Methods in Ecology and Evolution

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Journal:	*Methods in Ecology and Evolution*
Manuscript ID	Draft
Manuscript Type:	Perspective
Date Submitted by the Author:	n/a
Complete List of Authors:	Hsu, Gen-Chang; National Taiwan University Department of Life Science,
Keywords:	feeding trial, food web, intraguild predation, mesopredator, omnivory, stable isotope analysis, top predator, trophic interactions
Abstract:	1. Intraguild predation (IGP) is common in natural and human-managed systems and plays a critical role in food web dynamics. Although studies have documented the occurrence of IGP across a wide range of predator taxa, quantitative understanding regarding the degree/intensity of IGP remains lacking. 2. I propose an experimental framework combining controlled feeding trials and stable isotope analysis to quantify the degree of IGP in a three-species omnivorous food web (top predator + mesopredator + shared prey) in the field. The degree of IGP is defined as the proportion (in number) of mesopredator consumed in the total diet (shared prey + mesopredator) of the top predator. 3. Feeding trials along with stable isotope analysis are used to construct a standard curve of the relationship between top predator's diet and shift in its nitrogen isotope signatures. The nitrogen isotope signatures of field-sampled top predator individuals are then analyzed and interpolated to the curve to estimate the degree of IGP in the field. 4. The proposed framework leverages the strengths of different experimental approaches to studying trophic interactions, providing a practical tool for quantifying IGP in a more accurate (controlled feeding trials and standard IGP curve) and realistic (stable isotope analysis of field samples) fashion. The current framework can be further extended to food webs involving more complex interactions (e.g., cannibalism and multiple shared prey) and complemented with other approaches (e.g., molecular gut content analysis) to capture a more complete picture of IGP dynamics in the field.

Title

An experimental framework for quantifying the degree of intraguild predation in a three-species omnivorous food web in the field

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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 studies have documented the occurrence of IGP across a wide range of predator taxa, quantitative understanding regarding the degree/intensity of IGP remains lacking.
- I propose an experimental framework combining controlled feeding trials and stable isotope analysis to quantify the degree of IGP in a three-species omnivorous food web (top predator + mesopredator + shared prey) in the field. The degree of IGP is defined as the proportion (in number) of mesopredator consumed in the total diet (shared prey + mesopredator) of the top predator.
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- The proposed framework leverages the strengths of different experimental approaches to studying trophic interactions, providing a practical tool for quantifying IGP in a more accurate (controlled feeding trials and standard IGP curve) and realistic (stable isotope analysis of field samples) fashion. The current framework can be further extended to food webs involving more complex interactions (e.g., cannibalism and multiple shared prey) and complemented with other approaches (e.g., molecular gut content analysis) to capture a more complete picture of IGP dynamics in the field.

Keywords

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Introduction

Intraguild predation (IGP) is common in natural and human-managed ecosystems (Polis & Holt, 1992; Müller & Brodeur, 2002; Arim & Marquet, 2004) and is documented across a wide range of predator taxa (Polis et al., 1989; Gagnon et al., 2011). IGP could substantially affect the abundance and distribution of interacting species, generating ecological and evolutionary consequences for food web dynamics (Polis et al., 1989).

Previous studies have recorded the occurrence of IGP among arthropod predators through field observations of diet compositions (e.g., Nyffeler & Sunderland, 2003; Birkhofer & Wolters, 2012). Manipulative experiments in the field and laboratory have also been used to examine the intensity of IGP as a function of predator and prey density (e.g., Denno et al., 2004), allowing for causal inferences about the mechanisms underlying predator-predator interactions and its effect on prey population. Nonetheless, the confined settings in these experiments may potentially alter the encounter rates between organisms, thus leading to biased results (Uiterwaal et al., 2019).

Stable isotopes, particularly nitrogen isotope signatures ($\delta^{15}N$), have been used to estimate the trophic levels of predators for assessing IGP (e.g., Wise et al., 2006). It is suggested that IGP would increase the $\delta^{15}N$ of predators (Ponsard & Arditi, 2000). For example, Rickers et al. (2006) conducted feeding experiments on wolf spiders (*Alopecosa cuneata*) and found a higher $\delta^{15}N$ of these top predators in IGP treatment. However, the study did not quantify the degree of IGP as the IGP treatment was binary (absence vs. presence of mesopredator) with constant numbers of shared prey and mesopredator. On top of that, the trophic levels of top predators in previous studies were often calculated based on assumed trophic discrimination factors (TDFs) (Svanbäck et al., 2015). Since TDFs are often taxon-specific (Caut et al., 2009), this could lead to incorrect trophic level estimates and inferences about IGP in the field.

Recently, researchers have applied molecular gut content analysis and immunological techniques to reliably detect the presence of certain food items in predators' diet (Gagnon et al., 2011), allowing for calculating the incidence rates of IGP (i.e., the percentage of top predator individuals with mesopredator detected in the gut contents). Nonetheless, the incidence rates may not necessarily reflect the degree of IGP in the system (Raso et al., 2014). For example, it is possible that a high percentage of top predator individuals feed on mesopredator yet each of them consumes on average a low proportion of mesopredator in the diet. In this case, a high incidence rate of IGP only provides an incomplete picture of IGP dynamics.

Quantifying IGP is a critical step towards a deeper understanding of food web dynamics. Research has attempted to predict the intensity/degree of IGP based on allometric theory (Schneider et al., 2012), yet empirical evidence remains scarce. To address this gap, I propose an experimental framework combining controlled feeding trials and stable isotope analysis of field samples to estimate the degree of IGP in a three-species omnivorous food web (top predator + mesopredator + shared prey). The degree of IGP is defined herein as the proportion (in number) of mesopredator consumed in the total diet (mesopredator + shared prey) of top predator. The feeding trials will experimentally link different levels of mesopredator consumption by top predator to the changes in top predator's nitrogen isotope signatures via an IGP standard curve, to which the nitrogen isotope signatures of field-collected top predator individuals are interpolated to estimate the degree of IGP in the field.

The proposed experimental framework

The proposed experimental framework consists of three main stages: (1) first feeding trial for stable isotope calibration of mesopredator and top predator, (2) second feeding trial for construction of standard IGP curve, and (3) collection of field samples for IGP estimation. I will illustrate the framework using an example of a terrestrial arthropod food web involving a spider top predator, a spider mesopredator, and a planthopper shared prey (Fig. 1a) in the following paragraphs.

The first feeding trial is to calibrate the nitrogen isotope signatures of the mesopredator and top predator. In this trial, the two predators are fed the shared prey for a period of time (Fig. 1b). The actual duration of feeding may vary depending on the species. For arthropods, a period of 5–10 days will allow predators to incorporate isotope signatures into their tissues and reach an isotopic equilibrium state with the shared prey (Quinby et al., 2020).

The second feeding trial is to simulate a full range of omnivory that the top predator may exhibit in the field for constructing a standard IGP curve. In this trial, the top predator is fed different proportions of shared prey and mesopredator individuals from the first feeding trial: (1) 100% shared prey, (2) 75% shared prey + 25% mesopredator, (3) 50% shared prey + 50% mesopredator, (4) 25% shared prey + 75% mesopredator, and (5) 100% mesopredator (Fig. 1c). The actual numbers of shared prey and mesopredator supplied can be determined based on their feeding rates, obtained through either field observations or literature. To avoid the potential interfering effects of mesopredator feeding on the shared prey, the prey items are presented to the top predator one at a time in a randomized sequence instead of all at once. This also allows the researcher to ensure that a prey item is consumed by the top predator before the next item is presented.

At the end of the second trial (same duration as the first feeding trial to allow for the incorporation of prey isotope signatures into predator's tissues), the top predator individuals in each diet treatment as well as the shared prey are prepared for stable isotope analysis to obtain their $\delta^{15}N$ values. The difference in $\delta^{15}N$ between the top predator and the shared prey is computed ($\delta^{15}N_{predator} - \delta^{15}N_{prey}$; experimental $\Delta^{15}N$), and a standard curve is constructed by fitting a non-linear regression on the experimental $\Delta^{15}N$ against the proportion of mesopredator in the diet (Fig. 1d).

Finally, field samples of top predator and shared prey are collected for stable isotope analysis. The shared prey individuals are pooled to obtain an overall prey $\delta^{15}N$, while the $\delta^{15}N$ of top predator individuals are analyzed separately and thus each predator has its own empirical $\Delta^{15}N$ (i.e., $\delta^{15}N$ of each top predator individual − overall prey $\delta^{15}N$). The degree of IGP at the individual level can then be estimated by interpolating the individual empirical $\Delta^{15}N$ to the standard IGP curve (Fig. 1e). The mean and standard error of these individual IGP estimates can provide a measure of the average degree of IGP in the field and the uncertainty around the mean estimate at the population level.

A hypothetical example of standard IGP curve construction and estimation of IGP with field samples is shown in Fig. 2. In this example, five diet treatments are used; each treatment contains five top predator individuals, each of which is fed 12 prey items during the feeding period. After the feeding trial, the experimental $\Delta^{15}N$ of these predator individuals are determined and used to construct a standard IGP curve (Fig. 2a). 20 top predator and 30 shared prey individuals are then collected from the field for stable isotope analysis and determination of empirical $\Delta^{15}N$. An IGP estimate is calculated for each top predator individual and therefore there will be a total of 20 estimates, which are further averaged to quantify the degree of IGP at the population level (Fig. 2b).

Applications

The proposed framework leverages the strengths of different approaches to studying trophic interactions—the controlled feeding trials combined with stable isotope analysis can yield accurate experimental $\Delta^{15}N$ for constructing a standard IGP curve, whereas the empirical $\Delta^{15}N$ derived from field samples reflects the trophic interactions under natural settings. Additionally, the framework is robust to variations in background isotope signatures because the IGP estimation is based on the difference in nitrogen isotope signatures ($\Delta^{15}N$) rather than the original values ($\delta^{15}N$), thus allowing for comparisons across sites or systems with distinct background isotope signatures.

The framework can be implemented along environmental gradients or under different field treatments to investigate how various abiotic and biotic factors affect IGP interactions of a certain food web type (e.g., arthropod food web). For instance, one can quantify and compare the degree of IGP across altitudes to examine whether omnivory patterns change with temperature, precipitation, or vegetation. Moreover, this study gives an example of arthropod food web with spider as the top predator, but the framework applies to other generalist predators as well, provided that they are amenable to feeding trials and available for collection in the field.

Systems with clear IGP patterns and relatively simple trophic interaction networks are ideal for implementing the proposed framework, as this can minimize the potential interfering effects of non-focal species on the IGP interactions among focal organisms (Vance-Chalcraft et al., 2007). One of such systems is agricultural system, in which IGP occurs frequently (Polis et al., 1989; Rosenheim et al., 1995) and the food webs are generally less complex compared with most natural ecosystems. Furthermore, understanding the degree of IGP in agricultural field can have useful implications for practitioners, for example, evaluating the effectiveness of biocontrol agents in pest control programs (Müller & Brodeur, 2002).

A potential limitation of the proposed framework is that multiple mesopredators and shared prey with different isotope signatures may exist in the field, which could introduce variations into the IGP estimates for top predator individuals. The isotope signatures of top predators may represent multiple dietary items over time and space. Yet, given sufficiently large field samples of top predator, the average IGP estimate should fairly reflect the overall IGP patterns in the field at the population level. Additionally, one can adjust the isotope signatures of top predator individuals by adding an amount to (or deducting an amount from) the $\delta^{15}N$ of top predator that feeds on non-focal prey with a lower (or higher) $\delta^{15}N$ than that of the focal shared prey. Such calibration of $\delta^{15}N$ of top predator can yield a more accurate empirical $\Delta^{15}N$ for interpolation of IGP curve.

A better quantitative understanding of IGP can offer critical insights into the complex predator-predator-prey trophic interactions and help predict the community structure and stability (Arim & Marquet, 2004; Pahl et al., 2020). I am optimistic about the practical applications of the proposed framework and future experiments to validate and refine it. The current framework can also be extended to food webs involving more complex interactions (e.g., cannibalism and multiple shared prey) and further complemented with other approaches (e.g., combining the degree of IGP at the population level with the incidence rates derived from molecular gut content analysis to estimate the total IGP impact) to better elucidate the IGP dynamics in the field.

Acknowledgements

I thank William J.-A. Ou and Po-Ju Ke for the useful comments on this manuscript.

Conflict of interest

The author declares no conflict of interest regarding this manuscript.

Data accessibility statement

Data archiving and sharing are not applicable to this manuscript as no new data were generated or analyzed.

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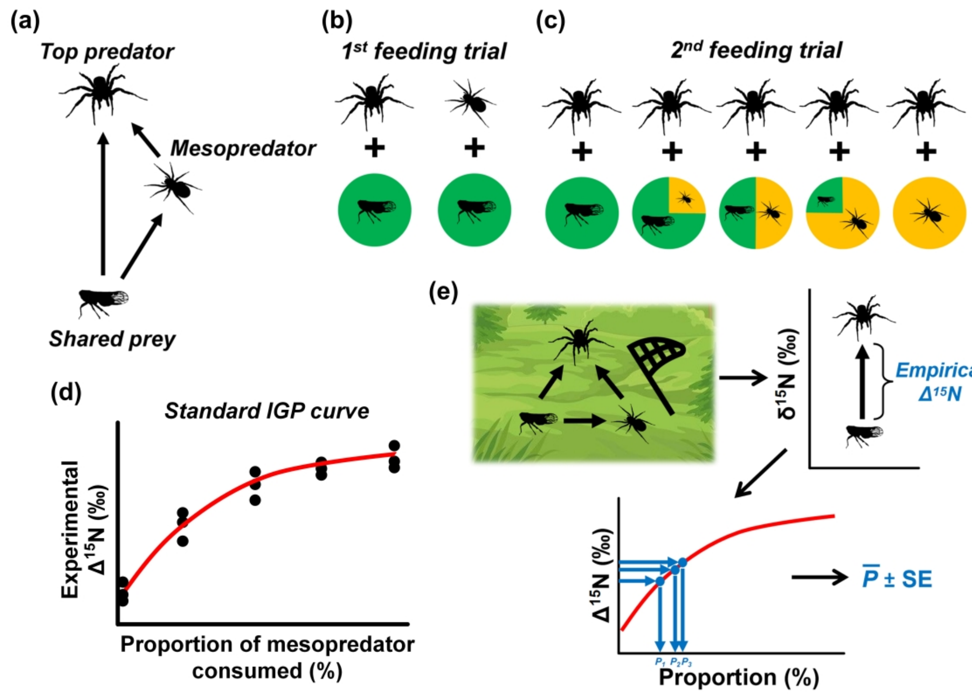

Figure 1. A schematic diagram of the proposed experimental framework for quantifying the degree of intraguild predation (IGP) in a three-species omnivorous food web involving a spider top predator, a spider mesopredator, and a planthopper shared prey. See “The proposed experimental framework” for detailed descriptions of the steps in the framework.

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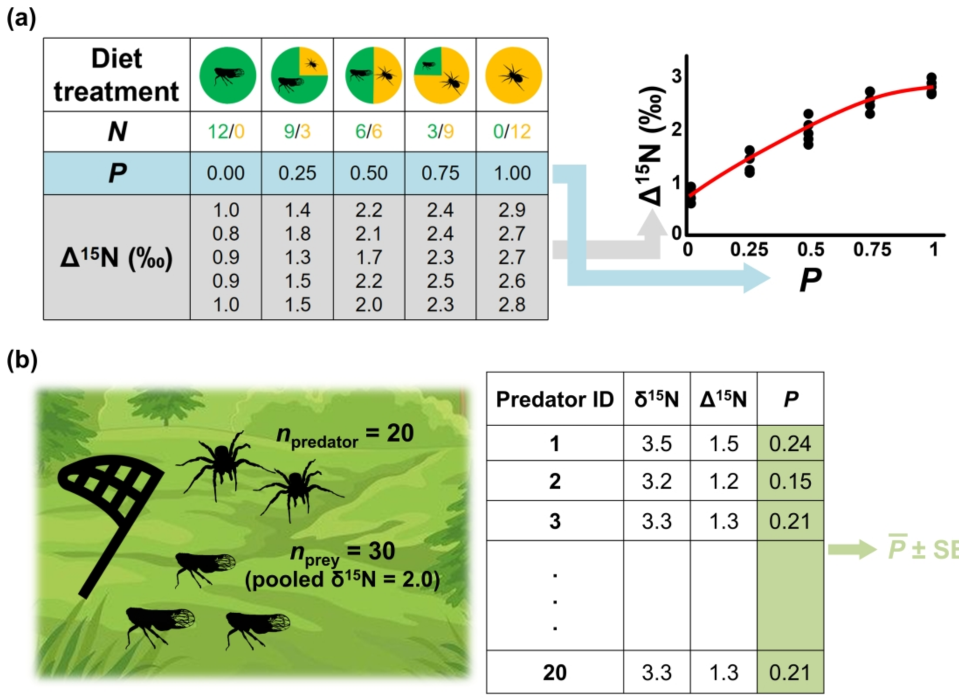

Figure 2. A hypothetical example of (a) standard IGP curve construction using data collected from the second feeding trial and (b) estimation of IGP with field samples of top predator and shared prey. N: number of shared prey/mesopredator in the mixed diet; P: proportion of mesopredator consumed (%).

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