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Using community science to identify predators of spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae), in North America

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Abstract

Spotted lanternfly, *Lycorma delicatula* (Hemiptera: Fulgoridae), is an invasive insect that was first detected in the United States in 2014 and feeds on a wide variety of plants, with economic impacts on the agricultural, ornamental, and timber industries. Part of what likely contributes to the success of *L. delicatula* in its invaded range is that it appears to be chemically defended by sequestering toxins from its host plant(s), which may deter predators in the introduced range. To determine the identity and behavior of North American predators that feed on spotted lanternfly, we performed a community science study in which we asked members of the public to contribute reports of animals feeding on spotted lanternfly through a Facebook page. The largest group of reported predators was arthropods followed by birds. Araneae was the arthropod order with the most reports and Phasianidae was the most frequently reported bird family. Using Pearson's χ^2 tests, we also identified significant relationships between predator behavior and (1) taxonomic group of the predator, (2) *L. delicatula* life stage, and (3) host plant *L. delicatula* was observed on. These results can help to guide future research on predator host shifting to spotted lanternfly and potential for biocontrol as a management tactic.

Introduction

Spotted lanternfly, *Lycorma delicatula* (White) (Hemiptera: Fulgoridae), is a planthopper, native to Southeast Asia, that was first detected in North America in Berks County, Pennsylvania (PA), USA, in 2014 (Dara *et al.*, 2015). Since then, *L. delicatula* has spread rapidly and currently has established populations in at least 51 counties in PA and 14 states in the USA (NYSIPM, 2023). This insect is highly polyphagous and has been found to feed on the phloem sap of more than 150 plant species in its known geographic distribution (Barringer and Ciafré, 2020). While *L. delicatula* is an economic pest impacting the ornamental, agricultural, and timber industries, the most serious damage is to grapevines (Harner *et al.*, 2022) and growth of maple saplings (Lavely *et al.*, 2022). Some Pennsylvania vineyards have reported winter mortality of grapevines that experienced heavy adult feeding during the late summer and fall months (Leach and Leach, 2020). In addition to a wide host range, the success of *L. delicatula* may also be attributed to its potential ability to sequester toxins from its preferred host, tree of heaven (*Ailanthus altissima* (Mill.) Swingle [Simaroubaceae]) (Song *et al.*, 2018).

Toxin sequestration is a process through which an organism acquires potentially harmful chemicals from its environment and then uses them to their benefit, often for defense against predators (Duffey, 1980). For example, the monarch butterfly sequesters toxins from its host plant, milkweed (*Asclepias spp.*), which renders them distasteful to vertebrate predators and which was first described more than 50 years ago (Parsons, 1965; Brower *et al.*, 1967). There is much to suggest that *L. delicatula* is capable of sequestering toxins from its preferred host, *A. altissima*, which is an invasive plant native to China that has quickly spread across much of North America since its introduction as an ornamental in the 18th century (Miller, 1990). The fourth instar and adult *L. delicatula* display aposematic coloration, which is a mechanism for prey to be recognized and avoided by predators that have previously encountered it (Prudic *et al.*, 2007). Onset of the bright red coloration of fourth instars and of the hindwings in adults coincides with the presence of two major classes of toxins that *A. altissima* produces, quassinoids and indole alkaloids (Polonsky and Fourrey, 1964; Anderson *et al.*, 1983; Souleles and Waigh, 1984; Tang and Eisenbrand, 1992; Xue and Yuan, 1996; Bucar *et al.*, 2007; Kim *et al.*, 2011; Song *et al.*, 2018). In addition to *A. altissima*, *L. delicatula* prefers native black walnut (*Juglans nigra*) as fourth instars and adults (Liu, 2019). In addition to its namesake juglone (5-hydroxy-1,4,-naphthoquinone), black walnut produces a wide range of compounds, including other phenolics, alkaloids, and triterpenoids (Houx *et al.*, 2008). These compounds could offer *L. delicatula* a new source of toxins for sequestration in the introduced range, especially as there are similarities in their chemical structures to toxins found in *A. altissima* (e.g., triterpenoids and quassinoids). Regardless of where *L. delicatula* is obtaining chemical defenses, they have the potential to affect predator behavior in ways that were previously unreported.

While predators of *L. delicatula* may learn to avoid defended prey over time, naïve predators in the introduced range may still consume them, potentially having harmful effects on the predator (Duffey, 1980; Prudic *et al.*, 2007). Detrimental effects in predators feeding on *L. delicatula* in areas where it has invaded have been reported prior to this project. For example, after the invasion of *L. delicatula* in South Korea, wild predatory birds were found to vomit after consuming *L. delicatula* (Kang *et al.*, 2011). In the USA, there are anecdotal reports of dogs and cats brought to their veterinarian suffering from drooling, vomiting, and loss of appetite after eating *L. delicatula* (Patton Veterinary Hospital, 2020). However, these reactions are inconsistent, potentially due to differences in the predators' tolerance to sequestered defenses or variability in concentrations of toxic compounds in prey at the time of consumption. As *L. delicatula* does not require *A. altissima* to complete its development and reproduce (Uyi *et al.*, 2020, 2021), it is reasonable to hypothesize that *L. delicatula* individuals that fed less or not at all on *A. altissima* could be less toxic and have little to no effect on their predators. Thus, it is important to study the potential interactions between *L. delicatula*, their host plants, and potential predators in North America. To begin disentangling these interactions, we used a community science approach that aimed to first determine which predators are feeding on *L. delicatula* in North America and investigate what effect *L. delicatula* diet may be having on predation.

Community science projects, in which volunteers from the public help collect or process data, have a long history. One of the oldest examples of a modern community science project is the Christmas Bird Count, which has been organized annually by the U.S. National Audubon Society since 1900 (Silvertown, 2009). Since this time, these types of studies have grown more common, especially as the development of social media has made it easier to reach interested people and collect a greater range of data (Liberatore *et al.*, 2018). Community science is useful for its ability to record far more data than a small group of researchers can collect, generate datasets that span a potentially large spatial and temporal range, are relatively low cost to conduct, and can potentially educate the public and explore ways to address issues most concerning to the community (Silvertown, 2009). Due to these advantages, we conducted a community science project for initial exploration of predation of *L. delicatula* in North America. The objectives of this study were to (1) identify North American predators of *L. delicatula*, (2) examine predator feeding behavior, and (3) test the interactions between predator feeding behaviors and predator type, *L. delicatula* life stage, and observed *L. delicatula* host plant.

Materials and methods

To solicit observations of predation of *L. delicatula* from the public, we created a Facebook page (facebook.com/birdsbitingbadbugs and http://facebook.com/birdsbitingbadbugs) in August of 2020 asking for reports of predators observed eating *L. delicatula* either by posting on the page or sending an email. We asked for reports to include the common name of the predator, time and location of the predation event, feeding behaviors performed by the predator, and any additional information, such as the host plant *L. delicatula* was on and/or photos. On 1 June 2021 and 2022, we submitted another post on this Facebook page to collect more information, with the same details requested above with the addition of *L. delicatula* life stage categorized as eggs, early nymph (first to third instars), late nymph (fourth instar), or adult, with an image guide to help people distinguish between life stages. The link for the page was widely shared by private organizations such as ornithology and Master Gardener groups, the media, and The Pennsylvania State University Extension. Reports were then collected and organized into larger taxonomic groups, including order for arthropod predators and family for avian predators.

To determine how our larger grouping of predator type (i.e., arthropod, bird, mammal, etc.), *L. delicatula* life stage, and known host plants had on predator behavior, we pulled out three subsets of our data that included reports of predator type and predator behavior, *L. delicatula* life stage and predator behavior, and known host plants and predator behavior, respectively. Pearson's χ^2 tests were performed on these subsets of data followed by post hoc analyses based on the residuals using the R package 'chisq.posthoc.test' (Ebbert, 2022) to determine if the observed frequency of a specific behavior differed significantly from the expected, with a *P*-value less than 0.05 considered statistically significant. We categorized predator feeding behaviors based on if, during, or after feeding on *L. delicatula*, the predator avoided it, dropped/released it, ate it whole, experienced illness, removed the wings, spat it out, or died. Avoidance was defined as a predator eating a *L. delicatula* and then refusing to do so again despite the presence of additional individuals available to consume, or a predator showing interest in feeding on other prey items in the area but not on *L. delicatula*. 'Dropping' is when the *L. delicatula* was held by the predator, either using their mouthparts or appendages, and then released. To be counted as spat out the prey would have to be fully in the predator's mouth before spitting it out. Illness includes reports of lethargy, nausea, and vomiting after eating a *L. delicatula*.

Results

As of 1 December 2022, we received 1294 unique reports of predation events of *L. delicatula*, 526 of which included pictures/video of the event and 719 of which included location data, with reports from Pennsylvania, New Jersey, Delaware, New York, Virginia, and Maryland. Of these, 655 (50.62%) were of arthropod predators and 533 (41.19%) were of avian predators, with mammals, fish, amphibians, and reptiles making up the remaining 106 (8.19%) reports (fig. 1). Of the arthropods, the three most reported orders were Araneae (206 reports, 31.45%), often only identified as 'spider,' Mantodea (196 reports, 29.92%), the majority of which were only identified as 'praying mantis,' and Hymenoptera (177 reports, 27.02%), with the most common report being 'yellow jacket' (fig. 2). There were also arthropods reported from an additional seven orders. Of the birds, the three most reported families were Phasianidae (97 reports, 20.64%), which were mostly chickens, Cardinalidae (73 reports, 13.27%), which were mostly cardinals, and Mimidae (65 reports, 10.07%), which were mostly catbirds (fig. 3). The remaining reported birds were in an additional 25 families.

We also examined feeding behaviors as reported for 255 predation events. Predators eating *L. delicatula* whole was the most frequently reported behavior (109 reports, 42.75%), followed by predators that removed the adult's wings (74 reports, 29.02%) (fig. 4). We did several tests to look for potential causes for

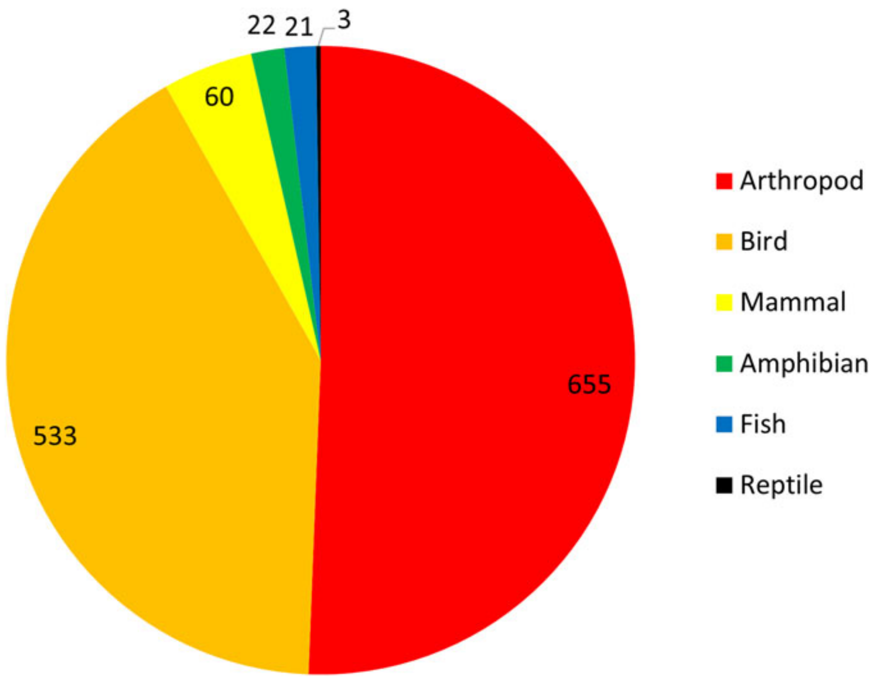

Figure 1. Predator types reported feeding on *L. delicatula* from 2020 to 2022. Of these reports, 50.62% were arthropods and 41.19% were birds.

differences in feeding behavior, which are summarized in table 1. We found a significant relationship between predator type (i.e., arthropod, bird, mammal, etc.) and predator behavior ($\chi^2 = 131.14$, df = 24, $P < 0.001$; fig. 5, $n = 255$). Of the 167 reported instances of birds eating *L. delicatula*, it was reported that they experienced illness afterwards only once, which was significantly less frequently than expected ($\chi^2 = 14.18$, $P = 0.006$). Arthropods removed wings in 24 out of the 47 reported instances of them feeding on *L. delicatula*, which was significantly more frequently than expected ($\chi^2 = 16.34$, $P = 0.002$). Of the 27 reports of mammals preying on *L. delicatula*, they ate the insect whole only twice, which was significantly less frequently than expected ($\chi^2 = 15.41$, $P = 0.003$), and experienced illness after eating *L. delicatula* 9 times, which was significantly more frequently than expected ($\chi^2 = 69.33$, $P < 0.001$). One out of the seven reported amphibians that fed on *L. delicatula* was reported to have died after doing so, which was more frequently than expected ($\chi^2 = 10.64$, $P = 0.039$).

L. delicatula life stage was also significantly associated with predator behavior ($\chi^2 = 43.97$, df = 18, $P < 0.001$; fig. 6, $n = 190$). Both early- and late-stage nymphs were eaten whole significantly more frequently than expected, with 18 of 21 early nymphs ($\chi^2 = 17.43$, $P < 0.001$) and 11 of 12 late nymphs being eaten whole ($\chi^2 = 12.29$, $P = 0.013$). Of the 153 reports of adults being preyed upon, they were eaten whole in 49 reports, which is significantly less frequently than expected ($\chi^2 = 39.69$, $P < 0.001$) and had their wings removed in 73 reports, which is more frequently than expected ($\chi^2 = 28.67$, $P < 0.001$).

There was a significant relationship between predator behavior and known *L. delicatula* host plant ($\chi^2 = 49.07$, df = 12, $P < 0.001$; fig. 7, $n = 91$). Of the 24 *L. delicatula* that were observed feeding

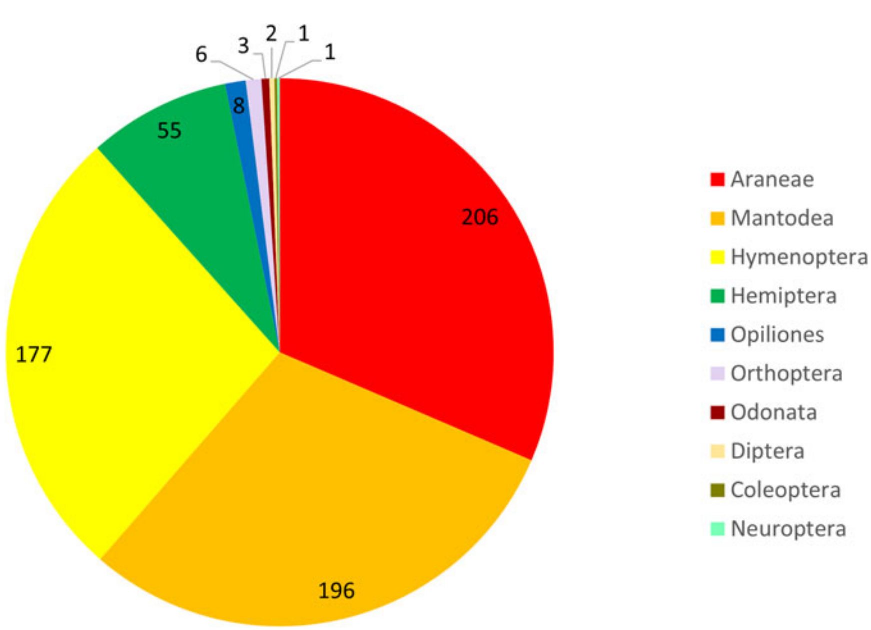

Figure 2. Arthropods reported feeding on *L. delicatula* by order from 2020 to 2022. Araneae was the most reported order, making up 31.45% of reports, followed by 29.92% Mantodea and 27.02% Hymenoptera of total reports.

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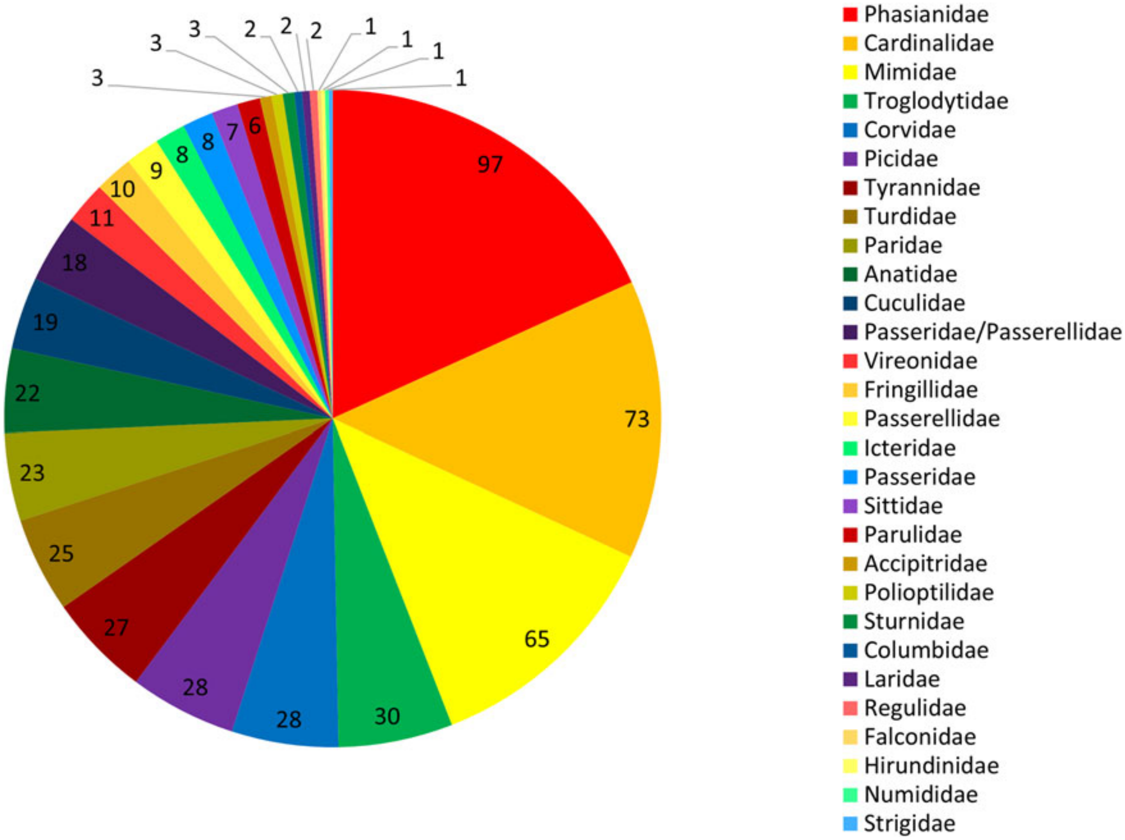

Figure 3. Birds reported feeding on *L. delicatula* by family from 2020 to 2022. Phasianidae was the most reported family with 20.64% of total reports, followed by 13.27% Cardinalidae and 10.07% Mimidae.

on *A. altissima*, only one was eaten whole, which is less frequently than expected ($\chi^2 = 32.37$, $P < 0.001$), and predators avoided eating additional lanternflies in 10 reports, which was more frequently than expected ($\chi^2 = 19.96$, $P < 0.001$). *L. delicatula* were reported feeding on host plants other than *A. altissima*, maple, and black walnut 40 times, and of these, 31 were eaten whole, which was more frequently than expected ($\chi^2 = 16.07$, $P = 0.001$). While not significant, it is worth noting that 10 of the 12 *L. delicatula* that were observed feeding on black walnut were eaten whole.

Discussion

Our findings indicate that many generalist predators in North America are feeding on *L. delicatula*, notably arthropods and birds. When comparing the major groups of predators to feeding

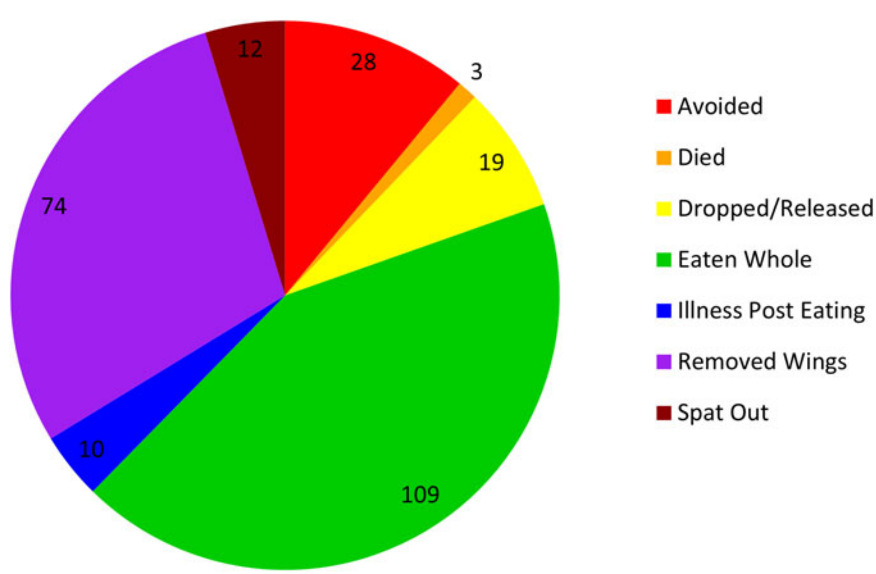

Figure 4. Reported feeding behaviors of *L. delicatula* predators from 2020 to 2022. Of these reports, 42.75% of predators were observed to eat *L. delicatula* whole and 29.02% removed the wings of adults prior to eating them.

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Table 1. Summary of *P*-values of Pearson's χ^2 tests and post hoc analyses performed

				$P < 0.001$			
Predator type	Avoided	Died	Dropped/released	Eaten whole	Illness post-eating	Removed wings	Spat out
Arthropod	1.000	1.000	1.000	1.000	1.000	0.002*	1.000
Bird	1.000	1.000	1.000	0.366	0.006†	1.000	1.000
Mammal	1.000	1.000	1.000	0.003†	<0.001*	1.000	0.305
Fish	1.000	1.000	1.000	1.000	1.000	1.000	0.087
Amphibian	1.000	0.039*	1.000	0.693	1.000	1.000	1.000
L. delicatula life stage							
Egg	1.000	1.000	1.000	0.570	1.000	NA	1.000
Early nymph	1.000	1.000	1.000	<0.001*	1.000	NA	1.000
Late nymph	1.000	1.000	1.000	0.013*	1.000	NA	1.000
Adult	1.000	1.000	1.000	<0.001†	1.000	<0.001*	1.000
Host plant							
Ailanthus	<0.001*		1.000	<0.001†		0.078	1.000
Maple	1.000		1.000	1.000		1.000	1.000
Walnut	1.000		1.000	0.557		0.716	1.000
Other	0.089		1.000	0.001*		1.000	1.000

An asterisk (*) indicates the predator behavior was observed significantly more frequently than expected while a † indicates the predator behavior was observed significantly less frequently than expected.

behaviors, birds were only reported to experience illness once, while mammals were reported to experience illness a third of the time after consuming *L. delicatula*, suggesting that birds have a greater tolerance than mammals of plant defensive compounds sequestered in *L. delicatula*. There was a frequent tendency of predators to remove the wings of *L. delicatula* prior to feeding on them, which occurred in more than half of the reported cases in arthropods and more than a quarter of the reports in birds (fig. 5). This behavior is similar to adaptations found in black-backed orioles, *Icterus abeillei* (Passeriformes: Icteridae), and black-headed grosbeaks, *Pheucticus melanocephalus* (Passeriformes: Cardinalidae), which are important predators of overwintering monarchs. These birds avoid eating the monarch wings and other areas consisting mainly of cuticle, as these areas have the highest concentrations of sequestered cardenolides (Fink and Brower, 1981). Our findings suggest that predators in North America may be learning to avoid a similar distribution of toxins in *L. delicatula* bodies, which could result in more effective top-down control. Further study of how naïve compared with experienced predators interact with *L. delicatula* is needed.

We also found significant differences in the feeding behaviors of predators in their interactions with different *L. delicatula* life stages. Adults were eaten whole less frequently than expected, while early and late instar nymphs were eaten whole more frequently than expected. These results may indicate that the levels of defenses present in *L. delicatula* vary over their life cycle,

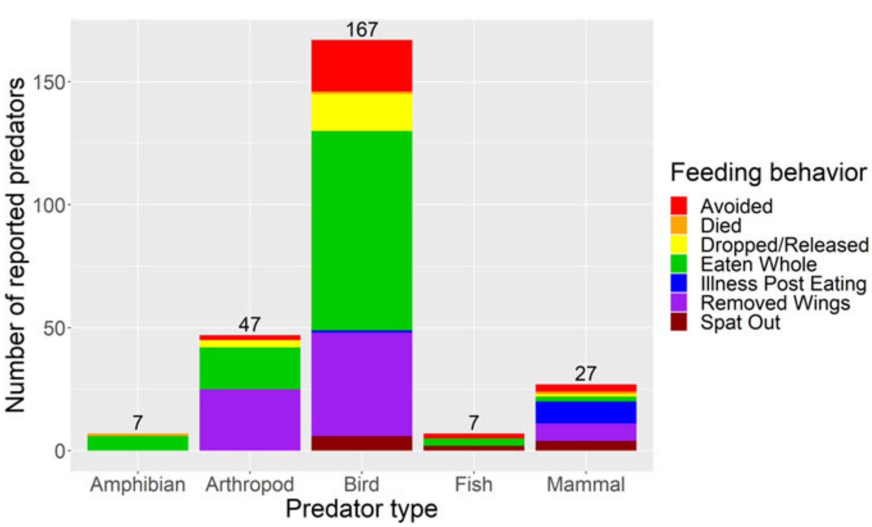

Figure 5. Feeding behaviors of *L. delicatula* predators by predator type. Birds experienced illness after eating *L. delicatula* less frequently than expected, arthropods removed wings more frequently than expected, mammals ate them whole less frequently than expected and experienced illness after eating more frequently than expected, and amphibians died more frequently than expected.

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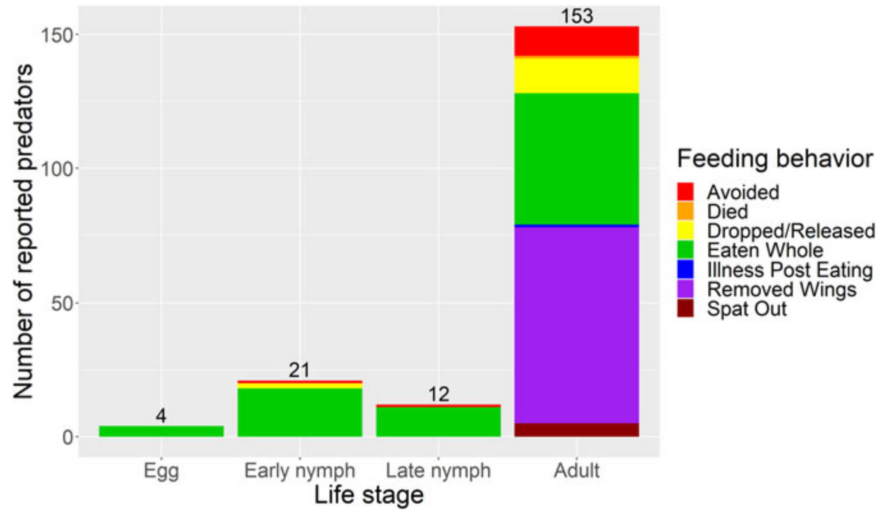

Figure 6. Feeding behaviors of *L. delicatula* predators by life stage. Early nymphs were eaten whole more frequently than expected, late-stage nymphs were eaten whole more frequently than expected, and adults were eaten whole less frequently than expected and their wings were removed more frequently than expected.

which is likely tied to changes in *L. delicatula* diet. In Kim *et al.* (2011), *L. delicatula* was reported to show an increasing preference for toxin-containing host plants, such as *A. altissima* during its development, with the strongest preference by adults just before egg laying. Murman *et al.* (2020) found a similar pattern, with the percentage of trees on which first through third instars were trapped being similar between *A. altissima* and other species, which are life stages that may not yet be sequestering toxins. In a choice test, Murman *et al.* (2020) also found that *L. delicatula* only began to display a consistent, significant preference for *A. altissima* over black walnut in adulthood. Since nymphs do not show as strong a preference for toxin-containing host plants as adults (Kim *et al.*, 2011; Liu, 2019; Murman *et al.*, 2020), they may not be as well defended and thus can more easily be eaten whole than adults.

There were significant relationships between the known host plants in the *L. delicatula* diet and predator behavior. Only once was a *L. delicatula* that was observed on *A. altissima* eaten whole; instead, most predators avoided or removed the wings of *L. delicatula* that were on *A. altissma*. *L. delicatula* that had fed on host plants other than *A. altissima* (i.e., maples, black walnut, or others) were frequently eaten whole, significantly so for those observed on host plants in the 'other' group and for all but two reported on black walnut. This could indicate that *A. altissima* provides *L. delicatula* with a source of sequesterable chemical defenses while other host plants do not, though reports only allowed us to know the host plant with certainty during the predation event, not what they fed on throughout their life.

Many of our results align with findings by Song *et al.* (2018). First, we found that *L. delicatula* likely had fewer defenses against predators in their earlier life stages; Song *et al.* (2018) found that when *L. delicatula* were collected on *A. altissima*, then crushed and mixed into butter balls, naïve birds pecked less and performed more head shakes and bill wipes when fed on balls containing adult *L. delicatula* than balls that contained third instars, indicating that balls containing adults collected from *A. altissima* were less palatable. We also found that the host plant affected predator behavior, with *A. altissima* likely providing a source of defenses against predators, which was also reported by Song *et al.* (2018) in which they found that butter or margarine balls containing crushed adult *L. delicatula* collected from *A. altissima* were pecked significantly less than balls containing adults collected from willow (*Salix* sp.) or control balls that did not contain *L. delicatula*. Birds also shook their heads and wiped their beaks more often after feeding on the *A. altissima*-collected *L. delicatula* balls than those that contained *L. delicatula* collected

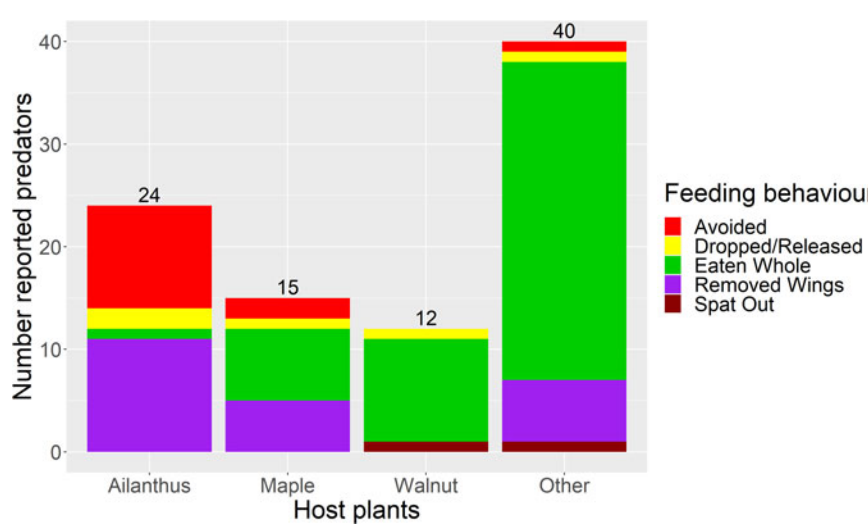

Figure 7. Feeding behaviors by predators of *L. delicatula* that were feeding on known *L. delicatula* host plants. Lanternflies observed feeding on *A. altissima* were eaten whole less frequently than expected and were avoided more frequently than expected, while those on host plants other than *A. altissima*, maple, and black walnut were eaten whole more frequently than expected.

on willow. Chemical analyses of fourth instar and adult *L. delicatula* showed that ailanthone and potentially four other quassinoids were present in *L. delicatula* collected from *A. altissima* but were not present in samples collected from persimmon trees. While the authors had limited availability of samples and standards to identify the chemical components other than ailanthone, they found differences in the composition of quassinoids between *L. delicatula* collected from Korean willow and *A. altissima*, with the differences being more pronounced for adults than nymphs. This is consistent with our findings that changes in diet across the life cycle of *L. delicatula* could lead to different levels of chemical defenses against predators.

It is worth noting that our results were undoubtedly affected by observer bias that is inherent to community science studies, with predators that were easier for participants to observe and identify likely overrepresented in their reports (Arazy and Malkinson, 2021). This could be one of the reasons that chickens were the most reported bird predators, since this is a domesticated species and many people in Pennsylvania keep chickens. This could also contribute to why arthropod predators such as grass spiders (family Agelenidae), jumping spiders (family Salticidae), orb weaver spiders (family Araneidae), praying mantises (all reported species were in family Mantidae), and yellow jackets (family Vespidae) were often reported, as these are relatively large, noticeable, and easily identified, while smaller or less well-known arthropods may have been overlooked. Likewise, most reports with the life stage of *L. delicatula* identified were of adults, which is the largest and most visible stage. Proper identification could also be an issue; for example, many wasps (identified through provided photos) were reported as 'bees.' We tried to counteract this by correctly identifying the predators when pictures were provided and by choosing taxonomic groupings, such as sorting arthropod predators by order (with both bees and wasps in Hymenoptera).

Another limitation of this study is that behaviors could be misinterpreted, notably the attribution of death of predators to feeding on *L. delicatula*. For the three reports of predator death, one was of a frog that the reporter believed to have fed on *L. delicatula* regularly throughout the season and was then found dead with no obvious injuries at the end of the summer. One was of a common finch that was observed eating four lanternflies before dying, and the last was a dog that ate a *L. delicatula* and then had a seizure that resulted in its death. It can be difficult to tell if these deaths were due to feeding on *L. delicatula* or other causes, yet this interaction could have serious ecological implications if they were in fact caused by ingestion of *L. delicatula* and should be further explored.

Our results provide evidence that predators could conceivably play a role in natural control of *L. delicatula*. Birds frequently feed on novel insects in their environment, making them excellent potential predators of *L. delicatula* (Fayt *et al*., 2005; Barbaro and Battisti, 2011), while wild insects, which made up the majority of reported arthropods, offer an estimated $4.5 billion of pest control in agricultural systems each year (Losey and Vaughan, 2006). While investigations of classical biocontrol agents are underway (Xin *et al*., 2021), natural predation could be enhanced through the implementation of purposeful augmentative or conservation biological control efforts once efficient predators are identified in the introduced range of *L. delicatula*.

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Author contributions. AJ and KH conceived the methods for this study. AJ compiled and analyzed the data and wrote the paper. All authors contributed to data interpretation, editing of the paper, and approved the paper for submission.

Competing interest. The authors declare none.

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