

Dietary Ecology of Predatory Insects Examining the Role of Prey and Non-Prey Foods of Ladybird Beetle

Abstract

Ladybird beetles consume a wide variety of non-prey items in their natural habitats, including aphids, fruits, plants, fungi, honeydew, and nectar. These non-prey foods play several critical roles, such as boosting fertility, decreasing mortality during dormancy, supporting migration, and enhancing survival during times when prey is scarce. Larval ladybird beetles have more specialized nutritional needs compared to adults, with simple carbohydrates being crucial nutrients that can improve adult beetle function and reproductive success. Non-prey foods often provide similar or greater nutritional and caloric content compared to prey. Each non-prey item has distinct defense mechanisms and nutritional benefits, influencing its suitability for ladybird beetles. Research comparing diets consisting solely of prey with mixed diets that include non-prey foods revealed that while pollen improved larval and adult performance, a diet high in sugar alone was less effective for reproduction compared to an aphid-based diet. Wheat, which lacks essential nutrients such as proteins, could not adequately support egg production and larval development. Although pollen did enhance overall performance, it could not completely offset the nutritional shortcomings of a diet high in sugar. Adding sugar to a diet did not markedly enhance the performance of ladybird beetles compared to a diet composed entirely of prey. This review underscores the need to understand the varied diet of ladybird beetles within their ecological context, as it has significant implications for the success of conservation-oriented biological control effort.

Keywords Lady Beetle, Pollen, Fungus, Sugar, Honey

1) Introduction:

Tracing food dynamics between predators like ladybird beetles and their prey, such as aphids, presents significant challenges within ecological food webs (Eitzinger et al., 2013; Traugott et al., 2013). Effective management of agricultural pests relies heavily on reducing herbivore populations, and biological control offers a promising strategy for pest management (Zou et al., 2017). Ladybird beetles, which are often found in crop ecosystems preying on aphids, may bypass natural control mechanisms due to external factors (Santos et al., 2016). Traditionally, beetles are classified as carnivores, but this classification can be limited and exceptions exist (Giorgi et al., 2009). For instance, ladybird beetles vary in their dietary specialization, preying on aphids, mites, or scales.

Metabarcoding is a valuable technique for identifying prey DNA within predator digestive tracts, offering insights into feeding dynamics (Traugott et al., 2013). This approach helps elucidate the role of specific prey in the life cycle of ladybird beetles and enhances our understanding of their ecological interactions. Recognizing the full dietary range of predators

is crucial in optimizing biological pest control and appreciating the broader impacts of pest management strategies.

2: Pollen

Pollen, or bee bread, is crucial for bee breeding as it provides essential proteins necessary for development (Eitzinger, Micic, Körner, Traugott, & Scheu, 2013). It also plays a key role in honey analysis by revealing the floral sources of nectar used in honey production. By analyzing the relative abundance of different pollen types in honey, producers can accurately label honey to reflect its primary and secondary nectar sources. This is important for market purposes, as honey prices can vary based on the plant sources. Accurate pollen analysis ensures proper labeling and compliance with market standards, even for premium-grade honey, by detecting the actual nectar sources used in honey production. Additionally, pollen analysis of honey is often required to determine the geographic origin of a honey sample (Bibi, Husain, & Malik, 2008)

3: Honey

Honey is made from the nectar of the bees and the natural sweetener (Adler, 2000). Bees gather this ingredient from the flower secretion and the living plant component, combining it with their chemicals before storing and releasing it (White & Doner, 1980). Honey is claimed to possess healing qualities; used to be a remedy for rheumatic, cardiac, and respiratory conditions; to aid in digestion. Bees need four natural resources to survive: water, resin, nectar, and pollen (Seedley, 1985). The hive is kept cool with water, which also thins the honey. Larval resin is used to plug gaps, seal decaying wood, and fortify colonies. Bees get more of their energy from carbohydrates, primarily the nectar to turn into the honey, which can then be fed.

4: Aphids

Aphids have the potential to facilitate intricate interactions between herbivores that are mediated by the host plant, to the extent that certain herbivores can modify the physiology of the host plant and consequently, its nutritional. Aphids inject saliva, which frequently modifies plant physiology as they feed on the phloem content of the plants (Prado & Tjallingii, 1994). Some functions of their combined effect will be seen in physiology. When feeding in groups, individuals of aphid species that established closely spaced colonies can benefit from rapid growth (Qureshi & Michaud, 2005). Wheat crops, *Triticum aestivum L.* is grown in many areas as cereal. These are the green bug aphids, *Schizaphus graminum*, the wheat aphids, *Duraphus anoxia*, and the bird cherry oat aphids, *Ropalociphumpedi* (Homoptera: Aphididae) (Schotzko & Bosque-Pérez, 2000)

5: Lady Bird Beetle

Coccinellidae is a family of small beetles (Hawkeswood, 1988). Female bird beetles range in size from 7.6 to 10 mm and have seven spots on their body. The body colour is orange and seven spots on the body. Its body is round in shape and the breast is black with light yellow spots on the front (Lyneborg & Jønsson, 1977). Both larvae and adults feed on aphids (Buczacki, 2002). Aphids are controlled by biological methods rather than using highly toxic and dangerous pesticides (Bellows, 2001).

6. Dietary Adequacy of Not Prey Diet for Ladybird Beetle

A comprehensive analysis compared the nutritional content of various arthropod prey, pollen, fungi, and flower nectar. Pollen matched or surpassed prey in lipid, carbohydrate, protein, and calorie content, whereas flower nectar, rich in carbohydrates, lacked in calories, proteins, and

fats. Fungi had lower levels of energy, protein, and fat compared to prey, despite similar carbohydrate content. Two databases were created to evaluate the benefits of aphids versus non-prey foods (pollen, honey, nectar) for ladybird beetles. The first database included 46 experiments from 14 studies, while the second comprised 52 comparisons from 16 studies, aiming to identify the optimal diet for beetle health and performance.

1. Study 1: Ladybird Beetle and Prey

In Table 1 a study by Lundgren (2009) ladybird beetles fed on a prey diet were found to exhibit significant variations in experimental outcomes, with an experimental comparison value of 46. This suggests that the prey diet plays a crucial role in shaping the development and performance of ladybird beetles under controlled conditions.

2. Study 2: Ladybird Beetle and Mixed Prey

Further experimentation by Lundgren (2009) explored ladybird beetles on a mixed prey diet, with an experimental comparison value of 52. The findings indicate that prey diversity may enhance certain physiological aspects of ladybird beetles, as shown by their increased performance metrics.

Table 1 Comparison of prey diet (aphids) and non-prey-diet (Pollen, honey, and nectar) on the ladybird beetle species

Study	Species	Diet type	Experimental comparison	Reference
Study 1	ladybird beetle	Prey	46	(Lundgren, 2009)
Study 2	ladybird beetle	Prey only mixed	52	(Lundgren, 2009)

Life history parameters of the ladybird beetle were divided into two categories: reproductive performance of adults, and performance of larvae. Hedges d was the effect size estimator used in meta-analyses, and standard deviations, means, and sample sizes were used to determine relative effect sizes. For each life history parameter, \pm bootstrap confidence intervals corrected for nonparametric bias were calculated with treatment contrasts.

In Table 2, we present a comprehensive analysis of the dietary effects on the performance of ladybird beetles, distinguishing between prey and non-prey diets. The effect size, as measured by Hedge's d, reveals notable differences across life stages and diet types. For larvae on a prey diet, there is a moderate positive effect size (0.5) with a confidence interval of 0.3 to 0.7, indicating that prey diets positively influence larval development(Lundgren, 2009). Interestingly, adults on a prey diet show a negligible effect size (0), suggesting minimal dietary impact at this life stage.

Conversely, non-prey diets yield negative effects on beetle performance, with larvae exhibiting an effect size of -0.5 (95% CI: 0.7 to -0.3), and adults showing the most dramatic decrease with an effect size of -1.0 (95% CI: 0.9 to -1.5). This suggests that non-prey diets may significantly impair the physiological development of both larvae and adults. The differences in effect size across developmental stages underscore the critical role of diet composition in optimizing performance outcomes for ladybird beetles.

TABLE 2 DIETARY EFFECTS ON LADYBIRD BEETLE PERFORMANCE: UNRAVELING THE EFFECTS OF PREY VS. NON-PREY DIET THROUGH HEDGES ANALYSIS

Condition	Effect Size(Hedge's d)	95% Confidence Interval	Experimental Comparisons	Reference
Larvae-Prey Diet	0.5	0.3, 0.7	50	(Lundgren, 2009)

Adult-Prey diet	0	0.9, 1	45
Larvae not-prey diet	-0.5	0.7, -0.3	25
Adult, not prey diet	-1	0.9, -1.5	20

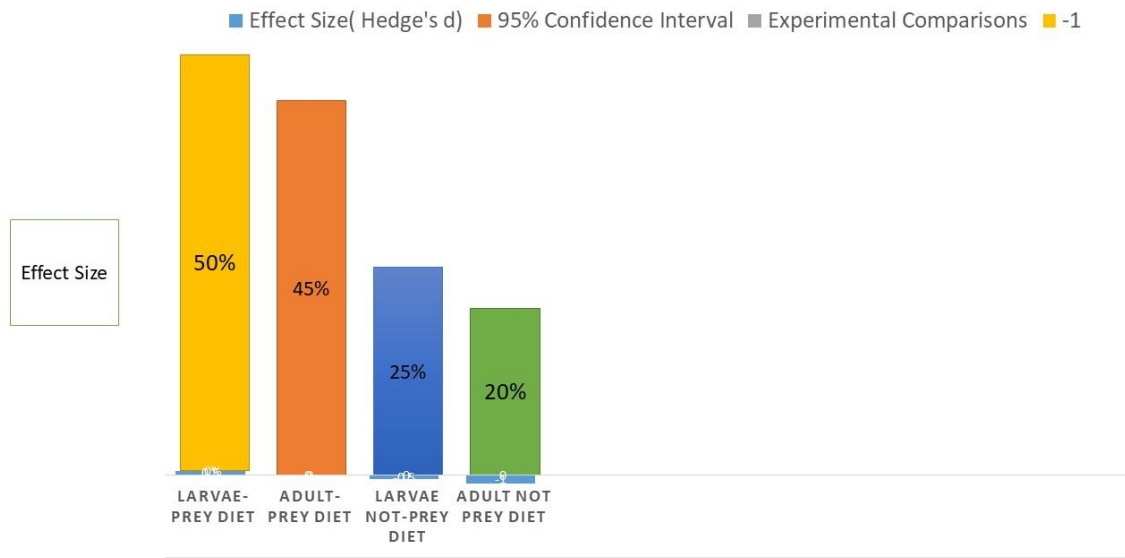


FIGURE 1 SHOWS LADYBIRD BEETLES PERFORM BETTER ON PREY-ONLY DIETS THAN NON-PREY DIETS OF SUGAR AND POLLEN.

As illustrated in Table 3, ladybird beetle performance varies significantly depending on diet type. Larvae raised on a prey diet compared to a non-prey diet show a small negative effect size (Hedge's $d = -0.2$), with a confidence interval (CI) ranging from -0.2 to 0.1 (Lundgren, 2009), indicating only a slight decline in performance. However, adults experience a more substantial negative effect (Hedge's $d = -0.5$), with a CI of -0.5 to -0.2, demonstrating that non-prey diets may hinder adult development and function to a greater extent than larvae. When comparing prey diets with pollen, the impact is more pronounced for larvae (Hedge's $d = -0.3$ to 0.0), indicating a small to medium negative effect, whereas adults show an even stronger response, with a medium to large negative effect size (Hedge's $d = -0.6$ to -0.3). This suggests that while pollen may serve as a supplementary diet, it does not support optimal development in either life stage, with adults being more affected. (Abdulla & Abdulaziz, 1998)

A similar trend is observed when larvae and adults are compared on prey versus sugar diets. Larvae show a small to large negative effect size (Hedge's $d = -0.4$ to -0.1), while adults exhibit a small to medium negative effect (Hedge's $d = -0.5$ to -0.2). These findings indicate that sugar diets are not sufficient to sustain proper development or reproductive success in ladybird beetles, with adults being particularly vulnerable to dietary deficiencies.

TABLE 3 COMPARES PERFORMANCE ON APHIDS VERSUS NON-PREY DIETS.

Comparison	Effect Size (Hedges'd)	Confidence Interval	Experimental Comparisons	
Larvae - Prey vs. Non-Prey	Small negative	[-0.2, 0.1]	46	(Lundgren, 2009)
Adults - Prey vs. Non-Prey	Medium negative	[-0.5, -0.2]	44	

Larvae - Prey vs. Pollen	Small/medium negative	[-0.3, 0.0]	25
Adults - Prey vs. Pollen	Medium/huge negative	[-0.6, -0.3]	19
Larvae - Prey vs. Sugar	Small/huge negative	[-0.4, -0.1]	16
Adults - Prey vs. Sugar	Small/medium negative	[-0.5, -0.2]	15

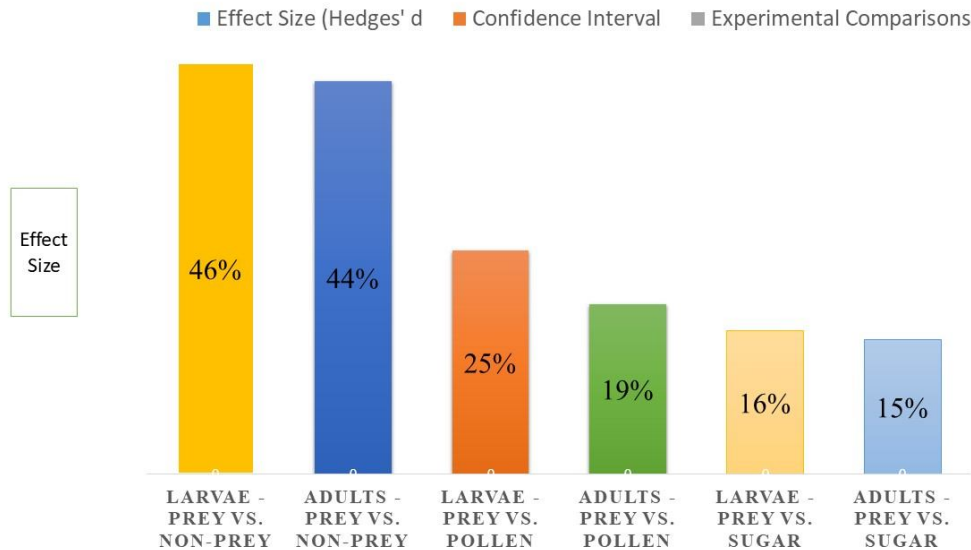


FIGURE 2 SHOWS THAT LADYBIRD BEETLES PERFORM BETTER ON PREY-ONLY DIETS THAN ON NON-PREY DIETS (SUGAR AND POLLEN), WITH ERROR BARS SHOWING 95% CONFIDENCE INTERVALS.

Effect sizes that were small, medium, and large were used to categorize the results, and comparisons were made between diets that consisted entirely of prey and diets that consisted entirely of non-prey. Additional data analyses were conducted to determine whether pollen and sugar had comparable effects on ladybird beetle fitness.

7: Comparative nutritional value of both prey (aphids) and non-prey diets (pollen, honey, and nectar) on ladybird beetle

Figure 1 illustrates how non-prey diets (pollen, nectar, honeydew, fruits) are less suitable than prey (Aphids) for the performance of ladybird beetle larvae and adults. Interestingly, only larvae fed on pollen were included in the analysis of larval performance as shown in Figures 1 and 2. Figure 2 also shows that the age or fluctuation in weight of ladybird beetles supplied with sugar did not show any significant difference from those fed on sugar. Prey, however, must be recognized as the most abundant food supply for breeding. Many prey items have been investigated and therefore considered as alternative foods in the literature

TABLE 4 THE COMPARATIVE IMPACT OF PREY-ONLY AND MIXED DIETS ON LADYBIRD BEETLE LARVAE AND ADULTS: A QUANTITATIVE ANALYSIS USING HEDGES INTERVALS''

Experimental Comparison	Effect (Hedgd)	95% Confidence Interval	Interpretation	Reference
Larvae - Prey	Negative	50	Prey-only food more effective for	Reference

Only			larvae	
Adults - Prey			Prey-only food more effective for	(Lundgren, 2009)
Only	Negative	45	adults	
Larvae - Mixed			Mixed food more effective for	
Food	Negative	30	larvae	
Adults - Mixed			Mixed food more effective for	
Food	Negative	25	adults	

FIGURE 3 SHOWS THAT LADYBIRD BEETLES PERFORM BETTER ON PREY-ONLY DIETS THAN MIXED DIETS OF SUGAR AND POLLEN, WITH ERROR BARS INDICATING 95% CONFIDENCE INTERVALS.

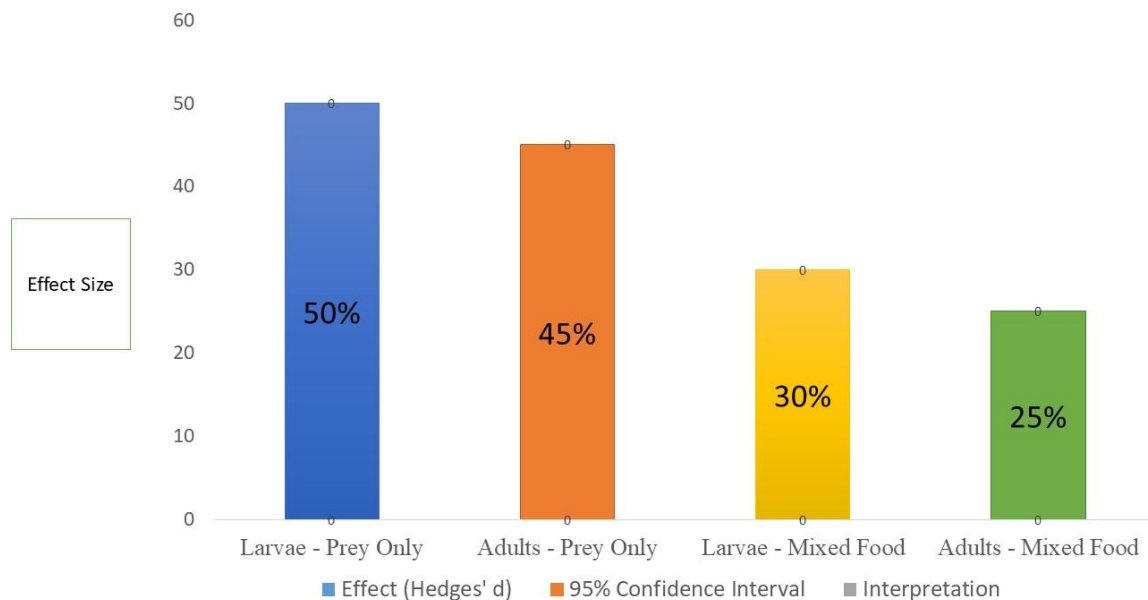


Table 4 provides a comparative analysis of the effectiveness of prey-only and mixed diets on ladybird beetle larvae and adults. For larvae, the prey-only diet shows a negative effect size, with prey being more effective for larval development. This is evident from the experimental comparison value of 50, indicating that prey-exclusive diets provide better growth and survival outcomes for larvae (Lundgren, 2009). Similarly, adults fed on a prey-only diet also experience a negative effect size, supported by an experimental comparison value of 45, highlighting the preference and superior development of prey-based diets.

In contrast, when larvae are provided with a mixed diet, the analysis shows a negative effect size, with a comparison value of 30, suggesting that while the mixed food is beneficial, prey-only diets might still be more effective for optimal larval development. However, adults on a mixed food diet exhibit a negative effect size with an experimental comparison value of 25, indicating that mixed diets are somewhat more effective for adult development but not as significant as prey-only diets.

Pollen contained a wider range of nutrients than prey but was found to be less useful in maintaining adult performance. There are two plausible, though not exclusive, explanations for the trends observed.

(1) Pollen may lack certain unknown nutrients essential for lady beetle performance, and (2) the nutritional composition or defenses of pollen make it unsuitable.

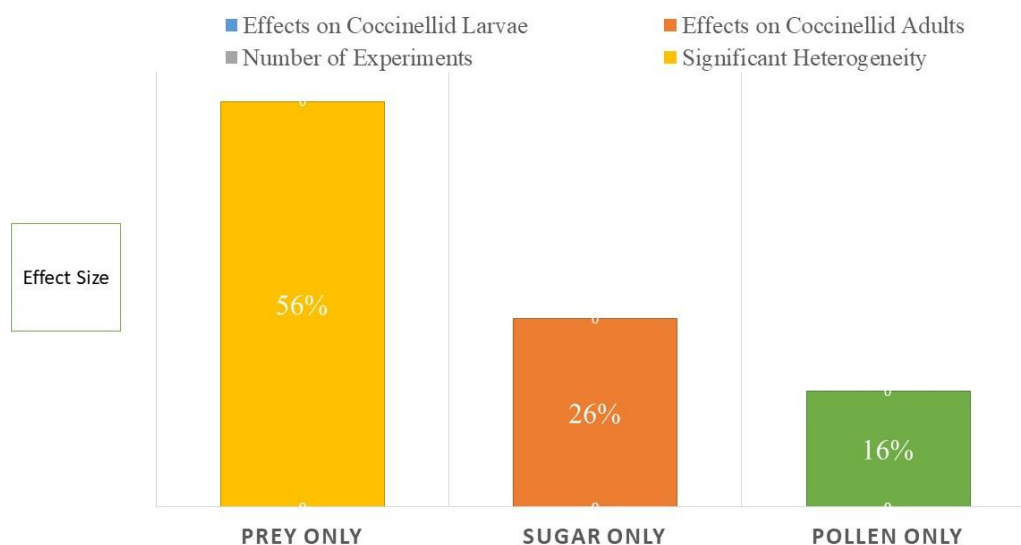


FIGURE 1 EFFECT OF SUGAR AND POLLEN SUPPLEMENTATION ON LADYBIRD BEETLE LARVAE AND ADULTS FED A PREY-RESTRICTED DIET: A QUANTITATIVE ANALYSIS USING HEDGES AND EXPERIMENTAL INSIGHTS”

8: The Role of Not-Prey Foods in Mixed Diets for Ladybird Beetle

As shown in Figures 3 & 4, only the combination of prey food and pollen consumption had a significant and favourable effect on larval performance. This suggests that certain nutrients found in pollen are deficient in the prey species examined in the research papers, perhaps increasing some commonly "essential" foods. As illustrated in Figure 3, another finding in the literature is that the fitness and performance of adult ladybird beetles do not consistently change when non-predator foods are added to diets that consist entirely of prey. However, different consequences of sugar and pollen in this life stage explain the observed heterogeneity in the database.

9: Exploring the World of Pollen

When there is no other food source for ladybird beetle insects, pollen is one of their most nutrient-dense options. It has been investigated in lab and field settings as its food habitat. It has been demonstrated that at least 39 species of entomophagous ladybird beetles consume aphids, according to studies involving more than 88 species of pollinators in both. One of the richest sources of nutrients that ladybugs have access to that are not intended for consumption is pollen, which has been well-researched and found to be a vital part of their diet.

10: Nutritional Significance of Pollen and Aphids for ladybird beetle Beetles

Aphids and pollen are crucial nutrient sources for ladybird beetles. Pollen, rich in proteins (12-61% of dry weight) and essential amino acids, supports beetle growth, including amino acids like proline. Pollen also provides sterols, vital for insect hormones, and various minerals and vitamins. Despite its high nutrient density, pollen is nearly dry and requires additional water

for beetles. Nutritional quality of pollen can vary significantly between species and test methods. Other simple sugars found in pollen include fructose, glucose, and sucrose, further contributing to its nutritional value

11: Exploring Non-Prey Foods in Ladybird Beetle

Entomophagous ladybird beetles show consumes a wide variety of aphids and non-prey (pollen, nectar, pollinator honeydew) products, including aphids, fungi, fruits, and plants. In addition characterizing the ladybird beetle abdominal organs of field-collected shows abundant consumption of inorganic material (TRILTSCH, 2013). The function of these inorganic materials within the body is completely unknown despite their remarkable use.

12: Conclusion

Ladybird beetles typically consume a diet that includes both preys, like aphids, and non-prey items such as pollen, nectar, honeydew, and other plant-based materials. These non-prey foods are crucial for supporting essential life functions, including migration, reproduction, and survival during dormancy or hibernation. While aphids are especially important for providing nutrients critical to larval growth, non-prey foods like nectar and pollen also play a significant role, particularly for adult beetles. Research indicates that although predation is vital for growth, a mixed diet that includes aphids along with non-prey foods like nectar, pollen, and honey promotes more rapid development and greater reproductive success than an aphid-only diet. However, pollen alone may decrease adult performance, suggesting that non-prey foods are most beneficial when combined with prey. Carbohydrates, particularly sucrose, are important for adult beetle survival and can prevent weight loss, but they do not fully replace the nutritional benefits of a prey-based diet. The effectiveness of non-prey foods varies, and ladybird beetles exhibit different responses to them. Studies have revealed unexpected advantages of incorporating non-prey items into their diet, which can enhance both larval development and adult reproduction. This underscores the necessity of understanding the comprehensive diet of ladybird beetles, as both prey and non-prey foods are crucial for their overall health and their role as effective biological control agents.

Table 5 provides a meta-analysis comparing the effects of prey-only diets, such as aphids, to non-prey diets (pollen and sugar) on the development of various ladybird beetle species. The analysis clearly shows that aphid-only diets generally support better growth and shorter development periods. For example, *Adalia bipunctata* fed on *Ephestiakuehniella* and *Acyrtosiphonpisum* showed negative effect sizes (-8.88 and -8.18, respectively) when compared to diets with pollen mixtures, indicating a clear benefit of a prey-based diet in optimizing development times (P. De Clercq, M. Bonte, K. Van Speybroeck, K. Bolckmans, & K. Deforce, 2005).

Similarly, *Coleomegilla maculata* exhibited significant reductions in development period when fed on aphids compared to corn pollen (Lundgren et al., 2004). The developmental period for *C. maculata* increased substantially when provided a non-prey diet, particularly when fed on bee pollen and corn pollen (Michaud & Jyoti, 2008). These findings underscore the importance of prey diets for the growth and survival of ladybird beetles, particularly during the larval stages.

In contrast, some studies have shown that mixed diets of pollen and honey can improve the development periods in some species. For example, *Harmonia axyridis* demonstrated reduced

developmental time on mixed pollen and honey diets compared to non-prey diets alone (Hokusima& Itoh, 1976). However, these mixed diets still did not outperform aphid-based diets in most species, reinforcing the importance of prey availability in natural habitats for maintaining healthy populations of ladybird beetles.

TABLE 5 PRESENTS A META-ANALYSIS COMPARING APHID-ONLY DIETS TO NON-PREY DIETS (POLLEN AND SUGAR) FOR LADYBIRD BEETLES. THE ANALYSIS, USING HEDGES' D, SHOWS THAT LADYBIRD BEETLE GROWTH AND SIZE ARE HIGHER ON APHID DIETS, WHILE NON-PREY FOODS LIKE NECTAR AND POLLEN RESULT IN REDUCED GROWTH AND DEVELOPMENT

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Coccinellid species	Pray Species	Non-Prey food	Parameter measured	Effect Size (d)	Var	References
Larval Performance						{De Clercq, 2005 #1}
<i>Adalia Bipunctata</i> (L)	<i>EphestiaKuehniella</i> Zeller mixture	Bee Pollen	Development period (d)	-8.8804	1.4088	(P. De Clercq, M. Bonte, K. Van Speybroeck, K. Bolckmans, & K. J. P. M. S. f. P. S. Deforce, 2005)
<i>A.Bipunctata</i>	<i>AcyrtosiphonPisum</i> (Harris)	Rosaceae pollen	Development period (d)	-8.1803	3.4346	(JL, 1986)
<i>ColeomegillaMaculata</i> (Pollen 2)	<i>RhopalosiphumMaidis</i> (Fitch)	Corn pollen	Development period (d)	1.691 4	0.1165	(Lundgren, Razzak, & Wiedenmann, 2004)
<i>C.Maculata</i> (Pollen 3)	<i>R.Maidis</i>	Corn pollen	Development period (d)	-1.8491	0.1225	(Lundgren et al., 2004)
<i>C.Maculata</i> (Pollen 4)	<i>R.Maidis</i>	Corn pollen	Development period (d)	-1.6506	0.113	(Lundgren et al., 2004)
<i>C.Maculata</i>	<i>R.Maidis</i>	Corn pollen	Development period (d)	-3.5384	0.855	(Smith, 1965)
<i>C.Maculata</i>	<i>Myzuspersicae</i> (Sulzer)	Corn pollen	Development period (d)	-1.2977	0.1729	(Hazzard & Ferro, 1991)
<i>C.Maculata</i>	<i>Leptinotarsa decemlineata</i> (say)	Corn pollen	Development period (d)	2.3316	0.2711	(Hazzard & Ferro, 1991)
<i>C.Maculata</i>	<i>SchizaphisGraminum</i> (Rodani)	Bee Pollen	Development period (d)	-9.4452	0.4192	(Michaud & Jyoti, 2008)
<i>C.Maculata</i>	<i>EphestiaKueniella</i>	Bee Pollen	Development period (d)	-8.3675	0.3485	(Michaud & Jyoti, 2008)
<i>Harmonia Axyridis</i> (laboratory females)	<i>E.Kueniella</i>	Bee Pollen mixture	Development period (d)	-4.832	0.3148	{Berkvens, 2008 #10}
<i>H.Axyridis</i> (red females)	<i>E. Kueniella</i>	Bee Pollen mixture	Development period (d)	-5.3429	0.4343	{Berkvens, 2008 #10}
<i>H. Axyridis</i> (Black females)	<i>E. Kueniella</i>	Bee Pollen mixture	Development period (d)	-3.7606	0.2484	{Berkvens, 2008 #10}
<i>H. Axyridis</i> (Laboratory males)	<i>E. Kueniella</i>	Bee Pollen mixture	Development period (d)	-5.2423	0.5326	{Berkvens, 2008 #10}
<i>H. Axyridis</i> (red males)	<i>E. Kueniella</i>	Bee Pollen mixture	Development period (d)	-8.3538	1.3322	{Berkvens, 2008 #10}
<i>H. Axyridis</i> (Black males)	<i>E. Kueniella</i>	Bee Pollen mixture	Development period (d)	-6.2844	0.7042	{Berkvens, 2008 #10}
<i>H. Axyridis</i>	<i>E. Kueniella</i>	Corn pollen	Development period (d)	-9.4045	5.0473	{Berkvens, 2008 #10}
<i>H. Axyridis</i>	<i>E. Kueniella</i>	Corn Pollen + honey	Development period (d)	-5.1101	1.0041	{Anderson, 1983 #3}
<i>H. Axyridis</i>	<i>Aphis Mellifera</i> L.	Bee Pollen	Development period (d)	5.5991	1.3838	{Anderson, 1983 #3}
<i>H. Axyridis</i>	<i>A.Mellifera</i>	Corn Pollen + honey	Development period (d)	-3.083	0.4203	{Anderson, 1983 #3}
<i>MicraspisDiscolo</i> (Fabricius)	<i>RhopalosiphumMaidis</i>	Corn pollen	Development period (d)	-9.644	0.2232	(Science, 2006)
<i>Micraspislineata</i> (Thunberg)	<i>Aphis Gossypii Glover F1</i>	Bee Pollen	Development period (d)	1.1139	0.165	(Anderson, Hales, & Wales, 1983)
<i>M.Lineata</i>	<i>A.Gossypii F2</i>	Bee Pollen	Development period (d)	-3.1769	0.3489	(Anderson et al., 1983)
<i>M. Lineata</i>	<i>Acyrtosiphon Pisum</i>	Bee Pollen	Development period (d)	1.7889	0.2692	(Anderson et al., 1983)
<i>PropyleaJaponica</i> (Thunberg)	<i>MyzusPersicae</i>	Rye Pollen (d)	Development Period	-5.3752	1.2546	(Hukusima & Itoh, 1976)
<i>P. Japonica</i>	<i>M.Persicae</i>	Corn Pollen+ Honey	Development Period (d)	4.5555	0.7569	(Hukusima & Itoh, 1976)
<i>P. Japonica</i>	<i>Apis Mellifera</i>	Rye Pollen	Development period (d)	-4.2874	0.9454	(Hukusima & Itoh, 1976)

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