Avian Behavior, Ecology, and Evolution

Tritrophic interactions with avian predators: the effect of host plant species and herbivore-induced plant volatiles on recruiting avian predators

Interacciones tritróficas con depredadores de aves: el efecto de las especies de las plantas hospederas y los volátiles de plantas inducidos por herbívoros en el reclutamiento de aves depredadores

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ABSTRACT. Herbivore-induced plant volatiles (HIPVs) are important signaling compounds released by plants upon wounding. These compounds have been shown to mediate tritrophic interactions in recruiting insect predators and parasitoids. Recent work has begun to show that avian species, which were once thought to have a very limited sense of smell, can cue in on these HIPVs to find insect prey. Here, we test the ability for two general HIPVs, methyl jasmonate and methyl salicylate, to recruit avian predators. We test the recruitment efficacies of these HIPVs across four different host plant species, black walnut (*Juglans nigra*), red maple (*Acer rubum*), cattail (*Typha latifolia*), and wheat (*Triticum aestivum*), and use clay caterpillars to quantify predation by insectivorous birds. We found no significant differences in predation between treatment groups across any of our host plants. However, there was a nearly significant effect of methyl salicylate in black-walnut trees. Interestingly, our results did show a significant effect of host plant species on predation levels. The two tree species, particularly black walnut, had higher levels of predation than the herbaceous species. We discuss the implications of these results and suggest a number of ideas and suggestions for future studies investigating the role of HIPVs in attracting insectivorous birds.

RESUMEN. Los compuestos volátiles de plantas inducidos por herbívoros (HIPV, por sus siglas en inglés) son importantes compuestos de señalización liberados por las plantas al sufrir un daño. Se ha demostrado que estos compuestos median interacciones tritróficas en el reclutamiento de insectos depredadores y parasitoides. Trabajos recientes han comenzado a mostrar que las especies de aves, que alguna vez se pensó que tenían un sentido del olfato muy limitado, pueden aprovechar estos HIPV para encontrar sus presas, insectos. Aquí, probamos la capacidad de dos HIPV comunes, jasmonato de metilo y salicilato de metilo, para reclutar aves depredadoras. Probamos las eficacias de reclutamiento de estos HIPV en cuatro especies diferentes de plantas hospederas, nogal negro (*Juglans nigra*), arce rojo (*Acer rubum*), totora (*Typha latifolia*) y trigo (*Triticum aestivum*), y usamos orugas de arcilla para cuantificar la depredación por aves insectívoras. No encontramos diferencias significativas en la depredación entre los grupos de tratamiento en ninguna de nuestras plantas hospederas. Sin embargo, hubo un efecto casi significativo del salicilato de metilo en los nogales negros. Curiosamente, nuestros resultados mostraron un efecto significativo de las especies de plantas hospederas sobre los niveles de depredación. Las dos especies de árboles, particularmente el nogal negro, tuvieron niveles más altos de depredación que las especies herbáceas. Discutimos las implicaciones de estos resultados y sugerimos una serie de ideas y sugerencias para futuros estudios que investiguen el papel de los HIPV en la atracción de aves insectívoras.

Key Words: *herbivore; herbivore-induced plant volatile (HIPV); insectivorous birds; methyl jasmonate; methyl salicylate; olfaction; tritrophic interactions*

INTRODUCTION

Historically, it was thought that birds lacked the ability to smell (Caro and Balthazart 2010, Caro et al. 2015). However, bird species do possess functional olfactory bulbs (Bang and Cobb 1968) and genomic studies into olfactory receptor (OR) gene diversity have shown the presence of many intact OR genes across a wide range of avian taxa, with evidence of positive selection on and ecological factors influencing the evolution of taxa-specific subgenomes (Khan et al. 2015). Two model avian species, the zebra finch (*Taeniopygia guttata*) and chicken (*Gallus gallus*), possess 134 and 214 intact OR genes, respectively, that contribute to their sense of smell (Steiger et al. 2009). Genomic investigations into the OR repertoire of other avian species, including the gamma-c subfamily, which is unique to birds, are continually receiving more attention (Driver and Balakrishnan 2021).

Further, much recent behavioral work has demonstrated that birds use odor in many important ecological contexts, such as in mate choice and species recognition (Bonadonna and Mardon 2013, Zhang et al. 2013, Van Huynh and Rice 2019, 2021), kin recognition (Fracasso et al. 2019), predator avoidance (Amo et al. 2008, 2011, Roth et al. 2008, Stanbury and Briskie 2015, Lee 2021), nesting (Petit et al. 2002, Gwinner and Berger 2008, Shutler 2019), foraging (Hutchinson and Wenzel 1980, Yang et al. 2015, Hiltpold and Shriver 2018, Saavedra and Amo 2018a, Potier et al. 2019, Potier 2020), and navigation (Pollonara et al. 2015, Abolaffio et al. 2018, Zannoni et al. 2020). Here, we assess the ability for birds to cue in on plant volatiles to locate insect prey.

Olfaction plays a key role for many vertebrate predators to identify and locate prey (Gardiner and Atema 2007, Conover 2007, Johannesen et al. 2012). Several songbird species have been shown

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to use the pheromones of their prey to find their location. For example, songbirds have been shown to cue in on the sex pheromones of winter moths (*Operophtera brumata*; Saavedra and Amo 2018a, Amo and Saavedra 2021) and the larval aggregation pheromone of carpenter worms (Díaz-Siefer et al. 2021). Other non-passerine species such as African penguins (*Spheniscus demersus*; Cunningham et al. 2008) and numerous procellariiformes (Nevitt 2000) have been shown to cue in on odor sources such dimethyl sulfide released by phytoplankton to find food.

In the context of herbivory, plants are known to mediate tritrophic interactions by recruiting herbivore predators through the production of herbivore-induced plant volatiles (HIPVs; Heil 2008). These volatile compounds are released by plants in response to wounding by herbivores (Arimura et al. 2009) and have been shown to attract insectivores (Kaplan 2012) and herbivore parasites, most notably parasitoid wasps (McCormick et al. 2012, Aartsma et al. 2017). These HIPVs show great structural variety, with many species showing unique species-specific blends of volatile organic compounds (Van Den Boom 2004, Mäntylä et al. 2008, 2017, Amo et al. 2013, Becker et al. 2015, Koski et al. 2015, Aartsma et al. 2017, Joo et al. 2017), while other more general HIPVs such as methyl jasmonate (Wasternack and Parthier 1997, Paré and Tumlinson 1999, Cheong and Choi 2003) and methyl salicylate (Rodriguez-Saona et al. 2011) are found across many plant taxa. Recent work has shown that species-specific HIPV blends may be used by birds to cue in on insect prey (Mrazova et al. 2019, Mäntylä et al. 2004, 2008, 2017, Hiltpold and Shriver 2018, Sam et al. 2021). For example, a field experiment conducted by Hiltpold and Shriver (2018) showed the attraction of a wild bird population to the specific HIPV released upon herbivory by maize. However, this effect may be specific to certain plant species. HIPVs of apple trees (*Malus silvestris*) seemed to attract insectivorous birds (Amo et al. 2013), while HIPVs of mountain birches (*Betula pubescens* and *Betula pendula*) seemed to have no such effect (Koski et al. 2015). A number of studies have attempted to investigate the ability for more general HIPVs found in many plant species, such as methyl jasmonate, to recruit avian predators; however, the results have been unclear (Amo et al. 2013, Mäntylä et al. 2014, Mrazova and Sam 2018, Saavedro and Amo 2018b, Mrazova et al. 2019). The general HIPV methyl salicylate has received less attention in this context but seems to show a clearer attractive effect (Rubene et al. 2019). In the current study, we aim to (1) further elucidate the role of these two common plant HIPVs methyl jasmonate and methyl salicylate in recruiting wild avian predators, and on which the previous literature is either in conflict or is lacking, respectively, and (2) investigate the capacity for wild birds to cue in on these general HIPVs across different plant species in the wild.

METHODS

Study location
We aimed to simultaneously assess the capacity for common plant HIPVs to attract insectivorous birds across several different host plants. We placed experimental setups at 15 sites on the DeSales University campus in east-central Pennsylvania (40°32′19″N, -75° 22′44″W; total area of experimental location: 1.5km x 1.5km). Each site contained one of four host plant species selected for this study: red maple trees (*Acer rubum*), black walnut trees (*Juglans nigra*), common wheat (*Triticum aestivum*), and broad-leaved cattails (*Typha latifolia*). We wanted to test two woody and two herbaceous plants within one general location (DeSales University campus) to control for location-specific variation. We chose these particular host species for their sufficient population size and distribution within our study location. Of the 15 sites, we used four wheat sites, three cattail sites, four red maple sites, and four black walnut sites.

Experimental setup
Methyl jasmonate and methyl salicylate are two general HIPVs found in many plant species (Wasternack and Parthier 1997, Paré and Tumlinson 1999, Cheong and Choi 2003, Rodriguez-Saona et al. 2011). However, the capacity for insectivorous birds to cue in on these HIPVs to find insect prey is unclear concerning methyl jasmonate (Amo et al. 2013, Mäntylä et al. 2014, Mrazova and Sam 2018, Saavedro and Amo 2018b, Mrazova et al. 2019) and has only been studied once in a non-natural context concerning methyl salicylate (Rubene et al. 2019). To assess the role of the methyl jasmonate and methyl salicylate in recruiting avian predators in the wild, we prepared three volatile treatments: methyl jasmonate (Methyl Jasmonate 95%, Sigma-Aldrich®) diluted to 0.76M in hexane, methyl salicylate (Methyl Salicylate ReagentPlus®, ≥ 99% (GC), M6752) diluted to 0.76M in hexane, and a pure hexane solution as a control. These solutions were aliquoted into 2 mL screw-cap dispenser vials (Thermo Scientific! 9 mm glass screw top vials) with rubber septa caps (9 mm screw thread cap, black polypropylene, natural rubber/PTEF septa, 1.0 mm thick).

In order to quantify instances of avian attacks, we prepared model caterpillars using green clay (Sculpey III®, Leaf Green, Polyform Product Company, USA). We rolled 2.5 g of clay into 5 cm lengths and then scrunched each caterpillar into an inchworm-like position. Using artificial caterpillars has been shown to be a reliable method to assess insectivorous bird predation (Mäntylä et al. 2008, Tvardikova and Novotny 2012, Low et al. 2014, Koski et al. 2015, Sam et al. 2015a, b, Mrazova and Sam 2018, Saavedra and Amo 2018a, b, Hiltpold and Shriver 2018).

Experimental setup occurred on 18 June 2021. At each site, we selected three host plant individuals (black walnut and red maple) or three host plant clusters (cattails and wheat) that were ~20 m apart. Each individual host plant or cluster was randomly assigned a different HIPV treatment group: methyl jasmonate, methyl salicylate, or a hexane control. Each host plant or cluster had three clay caterpillars spaced ~60 cm apart with a dispenser vial containing the HIPV treatment placed equidistant from all three caterpillars. A capillary tube (Chemglass Capillary Melting Point Tubes, 0.25 mm thick, 100 mm long, VWR 80061-548) was inserted into each treatment vial through the cap and sealed around the edges using parafilm, allowing for a slow release of the volatile mixture through the capillary tube (Fig. 1b). Clay caterpillars were attached to host plants using clear super glue (The Original Super Glue Corporation; Fig. 1a). Vials were attached to host plants using a combination of parafilm and SuperGlue (Fig. 1b). For woody host plants (black walnut and red maple), the caterpillars and vials were placed on the lowest branches ~1.5 m above the ground. For herbaceous host plants

(cattails and wheat), the caterpillars and vials were placed near the bottoms of the plants (~0.5 m and ~3 cm above the ground for cattails and wheat, respectively).

Fig. 1. (a) Clay caterpillar glued to a host red maple tree. (b) HIPV solutions or hexane controls were slow-released from glass vials punctured with a capillary tube. The glass vials were glued to the host plant and reinforced with parafilm. (c) Clay caterpillar with peck marks.

Data collection

Following setup, each of the 15 sites was visited and avian predation data was collected between 9:00 and 13:00 on the following dates: 20 June 2021, 23 June 2021, 25 June 2021, 27 June 2021, 29 June 2021, and 1 July 2021. We recorded the number of caterpillars pecked (0–3), the total number of unambiguous pecks found (1, 2, 3, 4, etc.), and if the site was visited by an avian predator, i.e., whether or not there was at least 1 peck (Y/N; Fig. 1c). Additional observations were also recorded, e.g., if a caterpillar was missing, destroyed beyond ability to distinguish peck marks, etc.

After we recorded the data on each collecting day, predated caterpillars were repaired and smoothed over using additional clay if necessary. If repair was not possible, the caterpillar was replaced. Missing caterpillars were also replaced. The amount of solution in the dispenser vials was checked and replaced with a new vial and solution if low.

Statistical analyses

Predation events that were not clearly of avian origin were ignored, as were events resulting in missing caterpillars. In total, of the 810 caterpillars that could have possibly been checked (15 sites x 3 treatments x 3 caterpillars x 6 days), 46 went missing. To conservatively account for the caterpillars that went missing over the course of the experiment, we divided two of our dependent variables, the total number of pecks and the total number of caterpillars pecked, by the total number of caterpillars that were checked over the 6 data collection days of the experiments for each site.

We ran all statistical analyses using the statistical software R (R Core Team 2021). We analyzed our data with a mixed-effects model using the R-package "lme4" (Bates et al. 2015) with the fixed effects of host plant, treatment, and their interaction (host plant x treatment). We also included the random effects of site location. We analyzed our mixed-effects model with a type II Anova using the R-package "car" (Fox and Weisberg 2019). We performed follow-up pairwise comparisons by comparing the marginal means with a Tukey-adjusted p-value to account for multiple comparisons using the R-package "emmeans" (Lenth 2021).

We observed variation in the collected data for each host plant across the different sites. To investigate this further, we performed Levene tests for homogeneity of variances between the different host plants. We performed follow-up pairwise comparisons by computing Tukey honest significant differences between the average variation between species.

RESULTS

Our mixed-effects model showed a near-significant effect of host plant as well as the interaction between host plant and treatment on the total relative number of pecks (Table 1, Fig. 2). Although these effects were not significant in the omnibus test, pairwise comparisons suggest that methyl salicylate attracted more predation than the control on black walnut trees (t-ratio: -3.514, p = 0.0053). There was a significant effect of the host plant species on the total relative number of caterpillars pecked (Table 1, Fig. 3) and on the total number of visits (Table 1, Fig. 4). Pairwise comparisons for the number of caterpillars pecked showed that black walnut trees attracted more predator activity than wheat (t-ratio: -1.127, p = 0.0313). Additionally, there was a significant difference between the number of visits recorded for black walnut trees vs. wheat (t-ratio: 4.269, p = 0.0062) as well as a near-significant difference between the number of visits recorded for red maple trees and for wheat (t-ratio: 2.956, p = 0.0547).

Table 1. Analysis of variance (type II test) of our mixed-effects models for three measures of predation: total relative pecks, total relative caterpillars pecked, and total visits. Each model included the fixed effects of treatment, host plant, and treatment x host plant. Significant p-values are denoted with an asterisk.

	χ^2	df	p-value
Total relative pecks			
treatment	3.29	2	0.193
host plant	6.83	3	0.078
treatment x host plant	10.83	6	0.094
Total relative caterpillars pecked			
treatment	2.53	2	0.283
host plant	12.1	3	0.007*
treatment x host plant	9.1	6	0.168
Visits			
treatment	1.75	2	0.42
host plant	20.29	3	< 0.001*
treatment x host plant	7.8	6	0.253

We found a significant difference in the variation of the total number of caterpillars pecked between host plants (Table 2). There was also a near-significant difference in the variation of the total number of pecks (Table 2). In contrast, there was no difference in the number of visits (Table 2). Specifically, there was the highest variation in the number of caterpillars pecked across the red maple sites in comparison to the wheat (p = 0.01). This variation was mainly driven by much higher overall predation activity at one red maple site.

Fig. 2. Mean number of relative total pecks per treatment group within each host plant over the duration of the experimental period. Standard error bars are shown as whiskers. Although the omnibus test was not significant, the pairwise comparison between methyl salicylate (MeSa) and the control on black-walnut host plants was significant. MeJa, Methyl jasmonate.
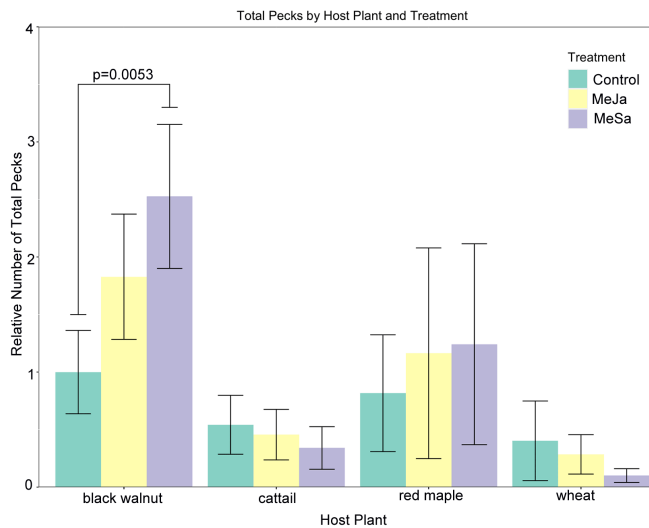

Total Pecks by Host Plant and Treatment

Fig. 4. Total number of avian predator visits per treatment group within each post plant over the duration of the experiment. Standard error bars are shown as whiskers. Black walnut host plants showed higher levels of overall visits compared to wheat host plants. MeJa, Methyl jasmonate; MeSa, methyl salicylate.

Total Visits by Host Plant and Treatment

Fig. 3. Mean number of relative caterpillars pecked per treatment group within each host plant over the duration of the experiment. Standard error bars are shown as whiskers. Black walnut host plants showed higher levels of overall relative caterpillars pecked compared to wheat host plants. MeJa, Methyl jasmonate; MeSa, methyl salicylate.
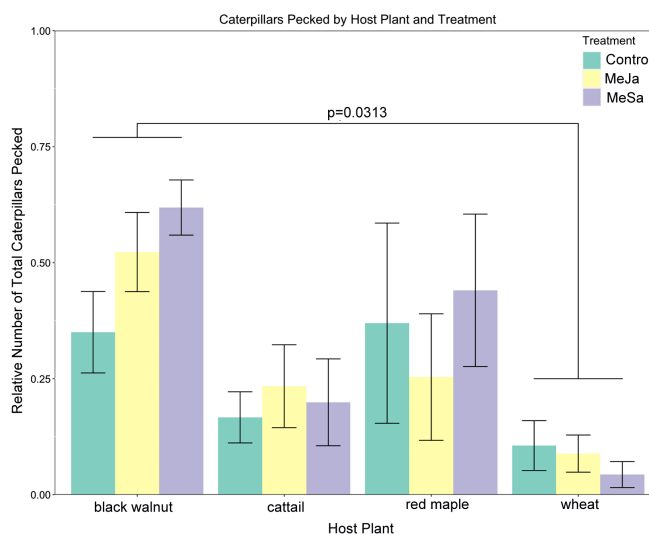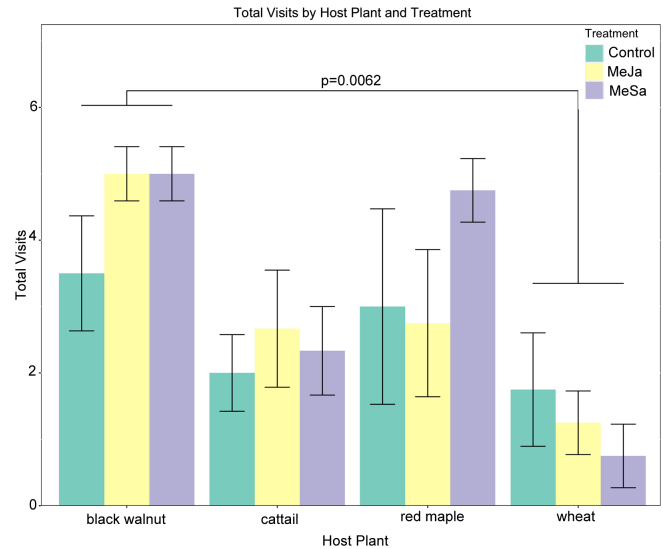

Caterpillars Pecked by Host Plant and Treatment

Table 2. Levene tests for homogeneity of variances between different host plants for three measures of predation: total relative pecks, total relative caterpillars pecked, and total visits.

	df	SS	MS	F	p-value
Total relative pecks					
host plant	3	4.776	1.5921	2.675	0.0597
residual	41	24.401	0.5951		
Total relative caterpillars pecked					
host plant	3	0.2159	0.07196	3.923	0.015*
residual	41	0.7521	0.01834		
Visits					
host plant	3	5.51	1.835	1.501	0.229
residual	41	50.14	1.223		

DISCUSSION

The role of odor in mediating ecologically important behaviors in birds has only recently started to receive interest (Caro and Balthazart 2010, Caro et al. 2015). Here, we tested the ability of insectivorous birds to cue in on two common HIPVs, methyl jasmonate and methyl salicylate, to find insect prey. These two compounds are important HIPVs known to mediate tritrophic interactions between plants, herbivores, and predators and parasitoids (Heil and Silva Bueno 2007).

We found many instances of predation on our model caterpillars (Fig. 1c). Although we did not directly observe or film these predation events, common insectivorous bird species in our study area include passerines such as catbirds, titmice, bluebirds, and blue jays, and near passerines such as woodpeckers. We did not

find any significant differences in any of our measures of predation between methyl jasmonate, methyl salicylate, and control treatments (Table 1). Past studies on the efficacy of methyl jasmonate in recruiting avian predators has yielded conflicting results (Amo et al. 2013, Mäntylä et al. 2014, Mrazova and Sam 2018, Saavedro and Amo 2018b, Mrazova et al. 2019). Together with this previous work, our results suggest that methyl jasmonate may not be a reliable cue used by birds to find insect prey. In several other plant species more complex blends species-specific HIPV compounds seem to show clearer attractive effects (Mäntylä et al. 2004, 2008, 2017, Hiltpold and Shriver 2018, Mrazova et al. 2019, Sam et al. 2021). We suggest that future studies focus on identifying and testing the species-specific volatile profiles released upon wounding. Interestingly, we did find a near-significant attractive effect of methyl salicylate on recruiting avian predators to black walnut trees (Table 1, Fig. 1). Although the literature is unclear on the recruitment effect of methyl jasmonate (Amo et al. 2013, Mäntylä et al. 2014, Mrazova and Sam 2018, Saavedro and Amo 2018b, Mrazova et al. 2019), methyl salicylate has previously been found to be attractive to birds (Rubene et al. 2019). Taken together, our results suggest that methyl salicylate may be a better general HIPV candidate for future study.

Although we did not find a significant omnibus effect of treatment, our data show a strong effect of host plant species on recruiting avian predators (Table 1). Specifically, predation levels were higher overall in the two tree species we tested compared to the two herbaceous species. This effect was significant in between black-walnut to wheat plants (Figs. 3 and 4). Investigating the use of odor cues by predatory birds as a form of biocontrol in agricultural settings is particularly interesting (Kaplan 2012, Hiltpold and Shriver 2018). However, for future investigations into the possible role of specific HIPVs in recruiting avian predators our data suggest that the more natural conditions around larger woody species may promote increased overall levels of avian activity. In such circumstances, the recruitment effect of HIPVs may still be an ecologically important form of biocontrol. For example, Mösch et al. (2018) found that insectivorous birds such as members of the Paridae can be a significant form of top-down control on horse chestnut leaf miners (*Cameraria ohridella* Deschka and Dimic, Lepidoptera, Gracillariidae). To this point, a near-significant attractive effect of methyl salicylate was seen on black walnut host plants (Fig. 2), the species that had the highest overall levels of predation. We suggest that future studies take careful consideration of the host plant species of study. Plant species with low levels of associated natural avian activity may not be well suited for study. Sipura (1999) found that only on willow (*Salix*) species with appreciable levels of herbivorous insects did the presence of avian predators contribute to increased fitness of the plant, i.e., growth. In contrast, host plants in environments with fewer natural non-avian predators of herbivores such as predatory arthropods may show larger effect sizes in the strength of plant-bird coevolutionary relationships (Tvardikova and Novotny 2012, Sam et al. 2015a)

We also found a significant difference in the amount of variation in predation between host plants (Table 2). Variation in the number of caterpillars pecked was greatest in red maple trees. We saw extreme differences in predation levels between the four red maple sites. Although we control for this site-specific variation in

our statistical model, we suggest that future research into the use of HIPVs by insectivorous birds try to select host plant sites with similar a priori levels of overall avian activity.

Here, we examine the capacity for the HIPVs methyl jasmonate and methyl salicylate to recruit avian predators. These HIPVs have been investigated in this context in other studies (Mäntylä et al. 2014, Mrazova and Sam 2018, Saavedra and Amo 2018b, Mrazova et al. 2019, Rubene et al. 2019). However, these compounds are known to produce varied additional physiological effects within individual plants (Ament et al. 2006, Yoon et al. 2009, Sayyari et al. 2011, Wang and Wu 2013, Shahzad et al. 2015, Kalaivani et al. 2016) and between neighboring plants, i.e., plant priming (Shulaev et al. 1995, 1997, Engelberth et al. 2004, Conrath et al. 2006, Kessler et al. 2006, Martinez-Medina et al. 2016). To our knowledge, these potential confounding effects have not been considered in other studies investigating the attractive effects of HIPVs on avian predators. In addition to future field studies, controlled aviary experiments verifying any attractive effects of the odor cue only, without live host plants is necessary to control for this possibility.

In conclusion, although we found no significant effect of HIPV treatment on increasing bird predation, there was a nearly significant effect of methyl salicylate on black walnut trees. We also saw higher levels of overall predation in our wood tree species compared to the herbaceous host plants. Our results provide valuable insight into the growing field of avian chemical ecology, especially as it relates to complex tritrophic interactions with other members of ecological communities. Finally, we discuss a number of important ideas and suggestions for future similar studies in this area including the choice of HIPV, host plant, field site, and possible off-target effects.

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Author Contributions:

M. N., C. M., and C. M. all contributed equally to this study. M. N., C. M., and C. M. designed and carried out the experiment. M. N., C. M., C. M., and A. V. H. analyzed the data and wrote the manuscript.

Data Availability:

The data and corresponding R code that support the findings of this study are openly available in Dryad at https://doi.org/10.5061/dryad.05qfttf49

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