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Pest control services on farms vary among bird species on diversified, low-intensity farms

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ABSTRACT

Avian species provide pest control services in some agricultural systems, which may incentivize farmers to conserve natural habitats for native biodiversity. A critical component of this equation, however, is verifying that avian species are consuming potential pest species in the agricultural ecosystems. We used a DNA metabarcoding approach to determine the frequency of pest presence in songbird fecal samples collected from birds caught on diversified, low-intensity farms in New England, USA, during the bird breeding season. Twelve species of insect pest were identified in fecal samples, and across all songbird species 12.6% of samples included DNA from at least one pest. Frequency of pest presence depended on songbird species, with Common Yellowthroats and Gray Catbirds eating pests more frequently than Song Sparrows. Pests were also more frequently found in fecal samples collected from hatch-year birds and birds caught later in the year. Although we observed a lower frequency of pest consumption than observed in previous comparable research, growers can likely improve pest control by songbirds by promoting the woody, non-crop habitat types preferred by insectivorous species, in our system specifically Gray Catbirds and Common Yellowthroats.

1. Introduction

Wildlife conservation and agricultural production are often tightly linked. With agricultural lands covering over 40% of the world's land (McLaughlin, 2011), production decisions have large impacts on global natural communities (Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Declines in wildlife populations are often linked to conventional agricultural intensification and conversion of natural habitat to active production (Rosenberg et al., 2019; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Agricultural intensification is generally marked by removal of non-crop vegetation, high chemical inputs (e.g., pesticides and herbicides), low crop diversity, large farm size, and mechanization (Donald et al., 2001; Sánchez-Bayo and Wyckhuys, 2019; Stanton et al., 2018; Tscharntke et al., 2005). Increasing demand for resource-intensive foods is likely to cause further declines to natural communities through the expansion of agricultural land or increasing agricultural intensity on currently productive land (Tomlinson, 2013; Zabel et al., 2019). However, farmland that supports native wildlife populations can take advantage of existing ecosystem services, like pollination and pest control, to enhance productivity (Gonthier et al., 2019; Kremen et al., 2007; Tscharntke et al., 2005). When natural habitat is left in the landscape, natural communities persist (Tscharntke et al., 2005), and depending on the ecosystem services provided, total production levels can be maintained with a smaller proportion of the

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land actively farmed (Garibaldi et al., 2020). Such an agricultural approach may be a strategy to conserve global wildlife populations, while meeting food production demands (Kremen, 2015).

Growers can maintain high food production while supporting native wildlife populations and ecosystem services by engaging in ecological intensification. Ecological intensification (also known as Diversified Farming Systems, or agroecology) is the practice of managing farmlands to support on-farm biodiversity which provides ecosystem services to aid in food production (Bommarco et al., 2013; Kremen, 2015; Kremen et al., 2012; Tittonell, 2014). In tropical cacao and coffee production, practices that maintain natural habitat support natural biodiversity and benefit from increased ecosystem services (Chain-Guadarrama et al., 2019; De Beenhouwer et al., 2013; Meylan et al., 2017). Many low intensity practices improve biodiversity and ecosystem services, leading to long term yield and profitability gains, though there is often a short-term economic cost (Rosa-Schleich et al., 2019). Increasing land complexity and natural enemy diversity usually results in increased crop pest control, though there is high variability between systems (Dainese et al., 2019; Karp et al., 2018; Letourneau et al., 2009; Rusch et al., 2016). Under agroecological systems, growers use their knowledge of ecological interactions to improve the efficiency of food production without the high inputs associated with conventional intensification (Kremen, 2015).

Farming systems in the northeastern USA have been trending more toward an agroecological approach in recent years. Consumers and growers in the region prefer the use of alternatives to pesticides when farmers are still able to maintain profitability (Anderson, 1993; Anderson et al., 1996; Hollingsworth et al., 1993; Martinez et al., 2010). In contrast with the rest of the US, northeastern farms are becoming smaller and more diversified, and the region is a hotspot for direct-to-consumer sales (United States Department of Agriculture USDA, 2017). All three of these factors are associated with lower-intensity farming approaches (Buttel and Larson, 1979; Kuo and Peters, 2017; Sassenrath et al., 2010) which are likely to be more wildlife friendly. Organic production in this region has seen steep growth, and several Integrated Pest Management (IPM) techniques to reduce pests without pesticides have seen broadening adoption (United States Department of Agriculture USDA, 2017). While more organic farmers are using practices such as biological pest control through the releasing of beneficial organisms, and growers are increasingly using pest resistant crops, other agroecological practices such as maintaining habitat for beneficial organisms and avoiding pests through careful plant placement are on the decline (United States Department of Agriculture USDA, 2017). These last two agroecological practices in particular could help maintain both wildlife populations and increased farm viability (Kremen, 2015; Kremen et al., 2012).

Songbird foraging in farm fields can have both positive and negative impacts for production (Garfinkel et al., 2020; Martin et al., 2013). In a prior study in this same system Mayne et al. (2023) reported that birds suppress crop pests in brassica and cucurbit crops, while they cause an increase in eggplant pests, likely due to ecological release from insect predators. Though in brassicas, cucurbits, and Solanaceae birds had positive or negligible impacts on crops, the potential for ecological release exists. The bird species responsible for pest suppression and ecological release are not known. Although for effective agroecological pest management it is crucial to thoroughly understand the ecological interactions of wildlife and pests (Kremen et al., 2007), relatively little research has attempted to quantify farmland bird diets (Garfinkel et al., 2020; Grass et al., 2017; Jedlicka et al., 2017). The only study with a comparable songbird community to that of the Northeast found that song sparrows (scientific names in Table 1) were the species most beneficial to corn production, while gray catbirds and common yellowthroats preyed on insect pests less frequently (Garfinkel et al., 2020). Though they also found that birds cause increased pest damage in soy, they were not able to link this directly to ecological release (Garfinkel et al., 2020). However, a study from another region was able to tie increased aphid populations directly to predation of their insect natural enemies by Eurasian Tree Sparrows (*Passer montanus*) (Grass et al., 2017). Given these species and crop-specific differences, to effectively manage farms for beneficial bird species, we must first know which species are most important in providing pest control.

It was the objective of this study to determine which bird species are most involved in agricultural insect pest control on diversified, low-intensity New England farms. Because habitat associations are known for this system's most abundant species (Brofsky, 2020), identifying the most important songbird species for natural pest control will allow growers to manage specifically for beneficial species. We hypothesized that birds on farms would consume pest insects as indicated by the frequency at which pest insect DNA was detected in songbird fecal sample, that the frequency of pest consumption would vary among bird species, and that birds might consume beneficial insects as well. This information will help stakeholders make decisions about on-farm habitat management and broader songbird conservation to enhance pest control services.

2. Methods

2.1. Study area

Fecal samples were collected from birds on 11 small, low-intensity farms in western Massachusetts. The study farms were located in Hampshire and Franklin counties, which together make up 26% of Massachusetts's cropland and 24% of the value of the state's agricultural production (United States Department of Agriculture USDA, 2017). Distance between farms ranged from 3 km to 42 km. All samples were collected along the edges of fields managed by 11 different growers during the summers of 2019 and 2020. Farmers' growing practices resemble those evident in the low-intensity trends in New England agriculture. Farms used IPM practices and were either certified organic or organic compliant. Farms produce a large variety of fruit and vegetable crops, and direct-to-consumer sales (farm stand, farmers' markets, or CSA) represented a major portion of their sales. Average farm size was 13.7 ha (SD 15.6, range 0.4 – 48.6). Although factors such as farm size and direct-to-consumer sales do not inherently affect farms' environmental impacts, small farms and those with direct-to-consumer business models typically apply lower intensity practices more friendly to wildlife (Donald et al., 2001; Kuo and Peters, 2017; Sassenrath et al., 2010). For this reason, we have focused on farms with these attributes, but this

Table 1

percentage of bird fecal samples containing agricultural insect pests. Fecal samples were collected from birds on 11 farms in Western Massachusetts during summer 2019 and 2020. Only bird species for which at least ten samples were collected are shown.

Species	n	Xestia dolosa	Xestia c-nigrum	Grapholita packardi	Lymantria dispar	Lygus lineolaris	Leptinotarsa decemlineata	Peridroma saucia	Byturus unicolor	Amphipyra pyramidoides	Agrotis ipsilon	Delia platura	Drosophila suzukii	Total
SOSP[1]	148	0.7	0	0	2.7	0	1.4	1.4	0	0.7	0	0	0	6.8
GRCA	143	0.7	0	1.4	3.5	1.4	1.4	4.2	2.1	2.8	0.7	0.7	1.4	17.5
COYE	99	0	0	0	1	5.1	0	6.1	1	4	1	0	2	16.2
BCCH	45	0	0	0	2.2	2.2	0	0	0	2.2	0	0	0	6.7
AMRE	30	0	0	0	0	0	3.3	0	0	3.3	0	0	0	6.7
HOWR	28	0	0	0	3.6	0	0	0	3.6	3.6	0	0	0	10.7
YEWA	23	0	0	0	0	4.3	0	0	0	8.7	0	0	0	13
CEDW	16	0	0	6.3	0	0	0	0	0	0	0	0	6.3	12.5
EAPH	14	0	7.1	0	7.1	0	0	0	0	7.1	0	0	0	21.4
AMGO	13	0	0	0	0	7.7	0	0	0	0	0	0	0	7.7
CHSP	13	0	0	0	0	7.7	15.4	0	0	0	0	0	0	23.1
WIFL	11	0	0	0	0	9.1	0	0	0	0	0	9.1	0	9.1
AMRO	10	0	0	0	0	0	0	0	0	0	0	0	0	0
NOCA	10	0	0	0	0	0	0	0	10	0	0	0	0	10
REVI	10	0	0	0	0	0	0	0	0	0	0	0	0	0
Total[2]	737	0.4	0.1	0.5	2.6	1.9	1.2	2.4	0.8	2.4	0.3	0.3	0.8	12.6

[1]SOSP = song sparrow (*Melospiza melodia*); GRCA = gray catbird (*Dumetella carolinensis*); COYE = common yellowthroat (*Geothlypis trichas*); BCCH = black-capped chickadee (*Poecile atricapillus*); AMRE = American redstart (*Setophaga ruticilla*); HOWR = house wren (*Troglodytes aedon*); YEWA = yellow warbler (*Setophaga petechia*); CEDW = cedar waxwing (*Bombycilla cedrorum*); EAPH = eastern phoebe (*Sayornis phoebe*); AMGO = American goldfinch (*Spinus tristis*); CHSP = chipping sparrow (*Spizella passerina*); WIFL = willow flycatcher (*Empidonax traillii*); AMRO = American robin (*Turdus migratorius*); NOCA = northern cardinal (*Cardinalis cardinalis*); REVI = red-eyed vireo (*Vireo olivaceus*).

[2] Total = all fecal samples collected, including from bird species not shown here.

does not preclude the effective adoption of lower intensity practices by larger farms without direct sales to consumers.

2.2. Field methods

Fecal samples were collected from songbirds between June 2nd and August 7th of 2019 and 2020. Songbirds were captured by mist net placed along field margins, within 50 m of actively cultivated crops (usually <15 m away). Playback of songbird breeding songs, alarm calls, raptor calls, and mobbing track were used to attract birds to the net. Once captured, birds were put in a clean paper bag until they defecated (maximum 30 min). The fecal sample was then transferred to a dry microcentrifuge tube and put on ice in an insulated cooler. Forceps used for transferring fecal material were thoroughly cleaned in hydrogen peroxide and ethanol and allowed to dry between uses. The bird was then banded, and standard morphological measurements were taken (sex, age, mass, breeding stage, flight feather length, tail feather length, body molt, flight feather molt, muscle rating, fat stores rating). Multiple fecal samples were collected from any individual that was captured more than 20 min after the previous sample was collected, with a maximum of 5 samples collected from an individual in one day. Jedlicka et al. (2017) found this to effectively limit the correlation between consecutive samples collected from an individual. Fecal samples were transferred to a − 80 °C freezer, where they were stored until DNA extraction.

2.3. Lab methods

Genetic material was extracted from fecal samples using the E.Z.N.A. Stool DNA Kit from Omega Bio-tek (Norcross, GA, USA) after a 15 s metal bead homogenization (FastPrep-24, MP Biomedicals, Illkirch, France). The arthropod cytochrome oxidase c subunit I (COI-5 P) gene was amplified and indexed in a two-step PCR using ZBJ primers (Zeale et al., 2011) and rhAmpSeq index primers made by Integrated DNA Technologies (Coralville, IA, USA). First round PCR reactions (25 μL total) included 0.75 μL DMSO, 0.25 μL Phusion High Fidelity Polymerase, 5 μL High Fidelity Buffer (all New England Biolabs, Ipswich, MA, USA), 0.5 μL of 10 M dNTP mix (Promega, Madison, WI, USA), 15 μL pure water, 1.25 μL each of 10 μM ZBJ forward and reverse primer, and 1 μL of template DNA from the DNA extraction. Thermocycler conditions were 98 °C for 30 s; 35 cycles of: 98 °C for 10 s, 50 °C for 30 s, 72 °C for 30 s; 72 °C for 10 min, and a final hold temperature of 12 °C. The index PCR (second round) used the same reaction components, but with the template DNA and ZBJ primers replaced by 1 uL of product from the first round of PCR and 1.25 uL each of 10 μM i5 and i7 rhAmpSeq index primers. Thermocycler conditions for the second round were the same but with only 10 cycles. A bead cleanup was performed between PCR rounds to remove nontarget amplification (primer dimer), using Mag-Bind TotalPure NGS beads and protocol (Omega Biotek, Norcross, GA, USA) at a 0.8:1 bead to PCR product ratio.

Final PCR products were combined into 4 indexed libraries and cleaned before sequencing. Two to four rounds of bead cleaning (Mag-Bind TotalPure NGS beads, Omega Biotek, Norcross, GA, USA) at a bead to PCR product ratio of 0.85:1 were used to remove nontarget amplification (primer dimer). Between each round of cleaning, 5 μL of the cleaned library was run on a 1.5% agarose gel, and if the nontarget DNA was low enough for sequencing, no more bead cleanups were performed. The four indexed libraries were sequenced by the Genomics Resource Laboratory (University of Massachusetts Amherst, MA 01003) on an Illumina MiSeq Nano v2–500 (Illumina, San Diego, CA, USA). Blank control samples run in parallel with both DNA extractions and PCR (n = 18), and PCR only (n = 21) were sequenced alongside samples.

2.4. Genetic database construction

Raw sequencing reads were processed in the QIIME 2 pipeline (Bolyen et al., 2019). Sequences were demultiplexed, denoised, and assigned to amplicon sequence variants (ASVs) using DADA2 (Callahan et al., 2016). A number of quality filters were applied to remove data that were the result of contamination or PCR errors. Samples with fewer than 1000 reads before denoising were removed from analyses. ASVs present in blank control samples, identified as non-Animalia, or with bad sequence lengths (must be 144–162 bp and divisible by 3) were removed from all samples for analyses, and ASVs with a read frequency less than 5 in a given sample were removed from that sample. DNA extractions and PCR amplifications were performed in a laboratory that routinely conducts molecular work focused on the invasive winter moth, *Operophtera brumata*; therefore, all sequences assigned to this genus were also removed from analyses. ASVs were assigned taxonomic classifications using two naïve-Bayes (Bokulich et al., 2018) classifiers. The "tidybug" reference dataset described by O'Rourke et al. (2020), filtered to include only records from the United States and Canada, was used to train one naïve-Bayes classifier. The tidybug reference dataset includes all COI-5 P records from the Barcode of Life Database (BOLD) (downloaded July 2020), filtered for quality, and trimmed to the region amplified by the ANML primers described by (Jusino et al., 2019), which includes the region amplified by the ZBJ primers used in this study. The other naïve-Bayes classifier was trained on untrimmed BOLD records from a selection of northeastern US and Canadian states and provinces, filtered for quality using a custom Python script. The taxonomic classifications of our sequence library were combined using RESCRIPt (Robeson et al., 2020), maintaining identifications to the level at which both classifiers agreed where there were discrepancies, but with the more specific classification accepted when lower-level classifications agreed. Once ASVs were collapsed to taxonomic levels and converted to presence-absence, all data were exported to R (R Core Team, 2021) for statistical analysis using the vegan (Oksanen et al., 2020) and glmmTMB (Brooks et al., 2017) packages.

2.5. Statistical methods

For analyses, pest and natural enemy species were identified as any listed in the 2020–2021 Northeast Vegetable Management Guide (Campbell-Nelson et al., 2020), 2021 New England Tree Fruit Management Guide (https://netreefruit.org/), or 2019–2020 New England Small Fruit Management Guide (https://ag.umass.edu/fruit/ne-small-fruit-management-guide). In R, separate PERMANOVA tests (2000 permutations) were applied to determine whether the frequency at which pest species were present in fecal samples was dependent on bird species, age (hatch year, HY or after hatch year, AHY), breeding stage (breeding or not breeding), sex (for adult birds), capture location (site), or capture year (year). Only bird species for which at least 30 samples were collected and passed all quality filters were included in bird species analyses. Since a significant PERMANOVA result can indicate a difference in the makeup of the communities being compared without a difference in total abundance, binomial GLMs were used to determine whether the predictors found to be significant through PERMANOVA impacted the frequency of consuming any pest species. GLMs were also used for the additional predictor day of year. Because DOY (day of year) and age were correlated, any GLM in which DOY was significant was also tested with age to determine which was a better predictor. DOY and age were also examined for collinearity using their Variance Inflation Factor (VIF). DOY was standardized for all statistical tests by first subtracting the mean and then dividing by the standard deviation. Where bird species was found to be a significant predictor, pairwise comparisons (PERMANOVA and GLM) were performed to determine between-group differences for those groups for which at least one pairwise PERMANOVA test had statistical power of at least 80%. To determine test power, we simulated bird diet data for each species based on our observed frequencies of preying on each pest species and our sample sizes. We repeated this process 3000 times, performing pairwise PERMANOVA tests between all simulated species samples each time, and the percentage of significant results ($p < 0.05$) was considered the test's power. The p-value adjustment proposed by Benjamini and Hochberg (1995) was used to control inflation of type I error rates in pairwise comparisons. For each of the bird species for which pairwise comparisons were sufficiently powerful, PERMANOVA tests were used to determine whether any of the previously mentioned predictors significantly affected that species' pest consumption, with follow-up GLMs used as above. The statistical approach was exactly the same for natural enemy presence in fecal samples as it was for crop pests.

3. Results

During the two summers of field work, 931 samples were collected from 864 unique birds of 53 species. Seven hundred thirty-seven of these samples passed all data quality filters, 93 of which contained a known insect crop pest (12.6%), and 15 of which contained a known natural enemy of crop pests (2.0%). Fifty-three percent of the samples that passed quality filtering were from either song sparrows, gray catbirds, or common yellowthroats. Taxa identified to the species level accounted for 56.3% (n = 2001) of the total ASVs across all samples (n = 3554). ASVs were grouped into 590 unique taxonomic groups, with 416 (70.5%) of these identified by the taxonomic classifier to the species level. Samples included an average of 6.0 species with a standard deviation of 17.3. Twelve pest species were identified in fecal samples: *Drosophila suzukii, Delia platura, Agrotis ipsilon, Amphipyra pyramidoides, Byturus unicolor, Peridroma saucia, Leptinotarsa decemlineata, Lygus lineolaris, Lymantria dispar, Grapholita packardi, Xestia c-nigrum, Xestia dolosa*. Five species of pest natural enemy were found in fecal samples: *Chrysopa oculata, Chrysoperla rufilabris, Orius insidiosus, Toxomerus geminatus*, and *Toxomerus marginatus*. Tables 1 and 2 show the frequency of pest and natural enemy presence in samples for a selection of bird species, while Table 1 shows the pest frequency and total sample size for all bird species. The host plants of pests and the prey of natural enemies, with the references supporting this designation, are presented in Appendix A.

We found that bird species, age, DOY (Fig. 1), and year had a significant impact on the pests present in fecal samples ($p < 0.05$), while site, sex, and breeding stage did not ($p > 0.05$). Results were consistent between PERMANOVA and GLM tests (Table 3). Though DOY and age were correlated (Pearson correlation = 0.45), they were not overly collinear (VIF = 1.25). However, when both DOY and bird age were included in the same GLM, bird age was no longer a significant predictor ($p = 0.35$). Power analysis indicated that the only bird species for which at least one pairwise test had an acceptable (<20%) type II error rate were song sparrow, gray catbird, and common yellowthroat. Pairwise PERMANOVA comparisons indicated that both gray catbird ($p = 0.014$) and common yellowthroat ($p = 0.014$) diets differed from those of song sparrow, but that gray catbird and common yellowthroat diets did not significantly differ

Table 2

The percentage of fecal samples for each bird species containing agricultural insect pest natural enemies. Fecal samples were collected from birds on 11 farms in Western Massachusetts during summer 2019 and 2020. Only bird species for which at least one sample included a natural enemy are shown.

Bird Species	N	Total	*Toxomerus geminatus*	*Toxomerus marginatus*	*Chrysopa oculata*	*Chrysoperla rufilabris*	*Orius insidiosus*
SOSP[1]	148	0.7	0	0	0	0.7	0
GRCA	143	4.2	4.2	0	0	1.4	0
COYE	99	1.0	1.0	0	0	0	0
HOWR	28	10.7	10.7	0	0	0	0
AMRO	10	20.0	10.0	10.0	10.0	0	0
HOSP	7	14.3	0	0	0	0	14.3
DOWO	4	25.0	0	0	0	0	25.0
Total	737	2.0	1.5	0.1	0.1	0.4	0.3

SOSP = song sparrow; GRCA = gray catbird; COYE = common yellowthroat; BCCH = black-capped chickadee; HOWR = house wren; AMRO = American robin; HOSP = house sparrow; DOWO = downy woodpecker.
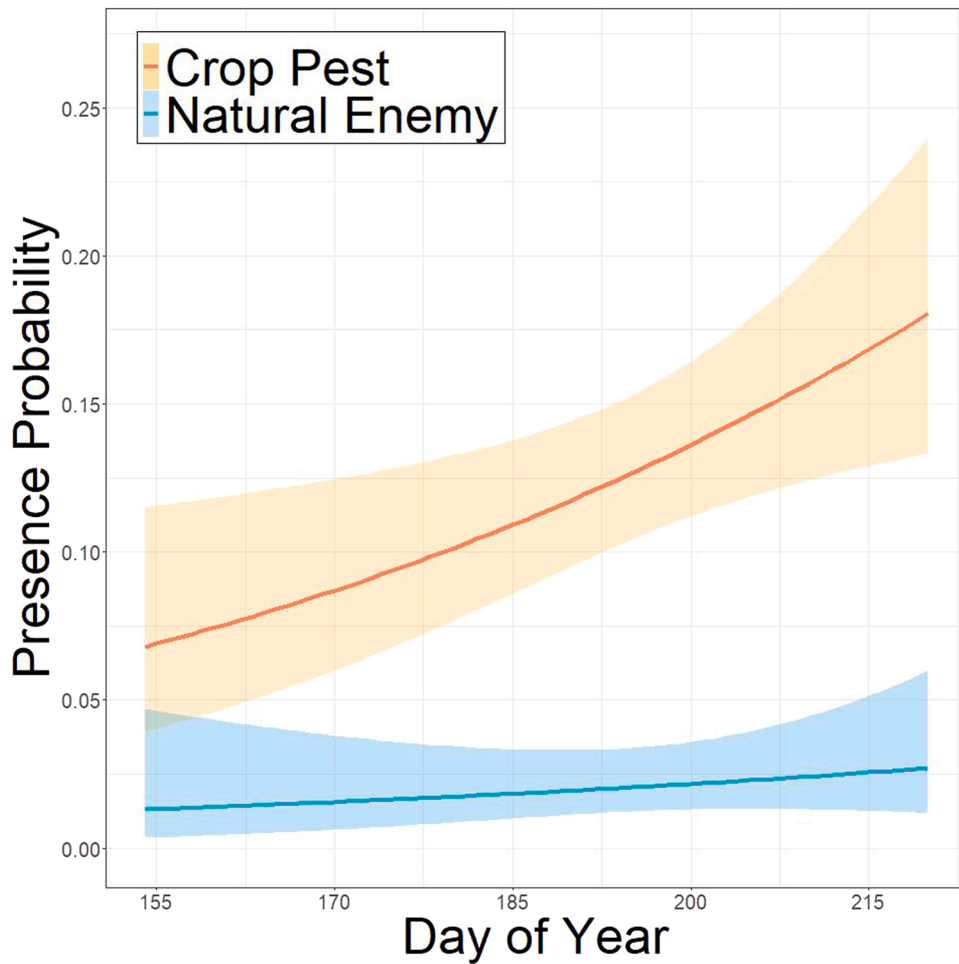
Fig. 1. The probability of presence of crop pests and pest natural enemies in bird fecal samples over the course of the growing season. Fecal samples were collected from birds captured on field edges on 11 western Massachusetts farms during the summers of 2019 and 2020. Pests were present more frequently in fecal samples collected later in the year, while there was no significant effect on natural enemy frequency.

from each other (p = 0.78, Table 4, Fig. 2). Pairwise GLM results were similar to those of the pairwise PERMANOVA tests (song sparrow-gray catbird: p = 0.029; song sparrow-common yellowthroat: p = 0.047; gray catbird-common yellowthroat: p = 0.77). Our single species analyses showed that song sparrow pest consumption was not affected by site, age, DOY, breeding stage, sex, or year (p > 0.05). Of those predictors, only year significantly impacted common yellowthroat pest consumption (PERMANOVA: p = 0.032; GLM: p = 0.013), and only DOY significantly affected gray catbird pest consumption (GLM: p = 0.020).

No predictors were found to significantly affect bird consumption of pest natural enemies in our PERMANOVA tests (p > 0.05), though site and bird species exhibited a non-significant trend (p < 0.1). Single-species PERMANOVAs showed no significant predictors for song sparrows and common yellowthroats. Gray catbird consumption of natural enemies was significantly impacted by site and year for PERMANOVA tests (p < 0.05), and only year for GLMs (p = 0.015).

4. Discussion

We found direct evidence that songbirds on low intensity farms prey on agricultural insect pests. In combination with our experimental demonstration of insect pest control by birds in this same system, the data suggest that this predation leads to significant biological control of some pests (Mayne et al., 2023). This is in line with the findings of Garfinkel et al. (2020), who found direct evidence of songbird predation leading to decreased pest damage. However, unlike Garfinkel et al. (2020), we did not observe birds in our system preying on the pest species which were demonstrably lowered by songbird predation by Mayne et al. (2023). In fact, Colorado Potato Beetle (*Leptinotarsa decemlineata*), the only species found in fecal samples which was also studied by Mayne, was found to increase in abundance when birds were excluded from crops (Mayne et al., 2023). Garfinkel et al., (2020, 2022) found a markedly higher frequency of pest presence in samples than we did and estimated bird density to be higher than Brofsky (2020) observed in our system. The difference in diet may be due to a higher diversity of prey insects available in our lower intensity system (Rosa-Schleich

Table 3

a. Statistical test results, sample sizes, and observed pest and natural enemy frequencies for several potential predictors of songbird pest and natural enemy consumption on 11 low intensity farms in Western Massachusetts. Tests were performed on the entire bird community, and each of the three most abundant bird species independently. PERMANOVA tests were applied separately to the multivariate frequency of pest and natural enemy presence in songbird diets, and GLMs were applied separately to aggregated pest and natural enemy occurrence where significant PERMANOVA results were observed. Pest and natural enemy frequency are reported as the observed percentage of fecal samples including any agricultural pests or natural enemies.

All species		n	Crop Pests				Natural Enemies			
					P				*P*	
Predictor			Frequency[‡]	Coefficient	PERM	GLM	Frequency	Coefficient	PERM	GLM
Species		465			0.04	0.02			0.07	
Site		737			0.94				0.06	
Year	2019	293	8.9		0.009	0.01	2.4		0.66	
	2020	444	15.1				1.8			
Sex	Female	225	12.9		0.13		2.7		0.26	
	Male	235	8.5				1.3			
Age	HY	202	16.8		0.03	0.04	3.0		0.12	
	AHY	510	11.0				1.8			
Breeding	Yes	307	11.6		0.20		2.6		0.51	
	No	309	15.0				1.9			
DOY†	Intercept			-5.20		0.0003		-6.08		0.03
	DOY	465		0.017		0.007		0.011		0.43

Song

b. Statistical test results, sample sizes, and observed pest and natural enemy frequencies for Song Sparrows only. As per Table 3a

Song Sparrow		n	Crop Pests				Natural Enemies			
					P				*P*	
Predictor			Frequency	Coefficient	PERM	GLM	Frequency	Coefficient	PERM	GLM
Site		148			0.63				1.00	
Year	2019	63	4.8		0.18		0.0		1.00	
	2020	85	8.2				1.2			
Sex	Female	20	5.0		0.78		5.0		0.23	
	Male	64	4.9				0.0			
Age	HY	56	8.9		0.53		0.0		1.00	
	AHY	87	5.7				1.1			
Breeding	Yes	60	10.0		0.33		0.0		1.00	
	No	71	5.6				1.4			
DOY†	Intercept			-1.48		0.67		-30.7		0.24
	DOY	148		-0.006		0.74		0.13		0.16

c. Statistical test results, sample sizes, and observed pest and natural enemy frequencies for Gray Catbird only. As per Table3a.

Gray Catbird		n	Crop Pests				Natural Enemies			
					P				*P*	
Predictor			Frequency	Coefficient	PERM	GLM	Frequency	Coefficient	PERM	GLM
Site		143			0.75				0.01	0.15
Year	2019	52	17.3		0.88		9.6		0.03	0.02
	2020	91	17.6				1.1			
Sex	Female	39	20.5		0.28		7.7		0.38	
	Male	40	10.0				2.5			
Age	HY	44	25.0		0.07		4.5		0.81	

Table 3 (*continued*)

		n	Frequency	Coefficient	PERM	GLM	Frequency	Coefficient	PERM	GLM
	AHY	91	14.3				4.4			
Breeding	Yes	49	22.4		0.29		4.1		1.00	
	No	64	14.1				4.7			
DOY†	Intercept			-7.48		0.007		-1.05		0.81
	DOY	143		0.030		0.03		-0.011		0.64

d. Statistical test results, sample sizes, and observed pest and natural enemy frequencies for Common Yellowthroat only. As per Table 3a.

Common Yellowthroat			Crop Pests				Natural Enemies			
					P				*P*	
Predictor		n	Frequency	Coefficient	PERM	GLM	Frequency	Coefficient	PERM	GLM
Site		99			0.93				0.97	
Year	2019	38	5.3		0.03	0.02	0.0		1.00	
	2020	61	23.0				1.6			
Sex	Female	22	13.6		0.93		4.5		0.35	
	Male	43	11.6				0.0			
Age	HY	32	21.9		0.26		0.0		1.00	
	AHY	63	12.7				1.6			
Breeding	Yes	46	19.6		0.61		0.0		0.40	
	No	30	13.3				3.3			
DOY†	Intercept			-1.70		0.56		-4.74		0.66
	DOY	99		0.0003		0.99		0.0008		0.99

†DOY (day of year) Frequency reported as model estimates on the logit scale in standardized units; HY = hatch year, AHY = after hatch year.

et al., 2019; Sirami et al., 2019). Our results and those from Mayne et al. (2023) indicate that even with a lower density of birds and pests making up a lower portion of their diets, birds can still significantly impact pest populations. The relative farming intensity of Garfinkel et al.'s study system compared to ours likely contributed to these differences, with our lower intensity system providing birds with a larger diversity of insect prey (Rosa-Schleich et al., 2019; Sirami et al., 2019). Thus, birds still had a significant impact on pest populations in our system even with a lower density and lower frequency of pest consumption than reported by Garfinkel et al., (2020, 2022).

Of species for which enough data were collected, gray catbirds and common yellowthroats appear to be more beneficial than song sparrows, though a number of factors can affect that conclusion. For example, though we showed that gray catbirds and common yellowthroats prey on agricultural pests at a higher frequency than song sparrows, differences in maximum bird densities and total individual food consumption would be required to determine which species' population removes pests at a higher rate. For example, common yellowthroat individuals (10.3 ± 0.98 g in our study) likely consume less total biomass than either song sparrows (20.3 ± 1.54 g) or gray catbirds (35.9 ± 2.40 g) based on the allometric relationship between mass and energy consumption (Daan et al., 1990). Additionally, song sparrows are more than twice as abundant in our system than gray catbirds or common yellowthroats (Brofsky, 2020), making total pest consumption by song sparrows higher in comparison than their pest consumption per individual. Assuming that fecal samples are proportional to total food intake, a rough calculation of population level pest removal can be found by multiplying together pest consumption and species abundance (from Brofsky, 2020). This shows that gray catbirds and song sparrows provide a similar total reduction in pests, while common yellowthroats provide slightly over a third of the pest removal as the other two species. Pest DNA was also detected in black-capped chickadee and American redstart feces, and thus they were also likely providers of insect pest control, though their sample sizes were too small to allow robust statistical analyses.

Another important consideration in the economic value of each species is their negative effects on crops. One of the major complaints directed at birds in our system was their direct frugivory on berry crops (e.g., blueberries, strawberries, blackberries). While we could not determine crop frugivory, we did note whether berries (wild or cultivated) were present in a subset of our fecal samples during collection. We found that 60 of 78 gray catbird fecal samples (76.9%) included berries, while only 1 of 71 song sparrow samples (1.4%) and 0 of 49 common yellowthroat samples contained berries. While it is likely that many or most of these berries were not from crops, there appears to be a higher risk of crop frugivory by gray catbird than the other two species. Though direct frugivory can be an issue, a recent study in strawberry production determined that the damage from frugivory by birds was roughly comparable to the amount of damage they prevented through insect pest control (Gonthier et al., 2019). They also found that increased semi-natural habitat was associated with decreased frugivorous bird abundance, leading to lower crop damage (Gonthier et al., 2019). When determining which species are the most beneficial, it is important to consider the trade-offs between pest consumption, natural enemy consumption, and direct crop damage.

Birds may also decrease crop output by suppressing arthropod natural enemies of crop pests (Martin et al., 2013). The bird community in our study preyed on pest species at approximately 6 times the rate that they preyed on natural enemies (12.6% vs 2.0%). However, because predation does not always affect lower trophic levels at a 1:1 ratio (Müller and Brodeur, 2002; Rosenheim et al., 1995), this does not necessarily mean that birds provide more services through pest control than disservices through natural enemy suppression. Nonetheless, for three crop types in this system (brassica, cucurbit and solanaceous), bird predation appears to be beneficial or have negligible effects on pest abundance and damage in this system (Mayne et al., 2023). Our reference list of pest natural enemies (19 species) may also be less comprehensive than that of crop pests (193 species), which would result in missed natural enemies in fecal samples and a lower natural enemy presence estimate. While the publications used to identify pests were designed to give detailed information about economically important pest species, they were not necessarily made to do the same for beneficial species.

Using Brofsky's (2020) survey of New England farmland birds and their habitat associations, we can make some management recommendations to promote pest control, but it is important to note that many of the abundant species in our system are not well represented in our dataset: Common yellowthroats, gray catbirds, and song sparrows are all associated with tall, woody habitats (generally nonproductive) as opposed to productive herbaceous cover. Increasing natural habitat features (e.g., hedgerows) and land cover will likely promote gray catbird and common yellowthroat abundance, while increased productive and developed cover will have negative impacts (Brofsky, 2020). Several other relatively abundant farmland species frequently had pests in their feces (>20% of samples), including eastern phoebes, chipping sparrows, and house sparrows, warranting further study. Our observation that the three bird species that were responsible for the majority of the pest consumption (song sparrow, gray catbird and common yellowthroat) are shrubland birds associated with open canopy conditions (Schlossberg and King, 2007) and thus would be most likely to occur in crops (Brofsky, 2020) makes it unclear whether their relative effectiveness as predators of agricultural pests is due to dietary preferences by birds, or just an artifact of their habitat associations that make them more likely to encounter pests during foraging. Regardless,

Table 4

Pairwise comparisons of pest consumption frequency between the three bird species for which sample sizes provided enough power to perform statistical tests. PERMANOVA tests were applied to the multivariate frequency of pest presence in songbird diets, and GLMs were applied to aggregated pest occurrence across insect species. Scientific names provided in Table 1.

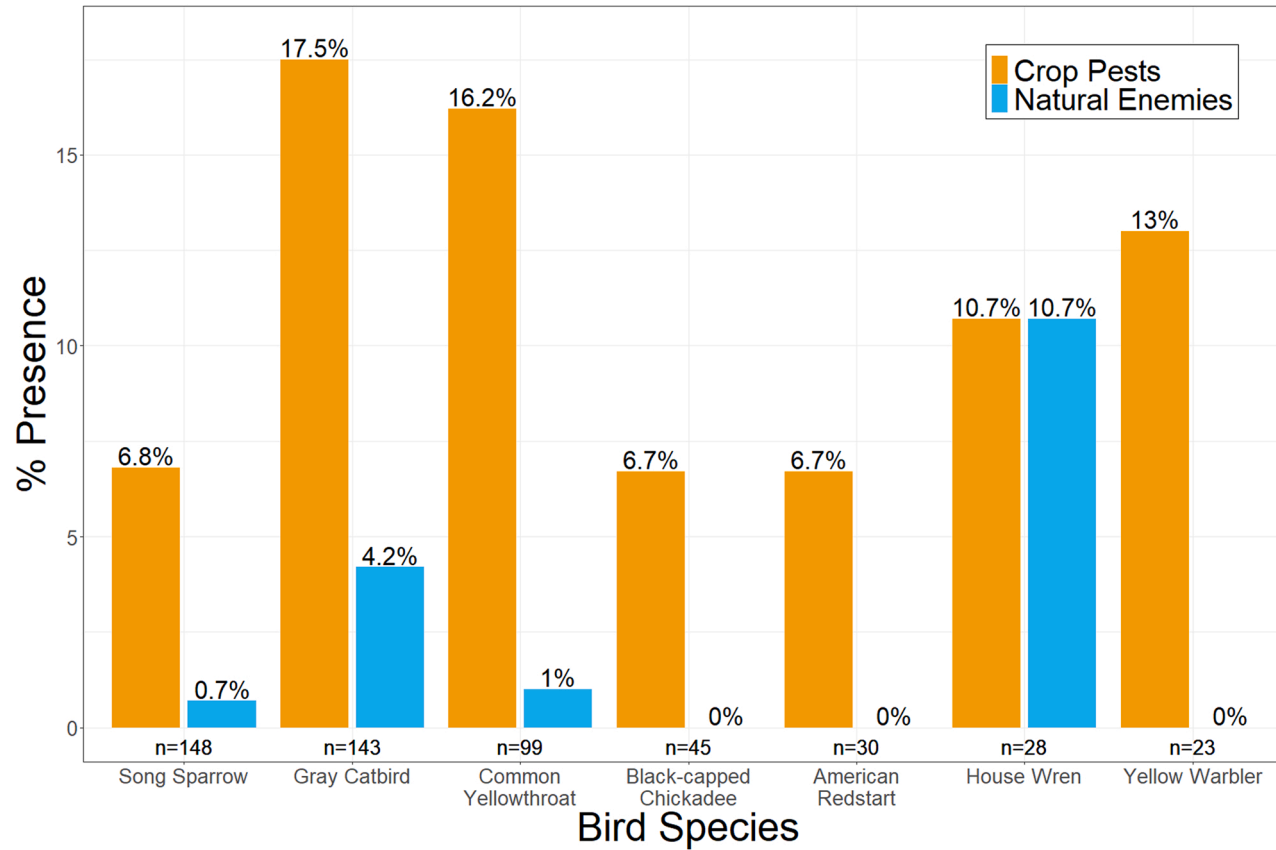|	Song sparrow		Gray catbird	
	PERM	GLM	PERM	GLM
Gray catbird	0.014 *	0.029 *		
Common yellowthroat	0.014 *	0.047 *	0.783	0.771

Fig. 2. The percentage of fecal samples, collected from birds on 11 Western Massachusetts farms, that contained crop pests and pest natural enemies is shown. The percentage containing crop pests is shown in orange, and the percentage containing natural enemies is shown in blue. The total number of samples collected for each bird species is shown below the bars. Bird scientific names can be found in Table 1.

enhancing habitat for these three species should enhance pest control.

We did not find that American robins, the second most abundant species on New England farms, preyed on pests, but were able to collect ten fecal samples for this species, limiting our ability to draw conclusions. Notably, two of the ten fecal samples from American robin included natural enemies. House wrens also preyed on natural enemies at a rate higher than most species, with 3 of 28 fecal samples (10.7%) including a natural enemy, the same proportion as included crop pests. Barn swallows, eastern kingbirds, and killdeer are all highly insectivorous species that frequently forage in and above farm fields, but our bird capture technique was not suited to collecting samples from them. Targeted approaches to determine these species' diets may be warranted due to their high potential for pest control. While we show the relative level of pest consumption between three of the most abundant New England farmland birds and present qualitative findings on many others, many important species, due to abundance or high insectivory, merit further study.

Several factors other than species identity predicted pest consumption. Birds ate pests more frequently later in the year, and hatch-year birds were more likely to eat pests. These two variables were moderately correlated (Pearson correlation = 0.45), so it is possible that one or the other is primarily driving the relationship. In fact, when the two predictors were included in the same GLM, bird age was no longer a significant predictor, suggesting that day of year was driving the relationship. This may be a result of birds taking greater advantage of pests later in the year when pest abundance has Increased drastically. There was also a significant difference in pest frequency between collection years, with pests more prevalent in 2020 than 2019. This may be a response of birds to changes in pest population abundance, but no data are available on the relative abundance of pests between the two years. It is also possible that this represents decay of DNA in fecal samples over time, as the 2019 samples were frozen for a longer time before DNA extraction than those from 2020. Samples should be stable at $-80\,^{\circ}C$, but presence of digestive fluids along with fluctuations in freezer temperature may have had an impact on genetic material over time. We found no evidence that pest consumption differed between sexes or that breeding affected birds' pest or natural enemy consumption. Site also did not affect pest consumption, likely because all farms practiced heavy intercropping and crop rotation, meaning that a wide variety of pests would be available to any given bird and availability changed over the course of the year and between years. Ultimately, bird species appears to be the most important determinant of pest consumption that growers can control through land management.

Finally, it is important to recognize the limitations to our study because of the genetic techniques used. While DNA metabarcoding is a powerful minimally invasive method to determine insect presence in fecal samples, it comes with several built-in constraints. The primers used in PCR often have taxon-specific rates of DNA amplification. This means that 1) at present, we cannot accurately determine relative abundance of species in a sample, limiting us to presence-absence data (Elbrecht and Leese, 2015; Jusino et al., 2019), and 2) the presence or absence of species may depend on the primer pairs used (Jusino et al., 2019). Additionally, PCR conditions can have significant impacts on amplification, and bias can occur at the sequencing stage as well (Jusino et al., 2019). Though we used the more biased primers (ZBJ) according to Jusino et al. (2019), we found that PCR success assessed by gel electrophoresis was more consistent with these primers than the lower bias ANML primers they present, under a wide range of PCR conditions. PCR is also capable of detecting the gut contents of insects present in bird fecal samples, making it possible that observed species are present due to consumption of their predators. This could explain the prevalence of *L. decemlineata* in fecal samples even though bird predation appears to release them from biocontrol in this system (Mayne et al., 2023), though we did not find *L. decemlineata* DNA in the same samples as any of its known natural enemies (Mayne et al., 2023).

Multiple decisions along the bioinformatic pipeline may also affect results. For instance, Ie method by which ASVs are assigned to taxa, and the reference data used for those classifications can have profound impacts on the classifications (O'Rourke et al., 2020). Our approach, using two reference databases and naïve-Bayes classifiers, was designed to maximize specificity of taxonomic classification, while minimizing inaccurate classifications. Differences in lab and data processing can have large impacts on results, making it crucial to consider these factors when making comparisons between studies.

5. Conclusion

We present the relative frequency of agricultural pests in the diets of a number of farmland bird species. We found crop pests in fecal samples more frequently than pest natural enemies. Though we found that pests were present in a smaller percentage of fecal samples than in a previous, similar study (Garfinkel et al., 2020), when considered alongside the conclusions of Mayne et al. (2023) based on exclosure experiments in this same system we can see that birds can provide significant pest reduction without pests making up a large portion of their diet. Of the species for which we had at least 30 samples, gray catbirds and common yellowthroats ate pest insects most frequently. While these species are only a portion of the likely biocontrol providers in the area, promotion of their preferred habitats, non-crop woody vegetation, will likely provide increased pest control. Further work to evaluate the role of other bird species and to determine population characteristics of the region's songbirds would allow more fine-tuned land management to improve ecosystem services. Additionally, improvement and standardization of diet analysis techniques would allow more precise conclusions and better comparisons between studies. In general, our results lend more support to the common conclusion that increasing non-crop habitats promotes agricultural insect pest control by supporting pest natural enemy abundance.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

Acknowledgments

Appendix A. The classification of pests and natural enemies as generalists or specialists, and which crops or pests (respectively) they impact, for species encountered on 11 farms in Western Massachusetts during summer 2019 and 2020. The information presented is from the following University of Massachusetts fact sheets and growing guides, except where otherwise noted: https://ag.umass.edu/vegetable/fact-sheets/insects; https://ag.umass.edu/fruit/publications; https://ag.umass.edu/vegetable/publications

Pest species	Host
Drosophila suzukii	fruits
Delia platura	corn, beans, peas, other seeds & seedlings
Agrotis ipsilon	most vegetable pants, alfalfa/clover, strawberry
Amphipyra pyramidoides[1]	leaves of apple, raspberry, grape, walnut
Byturus unicolor	fruit, fruit flowers
Peridroma saucia	vegetables, fruits, orchard fruits
Leptinotarsa decemlineata	Solanaceae
Lygus lineolaris	fruits, veggies, orchard fruits, very broad, disease transfer
Lymantria dispar[2]	apple
Grapholita packardi	fruits, Rosaceae, blueberry
Xestia c nigrum[3]	peppermint, alfalfa, other vegetables, grasses, grains
Xestia dolosa[4]	barley, clovers, corn, tobacco, apples
Natural Enemy Species	Prey
Chrysopa oculata[5]	larvae/soft, small insects, eggs/aphids, eggs, mites, mealybugs, small caterpillars
Chrysoperla rufilabris[6]	larvae/soft, small insects, eggs/aphids, eggs, mites, mealybugs, small caterpillars, beetle larvae (incl. Colorado potato beetle)
Orius insidiosus[7]	thrips, mites, aphids
Toxomerus geminatus[8]	aphids, thrips, leaf hoppers, small caterpillars
Toxomerus marginatus[8]	aphids, thrips, leaf hoppers, small caterpillars

[1] https://www.canr.msu.edu/ipm/diseases/humped_green_fruitworm

[2] https://ag.umass.edu/landscape/fact-sheets/spongy-moth

[3] http://pnwmoths.biol.wwu.edu/browse/family-noctuidae/subfamily-noctuinae/tribe-noctuini/xestia/xestia-c-nigrum/, Floate, K.D. 2017. Cutworm pests on the Canadian Prairies: Identification and management field guide. Agriculture and Agri-Food Canada, Lethbridge, Alberta.

[4] Floate, K.D. 2017. Cutworm pests on the Canadian Prairies: Identification and management field guide. Agriculture and Agri-Food Canada, Lethbridge, Alberta.

[5] https://biocontrol.entomology.cornell.edu/predators/Chrysoperla.php

[6] https://biocontrol.entomology.cornell.edu/predators/Chrysoperla.php

[7] https://ag.umass.edu/greenhouse-floriculture/fact-sheets/western-flower-thrips-management-tospoviruses

[8] Skevington, J. H., Locke, M. M., Young, A. D., Moran, K., Crins, W.J., and Marshall, M. A. 2019. Field Guide to the Flower Flies of Northeastern North America. Princeton University Press, 2019. ISBN: 9780691192512; https://ag.umass.edu/sites/ag.umass.edu/files/pdf-doc-ppt/insectary_2018_report.pdf

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