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Review

Exploring the Role of Supplemental Foods for Improved Greenhouse Biological Control

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Abstract

Small modifications in greenhouse agroenvironments can have a big impact on the success of biological control programs. For instance, the application of supplemental foods during and after the release of natural enemies onto crop plants, could considerably improve their long-term reproductive and population growth prospects. As such, food supplementation represents a valuable biological control supportive strategy, helping to grow natural enemy populations before pest establishment, akin to creating a standing-army to defend crops against future pest invasions. In many places of the world, food supplementation represents a relatively new but growing component of biological control research, with increasingly better resources available to guide producers, IPM practitioners, or researchers wanting to apply or optimize such strategies to their local agents and environments. In this review, we summarize the current stage of knowledge associated with various supplemental food types, which work best to support specific beneficial arthropods as well as some tools and techniques for successfully applying this biological control-enhancing strategy. We also summarize some current challenges to the use of supplemental foods and discuss what future research is needed to adapt and optimize food supplementation for a diversity of natural enemy species.

Key words: supplemental food, predators, biological control

In greenhouse agroecosystems, pest management has the tendency to become more complex over a given cropping cycle. This can be attributed to both the exponential buildup of pest populations, as well as to the cumulative need to mediate a diversity of arthropod pest species as they invade and colonize the same crop space. In this way, both native and exotic pests contribute to the potential for reduced crop yield and market value (Knapp et al. 2020). To mitigate such risks, growers can choose to apply a variety of management tools, including conventional chemical or biological control agents. Due to their inherent ease of application and initial cost-effectiveness, insecticidal and miticidal agents are commonplace in pest management arsenals around the globe (Gullino and Tavella 2020). However, pest populations can exhibit a staggering variation in their response to such agents, a factor that becomes particularly problematic when multiple historical pesticide exposures lead to resistance (van Lenteren 2000, Gullino and Tavella 2020). Furthermore, the application of many conventional agents can not only immediately negatively impact the populations of nontarget natural enemy species used for control of other crop pests, but their persistence on crops can also jeopardize the use of these biologicals following a pesticide treatment (Gradish et al. 2011).

However, there can also be major challenges with the successful implementation of biological control programs. Firstly, many of these are best applied on a preventative instead of curative basis and therefore may not be useful if a pest population has reached its economic threshold (De Backer et al. 2015, Weintraub et al. 2017). Biological control pest management can also fail when the conditions responsible for establishing and maintaining such natural enemy populations onto crops are not met. This can be the case when predators, parasitoids, or entomopathogens initially and rapidly deplete a pest population, but disappear shortly thereafter when the pest is no longer abundant and the natural enemy is faced with starvation (Henaut et al. 2002, Knapp et al. 2020), subsequently inviting a pest recurrence. In addition to prey population size limitations, mismatches between natural enemy life stage and size relative to those of available pest species can also be problematic and limit agent establishment on crops (Hoelmer et al. 1993, Gerling et al. 2001). Some predators such as *Orius laevigatus* (Fieber) (Hemiptera: Anthocoridae) avoid feeding on eggs or juvenile stages of target prey such as spider mite, *Tetranychus urticae* Koch (Acari: Tetranychidae) (Sabelis 1992, Symondson et al. 2002, Venzon et al. 2002). Or in the converse, a predator may only consume prey when the predator is at a specific life stage, such as syrphid flies (Diptera: Syrphidae), whose

larvae can devour aphids (Hemiptera: Aphididae), while adults are limited to feeding on nectar and pollen (Dunn et al. 2020).

Towards mitigating such limiting factors, the biological control practitioner can introduce specialist agents at regular intervals to specifically control the pest of interest. Through this, the specialist is always present, and at the right life, stage to exert pest control. Historically, most of the earliest biological control agents released in commercial greenhouses were classified as specialist agents (van Lenteren and Woets 1988). However, over a given cropping cycle, these repeated introductions can represent a costly option, and occasionally also an ineffective one. For instance, routine control of greenhouse whitefly, *Trialeurodes vaporariorum* Westwood (Homoptera: Aleyrodidae) on tomato crops by the specialist whitefly parasitoid, *Encarsia formosa* Gahan (Hymenoptera: Aphelinidae) can cost approximately US\$1.08 per m² per year (Lambert et al. 2005, Payton Miller and Rebek 2018). However, the application of this specialist alone can be inadequate faced with the invasion of another pest species that lies outside its host range.

Alternatively, biological control practitioners may choose to introduce a generalist agent, which owing to its flexible plant and prey feeding habits, can provide more sustained control of the target pest (Symondson 2002). For example, the mirid predator *Dicyphus hesperus* Knight (Hemiptera: Miridae) can provide good and cost-effective whitefly control when supported by a mullein banker plant system and the addition of *Ephesia* (*Anagasta*) *kuehniella* Zeller (Lepidoptera: Pyralidae) eggs. Furthermore, while its initial application costs are higher at US\$0.99 per m² per year, this amount is significantly reduced after an initial predator establishment period of about five months to US\$0.60 per m² per year, at which point, sufficient pest prey is available and no new predator releases are required (Lambert et al. 2005, Payton Miller and Rebek 2018). Ultimately, employing a generalist agent along with supportive foods on either banker or crop plants (Pandey et al. 2020) can represent an important cost saving to growers.

Furthermore, the application of generalist biological control agents can effectively serve to mitigate a broad range of pest species (Albajes and Alomar 1999, Jaworski et al. 2013, Banihashemi et al. 2017) and even complement the inundative

release of specialists (Symondson et al. 2002). For instance, generalist predators, *Amblyseius swirskii* Athias-Henriot (Mesostigmata: Phytoseiidae), and *Macrolophus pygmaeus* Rambur (Hemiptera: Miridae) can both consume and control populations of whitefly and thrips (Messelink et al. 2008, Calvo et al. 2011, Leman et al. 2020). However, in the case of *A. swirskii*, effective whitefly control is only possible when more than one prey type is available, providing a dietary benefit that results in higher rates of juvenile predator survival, faster development, and greater predator densities, which all contribute to rapid pest population control (Messelink et al. 2008). In addition, the flexible feeding habits of generalists can permit predator crop establishment even before pest populations are present or during periods of prey scarcity (Ingegno and Messelink 2016). This is especially true when supportive foods are also available, which help build an actively growing natural enemy population (Perdikis et al. 2011, Messelink et al. 2012; Fig. 1).

Generalist predators, including omnivorous species who also feed on pollen, floral and extrafloral nectar and plant tissue (Limburg and Rosenheim 2001), have a vast and flexible biological control potential (Ehler 1990, Coll and Guershon 2002). While non-pest foods, such as flower nectar, are also valuable to specialist parasitoids and predators (Jervis et al. 1992, Heimpel and Jervis 2005), this review focuses principally on the benefits alternate food provisioning has on generalist and omnivorous predators. Relative to specialists who have a direct dependence on target pest prey abundance, many generalists can readily engage in trophic switching, whereby omnivorous predators exploit foods at multiple trophic levels (Cohen 1996, Walzer and Schausberger 1999).

Omnivory among arthropods has evolved many times independently and is exhibited by diverse biological control organisms belonging to multiple orders including; Hemiptera, Coleoptera, Heteroptera, Thysanoptera, and Neuroptera, as well as by acarids such as the omnivorous phytoseiidae (Li et al. 2017, Puentes et al. 2018). In contrast to specialist agents who have a limited capacity to digest or parasitize organisms other than their target pest prey, generalist agents can feed on a diversity of foods to meet their nutritional requirements, which can also be met as the availability of pest species change over time (Gerling et al. 2001).

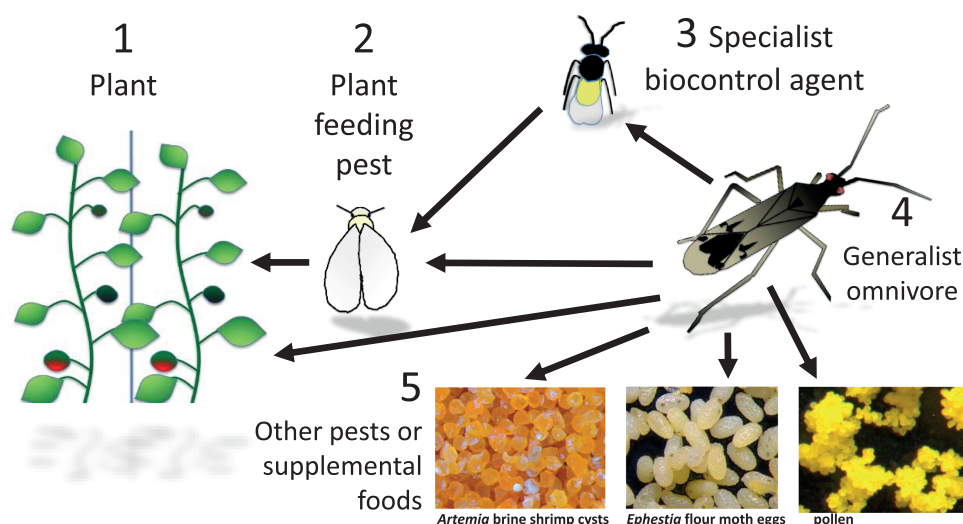


Fig. 1. Summary of trophic links between generalist omnivores and specialist natural enemies. Omnivorous predators, unlike specialist natural enemies, rely on multiple trophic levels to derive the necessary nutritional requirements for development, reproduction, and population establishment. This can include feeding on plant pests, the host plant itself, supplemental foods or other arthropods present in the greenhouse environment. By exploiting multiple resources, generalist agents employed for pest management can have a stabilizing effect on crop protection.

The capacity to feed on plants, as exhibited by omnivorous arthropods known as zoophytophages, can have a dichotomous impact on biological control. The ability to exploit alternative food sources serves to improve predator life history and population growth, even in the absence of arthropod prey (Naranjo and Gibson. 1996, Wiedenmann et al. 1996). However, fruit and plant feeding by zoophytophagous predators, such as is the case for many mirid species, can lead to significant yield losses (reviewed by Castañe et al. 2011). Plant feeding can be especially costly in the case of plant vascular tissue feeding species such as *Nesidiocoris tenuis* (Reuter) and *Engytatus varians* (Distant) (Hemiptera: Miridae), for whom plant feeding can incur significant crop damage at high densities, particularly when food is scarce (Castañe et al. 2011, Sanchez and Lacasa 2008, Arno et al. 2010). However, zoophytophagy can also be an asset when plant damage is mitigated by careful population monitoring or by food supplementation. For instance, *N. tenuis* is an excellent predator of many greenhouse and field pests, including the invasive *Tuta absoluta* Meyrick (Lepidoptera: Gelechiidae) (Sanchez and Lacasa 2008, Calvo et al. 2012).

In contrast, other plant-feeding mirids such as from *Macrolophus* and *Dicyphus* species (Hemiptera: Miridae), do not exhibit the same vascular tissue damage associated with significant yield loss (Castañe et al. 2011). Furthermore, plant damage by these predators can largely be mitigated by food supplementation, which can be considered a decisive factor for achieving durable and cost-effective crop protection (Castañe et al. 2011, Nannini et al. 2017).

In addition to the benefits of a mixed diet, generalist predators also frequently require a diversity of prey types to sustain their development and population growth. When predators such as *M. pygmaeus* are provided a mixed prey diet including whitefly *Bemisia tabaci* Gennadius (Hemiptera: Aleyrodidae) and the invasive microlepidopteran moth *Tuta absoluta*, the mirid predator necessarily exhibits prey switching, whereby it exploits both prey sources and stabilizes each of their populations (Jaworski et al. 2013). In this instance, the predator is incapable of controlling *T. absoluta* unless there is an alternate prey present, likely because *T. absoluta* alone does not provide all nutrients this predator requires for growth, development, and egg-laying (Jaworski et al. 2013, Molla et al. 2014, Sylla et al. 2016). Studies such as these demonstrate that generalist predators can benefit from the availability of a diversity of food types, which helps them achieve greater population growth and better pest control (Bompard et al. 2013, Jaworski et al. 2013, Molla et al. 2014). This notion of natural enemy provisioning is not new to biological control but instead represents an element of conservation biological control.

In field agroecosystems, conservation biological control or ecological engineering has sparked the interest of biological control practitioners over the past two decades, as it was seen as a way to improve natural enemy establishment and decrease the incidence of pest outbreaks in monocultures (Altieri 1999, Gurr et al. 2004). It serves to address an important challenge in conventional agricultural systems, that they often lack suitable sources of food or the habitats needed to support natural enemies (Wackers et al. 2008, Pekas and Wackers 2017). Agroenvironments without suitable food sources tend to have natural enemy populations that are undernourished and unable to effectively fulfill their ecosystem services (Olson and Wackers 2007). Similar limitations exist in the absence of adequate oviposition sites or the use of agricultural practices that hinder natural enemy presence. To address this, conservation biological control practices serve to provision naturally occurring biological control agents with the resources and conditions they require for population growth and persistence on crop plants, translating to

an overall improved pest suppression potential (Ehler 1998, Landis et al. 2000, Messelink et al. 2014a). In fields, conservation biological control practices include minimizing the use of pesticides, habitat management by surrounding crops with flowering plants or cover crops which provide shelter and food, or the direct provisioning of food resources (Van Driesche and Bellows 1996, Mensah 1997).

While distinct from conservation biological control practiced in fields, improving the persistence of natural enemies introduced on greenhouse crops is also possible by adopting several measures and tools (Pekas and Wackers 2017, Li et al. 2020). This includes, for instance, the introduction of banker or companion plants in and around greenhouse crops (Payton Miller and Rebek 2018, Xu et al. 2020), flower strips adjacent to greenhouses (Li et al. 2020, Xu et al. 2020) or by providing structural shelters (Pekas and Wackers 2017), which offer natural enemies with oviposition sites that would otherwise be limited in availability in a greenhouse environment (Ehler 1998, Messelink et al. 2014a). In addition to this, the application of factitious, artificial, or natural foods of either animal or plant origin, which are distributed either directly onto or around crop plants can also help meet the nutritional requirements for many predators, thereby increasing their fecundity, rate of development and overall survival (Moran and Hurd 1997, Landis et al. 2000, Wade et al. 2008, Messelink et al. 2014a).

According to current commercial greenhouse practices, biological control agents are not always provided with the elements needed to maximize their crop establishment and pest management potential. Furthermore, the combined provisioning of multiple inputs, including shelter and different forms of foods (pollen and sugar, etc.) appear to work synergistically to drastically improve the abundance of predators such as *Euseius stipulatus* Athias-Henriot (Mesostigmata: Phytoseiidae) (Pekas and Wackers 2017). As such, it is not unrealistic to suggest that the full potential of many omnivorous and zoophytophagous predators to provide pest suppression in commercial greenhouse settings remains underexploited (Pérez-Hedo et al. 2021). As an example of an improved biological control strategy, the combined and early release of zoophytophagous predator *M. pygmaeus* along with weekly applications of flour moth eggs of *Ephestia kuehniella* and decapsulated cysts of brine shrimp *Artemia franciscana* Kellogg (Anostraca: Artemiidae), can successfully reduce populations of a challenging pest, the green peach aphid *Myzus persicae* Sulzer (Hemiptera: Aphididae) (Messelink et al. 2015). Without the application of supplemental foods, the establishment of this predator before prey pest would not be possible, and due to the rapid growth of aphid populations, control of such species would otherwise be extremely challenging.

Much evidence suggests that supplemental foods can support a diversity of predators under many crop conditions (Pilkington et al. 2010, Messelink et al. 2014a), though such foods are as of yet, infrequently applied in commercial greenhouses (Messelink et al. 2014a, Seko et al. 2019). Part of the reason for this is that in many cases, predator/food combinations remain untested at the scale and complexity of commercial greenhouse settings. This, combined with the lack of practical delivery methods and the high costs associated with the production of certain foods, have represented barriers to the adoption of such biological control supportive strategies. Despite this, the global scale of greenhouse production continues to expand and research has only begun to investigate how various supplemental foods could be used to benefit the unique array of generalist predators present around the world (Calvo et al. 2016, Labbe et al. 2018).

In the following sections, we summarize the current state of knowledge with respect to how different food resources support predators both generally, as well as some specific predator families or species.

These are complemented by an extensive summary of the variety of predators from around the world, who have been previously studied for the impact supplemental foods have on their life history and or biological control potential (Table 1). This comprehensive summary is the result of literature searches conducted in multiple peer-reviewed journal databases including Scopus, the OVID database platform (including Agricola, CAB, Biological Abstracts), and the Canadian Federal Science Library (FSL). Over 60 search terms or their combinations were used to identify relevant literature that spans over 20 yr of published research on this subject. Subsequently, we follow specific predator examples with a summary of the application methods and rates for various food types, as well as a discussion on the current challenges to the use of supplemental foods in commercial settings. Finally, we propose how future research could assist in developing the best practices required for the successful application of supplemental foods in various greenhouse cropping systems.

Common Supplemental Food Types

While there exists a myriad of food types which arthropods can derive nutrients from, a large part of the artificial or factitious diets developed and used in greenhouses today originate from beneficial arthropod mass-rearing systems (reviewed in De Clercq 2008). Food types that are most commonly evaluated for their biological control supporting function in crop systems include the eggs of pyralid moths such as *E. kuehniella*, the cysts of brine shrimp, including from *Artemia* species, as well as various types of pollen and sugar. In addition to these, several other diets have also been explored for their capacity to serve in support of rearing systems, including the eggs of fruit flies and astigmatid mites which are also briefly discussed. Among these food supplements, most except for pollen, are referred to as factitious foods, defined as live or dead organisms not naturally present in the habitat of a predator, which are added to support predator survival, development, and reproduction (De Clercq 2008). These food types have each been comprehensively investigated over time, shedding light on the considerable differences in value each has to diverse predator species.

Pyralid Moth Eggs

The eggs of pyralid species such as flour moths, *Ephestia kuehniella* or *Cadra cautella* Walker (Lepidoptera: Pyralidae), have previously been employed in mass-rearing systems to support the reproduction and development of a diversity of predators including; coccinellid beetles such as *Adalia bipunctata* L. (Coleoptera: Coccinellidae) (De Clercq et al. 2005a), lacewings such as *Chrysoperla rufilabris* Burmeister (Neuroptera: Chrysopidae) (Kathiar et al. 2015), phytoseiid mites including *Amblyseius eharai* Amitai et Swirski, *A. swirskii*, *Neoseiulus cucumeris* Oudemans and *Typhlodromus transvaalensis* Nesbitt (Acari: Phytoseiidae) (Delisle et al. 2015b, Kishimoto 2015) as well as many species of predaceous heteropterans including *Orius laevigatus* and *O. strigicollis* Poppius (Cocuzza et al. 1997, Arjis and De Clercq 2001, Lu et al. 2011, Oveja et al. 2016). However, they are also the most costly type of supplemental food available for commercial use due to the technically demanding process their production requires (De Clercq 2008). For instance, an initial diet is required to support female moths, and mechanizing the rearing and harvesting process requires costly human resources and facility investments. In addition, once eggs are harvested, they must be preserved by irradiation or freezing. Finally, the cost for healthcare of rearing workers must be accounted for, since the risk of allergic reaction runs high due to the repeated inhalation of adult moth scales and eggs.

Brine Shrimp Cysts

Compared to *Ephestia* spp. eggs, the cysts of brine shrimp from genus *Artemia* are much less costly to produce and when offered to predators, often lead to comparable fecundity levels (De Clercq 2005b). For instance, encapsulated brine shrimp cysts represent an economically feasible resource on which to rear *Orius strigicollis* (Poppius), giving similar nymphal survival and female reproductive output relative to *Ephestia* eggs (Nishimori et al. 2016). Furthermore, *Artemia* cysts can also be sourced from many diverse geographical regions, each having a different value to arthropod nutrition. For instance, De Clercq (2005b) compared *Artemia franciscana* cysts from the San Francisco Bay area (United States), the Great Salt Lake area (United States), and Macau (Brazil) and found that decapsulated cysts from the Bay area yielded *Orius laevigatus* (Fieber) predators that developed 0.5–1 d faster than others. De Clercq (2005b) also conducted biochemical analyses to examine nutritional differences between *Ephestia* eggs and *Artemia* cysts that may affect the development and fecundity of this predator. Initially, both supplemental food types appear comparable in amino acid makeup, having similar levels of glutamine/glutamic acid, glycine, and alanine. However, differences arise when comparing the fatty acid content in each food type. Overall, *Ephestia* eggs have approximately three times the fatty acid content (360.0 µg/mg) relative to *Artemia* cysts (130.3 µg/mg). As a consequence, nutritional imbalances related to feeding on *Artemia* cysts eventually do appear in subsequent generations (De Clercq 2005b).

Pollen

Pollen is another type of supplemental food that is commonly used to support diverse predator populations during periods of prey scarcity (Table 1). The particular value of pollen is twofold. First, it serves to improve the performance of predators such as *Amblydromalus limonicus* Garman & McGregor (Acari: Phytoseiidae) when these are employed to control nutritionally inadequate pest prey such as spider mites *Tetranychus urticae* (Samaras et al. 2019). For this predator, a mixed diet of cattail pollen and spider mites significantly reduces its developmental time and increases its survival and oviposition rates. It is also beneficial to predators such as *Amblyseius swirskii*, in periods of prey scarcity (Mortazavi et al. 2019), allowing it to develop to adulthood on this food source alone (Park et al. 2010). With respect to the control of *T. urticae*, pollen supplementation serves a key function as it allows the predator to establish onto crops prior to pest establishment, mitigating the presence of spider mite webbing associated with high pest densities, which otherwise negatively impacts predator performance (Mortazavi et al. 2019).

Pollen is a particularly valuable food source for supporting both Type III generalist phytoseiid predators, for whom pollen feeding can support reproduction, as well as for Type IV predators for which pollen feeding is permissive to a high reproductive capacity (Swirskii et al. 1967, Van Rijn and Tanigoshi 1999, Mc Murtry et al. 2013, Kumar et al. 2014). For Type IV predator *Euseius cojaensis* (Ehara), feeding on pine pollen supports predator population growth, which in turn allows the predator to effectively control the pink citrus rust mite, *Aculops pelekassi* (Keifer) (Acari: Eriophyidae) (Tsuchida and Masui 2020). For *Neoseiulus cucumeris*, a Type III-e predator, its biological control potential of thrips is also directly improved by the presence of pollen (Skirvin et al. 2007). For other mite species however, such as Type III-a predator *Phytoseius finitimus*, pollen feeding can sustain its development and reproduction but reduces its consumption of various greenhouse pests (Pappas 2013). Clearly, for pollen to be effective in a biological control setting, the types

Table 1. Summary of organisms for which the function of supplemental foods has been investigated

Family	Species	Food type	Study source
Anthorcoridae	<i>Orius albidipennis</i> (Reuter)	<i>Ephestia</i> eggs pollen	Cocuzza et al. (1997) Sobhy et al. (2010) Rajabpour et al. (2018)
	<i>Orius insidiosus</i> (Say)	<i>Ephestia</i> eggs pollen <i>Tyrophagus putrescentiae</i> <i>Plodia</i> eggs BSA chicken/beef liver chicken egg albumin	Ferkovich and Shapiro (2004) Calixto et al. (2013) Wong and Frank (2013) Bernardo et al. (2017)
	<i>Orius laevigatus</i> (Fieber)	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen <i>Trichoderma viride</i> fungus	Cocuzza et al. (1997) Arjis and De Clercq (2001) De Clercq et al. (2005b) Skirvin et al. (2007) Arslan and Cencer (2017) De Puyssseleir et al. (2014) Oveja et al. (2016)
	<i>Orius majusculus</i> (Reuter)	<i>Artemia</i> cysts <i>Ephestia</i> eggs	Pumarino and Alomar (2012) Oveja et al. (2016)
	<i>Orius minutus</i> (Linnaeus)	<i>Tyrophagus putrescentiae</i> pollen	Kakimoto et al. (2005) Song et al. (2018)
	<i>Orius naivashae</i> (Poppius)	<i>Ephestia</i> eggs <i>Ephestia</i> eggs pollen <i>Artemia</i> cysts <i>Ceratitidis capitata</i> eggs <i>Tyrophagus putrescentiae</i> <i>Carpoglyphus lactis</i>	Bonte et al. (2012, 2017)
	<i>Orius pumilio</i> (Champion)	<i>Ephestia</i> eggs	Shapiro et al. (2009)
	<i>Orius sauteri</i> (Poppius)	<i>Mythimna separate</i> eggs <i>Ephestia</i> eggs	Kakimoto et al. (2005) Guo et al. (2020)
	<i>Orius strigicollis</i> (Poppius)	<i>Artemia salina</i> <i>Ephestia</i> eggs <i>Artemia</i> cysts <i>Cadra cautella</i> eggs	Kakimoto et al. (2005) Lu et al. (2011) Nishimori et al. (2016)
	<i>Orius thripoborus</i> (Hesse)	<i>Ephestia</i> eggs pollen <i>Artemia</i> cysts <i>Ceratitidis capitata</i> eggs <i>Tyrophagus putrescentiae</i> <i>Carpoglyphus lactis</i>	Bonte et al. (2012, 2017)
	<i>Orius thyeses</i> Herring	<i>Ephestia</i> eggs	Pedroso et al. (2006)
	<i>Wollastoniella rotunda</i> Yasunaga et Miyamoto (Heteroptera: Anthorcoridae)	<i>Tyrophagus putrescentiae</i> <i>Ephestia</i> eggs	Carvalho et al. (2005) Nagai et al. (2013)
Chrysopidae	<i>Chrysoperla lucasina</i> (Lacroix)	<i>Ephestia</i> eggs	Messelink et al. (2016)
	<i>Chrysoperla rufilabris</i> (Burmeister)	<i>Ephestia</i> eggs	Kathiar et al. (2015)
Coccinellidae	<i>Adalia bipunctata</i> (L.)	<i>Ephestia</i> eggs pollen	De Clercq et al. (2005a)
	<i>Harmonia axyridis</i> Pallas	<i>Ephestia</i> eggs	Specty et al. (2003)
	<i>Hippodamia variegata</i> (Goeze)	pollen	Schuldiner-Harpaz and Coll (2017)
	<i>Coleomegilla maculata</i> (DeGeer)	pollen	Lundgren et al. (2009)
	<i>Coccinella septempunctata</i> (L.)	pollen	Schuldiner-Harpaz and Coll (2017)
Miridae	<i>Cambyloneuropsis infumatus</i> (Carvalho)	<i>Ephestia</i> eggs	Bueno et al. (2018)
	<i>Deraeocoris pallens</i> (Reuter)	<i>Ephestia</i> eggs <i>Artemia</i> cysts	Messelink et al. (2015)
	<i>Dicyphus bolivari</i> (Lindberg)	<i>Ephestia</i> eggs	Madeira et al. (2019)
	<i>Dicyphus errans</i> (Wolff)	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen milk powder	Messelink et al. (2015) Arvaniti et al. (2018) Madeira et al. (2019)

Table 1. Continued

Family	Species	Food type	Study source
Phytoseiidae	<i>Dicyphus hesperus</i> Knight	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen	Gillespie and McGregor (2000) Sanchez et al. (2004) Calvo et al. (2018) Labbe et al. (2018) Pandey et al. (2020)
	<i>Dicyphus maroccanus</i> Wagner	<i>Ephestia</i> eggs	Salas Gervassio et al. (2017)
	<i>Dicyphus tamaninii</i> Wagner	<i>Ephestia</i> eggs <i>Artemia</i> cysts	Messelink et al. (2015)
	<i>Engytatus varians</i> (Distant)	<i>Ephestia</i> eggs <i>Sitotroga cerealella</i> eggs sucrose	Bueno et al. (2018) Palma-Castillo et al. (2019)
	<i>Macrolophus basicornis</i> (Stal)	<i>Ephestia</i> eggs	Bueno et al. (2018)
	<i>Macrolophus pygmaeus</i> (Rambur)	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen	Perdikis and Lykouressis (2000) Vandekerkhove and De Clercq (2010) Put et al. (2012) De Backer et al. (2015) Hamdi et al. (2013) Molla et al. (2013, 2014) Messelink et al. (2015) Oveja et al. (2016) Moerkens et al. (2017) Brenard et al. 2018, (2019) Urbaneja et al. (2005) Molla et al. (2014) Salas Gervassio et al. (2017) Mori et al. (2018) Owashi et al. (2020)
	<i>Nesidiocoris tenuis</i> Reuter	<i>Artemia</i> cysts <i>Ephestia</i> eggs	Burla et al. (2014) van Rijn et al. (1999) Vangansbeke et al. (2014a,b) Cavalcante et al. (2015) Leman and Messelink (2015) Nguyen et al. (2015) Lee and Zhang (2018) Samaras et al. (2015, 2019) Ferreira et al. (2020) Nguyen et al. (2015) van Rijn et al. (1999) Kishimoto (2015) Masui et al. (2019) Tsuchida and Masui (2020) Cavalcante et al. (2015) Marcossi et al. (2020) Cavalcante et al. (2015) Nomikou et al. (2001, 2003) Hoogerbrugge et al. (2008) Park et al. (2010) Goleva and Zebitz (2013) Kumar et al. (2014) Delisle et al. (2015a,b) Leman and Messelink (2015) Pijnakker et al. (2016a) Vangansbeke et al. (2016b) Pijnakker et al. (2016a,b) Muñoz-Cárdenas et al. (2017) Riahi et al. (2017) Pirayeshfar et al. (2020) Cavalcante et al. (2015) Massaro et al. (2016)
	<i>Tupicoris cucurbitaceus</i> (Spinola)	<i>Ephestia</i> eggs	
	<i>Amblydromalus limonicus</i> (Garman & McGregor)	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen grain mite <i>Aleuroglyphus ovatus</i>	
		<i>Carpoglyphus lactis</i> <i>Ceratitis capitata</i>	
	<i>Amblyseius aerialis</i> (Muma)	pollen	
	<i>Amblyseius andersoni</i> Chant	pollen	
	<i>Amblyseius degenerans</i> (Berlese)	pollen	
	<i>Amblyseius eharai</i> Amitai and Swirski	pollen <i>Ephestia</i> eggs	
	<i>Amblyseius herbicolus</i> (Chant)	grain mite <i>Aleuroglyphus ovatus</i> pollen	
	<i>Amblyseius largoensis</i> (Muma)	grain mite <i>Aleuroglyphus ovatus</i>	
	<i>Amblyseius swirskii</i> (Athias-Henriot)	<i>Ephestia</i> eggs <i>Artemia</i> cysts pollen honey bee pollen <i>Carpoglyphus lactis</i> astigmatid mites	
	<i>Amblyseius tamatavensis</i> Blommers	15 Astigmatid mite species bacteriophagous nematodes pollen grain mite <i>Aleuroglyphus ovatus</i>	

Table 1. Continued

Family	Species	Food type	Study source
	<i>Amblyseius tsugawai</i> Ehara	<i>Ephestia</i> eggs	Kishimoto (2015)
	<i>Cydnodromus californicus</i> (McGregor)	pollen	Ragusa et al. (2009)
	<i>Euseius concordis</i> (Chant)	multiple astigmatid mite species bacteriophagous nematodes	Barbosa and de Moraes (2015) Massaro et al. (2016)
		pollen	de Figueiredo et al. (2018)
	<i>Euseius gallicus</i> Kreiter and Tixier	pollen	Leman and Messelink (2015) Van Houten et al. (2016) Pijnakker et al. (2016a,b)
	<i>Euseius finlandicus</i> (Oudemans)	pollen	Puchalska and Kozak (2016)
	<i>Euseius ovalis</i> (Evans)	pollen	Pijnakker et al. (2016a)
	<i>Euseius scutalis</i> (Athias-Henriot)	pollen	Nomikou et al. (2001, 2004) Pijnakker et al. (2016a)
	<i>Euseius sojaensis</i> Ehara	pollen <i>Ephestia</i> eggs	Nomikou et al. (2003) Kishimoto (2015) Tsuchida and Masui (2020)
	<i>Euseius stipulatus</i> (Athias-Henriot)	15 Astigmatid mite species bacteriophagous nematodes	Massaro et al. (2016) Beltrà et al. (2017)
		pollen	Pekas and Wackers (2017)
		sucrose	Calabuig et al. (2018)
	<i>Gaeolaelaps aculeifer</i> (Canestrini)	<i>Aleuroglyphus ovatus</i> <i>Ephestia</i> eggs <i>Artemia</i> cysts saprophytic nematodes	Navarro-Campos et al. (2016) Rueda-Ramírez et al. (2018)
		pollen	
	<i>Iphiseius degenerans</i> (Berlese)	pollen	Pijnakker et al. (2016a) Tsolakis et al. (2016) Calabuig et al. (2018)
	<i>Iphiseiodes zuluagai</i> Denmark and Muma	multiple astigmatid mite species	Barbosa and de Moraes (2015) Ferreira et al. (2020)
	<i>Neoseiulus anonymus</i> (Chant and Baker)	15 Astigmatid mite species bacteriophagous nematodes	Massaro et al. (2016)
		pollen	
	<i>Neoseiulus baraki</i> Athias-Henriot	<i>Steneotarsonemus concavuscutum</i> <i>Tyrophagus putrescentiae</i>	Domingos et al. (2010)
	<i>Neoseiulus barkeri</i> Hughes	multiple astigmatid mite species	Nomikou et al. (2001)
		pollen	Barbosa and de Moraes (2015)
	<i>Neoseiulus californicus</i> McGregor	pollen <i>Ephestia</i> eggs multiple astigmatid mite species	Castagnoli et al. (2006) Barbosa and de Moraes (2015) Pina et al. (2012) Kishimoto (2015) Nguyen et al. (2015) Vacacela Ajila et al. (2019) Urbaneja-Bernat and Jacques (2020) Pascua et al. (2020) Soltaniyan et al. (2020)
	<i>Neoseiulus cucumeris</i> (Oudemans)	pollen <i>Ephestia</i> eggs <i>Sitotroga cerealella</i> eggs <i>Spodoptera littoralis</i> eggs <i>Tyrophagus putrescentiae</i>	Skirvin et al. (2007) Sarwar (2016) Delisle et al. (2015a,b) Nguyen et al. (2015) Al-Shemmary (2018) Tsolakis et al. (2019)
	<i>Neoseiulus longilaterus</i> (Athias-Henriot)	pollen	
	<i>Neoseiulus tunus</i> (De Leon)	grain mite <i>Aleuroglyphus ovatus</i>	Cavalcante et al. (2015)
	<i>Neoseiulus womersleyi</i> (Shicha)	<i>Ephestia</i> eggs	Kishimoto (2015)
	<i>Phytoseiulus persimilis</i> (Athias-Henriot)	pollen	Urbaneja-Bernat and Jacques (2020)
	<i>Phytoseius finitimus</i> Ribaga	pollen	Nomikou et al. (2001) Pappas et al. (2013)
	<i>Phytoseius</i> (<i>Dubininellus</i>) <i>nipponicus</i> Ehara	<i>Ephestia</i> eggs	Kishimoto (2015)
	<i>Proprioseiopsis cannaensis</i> (Muma)	pollen	Bellini et al. (2010)

Table 1. Continued

Family	Species	Food type	Study source
Thripidae	<i>Stratiolaelaps scimitus</i> (Womersley)	<i>Ephesia</i> eggs <i>Artemia</i> cysts saprophytic nematodes pollen pollen	Navarro-Campos et al. (2016)
	<i>Typhlodromus athiasae</i> (Porath and Swirski)	pollen pollen	Nomikou et al. (2001)
	<i>Typhlodromus laurentii</i> Scheuten	pollen	Tsolakis et al. (2016)
	<i>Typhlodromus negevi</i> (Swirski and Amitai)	pollen	Hussein et al. (2016)
	<i>Typhlodromus pyri</i> Scheuten	pollen	Bermúdez et al. (2010) Puchalska and Kozak (2016)
	<i>Typhlodromus vulgaris</i> Ehara	<i>Ephesia</i> eggs	Kishimoto (2015)
	<i>Typhlodromus transvaalensis</i> (Nesbitt)	<i>Ephesia</i> eggs	Kishimoto (2015)
	<i>Frankliniella occidentalis</i> (Pergande)	<i>Ephesia</i> eggs <i>Artemia</i> cysts pollen milk powder and yeast	Hulshof et al. (2003) Vangansbeke et al. (2014b) Leman and Messelink (2015)
	<i>Thrips hawaiiensis</i> Morgan	honey solution pollen	Fu et al. (2019)
	<i>Propylea japonica</i> (Thunberg)	<i>Ephesia</i> eggs	Hamasaki and Matsui (2006)

of predator, pest and pollen need to be validated first for their complementarity.

In addition to its benefit to phytoseiid predators, pollen is also known to support a diversity of other predator types. Neuropteran and coccinellid predators for instance, naturally feed on pollen and nectar from a diversity of up to 21 plant families localized in and around field crops, which contributes to their improved longevity and reproductive capacity (Medeiros et al. 2010). The anthocorid bug *Orius laevigatus* also derives benefit from pollen feeding (Skirvin et al. 2007).

While there is a great variety of plant species from which pollen can be obtained, not all support biological control agents equally (Van Rijn and Tanigoshi 1999, Ragusa et al. 2009, Bermúdez et al. 2010, Goleva and Zebitz 2013, Samaras et al. 2015, Soltaniyan et al. 2020). For instance, in a study comparing pollen from 25 plant species, pollen from apple, *Malus domestica* Borkh. and cattail, *Typha latifolia* L. were among the best to improve the oviposition rate for *N. cucumeris* (Van Rijn and Tanigoshi 1999). Goleva and Zebitz (2013) also compared the impacts of pollen from 21 plant species to the survival and development of predator *Amblyseius swirskii*. Among the pollens evaluated, some such as from *Lilium martagon* and *Hippeastrum* sp. were actually toxic to predators and caused complete mortality of preimaginal life stages (Goleva and Zebitz 2013). In contrast, pollen from *Aesculus hippocastanum*, *Crocus vernus*, *Echinocereus* sp. and *Paulownia tomentosa* most improved *A. swirskii* life history parameters (Goleva and Zebitz 2013).

Another study compared the benefits of four pollen types including *Typha latifolia*, pine, corn, and olive for the phytoseiid predator *Amblydromalus limonicus* (Garman and McGregor) (Acari: Phytoseiidae) (Samaras et al. 2015). This study showed that the greatest rate of population increase resulted from feeding on cattail pollen. To date, pollen from cattail *Typha latifolia*, has been studied extensively for its support of a variety of predator species, with evidence suggesting that congeneric pollens from *T. angustifolia* and *T. domingensis* L. may also similarly support

many predatory mites (Messelink et al. 2014a, Cavalcante et al. 2015, de Figueiredo et al. 2018). Worth noting however is that such pollens, from *T. angustifolia* L. for instance, may not have the same value to soil-dwelling predatory mites *Gaeolaelaps aculeifer* Canestrini and *Stratiolaelaps scimitus* Womersley (Mesostigmata: Laelapidae) for which oviposition remained unaffected by this supplement (Navarro-Campos et al. 2016). It is quite possible then, that the vastly different soil dwelling niche and biology of such predators may have a role to play in this differential response.

With respect to the production of pollens, *Typha* spp. pollens require a labor-intensive process of hand-collection, which can make them costly to produce and may consequently be infrequently applied at commercial scales (Messelink et al. 2014a). This is why other types of pollen are also frequently applied since they can be easier to harvest. Corn pollen, for example, can be mechanically harvested in large quantities and has the potential to be more economically feasible to apply in a commercial greenhouse compared to *Ephesia* eggs (Adar et al. 2014). Bee pollen is available at a low cost while apple pollen can be abundantly produced in orchards and is therefore made commercially available (Adar et al. 2014, Delisle 2015a, Messelink et al. 2014a).

Eggs of Tephritid Fruit Flies

The eggs of tephritid fruit flies have for some time been suggested to represent a nutritionally valuable food source for rearing predatory arthropods, and may also one-day support predators during or after their release onto crop plants. Eggs of the Mediterranean fruit fly (Medfly), *Ceratitis capitata* (Wiedemann) (Diptera: Tephritidae), were first used by Liquido and Nishida (1985), to rear the mirid bug *Cyrtorhinus lividipennis* Reuter (Heteroptera: Miridae). Both predatory hemipterans *Tytthus mundulus* Breddin (Heteroptera: Miridae) and *Orius insidiosus* Say (Heteroptera: Anthocoridae) were also successfully reared on eggs of the oriental fruit fly, *Dacus (Bactrocera) dorsalis* Hendel (Diptera: Tephritidae) (Takara

and Nishida 1981). Steinberg and Cayol (2009) also showed that rearing *Orius laevigatus* Fieber on Medfly eggs, could be comparable to rearing on eggs of *E. kuehniella*. Given this evidence, De Clercq et al. (2014) proposed that fruit fly eggs could serve as a possible factitious food source for mass rearing predatory arthropods. For two additional anthocorid bugs, *Orius naivashae* (Poppius) and *O. thripoborus* (Hesse), a Medfly diet supported complete predator development and reproduction for four consecutive generations, suggesting that this food source had a similar value to eggs of *E. kuehniella* (Bonte et al. 2017). In contrast, diets of astigmatid mites *Tyrophagus putrescentiae* (Schränk) or *Carpoglyphus lactis* L. (Acari: Carpocephidae) were nutritionally inadequate for these predators. Subsequent work however, showed that Medfly eggs may be less valuable for rearing phytoseiid species. For *Amblydromalus limonicus* a diet of *C. capitata* Medfly eggs offered high immature survival rates, comparable to diets of *Typha* pollen or *Ephesia* eggs, however, females cannibalized their own offspring eggs when maintained on this diet, which resulted in an overall reduced rate of population growth (Vangansbeke et al. 2014a).

Astigmatid Mites

Astigmatid mites have been studied and used extensively for rearing phytoseiid predators. One major benefit to such food sources is that, contrary to pollen, they do not generally support populations of some pests such as thrips *Frankliniella occidentalis* Pergande (Thrips: Thripidae) (Pirayeshfar et al. 2020). When provided in their frozen form, mites such as *Tyrophagus putrescentiae* can improve crop establishment of predators such as *Amblyseius swirskii*, and when supplied alive along with pollen, can even promote predator population growth (Pirayeshfar et al. 2020). Furthermore, such alternate food sources can be distributed both directly onto crop plants as well as to growth substrates. The latter distribution area serves to benefit litter-dwelling predators including *A. swirskii*, for which this food source improves its population growth as well as its biological control potential (Muñoz-Cárdenas et al. 2017).

Other mite species used for rearing phytoseiids include the dried fruit mite, *Carpoglyphus lactis*, which is an excellent food source for predators such as *Amblydromalus limonicus* (Vangansbeke et al. 2014a). In contrast, this fruit mite does not appear to be suitable for rearing anthocorid bugs (Bonte et al. 2017). Grain mite *Aleuroglyphus ovatus* (Troupeau) (Astigmatina: Acaridae) is also used for rearing phytoseiid predators including *Amblyseius swirskii* (Cavalcante et al. 2015) and *Gaeolaelaps aculeifer* (Rueda-Ramírez et al. 2018).

As with other food types, a diversity of astigmatid mite species are currently available, but not all serve predators equally (Castagnoli et al. 2006, Barbosa and De Moraes 2015). For instance, the nutritional suitability of ten different astigmatid mite species was compared for predatory mites *Euseius concordis* (Chant), *Iphiseiodes zuluagai* Denmark and Muma, *Neoseiulus barkeri* Hughes and *Neoseiulus californicus* McGregor (Mesostigmata: Phytoseiidae) (Barbosa and De Moraes 2015). From this study, astigmatid mites from *Thyreophagus* species were best suited to support *N. barkeri* while *Austroglyphus lukoschusi* (Fain) and *Blomia tropicalis* Oudemans (Acari: Glycyphagidae) were more suited for rearing *N. californicus*. These clear discrepancies in value between astigmatid species indicate that each predator type should be evaluated independently to identify their optimal astigmatid prey type. Finally, while astigmatid mites are beneficial in the sense that they support phytoseiid predator populations, multiple astigmatid species such as *T. putrescentiae* do pose some disadvantages as they are associated

with both crop damage as well as with triggering allergic reactions in humans, factors which would need to be considered before their use on crops (Green and Woolcock 1978; Johansson et al. 1994; Arlian et al. 1997).

Artificial Foods

Along with factitious foods, artificial foods have also been developed and evaluated for supporting biological control organisms. Artificial diets were first used for mass rearing applications, and their components were selected based on their known nutritional benefits to arthropod reproduction and population growth (De Clercq 2008). Some common artificial diets include mixtures of liver (chicken/beef) extract, as well as protein extracts from egg yolks or bovine sources (Ferkovich and Shapiro 2004). However, artificial diets are not as practical to implement in greenhouses due to a variety of issues. Firstly, their use has not extensively been tested or optimized, so that mixtures with ideal nutritional components remain largely unidentified (De Clercq 2008). Furthermore, when applying such food supplements, their physical characteristics can affect how accessible they are for predator feeding and oviposition (De Clercq 2008). Finally, to improve their useful lifespan on crops, the addition of anti-microbial and anti-fungal agents are required to prevent spoiling, which increases production costs (De Clercq 2008). While future research may one day develop less expensive artificial diets that are compatible for use in greenhouse settings, as they currently stand, these diet types remain impractical and rarely used in such environments.

Sucrose

Sugar provisioning to natural enemies, can represent a nutritive, economically feasible and complimentary option to other more expensive supplemental foods (Urbaneja-Bernat et al. 2013). Sucrose, which is naturally abundant in flower nectar, along with its components glucose and fructose (Percival 1961) has long been known to greatly increase the longevity of several species of parasitoids (reviewed in Wackers et al. 2008). More recently, attention has been turned to the role of sugars for improving the life-history parameters of predators. Zoophytophagous mirids are already known to derive sugars through plant feeding (Gillespie and McGregor 2000) and evidence suggests that they also benefit directly from extrafloral nectar (Portillo et al. 2012).

Sucrose application has also been studied in field trials where it has been shown to increase the abundance and diversity of multiple natural enemy species including coccinellid predators *Coccinella septempunctata*, L., *Hippodamia convergens* Guerin-Meneville, and *Harmonia axyridis* Pallas (Coleoptera: Coccinellidae) (Seagraves et al. 2011). In a laboratory setting, adding sucrose to a pollen diet increases the fecundity of predators such as *Chrysoperla carnea* (Stephens) (Neuroptera: Chrysopidae) (Li et al. 2010) and the population growth rate for phytoseiid *Euseius stipulatus* (Beltrà et al. 2017). At a 0.5 M concentration, sucrose can also increase the progeny number and crop establishment of hemipteran predator *Nesidiocoris tenuis*, particularly when added to a diet of *Ephesia* eggs, and has the effect of significantly reducing the number of *Ephesia* eggs the predator needs to consume (Urbaneja-Bernat et al. 2013, 2015). Indeed, other predatory bugs including *Orius sauteri*, also respond positively to sucrose. For this species, a 30% sucrose solution improved nymphal survival relative to predators offered water alone (Maeda et al. 2002). Furthermore, the longevity of mirid *Engytatus varians* can be greatly improved by provisioning an arthropod-based diet with a 5% sugar solution (Palma-Castillo

et al. 2019). As such, sucrose provisioning has the potential to both reduce the quantity of other supplemental foods required to improve predator establishment, as well as the overall cost of adopting a supplemental food strategy.

The provisioning of sugar for *N. tenuis* also has the added benefit of significantly reducing the incidence of phytophagy in this species, helping to mediate the damage it poses to tomato crops (Urbaneja-Bernat et al. 2019). Similar benefits of sucrose provisioning are likely to exist for other zoophytophagous species. Unsurprisingly, this diet does have its limitations, as long-term improvements to adult longevity and fecundity can only be achieved by providing diets that include other critical dietary components including fatty acids or protein (Maeda et al. 2002).

Finally, while sucrose provisioning is generally beneficial to arthropods, delivering it efficiently poses a challenge as it can be susceptible to microbial colonization when in an aqueous solution. However, as a possible solution, sucrose can be encapsulated within polymeric shells called hydrocapsules, which represents an efficient way to preserve and control sugar delivery (Urbaneja-Bernat et al. 2013) and one to consider for commercial application.

How Does Diet Affect the Survival and Development of Specific Predator Types?

In this section, examples of some commonly applied generalist predator species are reviewed for their response to a variety of supplemental food types including predatory mirids, anthocorids, phytoseiids, and coccinellids (Table 1). These summaries serve to highlight instances in which supplemental foods have been evaluated for their potential to improve the establishment, development, and growth of predator populations, and describes the conditions under which these combinations were either successful or not.

Miridae

Macrolophus pygmaeus

Macrolophus pygmaeus (Rambur) (Hemiptera: Miridae) is a zoophytophagous predator that preys on whiteflies and other small arthropod pests (Perdikis and Lykouressis 2003). As with other mirid predators, it can reproduce on tomato, pepper, cucumber, eggplant, and other crops, and can even establish on some of these before pest prey are available (Vandekerckhove and De Clercq 2010, Put et al. 2012). For this predator, feeding on pollen can have mixed outcomes. While consuming frozen moist honey bee pollen alone amounted to a lower fecundity and weight for adult *M. pygmaeus* relative to predators fed a diet of *Ephestia kuehniella* eggs in one study (Vandekerckhove and De Clercq 2010), other studies show that it is beneficial alone or in combination with other prey diets. For instance, Perdikis and Lykouressis (2000) found that bee pollen and pollen from *Ecbalium elaterium* L. (Cucurbitaceae), could support *M. pygmaeus* nymphal development and survival to adulthood, and was particularly valuable when added to other plant or prey diets. Similarly, Put et al. (2012) found that population growth of *M. pygmaeus* was greater when predators were fed a diet of *Ephestia* eggs alone or in combination with *Typha latifolia* pollen. Overall, pollen appears to represent a good complement to other nutrient and energy-rich foods such as *Ephestia* eggs. This combination could be especially useful in crops that produce less pollen such as cucumber, whereby the addition of pollen could improve *M. pygmaeus* crop establishment (Vandekerckhove and De Clercq 2010).

Pollen remains an important food type for *M. pygmaeus*, who can complete nymphal development on this food source (Vandekerckhove and De Clercq 2010). However, when pollen consuming pests are present, pollen should be applied carefully to avoid unintended impacts. A study from Lykouressis et al. (2013) suggested *M. pygmaeus* should be introduced in pollen-producing crops when crop flowers first begin to appear, and before pest presence. This is to ensure that *M. pygmaeus* establishment and initial population growth occurs before pest prey is present.

With respect to other food sources, Messelink et al. (2014b) found that a combination of *Ephestia* eggs and *Artemia franciscana* cysts applied weekly during the *M. pygmaeus* establishment period, and prior to aphid infestations, was the best combination for pest control on sweet peppers. Alternatively, Brenard et al. (2019) suggest that applying *Artemia* spp. cysts biweekly in sweet pepper greenhouses for up to 6–8 wk after the introduction of *M. pygmaeus*, yields optimal *M. pygmaeus* population growth and dispersal, even when compared to *Ephestia* eggs. Similar findings from earlier studies also suggest that an *Ephestia* egg diet does not lead to better aphid control, despite promoting more uniform and greater predator populations (De Backer et al. 2015).

Another important consideration is how food supplements are distributed within the crop. Put et al. (2012) found that a much more uniform distribution of *M. pygmaeus* predators was obtained when *Ephestia* eggs and *Typha* pollen were distributed evenly over the entire crop area (15 g of *E. kuehniella* eggs distributed over 3 rows each with 12 plants, rows spaced 3m apart) as compared to distributing the food supplements in fewer, more concentrated areas (6 g of *E. kuehniella* eggs distributed over the two outermost localized plants of each row). Similarly, Brenard et al. (2018) found that a local application of *Artemia franciscana* cysts led to lower predator dispersal rates as well as higher rates of competition between *M. pygmaeus* females, which could incur higher rates of cannibalism. Thus, while the broadcast of foods over a full crop may be a more time consuming option, it would ultimately lead to better pest control, since *M. pygmaeus* predators would more evenly disperse throughout the crop and better exploit all available pest resources.

Dicyphus spp.

Members of the genus *Dicyphus* (Hemiptera: Miridae) represent another group of mirid predators often used in greenhouse tomato and sweet pepper crops where they commonly feed on whitefly and aphid pests (Lambert et al. 2003, Messelink et al. 2014b). As an omnivore, *Dicyphus* species predators require a source of water in order to complete nymphal development, which complements arthropod prey consumption (Gillespie and McGregor 2000, Arvaniti et al. 2018). For many *Dicyphus* predator species, a diet of *Ephestia* eggs can greatly improve the survival, rate of nymphal development, egg production, and distribution of predators on greenhouse tomato crops (Gillespie and McGregor 2000, Lambert et al. 2003, Calvo et al. 2016, Madeira et al. 2019). Recent studies have shown that *D. hesperus* can benefit from a combined diet of *Ephestia* eggs and *Artemia* cysts (in 1:5 ratio), achieving a similar predator survival rate and nymphal development time on this diet relative to a diet of *Ephestia* eggs, suggesting the combination represents a cost-effective supplemental food option (Labbe et al. 2018). A similar result was documented for *Dicyphus errans* (Wolff) (Hemiptera: Miridae) for which a diet of *Ephestia* eggs and *Artemia* cysts significantly enhanced the rate of nymph development in comparison to predators fed other food types such as pollen and milk powder (Arvaniti et al. 2018). Importantly, these supplementary foods appear to most

improve nymphal development when they are applied to plant leaves, which is supported by the fact that zoophytophagous species use plant matter to obtain essential and complementary sugars, nutrients, and moisture (Gillespie and McGregor 2000, De Puyseleir et al. 2013, Messelink et al. 2014b).

Nesidiocoris tenuis

As discussed previously, the value of multiple supplemental foods has also been investigated for *Nesidiocoris tenuis* Reuter (Hemiptera: Miridae) (Urbaneja-Bernat et al. 2013, Owashi et al. 2020). From a strictly nutritional perspective, cysts of *Artemia salina* L. supplied in their dry form were shown to support the similar developmental and reproductive performance of this predator relative to *Ephestia* eggs (Owashi et al. 2020). In addition, the provisioning of sucrose along with *Ephestia* eggs serves to increase egg production for this predator, as well as to mediate levels of plant injury (Urbaneja-Bernat et al. 2013).

Anthocoridae

Orius spp.

Predatory anthocorids belonging to the genus *Orius* (Hemiptera: Anthocoridae) are numerous, originating from many diverse parts of the globe (Table 1). A handful of these species are regularly employed for the control of greenhouse crop pests. The insidious flower bug *Orius insidiosus* is a zoophytophagous predator used for suppression of many pest species, including thrips (Ferkovich and Shapiro 2004, Doğramaci et al. 2011). Its populations also derive considerable benefits from the availability of supplemental foods. Calixto et al. (2013), found that eggs of *Ephestia kuehniella* improved *O. insidiosus*, fecundity and duration of its oviposition period. A similar improvement in the crop establishment of *O. insidiosus* was observed when a combination of *Ephestia* eggs and *Typha latifolia* pollen was applied to sweet pepper crops (Labbe et al. 2018). In addition, *Ephestia* eggs also improved *O. albidipennis* (Reut), but not *O. laevigatus* (Laevigatus) establishment on sweet pepper plants (Cocuzza et al. 1997). For *Orius majusculus* (Reuter), the addition of *Ephestia* eggs to host plants significantly increased predator fecundity and fertility (Pumarino and Alomar 2012).

Despite the fact that pollen-only diets may not support reproduction of *O. insidiosus*, it can help the predator maintain populations during periods of prey scarcity (Calixto et al. 2013, Bernardo et al. 2017). Similar to the effects of sweet pepper pollen on *M. pygmaeus*, *O. insidiosus* can also make use of pollen derived from crop, banker, or companion plants in the greenhouse environment to support its development and survival, benefitting most from a mixed diet of pollen and prey (Wong and Frank 2013).

Interestingly, research has shown that protein extracts from eggs of the Indian Mealmoth *Plodia interpunctella* (Hübner) (Lepidoptera: Pyralidae) could serve as an artificial diet for *O. insidiosus*, which led to higher egg production and a longer oviposition period in females, compared to when they fed on other non-insect protein supplements (Ferkovich and Shapiro 2004). Overall, Mealmoth eggs could prove to be a cost-effective nutrition source relative to *Ephestia* eggs or other noninsect diets, since it requires 80–800 fold less *Plodia* protein extract, compared to a non-insect based diet, to reach the same level of predator egg production (Ferkovich and Shapiro 2004).

When comparing *O. laevigatus* feeding on different factitious foods, the fastest development time and similar fecundity level was observed with *Artemia franciscana* cysts, provided they are in the

dry decapsulated form as opposed to the encapsulated form, which presents some accessibility issues for the predator due to the difficult to penetrate outer alveolar layer on the cysts (Arijs and De Clercq 2001). A similar finding was reported for two *Orius* spp. native to South Africa—*Orius thripoborus* and *Orius naivashae* (Bonte et al. 2012). These two *Orius* species had improved development times and reproduction rates when *E. kuehniella* eggs and *A. franciscana* cysts were offered as food sources relative to moist honey bee pollen alone. However, after three generations of rearing *O. laevigatus* on *A. franciscana* cysts alone, slower predator development and lower fecundity were observed, pointing to nutritional imbalances of predators on this food source relative *E. kuehniella* eggs (De Clercq et al. 2005b).

Phytoseiidae

Amblyseius swirskii

Generalist phytoseiid predators are capable of switching from one food type to another and can benefit greatly from this diversity. In addition to the large number of pest prey phytoseiid predators can consume including; tetranychid, tenuipalpid, eriophyid, tarsonemid, and tyneid mites, thrips, scale, and whitefly pests, they also feed on other resources including pollen, nectar, honeydew, and fungi (McMurtry and Rodriguez 1987).

The phytoseiid mite *Amblyseius swirskii* (Athias-Henriot) (Mesostigmata: Phytoseiidae) is a predator associated with the control of many greenhouse crop pests, namely whiteflies and thrips (Bolckmans et al. 2005). As with other predatory phytoseiids, *A. swirskii* is more likely to survive on pollen alone relative to many other predatory insect species, making them valuable for use on both high pollen-producing crops, or crops supplemented with the addition of pollen (Hoogerbrugge et al. 2005). Pollen supplementation can support phytoseiid predator population establishment and growth when crop pollen is less abundant or absent, facilitating the success of inoculative predator releases (Hoogerbrugge et al. 2008, Pijnakker et al. 2016a). *Amblyseius swirskii*, for example, is capable of surviving on cucumber plants in the absence of *Bemisia tabaci* whitefly, as long as *T. latifolia* pollen is provided as a supplemental food source (Nomikou et al. 2004). Similarly, Delisle et al. (2015a) found that biweekly applications of apple pollen support the establishment and population growth of *A. swirskii* and improved the control of western flower thrips on cucumber and chrysanthemum plants. In contrast, another study showed that an overall lower thrips predation rate was observed for *A. swirskii* who consumed pollen compared to *Ephestia* eggs (Leman and Messelink 2015). Despite this, there can still be overall enhanced control of thrips when either supplemental food is available due to the numerically larger populations of predators produced under such dietary treatments (Leman and Messelink 2015). Finally, unlike many species of Miridae for which, *Artemia* cysts are a valuable food source, these are not considered suitable food sources for phytoseiid species such as *A. swirskii* (Leman and Messelink 2015).

Coccinellidae

Harmonia axyridis

The multicolored Asian lady beetle, *Harmonia axyridis* (Coleoptera: Coccinellidae) is native to East Asia but is now established in many continents around the globe including; Europe, North America, South America, and Africa (Brown et al. 2011). It is also commercially available in Europe for the control of aphid pests (Specty et al.

2003, Berkvens et al. 2010). Specty et al. (2003) examined the value of *H. axyridis* feeding on *Ephestia kuehniella* eggs versus on the aphid *Acyrtosiphon pisum* Harris (Hemiptera: Aphididae) and compared predator biological parameters including immature development time, adult fecundity, and fertility. They also examined the lipid and amino acid content of the different prey types or of predators consuming these prey. They showed that predators consuming *A. pisum* alone had reduced protein and lipid contents and that overall, beetle weight was greater when offered *Ephestia* eggs, providing evidence of its potential use as a supportive tool for coleopteran predators. Subsequent work showed that the number of predator egg-laying days, adult lifespan, as well as adult body weight, could increase in *H. axyridis* when fed *Ephestia* eggs relative to aphid prey (Berkvens et al. 2008b).

Artemia salina L. (Anostraca: Artemiidae) cysts also have the potential for use as a food source for *H. axyridis*. Seko et al. (2019) recently found that offering *H. axyridis* a combination of encapsulated dried *A. salina* cysts and sucrose could reduce aphid incidence in greenhouse trials. Furthermore, this supplemental food combination eliminated the need for any subsequent release of *H. axyridis*, representing a net benefit of food supplementation. In this instance, sucrose may have played a role as a feeding stimulant for the consumption of the encapsulated *A. salina* due to the hygroscopic effect that it has towards the hydration of cysts when these are combined, increasing their overall availability for predators (Seko et al. 2019). Lundgren (2009) also posits that sugar feeding is beneficial for coccinellids and can shorten preoviposition periods and increase survival.

Finally, *H. axyridis* is also able to feed on pollen, a food which can support its development to adulthood (Berkvens et al. 2008a). In fact, a gut analysis conducted on adult *H. axyridis* collected from aphid infested fields in Belgium showed that 90% of adults were positive for the presence of pollen grains suggesting the predator readily seeks out this food source (Berkvens et al. 2010). It also supports the idea that pollen may be beneficial as a non-prey food source for predatory coleoptera applied for biological control in greenhouse settings.

Technical Considerations for Application of Supplemental Foods

How supplemental foods are delivered to a crop is a critical component to their commercial usefulness and viability. Supplemental foods must be applied to plants in a way that maximizes predator availability and persistence on the crop, and provides a significant benefit to growers wanting to reduce long-term costs associated with the application of biological control. In this section, we highlight the state of knowledge associated with the diverse ways foods have been and continue to be applied.

Pollen Delivery Methods

Over the years, multiple pollen types and delivery methods have been developed to improve phytoseiid predator establishment and population growth on greenhouse crops. At the commercial scale, the pollen of *Typha latifolia* is available in at least two continents Europe and North America (e.g., Nutrimite, Biobest, Westerlo, BE). This pollen can be applied manually by dusting it on individual leaves. However, this is a labor-intensive and time-consuming process and not efficient for large-scale greenhouses (Nomikou et al. 2002). Researchers have also delivered pollen by placing it in containers or sachets that hang from plant stems, however, this is also labor-intensive considering growers would have to put the pollen in the containers themselves (Nomikou et al. 2010). Recent developments have created more

efficient systems of pollen application, although they do not represent ideal systems. For instance, Weintraub et al. (2009) created a prototype of an electrostatic pollen applicator with a viscosity enhancer (EPAVE) that was able to effectively apply corn pollen to sweet pepper plants and aid the establishment of *A. swirskii*. A proposed alternative to this method is the “pollen on-twine” technique proposed by Adar et al. (2014). It has two benefits: not only does it provide a less wasteful approach to electrical blowers, since the pollen-coated twine can be distributed throughout greenhouse crops without the problem of pollen falling to the ground, but it also provides an oviposition site for predatory mites such as *A. swirskii* or *E. scutalis*. In this application method, corn pollen is shaken over a segment of rayon-jute twine tied into rings, which is then suspended over individual preflowering pepper plants. Although this technique is not yet commercially available, it may be more economically feasible to use in the future to prevent pollen loss, and because pollen on-twine develops mold more slowly than pollen applied to leaves (Adar et al. 2014). This method allowed *E. scutalis* populations to increase tenfold and *A. swirskii* populations to double in a 2–3 wk period before plant flowering (Adar et al. 2014). Although these possible means for pollen application are promising, they are not commercially available to growers, meaning this would require growers extra labor costs to create these systems themselves.

The technique that is currently commercially available involves using an electrical blower device. However, this requires large quantities of pollen and can be wasteful when pollen falls to the ground (Adar et al. 2014). Nonetheless, this technique is being widely used by growers due to its ease of application. Pollen applicators are commercially available which can be attached to a wireless unit blower to apply pollen quickly to plants at a recommended biweekly rate of 500 g/ha, or 10 mg/plant/week (Van Rijn and Tanigoshi 1999, Pijnakker et al. 2016a). While this represents a labor-saving method for applying pollen to crops, it can also be improved by better targeting the plant space in which predators are likely to occur in.

Artemia and Ephestia Delivery Methods

Similar to pollen, multiple techniques have been developed for the delivery of *Artemia* spp. cysts and *Ephestia* eggs onto crops. This section will first focus on the application of *Artemia* spp. cysts, then address methods for delivery of *Ephestia* eggs either alone or in combination with *Artemia* cysts.

Studies have shown that decapsulated *Artemia* spp. cysts have greater value on crops relative to encapsulated cysts, since the outer alveolar layer is removed, which otherwise makes it difficult for nymphs like *O. laevigatus* to reach the nutritious embryo within (Arijs and De Clercq 2001). Additionally, since dry cysts contain only 8% moisture compared to 90% when rehydrated, dry decapsulated cysts must be rehydrated in water for two hours for successful development of the predator to occur (Arijs and De Clercq 2001). It is also important to keep greenhouses at relatively constant temperature and humidity since the rehydration and dehydration of cysts due to fluctuations in these parameters can result in a loss of nutrients for predators (Vangansbeke et al. 2016a). Dry decapsulated cysts are also a good alternative because they can be stored in dry form for years before spoiling occurs. Overall, *Artemia* spp. cysts are a viable option for supporting predators such as *Orius laevigatus* (Arijs and De Clercq 2001), particularly because they are inexpensive to mass-produce, costing about three percent on a per gram basis relative to *Ephestia* eggs (Labbe et al. 2018).

In terms of application methods, *Artemia* cysts and *Ephestia* eggs can be applied manually, by sprinkling directly on leaves for

smaller crops, although this is very time-consuming and labor-intensive (Messelink et al. 2014a). Dusting applicators, such as those used for pollen application, can also be employed for *Artemia* cysts delivery, typically being applied at 500 g/ha (Vangansbeke et al. 2016a). For more local applications, Oveja et al. (2016) supplied *Artemia* cysts glued on to a 2 cm² area plastic labels (8 ± 0.2 mg/cm²) on a single plant, although this method is not yet commercially available and would require growers to create these label delivery systems themselves.

An alternative form of cyst application that has recently become commercially available consists of a long adherent ribbon, onto which decapsulated *Artemia* cysts are attached on either side. This ribbon can be rolled out along each crop row (e.g., BioArtLine, Biobee, Brownbridge 2018). This delivery method has many benefits over *Artemia* cyst distribution using a blower applicator. Not only does it reduce waste by ensuring no *Artemia* cyst is lost due to falling to the ground, but it also permits the cysts to remain viable on the ribbon for up to 10 wk, since it is not exposed to humid crop leaves. This method may also be cost-effective in that it requires relatively low labor and fewer applications that last for extended periods of time.

However, there are some instances where *Artemia* cysts alone may not be a viable option as the sole source of nutrition for predators. Rather than turning to the sole use of *Ephestia* eggs, a combination of both *Artemia* cysts and *Ephestia* eggs in a 5:1 ratio can often provide similar results and represent a more economical option to *Ephestia* alone (Labbe et al. 2018, Brenard et al. 2019). One way that growers can save when using this method is by employing less frequent applications. Brenard et al. (2019) found that biweekly, as compared to weekly application of combined *Artemia franciscana* cysts and *Ephestia kuehniella* eggs was sufficient to support the establishment of *M. pygmaeus* on crops. Moerkens et al. 2017 also tested weekly supplemental food applications of *Ephestia* eggs and *Artemia franciscana* cysts to support *M. pygmaeus* in a semi-commercial greenhouse tomato crop. While weekly food applications resulted in larger populations for the predator, it also incurred more fruit damage as densities of predators were high. Thus, while these foods are clearly useful, too frequent applications should be avoided.

Overall, the current application methods for these common supplemental foods are focused on using blowers and food sprayers to quickly deliver the food across the entire crop. For instance, Brenard et al. (2019) used a blower to distribute 0.04 g of *Artemia* and *Ephestia* combined in 5:1 ratio per plant every two weeks, in a full-crop fashion to achieve the best dispersal of predators. *Ephestia* eggs, on the other hand, can be applied locally without a blower, directly to where predators are released to maximize the impact they have on their population growth. However, the future focus should continue to explore the use of other delivery methods as these may represent less wasteful ways for applying foods. For example, *Ephestia* eggs could one day also be applied onto an adherent ribbon that runs between crop plants or onto small adherent cards that can be attached to individual plant stems, providing good local food supplies. This area of research should be a future focus for the biological control industry, with the goal to develop the most effective and economical ways to deliver supplemental foods in commercial settings.

Current Challenges With the Application of Supplemental Foods

Foods That Support Pest Populations

One of the major challenges in the use of supplemental foods is that in some instances, these can also support pest population

growth. This is the case of pests such as the western flower thrips *F. occidentalis* who can also feed on pollen (Hulshof et al. 2003, Messelink et al. 2014a, Vangansbeke et al. 2016b), representing a potential issue when this food is employed as a supplement. This can also inherently be problematic when pollen is naturally abundant on crop plants. Thus, in situations where predators are either absent or at low numbers, the addition of foods to crops can disproportionately benefit pests such as thrips, whose populations may then expand rapidly (Hulshof et al. 2003). Furthermore, even a combination of dry *Artemia* cysts and pollen used to support predators such as *Orius laevis* and *O. majusculus*, can result in overall reduced control of *F. occidentalis* as pollen will promote thrips population increases relative to a diet of *Artemia* cysts alone (Oveja et al. 2016). In contrast to these findings, other studies have shown that when pollen continues to be applied in the presence of thrips, thrips control can still be successful due to better predator population establishment (van Rijn et al. 1999, Leman and Messelink 2015). Ultimately, the outcome of employing pollen depends critically on the timing of applications as well as on the regular monitoring of predator and prey ratios. When pest populations are absent or minimal in size, predator populations can be built up through pollen supplementation, and populations of thrips will be kept in check over a prolonged period of time (Leman and Messelink 2015). However, when pests are detected in the crop, it is recommended that pollen applications cease (Pijnakker et al. 2016a) or are limited to areas where pests are absent.

Despite instances where pollen feeding incurs negative effects on crop protection, it is also apparent that pollen reduces antipredator behaviors in *F. occidentalis*, such as when thrips larvae kill the eggs of phytoseiid predators such as *A. limonicus* (Vangansbeke et al. 2014b). This finding suggests that food supplementation influences interactions at multiple trophic levels, each of which can alter the success of biological control programs. It is also critical to know that not all thrips species respond the same way to pollen supplements. For instance, pollen was not found to support the population growth of poinsettia thrips, *Echinothrips americanus* Morgan (Thysanoptera: Thripidae), so could be used readily for supporting phytoseiid predator populations in its presence (Ghasemzadeh et al. 2017). This finding suggests that further research is needed to identify selectively beneficial foods which could be applied in various biological control scenarios.

Predator Satiation

Another important factor in the application of supplemental foods is predator satiation, whereby a predator is diverted from its target prey or favors the consumption of the supplemental food. For instance, when offered *E. kuehniella* eggs, a predator such as *M. pygmaeus* who is tasked with controlling the aphid *Myzus persicae*, will reduce its consumption of this pest, exhibiting a negative predator satiation effect (De Backer et al. 2015). Since these nutrient-rich eggs represent a preferred alternate food source for such predators, aphid populations can expand rapidly when this supplemental food is offered, compared to when it is absent.

This issue can also be present for many other food types and predator species. For instance when two ladybeetle species: *Hippodamia variegata* (Goeze) and *Coccinella septempunctata* (L.) are offered pollen from canola plants, *Brassica napus* L., they will reduce predation of their target aphid prey *Rhopalosiphum padi* L. (Hemiptera: Aphididae) (Schuldiner-Harpaz and Coll 2017). Despite this, the supplemental food continues to provide a benefit to the survival and oviposition rates of predators (Schuldiner-Harpaz

and Coll 2017). Similar findings were uncovered for green lacewing *Chrysoperla lucasina* (Lacroix), for whom feeding on *Ephesia* eggs reduces the consumption of the suboptimal mealybug target pest *Planococcus citri* Risso (Hemiptera: Pseudococcidae) (Messelink et al. 2016). Overall better control by lacewings can be achieved in the absence of *Ephesia* eggs. Finally, pollen supplementation for phytoseiid predators *Neoseiulus californicus* and *Phytoseiulus persimilis* improved predator survival, but reduced predation of target prey, *T. urticae* (Urbaneja-Bernat and Jacques 2020). Ultimately, the intensity of predator satiation observed may depend greatly on the preference a predator has for the supplemental food relative to its available target pest prey. The overall goal in these instances would be to choose supplemental foods that are beneficial, but not too good or too abundant that they distract the biological control agent from their role in pest suppression.

Spoiling of Supplemental Foods

One would expect that many types of foods dispersed onto crop plants would have a limited amount of time during which they are useful to natural enemies. For instance, considerations must be made when applying pollen to crops, since it is prone to spoiling, fungal infections and clumping, which can decrease its nutritional value or accessibility to predators (Messelink et al. 2014). While foods such as pollen, the eggs of *Ephesia*, and the cysts of *Artemia* are generally sufficiently low in moisture content to immediately deter pathogen colonization and degradation, other food types including sucrose solutions or artificial diets formulated for delivery on a crop, are more vulnerable. However, new technologies such as the encapsulation of sucrose into hydrocapsules (Urbaneja-Bernat et al. 2013), or the microencapsulation of artificially formulated diets (Tan et al. 2015) have the potential to prolong the integrity of such nutrient sources and represent an area where future research and development can make great strides.

Reducing the Cost to Benefit Ratio

Certainly, one of the big challenges to the general implementation of biological control supportive foods remains achieving a suitable benefit for the cost of adopting such a strategy. While there is evidence for the value of supplemental food strategies (Lambert et al. 2005, Payton Miller and Rebek 2018), there are still too few economic analyses conducted to show that these are feasible and in which biological control contexts. Furthermore, field conservation biological control studies focusing on the cost to benefit ratio of applying food sprays, to outdoor crops, simply do not demonstrate this value (Wade et al. 2008). With this said, it is clear that economic models for protected crop production, are distinct from field production as the large investments in augmentative and inundative biological control made to high value greenhouse crops, dwarf those of most field crops. As a consequence, it is quite likely that preserving natural enemies in protected crops ultimately represents a tangible cost saving and an improvement to the sustainability of pest management.

Conclusions and Future Directions

Food supplementation has an important role to play to address some key issues in greenhouse biological control. One area of interest is how it will serve to mitigate challenges including cannibalism and intraguild predation. For instance, when too few food resources are available on crops, many species of generalist predators engage in cannibalism, which directly impacts the population growth of these

natural enemies (Hamdi et al. 2013, Calabuig et al. 2018, Arvaniti et al. 2019, Marcossi et al. 2020). The absence of sufficient foods also increases the risks and intensity of intraguild predation (Shakya et al. 2009, Calabuig et al. 2018). To address this, food provisioning can serve to reduce the incidence of predator feeding on intraguild prey. This has been demonstrated by pollen supplementation which reduced intraguild predation by female phytoseiid mites on immature stages of other predator species (Maleknia et al. 2016). In such instances, there is a clear benefit to providing predators with alternate resources with which to mitigate periods of prey scarcity. These results also suggest that further research is needed to determine what other effects supplemental foods can have on biological control programs.

As a biological control supporting strategy, implementing food supplementation can increase the overall complexity of a pest management program. It requires an investment of time and money and depends on the effective application of knowledge and technique to generate durable pest management. There is also, now more than ever, a need to know how specific predators from around the world will respond to various and new biocontrol supportive strategies. This comes in addition to the need to optimize crop delivery methods for distinct and new food types. Finally, it is critical that future research focus on data collection at spatial and time scales relevant to commercial production. Large greenhouse operations regularly see a multitude of pests and other variables that laboratory or research greenhouse environments do not exhibit. Future research will help to address these voids and provide a well-rounded understanding of how such biological control supportive techniques can be implemented with long-term benefits to growers.

As of today, the knowledge generated from food supplementation research has shown that such additives can have a practical use in commercial crop pest management. The ability to decrease the length of time it takes to establish a predator species onto a crop, combined with increasing the amount of time it remains present, are important factors that improve the success of biological control programs and the likeliness these will be adopted in commercial production. At a time when insecticide resistance remains either a persistent or growing issue for management of greenhouse pests, access to diverse and new strategies, such as food supplementation, can help mitigate pest pressure and improve the long-term success of greenhouse crop protection.

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