**Running title**

Stable isotope analysis reveals consistent pest consumption by generalist arthropod predators (ladybeetles and spiders) in rice farms

* A predator in need is a predator indeed
* Generalist predators are specialists when things matter (during high pest density)

**Abstract**

* 3 years of field data, over 1,000 stable isotope samples
* This study aims to help fill the three aforementioned knowledge gaps by quantifying generalist predators’ diet composition, examining their consistency in pest consumption, and investigating how local abiotic and biotic factors affect the diet composition in rice system.

**Introduction**

Using natural arthropod enemies for pest control has a long history in agriculture. For example, the earliest record of biocontrol was documented in the book *Plants of the Southern Regions* (*ca.* 304 A.D.) that people in Southern China sold ants and their nests (attached to branches) in market to control citrus insect pests (Huang and Yang 1987). With the advent of new technologies in the past century, synthetic pesticides have become the main method to control pests in agriculture. However, this comes at a cost, such as posing risks to people, reducing biodiversity (e.g., decline in top predators) and hampering ecosystem functions (e.g., decline in pollinator service) (Geiger et al. 2010, Kehoe et al. 2017). As agriculture has become the largest land use type worldwide and the major driver for global biodiversity crisis and environmental degradation in Anthropocene (Campbell et al. 2017), a shift from synthetic pesticides to environmental-friendly practices (e.g., biocontrol) is urgently needed to make agriculture more sustainable (Gomiero et al. 2011). For example, the European Commission has recently announced its plan to reduce the use chemical pesticides in European Union’s agricultural systems by 50% by 2030 (EC 2020). Such large-scale plan for pesticide reduction will open great opportunities for pest control by natural enemies. In light of this, biocontrol by enemies to reduce pesticide applications has regained its importance nowadays and become an area of increasing focus in sustainable agriculture.

The natural arthropod enemies for herbivorous insect pest control can be classified into two major groups based on their host/prey range—specialists and generalist predators. While specialist enemies (e.g., parasitoids) have been widely advocated in agriculture because they target specific pest species and produce less undesirable non-target effects (Stiling and Cornelissen 2005), generalist predators (e.g., spiders) have been increasingly appreciated for their conspicuous existence and consistent top-down control on pest (Symondson et al. 2002, Stiling and Cornelissen 2005, Michalko et al. 2019b, Hsu et al. 2021) For example, generalist predators were commonly reported in various agro-ecosystems and significantly decreased pest abundances in about 75% cases of 181 field manipulative studies (Symondson et al. 2002). Moreover, generalist predators may even exert stronger suppressing effects on pest populations compared with specialists according to a meta-analysis (Stiling and Cornelissen 2005).

While the value of generalist predators has been increasingly appreciated, a few fundamental knowledge gaps need to be filled to validate their biocontrol potential and the underlying mechanisms in agro-ecosystems. For example, although studies have qualitatively analyzed generalist predators’ diet (e.g., using molecular gut content analysis to identify prey species) (Eitzinger and Traugott 2011, Ingrao et al. 2017, Albertini et al. 2018), very few have quantified these predators’ diet compositions over growth season in the field *(knowledge gap 1)* (Hsu et al. 2021). Quantifying the diet composition will provide critical information to address the concern that generalist predators may switch their diet from pests to alternative prey and thus weakens pest control (Michalko et al. 2019b). If generalist predators consume a high proportion of pests in their diet in field conditions with the presence of alternative prey, the result may help end a long debate on whether generalist predators serve well as biocontrol agents (Symondson et al. 2002, Krey et al. 2017, Michalko et al. 2019b). Moreover, the relevant time scale to assess the effectiveness of generalist predators as biocontrol agents should not be limited to a single growing season. To assess the reliability of these predators as biocontrol agents in real agricultural applications, it is also important to examine their consistency in pest consumption over years in the field, although this information is lacking *(knowledge gap 2)*. Given that dynamics in population density or species compositions are common in agro-ecosystems (Settle et al. 1996, Dominik et al. 2018), a consistently high consumption of pest by generalist predators, if it occurs, will provide strong support for applying these predators in pest management programs.

To better understand the underlying mechanisms for the biocontrol effect of generalist predators, we also need to examine how various abiotic and biotic factors affect the diet compositions of generalist predators in agro-ecosystems *(knowledge gap 3)*. First, arthropod community composition (e.g., pest vs. alternative prey density) may vary with crop stages over the growth season and affect predator-prey trophic interactions (Roubinet et al. 2017). Therefore, examining crop stage effect would help reveal how the biocontrol value of generalist predators varies within a growth season. Second, studies should examine whether farming practices (e.g., organic and conventional) influence the diet compositions of predators (e.g., pest consumption) (Birkhofer et al. 2011). In general, compared to conventional farming, organic farming promotes arthropod diversity (both pest and alternative prey) (Bengtsson et al. 2005), potentially lowering the consumption of pest by generalist predators (Hsu et al. 2021). In contrast, the application of synthetic chemicals in conventional farms may promote the abundance or even resurgence of pest herbivores (Hardin et al. 1995, Settle et al. 1996, Birkhofer et al. 2008a, Guedes et al. 2016), potentially leading to higher pest consumption in predators’ diet. Third, studies should investigate the relationship between the relative prey abundance and predators’ diet composition. This will clarify whether pest consumption by predators is due to pest availability (e.g., density effect) (Roubinet et al. 2017) or feeding preference for pests (Wise et al. 2006, Kuusk and Ekbom 2012, Eitzinger et al. 2019). Lastly, we should examine how surrounding vegetation (e.g., forest cover) affects the diet composition of generalist predators. Previous studies have shown that surrounding vegetation could affect arthropod diversity and predator-prey interactions in agro-ecosystems (Altieri and Letourneau 1982, Altieri 1999, Barbosa and Castellanos 2005, Diehl et al. 2013, Lichtenberg et al. 2017). However, little is known about the effect of surrounding vegetation on predators’ diet compositions. Understanding this will provide insights for managing agricultural landscape and promoting biocontrol services by generalist predators.

The objective of this study is to address the aforementioned critical knowledge gaps: 1) quantify the diet composition of generalist predators, 2) examine the predators’ consistency in pest consumption, and 3) investigate how abiotic and biotic factors affect these predators’ diet composition. Filling these gaps will provide insights for biocontrol potential and application of generalist predators. Specifically, this study sampled arthropod prey and generalist predators in sub-tropical organic and conventional rice farms over rice growth season (seedling, tillering, flowering, and ripening stages) in Miaoli County, Taiwan and from 2017 to 2019. This study aimed to (1) quantify the diet compositions of generalist arthropod predators (ladybeetles and spiders) at each rice stage using stable isotope analysis (δ13C and δ15N), (2) examine predators’ consistency in pest consumption over years (i.e., the proportion of rice pests in predators’ diet in 2017-2019), and (3) investigate how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect pest consumption by predators. Stable isotope analysis has been widely applied in ecological studies to infer predator-prey trophic interactions and to estimate the proportion contribution of different prey sources to predators’ diet (Post 2002, Boecklen et al. 2011, Layman et al. 2012). This quantification method reflects accumulated prey consumption in predators’ diet, which may not be achieved by some “snap-shot” techniques (e.g., field observations and molecular gut content analysis) (Newton 2016). We find that predators consumed high proportions of rice pests in their diet at late crop stages (e.g., from *ca.* 25-40% at the tillering stage to *ca.* 87-94% at the ripening stage in all rice farms during 2017-2019). Such high pest consumption patterns were similar across the three study years, suggesting that i) generalist predators’ top-down control of pest are consistent over years, and ii) generalist predators may function as “specialist predators” of pests at late crop stages (when pests are abundant). Moreover, predators in conventional farms consumed higher proportion of rice pests than those in organic farms. By quantifying diet composition over crop stages and years, our study lends strong support to applying generalist predators as biocontrol agents in agro-ecosystems (e.g., high pest consumption regardless of organic and conventional rice farms). To promote sustainable agriculture, we encourage studies to investigate if generalist predators may commonly function as “specialist predators” of crop pests in various agro-ecosystems.

**Materials and Methods**

*Study system and sample collection*

We collected terrestrial arthropods in organic and conventional rice farms in subtropical Taiwan (latitude and longitude ranges) from 2017 to 2019 (three farms each in 2017 and seven farms each in 2018 and 2019). These farms were irrigated with surface water and averaged at 0.2 hectares. The organic farms were managed with organic fertilizers (manure; 2-3 applications/crop season) and natural pesticides (tea saponins; 1 application/crop season). The conventional farms were managed with synthetic nitrogen fertilizers (2-3 applications/crop season) and organophosphate pesticides (1 application/crop season). At each major rice crop stages (seedling, tillering, flowering, and ripening stage) during the growing season (April - July) in each study year, we collected arthropod samples by sweep-netting (36 cm in diameter with a mesh size of 0.2 × 0.2 mm) the crop canopy 60 times along the farm ridges. Samples were sealed in bags without chemical preservatives, iced, and transferred to refrigerator (−20ºC) in the laboratory. We identified and counted arthropods under a dissecting scope to the lowest possible taxonomic level. Main orders, families, and genera have been documented in (Hsu et al. 2021).

*Stable isotope analysis of arthropod samples*

After identification, arthropod samples were prepared for stable isotope analysis. First, samples were oven dried (50ºC) for one week, ground, and weighed into individual tin capsules (5 × 9 mm). If a species had low biomass, several conspecifics would be pooled into a capsule to meet the minimum weight required for stable isotope analysis (i.e., 2 mg in this study). Stable isotope analysis was conducted at the UC Davis Stable Isotope Facility using a PDZ Europa ANCA-GSL elemental analyzer interfaced to a PDZ Europa 20-20 isotope ratio mass spectrometer (Sercon Ltd., Cheshire, UK). The standards for carbon and nitrogen stable isotope ratios were Vienna PeeDee Beleminte and atmospheric N2, respectively. The results of our samples were expressed in per mil (‰) relative to the aforementioned international standards (δ13C and δ15N).

*Arthropod trophic guild assignment*

A trophic guild represents a group of species using similar resources and forms a basic component of food webs (Root 1967, Hawkins and Macmahon 1989). The concept has been proved to be practical in current ecology because it condenses broad taxonomic information into distinct functional groups in communities (Blondel 2003). In this study, we classified arthropod samples into four trophic guilds based on their dietary information and isotope signatures (see Hsu et al. [2021] for more details): (1) “Predators” consisted of spiders and ladybeetles, which are the primary generalist arthropod predators inhabiting rice farms. (2) “Rice herbivores” consisted of major rice pests, including planthoppers, leafhoppers, and stink bugs. (3) “Tourist herbivores” consisted of herbivorous species without direct trophic association with rice plants, including grasshoppers and leaf beetles. (4) “Detritivores” consisted of arthropods that feed on decaying organic material or plankton, including various midge and fly species. Detailed information of the arthropod families/genera in each trophic guild is provided in Appendix S1: Table S1. This study focused on the trophic interactions between generalist predators and their prey sources and therefore did not consider other trophic guilds (e.g., parasitoids) in subsequent analyses.

*Data analysis*

To quantify the diet compositions of predators, we constructed a Bayesian stable isotope mixing model using the R MixSIAR package (Stock and Semmens 2017) to estimate the proportions of different prey sources (i.e., the three prey guilds including rice herbivores, tourist herbivores, and detritivores) in predators’ diet. In the mixing model, individual farm-year combination and crop stage were included as fixed effects for predator isotope data (in order to examine their effect on predators’ diet composition); isotope data for the three prey guilds were pooled respectively to generate fixed source values due to their high mobility across farms (Mazzi and Dorn 2012, Sun et al. 2015). Isotope data at the seedling stage for the three study years were omitted from the analysis due to insufficient sample sizes for model estimation. To improve our model estimates, carbon and nitrogen concentration dependencies as well as the residual/process errors were incorporated (Phillips and Koch 2002, Stock and Semmens 2016). Trophic discrimination factors (TDFs) were estimated from the diet-dependent discrimination equation proposed by Caut et al. (2009). We ran three Markov Chain Monte Carlo (MCMC) chains, each with 50,000 iterations and a burn-in number of 25,000, along with a non-informative Dirichlet prior. Chain convergence was assessed via Gelman-Rubin and Geweke diagnostics. Bayesian posterior mean estimates of diet compositions (for each farm-year-stage combination) were extracted for further analysis.

To examine how local abiotic and biotic factors (e.g., farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect the pest consumption by predators, we first fit beta regression models with year, farm type, crop stage, percent forest cover, and the relative abundance of rice herbivores as fixed effects without interactions and the proportion of rice herbivores consumed in predators’ diet as the response variable using the R betareg package (Zeileis et al. 2016). We then refit the first model by adding the interaction terms among all the significant factors to create the final model. Model parameters were estimated using maximum likelihood, and the significance of factor terms were then analyzed by a two-way ANOVA (type II test) using the “Anova” function in the R car package (Fox and Weisberg 2018). Tukey’s post-hoc tests were performed for the significant factors using the “cld” function in the R emmeans package (Lenth and Lenth 2018). Note that the percent forest cover around each study farm was estimated from Google Earth images by manually delimiting the forested areas within a 1-km radius circular buffer surrounding the farm and computing the fraction of these areas in the buffer zone. Because spiders and ladybeetles were the most abundant generalist predator groups in our agro-ecosystem and exhibited distinct foraging behavior (e.g., sit-and-wait vs. active hunting) and microhabitat use, we also performed all the aforementioned analyses separately for each of the two predator groups. All analyses were conducted in R version 4.0.3 (R Core Team 2021).

**Results**

*Diet compositions of predators in rice farms*

Across organic and conventional farms during 2017-2019, the proportion of rice herbivores in all predators’ diet increased over the course of the crop season from ca. 25-40% at the tillering stage to over 87-94% at the ripening stage; the proportion of detritivores in predator’s diet decreased from ca. 45-55% at the tillering stage to 1-2% at the ripening stage; the proportion of tourist herbivores in the diet also decreased from ca. 16-20% at the tillering stage to 5-10% at the ripening stage (Fig. 1a).

Regarding individual predator groups, spiders and ladybeetles showed a marked difference in their diet compositions over crop stages during 2017-2019. Spiders consumed higher proportion of detritivores (ca. 40-50%) in their diet in the beginning of crop season (tillering stage) and substantially increased the consumption on rice herbivores up to 80-93% in late crop season (ripening stage) (Fig. 1b). On the contrary, ladybeetles in both organic and conventional farms steadily consumed a low proportion of detritivores (e.g., less than 10%) and over 82% of rice herbivores in their diet throughout the crop season (Fig. 1c). For both predator groups, tourist herbivores did not constitute an important prey source and contributed less than 25% to their diet (Fig. 1b, c).

*Patterns of rice herbivore consumption by predators*

We further analyzed rice herbivore consumption by predators since these herbivores are the main pests of concern. The patterns of rice herbivore consumption by all predators in organic and conventional rice farms were generally similar across the three study years, suggesting consistency in their feeding habits (Fig. 2). The consistency in herbivore consumption over years was also revealed by our beta regression model, which indicated that the proportion of rice herbivores consumed in all predators’ diet did not vary across years (*χ*2 = 1.99, *P* = 0.37; Table 1).

Interestingly, spiders and ladybeetles exhibited distinct within-season patterns of rice herbivore consumption. For spiders in organic and conventional farms, the proportion of rice herbivores in their diet increased toward later crop season, ranging from 25-41% (tillering) to 80-93% (ripening) (Fig. 2b), whereas for ladybeetles in organic and conventional farms, the proportion of rice herbivores in their diet remained relatively stable throughout the season, ranging from 82-83% (tilling) to 94% (ripening) (Fig. 2c).

*Factors associated with rice herbivore consumption by predators*

The proportion of rice herbivores consumed in predators’ diet differed between organic and conventional farms (All predators: *χ*2 = 15.98, *P* < 0.001; Spiders: *χ*2 = 13.38, *P* < 0.001; Ladybeetles: *χ*2 = 6.70, *P* = 0.001; Table 1). In particular, all predators in conventional farms consumed higher proportion of rice herbivores in the diet compared with predators in organic farms (Tukey’s post-hoc test, *P* < 0.05; Table 2), although there was an interactive effect of farm type and year on spiders’ diet composition (*χ*2 = 7.64, *P* = 0.02; Table 2).

The proportion of rice herbivores consumed in predators’ diet also differed among crop stages (All predators: *χ*2 = 227.93, *P* < 0.001; Spiders: *χ*2 = 115.43, *P* < 0.001; Ladybeetles: *χ*2 = 152.60, *P* < 0.001; Table 1). Specifically, predators consumed higher proportion of rice herbivores in their diet at the flowering and/or ripening stage than they did at the tillering stage (Tukey’s post-hoc test, *P* < 0.05; Table 3).

Contrary to previous studies showing the importance of surrounding landscape in determining arthropod community structure and pest control by predators (Rusch et al. 2016) , but see Karp et al. (2018), the proportion of rice herbivores consumed in predators’ diet was not associated with the percent forest cover within a 1-km radius buffer surrounding the study farms (All predators: *χ*2 = 0.30, *P* = 0.58; Spiders: *χ*2 = 1.28, *P* = 0.26; Ladybeetles: *χ*2 = 0.77, *P* = 0.38; Table 1). Furthermore, the proportion of rice herbivores consumed was not associated with the relative abundance of rice herbivores in the field (All predators: *χ*2 = 0.36, *P* = 0.55; Spiders: *χ*2 = 1.38, *P* = 0.24; Ladybeetles: *χ*2 = 0.93, *P* = 0.33; Table 1).

Table 1. Analysis of deviance (type II test) for the beta regression models fitted to data for all predators, spiders only, and ladybeetles only. The results were obtained from the Anova() function in the R “car” package (Fox and Weisberg 2018). For each model, interactions were tested only between significant factors.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Factor | *d.f.* | *χ*2 | *P* |
| All predators | Year | 2 | 1.99 | 0.37 |
|  | Farm type | 1 | 15.98 | <0.001 |
|  | Crop stage | 2 | 227.93 | <0.001 |
|  | Percent forest cover | 1 | 0.30 | 0.58 |
|  | Relative abundance of rice herbivores | 1 | 0.36 | 0.55 |
|  | Farm type × Crop stage | 2 | 2.06 | 0.36 |
| Spiders | Year | 2 | 7.92 | 0.02 |
|  | Farm type | 1 | 13.38 | <0.001 |
|  | Crop stage | 2 | 115.43 | <0.001 |
|  | Percent forest cover | 1 | 1.28 | 0.26 |
|  | Relative abundance of rice herbivores | 1 | 1.38 | 0.24 |
|  | Year × Farm type | 2 | 7.64 | 0.02 |
|  | Year × Crop stage | 4 | 0.99 | 0.91 |
|  | Farm type × Crop stage | 2 | 1.12 | 0.57 |
|  | Year × Farm type × Crop stage | 4 | 0.44 | 0.98 |
| Ladybeetles | Year | 2 | 13.20 | 0.001 |
|  | Farm type | 1 | 6.70 | 0.001 |
|  | Crop stage | 2 | 152.60 | <0.001 |
|  | Percent forest cover | 1 | 0.77 | 0.38 |
|  | Relative abundance of rice herbivores | 1 | 0.93 | 0.33 |
|  | Year × Farm type | 2 | 5.78 | 0.06 |
|  | Year × Crop stage | 4 | 6.80 | 0.15 |
|  | Farm type × Crop stage | 2 | 1.95 | 0.38 |
|  | Year × Farm type × Crop stage | 4 | 2.37 | 0.67 |

Table 2. Tukey’s post-hoc tests comparing the proportion of rice herbivores consumed in predators’ diet in organic and conventional rice farms. The tests were performed using the function cld() from the R “multcomp” package (Hothorn et al. 2008). Different superscript letters indicate significant differences in the means (α = 0.05) within each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Farm type | Mean (± SE) | Lower 2.5% | Upper 2.5% |
| All predators | Organic | 0.66a (± 0.015) | 0.63 | 0.69 |
|  | Conventional | 0.73b (± 0.014) | 0.70 | 0.76 |
| Spiders | Organic | 0.64a (± 0.020) | 0.60 | 0.68 |
|  | Conventional | 0.73b (± 0.019) | 0.69 | 0.77 |
| Ladybeetles | Organic | 0.86a (± 0.007) | 0.85 | 0.87 |
|  | Conventional | 0.88b (± 0.005) | 0.87 | 0.89 |

Table 3. Tukey’s post-hoc tests comparing the proportion of rice herbivores consumed in predators’ diet among the three crop stages (tillering, flowering, and ripening stage). The tests were performed using the function cld() from the R “multcomp” package (Hothorn et al. 2008). Different superscript letters indicate significant differences in the means (α = 0.05) within each model.

|  |  |  |  |  |
| --- | --- | --- | --- | --- |
| Model | Crop stage | Mean (± SE) | Lower 2.5% | Upper 2.5% |
| All predators | Tillering | 0.32a (± 0.029) | 0.27 | 0.38 |
|  | Flowering | 0.84b (± 0.016) | 0.81 | 0.87 |
|  | Ripening | 0.92c (± 0.013) | 0.90 | 0.95 |
| Spiders | Tillering | 0.35a (± 0.036) | 0.28 | 0.42 |
|  | Flowering | 0.82b (± 0.021) | 0.78 | 0.86 |
|  | Ripening | 0.89b (± 0.024) | 0.84 | 0.93 |
| Ladybeetles | Tillering | 0.82a (± 0.012) | 0.80 | 0.85 |
|  | Flowering | 0.85a (± 0.007) | 0.84 | 0.87 |
|  | Ripening | 0.94b (± 0.004) | 0.93 | 0.95 |

Diet_proportion.tiff

Figure 1. The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in predators’ diet in organic and conventional rice farms over crop stages. (a) All predators as a whole feeding guild; (b) spiders only; (c) ladybeetles only. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models averaged over all replicate farms and across three study years.

Rice_herb_consumption.tiff

Figure 2. The proportion of rice herbivores consumed in predators’ diet in organic and conventional rice farms over crop stages in the three study years. (a) All predators as a whole feeding guild; (b) spiders only; (c) ladybeetles only. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models.

Rel_abd.tiff

Figure 3. The relative abundances of prey sources in organic and conventional rice farms over crop stages in the three study years. The relative abundances were determined from the sweep-net samples pooled across the replicate farms.

**Discussion**

To investigate the potential of generalist arthropod predators as biocontrol agents in agro-ecosystems, we collected field samples of arthropod communities in organic and conventional rice farms and conducted stable isotope analysis to examine the diet compositions of predators over the course of the crop season in three consecutive years. Our results showed that, across the three study years, predators in both organic and conventional farms increased their consumption on rice herbivores over the crop season, from around 25-40% at the tillering stage to over 87-94% at the ripening stage (Fig. 1a). This indicates that generalist arthropod predators by nature could become specialists in function depending on the context and underlines their high biocontrol potential at later crop stages. Interestingly, individual predator groups (spiders and ladybeetles) exhibited distinct within-season patterns of rice herbivore consumption. The proportion of rice herbivores consumed in spiders’ diet gradually increased from early toward later crop season (Fig. 2b), whereas that consumed in ladybeetles’ diet remained relatively stable throughout the season (Fig. 2c). Our results also revealed similar among-year patterns in rice herbivore consumption by predators in organic and conventional rice farms, suggesting consistency in their feeding habits (Fig. 2; Table 1). The proportion of rice pests consumed in predators’ diet differed between farm types as well as among crop stages. However, contrary to expectation and previous studies, pest consumption by predators was not associated with the vegetation (percent forest cover) surrounding the farms, neither was the relative abundance of rice herbivores in the field (Table 1). We discuss in the following a) the patterns of diet compositions of generalist arthropod predators, b) the effect of various abiotic and biotic factors on pest consumption by predators, and c) the limitations and potential caveats of this study. We finish by highlighting the implications of our results for agricultural management.

*Patterns of diet compositions of generalist arthropod predators*

Across the three study years, predators in both organic and conventional farms consumed increasing proportion of rice herbivores over the crop season, reaching around 90% in predators’ diet at the ripening stage, whereas the proportion of detritivores and tourist herbivores gradually decreased and contributed less than 10% to the diet at the ripening stage (Fig. 1; Appendix S1: Table S2). The increase in rice herbivore consumption suggests increasing biocontrol value of predators over time, particularly during the later crop season where they fed predominantly on rice pests. Interestingly, generalist predators are known to exploit a wide range of prey items (Albajes and Alomar 1999, Prasad and Snyder 2006), yet our diet analysis indeed revealed a previously under-appreciated aspect of their feeding habits—a generalist by nature could become a specialist in function depending on the context. It is also noteworthy that, although we did not experimentally test this proposal in our study, the consumption of alternative prey (detritivores and tourist herbivores) during early crop stages might have supported predator populations in the later season (Settle et al. 1996, Bilde et al. 2000, Harwood and Obrycki 2005). Environmentally friendly agricultural practices promoting the establishment of predator populations during early crop season would likely benefit pest control in the field.

The two main predator groups in our study system, spiders and ladybeetles, exhibited distinct dietary patterns over the crop season (Fig. 1; Fig. 2). Such distinct patterns may be due to the difference in their foraging modes—sit-and-wait vs. active-pursuit, which could largely affect prey capture and thus diet compositions (Allan et al. 1987, Nyffeler 1999, Klecka and Boukal 2013). Long-jawed orb-weavers (Tetragnathidae), the most abundant family in our spider samples, are sit-and-wait predators and encounter prey in a passive manner. Therefore, its diet compositions would be associated with the relative abundances of the prey items in close proximity (Nyffeler 1999). Our findings support this explanation that the proportions of different prey sources consumed in spiders’ diets partly correspond to the relative abundances of these sources in the field (Fig. 1b; Fig. 3). Moreover, sit-and-wait predators are more likely to capture prey with higher mobility and activity levels (Haraguchi et al. 2013). Since detritivores and tourist herbivores are comparatively more active than rice herbivores, they could be more vulnerable to capture by these orb-weavers and thus contribute more to the diet at early crop stage (Fig. 1b). By contrast, ladybeetles are active-pursuit predators and may preferentially feed on rice herbivores, which are relative sedentary and thus easier to capture. Furthermore, ladybeetles are generally more active in the crop canopy, where the densities of rice herbivores are also higher compared with the lower part of the rice plant. Consequently, their diets may deviate from the relative abundance of prey sources in the field and consist of mainly rice herbivores (Fig. 1c; Fig. 2c; Fig. 3). Despite the distinction in dietary patterns, both spiders and ladybeetles consumed predominantly rice herbivores at the ripening stage and may contribute significantly to pest regulation during this period. Since predator foraging behavior plays a key role in mediating predator-prey trophic interactions (Schmitz 2008, Liu et al. 2015), it would be critical to further examine how assemblages of predators with different foraging strategies and habitat domains may jointly influence the overall effectiveness of top-down control on pests.

Rice herbivore consumption by predators, both as a whole and as individual groups, showed consistent patterns across years (Fig. 2), despite the annual variation in environmental conditions during the crop season (Appendix S1: Fig. S2). The foraging behavior of generalist predators could be influenced by environmental factors (Whitney et al. 2018, Eitzinger et al. 2021). However, our results suggest that their feeding habits might not be as variable and unpredictable as previously thought. The consistency in generalist predators’ dietary patterns across years hints at their stable and reliable top-down effect on pest herbivores, offering a promising opportunity for practitioners to incorporate these predators as biocontrol agents in pest management programs.

*Factors associated with pest consumption by predators*

Overall, generalist predators in conventional farms consumed higher proportions of rice pests in their diet compared with those in organic farms did (Table 2). Previous studies have shown that organic farming generally promotes arthropod diversity in the farms (Bengtsson et al. 2005, Lichtenberg et al. 2017). Such increase in prey availability may distract predators from feeding on target species and thus result in lower consumption of pests (Birkhofer et al. 2008b). Another possibility is that conventional farming may cause higher pest densities (Porcel et al. 2018), thus increasing pest consumption in predators’ diet owning to higher encounter rates. This explanation is partly supported by the observed higher relative abundance of rice herbivores in conventional farms based on our sweep net samples in 2018 and 2019 (Fig. 3b, c). Our results highlight the high potential of using generalist arthropod predators as biocontrol agents in conventional farming systems. Further investigation in various agricultural systems is needed to test the generality of higher consumption of crop herbivores (pests) in the diet of predators, as well as the mechanisms underlying such patterns.

Pest consumption by predators increased from the tillering to the ripening stage (Fig. 2; Table 3), consistent with previous studies showing that predators consumed more pests in the diet over the crop season (Roubinet et al. 2017). There were not many rice herbivores in our study farms at the early crop stage (Fig. 2). As a result, the proportion of these herbivores in predators’ diet was relatively low. Through the development of rice plants, rice herbivore populations rose and predominated at the ripening stage (Fig. 2), leading to high pest consumption by predators during this period. These findings suggest a higher biocontrol value of predators during later crop season, when the crop production is most vulnerable to pest damage. Therefore, farm management (e.g., chemical applications) that could potentially impact predator populations should be minimized during later season to maintain healthy populations of predators in the field.

Habitat structure plays critical roles in governing the trophic dynamics of terrestrial arthropods (Barbosa and Castellanos 2005). Higher vegetation complexity in the surrounding landscape could promote the abundance and diversity of natural enemies by facilitating access to various prey resources as well as providing refuge from intra-guild predation (Langellotto and Denno 2004, Sanders et al. 2008, Diehl et al. 2013). However, our results showed that pest consumption by predators was not related to the vegetated area (percent forest cover) surrounding the farms. In fact, a meta-analysis reveals no significant changes in potential prey (crop herbivore) density in agricultural fields in response to habitat complexity (Langellotto and Denno 2004). Consequently, we speculate that the lack of vegetation effects in our study may be partly due to no difference in prey availability, which ultimately determines the diet compositions of generalist predators. Increasing surrounding vegetation complexity may benefit pest control through enhancing overall predator density and diversity but not per capita pest consumption by predator.

Surprisingly, the beta regression model suggests no effect of the relative abundance of rice herbivores in the field on the proportion of these herbivores consumed in predators’ diet (Table 1). Although the feeding habits and diet compositions of generalist predators could be largely influenced by the prey availability in the habitat (Madsen et al. 2004, Wise et al. 2006, Hsu et al. 2021), we failed to detect such effect in our analysis. An explanation for this is that the relative abundance of rice herbivore was highly related to crop stage, which was also included as a factor in the model (Fig. 3). This could potentially lead to the confounding effects between these two factors. In fact, the model did reveal a significant effect of crop stage on pest consumption (Table 1). As a result, the relative abundance of rice herbivores appeared to have no effect since most of the variation may have been explained by crop stage, a broader factor that is associated with various covariates (e.g., rice plant height). More experiments, both observational and manipulative, are needed to clarify the link between prey availability and diet compositions of generalist predators in the field and to shed light on the potential mechanisms underlying the foraging patterns of predators. (Discuss feeding experiment results here)

*Potential caveats and limitations*

Our study provides three-year quantitative information on the diet compositions of generalist arthropod predators in the field over three consecutive years and examines the potential factors that may influence predators’ dietary patterns, providing more convincing evidence for the biocontrol potential of these predators. Nonetheless, some potential caveats and limitations exist. First, high consumption of rice pests in predators’ diet does not necessarily imply a strong suppression of pest populations in the farms, as the population dynamics of pests depend on not only the per capita effect of predators but also their density and diversity in the field (Duelli and Obrist 2003, Letourneau et al. 2009, Rusch et al. 2016). The effectiveness of biocontrol can only be realized in the context of pest density. Therefore, future work would require complementing stable isotope analysis with field observations of predator and pest populations to unveil the connection between the per capita pest consumption and the overall pest dynamics. Second, intra-guild predation has been shown to impact the pest control by generalist predators (Straub et al. 2008). Estimating the degree of intra-guild predation in the field remains challenging and was not accounted for in our study. Although intra-guild predation among spiders is common in agro-ecosystems (Michalko et al. 2019a), the predation pressure can be substantially relaxed by increased habitat complexity (Finke and Denno 2006, Janssen et al. 2007). Such effects would likely occur in our study system, where the rice plants grew rapidly and formed dense clumps throughout the crop season. In fact, some studies have suggested that intra-guild predation usually does not lead to the disruption of pest control (Janssen et al. 2006). For example, intra-guild predation among spiders was relatively minor compared with their predation on pests (Petrakova et al. 2016). Still, we caution that our diet estimates of predators represent the situations without predator-predator interferences and thus might be biased if such interactions do occur in our system. Lastly, our study reveals the dietary patterns of predators in the field. However, we did not examine the causal effects regarding their diet compositions, which would require experimental manipulations to demonstrate. We encourage more studies to combine both field and experimental approaches to elucidate the dynamics underlying the observed patterns herein.

*Conclusions*

* Value of this study: Among the first to quantify over seasons and years, solve a previous GAP puzzle by providing strong and consistent evidence for the important value of GAP for biocontrol (sustainable agriculture)
* The first study to quantify the diet compositions of arthropod generalist predators in the field over three consecutive years as well as examine potential factors that may influence predators’ dietary patterns, providing more convincing evidence for the biocontrol potential of these predators
* Implications for agriculture: Our study provides evidence for consistent pest consumption by generalist predators, reducing previous concerns about whether generalist predators can exert effective top-down control on pest. Therefore, agricultural management should incorporate farming practices promoting arthropod generalist predators in the field to enhance biocontrol

**Acknowledgement**

We thank Miaoli District Agricultural Research and Extension Station for providing field assistance and logistic support. This study was funded by Council of Agriculture, R.O.C..

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**Appendix S1**

**Table S1**. The taxonomic information and trophic guilds of the arthropod samples in the three study years.

(a) Year 2017

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Carabidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Pyralidae |
|  | Lepidoptera | Nymphalidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Muscidae |
|  | Diptera | Sphaeroceridae |
|  | Diptera | Stratiomyidae |
|  | Diptera | Tephritidae |
|  | Orthoptera | Tetrigidae |

(b) Year 2018

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Hemiptera | Alydidae/*Leptocorisa* |
|  | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Pyralidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Muscidae |
|  | Diptera | Sciomyzidae |
|  | Diptera | Stratiomyidae |
|  | Orthoptera | Tetrigidae |

(c) Year 2019

|  |  |  |
| --- | --- | --- |
| Trophic guild | Order | Family/Genus |
| Predators | Araneae | Araneidae |
|  | Araneae | Clubionidae |
|  | Araneae | Oxyopidae |
|  | Araneae | Tetragnathidae |
|  | Araneae | Thomisidae |
|  | Coleoptera | Coccinellidae |
| Rice herbivores | Diptera | Agromyzidae |
|  | Hemiptera | Alydidae/*Leptocorisa* |
|  | Hemiptera | Cicadellidae/*Nephotettix* |
|  | Hemiptera | Coreidae |
|  | Hemiptera | Delphacidae/*Nilaparvata* |
|  | Hemiptera | Lygaeidae/*Pachybrachius* |
|  | Hemiptera | Miridae |
|  | Hemiptera | Pentatomidae/*Scotinophara* |
|  | Hemiptera | Ricaniidae |
|  | Lepidoptera | Hesperiidae |
|  | Lepidoptera | Nymphalidae |
|  | Lepidoptera | Pyralidae |
|  | Orthoptera | Pyrgomorphidae/*Atractomorpha* |
| Tourist herbivores | Coleoptera | Chrysomelidae |
|  | Orthoptera | Acrididae |
| Detritivores | Diptera | Calliphoridae |
|  | Diptera | Chironomidae |
|  | Diptera | Chloropidae |
|  | Diptera | Ephydridae |
|  | Diptera | Lauxaniidae |
|  | Diptera | Muscidae |
|  | Diptera | Phoridae |
|  | Diptera | Platystomatidae |
|  | Diptera | Sarcophagidae |
|  | Diptera | Sciomyzidae |
|  | Diptera | Sphaeroceridae |
|  | Diptera | Stratiomyidae |
|  | Diptera | Tephritidae |
|  | Orthoptera | Tetrigidae |
|  | Orthoptera | Tridactylidae |

**Table S2.** The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in predators’ diet in organic and conventional rice farms over crop stages in each study year. *n* represents the number of replicate farms for the diet estimation. (Note that the differences in *n* were due to the absence of predators in the sweep-net samples in some replicate farms.)

|  |  |  |  |  |  |  |  |
| --- | --- | --- | --- | --- | --- | --- | --- |
| Year | Farm type | Crop stage | Predator | Source | | | *n* |
| Rice herbivore | Tourist herbivore | Detritivore |
| 2017 | Organic | Tillering | All | 0.27 ± 0.08 | 0.19 ± 0.05 | 0.54 ± 0.12 | 3 |
|  |  |  | Spider | 0.21 ± 0.13 | 0.33 ± 0.16 | 0.46 ± 0.18 | 3 |
|  |  |  | Ladybeetle | 0.74 | 0.09 | 0.17 | 1 |
|  |  | Flowering | All | 0.82 ± 0.04 | 0.13 ± 0.04 | 0.05 ± 0.03 | 3 |
|  |  |  | Spider | 0.69 ± 0.15 | 0.25 ± 0.15 | 0.06 ± 0.04 | 3 |
|  |  |  | Ladybeetle | 0.79 | 0.09 | 0.12 | 1 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.07 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Spider | 0.78 ± 0.12 | 0.19 ± 0.12 | 0.03 ± 0.02 | 3 |
|  |  |  | Ladybeetle | 0.93 ± 0.01 | 0.04 ± 0.01 | 0.03 ± 0.01 | 3 |
|  | Conventional | Tillering | All | 0.23 ± 0.01 | 0.17 ± 0.05 | 0.59 ± 0.05 | 3 |
|  |  |  | Spider | 0.25 ± 0.01 | 0.2 ± 0.06 | 0.55 ± 0.08 | 3 |
|  |  |  | Ladybeetle | 0.8 | 0.08 | 0.12 | 1 |
|  |  | Flowering | All | 0.83 ± 0.03 | 0.12 ± 0.03 | 0.05 ± 0.01 | 3 |
|  |  |  | Spider | 0.85 ± 0.02 | 0.11 ± 0.03 | 0.04 ± 0.01 | 3 |
|  |  |  | Ladybeetle | 0.88 ± 0.02 | 0.06 ± 0.01 | 0.06 ± 0.01 | 2 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.06 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Spider | 0.91 ± 0.01 | 0.07 ± 0.02 | 0.02 ± 0.01 | 3 |
|  |  |  | Ladybeetle | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 2 |
| 2018 | Organic | Tillering | All | 0.23 ± 0.03 | 0.22 ± 0.05 | 0.55 ± 0.06 | 7 |
|  |  |  | Spider | 0.20 ± 0.02 | 0.28 ± 0.07 | 0.52 ± 0.07 | 7 |
|  |  |  | Ladybeetle | 0.81 ± 0.02 | 0.08 ± 0.01 | 0.11 ± 0.01 | 6 |
|  |  | Flowering | All | 0.75 ± 0.04 | 0.17 ± 0.04 | 0.07 ± 0.02 | 6 |
|  |  |  | Spider | 0.73 ± 0.07 | 0.20 ± 0.07 | 0.08 ± 0.04 | 5 |
|  |  |  | Ladybeetle | 0.82 ± 0.01 | 0.09 ± 0.01 | 0.09 ± 0.01 | 3 |
|  |  | Ripening | All | 0.92 ± 0.02 | 0.05 ± 0.01 | 0.02 ± 0.01 | 5 |
|  |  |  | Spider | 0.85 ± 0.04 | 0.11 ± 0.03 | 0.05 ± 0.03 | 4 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
|  | Conventional | Tillering | All | 0.47 ± 0.07 | 0.15 ± 0.02 | 0.38 ± 0.05 | 7 |
|  |  |  | Spider | 0.48 ± 0.10 | 0.19 ± 0.03 | 0.33 ± 0.08 | 7 |
|  |  |  | Ladybeetle | 0.83 ± 0.02 | 0.07 ± 0.01 | 0.10 ± 0.01 | 4 |
|  |  | Flowering | All | 0.90 ± 0.03 | 0.07 ± 0.02 | 0.02 ± 0.01 | 6 |
|  |  |  | Spider | 0.87 ± 0.06 | 0.10 ± 0.04 | 0.03 ± 0.02 | 6 |
|  |  |  | Ladybeetle | 0.86 ± 0.03 | 0.07 ± 0.01 | 0.07 ± 0.02 | 2 |
|  |  | Ripening | All | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.01 ± 0.01 | 7 |
|  |  |  | Spider | 0.93 ± 0.05 | 0.06 ± 0.04 | 0.01 ± 0.01 | 2 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
| 2019 | Organic | Tillering | All | 0.25 ± 0.08 | 0.19 ± 0.06 | 0.55 ± 0.06 | 7 |
|  |  |  | Spider | 0.31 ± 0.10 | 0.15 ± 0.06 | 0.54 ± 0.09 | 7 |
|  |  |  | Ladybeetle | 0.85 ± 0.04 | 0.08 ± 0.01 | 0.07 ± 0.03 | 3 |
|  |  | Flowering | All | 0.74 ± 0.12 | 0.20 ± 0.11 | 0.06 ± 0.01 | 7 |
|  |  |  | Spider | 0.77 ± 0.15 | 0.18 ± 0.14 | 0.05 ± 0.02 | 6 |
|  |  |  | Ladybeetle | 0.87 ± 0.02 | 0.07 ± 0.01 | 0.06 ± 0.02 | 3 |
|  |  | Ripening | All | 0.79 ± 0.16 | 0.19 ± 0.16 | 0.02 ± 0.01 | 5 |
|  |  |  | Spider | 0.78 ± 0.17 | 0.19 ± 0.16 | 0.03 ± 0.01 | 5 |
|  |  |  | Ladybeetle | 0.94 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 5 |
|  | Conventional | Tillering | All | 0.37 ± 0.04 | 0.17 ± 0.04 | 0.46 ± 0.06 | 7 |
|  |  |  | Spider | 0.41 ± 0.06 | 0.17 ± 0.05 | 0.42 ± 0.08 | 7 |
|  |  |  | Ladybeetle | 0.84 ± 0.01 | 0.07 ± 0.01 | 0.09 ± 0.01 | 2 |
|  |  | Flowering | All | 0.89 ± 0.02 | 0.08 ± 0.02 | 0.03 ± 0.01 | 7 |
|  |  |  | Spider | 0.91 ± 0.02 | 0.06 ± 0.02 | 0.02 ± 0.01 | 7 |
|  |  |  | Ladybeetle | 0.89 ± 0.01 | 0.06 ± 0.01 | 0.05 ± 0.01 | 6 |
|  |  | Ripening | All | 0.95 ± 0.01 | 0.05 ± 0.01 | 0.01 ± 0.01 | 5 |
|  |  |  | Spider | 0.94 ± 0.02 | 0.05 ± 0.02 | 0.01 ± 0.01 | 5 |
|  |  |  | Ladybeetle | 0.95 ± 0.01 | 0.04 ± 0.01 | 0.02 ± 0.01 | 3 |

Diet_proportion_2017.tiff Diet_proportion_2018.tiffDiet_proportion_2019.tiff

**Figure S1**. The proportions (mean ± SE) of prey sources (rice herbivores, tourist herbivores, detritivores) consumed in predators’ diet in organic and conventional rice farms over crop stages in each study year. (a), (d), (g) All predators as a whole feeding guild; (b), (e), (h) spiders only; (c), (f), (i) ladybeetles only. The proportions are the posterior mean estimates from the Bayesian stable isotope mixing models averaged over all replicate farms.

**Figure S2.** Daily mean temperature and precipitation of the study site during the first rice growth season (April to July) in the three study years. Observations from the two local weather stations (SanYi and YuanLi station) closest to the study farms were averaged. Data were retrieved from Central Weather Bureau Observation Data Inquire System (https://e-service.cwb.gov.tw/HistoryDataQuery/index.jsp).

* Download monthly weather data from San-Yi and Yuan-Li weather station on CWB as CSV files
* Two facets: temperature and precipitation
* Three lines + dots for each year

**Appendix S2**

Methods—feeding experiment of spiders