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**Title**

Idea paper: An experimental framework for determining the degree of intraguild predation in a three-species omnivorous food web

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## **Abstract**

Intraguild predation (IGP) is common in natural and human-managed systems and plays a critical role in food web dynamics. Although previous studies have documented the occurrence of IGP across a wide range of predator taxa, few have qualitatively examined the degree of IGP. Here, I propose an experimental framework combining controlled feeding trials and stable isotope analysis of field samples to determine the degree of IGP in a three-species omnivorous food web. Such an approach can provide a useful tool for studying IGP in a more accurate (controlled feeding trials) and realistic (stable isotope analysis of field samples) fashion. If proven successful, the present framework can be extended to food webs involving more complex interactions (e.g., cannibalism, multiple prey) and further complemented with other approaches to capture a more complete picture of IGP dynamics in the field.

## **Systematic keyword selection**

community, experiment, ideas for fundamental questions, intraguild predation, stable isotope analysis

## **Research question**

Intraguild predation (IGP) is common in natural and human-managed ecosystems (Arim & Marquet, 2004; Muller & Brodeur, 2002; Polis & Holt, 1992). Previous studies have documented the occurrence of IGP across various taxa (Polis et al., 1989). However, few have qualitatively examined the intensity/degree of IGP among predators. To address this gap, here I propose an experimental framework combining controlled feeding trials and stable isotope analysis of field samples to determine the degree of IGP in a three-species (top predator, mesopredator, and shared prey) omnivorous food web. The degree of IGP in this study is defined as the relative consumption of mesopredator (compared to shared prey) in the diet of top predator (i.e., a high degree of IGP means that the top predator consumes a high proportion of mesopredator in its diet).

## **Value**

IGP could substantially affect the abundance and distribution of interacting species (Polis et al., 1989), which may have profound ecological and evolutionary consequences for food web dynamics. A better quantitative understanding of IGP can provide insights into the complex predator-predator-prey trophic interactions and may help predict the community structure and stability (Arim & Marquet, 2004; Nakazawa & Yamamura, 2006; Pahl et al., 2020). Furthermore, such understanding can have useful implications for agricultural management, for example, evaluation of the effectiveness of biocontrol agents in pest control programs (Muller & Brodeur, 2002).

## **Relevant hypothesis**

Previous studies have used manipulative experiments (e.g., cage experiments) to assess the intensity of IGP by comparing the differences in the numbers of prey or mesopredator in the presence vs. absence of top predator (Denno et al., 2004; Provost et al., 2005). This approach can reveal the causal relationships between predator-prey interactions, allowing for strong inferences

about IGP. However, the use of enclosures could potentially alter the encounter rates between individuals and thus lead to biased results.

Stable isotopes, particularly nitrogen isotope ratios ( $\delta^{15}\text{N}$ ), have been used to estimate the trophic level of predators in the field (Abd El-Wakeil, 2009; Halaj et al., 2005; Rickers et al., 2006). It is suggested that IGP would increase the  $\delta^{15}\text{N}$  of predators and thus their trophic level (Ponsard & Arditi, 2000), but this proposal has not been experimentally verified. In addition, the trophic level of predators in previous studies was often calculated based on assumed trophic enrichment factors (TEFs) (e.g., Klarner et al., 2013; Ponsard & Arditi, 2000; Svanbäck et al., 2015), which can affect the subsequent inferences made about IGP in the field.

Recently, researchers have applied molecular gut content analysis (MGCA) and immunological techniques to reliably detect the presence of certain food items in predators' diet (Gagnon et al., 2011; Hagler, 2006; Mansfield & Hagler, 2016). These advances in technology have allowed researchers to compute the incidence rates (i.e., the percentage of top predator individuals with mesopredator detected in the gut contents) of IGP among predator individuals. Nonetheless, a high incidence of IGP does not necessarily imply a high degree of IGP (Raso et al., 2014). For example, it is possible that a high percentage of individuals in a top predator population feed on other predator species despite on average low consumption in the diet. In this case, the high incidence rates of IGP could be misleading and may result in incorrect inferences of high degree of IGP among predators in the field.

## **New research idea**

In this study, I propose an experimental framework combining controlled feeding trials and stable isotope analysis of field samples to more accurately determine the degree of IGP in a three-species omnivorous food web. Specifically, I predict that the  $\delta^{15}\text{N}$  of top predator individuals engaged in IGP will be higher than the  $\delta^{15}\text{N}$  of individuals not engaged in IGP. Moreover, the more the top predator consumes the mesopredator in the diet, the higher the  $\delta^{15}\text{N}$  of top predator would be, and the increase in  $\delta^{15}\text{N}$  (i.e., trophic enrichment) can be used to determine the degree of IGP.

## How to tackle the question through the proposed new idea

Consider a three-species omnivorous food web, in which a top predator and a mesopredator feed on a shared prey, while the top predator also feeds on the mesopredator (Fig. 1a). Two sets of controlled feeding trials will be conducted. In the first trial, the top predator and the mesopredator will be fed the shared prey for two weeks to allow for the incorporation of isotopes into the tissues (Gratton & Forbes, 2006) (Fig. 1b). The purpose of the first feeding trial is to ensure that both predators have reached an isotopic equilibrium state with the shared prey. In the second trial, the top predator will be fed mixed diets with different proportions of shared prey and mesopredator individuals (the organisms are from the first feeding trial): (1) shared prey only, (2) 75% of shared prey + 25% of mesopredator, (3) 50% of shared prey + 50% of mesopredator, (4) 25% of shared prey + 75% of mesopredator, and (5) mesopredator only (Fig. 1c). The exact numbers of shared prey and mesopredator individuals used in each diet treatment will be determined based on their field densities. The purpose of the second feeding trial is to simulate different degrees of IGP under different encounter rates among the organisms.

After two weeks of feeding, the  $\delta^{15}\text{N}$  of top predator individuals in each diet treatment will be analyzed, and their TEFs (relative to the  $\delta^{15}\text{N}$  of shared prey) are used to construct a standard IGP curve (Fig. 1d). Finally, field samples of top predator and shared prey individuals will be collected, with their  $\delta^{15}\text{N}$  analyzed to obtain the empirical TEF for the top predator. The degree of IGP in the field can then be determined by comparing the empirical TEF to the standard curve (Fig. 1e).

The proposed experimental framework combines the strengths of previous approaches to studying IGP—the controlled feeding trials can yield accurate trophic enrichment factors to construct a standard curve, whereas the stable isotope analysis of field samples allows for trophic interactions under natural settings. Therefore, this framework provides a useful tool for determining the degree of IGP in the field in a more quantitative and realistic fashion.

Agricultural systems are ideal for testing the proposed framework. IGP has been frequently documented among predators in such systems (Rosenheim et al., 1995). In addition, the species compositions are relatively simple compared to natural systems, which can largely reduce the potential confounding effects of other species on the trophic interactions among focal

organisms. If proven successful, this framework can be extended to food webs involving more complex interactions (e.g., cannibalism, multiple shared prey) and further complemented with other approaches (e.g., MGCA) to provide a more complete picture of the IGP dynamics in the field. Hopefully, it will provide an important piece of the puzzle in food web ecology.

## **Motivation**

I have been using stable isotope analysis to quantify the diet compositions of generalist arthropod predators in rice agro-ecosystems in Taiwan. In my previous manuscript (published in the journal *Ecosphere*), a few reviewers expressed the concern over whether IGP would affect the diet compositions of predators. In fact, IGP may occur among the predators in our system, yet we were not able to quantify IGP due to the limitations of stable isotope mixing models. This question really puzzled me at that time and haunted my mind for long, which eventually brought me to the idea of using controlled feeding experiments along with stable isotope analysis to determine the degree of IGP in the field. I hope that this study can inspire new ideas and we will be able to develop a more thorough method to solve this question in the future.

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## Figure legend

**Figure 1.** Schematic diagram of the proposed experimental framework for determining the degree of intraguild predation in a three-species omnivorous food web, in which a top predator and a mesopredator feed on a shared prey, while the top predator also feeds on the mesopredator (a). In the first feeding trial (b), the top predator and the mesopredator are fed the shared prey for two weeks to ensure that both predators have reached an isotopic equilibrium state with the shared prey. In the second feeding trial (c), the top predator is fed mixed diets with different proportions of shared prey (from the stock) and mesopredator (from the first feeding trial) individuals to simulate different degrees of IGP. (d) The trophic enrichment factors ( $\Delta^{15}\text{N}$ ) of top predator individuals (relative to the shared prey) in each diet treatment are used to construct a standard IGP curve. Note that the curve may not necessarily be linear due to complex isotope routing. (e) Field samples of top predator and shared prey individuals are collected, and their  $\delta^{15}\text{N}$  values are analyzed to obtain the empirical  $\Delta^{15}\text{N}$  for the top predator. The degree of IGP in the field can then be determined by comparing the empirical  $\Delta^{15}\text{N}$  to the standard curve.