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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 (defined herein as the proportion of mesopredator in the total numbers of prey [shared prey + mesopredator] consumed by the top predator) in a three-species omnivorous food web in the field. 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 current 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 specific organisms/systems, 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 in the field. 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 proportion of mesopredator in the total numbers of prey (shared prey + mesopredator) consumed by the top predator (e.g., a high degree of IGP means that the top predator consumes a high proportion of mesopredator individuals in its total 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 (δ15N), have been used to estimate the trophic levels of predators in the field and to make inferences about IGP (Halaj et al., 2005; Sanders & Platner, 2007; Wise et al., 2006). It is suggested that IGP would increase the δ15N of predators (Ponsard & Arditi, 2000), yet few studies have experimentally verified this proposal. Rickers et al. (2006) conducted feeding experiments on wolf spiders (*Alopecosa cuneata*) and revealed a higher δ15N of these top predators under IGP. However, the study did not attempt to quantify the degree of IGP as the IGP treatment was binary (absence vs. presence of mesopredator) with constant numbers of shared prey and mesopredator. Moreover, the trophic levels of predators in previous studies were often calculated based on assumed trophic discrimination factors (TDFs) (e.g., Klarner et al., 2013; Ponsard & Arditi, 2000; Svanbäck et al., 2015). Since TDFs are quite taxon-specific (Caut et al., 2009), these trophic level estimates could be biased and thus lead to incorrect inferences 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 false 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 determine the degree of IGP in a three-species omnivorous food web. Specifically, I predict that the δ15N of top predator engaged in IGP will be higher compared with not engaged in IGP, and the more the top predator consumes the mesopredator in the diet, the higher the δ15N of top predator would be, leading to greater difference in δ15N between the top predator and the shared prey (Δ15N). By experimentally linking different levels of mesopredator consumption and the resulting Δ15N of top predator, the degree of IGP in the field can be determined using field-derived Δ15N in a more accurate fashion.

**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 both 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 an appropriate period of time 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 (with the same duration as the first trail), the top predator will be fed mixed diets with different proportions of shared prey and mesopredator individuals (from the first 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 used in each diet treatment will be based on their field densities. The purpose of the second feeding trial is to simulate a full range of potential encounter rates that the focal organisms might experience in the field.

At the end of the second feeding trail, the actual numbers of shared prey and mesopredator consumed by the top predator in each diet treatment will be recorded, and the δ15N of each top predator individual will be analyzed. A standard curve can be constructed by plotting the Δ15N of top predator against the proportion of mesopredator consumed (Fig. 1d). Finally, field samples of top predator and shared prey individuals will be collected, with their δ15N analyzed to obtain the empirical Δ15N. The degree of IGP in the field can then be assessed by interpolating the field-derived Δ15N to the standard curve (Fig. 1e). A hypothetical example of data collection in the second feeding trail for standard curve construction is provided in Fig. 2.

The proposed experimental framework combines the strengths of previous approaches to studying IGP—the controlled feeding trials along with stable isotope analysis can yield accurate Δ15N to construct a standard curve, whereas the stable isotope analysis of field samples allows for trophic interactions under natural settings. Together, this framework provides a useful tool for determining the degree of IGP in the field in a more quantitative and realistic fashion, and can be used to investigate how the degree of IGP may change in response to various abiotic and biotic factors (e.g. temperature, habitat complexity, and predator and prey densities).

Agricultural systems are ideal for testing the proposed framework. IGP has been frequently documented among predators in such systems (Rosenheim et al., 1995). Furthermore, the species compositions are relatively simple compared with natural systems. Therefore, the potential confounding effects of other species on the trophic interactions among focal organisms can be largely reduced. 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 capture a more complete picture of the IGP dynamics in the field. Such understanding will provide an important piece of the puzzle in food web ecology.

**Motivation**

In my previous study, I have been using stable isotope analysis to quantify the diet compositions of generalist arthropod predators in rice agro-ecosystems, and 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, but we were not able to quantify that due to the limitations of stable isotope mixing models. This question really puzzled me at that time and haunted my mind for long. After doing some literature review, I felt that previous studies on IGP have focused mainly on the qualitative aspect of IGP (e.g., how IGP might affect predator-prey population dynamics), yet relatively few have experimentally examined the quantitative aspect of IGP (e.g., how intense IGP is in the system). This 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. Notwithstanding the limitations, I hope the proposed framework can serve as a starting point to generate new ideas refining the present method, or even inspire other researchers to develop a more thorough method to address this question in the future.

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**Conflict of interest**

The author declares no potential conflict of interest.

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**Figure legend**

**Figure 1. A** 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 both 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 an appropriate period of time to ensure that both predators have reached an isotopic equilibrium state with the shared prey. In the second feeding trial (with the same duration as the first trail) (c), the top predator is fed mixed diets with different proportions of shared prey and mesopredator individuals (from the first trial) to simulate a full range of potential encounter rates that the focal organisms might experience in the field. (d) A standard curve can be constructed by plotting the difference in δ15N between the top predator and the shared prey (Δ15N) against the proportion of mesopredator consumed. (Note that the curve may not necessarily be linear due to the differences in the biomass of shared prey and mesopredator individuals.) (e) The δ15N values of field-sampled shared prey and top predator individuals are analyzed to obtain the empirical Δ15N, which is then interpolated to the standard curve to determine the degree of IGP in the field.

**Figure 2.** A hypothetical example of data collection in the second feeding trail for standard curve construction. Each diet treatment consists of five replicates (different top predator individuals). *N*: number of prey supplied in the mixed diet (shared prey/mesopredator); *C*: number of prey consumed by the top predator (shared prey/mesopredator); *P*: proportion of mesopredator consumed (%).