unfed individuals, suggesting that nectar can be used immediately as fuel that prevents the burning of energy reserves (Limburg and Rosenheim, 2001). Sugar-feeding can reduce prey consumption (McEwen et al., 1993a), and distracts larvae from foraging for prey in the field (Limburg and Rosenheim, 2001). Still, sugar-fed larvae survive substantially longer than those fed water alone (Limburg and Rosenheim, 2001; McEwen et al., 1993b, 1996), and so prey consumption over their extended lifetimes is probably much higher than for those that are sugar-limited. Larvae fed prey in addition to sugarmeals generally perform better than those on sugar alone (Limburg and Rosenheim, 2001; McEwen et al., 1993b), although natural sugar sources seem to provide additional nutrients not found in a prey-only diet (McEwen et al., 1996).

### 2.1.6 *Diptera: Syrphidae*

Hoverflies are renowned flower visitors, and the physiological adaptations to sugar feeding are remarkably well described for members of this group. Syrphid adults are fairly fussy over which flower species they prefer, and different fly species specialize on specific flower types (Colley and Luna, 2000). Pollen is one floral reward gleaned from this flower feeding (Gilbert, 1985b), although various adaptations bolster the case that nectar is another important food source. The diet of syrphids is associated with their body size; larger body size is correlated with nectar feeding, whereas smaller-bodied syrphids feed more frequently on pollen (Gilbert, 1985b). Also, longer-winged individuals are more likely to feed on pollen, and less on nectar. Pollinivorous species need to spend more time airborne to collect the pollen grains from anthers, and so the smaller body size facilitates the stationary flight necessary for this task. Honeydew is another important sugar source for syrphids in the field (Hogervorst et al., 2007; Belliure and Michaud, 2001). Adults of some aphidophagous species are attracted to the volatiles of honeydew (Belliure and Michaud, 2001; Budenberg and Powell, 1992), and also show a gustatory response to honeydew that is proportional to the concentration of this substance (Sutherland et al., 2001).

Sensing of sugar appears to be accomplished by the labellar taste hairs, rather than the antennae (Hood Henderson and Wellington, 1982). Interestingly, chemosensilla on the ovipositors of two aphidophagous species (*Eupeodes fumipennis* and *E. volucris*) are sensitive to aphid honeydew, and the honeydew components sucrose, tryptophan (and its oxidation product) and alanine (Hood Henderson, 1982). In the non-predaceous hoverfly, *Eristalis tenax*, the flower-visiting adults have labellar taste hairs with receptor cells that only register sugar (sucrose) solutions (Wacht et al., 1996, 2000). Thus, they have the capabilities to taste sugar on potential food sources.

The process of nectar consumption by syrphids illustrates the complex evolutionary developments that have occurred to allow these flies to consume this important food source. The feeding process was first described by Müller (1883), and was advanced substantially by Gilbert (1981). Once the sugar source is identified by the fly, the proboscis is extended until the labellum comes in contact with the sugary fluid. The folds of the labella then separate so that they lie flush with the nectar droplet. Cibarial pumping motions suck the fluid into the mouth (Gilbert, 1981). The labella does not always have to touch the nectar; it can be wicked up along creases in the corolla through capillary functions of the hydrophilic labella (Gilbert, 1981). Several morphological features of the mouthparts are diagnostic for glucophagous syrphid species. Longer, thinner proboscises are associated with nectar feeding (Gilbert, 1985b), and the pseudotracheae of the labella may have spinose closing apparatuses that filter heterogenous materials out of nectar meals (Zaitsev, 1982). The fidelity to different flower species described above may be reflected by their mouthpart morphology. Gilbert (1985b) found that the length of the tongue is strongly correlated with the corolla length of the flowers that they visit (Fig. 2.3). It is presumed that long-tongued flies feed at deeper flowers because the quality of the nectar is



**Fig. 2.3** The relationship between the proboscis length and the average corolla depth (CD), weighted by the frequencies of visitation (weighted average = sum of (% x CD)/10). Species are: 1. *Syrphus ribesii*, 2. *Eupeodes corollae*, 3. *Episyrphus balteatus*, 4. *Melanostoma*, 5. *Melanostoma mellinum*, 6. *Syrpita pipiens*, 7. *Eristalis interrupta*, 8. *Eristalis tenax*, 9. *Eristalis nemorum*, 10–12. *Sphaerophoria* (Reproduced from Gilbert, 1985. With permission by the Royal Society)

superior for these species (see Chapter 3). In this way, a community of syrphids can separate the floral resources to reduce competition much the way that parasitoids do (described below).

### 2.1.7 Hymenoptera: Formicidae

The vast majority of ants consume sugar of one type or another, and the availability and abundance of sugar strongly shapes the dynamics of ant colonies and communities in which they live. In ants, sugar functions to

*make water more drinkable, it stimulates worker activity, and it conserves protein* (Brian, 1973)

Within a colony, most sugar is used by the worker castes. As major nutrient classes (carbohydrates, proteins, and lipids) enter the colony, it is clear that workers receive sugars first, while larvae and queens are the first recipients of lipid and proteinaceous foods (the fate of these higher calorie foods will be discussed more at length in Chapter 10) (Beattie, 1985; Brian, 1973; Carroll and Janzen, 1973; Tschinkel, 2006). The workers use sugary fluids as a fuel for foraging, hunting, and hauling their horde back to the nest (Beattie, 1985). The distribution of sugar among the workers is more rapid and widespread when the colony is starved than when the workers are sated, reaffirming that the workers use sugar for maintaining normal activity patterns (Tschinkel, 2006). By examining respiration rates of the different life stages, Brian (1973) presents evidence that larvae and workers are found to burn up sugary foods before digesting the protein sources. In the laboratory, an average worker of *Labidus rubra* consumes 22  $\mu\text{g}$  of sucrose daily (Brian, 1973). Approximately 20–40% of *Solenopsis* workers return to the nest with a sugar meal, often comprising 35% of their body weight (Tennant and Porter, 1991). When fed honey in addition to a standard, animal protein diet, *Solenopsis invicta* colonies survive better and have greater weight gain than those offered only an artificial diet (Williams et al., 1980).

Physiological characteristics of the ants help to understand the intra-colony dynamics of sugar feeding. One reason that nectar and honeydew are such an important source of food is that worker ants are restricted to a liquid diet, and there simply aren't many non-prey sources of nutritious fluids to eat that don't need processing. Solid food particles are prevented from entering the digestive system of ants by the infrabuccal pocket (Eisner and Happ, 1962; Glancey et al., 1981); workers bring foods like seeds and insect fragments to their 4th instars, who are able to masticate and digest the foods and recirculate the nutrients back to the rest of the colony (this process is discussed at length in Section III). The crop of the workers represents an important evolutionary development that increases the sugar feeding capacity of ants. *Solenopsis invicta* ants that take a sugar meal are externally distinguishable because their crop is so full of fluid (Tennant and Porter, 1991). A more extreme example that illustrates the importance of sugar sources to ant colonies is when the colony devotes a portion of their worker caste specifically to sugar storage,

these workers are called repletes (Wheeler, 1910; Carroll and Janzen, 1973; Holldobler and Wilson, 1990). The repletes in honeypot ants have grossly distended abdomens filled with sugary solutions that are transferred as needed to their attending sisters. These more extreme examples are best noted in arid environments, where environmental conditions are either unpredictable or predictably harsh. Other ants living in arid environments have simply stopped trying to find rare sugarmeals; *Messor* ants in the desert are not attracted to sugar or water sources (Went et al., 1972). Instead they obtain their nutrients exclusively from seeds, rodent and bird droppings, and dead insects.

One of the best studied forms of glucophagy in ants is honeydew feeding. In 1914, William Morton Wheeler found *Iridomyrmex* preserved with aphids in Baltic amber, dating back to the early Oligocene Epoch (38 mya) (Holldobler and Wilson, 1990), and Beattie (1985) believed ant-sternorrhynchan associations to extend as far back as the Cretaceous (135 mya). Ants are primitively carnivorous, but even the most predatory clades will consume honeydew when it drops to the ground or when they encounter it on foliage (Holldobler and Wilson, 1990; Wheeler, 1910). Carroll and Janzen (1973) postulated that the majority of ants will harvest honeydew from Sternorrhyncha, and this substance can comprise a major portion of the diet of many species. As a case in point, *Oecophylla longinoda longinoda* colonies can thrive when fed solely the honeydew of the scale *Saissetia zanzibarensis* (Way, 1954). Ants often call on multiple species of Sternorrhyncha (Beattie, 1985; Way, 1954), and many sternorrhynchans are visited by several species of ants (Nickerson et al., 1977). On cacao in Africa, at least 50 ant species were found to collect the honeydew from the coccid, *Formicococcus njalensis* (Strickland, 1947). The relative contributions of honeydew and prey to the diet of an ant species varies among species, and may even change based on the physiological status of the colony (Way, 1963). One estimate is that honeydew comprises 62% of the diet of *Formica rufa rufa*, whereas prey constitutes only 33% (Way, 1963, and references therein).

Hundreds of species are known to actually tend sternorrhynchans (although many sternorrhynchans are untended by ants), and the strongest mutualisms result in a fascinating sort of pseudo-domestication of the sternorrhynchans by the ants. The three most phylogenetically advanced subfamilies of Formicidae (Dolichoderinae, Formicinae, and Myrmicinae) are comprised of numerous species that tend sternorrhynchans for their honeydew (Holldobler and Wilson, 1990). The mutualism may have resulted from sternorrhynchans evolving to exploit a trophallactic appeasement behavior in ants (Choe and Rust, 2006). When two ants display aggression toward one another, they offer each other food which serves to curb the aggression. The result of providing ants food is that they are less aggressive to the donor. The importance of the mutualistic association between honeydew-producing sternorrhynchans and ants is evidenced in some of the behavioral and morphological adaptations observed in both participants (Way, 1963). In the absence of ants, sternorrhynchans frequently will kick off or simply drop their honeydew droplets. Ants have been shown to palpate the aphid's abdomen with their antennae (Wheeler, 1910), which then exudes a honeydew droplet (a similar behavioral solicitation occurs with mutualistic lycaenid caterpillars; Way, 1963). In fact, ant-tended

sternorrhynchans often possess a ring of small hairs near the anus that actually suspends the honeydew droplet until it can be collected by the ants; untended sternorrhynchans lack this ring of hairs (Wheeler, 1910) a similar behavior solicits honeydew from lycaenid caterpillars. Morphologically, it is thought that some aphid hind-quarters have evolved to resemble the morphology of a donor ant. Thus, ants use similar behaviors to solicit honeydew from sternorrhynchans as they do when soliciting sugar-meals from their nestmates (Way, 1963). In exchange for providing the ants a meal, the sternorrhynchans receive a number of services. The first is that the ants look after the sternorrhynchans; the ants protect their livestock from natural enemies, move them to prime feeding spots on the plant, and may even provide shelter within the ant's nest or through building special structures that harbor the sternorrhynchans (Way, 1954, 1963). Perhaps as importantly, the ants keep the sternorrhynchans clean from microorganisms that would ordinarily colonize the copious amount of honeydew and cause disease within the sternorrhynchans (Way, 1954, 1963). To keep the ants happy, the tended sternorrhynchans increase their feeding rates to provide more honeydew to their bodyguard/butlers. The end result is greater fitness and higher population growth rates in ant-tended sternorrhynchans versus untended colonies. The ants benefit as well, and some species go to extraordinary lengths to ensure that their relationship with sternorrhynchans continue (Holldobler and Wilson, 1990). The queens of one ant species will actually carry sternorrhynchans in their mandibles during the nuptial flight, to ensure that they have a new food source when they land!

There is no doubt that ants are frequent visitors to EFNs, and many ecologists would go so far as to say that ants are the *raison d'être*s of these plant structures. EFNs from a single plant species can attract a wide array of ant species (Barton, 1986; Beattie, 1985; Bentley, 1977b; Keeler, 1978; Stephenson, 1982b), the greatest number that was found in the literature being 22 ant species visiting the EFNs of *Turnera ulmifolia*, eight of which fed only at EFNs (Cuautle et al., 2005). Carroll and Janzen (1973) said it well when they explained that nectar from EFNs “*is eaten by practically any ant that encounters it.*”

In the absence of EFNs, ants are less interested in a plant (Agnew et al., 1982). For example, 75% of nectaried *Cassia fasciculata* plants were tended by ants, compared with <10% of plants lacking nectaries (Barton, 1986). A major benefit provided by ants that visit the EFNs is protection from herbivores. Beattie (1985) laid out several tenets of what makes an ant a good mutualist, some of the most valuable of which are paraphrased as:

1. A dietary need for the nectar
2. Aggressive toward herbivores
3. Are able to defend the plants where and when the plant needs it most

Essentially, the ideal situation for the plant is to develop a strong sense of ‘ownership behavior’ in their EFN visitors. This term refers to the degree to which an ant protects a plant from all interlopers, and the highest degree of ownership behavior is evident when the ants nest directly on the plant within plant-provided domatia (Way, 1963). Sometimes, this ownership can result in plants being kept free of

beneficial insects, such as generalist predators or pollinators that the plant would like to keep around (McLain, 1980).

Compared to the topics of honeydew consumption and EFN visitation, the utilization of floral nectar by ants has received little attention by myrmecologists. Indeed, this has been the case for many years. Wheeler (1910) explains that the dearth of information on flower-visiting ants is

*probably because [ants] treat the flowers very cavalierly, for unlike the bees, they do not concentrate attention on particular plants and make cross-fertilization one of their main avocations.*

Janzen (1977) hypothesizes that floral nectar sources are chemically defended against nectar thieves. It is certainly true that nectars are defended against thieves (see the next chapter), but the bottom line is that floral nectars are not universally toxic to ants, and more work should fill the void on this topic. Given the sexiness of domestication of sternorrhynchans by ants and the use of ants attracted to EFNs as a type of plant immune response against herbivory, it isn't surprising that the comparatively ho-hum consumption of floral nectar has been given short-shrift in the world of ant glucophagy.

## 2.2 Parasitoids

### 2.2.1 Parasitoid Diptera

*The mouthparts of virtually all fly families are specialized fundamentally for fluid feeding* (Gilbert and Jervis, 1998)

With the above statement in mind, it is not surprising to find that parasitoid members of the families Phoridae, Tachinidae, and Bombyliidae consume nectar and honeydew under a variety of circumstances, and that their morphology is well adapted to glucophagy. In fact, honeydew may be a more important food source evolutionarily to calypterate flies than nectar (Downes and Dahlem, 1987). Some of Downes and Dahlem's arguments for the importance of honeydew to the evolutionary history of parasitoid flies (and other non-parasitoid calypterates) are: (1) Flies taste sugars with their feet, so it seems likely that as they evolved, these flies must have walked on sugars. Honeydew is much more likely to be walked upon than nectar. (2) Tachinids skim leaf surfaces while in flight, and regularly touch down at shiny objects on the leaf surface; this is likely related to honeydew foraging. (3) The pseudotracheate labellum of most Diptera is an adaptation to suck up dried honeydews with a minimum loss of water. If nectar were an important source of nutrition, the proportion of long-tongued Diptera would be greater. Moreover, the pseudotracheate labellum is ancestral to the group, which evolved in the Triassic Period. Flowering plants didn't rise to dominance until the Cretaceous, but Sternorrhyncha were widespread in the Permian, long before the radiation of

Diptera. (4) Downes and Dahlem anecdotally point out that there are fewer Diptera found in areas where honeydew is scarce, resulting either as a function of the habitat or resulting from high numbers of ants that protect the honeydew. This final relationship bears further investigation. But certainly there are many instances of honeydew feeding in the literature on parasitoid Diptera. A case in point is with the phorid *Pseudacteon tricuspis*, which survive better on *Aphis gossypii* honeydew than on buckwheat nectar (Fadamiro and Chen, 2005).

Despite the convincing arguments put forth by Downes and Dahlem, parasitoid Diptera frequently are observed feeding on floral and EFN sources (Kost and Heil, 2005; Opler, 1983; Tillman, 2006). In a comprehensive examination, Allen (1929) found many species feeding on floral and extrafloral nectar, and Opler (1983) found that Tachinidae are some of the most frequent nectar-feeding visitors to Costa Rican plants. To some degree, flower feeding parasitoid Diptera can be distinguished from the honeydew feeders based on their mouthpart morphology (Allen, 1929; Gilbert and Jervis, 1998). In Allen's survey, he found that those species that have proboscises that are longer than the height of their head are more inclined to feed on nectar from flowers (only five of 18 feed on non-nectar sources, and never exclusively). Shorter mouthparts are typically associated with feeding at EFN sources (28 of 33 feed on non-nectar sources) (Table 1 of Gilbert and Jervis, 1998, taken from data of Allen, 1929).

*The habitual flower feeder has a slender, strongly-chitinized, elongate proboscis with a small labella at the tip, well adapted for reaching deeply seated secretions of nectar in flowers. The honeydew and surface-nectary feeder, on the other hand, has a short, stout, more flexible proboscis with a large, fleshy labella, better adapted to feeding from exposed surfaces, but very poorly adapted to sucking nectar from flowers* (Allen, 1929)

Gilbert and Jervis (1998) built upon Allen's early description of the relationship between diet and morphology in the parasitoid Diptera. First, nectar specialists in the parasitoid Diptera and Hymenoptera have developed a concealed nectar extraction apparatus (CNEA; Jervis, 1998), which is basically a longer, thinner labellum with fewer pseudotracheal canals. Bombyliids with this CNEA also have spinose edges that may function as nectar filters (Zaitsev, 1982). Those species that feed on honeydew or dried nectar likely have wider labellar surfaces with more pseudotracheal grooves.

The actual process of nectar feeding is described nicely by Gilbert and Jervis (1998), and is summarized here. First, the pseudotracheal canal transports saliva out of the mouth and onto the food. The fluids containing the nectar are then sucked through the interpseudotracheal folds of the labella and into the labral food canal. The prelabral pump is responsible for generating the pressure necessary for this process. Drinking dried sugars requires dissolving them in saliva, hence the wider labella with more pseudotracheae for salival transport. Another observation that merits further research is that the CNEA is disproportionately found in parasitoid Diptera that live in arid regions. Gilbert and Jervis believe that this form of mouthparts may have been selected for more strongly in arid habitats because these flies use nectar as a water source.

### 2.2.2 Parasitoid Hymenoptera

Several exquisite reviews of glucophagy in parasitoid Hymenoptera are currently available (Jervis, 1998; Jervis et al., 1993, 1996a; Wäckers et al., 2005), and I certainly cannot hope to recreate or pre-empt these sources. Still, all shapes and sizes of parasitoids use sugar, and some of the best instances of the function of this food are known from the parasitoid literature. Therefore, sugar-feeding in parasitoids is a topic worthy of at least a brief discussion here.

A number of gut analyses have been applied to indirectly substantiate sugar-feeding by parasitoids in the field. In crucifer fields, nearly 70% of *Cotesia* (spp.) test positive for the presence of sucrose (Wäckers and Stepphun, 2003). Fructose, a sugar that is not commonly encountered in unfed insects but is commonly found at greater levels in plant tissues and exudates, is detectable in less than 21% of the field populations of *Aphelinus albipodus*, *Aphytis aonidiae*, *Macrocentrus grandii* and *Trichogramma ostrinia* (Heimpel et al., 2004). Around 75% of *Diadegma semiclausum* test positive for fructose in the broccoli fields when *Fagopyrum esculentum* flowers are adjacent (Lavendero et al., 2005).

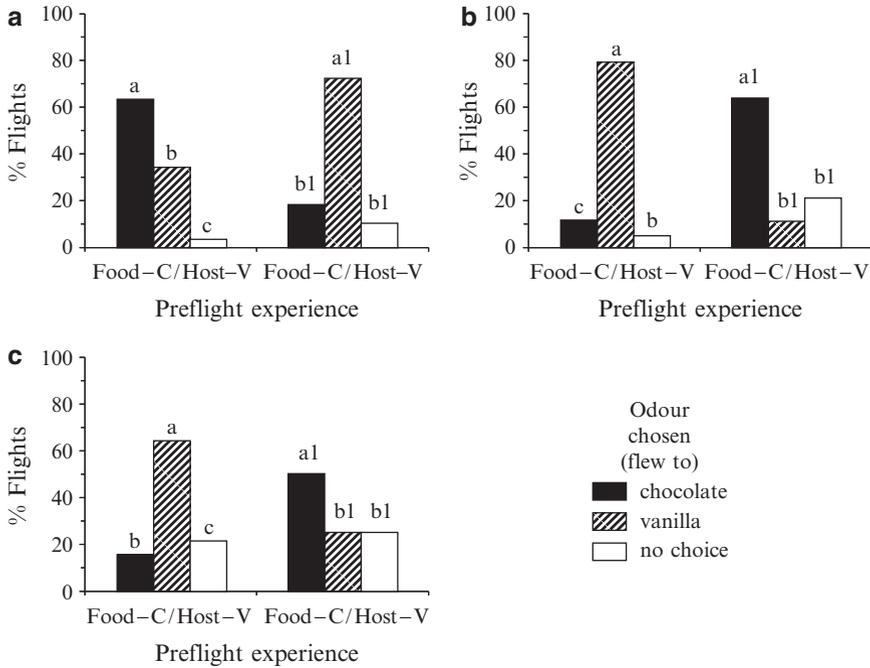
Members of over 30 families of Hymenoptera consume non-host foods (Jervis et al., 1993). In observing a particular habitat, 33 of 53 flowering plants are visited by parasitoids, roughly 25% of which (of nearly 1,000 specimens) actually feed at the flowers. As if this monumental set of field observations is not enough, Jervis and Kidd go on to report another 330 parasitoid species from the literature also feed at floral nectaries. In another comprehensive examination of flower-visiting parasitoids, Tooker and Hanks (2000) revisit a dataset from 1928 created by Robertson that documents flower visiting insects from 453 plant species found in central Illinois. Parasitoids comprise a large portion of these insects, 15,172 specimens to be exact. Ichneumonids are the most frequent visitors (48 species; almost twice as many as the next most frequent family). Most species feed from a narrow range of flower species; the exceptions to this rule are the largest-bodied families (Tiphidae, Leucospididae, and Scoliidae) which visit the most flower species per wasp (Tooker and Hanks, 2000). In the Canadian arctic, at least 18 parasitoid species were observed feeding on nectar at flowers (Kevan, 1973). Although floral architecture likely plays a role in which flowers are accessible to a parasitoid (see next chapter), Patt et al. (1997) show that some parasitoids are behaviorally more disposed to feeding from a greater breadth of flowers. Specifically, *Edovum putleri* feeds on the nectar of a large number of flowers, all except those where the nectaries are completely hidden at the base of a long corolla. *Pediobius foveolatus*, a larger parasitoid, feeds on a very restricted set of these nectar sources, regardless of whether the nectar is accessible. As more data is collected on the feeding patterns of a greater number of wasp species, the factors that ultimately drive floral preferences will likely become more consistently apparent.

Honeydew (Eijs et al., 1998; Fuchsberg et al., 2007; Hagley and Barber, 1992; Irvin et al., 2007; Leijs, 1961a) and EFN (Lingren and Lukefahr, 1977; Patt et al., 1997) are other sugar sources important to parasitoids. Some parasitoids

(e.g. *Encarsia formosa*) will even take the fluid droplets directly from an aphid's anus (Jervis and Heimpel, 2005)! In the field, 80% of *Cotesia glomerata* and 55% of *Microplitis mediator* consume honeydew (determined using indicator sugars) in crucifer fields (Wäckers and Stepphun, 2003). Most of this feeding occurs in association with field margins where buckwheat is planted, but the majority of these parasitoids also consume honeydew. Sugar profiles found in the guts of field-collected *Diadegma insulare* suggest that this parasitoid will consume both honeydew (from *Aphis glycines*) and nectar (likely from buckwheat) (Heimpel et al., 2004). Parasitoids are also commonly recorded visitors to EFNs; for example, *Cotesia congregata* is one of the most frequent visitors to the EFNs of *Catalpa speciosa* (Stephenson, 1982b).

The first step in glucophagy is that the wasp needs to recognize a sugar source as food; odor is an important cue for recognizing sugar meals (Jervis et al., 1996b). The use of odors by parasitoids to fulfill their physiological needs has been best explored for the wasp, *Microplitis croceipes* (Lewis and Takasu, 1990). Female wasps are eternally torn between feeding themselves and foraging for hosts; feeding prolongs their life, but may come at the expense of laying eggs since food and hosts are not always found together. Work on *M. croceipes* has shown that female wasps learn odors and respond to them in correspondence to their immediate physiological status- starved females are attracted to sugar-associated odors, and satiated females go hunting for hosts (Lewis and Takasu, 1990) (Fig. 2.4). The learned odors appear to be somewhat arbitrary, and wasps can be taught to associate a broad range of chemicals with a potential sugar meal. Research has shown that *M. croceipes* can be trained to use natural odors such as vanilla and chocolate, or entirely synthetic chemicals (cylcohexanone, diisopropylaminoethanol, 3, 4-dinitrotoluene, and 3, 4-octanone & octanol) as a sign to dine (Olson et al., 2003). Inexperienced wasps also show specific innate behavioral responses to odors and colors depending on their physiological state (Siekman et al., 2004; Wäckers, 1994). One of the few chemicals that is not attractive to many parasitoids is sucrose, one of the prevailing sugars found in most phloem-derived foods (Leius, 1961b; Patt et al., 1997; Rose et al., 2006; Tertuliano et al., 2004; Wäckers et al., 2002). This is likely since sucrose is non-volatile, but upon contact, sucrose is phagostimulatory. Thus it seems that other chemical cues associated with nectar or honeydew beyond the sugars themselves are necessary for parasitoids to locate food (Patt et al., 1997; Rose et al., 2006). Another pattern that is repeatedly shown in the literature is that parasitoids with experience are better at locating specific food-associated odors (Patt et al., 1999). Again, inexperienced parasitoids are also well capable of locating food sources (Siekman et al., 2004; Stapel et al., 1997; Wäckers, 1994, 2004). As a case in point, Stapel et al. (1997) reveal that naïve wasps locate EFN from cotton faster than sucrose spiked with vanilla. When these same parasitoids are tested a second time with the same food sources, the wasps find the sucrose and nectar equally fast.

Once they have located a sugar meal, wasps have evolved a variety of means for actually eating it. The morphological and physiological adaptations to sugar feeding are easily seen when the feeding process is described. Jervis (1998) adapted the proc-



**Fig. 2.4** Flight responses to vanilla or chocolate extract by hungry (a), well feed (b), or trained hungry then well fed (c) *Microplitis croceipes* females, with preflight training indicated. Food-C/Host-V: females given training experience of chocolate-to-food and vanilla-to-hosts; Food-V/Host-C: females given training experience of vanilla-to-food and chocolate-to-hosts (the order of food-odour and host-odour training was alternated and the results combined). Bars within same treatment group capped by different letters are significantly different (Reproduced from Lewis and Takasu, 1990. With permission by Nature Publishing Group)

ess of liquid feeding in bees (detailed by Kingsolver and Daniel, 1995) to parasitoid wasps. First, it appears that the mouthparts of the parasitoid need to contact the sugar solution to elicit a gustatory response (Beach et al., 2003; Wäckers, 1999). Acceptable sugars are then loaded onto the glossa, probably because of hydrophilic properties (often involving hairs) present on the tongue of the parasitoid. The glossal hairs likely function to filter heterogenous material out of the nectar. Saliva issues down the glossa and mixes with the sugar meal. The saliva-sugar mixture is then pumped into the oral cavity through movements of the cibarial pump.

The morphology of the mouthparts can be categorized to yield some inference on the feeding ecology of specific parasitoids. Perhaps the morphological structure that has received the most attention in parasitoids is the CNEA. This is a bit surprising, since only 1 in 30 species actually possesses this specialized adaptation to feeding on floral nectar (this is contrast to one-third of dipteran parasitoids) (Jervis, 1998). Jervis groups parasitoids into two major feeding guilds, those with and without the CNEA, which in parasitoids is an elongated labiomaxillary complex (this is reiterated by Olson et al., 2005). He then goes on to subdivide the CNEA

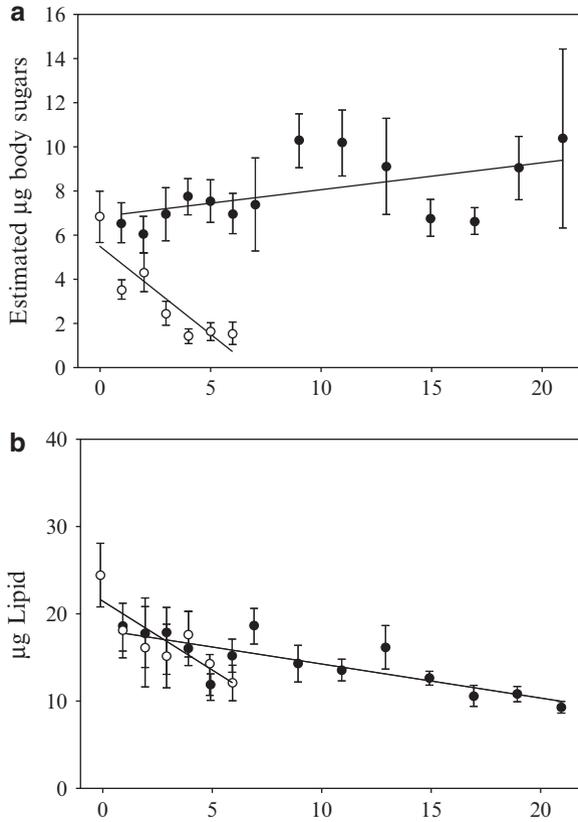
species into seven functional groups, based largely on the morphological arrangements of the labiomaxillary process. The Braconidae and Ichneumonidae are particularly noted for having the CNEA which facilitates the removal of nectar from flowers with deep corollas (Jervis et al., 1996b). Beach et al. (2003) raise the idea that gustatory response may reinforce the ecomorphological relationships of the mouthparts. Specifically, wasps with unspecialized mouthparts feed on a broader range of sugar sources in nature, and may then be expected to show gustatory responses to a wider range of sugars. Their observations with *Anaphes iole* support this hypothesis, which merits further examination.

Food must be digested for it to yield any benefits to the wasps, and even oligosaccharides may require a suite of specialized enzymes to digest them. Williams et al. (2005) found that melizitose is not digested by *Anaphes iole*, while other sugars are completely digested within 24 h of feeding. Wäckers (2001) believes that the digestive capabilities of wasps for different sugars are directly affected by the suite of digestive enzymes present in a parasitoid, and this may limit which sugars are fed upon and which can support the life processes of the wasps.

The most conspicuous function of sugar feeding in parasitoids is that sugar improves longevity, even for species that host feed (Heimpel et al., 1997; Leius, 1961b). There is no shortage of laboratory studies that exemplify the importance of sugar sources (floral and extrafloral nectar, and honeydew) in prolonging the lives of parasitoids big and small (Foster and Ruesink, 1984; Heimpel et al., 1997; Lundgren and Heimpel, 2003; Olson et al., 2000; Putnam, 1963; Rose et al., 2006; Takasu and Lewis, 1993; Williams et al., 2005 are just a few). Indeed, as little as one sugar feeding can have dramatic effects on the lifespan of wasps (Wäckers, 2001; Hausmann et al., 2005), although most parasitoids require many feedings to reach maximum longevity. Azzouz et al. (2004) show that *Aphidius ervi* survive best when continuously offered sugar. Olson et al. (2000) demonstrate that sugar-feeding in *Macrocentrus grandii* reduces the catabolism of carbohydrate and lipid reserves over unfed wasps (Fig. 2.5). EFN from cotton promotes longevity of *Campoletis sonorensis* better than floral sources (Lingren and Lukefahr, 1977), and Idris and Grafius (1995) show that different flowers yield nectars of varying suitability in maintaining the lives of *Diadegma insulare*. With these studies in mind, most parasitoids live an abbreviated and likely despondent life if they don't find a sugar meal of one sort or another. The reproductive and dispersal functions of sugar for parasitoids are discussed at length in Chapter 1. Suffice it to say that sugar-feeding may affect the egg viability, rate of egg resorption, diapause rate and primary sex ratio of progeny, and flight initiation and duration in parasitoids.

## 2.3 Conclusions

The general pattern in the research which has provided the basis for this chapter is that most natural enemies will consume a sugar meal if given a chance. Indeed, many predators and parasitoids have evolved sensory organs specifically for



**Fig. 2.5** Estimated amounts of body sugars (*top*) and lipids (*bottom*) over the lifespans of female *Macrocentrus grandii* that were provided with sucrose and water (●) and water only (○) (Reproduced from Olson et al., 2000. With permission by Blackwell)

perceiving sugar, and seek this non-prey food source out when in need of food. Another recurring theme in this chapter is that although sugar meals are coveted by a wide range of entomophagous species, very few can persevere through an entire generation without some other nutrient. Thus, simple carbohydrates cannot replace prey in the diets of these arthropods, but can sustain them for long periods of time in the absence of prey, and generally fitness is improved in sugar-fed natural enemies even when prey is available. As we shall see in subsequent chapters, the nutrition and defenses of different sugar sources have led to fascinating ecological interactions among natural enemies and their environments. Indeed, their lust for sugar even drives many entomophagous arthropods to kill.