SPECIALIST INVASIVE HERBIVORE REVEALS A POSITIVE PREFERENCE-PERFORMANCE RELATIONSHIP ON DEFENDED HOST PLANTS

by

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(Under the Direction of Carmen Blubaugh)

ABSTRACT

Herbivorous insects generally choose host plants that optimize growth. However, many specialists choose chemically defended host plants that slow growth, prioritizing protection from natural enemies. Invasive specialist herbivores may also be unpalatable in their non-native range where they lack co-evolved natural enemies. Here, we explore the diet choices of the invasive yellowmargined leaf beetle, *Microtheca ochroloma*. We measured *M. ochroloma* preferences among six *Brassica* plants varying in glucosinolate concentrations. In both field and laboratory experiments, *M. ochroloma* preferred the less-toxic host plants mizuna and Chinese cabbage. In the field, predatory insects were least common on mizuna, suggesting that less-defended plants may not increase the invader's susceptibility to predation. The positive preference-performance relationship we observed suggests that *M. ochroloma* prioritizes growth over protection against natural enemies. By identifying mizuna as a highly-preferred host for this invasive pest, our results may inform trap cropping strategies that limit damage in agricultural systems.

INDEX WORDS: invasive insect, preference-performance hypothesis, enemy release, *Microtheca ochroloma,* trap crop, intercrop

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BS, Clemson University, 2020

A Thesis Submitted to the Graduate Faculty of The University of Georgia in Partial Fulfillment of the Requirements for the Degree

MASTER OF SCIENCE

ATHENS, GEORGIA

2023

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May 2023

ACKNOWLEDGEMENTS

I would like to acknowledge the following people and groups who inspired me and offered immeasurable help during my time at UGA:

- Growing Green Family Farm who inspired me to research the yellowmargined leaf beetle and taught me about intercropping while I worked on their farm.
- Organic Farmer Research Foundation for funding my intercropping and trap cropping experiments.
- The five farms who participated in an on-farm trap cropping experiment: Growing Green Family Farm, Foster-Brady Farm, Oxford Farm, Bioway Farm, and Little Toccoa River Farm.
- The employees at the Durham Horticulture Farm who helped prepare and maintain my field experiments.
- My PI, Carmen Blubaugh, my field technicians: Jon Golan and Avery Ryan, and all the members of our wonderful lab who helped execute my experiments.

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CHAPTER 1

INTRODUCTION

The preference-performance hypothesis predicts that insects will oviposit on host plants that are best suited for larval development (Gripenberg et al., 2010, Jaenike 1978, Bradley et al. 2018). In bi-trophic systems which include an herbivore and host plant, host plant preferences often align with increases in larval performance (Xue et al. 2007, reviewed in Gripenberg et al 2010, but see Courtney and Kibota 1990, Berenbaum and Feeny 2008), yet in tri-trophic contexts including natural enemies, preference-performance relationships are often decoupled or even negative (Courtney and Kibota 1990, Singer et al 2004, Friberg et al. 2015). This is because some herbivorous insects consume more toxic host plants that slow their larval growth (Hufnagel et. al 2017, Brown et al., 2017), yet make them unpalatable to predators (Kos et al. 2012), or improve their resistance/immunity to parasitism (Singer et al. 2009, Ghosh et al. 2022; Smilanich et al. 2009). Short-term costs of consuming toxic host plants can pay off in long-term optimization of fitness when we consider those choices in a multi-trophic context (Price et al. 1980, Mayhew 2001) and across life stages (Brown et al 2017). For example, the tobacco hornworm, *Manduca sexta* L. (Lepidoptera: Sphingidae), is more likely to lay eggs on more-toxic solanaceous plants within their host range that decrease larval growth (Hufnagel et al. 2017). Yet, parasitoid wasps are less likely to oviposit and survive in caterpillar larvae that have consumed these plants, suggesting that larval growth comes secondary to predator protection (Garvey et al., 2020).

Mismatches between herbivore preference and performance are common on host plants in the highly defended Brassicaceae family (Fei et al. 2017). Most herbivores in this system are specialists uniquely adapted to consume glucosinolates, (i.e. mustard oils that crucifer plants synthesize for herbivore defense; Hopkins et al. 2009), and many selectively sequester and weaponize them in defense against natural enemies (Aliabadi et al. 2002, Kazana et al. 2007, Beran et al. 2014). For example, cabbage aphids, *Brevicoryne brassicae*, commonly select *Brassica* host plants with higher glucosinolates concentrations (Staley et al. 2010) that slow their colony growth (Kos et al. 2011, but see Kos et al. 2012), while concentrations of sequestered glucosinolates decrease preference and performance of generalist predators. Curiously, higher concentrations of sequestered glucosinolates increase preferences of specialist parasitoids without inflicting performance costs, suggesting that they are coevolved to exploit and/or detoxify sequestered glucosinolates (Kos et al. 2012). The diamondback moth, *Plutella xylostella* L. (Lepidoptera: Plutellidae), often prefers to lay eggs on more-toxic *Brassica* species and/or plant parts despite worse performance (Marchioro and Foerster 2014, Moreira et al. 2016, Ghosh et al. 2022, but see Staley et al. 2010, Zhang et al. 2012). Toxic host plants elevate the diamondback moth's immune response, and some parasitoid wasps prefer to oviposit on larvae fed less-toxic plants (Ghosh et al., 2022). Likewise, cabbage white butterflies (*Pieris rapae* L.) also selectively oviposit on plants misaligned with rapid larval growth, yet ultimately optimize survival (Friberg et al. 2015, Griese et al. 2020), and decrease parasitism (Ohsaki and Sato 1994).

Invasive specialist herbivores feeding on toxic host plants have the additional advantage of being especially unpalatable to native natural enemies (Callaway and Ridenour 2004), while escaping coevolved specialist natural enemies from their invaded range (Torchin et al., 2003, Keane & Crawley, 2002). Sequestered secondary metabolites may act as ‘novel weapons’ that confer even stronger protection from natural enemies than native herbivores (Callaway and Ridenour 2004), further releasing them from interspecific competition (Keane and Crawley 2002). This could enable them to dominate native herbivore communities (Fortuna et al. 2022) and inflict massive damage to crops (Bradshaw et al. 2016). Here, we explore preference-performance host plant relationships for the invasive yellow-margined leaf beetle, *Microtheca ochroloma* Stål (Coleoptera: Chrysomelidae) a Brassicaceae host specialist native to South America, which has expanded its range in the Southeastern United States since the 1940s (Staines 1999, Balusu et al., 2017, Chamberlin & Tippins, 1947).

Microtheca ochroloma causes extensive chewing damage to many *Brassica* crops and is one of the most damaging pests vegetable farmers face (Balusu and Fadamiro 2012), especially for farmers who prefer organic, low-input, or no-spray pest management methods (Bowers, 2003). There is little evidence of biocontrol by native natural enemies of *M. ochroloma* in its invaded range (Montemayor & Cave 2009, Balusu et al. 2017). Like many *Brassica* specialist herbivores (Jeschke et al. 2016), it has been hypothesized that *M. ochroloma* sequesters toxic secondary metabolites from their host plants which makes them unpalatable to natural enemies (Niño and Cave 2015, Balusu and Fadamiro 2012). Host plant preferences for *M. ochroloma* have been examined in both the native and invaded range (Table 1), and this prior work suggests that while *M. ochroloma* can feed on hosts throughout the Brassicaceae family, they tend to select cultivars within *Brassica rapa* and *Brassica juncea*. However, it’s unknown how host plant preferences might vary among these preferred cultivars.

Table 1. Host plant preference and performance trials of *Microtheca ochroloma.*

Reference	*Plants tested*	*Most-preferred*	*Choice/ no choice*	*Method/Metric*	*Location*
Balusu and Fadamiro 2011	cabbage, collards, Napa cabbage, and turnip	Turnip, napa cabbage	Choice	Cage experiment: number of beetles on plants and damage ratings	Alabama, USA (invaded range)
Farinha et al., 2021	Chinese cabbage, mustard, watercress, arugula, and radish	Chinese cabbage, mustard, arugula	Choice	Occurrence of beetles on field plots	Brazil (native range)
Menezes et al., 2005	watercress, mustard, Chinese cabbage, and wild radish	Chinese cabbage	Choice	Leaf tissue consumed by 1 larva in petri dish choice trial	Brazil (native range)
Menezes et al., 2005	watercress, mustard, Chinese cabbage, and wild radish	mustard	Choice	Leaf tissue consumed by 1 adult in petri dish choice trial	Brazil (native range)
Menezes et al., 2005	spinach, radish, collard, watercress, arugula, mustard, Chinese cabbage, and wild radish	mustard, Chinese cabbage	Choice	Leaf tissue consumed by 10 larvae in petri dish choice trial	Brazil (native range)
Balusu et al., 2015	turnip, cabbage, Napa cabbage, mustard	turnip, mustard, napa cabbage	Choice	Trap crop field experiment: number of beetles on plants and damage ratings	Alabama, USA (invaded range)
Ameen and Story 1997b	cabbage, collards, mustard, turnip, and radish	turnip	Choice	Leaf disk choice for 1st instar larvae	Louisiana, USA (invaded range)
Ameen and Story 1997b	cabbage, collards, mustard, turnip, and radish	turnip, mustard	Choice	Leaf disk choice for 3rd instar larvae	Louisiana, USA (invaded range)
Ameen and Story 1997c	cabbage, collards, mustard, turnip, and radish	turnip, mustard, radish	Choice	Leaf disk choice for adult beetles	Louisiana, USA (invaded range)

Ameen and Story 1997c	cabbage, collards, mustard, turnip, and radish	Turnip, radish, mustard, cabbage	No choice	Fecundity (eggs laid per female)	Louisiana, USA (invaded range)
Ameen and Story 1997c	cabbage, collards, mustard, turnip, and radish	Turnip, mustard, cabbage, radish	No choice	Fecundity (eggs laid per day)	Louisiana, USA (invaded range)
Ameen and Story 1997c	cabbage, collards, mustard, turnip, and radish	radish	No choice	Adult longevity	Louisiana, USA (invaded range)

To examine the relationship between an invasive herbivore's diet selection and larval performance, we performed host plant choice trials on *M. ochroloma*, over a range of six host plant cultivars within *Brassica rapa* that vary in their concentrations of glucosinolates (Table 2). We then compared host plant choices from the lab assay to patterns of herbivore and natural enemy abundances across the same host plants in the field. We predicted that, like other *Brassica* specialist herbivores, *M. ochroloma* would prefer more-toxic host plants such as mustard and turnip (Table 2) that slow their growth, while natural enemies will more commonly assemble on less-toxic host plants such as Chinese cabbage and mizuna.

CHAPTER 2

METHODS AND RESULTS

Methods

In previous studies, *M. ochroloma* almost always preferred more tender *Brassica* greens such as turnip, Chinese cabbage, and mustard instead of waxy-leafed *Brassica oleracea* crops (Table 1). For this reason, our study focused on the more preferred *Brassica rapa* and *Brassica juncea* plants. To measure *M. ochroloma* host plant preference, we chose six *Brassica* species plants: purple-top white globe turnip (*Brassica rapa* L. var *rapa*), broccoli raab (*Brassica rapa* Bailey var. *ruvo*), yellow mustard (*Brassica* L. *juncea*), mizuna (*Brassica rapa* Shebalina var. *japonica*), Chinese cabbage (*Brassica napa* Lour var. *pikinensis*), and choi sum (*Brassica rapa* L. var. *chinensis*). These plants vary in glucosinolate concentrations: the plant defense compound found in Brassicaceae plants (Table 2). We measured *M. ochroloma*'s preference to these six plants in both petri dish and field experiments as well as predator assemblages on the host plants.

Table 2: Glucosinolate concentrations (µmol/g) in foliar leaf tissue of six *Brassica* species plants according to literature review.

Toxicity	Plant		Reference	GSL µmol/g
Highest	Mustard	*Brassica juncea*	Bhandari et al., 2015	61.78 dry weight
High	Purple-top turnip	*Brassica rapa* var *rapa*	Carlson et al 1987	1.94-3.89 fresh
	Purple-top turnip	*Brassica rapa* var *rapa*	Yang and Quiros 2010	~1.8 fresh (average of 18 varieties)
	Purple-top turnip	*Brassica rapa* var *rapa*	Bradshaw et al., 1984	24.42 dry weight
Low	Broccoli raab	*Brassica rapa* var. *ruvo*	Yang and Quiros 2010	1.454-1.57 fresh weight
Low	Mizuna	*Brassica rapa* var. *japonica*	Park et al., 2020	15.81 dry weight
Low	Choi sum	*Brassica rapa* var. *chinensis*	Bhandari et al., 2015	14.48 dry weight
	Choi sum	*Brassica rapa* var. *chinensis*	Yang and Quiros 2010	0.563 (average of 3) fresh
Lowest	Chinese cabbage	*Brassica rapa* var. *pikinensis*	Bhandari et al., 2015	3.53 dry weight
	Chinese cabbage	*Brassica rapa* var. *pikinensis*	Yang and Quiros 2010	~0.424 fresh weight (average of 39 varieties)

Laboratory host plant choice trials:

To determine *M. ochroloma* plant preference, we provided freshly hatched *M. ochroloma* the choice between 1 cm leaf disks of each plant (Fig. 1). We planted each of the six host plants on 29 April 2021 and placed them into mesh cages outside. When plants were three weeks old, we cut out 1 cm leaf disks from the third leaf of each plant, and randomly arranged the six discs in a 14 cm diameter petri dish. We placed a first-instar *M. ochroloma* larva in the center of each dish (34 replicates) and recorded which plant the beetle larva began eating first.

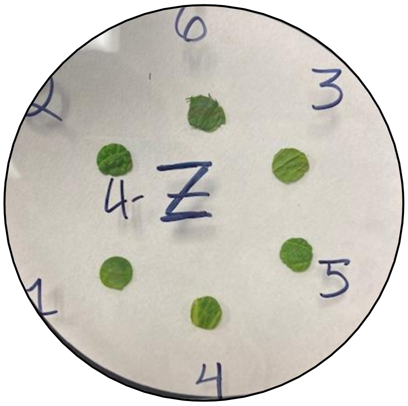

Figure 1: Photo of laboratory host plant trial experimental setup in a petri dish.

<u>Greenhouse performance assays:</u>

To estimate *M. ochroloma* performance on each of the host plants, we monitored their growth and mortality when consuming each host plant. We purchased seeds from Johnny's Selected Seeds and planted 48 seeds of each of the six plants in the greenhouse on 29 July 2021. After three weeks, we placed one 1st-instar *M. ochroloma* larva on 15 replicated plants of each species (90 replicates total). Three plants of each cultivar were placed in a cage (30 cages total). The cages were set up in five randomized blocks in the greenhouse. After three days, plants that had no leaf damage were assumed to have dead larva and were replaced with live larva. We measured larval weight after five days and recorded the number of beetles that survived to adulthood.

<u>Field estimates of *M. ochroloma* and natural enemies:</u>

We conducted our field experiment at the University of Georgia Durham Horticulture Farm in Watkinsville Georgia (33°53'11.8"N 83°25'18.7"W). We planted five small plots (1.2 m x .9 m) of each of the six *Brassica* cultivars, totaling 30 plots. The plots were arranged in a randomized block design. Each plot had two rows of crops. We fertilized the 62 m^2 site with 6.8

kg of 12-0-0 blood meal (1.00% water soluble nitrogen and 11.00% insoluble nitrogen) and 4 kg of "Nature Safe" 9-0-9 organic fertilizer (0.25% ammoniacal nitrogen, 8.00% water insoluble nitrogen derived from bone and meat meal, 0.75% other water-soluble nitrogen, 9.00% K_2O, and 3.00% sulfur) on 21 April 2021. Seeds were directly sown and spaced according to seed-packet instructions on 1May 2021. We re-planted seeds in areas that did not germinate on 17 May 2021. Plots were weeded by hand and with a stirrup hoe weekly and watered using drip irrigation. To characterize the insect community on our six host plants, we counted and identified all insects in visual surveys on three randomly selected plants as well as within three 0.04 m^2 ground quadrats for each of the 30 plots. During ground surveys, we turned over dead leaves and scratched the ground to reveal *M. ochroloma* eggs and pupae. Surveys were conducted once a week between 18 May 2021 – 25 June 2021. To account for the size variation across our 6 host plants, we standardized our insect quantities by plant biomass. Each week, three randomly selected plants of each species were collected from the field, dried for approximately 72 hours in a 70˚C oven, and weighed.

Plant Damage Surveys

We estimated herbivore damage on our sampled plants visually using an ordinal scale between 0-5 (Fig.1), and analyzed mean damage scores across the three subsamples in each plot.

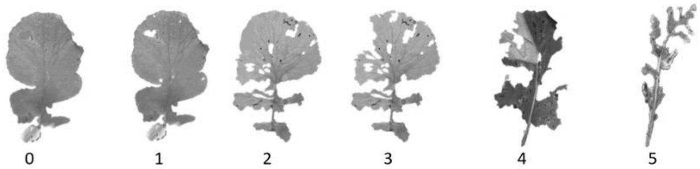

Figure 2: Plant damage pictorial scale used to quantify chewing herbivore damage on our six host plants.

Preliminary Predator Choice Trials

As a preliminary study to gauge how likely predators are to consume *M. ochroloma* versus native prey, we placed two medium sized *M. ochroloma* larvae and five aphids collected from a kale plant into a petri dish. We collected an assortment of 16 predators of including larval and adult lady beetles and damsel bugs to use for our trial. We placed one predatory insect into each petri dish (16 total replicates) and reported the proportion of aphids and *M. ochroloma* consumed to determine general predator preference (Appendix Fig. A.1). To determine predator preference, we gave 16 *Hippodamia convergens* the choice among six *M. ochroloma* that had exclusively fed on one of each *Brassica* plants. When *M. ochroloma* larvae were one week old, we removed them from plants and affixed them to sticky cards, which were placed in random order in a 14 cm diameter petri dish. We placed one predatory adult *H. convergens* into the center of each dish (16 total replicates) and recorded their first larval choice (Appendix Fig. A.2). Insects that did not make a choice after 24 hours were recorded as “no choice”.

Statistical analyses

All analyses were performed in R version 4.1.2 (R Core Team 2021). To evaluate herbivore preferences of 34 *M. ochroloma* larvae in lab-choice assays, we used chi-square tests assuming equal numbers of larvae would choose each host plant. To evaluate herbivore performance across the six host plants, we used ANOVA, with *M. ochroloma* larval weights after five days of feeding as the dependent variable, and host plant as the independent variable. We used logistic regression to evaluate host plant effects on pupation success. To evaluate densities of *M. ochroloma* and their predators across host plants in the field study, we used generalized linear mixed models using the lme4 package of R (Bates et al., 2015), assuming a Poisson distribution, with annual sums of insects as the dependent variable, host plant species as the independent variable, and dry plant biomass (grams) as a random effect to control for differences in plant sizes across host plants. Herbivore damage values did not meet normality assumptions, so we evaluated herbivore damage across host plants with nonparametric Kruskal-Wallis tests. We checked model assumptions by examining residual plots and histograms where relevant. We used Tukey post-hoc tests to separate means between groups. We extracted test statistics for host plant main effects in mixed models using the ANOVA function in the car package, reporting type II sums of squares (Fox and Weisberg 2019).

Results

Laboratory *M. ochroloma* choice and performance trials:

In lab choice experiments, *M. ochroloma* first-instar larvae numerically preferred mizuna and Chinese cabbage over other taxa ($\chi 2 = 10.471$, df = 5, n = 34, P = 0.063, Fig. 3).

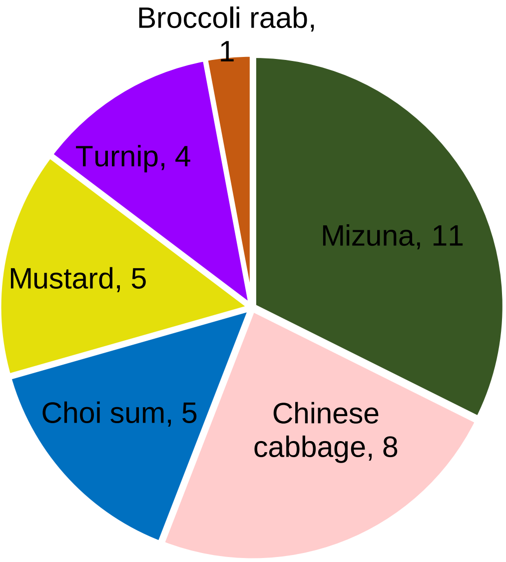

Figure. 3 Pie chart indicating numbers of host plants (*Brassica* species and varieties) chosen by 34 *M. ochroloma* first-instar larva in a six-way lab choice trial.

After five days of feeding in the no-choice performance assay, mean larval weights of *M. ochroloma* were 50% higher on mizuna than on Chinese cabbage and broccoli raab, and intermediate on turnips, mustard, and choi sum ($F_{5,69} = 68.81$, $P = 0.021$; Fig. 4). *M. ochroloma* survival to adulthood did not differ across host plants (Wald $\chi^2 = 3.0561$, df = 5, $P = 0.6913$), nor did adult weight ($F_{5,30} = 44.75$, $P = 0.23$). Together, choice assays and performance assays revealed a positive preference-performance relationship for *M. ochroloma* across the six host plants (Appendix Fig. A.3).

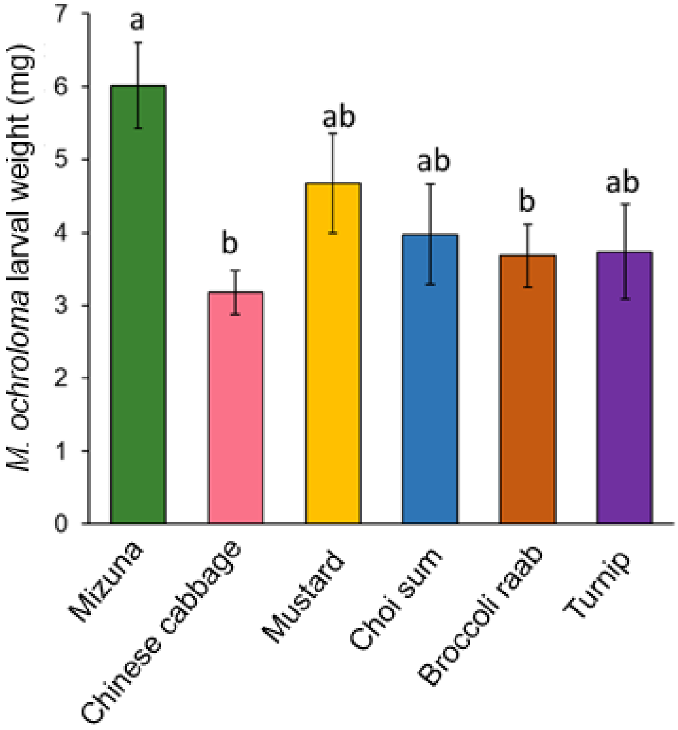

Figure 4. Mean larval weights (± SE) of *M. ochroloma* after five days of feeding on six *Brassica* host plants in a no-choice growth assay. The letters above each bar indicate significant differences ($P < 0.05$) among groups according to Tukey's post-hoc test.

Host plant preferences in the field.

In the field experiment, we found more than twice as many *M. ochroloma* adults and larvae on mizuna and Chinese cabbage, relative to other host plants ($F_{5,27,}$ = 51.327, P = < 0.00001) while Chinese cabbage, broccoli raab, and turnip supported the largest number of natural enemies ($F_{5,27,}$ = 27.441, P = < 0.00001) and mizuna, turnip, and mustard having the fewest herbivores ($F_{5,27,}$ = 15.502, P = < 0.00001) (Fig 4). Mizuna exhibited the highest plant damage score (χ^2 = 12.661, df = 5, P = 0.268).

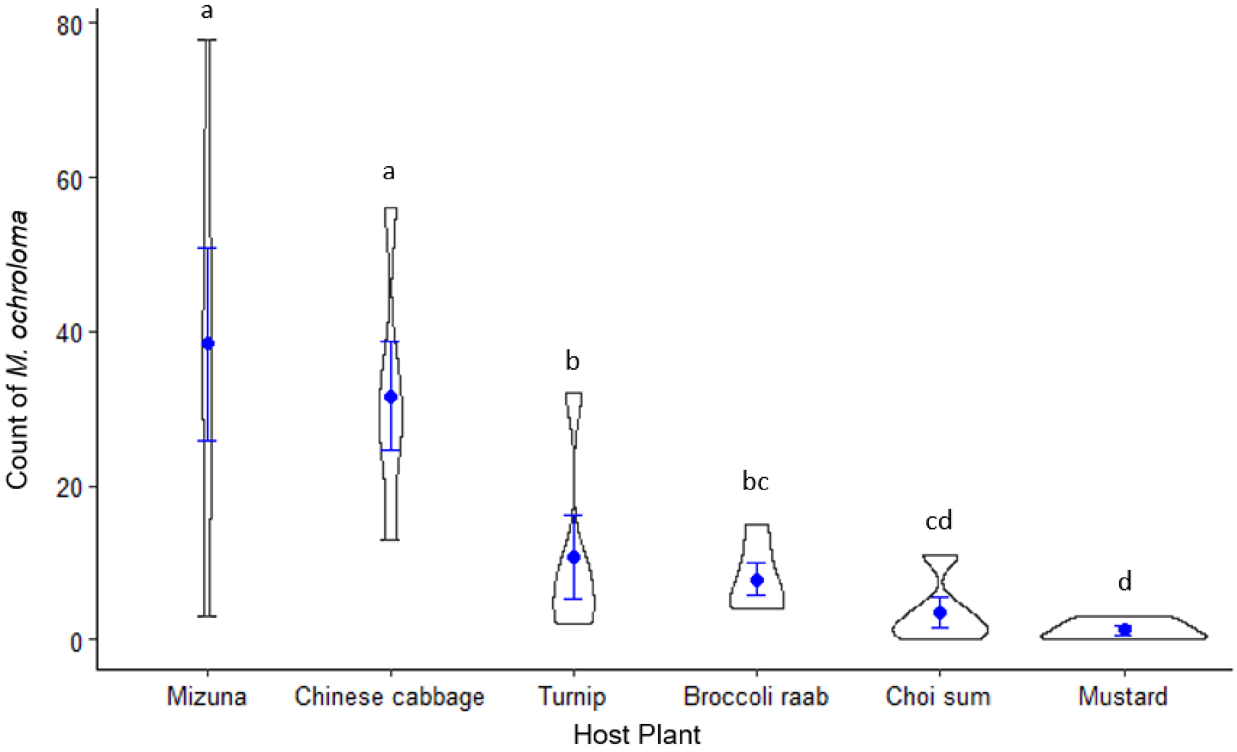

Figure 5: Mean annual counts (±SE) of *M. ochroloma* on each host plant (*Brassica* species and varieties) according to foliar count data. The top and bottom of the violin plot are the minimum and maximum values and the thickness of the shapes represents the probability density of the data. The letters above each plot indicate significant differences ($P < 0.05$) among groups according to Tukey's post-hoc test.

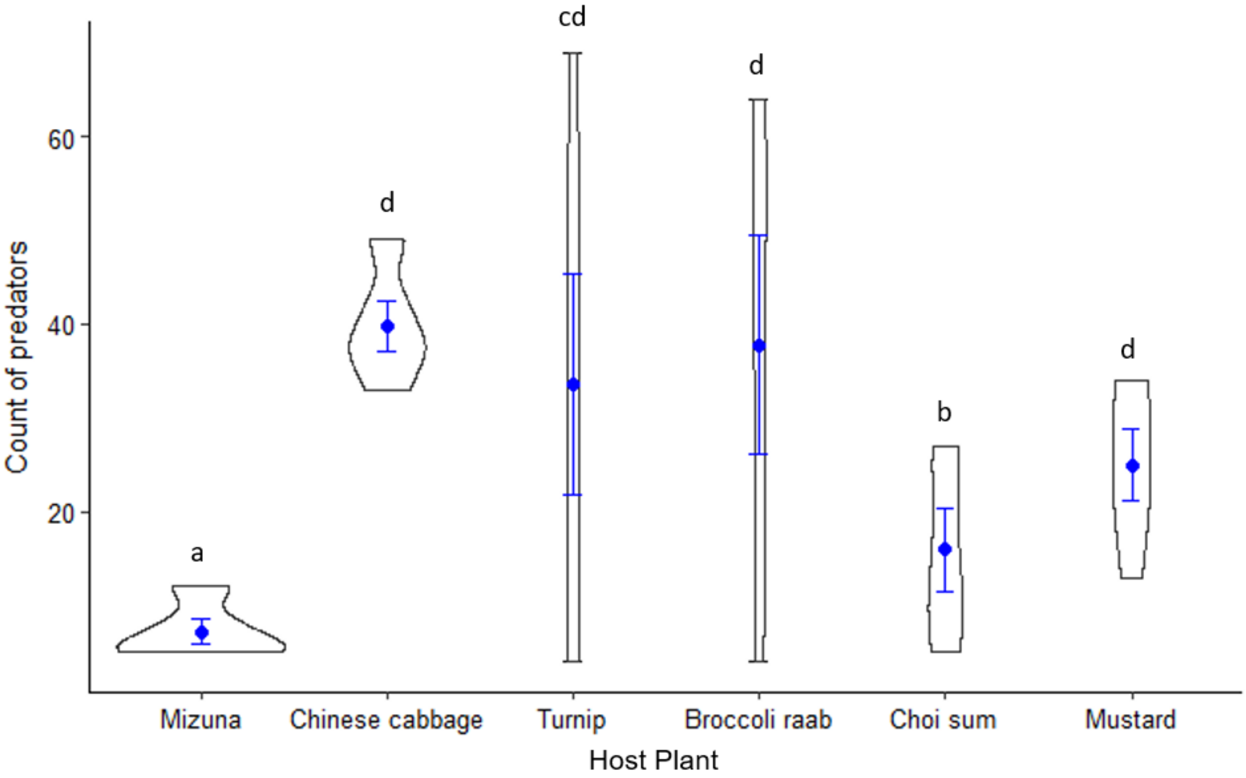

Figure 6: Mean annual counts (±SE) of natural enemies on each host plant according to foliar count data. The top and bottom of the violin plot are the minimum and maximum values and the thickness of the shapes represents the probability density of the data. The letters above each plot indicate significant differences ($P < 0.05$) among groups according to Tukey's post-hoc test.

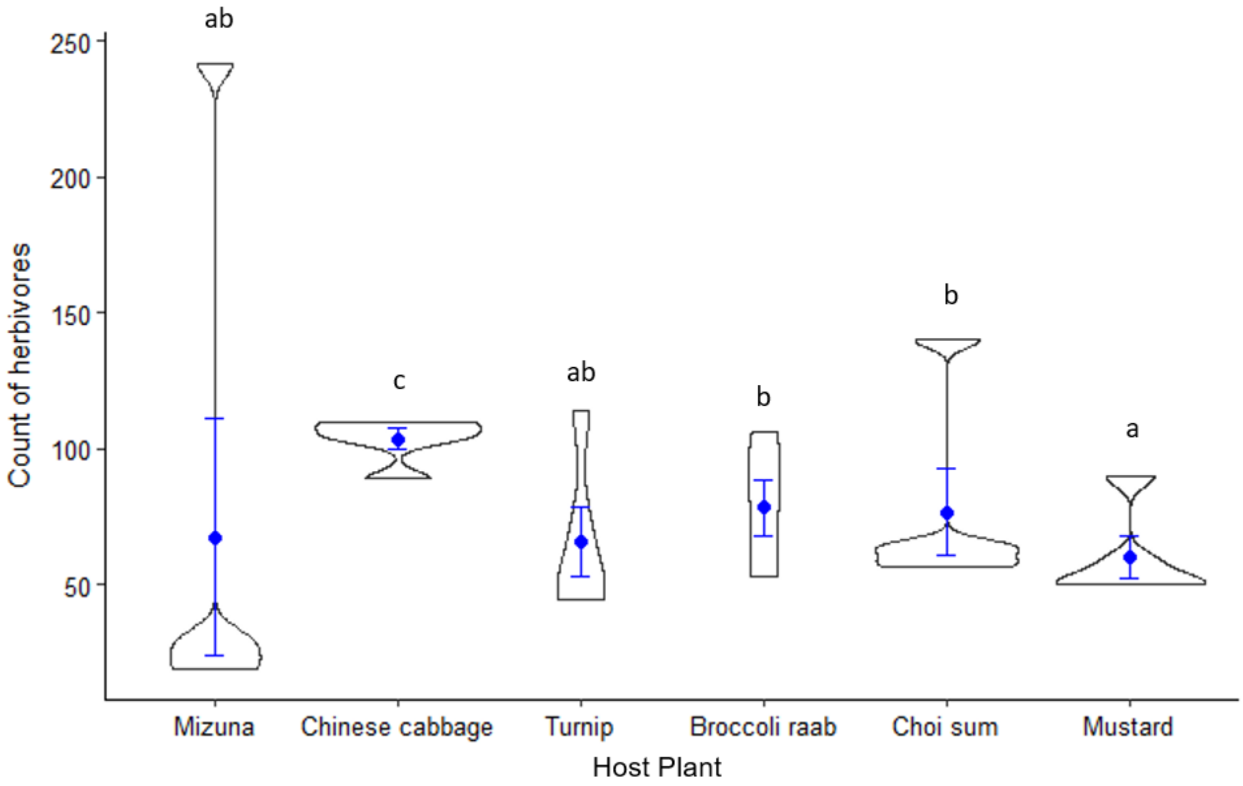

Figure 7: Mean annual counts (±SE) of all herbivorous insects excluding *M. ochroloma* on each host plant according to foliar count data. The top and bottom of the violin plot are the minimum and maximum values and the thickness of the shapes represents the probability density of the data. The letters above each plot indicate significant differences (P < 0.05) among groups according to Tukey's post-hoc test.

CHAPTER 3

DISCUSSION

To examine preference-performance relationships for an invasive specialist herbivore, we evaluated diet choice and its influence on *M. ochroloma* larval growth. Both our field and laboratory experiments revealed that *M. ochroloma* are selecting diets that maximize larval growth, in contrast to our predicted negative preference-performance relationships commonly found with *Brassica* specialist herbivores (Ghosh et al. 2022, Marchioro and Foerster 2014, Moreira et al. 2016). It appears that instead of consuming and high levels of toxic glucosinolates, *M. ochroloma* is able to prioritize growth over potential predator protection.

Although *M. ochroloma* arrived in the United States more than 80 years ago (Chamberlin and Tippins 1948), no native natural enemies are yet known to provide effective regulation of *M. ochroloma* in its invaded range (Balusu et al 2017). Other invasive herbivores like the brown marmorated stink bug, kudzu bug, and spotted wing drosophila were eventually discovered and suppressed by native or introduced natural enemies after initial population explosions (Lee et al., 2019, Tilman et al., 2020, Rice et al.,2020, Ragsdale et al., 2011, Diedrick et al., 2022). Yet, only a few anecdotal observations of biological control of *M. ochroloma* by native natural enemies have been recorded (Montemayor & Cave 2009, C. Huss and C. Blubaugh, personal observation). Indeed, controlled predator-choice trials suggest that native predators strongly prefer native *Brassica* herbivores over *M. ochroloma* (Montemayor and Cave, 2023, Appendix Fig. S.2). We originally predicted that *M. ochroloma* would reveal negative preference - performance relationships demonstrated by many other herbivores that specialize on highly-defended host plants (Ghosh et al. 2023, Marchioro et al. 2014, Moreira et al. 2016), yet in the absence of any meaningful top-down regulation in the invaded host range, perhaps *M. ochroloma* can opt to forego protection.

Some herbivores that specialize on toxic host plants are unpalatable to generalist predators regardless of their concentrations of sequestered chemicals (Kelly and Bowers 2018), so even the lowest concentrations of glucosinolates in *M. ochroloma*’s *Brassica rapa* host plants might render them sufficiently distasteful to preclude high rates of predation in the invaded range. Future research must examine the defensive chemistry of *M. ochroloma*. We suspect that they sequester glucosinolates because other closely related chrysomelids take advantage of glucosinolates for effective protection (Beran et al. 2014). Yet over time, a toxic invader might surrender its unnecessary defenses to evolve increased competitive ability in its novel host range (Blossey and Notzgold 1995). While hundreds of studies test the evolution of increased competitive ability (EICA) hypothesis among native plants, with mixed support (Felker-Quinn et al. 2013, Rotter and Holeski 2018), to our knowledge, no tests of EICA exist for invasive herbivores. Future research examining *M. ochroloma*’s preference-performance relationships in both the native and along the invasion front, along with an investigation of host preferences among natural enemies in both ranges could resolve whether enemy release is enabling the positive preference-performance relationship we observed. Little is known about *M. ochroloma*’s South American natural enemies. *Toxomerus duplicatus* Wiedemann, (Diptera: Syrphidae; Sturza et al., 2014) and *Stiretrus decastigmus* Herrich-Schaeffer (Heteroptera: Pentatomidae; Poncio et al., 2010) have been recorded consuming *M. ochroloma* in Brazil, but no specialized natural enemies are currently known.

In our field trial, we found the fewest predators on mizuna, choi sum, and mustard. Mustard, mizuna, and turnip contained the lowest number of herbivores (not including *M. ochroloma*; Fig. 6) which might explain why predators were less common on mizuna and mustard. Mustard and turnip's high toxicity relative to our other host plants (Bhandari et al., 2015) may further explain why herbivores were generally less likely to infest these plants. Mizuna was dominated by *M. ochroloma,* possibly out-competing other herbivores, yet few predators visited this plant. This may provide further evidence that native predators are not tracking *M. ochroloma* populations. Indeed, in a preliminary predator choice assay comparing *M. ochroloma* prey fed the six host plants, we found that lady beetles' most common choice was to starve rather than consume any of the larvae (Appendix Fig. A.2). Although *M. ochroloma* were equally likely to choose Chinese cabbage, this plant caused *M. ochroloma* to grow the slowest within a five-day period (Fig. 4). This lower weight may be explained by a lower protein, carbohydrate, and phosphorus density found in Chinese cabbage greens compared to the other host plants (USDA, 2019). Instead of choosing Chinese cabbage for its nutrient content, they may be utilizing the folded structure of the cabbage as habitat/refuge.

While *Brassica* specialists often choose highly-defended plants, *M. ochroloma* revealed a preference in both the field and lab for mizuna and Chinese cabbage, which are both relatively less-toxic plants to the others tested (Park et al., 2020; Bhandari et al., 2015). In addition to inspiring new hypotheses about why this invader has become such a serious pest, our results can be leveraged as cultural pest management tools by farmers. For example, trap cropping (Hokkanen, 1991) with highly preferred mizuna or Chinese cabbage could lure *M. ochroloma* away from the main *Brassica* crops. Importantly, mizuna attracted the fewest number of predators; this means that selectively applied pesticides in a 'dead end' trap crop strategy

(Shelton and Badenes-Perez, 2006) might inflict less damage to natural enemies on mizuna. If additional *M. ochroloma* predators are identified, then intercropping strategies can be used to attract those insects and increase *M. ochroloma* predation control (Gurr et al., 2017, Huss et al., 2022). Overall, our results reveal that the invasive *M. ochroloma* might be successful because of the absence of specialist natural enemies in their invaded range, allowing them to consume less-toxic host plants and prioritize growth over defense.

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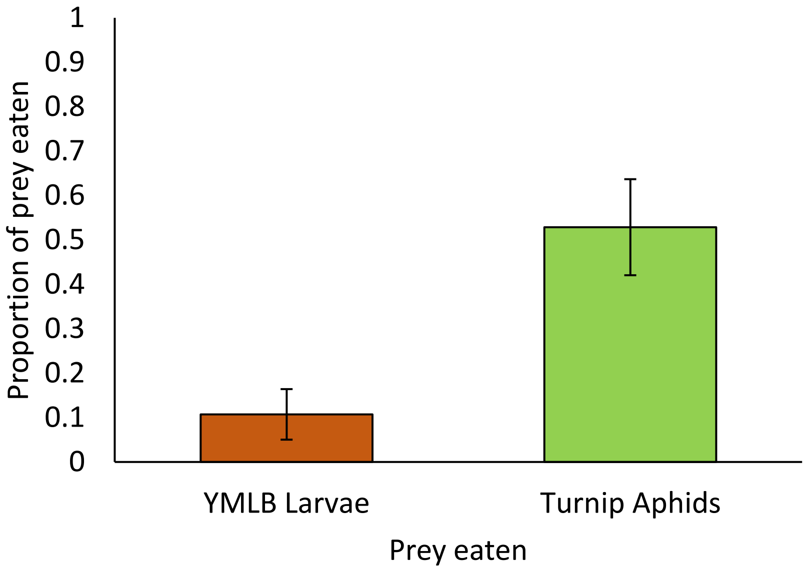
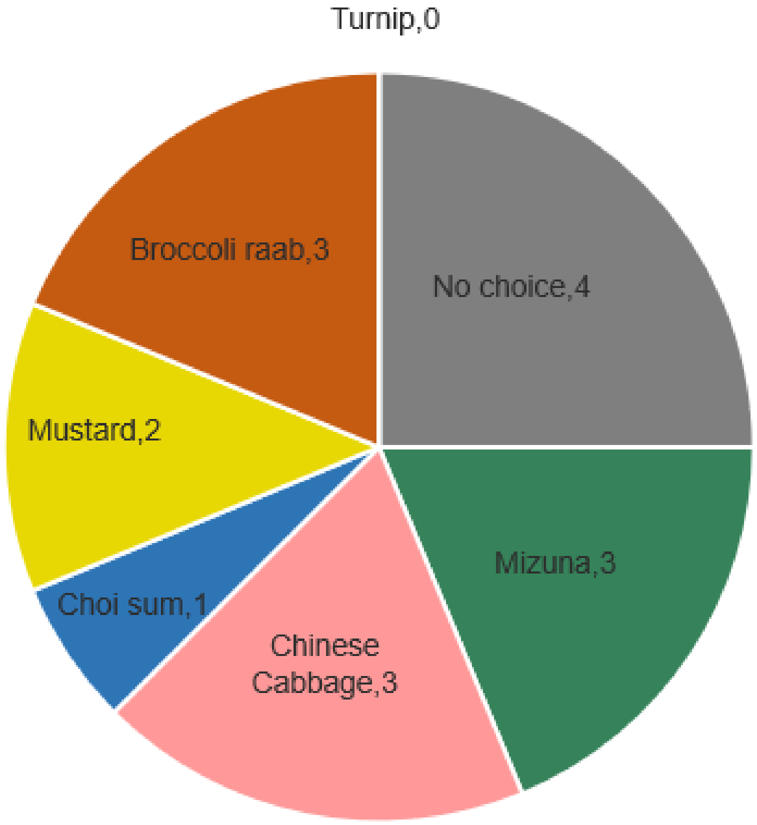
APPENDIX A

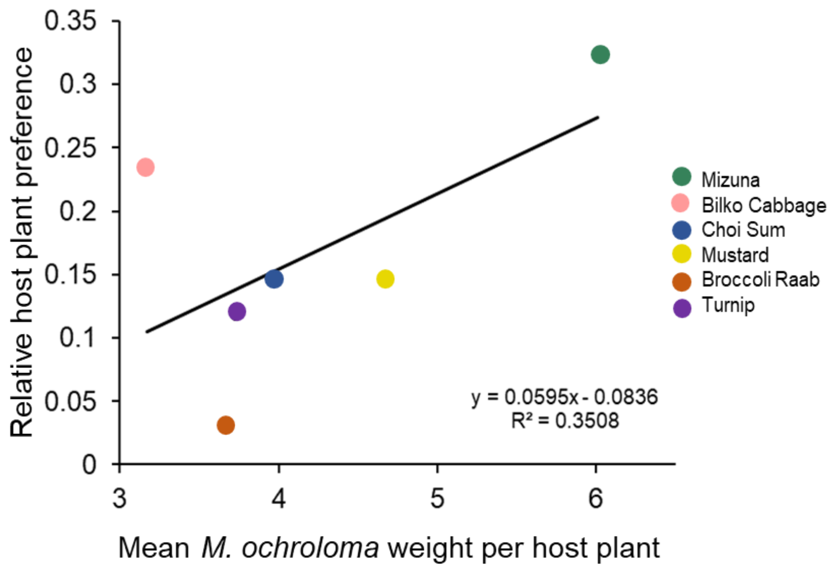
PRELIMINARY PREDATOR CHOICE TRIALS



Supplementary Figure 1. *The proportion of prey eaten by predatory insects in a petri dish choice trial.*



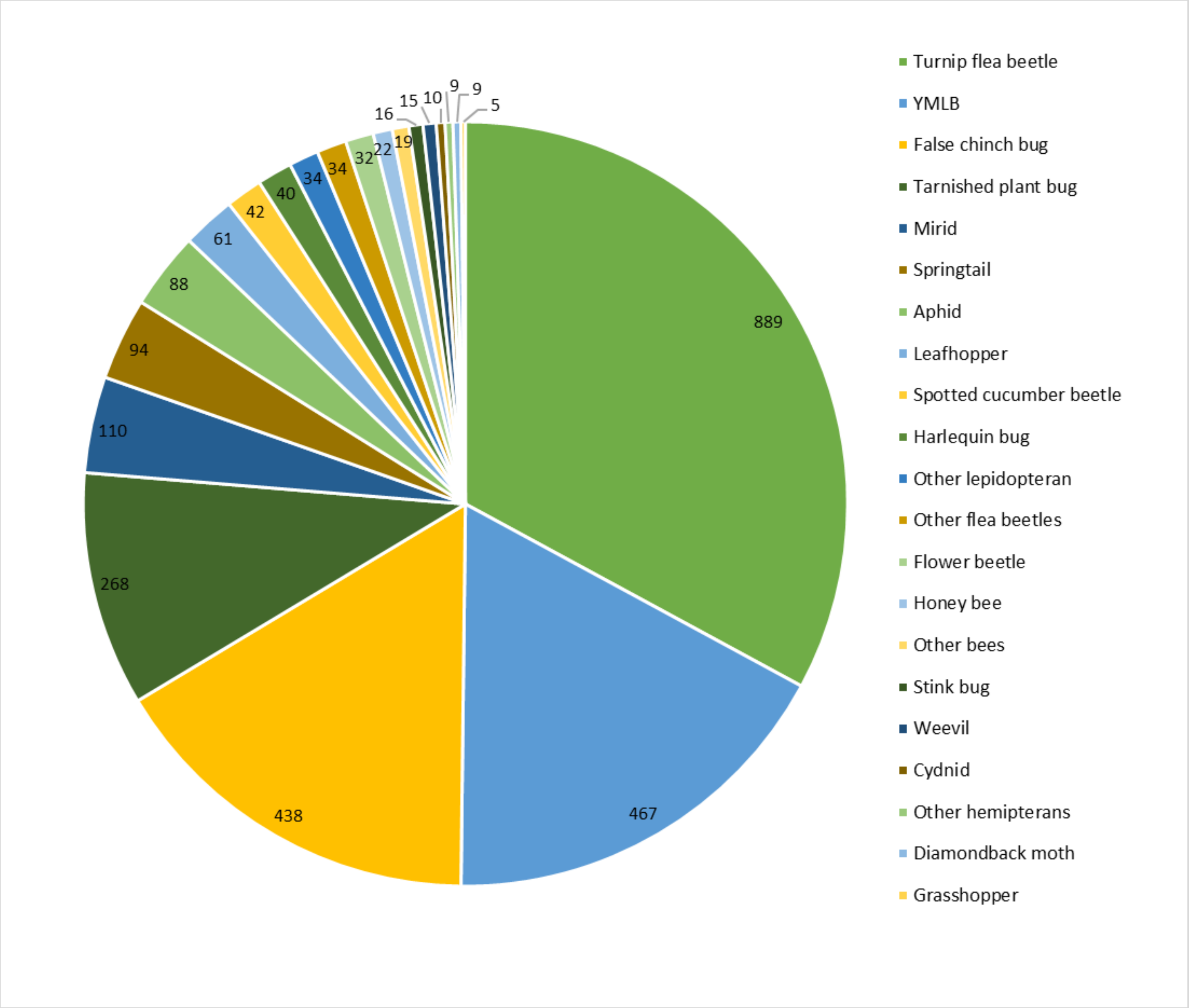
Supplementary Figure 2: *Proportion of lady beetles who ate M. ochroloma larva that were fed exclusively mizuna, Chinese cabbage, choi sum, mustard, broccoli raab, or turnip. The numbers indicate how many lady beetles chose that larva.*



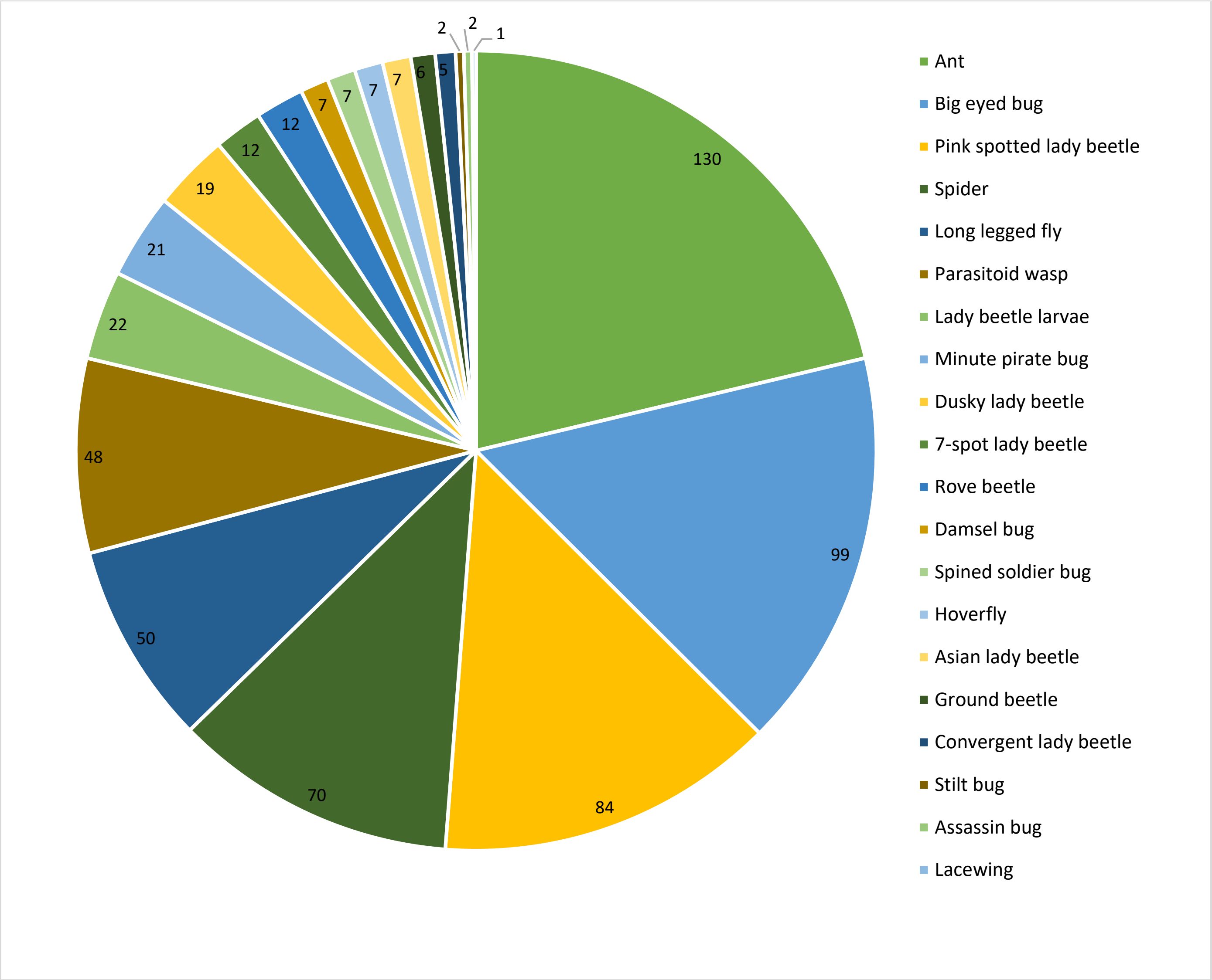
Supplementary Figure 3. *Preference-performance relationship for M. ochroloma on different host plants. The y-axis shows the proportion of M. ochroloma individuals that chose each host plant. The x-axis shows the average weight of M. ochroloma after five days of feeding. Each point represents a different host plant.*

APPENDIX B

ARTHROPOD COMMUNITY MAKEUP



Supplementary Figure 4*. Herbivorous insects counted in visual surveys of foliar plant tissue. Eggs and insects recorded less than five times are excluded.*



Supplementary Figure 5*. Predatory insects counted in visual surveys of foliar plant tissue. Eggs are excluded.*