**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 has been 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 demonstrated 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. However, 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 level 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 terrestrial omnivorous arthropod 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 predators to the changes in their nitrogen isotope signatures (δ15N) via a standard curve, to which the isotope signatures of 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 standard IGP curve construction, 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 focal 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: (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 in the supplied diet 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 plotting 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, with their δ15N analyzed to obtain the empirical Δ15N. The degree of IGP in the field can then be estimated by interpolating the empirical Δ15N to the standard curve (Fig. 1e).

A hypothetical example of standard IGP curve construction and estimation of IGP with field samples is shown in Fig. 2. In this example, there are five top predator individuals in each diet treatment; each predator individual is fed 10 prey items during the experimental period, after which the Δ15N values of these predator individuals are obtained to construct a standard IGP curve using non-linear fitting methods. 20 top predator and 20 shared prey individuals (pooled to obtain a single baseline reference) are then collected from the field for stable isotope analysis and determination of empirical Δ15N values, and an IGP estimate is obtained for each top predator individual (i.e., a total of 20 IGP estimates). The mean of these IGP estimates represents the average degree of IGP in the field, whereas the variance of these estimates provides a measure of the variation around the mean IGP estimate.

**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. Although it is possible that the isotope signatures of predators in the field may represent multiple dietary items over time and space, the framework could still provide a useful tool for assessing IGP in more quantitative and realistic fashion.

* Also note that the example here is given as spider, but the framework applies to generalist predators, provided that they are amenable to feeding trials and easy to collect samples in the field.
* Mean and variance of field samples
* This framework works at the community level. There could be quite a few variations at the individual level, but if we collect enough shared prey and top predator samples, then the average responses should be reflective the overall situation in the field.
* One potential caveat of this framework is that there could be multiple mesopredators and even shared prey in the field, with different isotopic signatures. This is indeed one of the limitations of this approach. However, as mentioned, the framework will first be tested in systems where the food webs are relatively simple so that the potential interfering effects from other species can be minimized. In fact, even if there are some variations, the average responses should still fairly reflect the reality given large enough samples. So again, this framework aims to quantify IGP at community level, not IGP for each individual.

Agricultural systems, in which IGP has been frequently documented (Polis et al., 1989; Rosenheim et al., 1995), are ideal for implementing the framework. As the food webs are relatively simple compared with other natural ecosystems, the potential effects of non-focal species on the trophic interactions among focal organisms can be minimized (Vance-Chalcraft et al., 2007).

Moreover, the framework can be implemented along environmental gradients or under different field treatments to examine how various abiotic and biotic factors may affect the degree of IGP in natural settings. Finally, 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.

* proposing a new experimental framework idea and can be tested later in the field, so at this current stage is purely theoretical but later will test it our with empirical data

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). Furthermore, such an understanding can have useful implications for practitioners, for example, evaluation of the effectiveness of biocontrol agents in pest control programs (Müller & Brodeur, 2002). 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.

