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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 predator taxa, yet there is still a lack of quantitative understanding regarding the degree/intensity of IGP in these systems.
2. Here, I propose an experimental framework combining controlled feeding trials and stable isotope analysis to determine the degree of IGP in a three-species omnivorous food web (shared prey + mesopredator + top predator) 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 more accurate (controlled feeding trials and standard IGP curves) 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.

Keywords

feeding experiment, food webs, intraguild predation, omnivory, stable isotope analysis, trophic interactions

Introduction

Intraguild predation (IGP) is common in natural and human-managed ecosystems (Arim & Marquet, 2004; Müller & Brodeur, 2002; Polis & Holt, 1992) and has been documented across a wide range of animal taxa (Fonseca et al., 2017; Polis et al., 1989). IGP could substantially affect the abundance and distribution of interacting species, which may have profound ecological and evolutionary consequences for food web dynamics (Polis et al., 1989).

Previous studies have used manipulative experiments (e.g., field cages) to assess the intensity of IGP by comparing the differences in the densities of prey or mesopredator in the presence vs. absence of top predator (Denno et al., 2004; Provost et al., 2005). This approach could reveal the mechanisms underlying predator-prey interactions, allowing for strong causal inferences about IGP. However, the confined settings in these experiments could potentially alter the encounter rates between organisms and thus lead to biased results.

Stable isotopes, particularly nitrogen isotope signatures ($\delta^{15}N$), have been used to estimate the trophic level of predators in the field for inferences about IGP (Halaj et al., 2005; Sanders & Platner, 2007; Wise et al., 2006). It is suggested that IGP would increase the $\delta^{15}N$ of predators (Ponsard & Arditi, 2000). Rickers et al. (2006) conducted feeding experiments on wolf spiders (*Alopecosa cuneata*) and revealed 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. Moreover, the trophic levels of top predators in previous studies were often calculated based on assumed trophic discrimination factors (TDFs) (e.g., Klarner et al., 2013; Svanbäck et al., 2015).

Since TDFs are quite taxon-specific (Caut et al., 2009), these trophic level estimates could 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 rate of IGP (i.e., the percentage of top predator individuals with mesopredator detected in the gut contents). Nonetheless, the incidence rate 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 top predator individual consumes on average low proportion of mesopredator in the diet. In this case, a high incidence rate of IGP could be misleading and may fail to capture the overall IGP dynamics in the field.

So far, there is still a lack of quantitative information regarding the intensity/degree of IGP in the field, and such information is the first step towards a deeper understanding of food web dynamics. 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) in the systems of interest. 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 ($\delta^{15}N$) via a standard curve, to which the isotope signatures of field samples are compared to estimate the degree of IGP in the field.

Experimental framework

Here, I illustrate the proposed framework using an example of a three-species omnivorous arthropod 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 feeding trial, the top predator and the mesopredator are fed the shared prey for an appropriate period of time to allow for the incorporation of isotopes into the tissues (Fig. 1b). The purpose of the first trial is 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 trial), the top predator are 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 numbers of shared prey and mesopredator in the presented diet can be determined based on their field densities. The purpose of the second 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 trial, the actual numbers of shared prey and mesopredator consumed by the top predator in each diet treatment are recorded, and the difference in nitrogen isotope signatures between the top predator individuals and the shared prey (baseline) are analyzed ($\delta^{15}N_{predator} - \delta^{15}N_{prey}$; $\Delta^{15}N$). A standard curve can be constructed by plotting the experimental $\Delta^{15}N$ of top predator against the proportion of mesopredator consumed (Fig. 1d). Finally, field samples of shared prey and top predator individuals are collected, with their $\delta^{15}N$ analyzed to obtain the empirical $\Delta^{15}N$. The degree of IGP in the field can thus be estimated by interpolating the empirical $\Delta^{15}N$ to the standard curve (Fig. 1e). A

hypothetical example of data collection in the second feeding trial for standard curve construction is provided in Fig. 2.

Applications

The proposed experimental framework leverages the strengths of previous approaches to studying IGP—the controlled feeding trials combined with stable isotope analysis can yield accurate experimental $\Delta^{15}N$ to construct a standard curve, whereas the empirical $\Delta^{15}N$ derived from stable isotope analysis of field samples reflects the 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.

Agricultural and aquatic ecosystems, in which IGP has been frequently documented (Polis et al., 1989; Rosenheim et al., 1995), are ideal for testing the proposed framework. The food web structures in these systems are relatively simple compared with other ecosystems. Therefore, the potential confounding effects of non-focal species on the trophic interactions among focal organisms can be minimized (Vance-Chalcraft et al., 2007). Moreover, this framework is useful for quantifying the effects of various abiotic and biotic factors on IGP under field settings. For instance, the framework can be implemented along a gradient of habitat complexity to examine how different levels of habitat complexity might affect the degree of IGP in the field. 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 ($\Delta^{15}N$) rather than their original values ($\delta^{15}N$), thus allowing for comparisons across sites or systems with distinct background isotope signatures.

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; Nakazawa & Yamamura, 2006; Pahl et al., 2020). Furthermore, such an understanding can have useful implications for practical issues, for example, evaluation of the effectiveness of biocontrol agents in pest control programs (Müller & Brodeur, 2002). If proven successful, 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., MGCA) to elucidate the IGP dynamics in the field.

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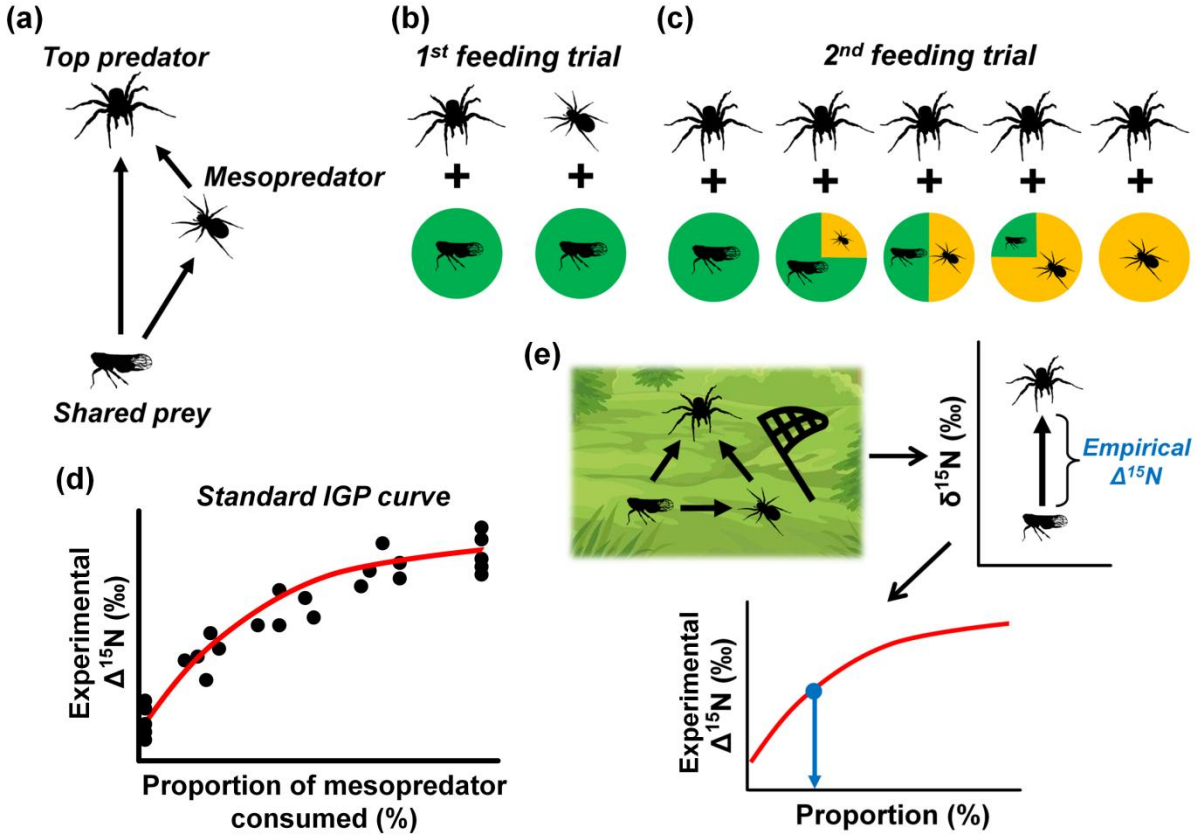
Figures

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 (c), the top predators are fed mixed diets with different proportions of shared prey and mesopredator 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) ($\delta^{15}N_{predator} - \delta^{15}N_{prey}$; experimental $\Delta^{15}N$) 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 $\delta^{15}N$ of field-sampled shared prey and top predator individuals are analyzed to obtain the empirical $\Delta^{15}N$, which is then interpolated to the standard curve to estimate the degree of IGP in the field.


(a)
Top predator
Mesopredator
Shared prey
(b)
1st feeding trial
(c)
2nd feeding trial
(d)
Standard IGP curve
Experimental Δ15N (‰)
Proportion of mesopredator consumed (%)
(e)
δ15N (‰)
Empirical Δ15N
Experimental Δ15N (‰)
Proportion (%)

210

211

Figure 2. A hypothetical example of data collection in the second feeding 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.

Diet treatment					
N	20/0	15/5	10/10	5/15	0/20
C	12/0 11/0 12/0 10/0 13/0	8/3 7/5 9/3 8/4 7/3	6/5 6/4 7/4 5/5 6/4	3/6 3/5 4/5 2/5 3/5	0/4 0/5 0/5 0/3 0/6
***P* (%)**	0 0 0 0 0	27.2 41.7 25.0 33.3 30.0	45.5 40.0 36.3 50.0 40.0	66.7 62.5 55.6 71.4 62.5	100 100 100 100 100
Δ^{15}N (‰)	1.0 0.8 0.9 0.9 1.0	1.4 1.8 1.3 1.5 1.5	2.2 2.1 1.7 2.2 2.0	2.4 2.4 2.3 2.5 2.3	2.9 2.7 2.7 2.6 2.8