ECOLOGICAL RESEARCH

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

Journal:	*Ecological Research*
Manuscript ID	ERE-2021-0114.R1
Wiley - Manuscript type:	Special Feature
Date Submitted by the Author:	n/a
Complete List of Authors:	Hsu, Gen-Chang; National Taiwan University Department of Life Science,
Manuscript Category:	5: Species interaction, 40: Stable isotope
Manuscript Keywords:	community, experiment, intraguild predation, stable isotope analysis, ideas for specific organisms/systems
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.

Article category

Special features

Title

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

Author

Gen-Chang Hsu[1]

Author's institutional affiliation

[1]Department of Life Science, National Taiwan University, Taipei, Taiwan

Correspondence

Gen-Chang Hsu, Department of Life Science, National Taiwan University, Taipei 10617, Taiwan.

Email: genchanghsu@gmail.com

ORCID: https://orcid.org/0000-0002-6607-4382

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 ~~present~~ 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~~ideas for fundamental questions~~, 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 ~~relative~~ proportion of ~~consumption of~~ mesopredator ~~(compared to shared prey)~~ in the total numbers of prey (shared prey + mesopredator) consumed ~~in the diet of~~by the top predator (e.g.,~~i.e.,~~ 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 ($\delta^{15}N$), have been used to estimate the trophic levels of predators in the field and to make inferences about IGP (~~Abd El-Wakeil, 2009;~~ Halaj et al., 2005; Sanders & Platner, 2007; Wise et al., 2006)~~; Rickers et al., 2006)~~. It is suggested that IGP would increase the $\delta^{15}N$ of predators ~~and thus their trophic level~~ (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 $\delta^{15}N$ 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 ~~but this proposal has not been experimentally verified~~. ~~In addition~~Moreover, the trophic levels of predators in previous studies were~~as~~ often calculated based on ~~assumed~~ assumed trophic ~~enrichment~~ discrimination factors (TD~~E~~Fs) (e.g., Klarner et al., 2013; Ponsard & Arditi, 2000; Svanbäck et al., 2015). Since TDFs are quite taxon-specific (Caut et al., 2009),~~,~~ ~~which can affect the~~ these trophic level estimates could be biased and thus lead to incorrect~~subsequent~~ inferences ~~made~~ 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 ~~incorrect~~ 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 ~~more accurately~~ determine the degree of IGP in a three-species omnivorous food web. Specifically, I predict that the δ^{15}N of top predator ~~individuals~~ engaged in IGP will be higher ~~than the δ^{15}N of individuals~~compared with not engaged in IGP, and ~~. Moreover,~~ the more the top predator consumes the mesopredator in the diet, the higher the δ^{15}N of top predator would be, leading to greater difference in δ^{15}N between the top predator and the shared prey (Δ^{15}N)~~of top predator would be~~. By experimentally linking different levels of mesopredator consumption and the resulting Δ^{15}N of top predator, the degree of IGP in the field can be determined using field-derived Δ^{15}N 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 ~~two weeks~~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 (~~the organisms are~~ from the first ~~feeding~~ 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 ~~individuals~~ used in each diet treatment will be ~~determined~~ 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~~different degrees of IGP under different encounter rates among the organisms~~.

At the end of the second feeding trail,~~After two weeks of feeding,~~ the actual numbers of shared prey and mesopredator consumed by the top predator in each diet treatment will be recorded, and the δ^{15}N of each top predator individual ~~individuals in each diet treatment~~ will be analyzed. A standard curve can be constructed by plotting the Δ^{15}N of top predator against the proportion of mesopredator consumed ~~, and their TEFs (relative to the δ^{15}N of shared prey) are used to construct a standard IGP curve~~ (Fig. 1d). Finally, field samples of top predator and shared prey individuals will be collected, with their δ^{15}N analyzed to obtain the empirical Δ^{15}N~~TEF for the top predator~~. The degree of IGP in the field can then be assessed~~determined~~ by interpolating~~comparing~~ the field-derived ~~empirical~~ Δ^{15}N~~TEF~~ 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 ~~trophic enrichment factors~~Δ^{15}N to construct a standard curve, whereas the stable isotope analysis of field samples allows for trophic interactions under natural settings. ~~Therefore~~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~~In addition~~, the species compositions are relatively simple compared with~~to~~ natural systems.~~, which can largely reduce~~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 ~~provide~~ 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~~ in Taiwan. In my previous manuscript (published in the journal *Ecosphere*)~~, 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, ~~yet~~ but we were not able to quantify ~~IGP~~ 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 ~~, which e~~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 ~~that this study~~ can serve as a starting point to generate ~~inspire~~ new ideas~~ and~~ refining the present method, or even inspire other researchers to ~~we will be able to~~ develop a more thorough method to ~~solve~~ address this question in the future~~ in the future~~.

Acknowledgements

I would like to thank Jia-Ang (William) Ou for ~~his~~ the useful comments and editing work on this manuscript.

Conflict of interest

The author declares no potential conflict of interest.

References

~~Abd El-Wakeil K. F. (2009). Trophic structure of macro-and meso-invertebrates in Japanese coniferous forest: Carbon and nitrogen stable isotopes analyses. *Biochemical Systematics and Ecology*, *37*, 317-324.~~

Arim M., & Marquet P. A. (2004). Intraguild predation: a widespread interaction related to species biology. *Ecol Lett*, *7*, 557-564.

Caut S., Angulo E., & Courchamp F. (2009). Variation in discrimination factors (Δ15N and Δ13C): the effect of diet isotopic values and applications for diet reconstruction. *Journal of Applied Ecology*, *46*, 443-453.

Denno R. F., Mitter M. S., Langellotto G. A., Gratton C., & Finke D. L. (2004). Interactions between a hunting spider and a web-builder: consequences of intraguild predation and cannibalism for prey suppression. *Ecological entomology*, *29*, 566-577.

Gagnon A. E., Heimpel G. E., & Brodeur J. (2011). The Ubiquity of Intraguild Predation among Predatory Arthropods. *PLoS One*, *6*, 7.

Gratton C., & Forbes A. E. (2006). Changes in δ 13 C stable isotopes in multiple tissues of insect predators fed isotopically distinct prey. *Oecologia*, *147*, 615-624.

Hagler J. (2006). Development of an immunological technique for identifying multiple predator–prey interactions in a complex arthropod assemblage. *Annals of Applied Biology*, *149*, 153-165.

Halaj J., Peck R. W., & Niwa C. G. (2005). Trophic structure of a macroarthropod litter food web in managed coniferous forest stands: a stable isotope analysis with δ15N and δ13C. *Pedobiologia*, *49*, 109-118.

Klarner B., Maraun M., & Scheu S. (2013). Trophic diversity and niche partitioning in a species rich predator guild–Natural variations in stable isotope ratios (13C/12C, 15N/14N) of mesostigmatid mites (Acari, Mesostigmata) from Central European beech forests. *Soil Biology and Biochemistry*, *57*, 327-333.

Mansfield S., & Hagler J. R. (2016). Wanted dead or alive: scavenging versus predation by three insect predators. *Food Webs*, *9*, 12-17.

Muller C. B., & Brodeur J. (2002). Intraguild predation in biological control and conservation biology. *Biol Control*, *25*, 216-223.

Nakazawa T., & Yamamura N. (2006). Community structure and stability analysis for intraguild interactions among host, parasitoid, and predator. *Population Ecology*, *48*, 139-149.

Pahl K. B., Yurkowski D. J., Lees K. J., & Hussey N. E. (2020). Measuring the occurrence and strength of intraguild predation in modern food webs. *Food Webs*, e00165.

Polis G. A., & Holt R. D. (1992). Intraguild predation: the dynamics of complex trophic interactions. *Trends in ecology & evolution*, *7*, 151-154.

Polis G. A., Myers C. A., & Holt R. D. (1989). The ecology and evolution of intraguild predation: potential competitors that eat each other. *Annual review of ecology and systematics*, *20*, 297-330.

Ponsard S., & Arditi R. (2000). What can stable isotopes (δ15N and δ13C) tell about the food web of soil macro-invertebrates? *Ecology*, *81*, 852-864.

Provost C., Coderre D., Lucas E., Chouinard G., & Bostanian N. J. (2005). Impact of intraguild predation and lambda-cyhalothrin on predation efficacy of three acarophagous predators. *Pest Management Science: formerly Pesticide Science*, *61*, 532-538.

Raso L., Sint D., Mayer R., Plangg S., Recheis T., Brunner S., Kaufmann R., & Traugott M. (2014). Intraguild predation in pioneer predator communities of alpine glacier forelands. *Molecular ecology*, *23*, 3744-3754.

Rickers S., Langel R., & Scheu S. (2006). Stable isotope analyses document intraguild predation in wolf spiders (Araneae: Lycosidae) and underline beneficial effects of alternative prey and microhabitat structure on intraguild prey survival. *Oikos*, *114*, 471-478.

Rosenheim J. A., Kaya H. K., Ehler L. E., Marois J. J., & Jaffee B. A. (1995). Intraguild predation among biological-control agents: theory and evidence. *Biol Control*, *5*, 303-335.

Sanders D., & Platner C. (2007). Intraguild interactions between spiders and ants and top-down control in a grassland food web. *Oecologia*, *150*, 611.

Svanbäck R., Quevedo M., Olsson J., & Eklöv P. (2015). Individuals in food webs: the relationships between trophic position, omnivory and among-individual diet variation. *Oecologia*, *178*, 103-114.

Wise D. H., Moldenhauer D. M., & Halaj J. (2006). Using stable isotopes to reveal shifts in prey consumption by generalist predators. *Ecological Applications*, *16*, 865-876.

Figure legend

Figure 1. A s~~S~~chematic 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 ~~two weeks~~ 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 ~~(from the stock)~~ and mesopredator individuals (from the first ~~feeding~~ trial) ~~individuals~~ to simulate a full range of potential encounter rates that the focal organisms might experience in the field.~~simulate different degrees of IGP.~~ (d) A standard curve can be constructed by plotting the difference in $\delta^{15}N$ between the top predator and the shared prey ($\Delta^{15}N$) against the proportion of mesopredator consumed. ~~The trophic enrichment factors ($\Delta^{15}N$) of top predator individuals (relative to the shared prey) in each diet treatment are used to construct a standard IGP curve.~~ (Note that the curve may not necessarily be linear due to the ~~complex isotope routing.~~differences in the biomass of shared prey and mesopredator individuals.) (e) The $\delta^{15}N$ values 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 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 (%).

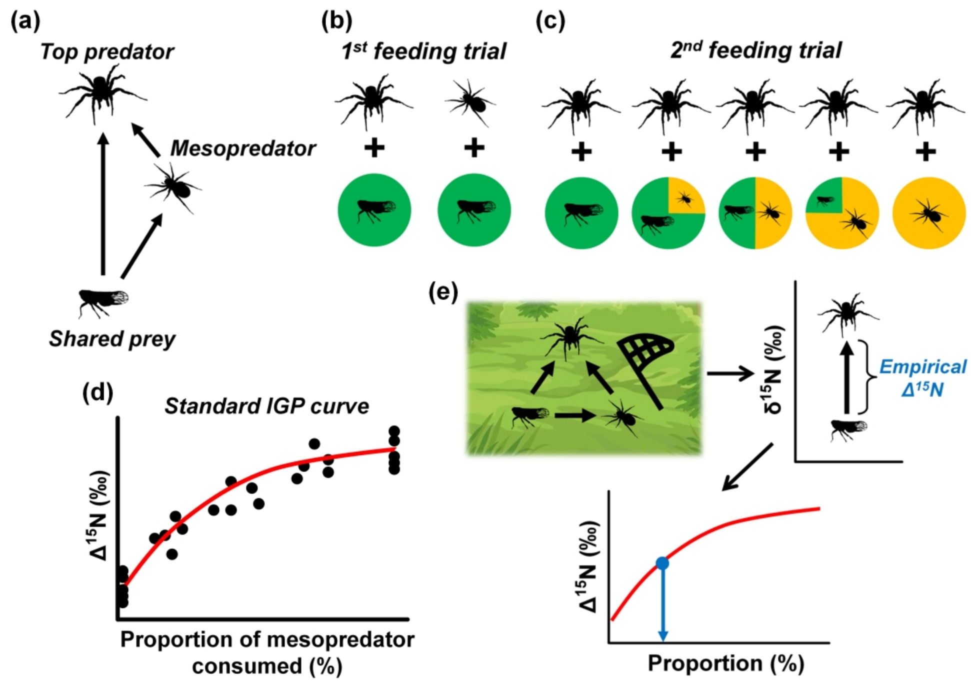

Figure 1

644x483mm (121 x 121 DPI)

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
Δ15N (‰)	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

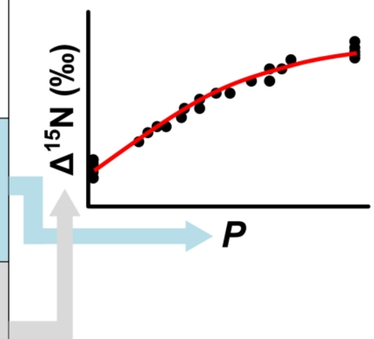

Figure 2

644x483mm (121 x 121 DPI)