The impact of adult diet on parasitoid reproductive performance

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Abstract

Diet is one of the most common influences on parasitoid reproductive traits. The life span, mating ability, fecundity, fertility and sex ratio of parasitoids can be affected by the quality of the adult diet. In the field, parasitoids can rely on different hosts and non-host nutrient sources, such as floral and extra floral nectar, hemipteran honeydew and pollen, and various artificial diets have been used in mass rearing. In addition, some parasitoid species obtain nutrients by feeding on their host while adult (host feeding). In this review, we summarize current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids, with a particular focus on longevity, offspring production and host searching traits. First, we focus on food preferences and learning abilities of parasitoids to discriminate high quality diets. Second, we analyze the impact of the adult diet on longevity, examining different natural and artificial food sources as well as the effect of their concentration and frequency. Third, we highlight the impact of the adult diet on host foraging. Fourth, we review the impact of adult diet on parasitoid offspring with special reference to (i) egg load, maturation and resorption, (ii) parasitism, and (iii) progeny production and sex ratio. Finally, a number of implications for biological control and Integrated Pest Management are discussed.

Keywords: biological control; Diptera; Hymenoptera; host searching; longevity; offspring production
Key Message

- Here we review current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids.
- The impact of the adult diet on parasitoid longevity is analyzed, examining different natural food sources, their concentration and frequency, as well as artificial diets currently employed in mass-rearing programs.
- We examine the impact of adult diet on parasitoid offspring, with special reference to egg load, maturation and resorption, parasitism, progeny production and sex ratio.
- Furthermore, we highlight the impact of the adult diet on host searching, then a number of implications for biological control and IPM are discussed.

Author Contribution Statement

GB and GG conceived and designed research. GB, GG, AT, ND, AIC, and AnC selected the literature. GB, GG, AT, ND, AIC and AnC analyzed the data. GB, GG, ND and AT wrote the manuscript.
Parasitoids are important organisms in both natural and human-modified environments. In nature, they form important components of ecological food webs and in agriculture they can be used as biological control agents against a number of crop pests of economic importance. Adult female parasitoids have to decide how to allocate their time, mainly dedicated to host or food foraging, to minimize energy waste. Food foraging is usually mediated by the exploitation of visual and olfactory cues, which can cover innately attractive stimuli (Wäckers 1994) as well as learned ones (Giunti et al. 2015). Both play a pivotal role in minimizing costs associated with food searching activities and on adaptation to spatial and temporal variation of food availability (Giunti et al. 2015). Because of their direct implication in biological control programs, parasitoid host-foraging behavior has been widely investigated, but even food-foraging behavior has a key role for biological control since nutrition affects the parasitoid reproductive traits (Jervis and Kidd 1986; Tena et al. 2015).

Previous review papers discussed peculiar aspects of adult parasitoid nutrition, such as the benefits associated to certain food sources (i.e. host feeding reviewed by Jervis and Kidd 1986; floral nectar by Heimpel and Jervis 2005; nectar, pollen and honeydew by Wäckers 2005 and Wäckers et al. 2008), the impact of natural (i.e. flowering species Jervis et al. 1996 and Russell 2005) and artificial (i.e. food spray Wade et al. 2008 and Tena et al. 2015) foods on parasitoid survival in field conditions, as well as the allocation and utilization efficiency of essential nutrients (Jervis et al. 2008). In this review, we summarize current knowledge on the impact of the adult diet on reproductive behavior of hymenopteran and dipteran parasitoids, highlighting the
impact of a broad range of natural and artificial diets on a number of parasitoid life-history traits. In the first section, we focus food searching (mostly preferences and learning abilities of parasitoids). In the second section, we analyze the impact of the adult diet on parasitoid longevity, examining different natural food sources (i.e. plant nectar and pollen, honeydew and host feeding), as well as artificial diets currently employed in mass-rearing programs. In the third section, we highlight the impact of the adult diet on host searching. In the fourth section, we review the impact of adult diet on parasitoid offspring, with special reference to (i) egg load, maturation and resorption, (ii) fecundity, fertility and parasitism, and (iii) sex ratio. Finally, we outline a number of implications for biological control and Integrated Pest Management. Information about dipteran parasitoids are limited and, when available, is presented in a separate paragraph at the end of every section.

The reviewed literature presented here is mainly focused on laboratory studies, whereas field applications are outlined in the conclusion section. In the field, parasitoids can rely on host and non-host nutrient sources, such as floral and extra floral nectar (Lee et al., 2006; Winkler et al. 2006), hemipteran honeydew (Tena et al. 2013a) and pollen (Zhang et al. 2004). Host feeding is not unusual among parasitoids (Jervis and Kidd 1986; Jervis et al. 1996), and at least one species obtains proteins and carbohydrates from host hemolymph (Giron et al. 2002). Moreover, at population level, the host-parasitoid interaction may be altered by parasitoid energetic requirements (Briggs et al. 1995; Evans and England 1996). For this reason, field researchers aim to increase the amount of sugars in the field improving parasitoid efficiency.

In contrast to previous reviews, which have generally focused on a specific food source, here we review the influence of a broad range of nutritional resources on
parasitoid life traits. The nutrients necessary to parasitoid reproduction are partially acquired during the larval stages, and they may be allocated directly to egg production (i.e. proovigenic egg maturation), but also stored as teneral reserves for adult maintenance and reproduction (Jervis et al. 2008). Storage resources may also arise from excess nutrients assimilated during adult nutrition, considering storage a different way to invest resources, comparable to maintenance or reproduction. Nutrients stored in the fat body may be subsequently remobilized through metabolic costs, which are small in comparison to costs associated with egg resorption (Boggs 1992). Overall, insects seem to use carbohydrates as their basic energy resource, while lipids function as long-term energy stores, although in the parasitoid diet the amount of lipid is moderate (Rivero and Casas 1999; Mondy et al. 2006) and most species are unable to synthesize lipids during their adulthood (Ellers 1996; Visser and Ellers 2008).

Food preferences and learning abilities

Among insects, food selection is a common behavior (Waldbauer, 1968). Food sources present in the ecosystem can vary in nutrient composition and diet selectivity is crucial to optimize parasitoid fitness. In nature, adult parasitoids may exploit as sugary sources a broad range of foods, including nectars and honeydew. This latter food source is considered of lower nutritional value (Wäckers et al., 2008); and simulation models indicate that the ability to select for nectar makes parasitoids more efficient under field conditions (Vollhardt et al. 2010). However, honeydew is largely available in agroecosystems and parasitoids’ preferences may become adapted to this resource, when they forage in a honeydew-rich microhabitat (Wäckers 2005; Tena et al., 2016).
the case of the parasitoid *Aphytis melinus* DeBach (Hymenoptera: Aphelinidae), which can feed on honeydews excreted by different hemipteran species (Tena et al. 2013a), naïve parasitoids prefer to feed on sugar-rich honeydew than on poor ones (Tena et al. 2013b).

The preference and selection of artificial sugars by hymenopteran parasitoids have been explored more in detail. *Cotesia glomerata* (L.) (Hymenoptera: Braconidae) feeds on a wide range of natural carbohydrates, but does not accept certain sugars (i.e. galactose, mannose, rhamnose, lactose, raffinose and melibiose at 2 M concentration) when previously provided with water (Wäckers 1999). However, the addition of fructose (1/8 M), but not that of sucrose, increased the response of *C. glomerata* mannose and raffinose (Wäckers 1999), highlighting the effect of food composition on its suitability for parasitoid alimentation. The ichneumonid *Diadegma semiclausum* (Hellén) also exploits trehalose, a peculiar sugar present in hemolymph and in some honeydews, whereas it shows low responses to lactose and melibose (Winkler et al. 2005). Moderately stimulatory sugars are also readily accepted by the egg parasitoid *Anaphes iole* Girault (Hymenoptera: Mymaridae) when wasps have been deprived of water and food (Beach et al. 2003).

Parasitoids should balance nutrient intake, avoiding toxicity of over-ingestion of plant secondary metabolites or herbivorous digestive excretions and, therefore, experience may alter innate parasitoid preferences, increasing responses for innately unattractive food sources (Kugimiya et al. 2010). Vollhardt et al. (2010) demonstrated that, while naïve *A. ervi* shows no preferences for either flower nectar or honeydew, wasps, which have experienced honeydew nutrition, prefer to feed on nectar. Several studies investigated the ability of parasitoids to learn both non-host (Sato and Takasu
Impact of the adult diet on parasitoid longevity

The access to appropriate food sources is fundamental for the survival of parasitoids (Idris and Grafius 1995; Jervis et al. 1996; Wyckhuys et al. 2008). Carbohydrate sources as sugar, nectar and honeydew are not always readily available in the agro-ecosystems and this may play a detrimental role in biocontrol programs, since longevity affects directly the impact of parasitoids as biological control agents (Wäckers 2004).

Natural food sources

Nectar and pollen

Plant nectar is an aqueous solution of sugars, amino acids and other compounds, which quantitatively and qualitatively vary among plant species. Generally, the main compounds of nectar are sucrose, glucose and fructose, quickly digestible carbohydrates with high-energy content, equally suitable for parasitoid alimentation (Hogervorst et al. 2007b), which, with few exceptions (Tompkins et al. 2010), can positively influence parasitoid longevity (Jervis et al. 1996). Floral and extra-floral nectars boost adult longevity (Olson and Nechols 1995; Russell 2005). However, flower availability usually
causes a higher increase of longevity in braconid (Olson et al. 2000; Sisterson and Averill 2002; Berndt and Wratten 2005) and mymarid (Cronin and Strong 1990; Jacob et al. 2006; Mutitu et al. 2013) female parasitoids.

The mating status may affect the beneficial effect of nectar on the longevity of female parasitoids. For example, virgin females of *Bathyplectes curculionis* (Thomson) (Hymenoptera: Ichneumonidae) live longer than mated ones when provided with flower nectar of dandelion, phacelia, alfalfa, and even with water alone, whereas no survival effect is recorded when wasps feed on honey solution (Jacob and Evans 2000).

Conversely, the mating status does not seem to influence the fitness of male parasitoids fed on nectar. In *Pteromalus cerealellae* (Ashmead) (Hymenoptera: Pteromalidae), food provisioning increases male longevity, irrespective to mating status, while in females, which have longer lifespans respect to males, a negative effect of mating is recorded when nectar is not associated to host-food presence (Onagbola et al. 2007).

The suitability of pollen as food source for parasitoid is narrowly investigated, since is usually considered as less valuable (e.g. for aphid parasitoids see Starý 1969). Females of the trichogrammatid parasitoid *Trichogramma brassicae* Bezdenko (Hymenoptera: Trichogrammatidae) live longer in presence of corn pollen respect to unfed females, although significantly less than those fed with honey or a mixture of honey and corn pollen (Zhang et al. 2004). *Cotesia plutella* (Kurdjumov) (Hymenoptera: Braconidae) also exploits beebread food (i.e. a mixture of pollen and nectar collected by honeybees), which is rich in proteins, lipids, carbohydrates, enzymes, vitamins and hormone precursors, by prolonging the adult life of both sexes (Soyelu 2013).
Honeydew

On contrast to other natural food sources, such as floral and extrafloral nectars, honeydew is primarily a byproduct. Honeydew has not evolved to attract sugar-feeding arthropods and contains plant-derived and aphid synthesized compounds, which can reduce its nutritional suitability (Wäckers et al. 2008). Sugars from hemolymph and honeydew promote *Eretmocerus melanoscutus* and *Encarsia formosa* lifespan, even if *E. formosa* wasps receive no benefits from feeding on trehalose (Hirose et al. 2009), a peculiar carbohydrate of aphid hemolymph present in some honeydews (Hogervorst et al. 2007a). Similar negative responses to trehalose are reported also for *C. glomerata* (Wäckers 2001), *D. semiclausum* (Winkler et al. 2005) and *B. curculionis* (Jacob and Evans 2004), suggesting that insect-produced oligosaccharides are poor food source for parasitoids (Wäckers 2000). Although the sugar profile of honeydew does not always explicate its lower nutritional value, the relatively high viscosity and the tendency of some honeydew sugars to rapidly crystallize could explain its lower suitability compared to nectar (Faria et al. 2008).

Despite the general assumption, some honeydews can increase parasitoid longevity as other sugar sources; the ichneumonid *B. curculionis*, as well as the trichogrammatid *Trichogramma ostriniae* Pang and Chen, the pteromalid *Scutellista caerulea* (Fonscolombe) and braconid *Psyttalia humilis* (Silvestri) and *Diaeretiella rapae* (McIntosh) successfully uses host or non-host honeydew as food source to prolong adult life, with comparable results to honey or nectar nutrition (England and Evans 1997; Fuchsberg et al. 2007; Wang et al. 2011; Varennes et al. 2016). When flower or extra-flower nectars are not available, parasitoids can detect and feed on
honeydew from hosts and non-hosts as it has been reported for *A. ervi* (Hogervorst et al. 2007a, b) and *A. melinus* (Tena et al. 2013a, b). Even when nectar is available, some parasitoids prefer to feed on honeydew (Lee et al. 2006), which increases adult lifespan less than nectar sources (Lee et al. 2004). Nevertheless, the effects of honeydew on parasitoid longevity greatly depend on the parasitoid species. Dulaurent et al. (2011) investigated the effect of different kind of honeydews on a generalist [*Ooencyrtus pityocampae* (Mercet) (Hymenoptera: Encyrtidae)] and a specialist [*Baryscapus servadeii* (Domenichini) (Hymenoptera: Eulophidae)] parasitoid. Honeydew feeding had a significant impact on the longevity of the generalist parasitoids, while the specialist species benefited from just specific honeydew types (Dulaurent et al. 2011).

Since honeydew-producers directly feed on phloem sap and do not degrade several compounds (Douglas 2003), honeydew reflect phloem sap composition. In this scenario, honeydew may be greatly altered in presence of transgenic plants producing insecticidal proteins. Indeed, *Galanthus nivalis* agglutinin (GNA) ingestion reduces *A. ervi* longevity, either when provided directly in a sugar solution or through contaminated honeydew (Hogervorst et al. 2009). Similarly, high concentrations (0.5% w/v) of GNA and concanavalin agglutinin (Con A) significantly reduce the survival chances of *Eulophus pennicornis* (Nees) adult females, altering parasitoid food consumption rates and decreasing food intakes (Wakefield et al. 2010). Moreover, even if generally sap-feeding insects excrete carbohydrates over nitrogen rich nutrients (Wäckers 2000), honeydews with highly concentrated amino acids are not appropriate to prolong lifespan of *Trichogramma* spp. wasps, which can handle their entire life using nitrogen reserves from the larval stages (Ashley and Gonzalez, 1974; McDougall and Mills 1997).
A wide range of parasitoids, estimated at nearly a third of all parasitoids, feed on their host during adulthood (Kidd and Jervis 1991), through both non-destructive (i.e. the host survives after being fed on) and destructive (i.e. the host dies) feeding (Jervis and Kidd 1986). Parasitic wasps host-killing behaviors, over parasitization, comprise also destructive feeding and eventually host stinging. In this context, it is useful to understand how parasitoids decide to exploit the host as food or reproductive resource. Generally, when parasitoid microhabitat includes both sugar-rich foods and hosts, wasps benefit from host feeding coupled with honey (Heimpel et al. 1997; Schmale et al. 2001; Kapranas and Luck 2008) or non-host honeydew (McDougall and Mills 1997), but not from host feeding alone. The exclusive presence of host food may cause divergent effects; while the pteromalid Dinarmus basalis Ashmed (Pteromalidae) nearly doubles life expectancy, respect to food-deprived wasps, when only host is provided, no effect is observable on Heterospilus prosopidis (Viereck) (Braconidae) and Anisopteromalus calandrae (Howard) (Pteromalidae) (Schmale et al. 2001). In contrast, host feeding is fundamental to increase the longevity of the eupelmid parasitoid Eupelmus vuilletti (Crawford), mainly due to carbohydrates obtained during host feeding, over lipids and proteins (Giron et al. 2004). Similarly, the presence of host increase adult longevity by itself in Neochrysocharis formosa (Westwood) (Hymenoptera: Eulophidae), but the provisioning of honey greater improves wasp lifespan (Liu et al. 2015). Indeed, while non-host food (10% honey solution) increases levels of gut sugar, body sugar and glycogen of Diglyphus isaea Walker (Hymenoptera:
Eulophidae) females, host-feeding is related to higher levels of lipids, suggesting the essential connection of this kind of feeding to lipid assimilation (Zhang et al. 2011).

**Artificial diets**

Artificial diet suitability has been widely investigated to select food supplements in the field or in the mass rearing. The encyrtid parasitoid *Ooencyrtus nezarae* Ishii naturally uses different kind of food sources, as floral and extra-floral nectars and honeydews (Teraoka and Numata 2000). However, when female wasps are fed continuously with a single food source during autumn, none of them overwinter (Teraoka and Numata 2000). Various artificial diets were proposed to improve longevity, but, even if honey, glucose, galactose and sucrose were profitable supplies for wasps, none of the artificial diets had greater impact respect to natural foods (Teraoka and Numata 2000). Furthermore, Bautista et al. (2001) also investigated the consequence of honey, maple syrup, molasses, sugar cane and ripe coffee on *Fopius arisanus* (Sonan) (Hymenoptera: Braconidae) adult longevity, highlighting the unsuitability of sugar cane to prolong parasitoid life (Bautista et al. 2001). On the other hand, Zamek et al. (2013) found that sugar cane diets prolong adult life of *Diachasmimorpha tryoni* females (Cameron) (Hymenoptera: Braconidae) 50% more than honey and golden syrup.

Honey is presumably the most studied artificial diet for parasitoid, since it is palatable and cheap. Provision of honey solutions boost mymarid and trichogrammatid parasitoid longevity similarly to flower and extra-flower nectars and even more than honeydew (Irvin et al. 2007; Tunçbilek et al. 2012). Good examples of parasitoid
species which impressively benefit of artificial diet are the ectoparasitoid *Mastrus ridibundus* (Gravenhorst) (Hymenoptera: Ichneumonidae) and the endoparasitoids *Trichogramma carverae* Oatman and Pinto and *T. brassicae*, which respectively respond to honey diet decoupling (*Bezemer et al. 2005*) or doubling their life expectancy (*Gurr and Nicol 2000*). Overall, honey solution, as well as dried grape extract, which present high sugar and low protein content, are able to greatly prolong life of the encyrtid parasitoid *Acerophagus papayae* Noyes and Schauff (*Divya et al. 2011*). Indeed, the addition of protein yeast hydrolysate to sugary sources acts as feed-deterrent and is toxic to *F. arisanus* wasps (*Bautista et al. 2001*). Also the hyperparasitoids *Lysibia nana* Gravenhorst and *Gelis agilis* Fabricius (Hymenoptera: Ichneumonidae, Cryptinae) benefit from honey diet over a mimic honey composed of pure saccharides (*Harvey et al. 2012*). The latter result suggests that the amino acids and vitamins present on the honey, as well as other components, are also responsible of its positive effect on parasitoid longevity. Furthermore, no differences on longevity between male and female, as well as between virgin and mated wasps, are recorded for the braconids *C. plutellae* and *Phanerotoma franklini* Gahan when fed on artificial solution of sucrose (20%) or honey (50%), suggesting that these two diets have similar nutritional value and that food may quickly replace the energy spent for reproduction (*Sisterson and Averill 2002; Mitsunaga et al. 2004*).

On contrast to the majority of parasitic wasp species, honey provisioning does not alter longevity of the aphelinid parasitoids *E. melanoscutus* and *E. formosa*. The adult life of these hymenopterans ranges from 1 to 7 days, and presumably the energy intake at the emergence is of pivotal importance for the longevity of these wasps (*Zang and Liu 2010*).
Fruit exudates can be also exploited as food sources by parasitoids. Sivinski et al. (2006) noticed that adult *Diachasmimorpha longicaudata* (Ashmead) (Hymenoptera: Braconidae) can exploit diets of fruit juice or fruit pulp (e.g. orange or peach), with comparable lifespans to those achieved on honey diet. In contrast, simple guava juice administration reduces longevity, by a decreasing of total sugars and glycogen levels, both for *D. longicaudata* and for the figitid *Aganaspis pelleranoi* (Brèthes) (Narváez et al. 2012).

Sugar composition of artificial diet can deeply influence adult parasitoid longevity. Önalp and Emre (2001) investigated the effect of 23 carbohydrates, including mono-, di-, tri- and polysaccharides, on the survival of the parasitoid *Pimpla turionellae* L. (Hymenoptera: Ichneumonidae). The best results were achieved with sucrose diet while some pure monosaccharides (e.g. fructose and galactose) showed detrimental effects (Önalp and Emre 2001). Similarly, the ichneumonid *D. semiclausum* exploits sucrose, maltose, glucose and melibose, while raffinose, lactose and melezitose have no effect on adult longevity (Winkler et al. 2005). Conversely, the egg parasitoid *A. iole* is able to exploit a broad range of sugars, including those from nectar and honeydew, and it shows the higher acceptance rate for the homopteran honeydew sugar trehalulose, with comparable results to sucrose and maltose (Williams and Roane 2007). However, *A. iole* survival is generally greater when provisioned with a mixture of the major nectar sugars (sucrose, glucose, and fructose) than with other suitable saccharides (Williams and Roane 2007).

Many parasitoids do not accumulate lipids as adults and do not replenish lipid levels after emergence from their host (Olson et al. 2000; Giron and Casas 2003; Visser et al. 2010). However, addition of lipids (i.e. olive oil) in the diet increases *C. glomerata*
female lipid levels, but the survival is negatively affected in both males and females in presence of olive oil, whose toxicity increases with concentration (Visser and Ellers 2012).

Similarly to hymenopteran parasitoids, also dipteran ones can improve their life expectancy in response to an appropriate adult nutrition. *Trichopoda giacomellii* (Blanchard) (Diptera: Tachinidae) increases its longevity of over three times when raisins are added to a water-only diet (Coombs 1997). Furthermore, Chen et al. (2005) investigated longevity variations in male and female of *Pseudacteon tricuspis* (Borgmeier) (Diptera: Phoridae) according to exposure to sugar source and temperature. Both males and females lived longer when fed on sugar sources than when sugar-starved, irrespective of temperature (Chen et al. 2005).

**Effect of food concentration and frequency**

Concentration and availability of the food sources in nature vary greatly depending on biotic factors and environmental conditions (Corbet et al. 1979). Usually, life span of sugar fed parasitoids increases with sugar concentration up to a limit (Azzouz et al. 2004; Ellers et al. 2011). In a laboratory assay with five concentrations from 0 to 70% (w/v) solution of glucose-fructose (1:1), *A. ervi* reached the maximum longevity when males and females feed on a 70%. The parasitoid wasps *Asobara tabida* Förster (Hymenoptera: Braconidae) and *Trichopria drosophilae* Perkins (Hymenoptera: Diapriidae) consume the same intake of differentially concentrated sucrose solutions, but they display detrimental effects when provided with a 100% dilution (w/v), while the higher longevity has been recorded for the 80% sucrose solution. Presumably, wasps
do not differentiate intake on the basis of the amount of calories consumed, but just on the volume of their stomach, leading to negative effect when ingesting high-concentrated foods (Ellers et al. 2011). The ectoparasitoid *Catolaccus grandis* (Burks) (Hymenoptera: Pteromalidae) also benefits of low-concentrated sugar solution (Morales-Ramos et al. 1996). The viscosity of highly concentrated sugar solutions may also affect the ingestion facility of parasitoids. Intermediate concentrations revealed to greater contribute to *P. lounsburyi* longevity (Williams et al. 2015), increasing the time spent searching for hosts and reducing resting and feeding periods, when wasps are more subjected to predator attacks (Völkl and Kroupa 1997; Lightle et al. 2010).

The value of a single meal can be crucial for survival when sources are spatially or temporally scarce. Different concentrations of *Brassica* flower nectar act differentially on the braconid *C. rubecula* when a single honey meal is offered, with greater benefits when sugar concentration is just below 50% (Siekmann et al. 2001).

Timing and sugar concentration of a single feeding activity may also influence *Psyttalia lounsburyi* (Silvestri) (Hymenoptera: Braconidae) longevity, increasing the survival chances from 32.3% to 95.4% compared to water control after 2 days (Williams et al. 2015). Furthermore, parasitoids exposed to longer food-deprivation periods show longest feeding durations, and thus major energy intakes (Williams et al. 2015).

Feeding frequency is crucial for parasitoid survivorship. Overall, daily food provisioning produces major longevity benefits, respect to longer feeding intervals (Lee and Heimpel 2008a). For example, *T. platneri* wasps prefer honey or sugars daily nutrition supplies respect to longer feeding intervals, mainly to overcome the evaporation of sugar solutions. However, the addition of stabilizing agents does not reduce evaporation nor enhance adult longevity (McDougall and Mills 1997). In this
scenario, it is raising the hypothesis that dietary restriction, in absence of strong malnutrition, may prolong invertebrates’ life (Ellers et al. 2011). Proovigenic parasitoid species, which emerge with an egg-load ready for oviposition (Jervis et al. 2001) and which present a relatively simple diet, mainly or exclusively constituted by carbohydrates (Wäckers 2001), can exploit dietary restriction. For Macrocentrus grandii (Goidanich) a constant supply of sugars is not necessary to achieve the maximum survivorship (Fadamiro and Heimpel 2001). Indeed, the maximum level of gut sugars is obtained after a single day of food provisioning and decreases substantially one day post-feeding, suggesting that, during starvation intervals, gut sugars are mobilized to maintain constant the level of parasitoid body sugars (Fadamiro and Heimpel 2001). Nevertheless, no beneficial effect of caloric restriction in the intermittent feeding has been recorded so far, since ad libitum and daily provisioning of food positively influence the wasps’ lifespan (Azzouz et al. 2004; Wu et al. 2008; Ellers et al. 2011). As infrequent feeding opportunities seem to have limited benefits, the habitat manipulation and the mass rearing programs should provide a continuous supply of sugar or nectars to parasitoids.

Impact of the diet on host searching

Host searching is a key behavior, which should be efficient and reduce the parasitoid exposure time to predation. Indeed, for parasitic wasps, food and host sources are often spatially distant. Whereas, host feeding and host honeydew are strictly dependent on host presence, many other suitable food sources, as plant nectars and non-
host honeydew, are not always associated with host and parasitic wasps need to move between different microhabitats during their foraging activities.

Nutrition may positively alter parasitoid physiology, reflecting on responsiveness to different olfactory sources and orientation toward the host, but likely up to a limit. For example, the endoparasitoid *Apanteles aristoteliae* Viereck (Hymenoptera: Braconidae) increases its nutritional state when feeds on sugar-rich sources. However, females with the highest levels of sugars are less prone to make a choice in olfactometer bioassays, while wasps with intermediate level are more expected to orient toward the host (Lightle et al. 2010). In other species, on contrast, females do not profit from nutrition, since starvation does not decrease searching ability (Gomez et al. 2012), usually preferring host cues to food (Pietrantuono et al. 2012).

High abundance of rich food sources is typically associated with an increasing of searching ability respect to the absence of nutrient supply (Takasu and Hirose 1991). Indeed, food provisioning could reduce time spent to locate and accept the hosts, by increasing parasitoid mobility and sensitivity to olfactory cues, but also host acceptance itself (Sisterson and Averill 2002). The frequency of food administration plays a pivotal role on olfactory orientation in parasitic wasps. In wind tunnel assays, female wasps modify their preferences toward host- and flower-associated odors in relation to their feeding status. While well-fed wasps prefer host stimuli, host and food stimuli seem equally attractive for hungry females, which employ more time to start searching behavior and to locate a cue (Jacob and Evans 2001, Siekmann et al. 2004).

Among parasitic wasps, flight ability is generally related to the presence of peculiar diet components, which may alter parasitoid in-flight orientation. The main fuel source employed for flight seems to be glycogen. Indeed, *Venturia canescens* (Grav.)
(Hymenoptera: Ichneumonidae) wasps decreased their glycogen content during flight, and females consume about the 50% of their glycogen storage in one hour of active flight, while glucose, protein and lipid remain constant (Amat et al. 2012). Furthermore, an arrhenotokous strain, which flies more frequently between host and food, has a higher glycogen load at emergence compared to thelytokous strain, reflecting also on a higher flight speed (Amat et al. 2012). Wanner et al. (2006) reported that *C. glomerata* females showed different flight ability according to source type, whereas no differences were noted for males. Furthermore, *ad libitum* feeding on *Anethum graveolens*, as well as on honey solution, increases the total distance flown, the number and the duration of flights completed by female parasitoids. Conversely, other diets have lower or none effects on parasitoid flight behavior (Wanner et al. 2006). Contrasting findings were instead reported for proovigenic species. Indeed, while synovigenic wasps need food provisioning for both somatic and reproductive functions, nutrition has a moderate impact on proovigenic females, which could not benefit from food supply and could eventually rely on their larval energy storage to respond to maintenance and locomotion (Fischbein et al. 2011).

In field condition, the interaction between nutritional state of parasitoids and the presence of food sources may influence the foraging behavior of females. In small corn and soybean plots without food sources, well-fed *Microplitis croceipes* (Cresson) (Hymenoptera: Braconidae) wasps spend more time for host searching and parasitize a higher number of host rather than unfed ones (Takasu and Lewis 1995). However, when supplemental food sources are provided, unfed females are more ready to feed on it and start immediately to search and parasitize hosts (Takasu and Lewis 1995). Similarly, in citrus groves, Tena et al. (2015) found that *A. melinus* females lay more eggs in trees
where artificial sugars are provided than in control ones, suggesting an increase of searching ability.

**Impact of adult diet on parasitoid offspring**

It is acknowledged that carbohydrate rich diets enhance the lifespan fecundity of parasitoids under laboratory condition (Jervis et al. 1996; Wäckers 2005), while lipids and proteins, either from diet and teneral reserves, are usually necessary for successful productions of the eggs (Ellers and van Alphen 1997). Furthermore, egg hatching and parasitization ability are also processes depending on nutritional status of female parasitoids, and the balanced acquisition of nutrients has great influence also on the size and the number of egg produced (Wheeler 1996; Harvey et al. 2012).

**Egg load, maturation and resorption**

Egg maturation in female parasitoids is considered a fitness-related parameter, which may influence the reproductive potential of biological control agents and thus population dynamics of hosts. However, different diets may affect the lifetime egg maturation patterns of synovigenic parasitoid species, whose females emerge with no or few mature oocytes, maturing the remaining eggs throughout their adult life. In contrast, for proovigneic species, whose females emerge with their set of eggs completely mature, the effect of diet is almost insignificant (Jervis et al. 2001). The effect of sugar-rich diet on lifetime egg maturation patterns of synovigenic species, both in presence or absence of host prey, has been widely investigated. Typically, parasitoid egg load
depends on the diet provided to adult females, as reported for the parasitoid *P. cereallellae* (Onagbola et al. 2007). Honey is usually the most effective sugar source to promote egg maturation (Hogervorst et al. 2007a; Hopkinson et al. 2013), and when it is replaced with sugar-poor diets, ovaries of gravid *F. arisanus* females show deterioration, by decreasing egg load from over 100 eggs to less than 70 immediately before their death (Bautista et al. 2001). The maximum egg load of the ichneumonid parasitoid *B. curculionis* greater benefits from honey (+15%) than from honeydew excreted by the pea aphid, *Acyrthosiphon pisum* (Harris) (England and Evans 1997). Nevertheless, distinct parasitoid species can differently benefit from artificial diets, as noted for hymenopteran parasitoids of tephritids. Thus, although the egg load of *D. longicaudata* is not altered by diet, *A. pelleranoi* has higher egg loads when fed on honey or pollen than on juice (Narváez et al. 2012). Similarly, egg production is improved by various pure carbohydrates solutions in *P. turionellae*, whereas galactose and trehalose have a detrimental effect (Özalp and Emre 2001). Apart from the intrinsic quality of food, its availability over time can also affect fitness-related traits and may alter egg maturation. Ellers et al. (2011) investigated the effect of dietary restriction (i.e. diet dilution and intermittent feeding) on *A. tabida* and *T. drosophilae*, nonetheless no effect of dietary regime is recorded on fecundity of both species.

Parasitoids feeding with diets lacking in sugars generally have to accept compromises, and thus to relocate energy, to mature eggs. For example, starved *Mastrus ridibundus* (Gravenhorst) (Hymenoptera: Ichneumonidae) wasps reduce their reproductive potential by decreasing egg size and maturation, as well as the number of attacked host (Bezemer et al. 2005). To economize energy for egg maturation, parasitoids can produce smaller and nutrient poor eggs, can use reserve energy obtained
during immature development, and can minimize energy employed for other activities (Rivero and Casas 1999; Olson et al. 2000; Jervis et al. 2008). In addition, body size, generally reflects the putative energetic reservoirs. Indeed, the egg maturation, either when nutrition is provided or not, is higher in largest $M. \text{rudibundus}$ females respect to smallest ones (Bezemer et al. 2005). In contrast to general patterns, maturation rates are not correlated with size in $Trichogramma nubilale$ Ertle & Davis (Hymenoptera: Trichogrammatidae), thus implying that size-related differences are attributable to first day’s egg load rather than to maturation rate in this species (Olson and Andow 1998).

Unlike previous reports, adult females of the solitary koinobiont I. leucospoides do not increase their post-emergence egg maturation according to food supply. However, this synovigenic species shows a high ovigeny index (the ratio between the initial egg load and the potential lifetime fecundity), which is more similar to those of proovigenic species respect to synovigenic, thus adult feeding has not effect on egg production (Fischbein et al. 2013).

Usually, the rate of egg resorption is higher for starved wasps (Jervis and Kidd 1986; Antolin and Williams 1989; Heimpel et al. 1997; Stokkebo and Hardy 2000), since females generally increase life expectancy and the eventuality of find suitable food sources (Collier 1995; Heimpel et al. 1997). Several parasitoids species can resorb eggs to improve their lifespan when exposed to water diet (Heimpel et al. 1997; Lee and Heimpel 2008b; Richard and Casas 2009). Nevertheless, when egg resorption is not allowed or does not considerably raises life expectancy, the increasing of egg maturation by starved wasps may be an advantageous adaptive strategy to improve the lifetime fecundity (Roitberg et al. 1992; Fletcher et al. 1994). For instance, starved $Macrocentrus cingulum (=grandii)$ Brischke (Hymenoptera: Braconidae) females have
a significant higher number of egg load respect to sugar-fed ones, since they no
evidence egg resorption, which is recorded for well-fed wasps (Olson et al. 2000).
Similarly, during the early adult life of the braconid Microplitis rufiventris Kokujev,
potential fecundity seems subjected to feeding status, since higher rates of egg
maturation are related to starved wasps, which potentially compensate shorter life
(Hegazi et al. 2013). In contrast, when lacking both suitable food and host, starved
females may invest their residual energy in locomotion to find a more profitable
microhabitat.

Host hemolymph absorbed through host feeding may also play a pivotal role in
egg maturation, usually increasing egg maturation rate and deterring egg resorption. The
synovigenic O. nezarae is a concurrent host feeder, usually exploiting this nutritional
source before oviposit. Females emerge with no mature eggs, but they mature two eggs
after a single host feeding (Aung et al. 2012). Furthermore, host feeding is not crucial
but helpful to enhance egg maturation in A. melinus, Metaphycus flavus Howard and M.
luteolus Timberlake, since the host meal contributes to egg maturation just when
coupled with honey supplement (Heimpel et al. 1997, Kapranas and Luck 2008). Some
amino acids and minerals readily available in host hemolymph are found to be essential
for egg maturation in an ichneumonid parasitoid (Bracken 1965), whereas protein
supplementation seems to have no impact on trichogrammatid species (Ashley and
Gonzalez 1974). Also Giron et al. (2004) investigated the effect of a single host-meal on
parasitic wasp egg production. Females of E. vuilletti obtained energy to produce just
1.53 eggs per host meal, due to the low lipid content of hemolymph (Giron et al. 2004).
Conversely, the strong synovigenic parasitoid D. isaea improves its potential fecundity
respect to water supply and increase the lipid level when it feeds on hosts, highlighting
the presence of a lipogenesis pathway (Zhang et al. 2011), which is absent in other species (Olson et al. 2000). Among lipids, poly-unsaturated fatty acids (PUFA) are known to be suitable for energetic purposes, but most insect are unable to synthesize long-chain lipids (Visser et al. 2010). As reported for carbohydrates, different fatty acids may influence differently on parasitoid life-history traits. P. turionellae produces eggs differentially in response to several fatty acid free diets. While the absence of single fatty acid (palmitic, stearic, oleic and linolenic acid) does not influence the egg loads in comparison to fatty acid-rich or natural diets, fatty acid-free and linoleic acid-free diets dramatically decrease the potential fecundity (Nurullahoglu and Ergin 2009). The crucial importance of linoleic acid may be attributed to its role as structural component of membranes and as precursor of eicosanoids, which act as oviposition stimulants (Stanley-Samuelson 1994). Furthermore, host feeding is generally crucial for amino acid intakes. However, the addition of synthetic amino acids or host hemolymph to honey diets does not increase oogenesis in inexperienced C. grandis, whereas females with ovipositional experience increase their egg maturation rate when fed on the supplemented diet (Morales-Ramos et al. 1996). Furthermore, host-food does not prevent egg resorption in absence of a supplemental food source (Heimpel et al. 1997), even if it seems fundamental to prevent this phenomenon in the eulophid species Tamarixia radiata (Waterston) (Chen and Stansly 2014).

Generalist species, which usually feed in highly variable microhabitats, are typically more flexible and adaptable to nutrient and host deficiency than specialist species. Cicero et al. (2012) investigated the effect of different diets, including hosts of different quality, on four braconid species: D. longicaudata, Doryctobracon crawfordi (Viereck), Utetes anastrephae (Viereck) and Opius hirtus (Fisher). Whereas the
generalist *D. longicaudata* increases its egg load and maturation rate when feeds on
different quality hosts, the specialist *O. hirtus* increases its egg load only when feeds on
low quality hosts (Cicero et al. 2012).

Lastly, the potential fecundity can also be influenced by food provisioning in
dipteran parasitoids. Feeding on raisins greatly increases the number of egg produced by
*T. giacomellii* females, respect to water-fed insects, although no effect is detectable on
number of ovarioles and body size (Coombs 1997).

**Fecundity, fertility and parasitism**

Here the effects of diet composition and frequency on (*i*) parasitism behavior
(i.e. number of oviposition or eggs laid), (*ii*) fertility (i.e. the natural ability to produce
offspring) (*iii*) and daily and lifetime fecundity (i.e. the actual reproductive rate) of
parasitic wasps are reviewed.

Natural or artificial diets can alter the oviposition behavior of parasitoids,
modifying either the propensity to oviposit or the number of egg laid. Overall, the
supply of optimal sugar-rich diet to parasitoid female increases the oviposition behavior.
The effect of nectar, honeydew, hosts and artificial diets on parasitism of the
proovigenic parasitoid *Copidosoma koehleri* Blanchard (Hymenoptera: Encyrtidae) was
investigated by Baggen and Gurr (1998). While host presence does not influence
parasitization rate, supplemental nutrition of honey or suitable nectar plants nearly
doubles the oviposition behaviors of *C. koahleri* females (Baggen and Gurr 1998).
Honey-based diet and sucrose syrup-based ones are reported as the best options to
increase parasitization rates in *Trichogramma euproctidis* (Girault) (Hymenoptera:
Trichogrammatidae), probably due to the high suitability of this sugary source coupled to a quick access to food (Tunçbilek et al. 2012). Similarly, O. nezarae lays more eggs in presence of honey, suitable flower nectar or sugar (glucose, galactose and sucrose) nutrition, if compared to aphid honeydew (Teraoka and Numata 2000). Nevertheless, the exposure to hosts coupled with sugar or honey food increase parasitization rates in C. plutellae, whereas the total absence of supplemental food does not enhance oviposition behavior neither in presence of high host-density scenarios (Mitsunaga et al. 2004). Food deprivation affects also the ratio between host feeding and parasitism in the aphelinids E. melanoscutus and E. formosa. In both species, food-deprived wasps killed more hosts by feeding, while fed females had greater parasitization rates (Zang and Liu 2010). Similarly, also the eulophid parasitoid N. formosa benefits from honey supplement by reducing the host-feeding events in favor of oviposition, increasing also the total host mortality (Liu et al. 2015). Oviposition behavior may also be deterred by the direct exposure to food contaminants, such as lectins, reducing the number of total egg laid by the parasitoid E. pennicornis (Wakefield et al. 2010).

The presence of optimal food sources is considered helpful to improve parasitoid fertility and fecundity. Fertility of braconid parasitoid O. hirtus is improved when females feed on sugar-rich artificial diets (Cicero et al. 2012), whereas the administration of aphid honeydew to T. ostriniae females showed no effect on fertility of egg laid, even if the parasitization rate were higher (Fuchsberg et al. 2007). Host feeding strategy is also important to improve lipid levels and consequently egg fertility (Zhang et al. 2011) in those species that are able to exploit a lipidic nutrition during adulthood (Visser et al. 2010). Indeed, the presence of fatty acid in the diets administrated to P. turionellae wasps is strictly related to higher egg fertility and
hatching percentage (Nurullahoglu and Ergin 2009).

Fecundity and progeny production are heavily affected by diet composition, either by directly improving female reproductive mechanisms, as well as by prolonging adult lifespan and consequently parasitoid lifetime fecundity. In several mymarid and braconid parasitoids, the lifetime fecundity increases when reared on honey diet, mainly boosting daily fecundity (Jacob et al. 2006; Wu et al. 2008; Mutitu et al. 2013).

Furthermore, the fecundity of *F. arisanus* is high when fed on honey, molasses, maple syrup and sugar cane, but daily fecundity varies accordingly to quality of diet (Bautista et al. 2001). Similarly, Tena et al. (2013b) compared the effect of five kinds of honeydew on the realized fecundity of *A. melinus*. The realized fecundity of females with access to low-value food, as the honeydew excreted by the aphid *Aphis spiraecola* Patch (Aphididae), was similar to unfed females. In contrast, females fed on honeydew of *Coccus hesperidum* L. (Coccidae) and *Icerya purchasi* Maskell (Monphlebidae), which contain high nutritional valuable carbohydrates, had a realized fecundity six times greater (Tena et al. 2013b). Even pollen may be exploited as food source to improve fecundity. *T. brassicae* wasps increase their lifetime fecundity when fed with pollen and water mixture respect to water-fed females, but since pollen is a sub-optimal food source, the addition of honey or the supply of honey solution determine greater positive effects on progeny production (Zhang et al. 2004). Low-quality diets can also lack impact on fecundity of females, with similar results to starved ones. Schmale et al. (2001) reported no differences in fecundity for the pteromalid parasitoids *D. basalis* and *A. calandrae*, as well as for the braconid *H. prosopidis*, three putative hymenopteran parasitoids of *Acanthoscelides obtectus* (Say) (Coleoptera: Bruchidae) when fed on sugarcane or without food supplements. On contrast, for all three tested species, females
produced more offspring when provided with a honey-based diet (Schmale et al., 2001). Although different nutritional sources generally alter parasitoid fecundity, this is not the case of the encyrtid *A. papayae*, which can equally benefit from honey solution, as well as from honey and yeast extract diet, dried grapes extract and fructose solution (Divya et al. 2011). Frequency of feeding may also play a role on wasps’ fecundity. Indeed, *C. marginiventris* females produce more offspring when sugar-rich nutrition is continuously provided (Faria et al. 2008). Similarly, when fed *ad libitum*, *M. pulchricornis* females produced significantly more progeny than those subjected to lower feeding frequencies, increasing daily fecundity rather than extending their reproductive period (Wu et al. 2008).

Food supply may evoke different effect on daily offspring production and on duration of the reproductive period. *D. basalis* and *H. prosopidis* shows higher daily fecundity when allowed to feed on honey, respect to sugarcane, but no differences are recorded after 25 day on cumulative progeny production of *D. basalis* (Schmale et al. 2001). Similar results are described for *M. rufiventris* wasps, since starved females lay more eggs than do honey-fed ones in the first day after emergence, probably as consequence of exclusive energy allocation for reproductive activities (Hegazi et al. 2013). The impact of nutrition on lifetime fecundity depends also on the interaction with parasitoid physiology, mostly size and age. For example, the realized lifetime fecundity of *T. nubilale* varies according to the wasp’s size, and the honey impact on fecundity is higher for small females, while no differences are reported for unfed wasps (Olson and Andow 1998). Parasitoid age plays a pivotal role for *P. cerealellae* wasps, which behave differently to various diet accordingly to age. Whereas the young females are not immediately conditioned by different diet composition or even by the absence of food,
the older females benefit from sugar feeding, increasing lifetime fecundity (Onagbola et al. 2007).

**Sex ratio**

Several parasitic wasps are able to adaptively control sex ratios, selecting offspring sex ratio in response to various factors, mainly represented by local mate competition and by host quality (Godfray and Werren 1996). Commonly, well-fed female parasitoids alter the progeny sex ratio producing a higher proportion of female offspring. Accordingly to Berndt and Wratten (2005), in absence of flower nectaries, *D. tasmanica* sex ratio is strongly male biased, but, when wasps feed on flowers, approximately an equal sex ratio was produced, with exclusive male production at the end of female’s life. The diet of adult parasitoids is unlikely to affect inbreeding, superparasitism and host size, while it could play a role in mating success, sperm viability or fertilization, which may explain sex ratio variation. Well-fed *Pachycrépoideus vindemmiae* (Rondani) females also exploit nutrition by producing a higher proportion of female offspring (Hu et al. 2012). In absence of honey, progeny sex ratio is always female biased but with an increase of male percentage, while total progeny production is significantly lower (Hu et al. 2012). Furthermore, also *T. ostriniae* produces a higher proportion of females and a greater daily fecundity when parasitoids were fed with aphid honeydew compared to unfed wasps (Fuchsberg et al. 2007). Similarly, honeydew feeding increases the total progeny and the relative number of females in *Lipolexis scutellaris* Mackauer (Hymenoptera: Braconidae) (Singh et al. 2000). Conversely, the solitary egg parasitoid *C. noackae*, if allowed to fed on sugary-
A prerequisite for parasitoid effectiveness against pests in the field is nectar and/or honeydew accessibility, which typically enhance survival, dispersal and fertility (Wäckers et al 2008). Nevertheless, modern agriculture had led to agro-ecosystem landscape simplification, which contributes to an increase in pest density and to a reduction to alternative non-crop food sources available for natural enemies. Moreover, the commuting behavior (i.e. the return of a parasitoid to the original host location, after feeding elsewhere) (Jervis et al. 1993) is still poorly understood and, apart from the energetic costs and predatory risk, longer distances between food and host locations and the presence of alternative hosts may make commuting less profitable for parasitoids, decreasing host fidelity.

In this scenario, a better understanding of parasitoid feeding ecology is needed to identify suitable food sources in the field. Besides the well-known HPLC-sugar analysis of food sources available in the agro-ecosystems, molecular approaches may be helpful to identify both plant and animal-borne foods suitable for adult parasitoids (reviewed by Traugott et al. 2013). DNA-based techniques (i.e. next-generation sequencing and multiplex PCR) may be employed to investigate which kind of food is used by parasitoid in field, while stable isotope and fatty acids may be helpful to examine the
differential assimilation and metabolism of a broad range of food sources, highlighting the nutrient and energy fluxes in the food web and the presence of nutrient limitations. Indeed, for parasitoids the presence of adequate sugary sources is fundamental to ensure appropriate host parasitization rates. Segoli and Rosenheim (2013) reported that Anagrus parasitoids in unsprayed vineyards survive less than a day and the proportion of fed wasps is generally really low (about 10% on average). In addition, seasonal changes in nutrient availability and quality may also play a key role in parasitoid efficiency, as reported for A. melinus, which could be limited by honeydew paucity and accordingly could reduce its potential as biological control agents (Tena et al. 2013a).

To overcome occurred field limitations, the employment of artificial sugar sources, flowering cover crops and the management of flowering field margins may be helpful to improve natural populations and to enhance the performance of parasitic wasps in both conservative and augmentative biological control programs. Indeed, since crops usually provide nectar for a limited period, commonly the only source of non-host food are wildflowers, including weeds (Altieri et al. 1977; Rollin et al. 2016), and honeydew (Tena et al. 2016). However, plant nectar and honeydew are not always profitable for parasitoids, since accessibility, quantity, quality and detectability of resources may be weak (Bianchi and Wäckers 2008; Tena et al. 2013a, b; Tena et al. 2016). Many parasitoid species exploit nectars from various cover crops and field margins’ plants differently, accordingly to sugar composition and content (Vattala et al. 2006), and accessibility of nectars (Idris and Grafius 1995; Baggen and Gurr 1998). Thus, the mere presence of flowering weeds or cover crops does not ensure food accessibility for parasitoids (Lee et al. 2006), since a great number of natural occurred plants are or not attractive or even repellent for them (Heimpel and Jervis 2005;
On this basis, intercrop plant varieties, with an increased number of nectaries, as well as with an extended nectar production period (Rollin et al. 2016), can highly benefit parasitoids, by providing high quality food and influencing various life traits (Jamont et al. 2013).

In the case of honeydew, its exploitation by parasitoids depends greatly on its quality. Therefore, it is essential to test the quality of the honeydew for parasitoids to determine whether this sugar source can increase parasitoid fitness (Tena et al. 2013b; Tena et al. 2016).

Furthermore, additional energy may be obtained by artificial sugar supplementation, as reported for A. melinus in field (Tena et al. 2015). Commercial food spray (Eliminate) has been proved to expand survival of some parasitoid species, but also among closely related species variations of nutrition benefits could be recorded (Irvin et al. 2007), while proteic supplement was not effective (Wade et al. 2008a). Nevertheless, the use of artificial sugar spray and food supplementation has not proven effective in many agroecosystems (Wade et al. 2008b). Since food is not always limiting in field, food supplements need to be appropriate and the nutrients suitable to enhance not only parasitoid longevity and fitness, but also their parasitization ability under field conditions (Sigsgaard et al. 2013). Concerning sugar-spray food, limited information has been provided for the effectiveness of other feeding devices containing mixture of honey and/or carbohydrates, mainly used in greenhouse crop systems (Shimoda et al. 2014). In some tri-trophic microhabitats, pest and parasitoid food resources are the same, and to control herbivorous populations various insecticidal-bait formulation containing food attractants are used. In this context, baits may also attract non-target species, as parasitoids, which may be killed by insecticides, but also may indirectly alter...
their foraging behavior in presence of a competitive food source (Wang et al. 2011).

The major challenge, however, is the selection of plant species and/or artificial sugars that encourage beneficial arthropods but not the pest. Indeed, it has been reported that flowering plants exploited by hymenopteran parasitoids are also an appropriate food source for their lepidopteran pests, although nectar has a much greater effect on parasitoid longevity than on herbivores (Winkler et al. 2009). However, peculiar carbohydrates present in hemipteran hemolymphs (i.e. trehalose) are not beneficial for herbivores and could be applied as selective food source (Winkler et al. 2005).

Moreover, beside the majority of research being focused on selectivity of food supplementation in a specific tri-tropic interaction (Begum et al. 2006), little attention has been given to the effect of sugar supplement toward non-target pests, which could benefit from additional food provisioning and make decrease crop yields (Mitsunaga et al. 2006). Furthermore, also hyperparasitoids may exploit supplemental nutrition, including honeydew saccharides that are not profitable for herbivorous pests, and this can boost their longevity and double their fecundity (Harvey et al. 2012). Even if hyperparasitoids lead to herbivore death, a large presence of these arthropods can cause the failure of a biological control program by dramatically decreasing parasitoid populations.

Finally, implementation of food sources under field condition, via artificial diet provisioning or flowering plant management, has to consider the innate preferences of parasitoids. Alternatively, also the ability to learn peculiar odor in association with sugary diets may be helpful to prime parasitoid responses during mass rearing or to increase food fidelity in field. Beside direct field application of food supplements, knowledge about diet influence on parasitoid life-history traits is essential to improve
mass-rearing techniques of biocontrol agents employed in inundative and
augmentative programs. Prior the field release, it seems therefore advisable to supply
insects with sugar-rich diets and host food to improve their performances in fields and
to optimize parasitoid egg expenditure (Hougardy et al. 2005; Hougardy and Mills
2006, 2007). Furthermore, little research on the effects of the adult diet on parasitoid
courtship and mating traits has been conducted. Further studies on this issue, as well as
on the employment of food sources as effective baits for parasitoid monitoring (Li et al.
2015) are urgently needed to maximize the field effectiveness of these biological control
agents.

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