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Chapter 9

PICK AND MIX:
SELECTING FLOWERING
PLANTS TO MEET THE
REQUIREMENTS OF
TARGET BIOLOGICAL
CONTROL INSECTS

Felix L. Wäckers and Paul C.J. van Rijn

INTRODUCTION

Many pollinators and entomophagous arthropods rely on floral food (pollen and nectar) at some point during their life cycle (Baggen *et al.*, 1999; Pontin *et al.*, 2006; Wäckers, 2005). The lack of floral resources in modern intensified agricultural systems has long been suspected to be an important bottleneck for natural pest control and pollination (Illingworth, 1921; van Emden, 1962; Hagen, 1986; Biesmeijer *et al.*, 2006). In conservation biological control, diversification of the agroecosystem with flowering vegetation is seen as an important tool to support the broad range of predators and parasitoids that require nectar and pollen sources to survive and reproduce. However, direct and quantitative evidence for the impact of such landscape management approaches has been scarce (Heimpel and Jervis, 2005). New biochemical techniques allow us to analyse the gut content of field collected insects (Heimpel *et al.*, 2004). These methods not only quantify the nutritional state of even the smallest individual predator or parasitoid in the field, but also provide information on their feeding history and food source use (Wäckers and Steppuhn, 2003). This methodology has generated the first proof that insects in agricultural landscapes lacking floral resources can be severely food-deprived (Olsen and Wäckers, 2007; Winkler *et al.*, 2009a). It has also proven to be an effective tool to quantify the impact of landscape management strategies on the nutritional state of predators and parasitoids in the field. This provides sound data for the optimisation of conservation biological control programmes (Box 9.1). This shows that enhancing beneficial arthropods through diversification of agroecosystems is not a function of increased botanical diversity per se, but depends on the selection of the 'right' flowering plants. We know from pollination ecology that plant–pollinator interactions can be often highly specific and that plants have evolved many mechanisms through which they can exclude visitors other than the intended specialised pollinators (Waser *et al.*, 1996). Specificity of flower exploitation can be based on the apparency and accessibility of flowers, as well as the nectar/pollen composition (Wäckers, 2005). It is thus not surprising that groups of entomophagous arthropods may differ in the range of nectar and pollen sources they can exploit. The impact of floral resources on biological control can be optimised by selecting those flowers whose availability, appearance, accessibility and chemical com-

Box 9.1 The 'right kind' of diversity

Olsen and Wäckers (2007) demonstrated that *Meteorus autographae* parasitoids collected from cotton fields bordered by pure stands of cahaba white vetch (*Vicia sativa* × *Vicia cordata* L.), a species selected on the basis of its suitability in providing nectar, had threefold higher energy reserves as compared to unfed individuals. In sharp contrast, *M. autographae* collected from cotton fields bordered by botanically diverse bird conservation margins showed no elevation in energy levels and were actually starving. This shows that enhancing beneficial arthropods through diversification of agroecosystems is not a function of increased botanical diversity per se, but depends on the selection of the 'right' flowering plants.

position matches the behaviour, morphology and physiology of target organisms (Wäckers, 2005; Fiedler *et al.*, 2008).

While recent studies have increased insight into the suitability of flowering plants for entomophagous arthropods, seed mixes for conservation biological control programmes have long been selected more or less arbitrarily (Gurr *et al.*, 2005). These shotgun approaches have been 'hit and miss' in terms of their effectiveness in supporting beneficial arthropods (Andow, 1991). An uninformed choice of non-crop vegetation not only means missing out on potential benefits but may also actually generate negative effects. Figure 9.1 illustrates the complexities inherent in the notion that floral resources might benefit biological control; achieving this outcome depends on avoiding a series of potential negative effects. It is, therefore, no surprise that arbitrarily composed floral vegetation can increase pest populations (Baggen and Gurr, 1998; Wäckers *et al.*, 2007; Winkler *et al.*, 2010) and populations of higher trophic level organisms (Araj *et al.*, 2008), while these structures can also serve as a sink, attracting beneficial species away from the crop (Dunning *et al.*, 1992).

The selection of floral vegetation to maximise ecosystem services, such as biological control and pollination, requires an understanding of the biology and

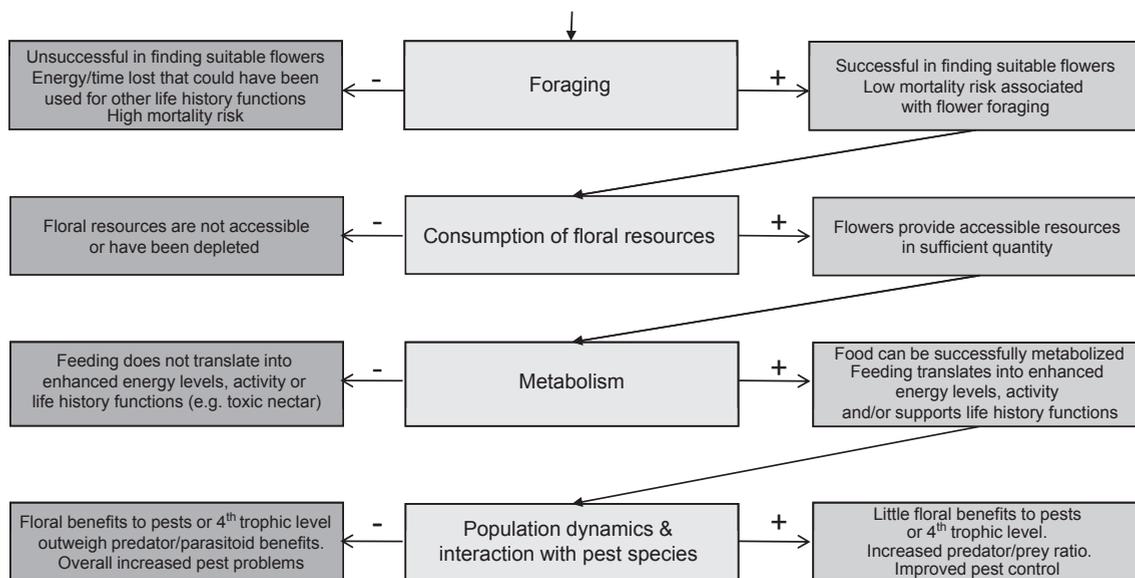


Figure 9.1 The interactions with and at floral resources can have positive as well as negative effects on predators and parasitoids at various levels. At each level examples of positive and negative impacts are presented.

ecology of the beneficial species delivering these services. Based on existing insights in insect–plant interactions, specific floral seed mixtures can be developed which target specific pollinators and/or flower-visiting biocontrol agents (Wäckers *et al.*, 1996; Pontin *et al.*, 2006; Van Rijn and Wäckers, 2010). This habitat management strategy has been demonstrated to be effective in enhancing the nutritional state of targeted beneficial insect groups (Olsen and Wäckers, 2007; Lee *et al.*, 2006), as well as their local abundance (Baggen *et al.*, 1999; Vattala *et al.*, 2006; Pontin *et al.*, 2006; Carvell *et al.*, 2007).

The first part of this chapter gives an overview of the various methods that have been used to study the exploitation of specific flowering plants by parasitoids and predators, while discussing the respective advantages and drawbacks of the various methods. In the second part, the specific floral requirements of different groups of biological control agents are discussed. The focus will be on parasitoids, syrphids, lacewings, predatory bugs and ladybeetles, representing important taxa of biological control agents. The level of specificity that emerges from this comparison underscores the importance of selecting the right floral resources to optimise the biological control services of agroecosystems.

METHODS OF STUDYING FLOWER EXPLOITATION

Previously, Jervis *et al.* (2004) reviewed approaches used to study the effect of habitat manipulation on parasitoids and biological control. Here this review is extended to include methods used to study various predators, with the focus on methods to select flowering species for use in such habitat manipulation programmes. Various methods have been employed to assess the suitability of individual flowering plant species as insect food sources (Table 9.1). These can be divided into five main categories:

- Recordings of flower choice
- Morphometric studies (i.e. measurements of flower and arthropod mouthpart morphology to assess whether the mouthparts of the arthropods would theoretically allow access to nectaries and anthers)
- Establishing consumption, either by assessing weight increase and/or fitness benefits in laboratory studies or through (palynological or biochemical) analyses of field collected individuals
- Study of nutritional suitability through lifetable/performance experiments
- Impact of mono-flower plots on insect populations in the field

Table 9.1 Compilation of studies showing the range of methods employed to assess suitability of flowering plant species as insect food sources.

Type of study	Methodology	Field/Lab	Establishes		References
			Attractiveness	Nectar/pollen accessibility/consumption	
Recording of flower choice	Olfactometer experiments	Lab	Possible given adequate choice experiments (only olfactory response)	–	Wäckers and Swaans, 1993; Wäckers, 2004
	Flower visits in flight cage	Lab	Possible given adequate choice experiments (olfactory as well as visual response)	Only if observations of nectar or pollen feeding are included	Patt <i>et al.</i> , 1997; Begum <i>et al.</i> , 2004; Van Rijn and Wäckers, 2010
	Direct observations	Field	Often implied but not established	Only if observations of nectar or pollen feeding are included	Gilbert, 1981; Weiss and Stettmer, 1991; Ambrosino <i>et al.</i> , 2006
	Sampling flowers (for small arthropods)	Field/Lab	Often implied but not established	Only if observations of nectar or pollen feeding are included	Silveira <i>et al.</i> , 2005; Fiedler and Landis, 2007a; Bosco and Tavella, 2008; Atakan and Tunc, 2010
Morphometric studies	Measurements of flower morphology and insect mouthparts	Lab	–	theoretical	Gilbert, 1985; Winkler <i>et al.</i> , 2009b; van Rijn and Wäckers, 2010
Establishing consumption	Weighing by microbalance	Lab/semi-field	–	+ (quantitative) (non-destructive)	Wäckers <i>et al.</i> , 1996; Wäckers, 2004; Winkler <i>et al.</i> , 2009b
Analysis of field-collected individuals	Sugar analysis	Field/Lab	– May be implied but not established	+ (quantitative and to some extent qualitative on basis of sugar profiles)	Wäckers and Steppuhn, 2003; Heimpel <i>et al.</i> , 2004; Lee <i>et al.</i> , 2006
	Pollen analysis	Field/Lab	– May be implied but not established	+ (quantitative and qualitative)	Jones and Rowe, 1999; Golding and Edmunds, 2003; Silberbauer <i>et al.</i> , 2004; Villenave <i>et al.</i> , 2006; Davidson and Evans, 2010

Plant secondary metabolites DNA analysis	Field/Lab	-	May be implied but not established	+	(quantitative and qualitative)	-	Ferreres <i>et al.</i> , 1996
	Field/Lab	-	May be implied but not established	+	(quantitative and qualitative)	-	Weber and Lundgren, 2011; Wilson <i>et al.</i> , 2010
Marking of nectar or pollen	Field/Lab	-	May be implied but not established	+	(quantitative and qualitative)	-	Gu <i>et al.</i> , 2001; Patt <i>et al.</i> , 2003; Scarratt <i>et al.</i> , 2008; Wanner <i>et al.</i> , 2006
	Field/Lab	-	May be implied but not established	+	(quantitative and qualitative)	-	DeGrandi-Hoffman and Hagler, 2000
Life history/ Performance studies	Lab	-		+		+	Vacante <i>et al.</i> , 1997; Patt <i>et al.</i> , 2003; Lundgren and Wiedermann, 2004
	Lab/semi-field	-		+	(if survival is prolonged compared to control)	+	(see text for pitfalls) Wäckers, 2004; Baggen and Gurr, 1998; Begum <i>et al.</i> , 2006; Irvin and Hodde, 2007; Winkler <i>et al.</i> , 2009b; Van Rijn and Wäckers, 2010
Fecundity	Lab/semi-field	-		+		+	Van Rijn <i>et al.</i> , 2006; Venzon <i>et al.</i> , 2006; Winkler <i>et al.</i> , 2006; Bertolaccini <i>et al.</i> , 2008
Flight capacity following flower/ food exposure	Lab	-		+		+	(convertibility of sugar/ nectar to flight energy) Hausmann <i>et al.</i> , 2005; Wanner <i>et al.</i> , 2006
	Field	-		-	(May be implied but not established)	-	Pemberton and Lee, 1996; Chaney, 1998
Impact of mono-flower plots on insect field populations	Field	-		-	(May be implied but not established)	-	

These methods differ in terms of required input (labour and equipment) as well as the informational output they provide (Table 9.1). Below the different methodologies are described in more detail and their advantages and limitations are discussed.

Recordings of flower choice

Flower choice can be addressed in a number of laboratory, semi-field or field experiments. Laboratory experiments include olfactometer studies which establish responses to flower odour, as well as flight chamber and cage experiments. Cages can also be used in semi-field experiments, whereas field experiments typically record and count arthropods on flowers in their (semi-) natural environment.

Olfactometer studies assess responses to flower odours. This is achieved by giving an organism a choice between two or multiple air plumes, which should be of equal size and have equal laminar flow and humidity. Humidifying the air improves odour detection. Based on the number of air plumes, we distinguish for instance between two-arm (Y-tube), four-arm, or eight-arm olfactometers. At least one arm should feature a control (clean air). Air pumps, in combination with flow-meters, should be used to attune airflow. The insect should be introduced downwind from the place where the odour plumes join. At this point it should be able to perceive the odour from both sources without too much mixing, which can be checked with smoke. Above-average choice for an odour alternative indicates olfactory attraction. Above-average choice for the control can indicate odour repellency. Most olfactometers require that the insect tested moves upwind in response to an attractive odour. Sometimes this requires specific adjustments. For *Orius* flower bugs for instance, the olfactometer has to be positioned vertically (Venzon *et al.*, 1999). While arthropods commonly exhibit upwind orientation in response to an attractive odour source, it has to be considered that organisms may also orient to odour gradients or show an arrestment in response to an odour. Most olfactometers are not designed to assess the latter two responses.

A second type of laboratory set-up is the use of flight chambers or flight cages where the insects can respond to chemical, as well as visual, flower stimuli. Visual stimuli are likely to be affected by the light conditions chosen. Artificial light, plastic, plexiglass and glass modify the light spectrum and intensity, which may

affect how flowers are perceived by the insect. To establish flower preference the use of an appropriate choice set-up is required, where factors other than the flower species tested are excluded or standardised as much as possible. For instance, it would be advisable to standardise the biomass of the flowers used in choice trials to ensure that increased responses are not simply a reflection of an increased chance of randomly landing on a larger flower. Another aspect to consider is that the behavioural response of an insect is the result of the interplay between its innate preference and previous experience (associative learning). Feeding on a particular flower will not only affect the response to this particular flower species, but also to other flowers. Interference from prior feeding experience can be excluded when unfed insects from laboratory rearing are used in the tests. If individuals need to be fed, it is important to ensure that their nutritional state is standardised, given that this factor is crucial to the expression of behavioural responses to flower stimuli (Wäckers, 1994).

Results of flower choice experiments are often interpreted in terms of flowers being 'attractive' (i.e. being able to draw in insects from a distance). While this attractiveness is usually presented as an absolute quality, bioassays frequently assess relative responses. When giving an insect the choice between flowers, the one receiving most visits may be attractive, or the alternatives may be repellent. Actual attraction can be established in choice experiments in which flowers are offered against an appropriate control, such as humidified clean air.

Field experiments on larger mobile species typically record the number of visits to particular flowering species within a predefined time frame (Kevan, 1973; Jervis *et al.*, 1993; Winkler *et al.*, 2005). Such recordings will be more difficult for smaller, less mobile species such as flower bugs and small parasitoids as they tend to remain on a given flower/plant for much longer periods. For these insects, as well as for non-flying arthropods such as mites, flower choice can be studied by assessing their distribution among flower species. The number of insects present per flower can be determined by vacuuming the flowers (Fiedler and Landis, 2007a; 2007b), by tapping flowers onto a white surface and subsequently collecting the insects with an aspirator (Bosco and Tavella, 2008), or by collecting the flowers in bags and extracting the arthropods in the lab (van Rijn, unpublished results). Generally the numbers are expressed per flower or per unit of soil surface area (m²).

Interpreting these field recordings is often difficult, as floral visits depend largely on the relative abundance of the flower species tested, the background vegetation, and the presence of arthropod competitors. Moreover, in the field it usually remains unknown whether an observed response to a flower represents an innate attraction or is the result of associative learning during previous successful or unsuccessful feeding events. Rewarding feeding experiences can change innate repellency or neutral responses to attraction, whereas lack of reinforcement may extinguish a response to stimuli that are innately attractive. Furthermore, aggregation at particular plant species is not necessarily proof of attraction, as it may also be a result of random flower visits followed by arrestment after successful feeding. Spatial, rather than olfactory or visual learning may enhance this aggregation, as it enables insects to return to rewarding food sites (Wäckers *et al.*, 2007). These mechanisms can underlie variations in responses to particular flowers between different studies and at different sites.

A final point to be considered in any study on nectar or pollen foraging is the fact that insects may be visiting flowers for resources other than nectar or pollen. These may include shelter, mates, prey or heat, as flowers may reflect/concentrate infrared radiation from the sun or even produce heat themselves through chemical reactions. Actual observations of nectar or pollen feeding can help eliminate these confounding factors.

Morphometric studies

Flower morphology has been recognised as an important factor limiting floral nectar use (Faegri and van der Pijl, 1979; Jervis *et al.*, 1993). Floral nectaries and the pollen-bearing anthers are often hidden within complex floral structures. Accessing these floral resources requires that the (mouthpart) morphology and the behaviour of the flower visitor match the floral architecture (Patt *et al.*, 1997; Jervis, 1998). Most hymenopteran parasitoids (Jervis *et al.*, 1993; Gilbert and Jervis, 1998) and many predators have short mouthparts that largely restrict their feeding to exposed nectar and pollen. For these species head width is the limiting factor hampering nectar exploitation from deep, narrow flower corollas. Small parasitoids and predators may not be restricted by flower morphology, but complex floral structures might nevertheless prevent them from finding nectar and pollen (Patt *et al.*, 1997).

In morphometric studies the length of the mouthparts and head width of the insect are measured, as well as the depth and width of the corolla (Vattala *et al.*, 2006; Winkler *et al.*, 2009b; van Rijn and Wäckers, 2010). The corolla depth is measured from the most proximal point of the corolla to the location of the nectaries or anthers. By combining these measurements it is possible to identify whether nectar or pollen from a particular flower could potentially be reached by a particular insect.

While this method is attractive due to the fact that it requires little more than a microscope, its drawback lies in the fact that it determines potential accessibility rather than establishing actual access. A number of issues are not accounted for. These include the fact that nectar or pollen foragers might be thwarted by complex flower morphology (Patt *et al.*, 1997), nectar viscosity (Winkler *et al.*, 2009b) or competition by other flower visitors (see Box 9.2). Finally, consumption may be inhibited by particular flower odours (Wäckers, 2004) or through nectar/pollen chemistry (Feinsinger and Swarm, 1978). Behavioural recording of insects foraging on real or artificial flowers can be used to test the predictions on nectar and pollen accessibility (Patt *et al.*, 1997).

On the other hand, flower visitors may be able to exploit floral resources that appear inaccessible on the basis of morphological measurements. This applies when nectar or pollen has been spilled from the nectar/stamen either by previous visitors or due to physical disturbance (wind) or simply by pollen dropping during flower maturation. Also, in a number of flowers the corolla opening is flexible. In the Fabaceae, for example, the wing and keel petals can be pushed apart to create a widened access to the floral resources. Here the strength and weight of the flower visitor as much as its size can determine foraging success. Some insects are also known to circumvent the floral structures and use their biting mouthparts to gnaw their way to the hidden resources (Inouye, 1983; Idris and Grafius, 1997).

Establishing consumption

To test whether floral resources are actually consumed a number of methods are available (Table 9.1). The approaches include gravimetric methods, as well as methods identifying food source markers in the arthropods. Depending on the method chosen quantitative and/or qualitative information on food uptake is obtained.

Box 9.2 Competition for floral resources

Under field conditions a broad range of insects compete for the often limited nectar and pollen resources. Insects can compete either through physical interactions (interference competition) (Kikuchi, 1963; Morse, 1981; Beattie, 1985; Blüthgen *et al.*, 2000) or through depletion of the resource (exploitative competition) (Comba *et al.*, 1999; Hansen *et al.*, 2002).

Interference competition occurs when flower visitors monopolise floral resources through aggressive behaviour towards other flower visitors, or simply because they are bigger and avoided by the other species. Kikuchi (1963) established dominance rankings between flower visitors, showing that bumblebees chase away syrphids, which in turn outcompete butterflies. Even among syrphid species interference competition may occur. Ambrosino *et al.* (2006) observed that where the *Eristalis* spp. were numerous they displaced the smaller zoophagous species from their preferred *Coriandrum* flowers.

Exploitative competition is based on depletion of the nectar or pollen resources by the earlier flower

visitor (first come, first served). In this way even bigger or more aggressive insects can suffer from the actions of smaller species when foraging on the same flowers (Reader *et al.*, 2005).

Competition for nectar is likely to be most fierce at accessible nectaries, as these can be exploited by a large pool of nectar feeders. Chances for direct interference competition to occur are further increased by the fact that exposed nectar tends to be more viscous, increasing intake time.

Resource partitioning is a way to avoid or alleviate competition. Deep and narrow flowers cater for a more restricted subset of nectar feeders and may thus provide a nectar refuge for specialised pollinators (Comba *et al.*, 1999). An example of temporal avoidance of competition is provided by Morse (1981), who showed that the hoverfly *Melanostoma mellinum* (L.) performs its highest foraging activity early in the morning when bumblebee activity is still very low.

Microbalances can be used on individual arthropods to establish weight increase following flower visits (Wäckers *et al.*, 1996; Winkler *et al.*, 2009b). Such a weight increase can indicate successful access to and consumption of floral nectar or pollen. In those species that do not feed on pollen (e.g. most parasitoids), any weight increase can be attributed to nectar feeding. Before being tested, individuals should be kept with water only to ensure that they are food deprived and motivated to search for food. Any external contamination with pollen should be excluded by assessing the insect under a loupe or microscope for external pollen deposition before the second weight assessment. The established weight increase provides a quantitative yet conservative measure of food consumption, as control individuals exposed to non-flowering plants typically lose weight during the exposure. It is important to ensure that test plants are not contaminated with honeydew or plant sap (exuding from damage), as this could invalidate conclusions. To ensure nectar availability flowers can be caged or covered with nylon bags for a few hours before releasing the test arthropod.

Another way of proving consumption is based on the detection of food-specific markers in the arthropod.

The advantage of these methods is that they can be used to study food consumption under various field conditions. Various markers can be used, including the food itself (specifically pollen grains), naturally occurring food compounds, such as specific carbohydrates, secondary metabolites, or DNA. The use of carbohydrate analyses to identify and quantify feeding on nectar and other sugar sources has been covered in previous reviews (Heimpel *et al.*, 2004; Steppuhn and Wäckers, 2004; Wäckers *et al.*, 2006a). Markers may also be added to the food plant in the form of stable isotopes or protein (Table 9.1). While these methods can be powerful tools to establish whether a particular nectar or pollen source is consumed, not all generate quantitative data. Quantitative data on pollen feeding can be derived from identifying the pollen grains found in the gut (e.g. Villenave *et al.*, 2006) or in the frass (Davidson and Evans, 2010). The latter, non-destructive method may also be interesting for educational projects (Golding and Edmunds, 2003).

When using these methods under non-standardised field conditions, the possibility of contamination has to be considered. Contamination can occur when omnivorous predators consume prey that has been feeding on pollen or nectar. Arthropods may also be exposed to

markers through feeding on plant-derived material other than floral nectar and pollen, such as plant sap, fruits or honeydew (Wäckers, 2005). Various types of pollen grains might be stuck in nectar or honeydew and be consumed inadvertently.

Life history/performance studies

The best proof that floral food resources benefit a biological control agent is by showing an effect on its life-table parameters (development, longevity, fecundity) or its (flight) activity. These parameters are typically studied in laboratory bioassays in which caged insects are provided with a particular flower species, or with nectar/pollen. Many landscape management projects employing floral resources base their selection of flowering plants on such laboratory studies.

Longevity (or survival) is the parameter most commonly studied as the experiments require generally little more than the insect and the floral resource. However, for long-lived arthropods, assessing longevity can require long-term commitment. Longevity is strongly affected by temperature. Within the range of temperatures acceptable for a given organism, a temperature increase/decrease of 10 °C will roughly increase/decrease longevity by a factor 2. This can be used to extend survival in longevity studies for short-lived organisms, or reduce longevity for those that are long-lived.

Impact of nectar or pollen on fecundity can be seen through an increase in daily fecundity, oviposition time, and/or lifetime fecundity (Winkler *et al.*, 2006). Studying fecundity in zoophagous insects often requires a supply of suitable prey or hosts. With a few exceptions, parasitoids only oviposit in or on suitable hosts, but also aphidophagous hoverflies and lady beetles require (cues from) their aphid prey (especially honeydew) to trigger oviposition (Scholz and Poehling, 2000). For flowerbugs, who insert their eggs in green plant tissue, a suitable oviposition substrate is essential.

To assess if juvenile development is affected by pollen or nectar, a supply of prey is required in the positive control (Patt *et al.*, 2003). In some cases the commercially produced eggs of *Ephestia* can be a suitable substitute.

Another way to show that floral resources are utilised by the insect is by assessing its flight capacity following flower exposure. Flight capacity can be assessed

in simple flight bioassays measuring the time it takes for flight ability to be restored in food deprived individuals (Hausmann *et al.*, 2005) or on flight mills assessing flight duration (Wanner *et al.*, 2006).

When using actual flowering plants, enhanced performance indicates that a food source is both accessible and nutritionally suitable. On the other hand, in cases of poor performance it usually remains unclear whether this is due to limited food intake or poor nutritional value. When the interest lies primarily with the nutritional suitability of floral resources, insects can be tested with collected nectar or pollen. When collected nectar and pollen are not used directly, they should be stored frozen. Also, the way the pollen is treated affects its quality as a food source (van Rijn and Tanigoshi, 1999). When testing nectar, it is advisable to offer this at high relative humidity (RH), to avoid limited consumption due to high viscosity. When testing pollen, high humidity should be avoided as this can lead to deterioration of pollen quality (van Rijn and Tanigoshi, 1999), while free water should always be available to compensate for the low water content of pollen (Michaud and Grant, 2005). Bee-collected pollen is nutritionally different from fresh pollen, due to nectar and enzymes being added by the bees (Human and Nicolson, 2006). For arthropods that feed on the content of individual pollen grains feeding success can be limited not only by nutritional content but also by pollen wall morphology (Ouyang *et al.*, 1992). Conclusions on nutritional suitability may also be confounded when a food source fails to stimulate feeding or is actually repellent. One way to control for this is to measure both food intake and survival. Wäckers (2001) determined the quantity of sugar consumption during a single feeding bout and subsequently assessed the effect of this known quantity on parasitoid survival. Nutritionally suitable sugars such as sucrose, fructose and melibiose showed a positive correlation between amount of sugar consumed and longevity with R^2 values between 0.7 and 0.81, whereas unsuitable sugars such as rhamnose, lactose, galactose and raffinose showed no such correlation.

Lifetable or performance studies should ideally include two control treatments: a water-only treatment, as a negative control, and a known suitable food (e.g. sucrose for nectar studies) as a positive control. When a treatment results in poorer performance relative to the negative control, this could indicate that the food source is toxic (Wäckers, 2001). Some foraging studies also show that certain flowers may have a

negative impact on both insect energy levels and survival (Winkler *et al.*, 2009b). This can occur when flowers stimulate nectar foraging without providing accessible nectar or pollen (Wäckers, 2004).

Data from laboratory survival studies are unlikely to be fully representative of the effect of food under natural conditions. On the one hand, they may underestimate the impact of nectar feeding as most experiments are conducted with caged individuals that are restricted in their mobility and are presented with *ad libitum* oviposition sites and food. Under natural conditions, mobile arthropods may need to cover long distances searching for oviposition and foraging sites. As a result they are likely to use considerably more energy, which would increase the need for adult feeding and enhance its impact on longevity and fecundity (Stephuhn and Wäckers, 2004). On the other hand, laboratory studies may also overestimate fitness benefits of feeding. Arthropods in the field are subject to a range of biotic and abiotic mortality factors that may limit fitness irrespective of feeding.

Impact of mono-flower plots on insect field populations

A final method to assess the impact of particular flower species on predators/parasitoids are field studies comparing the impact of plots with individual flowering species on the populations of the biological control agents or the pests they control. The appeal of such field studies lies in the fact that they are closest to the actual objective of using flowering plants to boost biological pest control. However, performing independent replicates in this set-up requires a lot of space and labour, and this will often limit the number of flower species that can be compared.

Under field conditions, the availability of floral resources depends not only on floral traits but also on competition by other flower visitors such as bees. The level of this competition can vary significantly from site to site and could be an important factor in determining the impact of landscape management programmes (see Box 9.2).

Typically, field studies monitor insect populations in the flowering plots themselves or the adjacent crop, comparing this with plots lacking the floral vegetation. Flower suitability is usually deduced based on enhanced predator/parasitoid numbers or increased levels of predation/parasitism. However, these population responses may also occur when the flowering

plants simply act as a sink (Dunning *et al.*, 1992), drawing in predators or parasitoids from the field, without necessarily providing any fitness benefit. In this case, the impact of a flowering field margin might actually be counterproductive, as the concentrating of biological control agents would result in a depletion of predators/parasitoids in the crop field. To substantiate that the biological control agents actually obtain nutritional benefits from the flowering vegetation it is advisable to combine field tests with studies demonstrating nectar/pollen consumption or quantifying energy reserves (Olsen and Wäckers, 2007). Nutritional benefits are also expected to be reflected in enhanced longevity in the field. A number of methods have been used to establish a relative estimate of age or activity in field-collected arthropods (e.g. by assessing mandible wear for carabids and wing wear for flying insects) (Hayes and Wall, 1999; Lee and Heimpel, 2008).

Choosing and combining methods

The listed approaches represent a broad arsenal of methodologies that can be used to study the suitability of flowering plants for conservation biological control. The specific characteristics of the listed methods and their respective advantages and limitations highlight the importance of choosing the right experimental approach and conducting the tests under ecologically relevant experimental conditions.

As some of the methodologies are costly and labour-intensive, it could be sensible to examine whether methods requiring lower inputs can serve as an adequate proxy. Van Rijn and Wäckers (2010) assessed hoverfly survival on 30 different flowers and correlated this with flower depth. With very few exceptions, flower depth explained hoverfly survival with the cut-off point for successful flower feeding being at 2 mm corolla depth. Winkler *et al.* (2009b) compared three methods to study the exploitation of 19 flowering plants by two lepidopteran pests (*Pieris rapae* (L.) and *Plutella xylostella* (L.)), and their respective hymenopteran parasitoids, *Cotesia glomerata* (L.) and *Diadegma semiclausum* (Hellen). First, theoretical nectar accessibility was established on the basis of floral architecture and the mouthpart structure of the arthropods. Second, it was tested whether the arthropods could actually access the nectar by quantifying weight gain of individual insects when exposed to individual flowering species. Finally, the impact of various flowers on longevity of the herbivores and parasitoids was assessed. For the parasitoids tested the theoretical

nectar accessibility was shown to be suitable as a first step in selecting plant species. Also there was a good fit between results from the short-term flower exposure bioassay and the results from the longevity study. This means that for these species, the theoretical nectar accessibility and/or the short-term bioassay would have been sufficient to assess flower suitability. For the herbivores, however, there were more disagreements between the methods. In this case, the gravimetric bioassay provided information that would have been missed on the basis of morphological measurements or longevity experiment alone. These results indicate that measurements of floral architecture and insect mouthpart structure can provide a good first assessment of potential nectar/pollen feeding. However, for an accurate understanding of the contribution of individual flowering plant species to the survival of arthropods in the field, these data need to be complemented with more detailed studies.

Since laboratory studies are at best an approximation of the complex interactions acting in the field, ultimately results from laboratory studies have to be confirmed in semi-field or field studies. For instance, the impact of floral nectar on longevity and fecundity of *D. semiclausum* has been found to be much more pronounced in the field than in the laboratory (Stephuhn and Wäckers, 2004; Winkler *et al.*, 2006). Other factors may also affect the exploitation of flowers under field conditions. For instance *P. rapae* was shown to be unable to feed on a number of exposed floral nectar sources in dry climatic conditions (45% RH), whereas the nectar from these plants was successfully exploited at 90% RH, presumably due to the resulting decrease in nectar viscosity (Winkler *et al.*, 2009b).

FLORAL FOOD REQUIREMENTS FOR DIFFERENT GROUPS OF BIOLOGICAL CONTROL AGENTS

A number of studies have shown that there can be clear differences in the exploitation of floral foods between arthropod pests and their natural enemies (Baggen *et al.*, 1999; Wäckers *et al.*, 2007; Winkler *et al.*, 2009b). These differences can be exploited to select flowering plants for conservation control programmes that provide nutritional resources for target beneficial insects, while minimising or excluding benefits to crop pests.

Given the reported specificity of flower exploitation patterns between pests and their natural enemies, one

can also expect differences in flower associations among the various groups of entomophagous arthropods. To explore these potential differences, the floral requirements of a range of nectar/pollen feeding biological control agents are reviewed below with a focus on parasitoids, syrphids, lacewings, coccinelids and predatory bugs. Table 9.2 shows results from survival studies with representatives of these groups. To allow for comparisons only those flowers are included which had been tested with at least two groups.

Hymenopteran parasitoids

While most parasitoid species are highly specialised in terms of their larval food requirements (host associations), the feeding requirements of the adult stages are less specific. The majority of hymenopteran parasitoids are dependent on sugar sources to cover their energy needs. For many parasitoid species the adult diet is restricted to nectar or other sugar-rich substrates. However, synovigenic parasitoid females may also feed on their host whose haemolymph provides protein and lipids for egg maturation. However, as haemolymph usually contains relatively low levels of carbohydrates (often trehalose and glycogen) carbohydrate sources are usually still required for energy. Morevoer, carbohydrates found in haemolymph are typically poor in terms of supporting survival (Wäckers, 2001; Williams and Roane, 2007).

Parasitoids can be further divided according to the association between host and carbohydrate sources (Wäckers *et al.*, 2008). One group includes those parasitoid species whose hosts are closely linked to carbohydrate-rich food sources. This applies to species whose hosts excrete sugars (e.g. honeydew) or whose hosts occur on sugar-rich substrates like fruits or nectar-bearing plant structures. For these parasitoids the task of locating hosts and carbohydrates is linked. Parasitoids from this group may show few specific adaptations to the exploitation of additional carbohydrate sources and little or no task differentiation between food foraging and host search (Wäckers *et al.*, 2008). The second group comprises those parasitoids whose hosts are not reliably associated with a suitable carbohydrate source. These parasitoids have to alternate their search for hosts (reproduction) with bouts of food foraging, which requires a clear task differentiation. The latter group must decide whether to stay in a host patch, thereby optimising short-term reproductive success, or leave the host patch in search of food

Table 9.2 Effect of flowering plant species on adult flower choice (for hoverflies) and adult longevity for three types of natural enemies.

Family	Species	Floral Nectar depth	Choice		Longevity (AFLI)			References parasitoids (species)
			Hoverfly <i>E. balteatus</i>	Hoverfly <i>E. balteatus</i>	Hoverfly <i>E. balteatus</i>	Lacewing <i>C. carnea</i>	Parasitoids	
Apiaceae	<i>Ammi majus</i> (L.)	0	+	+	+	+	-	Geneau <i>et al.</i> , unpubl. (<i>Microplitis mediator</i> (Haliday))
Apiaceae	<i>Coriandrum sativum</i> (L.)	0	+	+	+	+	+/-	Vattala <i>et al.</i> , 2006 (<i>Microctonus hyperodae</i> (Loan))
Apiaceae	<i>Daucus carota</i> (L.)	0	+/-	+	+	+	+	Winkler <i>et al.</i> , 2009b (<i>Cotesia glomerata</i> (L.))
Apiaceae	<i>Foeniculum vulgare</i> (Miller)	0	+	+	+	+	+	Winkler <i>et al.</i> , 2009b (<i>Cotesia glomerata</i>)
Apiaceae	<i>Heracleum spondylium</i> (L.)	0	+/-	+	+	+	+/-	Winkler <i>et al.</i> , 2009b (<i>Cotesia glomerata</i>)
Apiaceae	<i>Pastinaca sativa</i> (L.)	0	+	+	+	++	+/-	Foster and Ruessink, 1984 (<i>Meteorus rubens</i> (Nees))
Polygonaceae	<i>Fagopyrum esculentum</i> (Moench)	0	+	+	+	+	+	Winkler <i>et al.</i> , 2009b (<i>Cotesia glomerata</i>)
Boraginaceae	<i>Borago officinalis</i> (L.)	0	-	+	+	++	-	Nilsson <i>et al.</i> , unpubl. (<i>Trybliographa rapae</i> (Westwood))
Ranunculaceae	<i>Ranunculus acris</i> (L.)	0	+	+	+	+	-	Kehrl and Bacher, 2008 (<i>Minotetrastichus frontalis</i> (Nees))
Caryophyllaceae	<i>Gypsophila elegans</i> (Bieb)	1	+/-	+	+	+	-	Nilsson <i>et al.</i> , unpubl. (<i>Trybliographa rapae</i>)
Asteraceae	<i>Matricaria chamomilla</i> (L.)	1	+/-	+	+	+/-	-	Wäckers, 2004 (<i>Cotesia</i> <i>glomerata</i>)
Asteraceae	<i>Achillea millefolium</i> (Yarrow)	1	+/-	+	+	+/-	-	

Asteraceae L	<i>Cichorium intybus</i> (L.)	1	-	-	+/-	
Asteraceae	<i>Chrysanthemum segetum</i> (L.)	2	+/-	+	+/-	
Asteraceae	<i>Anthemis tinctoria</i> (L.)	2	-	+/-	+/-	Wäckers, 2004 (<i>Cotesia glomerata</i>)
Asteraceae	<i>Leucanthemum vulgare</i> (Lamarck)	2	-	+/-	+	
Asteraceae	<i>Tanacetum vulgare</i> (L.)	2	-	-	+/-	
Asteraceae	<i>Calendula officinalis</i> (L.)	3	-	-	-	Rahat et al., 2005 (<i>Trissolcus basaliss</i> (Wollaston)) Winkler et al., 2009b (<i>Cotesia glomerata</i>)
Asteraceae	<i>Centaura cyanus</i> (L.) (+EFN)	3	+/-	+	+	+/-
Asteraceae	<i>Helianthus annuus</i> (L.) (+EFN)	3	-	+	+	
Asteraceae	<i>Cosmos bipinnatus</i> (Cosmos)	4	-	-	+/-	+
Malvaceae	<i>Malva sylvestris</i> (L.)	4	-	-	-	Rahat et al., 2005 (<i>Trissolcus basaliss</i>)
Boraginaceae	<i>Phacelia tanacetifolia</i> (Bentham)	4	+/-	+/-	+/-	Irvin and Hodde, 2007 (<i>Gonatocerus</i> spp.) Kehri and Bacher, 2008 (<i>Minotetrastichus frontalis</i>) Geneau et al., unpubl. (<i>Microplitis mediator</i>)
Fabaceae	<i>Medicago sativa</i> (L.)	4	-	-	-	
Fabaceae	<i>Vicia sativa</i> (L.) (+EFN)	4	-	+	++	
Fabaceae	<i>Lotus corniculatus</i> (L.)	4	-	-	-	

Plants are ranked according to corolla depth measured up to floral nectaries. Data for *Episyrphus balteatus* (DeGeer) and *Chrysoperla carnea* (Stephens) from van Rijn and Wäckers (2010) and van Rijn (unpublished results). Data for various hymenopteran parasitoids from literature indicated in last column. Floral nectar depth, 0: <0.2 mm, 1: 0.2–1.0 mm, 2: 1.0–2.0 mm, 3: 2.0–3.0 mm, 4: >3.0 mm.

Flower choice, -: less than average, +/-: average, +: more than average. Adult longevity increase relative to control ('Adult food longevity index', AFLI), -: not significant, +/-: 2–4 fold, +: 4–8 fold, ++: more than 8 fold. L: Asteraceae without tubular florets. EFN: plant with extrafloral nectaries.

sources – a strategy that may optimise reproduction in the long term.

Carbohydrates can have a strong impact on several key lifetable parameters. Numerous studies have shown that sugar feeding is indispensable to parasitoid survival; a factor applying both to females and males (Azzouz *et al.*, 2004; Wyckhuys *et al.*, 2008). In addition, sugar feeding can also raise a female's propensity to search for herbivorous hosts and increase her daily fecundity. When combined, these factors can have a considerable cumulative effect on parasitisation rates and parasitoid reproductive success. Using semi-field Brassica patches Winkler *et al.* (2006) showed that the addition of flowering buckwheat increased the average reproductive lifespan of *D. semiclausum* from 1.2 days (control) to 28 days. In the absence of the floral resource the majority of wasps failed to attack any diamondback moth larvae but all parasitoids in the Brassica/buckwheat plots parasitised in excess of 300 larvae. These results demonstrate that access to carbohydrate-rich food may be indispensable to parasitoid fecundity. The impact of food sources on *D. semiclausum* fecundity was more pronounced in the semi-field experiments compared with laboratory studies, emphasising the importance of studying lifetable parameters under more natural conditions.

Parasitoids can fulfil their energy requirements by feeding on a broad range of accessible sugar sources such as floral nectar, extrafloral nectar or honeydew. While honeydew is often the most prevalent sugar source, especially in agricultural ecosystems, it is usually less suitable for supporting parasitoid survival when compared to nectar (Wäckers *et al.*, 2008). Parasitoids appear to be able to select sugar sources on the basis of their nutritional suitability (Wäckers, 2001; Vollhardt *et al.*, 2010).

As far as flower associations are concerned, most parasitoids are limited to the exploitation of exposed, easily accessible nectaries. This includes flower species such as buckwheat (*Fagopyron esculentum* (Moench)) and sweet alyssum (*Lobularia maritima* (L.)) as well as most species from the families Euphorbiaceae and Apiaceae. The flowers from the latter family are well known among taxonomists, who single them out to collect parasitic Hymenoptera. Tooker and Hanks (2000), based on records of flower visitations collected by Robertson (1928), showed that among 112 flowering plant species included in the records the top five in terms of parasitoid visits were all Apiaceae. Interestingly, Euphorbiaceae, while featuring similarly exposed

and accessible floral nectar, were visited far less frequently. This indicates that factors other than accessibility drive flower choice by hymenopteran parasitoids. Other plant species that are frequently visited by hymenopteran parasitoids are those species that produce extrafloral nectar (EFN) (Bugg *et al.*, 1989). EFN glands can usually be successfully exploited due to their exposed nature. EFN is available on a number of flowering herbs used in conservation biological control, such as cornflowers, sunflowers and some vetches (Table 9.2). In addition extrafloral nectaries are found on some crops, including some beans, peach, cherry, plum, cotton and zucchini.

Parasitoids are equipped with a number of mechanisms that enable them to forage effectively for floral nectar. They possess innate preferences for certain floral odours as well as for common flower colours (Wäckers, 1994). Following feeding, parasitoids ignore these floral cues and start responding to host-associated cues (Wäckers, 1994). Associative learning of food-associated stimuli enables parasitoids to concentrate foraging on those flowers where they previously experienced successful feeding (Takasu and Lewis, 1993; Wäckers *et al.*, 2006b).

Hoverflies (Syrphidae)

Hoverflies or flowerflies (Syrphidae) are a diverse group of insects regarding the feeding habits of the larvae. Some species feed on plants while many are saprophagous (i.e. feeding on decaying plant material) either on land or in fresh water. More than one-third of all species are zoophagous, mostly aphidophagous (feeding on aphids) and sometimes also feeding on other small insects (Reemer *et al.*, 2009). Some of these zoophagous species are relatively common in agricultural areas, and can under suitable conditions play an important role in suppressing aphid populations in agricultural crops. Despite the large differences in feeding habits of the larvae, all adult hoverflies feed on pollen and nectar from flowers (Figures 9.2 and 9.3). The protein-rich pollen is needed by both the males and the females for sexual maturation (Haslett, 1989; van Rijn *et al.*, 2006), whilst nectar is an important energy source. The typical hovering flight is an important part of male territorial courtship behaviour. It is therefore suggested that males demand more energy (nectar) but less pollen than females (Gilbert, 1981; Haslett, 1989; Hickman *et al.*, 1995). Further, between species, large



Figure 9.2 *Episyrphus balteatus* feeding on pollen of *Phacelia tanacetifolia* (photo by Paul van Rijn).



Figure 9.3 *Syrphus ribesii* feeding on nectar and/or pollen of *Chrysanthemum segetum* (photo by Paul van Rijn).

differences seem to occur in the relative need for nectar vs. pollen. Some *Melanostoma* and *Platycheirus* species are observed to contain mainly pollen from non-nectar flowers such as grasses and plantain (Ssymank and Gilbert, 1993). These small species are apparently able to obtain enough energy from pollen only. For larger hoverflies nectar makes up a larger part of the diet (Gilbert, 1985).

Although most studies consider hoverflies as one pollination guild (e.g. Comba *et al.*, 1999), large differences exist between species in the types of flowers used as a nectar source (Gilbert, 1981; 1985). Tongue length is one characteristic that can explain such differences, as it clearly limits the range of flowers from which nectar can be obtained (see Figures 9.2 and Figure 9.3). The data from Gilbert (1981; 1985) as well as from Branquart and Hemptinne (2000) indicate (within the nectar feeding species) a correlation between tongue length and the average depth of the flowers they visit. These data also show that most zoophagous hoverflies have much shorter mouthparts than common saprophagous species (e.g. *Eristalis* spp.). Conclusions on food plant ranges for hoverflies in general may therefore not always be applicable for the group of zoophagous hoverflies.

In a similar way to parasitoids, hoverflies show a propensity to visit umbelliferae (Apiaceae). In the analysis by Tooker *et al.* (2006), seven out of the ten plant species most visited by zoophagous hoverflies were from the family Apiaceae, even though they made up only a small proportion of all plant species sampled.

In several other American studies the visit frequencies were studied under more standardised conditions for a small range of flower species. In Hogg *et al.* (2011) hoverflies and other pollinators were observed on nine plant species that were sown in the experimental plots. In all periods where sweet alyssum was flowering this flower received most hoverfly visits (predominantly *Toxomerus marginatus* (Say)), with the exception that buckwheat was visited equally during the short period it was flowering. Alyssum and buckwheat have open flowers. However, the same applies for some of the alternative species (*Brassica* sp., *Diplotaxis muralis* (L.), *Borago officinale* (L.)) that attracted far fewer hoverflies. Some of the latter attracted more bees, which may have interfered with the (smaller) hoverflies (see Box 9.2). In the study by Colley and Luna (2000), featuring 11 plant species, alyssum, buckwheat and mustard were highly visited, but here the most visits were recorded on coriander (*Coriandrum sativum* (L.)). The latter result was confirmed by Ambrosino *et al.* (2006).

Until recently the range of suitable flowers for zoophagous hoverflies has been inferred from direct behavioural observations in the field only. In recent studies, using *Episyrphus balteatus* (DeGeer) as a model organism, results for flower choice studies in flight cages were compared with survival experiments in laboratory cages and morphometric measurements for

about 30 plant species (van Rijn and Wäckers, 2010). Females of *E. balteatus* start reproducing within six days of emergence. Therefore, a food source was considered adequate when females survived for at least six days (van Rijn *et al.*, 2006). In control experiments with only water *E. balteatus* lives for a mere two days, emphasising the importance of floral resources for hoverflies. The study by van Rijn and Wäckers (2010) showed that all plants with exposed nectaries, such as buckwheat and Apiaceae, were suitable food sources. On the other hand, the composites (Asteraceae) tested, featuring tubular florets, showed large differences in suitability for *E. balteatus*. Out of 15 species, 6 were insufficient food sources; 3 species were marginal food sources (resulting in a mean survival just above 6 days) and 6 species allowed the females to survive for 10 days or more. The morphometric data from these plants showed that longevity is generally well correlated with the depth of the tubular florets (see Table 9.2 for a selection of plants). When the florets are 1.6 mm deep or less (e.g. *Matricaria chamomilla* (L.) and *Achillea millefolium* (yarrow)) the flowers were suitable for *E. balteatus*. When the florets were 2.1 mm deep or more (as in *Calendula officinalis* (L.)) the flowers were unsuitable as food sources. The only exception to this latter category was *Jacobaea vulgaris* (Gaertn) where the hoverflies survived despite the floret depth of 2.8 mm. The presence of extrafloral nectaries (EFN) allowed hoverflies to survive long enough, even when the floral nectar is beyond reach. This is the case in cornflowers (*Centaurea cyanus* (L.)), sunflowers (*Helianthus annuus* (L.)) and the common vetch (*Vicia sativa*). Since pollen in most species tested (except Fabaceae species) is well exposed, the results clearly indicate that it is their nectar accessibility that determines hoverfly survival. Floral choice in flight cages appears to be correlated with the longevity performance (excluding plants with EFN: $R^2=0.28$, $n=25$, $p < 0.01$). When floral choice is categorised in 'preferred', 'neutral', and 'avoided', 12 out of 14 species with accessible floral nectar are classified as neutral or 'preferred'. Of the plants with apparent inaccessible nectar only 2 out of 11 species were neutral or 'preferred' (see Table 9.2 and van Rijn and Wäckers, 2010).

These results indicate that flower choice mainly reflects nectar accessibility rather than pollen accessibility. This is in agreement with the field studies by Gilbert (1981) and Branquart and Hemptinne (2000) showing a correlation between (relative) tongue length of the hoverfly species and the average depth of the

flowers visited. At the same time, it is in contrast with the observations by Gilbert (1981; 1985) that in urban gardens *E. balteatus* spends most of its time feeding on pollen: only 10% of the overall feeding time is spent consuming nectar. In fact, since these studies by Gilbert, *E. balteatus* and several other zoophagous species (including *Syrphus ribesii* (L.)) have been categorised as pollen feeders or pollen specialists (Gilbert and Owen, 1990; Branquart and Hemptinne, 2000; Reemer *et al.*, 2009). Accepting that the basic time allocation observations are correct, we have to assume that either pollen feeding requires a longer handling time as compared to the consumption of nectar required survival and flight (at least in the urban garden environment), or feeding on honeydew (which occur on vegetative plant parts not observed by the authors) is an important way of obtaining sugars. Hogervorst *et al.* (2007) concluded on the basis of sugar composition of field-collected adults that 40% of *E. balteatus* collected from one field had been feeding on honeydew, while no honeydew indicating sugars could be detected from those collected in a second field.

Lacewings (Chrysopidae)

Green lacewings (Chrysopidae) and brown lacewings (Hemerobiidae) are families within the order of Neuroptera. The larvae of these lacewings are predators of aphids, caterpillars and other soft-bodied insects. Some species are common within crop habitats, and are considered as important natural enemies of crop pests. Brown lacewing adults and some green lacewing adults feed on prey as well on floral food, while adults of other species (e.g. *Chrysoperla* and *Dichochrysa*) feed on pollen, nectar and honeydew only (Stelzl, 1991). Adult lacewings of *Chrysoperla* species (see Figure 9.4) require a sugar source (nectar or honeydew) and pollen for maximal survival and reproduction. With only a sugar source (sucrose or honey) no oviposition occurs. With only pollen some reproduction occurs, but at a much lower rate than when pollen and sugar are provided together. Moreover, survival is reduced in the absence of a sugar source (Venzon *et al.*, 2006; Li *et al.*, 2010). *Chrysoperla* adults house yeasts in their crop (diverticulum) that are assumed to provide the insects with essential amino acids that may not be present in their floral or honeydew diet (Hagen *et al.*, 1970; Gibson and Hunter, 2005).



Figure 9.4 *Chrysoperla carnea* (s.l.) feeding on pollen of *Chrysanthemum segetum* (photo by Paul van Rijn).

The range of plants that are used as pollen source can be assessed from crop content analyses of field collected lacewings. Females of *Chrysoperla carnea* (Stephens) collected in flowering maize fields contained around 5,000 pollen grains each (Li *et al.*, 2010). Adult lacewings (*C. externa*) collected in vegetable fields in Brazil contained much lower numbers (on average 252 grains/predator) which appeared to be mainly (greater than 99%) pollen from grasses (Medeiros *et al.*, 2010). Possibly these anemophilous (i.e. wind dispersed) pollen grains are collected from leaves rather than from the flowers. Villenave *et al.* (2005; 2006) found pollen from a large range of plant families within the crops of *Chrysoperla* species in western France from field crops and surrounding vegetation. Based on the assumed activity pattern of lacewings, scrubs and trees were sampled in daytime and herbs during twilight. They concluded that these lacewings were opportunistic foragers feeding on all flowers that are readily available, including shrubs from *Sambucus* and *Corylus* and Rosaceae, and herbs from the families Brassicaceae, Cayophyllaceae and Asteraceae (Villenave *et al.*, 2005). Other plant families that are fed upon in proportion to their presence are Chenopodiaceae, grasses (Poaceae) and Liliaceae (Villenave *et al.*, 2006). However some families are absent or clearly underrepresented in the lacewing crop. In the case of Convolvulaceae, Cucurbitaceae, Geraniaceae and Malvaceae this could be explained by the closure of the flowers at twilight, when the lacewings are active. For other families (e.g. Rubiaceae, Resedaceae, Primulaceae, Onagraceae, Verbenaceae, Violaceae) no direct expla-

nation is available without complementary experimental studies.

Various laboratory studies have shown the suitability of different pollen for survival and reproduction of *Chrysoperla* adults. Elbadry and Fleschner (1965) found reproduction was higher when *Chrysoperla* adults were kept on a diet of *Mesembryanthemum* pollen compared to pollen of *Capsicum* or *Cedrus*. Venzon *et al.* (2006) showed that pollen from leguminous cover crops (*Cajanus cajan* (L.) and *Crotalaria juncea* (L.)) allows for high reproduction rates, especially when complemented with honey, whereas pollen of the euphorbic castor bean *Ricinus communis* (L.) was less suitable.

Pollen analysis may reveal which plant species are exploited as source of pollen, but these do not necessarily constitute a suitable nectar source. Since the mouthparts of lacewings are rather small, only a limited number of plant species have nectar that is accessible to them. The sugar content of *C. carnea* adults collected in wheat fields by Hogervorst *et al.* (2007) indicated that 98% of the adults has been feeding on a sugar source, with a remarkably high average sugar level that was 45–90% of the maximum level measured in lacewings that had unlimited access to sucrose. The sugar spectrum, however, was not conclusive to establish whether these sugars originated from honeydew or nectar.

Survival experiments performed by van Rijn (unpublished results) to assess the suitability of various flowering plants as food sources for adult lacewings show the combined impact of pollen and nectar. Adult longevity was higher for all species with exposed nectaries compared to all other plant species (Table 9.2), which indicates the importance of nectar accessibility for flower suitability. However, on many plants with deeper corollas or inaccessible nectar, lacewings live on pollen long enough to start ovipositing, making the range of flowers suitable for lacewings broader as compared to those for hoverflies.

While larvae of *Chrysoperla* primarily feed on aphids and other prey, they will also consume (extrafloral) nectar and pollen when available. Nectar feeding is especially prevalent among neonate larvae and when prey is scarce (Limburg and Rosenheim, 2001), but occurs even when access to prey is unlimited (Hogervorst *et al.*, 2008). The nectar (of cotton) by itself does not allow for larval development but supports their survival and searching activity considerably (Limburg and Rosenheim, 2001). When the prey diet is relatively

poor, the addition of pollen and nectar enhances larval growth, and beyond the second stage allows further development even in the absence of prey (Patt *et al.*, 2003).

Flowerbugs (Anthocoridae)

Flowerbugs or Anthocoridae have, like all Heteroptera, a pointed rostrum with which they feed on mites and small insects such as thrips, aphids, psyllids, small caterpillars and eggs. Various *Anthocoris* and *Orius* species are considered important predators of insect pests. In addition to prey, many anthocorids also feed on plant material, such as plant juices, pollen and nectar. By feeding on plant juices they increase their longevity when prey is scarce (Salas-Aguilar and Ehler, 1977; Kiman and Yeargan, 1985; Coll, 1996). Other predatory bugs (from the related family Miridae) are thought to feed on plant sap only. However, a recent study showed that survival of *Macrolophus pygmaeus* (Rambur) is prolonged on broad bean plants providing extrafloral nectar as compared to broad bean with EFN removed. It also demonstrated that a greater proportion of mirid females laid eggs when extrafloral nectar was available compared to those confined on nectariless plants (Portillo *et al.*, 2012).

Feeding on pollen occurs in many anthocorids, but its impact on life history varies. *Orius pallidicornis* (Carayon) seem to feed almost exclusively on pollen (Carayon and Steffan, 1959). *Orius insidiosus* (Say), an important predator of corn pests, is reported to complete development and to oviposit on a diet of corn pollen only (Kiman and Yeargan, 1985), but this result was not confirmed by other studies (Richards and Schmidt, 1996). *Orius sauteri* (Poppius) is able to develop and oviposit on a diet of pollen, but at much lower rates than with prey diets (Funao and Yoshiyasu, 1995; Yano, 1996). In other species (*Orius tricolor* (White), *Orius laevigatus* (Fieber) and *Orius albidipennis* (Reuter)) pollen increases longevity but does not allow for full development or oviposition (Salas-Aguilar and Ehler, 1977; Cocuzza *et al.*, 1997; Vacante *et al.*, 1997). However, supplementing prey diet with pollen increases their development and oviposition. These results explain why various *Orius* spp. are generally more successful in pollen-bearing crops (e.g. strawberry, eggplant, sweet pepper), as opposed to crops without pollen (e.g. cucumber) (Van den Meiracker and Ramackers, 1991; Dissevelt *et al.*, 1995). It also explains why

these anthocorids often become more abundant in periods of increased pollen availability within the crop (Dicke and Jarvis, 1962; Isenhour and Yeargan, 1981; Coll and Bottrell, 1995).

In contrast with the previously discussed insect groups, the anthocorids are true omnivores that can feed both on prey and pollen in each life stage. Consequently, feeding on pollen may also directly affect their feeding on prey through satiation. Indeed, Skirvin *et al.* (2007) found that the presence of pollen led to a 40% reduction in thrips predation by *O. laevigatus*. Corey *et al.* (1998) concluded from electrophoresis of gut contents that in flowering corn, *O. insidiosus* fed mostly on corn pollen and much less on prey. In this way pollen can diminish the pest control capacity of the predator in the short term. On longer time scales, however, the enhanced production or attraction of predators is likely to tip the balance in the other direction (van Rijn *et al.*, 2002).

Flowers produced by plants other than crop plants can affect the anthocorid populations in and around crop fields as well. Letourneau and Altieri (1983) found that intercropping squash with corn and cowpea increased the number of *Orius*, possibly due to corn pollen. Frescata and Mexia (1995) observed more *O. laevigatus* and less thrips in a strawberry patch where a composite weed (*Chamaemelum mixtum* (L.)) was flowering compared to all other patches. Atakan (2010) found that numbers of *Orius niger* (Wolff) were significantly greater in faba bean plots with weedy margins than in weed-free plots.

The suitability of plants species for supporting anthocorids is little studied. Due to their small size direct observations on flower choice is not possible, but by tapping or collecting flowers from vegetation in and around crop fields and sorting out its content the distribution over various plant species can be assessed. Silveira *et al.* (2003) collected anthocorids on crops and weeds in south-east Brazil. The main species, *O. insidiosus*, was found on plants belonging to the families Poaceae, Fabaceae, Asteraceae and Amaranthaceae. Since they also found an association between *Orius* and thrips, its main prey, this species distribution of *Orius* may both be a direct and an indirect effect (through prey distribution) of plant features (Silveira *et al.*, 2005). Fiedler and Landis (2007a; 2007b) vacuumed flowers in plots of 43 native perennial plant species and found that *O. insidiosus* made up 30% of all natural enemies on these flowers, with chalcidoid parasitoids as the second most important group (25%).

The total number of natural enemies (all groups taken together) was positively correlated with the flowering period and with the flower surface. Within each seasonal period the highest numbers of natural enemies were found on species with well exposed nectaries belonging to the families of Apiaceae (3/3), Rosaceae (3/4), and Ranunculaceae (1/1), as well as species with less exposed nectaries including Asteraceae (5/13), Apocynaceae (1/1), Lamiaceae (1/2), Scrophulariaceae (1/2) and Onagraceae (1/1). No patterns are provided for the individual groups of natural enemies. Bosco and Tavella (2008) sampled the wild vegetation surrounding pepper greenhouses in north-western Italy for *O. niger*, *Orius majusculus* (Reuter) and *Orius minutus* (L.). They showed that *Orius* exhibits species-specific plant associations, with *O. niger* exhibiting a marked preference for Fabaceae. Van Rijn (unpublished results) regularly sampled flowers from flower strips along onion fields in the Netherlands. He found *Orius* spp. (mainly *O. minutus*) almost exclusively on Asteraceae plants (see Figure 9.5), with the highest numbers on *H. annuus* and *Cosmos bipinnatus* (Cavanilles). These results suggest that these bugs prefer flowers with deeper (and wider) corollas, possibly because these can serve as a hiding place as well.

Lady beetles (Coccinellidae)

Lady(bird) beetles are probably the most emblematic biological control agents. In some agroecosystems their presence may contribute considerably to natural pest control. Although they seem to lack the ability to regulate aphid populations in summer (Dixon, 2000) early-season pest suppression may benefit from conservation measures that promote lady beetle subsistence on prey and non-prey food in spring (Obrycki *et al.*, 2009).

Both larvae and adults have chewing mouthparts and can utilise similar food sources. Most entomophagous species of Coccinellidae feed on aphids or scale insects. Although floral food sources are not essential for these predators, they may be dependent on them when prey is temporarily scarce (Lundgren, 2009). Feeding on nectar, especially from extrafloral nectaries, is well known among coccinellids (Pemberton and Vandenberg, 1993; see also Figure 9.6). In absence of prey these sugar sources can strongly support survival (Putman, 1955) as well as flight capacity (Nedved *et al.*, 2001). Pollen provides the beetles with enough



Figure 9.5 A ladybird *Harmonia axyridis* and three *Orius* feeding on *Chrysanthemum segetum* (photo by Paul van Rijn).



Figure 9.6 *Coccinella septempunctata* feeding on extrafloral nectaries of cornflower (photo by Paul van Rijn).

proteins and other nutrients for some to complete their development on a diet of pollen only. The development rate and the final weight, however, are always lower than on a suitable prey diet (Lundgren, 2009). Pollen allows adults to survive longer, but generally does not support reproduction. An exception is *Coleomegilla*

maculata (DeGeer), which can complete its life cycle on a diet of pollen only (Lundgren and Wiedenmann, 2004). In the presence of prey, both nectar and pollen generally enhance development and reproduction (Lundgren, 2009). The fact that combining floral food and prey can benefit biological control is shown by Harmon *et al.* (2000), who observed that alfalfa plots with flowering *Taraxacum* (dandelion) plants had higher numbers of *C. maculata* and lower number of aphids than plots without these flowers.

Intensive inspection of more than 60 plant species in weed strips within a wheat field in Switzerland revealed 20 species that were frequently visited by local coccinellids (Schmid, 1992). For 11 plant species this could be attributed to the presence of abundant aphid populations. On other plant species floral resources seems to be the main food source for the lady beetles. The relative importance of the two food sources appears to be different for the various species of coccinellids. *Coccinella septempunctata* (L.) mainly occurs on plants with high number of aphids, such as *Symphytum officinale* (L.), *Silene alba* (Miller) and *Urtica dioica* (L.), on which also the juveniles are found. *Adonia variegata* (Goeze) on the other hand is mainly abundant on plants with floral resources, such as *Tripleurospermum inodora* (L.), *Myosotis arvensis* (L.), *Leucanthemum vulgare* (Lamarck), *Daucus carota* (L.), and *Verbascum thapsus* (Mullein). The same is true for *Propylea quatuordecimpunctata* (L.) showing high numbers on *Lamium purpureum* (L.) and *Plantago major* (L.). Juveniles are only observed when aphids are present as well, as on *T. inodora*. The large variation in flower types and nectar accessibility among these plants suggests that the beetles feed on pollen more than on floral nectar. Extrafloral nectar was present only on *C. cyanus* (see Figure 9.6), which showed intermediate numbers of three coccinellid species.

Few other studies have considered the association between plant species and coccinellids (Honěk, 1985; Burgio *et al.*, 2004), and even fewer have separated the impact of flowers from that of prey on these plants. In a mono-flower plot set-up comparing different Apiaceae, Lixa *et al.* (2010) found higher densities of various coccinellid species on *Anethum graveolens* (L.) (dill) compared to *C. sativum* (coriander) and *Foeniculum vulgare* (Miller) (fennel). In olfactometer tests *Harmonia axyridis* (Pallas) prefers odours from sunflower and dill over eight other plant species (Adedipe and Park, 2010). Visual preference tests were in concurrence with these results showing that this species

prefers the common flower colour yellow over all other colours. In an experimental set-up Bertolaccini *et al.* (2008) found that the egg production of *Hippodamia variegata* (Goeze) on plants with aphids increased when flowers of *Brassica* and *Sonchus* were present but not when flowers of *Daucus* were present. There is an obvious need for more of these experimental studies to establish which plant species and plant features can support lady beetle survival and reproduction in the absence of prey.

CONCLUSION

The detailed information on flower suitability generated by various laboratory and field studies has been used to underpin the selection of seed mix prescriptions for programmes aiming at arthropod conservation and/or enhancement of ecosystem services, such as pollination and biological control. These seed mixes typically target one particular group of arthropods (Wäckers, 2004; Carvell *et al.*, 2007; Coll, 2009). It is often implicitly assumed that flower-rich vegetation that has been selected to cater for one particular target group will generate benefits to nectar and pollen feeders across the board. This ignores the fact that flower associations can often be highly specific, and that plants have evolved many mechanisms through which they can exclude visitors other than the intended specialised pollinators (Faegri and van der Pijl, 1979; Kevan and Baker, 1998; Waser and Ollerton, 2006). Comparing pollinator and biological control targeted seed mixes, Campbell, Biesmeijer and Wäckers (unpublished) showed recently that flower visitation differed significantly between pollinators and biological control agents. Bumblebees almost completely refrained from visiting biological control seed mixes, whilst parasitoids were all but absent from flowers in the pollinator plots. These results highlight that insects providing ecosystem services differ distinctly with regard to their flower associations and that flower mixes targeting particular insect groups are not necessarily effective in supporting other beneficial arthropods.

The studies described in this chapter demonstrate that there can also be considerable variation within one functional group (i.e. among various categories of entomophagous arthropods). The data presented in Table 9.2 show the survival of hoverflies, lacewings and parasitoids on a range of flowering plants ranked by the depth of floral nectaries. The overview shows

that parasitoids are more constrained by the accessibility of floral nectaries, exhibiting enhanced survival only on those flowers where the nectaries are fully exposed. The examples where parasitoids show enhanced longevity on flowers with deeper corollas can be explained by the fact that *V. sativa* and *C. cyanus* feature EFN. The fact that the parasitoid *Trissolcus basalis* (Wollaston) is able to exploit nectar from *C. bipinnatus* can be explained by the small size of the (egg) parasitoid, allowing it to enter the relatively deep flower.

Zoophagous hoverflies can access flowers up to a nectar depth of 2 mm, but appear to be constrained by flowers with deeper lying nectaries. Exceptions to this are *Phacelia tanacetifolia* (Bentham) and plants which feature EFNs (Table 9.2).

Chrysoperla lacewings can probably use nectar from a smaller range of flowers than indicated in Table 9.2. The study of lacewing nectar exploitation can be skewed by the fact that *Chrysoperla* can also survive for some time by feeding on the often more accessible pollen (Venzon *et al.*, 2006). The lower nectar dependency of lacewings relative to hoverflies may be explained by the much reduced flight activity of the former.

Anthocorids (especially *Orius* spp.) are thought to be even less dependent on nectar feeding (but see examples described above). Moreover, their much smaller size and prolonged mouthpart structure relative to hoverflies and lacewings results in very different flower type relationships. Their specific morphology allows them to access or enter flowers with deep corollas as well as flowers of the flag type (Fabaceae) that are inaccessible to other beneficial insect groups. They even seem to prefer these flowers, possibly as these provide shelter, or prey, such as thrips, commonly associated with these flowers (Silveira *et al.*, 2005).

The specificity that emerges from these studies underscores the importance of selecting the right flowers when composing seed mixtures to optimise the biological control services of agroecosystems. Earlier approaches using flowering plants to support biological pest control could not draw upon the specific information that is currently available. As these studies make up a substantial part of the examples included in meta-analyses of the impact of habitat diversification on pest control, such analyses probably still underestimate the potential of using informed selection of flowering vegetation in conservation biological control.

When selecting flowering plant mixes that effectively support biological control in a particular crop, a sound approach would be to:

- identify the main pests in that particular crop as well as their key natural enemies,
- identify floral resource requirement of these target organisms, both in terms of which floral resource they need and when they need it,
- identify plant species that are effective in providing these resources to the natural enemies at the right time, while preferably excluding nutritional benefits to the pests.

Additional criteria should be considered when selecting flowering plants for targeted seed mixes (see the Ecostac website for more information: http://www.ecostac.co.uk/seed_selection.php). These criteria could be soil and climate requirements of the flowering plants; plant phenology (e.g. height); whether plants are annual/biannual/perennial; native/naturalised/non-native; seed availability/quality/price. Plants with negative traits such as weed potential, or those serving as potential alternative host to crop diseases or pests should be excluded. The hosting of non-pest herbivores, on the other hand, is often advantageous as it allows populations of natural enemies to develop in absence of the crop pest (banker plants). Competitive interactions between flowering plants and crop plants can occur when flowering vegetation is used in close proximity to the crop, such as in cases of flowering undergrowth in orchards, mixed cropping, or companion planting. These competitive interactions can be averted through the selection of specific compatible combinations.

The combining of flowering plants in flower mixes requires some other points to be considered. For instance, the compatibility of the separate plants and their competitive strength in the mixture can be issues. Important is the issue of whether individual plant species are complementary in their traits, for instance in terms of resources provided, accessibility, or flowering time. While it is usually of little benefit to have too much redundancy between floral offerings, some level of redundancy can be useful as an insurance policy in case some plants do not germinate or establish.

Overall, the informed choice of flowering plants and the spatial setting of floral vegetation relative to crops and other landscape elements gives us a powerful tool to shape the composition of the agricultural arthropod fauna and to maximise the ecosystem services they provide. It is all in the mix!

REFERENCES

- Adedipe, F. and Park, Y.L. (2010) Visual and olfactory preference of *Harmonia axyridis* (Coleoptera: Coccinellidae) adults to various companion plants. *Journal of Asia-Pacific Entomology*, 13, 319–323.
- Ambrosino, M.D., Luna, J.M., Jepson, P.C. and Wratten, S.D. (2006) Relative frequencies of visits to selected insectary plants by predatory hoverflies (Diptera: Syrphidae), other beneficial insects, and herbivores. *Environmental Entomology*, 35, 394–400.
- Andow, D.A. (1991) Vegetational diversity and arthropod population response. *Annual Review of Entomology*, 36, 561–586.
- Araj, S.E., Wratten, S., Lister, A. and Buckle, H. (2008) Floral diversity, parasitoids and hyperparasitoids – A laboratory approach. *Basic and Applied Ecology*, 9, 588–597.
- Atakan, E. (2010) Influence of weedy field margins on abundance patterns of the predatory bugs *Orius* spp. and their prey, the western flower thrips (*Frankliniella occidentalis*), on faba bean. *Phytoparasitica*, 38, 313–325.
- Atakan, E. and Tunc, I. (2010) Seasonal abundance of hemipteran predators in relation to western flower thrips *Frankliniella occidentalis* (Thysanoptera: Thripidae) on weeds in the eastern Mediterranean region of Turkey. *Biocontrol Science and Technology*, 20, 821–839.
- Azzouz, H., Giordanengo, P., Wäckers, F.L. and Kaiser, L. (2004) Effects of sugar availability and concentration on behavior and longevity of the aphid parasitoid *Aphidius ervi* (Haliday) (Hymenoptera: Braconidae). *Biological Control*, 31, 445–452.
- Baggen, L.R. and Gurr, G.M. (1998) The influence of food on *Copidosoma koehleri* (Hymenoptera: Encyrtidae), and the use of flowering plants as a habitat management tool to enhance biological control of potato moth, *Phthorimaea operculella* (Lepidoptera: Gelechiidae). *Biological Control*, 11, 9–17.
- Baggen, L.R., Gurr, G.M. and Meats, A. (1999) Flowers in tri-trophic systems: mechanisms allowing selective exploitation by insect natural enemies for conservation biological control. *Entomologia Experimentalis et Applicata*, 91, 155–61.
- Beattie, A.J. (1985) *The evolutionary ecology of ant-plant mutualisms*. Cambridge University Press, Cambridge.
- Begum, M., Gurr, G.M., Wratten, S.D. and Nicol, H.I. (2004) Flower color affects tri-trophic-level biocontrol interactions. *Biological Control*, 30, 584–590.
- Begum, M., Gurr, G.M., Wratten, S.D., Hedberg, P.R. and Nicol, H.I. (2006) Using selective food plants to maximize biological control of vineyard pests. *Journal of Applied Ecology*, 43, 547–554.
- Bertolaccini, I., Núñez-Pérez, E. and Tizado, E.J. (2008) Effect of wild flowers on oviposition of *Hippodamia variegata* (Coleoptera: Coccinellidae) in the laboratory. *Journal of Economic Entomology*, 101, 1792–1797.
- Biesmeijer, J.C., Roberts, S.P.M., Reemer, M. et al. (2006) Parallel declines in pollinators and insect-pollinated plants in Britain and the Netherlands. *Science*, 313, 351–354.
- Blüthgen, N., Verhaagh, M., Goitia, W., Jaffé, K., Morawetz, W. and Barthlott, W. (2000) How plants shape the ant community in the Amazonian rainforest canopy: the key role of extrafloral nectaries and homopteran honeydew. *Oecologia*, 125, 229–240.
- Bosco, L. and Tavella, L. (2008) Collection of *Orius* species in horticultural areas of northwestern Italy. *Bulletin of Insectology*, 61, 209–210.
- Branquart, E. and Hemptinne, J.L. (2000) Selectivity in the exploitation of floral resources by hoverflies (Diptera: Syrphidae). *Ecography*, 23, 732–742.
- Bugg, R.L., Ellis, R.T. and Carlson, R.W. (1989) Ichneumonidae (Hymenoptera) using extrafloral nectar of faba bean (*Vicia Faba* L., Fabaceae) in Massachusetts. *Biological Agriculture and Horticulture*, 6, 107–114.
- Burgio, G., Ferrari, R., Pozzati, M. and Boriani, L. (2004) The role of ecological compensation areas on predator populations: an analysis on biodiversity and phenology of Coccinellidae (Coleoptera) on non-crop plants within hedgerows in Northern Italy. *Bulletin of Insectology*, 57, 1–10.
- Carayon, J. and Steffan, J. (1959) Observations sur le regime alimentaire des *Orius* et particulièrement d' *Orius pallidicornis* (Peuter) (Hemiptera: Anthocoridae). *Cahiers des Naturalistes*, 15, 53–63.
- Carvell, C., Meek, W.R., Pywell, R.F., Goulson, D. and Nowakowski, M. (2007) Comparing the efficacy of agri-environment schemes to enhance bumble bee abundance and diversity on arable field margins. *Journal of Applied Ecology*, 44, 29–40.
- Chaney, W.E. (1998) Biological control of aphids in lettuce using in-field insectaries, in *Enhancing Biological Control: Habitat management to promote natural enemies of agricultural pests* (eds C.H. Pickett and R.L. Bugg), University of California Press, Berkeley, pp.73–83.
- Cocuzza, G.E., DeClercq, P., VandeVeire, M., DeCock, A., Degheele, D. and Vacante, V. (1997) Reproduction of *Orius laevigatus* and *Orius albidipennis* on pollen and *Ephestia kuehniella* eggs. *Entomologia Experimentalis et Applicata*, 82, 101–104.
- Coll, M. (1996) Feeding and oviposition on plants by an omnivorous insect predator. *Oecologia*, 105, 234–220.
- Coll, M. (2009) Conservation biological control and the management of biological control services: are they the same? *Phytoparasitica*, 37, 205–208.
- Coll, M. and Bottrell, D.G. (1995) Predator–prey association in mono and dicultures: effect of maize and bean vegetation. *Agriculture, Ecosystems and Environment*, 54, 115–125.
- Colley, M.R. and Luna, J.M. (2000) Relative attractiveness of potential beneficial insectary plants to aphidophagous hoverflies (Diptera: Syrphidae). *Environmental Entomology*, 29, 1054–1059.

- Comba, L., Corbet, S.A., Hunt, L. and Warren, B. (1999) Flowers, nectar and insect visits: evaluating British plant species for pollinator-friendly gardens. *Annals of Botany*, 83, 369–383.
- Corey, D., Kambhampati, S. and Wilde, G. (1998) Electrophoretic analysis of *Orius insidiosus* (Hemiptera: Anthocoridae) feeding habits in field corn. *Journal of the Kansas Entomological Society*, 71, 11–17.
- Davidson, L.N. and Evans, E.W. (2010) Frass analysis of diets of aphidophagous lady beetles (Coleoptera: Coccinellidae) in Utah alfalfa fields. *Environmental Entomology*, 39, 576–582.
- DeGrandi-Hoffman, G. and Hagler, J. (2000) The flow of incoming nectar in a honey bee (*Apis mellifera* L.) colony as revealed by a protein marker. *Insectes Sociaux*, 47, 302–306.
- Dicke, F.F. and Jarvis, J.L. (1962) The habits and seasonal abundances of *Orius insidiosus* (Say) (Hemiptera-Heteroptera: Anthocoridae) on corn. *Journal of the Kansas Entomological Society*, 35, 339–344.
- Dissevelt, M., Altena, K. and Ravensberg, W.J. (1995) Comparison of different *Orius* species for control of *Frankliniella occidentalis* in glasshouse vegetable crops in the Netherlands. *Mededelingen Faculteit Landbouwwetenschappen, Universiteit Gent*, 60/3a, 839–845.
- Dixon, A.F.G. (2000) *Insect predator-prey dynamics – ladybird beetles and biological control*, Cambridge University Press, Cambridge.
- Dunning, J.B., Danielson, B.J. and Pulliam, H.R. (1992) Ecological processes that affect populations in complex landscapes. *Oikos*, 65, 169–175.
- Elbadry, E.A. and Fleschner, C.A. (1965) The feeding habits of adults of *Chrysopa californica* Coquillett. (Neuroptera: Chrysopidae). *Bulletin de la Societe Entomologique d’Egypte*, 49, 359–366.
- Faegri, K. and van der Pijl, L. (1979) *The Principles of Pollination Ecology*, Pergamon Press, Oxford.
- Feinsinger, P. and Swam, L.A. (1978) How common are ant-repellent nectars? *Biotropica*, 10, 238–239.
- Ferrerres, F., Andrade, P., Gil, M.I. and Tomas-Barberan, F.A. (1996) Floral nectar phenolics as biochemical markers for the botanical origin of heather honey. *Zeitschrift für Lebensmitteluntersuchung und Forschung A*, 202, 40–44.
- Fiedler, A.K. and Landis, D.A. (2007a) Attractiveness of Michigan native plants to arthropod natural enemies and herbivores. *Environmental Entomology*, 36, 751–765.
- Fiedler, A.K. and Landis, D.A. (2007b) Plant characteristics associated with natural enemy abundance at Michigan native plants. *Environmental Entomology*, 36, 878–886.
- Fiedler, A.K., Landis, D.A. and Wratten, S.D. (2008) Maximizing ecosystem services from conservation biological control: the role of habitat management. *Biological Control*, 45, 254–271.
- Foster, M.A. and Ruesink, W.G. (1984) Influence of flowering weeds associated with reduced tillage in corn on a black cutworm (Lepidoptera: Noctuidae) parasitoid, *Meteorus rubens* (Nees von Esenbeck). *Environmental Entomology*, 13, 664–668.
- Frescata, C. and Mexia, A. (1995) Biological control of western flower thrips with *Orius laevigatus* (Heteroptera: Anthocoridae) in organic strawberries in Portugal, in *Thrips biology and management* (eds B.L. Parker, M. Skinner and T. Lewis), NATO ASI Series A, Life Sciences Vol. 276, Plenum Press, New York, pp. 249–250.
- Funao, T. and Yoshiyasu, Y. (1995) Development and fecundity of *Orius sauteri* (Poppius) (Hemiptera: Anthocoridae) reared on *Aphis gossypii* Glover and corn pollen. *Japanese Journal of Entomology and Zoology*, 39, 84–85.
- Gibson, C.M. and Hunter, M.S. (2005) Reconsideration of the role of yeasts associated with *Chrysoperla* green lacewings. *Biological Control*, 32, 57–64.
- Gilbert, F.S. (1981) Foraging ecology of hoverflies: morphology of the mouthparts in relation to feeding on nectar and pollen in some common urban species. *Ecological Entomology*, 6, 245–262.
- Gilbert, F.S. (1985) Ecomorphological Relationships in Hoverflies (Diptera, Syrphidae). *Proceedings of the Royal Society B*, 224, 91–105.
- Gilbert, F.S. and Jervis, M.A. (1998) Functional, evolutionary and ecological aspects of feeding-related mouthpart specializations in parasitoid flies. *Biological Journal of the Linnean Society*, 63, 495–535.
- Gilbert, F.S. and Owen, O. (1990) Size, shape, competition, and community structure in hoverflies (Diptera: Syrphidae). *Journal of Animal Ecology*, 59, 21–39.
- Golding, Y. and Edmunds, M. (2003) A novel method to investigate the pollen diets of hoverflies. *Journal of Biological Education*, 37, 182–185.
- Gu, H., Wäckers, F.L., Steindl, P., Günther, D. and Dorn, S. (2001) Different approaches to labelling parasitoids using strontium. *Entomologia Experimentalis et Applicata*, 99, 173–181.
- Gurr, G.M., Wratten, S.D., Tylianakis, J., Kean, J. and Keller, M. (2005) Providing plant foods for natural enemies in farming systems: balancing practicalities and theory, in *Plant-Provided Food for Carnivorous Insects A Protective Mutualism and its Applications* (eds F.L. Wäckers and P.C.J. van Rijn), Cambridge University Press, Cambridge, pp. 326–347.
- Hagen, K.S. (1986) Ecosystem analysis: Plant cultivars, entomophagous species and food supplements, in *Interactions of Plant Resistance and Parasitoids and Predators of Insects* (eds D.J. Boethel and R.D. Eikenbary), John Wiley & Sons, Inc., New York, pp. 153–197.
- Hagen, K.S., Tassan, R.L. and Sawall Jr., E.F. (1970) Some ecophysiological relationships between certain *Chrysopa*, honeydews and yeasts. *Bollettino Laboratorio Entomologia Agraria Filippo Silvestri*, 28, 113–134.
- Hansen, D.M., Olesen, J.M. and Jones, C.G. (2002) Trees, birds and bees in Mauritius: exploitative competition between

- introduced honey bees and endemic nectarivorous birds? *Journal of Biogeography*, 29, 721–734.
- Harmon, J.P., Ives, A.R., Losey, J.E., Olson, A.C. and Rauwald, K.S. (2000) *Colemegilla maculata* (Coleoptera: Coccinellidae) predation on pea aphids promoted by proximity to dandelions. *Oecologia*, 125, 543–548.
- Haslett, J.R. (1989) Adult feeding by holometabolous insects – pollen and nectar as complementary nutrient sources for *Rhingia campestris* (Diptera, Syrphidae). *Oecologia*, 81, 361–363.
- Hausmann, C., Wäckers, F.L. and Dorn, S. (2005) Sugar convertibility in the parasitoid *Cotesia glomerata* (Hymenoptera: Braconidae). *Archives of Insect Biochemistry and Physiology*, 60, 223–229.
- Hayes, E.J. and Wall, R. (1999) Age-grading adult insects: a review of techniques. *Physiological Entomology*, 24, 1–10.
- Heimpel, G.E. and Jervis, M.A. (2005) Does floral nectar improve biological control by parasitoids? in *Plant-provided food for carnivorous insects: a protective mutualism and its applications* (eds F.L. Wäckers, P.C.J. van Rijn and J. Bruin), Cambridge University Press, Cambridge, pp. 267–304.
- Heimpel, G.E., Lee, J.C., Wu, Z. et al. (2004) Gut Sugar Analysis in Field-Caught Parasitoids: Adapting Methods Used on Biting Flies. *International Journal of Pest Management*, 50, 193–198.
- Hickman, J.M., Lovei, G.L. and Wratten, S.D. (1995) Pollen feeding by adults of the hoverfly *Melanostoma fasciatum* (Diptera: Syrphidae). *New Zealand Journal of Zoology*, 22, 387–392.
- Hogervorst, P.A.M., Wäckers, F.L. and Romeis, J. (2007) Detecting nutritional state and food source use in field-collected insects that synthesize honeydew oligosaccharides. *Functional Ecology*, 21, 936–946.
- Hogervorst, P.A.M., Wäckers, F.L., Carette, A.-C. and Romeis, J. (2008) The importance of honeydew as food for larvae of *Chrysoperla carnea* in the presence of aphids. *Journal of Applied Entomology*, 132, 18–25.
- Hogg, B.N., Bugg, R.L. and Daane, K.M. (2011) Attractiveness of common insectary and harvestable floral resources to beneficial insects. *Biological Control*, 56, 76–84.
- Honěk, A. (1985) Habitat preferences of aphidophagous coccinellids [Coleoptera]. *BioControl*, 30, 253–264.
- Human, H. and Nicolson, S.W. (2006) Nutritional content of fresh, bee-collected and stored pollen of *Aloe greathedii* var. *davyana* (Asphodelaceae). *Phytochemistry*, 67, 1486–1492.
- Idris, A.B. and Grafius, E. (1997) Nectar-collecting behavior of *Diadegma insulare* (Hymenoptera: Ichneumonidae), a parasitoid of diamondback moth (Lepidoptera: Plutellidae). *Environmental Entomology*, 26, 114–120.
- Illingworth, J.F. (1921) Natural enemies of sugar-cane beetles in Queensland. Queensland Bureau of Sugar Experiment Stations, Division of Entomology, *Bulletin* 13, 1–47.
- Inouye, D.W. (1983) The ecology of nectar robbing, in *The Biology of Nectaries* (eds B. Bentley and T. Elias), Columbia University Press, New York, pp. 153–173.
- Irvin, N.A. and Hoddle, M.S. (2007) Evaluation of floral resources for enhancement of fitness of *Gonatocerus ashmeadi*, an egg parasitoid of the glassy-winged sharpshooter, *Homalodisca vitripennis*. *Biological Control*, 40, 80–88.
- Isenhour, D.J. and Yeargan, K.V. (1981) Predation by *Orius insidiosus* (Hemiptera: Anthocoridae) on the soybean thrips *Sericothrips variabilis* (Thysanoptera: Thripidae): effect of prey stage and density. *Environmental Entomology*, 10, 496–500.
- Jervis, M. (1998) Functional and evolutionary aspects of mouthpart structure in parasitoid wasps. *Biological Journal of the Linnean Society*, 63, 461–493.
- Jervis, M.A., Kidd, N.A.C., Fitton, M.G., Huddleston, T. and Dawah, H.A. (1993) Flower-visiting by hymenopteran parasitoids. *Journal of Natural History*, 27, 67–105.
- Jervis, M.A., Lee, J.C. and Heimpel, G.E. (2004) Use of behavioural and life-history studies to understand the effects of habitat manipulation, in *Ecological engineering for pest management advances in habitat manipulation for arthropods* (eds G.M. Gurr, S.D. Wratten and M.A. Altieri), CSIRO Publishing, Collingwood, pp. 65–101.
- Jones, T.P. and Rowe, N.P. (1999) *Fossil Plants and Spores*, The Geological Society of London, London.
- Kehrli, P. and Bacher, S. (2008) Differential effects of flower-feeding in an insect host-parasitoid system. *Basic and Applied Ecology*, 9, 709–717.
- Kevan, G. (1973) Parasitoid wasps as flower visitors in the Canadian high arctic. *Anz Schädlingskd Pflanz Umweltschutz*, 46, 3–7.
- Kevan, P.G. and Baker, H.G. (1998) Insects on flowers, in *Ecological Entomology* (eds C.B. Huffaker and A.P. Gutierrez), John Wiley & Sons, Inc., New York, pp. 553–83.
- Kikuchi, T. (1963) Studies on the coaction among insects visiting flowers. III. Dominance relationship among flower-visiting flies, bees and butterflies. *Scientific Reports of the Tohoku University*, 29, 1–8.
- Kiman, Z.B. and Yeargan, K.V. (1985) Development and reproduction of the predator *Orius insidiosus* (Hemiptera: Anthocoridae) reared on diets of selected plant material and arthropod prey. *Annals of the Entomological Society of America*, 78, 464–467.
- Lee, J.C. and Heimpel, G.E. (2008) Floral resources impact longevity and oviposition rate of a parasitoid in the field. *Journal of Animal Ecology*, 77, 565–572.
- Lee, J.C., Andow, D.A. and Heimpel, G.E. (2006) Influence of floral resources on sugar feeding and nutrient dynamics of a parasitoid in the field. *Ecological Entomology*, 31, 470–480.
- Letourneau, D.K. and Altieri, M.A. (1983) Abundance patterns of a predator, *Orius tristicolor* (Hemiptera: Anthocoridae), and its prey, *Frankliniella occidentalis* (Thysanoptera:

- Thripidae): habitat attraction in polycultures versus monocultures. *Environmental Entomology*, 12, 1464–1469.
- Li, Y., Michael, M. and Romeis, J. (2010) Use of maize pollen by adult *Chrysoperla carnea* (Neuroptera: Chrysopidae) and fate of Cry proteins in Bt-transgenic varieties. *Journal of Insect Physiology*, 56, 157–164.
- Limburg, D.D. and Rosenheim, J.A. (2001) Extrafloral nectar consumption and its influence on survival and development of an omnivorous predator, larval *Chrysoperla plorabunda* (Neuroptera: Chrysopidae). *Environmental Entomology*, 30, 595–604.
- Lixa, A.T., Campos, J.M., Resende, A.L., Silva, J.C., Almeida, M.M. and Aguiar-Menezes, E.L. (2010) Diversity of Coccinellidae (Coleoptera) using aromatic plants (Apiaceae) as survival and reproduction sites in agroecological system. *Neotropical Entomology*, 39, 354–359.
- Lundgren, J.G. (2009) Nutritional aspects of non-prey foods in the life histories of predaceous Coccinellidae. *Biological Control*, 51, 294–305.
- Lundgren, J.G. and Wiedenmann, R.N. (2004) Nutritional suitability of corn pollen for the predator *Coleomegilla maculata* (Coleoptera: Coccinellidae). *Journal of Insect Physiology*, 50, 567–575.
- Medeiros, M.A., Ribeiro, P.A., Morais, H.C., Castelo, B.M., Sujii, E.R. and Salgado-Laboriau, M.L. (2010) Identification of plant families associated with the predators *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae) and *Hippodamia convergens* Guerin-Meneville (Coleoptera: Coccinellidae) using pollen grain as a natural marker. *Brazilian Journal of Biology*, 70, 293–300.
- Michaud, J.P. and Grant, A.K. (2005) Suitability of pollen sources for the development and reproduction of *Coleomegilla maculata* (Coleoptera: Coccinellidae) under simulated drought conditions. *Biological Control*, 32, 363–370.
- Morse, D.H. (1981) Interactions among syrphid flies and bumblebees on flowers. *Ecology*, 62, 81–88.
- Nedved, O., Ceryngier, P., Hodkova, M. and Hodek, I. (2001) Flight potential and oxygen uptake during early dormancy in *Coccinella septempunctata*. *Entomologia Experimentalis et Applicata*, 99, 371–380.
- Obrycki, J.J., Harwood, J.D., Kring, T.J. and O'Neil, R.J. (2009) Aphidophagy by Coccinellidae: Application of biological control in agroecosystems. *Biological Control*, 51, 244–254.
- Olsen, D. and Wäckers, F.L. (2007) Management of field margins to maximize multiple ecological services. *Journal of Applied Ecology*, 44, 13–21.
- Ouyang, Y., Grafton-Cardwell, E.E. and Bugg, R.L. (1992) Effects of various pollens on development, survivorship, and reproduction of *Euseius tularensis* (Acari: Phytoseiidae). *Environmental Entomology*, 21, 1371–1376.
- Patt, J.M., Hamilton, G.C. and Lashomb, J.H. (1997) Foraging success of parasitoid wasps on flowers: interplay of insect morphology, floral architecture and searching behavior. *Entomologia Experimentalis et Applicata*, 83, 21–30.
- Patt, J.M., Wainright, S.C., Hamilton, G.C. et al. (2003) Assimilation of carbon and nitrogen from pollen and nectar by a predaceous larva and its effects on growth and development. *Ecological Entomology*, 28, 717–728.
- Pemberton, R.W. and Lee, J.H. (1996) The influence of extrafloral nectaries on parasitism on an insect herbivore. *American Journal of Botany*, 83, 1187–1194.
- Pemberton, R.W. and Vandenberg, N.J. (1993) Extrafloral nectar feeding by ladybird beetles (Coleoptera: Coccinellidae). *Proceedings of the Entomological Society of Washington*, 95, 139–151.
- Pontin, D.R., Wade, M.R., Kehrl, P. and Wratten, S.D. (2006) Attractiveness of single and multiple species flower patches to beneficial insects in agroecosystems. *Annals of Applied Biology*, 148, 39–47.
- Portillo, N., Alomar, O. and Wäckers, F.L. (2012) Nectarivory by the plant-tissue feeding predator *Macrolophus pygmaeus* Rambur (Heteroptera: Miridae): nutritional redundancy or nutritional benefit? *Journal of Insect Physiology* (in press).
- Putman, W.L. (1955) Bionomics of *Stethorus punctillum* Weise (Coleoptera: Coccinellidae) in Ontario. *Canadian Entomologist*, 87, 9–33.
- Rahat, S., Gurr, G.M., Wratten, S.D., Mo, J.H. and Neeson, R. (2005) Effect of plant nectars on adult longevity of the stinkbug parasitoid, *Trissolcus basalidis*. *International Journal of Pest Management*, 51, 321–324.
- Reader, T., MacLeod, I., Elliott, P.T., Robinson, O.J. and Manica, A. (2005) Inter-order interactions between flower-visiting insects: Foraging bees avoid flowers previously visited by hoverflies. *Journal of Insect Behavior*, 18, 51–57.
- Reemer, M., Renema, W., van Steenis, W. et al. (2009) *De Nederlandse zweefvliegen (Diptera: Syrphidae) – Nederlandse Fauna 8. Leiden*. Nationaal Natuurhistorisch Museum Naturalis, KNNV Uitgeverij, European Invertebrate Survey Nederland.
- Richards, P.C. and Schmidt, J.M. (1996) The effects of selected dietary supplements on survival and reproduction of *Orius insidiosus* (Say) (Hemiptera: Anthocoridae). *Canadian Entomologist*, 128, 171–176.
- Robertson, C. (1928) *Flowers and insects: lists of visitors of four hundred and fifty three flowers*, The Science Press, Lancaster.
- Salas-Aguilar, J. and Ehler, L.E. (1977) Feeding habits of *Orius tristicolor*. *Annals of the Entomological Society of America*, 70, 60–62.
- Scarratt, S.L., Wratten, S.D. and Shishehbor, P. (2008) Measuring parasitoid movement from floral resources in a vineyard. *Biological Control*, 46, 107–113.
- Schmid, A. (1992) Untersuchungen zur Attraktivität von Ackerwildkräutern für aphidophage Marienkäfer (Coleoptera, Coccinellidae). *Agrarökologie*, 5, Paul Haupt, Bern.
- Scholz, D. and Poehling, H.M. (2000) Oviposition site selection of *Episyrphus balteatus*. *Entomologia Experimentalis et Applicata*, 94, 149–158.

- Silberbauer, L., Yee, M., Del Socorro, A., Wratten, S., Gregg, P. and Bowie, M. (2004) Pollen grains as markers to track the movements of generalist predatory insects in agroecosystems. *International Journal of Pest Management*, 50, 165–171.
- Silveira, L.C.P., Bueno, V.H.P., Pierre, L.S.R. and Mendes, S.M. (2003) Crops and weeds as host plants *Orius* species (Heteroptera: Anthocoridae). *Bragantia Campinas*, 62, 261–265.
- Silveira, L.C.P., Bueno, V.H.P., Louzada, J.N.C. and Carvalho L.M. (2005) Species of *Orius* (Hemiptera, Anthocoridae) and thrips (Thysanoptera): interaction in the same habitat? *Revista Árvore Viçosa-MG*, 29, 767–773.
- Skirvin, D.J., Kravar-Garde, L., Reynolds, K., Jones, J., Mead, A. and Fenlon, J. (2007) Supplemental food affects thrips predation and movement of *Orius laevigatus* (Hemiptera: Anthocoridae) and *Neoseiulus cucumeris* (Acari: Phytoseiidae). *Bulletin of Entomological Research*, 97, 309–315.
- Szymank, A. and Gilbert, F. (1993) Anemophilous pollen in the diet of Syrphid flies with special reference to the leaf feeding strategy occurring in Xylotini (Diptera, Syrphidae). *Deutsche Entomologische Zeitschrift*, 40, 245–258.
- Stelzl, M. (1991) Investigations on food of Neuroptera-adults (Neuropteroidea, Insecta) in Central-Europe – with a short discussion of their role as natural enemies of insect pests. *Journal of Applied Entomology*, 111, 469–477.
- Steppuhn, A. and Wäckers, F.L. (2004) HPLC sugar analysis reveals the nutritional state and the feeding history of parasitoids. *Functional Ecology*, 18, 812–819.
- Takasu, K. and Lewis, W.J. (1993) Host- and food-foraging of the parasitoid *Microplitis croceipes*: learning and physiological state effects. *Biological Control*, 3, 70–74.
- Tooker, J.F. and Hanks, L.M. (2000) Flowering plant hosts of adult hymenopteran parasitoids of central Illinois. *Annals of the Entomological Society of America*, 93, 580–588.
- Tooker, J.F., Hauser, M. and Hanks, L.M. (2006) Floral host plants of Syrphidae and Tachinidae (Diptera) of central Illinois. *Annals of the Entomological Society of America*, 99, 96–112.
- Vacante, V., Cocuzza, G.E., De Clercq, P., van de Veire, M. and Tirry, L. (1997) Development and survival of *Orius albipennis* and *O. laevigatus* (Het.: Anthocoridae) on various diets. *Entomophaga*, 42, 493–498.
- van den Meiracker, R.A.F. and Ramakers, P.M.J. (1991) Biological control of the western flower thrips, *Frankliniella occidentalis*, in sweet pepper with the anthocorid predator *Orius insidiosus*. *Mededelingen van de Faculteit Landbouwwetenschappen, Rijksuniversiteit Gent*, 56, 241–249.
- van Emden, H.F. (1962) Observations on the effect of flowers on the activity of parasitic Hymenoptera. *Entomologist's Monthly Magazine*, 98, 265–270.
- van Rijn, P.C.J. and Tanigoshi, L.K. (1999) Pollen as food for the predatory mites *Iphiseius degenerans* and *Neoseiulus cucumeris* (Acari: Phytoseiidae): dietary range and life history. *Experimental and Applied Acarology*, 23, 785–802.
- van Rijn, P.C.J. and Wäckers, F.L. (2010) The suitability of field margin flowers as food source for zoophagous hoverflies. *IOBC/WPRS Bulletin*, 56, 125–128.
- van Rijn, P.C.J., van Houten, Y.M. and Sabelis, M.W. (2002) How plants benefit from providing food to predators even when it is also edible to herbivores. *Ecology*, 83, 2664–2679.
- van Rijn, P.C.J., Kooijman, J. and Wäckers, F.L. (2006) The impact of floral resources on syrphid performance and cabbage aphid biological control. *IOBC/WPRS Bulletin*, 29, 149–152.
- Vattala, H.D., Wratten, S.D., Phillips, C.B. and Wäckers, F.L. (2006) The influence of flower morphology and nectar quality on the longevity of a parasitoid biological control agent. *Biological Control*, 39, 179–185.
- Venzon, M., Janssen, A. and Sabelis, M.W. (1999) Attraction of a generalist predator towards herbivore-infested plants. *Entomologia Experimentalis et Applicata*, 93, 305–314.
- Venzon, M., Rosado, M.C., Euzebio, D.E., Souza, B. and Schorereder, J.H. (2006) Suitability of leguminous cover crop pollens as food source for the green lacewing *Chrysoperla externa* (Hagen) (Neuroptera: Chrysopidae). *Neotropical Entomology*, 35, 371–376.
- Villenave, J., Thierry, D., Al Mamun, A., Lode, T. and Rat-Morris, E. (2005) The pollens consumed by common green lacewings *Chrysoperla* spp. (Neuroptera: Chrysopidae) in cabbage crop environment in western France. *European Journal of Entomology*, 102, 547–552.
- Villenave, J., Deutsch, B., Lode, T. and Rat-Morris, E. (2006) Pollen preference of the *Chrysoperla* species (Neuroptera: Chrysopidae) occurring in the crop environment in western France. *European Journal of Entomology*, 103, 771–777.
- Vollhardt, I.M.G., Bianchi, E.J.J.A., Wäckers, F.L., Thies, C. and Tschardt, T. (2010) Nectar versus honeydew feeding by aphid parasitoids: does it pay to have a discriminating palate? *Entomologia Experimentalis et Applicata*, 137, 1–10.
- Wäckers, F.L. (1994) The effect of food deprivation on the innate visual and olfactory preferences in *Cotesia rubecula*. *Journal of Insect Physiology*, 40, 641–649.
- Wäckers, F.L. (2001) A comparison of nectar- and honeydew sugars with respect to their utilization by the hymenopteran parasitoid *Cotesia glomerata*. *Journal of Insect Physiology*, 47, 1077–1084.
- Wäckers, F.L. (2004) Assessing the suitability of flowering herbs as parasitoid food sources: flower attractiveness and nectar accessibility. *Biological Control*, 29, 307–314.
- Wäckers, F.L. (2005) Suitability of (extra-)floral nectar, pollen, and honeydew as insect food sources, in *Plant-provided food for carnivorous insects: a protective mutualism and its applications* (eds F.L. Wäckers, P.C.J. van Rijn and J. Bruin), Cambridge University Press, Cambridge, pp. 17–74.
- Wäckers, F.L. and Steppuhn, A. (2003) Characterizing nutritional state and food source use of parasitoids collected in

- fields with high and low nectar availability. *IOBC/WPRS Bulletin*, 26, 203–208.
- Wäckers, F.L. and Swaans, C.P.M. (1993) Finding floral nectar and honeydew in *Cotesia rubecula*: random or directed? *Proceedings of Experimental and Applied Entomology*, 4, 67–72.
- Wäckers, F.L., Björnsten, A. and Dorn, S. (1996) A comparison of flowering herbs with respect to their nectar accessibility for the parasitoid *Pimpla turionellae*. *Proceedings of Experimental and Applied Entomology*, 7, 177–182.
- Wäckers, F.L., Lee, J.C., Heimpel, G.E., Winkler, K. and Wagenaar, R. (2006a) Hymenopteran parasitoids synthesize “honeydew-specific” oligosaccharides. *Functional Ecology*, 20, 790–798.
- Wäckers, F.L., Bonifay, C., Vet, L.M. and Lewis, W.J. (2006b) Gustatory response and appetitive learning in *Microplitis croceipes* in relation to sugar type and concentration. *Animal Biology*, 56, 193–203.
- Wäckers, F.L., Romeis, J. and van Rijn, P.C.J. (2007) Nectar and pollen feeding by insect herbivores and implications for multitrophic interactions. *Annual Review of Entomology*, 52, 301–323.
- Wäckers, F.L., van Rijn, P.C.J. and Heimpel, G.E. (2008) Exploiting honeydew as a food source. Making the best of a bad meal? *Biological Control*, 45, 176–185.
- Wanner, H., Gu, H., Gunther, D., Hein, S. and Dorn, S. (2006) Tracing spatial distribution of parasitism in fields with flowering plant strips using stable isotope marking. *Biological Control*, 39, 240–247.
- Waser, N.M. and Ollerton, J. (eds) (2006) . *Plant–pollinator interactions: from specialization to generalization*, The University of Chicago Press, Chicago.
- Waser, N.M., Chittka, L., Price, M.V., Williams, N.M. and Ollerton, J. (1996) Generalization in pollination systems, and why it matters. *Ecology*, 77, 1043–1060.
- Weber, D.C. and Lundgren, J.G. (2011) Effect of prior diet on consumption and digestion of prey and non-prey food by adults of the generalist predator *Coleomegilla maculata*. *Entomologia Experimentalis et Applicata*, DOI: 10.1111/j.1570-7458.2011.01141.x.
- Weiss, E. and Stettmer, C. (1991) Unkräuter in der Agrarlandschaft locken blütenbesuchende Nutzinsekten an. *Agrarökologie*, 1, 1–104.
- Williams, L. and Roane, T.M. (2007) Nutritional ecology of a parasitic wasp: food source affects gustatory response, metabolic utilization and survivorship. *Journal of Insect Physiology*, 53, 1262–1275.
- Wilson, E.E., Sidhu, C.S., Levan, K.E. and Holway, D.A. (2010) Pollen foraging behaviour of solitary Hawaiian bees revealed through molecular pollen analysis. *Molecular Ecology*, 19, 4823–4829.
- Winkler, K., Wäckers, F.L., Buitrago, L. and van Lenteren, J.C. (2005) Herbivores and their parasitoids show differences in abundance on eight different nectar producing plants. *Proceedings of Experimental Entomology*, 16, 36–42.
- Winkler, K., Wäckers, F.L., Bukovinszkyne-Kiss, G. and van Lenteren, J.C. (2006) Nectar resources are vital for *Diaegma semiclausum* fecundity under field conditions. *Basic and Applied Ecology*, 7, 133–140.
- Winkler, K., Wäckers, F.L. and Pinto, D. (2009a) Nectar-providing plants enhance the energetic state of herbivores as well as their parasitoids under field conditions. *Ecological Entomology*, 34, 221–227.
- Winkler, K., Wäckers, F.L., Kaufman, L.V., Larraz, V.G. and van Lenteren, J.C. (2009b) Nectar exploitation by herbivores and their parasitoids is a function of flower species and relative humidity. *Biological Control*, 50, 299–306.
- Winkler, K., Wäckers, F.L., Termorshuizen, A.J. and van Lenteren, J.C. (2010) Assessing potential risks and benefits of floral supplements in conservation biological control. *Biological Control*, 55, 719–727.
- Wyckhuys, K.A.G., Strange-George, J.E., Kulhanek, C.A., Wäckers, F.L. and Heimpel, G.E. (2008) Sugar feeding by the aphid parasitoid *Binodoxys communis*: how does honeydew compare to other sugar sources? *Journal of Insect Physiology*, 54, 481–491.
- Yano, E. (1996) Biology of *Orius sauteri* (Poppius) and its potential as a biocontrol agent for *Thrips palmi*. *IOBC/WPRS Bulletin*, 19, 203–206.