MAINTENANCE OF INTRAGUILD PREDATION IN JUMPING SPIDERS

By

TOSHINORI OKUYAMA

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by

Toshinori Okuyama
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Intraguild predation (IGP), defined as predation among individuals of the same guild, is predicted on theoretical grounds to destabilize ecological communities. However, IGP is found in most communities. In an attempt to resolve this discrepancy between theory and observation, I explored mechanisms that may maintain IGP in ecological communities, focusing on two ecological factors: animal behavior and spatial structure. Jumping spiders were used as model organisms because IGP is common among them and because behavioral observations are tractable with these animals.

Theoretical investigations predict that both spatial structure and behavior can have independent positive or negative effects on the persistence (ability of all species to coexist) of an IGP community. Empirical evidence suggests that real systems lie in a parameter region of the model where spatial structure enhances IGP persistence relative to its non-spatial counterpart.

Simultaneous examination of behavior and spatial structure indicate that commonly used analyses in community ecology overestimate the magnitude of behavioral effects on community dynamics. Empirical examinations of antipredator
behavior in jumping spiders confirms this prediction; although spiders change their behavior based on experiences such as predator encounters, such changes in behavior do not persist long enough to induce the magnitude of behavioral effect typically predicted by the models.

Field observations of spider activity reveals the potential for complex activity dynamics. In particular, jumping spiders exhibit distinct active and inactive phases (biphasic activity) where inactive individuals stay in a retreat even during the day when they are normally active. Thus, activity dynamics of jumping spiders is more complex than its representation in previous models, where individuals alter activity only with respect to the external variables such as density of predators or density of prey.

An individual-based model built on the theoretical and empirical results of this study shows that typical adaptive behavior, such as lowering activity level after encountering a predator, had only weak influences on overall community dynamics. In contrast, biphasic activity allowed the IGP community to persist.

Taken together, this work suggests that common models linking behavioral and community dynamics neglect important behavioral details. Both within-individual behavioral variation (e.g., biphasic activity) and between-individual behavioral variation (e.g., caused by spatial structure) need to be carefully examined when attempting to scale behavioral dynamics up to the level of communities.
CHAPTER 1
GENERAL INTRODUCTION

This dissertation examines the dynamics of ecological communities that include intraguild predation. This introduction will first define (and describe) intraguild predation and outline the general questions addressed in this study. This problem description is followed by an outline that describes each chapter in relation to the overall goal of the project.

1.1 Intraguild Predation

Intraguild predation (IGP) is defined as predation among individuals of the same guild, i.e., individuals from species that share similar resources. Thus, broadly speaking, cannibalism is considered a form of IGP unless there is a distinct ontogenetic niche shift that differentiates the resource profile of cannibals and their victims (but see Wise, 2006). For example, most spiders are generalist predators that feed on a variety of prey items such as mosquitoes and flies, making them members of the same guild. However, spiders also eat other spiders; we count this cannibalism as intraguild predation. IGP commonly involves larger individuals feeding on smaller individuals (Polis, 1988). We call the victim intraguild prey (IGprey) and the predator intraguild predator (IGpredator). IGP is common in nature and is found in a variety of taxa (Polis, 1981; Polis et al., 1989; Polis and Holt, 1992; Williams and Martinez, 2000; Arim and Marquet, 2004). One characteristic of IGP is the simultaneous existence of competitive and trophic interactions between the same species (Figure 1–1).

Theoretical models predict that coexistence of IGpredators and IGprey is difficult (Holt and Polis, 1997), because IGprey experience the combined negative effects of competition and predation. In systems with competition only, IGprey
suffer no predation; in standard predator-prey interactions without competition, IGprey suffer no exploitative competition from the IGpredator (Figure 1–1). Thus, IGP is more stressful for the intermediate consumer (IGprey) than either exploitative competition or trophic interaction alone (Figure 1–1).

The theoretical difficulty in explaining IGP persistence and its observed ubiquity have identified IGP as an ecological puzzle (Holt and Polis, 1997) and led to a series of studies that have attempted to resolve this puzzle. These studies have considered factors such as top predators (food web topology) (Yurewicz, 2004), size structure (Mylius et al., 2001; Borer, 2002; MacNeil and Plavoet, 2005), habitat segregation (MacNeil and Platvoet, 2005), metacommunity dynamics (Melián and Bascompte, 2002), intraspecific predation (Dick et al., 1993), and adaptive behavior (Krůvan, 2000; Křivan and Diehl, 2005). However, it is not clear whether the most important interactions have yet been identified, and consensus has yet to
emerge from these studies about the relative frequency and strength of different possible mechanisms in maintaining IGP.

Understanding the dynamics of IGP has practical importance because IGP occurs in agricultural systems and also affects species of conservation concern (Muller and Brodeur, 2002; Harmon and Andow, 2004; Koss and Snyder, 2005; Harmon and Andow, 2005). Despite the need for solid understanding about IGP in order to manage these systems successfully, the unresolved puzzle suggests that we still do not understand how IGP communities persist in nature. Thus, in this dissertation, I examine how an IGP system can persist by examining both theoretical and empirical issues, using jumping spiders as model organisms, in an attempt to resolve the discrepancy. I focused on two classes of ecological phenomena, animal behavior and spatial structure, as possible explanations; each is further discussed below.

1.2 Jumping Spiders

Jumping spiders are the largest spider family (Salticidae) (Coddington and Levi, 1991). They are generalist predators that prey primarily on arthropod species, including other spiders (Jackson and Pollard, 1996). The frequency of IGP is known to be high in some species. For example, approximately 20% of Phidippus audax’s diet consists of other spider species that also consume similar resources (Okuyama, 1999). Intraguild predation among jumping spiders is always size-dependent, with large-bodied individuals consuming smaller individuals (Okuyama, 1999). Nevertheless, smaller species of jumping spiders appear to coexist in local communities with large species of jumping spiders for many years, posing the puzzle of persistence discussed above.

The focus of this study on behavior makes jumping spiders particularly good study subjects. These spiders are visual foragers and their complex foraging tactics are often compared to those of vertebrate species (Land, 1972; Hill, 1979; Jackson
and Pollard, 1996). In fact, the majority of studies on jumping spiders concern their behavior, rather than their ecological dynamics. Complex behavior does not occur in microcosms of microorganisms (or is difficult to examine at the individual level when it exists), whose rapid dynamics otherwise make them well suited for community level studies.

1.3 Spatial Structure

Although spatial processes are well recognized as an important factor in ecology (Kareiva and Tilman, 2000), the majority of theoretical models of IGP, including those that pose the discrepancy with observation (e.g., Holt and Polis, 1997), are non-spatial. Non-spatial models assume that individuals are mixed homogeneously in space, ignoring various forms of spatial structure that are ubiquitous in nature (Figure 1–2). For example, except in landscapes that have been artificially homogenized by humans (lawns, crop fields), we observe distinct spatial vegetation patterns in all terrestrial communities.

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Figure 1–2. Spatial distribution of predators $P$ and prey $N$. In the right figure, each species is well mixed. In the left figure, the two species are spatially segregated.

Regardless of whether spatial structure is generated exogenously or endogenously (e.g., Bolker, 2003), it can have a large impact on species interactions. If species are well mixed (Figure 1–2, left), the community’s dynamics can be well approximated by traditional non-spatial models. However, if there is a spatial pattern in animal distribution and if individuals interact only with individuals in a local
neighborhood, spatial models describing the true dynamics are more accurate (Bolker et al., 2000; Iwasa, 2000; Satô and Iwasa, 2000). In Chapter 2, I examine the role of spatial structure in a simple IGP community. The analysis presented in Chapter 2 shows that the nutrient content of IGprey is an important model parameter; Chapter 3 explores this parameter experimentally.

### 1.4 Animal Behavior

Animal behavior is an ecological factor that is considered to play a pivotal role in ecological communities (Fryxell and Lundberg, 1998). While traditional models such as the Lotka-Volterra model and its numerous variants assume that behavior (e.g., foraging activity) of individuals is constant and independent of environmental factors, there is considerable evidence for dynamic variation in behavior. In particular, there is a large body of evidence that animals alter their foraging activity with respect to predation risk (Caro, 2005) (Figure 1–3).

![Figure 1-3](image)

Figure 1–3. Hypothetical activity dynamics. The top figure shows the dynamics of predator density. The bottom figure shows the corresponding foraging activity of adaptive (solid) and non-adaptive (dashed) foragers.
Community models that include behavior typically assume that animals forage optimally, balancing the risks of starvation and predation (Stephens and Krebs, 1986). As a consequence, these models predict that foragers decrease their foraging effort (e.g., search rate) when predation risk is high (Figure 1–3). This type of behavioral analysis has been done for a variety of food web modules (Bolker et al., 2003).

However, the inclusion of animal behavior in community dynamics has overlooked many important aspects of behavior. For example, theoretical models that include adaptive behavior have largely ignored intraspecific interactions. In other words, the model shown in Figure 1–3 overlooks the possible effects of changes in forager densities over time, despite the fact that animals are known to alter their behavior based on the behavior and density of their peers (Giraldeau and Caraco, 2000; Caro, 2005). In chapter 4, I examine the evolution of adaptive foraging behavior in a simple predator-prey model based on Evolutionarily Stable Strategy (ESS) analysis. This model incorporates a Holling type II functional response. When even this basic ecological detail is included in an otherwise standard model of behavioral responses, it results in infinitely many ESSs due to the evolution of intraspecific interaction caused by the predator’s handling constraint. This result cautions us in the interpretation of results from existing models and suggests that consideration of behavior in existing models may be too simplistic.

Empirical ecologists, however, do not tend to focus on individual behavior. Even studies that directly examine behavior have collected behavioral data at the level of populations rather than measuring individual responses (e.g., Anholt et al., 2000). Instead, much of the effort of examining animal behavior has focused on indirect effects generated by such behavior. For example, trait-mediated indirect interactions (TMIIs) are induced by changes in a trait (behavior) of an
intermediate species. In a three-species food web, the intermediate consumers may reduce their foraging effort in response to predation risk, reducing their consumption rate of resources (Figure 1–3). Thus, predators have a positive indirect effect on resource (Figure 1–4). Another class of well-recognized indirect interactions, density-mediated indirect interactions, are transmitted via changes in density of intervening species rather than via trait changes.

![Figure 1-4. Indirect interactions. Black arrows indicate the consumption of one species by another (lethal/direct density effect). Thickness of the arrow represents the rate of consumption. Gray arrow indicates a non-lethal effect (direct trait effect). The community in (a) includes only a single consumer species and the resource, and thus has no indirect interactions. In (b), the predator species P consumes the consumer species thus decreasing the density of consumers (depicted by the small font). Because the consumer density is smaller, the consumer population removes fewer resources. In (c), although they do not consume the consumer, predators induce antipredator behavior by the consumer, which decreases the consumption of resource by consumer.]

Although TMII and DMII are widely described (Werner and Peacor, 2003), quantifying them is not straightforward. In Chapter 5, I examine indices of indirect effects that are commonly used in ecological experiments, focusing on how they can be used to facilitate the connection between indirect effects and community dynamics.

### 1.5 Adaptive Behavior Under Spatially Structured Environments

Although I demonstrate that spatial and behavioral factors are both important when considered independently in the previous chapters, this does not guarantee that both components are still important when they operate together. For example,
in the presence of spatially structured interactions, behavior may have little effect on the dynamics of community and vice versa (e.g., if they interact in a non-additive manner).

Figure 1–5. Spatial distribution of predators P and prey N. Two prey individuals are labeled as A and B.

A simple scenario illustrates the possible effect of spatial structure on adaptive behavior. In Figure 1–5, the distribution of predators is concentrated in the upper left corner. Prey are randomly distributed. In this scenario, prey individual A may forage much less than prey individual B because its perceived predation risk is higher (Figure 1–5). Thus spatial structure leads to considerable spatial variation in individual behavior, variation that the common non-spatial models neglect (Abrams, 2001). Chapter 6 examines how adaptive behavior and spatially structured species interactions can produce qualitatively different outcomes in community dynamics.

1.6 Dynamics of Jumping Spider Activity

The chapters described above establish that the dynamics of activity is an important component and is sensitive to details of the models such as spatial structure. Thus, in Chapters 7, 8, and 9, I examine experimentally the assumptions of the models and the dynamics of jumping spiders to identify how their behavior should be incorporated into a community model, and whether the details of their
natural history tell us anything further about how to model their community dynamics.

First, consider Figure 1–3 again. Although antipredator behavior is widely described and thus the qualitative pattern we observe in the figure makes sense, behavioral tracking of the environment in this way implies that individuals can maintain information on the changing state of the environment. If environmental cues indicating predator density are not continuously present and prey can respond only to direct encounters with predators, foraging effort is unlikely to track predator density as cleanly as shown in Figure 1–3. How individuals exhibit antipredator behavior in the absence of immediate threats and how their behavior affected by the environmental variables such as the density of predators? I address this question in a series of three studies, each focusing on a specific time scale. In Chapter 7, I examine the behavior of jumping spiders after an encounter with a predator, behavior that has the potential to produce tracking behavior such as that shown in Figure 1–3 (short time scale). In Chapter 8, I examine how the resting metabolic rates of jumping spiders are affected by their previous experience with predators or prey during the previous day (intermediate time scale). In chapter 9, I examine the general activity level of jumping spiders in the field (long time scale). These results, combined with the results from previous chapters, suggest that the commonly used modelling framework is inappropriate for studying the community dynamics of jumping spiders.

1.7 Synthesis

In the final chapter (Chapter 10), I synthesize the findings obtained from each piece of this project and discuss how they apply to the problem of long-term persistence of jumping spider communities. To assist in this synthesis, I create an individual based model that combines many of the factors discussed and measured in the previous chapters. I also consider an additional detail of spider
behavior, which is not specifically examined in this project (i.e., ballooning, [Bell et al., 2005]), because it strongly affects the spatial structure of the model and exclusion of the behavior may result in an unrealistic degree of spatial structure.

Taken together, this model demonstrates that the activity patterns of jumping spiders that are described in this project play key roles in allowing the two species of jumping spiders that exhibit IGP to coexist. This result incorporates natural history characteristics of spiders such as ballooning, further strengthening the validity of this conclusion. Without the simultaneous consideration of spatial and behavioral factors together, it would not be possible to derive this conclusion. Although the focus of the study is IGP, my results about the relationship between behavior and community ecology are more general. Based on the findings of this project, a general discussion about behavioral modelling in community ecology is also provided to facilitate reexaminations of relationships between behavior and community ecology.
CHAPTER 2
INTRAGuild PREDATION WITH SPATIALLY STRUCTURED SPECIES INTERACTIONS

2.1 Introduction

Intraguild predation (IGP) is a common and important species interaction in many ecological systems (Polis and Holt, 1992; Arim and Marquet, 2004). Effective implementation of biological control, for example, must take IGP into consideration (Harmon and Andow, 2004; Koss and Snyder, 2005). IGP has also affected the success of conservation and wildlife management programs (e.g., Palomares and Caro, 1999; Longcore, 2003). It is now well established that IGP dynamics have strong implications for both basic and applied ecology.

Theoretical studies of IGP suggest that the coexistence of species in IGP food webs is difficult. Due to the double pressure of competition and predation from intraguild predators (IGpredators), models predict that intraguild prey (IGprey) will be eliminated in a wide range of parameter space. Because IGP is ubiquitous in nature (Arim and Marquet, 2004), there is a discrepancy between theory and observations. This discrepancy continues to puzzle ecologists (Holt and Polis, 1997; Krivan and Diehl, 2005).

Simple models show that

1. IGprey must be better at exploiting the basal resource than IGpredators in order to coexist.
2. At low productivity levels, IGprey can outcompete IGpredators. When productivity is high, IGpredators will drive IGprey to extinction. At intermediate productivity levels, the two species may coexist.
3. As productivity increases within the range that allows coexistence, the equilibrium IGprey density decreases while the equilibrium of IGpredator density increases.
All these predictions have been empirically verified in parasitoid systems (predictions 1 and 2, Amarasekare (2000); prediction 3, Borer, Briggs, Murdoch, and Swarbric (2003)), and in microcosms (prediction 1, Morin (1999); all predictions, Diehl and Feissel (2000)).

These empirical studies confirm that simple models capture some qualitative properties of IGP interactions. However, the real challenge to theory lies not in the qualitative (im)possibility of IGP coexistence but in its predicted improbability. The narrow parameter space that models suggest could allow coexistence does not seem to support the ubiquitous occurrence of IGP in ecological communities. Several ecological factors (e.g., size-structure and adaptive behavior) have been examined to see whether they allow an increased probability of coexistence (Mylius et al., 2001; Křivan and Diehl, 2005); the coexistence parameter region may or may not expand depending on the details of the models. Although these factors are important, it is likely that we still lack some important ecological components in IGP models.

One factor that has not been examined in IGP models is spatial structure (but Amarasekare (2000a,b) concluded that the competition-dispersal tradeoff is not important in the coexistence of a parasitoid community that includes IGP in a patchy environment). Spatially explicit modelling (e.g., distinguishing local and global interactions) has generated a number of new hypotheses (Amarasekare, 2003a). Furthermore, spatial structure is known to stabilize simple predator-prey models (Keeling et al., 2000). As all organisms in an IGP food web inherently interact with other species in a spatially structured manner, this is an important as well as a realistic axis to examine. In this study, I use pair approximations (Satō and Iwasa, 2000) and an individual based model (IBM) to examine a simple IGP food web in a spatially structured environment. The so-called pair approximation keeps track of local dynamics as well as global dynamics, while the mean field
approximation makes no distinction (non-spatial); pair approximation reduces to the mean field approximation in its non-spatial limit (discussed below). Thus, using pair approximation allows one to examine the effect of local interactions by comparing the results with the analogous mean field model. With IBMs, I examine the effects of spatial heterogeneity in productivity, which Holt and Polis (1997) suggested should be important in IGP systems. The three main questions are (1) how the qualitative predictions of IGP models are affected by taking space into account, (2) whether spatial structure expands the possibility of coexistence, and if so, under what conditions, and (3) how spatial heterogeneity in resource distribution affects IGP dynamics.

2.2 Materials and Methods

To examine the effect of spatial structure on IGP dynamics, a simple IGP community was constructed in a lattice environment (see below). Both homogeneous and heterogeneous resource distributions were examined. For homogeneous resources, pair approximations worked well and allowed for simple comparisons to a standard non-spatial model. The heterogenous model makes the pair approximation model complex and thus was analyzed with individual based computer simulations. This section first describes the spatially structured IGP community, then describes how it can be analyzed using either pair approximation or an individual based model.

2.2.1 Lattice Model of Intraguild Predation

We consider two predators of the same guild interacting on a lattice space (i.e., IGpredator $P$ and IGprey $N$). IGpredators and IGprey consume the same basal resource and IGpredators also eat IGprey. Basal resources are not explicitly represented in this model: instead, each cell is characterized by a fixed resource level, $R$. Because resources are fixed in space and are not depleted, competition is for space in lattice cells (IGprey and IGpredators cannot coexist in a cell).
Each lattice site has \( z \) neighbors (e.g., hexagonal neighborhoods would have \( z = 6 \)) and is either occupied by \( P \) or \( N \), or is vacant (\( E \)). The two species can have distinct neighborhood sizes (\( z_N \) for IGprey and \( z_P \) for IGpredators); however, unless otherwise stated, we assume that IGprey and IGpredators have the same neighborhood sizes (\( z = z_N = z_P \)). The fraction of sites in state \( P \), \( N \), and \( E \) are called global densities and are designated \( \rho_P \), \( \rho_N \) and \( \rho_E \). We define \( q_{i/j} \) as the local density of sites in state \( i \) with a neighbor in state \( j \). For example, \( q_{P/N} \) is the fraction of \( P \) sites that are next to an \( N \) site (i.e., the probability that a randomly chosen \( N \) site is located next to a \( P \) site).

IGprey (\( N \)) and IGpredators (\( P \)) can reproduce (at a rate depending on basal resource consumption) only if they are adjacent to a vacant site, and their reproductive rate per vacant site is \( Rb_N/z \) and \( Rb_P/z \), respectively. Therefore, \( Rb_N \) and \( Rb_P \) are the maximum rates of reproduction in an empty neighborhood. Hence, the reproduction rate of a randomly chosen IGprey is \( z(Rb_N/z)q_{E/N} = Rb_Nq_{E/N} \), the product of the maximum birth rate and the expected fraction of vacant sites in the neighborhood. For simplicity, I assume that spatial movement occurs only by means of reproduction.

IGprey die due to predation by IGpredators at a rate \( \lambda \), which together with conversion efficiency (\( e \)) also determines the reproduction of IGpredators. We define \( \lambda \) as the maximum predation rate which is attained when the IGpredator is completely surrounded by IGprey.

Based on these rules, the equations for the global population densities are

\[
\frac{d\rho_N}{dt} = \rho_N(Rb_Nq_{E/N} - \lambda q_{P/N} - m_N) \tag{2-1}
\]
\[
\frac{d\rho_P}{dt} = \rho_P(Rb_Pq_{E/P} + e\lambda q_{N/P} - m_P). \tag{2-2}
\]

where \( m_N \) and \( m_P \) represent the background mortality rate for IGprey and IGpredators, respectively.
2.2.2 Mean Field Approximation

By making the approximations \( q_{i/j} \approx \rho_i \) (i.e., the probability that an adjacent cell occupied by \( i \) is the same as the global distribution of the species \( i \)) and applying the identity \( \rho_E = 1 - \rho_N - \rho_P \), we obtain the following non-spatial mean field approximation model,

\[
\begin{align*}
\frac{d\rho_N}{dt} &= Rb_N \rho_N (1 - \rho_N - \rho_P) - m_N \rho_N - \lambda \rho_N \rho_P \\
\frac{d\rho_P}{dt} &= Rb_P \rho_P (1 - \rho_N - \rho_P) - m_P \rho_P + e \lambda \rho_N \rho_P.
\end{align*}
\]

This mean field model is essentially the same as previously studied non-spatial IGP models: in particular eqs. 2–3 and 2–4 represent a special case of the model described in Figure 4 of Polis et al. (1989) when the intensities of inter- and intra-specific competition are the same. Although competition is for space rather than for a resource with explicit within-cell dynamics, the non-spatial version of the model matches a model derived with resource competition in mind.

2.2.3 Pair Approximation

As discussed above, pair approximation keeps track of local densities in addition to the global densities described above. To derive the dynamics of local densities, we first need to resolve the dependencies among possible variables. For example, there are three global densities \( \rho_N, \rho_P, \rho_E \) and nine local densities \( (q_{N/N}, q_{N/P}, \ldots, q_{E/E}) \), but because of the following constraints, they are not independent:

\[
\begin{align*}
\rho_N + \rho_P + \rho_E &= 1 \\
q_{N/i} + q_{P/i} + q_{E/i} &= 1 \quad (i = N, P, \text{or } E) \\
q_{i/j} \rho_j &= q_{j/i} \rho_i \quad (i = N, P, \text{or } E).
\end{align*}
\]
Due to these dependencies, we have only five independent variables, which can be chosen arbitrarily. We will choose $\rho_N, \rho_P, q_{N/N}, q_{P/P}$ and $q_{P/N}$ as the independent variables and express all the others in terms of these five variables based on the above constraints.

In order to calculate the dynamics of local density, for example $q_{N/N}$, we first derive the dynamics of the doublet density $\rho_{NN}$ (i.e., two cells that are adjacent to each other are both occupied by IGprey).

\[
\frac{d\rho_{NN}}{dt} = -2m_N \rho_{NN} + 2Rb_N \left( \frac{1 + (z-1)q_{N/EN}}{z} \right) \rho_{EN} - 2\lambda \left( \frac{(z-1)q_{P/NN}}{z} \right) \rho_{NN}.
\]

The first term on the right hand side indicates the loss of an IGprey doublet (i.e., $NN \rightarrow NE$ or $EN$) due to density independent mortality. The second term indicates the gain of an IGprey doublet from an $EN$ or $NE$ doublet due to reproduction either by the IGprey within the doublet or by any other potential IGprey individual located in one of the $(z-1)$ neighbors of the vacant cell. $q_{i/jk}$ indicates that $i$ is located adjacent to the doublet $jk$. The last term describes the loss of the IGprey doublet, $NN$, due to intraguild predation by an IGpredator located in the neighborhood of the doublet.

The equations for the other two doublets are:

\[
\frac{d\rho_{PP}}{dt} = -2m_P \rho_{PP} + 2Rb_P \left( \frac{1 + (z-1)q_{P/EP}}{z} \right) \rho_{EP} + 2\epsilon \lambda \left( \frac{1 + (z-1)q_{P/NP}}{z} \right) \rho_{NP}
\]

\[
\frac{d\rho_{NP}}{dt} = -(m_N + m_P) \rho_{NP} + Rb_P \left( \frac{(z-1)q_{P/EN}}{z} \right) \rho_{EN} + Rb_N \left( \frac{(z-1)q_{N/EP}}{z} \right) \rho_{EP}
\]

\[
- \lambda \left( \frac{1 + (z-1)q_{P/NP}}{z} \right) \rho_{NP} + \epsilon \lambda \left( \frac{(z-1)q_{P/NN}}{z} \right) \rho_{NN}
\]

Pair approximation substitutes triplets for pair densities (i.e., $q_{i/jk} \approx q_{i/j}$), assuming conditional independence between pairs of points. Interested readers should refer to Satō and Iwasa (2000) and Iwasa et al. (1998) for discussions/details. These doublet densities are transformed to conditional
probabilities. For example, the dynamics of \( q_{P/P} \) are found to be,

\[
\frac{dq_{P/P}}{dt} = \frac{d(\rho_{PP}/\rho_P)}{dt} = -\frac{\rho_{PP}}{\rho_P^2} + \frac{1}{\rho_P} \frac{d\rho_{PP}}{dt}.
\]

### 2.2.4 Invasibility Analysis

The pair approximation model is too complex to analyze algebraically, so we used invasion analysis to examine the outcomes of community dynamics. Invasibility was examined by asking whether one of the species could increase its population from low initial densities when the other species was present at its equilibrium density. For example, to examine the possibility of IGprey invasion, we evaluated the values for \( \rho_P \) and \( q_{P/P} \) when \( \rho_N = 0 \). Based on these equilibria, we then obtained \( q_{N/N} \) and \( q_{P/N} \) that in turn were used to examine whether \( \rho_N \) increased based on equation 2–1. The outcome was classified into one of four cases: IGprey can invade IGpredators, but IGpredators cannot invade IGprey (IGprey win), IGpredators can invade IGprey, but IGprey cannot invade IGpredators (IGpredators win), each species is able to invade the other (coexistence), and neither IGprey nor IGpredators can invade the other (bistability) (Murrell and Law, 2003).

### 2.2.5 Individual Based Model

The pair approximation described above assumes a homogeneous environment, characterized by constant productivity \( R \) in every cell. In order to examine the role of a heterogeneous environment, an individual based model that corresponds to the pair approximation model was created. For simplicity, simulations were run in discrete time; thus, the model did not exactly match the differential equation model (e.g., it ignores action of offspring within the time step), but it maintained the qualitative behavior of the model.

At the beginning of each iteration, the number of IGprey and IGpredators that died due to density-independent mortality were determined as Poisson deviates.
Reproduction and death events were randomly ordered for each individual in each iteration; an animal that died in a time step may or may not have reproduced before death. The potential fecundity for each individual was simulated as a Poisson deviate with mean $Rb_N$ (IGprey) or $Rb_P$ (IGpredators) where $R$ is the productivity of the cell where individuals reside (i.e., either $R_L$ or $R_H$: see below for the description). For each potential offspring, the probability of actual reproduction was fraction of vacant adjacent cells (e.g., the probability of converting one potential reproduction to an actual offspring is $1/4$ if only one adjacent cell is empty). Reproduction of offspring was realized sequentially, allowing for depletion of free space in the neighborhood. IGpredator updating includes predation, which resulted in a Poisson reproduction process (number of offspring) with mean $e$.

A 51-by-51 square lattice with periodic boundaries was used as the environment. Simulations always began with 200 IGprey and 100 IGpredators, both randomly distributed in the environment. Persistence was defined as fraction of simulations out of 50 resulting in $P > 0$ and $N > 0$ at $t = 5000$. The model was implemented in Netlogo (Wilensky, 1999).

#### 2.2.6 Heterogeneous Environment

Each cell in the environment was assigned a random productivity value $R$ from $[0,1]$. Spatial correlation was generated by letting each cell share 50% of its productivity value with its neighboring cells; this procedure is called diffuse and is a standard function in Netlogo. Increasing the number of sequential uses of the diffuse function increases the spatial correlation of productivity values. We call the number of diffuse iteration the patch scale. Two different productivity values (high and low) were assigned based on whether a patch was higher or lower than the median value. To alter the mean productivity, the high productivity cells were always set to $R_H = 1$ while the low productivity patch value, $R_L$, varied. Because
half the cells were assigned to high or low, the average environmental productivity was always \((R_H + R_L)/2\). Examples of patches of different scales are shown in Figure 2–1.

![Figure 2–1. Examples of random binary landscapes based on different patch scales. Patch scale refers to the number of times the procedure diffuse was applied (see text).](image)

### 2.3 Results

#### 2.3.1 Mean Field Approximation

In addition to the trivial equilibrium where no species can survive (which occurs when \(R < m_N/b_N\) and \(R < m_P/b_P\)), four outcomes are possible (Figure 2) in the mean field approximation model (eqns 2–3 and 2–4): IGprey win (when \(R < c_1\) and \(R < c_2\)), IGpredators win (when \(R > c_1\) and \(R > c_2\)), coexistence (when \(R < c_1\) and \(R > c_2\)), and bistability (when \(R > c_1\) and \(R < c_2\)) where

\[
    c_1 = \frac{m_P \lambda}{b_P (m_N + \lambda) - m_P b_N}, \quad c_2 = \frac{m_N e \lambda}{b_N (e \lambda - m_P) + b_P m_N}.
\]

Although the basal resource is not explicitly modelled here, the model’s properties are equivalent to those of a standard non-spatial IGP model with explicit resources (Holt and Polis, 1997).
Figure 2-2. Parameter regions indicating the outcome of IGP in a non-spatial model. Parameters: \( m_P = 0.3, m_N = 0.2, b_P = 0.5, b_N = 0.8, e = 0.4 \). When \( R < 0.25 \), neither species can survive.

For example, IGprey will outcompete IGpredators when the productivity level is low and IGpredators will win when the productivity level is high provided \( \lambda > 0.5 \) (Figure 2-2). At intermediate productivity, both species can coexist. When both species coexist, the amount of resource in vacant cells, \( R_{pE} \), (analogous to the standing stock of unused basal resource in an explicit resources model) is at an intermediate proportion between that with IGprey alone and that with IGpredator alone. When the species coexist, increasing productivity will decrease the density of IGprey while increasing that of IGpredators. The coexistence condition based on the productivity level above (i.e., \( R < c_1 \) and \( R > c_2 \)) can be rewritten as \( b_N/m_N > b_P/m_P \). Thus for species with equal background mortality rates, coexistence is only possible when IGprey is a better competitor for resource than IGpredators (i.e., \( b_N > b_P \)).

2.3.2 Pair Approximation

The qualitative results of pair approximation based on one dimensional (\( z = 2 \)), square lattice (\( z = 4 \)), and hexagonal lattices (\( z = 6 \)) are similar to those of
the mean field approximation model (Figure 2–3). As the neighborhood size grows (e.g., Figure 2–3, $z = 9999$), the dynamics of the pair approximation approaches the limiting case, the mean field approximation model. In a bistability region, one species ($N$ or $P$) can win depending on the initial densities (i.e., founder control).

![Figure 2–3. Results of invasion analysis in the pair approximation model. The parameters used are the same as in Figure 2–2. When neighborhood size ($z$) is large, the results are indistinguishable from the non-spatial model (Figure 2–2).](image)

### 2.3.3 Unequal Neighborhood Sizes

The above results assume that neighborhood sizes of IGprey and IGpredators are the same (i.e., $z = z_N = z_P$). To examine the effect of unequal neighborhood sizes (i.e., $z_N > z_P$), the neighborhood size of IGpredators was fixed at $z_P = 4$ and $z_N$ was varied, and the same invasion analysis was applied (Figure 2–4).

Both reproduction and mortality parameters for the IGprey and IGpredators were fixed at the same value ($b_N = b_P$ and $m_N = m_P$; see the figure caption for the actual values). This condition prevents IGprey from persisting in the non-spatial model (see introduction) or when both IGprey and IGpredators had the same neighborhood size (i.e., $z_N = z_P = 4$ resulted IGpredator dominance in all the parameter regions in Figure 2–4). However, as IGprey’s neighborhood size became
Figure 2-4. Results of invasion analysis in the pair approximation model. Spatial scale of IGpredators was fixed at $z_P = 4$ while that of IGprey varied. When $z_N = 4$ (i.e., $z_N = z_P$), IGpredators dominate in the entire parameter space shown. Parameters: $m_N = m_P = 1, b_N = b_P = 1, e = 1$.

greater than that of IGpredators, coexistence between IGprey and IGpredators became possible.

**2.3.4 Quantitative Comparison Between Spatial and Non-spatial Models**

However, the pair approximation and mean field approximation make different quantitative predictions about coexistence as a function of environmental productivity (Figure 2-3). For example, in Figure 2-4, when $\lambda = 0.6$ for the range of productivity examined, strong spatial structure ($z = 2$) predicts coexistence is impossible while coexistence may be possible in the case of weaker spatial structure such as ($z = 6$). In the other words, the interval of productivity levels that allows for coexistence changes with $z$.

Thus, to make a quantitative comparison between spatial and non-spatial models, we compared the range of productivity levels that allows coexistence in the two models. Let $I_{\text{spatial}}$ and $I_{\text{non-spatial}}$ be the coexistence interval in productivity for spatial and non-spatial model, respectively (The parameter values used to
obtain $I_{\text{spatial}}$ and $I_{\text{non-spatial}}$ are described in the caption of Figure 2–5). The ratio of intervals, $I_{\text{spatial}}/I_{\text{non-spatial}}$, were examined: values greater than 1 indicate that spatial structure enhanced the probability of coexistence with respect to the non-spatial model.

![Diagram](image)

Figure 2–5. Parameter intervals resulting in expansion and reduction of the coexistence interval. The line indicates the contour at $I_{\text{spatial}}/I_{\text{non-spatial}} = 1$. When this ratio is greater than 1, spatial structure increased the size coexistence intervals. Parameters: $m_P = 0.3, m_N = 0.2, b_P = 0.3, b_N = 0.6, R \in (0.1, 10), z = 4$.

Depending on the parameter values, spatial structure can either decrease or increase the coexistence interval (Figure 2–5). High conversion efficiency $e$ and a high attack rate of IGpredators $\lambda$ meant that spatial structure increased the probability of coexistence (Figure 2–5). Although the comparison between the spatial model with $z = 4$ and the non-spatial model is shown, the results for other neighborhood sizes (e.g., $z = 6, z = 8$) are similar.

2.3.5 Heterogeneous Environments

The IBM model captures the same qualitative characteristics as the differential equation models in terms of the dominance of IGprey and IGpredators along the
productivity gradient: IGpredators are eliminated at low productivity levels and IGprey are eliminated at high productivity levels (Figure 2–6).

Figure 2–6. Persistence probability (squares) and density of IGprey (circles) and IGpredators (triangles). Parameters: $m_P = 0.2, m_N = 0.2, b_P = 0.5, b_N = 0.8, \lambda = 0.9, e = 0.9, z = 4$.

In heterogeneous environments (i.e., each cell is assigned either $R_H$ or $R_L$), when the productivity of a low resource patch is small (e.g., if the environments were homogeneous at this productivity, even IGprey alone could not persist), a small patch scale was favorable to IGprey and IGpredators went extinct quickly. When the patch scale was large, however, IGprey were eliminated. At intermediate patch scales, both species coexist. Because average productivity at different patch scales is the same, this suggests that the spatial configuration of patches may strongly affect the outcome of IGP. This relationship, however, flipped as the productivity of low-resource patches ($R_L$) increased. When $R_L$ was relatively high, persistence of the IGP system was higher when the patch scale was either low or high. Persistence probability was lowest at an an intermediate level of patch scale.

Spatial heterogeneity also modified the effect of productivity level on numerical dominance. For example, the non-spatial model predicts that when IGprey and
IGpredators coexist, as productivity increases, IGprey will decline in density. However, when spatial heterogeneity is introduced, IGprey density may remain constant as productivity increases (Figure 2–8).

2.4 Discussion

2.4.1 Effects of Spatial Structure on the Basic Results of Nonspatial Models

The homogeneous environment model (i.e., pair approximation) maintained the qualitative predictions of non-spatial models. As suggested by the non-spatial model, resource utilization ability of IGprey had to be be greater than that of IGpredators in order for the two species to coexist when they have the same neighborhood sizes. Nonetheless, the pair approximation model predicts that IGprey and IGpredators can coexist even when the resource utilization condition (i.e., $b_N > b_P$) is not met as long as the spatial scale for IGprey is larger than that of IGpredators (Figure 2–4). Amarasekare (2000) considers this phenomenon a dispersal-colonization tradeoff. Recognizing this potential tradeoff is important because laboratory measurement of parameters such as $b_N$ and $b_P$ overlooks the
Figure 2–8. Persistence probability (squares) and density of IGprey (circles) and IGpredators (triangles). Densities of consumers are presented as fraction of total cells occupied by the species. Parameters: $m_P = 0.2, m_N = 0.2, b_P = 0.5, b_N = 0.8, \lambda = 0.9, e = 0.9, z = 4$, and Spatial scale = 7.

Differences in spatial scale of foraging, which may be essential in order to tease apart mechanisms of coexistence in IGP communities (Amarasekare, 2003b). Explicitly considering these factors, Amarasekare (2000a,b) concluded that local resource utilization differences (e.g., $b_N > b_P$) were more important than dispersal-colonization tradeoff (e.g., $z_N > z_P$) in coexistence of a parasitoid community.

Spatial heterogeneity can overturn the second prediction (species dominance shifts from IGprey to coexistence, and then to IGpredators as productivity increases). For example, even when average productivity is low (i.e., the homogeneous model predicts that IGprey will exclude IGpredators), IGpredators can still outcompete IGprey when resources are distributed at particular patch scales (Figure 2–7). Thus, although the homogeneous model predicts a dominance shift (i.e., IGprey dominance $\rightarrow$ coexistence $\rightarrow$ IGpredator dominance), this prediction can be violated in the presence of resource heterogeneity if patch scale is large in
low productivity environments and small in intermediate and high productivity environments. In other words, without knowing how the spatial scale of resource changes, we cannot reliably predict changes in species dominance with increasing average productivity.

Furthermore, spatial heterogeneity affects the qualitative prediction that the density of IGprey will decrease while that of IGpredator increases as productivity level increases. On the contrary, we see that density of IGprey may remain roughly constant as productivity increases in the coexistence region (Figure 2–8) in a heterogenous environment. In the field, Borer et al. (2003) observed the same phenomenon that density of IGprey was unaffected by the resource level. Thus the spatial model can potentially explain unresolved results observed in nature. The results shown in Figure 2–8 assume a constant patch scale. If the patch scale varied (e.g., different scales for each productivity value), we could potentially see many different trends.

2.4.2 Quantitative Effect of Spatial Structure

The qualitative results of the mean field approximation and pair approximation models were similar (e.g., Figure 2–3), but the models gave different quantitative predictions of coexistence probability. As spatial structure becomes stronger (i.e., \( z \) decreases), the coexistence region expands while shifting in the parameter space. For example in Figure 2–3, as \( z \) decreased, lower values of \( \lambda \) (attack rate of IGpredators on IGprey) that previously allowed for coexistence (e.g., \( R = 1, \lambda = 0.8 \)) instead allowed IGprey dominance. In the parameter region of coexistence near IGprey dominance, IGpredators become less effective in utilizing IGprey as \( z \) decreases. At the same time, the parameter region that allowed IGpredator dominance but was near the boundary of coexistence parameter region (e.g., \( R = 1.5, \lambda = 0.6 \)) shifted to coexistence because IGprey became less vulnerable to intraguild predation. The parameter \( e \) has a similar influence in the
model because reproduction due to IGP is realized only if IGpredators can capture IGprey.

In general, given a high attack rate of IGpredators ($\lambda$) and high profitability of IGprey ($e$) (i.e., intraguild predation is more beneficial to the IGpredators than resource consumption), spatial structure favors the persistence of the IGP system. One hypothesis for the evolution of IGP is based on stoichiometry (Denno and Fagan, 2003); IGpredators consume IGprey because IGprey have the right balance of nutrients (i.e., $e$ is large). For example, Matsumura et al. (2004) documented that wolf spiders grow better if other spiders (i.e., IGprey) were included in their diet than when they were raised on a diet that did not include other spiders as diet. Thus, the parameters of natural systems are likely to lie in the region where spatial structure favors IGP persistence. This relationship between the benefit of IGP and spatial structure suggests that understanding the proximal consequences and determinants of IGP (e.g., Matsumura et al., 2004; Rickers and Scheu, 2005) and the roles of spatial structure should facilitate our understanding of the ecological and evolutionary significance of IGP.

2.4.3 Effect of Spatial Heterogeneity

Individual based model simulations in spatially heterogeneous environments revealed that even at the same average productivity of the environment, changes in patch scale can result in different IGP dynamics. When patch scale is small, each cell’s productivity is independent of the neighboring cells, and individuals will experience the same average productivity level no matter where they are (as long as their neighborhood includes at least few different cells). Therefore, the prediction of IGP coincides with the case from a homogeneous environment. However, as patch scale increases, the expected productivity level experienced by individuals will diverge depending on their location. If a parent is in a low resource patch, for example, its offspring will experience a lower than average productivity level.
Accordingly, predictions of IGP outcomes in a heterogeneous environment depart from predictions when the environment is homogeneous.

When average productivity level was low (e.g., 0.65 in Figure 2–7), IGP dynamics changed from IGprey dominance to coexistence and then to IGpredator dominance as patch scale increased. In this example, the low patch productivity was very low \(R_L = 0.3\), and neither IGprey or IGpredators could persist in a large scale low patch. The high resource patches, in contrast, were very productive \(R_H = 1\) so that IGpredators dominated (Figure 2–7). Therefore, as patch scale increased and patch productivity diverged, neither species could persist in the low-resource patches while IGpredators won in the high-resource patches. At intermediate patch scales, patch heterogeneity created an environment that allowed both species to coexist, creating a hump shaped relationship in persistence. This hump-shape was flipped at high mean productivity levels (e.g., 0.835 in Figure 2–7 corresponding to \(R_L = 0.67\)). In high-resource patches \(R_H\), IGpredators dominated, and in low-resource patches \(R_L\), IGprey dominated; habitat segregation resulted, causing an increase in persistence. If patch scale was further increased, persistence would eventually approach 1. For habitat segregation to be effective, each patch type must be sufficiently large. For example, continuous “spill over” of IGpredators from the high productivity patch can wipe out a small low productivity patch with IGprey. This result suggests that details of landscape configuration may significantly alter characteristics of community stability. Further investigations on how landscape structure affects movement of species and community dynamics is needed (van Dyck and Baguette, 2005).

Although spatially structured species interaction and spatially heterogeneous environment are well recognized factors in ecology, systematic exploration of this axis has only begun recently (Bolker, 2003; Hiebeler, 2004a,b), and we do not yet have clear general hypotheses about the effects of space even in simple models.
Further explorations of the roles of both spatial structure and spatial heterogeneity are needed. Furthermore, although spatial interactions may be difficult to analyze, some spatial data are relatively easy to collect once we know exactly what to collect. In fact, field studies have often collected these data as auxiliary information even when their analyses ignored space. The development of spatial theories will create more testable hypotheses and increase our ability to utilize data more efficiently, which may resolve some of the discrepancies between theory and data.
CHAPTER 3
NITROGEN LIMITATION IN CANNIBALISTIC JUMPING SPIDERS

3.1 Introduction

The nutrient content of food resources has a direct influence on consumer behavior, fitness and population dynamics. For example, dietary nitrogen level influences the demographic parameters (i.e., growth and fecundity) of grasshoppers (Joern and Behmer, 1997); feeding activity and growth rate of zooplankton are strongly influenced by phosphorus levels in their algal diet (Plath and Boersma, 2001). Theory suggests that animals should forage selectively to maximize their nutrient requirements (e.g., Simpson et al., 2004). These considerations are important not only for understanding the behavioral and physiological mechanisms of foraging but also for understanding the dynamics of ecological communities. Nutrients directly affect the functional and numerical responses of species interactions (Andersen et al., 2004). In recent years, analysis of community models with nutrient specific interactions has became common (e.g., usually called ecological stoichiometry (Loladze et al., 2004) or nutrient homeostasis (Logan et al., 2004)) and these studies have helped to understand previously unexplained patterns in nature (reviewd in Moe et al., 2005).

Intraguild predation (IGP), predation within a guild (i.e. between members of different species at the same level in a food chain), has been suggested to be a response to the mismatch in the ratio of carbon to nitrogen (C:N) between predators and herbivorous prey (Denno and Fagan, 2003). C:N decreases as trophic level increases (Fagan et al., 2002). This type of predation (IGP, or omnivory more broadly) benefits the consumers because consuming other nitrogen-rich predators (and thus decreasing the C:N imbalance) helps satisfy their nutrient requirements.
and facilitates growth (Fagan and Denno, 2004). If IGP facilitates the growth of intraguild predators, it will directly affect the size-structure of individuals within the community because occurrence of IGP is size-dependent (Polis, 1988). However, direct examination of this hypothesis is rare (but see Matsumura et al., 2004).

In this study, I examined whether the nitrogen content of prey affects the growth of jumping spiders. Specifically, I showed that spider growth rate is facilitated by nitrogen content of prey.

3.2 Materials and Methods

Eggs of the jumping spiders Phidippus audax were collected in the field near the campus of the University of Florida, Gainesville, FL, USA. First instar spiderlings do not eat before becoming second instars. Once they moulted to second instar, spiders were assigned to one of two treatment groups: control and N-rich. Individual spiders were reared separately in plastic cup containers (62 mm in diameter and 30 mm in height; approximately cylindrical). Forty spiders were used in each treatment. The mean (±sd) carapace widths of the spiders in the beginning of the experiment were 0.83±0.05mm (N-rich) and 0.84±0.04mm (control) and were not statistically different (t-test: \( p = 0.1633 \)).

3.2.1 Experimental Treatments

Spiders in the two treatment groups received prey (Drosophila melanogaster) that were reared on different media to alter their nutrient profiles (Mayntz and Toft, 2001). In the control group, fruit flies were raised on Drosophila medium (Carolina Biological Supply). In the N-rich group, blood meal (Pennington Enterprizes, Inc) was added to the medium (3:1 = medium:blood meal).

In order to examine potential confounding factors of the treatment (i.e., treatment may create difference in aspects of prey in addition to N level), the energetic content of prey was also quantified based on a whole-animal assay with a dichromate oxidation method described in McEdward and Carson (1987).
3.2.2 Effect on Growth

The spiders were kept in a controlled environmental chamber (28 Celsius, light:dark = 14:8 hrs). One fruit fly was given every three days during the second instar. Two fruit flies were given every three days during the third and the fourth instars. Spiders were able to consume all the prey within a day although prey were given only once every three days. Water was supplied daily in the form of a water-soaked sponge. Carapace widths of spiders were recorded within 24 hours of moulting to examine the treatment effect on size, while durations in each instar were recorded to examine the effect on growth rate.

One spider in the N-rich group died during the experiment and was excluded from the analyses. Thus, for all the following analyses, the sample size for the control group was 40 while the sample size for the N-rich group was 39. Treatment effects on growth (size and instar duration) were analyzed with t-tests.

3.3 Results

The treatment created prey individuals that were statistically different in their nitrogen content but were equivalent in energetic content and were similar in composition to spiderlings (Table 3–1).

Table 3–1. Nutrient and energy contents of prey (standard errors in parentheses).

<table>
<thead>
<tr>
<th>Prey</th>
<th>N%</th>
<th>C%</th>
<th>Energy (J)</th>
</tr>
</thead>
<tbody>
<tr>
<td>flies (control)</td>
<td>7.64 (0.08)</td>
<td>50.38 (0.26)</td>
<td>2.20 (0.48)</td>
</tr>
<tr>
<td>flies (blood)</td>
<td>10.36 (0.28)</td>
<td>49.59 (0.94)</td>
<td>1.71 (0.36)</td>
</tr>
<tr>
<td>spiderlings</td>
<td>10.06 (0.57)</td>
<td>35.88 (1.27)</td>
<td>1.50 (0.26)</td>
</tr>
</tbody>
</table>

Figure 3–1 shows the carapace widths of spiders for each treatment. The N-rich group had wider carapaces on average for all the instars examined, but the differences were not statistically significant (Figure 3–1, t-test: $p > 0.05$ in all
cases). The size differences were insignificant even when the cumulative difference in growth was considered (i.e., the changes in size from the second instar to the fifth instar).

Figure 3–1. Growth in carapace width of spiders. *n*th instar data indicate the difference in size between (*n* + 1)th and *n*th instar. No significant differences were found between treatments, for any instar. Treatments: N-rich (N) and control (c). Top and bottom lines of box indicate the 75% quartile and 25% quartile of sample, respectively. The horizontal bar in the box indicates the median. Top and bottom bars around the box indicate 90% quartile and 10% quartile, respectively. The upper and lower notches corresponds to the upper and lower 95% CI about the median.

The mean durations of instars were always shorter for the N-rich group (Figure 3–2); thus, spiders grew faster while moulting between instars at the same sizes. The differences in duration were statistically significant for the 2nd instar (*t*-test: *p* = 0.0006) and 4th instar (*p* = 0.0003), but not for the 3rd instar (*p* = 0.839).
3.4 Discussion

In support of Denno and Fagan’s (2003) hypothesis, the consumption of N-rich prey facilitated the growth of jumping spiders, which would provide a selective advantage to IGP behavior. Furthermore, because the outcome of IGP and cannibalism in these spiders is size-dependent (i.e., large individuals eat small individuals), the degree to which this predation occurs will have direct consequences for their size-structured dynamics (de Roos et al., 2003). Because occurrence of IGP depends on the size-structure, the growth consequences of stoichiometry may have strong implications for IGP community dynamics.

Future work should consider the prey’s nutrient profile more carefully. Matsumura et al. (2004) have done experiments similar to this study examining the effects of prey type on the growth level of wolf spiders (genus *Pardosa*), finding
that spiders that fed on intraguild prey (i.e., other spiders) alone did not enhance their growth rate. Yet, they found that a mixed diet (i.e., addition of intraguild prey to herbivorous prey) facilitated the growth of wolf spiders. Researchers have found similar results (i.e., advantages of mixed diets) in other ecological systems (Agrawal et al., 1999; Cruz-Rivera and Hay, 2000). We still do not clearly understand the optimal nutrient requirements for these carnivores, nor how those nutrients are distributed among prey in the field. Nor do we know whether simplifying the description of stoichiometry to a single C:N ratio, or C:N:P (Logan et al., 2004), is adequate for understanding community dynamics. For example, Greenstone (1979) found that wolf spiders forage selectively to optimize amino acid makeup, which suggests that more complex stoichiometric descriptions may be necessary if we hope to study stoichiometric community ecology.

In this experiment, the food (i.e., fruit fly medium) of prey items was varied to manipulate the nitrogen content of prey (Mayntz and Toft, 2001). We do not know whether the level of nitrogen difference between treatment and control groups was created as a result of nitrogen assimilation into fly tissues or blood meal in their gut content. This difference is not crucial to the interpretation of this study as spiders nonetheless consumed nitrogen rich prey and increased their growth rate (Figure 3–2). However, the results have other implications. For example, nitrogen content varies greatly among plants (Mattson, 1980). Anthropogenic environmental changes (e.g., increased CO₂ and soil pollution) alter nutrient levels of plants (Newman et al., 2003). The blood meal used in this study is a common agricultural fertilizer. If herbivores that consume different plants of different qualities influence predators as shown in this study, the effect of stoichiometric interaction on systems with IGP could occur at very large temporal and spatial scales. By carefully examining the nutrient requirement of organisms as well as the flow of nutrients, we may obtain deeper insights not only into a specific ecological
community with IGP but also into general properties of the persistence of complex food webs.
CHAPTER 4
EVOLUTIONARILY STABLE STRATEGY OF PREY ACTIVITY IN A SIMPLE PREDATOR-PREY MODEL

4.1 Introduction

Incorporating adaptive traits into community models has shed light on a number of ecological problems such as complexity-stability and phases of population cycles (e.g., Kondoh, 2003; Yoshida et al., 2003). Antipredator behavior (e.g., activity level) is one of the most well studied classes of adaptive traits both empirically and theoretically; it is widely observed in nature (Werner and Peacor, 2003; Benerd, 2004; Preisser et al., 2005; Luttbeg and Kerby, 2005) and its community level consequences can be significant (Fryxell and Lundberg, 1998; Bolker et al., 2003).

One of the earliest approaches to the study of evolutionary adaptation (Maynard Smith and Price, 1973) goes under the general name of evolutionary game theory. This approach seeks to identify the set of all strategies (trait values) that are evolutionarily stable by applying an ESS (Evolutionarily Stable Strategy) criterion. A strategy is called evolutionarily stable if a population of individuals adopting this strategy cannot be invaded by a mutant strategy. The usual indicator for measuring invadability is the fitness (contribution to the next generation’s gene pool) of the individual (Roughgarden, 1996). Thus, a strategy is called an ESS if when it is adopted by almost all members of a population, then any mutant individual will have a lesser fitness than that of an individual of the general population. One shortcoming of this approach to studying ecological dynamics is that while the ESS criterion makes good intuitive sense, it is based on a static analysis of the population and does not indicate how the population may have
come to evolve to such an ESS. In fact, it has been shown that the non-invadability of a trait value (a particular ESS) does not imply that a population with a nearby different trait value will evolve to the ESS over time (Taylor, 1989; Christiansen, 1991; Takada and Kigami, 1991). In other words, if we regard evolution as a dynamic process, there can exist strategies that are evolutionarily stable according to the ESS criterion, but that are not attainable in the dynamics of evolution.

The dynamical approach to evolution of a trait \( C \) is commonly modelled by including the following equation:

\[
\frac{d\tilde{C}}{dt} = g \left. \frac{\partial W(\tilde{C}, C)}{\partial \tilde{C}} \right|_{\tilde{C}=C}.
\]  

(4–1)

Here, \( W(\tilde{C}, C) \) is the fitness of an individual with trait value \( \tilde{C} \) in a population that is numerically dominated by individuals with resident trait values \( C \). The coefficient \( g \) scales the rate of evolutionary change. Adaptive dynamics of the kind given by Eq. 4–1 have been motivated by the general principle that regards evolution as a gradient-climbing process on an adaptive landscape (Gavrilets, 2004), and by similar principles (Brown and Vincent, 1987, 1992; Rosenzweig et al., 1987; Takada and Kigami, 1991; Vincent, 1990; Abrams, 1992; Abrams et al., 1993). It has also been shown that one can obtain an equation similar to the dynamics (Eq. 4–1) as a limiting case of results from quantitative genetics (Lande, 1976; Abrams, 2001). In the derivation of Eq. 4–1 by quantitative genetics it is assumed that the trait in question is determined by a large number of genetic loci, each contributing a small additive effect. In this setting, the rate of evolution \( g \) may be interpreted as the ratio of additive genetic variance to population mean fitness (Iwasa et al., 1991; Abrams, 2001).

When the focus of study is ecological dynamics, we assume that foragers behave optimally (with an evolutionarily stable strategy) and we study the consequences of this behavior to community dynamics (e.g, Abrams, 1992; Křivan,
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1996; Krivan and Sirot, 2004). Thus, instead of incorporating the evolutionary trait equation, Eq. 4–1, an optimal solution (ESS) for the trait $C$ is calculated by the ESS criterion and then substituted into the ecological dynamics equations. In other words, we assume that evolution has already taken place to shape the adaptive behavior, and that an evolutionarily stable value for $C$ is in place. An understanding of the relationship between genes and behavior is not necessary when using this approach. However, as we shall see, even in a simple model, such an optimal behavior may be very complex.

In this paper, using a simple Lotka-Volterra type predator-prey model with a type II functional response (Holling, 1959; Royama, 1971; Jeschke et al., 2002) in which the prey have a density-dependent foraging effort, we analytically derive the ESS of prey activity, as defined by the ESS criterion. Specifically, we show that at particular densities of predators and prey, there are multiple ESSs. To examine the relationship between the ESSs and trait evolution, we also examine the common dynamical model of evolution (i.e., Eq. 4–1). To examine ecological implications of adaptive behavior, we explore the differences that may arise in community dynamics between the evolutionary dynamical approach and the situation where any one of the multiple ESSs of prey behavior is fixed in the base ecological model.

4.2 The Model

The base model we consider is the Lotka-Volterra model with a type II predator functional response.

\[
\frac{dN}{dt} = N \left( b_c - \frac{ac^2P}{1 + ac^2hN} - m_N \right)
\]

\[
\frac{dP}{dt} = P \left( \beta \frac{ac^2N}{1 + ac^2hN} - m_P \right)
\]

where $P$ is predator density, $N$ is prey density, and $c \in [0,1]$ is a dimensionless quantity interpreted as the foraging effort of prey. When $c = 1$ (or a constant),
the model reduces to the standard Lotka-Volterra model with a type II functional response. The parameters $b, \beta, h, a, m_N, m_P$ we regard to be constants, but the foraging effort $c$ we regard to be a function $c(N, P)$, so that $c$ is modelled here as an adaptive behavior of the prey that is dependent on the densities $N$ and $P$. We interpret $b$ as the maximum rate of benefit (reproduction) of prey when they forage maximally. Handling time, $h$, is the time required for predators to consume a prey. The density-independent death rates of prey and predators are denoted by $m_N$ and $m_P$, respectively. The search efficiency, $a$, is a characteristic of the predators that measures their success rate of finding prey. The search efficiency $a$ of the predators is modified by the vulnerability $\phi(c)$ of the prey. The usual assumption is that vulnerability of the prey increases with their foraging effort as a convex function of $c$. The reason for choosing a linearly increasing function of $c$ to modify the prey benefit rate $b$ and a convex increasing function to modify predation efficiency $a$ is so that the risk of predation does not outweigh the benefit of enhanced reproduction when increasing foraging effort from $c = 0$ in the presence of a large predator population. No matter what the densities $N$ and $P$ are, there will always be some positive value of $c$ which is better for the prey than $c = 0$. For simplicity we use the vulnerability function $\phi(c) = c^2$. For example, if the prey decrease their effort from $c = 1$ to $c = 0.5$, then the effective search efficiency of the predators decreases from $a$ to $0.25a$ while effective benefit decreases from $b$ to $0.5b$. Food assimilation efficiency in converting ingested prey into new predators is denoted by $\beta$. Note again that we assume the foraging effort has bounded values. Since we assume $c(N, P) \in [0, 1]$, $c$ may be interpreted as a fraction of the maximum foraging effort.

A method for calculating all possible ESSs for an adaptive behavior is based on the following
**ESS criterion:** A strategy is an ESS if when used by almost all members of the population, results in the fitness of an individual from the general population being greater than or equal to the fitness of any mutant individual in the population.

We remark that this criterion in and of itself does not guarantee the existence of an ESS and also does not rule out the possibility that more than one (or infinitely many) ESS can exist. Furthermore, it assumes that the population is homogeneous in the sense that almost all individuals in the population use the same strategy.

In our model, suppose a mutant prey individual (e.g., \(c = B\)) emerges in a population where every other prey individual employs the foraging effort \(c = A\). The fitness \(W_N\) of an individual in the general population is derived from Eq. 4–2:

\[
W_N = bA - \frac{aA^2P}{1 + aA^2hN} - m_N.
\]

The fitness \(W_m\) of a mutant individual (with \(c = B\)) is very closely approximated by

\[
W_m = bB - \frac{aB^2P}{1 + aA^2hN} - m_N.
\]

The mutant fitness is of this form, because in the expression for a type II functional response, the denominator \(1 + ac^2hN\) (a dimensionless quantity) is the factor by which the risk of predation is reduced due to the time that a predator spends handling prey, and by assumption essentially all prey that are being handled are non-mutant \((c = A)\). On the other hand, the numerator is the risk to the focal (i.e., mutant) prey type, which has \(c = B\).

The ESS criterion for adaptive foraging in our model is:

An effort \(E \in [0, 1]\) is an ESS if and only if

\[
bx - \frac{aPx^2}{1 + ahNE^2} \leq bE - \frac{aPE^2}{1 + ahNE^2} \quad \text{for all } x \in [0, 1].
\]
We remark again that we regard such strategies $E$ and $x$ to be density-dependent functions $E(N, P)$ and $x(N, P)$.

4.3 Results

4.3.1 Evolutionarily Stable Strategy (ESS) of Foraging Effort

The derivation of evolutionarily stable strategies (ESSs) for the trait $c$ is shown in Appendix A. There are three possible functional types of ESS: $c = y_1$, $c = y_2$ and $c = 1$, where

$$y_1 = \frac{1}{bhN} \left( P - \sqrt{P^2 - \frac{b^2hN}{a}} \right), \quad y_2 = \frac{1}{bhN} \left( P + \sqrt{P^2 - \frac{b^2hN}{a}} \right)$$

Each of the three ESSs is valid only in a certain region of the $NP$-plane, as shown in Figure 4–1.

When predator density is relatively low (Region I, Figure 4–1), the only ESS is for prey to forage with the maximal effort of $c = 1$. When predator density is high relative to the prey density (Region II, Figure 4–1), the only ESS is for prey to forage with effort of $c(N, P) = y_1(N, P)$. The value of $y_1$ throughout most of Region II is generally low ($\ll 1$), although $c = y_1$ agrees with $c = 1$ at the boundary between Region I and Region II. At all points in the $NP$-plane of intermediate predator density (Region III, Figure 4–1), each of $c = y_1, c = y_2$ and $c = 1$ is an ESS.

When we refer to a particular ESS, $c(N, P)$, it is with the understanding that at each point $(N, P)$ of the $NP$-plane $c$ has a well defined value that is among the possible values given above. The existence of multiple ESS values in Region III implies that there do exist complicated ESS, because the criterion does not require that just one of $c = y_1, c = y_2$ and $c = 1$ must apply uniformly to all points in Region III. One such complicated, and perhaps unlikely, strategy is depicted in Figure 4–2, where Region III is divided into many subregions, with each subregion associated to one of the three possible ESSs. For simplicity in the subsequent
Figure 4–1. Solutions for the ESS for $c$ in each of three regions of the nondimensionalized $NP$-plane ($s = ahN$ and $r = \frac{a}{b}P$). In both Region I and Region II there is precisely one ESS function. In Region III there are three possibilities for an ESS. For the expressions for $y_1$ and $y_2$ in terms of $r$ and $s$, see Appendix A.

analysis we will consider three basic ESSs, one for which $c = y_1$ is chosen uniformly for all points in Region III, and similarly those for which $c = y_2$ and $c = 1$ are chosen uniformly in Region III. No matter which of the three possible ESSs is chosen uniformly for Region III, there will be a discontinuity of the ESS function. If $c = 1$ is chosen for Region III, then there is a discontinuity at all points on the boundary between Regions III and II (Figure 4–3); if $c = y_1$ is chosen for Region III, then there is a discontinuity at all points on the boundary between Regions III and I; if $c = y_2$ is chosen then there is a discontinuity at all points on both boundaries of Region III.

We note that the strategy $c = y_2$ (in Region III) is a strategy that is counter to intuition in the sense that for fixed prey density $N$, as $P$ increases then $y_2$ increases in value, so that a prey individual that has adopted the strategy of $c = y_2$ in Region III would increase its foraging effort as the predator density increases.
A prey individual that has adopted the strategy of \( c = y_1 \) in Region III would decrease its foraging effort as the predator density increases.

For a fixed predator density, similar characteristics of the three ESS functions are observed as prey density increases from \( N = 0 \) (Figure 4–3).

![Diagram showing ESS functions with different strategies](image)

**Figure 4–2.** A complicated ESS function, where Region III is split into many subregions, with each subregion associated with one of the three possible basic ESSs.

The functional response of predators will be very different, depending on the strategy that prey employ in Region III. Considering each of \( y_1, y_2, \) and 1 as a strategy employed uniformly in Region III by the prey, the type II functional responses appear as shown in Figure 4–4. The choice of \( c = 1 \) while in Region III, naturally yields a response that is equivalent to a standard type II response. The choice of \( c = y_2 \) however yields a functional response that is opposite in trend to the standard response - increasing prey density results in decreased kill rate for the predators while in Region III.
Figure 4–3. The three basic ESS functions determined by which of the three strategies is chosen uniformly in Region III. Top ($c = 1$), bottom left ($c = y_1$), bottom right ($c = y_2$). Plots of the ESS functions are shown on the nondimensionalized $NP$-plane ($s = ahN$ and $r = \frac{a}{b}P$).

4.3.2 Incorporating ESS into the Community Dynamics

The calculation of ESS in the previous section was done without any consideration of the population dynamics, other than to use Eq. 4–2 in deriving the ESS criterion. In this section we take the basic ecological model (Eqs. 4–2 and 4–3) and replace the foraging effort $c$ in these equations with one of the three basic ESS strategies. Thus the right-hand sides of equations (4–2) and (4–3) are now formulated as three-part functions, since there are three functional forms for a basic ESS for $c$, depending on which of three regions of the $NP$-plane the point $(N, P)$ lies in. In Region III we choose just one of the three possible ESSs to incorporate into the system, and we look at each of these three choices in turn to compare the
effects on the ecological dynamics with these choices. Conceptually, we are now looking at community dynamics with the assumption that evolution has already taken place and has arrived at one of the three basic ESSs. The analysis in this section includes equilibrium and stability results of the community dynamics.

For any fixed positive values of the parameters $a, h, m_N$ and $m_P$, if both $b$ and $\beta$ are sufficiently large, then there is exactly one nonzero equilibrium $(N^*, P^*)$ possible and this equilibrium is guaranteed to occur for one of the three choices of ESS in Region III. This nonzero equilibrium is locally stable only if both $b$ and $\beta$ are further sufficiently large. In particular, with $b$ and $\beta$ sufficiently large, a locally stable equilibrium will occur if and only if $c = y_1$ is the ESS in Region III.

In the results listed below, for given strategy $c(N, P)$, the ecological equilibrium $(N^*, P^*)$ is recorded along with the effort $c^*$ evaluated at this equilibrium, i.e. $c^* = c(N^*, P^*)$. 

Figure 4–4. Apparent functional responses of predators when $P = 10$, $a = 1$, $h = 1$, $m_N = 0.1$, $m_P = 0.1$. In this parameter region, there are three ESSs (Figure 4–1). These functional responses were plotted assuming that the three ESS values are distinct strategies. Left: $c = y_1$. Middle: $c = y_2$. Right: $c = 1$. 
1. If \( b < m_N \) or \( \beta/h < m_P \), there is no nonzero equilibrium.
   - If \( b < m_N \), then both species will go extinct.
   - If \( b > m_N \) and \( \beta/h < m_P \), then \( P \) will die, but \( N \) will grow without bound.

2. If \( m_N < b < 2m_N \) and \( \beta/h > m_P \), then an equilibrium is guaranteed to exist if \( c = 1 \) is chosen for Region III. This equilibrium is given by
   \[
   N^* = \frac{m_P}{a(\beta - hm_P)}, \quad P^* = \frac{\beta(b - m_N)}{a(\beta - hm_P)}, \quad c^* = 1
   \]
   This equilibrium is unstable. The location of this equilibrium \((N^*, P^*)\) may lie in either Region I or Region III, depending further on the values of \( b, \beta/h, m_N, m_P \).

3. If \( b > 2m_N \) and \( m_P < \frac{\beta}{h} < 2m_P \), then an equilibrium is guaranteed to exist if \( c = y_2 \) is chosen for Region III. The location of this equilibrium and the corresponding value of the ESS at equilibrium is given by
   \[
   N^* = \frac{m_P b^2}{4a m_N^2(\beta - hm_P)}, \quad P^* = \frac{\beta b^2}{4a m_N(\beta - hm_P)}, \quad c^* = y_2^* = \frac{2m_N}{b}
   \]
   This equilibrium is unstable. The location of this equilibrium \((N^*, P^*)\) lies in Region III.

4. If \( b > 2m_N \) and \( \frac{\beta}{h} > 2m_P \), then an equilibrium is guaranteed to exist if \( c = y_1 \) is chosen for Region III.
   The location of this equilibrium and the corresponding value of the ESS at this equilibrium is given by
   \[
   N^* = \frac{m_P b^2}{4a m_N^2(\beta - hm_P)}, \quad P^* = \frac{\beta b^2}{4a m_N(\beta - hm_P)}, \quad c^* = y_1^* = \frac{2m_N}{b}
   \]
   Note that this expression for the equilibrium is the same as in item (3) above, but the stability is different. This equilibrium may be locally stable or unstable:
Table 4–1. Equilibrium analysis. The $c$ specified is the choice of ESS in Region III that guarantees the existence a nonzero equilibrium.

<table>
<thead>
<tr>
<th>Condition</th>
<th>$b &lt; m_N$</th>
<th>$m_N &lt; b &lt; 2m_N$</th>
<th>$b &gt; 2m_N$</th>
</tr>
</thead>
<tbody>
<tr>
<td>$\frac{\beta}{h} &lt; \frac{m}{P}$</td>
<td>none</td>
<td>none</td>
<td>none</td>
</tr>
<tr>
<td>$m_P &lt; \frac{\beta}{h} &lt; 2m_P$</td>
<td>none</td>
<td>$c = 1$ unstable</td>
<td>$c = y_2$ unstable</td>
</tr>
<tr>
<td>$\frac{\beta}{h} &gt; 2m_P$</td>
<td>none</td>
<td>$c = 1$ unstable</td>
<td>$c = y_1$ locally stable iff $\frac{\beta}{h} &gt; \max{2m_P, m_P + \frac{1}{2}m_N}$</td>
</tr>
</tbody>
</table>

- If, in addition to the above conditions, $\frac{\beta}{h} < m_P + \frac{1}{2}m_N$, then the equilibrium is unstable.

- If, in addition to the above conditions, $\frac{\beta}{h} > m_P + \frac{1}{2}m_N$, then the equilibrium is locally stable.

The location of this equilibrium $(N^*, P^*)$ may lie in either Region II or Region III, depending on the values of $b, \beta/h, m_N, m_P$.

Table 1 summarizes the equilibrium analysis results.

4.3.3 Comparison with the Quantitative Genetics Model

The quantitative genetics (QG) model analyzes the community dynamics along with the evolutionary adaptation of $c$ by taking the ecological system and incorporating the dynamics of $c$. To the ecological system of Eqs. 4–2 and 4–3 we add the following differential equation, which is Eq. 4–1 applied to the fitness function of the prey.

$$\frac{dc}{dt} = g \left( b - 2 \frac{acP}{1 + ac^2hN} \right)$$

where $g$ indicates the rate of evolution. The usual QG model (e.g., Matsuda and Abrams, 1994) assumes that $c$ can take on an arbitrarily large value and so the system of three differential equations always has well defined solutions, although
solutions will generally have unbounded $c$ values. In our model, we assume that the value of $c$ is restricted to $c \in [0, 1]$, and so we restrict the third differential equation to limit the growth of $c$.

$$
\frac{dc}{dt} = \begin{cases} 
g \left( b - 2 \frac{acP}{1 + ac^2hN} \right), & \text{if } c < 1 \text{ or } g \left( b - 2 \frac{acP}{1 + ac^2hN} \right) < 0 
g \left( b - 2 \frac{acP}{1 + ac^2hN} \right) > 0, & \text{if } c = 1 \text{ and } g \left( b - 2 \frac{acP}{1 + ac^2hN} \right) > 0 
\end{cases}
$$

(4–4)

In any solution to this system, if the value of $c$ ever evolves to the value $c = 1$, then it will remain at $c = 1$ until the population densities reach levels at which $\frac{dc}{dt} < 0$, where $\frac{dc}{dt}$ is given by Eq. 4–4.

In a stability analysis of the system (Eqs. 4–2, 4–3, 4–4), solving the the equation $\frac{dc}{dt} = 0$ easily confirms that the equilibria values $c^*$ for the QG system are precisely the same as the ESSs derived by the ESS criterion in section 3.1. Thus we find, as expected, that the equilibria $(N^*, P^*, c^*)$ for the QG dynamical system are the same as those derived in section 3.2 from analyzing the ecological dynamics with ESS inserted.

4.3.3.1 Behavior of the system with fast evolution

Choosing $g$ to have a large value in the QG system assures that evolution of the trait $c$ occurs rapidly, and so in the QG model the value of $c$ is always at, or very near, an ESS for the current densities of $N$ and $P$. For example, if the QG system is in a state such that the current value of $(N, P)$ lies in Region I, then, with the assumption that the rate $g$ is fast relative to the ecological dynamics, we can conclude that foraging must be at $c = 1$ (or will evolve very quickly to $c = 1$), because there is only one equilibrium $c$-value in Region I. Similarly, if the current value of $(N, P)$ lies in Region II, then we may conclude that the value of $c$ is at $c = y_1(N, P)$ since evolution occurs quickly and there is only one equilibrium in Region II. But if the current value of $(N, P)$ lies in Region III, then it is not immediately clear at which level $c$ will be (or will quickly evolve to).
Figure 4–5. Evolutionary dynamics of foraging effort ($dc/dt$ versus $c$) in Region I (left), Region III (middle), and Region II (right), under the assumption of fast rate of evolution $g$.

Which of the three ESS in Region III is favored by evolution can be determined by examining the phase plane for $c$ with fixed $N$ and $P$. We may assume $N$ and $P$ to be essentially constant as $c$ evolves, because we have assumed a fast rate of evolution $g$. A phase plane diagram (plot of $dc/dt$ versus $c$) with value of $(N, P)$ in Region III is shown in Figure 4–5. The diagram shows that in the dynamics of the QG model, $c = y_1$ is stable, $c = y_2$ is unstable and $c = 1$ is stable when the system is in Region III. (Note that $c = 1$ is bounded above, so that it has nowhere to evolve but down, but the dynamics of $c$ will cause any small perturbation to a lesser $c$-value to quickly return to $c = 1$.) In particular, if the system is in a state such that $(N, P)$ is in Region III, then a value of $c$ that is greater than $y_2(N, P)$ will quickly evolve to $c = 1$ while a value of $c$ that is less than $y_2(N, P)$ will quickly evolve to $c = y_1(N, P)$. 
Which of the three ESSs is evolved to while in Region III is dependent on the trajectory of the ecological system. If the trajectory of the system in the $NP$-plane enters Region III with trait value $c$ greater than $y_2$, then the trait will converge to the ESS $c = 1$, while if the trait value is below $y_2$ when entering Region III, then $c$ will evolve to $c = y_1$. It is well known that the predator-prey dynamics of a Lotka-Volterra system involves counterclockwise trajectories in the $NP$-plane. The same is true of this system. Unless the parameters are such that one or both species are dying out, trajectories proceed in a counterclockwise fashion in the $NP$-plane. This means that if the initial state of the system is such that $(N, P)$ lies in Region I, the only way that the resultant trajectory of the system in the $NP$-plane may enter Region III is by crossing the boundary between Region I and Region III. In general, spiral trajectories that pass through each of the three regions proceed in counterclockwise cyclic order of (I, III, II). As noted before, any trajectory that passes through Region II quickly evolves to $c = y_1$ while in Region II, and any trajectory that passes through Region I quickly evolves to $c = 1$ while in Region I. Thus for any initial state $(N, P, c)$, unless the ecological dynamics are such that the resulting trajectory converges to an ecological equilibrium without ever entering Region I, it is necessarily the case that the trajectory will enter Region III with its trait value fixed at $c = 1$. As a general principle, we can say that in the QG model with fast $g$, any trajectory that involves a spiral or a cycle passing through Region I takes on the value $c = 1$ while in Region III.

It was shown in Section 3.2 that stability of the ecological system is possible only for certain values of the parameters, and only if the ESS being used has $c = y_1$ fixed in Region III. The above analysis shows however that even if the parameters are favorable to ecological stability, if the rate of evolution is fast (large $g$), then the potential ecological stability may not be realized, because the system evolves to $c = 1$ whenever Region III is entered on a trajectory that passes through Region I.
On the other hand, it is also possible that the trajectory of a stable ecological system may be contained entirely within Regions II and III, in which case a fast rate of evolution would not affect the stability.

Figure 4–6 shows typical trajectories in a simulation of the base ecological system when the three different ESSs in turn were fixed in Region III. (The simulation shown is for the base system without the dynamics of $c$ incorporated.) For the simulation in Figure 6, where $c = y_2$ is fixed in Region III, there are periodic outbreaks of prey. Where $c = 1$ is fixed in Region III, the system system is unstable with oscillations with very high magnitude (prey growth is much more rapid). Where $c = y_1$ is used in Region III, the result is a limit cycle that passes through each of the three regions. This stable limit cycle is possible if we regard evolution as having already occurred and further consider that evolution has terminated with the basic ESS that fixes $c=y_1$ in Region III. But this same cycle is not possible in the dynamics of the QG model with fast $g$, because the cycle passes through the three regions in cyclic order (II, I, III), thus resulting in the fixing of $c = 1$ in Region III.

Another interesting consequence of the above analysis of the evolutionary dynamics is that we have identified the basic strategy $c = y_2$ as unstable in the dynamics of evolution. Thus we have, at first glance, the seemingly paradoxical existence of an unstable strategy that is evolutionarily stable. The possible confusion lies in the two ways that the word “stable” is being used in this sentence. The strategy $c = y_2$ is stable relative to invasion by mutants. If the general population adopts the basic ESS strategy that fixes $c = y_2$ in Region III, then the population is not invadable by a small number of mutants. However this strategy is not stable relative to small shifts in the behavior of the general population. If by some happenstance the entire population experienced a small shift in behavior, due for example to environmental change or to a large scale mutation, then the entire
Figure 4-6. Simulation of the dynamics of predators and prey plotted on the effort diagram (Figure 4-1). \( s = a h N \) and \( r = (a/b)P \). The gray line indicates \( r = \sqrt{s} \) and the dotted line indicates \( r = (1 + s)/2 \). The area between these two curves with \( s > 1 \) indicates the region where there are multiple ESSs. Left figure: \( c = y_1 \), middle figure: \( c = y_2 \), and right figure: \( c = 1 \). \( h = 1.6, b = 1.25, m_N = 0.8, m_P = 0.5, \beta = 1.5 \).

population would evolve away from the strategy \( y_2 \) towards one of the dynamically stable strategies with \( c = y_1 \) or \( c = 1 \) in Region III. Similarly, we can say that the basic ESS that fixes \( c = 1 \) in Region III is stable relative to small shifts in the behavior of the population with fast \( g \), but this behavior does not allow ecological stability.

4.3.3.2 Behavior of the system with slow evolution

Choosing \( g \) to have a small value in the QG system relative to the ecological time scale assures that evolution of the trait \( c \) occurs slowly. In such a situation, if the community is not initially at ESS, then evolution to an ESS is not possible unless the community dynamics allow an ecological equilibrium of some sort, simply because the community must persist in order for evolution to take place. Assuming that a community is initially at ecological equilibrium and assuming that an initial non-ESS strategy is employed, then as evolution occurs (slowly), the ecological equilibrium will change, because mutants with superior genetics (superior foraging behavior \( c \)) will successfully invade the population, thus changing the
ecological dynamics. To attempt to calculate all possible effects of slow evolution on the community dynamics would be more difficult for this model, because we would need to characterize those foraging functions $c(N, P)$ that allow for an ecological equilibrium, and then determine for which of these initial foraging functions the QG dynamics will maintain stability of the community as evolution of $c$ occurs. We will leave such calculations for a future paper, but note that it is not implausible that slow evolution could lead to the destruction of ecological stability. It is also plausible that slow evolution could converge to an ESS that supports ecological stability and that is more complicated than one of the three basic ESSs (i.e. an ESS which is piecewise defined on several subregions of Region III, as in Figure 4–2)

4.4 Discussion

When studying dynamics of the evolution of an adaptive behavior it is essential to consider evolutionary dynamics along with ecological dynamics. Certain behaviors can be determined to be evolutionarily stable strategies without those behaviors being compatible with a stable ecological system. In a simple but commonly used predator-prey model, we found that the quantitative genetics model of evolution with fast rate of evolution $g$ often may converge to an ESS that promotes instability of the ecological system. In a wide parameter region for this same model, we found the existence of multiple ESSs (Figure 4–1). Among these we identified one simple such strategy that allows a stable ecological equilibrium. However, a system that is initially in ecological equilibrium and employing this ESS, may well evolve under the quantitative genetics model to an ESS that destabilizes the community dynamics. Even without considering the issue of ecological equilibrium, it is apparent that depending on which of the multiple ESS is adopted, community dynamics can be very different (Figure 4–6), and so we need to be cautious about the implications derived from results of these models.
Most community models with a component of adaptive behavior do not include intraspecific interactions such as the one imposed by a type II functional response. This study shows that the inclusion of one of the most commonly used functions in community ecology (i.e., type II functional response) induces the existence of multiple evolutionarily stable strategies of adaptive behavior. Any one of these ESS is by definition, a strategy that is stable relative to invasion by mutants. However, not all ESSs are attainable in the evolutionary dynamics that are derived from specific assumptions about how genes influence behavior.

The Type II functional response is generally considered to be a destabilizing factor in community ecology (Murdoch et al., 2003). Indeed, the same Lotka-Volterra system as used in this study, but without the adaptive foraging behavior $c$ incorporated, is known to be a globally unstable system without limit cycles. The result of the stability analysis of our system gives some evidence for the notion that inclusion of adaptive behavior along with a Type II functional response may have a stabilizing effect on community dynamics.

The analysis of the ESSs for this model was confined to what we referred to as the three “basic” ESSs, that is strategies that uniformly fix one of the three functional forms for an ESS throughout Region III. However, the existence of these three basic ESSs implies that there are theoretically infinitely many ESSs for the model (e.g., Figure 4–2). The analysis of apparent functional response (Figure 4–4) was done just for the three basic ESSs. However, a complicated ESS such as is shown in Figure 4–2 is a possible behavior, and if prey were to adopt such a strategy, the functional response would appear very erratic. The community dynamics associated with such an irregular, non-basic ESS would also be very hard to predict or analyze. The biological feasibility of a strategy set is difficult to assess with confidence. However, it is important to note that simple considerations (i.e., type II functional response) in a simple predator-prey model led to potentially
infinitely many ESSs, suggesting that analysis of behavioral data on activity level can be very difficult.

The present study also has implications for functional response studies. If multiple ESSs are possible, the apparent functional response can look very different depending on which ESS is employed by the prey (Figure 4–4), even though the underlying mechanism of predator activity is in each case the type II functional response (Holling, 1959; Royama, 1971). When faced with experimental functional response data that differs from the classical Type II curve, a type II functional response can still be fitted, provided that information about the about activity behavior of the prey can be incorporated into the model. Furthermore, although certain functional responses may look unfamiliar (e.g., Figure 4–4, middle), without carefully examining the intraspecific behavior of prey in the field, we should not dismiss such responses as possibilities. For example, jumping spiders are known to stay in their retreat even when they are starved (Okuyama, unpublished manuscript). Although, the mechanism behind this behavior is still unknown, if we were to estimate a functional response of predators of these jumping spiders by including the inactive individuals in the analysis, we may see a relationship that is very different from the case when only active individuals are used in the analysis. In laboratory experiments, such inactive behaviors of prey are often not recovered due to the use of a small arena, and so such analyses may artificially lead to the usual type II functional response. It is important to examine how activity level is really expressed in a natural environment.

In many theoretical investigations of adaptive behavior, no upper bound is imposed on the trait value (e.g. Matsuda and Abrams, 1994; Abrams, 1992). In the model studied here, if the foraging effort $c$ were allowed to take on arbitrarily large values, then there would be no ESS for $c$ possible in Region I. At all other points (in Region II and III), both of the strategies $y_1$ and $y_2$ would be ESSs,
and $y_2$ would take on very large value in Region II. The quantitative genetics model with no bound on $c$ would also yield drastic instability in Region I, since any trajectory that entered Region I would result in $c$ evolving to higher and higher, unbounded values. Although unbounded trait value is a commonly used assumption for its simplicity, it can have a strong influence on the conclusions that are made about community dynamics. In our model, the trait $c$ is a dimensionless quantity interpreted as foraging effort and so the only realistic interpretation is with $c$ taking values between 0 and 1.

Křivan and Sirot (2004) investigate community dynamics with type II predator functional response under the assumption that prey effort is determined by maximizing population fitness rather than by an ESS criterion for individual fitness. The dependence of prey effort on the densities of $N$ and $P$ is a very different relation when the criterion is maximizing population fitness compared to when the criterion is ESS. (Figure 4–7). When analyzing adaptive behavior in a community ecological context, for example when considering trait mediated indirect interactions, the criterion for “optimal behavior” needs to be considered carefully and stated explicitly. For a fixed prey density, an increasing predator density would

![Figure 4–7. Foraging effort as a function of $N$ and $P$ for an Evolutionary stable strategy (left) and for a strategy that maximizes population fitness (right). $a = 1, h = 1, b = 1$.](image)
increase the effect size of the trait-mediated indirect interaction in the case of an ESS, but may decrease it in a non-ESS solution (Figure 4–7).

As far as the interface of evolution and ecology is concerned, the current study highlights the importance of understanding the genetic basis of behavior. While more progress in this field has been made in recent years (e.g., Greenspan, 2004), we still have little information about the mechanisms of behavior for most traits, and thus about how behavior comes to fixation. It has not been well established that the assumptions of the quantitative genetics approach (Abrams, 2001) are appropriate for the study of adaptive behavior. Until the genetic basis of behavior is more well grounded, evolutionary ecological modelling remains highly phenomenological, even if the model is based on the mechanistic genetics argument. While research in behavioral genetics is already recognized as an exciting research front, the field of community ecology also awaits its exciting progress.
Appendix A: Derivation of the ESS

ESS Problem: Find $E \in [0, 1]$ such that

$$bx - \frac{aP x^2}{1 + ahNE^2} \leq bE - \frac{aPE^2}{1 + ahNE^2}$$

for all $x \in [0, 1]$

(Assume all parameters and variables $a, b, h, N, P$ have positive values.)

Let $r = (a/b)P$, $s = ahN$, and let $F(x, y) = (y - x) + \frac{r(x^2 - y^2)}{1 + sy^2}$.

Then the ESS problem is equivalent to:

Find $E \in [0, 1]$ such that $F(x, E) \geq 0$ for all $x \in [0, 1]$.

It is clear for any $E$, that $F(E, E) = 0$, so the problem is equivalent to:

Find $E \in [0, 1]$ such that $\min_{x \in [0, 1]} F(x, E) = 0$.

For any fixed $y$-value $E$, the function $F(x, E)$ is quadratic in $x$ so it is easy to locate the value $x_0$ that yields the min value for $F(x, E)$. That value is $x_0 = \frac{(1+sE^2)}{2r}$.

There are two cases to consider, because the value of $x_0$ may or may not lie in the interval $[0, 1]$. In particular, $x_0 \in [0, 1] \iff E^2 \leq (2r - 1)/s$.

1. If $E^2 \leq (2r - 1)/s$, then the min value of $F(x, E)$ occurs at $x = x_0$, and so the problem requires in this case that

$$F(x_0, E) = -\frac{1}{4r(1 + sE^2)}((1 + sE^2) - 2rE)^2 = 0.$$ 

If $E$ is to be an ESS in this case, then $E$ must satisfy

$$sE^2 - 2rE + 1 = 0.$$ 

2. If $E^2 \geq (2r - 1)/s$, then the min value of $F(x, E)$ occurs at $x = 1$, and so the problem requires in this case that

$$F(1, E) = \frac{(E - 1)((1 + sE^2) - r(1 + E))}{(1 + sE^2)} = 0.$$ 

It is not hard to show, with the assumption $E^2 \geq (2r - 1)/s$, that the only solution of this equation for $E$ in the interval $[0, 1]$ is $E = 1$. 
In summary, suppose $E$ is an ESS. Then the two cases to consider are:

1. If $E^2 \leq (2r - 1)/s$, then $E$ must satisfy $sE^2 - 2rE + 1 = 0$.

2. If $E^2 \geq (2r - 1)/s$, then $E$ must satisfy $E = 1$.

Next consider the polynomial equation given in Condition (1). The solutions of the equation $sy^2 - 2ry + 1 = 0$ are:

$$y = \frac{r \pm \sqrt{r^2 - s}}{s}.$$ 

Thus an ESS for condition (1) is possible only if $r^2 \geq s$. Furthermore, if we let

$$y_1 = \frac{r - \sqrt{r^2 - s}}{s} \quad \text{and} \quad y_2 = \frac{r + \sqrt{r^2 - s}}{s},$$

then both $y_1, y_2$ are positive and we have the following requirements for $y_1$ and $y_2$ to lie in the interval $[0, 1]$:

- $y_1 \in [0, 1] \iff r \geq \sqrt{s}$ and $(r \leq s$ or $r \geq (1 + s)/2$)
- $y_2 \in [0, 1] \iff r \geq \sqrt{s}$ and $(r \leq s$ and $r \leq (1 + s)/2$.

Formulas for ESS can now be given in terms of conditions involving just the parameters $r$ and $s$. It turns out that results are dependent on whether $s < 1$ or $s > 1$. There are a few subcases for each of these two cases. Here is a summary of the formulas:

**Assuming $s > 1$:** (so $s > \frac{1 + s}{2} > \sqrt{s}$.)

- If $r > \frac{(1+s)}{2}$, then $y_1$ is the only ESS. ($y_2 > 1$ in this case.)
- If $\sqrt{s} < r < \frac{(1+s)}{2}$, then $y_1 < y_2 < 1$ are both ESS, and $y = 1$ is also ESS.
- If $r < \sqrt{s}$, then $y = 1$ is the only ESS. ($y_1, y_2$ are not real in this case.)
Assuming $s < 1$: (so $s < \sqrt{s} < \frac{1+s}{2}$.)

- If $r > \frac{(1+s)}{2}$, then $y_1$ is the only ESS. ($y_1 < 1$ and $y_2 > 1$ in this case.)

- If $r < \frac{(1+s)}{2}$, then $y = 1$ is the only ESS. (Both $y_1, y_2$ are either $> 1$ or not real in this case.)
CHAPTER 5
ON THE QUANTITATIVE MEASURES OF INDIRECT INTERACTIONS

5.1 Introduction

Indirect interactions, whether density-mediated (DMII) or trait-mediated (TMII), can profoundly alter community dynamics (Werner and Peacor, 2003; Bolker et al., 2003). Two well-known phenomena in community ecology, trophic cascades and keystone predation, illustrate the importance of both trait and density effects (Schmitz, 1997; Wissinger et al., 1999; Schmitz et al., 2004); TMII can also promote coexistence in ecological communities (e.g., Damiani, 2005). Ecologists have quantified the strengths of TMII and DMII in a variety of systems (Werner and Peacor, 2003; Preisser et al., 2005), typically concentrating on the relative strengths of the two types of indirect interactions, and their effects on long-term community dynamics (Křivan and Schmitz, 2004; van Veen et al., 2005). In order for us to make progress in this area, however, we must quantify indirect interactions in ways that are accurate, consistent among studies, and consistent with the underlying community dynamics.

Here, we point out that the methods used in previous studies have been inconsistent and may inaccurately estimate the relative strength of trait and density effects, one of the main goals of these studies. We explore the strengths and weaknesses of different metrics using the example of a three-species linear food chain (predators-foragers-resources). Predators both kill foragers (density effects) and induce antipredator behavior in foragers (trait effects), in both cases reducing the absolute rate at which the forager population consumes resources and thus increasing the density of resources. We find that ratio-based metrics typically quantify TMII and DMII most consistently, although other metrics may
be required in specific cases where absolute differences in resource density are of interest or where the community is observed over a long time scale.

5.2 Quantifying Indirect Effects

5.2.1 Standard Experimental Design

Studies that aim to quantify the strength of TMII and DMII are typically short-term, usually much shorter than a generation time, with negligible reproduction or regrowth of any of the species in the community. Thus researchers typically quantify indirect effects based on the change in resource density between the beginning and end of the experiment (which is equivalent to the total resource consumed by foragers if the regrowth of resource is negligible).

Previous attempts to quantify the strength of indirect effects have used some or all of the following treatments.

1. The true predator treatment includes unmanipulated predators, foragers, and resource, mimicking the natural system;
2. The threat predator treatment includes predators (or predator cues), inducing antipredator traits in foragers, but prevents predators from consuming foragers (e.g., predators are disabled or caged);
3. The no predator treatment contains only foragers and resources, and thus eliminates indirect effects.
4. The culling treatment removes foragers in a way that matches the predation rate in the true predator treatment in the absence of predators.

While the first three treatments are standard, culling is rarer (Peacor and Werner, 2001; Griffin and Thaler, 2006). We will discuss the importance of culling below; we simply note here that the accuracy of the culling treatment (i.e., the degree to which it mimics the natural removal of foragers by predators) is important (Griffin and Thaler, 2006). Experimenters must record the number of surviving foragers in the true predator treatment at frequent intervals and remove foragers in a no-predator treatment to match the population trajectory in the predator treatment.
5.2.2 Indices of Indirect Effects

Suppose we run a short-term experiment with abundant resources, minimizing (1) the effects of both forager and resource depletion (and resulting variation in forager death and resource uptake due to functional responses of predators and foragers (Juliano and Williams, 1987)); (2) variation in forager strategy over time (Luttbeg et al., 2003); (3) differential mortality due to costs of antipredator behavior; and (4) intraspecific interference. Then we can define $F$ and $f$ as the per-forager uptake in the absence and presence of predators; since antipredator behavior generally reduces foraging effort or efficiency, we suppose $f < F$. Similarly, if $N$ and $n$ are the average numbers of foragers alive during the experiment in the absence and presence of predators, we expect $n < N$. The total uptake in different treatments, which should approximately equal the difference in resources between the beginning and end of the experiment, is:

$$
\text{no pred. threat culling true} \\
FN \quad fN \quad Fn \quad fn
$$

(5–1)

We can quantify TMII, DMII, and the total indirect effect (TII) by contrasting these treatments:

$$
\text{TMII}_{a^-} = \text{no pred} - \text{threat} = N(F - f) \\
\text{TMII}_{a^+} = \text{cull} - \text{true} = n(F - f) \\
\text{DMII}_{a^-} = \text{no pred} - \text{cull} = F(N - n) \\
\text{DMII}_{a^+} = \text{threat} - \text{true} = f(N - n) \\
\text{TII}_a = \text{no pred} - \text{true} = FN - fn
$$

(5–2)

In the subscripts, $a$ denotes “additive” and the + and − indices refer to the presence or absence of the other effect; for example, DMII$_{a^+}$ is the additive effect of predator-induced changes in density (present in the true predator treatment but not the threat treatment) in the presence of antipredator behavior (present in both treatments).
Alternatively, we can quantify the indirect effects based on proportional changes (ratios):

\[
\begin{align*}
\text{TMII}_r^- &= \frac{\text{no pred}}{\text{threat}} = \frac{F}{F} \\
\text{TMII}_r^+ &= \frac{\text{cull}}{\text{true}} = \frac{F}{F} \\
\text{DMII}_r^- &= \frac{\text{no pred}}{\text{cull}} = \frac{N}{n} \\
\text{DMII}_r^+ &= \frac{\text{threat}}{\text{true}} = \frac{N}{n} \\
\text{TII}_r &= \frac{\text{no pred}}{\text{true}} = \frac{FN}{fn}
\end{align*}
\]

or similarly (as used by all existing studies):

\[
\begin{align*}
\text{TMII}_{r2^-} &= 1 - \frac{\text{no pred}}{\text{threat}} = 1 - \frac{F}{F} \\
\text{TMII}_{r2^+} &= 1 - \frac{\text{cull}}{\text{true}} = 1 - \frac{F}{F} \\
\text{DMII}_{r2^-} &= 1 - \frac{\text{no pred}}{\text{cull}} = 1 - \frac{N}{n} \\
\text{DMII}_{r2^+} &= 1 - \frac{\text{threat}}{\text{true}} = 1 - \frac{N}{n} \\
\text{TII}_{r2} &= 1 - \frac{\text{no pred}}{\text{true}} = 1 - \frac{FN}{fn}
\end{align*}
\]

All existing studies that used ratio based indices have used eq. 5–4 rather than eq. 5–3. Using the ratio-based indices, the difference between + and − disappears (e.g., \(\text{TMII}_r = \text{TMII}_{r^-} = \text{TMII}_{r^+}\) and \(\text{DMII}_r = \text{DMII}_{r^-} = \text{DMII}_{r^+}\)). However, as we discuss below, the difference between indices with different subscripts (e.g., \(r^+\) vs. \(r^-\)) can become important in some circumstances.

Existing studies vary widely (Table 5–1), using both additive (eq. 5–2) and ratio (eq. 5–4) indices. In addition, some studies have calculated the indices of TMII and DMII directly from the contrasts shown above (direct method), while others have quantified TMII using the contrasts but derived DMII by subtracting TMII from the overall size of indirect effects: we discuss this indirect method further below.

### 5.2.3 Decomposing Total Effects

Our first criterion for metrics of indirect effects is that they should neatly decompose total indirect effects into trait- and density-mediated components. The
Table 5–1. Existing studies that have explicitly compared TMII and DMII.

<table>
<thead>
<tr>
<th>Study</th>
<th>Additive/Ratio</th>
<th>Direct/Indirect</th>
<th>Culling</th>
</tr>
</thead>
<tbody>
<tr>
<td>Huang and Sih (1991)</td>
<td>Additive</td>
<td>Indirect</td>
<td>No</td>
</tr>
<tr>
<td>Wissinger and McGrady (1993)</td>
<td>Additive</td>
<td>Indirect</td>
<td>No</td>
</tr>
<tr>
<td>Peacor and Werner (2001)</td>
<td>Additive</td>
<td>Direct</td>
<td>Yes</td>
</tr>
<tr>
<td>Grabowski and Kimbro (2005)</td>
<td>Ratio</td>
<td>Indirect</td>
<td>No</td>
</tr>
<tr>
<td>Wojdak and Luttbeg (2005)</td>
<td>Ratio</td>
<td>Direct</td>
<td>No</td>
</tr>
<tr>
<td>Griffin and Thaler (2006)</td>
<td>Ratio</td>
<td>Direct</td>
<td>Yes</td>
</tr>
</tbody>
</table>

metrics defined above lead to

\[ TII_a = FN - fn = DMII_{a-} + TMII_{a+} = DMII_{a+} + TMII_{a-} \]

\[ TII_r = \frac{FN}{fn} = DMII_r \cdot TMII_r \]

\[ TII_{r2} = 1 - \frac{FN}{fn} = 1 - (1 - DMII_{r2})(1 - TMII_{r2}). \]  

(5–5)

While one can decompose total effects in any of the three frameworks shown above, the ratio framework is simplest, and for some purposes can be simplified further by taking logarithms: \( \log TII_r = \log DMII_r + \log TMII_r \). Furthermore, the decomposition of total additive effects into components with different subscripts is problematic: we discuss this further below. Although some studies have used ratio measures (Griffin and Thaler, 2006), the general importance of assessing contrasts on an appropriate scale does not seem to have been appreciated as it has in the closely analogous problem of detecting multi-predator interactions (Billick and Case, 1994; Wootton, 1994).

However, additive indices may be preferable when the goal is to quantify the absolute change in resource depletion instead of the relative size of TMII and DMII. For example, in a study of eutrophication one might want to know the absolute change in phytoplankton in a lake due to TMII or DMII; in this case, \( TMII_{a+} \) and \( TMII_{a-} \) will quantify the change in resource depletion due to the antipredator behavior if we fixed the the density of foragers to that of the true predator and no predator treatments, respectively.
5.2.4 Incommensurate Additive Metrics

Comparing additive metrics with different subscripts (e.g., $\text{DMII}_{a-}$ vs. $\text{TMII}_{a+}$) is problematic. This invalid comparison arises when one tries to quantify $\text{DMII}$ indirectly by subtracting (additive) $\text{TMII}$ from the total (additive) indirect effects (eq. 5–5). For example, Huang and Sih (1991) quantified metrics similar to $\text{TMII}_{a-}$ and $\text{TII}_{a}$ and estimated $\text{DMII}$, which corresponds to $\text{DMII}_{a+}$, by subtracting trait effects from the total. To see the problem, suppose that predators reduced both the average density and the average uptake rate of foragers by a proportion $p$, in which case we would probably like to conclude that the magnitudes of $\text{DMII}$ and $\text{TMII}$ are equal. Carrying through the equations above with $f = (1 - p)F$, $n = (1 - p)N$ shows that trait effects ($\text{TMII}_{a-}$) are always estimated to be $1/(1 - p)$ times larger than density estimates in this case ($\text{DMII}_{a+}$). (The problem still applies if $F$ and $N$ are reduced by the same absolute amounts — although it would be hard to interpret this scenario in any case since $F$ and $N$ have different units.) Similarly, if one tries to use additive metrics without having run a culling treatment, one can only estimate $\text{TMII}_{a-}$ and $\text{DMII}_{a+}$. Indirect methods can work — for example dividing $\text{TII}_r$ by $\text{TMII}_r$ should give a consistent estimate of $\text{DMII}_r$ — but only in the case where all the simplifying assumptions stated above (no depletion, no intraspecific competition, etc.) hold.

5.3 Complications

5.3.1 Biological Complexities: Short-term

What if biological complexities such as depletion of resources or intraspecific interference do occur? Restating eq. 5–1 more generally as

$$
\text{no pred. threat culling true} \\
F_1 N_1 \quad f_1 N_2 \quad F_2 n_1 \quad f_2 n_2
$$

(5–6)
highlights our implicit assumptions above. For example, by assuming that $f_1 = f_2$, we are assuming that antipredator behavior is independent of population density; by assuming that $F_1 = F_2$, we are assuming that per capita foraging success in the absence of predator cues is independent of forager density (Luttbeg et al., 2003). Assuming $N_1 = N_2$ is safe unless significant numbers of foragers die due to the costs of antipredator behavior (easily detected in an experiment); assuming $n_1 = n_2$ may be reasonable since it is an explicit goal of the culling treatment.

In the standard experimental design without culling, we have three treatments with which to test two contrasts, and no remaining information with which to test our assumptions. The culling treatment provides a second pair of contrasts that were initially supposed (eq. 5–3) to be equivalent. Continuing in the tradition of the multiple-predator-effects literature (Billick and Case, 1994; Wootton, 1994), we may be able to use the log-ratio indices and interpret non-additivity or interaction terms as evidence for additional ecological mechanisms. For example, we can think of prey relaxing antipredator behavior under high conspecific density as an interaction between density and trait effects, in both the ecological and statistical sense: this phenomenon could be quantified (if $F_1 = F_2$) as $\log f_2/f_1 = \log \text{TMII}_{r-} - \log \text{TMII}_{r+}$. Unfortunately, as Peacor (2003) suggested, conspecific density may also change forager behavior even in the absence of predators, meaning $F_1 \neq F_2$. While the available contrasts do not provide enough information to disentangle all of the possible effects, at least the presence of an interaction tells us that something interesting may be happening. Auxiliary measurements of behavioral proxies for uptake, or measurements of resource uptake at a range of different forager densities, are more detailed potential solutions to the problem of additional interactions.

We have also assumed so far that the absolute rate of forager consumption is independent of the amount of resource available — given enough time, foragers
will reduce the resource density linearly to zero, which may be reasonable in small experimental arenas. If alternatively foragers deplete resource exponentially (so we can redefine $F$ and $f$ as predation probability of one unit of resource per forager in the absence and presence of predators respectively), then the change in the amount of resource (e.g. in the no predator treatment is proportional to $(1 - (1 - F)^N)$. We can define yet another set of indices in this case as (e.g.)

$$DMII_{r3} = \frac{\log(\text{threat})}{\log(\text{true})}$$

(5-7)

where (threat) and (true) are the proportional reduction of resources with respect to the previous time step. We call these “log-log-ratio metrics”, because the decomposition $\log TII_{r3} = \log TMII_{r3} + \log DMII_{r3}$ involves taking the logarithm of the response variables twice. The equivalence of the + and − indices, and the clean decomposition of TII into trait and density effects, still holds in this case.

Ecological systems are diverse, and we have certainly not covered all of the possible scenarios. For example, strongly nonlinear dynamics (e.g. self-competition among the resource) could, like most strongly nonlinear interactions, lead to peculiar results — for example, resource densities dropping as forager densities or foraging efforts decreased (Abrams, 1992). If strong, such dynamics should be obvious from unusual signs or magnitudes of the indices (e.g. $F/f < 1$); if weak, they could throw off interpretations of data. The only preventive measures we can suggest are common sense (avoid using resources with potential for such strong self-suppression) and auxiliary observations (behavior proxies) or experiments (ranges of forager densities).

5.3.2 Biological Complexities: Long-term

So far we have assumed that indirect-interaction experiments were run over short time scales — to estimate “instantaneous” effects, and to avoid potential complications of resource regrowth or variation in resource or forager densities.
However, indirect interactions clearly act over longer time scales as well. Luttbeg et al. (2003) have pointed out that forager strategies may vary even over the course of a fairly short-term experiment where densities are held constant, and of course the densities of predators, foragers, and resource may all vary over longer time scales. If we are to try to understand the longer-term dynamics of ecological communities, whether empirically or theoretically, we will eventually need to think about how to quantify indirect interactions that run over long enough time scales that population density and behavior vary significantly.

If we run an experiment over $T$ time steps and simply add together the log-ratio indices from (eq. 5–5), we do preserve the decomposition of indirect effects:

$$
\sum_{t=1}^{T} \log(TII_r)_t = \sum_{t=1}^{T} \log(TMII_r)_t + \sum_{t=1}^{T} \log(DMII_r)_t
$$

(5–8)

However, using the ratio indices we cannot expect that computing TMII and DMII from the total amount of resources consumed between the beginning and end of the experiment will give us the same answer as computing TMII and DMII period-by-period and adding them, because, e.g.

$$
\sum_{t}(\text{no pred})(\text{threat})_{\text{period-by-period}} \neq \frac{\sum_{t}(\text{no pred})}{\sum_{t}(\text{threat})}_{\text{overall}}.
$$

(see e.g. Earn and Johnstone (1997) for other biological implications of the fact that sums of ratios are not equal to the ratios of sums).

This difference can cause a large difference in the relative sizes of TMII and DMII even over a fairly short experiment. In this case the product of TMII$_r$ and DMII$_r$ computed from the endpoint data (the difference between beginning and ending resource levels) will no longer satisfy the decomposition given in eq. 5–5, and the $+$ and $-$ ratio indices will no longer be equivalent ($TMII_{r+} \neq TMII_{r-}$, $DMII_{r+} \neq DMII_{r-}$). Another consequence is that a culling treatment will be
necessary in order to compare trait- and density-mediated effects accurately. Griffin and Thaler (2006) found large differences between TMII\(_{+r}\) and TMII\(_{-r}\) as well as between DMII\(_{+r}\) and DMII\(_{-r}\) in a 3-day experiment; while differences between the TMII indices could be caused by intraspecific interactions as suggested above, differences in DMII are more constrained and may reflect the effects of variation in density and behavior over time.

A few possible solutions to these difficulties are to:

- **Use additive metrics**, including a culling treatment to avoid comparing unlike subscripts. Since the total amount of resource consumed over the course of the experiment equals the sum of the period-by-period consumption, period-by-period and endpoint calculations of indices are consistent.

- **Use log-log-ratio metrics**, i.e. assuming geometric depletion of resources. If we define the response variables in each treatment as the proportion of the resource being consumed in each time step, then the values of TII=TMII+DMII calculated at each time step sum to the value calculated at the endpoint (i.e. based on the ratio of initial to final resource densities).

- **Collect period-by-period data**, with frequency depending on the study system. For example, if behavior of foragers changes in a systematic way on a fast time scale (e.g., morning vs. afternoon), subsampling the data (e.g., collecting data only once a day) would result in bias. Similarly, if the forager density is depleted more than a few percent by predators, collecting data that does not reflect this forager depletion will also give biased answers.

- **Model the system**: while we have focused on very simple dynamics here (few interactions, simple functional responses, etc.) it is clear that we have neglected many possibilities. In the absence of detailed period-by-period data, the only way to estimate the effects of time-varying densities and behaviors is to build a simple model of resource dynamics, predation rate, and forager responses and parameterize it from the system (van Veen et al., 2005). Here even a little bit of period-by-period data, even if the sampling frequency is too slow to capture the details of the dynamics, can be enormously useful for validating the functional forms incorporated in the model.

5.4 Summary

While some of the metrics we have presented here appear to be generally better than others — in most cases it appears that ratio-based indices will
more clearly and consistently decompose total indirect effects into trait- and
density-mediated components — it is also clear that significant complexities lurk
once we go beyond short-term, highly controlled experiments in small arenas.
However, these complexities are actually the signature of interesting ecological
dynamics, representing the next stage beyond the now-familiar questions of “are
trait-mediated effects detectable?” and “what is the relative magnitude of trait-
vs density-mediated effects?” (Werner and Peacor, 2003; Preisser et al., 2005).
We suggest that, as in studies of multiple predator effects, ratio-based indices
should probably be the default, but that empiricists interested in quantifying
indirect effects should (1) consider metrics that are most appropriate for their
particular system and question (e.g. additive vs. log-ratio vs. log-log-ratio, linear
vs. geometric resource consumption); (2) report “raw” measures (e.g. resource
densities or consumption rates) to allow readers to calculate different indices
from the data; (3) incorporate culling treatments in their experiments and use
the additional contrasts to test for and interpret interactions between trait and
density effects; and (4) consider running longer experiments, despite the potential
added complexities, to gain information on a larger and richer set of ecological
phenomena.
CHAPTER 6
ADAPTIVE BEHAVIOR IN SPATIAL ENVIRONMENTS

6.1 Introduction

Optimal foraging theory has proven useful in analyzing feeding behaviors in a variety of contexts (Stephens and Krebs, 1986) as well as in understanding how those behaviors affect community dynamics (reviewed in Bolker et al., 2003). In the scenario where foragers adjust their foraging activity level based on their perception of the environment, the simplest case assumes a single homogeneous foraging arena with a known density of predator and prey (e.g., Abrams, 1992). In these models, foragers are assumed to react to the average predation risk of the environment. This behavior introduces trait interactions into the community (Abrams, 1995), which influence the dynamics of the community in important manner (Werner and Peacor, 2003). However, predation risk can vary spatially based on exogenous factors (e.g., microhabitats) (Schmitz, 1998; Bakker et al., 2005) and endogenous factors (Keeling et al., 2000; Liebhold et al., 2004). Thus, models assuming that a population of foragers responding to an average (i.e., spatial average) risk of predation may give inaccurate results if animals respond to spatially variable local cues (e.g., encounter with a predator) (Jennions et al., 2003; Hemmi, 2005b; Dacier et al., 2006).

Spatial properties of foragers and predators can influence the resulting species interactions. For example, while visual foragers can detect predators that are located within their perceptual range at any moment (Cronin, 2005), chemosensory foragers (Cooper, 2003; Greenstone and Dickens, 2005) may detect the presence of predators based on cues that may or may not be closely associated with predator’s actual location depending on how the predator’s chemical cues
travel the environment and how long the chemical cues persist. Thus, ecological communities with different spatial properties may exhibit different outcomes in species interactions. For example, a meta-analysis by Preisser et al. (2005) showed that trait-mediated effects are stronger in aquatic than in terrestrial systems. Whether or not this difference can be attributed to the spatial characteristics (e.g., physical properties of the predator cues) discussed here is not clear, but most community ecological studies that examined trait-effect of chemical foragers are based on aquatic systems (Werner and Peacor, 2003), suggesting the possibility that the observed trend is influenced by the spatial properties.

In this paper, I examined how spatial consideration may affect the strength of species interactions by constructing two types of foragers in a simple three species linear food chain (resource – forager – predator). The first type of foragers, Global Information Foragers (GIFs), represent the commonly used modelling framework (e.g., Krivan, 2000) where foragers detect the average predation risk of the environment regardless of their current activity (e.g., even when foragers are hiding) or the actual locations of the predators. This scenario may be appropriate if predator cues (e.g., chemical) diffuse rapidly in the environment. For example, aquatic chemical foragers can detect predator density based on the concentration of diffusing chemical cues (i.e., actual presence of predators is not required to induce antipredator behavior) (Holker and Stief, 2005). The second type of foragers, Local Information Foragers, only detect local predator cues that are associated with the actual predators. LIFs develop their perception of predator density based on their experience of encounters with predators (Chapters 7 and 8). The difference between GIFs and LIFs is not only the spatial range over which they estimate the predator density but also how they obtain the information. While GIFs can detect the predator density passively even when they stay in a refuge, LIFs must leave their refuge and sample the environment to gain information about predators.
I examined two important determinants of the fate of ecological communities; direct interactions (i.e., the performance of foragers) and indirect interactions (e.g., interactions between predators and resources). To quantify direct and indirect species interactions, I solved for the foraging effort for GIFs and LIFs that maximizes their fitness under their respective biological and physical constraints by using dynamic state variable models (Clark and Mangel, 2000). The solutions were then simulated in a spatially explicit lattice environment. This procedure allowed me to examine the performance (i.e. survival and reproduction) of foragers with different sensory properties. I also examined how these two different foraging strategies affect indirect species interactions. Specifically density- and trait-mediated indirect interactions (DMII and TMII, respectively) of predators on the resource population were examined. DMII is the indirect effect of predators on the foragers’ resource through reductions in forager density, while TMII is the effect of predators on the resource through reductions in forager activity (i.e., due to antipredator behavior) (Werner and Peacor, 2003).

6.2 The Model

A model similar to Luttbeg and Schmitz’s (2000) dynamic optimization model was developed for a $K \times K$ square lattice space with periodic boundary conditions (i.e., edges of the environment are connected to the opposite edges). The model is a three species linear food chain where predators consume foragers, while foragers consume resources. Each cell is occupied by a predator or a forager or is empty. Thus, predators and foragers have explicit spatial locations. Resources are randomly distributed across space, and are instantaneously renewed – hence they are only represented implicitly in the model. Predators and foragers reproduce at the end of one 40-day foraging season. The following fecundity rule from Luttbeg
and Schmitz (2000) was used for the foragers;

\[
\text{Number of offspring} = \frac{x^{0.75}}{3}
\]

where \( x \) is the energy state of foragers. The exponent reflects the allometric constraint of reproduction (Luttbeg and Schmitz, 2000).

The foraging effort \( C \) of foragers is described by the number of lattice cells searched each day. If a forager searches more cells, it is more likely to find resources, but it also becomes more vulnerable to predators. There are six possible levels of foraging effort \( C \) ranging from 0 to 80 (Figure 6–1).

![Figure 6–1. Schematic representation of foraging efforts. The black center square is the forager’s location. The gray squares indicate cells in which the forager will seek food i.e., \( C = 0, 4, 12, \) and 28 from left to right respectively. Foraging effort of \( C = 48 \) and 80 can be similarly characterized (not shown).](image)

Given a probability \( \pi \) of finding a resource in a single cell, and that resources are assumed to be independent between cells, the probability of finding a resource for a given level of effort is \( \lambda = 1 - (1 - \pi)^C \).

Foragers expend energy on metabolism at a rate of \( a \) per day; if a forager finds a resource, it increases its energy state by \( Y \). The maximum energy state obtainable was set to 40. Foragers starve to death if their energy state falls below 1.
GIFs’ perception of the probability of encountering a predator by searching one cell is

\[ \text{Prob}_G(\text{predator}) = \frac{P}{K^2} \]

where \( P \) is the actual number of predators in the entire lattice space (e.g., average risk). LIFs base their estimate of predator probability on past experience: based on the number of predators encountered \((p)\) while foraging in \(k\) cells over the past \(m\) time steps, foragers predict the encounter probability based on a binomial distribution

\[ p \sim \text{Binomial}(k, \text{Prob}_L(\text{predator})). \]

where \( \text{Prob}_L(\text{predator}) \) is the perception of forager about the encounter probability. LIFs have a prior knowledge about this encounter probability, which is set as \( \text{Beta}(\alpha, \beta) \) where \( \alpha \) and \( \beta \) constitute innate knowledge of the foragers (i.e., priors) about the environment. I chose a weak prior that corresponds to an intermediate predator density \((\alpha = 0.01, \beta = 0.99)\). This prior is weak and is equivalent to a single prior observation in a binomial process with 1% of probability of encountering a predator for a given cell (e.g., \(\approx 25\) predators in the environment).

These specifications lead to the posterior distribution for \( \text{Prob}_L(\text{predator}) \), \( \text{Beta}(\alpha + p, \beta + k - p) \), which is used by LIFs to determine their optimal strategies.

The perception of the probability of surviving a given foraging effort, \(C\), for GIFs is approximated by

\[ \text{Prob}_G(\text{survive}) = (1 - d \text{Prob}_G(\text{predator}))^C \]

where \( d \) is the probability of being killed given an encounter with a predator. LIFs’ perception of this probability is approximated by

\[ \text{Prob}_L(\text{survive}) = (1 - dU)^C, \quad U \sim \text{Beta}(\alpha + p, \beta + k - p). \]
The fitness functions $F(x, t)$ (for GIFs) and $F(x, p, k, t)$ (for LIFs) are defined as the maximum expected reproductive success between day $t$ and the end of the forager’s life given that its current energy state is $x$ and that it has encountered $p$ predators while searching $k$ cells in past $m$ time steps.

The dynamic optimization rules can be described by

$$F(x, t) = \text{Prob}_G(\text{survive})\{\lambda F(x + Y - a, t + 1) + (1 - \lambda)F(x - a, t + 1)\}$$

$$F(x, p, k, t) = \int_0^1 \text{Prob}_L(\text{survive})\text{Beta}(u; \alpha, \beta, p, k)\times \{\lambda F(x + Y - a, t + 1) + (1 - \lambda)F(x - a, t + 1)\}du$$

Then we can solve for the optimal foraging effort $C$ by using the backward iteration procedure (Clark and Mangel, 2000). Table 1 shows the parameters used for the backward solutions.

Table 6–1. Parameter values used for the simulations. For the description of parameters, see the text.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Notation</th>
<th>Value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Lattice</td>
<td>$K$</td>
<td>51</td>
</tr>
<tr>
<td>P(food</td>
<td>cell)</td>
<td>$\pi$</td>
</tr>
<tr>
<td>Memory</td>
<td>$m$</td>
<td>3</td>
</tr>
<tr>
<td>Predation</td>
<td>$d$</td>
<td>0.5</td>
</tr>
<tr>
<td>Resource value</td>
<td>$Y$</td>
<td>3</td>
</tr>
<tr>
<td>Dispersal</td>
<td>$D$</td>
<td>1,2,3,4,5</td>
</tr>
<tr>
<td>Metabolism</td>
<td>$a$</td>
<td>1</td>
</tr>
</tbody>
</table>

6.2.1 Lattice Simulations

6.2.1.1 Direct effects: performance of foragers

After the behavioral solutions for GIFs and LIFs were found, spatially explicit simulations were conducted with 100 foragers with an initial energy state of 5 units. Predators and foragers were randomly distributed over the lattice space at the beginning of the simulation.
The number of predators was varied from 5 to 50 in increments of 5. Predators are considered *encountered* if they are found in the cells that were searched (Figure 6-1) in accordance with the foraging solution. Foragers were set to their initial location throughout the season (i.e., they foraged around a random fixed location) whereas predators relocated daily. Predators dispersed randomly to an empty cell within a radius of $D$. For each possible parameter set (Table 6-1), 30 simulations were conducted. At the end of each simulation, the number of surviving foragers, fecundity of the survivors, and the depletion of resource by the forager population were recorded. The survival and fecundity represent the direct effect of predators on foragers, while resource uptake is used to quantify indirect effects (discussed below).

### 6.2.1.2 Indirect effects

In order to compare the strength of various indirect effects, I used three treatments in the simulation (Chapter 5). All the treatments contained the basal resource and foragers, but differed in the type of predators they included. The *true-predator treatment* incorporated unmanipulated predators that could both kill foragers and induced changes in traits of foragers. The *threat-predator treatment* contained predators that induced forager antipredator behavior but did not kill foragers. In the *culling* treatment, no predator was introduced, but foragers were artificially removed from the environment at the rate at which they were removed by predation in the true predator treatment.

Based on these treatments, TMII and DMII were quantified as follows (Chapter 5),

$$
\text{DMII} = \text{Resource eaten(threat)} - \text{Resource eaten(true)}
$$

$$
\text{TMII} = \text{Resource eaten(culling)} - \text{Resource eaten(true)}
$$

where “Resource eaten” indicates the cumulative amount of resource consumed
by the forager population at the end of the season. Thus, these measurements are approximations to the actual TMII and DMII that occur in the system throughout the season (Chapter 5).

6.3 Results

6.3.1 Direct Effects: Performance of GIFs and LIFs

When predator density was high (e.g., 50 predators), GIFs survived better than LIFs (Figure 6–2). On the other hand, the average fecundity of surviving LIFs was always higher than that of GIFs. Fitness (i.e., the product of survival and fecundity) of LIFs was uniformly higher when predators’ movement range was small, but as the dispersal range $D$ of predators increased, their advantage over GIFs diminished (Figure 6–2).

6.3.2 Indirect Effects

At any parameter and variable combinations, TMII for GIFs were always larger than TMII of LIFs (Figure 6–3). DMII was uniformly larger than TMII in LIFs. In GIFs, the relative strength of TMII and DMII changed depending on predator dispersal and resource level (Figure 6–3).

The strength of DMII decreased with increasing resource level while it increased with increasing predator dispersal $D$ and density $P$. The strength of TMII for GIFs was greater when the predator density was high than when the predator density was low, but was relatively unaffected by predators’ dispersal range.

6.4 Discussion

The current study indicates that differences in the way predator cues propagate leads to considerable differences in forager performance and in indirect effects on resource uptake. Because the model included only random predator movement (excluding behaviors such as aggregation and area-concentrated foraging (Kareiva and Odell, 1987; Schellhorn and Andow, 2005)), the spatial...
effects seen were due to the sampling error (i.e., random variability) of predation risk in the spatial environment. For example, if the environment contains a single predator, then a location near the predator and another location far from the predator have very different actual predation risk. This difference diminishes as predator density increases because every location becomes closer to a predator. Thus, sampling error is largest when the density of predators is low. When predator density is low, even when predator dispersal is high, LIFs have higher fitness than GIFs (results not shown). Dispersal of predators also acts to homogenize the predation risk in the environment. If dispersal is unlimited, the model loses its spatial characteristics. Limited dispersal of predators enhanced the
Figure 6–3. Effect size for TMII (T) and DMII (D) with variable number of predators (P).

sampling errors of predation risk in the environment and gave an advantage to LIFs (Figure 6–2).

In a spatially structured environment (e.g., with limited predator dispersal), GIFs survived better but sacrificed fecundity compared to LIFs (Figure 6–2). Because survival and fecundity represent direct density and trait effects of predators on foragers respectively, we can interpret that the different mechanisms (i.e., GIF vs. LIF) result in the tradeoff between direct trait and density effects. This result may be consistent with Preisser et al’s (2005) meta-analysis, which found that trait-mediated effects are stronger in aquatic system than in terrestrial systems. In aquatic systems, predator cues may diffuse in the environment more readily and/or persist longer and thus foragers cannot respond to the actual location of predators; they must act like GIFs. Consequently, aquatic chemical foragers may exhibit high levels of antipredator behavior even when actual predation risk is low.
The effect of the spatial structure on indirect interactions was large (Figure 6–3). Like direct trait effects, trait-mediated indirect interactions were generally stronger in GIFs than in LIFs. In particular, TMII of LIFs is almost negligible throughout the parameter space, indicating antipredator behavior alone does not produce much effect. This is because predation probability used in the simulation was relatively high ($d = 0.5$). Under the highly efficient predators, LIFs become more opportunistic and the value of antipredator behavior becomes small. Antipredator behavior induced through experience, as in LIFs, has value only when foragers have sufficiently good chance of surviving the encounter (Sih, 1992). When the probability of surviving an encounter is small, there is little chance of learning from the experience. If the predation risk is lowered ($d = 0.25$), the effect size of TMII increases, but the general characteristic discussed here is not affected by this change.

In LIFs, DMII was always stronger than TMII. On the other hand, in LIF, the relative magnitude of TMII and DMII were sensitive to the predator dispersal, the resource availability, and number of predators. GIFs change their behavior based on the number of predators in the environment, not where predators are located, thus predator dispersal does not affect trait expression. On the other hand, predators with a high dispersal ability can more effectively deplete foragers in the environment. Therefore, when predator dispersal is high, parameter region where DMII is greater than TMII becomes wide. Previously, the relative size of indirect effects were discussed potentially as an important index that helps determine community stability (Werner and Peacor, 2003). If true, this result indicates that we should consider spatial structure as well as the perception of foragers in these models as they can qualitatively alter such a relationship.

The results from direct and indirect effects also have implications for experimental designs that are commonly used to quantify trait effects (Werner
and Peacor, 2003). In experiments where foragers detect predators based on the cues that may spread far from predators (e.g., GIFs), artificial arenas may cause prey to exaggerate their trait expression. For example, in aquatic system with chemosensory foragers, antipredator behaviors are often studied by introducing water that held predator species because it contains chemical cues used for identifying the existence of predators by foragers (Holker and Stief, 2005) or introducing caged predators (Anholt and Werner, 1998). However, no study has examined how the chemical cue diffuses in water or how rapidly it decays. Thus although there is evidence that water that contained more predators is more effective in inducing antipredator behavior (Holker and Stief, 2005), emerging spatial interactions will be strongly affected by such unknown physical details. For example, chemical foragers in aquatic and terrestrial environment would mediate very different trait effects because of the differences between the physical properties of water and air. If the cue is quickly homogenized in the environment, the system becomes similar to GIFs examined in this paper. Relatively small arenas used in experiments may potentially create a bias because it prohibits foragers from moving to areas where the chemical cue is absent (e.g., eventually predator cues may fill up the arena).

To date, most community models with adaptive foraging behaviors have not incorporated spatial structure (Abrams, 1993; Fryxell and Lundberg, 1998; Krivan, 2000; Abrams, 2001). Thus, we do not understand how these adaptive behaviors result in community dynamics in a spatially explicit environment or the possible role of the physical environment. Furthermore, because conventional non-spatial models give results similar to GIFs, it is possible current general understanding about the effect of trait change on community dynamics (Bolker et al., 2003) may apply only to specific scenarios. Behaviorists have long known that physical environment affects behavior through sensory mechanisms (Endler, 1992), and
these specificities indeed seem to act distinctively in real ecosystems (Preisser et al., 2005). Although more studies are needed, investigation of adaptive behavior through sensory constraints may be a fruitful way to further advance the interface of adaptive behavior and community dynamics.
CHAPTER 7
PROLONGED EFFECTS OF PREDATOR ENCOUNTERS ON THE JUMPING SPIDER, *PHIDIPUS AUDAX* (ARANAE: SALTICIDAE)

### 7.1 Introduction

Prey species respond to the effect of predation risk on fitness by expressing a variety of antipredator traits (e.g., Lima and Dill, 1990; Eisner et al., 2000; Mappes et al., 2005; Caro, 2005). One common antipredator trait is vigilance behavior, where animals increase their ability to detect predators at the cost of reduced resource intake (e.g., Bertram, 1980; Bekoff, 1995; Bednekoff and Lima, 2002; Randler, 2005). Community ecologists have been increasingly interested in this type of behavior because it is known to affect the dynamics of ecological communities (Werner and Peacor, 2003; Bolker et al., 2003).

Most community models with adaptive behavior include a variable describing the level of foraging effort. The nature of this variable varies among studies. Some studies are vague about foraging effort (Matsuda and Abrams, 1994; Abrams, 1992; Luttbeg and Schmitz, 2000); some identify it with a measure of foraging intensity such as search speed (Leonardsson and Johansson, 1997); and others define it as frequency, the fraction of total time available that foragers spend foraging (Abrams, 1990). Empirical studies indicate that foragers can respond to environmental cues by changing both intensity and frequency of foraging (Johansson and Leonardsson, 1998; Anholt et al., 2000). The community implications of predator-induced changes in foraging effort depend on whether foragers change their intensity or frequency of foraging. Indeed, one of the central foci of community models are the indirect effects that arise on the prey’s resources in response to changes in the forager’s behavior induced by the predator.
Consider a forager whose resource intake is described by a Holling’s type II functional response (Holling, 1959; Royama, 1971; Jeschke et al., 2002). In the simplest case, the rate of consumption and therefore the rate of resource depletion by a foraging population is \( NaR/(1 + ahR) \) where \( a \) and \( h \) are attack rate and handling time, and \( N \) and \( R \) are densities of foragers and resource, respectively. Let \( c \) be a parameter that represents the effect of a predator on the foraging effort. If predators affect “intensity”, then the predator effect is represented by a reduction in the encourage rate:

\[
W_{\text{int}} = N \frac{acR}{1 + achR} \quad (7-1)
\]

On the other hand, if foraging effort is reduced by altering the frequency of foraging, then we must modify the density of foragers:

\[
W_{\text{freq}} = Nc \frac{aR}{1 + ahR} \quad (7-2)
\]

The difference between these two models (eqns. 7–1 and 7–2) can be substantial. For example, Figure 7–1 shows as much as a 17% difference in foraging effort depending on whether frequency or intensity is assumed. This can alter the community dynamics qualitatively (Okuyama, unpublished manuscript). Most community models that allow for adaptive foraging use a mathematical formulation based on intensity rather than frequency (although the distinction is irrelevant in models with type I functional response). Thus, we need empirical studies that help us differentiate between these models and thus better guide theoretical approaches.

Antipredator behavior also includes both escape behavior and avoidance behavior (Sih, 1985). Ecologists have rarely distinguished between escape and avoidance, and they are often used interchangeably (Hemmi, 2005a). Here, I consider escape behavior to be a direct response of prey to an encounter with a predator (e.g., running away) while avoidance is prey behavior that decreases the
Figure 7–1. Resource depletion rate under a Type II functional response based on the two different assumptions of foraging effort: intensity of effort ($W_{\text{int}}$, solid line) or frequency of effort ($W_{\text{freq}}$, dashed line). Parameters used were obtained from the damselfly *Ischnura elegans* feeding on *Daphnia* ($a = 1.38; h = 0.032$; Thompson (1975)). The vertical line (at foraging effort $C = 0.56$) corresponds to a reduction in foraging in response to a fish predator for the damselfly *Ischnura verticalis* feeding on *Daphnia* (Peacor and Werner, 2004). $N = 60$; $P$ (predator density) = 15.

Probability of encounter with, or detection by a predator. Just as with frequency and intensity of foraging, avoidance and escape behavior result in qualitatively different model predictions. For example, in eqn. 7–1, escape behavior reduces the realized attack rate by pushing $c$ below 1. In contrast, avoidance behavior would induce density-dependent effects because in order for a forager to escape from being detected by predators, it needs to reduce its activity level as predator density increases. Most mathematical models assume foragers closely track the density of predators and exhibit avoidance behavior.

One way to identify the type of activity expressions (e.g., intensity vs. frequency) and to validate the existing models is to extrapolate prey’s proximate responses (e.g., encounter with a predator). Decision theoretical models (Dall et al., 2005) describe how animals use proximate information to infer the density of predators and determine behavior. A typical model prediction from such a model is that a forager that had encountered a predator twice would increase
vigilance, foraging less intensely in return for increased predator detection when compared with a forager that had encountered one or zero predators (e.g., Luttbeg and Schmitz, 2000). Thus, foragers in an environment with a high predator density will exhibit lower foraging intensity than foragers in an environment with a low predator density because on average they encounter more predators. These proximate cue-based models have two advantages. First, the mechanistic nature of proximate models allows them to make context dependent predictions that other phenomenological models cannot. For example, a giving-up density model that incorporates a forager’s proximate cues (e.g., encounter frequency) for assessing the remaining resource density can predict changes in a forager’s strategy in response to the statistical distribution of resources among patches (Iwasa et al., 1981). In this case, a phenomenological model represents a specific case of a mechanistic model. Second, predictions from proximate cue models can be used to study how animals translate their experience into behavior. Despite these features of mechanistic models and numerous antipredator behavior studies (Caro, 2005), we know little about how animals perceive predation risk and adjust their behavior (Lima and Steury, 2005). As discussed above, details of behavior (i.e., intensity vs. frequency, or avoidance vs. escape) can cause large differences in community dynamics. Ecologists need to understand behavior in order to predict how they will scale up to community dynamics, because community dynamics are inherently summaries of behavioral processes such as predation and reproduction.

This study examines how an initial encounter with a predator influences the avoidance behavior (i.e., time to come out of a refuge) of jumping spiders over time. The study also examines how their behavior to come out of the refuge is influence by a neutral stimulus. The duration of their avoidance behavior gives some information about the type of dynamics they may produce (eqn. 7–1 vs. 7–2). Their response to the neutral stimulus after an encounter with a predator will give
us some information about their potential decision making processes that can be discussed in a decision-theoretical context (Dall et al., 2005).

7.2 Materials and Methods

Eggs of the jumping spider *Phidippus audax* were collected from their nests that are typically placed on solid substrates such as hard wood and artificial structure in the vicinity of the University of Florida, Gainesville, FL. Before spiders were used in the experiment, they were housed individually in a plastic container (62 mm in diameter and 30 mm in height; approximately cylindrical) with water supply, and were fed twice a week. Second-instar hatchlings were used in the experiment. All spiders were fed *ad libitum* food for 24 hrs and deprived of food for 2 days to standardize their degree of starvation, which is known to affect their foraging behavior (Gardner, 1964).

The experiment was done in a $2 \times 2$ factorial design. One of the factors was predator (encounter or no-encounter). This treatment was established to examine whether encounter with a predator had an effect on the spiders’ subsequent response to an ambiguous visual stimulus (the other factor). Jumping spiders, like other visual predators (Cronin, 2005), detect an object and subsequently identify it (as a prey, predator, etc). Thus, the response of spiders to an ambiguous stimulus can provide finer information on the duration of behavioral antipredator responses than their response to an actual prey visual cue. This is because an absence of response to an actual prey item does not necessarily indicate that that effect of predator has diminished.

The experimental arena was made of two 2 cm long circular rubber tubes (Figure 7–2). A smaller green semi-transparent tube (4 mm in interior diameter, 1 mm thickness) was placed inside a larger (10 mm in interior diameter, 1.5 mm thickness) clear tube, with an empty space between the inner and outer tubes. This space was closed at both ends with pieces of rubber. One end of the smaller tube
Figure 7–2. Schematic diagram of the experimental arena. The arena consists of two physically separated open spaces: an inner space and an outer space. The openings of both spaces are closed (colored gray) except for the front opening of the inner space. Numbers represent different time periods (steps). Step 1 represents the time spiders spent at location 1 before approaching the exit, Step 2 is the time spiders took from leaving location 1 to reaching location 3, and Step 3 is the time spiders spent at location 3 before leaving the tube.

was closed with a sponge so that only one end was open. In each experiment, a spider was placed inside the inner tube.

7.2.1 Study System

7.2.1.1 Predator treatment

Each trial started by introducing a jumping spider into the inner tube. When the spider came to the tip of the entrance/exit hole, a visual predator stimulus (a dead adult *Phidippus audax* female) was shown by placing it at the exit. Intraguild predation and cannibalism, where larger individuals consume smaller individuals, are common in jumping spiders. Because spiders possess an innate perception towards other spiders (*Land, 1972*), presentation of the dead adult individual resulted in spiders running back to the inner end of the tube, which was the reference point (location 1 in Figure 7–2) for subsequent movement (see Behavioral measures below).

For the no-predator treatment, it was impossible to make a spider retreat inside the tube without a stimulus. Even artificial visual stimuli such as human
fingers, forceps, and match sticks were insufficient to make spiders retreat back into the tube. Thus, to make spiders move to the end of the inner tube so that the behavioral assay could be run in a comparable manner, a match stick was used to nudge spiders to the back of the tube.

### 7.2.1.2 Ambiguous visual stimuli

The second treatment was the presence or absence of ambiguous visual stimuli. Jumping spiders visually detect and identify objects (Land, 1972). Spiders first detect movement of an object with their posterior lateral eyes (PLE), then orient towards the object and identify it with their anterior median eyes (AME). Thus, the initial detection of an object does not allow spiders to identify the object (i.e., the visual stimulus will be ambiguous) unless they have the object in clear view of the AME. To introduce such visual stimuli, five adult flour beetles, *Tribolium confusum*, were contained in the space between the two tubes (outer space) and the space was closed such that the beetles could only move around within the space (Figure 7–2). Because the inner tube was not completely opaque, a spider inside the inner space could visually sense the movement of the flour beetles but (arguably) not identify them.

### 7.2.2 Behavioral Measures

The time taken for spiders to walk the length of tube and come out of the tube entirely was divided into three steps (Figure 7–2). Step 1 is the duration from the time spiders touched the back wall or were nudged to the inner end of the tube to the time they began to move to the exit; step 2 is the time that spiders took to move from the inner end of the tube to the exit; and step 3 is the time interval from the spiders’ arrival at the exit of the tube to when they exited the tube completely. An observer could see the location of a spider through the inner and outer tubes, although the inner tube made it impossible to identify the orientation of an individual.
7.2.3 Statistical Analysis

The study used 26 spiders. All spiders experienced all treatments. To eliminate the bias caused by the treatment order, all 24 possible orders were allocated (the remaining two individual experienced the same treatment order as another individual). Each treatment for each subject was separated by at least 3 days. All individuals eventually came out of the tube (maximum of 2868 sec), at which time a trial was terminated.

Because of the repeated measures design (each individual was used for multiple treatments), mixed effects ANOVA accounting for between-individual variation was used. The statistical model was parameterized such that no-predator, no-ambiguous visual stimuli, and step 1 were set as the reference levels of the respective factors. The data were analyzed in two ways. First, treatment effects were examined without separating into the three time units. This result represents the treatment effects on individuals’ time to come out of the tube. In order to examine the temporal effect of treatment effects, the same data were also analyzed with the three explicit time steps. The model with the best AIC was utilized in the results. The duration measures were square root transformed so that the data are normally distributed based on a Pearson chi-square normality test for all treatments ($p > 0.15$ for all). Variances within the predator treatment were statistically not different with Levene’s test ($p > 0.05$ for both).

7.3 Results

Encounter with a predator prolonged the spiders’ stay in the tube (Figure 7–1, Table 7–1). The ambiguous visual stimuli did not affect the time to come out when spiders had not encountered a predator, but if they had encountered a predator, the ambiguous stimuli caused spiders to stay in the tube significantly longer (Table 7–1).
For each time step, spiders showed a similar behavior where they exhibited differential response to the ambiguous stimuli only when they encountered a predator stimulus (Figure 7–4).

The interactions between predator treatment and step were always negative except for the step 2 in the without ambiguous stimuli treatment (Table 7–2). These interactions were significant for step 3 in both cases (i.e., with and without ambiguous stimuli), but only significant for the treatment without ambiguous stimuli in step 2. A detailed biological interpretation is given in discussion.

Table 7–1. Estimated parameters from the random effect model. SE (standard error) and RE (random effect).

<table>
<thead>
<tr>
<th></th>
<th>Value</th>
<th>SE</th>
<th>RE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>13.61</td>
<td>1.23</td>
<td>3.28</td>
<td>11.04</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Predator</td>
<td>10.83</td>
<td>2.25</td>
<td>8.66</td>
<td>4.79</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Ambiguous stimuli</td>
<td>-0.99</td>
<td>0.148</td>
<td>-0.67</td>
<td>0.51</td>
<td></td>
</tr>
<tr>
<td>Interaction</td>
<td>9.12</td>
<td>2.10</td>
<td>4.33</td>
<td>0.01</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td></td>
<td></td>
<td>5.36</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Table 7–2. Statistical results for with and without ambiguous stimuli. RE indicates the random effect describing the standard deviations. Parameters with missing RE values are fixed effects.

### Without ambiguous stimuli

<table>
<thead>
<tr>
<th></th>
<th>Value</th>
<th>SE</th>
<th>RE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>6.11</td>
<td>0.72</td>
<td>0.96</td>
<td>8.45</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Predator</td>
<td>8.88</td>
<td>1.38</td>
<td>4.93</td>
<td>6.42</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Step 2</td>
<td>3.14</td>
<td>1.19</td>
<td>3.40</td>
<td>2.64</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Step 3</td>
<td>0.58</td>
<td>1.11</td>
<td>2.56</td>
<td>0.52</td>
<td>0.60</td>
</tr>
<tr>
<td>Predator × Step 2</td>
<td>-3.28</td>
<td>1.39</td>
<td>2.35</td>
<td>0.02</td>
<td></td>
</tr>
<tr>
<td>Predator × Step 3</td>
<td>-4.87</td>
<td>1.39</td>
<td>3.49</td>
<td>&lt; 0.01</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td></td>
<td></td>
<td></td>
<td>3.56</td>
<td></td>
</tr>
</tbody>
</table>

### With ambiguous stimuli

<table>
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<tr>
<th></th>
<th>Value</th>
<th>SE</th>
<th>RE</th>
<th>t-value</th>
<th>p-value</th>
</tr>
</thead>
<tbody>
<tr>
<td>Intercept</td>
<td>6.86</td>
<td>0.94</td>
<td>1.80</td>
<td>7.28</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Predator</td>
<td>13.39</td>
<td>1.60</td>
<td>5.16</td>
<td>8.38</td>
<td>&lt; 0.01</td>
</tr>
<tr>
<td>Step 2</td>
<td>0.80</td>
<td>1.63</td>
<td>5.37</td>
<td>0.49</td>
<td>0.62</td>
</tr>
<tr>
<td>Step 3</td>
<td>-0.49</td>
<td>1.37</td>
<td>3.06</td>
<td>-0.35</td>
<td>0.72</td>
</tr>
<tr>
<td>Predator × Step 2</td>
<td>0.72</td>
<td>1.74</td>
<td>0.41</td>
<td>0.68</td>
<td></td>
</tr>
<tr>
<td>Predator × Step 3</td>
<td>-9.38</td>
<td>1.74</td>
<td>-5.36</td>
<td>&lt; 0.01</td>
<td></td>
</tr>
<tr>
<td>Residual</td>
<td></td>
<td></td>
<td></td>
<td>4.46</td>
<td></td>
</tr>
</tbody>
</table>
Figure 7–4. Box plot for the duration of each step for each treatment.

7.4 Discussion

Spiders that did not encounter a predator emerged equally quickly whether they were exposed to ambiguous visual stimuli or not, but spiders that encountered a predator took significantly longer to come out of the refuge in the presence of visual stimuli (significant interactions: Table 7–1). Similar predator effect has been observed in other animals (Jennions et al., 2003; Hugie, 2004) suggesting that a hiding behavior is a typical antipredator behavior in wide variety of taxa.

The observed behavior qualitatively agrees with the predictions of decision-theoretical models (e.g. Luttbeg and Schmitz, 2000). In these models, individuals formulate their perception about the environment in light of both prior information (e.g., innate decision rules) and experience (e.g., encounters). This new perception
about the environment is called the posterior distribution, and animals base their subsequent decisions on this posterior distribution (Dall et al., 2005). In the current study, if we consider the predator treatment as manipulating prior information (spiders’ prior estimate of their predator encounter probability is higher when they are given a predator stimulus) and the ambiguous stimulus treatment as their experience, we can interpret the difference in the spiders’ response to the ambiguous stimulus as resulting from their difference in posterior distributions (i.e., spiders are more likely to interpret the ambiguous stimulus as a predator after the encounter). This is why this study is different from other studies that investigated the effect of predators only. For example, Jennions et al. (2003) examined hiding behavior (i.e., time to stay in a nest) of fiddler crabs after exposing them to a predator visual cue and found the significant predator effect similar to the jumping spiders. However, without examining the response to an ambiguous stimulus, it is not possible to examine how the perception with respect to the predation risk may operate in the decision-theoretic framework as discussed above. Similarly, the use of a prey stimulus in this study instead of the ambiguous stimuli would have been ineffective because the prey stimulus may not contribute any information towards the prior information of the predation risk unless animals possess some innate perception about the occurrence of predators and prey.

The adaptive behavioral models used in community ecology assume that foragers can keep track of the density of relevant stimuli (e.g., conspecifics, predators, resources) in order to adjust their behavior accordingly. The decision-theoretical mechanism described above can potentially lead to such behavior, but the short temporal effect shown here would not be strong enough to create a magnitude of trait effect that is exhibited by typical models. In Chapter 6, I have shown that even with a moderately persistent predator effect (more persistent effect than the result of this experiment), when an encounter with a predator is infrequent, the
model exhibits much weaker trait effect than typical models. However, this study only examined the predator effect on the time to come out of refuge, and it is possible that the predator effect is more persistent on other aspects of behavior (Chapter 8). Further studies on the effect of predators on a suite of trait expression are needed to examine the validity of the existing models of behavior in community ecology.

The interpretation of the two treatments (i.e., predator treatment and ambiguous stimuli treatment) requires some caution. First, it is uncertain whether spiders were unable to identify the ambiguous visual stimuli as the treatment intended. However, such identification of objects is unlikely because jumping spiders require a clear contrast of an object with its background for identification (Land, 1972), which was likely removed by the semi-transparent inner tubes. Second, the no-predator treatment did not consist of no-stimulus, but spiders were pushed to the reference point with a match stick. However, spiders did not respond to the artificial object (i.e., match stick) very strongly, while their response to a predator stimulus was very distinct (personal observation). Thus, the no-predator treatment effectively produced the response similar to the scenario where no stimulus was given to spiders. Otherwise, the no-predator treatment would have made the predator effect conservative because, if anything, the manipulation will likely to make spiders more cautious, but very large treatment effects were obtained.

When the statistical analysis incorporated different steps, the interaction (between predator and step 2) was significant only in the treatment without the ambiguous stimulus (Table 7–2). Biologically, this negative interaction between step 2 and the predator factor (−3.28, Table 7–2) may be interpreted as a waning of the predator effect (8.88, Table 7–2) over time. Thus, the predator effect diminished by about 37 % in the treatment when the ambiguous visual stimuli
was absent. This effect was not statistically different from zero when spiders were exposed to the ambiguous visual stimulus. Further studies are needed to understand latency of predator effect as it is a vital assumption in theoretical models that allow foragers to track dynamic environments (Luttbeg and Schmitz, 2000).

Community ecological models incorporating adaptive individual behavior are now common, but behavioral details, which may have significant effects on community dynamics (Figure 7–1), have rarely been examined. Though common models appear simple and transparent, they make implicit assumptions about behavioral expression. We do not know how well any specific model structure can approximate a variety of behavioral expressions (Caro, 2005). To respond to this issue, more mechanistic frameworks such as decision-theoretical models have been developed (Dall et al., 2005). This study examined the temporal carry over effect of the predator encounter, which is a central assumption in those mechanistic models. In order to further understand and validate existing community models with adaptive behavioral components, we need to understand how individuals translate their experience to behavioral expression rather than simply demonstrating a general pattern such as reductions in foraging in high-risk environments (Lima and Steury, 2005). Understanding the details of behavioral expression will allow us to examine more appropriately how behavior scales up to community dynamics.
CHAPTER 8
SUSTAINED EFFECTS OF VISUAL STIMULI ON RESTING METABOLIC RATES OF JUMPING SPIDERS

8.1 Introduction

Behavioral dynamics, especially changes in mean activity levels over time in response to predators, competitors, and prey, significantly affect the population dynamics of ecological communities (Werner and Peacor, 2003). In predator-prey communities, activity dynamics may cause qualitative changes in the community dynamics. For example, they may allow persistence (Kondoh, 2003) or induce population cycles (Abrams and Matsuda, 1997). A number of theoretical studies examining the relationship between activity and population dynamics (Bolker et al., 2003) have suggested that the predictions of community models are sensitive to the details of behavioral models.

Vigilance behavior is one of the best-studied mechanisms of activity dynamics (Lima and Dill, 1990; Caro, 2005). Typical mathematical models of vigilance behavior assume that animals adjust their vigilance in response to the densities of predators and resources (e.g., Abrams, 1992, 1995); many empirical studies support this assumption (Stephens and Krebs, 1986; Kagata and Ohgushi, 2002; Caro, 2005). For example, larval frogs reduce their activity level in response to increases in resource or predator densities (Anholt et al., 2000). However, these studies quantify changes in activity level under the influence of a persistent stimulus. For example, Anholt et al.’s (2000) study used caged predators to supply a chemical cue that varied in concentration among treatment, but persisted in time. The activity levels of prey under these typical experimental conditions (Anholt and Werner, 1998; Peacor and Werner, 2001; Holker and Stief, 2005), however, only reflect the
behavior of prey that are persistently exposed to predator cues (Chapter 5). Such a scenario is unlikely for prey that detect predators only intermittently (common in prey that detect predators visually). Most models used to predict the linked dynamics of behavior and populations implicitly assume that prey can modify their behavior in concert with changes in predator population densities; prey must show sustained responses with respect to predator cues in order to track predator densities when predator cues are intermittent.

This study examines how jumping spiders, which are exposed to predator and prey visual cues during the day, change their metabolic rates on subsequent nights. Spiders maintain only half the resting metabolic rate of other poikilothermic predators (Anderson, 1970, 1996), lowering metabolism still further when they experience prey shortages (Anderson, 1974). Although the effects of predator and prey stimuli on immediate responses (e.g., time to come out of a refuge; Chapter 7) are well studied in these spiders and other organisms (e.g., Jennions et al., 2003), little is known about the effects of such experiences during the day on longer-term responses such as changes in metabolism at night. In this study, I hypothesized that because jumping spiders visually detect objects, visual stimuli alone may be sufficient to maintain resting metabolic rate of starving spiders above the expected level in the absence of such stimuli. To test this idea, I examined how visual stimuli of predator or prey alone, in the absence of access to prey, affect the resting metabolic rates of starving jumping spiders.

8.2 Materials and Methods

Eggs of the jumping spider *Phidippus audax* were collected from their nests that are typically placed on solid substrates such as hard wood and artificial structures in the vicinity of the University of Florida, Gainesville, FL. Upon hatching, spiders were kept individually in plastic containers. Third instar spiderlings were used for study. Spiders were kept in a controlled environment
chamber (light:dark = 12:12, the shifts occurring at 0700 and 1900, temperature = 25 °C) during the second instar and a part of their third instar before being used in the experiment. During this time, spiders were fed one fruit fly (*Drosophila melanogaster*) every third day. For the three days before the experiment started, spiders were fed one fly daily. All individuals were fed on the same schedule to ensure similar starvation levels among test subjects at the beginning of the experiment.

8.2.1 Experimental Treatments

The goal of this study was to examine the effect of visual stimuli on the resting metabolic rate of starving spiders. The experiment consisted of four treatments that were intended to vary spiders’ experience based on their visual stimuli. Spiders in the first treatment (none treatment) were given neither prey for consumption nor visual stimuli; this treatment is comparable to other studies that examined the effect of starvation on metabolic rate (e.g. Anderson, 1974). Spiders in the second treatment (prey treatment) were shown prey (i.e., received visual prey stimuli) but were not allowed to consume them. Spiders in the third treatment (predator treatment) were shown a predator stimulus and were not given prey (i.e., neither consumption nor visual prey stimulus). Spiders in the last treatment (fed treatment), were given a single prey daily to consume (consumption and visual prey stimulus).

Groups of five spiders, representing a single sample (see Oxygen measurement below), were kept in an experimental arena consisting of two nested clear plastic containers. A smaller container (62 mm in diameter and 43 mm in height, approximately cylindrical) was placed inside the larger container (107 mm in diameter and 78 mm in height, approximately cylindrical) so that the walls of the inner container physically separated an inner from an outer space, but objects in each space were visible from the other space. Subject spiders were
kept inside the inner space. In the none treatment, both the inner and outer space were left empty except for the treatment subjects. In the fed treatment, five *D. melanogaster* prey were introduced into the inner space; although all prey were always consumed, it is uncertain how the prey were shared among the five subjects. In the prey treatment, five *D. melanogaster* were placed in the outer space, visible but inaccessible to the subjects. In the predator treatment, one adult female jumping spider *Plexippus paykulli* was placed in the outer space, visible but inaccessible. *Plexipplus paykulli* and *Phidippus audax* live in same habitats and intraguild predation is size-dependent; thus, in the field *Plexippus paykulli* adults prey on *Phidippus audax* juveniles (personal observation). Subject spiders and the predator stimulus spiders reacted to each other although separated by the wall of smaller container. In particular, subject spiders exhibited typical vigilance behavior towards the predator stimulus (e.g., halting motion, making slow backward movements, and running away). In contrast, subject spiders occasionally attempted to jump on prey that were separated from them in the outer space, indicating that subjects were able to distinguish the two visual stimuli in the arena.

The four treatments described above were applied from 1000-1600 daily. At 1600, spiders (in groups of five individuals) were gently transferred to a plastic syringe for their oxygen consumption measurement (followed by 2 hours of acclimation period, further described below). The oxygen measurement procedure lasted until the next morning at 0700. Thus, each treatment alternated between treatments and oxygen measurement. This regimen was continued for four days.

### 8.2.2 Oxygen Measurement

Oxygen consumption was measured by using the technique described in Lee (1995). The respiration measurements were conducted in a room with a controlled temperature of 25.76 ±2.2°C (mean±sd). Syringes (60 ml) connected to a glass pipet were used as the respirometric chambers. The syringe plungers were pushed...
in so that a 10 ml space was actually available to spiders. Because of the small size and low respiration rate of individual spiders, five individuals were grouped for measurements; each group of five spiders was contained in a separate syringe and was acclimated for approximately 2 hours each day. Although spiders are cannibalistic, cannibalism is rare at this early instar and was never observed in this experiment. After acclimation, the pipet openings of the syringes were closed with 15% KOH solution and left for stabilization (approximately 30 min). Measurements started at 1900 and ended at 0700 next day. Respired CO\textsubscript{2} in the closed air is absorbed by KOH solution, reducing the pressure inside the chamber and causing the KOH solution to move into the pipet, and thus converted to the volume of oxygen consumed by the spiders (Lee, 1995). The recorded values were calibrated from the measurements from two empty syringes. All treatments of all samples were collected simultaneously to minimize errors caused by potential temperature and humidity fluctuations. Estimates of size and weights were made from one random sample from each sample group of 5 spiders (hence 7 samples from each treatment). The pooled carapace widths and body weight were 0.98±0.0004 mm and 2.26±0.09 mg, respectively (mean±se). No statistical differences in either variables were observed among the treatments (ANOVA, \( p > 0.1 \) for both size and weight).

8.2.3 Statistical Analyses

Oxygen consumption data were converted to differences from the day-0 measurement (i.e., a value of 5 \( \mu l \) on day 1 indicates that oxygen consumption decreased by 5 \( \mu l \) from day 0). The comparison between the food deprivation treatments (i.e., none, predator, and prey treatments) and the fed treatment reveals the effect of food deprivation.

Four models were examined. Let \( \mu_{\text{None}}, \mu_{\text{Prey}}, \) and \( \mu_{\text{Predator}} \) be the mean decrease in oxygen consumption in the none, prey, and predator treatment,
respectively. Then the four models were: (1) visual stimuli (either prey or predator) do not affect metabolic rate (i.e., $\mu_{\text{None}} = \mu_{\text{Prey}} = \mu_{\text{Predator}}$); (2) only prey visual stimuli affect metabolism (i.e., $\mu_{\text{Prey}} \neq \mu_{\text{None}} = \mu_{\text{Predator}}$); (3) only predator visual stimuli affects metabolism (i.e., $\mu_{\text{Predator}} \neq \mu_{\text{Prey}} = \mu_{\text{None}}$); and (4) prey and predator visual stimuli affect metabolism differently (i.e., $\mu_{\text{None}} \neq \mu_{\text{Prey}} \neq \mu_{\text{Predator}}$). The best described model was chosen based on AIC ($= -2l + 2p$) where $l$ and $p$ are the log-likelihood and number of parameters of the model. All models were based on normal distributions with equal variances.

### 8.3 Results

In the fed treatment, spiders maintained their resting metabolic rates at a roughly constant level during the treatment (Figure 8–1). In the starvation treatments, individuals decreased their metabolism significantly regardless of the presence or absence of visual stimuli ($t$-tests, $p < 0.001$ for all comparisons).

![Figure 8–1. Average change (± SE) in oxygen consumptions of spiders ($\mu l/hr/individual$). Average weight of individual spiders was 2.26 mg.](image)

Model 2 (only prey visual stimuli affect metabolism) was selected on days 1 and 2. On day 3, the treatment effect disappeared — model 1 (all metabolic rates equal) was selected.
Table 8–1. AIC for each model. p = number of parameters.

<table>
<thead>
<tr>
<th>No.</th>
<th>Model</th>
<th>p</th>
<th>AIC (day 1)</th>
<th>AIC (day 2)</th>
<th>AIC (day 3)</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$\mu_{\text{None}} = \mu_{\text{Prey}} = \mu_{\text{Predator}}$</td>
<td>2</td>
<td>26.13</td>
<td>30.71</td>
<td>36.66</td>
</tr>
<tr>
<td>2</td>
<td>$\mu_{\text{Prey}} \neq \mu_{\text{None}} = \mu_{\text{Predator}}$</td>
<td>3</td>
<td>21.04</td>
<td>30.10</td>
<td>38.49</td>
</tr>
<tr>
<td>3</td>
<td>$\mu_{\text{Predator}} \neq \mu_{\text{Prey}} = \mu_{\text{None}}$</td>
<td>3</td>
<td>23.74</td>
<td>31.92</td>
<td>37.19</td>
</tr>
<tr>
<td>4</td>
<td>$\mu_{\text{None}} \neq \mu_{\text{Prey}} \neq \mu_{\text{Predator}}$</td>
<td>4</td>
<td>21.91</td>
<td>32.08</td>
<td>39.14</td>
</tr>
</tbody>
</table>

### 8.4 Discussion

Spiders that were given visual prey stimuli maintained higher metabolic rates on day 1 and day 2 compared to spiders in the none treatment and predator treatment (Figure 8–1). Thus visual stimuli as well as physiological state (degree of starvation) influence metabolic rate, although starvation is a primary driver of metabolic rate (as has been shown in other spiders: Anderson, 1974; Tanaka and Ito, 1982). Starvation rapidly induced lower metabolic rates (Figure 8–1), consistent with results found in wolf spiders (Anderson, 1974). Considering that spiders’ labile metabolic rate is often cited as an adaptation to unpredictable prey shortages (Anderson, 1974), it is surprising that their metabolic control is so sensitive to brief periods of starvation — temporary prey shortages can occur by chance even when overall prey availability is high, in which case shutting down metabolism would be inappropriate.

Visual stimuli may affect metabolic rates indirectly through changes in activity level. For example, spiders in the prey treatment may have been more active than those in the predator and none treatment in trying to capture prey. Similarly, spiders in the predator treatment may be minimizing their motion for most of the time in order to avoid predation. If these activity shifts occur, spiders’ proximate response to stimuli is to lower activity levels, and lowered metabolic rates may simply be a byproduct of lowered activity. However, earlier experiments have suggested a weak correlation between activity and metabolic rate in other spiders: wolf spiders exhibit dramatic changes in metabolic rate in response to fasting...
even when activity level was maintained during the fasting period (Anderson, 1974). Jumping spiders can also recover their oxygen consumption rate as well as removing lactate accumulated due to activity with a relatively short period (≈1 hour) (Prestwich, 1983). Thus, I suggest that spiders adjust their metabolic rates in direct response to visual stimuli, rather than as an indirect consequence of changes in foraging behavior. To tease apart the cause and effect relationship between metabolism and activity or other factors, a more elaborate experimental design is required.

Whether the observed results were direct responses or byproducts of changes in activity, this study indicates the possibility that changes in prey densities and predator densities can drive changes in spider behavior and hence that behavior and population dynamics can interact. For example, even when spiders fail to capture prey, a high density of prey may induce a higher degree of foraging activity that maintain a high metabolic rates. While individuals with high metabolic rates must feed more to meet their metabolic needs, a high metabolic rate may also increase the probability of prey capture by allowing energetically demanding activity (Speakman et al., 2004). Thus, spiders that maintain a higher metabolic rate may be successful not only in capturing prey but also in reproducing or escaping predation (Anilletta and Sears, 2000). In general, maintenance of metabolic rate has greater consequences in ectotherms than in endotherms. Thus, spiders altering their metabolic rates independently of actual prey consumption is another avenue for adaptive change in behavior as a function of the environment (Bolker et al., 2003). This result suggests that a failure to observe an obvious adaptive behavior (e.g., immediate response to predator encounter) does not prove the absence of adaptive dynamics predicted by common models. The sustained effect of experience (i.e., seeing prey) may induce a variety of trait effects. Further understanding the ecological consequences of metabolic
changes in response to experience will enhance our understanding of the linkages between behavior, physiology, and ecological dynamics.
CHAPTER 9
ACTIVITY MODES OF JUMPING SPIDERS

9.1 Introduction

A number of studies have revealed that animal behavior has substantial impact on community dynamics (Fryxell and Lundberg, 1998; Bolker et al., 2003; Werner and Peacor, 2003). Behavior affects community dynamics by altering the strength of species interactions (Abrams, 1991; Berlow et al., 2004), which in turn modify both functional and numerical responses of the species involved. For example, foragers that express antipredator behavior (e.g. by reducing their activity level) will lower the realized attack rate of their predators (Anholt et al., 2000). If foragers change their behavior adaptively, this attack rate may become density-dependent and can produce rich dynamics even in a simple model (e.g., Abrams, 1992). One conclusion from these studies is that changes in activity level (e.g., foraging intensity, Chapter 7) of animals can affect community dynamics profoundly.

To model activity dynamics, most theoretical models assume that activity level is determined solely by the trade-off between resource uptake and current predation risk (e.g., Abrams, 1993; Bolker et al., 2003), or by the relative abundances of resource species if the focus is on the switching behavior (Krīvan, 2000; van Baalen et al., 2001; Kondoh, 2003). However, this approximation is sensitive to a variety of details. For example, when animals exhibit antipredator behavior in the frequency rather than the intensity of their activity (Chapter 7), or when spatial constraints are imposed on the species interactions (Chapter 6), the approximation departs from the true dynamics. One reason why the approximation fails in these situations is because activity changes on a faster time scale than the models capture. For
example, common models usually predict a single optimal level of foraging activity with respect to each density of predators (e.g., Abrams, 1993; Křivan and Sirot, 2004). However, in nature, individuals change their behavior at a much faster time scale in response to environmental cues (e.g., Chapter 7). A prey individual may exhibit a variety of levels of activity in one hour or even in a minute while the density of predators may stay relatively constant for long periods (e.g., weeks). Nevertheless, an implicit assumption of the models is that behavioral dynamics that matter to the model are only as fast as the dynamics of the community; the common models ignore behavioral variation that occurs at a fast time scale (oddly, since these models were inspired by the need to include processes that acted at a fast time scale). These fast behavioral dynamics, however, may significantly affect community dynamics (Chapter 10) and need to be described in a manner that can be extrapolated to long-term community dynamics.

This paper investigated jumping spiders in the field to gain a better understanding of their activity dynamics. Because demographic dynamics of jumping spiders occur on a much slower scale than this study addresses (Edwards, 1980), the details of activity I describe in this study are examples of the details that are ignored by the conventional framework of community models with adaptive behavior. In particular, I will demonstrate that these spiders employ a biphasic activity pattern where individuals alternate between periods of activity and inactivity. In addition, I show that this activity pattern is not simply described by their food deprivation level. A simple behavioral model that predicts the observed pattern in the field was examined with laboratory experiments and computer simulations.

9.2 Part I: Quantification of Spider States in the Field

Jumping spiders are diurnal visual foragers (Land, 1972; Hill, 1979; Li et al., 2003). They actively forage (they move to find prey rather than building webs to capture prey) but do produce silk in order to construct retreats for shelter at
night and when not actively foraging (Hoefler and Jakob, 2006). We categorized individuals that were found in their retreat as inactive and individuals that were found outside a retreat as active based on our daytime observations. This classification is only approximate, because individuals that were found in the retreat may have been inactive for different amounts of time (e.g., they may have been active just prior to the observation). To obtain some idea about their previous activity, “food deprivation degree” – equivalent to the time since a spider had last fed to satiation – was also estimated.

9.2.1 Materials and Methods

Activity status and food deprivation level of the jumping spider, *Phidippus audax*, in the field was quantified. Observations were conducted in the vicinity of the University of Florida, Gainesville, FL, containing a variety of grasses, trees, and flowering plants. All observations were conducted between 11:00 and 15:00 when some of the individuals are known to be active. I walked slowly through the field. Once an individual spider was observed, its status was recorded (in retreat or not). The spiders were individually placed in a small cup and were brought to the laboratory within a few hours of observation, and each individual’s body mass were immediately recorded. Then each spider was housed in an individual plastic container (62 mm in diameter and 30 mm in height; approximately cylindrical) and fed *ad libitum* on fruit flies (*Drosophila melanogaster*) and flour beetle larvae (*Tribolium confusum*) for approximately 24 hrs, and its weight at satiation was recorded. Spiders were then deprived of food and their masses were measured daily for 40 days or until they either moulted or laid eggs. Water was supplied daily, because spiders in the field have free access to water, e.g., morning dew.

One way to quantify the degree of food deprivation is to establish a population level reference and compare individual status against it. For example, Bilde and Toft (1998) used a behavioral assay to quantify the food deprivation level of
sheet-web spiders; they created a population-level reference curve in the laboratory that translates a number of prey consumed in a short time period to a food deprivation level in days and then compared behavior of field-collected spiders to the reference curve. However, jumping spiders exhibit a large variation in their predation behavior (this was also apparent in the laboratory experiment described below). Thus, we based an index of food deprivation degree on body mass instead of behavior.

Food deprivation level of an individual was estimated by referencing its mass in the field to the individual mass loss profile. For example, if spider $i$’s mass in the field was $w_i$ and its mass at satiation was $f_i$, the food deprivation degree $T_i$ was estimated as the first day since the satiation that satisfied $w_i < f_i$. If spiders moulted or laid eggs before their mass became lower than $f_i$, values of $T_i$ were estimated from a power function (mass = $a X^b$) estimated from the data, where $X$ is the food deprivation degree (also see Part III below). This consideration was necessary because events such as moulting and egg-laying change spiders’ mass drastically, but we focused on the food deprivation degree based on daily metabolic costs. Differences in the inferred level of food deprivation level between active and inactive spiders were tested with a Wilcoxon Rank Sum test.

9.2.2 Results

A total of 188 individuals were observed (128 immature, 31 females, 29 males). On two occasions, estimates of $T_i$ were greater than 50. These samples were considered outliers and omitted from the following analyses, but their inclusion does not alter the qualitative conclusions. A total of 115 spiders (79 immature, 10 males, and 26 females) were observed as inactive.

On average, individuals classified as inactive were found to be significantly more deprived of food than individuals classified as active (Figure 9–1: $p < 0.05$ for all classes, Wilcoxon Rank Sum test).
Figure 9–1. Box plots for the food deprivation degrees of the spiders in the field. Spiders were classified based on sex and the location where they were found: outside retreat (active) or inside retreat (inactive).

9.2.3 Discussion

The results show that many individuals remain inactive and stay in the retreat during the day even though they may be deprived of food. Because we have not quantified prey density in the field, we cannot attribute these differences in food deprivation to the spiders’ activity levels alone. Nonetheless, the fact that inactive spiders are deprived of food indicates that their decision not to forage is not necessarily altered by food deprivation. This result contradicts other studies that showed hungry spiders eat more and are more risk-prone (e.g., Gardner, 1964; Walker and Rypstra, 2003). If spiders eat more when they are more deprived of food, we would have seen the opposite trend in the results — inactive spiders would have been more satiated.

9.2.4 A Simple Model

A simple mechanism that may explain the observed result (Figure 9–1) is that spiders have an active phase and an inactive phase, and that they switch between the two phases based on a physiological state variable that is related to the degree of food deprivation. The physiological variable (e.g., body mass)
decreases as they are deprived of food, and inactive spiders will become active once their physiological state drops below a threshold $L_{I\to A}$; active individuals become inactive once they capture enough prey to raise their physiological state above a (possibly different) threshold $L_{A\to I}$. If $L_{I\to A} < L_{A\to I}$, individuals at the same physiological state can either be active or inactive (as observed in the field). This will create a tendency for inactive spiders to be more deprived of food on average than active ones. Spiders’ low metabolic rates (Anderson, 1996, Chapter 8) allow them to remain inactive for prolonged periods after a period of successful foraging. If food-deprived spiders forage more intensely (Gardner, 1964; Walker and Rypstra, 2003) when they become active, the apparently contradictory results of this and previous studies may complement each other to explain the observed data (Figure 9–1).

9.3 Part II: Examining the Simple Model

The analysis in Part I determined that spiders in the field may be inactive even when they are deprived of food. To explain the pattern observed in the data (Figure 9–1), a simple model was developed (see discussion above). In this section, the model is experimentally tested. In particular, the model has two main assumptions: 1) spiders have distinct active and inactive phases, and 2) the transition between phases is influenced by their degree of food deprivation.

9.3.1 Materials and Methods

Eggs of the jumping spider Phidippus audax were collected from the same area where the previous observations were made (Part I). Fourth-instar juvenile hatchlings were used in this experiment. Until the spiders were used in the experiment, they were housed individually in plastic cups (62 mm in diameter and 30 mm in height; approximately cylindrical) and fed fruit flies (Drosophila melanogaster) twice a week.
Immediately prior to the experiment, the spiders were fed *ad libitum* for 24 hrs followed by six days of food deprivation. Their water supply was maintained daily with water-soaked sponges during the fasting.

### 9.3.1.1 The treatment

Spiders were randomly assigned to one of six treatment groups differing in the number of prey (*Drosophila melanogaster*) provided to each individual (0 to 5 flies). This treatment was intended to create differences in the spiders’ food deprivation states. Each treatment had eleven individuals (replications). The spiders were kept individually in cups with a small hole (6 mm in diameter) closed with plastic tape. At 0900, each spider was given an assigned number of prey based on its treatment group. The time required to capture the first prey was recorded for each individual. At 1300, numbers of prey consumed were counted. If any prey survived, they were removed from the container at this point. Subsequently, spiders were kept in a dark environmental chamber from 1300 to 1800 to facilitate their spinning of retreats because retreats are required for inactivity (Part I). All individuals created a thin retreat during this period.

### 9.3.1.2 Behavior measure

The spiders’ propensity to attack prey was examined each day for 10 days. Each day, one fly was given to each individual through the small hole in its cup such that the introduction of prey would not agitate the spiders in their retreat. This method was used because opening the lid of the cup will disturb the spiders as they usually build their retreats on the lids. Whether the spiders captured a fly within 10 min was recorded. The 10 min duration was determined because the longest that a spider took to capture a fly was 283 sec in the morning treatment trial, and the majority of spiders captured a fly within one min; thus 10 min was considered a conservative measure (i.e., if an individual attempted to capture a fruit fly, it was able to do so within 10 min in the small cup). If a spider captured a
fly, the prey was removed from the cup before the spider could consume it, so that
the spider did not gain any nutritional value from the prey. This procedure was
necessary to examine whether the transition back to an active phase is influenced
by the degree of food deprivation if the spiders became inactive (i.e., did not attack
prey). Except on the treatment day (Day 0), the observation was conducted at
1100 daily. Observations on the treatment day were conducted at 1800.

9.3.1.3 Statistical analysis

The data on the spider behavior (i.e., attack or not attack) were analyzed
using a repeated-measures logistic regression model. The formal description of the
model is:

\[ y_{ij} \sim \text{Binomial}(p_{ij}, 11) \]
\[ \logit(p_{ij}) = a_i + b_i \cdot j + e_i \]
\[ e_i = \rho e_{i-1} + u_i \]

where \( y_{ij} \) is the number of spiders that attacked a fly on day \( i \) in treatment \( j \). This
model incorporates binomial sampling variation; logistic dependence of the attack
probability on the number of flies initially fed to the spider (\( j \)); correlation between
capture rate on successive days (\( \rho \)); and additional variation in capture probability
over and above the binomial sampling variation (\( u_i \)). A simpler variant of the
model above (a reduced model) was tested, changing the arbitrary dependence
of attack rate on the day to a logistic dependence (\( a_i = a_1 + a_2 i \)) and similarly
changing the temporal variation in the parameter governing the dependence of
attack rate on initial feeding level (\( b_i \)) from arbitrary to logistic (\( b_i = b_1 + b_2 i \)).

To complete the model, noninformative priors were specified: \( \rho \sim \text{Uniform}(-1, 1) \),
and all other stochastic nodes were assumed to be Normal(0,100). The deviance
information criterion (DIC: Spiegelhalter et al. (2002)) was used to select the best
model.
Proportion of individuals that attacked a fly. Each treatment had 11 individuals.

Because these spiders were not satiated (except possibly for the 5-prey treatment, further discussed below), a significant treatment effect would suggest that spiders that are deprived of food do not necessarily forage (i.e., spiders may remain in an active or an inactive phase partly independently of their food deprivation status) but their tendency to attack is partially governed by their satiation (i.e., treatment effect). Furthermore, persistence of the treatment effect will provide information on the relationship between $L_{I\to A}$ and $L_{A\to I}$. For example, data showing that the treatment effect persists for more than 6 days (i.e., the initial food deprivation degree prior to the experiment) would support the hypothesis that $L_{I\to A} < L_{A\to I}$.

9.3.2 Results

All the spiders except for four individuals in the 5-prey treatment ate all the flies in the treatment conditioning (on Day 0). Although these four individuals only ate 4 flies they were still included in the 5-prey treatment group in the data analysis. Spiders that ate more flies were less likely to attack prey (Figure 9–2). Nearly all individuals in the 0-prey treatment attacked prey throughout the
Table 9–1. Estimated parameters of the reduced model. The model is an hierarchical logistic regression model with the intercept $a_1 + a_2j$ and slope $b_1 + b_2j$, where $j$ is the day of the experiment.

<table>
<thead>
<tr>
<th>Parameters</th>
<th>mean</th>
<th>2.5%</th>
<th>97.5%</th>
</tr>
</thead>
<tbody>
<tr>
<td>$a_1$</td>
<td>2.862</td>
<td>1.833</td>
<td>3.759</td>
</tr>
<tr>
<td>$a_2$</td>
<td>-0.2167</td>
<td>-0.348</td>
<td>-0.0678</td>
</tr>
<tr>
<td>$b_1$</td>
<td>-0.7793</td>
<td>-1.052</td>
<td>-0.4746</td>
</tr>
<tr>
<td>$b_2$</td>
<td>0.0594</td>
<td>0.0166</td>
<td>0.1009</td>
</tr>
<tr>
<td>$\rho$</td>
<td>0.1269</td>
<td>0.01558</td>
<td>0.2233</td>
</tr>
</tbody>
</table>

experiment. The effect of day varied depending on the treatment: increasing as well as decreasing trends were observed (Figure 9–2).

The reduced model was selected based on the model selection criteria (Full model: DIC = 222.291, Reduced model: DIC = 206.284).

Table 9–1 shows the estimated parameters. The negative value of $a_2$ indicates that spiders tend to forage less as they starve (approximately 30% reduction in attack rate between the first and the last day of the experiment). That food deprived individuals forage less is counterintuitive; we discuss this further below.

The treatment effect becomes weaker as spiders become deprived of food because positive $b_1$ and negative $b_2$ cancel out. For example, between the 0-prey and 5-prey treatments, spiders in the 5-prey treatment exhibited approximately 70% reduction in their attack rate on the first day, but this reduction was increased to 30% at the end of the experiment.

By day 6, spiders in the 5-prey treatment are roughly equivalent in terms of food deprivation level to all groups just prior to the experiment (because the duration of food deprivation conditioning after *ad libitum* feeding was 6 days). However, on day 6 of the experimental trial, many individuals did not attack a fly, while all individuals attacked a prey at the beginning, suggesting the food deprivation is not the sole factor that determines the activity of spiders. Furthermore, in the 5-prey treatment, although all of the spiders captured a fly
within 10 min on day 0, only 5 individuals captured a fly within 10 min at day 10. This difference is significant (Fisher’s exact test, \( p = 0.01238 \)). These results are consistent with the hypothesis \( L_{I \rightarrow A} < L_{A \rightarrow I} \).

9.4 Part III: Individual Based Model

In this section, I used an individual-based model to explore whether the simple model described above is consistent with the observed pattern in the field (Figure 9–1). First, the model is translated to a descriptive model.

9.4.1 The Model

The energy state (represented by mass) of an individual spiders \((i)\) at time \(t\) is denoted by \(S_i(t)\). Spiders suffer a daily metabolic cost of \(m\) (function of mass and activity phase), and inactive spiders become active and forage when their energy level goes below a critical level \(L_{I \rightarrow A}\). Active spiders become inactive once their energy state goes above a threshold \(L_{A \rightarrow I}\).
Thus the dynamics of mass can be described as

\[
S_i(t + 1) = \begin{cases} 
S_i(t) - m_{w,A}, & \text{if } A_i(t) = 0 \\
S_i(t) - m_{w,A} + Y, & \text{if } A_i(t) = 1 
\end{cases}
\]

If an individual is inactive (i.e., \( A_i = 0 \)), its mass decreases by \( m_{w,A} \) due to metabolic cost, which depends on its mass and activity phase. If an individual is active (i.e., \( A_i = 1 \)), it increases its mass by \( Y \) from prey consumption. However, \( Y \) will be a random variable, incorporating the probability of capturing a prey.

Activity transitions are governed by the following rules:

\[
A_i(t + 1) = \begin{cases} 
0, & \text{if } A_i(t) = 0 \text{ and } S_i(t) > L_{I\rightarrow A} \\
1, & \text{if } A_i(t) = 0 \text{ and } S_i(t) < L_{I\rightarrow A} \\
0, & \text{if } A_i(t) = 1 \text{ and } S_i(t) > L_{A\rightarrow I} \\
1, & \text{if } A_i(t) = 1 \text{ and } S_i(t) < L_{A\rightarrow I} 
\end{cases}
\]

The first two rows say that if an individual is currently inactive, it will remain inactive until its mass decreases below the threshold, \( L_{I\rightarrow A} \). The last two rows say that if an individual is currently active, it will remain active until its mass becomes greater than the threshold, \( L_{A\rightarrow I} \), due to its foraging successes.

### 9.4.2 Parameter Estimation

The data of juvenile spiders from the first section were used (Part I) to estimate some of the parameters of the model. The relationship between body mass \( (w_t) \) and the number of days deprived \( (t) \) was established as \( w_t = a(t + 1)^b \) where \( t = 0 \) indicates satiation, implying that \( a \) is interpreted as the mass at satiation. These parameters were estimated with least-squares from the average mass of individuals. Individuals with complete data (all 15 days of the experiment, including day 0) data were used for the estimation. The parameters \( a = 0.145, b = -0.063 \) were estimated (Figure 9–4).
Figure 9–4. Relationship between mass and food deprivation degree. The estimated function is $w_t = 0.145(t + 1)^{-0.063}$.

The metabolic loss rate for inactive individuals (i.e., $m_{w,A=0}$) can be derived from this relationship ($w = a(t + 1)^b$) and recognizing that $(t + 1)^{b-1} = (w/a)^{1/b}$,

$$\frac{dw}{dt} = ab(t + 1)^{b-1} = \frac{bw}{(w/a)^{1/b}} = ba^{1/b}w^{1-1/b}. \quad (9–1)$$

Because active individuals exhibit high metabolic rates (Chapter 8), metabolic loss for active individuals included an additional metabolic cost $u$ in eq. 9–1 (i.e., $m_{w,A=1} = ba^{1/b}w^{1-1/b} - u$).

Other parameters of the models were set arbitrarily. For example, the thresholds were set ($L_{I→A} = 0.116, L_{A→I} = 0.14$) such that the condition $L_{I→A} < L_{A→I}$ is satisfied. As discussed above, it is known that spiders’ foraging behavior is more intense when they are more deprived of food (Gardner, 1964). To reflect this biology, I determine the foraging success (i.e., probability of obtaining a prey) as a function of their food deprivation degree: $p = 1 - w_t/L_0$ where $L_0 = 0.149$ so that an individual with its mass slightly above the threshold $L_{A→I}$ still forages. For the actual value of prey, $Y$, an exponential distribution with
mean 0.01 was used to reflect the variation of prey size in the field. The additional metabolic cost for active individuals was set as $u = 0.008$.

### 9.4.3 Results

Based on the model rules, individuals alternate between a long inactive phase and relatively short active phase (Figure 9–5). When individuals are inactive, mass decreases slowly based on the metabolic loss relationship. Once spiders become active, they can quickly attain enough prey to become inactive again. Due to the low metabolic rate of spiders (Chapter 8), the loss is slow and thus the period of inactivity is longer than the active period.

Although the quantitative prediction differs from the actual observation, this activity pattern of the IBM produced patterns similar to those observed in the data (Figure 9–6). In particular, on average inactive individuals are more deprived of food than active individuals. Inactive individuals also vary more in their food deprivation degree than active individuals.
9.5 Conclusion

This study suggests that jumping spiders may not forage during the day even when they are deprived of food. Laboratory observations and the results of individual-based computer simulations, combined with the states of spiders captured in the field, suggests the existence of different thresholds for activity and inactivity.

Estimated food deprivation degrees suggest that spiders had typically spent many days without eating (Figure 1). This result is comparable to the field food deprivation degree of sheet web spiders Bilde and Toft (1998), although the overall food deprivation degree of jumping spiders appears to be larger than that of sheet web spiders. This difference may be due to their foraging tactics: while jumping spiders practice active foraging, sheet web spiders are specialized in a sit-and-wait behavior in their retreat. Because sheet-web spiders would have no clear distinction between staying in retreat and foraging, they may not enter a state of inactivity, and hence may experience less variation in nutritional state.

The observed trends (Figure 9–1) may be explained based on the mechanistic rules of the IBM. First, more individuals were observed inactive than active in the
field. This may be due to the low metabolic rate of the spiders and the biphasic activity pattern; the low metabolic rate makes the period of inactivity long because the time to reach the lower threshold \((L_{I\rightarrow A})\) becomes longer (Figure 9-5). This loss in mass may be easily compensated by a few successful prey captures, which makes active phases shorter than inactive phases on average provided prey are not scarce. Another important trend, that inactive individuals are more deprived of food than active individuals, may be explained by the nonlinear mass change in inactive and active phases. In inactive phase, the mass decreases exponentially such that on average, a spider’s mass is low (e.g., close to \(L_{A\rightarrow I}\)). On the other hand, active individuals’ masses will be on average higher because the lower the mass of an individual, the higher the probability it will capture a prey. Therefore, although as discussed above, the result that more starved individuals forage more intensely (Gardner, 1964) appears to contradicts the observed trend, it actually complements the model to produce the observed pattern if such a relationship between food deprivation and foraging behavior is expressed only when spiders are active.

The decline of treatment effect (the difference in foraging activity among differently food deprived spiders) over time was not only caused by an increasing foraging intensity of initially inactive spiders with food deprivation. In fact, in some treatments, the proportion of (attacking) individuals declined over time even though individuals became more deprived of food. I hypothesize that this effect was due to the quality of spiders’ retreats. The spiders built a thin retreat during the first day of the experiment, and in the subsequent days they continued to build upon it and created more robust retreats. Robust retreats are thick and less transparent. Existence of this retreat is probably essential for spiders to be inactive. For example, inactive spiders that were collected in the field ate many prey in the laboratory because they were separated from their retreat, which forced
them to become active in the laboratory. Therefore, although the treatment effect became insignificant on day 9, it may take longer than 9 days for spiders in the field to become active again (i.e., $L_{I \rightarrow A}$ may be overestimated). Ignoring such details of natural history may lead to misleading results: for example, if the same laboratory experiment were conducted in a common experimental arena (i.e., all spiders were removed from their retreats), we might have found effects neither of treatment nor of time.

These behavioral dynamics may have large implications for the dynamics of activity and population densities, which are ignored by the most commonly used models of activity dynamics (Chapter 10). Although the particular behavior described here may be specific to spiders that have high food deprivation tolerance, much smaller deviations from the standard model can have major effects on model predictions (Chapters 6 and 7). Although this study considers a longer time scale than many other behavioral studies (e.g., Chapter 6; Caro 2005), it still deals with a much faster time scale than is considered by typical community models: on the time scale of this experiment, densities of predators (e.g., other jumping spiders) are unlikely to change dramatically. In other words, all of the dynamics described in this study are details that are considered unimportant in the common framework of mathematical models. Nevertheless, because the approximations made by common models are sensitive to variation in behavior that occurs at fast time scales (Chapters 6, 7, and 10), we need to re-examine how activity dynamics and community dynamics are related to each other. Further careful examinations of activity dynamics in a variety of organisms will help to validate the assumptions of the existing models and improve their general robustness. More generally, they will identify what behavioral information we will need in order to reliably scale behavioral models up to the level of community dynamics.
CHAPTER 10
INTRAGUILD PREDATION IN A JUMPING SPIDER COMMUNITY: A SYNTHESIS

10.1 Introduction

Thus far (Chapters 2 through 9), I have explored the effects of various spatial and behavioral mechanisms on the dynamics of jumping spider communities. While spatial factors are likely to be important (Chapters 2 and 3), previous treatments of behavioral models may be too simple to appropriately scale behavior up to community dynamics.

Two main concerns were raised. First, conventional community models may overestimate the ability of prey to respond to predator densities, especially for foragers that do not receive predator cues persistently (e.g., visual foragers) (Chapter 6). Whether such biases lead to qualitative, or merely quantitative, changes in model predictions entirely has yet to be determined. Second, many important aspects of behavior vary on a faster time scale than demographic variables; such variation may alter community dynamics. For example, jumping spiders exhibit changes in activity from minute to minute (Chapter 7) in response to predator cues; they also exhibit biphasic activity patterns (Chapter 9). Inclusion of such behaviors is likely to have a large influence on the predictions of community models.

In this chapter, I reexamine the role of behavior and spatial structure on a jumping spider community by using an individual-based model to treat the issues discussed above explicitly, synthesizing the results from the previous chapters. Although concerns about behavioral modelling go beyond questions about the persistence of jumping spider communities and will require case-by-case treatments,
I will conclude this dissertation with a short general discussion about behavioral modelling in community ecology.

Indirect effects are almost certainly important in ecological dynamics (Wootton, 2002; Werner and Peacor, 2003). The behaviors described in this dissertation would create complex indirect interactions that may strongly interact with spatial structure. However, as discussed in Chapter 5, we are not yet at a stage where we can connect specific measures of indirect effects such as trait- and density-mediated indirect interactions (TMII and DMII, respectively) to community characteristics. This inability is in large part because indirect-effect experiments have focused strongly on quantifying the effect of attack rates on these measures and have neglected other information such as direct effects (e.g., cost in reproduction due to the trait change), which ecologists have long known to be key components governing community dynamics (Murdoch et al., 2003). This is not to say there is no underlying biological relationship that connects short-term TMII and DMII to long-term dynamics, but it has yet to be discovered. The further research that is needed to bridge these disciplines is beyond the scope of this dissertation. In this synthesis, I will focus on the effect of behavioral and spatial factors without explicitly focusing on indirect effects.

10.2 The Model

The model represents an IGP system containing two species of jumping spiders (i.e., IGprey and IGpredators) in a spatial environment. The model also explicitly tracks resource dynamics (i.e., the population of prey that IGprey and IGpredators utilize). An individual spider can occupy any point (i.e. floating point) in an environment that is 51 units long by 51 units wide. Individuals can interact with (compete, eat or be eaten by) individuals within a distance $U$, which defines the size of the neighborhood. Resources are modelled on a lattice (see Chapter 2). Resources grow independently on square patches with area 1 (i.e., there are
51 × 51 patches). Each independent patch can harbor an unlimited number of IGpredators and IGprey in the absence of biological constraints.

10.2.1 Activity of Spiders

The activity of IGprey and IGpredators is governed by the following process (Chapter 9). The weight $S_i(t)$ of the $i^{th}$ spider at time $t$ decreases by $m$ units per day due to metabolic costs; active spiders ($A_i = 1$) may gain $Y$ units of weight (a random variable) by foraging. Inactive spiders ($A_i = 0$) never gain weight; they return to foraging activity when their energy level goes below a critical level $L_{I→A}$. Active spiders become inactive once their energy state goes above a threshold $L_{A→I}$.

Thus the following equation describes the dynamics of mass:

$$S_i(t + 1) = \begin{cases} 
S_i(t) - m, & \text{if } A_i(t) = 0 \\
S_i(t) - m + Y, & \text{if } A_i(t) = 1
\end{cases}$$

If an individual is inactive (i.e., $A_i = 0$), its weight decreases due to metabolic cost $m$. Activity transition is governed by the following rules

$$A_i(t + 1) = \begin{cases} 
0, & \text{if } A_i(t) = 0 \text{ and } S_i(t) > L_{I→A} \\
1, & \text{if } A_i(t) = 0 \text{ and } S_i(t) < L_{I→A} \\
0, & \text{if } A_i(t) = 1 \text{ and } S_i(t) > L_{A→I} \\
1, & \text{if } A_i(t) = 1 \text{ and } S_i(t) < L_{A→I}
\end{cases}$$

In order to examine the effect of these activity dynamics, the situation where individuals are always active ($A = 1$) was also examined. Dynamics allowing for activity and inactivity are *biphasic*, while dynamics where individuals are always active are *monophasic*.

For IGpredator, $L_{I→A} = 10$ and $L_{A→I} = 30$, and for IGprey $L_{I→A} = 10$ and $L_{A→I} = 25$. The metabolic loss $m$ was assumed to be 1 for both species. To reflect
variation in prey benefits (Chapter 9), I assumed $Y$ is a random deviate from a Poisson distribution with mean 5.

### 10.2.2 Foraging Activity

The foraging activity (effort) of IGprey $C$ was modelled by

$$C = \exp(-\alpha P + \beta N)$$

where $P$ and $N$ are the numbers of IGpredators and IGprey respectively within a distance $U$ (Chapter 7).

Foraging activity is zero if an individual is inactive (i.e., $A = 0$ implies $C = 0$). The parameters $\alpha$ and $\beta$ describe the effects of antipredator behavior (Chapter 7) and intraspecific behavior (Chapter 4). I assume that antipredator behavior will increase (and hence foraging effort will decrease) as the number of predators $P$ increases while antipredator behavior will decrease (and foraging effort will increase) due to dilution effects as the number of conspecifics $N$ increases (Chapter 4). Two scenarios, where individuals are not adaptive (i.e., both parameters are zero) or adaptive ($\alpha = 1$ and $\beta = 0.1$), were examined.

### 10.2.3 Exploitation Competition

Each patch is characterized by its resource density $R$ whose dynamics are governed by the logistic growth equation with a carrying capacity $K$ and growth rate $r$. The probability of successful foraging of IGprey and IGpredators is determined by the average productivity of the neighborhood $\bar{R}$. A patch is considered to be within the neighborhood of an individual when its center falls within $U$ of the individual. Successful foraging by IGprey or IGpredator results in an increase in their weight of $Y$, and will decrease the resource density of all patches within the neighborhood by $\delta$. A carrying capacity of $K = 0.7$ was used in the analysis, and $r$ was varied to examine the effect of productivity change on the persistence of the community. For the depletion parameter, $\delta = 0.07$ was used.
10.2.4 Intraguild Predation

An IGpredator can consume an IGprey if there is an IGprey who is active (i.e., $A = 1$) in its neighborhood (defined by the same radius $U$ that governs resource competition). If an active IGprey exists, an IGpredator may either try to consume the IGprey or consume resource, but an IGpredator cannot consume both IGprey and resource within one time unit. The probability of IGP given an active IGprey is in the neighborhood is determined by a parameter $\pi$ in the model. Successful IGP will increase IGpredator’s energy state by $Z$. I assumed $Z > \bar{Y}$ to reflect the result that IGprey have higher nitrogen content than resource items (Chapter 3). In particular, I used $\pi = 0.5$ and $Z = 10$ as the base parameters, where $\bar{Y} = 5$ as described above.

10.2.5 Reproduction

Reproduction may occur when an individual’s energy state reaches $L_{A \rightarrow I}$ and results in a new individual of the same species that is located within radius $U$ whose energy state is $(L_{A \rightarrow I} + L_{A \rightarrow I})/2$. The probabilities of reproduction of IGprey and IGpredators were 0.3 and 0.1, respectively. Thus, the model assumed that IGprey could utilize the resource more efficiently than IGpredators.

The model also incorporated ballooning behavior of spiders. Reproduction of spiders is local; however, juvenile spiders are known to disperse long distances aerially (called ballooning) (Suter, 1991; Foelix, 1966; Bell et al., 2005). Thus, in the absence of ballooning behavior, the model may induce unrealistically strong spatial effects. To reflect the ballooning behavior, I assumed newborns dispersed globally rather than being restricted to the local neighborhood determined by $U$.

Each simulation was initiated with initial numbers of 15 IGpredators and 30 IGprey randomly distributed in the environment with an initial energy state of 15 for all individuals of both species. In the case of biphasic activity, individuals’
initial activity states were randomly determined. Each simulation was continued until either one of the two species were excluded or 1500 time steps had elapsed. Average duration of persistence was used to explore the effects of various ecological factors on the persistence of the community.

10.3 Results

Biphasic activity dynamics (Chapter 9) greatly increased community persistence (Figure 10–1). Under monophasic activity, persistence was highest at an intermediate level of productivity. Under biphasic activity, persistence increased with productivity level (Figure 10–1). In general, persistence was longer under biphasic than monophasic activity. Regardless of the activity dynamics, increasing spatial structure (i.e., smaller $U$) increased persistence.

![Figure 10–1. Effect of productivity level on the persistence of IGP community under various degrees of spatial structure. The smaller the neighborhood size $U$, the stronger the spatial structure. Local reproduction and non-adaptive behavior (i.e., $\alpha = \beta = 0$) are assumed.](image)

The effect of adaptive behavior (both $\alpha$ and $\beta$) was relatively weak compared to the effect of biphasic activity dynamics. This behavior represents IGprey’s change in foraging effort $C$ in response to their local environment. With monophasic activity dynamics,
activity, adaptive behavior shifted the peak in persistence to higher productivity levels (Figure 10–2).

\[ U = 7. \]

Local reproduction is assumed.

Ballooning behavior decreased persistence dramatically under monophasic activity dynamics. However, with biphasic activity, persistence was maintained even with ballooning behavior (Figure 10–3).

\[ U = 7. \]

Adaptive behaviors are included.
10.4 Discussion

The characteristics of the individual-based model discussed here, synthesizing many of the results of this dissertation could allow an IGP community to persist for longer than it would under a more conventional approach. When individuals were assumed to be continuously active (monophasic), the model behaved as predicted by conventional models; persistence peaked at an intermediate level of productivity level (Chapter 2). On the other hand, when individuals were assumed to have biphasic activity (Chapter 9), persistence increased with productivity (Figure 10–1). Furthermore, persistence based on biphasic activity was robust to global reproduction (i.e., ballooning); in contrast, global reproduction collapsed persistence under monophasic activity, suggesting the activity dynamics may be an important mechanism that allows IGprey and IGpredators to coexist in jumping spider communities.

10.4.1 Spatial Structure

The results of Chapters 2 and 3 suggest an explanation for the observed decrease in persistence with decreased spatial structure (increasing neighborhood size). One reason non-spatial IGP models predict that the persistence of IGP is difficult is because non-spatial models create a specific scenario that is disadvantageous to intraguild prey (IGprey) by constantly making IGprey vulnerable to IGpredators by eliminating spatial segregation between IGprey and IGpredators that would emerge when predators deplete prey locally (Hastings, 2000). This advantageous scenario (for IGpredators, and thus disadvantageous for IGprey) is further enhanced when IGprey are beneficial to IGpredators (Chapter 3) — which appears to be the case for jumping spiders, because nitrogen content of prey had a significant effect on the growth rate of the animals (Chapter 3).
10.4.2 Biphasic Activity

Biphasic activity is the strongest mechanism incorporated in the model. Including the inactive phase generally enhanced the persistence of the community. However, the precise dynamical mechanism by which biphasic activity reduces IGP (and hence increases persistence) is unclear. Is it possible to mimic the community dynamics obtained under biphasic activity by reducing the rate of IGP (\(\pi\)) under monophasic activity? The answer to this question is yes and no. When the probability of IGP was reduced from 0.5 to 0.025, the relationship between the productivity and persistence under monophasic activity behavior became closer to that of biphasic behavior with the standard rate of IGP (i.e., 0.5). However, even under the low rate of IGP, the community collapsed with ballooning behavior under monophasic activity. Nor could adjusting other parameters such as reproduction rate recover the dynamics seen with biphasic dynamics. This suggests that biphasic activity does more than simply reducing species interaction strengths. For example, because foraging success of individuals depends on the local productivity level, it is likely that an activity dynamics induced by the coupled local exploitative competition introduces behavioral dynamics that cannot be adequately approximated without including more biological details into the model.

10.4.3 Adaptive Behavior

The effects of adaptive behavior (e.g., \(\alpha\) and \(\beta\)) were relatively weak (Figure 10–2). At most, adaptive behavior caused a weak quantitative effect under monophasic activity. In light of the results of Chapter 6, the weak effect of adaptive behavior is not surprising because spatial effects weaken trait effects. In jumping spiders, although antipredator behavior is sustained temporarily (Chapters 7 and 8), the duration of the trait expression was relatively short and would not be strong enough to produce the magnitude of trait effect predicted.
by common models (Chapter 6). However, these results do not necessarily imply
that adaptive behavior is unimportant. For example, although biphasic activity
was modelled simply, spiders’ lowering of metabolic rate in response to predator
encounters (Chapter 8) might be associated with the threshold $L_{A\rightarrow I}$. If an
encounter experience with a predator increases spiders’ tendencies to become
inactive, this predator induced trait effect would be much stronger than what is
predicted by the current model. As discussed in Chapter 9, most empirical studies
have examined the effect of predators on immediate behavioral responses, such
as time to come out of a refuge (e.g., Jennions et al., 2003); however, predator
encounter can affect prey in a variety of ways. More comprehensive treatments
of the effects of predator threat will be useful to further appreciate the role of
adaptive behavior in community dynamics.

10.4.4 Modelling Behavior in Community Ecology

The variety of behavioral details ignored in conventional models is daunting.
For example, for a given jumping spider in the field, because IGP is size-dependent,
the actual density of IGpredators (large spiders) may not change dramatically
throughout the season while the density of IGprey (small spiders) may increase
with each reproduction event. Thus, the density of IGpredators for a particular
individual would decrease in time as the individual grows larger, while individuals
that were initially larger may die (de Roos et al., 2003). In this scenario,
conventional models predict that this individual would keep lowering its foraging
activity on average throughout its lifetime because the density of IGpredators
decreases. Whether or not this prediction based on average activity level is true
or not needs to be investigated, which would be a difficult task because it requires
more than simply documenting high predator density resulting in more encounters
with predators (and thus inducing escape behavior more frequently). Whether
or not this prediction based on average activity level is true or not needs to be
investigated, which would be a difficult task because it requires more than simply documenting high predator density resulting in more encounters with predators (and thus inducing escape behavior more frequently). However, it is easy to show that there is large variance around the average trait expression. For example, if an individual encounters and escapes a predator, it will subsequently lower its activity (Chapter 7). In other words, although typical models assume that animals respond to an average density of predators (e.g., Abrams, 1992), behavioral variance is induced by other details such as spatial structure (Chapters 2 and 6) and individual experience (Chapters 7 and 8). Furthermore, individual experience and spatial structure are not independent (Chapter 6) because prey in the region where the density of predators is high will experience predation risk differently from prey in the area where the density of predator is low. The effect of these ignored variations of behavior can be substantial. For example, if the relationship between foraging activity and resource intake is convex, including behavioral variation will lower the actual resource depletion due to Jensen’s inequality. Thus, simple models may overestimate resource depletion (cf. Chapter 7). Although the magnitude of particular biases can be estimated and corrected for if variances of behavior are known, the effects of such biases on the dynamics of multi-species community are unknown and need to be investigated.

Typical community models with adaptive behavior ignore more than just behavioral variation. As illustrated by biphasic activity of jumping spiders, some behaviors may not be able to be simply approximated by including variance in the model. In jumping spiders, community dynamics under biphasic activity could not be recovered by simply adjusting parameters of monophasic activity. As discussed above, this difference probably occurs because such dynamics not only lower the rate of IGP but also induce other dynamics that have yet to be described. Because theoretical investigations that scale behavior to community dynamics
are dominated by a common recipe that neglects the effect of rapid variation in behavior, we have little understanding of the importance of empirically observed behaviors.

The intent of this discussion is to point out persisting weaknesses in the connection between theory and data. While theoreticians have neglected behavioral variation (Bolker et al., 2003), empiricists have worked hard to quantify them (Werner and Peacor, 2003). While “all models are wrong” (Box, 1979; Sterman, 2002), we must never forget to examine the reliability of various approximations. While simple models are easier to understand, models are useless if they do not predict the dynamics of the target community (Peters, 1991). My work questions the robustness of common approximations made in models linking behavior and community dynamics.

Good experiments are notoriously difficult to conduct. The slow time scale of community dynamics makes many experiments logistically infeasible. Fortunately, inclusion of behavior allows empiricists to examine the models more rigorously, which makes this fusion a great place for theoreticians and empiricists to collaborate. In this dissertation, I showed that behavioral dynamics that occur at a faster time scale than the demographic dynamics can have a strong impact on community dynamics. Thus, theories that incorporate fast dynamics in the connection between behavioral and community dynamics will facilitate this collaboration dramatically. Without this effort, we cannot identify how much and or what kind of behavioral variation can be included into the model as variation, as mechanistic details, or ignored. Although simplifying behavioral dynamics is needed as it will allow more general analysis, ecologists have paid little attention to the goodness of their approximations. Consequently, we have surprisingly little general understanding how behavior scales up to community dynamics other than stating it is important. For example, despite the increasing popularity of
quantifying TMIII and DMIII (Preisser et al., 2005; Wojdak and Luttbeg, 2005), we have little idea what they imply in a long term community dynamics (Chapter 5). I hope that the information I have provided in this dissertation will motivate both empiricists and theoreticians to facilitate the connection between theory and data to further improve our understanding about the roles of behavior in ecological communities.
REFERENCES


BIOGRAPHICAL SKETCH

Toshinori Okuyama was born in Ise, Mie, Japan. He obtained a B.S. in zoology from Miami University of Ohio in 1996, an M.S. in biology from University of Nebraska-Lincoln in 1999, and an M.S. in mathematics from Clemson University in 2001.