**Title**

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

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**Abstract**

1. Intraguild predation (IGP) is common in natural and human-managed systems and plays a critical role in food web dynamics. Previous studies have documented the occurrence of IGP across a wide range of arthropod predator taxa, yet there is still a lack of quantitative understanding regarding the degree/intensity of IGP in these systems.
2. I propose an experimental framework combining controlled feeding trials and stable isotope analysis to determine the degree of IGP in a three-species terrestrial omnivorous arthropod food web (top predator + mesopredator + shared prey) in the field. The degree of IGP is defined herein as the proportion (in number) of mesopredator consumed in the total diet (shared prey + mesopredator) of top predator. The feeding trials are used to construct a standard curve for the degree of IGP in the focal system, to which the stable isotope signatures of field samples are compared to estimate the degree of IGP in the field.
3. The proposed framework leverages the strengths of different experimental approaches to studying trophic interactions, providing a useful tool for quantifying IGP in a accurate (controlled feeding trials and standard IGP curve) and realistic (stable isotope analysis of field samples) fashion.
4. If proven successful, the current framework can be extended to food webs involving more complex interactions (e.g., cannibalism and multiple shared prey) and further complemented with other approaches (e.g., molecular gut content analysis) to capture a more complete picture of IGP dynamics in the field.

**Key words**

intraguild predation, food webs, omnivory, generalist predators, stable isotope analysis, feeding experiment

**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 arthropod 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 (e.g., field cages) have also been used to assess the intensity of IGP (e.g., Denno et al., 2004), which could reveal the mechanisms underlying predator-prey interactions and allow for strong causal inferences about IGP. 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 (δ15N), have been used to estimate the trophic levels of predators in the field for inferences about IGP (e.g., Wise et al., 2006). It is suggested that IGP would increase the δ15N of predators (Ponsard & Arditi, 2000). For example, Rickers et al. (2006) conducted feeding experiments on wolf spiders (*Alopecosa cuneata*) and found a higher δ15N 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 quite 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 estimating 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 consumes on average only 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 and could be misleading.

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 determine 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 (δ15N) via a standard curve, to which the isotope signatures of top predator from the field samples are compared 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 focal organisms, (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 isotope signatures of the focal organisms. In this trial, the top predator and the mesopredator 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 mixed diets with different proportions of shared prey and mesopredator individuals (these prey items are from the first feeding trial): (1) 100% shared prey, (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) 100% mesopredator (Fig. 1c). The actual numbers of shared prey and mesopredator supplied can be determined based on their field densities. 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 sequential fashion 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 δ15N values. The differences in δ15N between the top predator and the shared prey (baseline) is computed (δ15N*predator*─ δ15N*prey*; Δ15N), and a standard curve can be constructed by fitting a non-linear regression model on the experimental Δ15N against the proportion of mesopredator in the diet treatments (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 a single baseline δ15N, while the δ15N of top predator individuals are analyzed separately and thus each predator has its own empirical Δ15N. The degree of IGP at the individual level can then be estimated by interpolating the individual empirical Δ15N to the standard curve (Fig. 1e). The mean and standard error of these individual IGP estimates can further 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, each diet treatment contains five top predator individuals, each of which is fed 10 prey items during the experimental period. After the feeding trial, the experimental Δ15N of these predator individuals are obtained to construct a standard IGP curve. 20 top predator and 30 shared prey individuals (pooled) are then collected from the field for stable isotope analysis and determination of empirical Δ15N. An IGP estimate is calculated for each top predator individual so that there is a total of 20 estimates, which can be further averaged to quantify the degree of IGP at the population level.

**Application**

The proposed framework leverages the strengths of previous approaches to studying IGP—the controlled feeding trials combined with stable isotope analysis can yield accurate experimental Δ15N to construct a standard curve, whereas the empirical Δ15N derived field samples reflects the trophic interactions under natural settings. Additionally, the framework is robust to variations in background isotope signatures because the degree of IGP is determined based on the difference between nitrogen isotope signatures of the focal organisms (Δ15N) rather than their original values (δ15N), 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 the degree of IGP in natural settings. For instance, one can quantify and compare the degree of IGP across altitudes to examine whether omnivorous interactions change with temperature, precipitation, or vegetation. Moreover, although an example is given using spider as the top predator, the framework applies to other generalist predators as well, provided that they are amenable to feeding trials and easy to collect in the field.

The systems ideal for implementing the framework are those with clear IGP patterns and relatively simple trophic interaction networks, which can minimize the potential interfering effects of non-focal species on the trophic interactions among focal organisms (Vance-Chalcraft et al., 2007). One of such systems is agricultural system, in which IGP is frequent (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, evaluation of the effectiveness of biocontrol agents in pest control programs (Müller & Brodeur, 2002).

A potential limitation of the proposed framework is that there could be multiple mesopredators and shared prey with different isotope signatures in the field, which may introduce variations into the IGP estimates for individual predators. Yet, given sufficiently large field samples, the average of these individual estimates should still be fairly reflective of the overall IGP patterns in the field at the population level. Therefore, although the isotope signatures of predators in the field could represent multiple dietary items over time and space, the framework still provides a useful tool for assessing IGP in a more quantitative and realistic fashion.

A better quantitative understanding of IGP can provide critical insights into the complex predator-predator-prey trophic interactions and could help predict the community structure and stability (Arim & Marquet, 2004; Pahl et al., 2020). Albiet conceptual at this stage, I am optimistic about validating the proposed framework with real data and further refining it. If proven successful, the current framework can be 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 better elucidate the IGP dynamics in the field.

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**Contribution of authors**

GCH conceived the idea and wrote the manuscript. No other person was entitled to authorship.

**Conflict of interest**

The author declares no conflict of interest regarding this paper.

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**Figure legends**

Figure 1.A schematic diagram of the proposed experimental framework for determining the degree of intraguild predation (IGP) in a three-species terrestrial omnivorous arthropod food web involving a spider top predator, a spider mesopredator, and a planthopper shared prey (a). In the first trial (b), the top predator and the mesopredator are fed the shared prey for 5–10 days to ensure an isotopic equilibrium state between the predators and the prey. In the second trial (c), the top predator is fed mixed diets with different proportions of mesopredator and shared prey individuals 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 nitrogen isotope signatures between the top predator individuals and the shared prey (baseline) (δ15N*predator*─ δ15N*prey*; experimental Δ15N) against the proportion of mesopredator consumed. Note that the curve may not necessarily be linear due to biomass differences between mesopredator and shared prey. (e) The δ15N of field-sampled top predator and shared prey individuals are analyzed to obtain the empirical Δ15N, which is then interpolated to the standard curve to estimate the degree of IGP in the field.

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

**Figures**

Figure 1.

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Figure 2.

