**Running title**

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

**Abstract**

**Introduction**

* [Importance of biocontrol]

1. Importance of biocontrol service in agriculture (e.g., using predators to control pests): a long history in agriculture (e.g., buy and place ant nests in orchards in China); critical as well in Anthropocene (e.g., 50% pesticide reduction in EU by 2030)

* [Importance of GAPs]

1. Previous studies on the potential of (underappreciated) generalist arthropod predators (GAPs) as biocontrol agents: cages, observations, molecular gut content analysis
2. Strengths and limitations of previous approaches (e.g., MGCA only provides qualitative information on predators’ diet compositions [presence/absence of prey in predators’ diet])

* [Knowledge gaps]

1. The diet composition of GAPs is a key determinant of the top-down control, reflecting their foraging habits and the trophic interactions with their prey. To fully realize the potential of GAPs, we need to quantify their diet compositions during crop growing season (crop stages). Moreover, to understand the reliability of GAPs as biocontrol agents over environmental fluctuations, it is also important to examine the consistency of pest consumption by GAPs across years in the field.
2. A better understanding of how various biotic and abiotic factors may affect the diet compositions of GAPs is crucial for predicting whether GAPs could provide reliable and stable biological control services in agro-ecosystems as well as provide insights (mechanisms) for a better agricultural management

* [Aims]

1. Quantify diet compositions of GAPs (predator guild, spider and ladybeetle group) over crop stages
2. Examine the consistency of rice herbivore composition by GAPs(rice herbivores) over time (years)
3. Investigate how biotic and abiotic factors may affect the diet compositions of GAPs.

* Brief introduction of our system: stable isotope approach and feeding guilds

Agriculture is the largest land use type worldwide and the major driver for global biodiversity crisis and environmental degradation. Agricultural expansion and intensification have contributed to habitat loss and climate change, posing substantial threats on species and ecosystems (Kehoe et al. 2017). To mitigate such impacts, there is an urgent need for modern industrial agriculture to shift toward more ecological- and environmental-friendly practices (Gomiero et al. 2011).

Using natural arthropod enemies for pest control is a critical component in agriculture (Heimpel and Mills 2017). Indeed, the earliest record of biocontrol dates far back in human history, long before synthetic chemicals were invented. It is 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 to control citrus insect pests (Huang and Yang 1987). Now, in the Anthropocene, biocontrol by enemies to reduce pesticide applications has become an area of increasing focus in sustainable agriculture. For example, the European Commission has recently announced its intention to reduce the use chemical pesticides in European Union’s agricultural systems by 50% by 2030 (EC 2020). Such plan for pesticide reduction will open great opportunities for pest control by natural enemies.

The natural arthropod enemies for herbivorous insect pest control can be classified into two major group based on their host/prey range—specialists and generalist predators. On one hand, specialist enemies (e.g., parasitoids) have been widely applied in agriculture because they are able to target specific pest species and thus minimizes the undesirable non-target effects (Stiling and Cornelissen 2005). On the other hand, generalist predators (e.g., spiders) could feed on not only target pests but also non-pest alternative prey due to their polyphagous nature. Consequently, their effectiveness as biocontrol agents has long been questioned (Symondson et al. 2002), and whether generalist predators can provide reliable top-down control on crop pests remains a subject of much debate.

Empirical evidence for the biocontrol effectiveness of generalist predators remains mixed and may be context-dependent. Some studies have suggested that generalist predators can be effective in controlling pest populations. For example, a review shows that generalist predators significantly decreased pest abundances in around 75% cases of the 181 field manipulative studies examined (Symondson et al. 2002). Moreover, a meta-analysis reveals that generalist predators exert stronger suppressing effects on pest populations compared with specialists (Stiling and Cornelissen 2005). On the other hand, it has also been shown that generalist predators can exhibit prey switching in the presence of alternative prey, which distracts predators from attacking target pests and thus weakens pest control (Michalko et al. 2019).

To fully realize the biocontrol potential of generalist predators, it is important to first understand their diet compositions in the field. The diet compositions of predators directly reflect their trophic interactions with prey and are key determinants of their top-down control on pests. Therefore, quantifying the diet compositions of predators in the farms over the course of the crop season is the critical step toward untangling the complex predator-prey trophic dynamics. Moreover, to assess the reliability of predators as biocontrol agents under temporal environmental fluctuations, it is also important to examine their consistency in pest consumption over years.

Various factors can affect the diet compositions of generalist predators in agro-ecosystems. First, arthropod communities may vary over the season through crop development, and such temporal variations in arthropod compositions can affect predator-prey trophic interactions and thus the diet compositions of predators (Roubinet et al. 2017). Second, farming practices (e.g., organic and conventional farming) can influence arthropod community compositions and densities in the field, which may in turn alter the diet compositions of predators (Birkhofer et al. 2011). For instance, organic farming generally promotes arthropod prey diversity in the farms (Bengtsson et al. 2005), and higher prey diversity may increase predators’ diet breadths as a result of greater prey availability. In contrast, the application of synthetic chemicals can reduce the abundances of non-pest alternative prey (e.g., detritivores) but increase those of certain pest herbivores (Birkhofer et al. 2008a), potentially leading to higher pest consumption in predators’ diet. Third, the relative abundances of different prey items in the field could largely determine predators’ diet if predators forage in a prey-density-dependent fashion. Yet, some predators may exhibit prey preferences and their diet compositions may not directly reflect prey availability (Kuusk and Ekbom 2012, Eitzinger et al. 2019). For example, a study found that wolf spiders fed continually on pest species even under increasing densities of alternative prey (Wise et al. 2006). Finally, surrounding vegetation could affect predators’ diet by influencing the local arthropod species pool as well as the spatial distributions of predator and prey individuals. Vegetation complexity has been shown to affect prey capture and thus the diet compositions of web-building spiders (Diehl et al. 2013); greater habitat heterogeneity increases the diet breadths of predators as a result of relaxed intraspecific competition (Staudacher et al. 2018). As prey capture and diet compositions of generalist predators are the key determinants of their biocontrol effectiveness, understanding how these aforementioned factors may affect prey consumption by predators can provide useful information for designing agricultural management schemes that enhance their biocontrol services.

A few limitations exist in previous studies on pest control by generalist predators in agro-ecosystems. First, recent studies have applied molecular gut content analysis to determine the trophic linkages between predators and their prey (Eitzinger and Traugott 2011, Ingrao et al. 2017, Albertini et al. 2018). However, this approach provides only qualitative information on predator’s diet but does not actually quantify their diet compositions. Moreover, many studies examining the effects of predators on pests were conducted with cage experiments (Birkhofer et al. 2008b, Crowder et al. 2010, Muñoz-Cárdenas et al. 2017). Although this approach can provide direct causal effects of predators on pests, it might not account for the natural predator and prey population fluctuations, which could largely influence predator-prey interactions and thus the biocontrol by predators. Furthermore, such confined settings may potentially increase the encounter rates between predators and pests (Sih et al. 1985), thus leading to biased biocontrol results. Therefore, more studies conducted under natural settings are needed to get a more realistic picture of pest consumption by predators in agro-ecosystems.

Stable isotope analysis has been widely applied in ecological studies to infer predator-prey trophic interactions and to estimate the proportions of different prey sources in predators’ diet (Post 2002, Boecklen et al. 2011, Layman et al. 2012). This approach has advantages over other “snap-shot” techniques (e.g., field observations and gut content analysis) in that it can provide time-integrated dietary information of predators (Newton 2016). In this study, we used stable isotope analysis to (1) quantify the diet compositions of generalist arthropod predators (ladybeetles and spiders) in rice agro-ecosystems over three consecutive years, (2) examine the annual patterns of pest consumption by predators (i.e., the proportion of rice pests consumed in predators’ diet), and (3) investigate how various local factors (farm type, crop stage, percent forest cover, and the relative abundance of pests in the field) may affect pest consumption by predators. Our results could provide a deeper insight into the potential of generalist arthropod predators as biocontrol agents in agro-ecosystems.

**Materials and Methods**

* Why we focused on spiders and ladybeetles for more detailed analysis (show abundance data to support our decision): the two most abundant GAP groups in our system, distinct foraging modes (active vs. sit-and-wait)

*Study system and experimental design*

*Sampling procedure and environmental data collection*

*Stable isotope analysis and arthropod trophic guild assignment*

*Data analysis (stable isotope mixing model and beta regression)*

**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, 1c).

*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 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).

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 across the 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.

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 et al. 2012). 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 |

**Discussion**

Key messages: 1) Consistent pest consumption over years: high potential in providing ecosystem service (biocontrol). 2) Different patterns between generalist predators: active vs. sit-and-wait. 3) Generalist predators (e.g., spiders) could be specialist when things matter (during high pest density) (context-dependent specialist)

* Summary of the main findings: (1) different dietary patterns of ladybeetles and spiders; (2) high consistency in pest consumption across the three study years for both predator groups; (3) factors that affect the proportions of rice herbivore consumed in predators’ diet
* Significance of this study: 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

CK: also complement with molecular analysis (limitation: qualitative study [presence/absence], snap shot, etc.)

* Different dietary patterns of the two generalist predator groups: This may be due to the differences in their feeding modes (active-pursuit vs. sit-and-wait). Ladybeetles are active-pursuit feeders and may prefer rice pests to detritivores. In addition, they are more active in the upper part of the rice plant, where the relative abundance of rice herbivores to detritivores is higher compared to the lower part of the rice plant. On the other hand, most spiders in our study (Tetragnathidae) are orb weavers and thus their diet composition might reflect the relative abundances of the prey items in the surroundings. In fact, our data support this explanation that the relatively high consumption of detritivores and tourist herbivores by spiders at the tillering stage corresponds to the high relative abundances of these prey sources in the field
* High consistency in rice herbivore consumption of both predator groups across years: the feeding habits of generalist predators might not be as variable and unpredictable as previously thought, and therefore they could provide stable and reliable top-down control on pest herbivores
* Factors that affect the pest composition by generalist predators: possible explanations, comparisons with previous studies, implications for agricultural management
* Implication based on our results: For example, 1) farm type: overlooked ecosystem service by GAPs particularly in conventional farms, 2) crop stage: not much herbivores in early season (tillering, Cite our Ecosphere), much higher herbivore density later on > Therefore, farm management should avoid hurt GAP populations during sensitive / highly valuable stages.
* Limitations: (1) Not able to quantify the degree of intraguild predation, (2) Diet compositions reflects only the per capita effects of predator on prey, yet the overall effects of predators on prey populations also depend on the density of predators in the field

* 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

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