Lepidoptera Host Records Accurately Predict Tree Use by Foraging Birds

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Abstract - The richness, abundance, and biomass of phytophagous arthropods like lepidopteran larvae is highly uneven among sympatric tree taxa. Optimal foraging theory predicts that predation pressure will be greatest on foraging substrates that support the highest abundance and/or diversity of prey, thus offering the greatest reward and maximizing fitness. Predation pressure can also vary with the nutritional or energetic needs of predators across the annual cycle. For insectivorous birds, prioritizing foraging effort in trees that support the most insect prey can benefit individuals by improving their foraging efficiency, condition, and ultimately fitness. However, we lack an understanding of how trees vary in their support of bird foraging activity across seasons and among plant taxa. We used plasticine caterpillar models to measure avian predation rates on 9 native North American tree species that vary in caterpillar-hosting potential. We measured avian predation rates during May, June, and October to compare caterpillar mortality in seasons that vary in life-history needs, abundance, and diversity of avian predators. We modeled daily survivorship and total mortality using Cox-proportional hazard models and logistic regression. We found that, across seasons, caterpillars had significantly higher predation rates on trees that are predicted by literature host records to support the most species of caterpillars ($\beta = 0.22 \pm 0.05$, 95% CI = [0.13,0.32], $z = 4.73$, $P < 0.0001$). Caterpillars had the highest mortality in June, coinciding with avian breeding seasons, and the lowest rates in October, coinciding with fall migration and dispersal. Our study suggests that birds disproportionately forage on trees that have the highest potential to support caterpillar richness and presumably prey biomass. The observed pattern of non-random foraging has many implications; for example, the utility of using informed tree selection to improve bird foraging in managed ecosystems or potential negative implications to bird populations of forest-composition shifts due to climate change. Applying this information to habitat restoration will enable land managers to better support avian populations by planting trees that best support foraging substrates for insectivorous birds in managed ecosystems.

Introduction

Optimal foraging theory predicts that birds should preferentially forage in microhabitats with the highest caloric returns per unit effort (Stephens and Krebs 1986). Thus, if high caterpillar diversity is correlated with high prey biomass (Alison et al. 2017, Bock et al. 2007, Richard et al. 2019), bird foraging activity should be positively related to caterpillar diversity and hence highest on plants that support the most caterpillar diversity and abundance, as documented from the host-plant literature. For *Poecile carolinensis* (Audubon) (Carolina Chickadee)

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breeding in residential neighborhoods, plants that supported the highest caterpillar diversity also were the most preferred by foraging individuals (Narango et al. 2017), suggesting caterpillar diversity derived from host records is a useful proxy for bird foraging preferences.

Insects are essential for passing the energy captured by plants to other animals, and caterpillars consume and pass on more plant energy than any other animal taxon (Janzen 1988). The importance of caterpillars in vertebrate food webs is particularly evident with birds. In 16 of 20 terrestrial bird families for which there are sufficient data, caterpillars dominate nestling diets (Kennedy 2019). One clutch of Carolina Chickadees, for example, can eat 6000–9000 caterpillars before fledging, depending on the number of chicks in the nest (Brewer 1961). Accordingly, many insectivorous birds time their breeding and adjust clutch size to align nestling development with peak caterpillar abundance in summer (Lany et al. 2016, Perrins 2008).

Although insects are the primary food source for over 70% of songbirds (Wilman et al. 2014), bird diet often varies by season (Parrish 2000). Preceding and during migration, many migratory songbirds will shift to a fruit-based diet (Parrish 1997). Feeding on fruit helps individuals accumulate lipids used to build necessary fat stores and lowers energy expenditure through a decrease in search and handling time as compared to feeding on insects, which are often less abundant and less reliable during migration (Parrish 2000). Then, during spring breeding, most birds return to a largely insect-based diet to provision their young (Kennedy 2019).

Among herbivorous insects, more than 90% are specialized to feed on 1 or a few host plants (Forister et al. 2015). However, plant genera vary by orders of magnitude in their ability to host caterpillar species (Narango et al. 2020). For example, in the Mid-Atlantic region of the US, entomological surveys over the last century have recorded 557 species of caterpillars on *Quercus* (oak) species, but only 21 species on *Liriodendron tulipifera* L. (Tuliptree), and no caterpillars using *Cladrastis kentukea* (Dum. Cours.) Rudd (Kentucky Yellowwood) (Tallamy and Shropshire 2009). Moreover, across ecological communities and geographic regions in North America, caterpillars use relatively few plant lineages for growth and reproduction, and most caterpillar diversity is supported by a small number of hyperproductive plants (i.e., keystone plants [Narango et al. 2020], also called "foundational species").

Recent surveys suggest that both birds (Rosenberg etal. 2019, Schipper et al. 2016) and insects (reviewed by Forister et al. 2019, Wagner 2020) are declining rapidly and globally. One of the major drivers of these declines is habitat loss (Dirzo and Raven 2003, Wilcox and Murphy 1985). In many regions facing rapid land development, habitat preservation will not be sufficient alone to reverse declines in biodiversity because the patches that remain are too small and too isolated from each other to sustain the species within them (Rosenzweig 2003). Many forests are also decreasing in tree richness and shifting in community assemblages and tree dominances due to climate change (Thompson et al. 2011) and selective "high-grade" logging (Nyland 2002). Climate change is negatively affecting remaining forest by disrupting disturbance cycles, bolstering invasive species and pathogens,

and increasing severe weather (Dale et al. 2001). Moreover, climate change might also influence land managers to plant tree species or adopt management techniques (e.g., prescribed burnings) adapted to future rather than contemporary climates (Park and Talbot 2018). To counteract these changes, successful conservation will require not only appropriate management of intact habitat, but also ecological restoration of the landscapes that lie between such habitats (Bullock et al. 2011). Because plants vary in their ability to support the food webs that determine the diversity and abundance of life in higher trophic levels (Lawson and Michler 2014, Messeder et al. 2020, Narango et al. 2020, Tallamy and Shropshire 2009), the success of restored landscapes in supporting biodiversity will depend on informed plant choices that favor species that support the most plant–animal interactions (Peters et al. 2016).

Herein we ask whether caterpillar host-associations described in the literature predict bird foraging activity across avian communities and seasons. We tested this hypothesis by measuring bird predation attempts on clay caterpillar surrogates distributed in even densities across tree species that varied widely in caterpillar-hosting potential. If bird foraging behavior reflects experience from previous encounters with caterpillars as suggested by Heinrich and Collins (1983), attacks on clay caterpillars should reflect the degree to which birds target tree species that are typically rich in caterpillars. We also examined whether bird foraging patterns were consistent across seasons (early breeding, late breeding, and fall migration) or are season dependent. The preference for caterpillar-rich tree species by foraging birds should be consistent across each season, even if overall foraging levels vary.

Field-Site Description

We conducted the experiment on a 4-ha (10-acre) property in Oxford, Chester County, PA. The study site, which D.W. Tallamy has been managing to encourage native plant communities, is a mixture of meadow, deciduous woodland, and marshland. Breeding birds frequently observed on the property that could be responsible for most predation attempts in our study included *Cardinalis cardinalis* (L.) (Northern Cardinal), *Sialis sialis* (L.) (Eastern Bluebird), Carolina Chickadees, *Baeolophus bicolor* (L.) (Tufted Titmouse), *Dumetella carolinensis* (L.) (Gray Catbird), *Mimus polyglottos* (L.) (Northern Mockingbird), *Cyanocitta cristata* (L.) (Blue Jay), *Spizella pusilla* (Wilson) (Field Sparrow), *Vireo griseus* (Boddaert) (White-eyed Vireo), and *Turdus migratorius* L. (American Robin). All of these species provision nestlings with diets composed primarily of insects and caterpillars during the breeding season (Cornell Lab of Ornithology 2020, Kennedy 2019).

Methods

We conducted the experiment in June 2018, October 2018, and May 2019. We chose these months to correspond with different periods in the annual cycle of local bird communities. In southeastern Pennsylvania, May corresponds with a peak in

nestling provisioning of breeding resident birds (e.g., Carolina Chickadee) and the passage of migratory birds in the spring, June corresponds with nestling provisioning by breeding migrants (e.g., Gray Catbird) as well as continued provisioning of breeding and previously fledged residents (e.g., Carolina Chickadee), and October corresponds with the fall passage of migratory birds to nonbreeding grounds, dispersal of fledged young, and the cessation of breeding for resident species (D.W. Tallamy, pers. observ.).

Using clay caterpillars, we measured bird foraging activity on 9 tree genera: *Quercus* (*Q. alba* L. [White Oak]), *Prunus* (*P. serotina* Ehrh. [Black Cherry]), *Ulmus* (*U. americana* L. [American Elm] and *U. rubra* Muhl. [Slippery Elm]), *Pinus* L. (*P. strobus* L. [Eastern White Pine]), *Juglans* (*J. nigra* L. [Black Walnut]), *Diospyros* (*D. virginiana* L. [Common Persimmon]), *Liriodendron* (*Liriodendron tulipifera* L.[Tulip Tree]), *Asimina* (*A. triloba* (L.) Dunal [Pawpaw]), and *Lindera* (*L. benzoin* (L.) Blume [Northern Spicebush]). These species were chosen because they represent plant genera that differ widely in the diversity of caterpillar species they host and were the most common taxa at the site. As a quantitative measure of caterpillar-hosting potential (i.e., host-plant quality), we used a comprehensive compilation of host records in the Mid-Atlantic states over the last century from over 400 primary literature sources (Tallamy and Shropshire 2009).

Artificial caterpillars made from non-hardening plasticine clay (or other malleable materials) are frequently used as a method of measuring predation rates and caterpillar mortality (Loiselle and Farji-Brener 2002, Posa et al. 2007, Roslin et al. 2017, Sam et al. 2014). When predators attempt to eat a caterpillar model, indentations in the clay leave a record of the predation attempt. Examining such marks can provide estimates of predation levels as well as the predator taxon responsible (Howe et al. 2015).

To measure predation rates at our sites, we molded artificial caterpillars from non-toxic, brown plasticine modeling clay. Because both clay scent (Sam et al. 2015) and model size (Remmel and Tammaru 2009) may affect avian predation attempts, we used the same material for all caterpillars and made each caterpillar to a standard size (0.4 cm x 3.0 cm). In the June 2018 run of the experiment, we gave caterpillars a straight shape and attached them to trees with Gorilla™ super glue adhesive, while in May and October 2019, we molded caterpillars with an arch to resemble geometrid inch worms and attached them to branches with 2-cm wire brads at the front of the model. We modified attachment because it was a scent-free, faster and more secure application process that resulted in more-successful deployments. We modified the caterpillar shape to produce a more realistic caterpillar model.

We affixed caterpillar models to branches ~3 m from the ground near branch terminals at least 0.75 cm thick to ensure that each branch could support the weight of an avian predator. Further, we placed only 1 caterpillar model on a branch and spread models out across each test tree as much as possible. We placed thumbtacks at the base of the branch by the central trunk to help identify where the models were placed. Because of inherent differences among tree species, tree size was variable (4–7 m tall); however, no trees were large, mature specimens (>15 cm dbh).

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To ensure that foraging activity was not related to tree location, we controlled for several aspects of caterpillar placement. Individual trees used in this study were all located on well-lit habitat edges at the study site. We also controlled for caterpillar visibility to predators by only placing models on well-lit areas of branches that were easily visible from outside the tree. Additionally, we ensured each tree had a vegetated groundcover to prevent unintended discrepancies in herbivore presence since many caterpillar species pupate within soil covered by vegetation. For each experimental run, we placed 4 caterpillars on each of 5 individuals per tree species ($n = 20$ per tree species per season). Thus, each season, we monitored 180 caterpillar decoys during each of the 3 runs.

To quantify caterpillar mortality and thus bird foraging rates, we recorded beak marks left on the clay caterpillars (Fig. 1). For 7 consecutive days, we surveyed all caterpillars each morning following their deployment. If a caterpillar had indentations that resembled beak marks or were torn apart, we recorded it as an avian attack and removed it from its host tree. If a caterpillar had detached from its branch and was unable to be recovered, we excluded it from the dataset. As we were primarily interested in avian foraging, we did not consider caterpillars with arthropod damage (i.e. typically very small pin holes or chew marks) as mortality events.

Statistical analysis

To test whether tree species and month were related to caterpillar predation, we used 2 complementary statistical approaches to assess (1) daily survival rates and (2) total mortality. We assessed both responses to understand differences in the speed of predation as well as total predation pressure on different trees and seasons.

Figure 1. Clay caterpillar with typical bird beak mark recorded as a predation attempt.

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We first modeled survival of our plasticine caterpillars using a survival-time analysis with a Cox-proportional hazard model (CPH). This model describes the probability that a caterpillar is attacked (i.e., predation risk) as a function of environmental features included as explanatory variables (e.g., month) as well as a baseline hazard over time. We were primarily interested in whether caterpillar survival was directly related to a tree's caterpillar-hosting potential, quantified as the number of caterpillar species a tree supports, and whether this relationship varied over months in the year. Therefore, in this model, we included fixed effects of tree caterpillar diversity, month (May, June, and October) and the interaction between tree potential and month. Prior to the analysis, we rescaled the caterpillar diversity variable by dividing by 100 so that each step increase of 1 represented an increase in 100 more potential species hosted. To run the survival model, we used the R package 'survival' (Therneau 2015, Therneau and Grambsch 2000). We tested for significance of our terms using a chi-square analysis of deviance test. If interaction terms were non-significant, we removed them and reran the model with only fixed terms.

Next, as an alternative metric to compare total predation pressure, we tested whether the total proportion of caterpillars attacked differed by month and tree host potential. For this comparison, we used a linear regression. We included proportion attacked as our response and caterpillar potential, month, and the interaction between caterpillar potential and month as fixed effects. We compared mortality between months using a pair-wise Tukey's test for significance using the functions glht and mcp in the R package 'multcomp' (Hothorn et al. 2008). All analyses and graphics were completed using Program R version 3.5.1 (R Core Team 2018).

Results

Clay caterpillars on trees with high caterpillar potential were attacked more quickly than caterpillars on trees that host few species of caterpillars (Table 1). Daily survival probability of clay caterpillars significantly declined as tree caterpillar potential increased (Table 2). Controlling for season, caterpillar daily mortality

Table 1. Percentage of clay caterpillar models (out of 20 individuals) attacked by birds after 1 week exposure on tree species varying in potential caterpillar diversity (the number of caterpillar species recorded in the literature as using a tree for growth and reproduction as per Tallamy and Shropshire (2009).

Tree species	Caterpillar host potential	May	June	October
Ulmus	215	0.05	0.32	0.00
Prunus	456	0.30	0.30	0.20
Juglans	129	0.20	0.35	0.30
Asimina	12	0.05	0.21	0.05
Dyospiros	46	0.30	0.26	0.10
Lindera	11	0.15	0.17	0.10
Lireodendron	21	0.10	0.10	0.00
Quercus	557	0.55	0.53	0.20
Pinus	201	0.05	0.33	0.00

probability increased by 25% for every increase in 100 caterpillar species that a tree potentially supports (Table 2, Fig. 2). Controlling for potential caterpillar diversity, caterpillar survival was also significantly different between months (Table 2, Fig. 2). Compared to May, caterpillars were 58% more likely to be attacked in June and half as likely to be depredated in October (Table 2). There was no significant interaction between potential caterpillar diversity and month ($\chi^2 = 0.84$, $P = 0.66$) indicating that, across all months, potential caterpillar diversity had the same negative relationship with caterpillar survival.

Table 2. Results from a Cox proportional hazards regression of caterpillar survival over time. Degrees of freedom, χ^2, and AOV-P are from an ANOVA test. Values in parentheses are the exponential of the β coefficient and 95% confidence intervals.

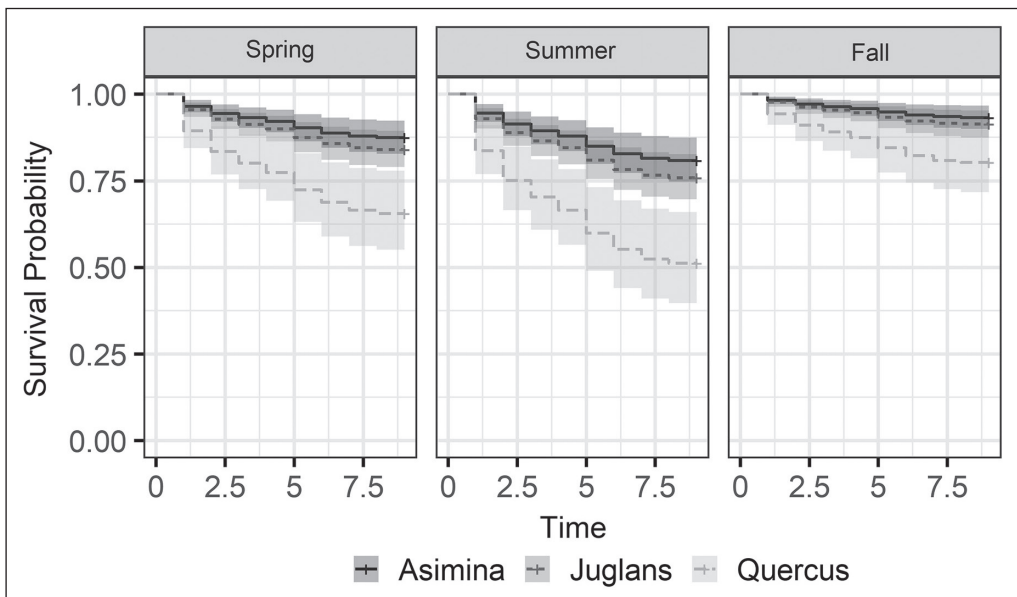| Factor	Categories	β ± SE	z	P	95% confidence interval	df	χ^2	AOV- P
Caterpillar potential		0.22 ± 0.05 (1.25)	4.73	<0.0001	0.13, 0.32 (1.14, 1.38)	1	21.08	<0.0001
Season	Reference: May					2	17.93	0.001
	June	0.46 ± 0.22 (1.58)	2.06	0.04	0.02, 0.90 (1.02, 2.45)			
	October	-0.65 ± 0.28 (0.52)	-2.29	0.02	-1.21, -0.09 (0.30, 0.91)			

Figure 2. Daily probabilities of plasticine caterpillar mortality by month for tree species with different potential caterpillar diversity. For visualization purposes, 3 species that represent high, medium, and low potential caterpillar diversity were used: *Asimina* (12 caterpillar species), *Juglans* (129 species), and *Quercus* (557 species). Lines represent the mean relationship between daily survival and time for each category, and shading represents the 95% confidence interval.

Similar to our survival model, the proportion of caterpillars attacked by the end of the trial was related to both potential caterpillar diversity and month (Fig.3, Table 3). Mean percent caterpillars attacked per tree increased with potential caterpillar diversity and were different between some months (Table 3). The interaction between caterpillar diversity and month was non-significant, indicating that this relationship was consistent across months ($\chi^2=0.99$, $P=0.38$). Controlling for potential caterpillar diversity, proportions of attacked caterpillars were similar between May and June and May and October but different between June and October (Table 3).
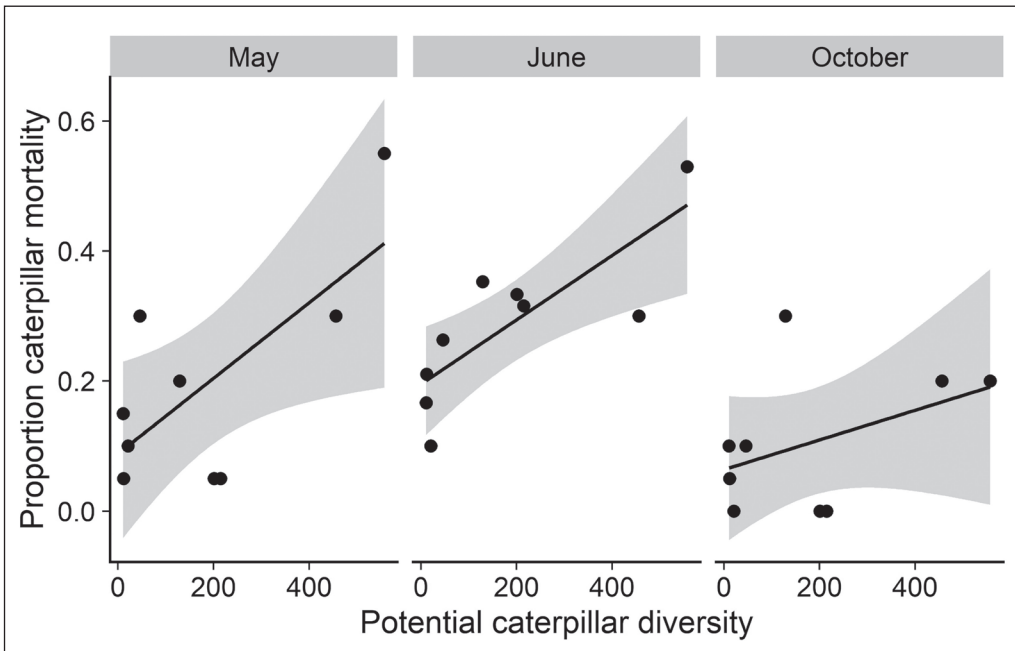

Figure 3. Relationship between tree potential caterpillar diversity and proportion of attacked caterpillars in May, June, and October. Lines represents the mean slope, and gray shading indicates the 95% confidence interval.

Table 3. Results from a linear regression of caterpillar mortality. Degrees of freedom, *F*, and AOV-*P* are from an ANOVA test comparison of models with and without the factor of interest. Comparison between each categorical month is from a Tukey's test for multiple comparisons.

Factor	Categories	β ± SE	*t*	*P*	95% confidence interval	df	*F*	AOV - *P*
Caterpillar potential		0.04 ± 0.01	4.08	0.0004	0.02, 0.07	1	16.61	0.0004
Season						2	6.63	0.005
	June–May	0.09 ± 0.05	1.85	0.18	-0.03, 022			
	October–May	-0.09 ± 0.05	-1.80	0.19	-0.21, 0.04			
	October–June	-0.18 ± 0.05	-3.64	0.004	-0.30, -0.06			

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Discussion

Our results show that caterpillar-host records in the literature are an accurate predictor of bird-foraging frequency and a convenient index of tree preferences and potential caterpillar abundance on tree species. Even though clay caterpillars were distributed in equal numbers across tree species, there were more avian predation attempts on models fixed to trees with high caterpillar-host potential than on trees that host few caterpillar species. Surrogate caterpillars on keystone trees such as *Quercus* (oak) and *Prunus* (cherry) that have been shown to host high caterpillar abundance and biomass (Richard et al. 2019, Tallamy and Shropshire 2009) were always attacked more than caterpillars on trees with lower caterpillar-host potential such as *Liriodendron* (tulip tree), *Asimina* (pawpaw), and *Lindera* (spicebush). These results support Heinrich and Collins's (1983) hypothesis that bird foraging behavior reflects experience from previous encounters with caterpillars. They are also consistent with the foliage palatability hypothesis that posits avian insectivores preferentially forage on trees with abundant arthropods resulting from high foliage nutrition and palatability (Greenberg and Bichier 2005). Several studies have found that foraging birds have distinct preferences for tree species that are highly productive for caterpillars (Airola and Barrett 1985, Beltrán and Wunderle 2013, Gabbe et al. 2002, Holmes and Robinson 1981, Peck 1989, Singer et al. 2012).

Attacks occurred at higher rates during the peak bird-breeding season of May and June compared to October after breeding had ended and southward migratory movements had commenced. Migratory birds also heavily use native trees like oaks that support high biomass of insect prey to complete migration (Richard et al. 2019, Wood and Esaian 2020, Wood et al. 2012). However, we were not surprised to find lower rates of attack on our surrogate caterpillars in October than in May or June; birds may not forage for caterpillars or other arthropods with the same intensity in the fall when they are not feeding young and instead include more fruit in their diet (Parrish 1997). Many birds add fruit to their diets in the fall because fruit supplies fat necessary for migratory flight and is an abundant and reliable food source during this season (Parrish 2000). However, many birds still forage heavily on arthropods during this period. For example, warblers, vireos, kinglets, and many other songbirds consume 60–80% insects during the fall (Martin et al. 1951). For frugivorous birds, some native plants that produce preferred high fat berries also support high insect biomass (e.g., cherry and *Viburnum* (arrow-wood); Gallinat et al. 2020, Tallamy and Shropshire 2009).

Migrants are occurring in increasingly high densities in human-dominated landscapes because of low habitat availability and attraction by artificial light (McLaren et al. 2018). These issues can be magnified by changing tree diversity, species dominance, and tree assemblages due to climate change (Thompson et al. 2011). Thus, restoring tree canopies that enhance foraging substrates for birds may be important for migrant conservation. Combining information on both insect and fruit preferences will help refine plant selection in managed landscapes to create bird habitat for both breeding and non-breeding periods.

The preferential foraging of birds on certain trees could also have effects on insect demography, particularly in urban and highly developed land uses. Smith and Sweatman (1974) found that *Parus major* L. (Great Tit) spend most of their foraging time in habitat patches with high prey abundance/size, and progressively less time in areas with less prey reward. Therefore, patches of trees that do not provide consistent high reward will be searched significantly less by foraging birds. In highly fragmented or developed areas, for example, this could cause unproductive fragments to be ignored by avian predators. Since foraging birds also consume a variety of nonpreferred prey (e.g., Hemiptera) while searching for high-reward prey (e.g., Lepidoptera) (Kennedy 2019), habitat patches ignored by birds could potentially cause spikes in nonpreferred prey due to reduced predation. Assessing this hypothesis requires further research. Even preferred prey species (e.g., Lepidoptera) could spike due to the failure of birds to respond to high prey rewards that suddenly appear where they previously were absent, a phenomenon displayed in Great Tits (Smith and Sweatman 1974). However, proximity of non-preferred trees to preferred trees could result in "spillover" predation pressure onto non-preferred trees by bird predators. This scenario has been shown in agricultural landscapes (non-preferred habitat) that receive significant spillover predation pressure from birds in neighboring native habitat (preferred habitat) (Boesing et al. 2017).

Regardless of seasonal differences, our data suggest that bird foraging reflects preferences for keystone tree species which host large numbers of caterpillar species and thus are more rewarding foraging substrates for birds than trees that host fewer species of caterpillars. Although foraging birds may be able to distinguish between tree species and recognize them as being either reliable or unreliable sources of caterpillars, it is also likely that birds recognize visual (e.g., mechanical herbivory or leaf light reflectance; Koski et al. 2017, Mäntylä et al. 2020) or chemical (e.g., volatile compounds; Hiltpold and Shriver 2018) cues of caterpillar presence that then attract foraging individuals to trees with larger caterpillar abundance and richness. Regardless of the mechanism, planting, restoring, and protecting trees that are preferred by foraging birds and provide abundant prey resources will be beneficial for both bird and insect populations. Thus, to improve the quality of avian-targeted restoration projects, it is important that high-quality trees for insectivorous birds be included in natural and human-dominated landscapes.

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