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NUTRITIONAL ASPECTS OF NON-PREY FOODS IN THE LIFE HISTORIES OF PREDACEOUS COCCINELLIDAE

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Abstract

Non-prey foods are an integral component of the diets of most predaceous coccinellids. Under field conditions, numerous coccinellids consume nectar, honeydew, pollen, fruit, vegetation, and fungus. These non-prey foods are used by coccinellids to increase survival when prey is scarce, reduce mortality during diapause, fuel migration, and enhance reproductive capacity. Each of these non-prey foods has unique nutritional and defensive characteristics that influence its suitability for lady beetles. Quantitatively, nutrient and energy contents of these foods are often competitive with, or even exceed that, present in prey. Meta-analyses of literature were used to assess whether 1) some non-prey foods and prey are equivalent foods for coccinellids, and 2) prey-only diets and mixed diets involving prey and non-prey foods are equally suitable for coccinellids. Response variables were categorized as larval performance (e.g., development time, weight at eclosion), adult performance (e.g., adult longevity, weight change), and reproduction (e.g., fecundity, oviposition period). The analyses revealed that pollen is inferior to prey for supporting larval and adult performance, but that adult performance in sugar-fed adults was equal to that of prey-fed adults (although sugar alone does not support reproduction). Larval performance was enhanced substantially when they were reared on mixed diets compared to prey-only diets. Adding sugar to mixed diets strongly improved adult performance and reproduction over prey-only diets, but this was not the case with pollen in mixed diets. These results suggest that coccinellid larvae have more stringent nutritional requirements than adults, and that non-prey foods provide unique nutrients that enhance prey-only diets. Moreover, it suggests that simple carbohydrates are important dietary constituents capable of enhancing both adult performance and reproduction, although it is important to note that a range of prey species of variable quality for coccinellids are evaluated in this database. The literature review presented

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here suggests that non-prey foods are a critical component of coccinellid nutritional ecology, and may influence the success of conservation biological control programs.

Keywords: biological control, fungus, lady beetles, mixed diets, meta-analysis, omnivory, pollen, polyphagy, sugar

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Introduction

The traditional approach to defining the trophic placement of an organism is narrowly defined, and often is based on an organism's primary function within a food web (e.g, herbivore, detritivore, predator, etc.). Lady beetles are no exception to this trend, and are often defined as predators (but see Giorgi et al 2009, this issue; Sutherland and Parrella, 2009 this issue). Within the predatory clades, lady beetles are sometimes further partitioned as specialists on aphids, mites, scales, etc. These designations have utility, both in terms of their application to biological control of agronomic pests and when one considers the importance of these prey groups to the life histories of individual lady beetle species. Nevertheless, it is important that the full dietary breadth of an organism be recognized, especially for those species involved in the biological control of pests.

In 1962, Ivo Hodek defined foods of predators as essential and alternative; essential foods support reproduction and development, and alternative foods do not (Hodek and Honěk, 1996). Since this basic distinction was made, it has often been presumed by scientists and biological control practitioners that coccinellids spend their time seeking out their respective essential foods. But nowhere in his initial definition of these terms does Hodek define essential foods as *optimal* foods for maximizing rates of growth, development and reproduction of a predator. This is underscored by the large number of studies that show that different essential foods vary in their suitability for supporting coccinellid fitness (even intraspecifically), and the fact that mixing different prey usually leads to higher fitness in the predator than eating a single prey item alone (Evans, 2009; Hodek and Honěk, 2009). Moreover, combining several alternative foods can ultimately lead to diets that support reproduction and development of a coccinellid species (Evans, 2000).

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Non-prey foods are an important component of most coccinellid diets, and although they receive less attention than prey in the scientific literature, these foods fundamentally shape the life histories of many coccinellid species. Nectar, honeydew, pollen, fruit, vegetation, and fungus are all regularly consumed by coccinellids under field conditions. Given that alternative foods such as these seldom support critical life functions, it is easy to dismiss them as inferior to essential foods in nutrition. An objective review of the literature shows that each of these non-prey foods represents a rich source of nutrients and energy, and a meta-analysis of published studies reveals that non-prey foods are often an integral component of optimal diets for coccinellids.

1. Characteristics of non-prey foods and their function in the life histories of coccinellids.

Although it has long been recognized that natural enemies rely on non-prey foods as part of their diet (Forbes, 1881; 1883), synthesis on the importance of these nutritional resources for natural enemies (including coccinellids) has only come about within the last 22 years. Hagen (1986) was one of the first to comprehensively review the role of plant-based foods in the nutrition of natural enemies. Wäckers (2005) defined several traits that affect the suitability of plant-based foods for natural enemies, including their availability, apparency, accessibility, nutritional composition/suitability, and foraging risks associated with each non-prey food. Most recently, Lundgren (2009) provided a comprehensive discussion on the physiological, morphological, nutritional and environmental factors that mediate the interactions among natural enemies and non-prey foods. Within the context of this review, non-prey foods aid in the survival of coccinellids (particularly when prey is scarce or of poor quality), but also support diapause, dispersal, and reproduction of these important natural enemies.

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1.1 Nectar. Floral and extrafloral nectars differ from each other in their nutrition and defensive properties. These differences are driven in large part by the distinct functions that floral and extrafloral nectars play in the life histories of the plants that produce them (Bentley, 1977). Floral nectar plays a crucial role in attracting (often very specific) pollinators and facilitates outbreeding in plants. As such, it is guarded against floral larceny by non-pollinators (like coccinellids). The function of extrafloral nectar (EFN) is to attract entomophagous natural enemies of herbivores (like coccinellids), essentially acting as an extension of the plant's defense response to herbivory (Heil et al., 2001; Heil, 2004; Choh et al., 2006; Kost and Heil, 2006). EFN is produced when the plant needs defense from herbivores the most, particularly during periods of vegetative growth. Under most circumstances, EFN is available for a much greater duration than flower-bound nectar. For these reasons, a review of the literature reveals that EFN is fed upon by coccinellids more frequently than floral nectar.

1.1.1. Nectar nutrition. At first glance, nectar is simply a source of sugar- it is primarily composed of sucrose, glucose, and fructose (Percival, 1961; Elias and Gelband, 1975; Petanidou et al., 1996; Heil et al., 2000; Wäckers, 2001; Lundgren, 2009). A closer examination reveals that a number of mono- and di-saccharides (as well as some oligo-saccharides) are present in many nectars, but at much lower concentrations than sucrose and its metabolites (Torres and Galetto, 2002; Petanidou, 2005). At least 18 sugars have been found in floral nectars, and 15 from EFN (Lundgren, 2009).

Other nutrients, when they occur, are found in much lower quantities. Amino acids give floral nectar its taste and are important in encouraging pollinator fidelity (Baker and Baker, 1977; Gardener and Gillman, 2002; Petanidou et al., 2006). EFN also frequently possesses amino acids (Hanney and Elmore, 1974; Baker et al., 1978; Smith et al., 1990), perhaps to attract specific beneficials. Lipids are reported (infrequently) in nectars (Keeler, 1977; Baker and Baker, 1983;

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Caldwell and Gerhardt, 1986), as are vitamins (Baker and Baker, 1983; Jakubska et al., 2005). The amount and types of nutrients found in nectar of a particular species depends on many factors, including plant genetics, floral architecture, physiological status of the plant, age of the bloom and previous feeding from them, and environmental conditions including soil (Shuel, 1955; Cruden et al., 1983; Gottsberger et al., 1984;). Usually, sugar concentrations from floral and extrafloral nectars are approximately 20% w/v (Baker, 1975; Guerrant and Fiedler, 1981; Adler, 2000).

1.1.2 Nectar defenses. The defenses that discourage nectar thievery from flowers can be categorized as architectural or chemical in nature. The position of the nectary within the flower has substantial influence on the number of insect species that feed on it. Except for the smallest of species, coccinellids (like other large entomophages; Tooker and Hanks, 2000; Galletto and Bernardello, 2004; Vattala et al., 2006) are largely excluded from floral nectar when it occurs deep within the corolla. Abundant stigmas or styles also inhibit some insects from accessing floral nectars. A wide range of secondary chemicals are found in floral nectar (Baker and Baker, 1978; Adler and Irwin, 2005). These secondary chemicals (which include phenolics, alkaloids, glycosides, saponins, non-protein amino acids, alcohols, and ammonia) deter or intoxicate many insects, play an important part in keeping pollinators that have adapted to feed on them loyal, and generally increase the likelihood of successful pollination of the plant (Adler, 2000; Kessler et al., 2008).

Because its role is to attract whatever beneficial arthropods reside in a given habitat, EFN is largely unprotected from nectar-feeding insects. Even so, a few secondary chemicals have been isolated from EFN (Keeler, 1977; Baker and Baker, 1978), but their role is not well understood.

1.1.3 Coccinellids that feed on nectar. Most entomophagous arthropods will feed on sugar if given the chance, and coccinellids are no exceptions. Few observations of flower-visiting

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coccinellids have irrefutably substantiated nectarivory (Bugg, 1987; Nalepa et al., 1992; Spellman et al., 2006). In contrast, coccinellids are often some of the most frequent visitors to extrafloral nectaries (EFNs) under field conditions (Putman, 1955; Banks, 1957; Putman, 1963; Keeler, 1978; Stephenson, 1982; Ricci et al., 2005). This is particularly so during the spring in temperate regions, when EFNs are most abundant on developing vegetation (Ewing, 1913; Watson and Thompson, 1933; Rockwood, 1952), and coccinellids frequently find themselves prey-limited. Pemberton and Vandenberg (1993) present a list of 41 coccinellid species found feeding at the EFNs of dozens of plant species from 15 families. Little has been added to this extensive review of EFN-coccinellid interactions during the past 16 years, except to further substantiate the place of coccinellids as some of the more frequent visitors to EFNs.

The sugars found in nectars are an easily digestible and high energy food, and can dramatically increase survival of coccinellids in the absence of prey (Geyer, 1947; Ibrahim, 1955; Matsuka et al., 1982; Dreyer et al., 1997). It is worth mentioning that not all mono- and oligosaccharides are equally suitable for coccinellids; clear preferences were displayed by *Harmonia axyridis* Pallas larvae for simple carbohydrates (n = 13 sugars tested) under choice conditions (Niijima et al., 1997). Sugar-feeding also supports the flight capacity of coccinellids (Nedved et al., 2001). Finally, although sugar-feeding seldom supports reproduction in coccinellids on its own, sugar consumption can shorten pre-oviposition periods of coccinellids (Smith and Krischik, 1999), and help females to survive reproductive diapause (Hagen, 1962; Reznik and Vaghina, 2006). In the latter case, reductions in prey density initiate a physiological shift in some coccinellids; essentially a trophically induced reproductive diapause. Nutritional resources are shifted from reproduction to fat storage, and sugar resources can help to increase survival and reduce the resorption of eggs during these periods of reproductive diapause (Reznik and Vaghina, 2006).

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1.2 Honeydew. Honeydew is a sugary exudate originating from phloem- and xylem-feeding hemipterans (and some lepidopterans), and it differs from nectars in subtle but important ways. Although honeydew production likely began simply as a sugary excretory product that necessarily accompanies the consumption of nutritionally simple plant sap, it also is a clear indicator to predators of the prey insects that produce it. The valuable sugar secreted by sternorrhynchans has since fueled mutualistic associations with ants, which deter predators such as coccinellids from attacking herbivores (Majerus et al., 2007). These complex interactions notwithstanding, honeydew is ubiquitous in most terrestrial habitats (Way, 1963; Downes and Dahlem, 1987), and is a valuable food source that is consumed by numerous coccinellid species.

1.2.1. Honeydew nutrition. Like the original ingested phloem contents, excreted honeydew is primarily comprised of sugars, especially glucose, fructose, and sucrose (Ewart and Metcalf, 1956; Mittler, 1958; Lamb, 1959). Unlike many nectars, honeydew also has a large complement of trisaccharides (some of which are found in few other places in nature), that are produced within the herbivore (Ashford et al., 2000). These trisaccharides have several roles that will be discussed below (section 1.2.2). In addition to sugars, honeydews possess a wide range of amino acids that often match the original phloem contents in quality if not in quantity; usually less than 2% of the dry weight of honeydew is amino acids (Ewart and Metcalf, 1956; DeVries and Baker, 1989; Yao and Akimoto, 2002; Woodring et al., 2006). Some sterols and vitamins are also found in honeydews at low concentrations (Gray, 1952; Lamb, 1959).

1.2.2. Honeydew defenses. Honeydew contains a number of chemicals that may help to protect the herbivore from foraging coccinellids. First, the trisaccharides created by the insect to offset the osmotic differential between hemipteran haemocoel and the copious amount of fluid ingested (Costa et al., 1999; Woodring et al., 2006) may have a dual function of making

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honeydew less palatable to natural enemies. In part, this may be nutritional; some sugars are indigestible or undetectable by natural enemies (Niijima et al., 1997; Wäckers, 2000; 2001; Williams et al., 2005). But trisaccharides also make honeydew evaporate more quickly, thereby reducing the number of natural enemies that can partake of the dry, sugary residue. Other defensive properties of honeydew can come from the host plant itself. Some of the defensive secondary chemicals found in plants are found in the honeydew of sternorrhynchans, and can in some instances make the area surrounding hemipteran colonies (where honeydew accumulates) repulsive to natural enemies (Molyneux et al., 1990; Bristow, 1991).

1.2.3. Coccinellids that feed on honeydew. In spite of the ants and aversive chemicals that guard it, honeydew is frequently encountered and of high energy value; thus it is not surprising that many coccinellids consume it as part of their diet (Simanton, 1916; Tedders and Schaefer, 1994). This sugar source can extend the lives of beetles in the absence of prey (Putman, 1955; Yinon, 1969). Also, when only poor quality prey are available, consumption of honeydew along with it can support modest reproduction in some coccinellids; e.g., *Coccinella transversalis* Fabricius (Evans, 2000).

In addition to being a source of nutrition, honeydew also arrests and intensifies the foraging of coccinellid adults and larvae (Banks, 1957; Carter and Dixon, 1984; van den Meiracker et al., 1990; Han and Chen, 2002; Seagraves, 2009, this issue). The presence of honeydew is a clear indication of a local population of prey, and coccinellids that encounter patches of honeydew turn more often, and forage more intensively in the hopes of encountering the honeydew-producing prey. This shift in foraging results in aggregations of coccinellids within hemipteran-infested areas of plants, and can lead to suppression of pests.

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1.3. Pollen. One of the most nutritious of non-prey foods consumed by coccinellids is pollen. This is one of the reasons that this non-prey food has been studied more extensively than any other as a dietary component for coccinellid beetles. Given the restrictions of flower-bound resources (described above in section 1.1.2), anemophilous pollen species are likely a more widely dispersed and apparent food source for lady beetles than zoophilous pollens. During peak anthesis within a given habitat, pollen grains are a significant food source for numerous insects (Cottrell and Yeargan, 1998; Hoheisel and Fleischer, 2007; Lundgren, 2009). Coccinellids are just one of the many organisms that recognize this abundant resource as food, and respond behaviorally to its availability within a habitat.

1.3.1 Pollen nutrition. Pollen is an excellent source of essential nutrients for insects (Stanley and Linskins, 1974). Fructose, glucose, and sucrose (among other simple sugars) are present within most pollens (Roulston and Buchmann, 2000). Starches are the most important storage carbohydrates, generally comprising less than 2.5% of pollen dry weight (Baker and Baker, 1979; 1982; Roulston and Buchmann, 2000). Protein is one of the most abundant nutrients in pollen, typically comprising 12-61% of dry weight (Roulston et al., 2000). All essential amino acids for insect growth are present, and of these proline is typically one of the most abundant (Erhardt and Baker, 1990; Lundgren and Wiedenmann, 2004; Carter et al., 2006). Lipids are also common to most pollens, comprising up to 19% of dry weight (Standifer, 1967; Barbier, 1970). While sterols are present in most pollens (Standifer et al., 1968), these precursors to insect hormones are a limiting nutrient for the development of pollen-fed lady beetles (Lundgren, unpublished data). A wide range of vitamins and inorganic minerals are also prevalent in many pollens (Stanley and Linskins, 1974). Pollen is practically devoid of water, and although this raises its per-unit nutrient value, coccinellids reared solely on pollen invariably require a supplemental source of water (De Clercq et al., 2005; Michaud and Grant, 2005). Finally, pollens

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vary in their nutrition both intraspecifically and among species (Lundgren and Wiedenmann, 2004; Lundgren, 2009), and as such the nutritional value of pollen for a coccinellid species can change substantially among testing systems.

1.3.2. Pollen defenses. In addition to the floral defenses discussed in Section 1.1.2., pollen has a range of physiological defensives that protect it from pollinivory. Structurally, the rigid pollen exine must be dismantled, either mechanically or chemically, before the internal nutrients of the grain can be accessed (Roulston and Cane, 2000). Also, numerous textures and appendages (hooks, spines, barbs, etc.) to the exine can inhibit pollinivory by lady beetles. As a case in point, *Coleomegilla maculata* DeGeer adults and larvae were killed when enclosed with the hooked grains of *Helianthus annuus* L. under laboratory conditions (Michaud and Grant, 2005).

Pollen can be chemically defended either through deficiency in key nutrients for insects, and/or with defensive secondary compounds. Anti-nutritive qualities of pollen are speculated based on the observation that anemophilous pollen (which does not benefit from insect dispersal) has a different nutritional composition than that of animal-pollinated plants (Baker and Baker, 1979). A comprehensive review of the literature reveals that many anemophilous plants have starchier pollens than zoophilous pollens (and thus have lower energy content), but it remains unclear whether this is a case of convergent evolution (Roulston and Buchmann, 2000; Roulston et al., 2000). Many pollens are conspicuously toxic to insects (Lundgren, 2009). Although toxic agents within pollens are seldom identified, alkaloids and galitoxins are reported in some pollens (Stanley and Linskins, 1974).

1.3.3. Coccinellids that consume pollen. In sum, at least 39 species of entomophagous coccinellids have been recorded as consuming more than 88 species of pollen under laboratory and field conditions (Lundgren, 2009). Pollen is believed to be most important as food when prey is scarce or of low quality, as is evident in the significant number of instances of spring and fall

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pollinivory, when prey is scarce in most temperate habitats (Conrad, 1959; Solbreck, 1974; Benton and Crump, 1981; Anderson, 1982; Hemptinne and Desprets, 1986; Triltsch, 1997; 1999). Consistent with this pattern, regions that experience a mid-summer dearth of prey experiences a concomitant increase in mid-summer pollinivory by coccinellids (Ewing, 1913; Hagen, 1962; Ricci et al., 2005; Michaud and Qureshi, 2006).

It should not be assumed that just because pollen is sought most intensively when prey is scarce that this non-prey food does not fulfill a vital role in the diet of coccinellids. At least several species can complete development on a diet of pollen alone, although the resulting adults may have lower fitness than those fed prey-based diets (Hukusima and Itoh, 1976; Smith, 1961; Berkvens et al., 2008). Others use pollen resources to fuel migrations (Solbreck, 1974) and survive dormancy (Anderson, 1981; Triltsch, 1999). Moreover, pollen is important in spermatogenesis (Hemptinne and Naisse, 1987) and, particularly when mixed with prey, may help to promote reproduction in some species (Hemptinne and Desprets, 1986; Michaud, 2000; De Clercq et al., 2005; Omkar, 2006; Berkvens et al., 2008).

Without question, pollinivory has been best studied for the highly omnivorous New World coccinellid, *Coleomegilla maculata*. The first description of pollen-feeding in this species was by Stephen Forbes in 1881, who substantiated pollinivory under field conditions using microscopic gut content analysis. This coccinellid can complete its development on a range of pollen species (Smith, 1961; Smith, 1965; Hodek et al., 1978; Hazzard and Ferro, 1991; Riddick and Barbosa, 1998; Michaud and Grant, 2005; Michaud and Jyoti, 2008;). Under field conditions, *C. maculata* frequently consumes pollen (Forbes, 1881; 1883; Conrad, 1959; Putman, 1964; Solbreck, 1974; Benton and Crump, 1981; Lundgren et al., 2004), and lays more eggs in cropland during anthesis (Smith, 1971; Cottrell and Yeargan, 1998; Lundgren et al., 2004). Females consume 10 times more corn pollen than males under field conditions (Lundgren et al., 2005),

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and this is one of the few coccinellid species that can reproduce on a diet consisting solely of pollen (Lundgren and Wiedenmann, 2004). Clearly, pollinivory has contributed to the widespread abundance of this lady beetle across many habitats and geographic areas.

1.4 Other Non-prey Foods. A number of other non-prey foods are consumed by entomophagous coccinellids, but the importance of these foods to their diet is poorly understood. These foods include fruit, foliage, and fungus. Also, several gut dissections of field-collected lady beetles reveal that coccinellids frequently consume inorganic materials that are noteworthy (Putman, 1964; Anderson, 1982; Triltsch, 1999), but their role in the nutritional ecology of coccinellids is entirely unknown.

1.4.1 Fruit. Fruits are an especially good source of simple carbohydrates, and as such it is not uncommon to find lady beetles feeding at damaged fruit under field situations (Hodek and Honěk, 1996). Within the laboratory, providing fruits can improve the longevities of some coccinellids. For instance, raisins (accompanied by peach EFN) can help improve survival of *Stethorus punctillum* (Weise) in the laboratory (Putman, 1955), and *Anatis ocellata* (L.) consumed bananas as part of their laboratory diet (Kesten, 1969). The only empirical examination of fruit as food for coccinellids involves *Harmonia axyridis*, which is a secondary pest of several fruit crops in North America. This coccinellid frequently aggregates to fruit crops during the fall, where it damages grapes, apples, peaches, plums, pears, pumpkins and raspberries (Kovach, 2004; Koch and Galvan, 2008). The wine industry is particularly concerned by this insect, since pungent alkylmethoxypyrazines from even a single beetle can taint the flavor of wine (Kovach, 2004; Koch and Galvan, 2008). Fruit feeding by *H. axyridis* significantly improves their overwintering survival over unfed individuals (Galvan et al., 2009).

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1.4.2 Foliage. Recent research shows (see also the report by Brassler, 1930) that coccinellids feed on plant foliage more often than previously believed, and thus are directly exposed to systemic insecticides and the insecticides produced by insect-tolerant GM crops. Moser et al. (2008) found that larvae (especially 4th instars) of *Coleomegilla maculata* and *Harmonia axyridis* fed on corn leaf tissue, even in the presence of water and aphids. Another laboratory assay found that *Harmonia axyridis* larvae (especially 1st and 4th instars) were adversely affected by soybean foliage possessing a soybean aphid (*Aphis glycines* Matsumura) resistance factor (the *Rag1* gene) (Lundgren et al., 2009). In this study, host plant resistance-induced reductions in prey quality were not an influence on the experimental results, since lepidopteran eggs that had not ingested plant material were used as the prey item. These results suggest that there was a direct (and likely nutritional) effect of the soybean plant on the coccinellid.

1.4.3 Fungus. Fungus is a highly nutritious food source that is consumed by numerous entomophagous coccinellids (and fungal specialists; see Sutherland and Parrella, 2009). The most abundant constituent in most fungal tissues is water (85% by weight) (Chang and Miles, 2004). Spores are an exception to this trend, and typically contain minimal water. Although carbohydrates can comprise a substantial amount of the dry weight of fungus, most of this carbohydrate is in the form of structural polysaccharides (Mueller et al., 2001; Chang and Miles, 2004). Proteins are one of the most abundant constituents of fungal tissue, and fungi possess all of the amino acids essential to insect growth and development (Mueller et al., 2001; Chang and Miles, 2004). Lipids are often less abundant than carbohydrates and proteins, usually representing less than 10% of dry fungal weight (Harwood and Russell, 1984). Most of the sterols present in fungus are ergosterol, a C28 sterol that is usable by many insects. Vitamins and

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inorganic compounds are often quite abundant in fungi relative to other non-prey foods (Chang and Miles, 2004).

A range of entomophagous coccinellids consume fungal spores as an integral part of their diet, and many believe that mycophagy may have been associated with the early evolution of aphidophagy (lady beetles first consumed the sooty molds on honeydew before consuming the honeydew producing sternorrhynchans; Sutherland and Parrella, 2009). Spores of at least 17 genera of fungus have been reported from the guts of coccinellids (Lundgren, 2009). Indeed, gut content analysis reveals that fungal spores are fed upon more frequently than prey by *Coccinella septempunctata* L., especially during the spring and fall (Triltsch, 1999). Another coccinellid, *Hippodamia convergens* Guérin-Méneville, consumes the spores of the plant pathogen, *Discula destructiva* Redlin, and is an important agent of its dispersal (Hed et al., 1999). Other species also use fungus to help build reserves before entering overwintering (Anderson, 1982; Ricci et al., 1983; Ricci et al., 2005).

2. Nutritional suitability of non-prey foods for coccinellids.

Lundgren (2009) statistically compared the nutritional contents (carbohydrates, protein, lipids, and calories) of hundreds of species of floral nectar, pollen, fungus, and arthropod prey. Pollen is quantitatively superior to prey in terms of energy (calories), protein, and carbohydrates, and is statistically similar to prey in lipid content. Floral nectar is deficient in lipids, proteins, and energy compared with prey, but has nearly three times the carbohydrate content. Fungus is statistically similar to prey in carbohydrate content, but is substantially lower in energy, protein, and lipid contents. Given the high nutritional content of some non-prey foods, it might be expected that coccinellids reared on non-prey foods such as pollen should have similar or superior fitness compared to those reared on prey. But considerable variability in the methods

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used to explore these questions experimentally, species-specific responses of coccinellids to prey and non-prey foods, and the nutritional properties of the non-prey foods themselves have challenged our ability to characterize trends in the nutritional suitability of non-prey foods for coccinellids.

Meta-analysis quantitatively and objectively examines cross-study trends in the literature to identify relationships that may be obscured or entirely overlooked by traditional literature reviews that either selectively report illustrative results of individual studies, or that use vote-counting approaches (presenting the proportion of studies that report a phenomenon) to characterize an ecological process (Bigger and Marvier, 1998; Osenberg et al., 1999; Rosenberg et al., 2000; Wolfenbarger et al., 2008). Here, meta-analysis was used to specifically address two questions:

1) Are prey or non-prey foods more suitable for coccinellids?

2) Are prey-only diets and mixed diets containing prey and non-prey foods equally suitable for coccinellids?

Two databases were created from the published literature to address these questions. The first compiled a series of 46 experimental comparisons from 14 published studies that made direct comparisons of a coccinellid species fed prey or non-prey diets (Table 1). Ten coccinellid species and 11 prey species (Hemiptera: Sternorrhyncha [n = 18 studies], Lepidoptera: Phycitidae and Noctuidae [13], Coleoptera: Chrysomelidae & Curculionidae [8], Hymenoptera: Apidae [6]), were examined in this first database. The second database compiles 52 experimental comparisons from 16 published studies comparing prey-only to mixed diets on coccinellid performance and fitness (Table 2). The second database includes 10 coccinellid species and nine prey species (Lepidoptera: Phycitidae and Noctuidae [n = 27 studies], Hemiptera: Sternorrhyncha [13], Coleoptera: Curculionidae [10], Hymenoptera: Apidae [2]).

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The numerous life history parameters measured in these studies were categorized as larval performance, adult performance, and reproduction. Some studies measured several aspects of these categories within a single experiment. To avoid non-independence within the database, only a single measurement was selected for each study for each category. For larval performance, larval developmental rate was prioritized over weight at eclosion. For adult performance, adult longevity was prioritized over adult weight change. For reproduction, lifetime fecundity was compared preferentially over ovipositional or pre-ovipositional period. For the comparison of prey and non-prey diets, there are few reports where coccinellids are able to lay eggs on non-prey foods without prey (Hodek et al., 1978; Lundgren and Wiedenmann, 2004; Omkar, 2006; Berkvens et al., 2008), and the effects of prey versus non-prey foods on reproduction were not analyzed for this comparison. In studies that evaluated the effects of Bt and non-Bt pollen on coccinellids, the non-Bt hybrid was preferentially selected for analysis.

The meta-analyses used Hedges' *d* as its effect size estimator (Hedges and Olkin, 1985), with relative effect sizes assigned to each study based on the sample sizes, means and standard deviations of the two treatments compared. Contrasts between treatments were conducted such that a positive effect size represents a beneficial effect of the mixed diet over the prey-only control diet. Comparisons were made using MetaWin 2.1, and mean ± non-parametric bias-corrected bootstrap confidence intervals (representing 95% confidence limits) were calculated for each life history parameter (Rosenberg et al., 2000). If the error intervals encompassed zero, the effect size was not considered to be significant. Small, medium, and large effect sizes were considered to be approximately 0.2, 0.4, and 0.6, respectively (Cohen, 1988). First, comparisons were made between prey-only diets and those involving non-prey foods as a whole. Then, the data was partitioned to determine whether pollen and sugar affected fitness of coccinellids similarly.

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2.1. The relative suitability of prey and non-prey foods. Non-prey foods are clearly and substantially less suitable than prey for coccinellid larval and adult performance (Fig. 1). Indeed, sugar-fed larvae seldom complete development through the second stadium, and so only pollen-fed larvae were included in the analysis on larval performance (Figs 1 & 2). What was surprising is that the longevity or weight change of sugar-fed coccinellids did not differ significantly from prey-fed beetles (Fig. 2). However, it should be noted that sugar is a poor food source for reproduction, and that many of the prey items tested in the literature are considered alternative foods. Although it has a greater breadth of nutrients, pollen was less effective in supporting adult performance than was prey. Two non-exclusive possible explanations for these trends are that 1) pollen is limiting in unidentified nutrients critical to lady beetle performance, and that 2) pollen defenses or the types of nutrients in pollen render it unsuitable for lady beetles in the absence of prey.

2.2. Non-prey foods as components of mixed diets. There is a strong and positive effect of mixing prey-only diets with pollen on larval performance (Figs. 3 & 4). This suggests that pollen contains certain nutrients that are not present in the wide breadth of prey evaluated in published studies, and that the nutrition in pollen helps to improve some normally “essential” foods. Another trend in the literature is that mixing prey-only diets with non-prey foods does not uniformly change the fitness and performance of adult coccinellids (Fig. 3). However, the relative effects of pollen and sugar on this life stage at least partially explain the heterogeneity present in the database.

When additions of pollen and sugar to prey-only diets were analyzed separately, it was clear that coccinellids are affected very differently by these two non-prey foods. Adult performance and reproduction were strongly and positively affected when sugar was added to

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prey-only diets (Figure 4). It should be added that the prey used in nearly all of these comparisons was not sternorrhynchan, although it was not necessarily of uniformly poor quality (Table 2). The benefits of sugar in the diet may have stemmed from its nutrition or from possible phagostimulatory effects that spurred consumption of the prey. In contrast, adult performance and reproduction was not significantly affected by the addition of pollen to prey-only diets. There was substantial heterogeneity in each of the datasets presented in Figures 1-4 except for the effects of sugar on reproduction.

3. Conclusions

Most, if not all, coccinellids rely on non-prey foods as part of their life history. Under field conditions, even the most stereotypical entomophagous coccinellids consume sugar, pollen, fungus, fruit and vegetation, often as an integral part of their diets. Non-prey foods serve as fuels for migration, support survival in the absence of prey, improve reproductive capacity, and increase survival through quiescent and overwintering periods. The importance of non-prey foods to coccinellids provides opportunities for pest managers to manipulate the abundance of and ecological services provided by coccinellids as biological control agents. For example, use of sugar sprays or habitat management to increase vegetational diversity often accompanies increases in biological control of key pests by coccinellid predators (Wade et al., 2008; Evans, 2009; Lundgren, 2009).

Meta-analyses of published literature on the suitability of non-prey foods suggest that coccinellid larvae have more stringent nutritional requirements than adults. Larvae perform poorly on non-prey foods alone, and while prey alone support successful development, mixing prey and non-prey foods leads to faster development and greater weight gain in coccinellid larvae than when they are reared on prey alone. Pollen is in some ways nutritionally superior to insect prey, and entomologists are only beginning to understand what nutrients and phytochemicals limit pollen's suitability as a sole food source, while enhancing the suitability of diets mixed with prey.

Carbohydrates are clearly an important dietary component for adult coccinellids. Sugar alone permits survival and reduces weight loss in adult coccinellids, and adding sugar to prey-only diets improves adult performance and increases reproduction substantially. Surprisingly, pollen has a very different effect on adult coccinellids, and generally reduces adult performance compared to prey-only diets when offered individually or in mixed diets. Pollen as a component of mixed diets has no effect on reproduction over prey-only diets. There was substantial heterogeneity in the effects on all tested interactions (except in the effects of sugar in mixed diets on coccinellid reproduction; Fig. 4), suggesting that not all coccinellids behave similarly to non-prey foods and that prey suitability differs widely among studies. Nevertheless, the significant and often dramatic positive effects of non-prey foods on these three life history parameters clearly show that prey and non-prey foods are both parts of an optimal diet for many coccinellid larvae.

Finally, the clear importance of "alternative" foods to the optimal diets of coccinellids makes it important not to misinterpret the definitions of alternative and essential foods. While "essential" foods enable reproduction and development, these foods are not necessarily optimal for achieving maximum reproduction and developmental rates. The meta-analysis shows that the suitability of essential foods is usually improved when they are mixed with other foods. The predictability and reliability of biological control programs will be enhanced when we understand the nutritional constraints faced by omnivorous biological control agents like coccinellids, such that resources integral to their survival and success are available within cropland.

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Table 1. Database included in the meta-analysis comparing prey-only controls with non-prey diets (sugar and pollen) on two life-history categories of coccinellids. Effect size (Hedges' *d*) and Var(*d*) were calculated from means, standard deviations, and sample sizes published in the reference, or from direct communications with the author. A negative effect size indicates that the non-prey diet was inferior to the prey diet.

Coccinellid species	Prey species	Non-prey food	Parameter measured	Effect size (Hedges' *d*)	Var (*d*)	Reference
			Larval performance			
Adalia bipunctata (L.)	*Ephestia kuehniella* Zeller	Bee pollen mixture	Development period (d)	-8.8804	1.4088	(De Clercq et al., 2005)
Adalia bipunctata	*Acyrthosiphon pisum* (Harris)	Rosaceae pollen	Development period (d)	-8.1803	3.4346	(Hemptinne and Desprets, 1986)
Coleomegilla maculata (Pollen 2)	*Rhopalosiphum maidis* (Fitch)	Corn pollen	Development period (d)	-1.6914	0.1165	(Lundgren and Wiedenmann, 2004)
Coleomegilla maculata (Pollen 3)	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	-1.8491	0.1225	(Lundgren and Wiedenmann, 2004)
Coleomegilla maculata (Pollen 4)	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	-1.6506	0.113	(Lundgren and Wiedenmann, 2004)
Coleomegilla maculata	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	-3.5384	0.855	(Smith, 1965)
Coleomegilla maculata	*Myzus persicae* (Sulzer)	Corn pollen	Development period (d)	-1.2977	0.1729	(Hazzard and Ferro, 1991)
Coleomegilla maculata	*Leptinotarsa decemlineata* (Say)	Corn pollen	Development period (d)	2.3316	0.2711	(Hazzard and Ferro, 1991)
Coleomegilla maculata	*Schizaphis graminum* (Rondani)	Bee pollen	Development period (d)	-9.4452	0.4192	(Michaud and Jyoti, 2008)
Coleomegilla maculata	*Ephestia kuehniella*	Bee pollen	Development period (d)	-8.3675	0.3485	(Michaud and Jyoti, 2008)
Harmonia axyridis (laboratory females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-4.832	0.3148	(Berkvens et al., 2008)
Harmonia axyridis (red females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-5.3429	0.4343	(Berkvens et al., 2008)
Harmonia axyridis (black females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-3.7606	0.2484	(Berkvens et al., 2008)
Harmonia axyridis (laboratory males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-5.2423	0.5326	(Berkvens et al., 2008)
Harmonia axyridis (red males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-8.3538	1.3322	(Berkvens et al., 2008)
Harmonia axyridis (black males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-6.2844	0.7042	(Berkvens et al., 2008)
Harmonia axyridis	*Myzus persicae*	Corn pollen	Development period (d)	-9.4045	5.0473	(Hukusima and Itoh, 1976)

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Harmonia axyridis	*Myzus persicae*	Corn pollen + honey	Development period (d)	-5.1101	1.0041	(Hukusima and Itoh, 1976)
Harmonia axyridis	*Apis mellifera* L.	Corn pollen	Development period (d)	-5.5991	1.3838	(Hukusima and Itoh, 1976)
Harmonia axyridis	*Apis mellifera*	Corn pollen + honey	Development period (d)	-3.6083	0.4203	(Hukusima and Itoh, 1976)
Micraspis discolor (Fabricius)	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	-0.9644	0.2232	(Omkar, 2006)
Micraspis lineata (Thunberg)	*Aphis gossypii* Glover F1	Bee pollen	Development period (d)	1.1139	0.165	(Anderson and Hales, 1983)
Micraspis lineata	*Aphis gossypii* F2	Bee pollen	Development period (d)	-3.1769	0.3489	(Anderson and Hales, 1983)
Micraspis lineata	*Acyrthosiphon pisum*	Bee pollen	Development period (d)	1.7889	0.2692	(Anderson and Hales, 1983)
Micraspis lineata	*Apis mellifera*	Bee pollen	Development period (d)	-0.1615	0.1433	(Anderson and Hales, 1983)
Propylea japonica (Thunberg)	*Myzus persicae*	Rye pollen	Development period (d)	-5.3752	1.2546	(Hukusima and Itoh, 1976)
Propylea japonica	*Myzus persicae*	Corn pollen + honey	Development period (d)	-4.5555	0.7569	(Hukusima and Itoh, 1976)
Propylea japonica	*Apis mellifera*	Rye pollen	Development period (d)	-4.2874	0.9454	(Hukusima and Itoh, 1976)
Propylea japonica	*Apis mellifera*	Corn pollen + honey	Development period (d)	-4.2135	0.6819	(Hukusima and Itoh, 1976)
Adult performance						
Adalia bipunctata (Exp. III)	*Ephestia kuehniella*	Bee pollen mixture	Weight gain (mg)	-4.3077	0.5474	(De Clercq et al., 2005)
Coccinella septempunctata (Exp. IV, females)	*Hypera postica* Gyllenhall	Sugar	Weight change (mg)	-0.3539	0.1354	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. IV, males)	*Hypera postica*	Sugar	Weight change (mg)	-0.9602	0.1394	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. VI, females)	*Hypera postica*	Sugar	Weight change (mg)	-0.1727	0.1673	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. VI, males)	*Hypera postica*	Sugar	Weight change (mg)	-1.2574	0.2994	(Richards and Evans, 1998)
Coccinella transversalis	*Myzus persicae*	Sugar	Weight change (mg)	-2.1611	0.5279	(Evans, 2000)
Coccinella transversalis	*Helicoverpa armigera* (Hübner)	Sugar	Weight change (mg)	0.2004	0.335	(Evans, 2000)
Coccinella transversoguttata Falderman (Exp. IV, females)	*Hypera postica*	Sugar	Weight change (mg)	-1.4877	0.2574	(Richards and Evans, 1998)
Coccinella transversoguttata (Exp. IV, males)	*Hypera postica*	Sugar	Weight change (mg)	-2.1065	0.2966	(Richards and Evans, 1998)

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Harmonia axyridis (laboratory population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-1.3202	0.107	(Berkvens et al., 2008)
Harmonia axyridis (red population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-0.6189	0.1117	(Berkvens et al., 2008)
Harmonia axyridis (black population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-1.8719	0.141	(Berkvens et al., 2008)
Harmonia axyridis	*Hypera postica*	Sugar	Weight change (mg)	-2.0175	0.3772	(Evans and Gunther, 2005)
Harmonia axyridis	*Acyrthosiphon pisum*	Sugar	Weight change (mg)	-5.157	1.0811	(Evans and Gunther, 2005)
Rodolia cardinalis (Mulsant)	*Icerya purchasi* Maskell	Sucrose	Longevity (d)	0.5884	0.1043	(Matsuka et al., 1982)
Rodolia cardinalis	*Apis mellifera*	Sucrose	Longevity (d)	2.703	0.1913	(Matsuka et al., 1982)

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Table 2. Database included in the meta-analysis comparing prey-only controls with mixed diets (prey + non-prey foods) on three life-history categories of coccinellids. Effect size (Hedges' *d*) and Var(*d*) were calculated from means, standard deviations, and sample sizes published in the reference, or from direct communications with the author. A negative effect size indicates that the mixed diet was inferior to the prey-only diet.

Coccinellid species	Prey species	Non-prey food	Parameter measured	Effect size (Hedges' *d*)	Var (*d*)	Reference
			Larval performance			
Adalia bipunctata Exp III	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	1.0121	0.0728	(De Clercq et al., 2005)
Adalia bipunctata Exp II	*Ephestia kuehniella*	Dry bee pollen mixture	Development period (d)	0	0.0774	(De Clercq et al., 2005)
Adalia bipunctata Exp II	*Ephestia kuehniella*	Frozen bee pollen mixture	Development period (d)	-0.305	0.0728	(De Clercq et al., 2005)
Adalia bipunctata	*Acyrthosiphon pisum*	Rosaceae pollen	Development period (d)	1.219	0.3174	(Hemptinne and Desprets, 1986)
Coleomegilla maculata	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	3.9205	0.2921	(Smith, 1965)
Coleomegilla maculata	*Rhopalosiphum maidis*	Corn pollen	Development period (d)	1.1096	0.2308	(Omkar, 2006)
Coleomegilla maculata	*Myzus persicae*	Rice pollen	Development period (d)	-1.1645	0.0557	(Bai et al., 2005)
Harmonia axyridis (laboratory females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	1.4913	0.0787	(Berkvens et al., 2008)
Harmonia axyridis (red females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	0.0202	0.067	(Berkvens et al., 2008)
Harmonia axyridis (black females)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	3.1458	0.1494	(Berkvens et al., 2008)
Harmonia axyridis (laboratory males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	1.1658	0.0936	(Berkvens et al., 2008)
Harmonia axyridis (red males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	-0.4368	0.0897	(Berkvens et al., 2008)
Harmonia axyridis (black males)	*Ephestia kuehniella*	Bee pollen mixture	Development period (d)	2.8001	0.1553	(Berkvens et al., 2008)
Harmonia axyridis	*Apis mellifera*	Brewer's yeast (50% of diet) + sucrose	Development period (d)	1.274	0.1203	(Niijima et al., 1997)
Micraspis discolor	*Acyrthosiphon pisum*	Corn pollen	Development period (d)	1.7389	0.0919	(Pilcher et al., 1997)
Propylea japonica	*Schizaphis graminum*	Corn pollen	Development period (d)	1.2066	0.0249	(Ahmad et al., 2006)
			Adult performance			
Adalia bipunctata	*Ephestia*	Bee pollen	Weight gain	3.2151	0.2292	(De Clercq et al.,

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(Exp III)	*kuehniella*	mixture	(mg)			2005)
Adalia bipunctata (Exp II)	*Ephestia kuehniella*	Dry bee pollen mixture	Weight gain (mg)	0.3509	0.0655	(De Clercq et al., 2005)
Adalia bipunctata (Exp II)	*Ephestia kuehniella*	Frozen bee pollen mixture	Weight gain (mg)	0.213	0.0778	(De Clercq et al., 2005)
Coccinella septempunctata (Exp. IV, females)	*Hypera postica*	Sucrose	Weight change (mg)	0.9217	0.1429	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. IV, males)	*Hypera postica*	Sucrose	Weight change (mg)	0.1614	0.1217	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. VI, females)	*Hypera postica*	Sucrose	Weight change (mg)	1.1311	0.2403	(Richards and Evans, 1998)
Coccinella septempunctata (Exp. VI, males)	*Hypera postica*	Sucrose	Weight change (mg)	0.2051	0.217	(Richards and Evans, 1998)
Coccinella transversalis	*Helicoverpa armigera*	Sucrose	Weight change (mg)	0.044	0.3334	(Evans, 2000)
Coccinella transversalis	*Helicoverpa armigera*	Aphid honeydew	Weight change (mg)	0.3842	0.3395	(Evans, 2000)
Coccinella transversoguttata (females)	*Hypera postica*	Sucrose	Weight change (mg)	-0.0426	0.2223	(Richards and Evans, 1998)
Coccinella transversoguttata (males)	*Hypera postica*	Sucrose	Weight change (mg)	-0.3561	0.2032	(Richards and Evans, 1998)
Coleomegilla maculata	*Schizaphis graminum*	Corn pollen	Longevity (d)	-0.182	0.0283	(Ahmad et al., 2006)
Harmonia axyridis (laboratory population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-1.0745	0.0776	(Berkvens et al., 2008)
Harmonia axyridis (red population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-0.362	0.0713	(Berkvens et al., 2008)
Harmonia axyridis (black population)	*Ephestia kuehniella*	Bee pollen mixture	Longevity (d)	-0.5994	0.0733	(Berkvens et al., 2008)
Harmonia axyridis	*Hypera postica*	Sucrose	Weight change (mg)	-0.9146	0.2761	(Evans and Gunther, 2005)
Hippodamia convergens	*Schizaphis graminum*	Bee pollen mixture	Longevity (d)	-0.1092	0.0589	(Michaud and Qureshi, 2006)
Rodolia cardinalis	*Icerya purchasi*	Sucrose	Longevity (d)	3.4656	0.2501	(Matsuka et al., 1982)
Rodolia cardinalis	*Apis mellifera*	Sucrose	Longevity (d)	3.2151	0.2292	(Matsuka et al., 1982)
Reproduction						
Adalia bipunctata (Exp. III)	*Ephestia kuehniella*	Bee pollen mixture	# eggs	1.198	0.2286	(De Clercq et al., 2005)
Adalia bipunctata (Exp. II)	*Ephestia kuehniella*	Dry bee pollen mixture	# eggs	0.3919	0.238	(De Clercq et al., 2005)
Adalia bipunctata (Exp. II)	*Ephestia kuehniella*	Frozen bee pollen mixture	# eggs	0.6981	0.232	(De Clercq et al., 2005)

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Adalia bipunctata	*Acyrthosiphon pisum*	Rosaceae pollen	# eggs	-0.2499	0.2699	(Hemptinne and Desprets, 1986)
Coccinella septempunctata	*Hypera postica*	Sucrose	# eggs	1.2846	0.1558	(Richards and Evans, 1998)
Coccinella transversalis	*Helicoverpa armigera*	Sucrose	# eggs	0.9332	0.3696	(Evans, 2000)
Coccinella transversalis	*Helicoverpa armigera*	Aphid honeydew	# eggs	0.7008	0.3538	(Evans, 2000)
Coccinella transversoguttata	*Hypera postica*	Sucrose	# eggs	1.231	0.2643	(Richards and Evans, 1998)
Coleomegilla maculata	*Ephestia kuehniella*	Corn pollen	# eggs	0.0336	0.1181	(Michaud and Grant, 2005)
Coleomegilla maculata	*Ephestia kuehniella*	Sorghum pollen	# eggs	0.2196	0.1151	(Michaud and Grant, 2005)
Harmonia axyridis (laboratory population)	*Ephestia kuehniella*	Bee pollen mixture	# eggs	-0.2298	0.076	(Berkvens et al., 2008)
Harmonia axyridis (red population)	*Ephestia kuehniella*	Bee pollen mixture	# eggs	0.1481	0.0819	(Berkvens et al., 2008)
Harmonia axyridis (black population)	*Ephestia kuehniella*	Bee pollen mixture	# eggs	-0.0622	0.0917	(Berkvens et al., 2008)
Harmonia axyridis	*Hypera postica*	Sucrose	# eggs	0.9881	0.2805	(Evans and Gunther, 2005)
Hippodamia convergens	*Schizaphis graminum*	Bee pollen mixture	# eggs	-2.4859	0.0821	(Michaud and Qureshi, 2006)
Micraspis discolor	*Rhopalosiphum maidis*	Corn pollen	# eggs	2.4475	0.3498	(Omkar, 2006)
Propylea japonica	*Myzus persicae*	Rice pollen	# eggs	0.7462	0.1535	(Bai et al., 2005)

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Figure 1. The effects of prey versus non-prey foods (sugar and pollen analyzed simultaneously) on the larval and adult performance of coccinellid beetles. Effects are measured by Hedges' d (see text), with negative effect size indicating that the non-prey foods were inferior to the prey-only diet. Error bars represent 95% confidence intervals, and the arabic number associated with each bar represents the number of experimental comparisons analyzed.

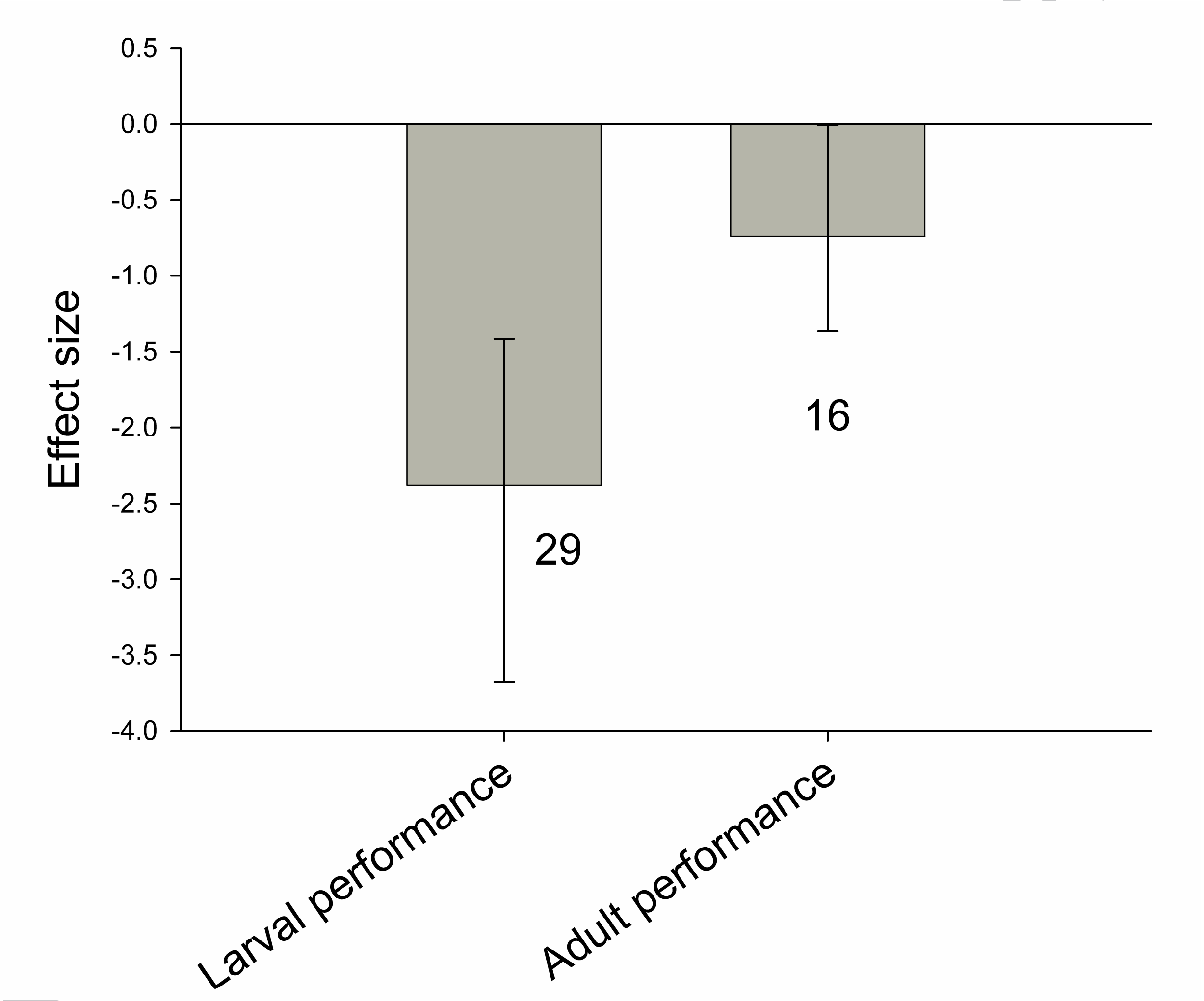

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Figure 2. The effects of prey versus non-prey foods (sugar and pollen analyzed independently) on the larval and adult performance of coccinellid beetles. Effects are measured by Hedges' d (see text), with negative effect size indicating that the non-prey foods were inferior to the prey-only diet. Error bars represent 95% confidence intervals, and the arabic number associated with each bar represents the number of experimental comparisons analyzed.

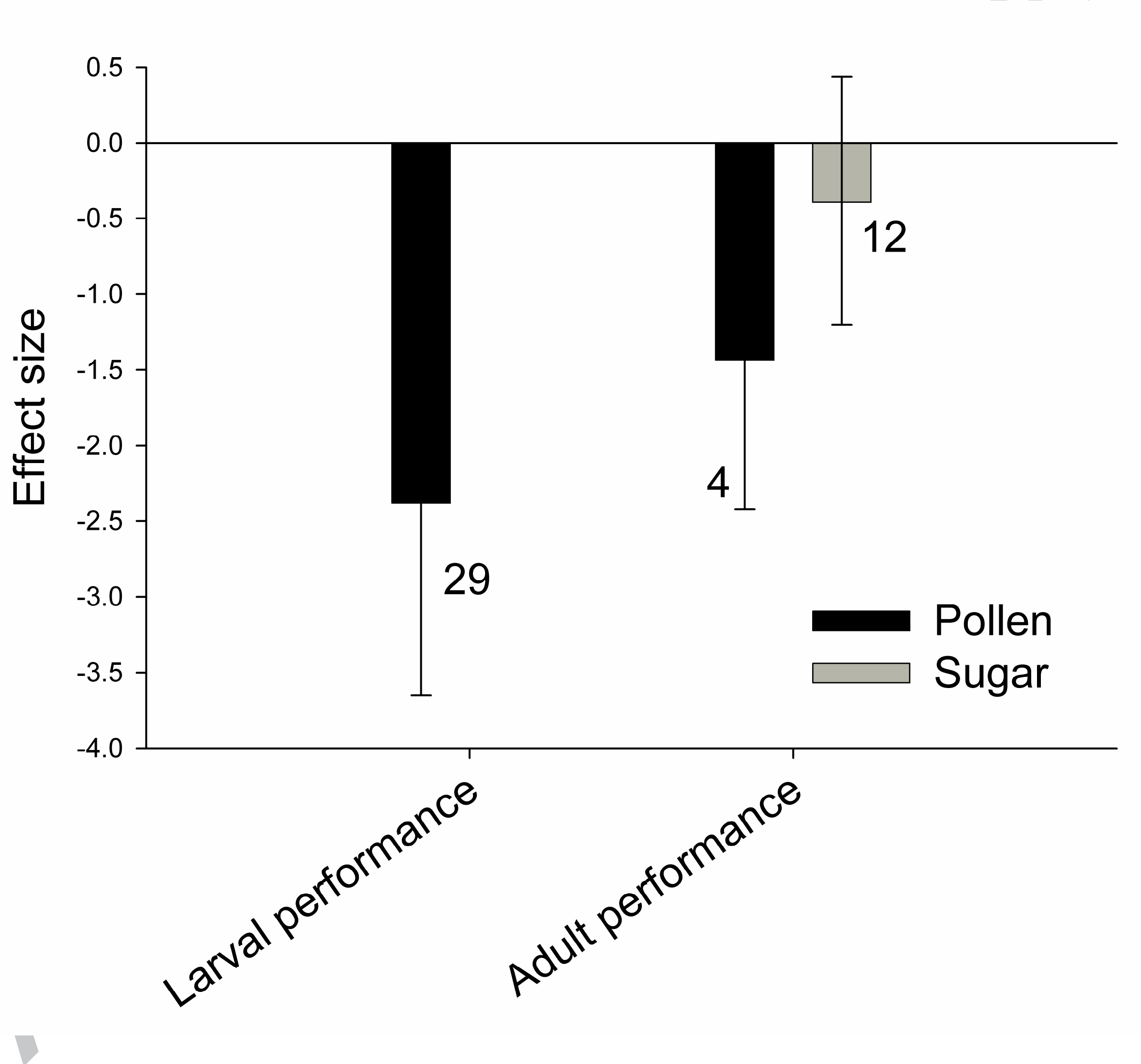

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Figure 3. The effect of mixing prey-only diets with non-prey foods (sugar and pollen analyzed simultaneously) on coccinellid larvae and adults. Effects are measured by Hedges' d (see text), with negative effect size indicating that the mixed diets were inferior to the prey-only diet. Error bars denote 95% confidence intervals, arabic numbers associated with each bar indicate the number of experimental comparisons analyzed.

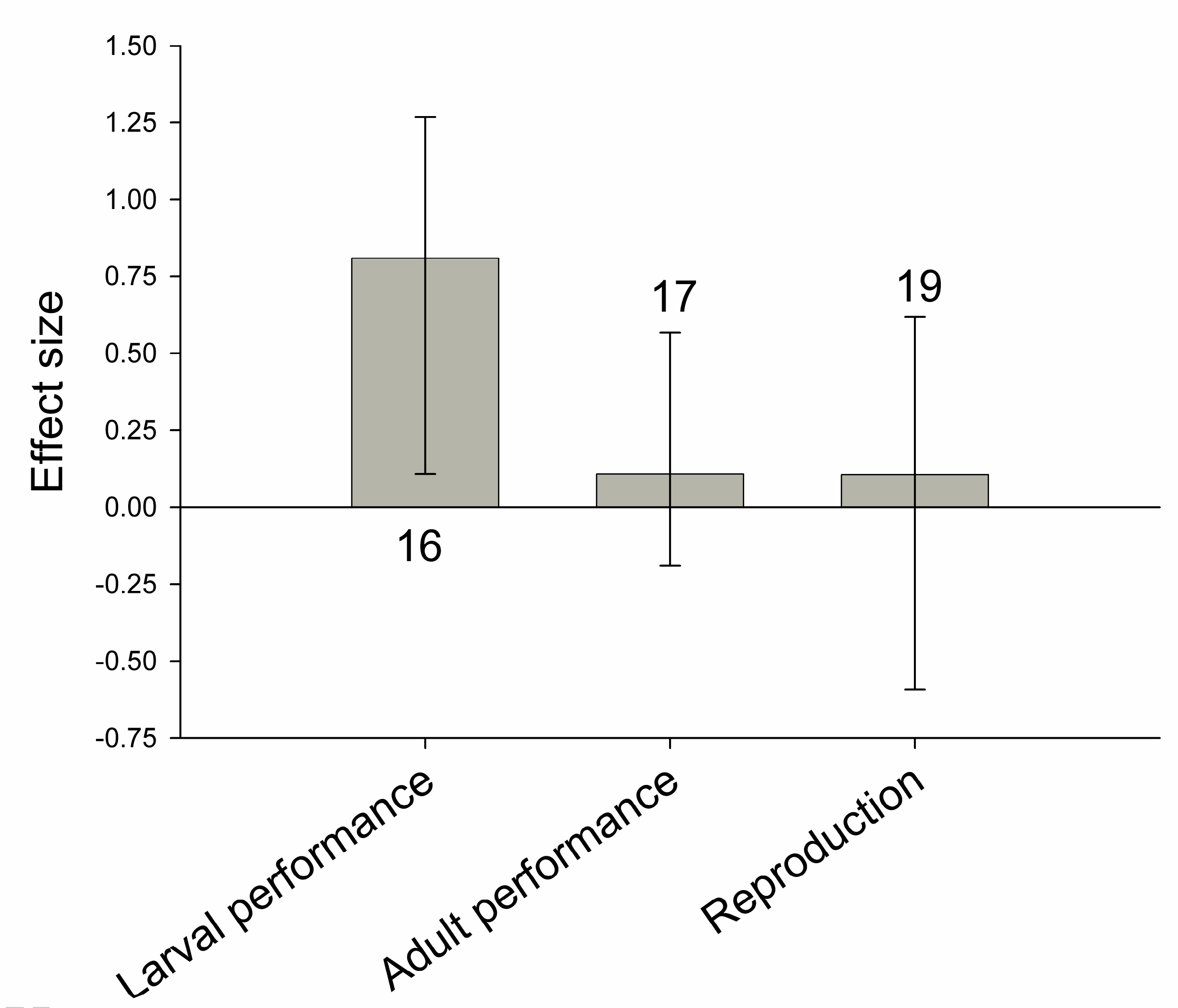

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Figure 4. The effect of mixing prey-only diets with sugar or pollen (non-prey foods analyzed independently) on coccinellid larvae and adults. Effects are measured by Hedges' d (see text), with negative effect size indicating that the non-prey foods were inferior to the prey-only diet. There was not a sufficient number of studies that compared prey with sugar in the larval performance for analysis. Error bars denote 95% confidence intervals, arabic numbers associated with each bar indicate the number of experiments analyzed. Asterisks indicate significant heterogeneity in the data ($P < 0.0001$).

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