

SYNTHESIZING INTRAGUILD PREDATION THEORY AND DATA**Short title:** Intraguild Predation**Name/contact:** Elizabeth Borer

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Summary:

Although intraguild predation (IGP), a form of omnivory, is widespread in natural communities and has received significant attention in the recent theoretical and empirical literature, a gulf exists between theoretical predictions about the role of IGP in food webs and our understanding of its role in real communities. With few exceptions, the IGP literature falls into two categories operating at different time-scales: (1) theory presenting long-term effects of IGP on species persistence and population densities, and (2) short-term studies demonstrating IGP and, from theory, extrapolating the outcome for populations and communities. In addition, IGP models have been formulated for predator-prey (e.g. Holt and Polis 1997), host-parasitoid (Briggs 1993), and host-parasite (or pathogen) (e.g. Hochberg and Holt 1990) systems. Although the broad predictions of all of these model formulations are the same, this commonality is not generally recognized. I propose to synthesize this diffuse body of theory, assess the information available from short-term empirical studies, and test theoretical IGP predictions with empirical data.

Problem Statement:

Background: Intraguild predation (IGP), predation on a consumer species by its guild member, is common in natural communities (Fig. 1., Polis et al. 1989) and has received substantial attention in the theoretical literature, particularly following the recent publication of a general theory of IGP by Holt and Polis (1997). Theory has shown that the presence of intraguild predation in a community has implications for important ecological issues including the relationship between food web stability and diversity, coexistence of resource competitors, suppression of the shared resource, and effects of productivity on trophic interactions. Thus, intraguild predation is relevant to both ecological theory and important applied problems such as biological control of pest species and conservation of threatened species.

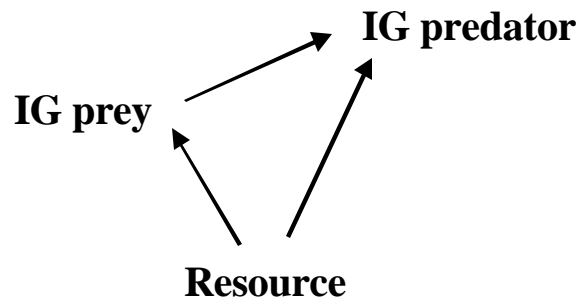


Fig. 1. Intraguild predation is a form of omnivory that combines exploitative competition by guild members for a shared resource and predation on one guild member by the other.

Since the concept of IGP was introduced into the ecological literature in 1987 (Polis and McCormick 1987), there have been >250 papers published specifically about IGP, with over half of them published in the past 5 years. Most of these papers fall into one of two categories: (1) theory presenting the long-term effects of IGP on populations and communities, and (2) short-

term studies demonstrating IGP but citing equilibrium IGP theory to extrapolate to long-term effects. Rigorous empirical tests of equilibrium IGP predictions, however, are rare (but see Morin 1999, Diehl and Feissel 2000), and even scarcer are long-term studies in natural systems. Thus, although IGP has received significant attention in recent theoretical and empirical literature, a gulf exists between the theoretical predictions about the role of IGP in species interactions and our understanding of its role in real communities.

Although the original IGP concept focused on predators and prey, several sub-disciplines within ecology have developed theory not specifically framed in terms of predation and competition, yet functionally quite similar. For example, in host-parasitoid systems, facultative hyperparasitoids, that can attack and consume either the host or the juveniles of another parasitoid species, act as intraguild predators. In parasite or disease systems, parasites that can successfully attack hosts already infected by a different parasite species also function as intraguild predators. In all cases, the second species attacks a resource that would not be available to it solely through exploitative competition. Moreover, the major predictions stemming from each of these formulations mirror those of theory framed in terms of predators and prey (e.g. Hochberg and Holt 1990, Briggs 1993).

The time is right to synthesize the theoretical literature on IGP, to evaluate what can be determined from short-term data, and to devise rigorous tests of IGP theory using existing data. Because food web form has implications for applications such as biological control, species invasions, and protection of endangered species, a clearer understanding of the role of IGP in natural communities would help resolve important applied and basic questions concerning community structure. As an NCEAS postdoctoral researcher, I will synthesize the divergent theoretical literature on intraguild predation and test IGP theory with empirical data.

Specifically, I propose to:

- 1) Synthesize existing model formulations that examine a combination of exploitative and interference competition.
- 2) Test IGP theory using existing field-collected data and determine what can be known from short-term field data.

1) Synthesize IGP model formulations:

Model formulations combining exploitative and interference competition have been developed for predator-prey (e.g. Holt and Polis 1997), host-parasitoid (Briggs 1993), and host-parasite (or pathogen) (e.g. Hochberg and Holt 1990) systems. In predator-prey models, predation provides a unique gain for the IG-predator that is independent of the shared resource. In host-parasitoid models, there is less of a distinction between gains from a host containing a parasitoid and gains from a healthy host. In host-parasite models, one parasite “wins” in competition and excludes the other to garner the host. System-specific formulaic differences, such as stage-structure (Briggs 1993), age-structure (Mylius et al. 2001), flexible behavior (Krivan 1997), and conversion efficiency (Holt and Polis 1997, Borer 2002) cause these models to appear more different than they are. In spite of formulaic differences, these models have broadly similar results: coexistence requires intermediate resource productivity and occurs only when the IG-predator is a poorer exploiter of the shared resource. Thus, in all model formulations, the resulting basal resource equilibrium is higher with both guild members present than with just the superior resource exploiter (IG-prey).

To demonstrate the similarities and examine the differences among IGP formulations, I propose to unify these modeling approaches by developing a new model that tracks movement and storage of nitrogen and carbon throughout a food web (DeAngelis 1992, Diehl 1995, Polis and Winemiller 1996). Using this unifying formulation and parameter estimates from the predator-prey, host-parasitoid, and host-parasite literature, I will examine the effects of system-specific formulations, including relative development rates and size differences of the IG-predator, IG-prey, and their resource, trophic position of the basal resource (e.g., producer or consumer), and conversion efficiency.

2) Use models and data to better understand the information available from short-term studies

Our understanding of IGP is based on equilibrium theory, an inherently multi-generational formulation, yet many recent studies have collected short-term non-equilibrium data but cited IGP theory in predictions about long-term community structure (e.g. Hurd and Eisenberg 1990, Rosenheim et al. 1993, Moran and Hurd 1994, Rosenheim et al. 1995, Chang 1996, Fagan et al. 1998, Moran and Hurd 1998). In addition, very few empirical studies have been published that explore extensively the equilibrium predictions of IGP theory (Diehl and Feissel 2000, Venzon et al. 2001).

I propose to address this conceptual disconnection in two ways.

- (i) Examine important predictions of IGP using existing, long-term field datasets that approximate the equilibrium assumptions of the theory.
- (ii) Use my new, general IGP model to assess the information available from short-term field IGP measures, and perform a meta-analysis of short- and long-term IGP datasets to examine effect sizes across single- and multi-generational studies.

(i) One of the most consistent predictions from all formulations of IGP theory is a unimodal species diversity-productivity relationship (Diehl and Feissel 2000). At extremely low productivity of the shared resource, neither IG-prey nor IG-predator can invade the system (Fig. 2, $K \ll 1$). If the IG-predator and IG-prey coexist under any conditions, the IG-prey must be a better exploiter of the basal resource. Therefore, with a small increase in the productivity of the basal resource, the IG-prey can invade (Fig 2., $K \approx 1$). The IG-predator uses the IG-prey as a second resource, so an increase in basal resource productivity that increases the IG-prey equilibrium density allows invasion by the IG-predator (Fig. 2, shaded region). When all three species are present, the equilibrium abundance of the basal resource increases with system productivity because the IG-predator increases in relative abundance, decreasing top-down control on the resource. At high productivity, species diversity declines again because the IG-predator extirpates the IG-prey and persists only on the basal resource (Fig. 2, $K > 6$).

Because this diversity-productivity relationship has not been thoroughly tested using non-laboratory data, I propose to analyze long-term field datasets appropriate for testing major IGP predictions. I have acquired two appropriate field datasets. The first dataset (permission of W.

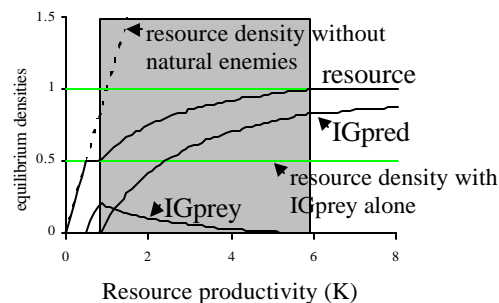


Figure 2. An example of the effects of increasing resource productivity the equilibrium densities of IG predator, IG prey, and resource. Coexistence of the IGprey and IGpred is possible only in the shaded region. Figure courtesy of C. Briggs.

Murdoch) is appropriate to quantitatively assess whether IG-predators increase relative to IG-prey and resource suppression declines along a gradient of productivity. The second dataset (permission of C. Briggs) includes time-series data of resource density with a factorial combination of IG-prey and IG-predators. Using these data, I will determine whether the system has reached equilibrium and quantitatively assess whether the basal resource increases when the IG-predator is present. I will parameterize and test my general IGP model with these field-collected data.

(ii) A major problem affecting the current state of IGP research is that empirical studies are often too short-term to appropriately test the theory (Morin 1999). In particular, short-term experiments cannot quantify several components of the IGP interaction that have implications for long-term dynamics, including the predator numerical response and conversion efficiency. Unfortunately, due to logistics, empirical field estimation of these and other parameters is often impossible, and ecologists must rely on short-term experiments to approximate long-term dynamics.

(a) I will examine conditions under which the short-term results of my general IGP model are consistent with equilibrium predictions. In addition, I will parameterize my general model to be system-specific for several published short-term studies to determine the conditions under which results of short-term IGP studies can predict long-term, equilibrium community structure.

(b) I also will perform a meta-analysis on existing short- and long-term datasets collected in communities with IGP (e.g. Hurd and Eisenberg 1990, Rosenheim et al. 1993, Moran and Hurd 1994, Rosenheim et al. 1995, Chang 1996, Fagan et al. 1998, Moran and Hurd 1998, Briggs and Latto 2001). Using this meta-analysis, I will examine the relationship between effect sizes of short- and long-term studies, as well as the role of such factors as resource productivity, community richness, and study length on effect size of the IG-predator on its community.

NCEAS Justification:

Intraguild predation has received much attention throughout the ecological literature and is of interest to a broad ecological audience. This trophic blurring of predation and competition has been examined theoretically and empirically in the food web, omnivory-stability, host-parasitoid, host-pathogen, and predator-prey literature, and the need for synthesis of this literature is great. Because the majority of work on IGP has been published in the past 5 years, this synthesis also would be timely.

This research should occur at NCEAS because synthesis of different approaches to IGP modeling represents a search for "general patterns and principles" among the sub-disciplines of ecology, part of the mission of NCEAS. In addition, NCEAS has computing facilities and expertise that would make possible the proposed modeling and data analysis. I will take advantage of this expertise to associate data from my meta-analysis with meta-data files and make it available on a public web site as well as to make my model code publicly available.

Activities and Timetable:

Start date: September 2003.

Proposed tasks:

- 1) Develop a general model with which to compare among IGP formulations (Part 1)
- 2) Conduct sensitivity analyses to identify parameters affecting short- and long-term model dynamics (Part 2-ii)
To ensure model generality, I will collaborate with researchers who have developed various IGP formulations. Dr. Cheryl Briggs (host-parasitoid, UC-Berkeley), Dr. Priyanga Amarasekare (host-disease and host-parasitoid, U. Chicago), and Dr. Sebastian Diehl (predator-prey, U. Munich, Germany) have all expressed their interest in this project and have agreed to provide input into formulation of a general IGP model. **6 months.**
- 3) Test predictions of IGP theory by analyzing existing long-term datasets (Part 2-i)
- 4) Examine long-term predictions of a subset of published short-term IGP studies (Part 2-ii)
I will modify my general IGP model and parameterize it for each system. **2 months per system.**
- 5) Examine the effect of IG-predators in published short- and long-term empirical datasets using meta-analysis (Part 2-ii)
I have identified several datasets appropriate to this meta-analysis, but will continue to search for more. The majority of time for this task will include data entry and statistical analysis. **2 months.**
- 6) Identify and analyze other short- and long-term IGP datasets (Part 2-i and 2-ii)
Ongoing.
- 7) Publish project results.
Each task will produce one to several publishable projects, and I consider publication of these results a high priority. **Ongoing.**

Anticipated Results and Beneficiaries:

The main product from this postdoctoral appointment will be publications in the primary literature. I expect to produce a few broadly conceptual papers that synthesize published material with new material and insights, as well as several conceptually narrower, though more thorough, publications describing work on particular systems.

Theoretical and empirical ecologists would be immediate beneficiaries of my work, however I hope that my work will eventually find applications for researchers, policy-makers, and resource managers working with biological control, invasive species, and endangered species.

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