

Abstract

Skalski, Garrick Tyson. Adaptive behavior and interference in the functional response of predator to prey. (Under the direction of James F. Gilliam and Nick M. Haddad)

The behavior of individuals in predator-prey interactions plays a fundamental role in population ecology and evolution. Accordingly, the development and assessment of theory that provides a conceptual framework for understanding and predicting behavior in predator-prey systems is of basic importance. This dissertation is focused on developing and assessing theory that provides a quantitative structure for predator-prey interactions.

Chapter 1 provides a theoretical treatment of the problem of modeling the behavior of an animal facing two- and three-way tradeoffs among growth, mortality and reproduction, three components of Darwinian fitness. In this situation benefits in terms of one fitness component can be obtained only with a cost in terms of another fitness component. Applying a dynamic optimization method, the theory describes the behavior of phenotypes that adaptively balance growth, mortality and reproduction in a size-structured population. One simple prediction of the theory is that non-growing adults in a stable population should behave so as to minimize the ratio of mortality rate to birth rate. A further extension of the theory using the idea of ideal-free distributions results in a prediction of a positive and linear relationship among the rates of growth, mortality and birth when measured across different habitat patches. These and other results lead to testable predictions and I discuss empirical examples of how subsets of the theory have been and can be assessed.

Chapter 2 is an empirical assessment of four alternative models of the functional response of predator to prey (the *per capita* feeding rate of a predator) using

19 data sets from the literature. The results show that predator-dependent functional responses (i.e., forms that are functions of predator and prey abundance because of predator interference) provide better descriptions of 18 of the 19 data sets than the Holling Type II model, a commonly used prey-dependent functional response (i.e., a model that depends only on prey abundance). Hence some form of predator interference is common in these data. However, no single functional response can best describe all of the data sets. A key result is that the best-fitting predator-dependent model depends on the presence or absence of predator-dependence when prey are very abundant.

Accordingly, I suggest use of the Beddington-DeAngelis or Hassell-Varley model when predator feeding rate becomes independent of predator density at high prey density, and use of the Crowley-Martin model when predator feeding rate is decreased by higher predator density even when prey density is high. These results suggest that predator-dependent functional responses should be more widely considered in the literature.

Chapter 3 is an empirical assessment of four alternative optimization models of behavior for animals facing a feeding-mortality tradeoff (i.e., increases in feeding rate can be obtained only at a cost of increasing mortality rate by predation). Using lab experiments, I measured the feeding and mortality of stream fish (bluehead chubs) in the presence of varying levels of food availability and green sunfish predators. The models vary in their specifications as to how bluehead chubs might value, in terms of fitness, rates of growth and mortality. Two models that emphasize the importance of growth or mortality alone fit the data poorly, whereas the two models that balance growth and mortality adaptively provide a much better description of the data because bluehead chubs continue to feed, albeit at a reduced level, in the presence of the predator-

maintained mortality hazard. A comparison of the two best-fitting models leads to the inference that reproductive value in the bluehead chub should be thought of as a function of body size and age rather than a function of body size alone. A key implication of this result is that risk-taking behavior in these fish can be quantitatively estimated using a parameter that incorporates the benefits of growth and the costs mortality into a single fitness-based metric. The metric, called the marginal rate of substitution of mortality rate for growth rate, provides a link between behavior and life history in the bluehead chub.

In summary, this dissertation provides some solutions to the challenge of how to conceptualize and predict animal behavior in predator-prey settings. The emphasis is on developing and assessing alternative hypotheses in a quantitative framework.

Adaptive behavior and interference in the functional response of predator to prey

by
Garrick Tyson Skalski
Garrick Tyson Skalski

A dissertation submitted to the Graduate Faculty of
North Carolina State University
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Biomathematics and Zoology

Raleigh

2001

Approved by:

James F. Gilliam
James F. Gilliam
Co-Chair of Advisory Committee

Montserrat Fuentes
Montserrat Fuentes

Nicholas M. Haddad
Nicholas M. Haddad
Co-Chair of Advisory Committee

George R. Hess
George R. Hess

Dedication

My dissertation is dedicated to my parents, James J. and Patricia M. Skalski. As I journey through stages of life that they have long since traveled, my appreciation and respect for their morality and work ethic only increases. Their definitions of right and wrong are my guide and I am thankful for all they have given me.

Personal Biography

I was born Garrick Tyson Skalski on March 20, 1973 in Detroit, M. I., U. S. A. Growing up in downtown Detroit, I acquired a respect for experiences that only urban living can generate: walking 100 yards to elementary school, walking 2000 yards to buy cheese, meat, and fresh produce from the farmer's market, the Detroit Tigers winning the 1984 World Series, skate boarding to Greektown to play in the arcade perpetually occupied with middle-aged Greek men dealing cards, football and baseball with pals in an undeveloped city lot, being white and male and in the minority in a community of folks with diverse ethnic histories, walking downtown to ice skate in the amphitheatre along the Detroit River, neighborhood unity tested by an occasional burglary or purse-snatching, having friends that also like teams from the Bad Boys era of the Detroit Pistons, playing street hockey at the farmer's market during a day off from school, dining out for Soul Food, and, finally, making fun of people that live in the suburbs.

Just before beginning the eighth grade my family and I moved to Asheville, N. C., U. S. A. Moving from a very urban setting to a very rural setting required a large adjustment for the entire family. Prior to the move south, my family was frequently engaged in outdoor activities, such as camping, hiking and fishing (in fact, my family discovered Asheville for themselves during a camping trip in the Smoky Mountains). However, it was during these early years in Asheville that my interest in biology and ecology began to emerge. Just what kinds of creatures lived in that creek along Highway 74 on the route to school? What did these creatures do all day long? All night long? What about the creek near my house by the Star Lanes bowling alley? What kinds of creatures lived in *that* creek? What did *they* do all day and night? After high school, I enrolled in

college at the University of North Carolina at Chapel Hill and settled on a major in Biology. After taking Biology 54, Ecology and Population Biology, I realized that this is the field where I can find out about what's happening in those creeks. I was fortunate to have the opportunity to conduct research on the ecology of stream invertebrates under Professor Seth. R. Reice. During this experience I read and wrote about the ecological literature and participated in discussion sessions with Dr. Reice, his graduate students, and other undergraduates in the Reice Lab. It was in this setting that I was encouraged to develop a taste for theoretical approaches to biology, especially ecology.

I realized that all aspects of college life at UNC should not be taken for granted, be they scholarly or otherwise. As such, I participated fully in the aesthetic and social experiences that can only be offered by Chapel Hill: the student section on a Saturday at Kenan Stadium, meeting friends for beer at He's Not Here on a warm afternoon, riding my bike (bike as in motorcycle) around town and through the countryside of Orange County, pulling for the Tarheels come tournament time in the TV lounge of Stacy dormitory, talking with friends the next morning about all of the stupid events of last night, picking up a keg from TJ's, living at the residences of Barclay and Ashley Forest, playing hoops after class on the outdoor court near Cobb Hall, eating at Time Out, and going for a leisurely, mainly pointless, stroll through campus on a clear blue day with roommates.

Of course all of this fun was not attained without a cost. While I pursued ecological coursework with enthusiasm, *other* classes, comprising the bulk of any undergraduate's curriculum, received less attention. This explains the C- in my 2nd semester of organic chemistry (isn't one semester enough, anyway?) and a few other

instances of underachievement. Thus during my senior year I faced the formidable task of gaining acceptance into a graduate school with a strong ecology program. I was rejected from all schools save N. C. State University where I was accepted to the Department of Zoology to work in the lab of Professor James F. Gilliam. It was in this environment that I became focused on quantitative ecology and evolution, earning a M. S. in Zoology and continuing my studies to pursue a Ph. D. in Biomathematics and Zoology. An important consequence of my moving to Raleigh was that I met my wife, Amy, in Raleigh, N. C. and we were married on March 7, 1998. Amy and I, and our two dalmations, Daisy and Edward, live in a small farmhouse near Raleigh where I am continuing my pursuits as a student and teacher of ecology and evolution.

Acknowledgments

I am thankful for the assistance of many individuals during the course of my graduate training. The staffs of the Departments of Zoology and Statistics kept the paperwork flowing and the computers running. I am appreciative of the many fun and intelligent fellow graduate students that I have gotten to know over the years - I'm glad that we never take ourselves too seriously. I benefited from many excellent classroom teachers on the faculty at N. C. State, especially Roger Berger, John Bishir, Ernest Burniston, David Dickey, Steve Ellner, Tim Elston, John Franke, Joe Hightower, Jacqueline Hughes-Oliver, and Carl Meyer. My research technician, Kateri Duncan, was extremely dependable and helpful. The members of my advisory committee, Montse Fuentes, Nick Haddad, and George Hess, have graciously provided their time and ideas. Jim Gilliam, the chair of my advisory committee, sets a fine example for his students to follow and has been supportive in all facets of my training. My wife Amy has been a source of advice and encouragement even as my studies permeate into our home life (to wit, our yard doubles as a mini biological preserve with its resident "weeds," mice and snakes – also known as biodiversity; but it's conservation biology in practice!).

Table of Contents

Preface	ix
List of Tables	xii
List of Figures	xiii
Chapter 1: Adaptive behavior in a size-structured population: three way tradeoffs among growth, mortality and reproduction	1
Abstract.....	2
Introduction.....	3
Adaptive Behavior in a Size Structured Population.....	5
Testing Optimization Models of Behavior.....	14
Conclusions.....	22
Literature Cited.....	24
Figure Legends.....	28
Chapter 2: Functional responses with predator interference: viable alternatives to the Holling Type II model	31
Abstract.....	32
Introduction.....	33
Methods.....	39
Results.....	43
Discussion.....	46
Acknowledgments.....	51
Literature Cited.....	52
Figure Legends.....	62
Appendix 1.....	65
Appendix 2.....	68
Chapter 3: Feeding under predation hazard: testing models of adaptive behavior with stream fish	73
Abstract.....	74
Introduction.....	75
Methods.....	77
Experimental System.....	77
Growth Experiment.....	77
Behavioral Experiments.....	79
Experiment One.....	81
Experiment Two.....	82
Alternative Optimization Models of Behavior.....	83
Statistical Model Selection.....	90
Results.....	93

Growth Experiment.....	93
Behavioral Experiments.....	94
Discussion.....	98
Acknowledgments.....	106
Literature Cited.....	107
Figure Legends.....	114

Preface

The content and philosophy of this dissertation reflect the content and philosophy of the training that I have received and pursued as a graduate student. I have attempted to apply the best concepts from my schooling to the problem of scientific discovery. Five themes form the philosophical basis for this work.

First, I believe that research in biology should be firmly rooted in natural history. Biological pattern and process, if we interpret it correctly, should fall directly within the context of evolution in the field. I have attempted to make my studies, no matter how abstract, based on observations and information from organisms in the wild. In my theoretical work this means tracking relevant state variables and generating predictions that can be measured. In my empirical work this means taking measurements that can be, at least by analogy, extrapolated to field settings.

“God does not care about our mathematical difficulties. He integrates empirically.” - Albert Einstein

Second, in the context of ecology and evolutionary research, I feel that the behavior of animals plays a vital, fundamental role. If we are interested in the population-level phenomena that form the core of ecological and evolutionary thought, then a reasonable reductionist approach is to study the properties of individuals. Rates of growth, birth, and mortality map to rates of population growth and genetic change and vice versa. Feeding, mating, and anti-predator behaviors are important components of the phenotype that drive a population's vital rates. Hence the focus of my dissertation is on understanding feeding and anti-predator behavior in predator-prey systems.

“The difficulty in most scientific work lies in framing the questions rather than in finding the answers.” - A. E. Boycott

Third, I believe that biological investigation is strengthened by the application of mathematical tools. Mathematical models make theory less ambiguous and statistics permits a determination of empirical uncertainty. As the science of biology progresses quantitative approaches will become increasingly relevant and prevalent in the discipline. Hence my dissertation draws heavily on some basic tools of applied mathematics.

“Every new body of discovery is mathematical in form, because there is no other guidance we can have.” - Charles Darwin

Fourth, I am an advocate of simultaneously utilizing empirical and theoretical approaches. It is clear that science can not progress on the strength of theory or empiricism alone. As such, it is reasonable to conclude that the integration of theory and data provides more information about the object(s) of inquiry than either approach used alone. My dissertation corroborates this notion: the models and data from Chapters 2 and 3 are hardly novel in isolation and only the assessment of the models using the data makes a substantial scientific contribution.

“The men of experiment are like the ant, they only collect and use; the reasoners resemble spiders, who make cobwebs out of their own substance. But the bee takes the middle course: it gathers its material from the flowers of the garden and field, but transforms and digests it by a power of its own. Not unlike this is the true business of philosophy (science); for it neither relies solely or chiefly on the powers of the mind, nor does it take the matter which it gathers from natural history and mechanical experiments and lay up in the memory whole, as it finds it, but lays it up in the understanding altered

and digested. Therefore, from a closer and purer league between these two faculties, the experimental and the rational (such as has never been made), much may be hoped.” -

Francis Bacon

Fifth, and finally, I adopt the philosophy that science is best advanced by considering the relative merits of alternative hypotheses. It's clear, in biology at least, that the available scientific hypotheses are approximations and incomplete descriptions of nature, at best. Thus, a reasonable approach is to hope to improve these approximations iteratively via application of the scientific method. Accordingly, in the analysis of data in my dissertation I embrace this approach and consider several alternative hypotheses.

“The young specialist in English Lit, ...lectured me severely on the fact that in every century people have thought they understood the Universe at last, and in every century they were proved to be wrong. It follows that the one thing we can say about our modern ‘knowledge’ is that it is wrong.

... My answer to him was, ‘... when people thought the Earth was flat, they were wrong. When people thought the Earth was spherical they were wrong. But if you think that thinking the Earth is spherical is just as wrong as thinking the Earth is flat, then your view is wronger than both of them put together.’ ” - Isaac Asimov

List of Tables

Chapter 2

Table 1: Functional Responses in the Ecological Literature..... 59

Table 2: Functional Response Data Sets..... 60

Chapter 3

Table 1: Model Selection via Schwarz Information Criteria..... 113

List of Figures

Chapter 1

- Figure 1: Two Hypothetical Behavioral Options Sets.....29
- Figure 2: Graphical Solutions for Optimal Behavior.....30

Chapter 2

- Figure 1: Comparative Fits of Functional Response Models..... 63
- Figure 2: Representative Fits of Predator-Dependent Forms..... 64

Chapter 3

- Figure 1: Graphical Solutions of Optimal Behavior..... 117
- Figure 2: Fit of the Growth Model to the Data..... 118
- Figure 3: Fit of Model 1 (maximize growth) to the Data..... 119
- Figure 4: Fit of Model 2 (minimize mortality) to the Data..... 120
- Figure 5: Fit of Model 3 (minimize mortality/growth) to the Data..... 121
- Figure 6: Fit of Model 4 (maximize $\theta g - \mu$) to the Data..... 122

Chapter 1

Adaptive behavior in a size-structured population: three way tradeoffs among growth, mortality and reproduction

Abstract

Predicting behavioral phenotypes is an important goal in ecology and evolution, but the task is made challenging by the fact that Darwinian fitness is comprised of several components that can not usually be simultaneously optimized (i.e., increases in one component are achieved only with the cost of decreasing other components). Here I explore a theoretical representation of the problem of an animal balancing two- and three-way tradeoffs among growth, mortality and reproduction in a size-structured population, review approaches used for testing some of the theory and consider two empirical examples from the literature. The formulation is a direct extension of earlier work and provides expressions that predict adaptive behavior in the presence of two- and three-way tradeoffs. One parsimonious result is that non-growing adults in a stable population should behave so as to minimize the ratio of mortality rate to birth rate. A further extension of the theory using the idea of ideal-free distributions results in a prediction of a positive and linear relationship among rates of growth, mortality and birth when measured across different habitat patches. My discussion of two empirical examples illustrates some challenges involved in testing the theory.

Introduction

Modern evolutionary biology rests upon the Darwinian theory that animals evolve so as to maximize fitness subject to certain constraints. Ecologists have applied ideas involving fitness maximization to a variety of ecological problems, especially the problems of predicting behavioral (e.g., MacArthur and Pianka 1966, Fretwell and Lucas 1970, Charnov 1976) and life history phenotypes (e.g., Williams 1966, Gadgil and Bossert 1970, Schaffer 1974, Taylor et al. 1974, Perrin and Sibly 1993) that could result from natural selection. Many mathematical representations of fitness are difficult to measure in nature and many of the attempts to predict behavior based on fitness considerations utilize a single component of fitness, such as feeding rate (e.g., Milinski 1979, Harper 1982), mortality rate (e.g., Godin and Dugatkin 1996), or birth rate (e.g., Parker 1978), as a proxy for fitness (Stephens and Krebs 1986, Krebs and Davies 1993, Houston and McNamara 1999). Other studies emphasize the idea that different components of fitness, such as feeding rate, mortality rate, and birth rate, contribute, perhaps in conflict, to determine an organism's fitness (e.g., Milinski and Heller 1978, Sih 1980, Werner et al. 1983, Mangel and Clark 1988, Houston and McNamara 1999). For example, a behavior that yields the highest feeding rate may also yield the highest mortality rate. In fact, a large literature now exists to support the statement that animals consider different components of fitness when making behavioral decisions (Lima and Dill 1990, Milinski 1993, Lima 1998). Moreover, a theoretical framework for understanding how organisms might explicitly balance conflicting components of fitness also exists (Leon 1976, Schaffer 1983, Mangel and Clark 1988, Houston and McNamara 1999).

While the empirical literature has shown that animals are likely to consider different components of fitness, data that assess how animals may quantitatively balance the conflicting demands of these components in terms of fitness consequences are lacking. Specifically, the available empirical analyses address the presence or absence of a role for potential fitness components, but do not explore how these components tradeoff using the framework of available theory. An empirical difficulty imposed by many theories is the need for estimates of marginal rates of substitution. These rates allow for the differing components of fitness to be assessed in terms of the common currency of reproductive value (Brown 1992, Houston and McNamara 1999). However, the marginal rates of substitution, as one might surmise, involve reproductive value, a quantity that is difficult to measure directly.

In an effort to facilitate empirical efforts, Gilliam (1982) introduced a simplification to the theory that partially negated the need to estimate marginal rates of substitution and quantities involving reproductive value in order to predict behavior (see also Werner and Gilliam 1984). Yet despite this simplification, Gilliam's most useful result, that some animals may behave so as to minimize the ratio of mortality rate to growth rate, has hardly been assessed (Lima and Dill 1990, Lima 1998). Accordingly, in this chapter my intent is stimulate empirical research along these lines: research that rigorously tests hypotheses concerning two-way and three-way behavioral tradeoffs involving rates of growth, mortality and reproduction.

I develop and analyze a generalization of the basic size-structured model proposed by Gilliam (1982). My findings extend Gilliam's results for two-way tradeoffs between growth and mortality by analyzing two-way and three-way tradeoffs involving

rates of growth, mortality and reproduction. I then discuss the most relevant set of empirical literature and approaches for testing the theory.

Adaptive behavior in a size-structured population

I propose a simple extension of Gilliam's (1982) size-structured model (see also Werner and Gilliam 1984). Except in one aspect, my model is essentially identical to Gilliam's (1982) earlier model. Like Gilliam (1982), I assume that the individuals in the model population can be categorized by a single state variable, s , which could be any biologically relevant feature of the organism's state, including, for example, age, body size, level of energy reserves, or territory size. For illustrative purposes I take the state variable to be body size. I assume that an individual's reproductive value, V , is given by a function of one variable, the state variable, giving $V=V(s)$. Hence reproductive value is independent of age and time of year with the implications that there exists no maximum age and all constraints are independent of age and time of year (e.g., no seasonality in mortality or reproduction).

My extension is to assume that individuals face behaviorally-mediated tradeoffs among rates of growth, g , (i.e., changes in the state variable), mortality, μ , and birth, b , giving a three-way tradeoff (in contrast, Gilliam (1982) considers the growth-mortality tradeoff only, a two-way tradeoff, and takes b as a given function of s). I model these tradeoffs by writing $\mu=\mu(s, g, b)$ with the constraint equation $h(s, g, b)\leq 0$. The functions $\mu(s, g, b)$ and $h(s, g, b)$ are given: they are taken to be completely determined by the details of the population (e.g., the habitat and density of the population) and its environment (e.g., the availability of food and the presence of predators). Behavior enters

the model through g and b . One can think of an organism as having a set of behavioral options, each resulting in a growth rate, g , and a birth rate, b , which then, along with the organism's state, s , determine the mortality rate via the function, μ . The equation $h(s, g, b) \leq 0$ can be thought of as a size-specific constraint on the set of biologically possible values for g and b (e.g., an animal can not allocate 100% of its time to feeding and 100% of its time to nest building). Thus each behavioral option can be specified by a vector (g, b, μ) which is sufficient to completely specify the fitness consequences of each behavior at each body size. Throughout my analysis I consider the functions μ and h to be increasing in g and b because I am studying tradeoffs among fitness components.

One can interpret mortality rate as a function of g and b in a variety of ways. For example, a set of behavioral options for an animal may be a finite number of choices of different habitats, with each habitat described by a point (g, b, μ) . In this case, the set of behavioral options is a finite number of points (Fig. 1a). For an animal that spends some proportion of its time in more than one habitat then the set may be extended to include all linear combinations of the available habitats resulting in a 3-dimensional polygon (Fig. 1a). In contrast, the set of behavioral options may be determined, for example, by the proportions of time that an animal spends feeding and building its nest. In this case the set of behavioral options may be a 3-dimensional region with a smooth surface if the vector (g, b, μ) is a smooth function of the proportion of time allocated to each activity (Fig. 1b). For the purposes of my analysis, I define the behavioral phenotype as the set of behavioral options employed by an organism over its lifetime (i.e., the choice of (g, b, μ) employed at each body size). My analytical approach is to identify and study the properties of behavioral phenotypes that are optimal in terms of maximizing fitness.

My analysis only considers the properties of phenotypes, and does not explicitly consider the genetics that may underlie these phenotypes. Hence my approach should be interpreted as identifying optimal behavioral phenotypes that can serve as evolutionary stable strategies, without consideration of the more complicated and general problem of describing dynamical evolution (Leon 1976, Charlesworth 1980, Houston and McNamara 1999, Kozlowski 1999). Although my model may indeed approximate the evolutionary dynamics of some particular genetic systems (Leon 1976, Charlesworth 1980), in general my results are best interpreted as representing potential phenotypic endpoints of evolution - with no explicit specification of how such endpoints may be reached by evolving populations (Houston and McNamara 1999).

Using reproductive value as the metric of fitness, I study the optimal behavioral phenotype of individuals within a small sub-population that is invading a larger base population (Leon 1976, Kozlowski 1999). By definition, reproductive value for a growing organism, when parameterized by body size (by employing the change of variables $ds/g=dx$ in the standard integral equation for reproductive value with age= x) is given by

$$V(s) = \frac{\int_s^{\infty} e^{-R(w)} l(w|s) \frac{b(w)}{g(w)} dw}{l(s|s_0)},$$

where

$$R(w) = \exp\left\{-\int_s^w \frac{r}{g(y)} dy\right\},$$

(with r representing the population growth rate of the base population) survivorship from body size s to body size w is given by

$$l(w|s) = \exp\left\{-\int_s^w \frac{\mu[y, g(y), b(y)]}{g(y)} dy\right\} ,$$

and s_0 is the body size of a newborn (Werner and Gilliam 1984). The growth and birth rates are written as functions of body size, $g=g(w)$ and $b=b(w)$, because behavioral decisions, and hence g and b , are expected to vary with body size. Thus, my goal is to identify the functions $g(s)$ and $b(s)$ such that fitness is maximized.

Parameterized by only the state variable, s , it suffices to track changes in reproductive value as body size changes. In a growing organism, reproductive value, for small changes in body size, Δs , satisfies the recursive relationship

$$V(s) = \frac{b}{g} \Delta s + \left[1 - \frac{r + \mu}{g} \Delta s\right] V(s + \Delta s) .$$

Taking the limit as Δs becomes small and applying the result that optimal behavioral phenotypes maximize reproductive value at every body size through the appropriate choices of g and b (e.g., Schaffer 1974, 1983, Taylor et al. 1974), gives the dynamic programming equation

$$-\frac{dV^*}{ds} = \max_{g,b} \left(\frac{b}{g} - \frac{r + \mu}{g} V^* \right) \quad \text{subject to } h(s, g, b) \leq 0, \quad (1)$$

where the asterisk denotes the value produced by the optimal behavioral phenotype (Houston and McNamara 1999, Mangel and Clark 1988). Equation (1) also follows directly from Gilliam's (1982) formulation via his assumptions that (i) there is no maximum age (i.e., individuals have finite, if arbitrarily small, survivorship to any arbitrarily large age) and (ii) the fitness components are independent of age. The consequence of these assumptions is that reproductive value is independent of age (i.e., reproductive value will only change over time if body size changes over time), which I

have assumed *a priori*. Accordingly, the functions μ and h along with the dynamic programming equation completely specify the problem of finding optimal choices for $g(s)$ and $b(s)$.

The computation of the optimal population growth rate of the invading sub-population, r^* , is a two-step process (Leon 1976, Gilliam 1982, Taylor et al. 1974). First one finds the optimal behavioral phenotype (i.e., the optimal functions $g^*(s)$ and $b^*(s)$) treating r (the growth rate of the base population) as a given parameter. In general, the functions $g^*(s)$ and $b^*(s)$ will also be functions of r . In the second step the functions $g^*(s)$ and $b^*(s)$ are substituted into the Euler-Lotka equation (i.e., the equation $V(s_0)=1$) which is then solved to obtain the optimal growth rate of the invading sub-population, r^* (r^* is thus a function of r). The actual computation of r^* is not necessary for this analysis, as I will not specify particular forms for the functions μ and h . Keeping these ideas in mind, in the following sections I treat r as a given parameter with $\frac{b}{V} - \mu \leq r$ at every size (otherwise the animal does not grow or reproduce).

The fundamental results of this analysis are given by carrying out the maximization indicated in Eq. 1. At each body size optimal behavioral phenotypes choose g and b so as to maximize the right hand side in Eq. 1. Equivalently, optimal choices of g and b are also given by the minimization

$$\frac{dV^*}{ds} \frac{1}{V^*} = \min_{g,b} \left(\frac{(r + \mu) - \frac{b}{V^*}}{g} \right), \quad (2)$$

a generalization of the criterion given by Gilliam (1982). Gilliam's (1982) criterion implements the minimization over g with b fixed at its given value whereas Eqs. 1 and 2

implement the optimization over both g and b . Rearrangement of Eq. 2 illustrates the solution to the optimization problem,

$$\mu^* = \frac{dV^*}{ds} \frac{1}{V^*} g^* + \frac{b^*}{V^*} - r, \quad (3)$$

where g^* , b^* , and μ^* are the optimal values. Optimal behavioral phenotypes yield a linear relationship among g , b and μ at each body size (the form of the linearity will change with body size). For a given body size s one can plot μ over the g - b plane. The solution can be found by considering the family of planes

$$\mu = \frac{\Delta\mu}{\Delta g} g + \frac{b}{V^*} - r, \quad (4)$$

where the intercept is fixed at $-r$, the slope in the b direction is fixed at $1/V^*$, and the

slope in the g direction, $\frac{\Delta\mu}{\Delta g}$, is free to vary. The solution is found by identifying the

smallest value of $\frac{\Delta\mu}{\Delta g}$ such that at least one point from the behavioral options set (i.e., the

(g, b, μ) points) lies in the plane given by Eq. 4 (Fig. 2a). When μ is a smooth function

(Fig. 2b) the marginal rates of change in mortality for changes in g and b at the optimal

solution are given by

$$\left. \frac{\partial\mu}{\partial g} \right|_{(g,b)=(g^*,b^*)} = \frac{\Delta\mu}{\Delta g} = \frac{dV^*}{ds} \frac{1}{V^*} = \frac{\mu^* + r - b^*/V^*}{g^*} > 0, \quad \text{and} \quad (5)$$

$$\left. \frac{\partial\mu}{\partial b} \right|_{(g,b)=(g^*,b^*)} = \frac{1}{V^*} > 0.$$

Equations 5 are necessary conditions for optimal behavioral phenotypes and can also be found by differentiating Eqs. 1 or 2 with respect to g and b and setting the results equal to zero.

In general, the current optimal behavior depends on V^* , the reproductive value of an organism that adopts the optimal phenotype for all future body sizes. If the functions μ and h are specified, then, in principle, V^* can be computed by solving the dynamic programming equation given in Eq. 1 (Mangel and Clark 1988, Houston and McNamara 1999). If μ and h are partially unspecified, as in the present case, one can still analyze the implications of Eqs. 1-5 by making some qualitative assumptions about the forms of μ and h and thereby determining the qualitative behavior of V^* (of course, V^* is always a positive number by definition).

I now consider a three-stage life history that illustrates the idea. I assume that μ and h are functions such that the life history has three distinct phases: the life history begins with a growing juvenile phase with $g>0$ and $b=0$, followed by a growing adult phase with $g>0$ and $b>0$, and ending with a non-growing adult phase with $g=0$ and $b>0$. I assume μ to be a continuous function of g and b .

Juveniles have $g>0$ and $b=0$, so reproductive value increases with body size in the juvenile stage according to

$$\frac{dV^*}{ds} = \frac{\mu^* + r}{g^*} V^*, \quad (6)$$

where the ratio $\frac{\mu + r}{g}$ is minimized at every body size according to Eqs. 1 and 2 with the constraint $b=0$. The particular shape of the increase of V^* with body size during the juvenile phase will depend on the particular mathematical forms of μ and h . However, it

is clear qualitatively that V^* is increasing during the juvenile phase. The most important result for the juvenile phase is that at each body size juveniles should choose the behavioral option (e.g., habitat or prey item) resulting in the smallest value of the ratio $\frac{\mu + r}{g}$. This is Gilliam's (1982) basic criterion for juvenile behavior in size-structured populations (Werner and Gilliam 1984). This optimization criterion is especially useful empirically because it does not involve marginal rates of substitution or other quantities involving reproductive value. If the population is at a steady state size ($r=0$), then the criterion maximizes the probability of survival to the next body size. This phenotype is optimal because reproductive value only depends on body size, hence the phenotype maximizes a juvenile's probability of surviving to the size at which reproduction begins (i.e., survives to be an adult). Using $r=0$ as the reference case, for a given μ juveniles with the optimal phenotype should adopt higher growth with higher mortality when the population is growing ($r>0$), and should adopt lower growth with lower mortality when the population is declining ($r<0$; Gilliam 1982, Werner and Gilliam 1984).

During the growing adult phase $g>0$ and $b>0$ with the implication that reproductive value is increasing with body size and changes according to

$$\frac{dV^*}{ds} = \frac{(\mu^* + r)V^* - b^*}{g^*} \quad (7)$$

where the optimal values for g and b follow from Eqs. 1 or 2. Reproductive value is again increasing. However, the addition of reproduction causes a factor of b^*/g^* to be subtracted from the change in reproductive value, decreasing the rate of increase. In this phase the mortality that is incurred by the organism is now partitioned to achieve an adaptive balance between the benefits of growth and reproduction and their resulting

mortality costs. The optimization criterion for predicting the behavior of growing adults (Eqs. 1 or 2) is less useful empirically because an estimate of reproductive value, V^* , is necessary to explicitly compute optimal behavior.

The final phase of the three stage life history is the non-growing adult stage with $g=0$ and $b>0$. When $g=0$ one can not track reproductive value as a function of body size; instead I parameterize reproductive value as a function of time, giving

$$\frac{dV^*}{dt} = b^* - (\mu^* + r)V^*.$$

When $g=0$ Eq. 3 implies that $\frac{\mu^* + r}{b^*} = \frac{1}{V^*}$, implying

$$\frac{dV^*}{dt} = 0 \quad \text{and} \quad \left. \frac{\partial \mu}{\partial b} \right|_{b=b^*} = \frac{1}{V^*} = \frac{\mu^* + r}{b^*}.$$

Thus, during the non-growing adult phase reproductive value is constant (because body size is not changing and V only depends on body size) and equal to the ratio $\frac{b^*}{\mu^* + r}$.

Accordingly, optimal behavioral phenotypes should behave so as to maximize the ratio

$\frac{b}{\mu + r}$ (or, equivalently, minimize the ratio $\frac{\mu + r}{b}$) at every age during the non-growing

adult phase. Accordingly, if the population is at a steady state ($r=0$), then the criterion maximizes the expected future lifetime production of offspring (i.e., reproductive value) by minimizing the mortality incurred per newborn. Analogously to the juvenile case, adults with the optimal phenotype should adopt higher birth rates with higher mortality when the population is growing ($r>0$), and should adopt lower birth rates with lower mortality when the population is declining ($r<0$). This criterion is analogous to Gilliam's

(1982) criterion for juveniles and is equally useful because it does not require estimates of marginal rates of substitution or reproductive value to predict optimal behavior.

To summarize, my results generalize those of Gilliam (1982) by incorporating reproduction as a behavioral decision in a size-structured population. For the three-stage life history that I consider, reproductive value increases during the juvenile and growing adult phases, and remains constant during the non-growing adult phase. Reproductive value never declines and changes through time only if body size changes through time. The resulting optimization criterion for adaptive behavior during the juvenile phase is identical to that presented by Gilliam (1982). Further, I show that the optimization criterion for adaptive behavior during the growing adult phase is also identical to that given by Gilliam (1982) save for one key feature. The present model invokes the optimization via a choice of a growth rate *and* a birth rate while Gilliam's (1982) model invokes the optimization via a single choice of a growth rate while the birth rate is taken as a given function. The results also show that the optimization criterion for adaptive behavior during the non-growing adult phase is for organisms to behave so as to minimize the ratio $\frac{\mu + r}{b}$. Gilliam's (1982) model did not explore behavior in the non-growing adult phase and my result complements his earlier finding for juveniles (i.e., minimize the ratio $\frac{\mu + r}{g}$).

Testing optimization models of behavior

Although I generalize Gilliam's (1982) earlier results, the model remains a simple characterization of a biological system. For example, I assume that one state variable is

sufficient to describe any differences among individuals in the model population and that there is no seasonality in the components of fitness. Clearly these two assumptions will often be violated in real systems. However, the intent behind my simplification of the theory is to facilitate empirical assessment by eliminating, as much as possible, the need to estimate marginal rates of substitution and other quantities involving reproductive value. Remarkably, the most salient result from Gilliam's (1982) foundational model, that juveniles in a population with $r=0$ may behave so as to minimize the ratio of mortality rate to growth rate (i.e., minimize the ratio $\frac{\mu}{g}$), has hardly been assessed empirically.

The large empirical literature on foraging under threat of mortality has shown that many kinds of animals consider both feeding and mortality when making behavioral decisions (Lima and Dill 1990, Lima 1998), but very few studies have offered evidence supporting or rejecting the concept that animals explicitly balance mortality versus growth by minimizing the ratio $\frac{\mu}{g}$. I now discuss some approaches for testing theories such as the one presented above with the intent of stimulating empirical evaluations.

One approach to testing the “minimize $\frac{\mu}{g}$ criterion” for juveniles is to experimentally manipulate the structure of the behavioral options set and measure the resulting behavior. To accomplish this, the experimenter must have estimates of the rates of growth and mortality that result from different behavioral options and compute the ratio $\frac{\mu}{g}$ for each behavioral option. Accordingly, the experimenter can then manipulate the set of behavioral options available to an organism and measure the resulting behavior.

If the observed behavior corresponds to the option with the smallest ratio $\frac{\mu}{g}$, then the theory is supported, otherwise the theory is rejected.

I am aware of only one study that has approached a test of the minimize $\frac{\mu}{g}$ criterion using the method outlined above. Gilliam and Fraser (1987) tested a related criterion, that individuals should behave so as to minimize mortality rate while obtaining a feeding rate, f , above some critical level. They tested the theory by measuring the habitat preferences of juvenile creek chubs presented with a choice of three experimental habitats (a refuge habitat and two alternative habitats) that varied in food availability and number of predators (adult creek chubs). Gilliam and Fraser (1987) emphasize that if one of the three habitats is a refuge (a habitat with effectively zero mortality and zero feeding rate) and that if the juvenile creek chubs have the potential to obtain the critical feeding level in either of the two alternative habitats (*if* the animal forages in the habitat for a sufficient amount of time), then the optimal behavior is to “use the refuge plus the habitat with the lowest ratio of mortality rate to feeding rate, $\frac{\mu}{f}$.” They first measured the rates of feeding and mortality of juvenile creek chubs constrained to habitats with varying levels of food availability and numbers of adult creek chubs. These measurements permitted the computation of the ratio $\frac{\mu}{f}$ for each habitat (i.e., each behavioral option). They then conducted a series of habitat selection experiments in which juvenile creek chubs were allowed to choose among habitats with varying levels of food availability and

numbers of adult creek chubs. Their results show that juvenile creek chubs spent more time in the habitats with the lowest ratio, $\frac{\mu}{f}$.

As mentioned above, the optimal behavior in Gilliam and Fraser's (1987) experimental design is to use the refuge plus whichever alternative habitat yields the lowest ratio, $\frac{\mu}{f}$. The implication of this result is that under Gilliam and Fraser's (1987) assumptions the optimal behavior is likely to be identical to the behavior that "uses the refuge plus whichever alternative habitat yields the lowest ratio $\frac{\mu}{g}$." Hence Gilliam and Fraser's (1987) results are consistent with the minimize $\frac{\mu}{g}$ criterion for predicting, qualitatively, which of the two alternative habitats should be occupied. In order for the two criteria to agree exactly, by predicting the precise amounts of time that the juvenile creek chubs should spend in each habitat, the critical feeding level must be the feeding rate at which the growth rate is g^* (i.e., the g that minimizes $\frac{\mu}{g}$). Gilliam and Fraser (1987) do not analyze the behavior at this level of detail and simply note that the critical feeding level may change as the behavioral options change (because, for example, g^* would change, in general, as the behavioral options change). Thus, I emphasize that, in general, the behavioral strategies "minimize $\frac{\mu}{f}$ " and "minimize $\frac{\mu}{g}$ " will yield different quantitative behaviors (e.g., the time spent in each habitat), and that Gilliam and Fraser's (1987) analysis is a case where the strategies predict the same qualitative behavior (i.e., which habitats are utilized for any amount of time).

As Gilliam and Fraser (1987) point out, the observed feeding rates of the juvenile creek chubs declined as food availability and the number of predators were increased in one of the alternative habitats. These results are consistent with the idea that the critical feeding rate is adjustable as the behavioral options set changes. The minimize $\frac{\mu}{g}$ criterion with nonlinear tradeoffs between mortality rate and feeding rate is one mechanism by which feeding rate could be adjusted adaptively by the juvenile creek chubs. The presence of nonlinear tradeoffs could also explain the use of both alternative habitats by the juvenile creek chubs (Gilliam and Fraser's (1987) model predicts use of the refuge plus only *one* of the two alternative habitats).

Also of note is the fact that Gilliam and Fraser (1987) measured feeding and mortality rates independently of one another to parameterize a model designed to predict behavior that balances feeding and mortality simultaneously. That is, feeding rates of juvenile creek chubs were measured at different levels of food availability in the absence of predators and the mortality rates of juvenile creek chubs were measured at different levels of predator abundance in the absence of food. Apparently these measurements were sufficient to parameterize their model for their analysis. However, as their own results suggest, behavior should depend simultaneously on factors such as food availability and predator abundance. For example, the feeding rate of juvenile creek chubs within an alternative habitat with a given level of food availability will probably vary with predator abundance in the habitat. Thus, there is no reason to believe that measurements of behavior taken with one factor held fixed at zero will be generally adequate for the prediction of behavior in the presence of varying levels of both factors.

In summary, Gilliam and Fraser's (1987) study is the only explicit experimental assessment (in the sense of experimentally creating and manipulating the behavioral options set) of any aspect of Gilliam's (1982) model (including my present generalization of that model). Many of the results in Gilliam and Fraser's (1987) study are consistent with the minimize $\frac{\mu}{g}$ criterion. However, the forms of the tradeoffs (linear versus nonlinear) and the details of the model parameterization warrant further investigation. With these ideas in mind, Gilliam and Fraser's (1987) study should serve as a helpful foundation for additional studies of this sort.

A second approach for testing the minimize $\frac{\mu}{g}$ criterion is to measure the ratio $\frac{\mu}{g}$ for a variety of behavioral options known to exist in the field and to then determine whether the behavioral options selected by organisms in the field correspond to those with lowest ratio $\frac{\mu}{g}$. Dahlgren and Eggleston (2000) report that juveniles of a coral reef fish, the Nassau grouper, appear to occupy two different reef habitats as they increase in body size. Through the use of caging and tethering experiments they estimated the rates of growth and mortality of three size classes of Nassau grouper in the two habitat types. Using these data they assessed the applicability of three optimization criteria as mechanisms underlying the observed ontogenetic habitat shifts: maximize g , minimize μ , and minimize $\frac{\mu}{g}$. Their results show that the maximize g criterion can be rejected for the smallest size class, that the minimize μ criterion can be rejected for the medium and large

size classes, and that the minimize $\frac{\mu}{g}$ criterion is never rejected for any of the three size classes. Accordingly, these results show that the minimize $\frac{\mu}{g}$ criterion is the best explanation (among the three explanations considered) for the observed ontogenetic habitat shifts.

The difficulty of measuring behavior-specific growth and mortality rates can hinder field assessments of the minimize $\frac{\mu}{g}$ criterion. Dahlgren and Egelston (2000) estimated mortality by measuring the mortality of tethered fish. As suggested by Gilliam (1982), a measurement of relative mortality for comparisons among habitats can be sufficient for testing the theory. In this case, tethering mortality need only be proportional to true mortality for the analyses of Dahlgren and Egelston (2000) to be accurate assessments of the theory. However, the constant of proportionality must be the same for every habitat. In general, it's important to note that the relationship between tethering mortality and natural mortality is unknown, and this fact must be taken into consideration when interpreting the results of Dahlgren and Egelston (2000).

To summarize, the study of Dahlgren and Eggleston (2000) is the only published field-derived test (in the sense of attempting to utilize a behavioral options set found in nature) of Gilliam's (1982) model. In addition to its measurements taken from a natural system, the scientific value of the Dahlgren and Egelston (2000) study rests in its explicit consideration of three alternative hypotheses. Of the three alternatives that they consider, the minimize $\frac{\mu}{g}$ criterion provides the best description of the data. The measurement of behavior-specific rates of growth and mortality in the field continues to

be a challenge and the work of Dahlgren and Eggelston (2000) can serve as a basis for future studies of this sort.

A third approach can, in principle, be utilized to test many predictions from a variety of optimization models, including my present generalization of Gilliam's (1982) model. This method requires the additional assumption that individuals from the study population are distributed among habitat patches (the habitat patches may be experimental or natural) according to an ideal-free distribution (Fretwell and Lucas 1970). The key assumption is that the individuals distribute themselves among the alternative habitats such that all individuals within a size class have equal fitness. If this scenario applies, then many optimization models make explicit predictions about how the components of fitness should relate to one another.

I illustrate the idea for the most general case in my model: growing adults. For $i=1,2,\dots,n$ habitats fitness among growing adults of identical size is equal across the habitats if and only if

$$\frac{dV^*}{ds} \frac{1}{V^*} = \frac{(r + \mu_1^*) - \frac{b_1^*}{V^*}}{g_1^*} = \frac{(r + \mu_2^*) - \frac{b_2^*}{V^*}}{g_2^*} = \dots = \frac{(r + \mu_n^*) - \frac{b_n^*}{V^*}}{g_n^*}$$

implying

$$\mu_i^* = \frac{dV^*}{ds} \frac{1}{V^*} g_i^* + \frac{b_i^*}{V^*} - r \quad (8)$$

for each i . Thus the ideal-free extension of the theory predicts that mortality rate is linear in growth rate and birth rate with intercept $-r$ when the fitness components are measured across habitats. The predictions for juveniles and non-growing adults follow from Eq. 8 directly with the substitution $g_i^*=0$ and $b_i^*=0$, respectively. This prediction motivates an empirical effort that would measure rates of mortality, growth, and birth across a variety

of habitats. The prediction of the linear relationship given in Eq. 8 could then be tested using linear regression. Estimates of the regression coefficients would be valuable in that they would provide estimates of the demographic parameters $\frac{dV^*}{ds}$ and $\frac{1}{V^*}$ (see Chapter 3 for a presentation of a method for estimating $\frac{dV^*}{ds} \frac{1}{V^*}$).

Conclusions

My view is that there are many opportunities for empirical tests of optimization theory and I illustrate three examples of how the theory may be evaluated. However, much more work remains to be done to adequately test available theory. As documented in reviews (Lima and Dill 1990, Lima 1998), the empirical literature covering two-way tradeoffs between feeding and mortality and reproduction and mortality is extensive. Yet, surprisingly, only the two published studies discussed above provide explicit assessments of any part of the available theory. These two studies both consider the minimize $\frac{\mu}{g}$ criterion only. The remaining published studies show convincingly that animals consider food intake and mortality hazard when making behavioral decisions, but fall short of carrying out the measurements and/or computations required to evaluate the minimize $\frac{\mu}{g}$ criterion. The other components of the theory remain quantitatively unevaluated.

For example, I know of no study (aside from my Chapter 3) that has attempted to (1) evaluate the relative merits of two or more alternative models that adaptively balance growth rate and mortality rate (e.g., the minimize $\frac{\mu}{g}$ criterion versus the maximize $\theta g - \mu$

criterion, where θ is the marginal rate of substitution of mortality for growth, Houston and McNamara 1999), (2) test the minimize $\frac{\mu + r}{b}$ criterion, in any form, or (3) test for three-way tradeoffs among growth, mortality and reproduction, such as those embodied in my present generalization of Gilliam's (1982) model. Studies that address these deficiencies in the literature will contribute substantially to our understanding of how natural selection may act on behavioral phenotypes and thereby contribute to our understanding of broader issues in ecology (e.g., Rosenzweig and Abramsky 1997, Post et al. 1999).

Literature Cited

- Brown, J. S. 1992. Patch use under predation risk: I. Models and predictions. *Annales Zoologici Fennici* 29: 301-309.
- Charlesworth, B. 1980. *Evolution in age-structured populations*. Cambridge University Press, Cambridge, U. K.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81: 2227-2240.
- Fretwell, S. D. and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. I. Theoretical development. *Acta Biotheoretica* 19: 16-36.
- Gadgil, M., and W. H. Bossert. 1970. Life historical consequences of natural selection. *American Naturalist* 104: 1-24.
- Gilliam, J.F. 1982. Foraging under mortality risk in size-structured populations. Ph. D. Thesis, Michigan State University, U.S.A.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68: 1856-1862.
- Godin, J. J. and L. A. Dugatkin. 1996, Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Science* 93: 10262-10267.
- Harper, D. G. C. 1982. Competitive foraging in mallards: 'ideal free' ducks. *Animal Behaviour* 30: 575-584.

- Houston, A. I., and J. M. McNamara. 1999. Models of adaptive behavior: an approach based on state. Cambridge University Press, Cambridge, U. K.
- Kozłowski, J. 1999. Adaptation: a life history perspective. *Oikos* 86: 185-194.
- Krebs, J. R. and N. B. Davies. 1993. An introduction to behavioural ecology. 3rd Edition. Blackwell Scientific Publications, Oxford, U. K.
- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
- Leon, J. A. 1976. Life histories as adaptive strategies. *Journal of Theoretical Biology* 60: 301-335.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27: 215-290.
- Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Mangel, M. and C. W. Clark. 1988. Dynamic modeling in behavioral ecology. Princeton University Press, Princeton, N. J., U. S. A.
- Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. *Zeitschrift für Tierpsychologie* 51: 36-40.
- Milinski, M. 1993. Predation risk and feeding behavior. In: *Behaviour of teleost fishes*. Ed. T. J. Pitcher. Chapman and Hall, New York, N. Y., U. S. A.
- Milinski, M. and R. Heller. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks. *Nature* 275: 642-644.

- Parker, G. A. 1978. Searching for mates. In: Behavioural ecology. 1st Edition. Eds. J. R. Krebs and N. B. Davies. Oxford University Press, Oxford, U. K.
- Perrin, N. and R. M. Sibly. 1993. Dynamic models of energy allocation and investment. *Annual Review of Ecology and Systematics* 24: 379-410.
- Post, E., R. O. Peterson, N. C. Stenseth and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401: 905-907.
- Rosenzweig, M. L., and Z. Abramsky. 1997. Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. *Evolutionary Ecology* 11: 733-756.
- Schaffer, W. M. 1974. Selection for optimal life histories: the effects of age structure. *Ecology* 55: 291-303.
- Schaffer, W. M. 1983. The application of optimal control theory to the general life history problem. *American Naturalist* 121: 418-431.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210: 1041-1043.
- Stephens, D. W. and J. R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, N. J., U. S. A.
- Taylor, H. M., R. S. Gourley, C. E. Lawrence, R. S. Kaplan. 1974. Natural selection of life history attributes: an analytical approach. *Theoretical Population Biology* 5: 104-122.
- Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393-425.

Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. *American Naturalist* 100: 687-690.

Figure Legends

Figure 1: Hypothetical sets of behavioral options corresponding to (a) a linear combination of a discrete set of behavioral options and (b) a smooth and nonlinear relationship among fitness components. The function h denotes a constraint between growth rate, g , and birth rate, b and can limit the boundary of the set of behavioural options (polygon defined by solid lines).

Figure 2: Hypothetical behavioral options sets identical to those in Figure 1. The planes through the origin identify optimal behaviors (denoted by a star) following from the dynamic programming equation when applied to each options set.

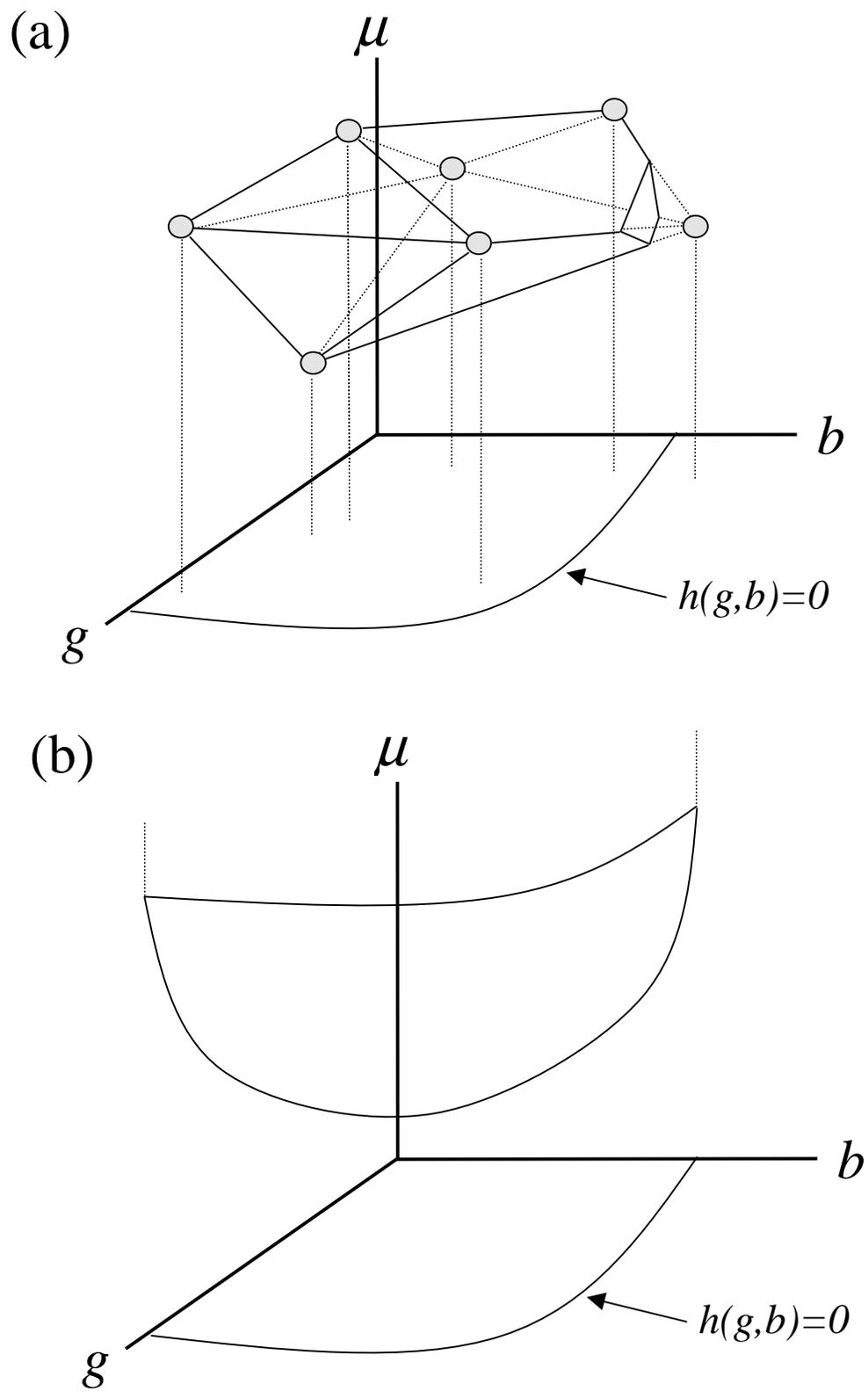


Figure 1

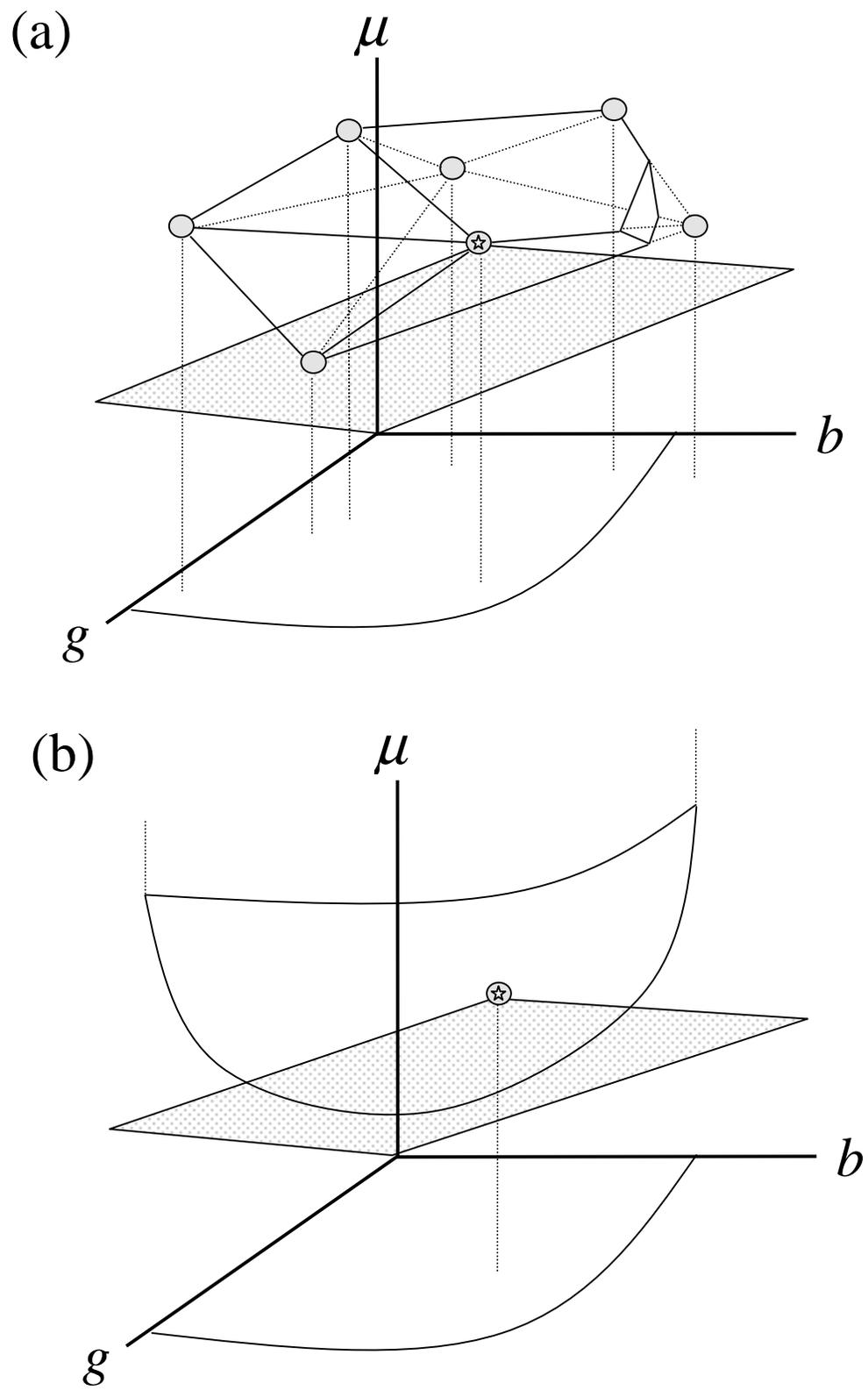


Figure 2

Chapter 2

Functional responses with predator interference: viable alternatives to the Holling

Type II model

(to appear in *Ecology*)

Abstract

A predator's *per capita* feeding rate on prey, or its functional response, provides a foundation for predator-prey theory. Since 1959, Holling's prey-dependent Type II functional response, a model that is a function of prey abundance only, has served as the basis for a large literature on predator-prey theory. I present statistical evidence from 19 predator-prey systems that three predator-dependent functional responses (Beddington-DeAngelis, Crowley-Martin, and Hassell-Varley), i.e., models that are functions of both prey and predator abundance because of predator interference, can provide better descriptions of predator feeding over a range of predator-prey abundances. No single functional response best describes all of the data sets. Given these functional forms, I suggest use of the Beddington-DeAngelis or Hassell-Varley model when predator feeding rate becomes independent of predator density at high prey density, and use of the Crowley-Martin model when predator feeding rate is decreased by higher predator density even when prey density is high.

Introduction

Understanding the relationship between predator and prey is a central goal in ecology, and one significant component of the predator-prey relationship is the predator's rate of feeding upon prey. The feeding rate describes the transfer of biomass between trophic levels and, in the simplest models, completely describes the dynamic coupling between predator abundance and prey abundance (e.g., Lotka 1925). Since the early development of predator-prey theory ecologists have recognized the theoretical importance of understanding the details of a predator's feeding rate (Nicholson and Bailey 1935, Holling 1959a). More recent theoretical work has demonstrated that the mathematical form of the feeding rate can influence the distribution of predators through space (van der Meer and Ens 1997), the stability of enriched predator-prey systems (DeAngelis et al. 1975, Huisman and De Boer 1997), correlations between nutrient enrichment and the biomass of higher trophic levels (DeAngelis et al. 1975), and the length of food chains (Schmitz 1992).

The description of a predator's instantaneous, *per capita* feeding rate, f , as a function of prey abundance, N , is the classic definition of a predator's "functional response" (Holling 1959a). One type of functional response derived by Holling (1959b), the "Type II," describes the average feeding rate of a predator when the predator spends some time searching for prey and some time, exclusive of searching, processing each captured prey item (i.e., handling time). In this case the instantaneous, *per capita* feeding rate of the predator is given by a function of the form

$$f_1(N, P) = \frac{aN}{1 + bN}, \quad \text{where} \quad (1)$$

parameters a (units: 1/time) and b (units: 1/prey) are positive constants that describe the effects of capture rate and handling time, respectively, on the feeding rate (handling time = b/a). Note that the feeding rate given by Eq. 1 is unaffected by predator abundance, P . Equation 1, known as the Holling Type II functional response (hereafter the H2 model), is widely used and has stood as the “null model” upon which much predator-prey theory has been constructed (Brown 1991).

Equation 1, as suggested by Holling’s (1959a) empirical results, assumes that predators do not interfere with one another’s activities; thus competition among predators for food occurs only via the depletion of prey. However, Beddington (1975) derived and DeAngelis et al. (1975) proposed, independently, a functional response that can accommodate interference among predators (see Huisman and De Boer 1997 for a mathematically detailed derivation). In this model individuals from a population of two or more predators not only allocate time to searching for and processing prey, but also spend some time engaging in encounters with other predators, resulting in a functional response that gives an instantaneous, *per capita* feeding rate

$$f_2(N, P) = \frac{aN}{1 + bN + c(P - 1)}, \quad (2)$$

where P is the predator abundance and c (units: 1/predator) is a positive constant describing the magnitude of interference among predators. When $c=0$ or $P=1$, Eq. 2, the Beddington-DeAngelis functional response (hereafter the BD model), reduces to Eq. 1, the H2 functional response. The precise form of the model proposed by DeAngelis et al. (1975) differs slightly from the Beddington (1975) derivation in that DeAngelis et al. use the term P instead of $P-1$. I retain Beddington’s original $P-1$ form here, and also retain the $P-1$ term in the Crowley-Martin functional response that follows below. The $P-1$ form

was used by Beddington and by Crowley and Martin (below) in building mechanistic models in which predator abundance is expressed as counts (integers), and the mechanism of predator dependence is interference via direct encounters with other predators. Hence the $P-1$ term is used because a predator does not interfere with itself in those models, and setting $P=1$ reduces the models exactly to the H2 model. However, when predator abundance is modeled as a continuous variable as in usual models of population dynamics, or when some other mechanism of predator dependence is hypothesized (e.g., prey behavior that depends on predator density), replacement of $P-1$ by P in predator-dependent functional responses will often be more appropriate.

The BD model assumes that handling and interfering are exclusive activities. Crowley and Martin (1989) removed that assumption in what they called their “pre-emption” model, allowing for interference among predators regardless of whether a particular individual is currently handling prey or searching for prey. The Crowley-Martin model (hereafter the CM model) thus adds an additional term in the denominator,

$$f_3(N, P) = \frac{aN}{1 + bN + c(P-1) + bcN(P-1)} = \frac{aN}{(1 + bN)(1 + c(P-1))}. \quad (3)$$

The parameters a , b , and c have the same interpretation as in the BD model, and, like the BD model, the CM functional response reduces to the H2 functional response when $c=0$. An important distinction between the BD and CM models is that the BD model predicts that the effects of predator interference on feeding rate become negligible under conditions of high prey abundance (because predators which are handling prey do not interfere), but the CM model predicts that interference effects on feeding rate remain important. That is, rearranging the BD model by dividing the numerator and denominator

by N , $\lim_{N \rightarrow \infty} f_2(N, P) = \lim_{N \rightarrow \infty} \frac{a}{\frac{1}{N} + b + \frac{c(P-1)}{N}} = \frac{a}{b}$ while the CM model

yields $\lim_{N \rightarrow \infty} f_3(N, P) = \lim_{N \rightarrow \infty} \frac{a}{\frac{1}{N} + b(1 + c(P-1)) + \frac{c(P-1)}{N}} = \frac{a}{b(1 + c(P-1))}$. Hence, as prey

abundance becomes large, the functional response asymptotes at a level independent of predator abundance in the BD model, but the asymptote depends on predator abundance in the CM model. In both models, the distance between the functional response and its asymptotic value depends on the relative abundance of predators and prey, specifically the value of $1/N + c(P-1)/N$, and the parameters a and b .

The H2, BD, and CM models all have mechanistic bases stated by their authors. However, they can also be viewed as phenomenological models with increasing complexity (in the denominator, for the H2, BD, and CM models, respectively, only a linear prey term, the addition of a linear predator term, and the addition of a prey X predator interaction term). Also, the BD model and the CM model can be derived from other premises. For example (P. Abrams, personal communication), the DeAngelis et al. (1975) form of the BD model (use of P instead of $P-1$) can be derived by assuming no direct interference among predators, but rather that the prey adjust their behavior in the presence of the predators. Writing the H2 model as $CN/(1+ChN)$, where C is a capture coefficient and h is handling time, and writing $C = C'/(1+iP)$ where C' and i are parameters, yields an equation identical to Eq. 2 if $P-1$ is replaced by P . The CM model can also be derived via a different route than the mechanistic approach of Crowley and Martin. Harrison (1995) divided the H2 functional response by a term, $1+\beta P$, where β is a positive parameter, to produce a predator-dependent functional response as a

phenomenological model rather than positing any particular mechanism. This division yields the CM model if $P-1$ in the CM model is replaced with P .

There is a vast literature of ecological theory resting upon the H2 model. I inspected papers in three leading ecology journals over the past four years (Table 1), and found that 69% of the papers specifying a functional response employ the H2 model. The second-most specified functional response was the linear Lotka-Volterra model, $f = aN$, as specified in 27% of the papers. In contrast, 7% and 0% of these studies employ the BD and CM models, respectively (two of the three studies employing the BD model are authored by DeAngelis, who introduced the model in 1975).

Four of the papers (9%) in Table 1 specified predator-dependent forms based on the Hassell-Varley model (Hassell and Varley 1969) and similar ratio-dependent forms (forms dependent on N/P rather than N) that have been the subject of many criticisms over the past 10 years (e.g., Abrams 1994, 1997). Because the BD and CM models are mechanistic extensions of the H2 model, I prefer them to the Hassell-Varley model, which was written without a stated mechanistic basis subject to test. However, because of its relatively high profile in the functional response literature, I also include a version of the Hassell-Varley model in my analyses. Also, recently Cosner et al. (1999) have shown that special cases of the Hassell-Varley model ($m = 1/3, 1/2, \text{ or } 1$ in Eq. 4, below) can arise from mechanistic assumptions about foraging by spatially grouped predators, and Abrams and Ginzburg (2000) discuss possible mechanistic bases leading to ratio dependence ($m = 1$).

Specifically, I analyze a version of the Hassell-Varley model, modified to include handling time following Sutherland (1983),

$$f_4(N, P) = \frac{aN}{bN + P^m}. \quad (4)$$

Hereafter, I call Eq. 4 the HV model. When $m=0$ or $P=1$ the HV model reduces to the H2 model. Arditi and Ackakaya (1990) compared this same model to the H2 model, and found $m>0$ in each of the ten predator-prey systems they analyzed, hence concluding that the HV model was a better descriptor of the data than the H2 model. They also concluded that ratio-dependent functional responses are likely because most of their confidence intervals for m contain one. When $m=1$ the HV model depends on N and P only through the ratio N/P , because Eq. 4 can then be rewritten as $f = a \cdot (N/P) / (1 + b \cdot (N/P))$.

However, the H2 model's relative monopoly of the theoretical literature and the debate over ratio dependence (including Arditi and Ackakaya's results) linger while empirically it remains unclear as to what form the functional response should take (Abrams and Walters 1996, Murdoch and Briggs 1996, Abrams and Ginzburg 2000). Indeed, Abrams and Walters (1996) conclude, "Although the idea of predator density dependence is very plausible, it is something that has not received much empirical investigation. The literature on ratio-dependent functional responses has yet to produce any conclusive evidence for density dependence of any kind affecting the functional response."

Given that large numbers of experiments and observations suggest that predators do indeed interfere with one another's activities so as to result in competitive effects (reviews in Schoener 1983, MacIsaac and Gilbert 1991) and that prey alter their behavior under increased predator threat (reviewed by Lima 1998), the BD, CM, and HV models stand as reasonable alternatives to the H2 model. Therefore, in this paper I expand on Arditi and Ackakaya's (1990) work by presenting the results of statistical tests that can

discriminate among these four alternative functional response models using data sets from 19 simple predator-prey systems.

Methods

I searched the literature via electronic database and literature citations for any study from which I could extract measured instantaneous or integrated feeding rates (defined below) for at least two prey abundances and two predator abundances. I located 19 data sets (Table 2) from 15 sources (14 from the peer-reviewed literature, one Ph.D. dissertation). I did not consider any study that measured a feeding rate but failed to report both predator abundance and prey abundance (e.g., many studies of predator feeding with continuous input of prey; Kennedy and Gray 1993). Some papers reported several similar data sets for the same predator, and in this case I randomly selected one of these data sets so as to include a maximum of one data set per predator-prey system in my analysis. I tested among the four functional response models by first testing each of the three predator-dependent forms against the H2 model, and then testing the alternative predator-dependent models against one another. In keeping with the assumptions of each model, the parameters a , b , c , and m are assumed to be non-negative. I distinguish between two types of data sets: those that attempted to measure instantaneous feeding rates by assuming a relatively constant prey abundance over the duration of the study, and those that measured integrated feeding rates because prey abundance was depleted by predator feeding over the duration of the study (Table 2). These two types of data sets require slightly different mathematical approaches.

I analyzed five data sets as representing direct estimates of instantaneous feeding rates, because the author(s) either (i) regularly replaced prey that had been consumed by predators (data sets 2 and 3), or (ii) directly measured the number of prey killed along with predator and prey densities (data sets 1, 4 and 5).

When prey are depleted over the course of the study by predator feeding then integrated feeding rates are measured, and the computations become more cumbersome. In this case, to compare model predictions with the observed data one must integrate the predators' instantaneous feeding rate over the duration of the empirical study, accounting for prey depletion, resulting in an integrated feeding rate, F_i (i.e.,

$$F_i(N(0), P) = \frac{N(0) - N(t)}{P}, \text{ where } N(0) \text{ is the initial number of prey and } N(t) \text{ is the}$$

number of prey remaining after time t). The prey remaining after time t , $N(t)$, is the solution to the appropriate differential equation, where the rate of prey depletion by P predators is

$$\frac{dN}{dt} = -f_i(N, P)P, \quad i=1,2,3,4 \quad (5)$$

for the H2, BD, CM, and HV functional responses, respectively. Predator abundance, P , and initial prey abundance, $N(0)$, are given as the treatment combinations and Eqs. 5 must be solved for the final prey abundance after time t , $N(t)$. These equations can be solved analytically, resulting in an implicit function which must then be solved numerically to find $N(t)$ (Beddington 1975). Alternatively, Eqs. 5 can be numerically integrated to obtain $N(t)$.

Using the method of maximum likelihood I fit model predictions of integrated feeding rates ($N(t)$) obtained by numerical integration of Eqs. 5 via a second order Runge-

Kutta algorithm; Kincaid and Cheney 1996) to the experimental observations of integrated feeding rates for different levels of initial prey abundance, $N(0)$, and predator abundance, P , to estimate the parameters a , b , c and m . For the j th observation I assumed the statistical models

$$W_j \sim \text{lognormal}(\log(f_i(N_j, P_j)), \sigma_{w,i}^2) \quad \text{and}$$

$$Y_j \sim \text{lognormal}(\log(F_i(N_j(0), P_j)), \sigma_{y,i}^2),$$

for instantaneous and integrated measurements of predator feeding rates, respectively (Hilborn and Walters 1992, Carpenter et al. 1994, Pascual and Kareiva 1996, Jost and Arditi 2000). Here the sets $\{W_j, N_j, P_j\}_{j=1}^n$ and $\{Y_j, N_j(0), P_j\}_{j=1}^n$ are the observed feeding rates, prey abundances, and predator abundances from experiments measuring instantaneous and integrated feeding rates, respectively. The parameter n is the sample size, and the parameters $\log(f_i(N_j, P_j))$ and $\log(F_i(N_j(0), P_j))$, and $\sigma_{w,i}^2$ and $\sigma_{y,i}^2$ are the expectations and variances of $\log(W_j)$ and $\log(Y_j)$, respectively. I estimated the parameters a , b , c , and m by maximum likelihood, minimizing the sums of squares

$$SS_{w,i} = \sum_{j=1}^n (\log(W_j) - \log(f_i(N_j, P_j)))^2,$$

for instantaneous feeding rates. The sums of squares for integrated feeding rates is analogous. I estimated the variances using

$$\hat{\sigma}_{w,i}^2 = \frac{\hat{SS}_{w,i}}{n - p},$$

where p is the number of parameters in the functional response and $\hat{SS}_{w,i}$ is the maximum likelihood estimate of $SS_{w,i}$ (Seber and Wild 1989; the variance estimator for integrated feeding rates is analogous).

To test the BD and CM models against the H2 model I tested whether $c=0$, because each of the three predator-dependent models reduces to the H2 model when $c=0$, by computing 95% confidence intervals for c for each of the predator-dependent forms. Similarly, for the HV model, I computed 95% confidence intervals for m , because the HV model reduces to the H2 model for $m=0$. I computed the 95% confidence intervals by computer simulation (i.e., I employed a parametric bootstrap with 500 bootstrap replicates per model per data set; Efron and Tibshirani 1993, Dennis and Taper 1994).

To test among the alternative predator-dependent forms I used the likelihood-ratio test statistic, defined, for instantaneous feeding rates, for example, as

$$T_{i,j} = n(\log[\hat{SS}_{w,j}] - \log[\hat{SS}_{w,i}])$$

(the test statistic for integrated feeding rates is analogous). If model i fits the data better than model j , then $T_{i,j}$ will be positive. Conversely, if model j fits the data better than model i , then $T_{i,j}$ will be negative. This test statistic is identical to the difference between two Akaike Information Criterion (AIC) values for the case of comparing two models with the same number of parameters (Hilborn and Mangel 1997), as is the case here.

My tests of each of the predator-dependent models versus the H2 model treat the H2 model as a null hypothesis in the classic sense in that my test manages Type I errors (i.e., incorrectly rejecting the H2 model), but does not control for Type II errors (i.e., incorrectly accepting the H2 model). This approach gives the H2 model the “benefit of the doubt” in a statistical sense when compared to the three-parameter models I consider

here. However, for testing among the three predator-dependent models I do not have justification for specifying any model as the null hypothesis and therefore I employ a test that puts the BD, CM, and HV models on “equal footing” by managing for errors in either direction. Accordingly, I defined the critical values for the test statistic $T_{i,j}$ as

$$L_{i,j} = \min(k_{i,j}^1, k_{i,j}^2) \quad \text{and} \quad U_{i,j} = \max(k_{i,j}^1, k_{i,j}^2)$$

where $k_{i,j}^1$ and $k_{i,j}^2$ satisfy

$$\Pr\{T_{i,j} < k_{i,j}^1 | H_i\} = 0.05 \quad \text{and} \quad \Pr\{T_{i,j} > k_{i,j}^2 | H_j\} = 0.05,$$

where H_i and H_j represent the hypothesized functional responses f_i and f_j , respectively.

The resulting test is: reject H_i if $T_{i,j} < L_{i,j}$, reject H_j if $U_{i,j} < T_{i,j}$, or reject neither H_i or H_j if $L_{i,j} \leq T_{i,j} \leq U_{i,j}$.

I parameterized the models with 95% confidence intervals for a , b , c and m and computed $L_{i,j}$ and $U_{i,j}$ by computer simulation (i.e., I used parametric bootstrap to compute confidence intervals and the distributions of the test statistics using 500 bootstrap replicates per model per data set). I report the outcomes of my hypothesis tests using the observed values of the test statistic $T_{i,j}^{obs}$, the P -values $\Pr\{T_{i,j} < T_{i,j}^{obs} | H_i\}$ and $\Pr\{T_{i,j} > T_{i,j}^{obs} | H_j\}$ for each pairwise test of the alternative predator-dependent models and the confidence intervals for c or m for the best-fitting (i.e., greatest likelihood) model for each data set.

Results

When compared with the Holling Type II (H2) model as the null hypothesis, all three alternatives show statistically significant improvement over the Holling model, by

the criterion that the 95% confidence interval for the interference parameter (c or m) does not contain zero (Fig. 1a, 1b, 1c). Treating the H2 model as the null hypothesis, comparison with the Beddington-DeAngelis (BD) model results in rejection of the H2 model in favor of the BD model in 18 of the 19 data sets (Fig. 1a). The Crowley-Martin (CM) comparison results in rejection of the H2 model in 15 of the 19 cases (Fig. 1b), and the Hassell-Varley (HV) comparison is essentially identical to the result of the BD versus H2 comparison: rejection of the H2 model in all but one case (data set 5, as in the BD comparison; Fig. 1c). Appendix 1 gives 95% confidence intervals for the interference parameters (c and m) and the other parameters for the best-fit model for each data set. Only for data set 5 is the H2 null hypothesis accepted.

To illustrate the fits of the three alternative predator-dependent models, in Fig. 2 I show the model fits for three cases, one for each of the three models. As explained in the Introduction, the CM model accommodates different asymptotic feeding rates for different predator levels as prey increase in density. Data set 11 (Fig. 2b) shows that phenomenon, and the CM model provides the best fit to that data set (Appendix 1); the asymptotic feeding levels for low predator abundances ($P=1, 2$) appear not to be reached over the range of prey abundances studied, but exceed the asymptotic feeding levels inferred for high predator abundances ($P=6, 8$). In contrast, the BD and HV models provide better fits (Appendix 1) to data sets without evidence for different asymptotes, such as data set 6 (Fig. 2a) and data set 12 (Fig. 2c). However, I note that for some data sets, e.g., Fig. 2a, the prey abundances studied were not sufficiently high to make a convincing case regarding the existence of an asymptotic feeding rate common to all predator abundances, versus asymptotes which depend on predator abundance.

Comparison of the BD, CM, and HV models (Fig. 1 and Appendix 2) shows that the CM model fits are often significantly different from the BD model fits (Fig. 1d) and the HV model fits (Fig. 1e), but that the BD and HV models are usually not distinguishable from each other (Fig. 1f). When compared to the BD model (Fig. 1d and Appendix 2), the CM model yields significantly better fits in three cases (data sets 3, 7, and 11), and inspection of those fits confirmed that those data sets indicate asymptotes that differ across predator level. Similarly, nine data sets favor the BD model over the CM model (Fig. 1d and Appendix 2), and in these data sets a common asymptote within each data set, across predator levels, is indicated. Comparison of the CM model with the HV model (Fig. 1e, Appendix 2) yields the identical result, except that eight data sets rather than nine data sets support the HV model over the CM model.

In contrast, the statistical distinction between the BD and HV models is quite subtle; their respective best-fitting predator-dependent terms in the denominator, $1 + \hat{c}(P - 1)$ and $P^{\hat{m}}$ (where \hat{c} and \hat{m} are the maximum likelihood estimates of c and m), are nearly identical over the relevant set of predator abundances for all of the data sets, including those data sets that statistically distinguish one form as superior to the other (e.g., data sets 6 and 12 in Fig. 2a and 2c). In 11 of the 19 cases, the data do not support one model over the other (Appendix 2, Fig. 1f). In the eight cases that reveal a difference, five support the BD model and three support the HV model. However, even in those cases where the models have significantly different statistical fits, the fits are qualitatively quite similar (Fig. 1f).

Discussion

My most salient finding is that predator dependence in the functional response is a nearly ubiquitous property of the published datasets. In 18 of the 19 studies, the classical Holling Type II model, which assumes only prey dependence, was rejected in favor of at least one of the three predator-dependent models.

While the result of predator dependence in all but one of the data sets is clear, I do not attempt to infer the mechanism(s) which produced the predator dependence in these studies. Several mechanisms can produce declining *per capita* intake with increasing predator abundance (e.g., Abrams and Ginzburg 2000). One mechanism is “direct” interactions among predators, such as those embodied in the Beddington-DeAngelis and the Crowley-Martin models, in which encounters between predator individuals is modeled as time lost from hunting for prey. A second mechanism is changes in prey behavior which result in less vulnerable prey under higher predator densities (Charnov et al. 1976), and a third mechanism, applicable when prey are depleted, is heterogeneity in vulnerability within the prey population, e.g., that there is a subset of the total prey population that is more vulnerable than others, with that subset depleted more rapidly at higher predator abundances (Abrams 1994). In some of the 19 studies, additional information was given which pointed to specific mechanisms. For example, Walde and Davies (1984) observed predator and prey behavior directly, and reported that the first two mechanisms appeared to play roles in producing the predator dependence. In other cases the experimental settings rule out some mechanism. For example, in data set 7 the parasitoid *Trichogramma* parasitizes the eggs of the host *Sitotroga* in a laboratory setting and I can presumably rule out altered prey (egg) behavior as the mechanism in that case.

The same argument applies to data sets 6 and 16 where the parasitoids lay eggs on fly pupae and moth eggs, respectively. However, given a large empirical and theoretical literature addressing changes in prey behavior across predator abundances (Lima 1998, Houston and McNamara 1999), prey behavior almost surely contributes to the phenomenon of predator dependence in some of the 19 data sets, and in many other predator-prey systems in nature.

The degree to which my results from 19 data sets can be extrapolated to some larger set of predator-prey systems is not known. The data sets measuring feeding rate across both prey abundance and predator abundance tend to be laboratory studies, and I agree with Osenberg et al. (1999) that the sample is likely to be biased towards systems in which the researchers suspected predator dependence in the first place, hence motivating their commitment of effort to measuring the functional response across multiple predator abundances. My study analyzes available data, but I caution against over-generalization, and point to the usefulness of an effort to randomly sample predator-prey systems from some population of systems.

Nonetheless, my statistical results suggest that the three predator-dependent models that I consider deserve more attention in the literature than they have received to date (Table 1). No single model best describes all of the 18 data sets that exhibit predator dependence. However, some patterns in the results are evident. Based on their different asymptotic properties as prey density becomes high, the CM model can be quite different from the BD and HV models, and some of the data sets strongly support the CM model whereas the remaining data sets support the BD and HV models over the CM model. Among the data sets that do not support the CM model, choosing between the BD and

HV models based on my statistical results is difficult. As I note in the results, the BD and HV models are very similar because their forms of predator dependence are very similar for any given data set. Moreover, five of the ten data sets that prefer the BD and/or HV models over the CM and H2 models do not distinguish between the BD and HV models.

My overall suggestion for choosing among these three predator-dependent functional responses is that the CM model be used for data sets that indicate an asymptotic feeding rate that is affected by predator density, and otherwise the BD or HV model be used. Statistically the BD and HV models are effectively equivalent in my study, and I recognize that the choice between the BD model and the HV model will largely be a matter of preference for either mechanistic or phenomenological models, respectively. I tend to prefer the mechanistic alternative, but Sutherland (1983) stated the opposite view, preferring the HV model specifically because it assumes no mechanistic basis. The special case of $m = 1$ in the HV model, which corresponds with ratio dependence, appears to have little general support in the data sets I examined. In the HV model fits, 13 of the 19 95% confidence intervals for m do not contain the value one, and many of the confidence intervals which do contain the value one are rather wide, indicating uncertainty in the estimate of m (examples in Appendix 1). Still, my analyses do not exclude ratio dependence as a simple two-parameter descriptor of some data sets.

I have limited my analysis to the four models considered here. However, Jost (1998, see also Jost 2000) catalogued 12 models of purely prey-dependent functional responses in the literature, and 15 models of predator-dependent functional responses. Four of the predator-dependent models listed by Jost (1998) have the property exhibited by the CM model, that the feeding rate at high prey abundance asymptotes at a level that

is dependent on predator abundance (Aiba et al. 1968, Hassell and Rogers 1972, Rogers and Hassell 1974, Harrison 1995). One simple phenomenological approach to producing that effect is to divide the H2 prey-dependent model or any other prey-dependent model by some term that depends on predator abundance, e.g., to divide the H2 model by P^m (Hassell and Rogers 1972), $1+\beta P$ (Harrison 1995), or e^{kP} (Aiba et al. 1968), where m , β , and k are parameters, hence producing simple three-parameter predator-dependent models. The other 11 predator-dependent models catalogued by Jost (1998) show either no saturation at high prey abundance, or a saturation level independent of predator abundance, as in the BD and HV models considered here. There is also a large literature on models of foraging behavior when under threat from predators, providing additional models of predator-dependent functional responses, or a path to writing such functional responses (e.g., Abrams 1982, Gilliam and Fraser 1987, Abrahams and Dill 1989, Gilliam 1990, Abrams 1992, Werner and Anholt 1993, Hugie and Dill 1994, Sih 1998, Brown et al. 1999, Houston and MacNamara 1999). These models of adaptive prey behavior are often written in general forms with the number of parameters depending on the choice of functional forms and level of detail included, but some of the models have the capability of dealing with complexities such as spatial structure and alternative prey, albeit at the cost of requiring substantially more parameters in the model. The predator-dependent models that I considered here fit the data reasonably well, and have the additional advantage of being simple three-parameter models, but they cannot be expected to describe all cases accurately.

In conclusion, my results suggest that predator-dependent functional responses, including the forms based on interference that I consider here, should be more widely

studied in the literature. Because some predator-dependent models of the functional response predict asymptotic feeding rates at high prey abundance that are independent of predator abundance (e.g., the BD and HV models), but others predict asymptotes that depend on predator abundance (e.g., the CM model), I recommend that measurements be taken for the limiting cases of low and high prey and predator abundance. Also, because there are multiple possible mechanisms for predator dependence, I advocate careful observations and measurements of predator and prey behavior in such experiments; while some of the papers containing the data analyzed here had such observations, behavioral observations and measurements were usually cursory or absent. Finally, while phenomenological models can suffice for many purposes, I feel that models derived from mechanistic principles will lead to clearer science because the resulting hypothesis tests provide a direct route for making inferences about the relationship between process and pattern.

Acknowledgments

I thank Peter Abrams, Steve Ellner, Nick Haddad, John Fieberg, Doug Fraser, Montserrat Fuentes, Jacqueline Hughes-Oliver, Nikkala Thomson, Kyle Shertzer, Jonathan Rowell, Christian Jost and two anonymous reviewers for useful advice, and Pajaro Morales for assisting with my programming efforts. The U. S. National Science Foundation and the Agricultural Research Service of North Carolina State University provided financial support.

Literature Cited

- Abrahams, M. V., and L. M. Dill. 1989. A determination of the energetic equivalence of predation. *Ecology* 70:999-1007.
- Abrams, P. A. 1982. Functional responses of optimal foragers. *American Naturalist* 120:382-390.
- Abrams, P. A. 1992. Predators that benefit prey and prey that harm predators: unusual effects of interacting foraging adaptations. *American Naturalist* 140:573-600.
- Abrams, P. A. 1994. The fallacies of "ratio-dependent" predation. *Ecology* 75:1842-1850.
- Abrams, P. A. 1997. Anomalous predictions of ratio-dependent models of predation. *Oikos* 80:163-171.
- Abrams, P. A., and L. R. Ginzburg. 2000. The nature of predation: prey dependent, ratio dependent or neither? *Trends in Ecology and Evolution* 15:337-341.
- Abrams, P. A., and C. J. Walters. 1996. Invulnerable prey and the paradox of enrichment. *Ecology* 77:1125-1133.
- Aiba, S., M. Shoda, and M. Nagatani. 1968. Kinetics of product inhibition in alcohol fermentation. *Biotechnology and Bioengineering* 10:845-864.
- Arditi, R., and H. R. Akcakaya. 1990. Underestimation of the mutual interference of predators. *Oecologia* 83:358-361.
- Beddington, J. R. 1975. Mutual interference between parasites or predators and its effect on searching efficiency. *Journal of Animal Ecology* 51:331-340.
- Brown, J. H. 1991. Methodological advances: new approaches and methods in ecology. Pages 445-455 in L.A. Real and J. H. Brown, editors. *Foundations of ecology:*

- classic papers with commentaries. University of Chicago Press, Chicago, IL, USA.
- Brown, J. S., J. W. Laundré, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80:385-399.
- Carpenter, S. R., K. L. Cottingham, and C. A. Stow. 1994. Fitting predator-prey models to time series with observation errors. *Ecology* 75:1254-1264.
- Chant, D. A., and A. L. Turnbull. 1966. Effects of predator and prey densities on interactions between goldfish and *Daphnia pulex* (De Geer). *Canadian Journal of Zoology* 4:285-289.
- Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. *American Naturalist* 110:247-259.
- Cosner, C., D. L. DeAngelis, J. S. Ault, and D. B. Olson. 1999. Effects of spatial grouping on the functional response of predators. *Theoretical Population Biology* 56:65-75.
- Crowley, P. H., and E. K. Martin. 1989. Functional responses and interference within and between year classes of a dragonfly population. *Journal of the North American Benthological Society* 8:211-221.
- DeAngelis, D. L., R. A. Goldstein, and R. V. O'Neill. 1975. A model for trophic interaction. *Ecology* 56:881-892.
- Dennis, B., and M. L. Taper. 1994. Density dependence in time series observations of natural populations: estimation and testing. *Ecological Monographs* 64:205-224.

- Edwards, R. L. 1961. The area of discovery of two insect parasites, *Nasonia vitripennis* (Walker) and *Trichogamma evanescens* Westwood, in an artificial environment. *Canadian Entomologist* 93:475-481.
- Efron, B., and R. J. Tibshirani. 1993. An introduction to the bootstrap. Chapman and Hall, New York, NY, USA.
- Eveleigh, E. S., and D. A. Chant. 1982. Experimental studies on acarine predator-prey interactions: the effects of predator density on prey consumption, predator searching efficiency, and the functional response to prey density (Acarina: Phytoseiidae). *Canadian Journal of Zoology* 60:611-629.
- Gilliam, J. F. 1990. Hunting by the hunted: optimal prey selection by foragers under predation hazard. Pages 797-818 in R. N. Hughes, editor. *Behavioural mechanisms of food selection*. Springer-Verlag, Berlin, Germany.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68:1856-1862.
- Harrison, G. W. 1995. Comparing predator-prey models to Luckinbill's experiment with *Didinium* and *Paramecium*. *Ecology* 76:357-374.
- Hassell, M. P., and D. J. Rogers. 1972. Insect parasite responses in the development of population models. *Journal of Animal Ecology* 41:661-676.
- Hassell, M. P., and G. C. Varley. 1969. New inductive population model for insect parasites and its bearing on biological control. *Nature* 223:1133-1136.
- Hilborn, R. and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, NJ, USA.

- Hilborn, R., and C. J. Walters. 1992. Quantitative fisheries stock assessment: choice, dynamics, and uncertainty. Chapman and Hall, New York, NY, U.S.A.
- Holling, C. S. 1959a. The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Canadian Entomologist* 91: 293-320.
- Holling, C. S. 1959b. Some characteristics of simple types of predation and parasitism. *Canadian Entomologist* 91: 385-398.
- Houston, A. I. And J. M. McNamara. 1999. Models of Adaptive Behaviour: An Approach Based on State. Cambridge University Press, Cambridge, UK.
- Huffaker, C. B., and B. M. Matsumoto. 1982. Group versus individual functional responses of *Venturia [=Nemeritis] canescens* (Grav.). *Researches on Population Ecology* 24:250-269.
- Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology* 45:151-169.
- Huisman, G., and R. J. De Boer. 1997. A formal derivation of the “Beddington” functional response. *Journal of Theoretical Biology* 185:389-400.
- Jost, C. 1998. Comparing predator-prey models qualitatively and quantitatively with ecological time-series data. Ph. D. thesis. Institut national agronomique Paris-Grignon.
- Jost, C. 2000. Predator-prey theory: hidden twins in ecology and microbiology. *Oikos* 90:202-208.
- Jost, C., and R. Arditi. 2000. Identifying predator-prey processes from time series. *Theoretical Population Biology* 57:325-337.

- Katz, C. H. 1985. A nonequilibrium marine predator-prey interaction. *Ecology* 66:1426-1438.
- Kennedy, M., and R. D. Gray. 1993. Can ecological theory predict the distribution of foraging animals? A critical analysis of experiments on the Ideal Free Distribution. *Oikos* 68:158-166.
- Kfir, R. 1983. Functional response to host density by the egg parasite *Trichogramma pretiosum*. *Entomophaga* 28:345-353.
- Kincaid, D. R., and E. W. Cheney. 1996. Numerical Analysis. Brooks/Cole, Pacific Grove, CA, USA.
- Kumar, A., and C. P. M. Tripathi. 1985. Parasitoid-host relationship between *Trioxys (Binodoxys) indicus* Subba Rao & Sharma (Hymenoptera: Aphidiidae) and *Aphis craccivora* Koch (Hemiptera: Aphididae): effect of host plants on the area of discovery of the parasitoid. *Canadian Journal of Zoology* 63:192-195.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27:215-290.
- Lotka, A. J. 1925. Elements of physical biology. Williams and Wilkins, Baltimore, MD, USA.
- MacIsaac, H. J., and J. J. Gilbert. 1991. Discrimination between exploitative and interference competition between cladocera and *Keratella cochlearis*. *Ecology* 72:924-937.
- Mertz, D. B., and R. B. Davies. 1968. Cannibalism of the pupal stage by adult flour beetles: an experiment and a stochastic model. *Biometrics* 24:247-275.

- Murdoch, W. M., and C. J. Briggs. 1996. Theory for biological control: recent developments. *Ecology* 77:2001-2013.
- Nicholson, A. J., and V. A. Bailey. 1935. The balance of animal populations. *Proceedings of the Zoological Society of London* 3:551-598.
- O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. *Ecology* 79:1193-1208.
- Osenberg, C. W., O. Sarnelle, S. D. Cooper, and R. D. Holt. 1999. Resolving ecological questions through meta-analysis: goals, metrics, and models. *Ecology* 80:1105-1117.
- Pascual, M. A., and P. Kareiva. 1996. Predicting the outcome of competition using experimental data: maximum likelihood and Bayesian approaches. *Ecology* 77:337-349.
- Rogers, D. J., and M. P. Hassell. 1974. General models for insect parasite and predator searching behaviour: interference. *Journal of Animal Ecology* 43:239-253.
- Salt, G. W. 1974. Predator and prey densities as controls of the rate of capture by the predator *Didinium nasutum*. *Ecology* 55:434-439.
- Schmitz, O. J. 1992. Exploitation in model food chains with mechanistic consumer-resource dynamics. *Theoretical Population Biology* 41:161-183.
- Schoener, T. W. 1983. Field experiments on interspecific competition. *American Naturalist* 122:240-285.
- Seber, G. A. F., and C. J. Wild. 1989. *Nonlinear regression*. John Wiley and Sons, New York, NY, U.S.A.

- Sih, A. 1998. Game theory and predator-prey response races. Pages 221-238 in L. A. Dugatkin and H. K. Reeve, editors. Game theory and animal behavior. Oxford University Press, New York, NY, USA.
- Sutherland, W. J. 1983. Aggregation and the 'ideal free' distribution. *Journal of Animal Ecology* 52:821-828.
- Taylor, A. D. 1988. Host effects on functional and ovipositional responses of *Bracon hebetor*. *Journal of Animal Ecology* 57:173-184.
- Uttley, M. G. 1980. A laboratory study of mutual interference between freshwater invertebrate predators. Ph. D. thesis. University of York, UK.
- van der Meer, J., and B. J. Ens. 1997. Models of interference and their consequences for the spatial distribution of ideal and free predators. *Journal of Animal Ecology* 66:846-858.
- von Westernhagen, H., and H. Rosenthal. 1976. Predator-prey relationships between Pacific herring, *Clupea harengus*, larvae and a predatory amphipod, *Hyperoche medusarum*. *Fishery Bulletin* 74:669-674.
- Walde, S. J., and R. W. Davies. 1984. The effect of intraspecific interference on *Kogotus nonus* (Plecoptera) foraging behavior. *Canadian Journal of Zoology* 62:2221-2226.
- Werner, E. E., and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142:242-72.

Table 1: The numbers and percentages of papers specifying different types of functional responses in papers during 1996-1999 in three major ecology journals (TPB=Theoretical Population Biology).

Functional Response	Number of Articles			Total (45 papers)	% of papers
	Ecology (14 papers)	American Naturalist (17 papers)	TPB (14 papers)		
Holling Type II	10	11	10	31	68.8
Lotka-Volterra (linear)	3	6	3	12	26.6
Hassell-Varley*	1	2	1	4	8.8
Beddington-DeAngelis	1	0	2	3	6.7
Crowley-Martin	0	0	0	0	0
Other	1	1	0	2	4.4

*Here Hassell-Varley refers to both ratio-dependent models using N/P and forms based on the model given in Hassell and Varley (1969).

Table 2: Characteristics of the nineteen data sets used in the analysis. Data sets are sorted into two groups: those measuring instantaneous feeding rates and those measuring integrated feeding rates.

Data Set	Predator-Prey	Reference	Data Source
Instantaneous Feeding Rates			
1	protozoan-protozoan	Salt 1974	Fig. 3, Table 1
2	stonefly-mayfly	Walde & Davies 1984	Figs. 2, 4
3	dragonfly-dragonfly	Crowley & Martin 1989	Fig. 2
4	coyote-hare	O'Donoghue et al. 1998	Figs. 1, 5
5	lynx-hare	O'Donoghue et al. 1998	Figs. 1, 5
Integrated Feeding Rates			
6	parasitoid-house fly	Edwards 1961	Table 1
7	parasitoid-moth eggs	Edwards 1961	Table 2
8	fish-cladoceran	Chant & Turnbull 1966	Table 1

9	beetle-beetle	Mertz & Davies 1968	Table 1
10	amphipod-fish	von Westernhagen & Rosenthal 1976	Fig. 3
11	damselfly-cladoceran	Uttley 1980	Fig. 4.3.1
12	back swimmer-cladoceran	Uttley 1980	Fig. 8.3.2
13	mite-mite	Eveleigh & Chant 1982	Tables 3, 5
14	mite-mite	Eveleigh & Chant 1982	Tables 7, 8
15	parasitoid-caterpillar	Huffaker & Matsumoto 1982	Table 1
16	parasitoid-moth eggs	Kfir 1983	Table 1
17	parasitoid-aphid	Kumar & Tripathi 1985	Table 1
18	snail-barnacle	Katz 1985	Figs. 4, 8
19	parasitoid-caterpillar	Taylor 1988	Fig. 1a

Figure Legends

Figure 1: The fits of the four alternative functional response models to the nineteen data sets, by the log-likelihood criterion. The 45 degree line indicates equal fits, so points lying above that line indicate a better fit by the model on the vertical axis. Cases in which one model provides a statistically better fit are indicated by filled circles. In some cases statistically significant differences occur despite similar fits (i.e., points very close to the 45 degree line) because of large sample sizes and/or small variances. Top row (a-c): comparisons of the predator-dependent models with the Holling Type II model. Bottom row (d-f): comparisons among the three predator-dependent models.

Figure 2: The measured and predicted integrated feeding rates plotted against prey abundance for each predator abundance treatment for data sets 6, 11, and 12. The best-fitting model is indicated for each data set. Some predator-levels are omitted from data set 6 to improve clarity. Data set 11 (Fig. 2b) indicates different asymptotes for different predator levels, in agreement with the Crowley-Martin model, while the other data sets are consistent with a common asymptote, in agreement with the Beddington-DeAngelis (2a) or Hassell-Varley model (2c).

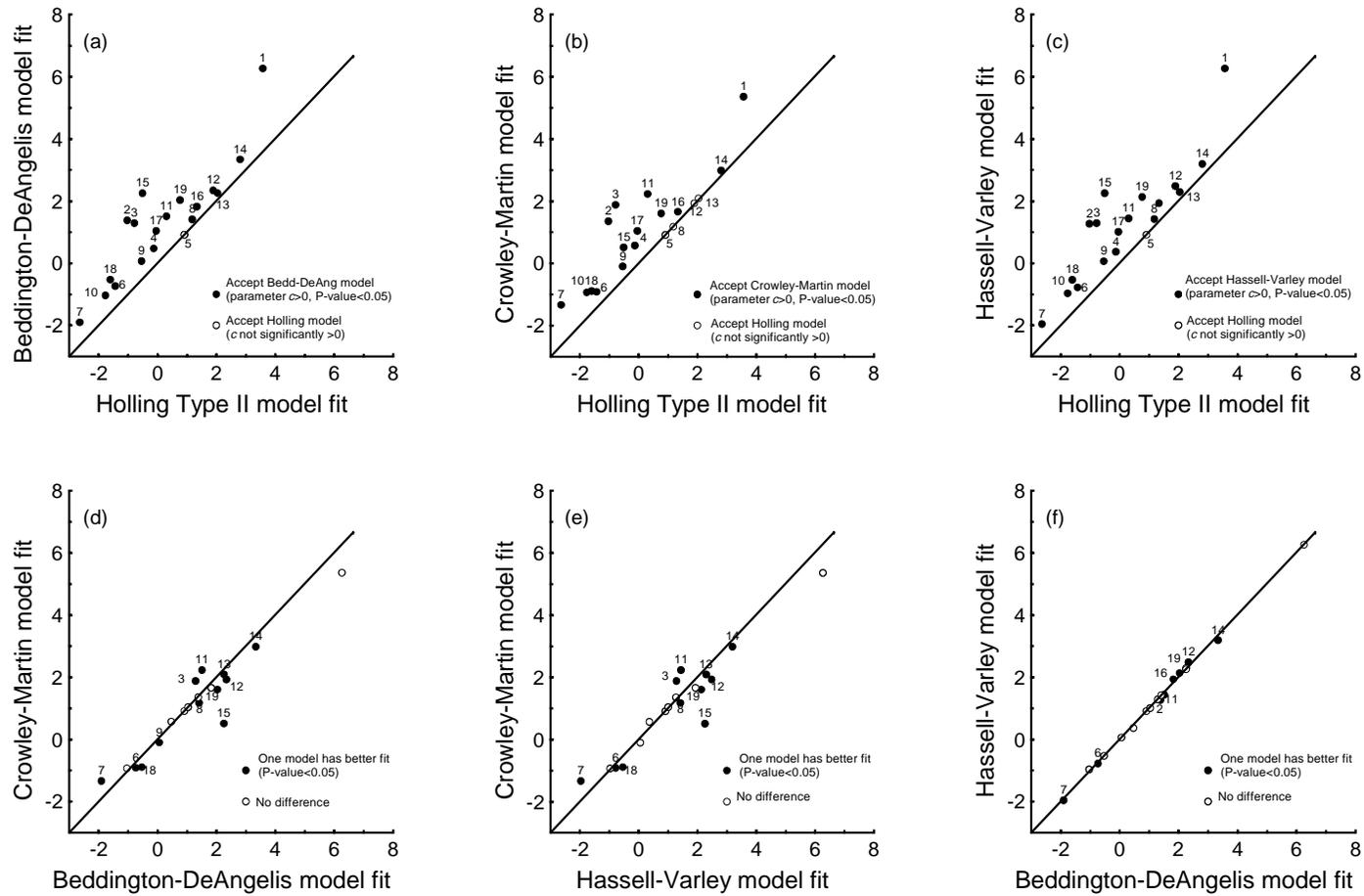


Figure 1

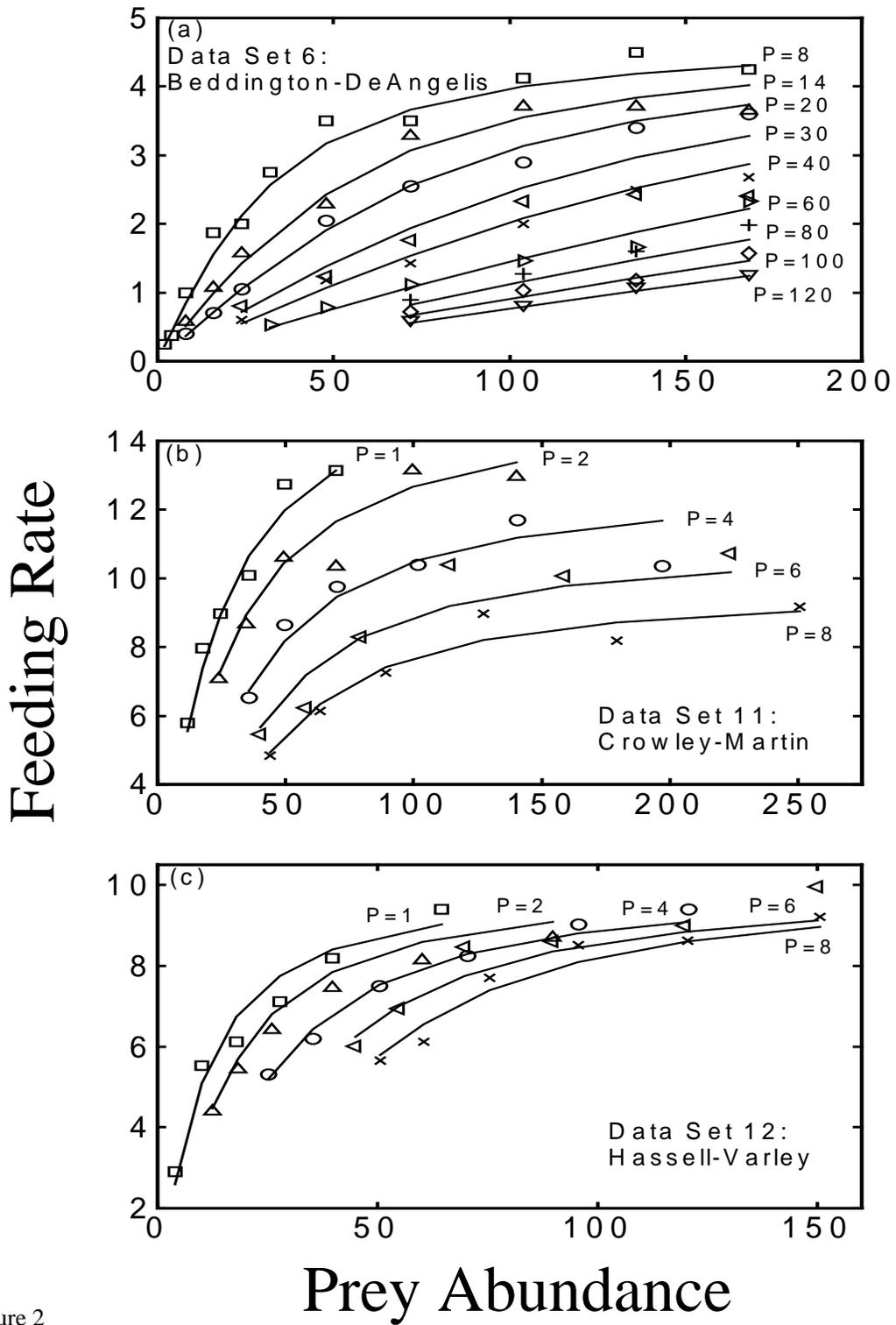


Figure 2

Appendix 1: Maximum likelihood parameter estimates (bootstrap 95% confidence intervals) for the nineteen data sets. For data set 5, the H2 model was accepted (c or m not different from zero for any of the predator-dependent models), and the H2 parameter estimates are shown. For the other data sets, the H2 model was rejected, and the parameters of the best-fit (greatest likelihood) predator-dependent model (BD, CM, or HV) are shown for each data set. H2=Holling Type II model, BD=Beddington-DeAngelis model, CM=Crowley-Martin model, HV=Hassell-Varley model.

65

Data Set	Parameter Estimates			Sample Size	Best-Fit Model
	a	b	c or m		
	Instantaneous Feeding Rates				
1	0.0596 (0.0504, 0.0711)	0.0298 (0.0238, 0.0372)	0.0316 (0.0181, 0.0486)	5	BD or HV*
2	0.8461 (0.6510, 1.202)	0.0752 (0.0482, 0.1221)	1.434 (0.9970, 2.063)	18	BD
3	2.087 (1.853, 2.363)	0.0244 (0.0172, 0.0329)	0.7296 (0.5795, 0.9345)	15	CM
4	0.0268 (0.0181, 0.0482)	0.0036 (0, 0.0203)	0.2927 (0.0056, 1.159)	8	CM

5	0.0392 (0.0234, 0.0864)	0.0334 (0.0152, 0.0997)	0 n/a	8	H2
Integrated Feeding Rates					
6	0.0312 (0.0248, 0.0409)	0.1557 (0.1187, 0.2116)	0.2442 (0.1757, 0.3429)	96	BD
7	0.0189 (0.0161, 0.0229)	0.0062 (0.0047, 0.0087)	0.1204 (0.0953, 0.1479)	75	CM
8	0.2338 (0.0839, 2.116)	0.0248 (0.0062, 0.2622)	1.197 (0.4042, 2.704)	15	HV
9	0.0106 (0.0079, 0.0156)	0.0581 (0.0406, 0.0852)	0.0566 (0.0374, 0.0903)	120	BD
10	0.0156 (0.0113, 0.0226)	0.0287 (0.0115, 0.0623)	0.1575 (0.0759, 0.3079)	20	CM
11	0.0402 (0.0358, 0.0464)	0.0576 (0.0478, 0.0708)	0.1017 (0.0833, 0.1239)	30	CM
12	0.1410 (0.1228, 0.1629)	0.1396 (0.1179, 0.1662)	0.3265 (0.1998, 0.4339)	30	HV

13	0.1625 (0.1324, 0.2086)	0.4353 (0.3423, 0.5766)	0.4790 (0.2256, 0.6905)	33	HV
14	0.0781 (0.0683, 0.0901)	0.0392 (0.0319, 0.0485)	0.2142 (0.1076, 0.3362)	19	BD
15	0.0595 (0.0388, 0.1113)	0.0541 (0.0285, 0.1218)	1.647 (0.9786, 3.172)	8	BD or HV*
16	0.0113 (0.0066, 0.0247)	0.0087 (0.0045, 0.0219)	0.4503 (0.1377, 0.8164)	12	HV
17	0.0192 (0.0139, 0.0264)	0.0045 (0, 0.0125)	0.4105 (0.1418, 0.8497)	9	BD
18	0.0065 (0.0046, 0.0107)	0.0153 (0.0068, 0.0353)	1.206 (0.5829, 2.165)	21	BD
19	0.1706 (0.1390, 0.2188)	0.0965 (0.0640, 0.1469)	0.7227 (0.4796, 0.9621)	13	HV

*Model fits identical to three decimal points. We report the parameter estimates for the BD model.

Appendix 2: Test statistics, P -values and inferences for hypothesis tests involving the three alternative predator-dependent models.

The hypothesis tests for distinguishing among the alternative predator-dependent models are of the form $H_i: f_i$ is the better model vs. $H_j: f_j$ is the better model (H_2 =Holling Type II model, BD =Beddington-DeAngelis model, CM =Crowley-Martin model, HV =Hassell-Varley model).

Data Set	Test	$T_{i,j}^{obs}$	$\Pr\{T_{i,j} < T_{i,j}^{obs} H_i\}$	$\Pr\{T_{i,j} > T_{i,j}^{obs} H_j\}$	Inference	
	H_i vs. H_j					
			Instantaneous Feeding Rates			
89	1	H_2 vs. H_3	4.53	0.329	0.127	BD or CM
		H_2 vs. H_4	0	0.348	0.620	BD or HV
		H_3 vs. H_4	-4.52	0.137	0.294	CM or HV
	2	H_2 vs. H_3	0.509	0.040	0.024	BD or CM
		H_2 vs. H_4	1.98	0.921	0.021	BD
		H_3 vs. H_4	1.47	0.049	0.046	CM or HV
	3	H_2 vs. H_3	-8.81	0.001	0.595	CM
		H_2 vs. H_4	0.053	0.592	0.408	BD or HV

	H_3 vs. H_4	8.86	0.997	0.003	CM
4	H_2 vs. H_3	-0.790	0.144	0.748	BD or CM
	H_2 vs. H_4	0.877	0.846	0.096	BD or HV
	H_3 vs. H_4	1.67	0.789	0.067	CM or HV
5	H_2 vs. H_3	0	0.500	0.485	H2
	H_2 vs. H_4	0	0.583	0.427	H2
	H_3 vs. H_4	0	0.605	0.400	H2

Integrated Feeding Rates

6	H_2 vs. H_3	17.28	0.109	<0.001	BD
	H_2 vs. H_4	4.13	0.227	0.016	BD
	H_3 vs. H_4	-13.15	<0.001	<0.001	CM or HV
7	H_2 vs. H_3	-42.43	<0.001	0.411	CM
	H_2 vs. H_4	4.35	0.396	0.020	BD
	H_3 vs. H_4	46.77	0.272	<0.001	CM
8	H_2 vs. H_3	3.50	0.851	0.009	BD

	H_2 vs. H_4	-0.139	0.359	0.659	BD or HV
	H_3 vs. H_4	-3.64	0.005	0.815	HV
9	H_2 vs. H_3	19.65	0.099	<0.001	BD
	H_2 vs. H_4	0.585	0.334	0.186	BD or HV
	H_3 vs. H_4	-19.07	<0.001	0.034	CM or HV
10	H_2 vs. H_3	-2.01	0.096	0.574	BD or CM
	H_2 vs. H_4	-1.31	0.136	0.655	BD or HV
	H_3 vs. H_4	0.694	0.721	0.178	CM or HV
11	H_2 vs. H_3	-21.57	<0.001	0.094	CM
	H_2 vs. H_4	2.12	0.927	0.018	BD
	H_3 vs. H_4	23.69	0.101	<0.001	CM
12	H_2 vs. H_3	12.30	0.913	<0.001	BD
	H_2 vs. H_4	-4.25	0.005	0.936	HV
	H_3 vs. H_4	-16.55	<0.001	0.94	HV
13	H_2 vs. H_3	5.50	0.711	0.013	BD

	H_2 vs. H_4	-1.14	0.118	0.679	BD or HV
	H_3 vs. H_4	-6.63	<0.001	0.652	HV
14	H_2 vs. H_3	6.79	0.824	0.001	BD
	H_2 vs. H_4	2.83	0.922	0.013	BD
	H_3 vs. H_4	-3.95	0.018	0.597	HV
15	H_2 vs. H_3	13.94	0.538	0.001	BD
	H_2 vs. H_4	0	0.519	0.505	BD or HV
	H_3 vs. H_4	-13.94	<0.001	0.504	HV
16	H_2 vs. H_3	1.97	0.592	0.111	BD or CM
	H_2 vs. H_4	-1.33	0.024	0.947	HV
	H_3 vs. H_4	-3.31	0.046	0.706	HV
17	H_2 vs. H_3	0.009	0.575	0.408	BD or CM
	H_2 vs. H_4	0.271	0.544	0.358	BD or HV
	H_3 vs. H_4	0.262	0.560	0.352	CM or HV
18	H_2 vs. H_3	7.69	0.927	<0.001	BD

	H_2 vs. H_4	0.149	0.775	0.276	BD or HV
	H_3 vs. H_4	-7.54	<0.001	0.907	HV
19	H_2 vs. H_3	5.62	0.515	0.014	BD
	H_2 vs. H_4	-1.26	0.039	0.897	HV
	H_3 vs. H_4	-6.88	0.009	0.592	HV

Chapter 3

Feeding under predation hazard: testing models of adaptive behavior with stream

fish

Abstract

Many empirical studies support the premise that animals consider both the benefits of feeding and the cost of mortality when making behavioral decisions and many theoretical studies predict animal behavior in the presence of a feeding-mortality tradeoff. Yet no existing empirical work has tested among alternative models that incorporate the benefits of feeding and the costs of mortality using the common currency of Darwinian fitness. Using data from two sets of behavioral experiments examining stream minnows (bluehead chubs) foraging in the presence of sunfish predators (green sunfish), I assess, via statistical model fitting, the utility of four basic optimization models of foraging behavior. The models vary in their specifications as to how bluehead chubs might value, in terms of fitness, rates of growth and mortality. As anticipated by many earlier studies, my results support the idea that animals suppress feeding so as to reduce mortality, but continue to feed even in the presence of predators. More importantly, I demonstrate, via a comparison of the two best-fitting models, that the precise manner in which animals may assess the relative fitness values of feeding and mortality can be estimated quantitatively using a parameter called the marginal rate of substitution of mortality rate for growth rate. Interpretation of my findings leads to several insights into the behavior and life history of the bluehead chub including the conclusion that reproductive value should be thought of as a function of body size and age rather than a function of body size alone.

Introduction

Ecologists have recognized that the behaviors of individual animals can be integrated to predict patterns in populations (Sutherland 1996). Consequently, ecologists have been motivated to develop a conceptual framework for understanding and predicting animal behavior. Optimization methods, which leverage the principle that behavior is molded by natural selection, provide a conceptual framework for predicting animal behavior in a variety of contexts (MacArthur and Pianka 1966, Charnov 1976, Fretwell and Lucas 1970, Houston and McNamara 1999, Mangel and Clark 1988). Taken literally, the approach asserts that behavioral phenotypes that maximize Darwinian fitness should be the behavioral phenotypes that are observed in nature. Clearly natural selection does not always proceed unconstrained in real populations, and while the evolutionary simplification of unconstrained natural selection should be acknowledged, the adaptationist approach has proved insightful as an explanation of phenotype (Houston and McNamara 1999, Kozłowski 1999, Pigliucci and Kaplan 2000).

Fitness is comprised of many components, such as feeding rate, mortality rate, and birth rate, all of which can be influenced by behavior. However, many studies rely on the assumption that fitness depends on behavior only through one fitness component, using feeding rate (e.g., Milinski 1979, Harper 1982), survivorship (e.g., Godin and Dugatkin 1996), or birth rate (e.g., Parker 1978), as a proxy for fitness (Stephens and Krebs 1986, Krebs and Davies 1993, Houston and McNamara 1999). However, in nature it is unlikely that a particular behavior will be optimal in terms of all fitness components. For example, a bird may increase its foraging effort by making more foraging trips only at the expense of alerting more predators to the location of its nest (e.g., Martin et al.

2000), or a juvenile fish may increase its feeding rate by entering pelagic habitat only at the cost of increasing its exposure to predators (e.g., Werner and Hall 1988). These types of tradeoffs have been widely studied in the literature (reviews in Lima and Dill 1990, Lima 1998), and the feeding-mortality tradeoff, in particular, has been the focus of a large subset of this work. Indeed, there exists a substantial body of theory that addresses (i) the quantitative manner in which animals may respond adaptively to the feeding-mortality tradeoff (Abrams 1982, Werner and Gilliam 1984, Ludwig and Rowe 1990, Houston and McNamara 1999), and (ii) the ecological implications of behaviors that adaptively balance the feeding-mortality tradeoff (Abrams 1982, Werner and Anholt 1993, Hugie and Dill 1994, Leonardsson and Johansson 1997, Brown et al. 1999). Likewise, there exists a voluminous empirical literature (Lima and Dill 1990, Lima 1998) showing that animals appear to weigh both feeding rate and mortality rate when making behavioral decisions (e.g., Milinski and Heller 1978, Sih 1980, Werner et al. 1983, Gilliam and Fraser 1987, Abrahams and Dill 1989, Fraser and Gilliam 1992). Yet, empirically, the literature has rarely approached the question of how animals may quantitatively integrate feeding rate and mortality rate so as to make adaptive behavioral decisions. In particular, the conceptual relationship between the various alternative theoretical models and much of the available data is far from clear.

In this study I address, using mechanistic modeling and laboratory experiments, the question of how animals (stream minnows) may balance, through adaptive behavior, opportunities for feeding versus the associated cost of mortality by predation. My analysis provides a novel empirical assessment of several alternative hypotheses of feeding under predation hazard. I formulate these hypotheses as optimization models and

use a model selection criterion to statistically assess the ability of these models to predict the results of laboratory experiments.

Methods

Experimental System

My experimental system is a simple three-level food chain comprised of green sunfish (*Lepomis cyanellus*), bluehead chubs (*Nocomis leptcephalus*), and pelleted fish food (Hikari Cichlid-Type floating baby pellets, 2.45 mg/pellet). Bluehead chubs and green sunfish occur in streams throughout the North Carolina Piedmont, including the study stream, Richland Creek, Wake County, NC, U. S. A. where I estimate their densities to be 1.6 and 0.6 individuals/m², respectively, in my study reach (the study reach is 75 m long and, on average, 1.87 m wide; population abundances estimated by two-pass removal electrofishing: Seber and LeCren 1967). In the laboratory environment green sunfish readily consume bluehead chubs and bluehead chubs readily consume pellets, but green sunfish rarely or never consume pellets (see below). All experiments described below took place during the summer of 2000 in a laboratory with the light cycle set to 14L:10D and the water temperature set to 25° C.

Growth Experiment

The goal of this study is to understand how bluehead chubs may adaptively balance benefits of feeding on pellets against any associated mortality cost due to predation by green sunfish. For many organisms, including fish, body size is often suggested as an important state variable in that many salient features of the animal's biology, including Darwinian fitness, may be described as functions of body size (Werner

and Gilliam 1984, Houston and McNamara 1999). As such, optimization theory often explores the manner in which behavior affects fitness through its influence on growth rate, or changes in body size. Thus the feeding-mortality tradeoff can also be studied as a growth-mortality tradeoff. Accordingly, I conducted a growth experiment to quantify the dynamic relationship between feeding rate and growth rate for different body sizes of bluehead chubs feeding on pellets.

I captured 48 bluehead chubs from Richland Creek ranging in size from 33 mm to 78 mm total length (TL). After acclimating the fish to the laboratory environment for 3 days I initiated a 21-day growth experiment in which bluehead chubs were weighed (wet mass) and measured (total length) and then housed individually in aerated 3 L tanks and supplied one of three daily rations of pellets (9.8 mg, 19.6 mg, or 39.2 mg). The ration treatment serves to experimentally manipulate feeding rate. At 24 hour intervals I cleaned each tank, counting and removing all unconsumed pellets, and exchanged 1 L of tank water with filtered water from a central tank containing 200 L of biologically filtered water. After 21 days I weighed and measured all individuals.

I estimated two important parameters using the data from the growth experiment: (i) k , an assimilation-conversion efficiency specifying the assimilation and conversion of pellet mass into bluehead chub biomass (unitless) and (ii) ω , a mass-specific maintenance rate specifying the loss of biomass attributable to all metabolic processes (units: 1/d). Using these two parameters the growth rate, g , of a bluehead chub over the course of an experiment can be modeled as

$$g = \frac{ds}{dt} = kf - \omega s ,$$

where s is body size (units: mg wet mass), f is feeding rate (units: mg/d), and t is time (Kooijman 2000, Lika and Nisbet 2000). For a bluehead chub with initial size $s(0)$ following this model, its growth over the course of the experiment (i.e., change in body size, $s(t)-s(0)$) is

$$s(t) - s(0) = \left[\frac{kf}{\omega} - s(0) \right] [1 - \exp\{-\omega t\}]. \quad (1)$$

Initial body size, $s(0)$, and feeding rate, f , were experimentally manipulated by applying the ration treatment to individuals of varying body size. I used my measures of daily feeding rates to supply the covariate f in the model because not all bluehead chubs consumed all rationed pellets every day during the experiment. I computed f for an individual as its average daily feeding rate over the course of the 21-day experiment. To estimate k and ω I fit the model given by Eq. (1) to my measurements of growth via ordinary least squares using $s(0)$ and f as covariates (the model is nonlinear in ω , but linear in the parameters $\beta_f = k[1 - \exp\{-\omega\}]/\omega$ and $\beta_s = [\exp\{-\omega\} - 1]$). I use my estimates of k and ω in my optimization models (see below) to provide the link between feeding rate, growth rate and fitness.

Behavioral Experiments

I conducted two sets of experiments, Experiment 1 and Experiment 2, in which I measured bluehead chub behavior in the presence of varying quantities of green sunfish predators and pellet food. The green sunfish treatment influences the mortality rate of bluehead chubs and the pellet treatment influences the feeding rate of bluehead chubs. Thus these experimental treatments permit the study of bluehead chub behavior in response to varying forms of a growth-mortality tradeoff, if such a tradeoff exists.

Different optimization models make different predictions of behavior as the form of the tradeoff is varied, so the experiments can be used to test among alternative optimization models of bluehead chub behavior when some relevant aspect of behavior is measured as a response variable (details on alternative models below).

The basic experimental setup for both sets of experiments consists of a 568 L oval stock tank (Rubbermaid Farm Tough #4245-00-GRAY livestock watering tank) containing 200 L of water and a concrete block (length x width x height: 39.5 cm x 19.4 cm x 19.4 cm) placed on its side on the bottom of the tank. The two 14.3 cm x 12.7 cm x 19.4 cm holes in the concrete block serve as a refuge for the green sunfish and the top of the concrete block serves as a partial refuge for the bluehead chubs as the water level was only a few centimeters above the surface of the block. For a given experimental trial I placed green sunfish, bluehead chubs, and pellets, in said order, into a stock tank at 22:00 hrs when the laboratory lights shut off (bluehead chubs feed readily at night in the lab and preliminary gut contents data indicate that bluehead chubs feed at night in the field). Bluehead chubs were randomly selected from two community aquaria and green sunfish were randomly assigned to predator treatments. The trials ran overnight at a light level of about 1 LUX. At 8:00 hrs the next day (after 10 hrs) the experimental trial ended, the laboratory lights turned on, and all remaining bluehead chubs and pellets were counted. Thus I measured two response variables per trial for both experiments: the number of bluehead chubs consumed by green sunfish and the mass of pellets consumed by bluehead chubs (each pellet has a mass of 2.45 mg, on average). I ran four trials per night, with treatments randomly assigned to tanks.

I captured all bluehead chubs and green sunfish from Richland Creek. Except for experimental trials, I held the two species in separate aquaria in the laboratory. I acclimated all fish to the laboratory environment (3 days acclimation to aquaria, 3 days acclimation to stock tanks, and 6 days acclimation to food supply) prior to the start of an experiment.

Experiment One

The first set of experiments used 65 one-year-old bluehead chubs (hatched during the spring of 1999; mean TL: 57.8 mm, standard deviation (SD): 5.5 mm, range: 47 mm-66 mm) and six green sunfish (TLs: 135 mm, 140 mm, 142 mm, 149 mm, 151 mm, and 154 mm). The stock tanks contained one concrete block placed on its side and across the center of the oval tank. I applied one of three predator treatments (0, 1, or 2 green sunfish) and one of four pellet treatments (240, 300, 600, or 750 mg pellets) to each experimental trial for a total of 12 treatment combinations. All trials received six bluehead chubs. Each night bluehead chubs not used in that night's experimental trials were fed a maintenance ration of approximately 10 pellets. Each morning all green sunfish were fed a ration of three female adult mosquitofish (*Gambusia holbrooki*). I repeated experimental trials until all 12 treatment combinations had been replicated four times. Because the relative errors varied across treatment combinations (relative error measured as standard error/mean), on each night thereafter, I repeated trials for the treatment combinations with the largest relative errors so as to homogenize the uncertainty across treatment combinations. I replicated each experimental trial 4-9 times and ended the experiment after 71 experimental trials had been completed. I assessed the green sunfish's propensity to consume pellets using control trials that isolated one green

sunfish with 240 mg of pellets for 10 hours overnight in the absence of bluehead chubs (five replicates). I found that green sunfish did not consume any pellets in these trials. The average wet mass of bluehead chubs over the course of Experiment 1 was 2120 mg (for use in my mathematical models, see below).

Experiment Two

The second set of experiments was designed to replicate Experiment 1 using smaller, younger bluehead chubs in a similar experimental environment. In Experiment 2 I used 82 young-of-the-year (age 0) bluehead chubs (hatched during the spring of 2000; mean TL: 39.1 mm, SD: 3.1 mm, range: 33 mm-45 mm) and three green sunfish (TLs: 102 mm, 104 mm, and 108 mm). In these experiments I designed the experimental environment so as to facilitate a tradeoff between feeding and mortality. Accordingly, I divided the oval stock tanks cross-wise into two equal-size halves with a 0.6 cm mesh partition that is impermeable to green sunfish and floating pellets but permeable to bluehead chubs. The concrete block was placed on its side in one of the halves of the tank each night. I applied one of two predator treatments (0 or 1 green sunfish) and one of four pellet treatments (40, 70, 100, or 160 mg pellets) to each experimental trial, adding pellets, green sunfish and the concrete block to one randomly chosen half of the tank each night. All trials received four bluehead chubs placed into the half of the tank lacking pellets and green sunfish. In this situation feeding bluehead chubs are forced to occupy the same half of the tank as the green sunfish, thereby facilitating a feeding-mortality tradeoff. I applied all eight of the treatment combinations except the 1 green sunfish and 100 mg pellet treatment combination for a total of seven treatment combinations. I

repeated experimental trials until all seven treatment combinations had been replicated four times (save for the 40 mg of pellets x 0 green sunfish treatment which was replicated only twice because it was apparent after two replicate trials that the bluehead chubs would probably consume all of the pellets on every trial). On each night thereafter, I repeated trials for the treatment combinations with the largest relative errors (so to homogenize uncertainty across treatment combinations). I replicated each experimental trial 2-12 times and ended the experiment after 51 experimental trials had been completed.

Each night bluehead chubs not used in that night's experimental trials were fed a maintenance ration of approximately three pellets. Each morning all green sunfish were fed a ration of two female adult mosquitofish. I assessed the green sunfish's propensity to consume pellets using control trials that isolated one green sunfish with 160 mg of pellets for 10 hours overnight in the absence of bluehead chubs. The green sunfish sometimes consumed a small amount of pellets in these trials (mean: 2.9 mg, standard error: 1.5 mg, replicates: 7), but I considered such consumption to be negligible and ignore it in my calculations. The average wet mass of bluehead chubs over the course of the Experiment 2 was 597 mg (for use in my mathematical models, see below).

Alternative Optimization Models of Behavior

I measured two response variables per trial in each experiment: the number of bluehead chubs consumed by green sunfish and the mass of pellets consumed by bluehead chubs. There are many hypothetical models that could feasibly describe the feeding rates and predation mortality of bluehead chubs in my experimental system. In this analysis, I focus on a set of four foundational alternative models of bluehead chub

behavior which map to a set of four different predictions of the number of bluehead chubs consumed by green sunfish and the amount of pellets consumed by bluehead chubs. The models vary in terms of one key feature: the hypothesized relationship between rates of feeding and mortality and fitness.

The relationship between feeding rate and mortality rate can be specified in a variety of ways. I posit that bluehead chub feeding behavior in my experimental system can be quantified by a parameter ρ that measures foraging effort (Abrams 1991, McNamara and Houston 1994). Foraging effort can depend on many factors, such as the proportion of time spent in foraging areas (Abrams 1982, Gilliam and Fraser 1987, Hugie and Dill 1994), searching speed (Werner and Anholt 1993, Leonardsson and Johansson 1997), or the proportion of time spent scanning for predators while foraging (Brown et al. 1999). I do not explicitly model the behavioral components that determine foraging effort. Rather I represent foraging effort with one parameter that is hypothesized to represent the rate at which bluehead chubs encounter pellet food. I posit that foraging effort, ρ , can range between 0 and 1 and represents a proportion of the maximum encounter rate that can be achieved by bluehead chubs in my experimental system.

The models specify the decline of pellets, $r(t)$ (units: mg), and bluehead chubs, $n(t)$ (units: number of individuals), over the course the 10-hr experimental trials. I assume that bluehead chubs consume pellets according to a Holling Type II functional response (Holling 1959) and that feeding rate is a nonlinear function of foraging effort, $f(\rho)$.

Therefore, the depletion of pellets over the course of an experimental trial is given by

$$\frac{dr}{dt} = -\frac{a\rho r}{1 + a\rho hr} n = -f(\rho)n, \quad (2)$$

where the parameters a and h are capture rate at maximum foraging effort (units: 1/hr) and the handling time (units: hr/mg), respectively, for bluehead chubs feeding on pellets. I assume that green sunfish consume bluehead chubs according to a linear functional response, so that the *per capita* mortality rate of bluehead chubs, $\mu(\rho)$, is linear in ρ . The depletion of bluehead chubs is given by

$$\frac{dn}{dt} = -\alpha p n = -\mu(\rho)n, \quad (3)$$

where α is the predator capture rate at maximum bluehead chub foraging effort (units: 1/hour) and p is the number of green sunfish predators.

These functional forms for feeding rate and mortality rate as functions of foraging effort produce a nonlinear relationship between feeding rate and mortality rate. The graph of mortality rate, $\mu(\rho)$, versus feeding rate, $f(\rho)$, when parameterized by foraging effort, ρ , is convex. Further, because I assume that growth rate is linear in feeding rate with $g(\rho) = kf(\rho) - \omega s$, the graph of mortality rate, $\mu(\rho)$, versus growth rate, $g(\rho)$, is also convex (Fig. 1). This convex function describes the growth-mortality tradeoff: growth rate and mortality rate increase simultaneously as foraging effort increases from 0 to 1.

I consider four different optimization models that specify bluehead chub foraging effort based on growth rate and mortality rate. These optimization models operate under the premise that behaviors evolve so as to maximize fitness. A wide variety of metrics of fitness have been suggested and utilized in the literature. Here I note that organisms within a population are not identical (that is, individuals can be classified into different categories, or states, according to age, body size, spatial position, parasite load, energetic condition, etc) and hence I rely on the set of optimization literature that models behavior in state-structured populations (Houston and McNamara 1999, Kozłowski 1999, Mangel

and Clark 1988) as my conceptual foundation. A variety of other optimization models exist, but they are principally relevant when all individuals within a population are identical (e.g., Abrams 1982, Abrams 1991, Leonardsson and Johansson 1997, Brown et al. 1999). Many authors have discussed alternative representations of fitness in optimization models (e.g., Abrams 1991, Brown et al. 1996, Houston and McNamara 1999, Kozłowski 1999).

I take reproductive value, V , as my basic metric of fitness. My general model assumes that the population is structured by body size, s , and age, t , so that reproductive value is a function of body size and age (that is, $V=V(s,t)$; introductions to the theory and literature upon which my general optimization model is based can be found in Houston and McNamara (1999) and Mangel and Clark (1988)). Under this assumption, the reproductive value of a juvenile animal in a stable population changes over time according to

$$-\frac{\partial V}{\partial t} = \frac{\partial V}{\partial s} g(\rho) - \mu(\rho)V,$$

where $g(\rho)$ is the growth rate, or change in body size per time (Ludwig and Rowe 1990, McNamara and Houston 1989, 1994). Optimal behaviors maximize fitness by maximizing the right hand side of this equation at every age, t . This optimization is equivalent to maximizing reproductive value at each age. Behavior of bluehead chubs is determined by foraging effort, ρ , so optimal behaviors satisfy the dynamic programming equation

$$-\frac{\partial V^*}{\partial t} = \max_{\rho} \left\{ \frac{\partial V^*}{\partial s} g(\rho) - \mu(\rho)V^* \right\}, \quad (4)$$

where $V^*=V^*(s,t)$ is the reproductive value of a bluehead chub at size s and time t that behaves optimally over the remainder of its lifetime.

I now discuss four possible models of foraging effort arising from the general model. All of the models assume that bluehead chubs forage with maximum effort so that $\rho=1$ when predation mortality is zero (i.e., when green sunfish predators are absent). However, the models differ in terms of their predicted foraging efforts when predation mortality is positive (i.e., green sunfish predators are present). It is important to note that in all four models bluehead chub fitness is independent of the number of bluehead chubs, so that $\partial V^*/\partial t$ is density and frequency independent (this framework is consistent with my observations of bluehead chub behavior which indicate that during the night bluehead chub individuals forage independently of one another). Further, Models 2-4 denote optimal foraging effort as a function of the mass of pellets so that foraging effort is predicted to change over the course of a trial as pellets are depleted.

Model 1 is the classic growth, or energy, maximization model that is a foundation of foraging theory (Stephens and Krebs 1986, Krebs and Davies 1993). It assumes that bluehead chubs always forage so as to maximize growth rate regardless of the presence of a growth-mortality tradeoff. Model 1 can arise if the growth-mortality tradeoff does not exist. In this case, mortality rate does not depend on foraging effort so mortality rate is the same for all levels of foraging effort and bluehead chubs maximize fitness by maximizing growth rate. Alternatively, Model 1 can arise under another scenario. If $\partial V^*/\partial s$ is sufficiently large relative to V^* in Eq. 4, then reproductive value will be maximized by maximizing growth rate. This assumption means that, in terms of fitness, bluehead chubs value growth much more than survival. Since feeding rate and

growth rate are increasing functions of foraging effort, Model 1 states that the optimal foraging effort is $\rho_1=1$ whether green sunfish are present (Fig. 1) or absent.

Model 2 assumes that bluehead chubs forage so as to maximize growth rate in the absence of a growth-mortality tradeoff (e.g., when green sunfish are absent), but fix foraging effort so as to exactly meet maintenance costs (i.e., $g(\rho)=0$) when a growth-mortality tradeoff exists (e.g., when green sunfish are present). Model 2 can arise if $\partial V^*/\partial s$ is very small relative to V^* in Eq. 4 and mortality rate increases steeply as growth rate becomes negative (i.e., $g(\rho)<0$, so that the feeding rate of bluehead chubs is not sufficient to meet maintenance costs and starvation is imminent). This assumption means that, in terms of fitness, bluehead chubs value survival much more than growth. Model 2 specifies foraging effort as maximal with

$$\rho_2 = 1$$

when green sunfish are absent and

$$\rho_2 = \frac{\omega s}{ar(k - \omega sh)},$$

or maintenance (i.e., the ρ such that $g(\rho)=0$), when green sunfish are present (Fig. 1).

Model 2 minimizes mortality rate when green sunfish are present.

Model 3 assumes that bluehead chubs adjust foraging effort so as to minimize the ratio of mortality rate to growth rate, $\mu(\rho)/g(\rho)$. This model follows from Eq. 4 with the additional assumption that reproductive value only depends on body size (Werner and Gilliam 1984). Bluehead chubs that adopt this strategy maximize their probability of surviving to the next body size. Model 3 specifies foraging effort as

$$\rho_3 = 1$$

when green sunfish are absent, and

$$\rho_3 = \sqrt{\frac{\omega s}{kh}} \frac{1}{ar(1 - \sqrt{\omega sh/k})} \quad \text{if} \quad \sqrt{\frac{\omega s}{kh}} \frac{1}{a(1 - \sqrt{\omega sh/k})} < r$$

$$\rho_3 = 1 \quad \text{otherwise,}$$

when green sunfish are present. The optimal foraging effort in this model can be illustrated graphically as the value of ρ at the intersection produced by taking the smallest slope of a straight line through the origin such that this line still touches the graph of $\mu(\rho)$ vs. $g(\rho)$ (Fig. 1).

Model 4 specifies foraging effort from the general model in Eq. 4 (Ludwig and Rowe 1990, McNamara and Houston 1989, 1994) subject to the constraint that $g(\rho) \geq 0$. The basic form in Eq. 4 follows from the assumption that reproductive value only depends on body size and age and states that bluehead chubs should adjust foraging effort so as to maximize a linear combination of growth rate and mortality rate (i.e., the right-hand side of Eq. 4 which is equivalent to maximizing $\theta g(\rho) - \mu(\rho)$ where $\theta = \frac{\partial V^*}{\partial s} \frac{1}{V^*}$).

Model 4 specifies foraging effort as

$$\rho_4 = 1$$

when green sunfish are absent and

$$\rho_4 = \frac{\omega s}{ar(k - \omega sh)} \quad \text{if} \quad r < \frac{\alpha p}{ka\theta}$$

$$\rho_4 = \left(\sqrt{\frac{ka\theta r}{\alpha p}} - 1 \right) \frac{1}{ahr} \quad \text{if} \quad \frac{\alpha p}{ka\theta} < r < \frac{\alpha p(1 +ahr)^2}{ka\theta}$$

$$\rho_4 = 1 \quad \text{otherwise}$$

when green sunfish are present. The parameter θ (units: 1/mg) is the marginal rate of substitution of mortality rate for growth rate (MRS) and is a measure of the relative contributions of growth and mortality to fitness. It is a function of body size and age and specifies the mortality rate that a bluehead chub is willing to incur per unit increase in body size. The optimal foraging effort in this model can be illustrated graphically as the value of ρ at the intersection produced by a taking the smallest intercept of a straight line with slope θ such that this line still touches the graph of $\mu(\rho)$ vs. $g(\rho)$ (Fig. 1).

Statistical Model Selection

My experimental treatments vary the initial mass of pellets, $r(0)$, and the number of green sunfish, p , in each trial. The initial number of bluehead chubs, $n(0)$, is given and is constant across treatment combinations within each set of experiments ($n(0)=6$ in Experiment 1 and $n(0)=4$ in Experiment 2). The two observed response variables, which I treat as random variables, are the mass of pellets consumed by bluehead chubs, $R_c(t)$, and the number of bluehead chubs consumed by green sunfish, $N_c(t)$. The differential equations, Eqs. 2 and 3, describe the depletion of pellets and bluehead chubs over the course of the trials given $r(0)$, $n(0)$, p and values for foraging effort, ρ , where foraging effort over the course of a trial is determined by one of the four alternative optimization models. Foraging effort may depend on the growth parameters k and ω and the body size, s , of bluehead chubs. In the model I assume that all individual bluehead chubs within a set of experiments have identical and constant body sizes over the duration of the experiments (i.e., $s=2120$ mg in fits to Experiment 1 data and $s=597$ mg in fits to Experiment 2 data; surviving bluehead chubs grew an average of 1.1 mm TL and 1.7 mm

TL over the course of Experiment 1 and Experiment 2, respectively). Moreover, I assume in the modeling that all parameters (a , h , α and λ in Models 1-3 and a , h , α , λ and θ in Model 4; λ is a covariance parameter defined below) are constant during each trial and across all treatments within each set of experiments. The parameters are assumed to differ across the two sets of independent experiments, Experiment 1 and Experiment 2, because the experimental conditions and the body sizes of the fish differ between the two sets of experiments.

Hence each of the four optimization models produces a prediction of the mass of pellets consumed, $r_c(t)=r(0)-r(t)$, and the number of bluehead chubs consumed, $n_c(t)=n(0)-n(t)$, for any given treatment combination. That is, for a given treatment combination for one of the sets of experiments, the i th optimization model predicts

$$\frac{dr}{dt} = -f(\rho_i)n \quad \text{and} \quad \frac{dn}{dt} = -\mu(\rho_i)n, \quad (5)$$

which have solutions for the amounts of pellets and bluehead chubs remaining at the end of a trial, $r_i(t)$ and $n_i(t)$, respectively, so that the predicted consumption of pellets and bluehead chubs is $r_{c,i}(t)=r(0)- r_i(t)$ and $n_{c,i}(t)=n(0)- n_i(t)$, respectively.

I model the stochastic variability in the outcomes of the experimental trials by assuming that the observed value of bluehead chubs consumed for a given treatment combination, $N_{c,i}(t)$, follows a binomial distribution with probability density $\Pi_n(n_{c,i}(t))$ determined by

$$N_{c,i}(t) \sim \text{Binomial}\left(p, \frac{n_{c,i}(t)}{p}\right)$$

for Experiment 1 and

$$N_{c,i}(t) \sim \text{Binomial}\left(2, \frac{n_{c,i}(t)}{2}\right)$$

for Experiment 2 because at most p bluehead chubs were actually consumed in any trial in Experiment 1 and at most 2 bluehead chubs were actually consumed in any trial in Experiment 2. I assume that the observed value of pellets consumed for a given treatment combination, $R_{c,i}(t)$, follows a binomial distribution conditional on $n_{c,i}(t)$ with probability density $\Pi_{r|n}(r_{c,i}(t) | n_{c,i}(t))$ determined by

$$R_{c,i}(t) \sim \text{Binomial}\left(r_i(0), \frac{r_{c,i}(t)}{r_i(0)} + \lambda_i \frac{N_{c,i}(t) - n_{c,i}(t)}{r_i(0)}\right)$$

where

$$\lambda_i = \text{Corr}(R_{c,i}(t), N_{c,i}(t)) \sqrt{\frac{\text{Var}(R_{c,i}(t))}{\text{Var}(N_{c,i}(t))}}$$

is a measure of the within-treatment covariance between $R_{c,i}(t)$ and $N_{c,i}(t)$ and is proportional to the correlation coefficient, $\text{Corr}(R_{c,i}(t), N_{c,i}(t))$. Accordingly $R_{c,i}(t)$ and $N_{c,i}(t)$ have the joint probability density

$$\Pi(r_{c,i}(t), n_{c,i}(t)) = \Pi_{r|n}(r_{c,i}(t) | n_{c,i}(t)) \Pi_n(n_{c,i}(t)) \quad (6)$$

with expectations $E(R_{c,i}(t)) = r_{c,i}(t)$ and $E(N_{c,i}(t)) = n_{c,i}(t)$.

Given this stochastic model of the experimental data, I fit the four alternative optimization models to the data from Experiments 1 and 2 via maximum likelihood using the joint density defined in Eq. 6 (Hilborn and Mangel 1997, Casella and Berger 1990). I implemented the optimization routine `fmincon` in the software application MATLAB to maximize the likelihood (Coleman et al. 1999). Solutions to the differential equations in Eq. 5 and those used to obtain the gradient required in `fmincon` were solved using a 4th order Runge-Kutta scheme with a fixed step size (Kincaid and Cheney 1996).

I computed Schwarz's Information Criterion (*SIC*) for each model fit to each data set so as to compare the alternative models which differ in their numbers of parameters. That is, Models 1-3 have parameters a , h , α and λ , but Model 4 has these same four parameters plus a fifth parameter, θ . The *SIC* is an asymptotic model selection criterion with a Bayesian foundation that incorporates both the model's fit to the data and the model's number of parameters (Schwarz 1978). The *SIC* for Model i fit to the data from one of the sets experiments with a total of m experimental trials is

$$SIC_i = -2L_i + \log_e(m)q_i,$$

where L_i is the \log_e -likelihood of Model i and q_i is the number of parameters in Model i . The *SIC* decreases as the \log_e -likelihood increases (i.e., as the model fit to the data improves) and decreases as the number of parameters decreases (i.e., as the model becomes more parsimonious). Thus smaller values of SIC_i relative to SIC_j provide support for Model i relative to Model j as a model of the data and I use the *SIC* to make this kind of inference in my analysis. I use the *SIC* rather than some other model selection criteria because it can select the correct model with high probability when sample sizes are large (i.e., it is asymptotically consistent) and it is less likely to select models with more parameters (i.e., it is less prone to overfitting) relative to some other criteria (McQuarrie and Tsai 1998).

Results

Growth Experiment

The growth model specified in Eq. 1 with parameters k and ω explained a significant amount of the variation in the data from the growth experiment ($F_{2,34}=80.46$,

$P < 0.001$). In particular, the specification of instantaneous growth rate as linear in feeding rate and body size provides a good fit to the data (Fig. 2). I take the estimates (95% confidence intervals), 0.455 (0.3785, 0.5302) and 0.005 (0.0041, 0.0058), as values for the parameters k (unitless) and ω (units: 1/day), respectively, in fitting the optimization models below. I also fit a more general four parameter model that specifies k and ω as allometric functions of body size and found that it does not explain any more variation in the data than the 2 parameter model given by Eq. 1 (i.e., the likelihoods for these two models are identical).

Behavioral Experiments

The results from both Experiments 1 and 2 with my corresponding statistical analysis indicate that bluehead chubs forage so as to balance the benefits of growth versus the cost of predation mortality. Moreover, my statistical ranking of the models using the data from the experiments results in the following ordering of the models from worst to best (highest SIC to lowest SIC): Model 2, Model 1, Model 3 and Model 4. This ranking of the models holds if the data from the two experiments are considered separately or pooled (Table 1), indicating that my result is applicable to both young of the year and one-year-old bluehead chubs. Moreover, application of the Akaike Information Criterion, another commonly used model selection criterion (McQuarrie and Tsai 1998), results in the same rankings. The graphical fits of the four alternative optimization models to the data illustrate the results in more detail.

Optimization Model 1 (statistical rank of 3 with the 2nd highest SIC) predicts that bluehead chubs forage with maximum effort so as to maximize growth rate regardless of the number of pellets or green sunfish present. However, my analysis indicates that

bluehead chubs behaviorally decrease their pellet consumption in the presence of green sunfish. Indeed, Model 1 (i) can not explain much of the variation in pellet consumption across green sunfish treatments (Fig. 3a, b) and (ii) overestimates the consumption of bluehead chubs by green sunfish (Fig. 3c, d). Model 1 does account for some of the variation in pellet consumption across green sunfish treatments via depletion effects. Specifically, bluehead chub mortality increases with increasing numbers of green sunfish, resulting in fewer individuals to consume pellets thereby decreasing pellet consumption. This depletion effect is more pronounced in Experiment 2 than Experiment 1 because mortality rates were higher in Experiment 2 (Fig. 3c, d; all trials in Experiment 1 began with six bluehead chubs whereas all trials in Experiment 2 began with four bluehead chubs, but more bluehead chubs were consumed, on average, per trial in Experiment 2). Accordingly, depletion can explain more of the variation in pellet consumption across green sunfish treatments in Experiment 2 than in Experiment 1 (Fig. 3a, b). Even with depletion effects Model 1 remains a poor predictor of both response variables in both experiments. These results indicate that the poor fit of Model 1 to the data is due to (i) its lacking of any behavioral flexibility of bluehead chubs in response to the presence of pellets and green sunfish and/or (ii) its assumption that, in terms of fitness, bluehead chubs value growth much more than survival.

Optimization Model 2 (statistical rank of 4 with highest *SIC*) predicts that bluehead chubs forage with maximum effort in the absence of green sunfish, but forage so as just to meet maintenance requirements when green sunfish are present. However, my analysis indicates that in the presence of green sunfish bluehead chubs are willing to incur greater mortality (so as to consume more pellets) than is predicted by Model 2.

Specifically, the data show that bluehead chubs fed at a rate much higher than their maintenance requirement during the trials as Model 2 underestimated pellet consumption in the presence of green sunfish (Fig. 4a,b). In fact, the data run counter to any model that assumes that bluehead chubs feed to acquire a target consumption rate because pellet consumption increased with initial pellets for all predator levels (Fig. 4a, b). Model 2 also underestimated the number of bluehead chubs consumed (Fig. 4c,d), suggesting that bluehead chubs assumed a higher mortality rate so as to acquire a higher feeding rate. These results indicate that the poor fit of Model 2 to the data is due to its assumption that, in terms of fitness, bluehead chubs value survival much more than growth.

Optimization Model 3 (statistical rank of 2 with 2nd lowest *SIC*) predicts that bluehead chubs forage so as to minimize the ratio of mortality rate to growth rate. Relative to Models 1 and 2, Model 3 provided a reasonable fit to the data in that it correctly predicted the approximate magnitude of the decrease in pellet consumption in the presence of green sunfish (Fig. 5a, b) and more closely approximated the observed numbers of bluehead chubs consumed (Fig. 5c, d). However, Model 3 tended to overestimate pellet consumption at low initial pellets and underestimate pellet consumption at high initial pellets. Further, Model 3 underestimated the consumption of bluehead chubs across all treatments. These discrepancies arise because Model 3 predicts that bluehead chub foraging effort increases as pellets decline in abundance making bluehead chub feeding rate over the course of a trial constant as pellets decline (that is $f(\rho_3)$ is independent of r ; this prediction holds when pellet abundance is sufficiently large so that $\rho_3 \neq 1$). Accordingly, Model 3 predicts that pellet consumption is largely constant across initial pellet treatments in the experiments (Fig. 5a, b). The consequence of this for

the overall fit of Model 3 to the data involves a conflict between fitting the pellet consumption data versus fitting the bluehead chub consumption data. Specifically, increases in the predicted number of bluehead chubs consumed by increasing the capture rate α can be acquired only with the result of decreasing the predicted pellet consumption. The resulting fit of Model 3 to the data is a balance of this conflict resulting in (i) a predicted pellet consumption that is an average across all green sunfish treatments and (ii) a predicted number of bluehead chubs consumed that underestimates the data. These results indicate that Model 3 is superior to Models 1 and 2 because Model 3 does predict a foraging effort that balances the growth-mortality tradeoff in some fashion. However, Model 3 fails to explain some features of the data resulting in systematic deviations in the model fit.

Of the four models I consider, Model 4 (statistical rank of 1 with lowest *SIC*) provides the best fit to the data by providing a good description of the pellets consumed and bluehead chubs consumed from both experiments. However, Model 4 has an additional parameter θ , and one should ask whether the improvement is “worth it” in two senses. The first sense is whether the extra parameter results in a qualitative improvement in fit to some feature(s) of the data. I feel it does. Relative to Model 3, Model 4 correctly predicts (i) that pellet consumption increases with initial pellets in the presence of green sunfish (Fig. 6a, b) and (ii) the approximate magnitude of the numbers of bluehead chubs consumed across all treatments (Fig. 6c, d). The second sense is the statistical assessment, via the *SIC*. Model 4 has the lowest *SIC* value, indicating that, among the four models I consider, Model 4 is the best representation of the data despite having one more parameter than Models 1-3.

In summary, the fits of the models to the data and my statistical ranking of the models by the *SIC* indicate several important and insightful results. First, the results do not differ across the two experiments, indicating that (i) the behavioral motivations of young-of-the-year and one-year-old bluehead chubs are similar in some fundamental features, and (ii) a feeding-mortality tradeoff was present in both of the experimental environments used in Experiments 1 and 2. Second, the fact that Model 1 has a lower *SIC* value than Model 2 indicates that a behavioral strategy that maximizes growth, even in the presence of green sunfish, is a better description of bluehead chub behavior than a behavioral strategy that minimizes mortality in the presence of green sunfish. This result is insightful because it illustrates the importance of growth to fitness. Third, Model 1, which lacks any behavioral flexibility, is a poor description of the data indicating that the inclusion of behavioral flexibility is crucial to understanding the experimental food chain. Fourth, Models 3 and 4 are both preferable, in terms of the *SIC*, to Models 1 and 2, indicating that models with behavior that considers both growth and mortality are better descriptions of bluehead chub behavior than models emphasizing growth or mortality alone. Fifth, Model 4 has a lower *SIC* than Model 3, indicating that modeling bluehead chub reproductive value as a function of body size and age is more appropriate than modeling bluehead chub reproductive value as a function of body size alone.

Discussion

My results indicate that bluehead chubs consider both growth and mortality when making behavioral decisions and suggest a particular structure for how growth and mortality may be balanced in the fitness currency of reproductive value. Data from two

sets of experiments, one involving young-of-the-year fish and the other involving one-year-old-fish, both indicate that Model 4 is a better model for fish behavior in the experimental system than Model 3. Model 4 assumes that bluehead chubs adjust foraging effort so as to maximize a linear combination of growth rate and mortality rate (i.e., maximize $\theta g(\rho) - \mu(\rho)$, Ludwig and Rowe 1990, McNamara and Houston 1989, 1994). Model 3 assumes that bluehead chubs adjust foraging effort so as to minimize the ratio of mortality rate to growth rate (i.e., minimize $\mu(\rho)/g(\rho)$, Werner and Gilliam 1984). Model 3 follows from the assumption that reproductive value is a function of body size alone, whereas Model 4 follows from the assumption that reproductive value is a function of body size and age.

Model 4 can account for time-related changes in reproductive value, such as those that may result from age-specific and seasonal effects on fitness components - effects that are not included in Model 3. Bluehead chubs in my study area live in a seasonal environment so that many factors that influence fitness, such as water temperature, for example, probably vary with time *per se*. Reproduction is seasonal because bluehead chubs only reproduce during a relatively small time interval in the spring. Moreover, other factors such as growth, metabolic rate, prey availability and many other variables are also likely to vary strongly through the year. Hence the structure of Model 4 is more appropriate for bluehead chub biology than that of Model 3.

The fits of Model 4 to the data allows the study of the resulting estimates of the parameter, θ , the marginal rate of substitution of mortality rate for growth rate (MRS). The MRS is a measure of the relative value, in terms of fitness, of growth and mortality. Large values for the MRS indicate that growth is more valuable relative to mortality and

small values indicate that growth is less valuable. The MRS is interesting because it provides a conceptual connection between bluehead chub behavior and bluehead chub life history. Based on the definition of the MRS as $\theta = \frac{\partial V^*}{\partial s} \frac{1}{V^*}$, I expect that young bluehead chubs of small body size should place more value on growth relative to mortality than older, larger bluehead chubs (McNamara and Houston 1999). In the presence of a feeding-mortality tradeoff this means that younger, smaller bluehead chubs should take more risks (in terms of exposure to predators) than their older, larger counterparts. My estimates of the MRS for young-of-the-year (fish from Experiment 2) and one-year-old (fish from Experiment 1) bluehead chubs support this expectation. I estimate the MRS (95% confidence intervals computed using likelihood ratios) to be 0.1194/mg (0.0993, 0.1446) and 0.0297/mg (0.0262, 0.0341) for young-of-the-year and one-year-olds, respectively. Moreover, the results from my experiments and my observations of bluehead chub behavior in the lab corroborate this idea. Averaging across treatments with green sunfish present, the young-of-the-year bluehead chubs in Experiment 2 fed at higher rates (relative to maintenance requirements) and incurred higher rates of mortality relative to their one-year-old counterparts in Experiment 1 (this comparison is only approximate because many factors, in addition to the age and size of bluehead chubs, differed across the two experiments). Additionally, the young-of-the-year fish more quickly resumed normal behavior after handling and disturbance and were generally less cautious than the one-year-olds. In summary, my results are consistent with the concept of the MRS and the connection it provides between behavior and life history in the bluehead chub.

Although the data make a convincing case for the appropriateness of Model 4 relative to the three alternatives, Model 3, in particular, remains a helpful representation of bluehead chub behavior. Model 3 is statistically and conceptually superior to Models 1 and 2 as a description of bluehead chub behavior because it incorporates a balance, in terms of fitness, between growth rate and mortality rate that is lacking in Models 1 and 2. Additionally, empirical estimates of the MRS, which can be difficult to obtain, can limit the utility of Model 4. Accordingly, if empirical estimates of the MRS are lacking, Model 3 can be used provisionally until sufficient data are available to make a rigorous inference regarding the appropriateness of Model 3 relative to Model 4.

I modeled the feeding-mortality tradeoff as a nonlinear tradeoff, but I can use my data to make inferences about models that assume a linear tradeoff. If I take feeding rate to be proportional to foraging effort in the four optimization models then the tradeoff becomes linear. In this case the predictions of Models 1 and 2 do not change and Model 3 becomes identical to Model 1. Thus all of these linear cases fit the data poorly. A linear tradeoff in Model 4 results in a prediction of maximum foraging effort (also maximum feeding rate and mortality rate) when pellets are abundant and maintenance foraging effort (also minimum feeding rate and mortality rate) when pellets are rare. There is no indication of such a pattern in the data and this model would fit both the pellet consumption and bluehead chub consumption data poorly. Thus although I do not explicitly consider models with a linear tradeoff between feeding rate and mortality rate, it is clear from a qualitative assessment that all such cases corresponding to the four optimization models that I consider here would compare poorly to their best-fitting nonlinear counterparts.

A large number of empirical studies have addressed the topic of feeding-mortality tradeoffs (Lima and Dill 1990, Lima 1998). Abrahams and Dill (1989) and Nonacs and Dill (1990) used titration-type methods in laboratory habitats to study the tradeoff between feeding rate and mortality rate and computed measures of the amount of mortality animals are willing to incur so as to obtain food. Houston and McNamara (1999) discuss how to interpret the results of these kinds of titration experiments in terms of the kinds of models that I test here, including the relevance of the MRS. Kotler (1997) and Mitchell et al. (1990) studied the foraging of desert gerbils and show that feeding rate maximization is a better description of their behavioral data than mortality rate minimization. Their results are similar to my result that Model 1 is superior to Model 2 for bluehead chubs. Other studies have explicitly considered the optimization hypothesis underlying Model 3, that foragers should behave so as to minimize the ratio of mortality rate to growth rate, μ/g . Gilliam and Fraser (1987) reported that habitat selection by juvenile creek chubs in an experimental stream was consistent with a minimize μ/f hypothesis (minimize μ/f can be related to, but is not identical to, minimize μ/g) and inconsistent with growth maximization and mortality minimization (i.e., feeding to obtain a fixed ration). Their results are also consistent with the minimize μ/g and maximize $\theta g - \mu$ hypotheses. Dahlgren and Eggleston (2000) obtained a similar result in their field study of ontogenetic habitat shifts in Nassau grouper. Using approximate calculations Turner and Mittelbach (1990) argue that the foraging behavior of bluegill sunfish in experimental ponds is consistent with the minimize μ/f hypothesis. All of these studies, and many others, show that animals consider both feeding rate and mortality rate when making behavioral decisions. However, none of the above studies, or any other work, to

my knowledge, has attempted to test among alternative models that incorporate feeding and mortality into the common currency of fitness. Thus, my empirical assessment of Models 3 and 4 relative to one another is a novel result.

Although my analysis may seem detailed, my study only begins to approach the general biological and theoretical complexity of foraging behavior. For example, the theory underlying Models 3 and 4 assumes that the forager's environment only changes as size and/or age changes. However, in my experiments the environment changes over the duration of every trial through the depletion of pellets. Yet, in my model fitting I take size and age to be constant even as the environment changes through pellet depletion. In Model 3 this means that the ratio $\mu(\rho_3)/g(\rho_3)$ is changing over the duration of a trial even though body size is assumed to be constant. In Model 4 this means that the MRS, θ , is assumed to be constant over the course of each set of experiments even though the environment is changing via pellet depletion within each trial. Hence while I attempted to design experiments that would satisfy the assumptions of the theory as closely as possible, there exist some subtle differences related to the details of the dynamic optimization theory. Thus one opportunity for future research is to study the relationship between the MRS (or a measure of the MRS) and the recent environment. The MRS depends on a forager's expectation of future environmental conditions and recent environmental conditions may be used by foragers to predict future conditions (Abrams 1991, McNamara and Houston 1994, Houston and McNamara 1999).

Many other avenues for future research are available. For example, additional state variables such as level of energetic reserves or parasite load could be considered. Future work should also take care to measure components of fitness, such as feeding rate

and mortality rate, as well as other metrics of foraging effort such as swimming speed and activity (Werner and Anholt 1993, Johansson and Leonardsson 1998, Anholt et al. 2000). The four alternative models make predictions concerning foraging effort, feeding rate, and mortality rate of bluehead chubs, but I only measured feeding rate and mortality rate. Measurements of foraging effort, such as swimming speed and time spent foraging, would improve my ability to test among more detailed hypotheses. Finally, many earlier studies used experiments that minimized or eliminated the depletion of foragers and/or their prey over the course of experimental trials. Some consequences of these efforts are that (i) the duration of trials is of the order of minutes with a nonzero predation hazard (e.g., Gilliam and Fraser 1987, Abrahams and Dill 1989, Johansson and Leonardsson 1998) or (ii) the trial duration is longer with zero or negligible predation hazard (e.g., Sih 1980, Anholt et al. 2000) or (iii) the trials are short and have a negligible predation hazard (e.g., Milinski and Heller 1978, Dugatkin and Godin 1996). However, as my analysis demonstrates, eliminating depletion is not necessary to test among several quantitative hypotheses when the depletion process can be explicitly modeled in the statistical analysis. In fact, measurements of depletion can be viewed as providing additional information over longer time intervals.

In conclusion, the two response variables, pellets consumed and bluehead chubs consumed, are measures of the functional response (in the Holling 1959 sense) of bluehead chubs feeding on pellets and green sunfish feeding on bluehead chubs, respectively. My results show that these functional responses are likely to depend on behavior that adaptively balances feeding and mortality (Abrams 1982, Abrams 1991)

thereby adding to the current evidence supporting a role for behavioral flexibility in the ecology of populations (e.g., Rosenzweig and Abramsky 1997, Post et al. 1999).

Acknowledgments

I thank Montse Fuentes, Nick Haddad and George Hess for comments on this manuscript, Kateri Duncan for help with the experiments, and Tom Kwak and the North Carolina State University Cooperative Research Unit for providing lab space. This research was supported by the United States National Science Foundation and the North Carolina Agricultural Research Service.

Literature Cited

- Abrahams, M. V. and L. M. Dill. 1989. A determination of the energetic equivalence of the risk of predation. *Ecology* 70: 999-1007.
- Abrams, P. A. 1982. Functional responses of optimal foragers. *American Naturalist* 120: 382-390.
- Abrams, P. A. 1991. Life history and the relationship between food availability and foraging effort. *Ecology* 72: 1242-1252.
- Anholt, B. R., E. Werner, and D. K. Skelly. 2000. Effect of food and predators on the activity of four larval ranid frogs. *Ecology* 81: 3509-3521.
- Brown, J. H., M. L. Taper, and P. A. Marquet. 1996. Darwinian fitness and reproductive power: reply to Kozlowski. *American Naturalist* 147: 1092-1097.
- Brown, J. S., J. W. Laundre, and M. Gurung. 1999. The ecology of fear: optimal foraging, game theory, and trophic interactions. *Journal of Mammalogy* 80: 385-399.
- Casella, G. and R. L. Berger. *Statistical inference*. Wadsworth Publishing, Belmont, C. A., U. S. A.
- Charnov, E. L. 1976. Optimal foraging, the marginal value theorem. *Theoretical Population Biology* 9: 129-136.
- Coleman, T., M. A. Branch, and A. Grace. 1999. *Optimization toolbox user's guide*. Mathworks, Natick, M. A., U. S. A.
- Dahlgren, C. P., and D. B. Eggeston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* 81: 2227-2240.

- Fraser, D. F. and J. F. Gilliam. 1992. Nonlethal impacts of predator invasion: facultative suppression of growth and reproduction. *Ecology* 73: 959-970.
- Fretwell, S. D. and H. L. Lucas. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretica* 19: 16-36.
- Gilliam, J. F., and D. F. Fraser. 1987. Habitat selection under predation hazard: test of a model with foraging minnows. *Ecology* 68: 1856-1862.
- Godin, J. J. and L. A. Dugatkin. 1996, Female mating preference for bold males in the guppy, *Poecilia reticulata*. *Proceedings of the National Academy of Science* 93: 10262-10267.
- Harper, D. G. C. 1982. Competitive foraging in mallards: 'ideal free' ducks. *Animal Behaviour* 30: 575-584.
- Hilborn, R. and M. Mangel. 1997. *The ecological detective: confronting models with data*. Princeton University Press, Princeton, N. J., U. S. A.
- Holling, C. S. 1959. Some characteristics of simple types of predation and parasitism. *The Canadian Entomologist* 91: 385-398.
- Houston, A. I. And J. M. McNamara. 1989. The value of food: effects of open and closed economies. *Animal Behaviour* 37: 546-562.
- Houston, A. I. and J. M. McNamara. 1999. *Models of adaptive behaviour: an approach based on state*. Cambridge University Press, New York, N. Y., U. S. A.
- Hugie, D. M. and L. M. Dill. 1994. Fish and game: a game theoretic approach to habitat selection by predators and prey. *Journal of Fish Biology* 45A: 151-169.

- Johansson, F. and K. Leonardsson. 1998. Swimming speeds and activity levels of consumers as various resource and consumer densities under predation risk. *Canadian Journal of Zoology* 76: 76-82.
- Kincaid, D. and W. Cheney. 1996. Numerical Analysis. Brooks/Cole Publishing, Pacific Grove, C .A., U. S. A.
- Kooijman, S. A. L. M. 2000. Dynamic energy and mass budgets in biological systems. Cambridge University Press, New York, N. Y., U. S. A.
- Kotler, B. P. 1997. Patch use by gerbils in a risky environment: manipulating food and safety to test four models. *Oikos* 78: 274-282.
- Kozłowski, J. 1999. Adaptation: a life history perspective. *Oikos* 86: 185-194.
- Krebs, J. R. and N. B. Davies. 1993. An introduction to behavioural ecology. 3rd Edition. Blackwell Scientific Publications, Oxford, U. K.
- Leonardsson K. and F. Johansson. 1997. Optimum search speed and activity: a dynamic game in a three-link trophic system. *Journal of Evolutionary Biology* 10: 703-729.
- Lika, K. and R. M. Nisbet. 2000. A dynamic energy budget model based on partitioning of net production. *Journal of Mathematical Biology* 41: 361-386.
- Lima, S. L. 1998. Stress and decision making under the risk of predation: recent developments from behavioral, reproductive, and ecological perspectives. *Advances in the Study of Behavior* 27: 215-290.
- Lima, S. L. and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. *Canadian Journal of Zoology* 68: 619-640.
- Ludwig, D. and L. Rowe. 1990. Life-history strategies for energy gain and predator avoidance under time constraints. *American Naturalist* 135: 686-707.

- MacArthur, R. H. and E. R. Pianka. 1966. On optimal use of a patchy environment. *American Naturalist* 100: 603-609.
- Mangel, M. and C. Clark. 1988. *Dynamic modeling in behavioral ecology*. Princeton University Press, Princeton, N. J., U. S. A.
- Martin, T. E., J. Scott, and C. Menge. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proceedings of the Royal Society of London B*. 267: 2287-2293.
- McNamara, J. M. and A. I. Houston. 1994. The effect of a change in foraging options on intake rate and predation rate. *American Naturalist* 144: 978-1000.
- McQuarrie, A. D. R., and C. L. Tsai. 1998. *Regression and time series model selection*. World Scientific Publishing, River Edge, N. J., U. S. A.
- Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. *Zeitschrift fur Tierpsychologie* 51: 36-40.
- Milinski, M. and R. Heller. 1978. Influence of a predator on the optimal foraging behaviour of sticklebacks. *Nature* 275: 642-644.
- Mitchell, W. A., Z. Abramsky, B. P. Kotler, B. Pinshow, and J. S. Brown. 1990. The effect of competition on foraging activity in desert rodents: theory and experiments. *Ecology* 71: 844-854.
- Nonacs, P. and L. M. Dill. 1990. Mortality risk vs. food quality trade-offs in a common currency: ant patch preferences. *Ecology* 71: 1886-1892.
- Parker, G. A. 1978. Searching for mates. In: *Behavioural ecology*. 1st Edition. Eds. J. R. Krebs and N. B. Davies. Oxford University Press, Oxford, U. K.

- Pigliucci, M. and J. Kaplan. 2000. The fall and rise of Dr. Pangloss: adaptationism and the *Spandrels* paper 20 years later. *Trends in Ecology and Evolution* 15: 66-70.
- Post, E., R. O. Peterson, N. C. Stenseth, and B. E. McLaren. 1999. Ecosystem consequences of wolf behavioural response to climate. *Nature* 401: 905-907.
- Rosenzweig, M. L. and Z. Abramsky. 1997. Two gerbils of Negev: a long-term investigation of optimal habitat selection and its consequences. *Evolutionary Ecology* 11: 733-756.
- Schwarz, G. 1978. Estimating the dimension of a model. *The Annals of Statistics* 6: 461-464.
- Seber, G. A. F. and E. D. LeCren. 1967. Estimating population parameters from catches large relative to the population. *Journal of Animal Ecology* 36: 631-643.
- Sih, A. 1980. Optimal behavior: can foragers balance two conflicting demands? *Science* 210: 1041-1043.
- Stephens, D. W. and J. R. Krebs. 1986. *Foraging Theory*. Princeton University Press, Princeton, N. J., U. S. A.
- Sutherland, W. J. 1996. *From individual behaviour to population ecology*. Oxford University Press, New York, N. Y., U. S. A.
- Turner, A. M. and G. G. Mittelbach. 1990. Predator avoidance and community structure: interactions among piscivores, planktivores, and plankton. *Ecology* 71: 2241-2254.
- Werner, E. E. and B. R. Anholt. 1993. Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142: 242-272.

Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* 15: 393-425.

Werner E. E. and D. J. Hall. 1988. Ontogenetic habitat shifts in bluegill: the foraging rate-predation risk trade-off. *Ecology* 69: 1352-1366.

Werner, E. E., J. F. Gilliam, D. J. Hall, and G. G. Mittelbach. 1983. An experimental test of the effects of predation risk on habitat use in fish. *Ecology* 64: 1540-1548.

Table 1: Values of the Schwarz Information Criterion (*SIC*) for each of the four models for each data set. Lower values of the *SIC* indicate that the model provides a more parsimonious fit to the data. The values have been standardized within each column so that the model with the lowest *SIC* value is set to zero.

Model	Schwarz Information Criterion		
	Experiment 1	Experiment 2	Both Experiments
1	450.7	314.7	764.0
2	4901.8	1457.2	6357.6
3	131.4	189.7	319.7
4	0	0	0

Figure Legends

Figure 1: A graphical illustration of the foraging behavior predicted by the four alternative optimization models when there is a convex tradeoff between growth rate and mortality rate. Model 1 predicts that bluehead chubs forage with maximum effort so that $\rho_1=1$ and growth rate is maximized at $g=g_{max}$. Model 2 predicts a foraging effort that exactly meets maintenance needs resulting in $g(\rho_2)=0$. Model 3 predicts that bluehead chubs forage so as to minimize the ratio of mortality rate to growth rate. Model 4 predicts a foraging effort that maximizes a linear combination of growth rate and mortality rate according to a dynamic programming equation, Eq. 4. The dashed lines tangent to the curve identify optimal foraging efforts for Models 3 and 4 (see text).

Figure 2: Predictions of the growth model described by Eq. 1 and the data from the growth experiment (each data point corresponds to an individual bluehead chub). Growth decreases with body size and increases with ration in both the data and the model. The lines indicating the model fit only approximate the true best-fitting model value for each individual data point because there is not an exact one-to-one correspondence between ration level and the observed feeding rate of an individual bluehead chub (that is, bluehead chubs receiving the same ration level could have fed at different rates). However, the graph is sufficiently accurate to show the effect of feeding rate on growth because within-ration variability in bluehead chub feeding rate is sufficiently small.

Figure 3: The fits of optimization Model 1 to the bivariate data from Experiments 1 (left column: panels a and c) and 2 (right column: panels b and d). Model 1 predicts that

bluehead chubs maximize foraging effort across all treatments. The two response variables, pellets (top row) and bluehead chubs consumed (bottom row), are plotted against initial pellet treatments for different levels of the green sunfish treatment. Symbols indicate data (treatment means), error bars denote one standard error and lines indicate model predictions. Data symbols are slightly offset in some cases so as to improve clarity.

Figure 4: The fits of optimization Model 2 to the bivariate data from Experiments 1 and 2. Model 2 predicts that bluehead chubs adjust their foraging effort in the presence of green sunfish so as to exactly meet maintenance costs. The format of the figure is identical to that in Figure 3. Note that Model 2 predicts identical results for pellets consumed, and nearly identical results for bluehead chubs consumed, across green sunfish levels 1 and 2 so that the lines for these values overlap substantially.

Figure 5: The fits of optimization Model 3 to the bivariate data from Experiments 1 and 2. Model 3 predicts that bluehead chubs adjust foraging effort so as to minimize the ratio of mortality rate to growth rate. The format of the figure is identical to that in Figure 3. Note that Model 3 predicts nearly identical results for pellets consumed across green sunfish levels 1 and 2 so that the lines for these values overlap substantially.

Figure 6: The fits of optimization Model 4 to the bivariate data from Experiments 1 and 2. Model 4 predicts that bluehead chubs adjust foraging effort so as maximize a linear

combination of growth rate and mortality rate given by a dynamic programming equation. The format of the figure is identical to that in Figure 3.

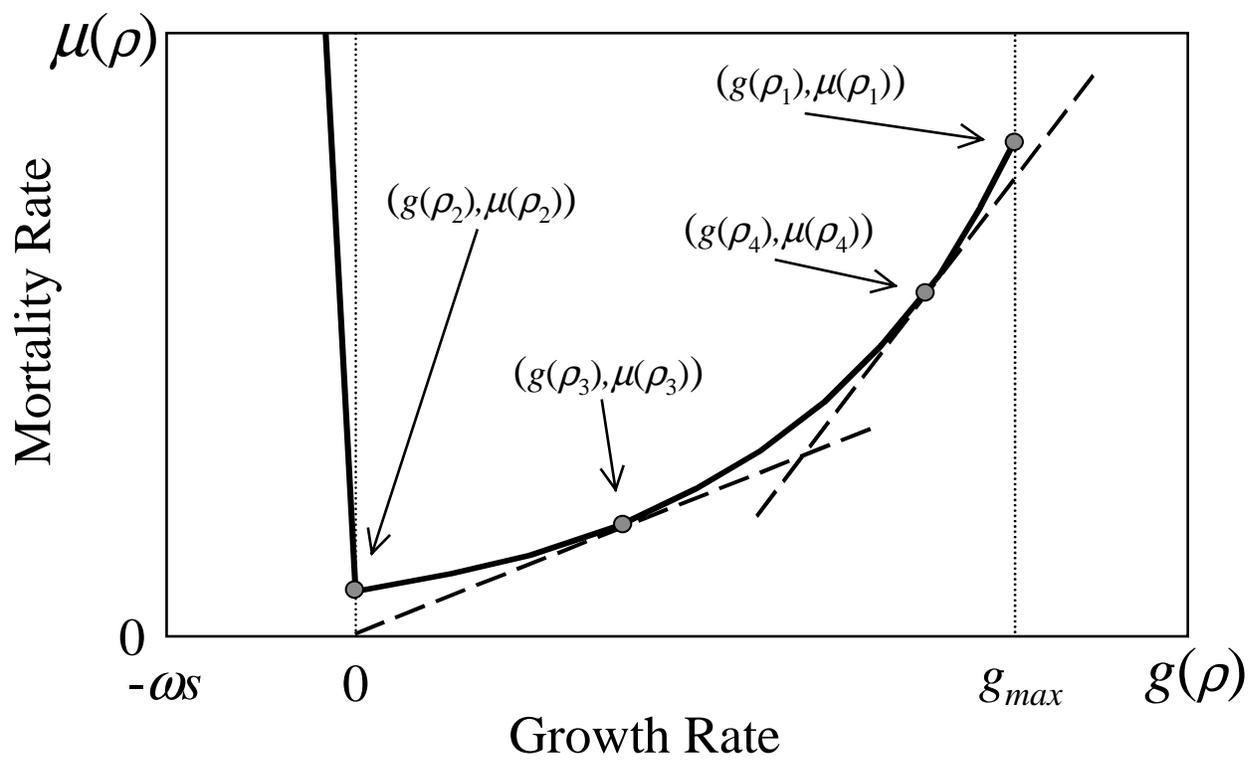


Figure 1

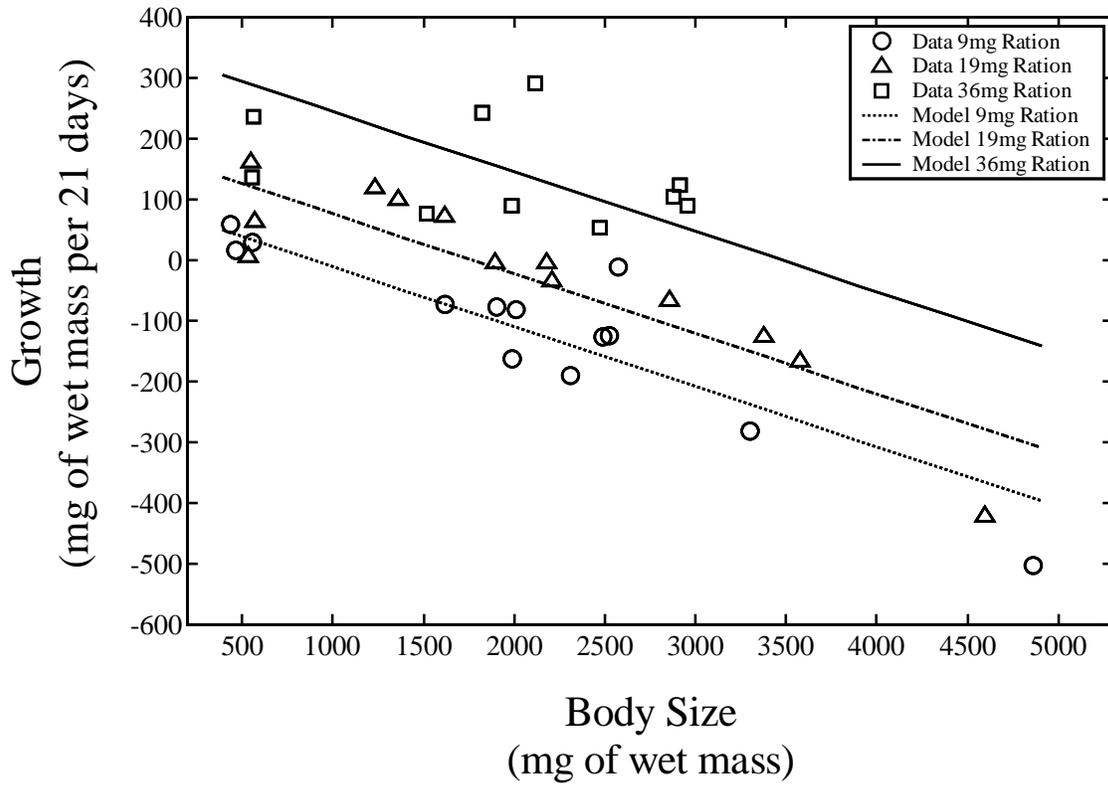


Figure 2

Model 1 (maximize growth)

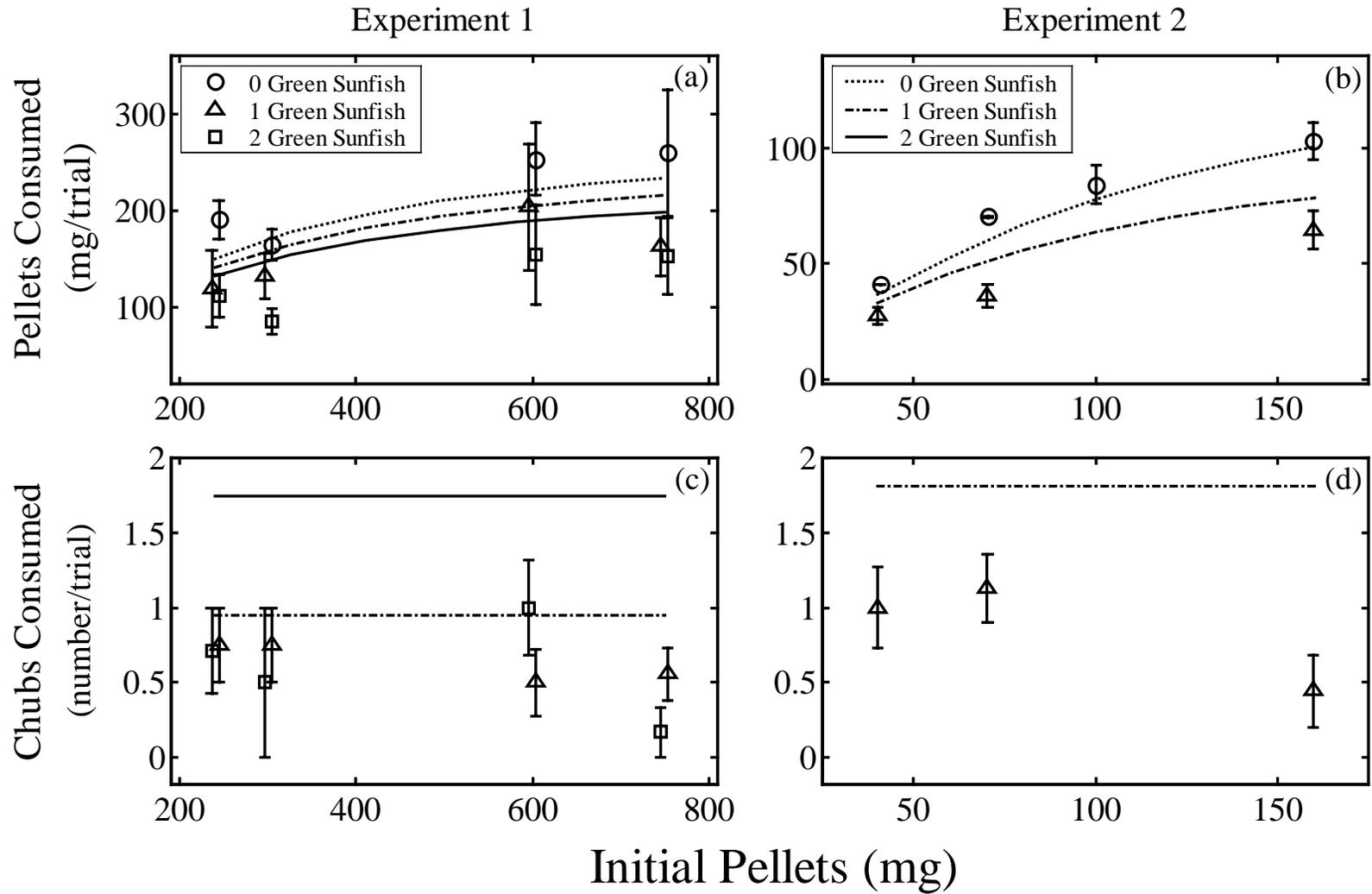


Figure 3

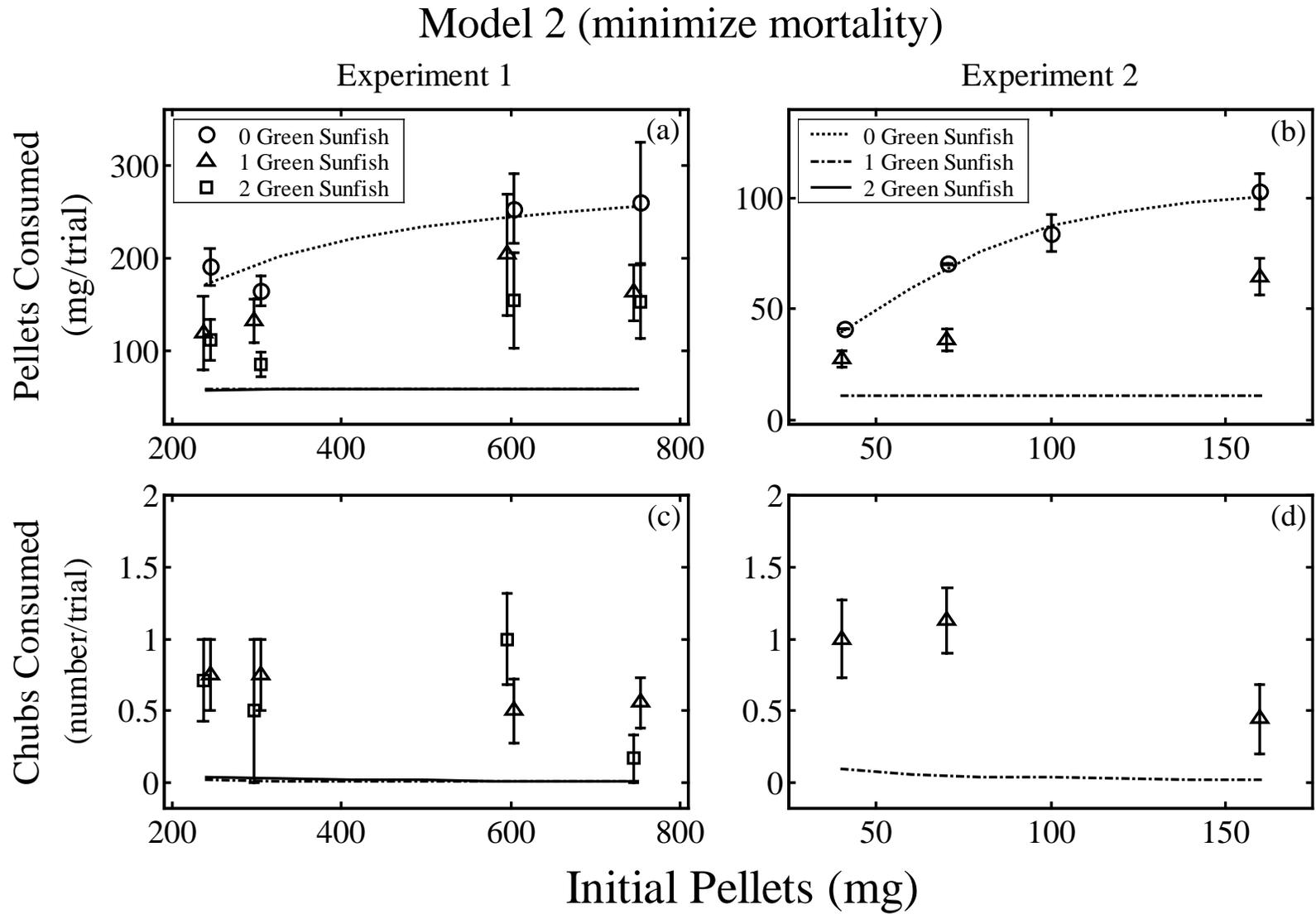


Figure 4

Model 3 (minimize mortality/growth)

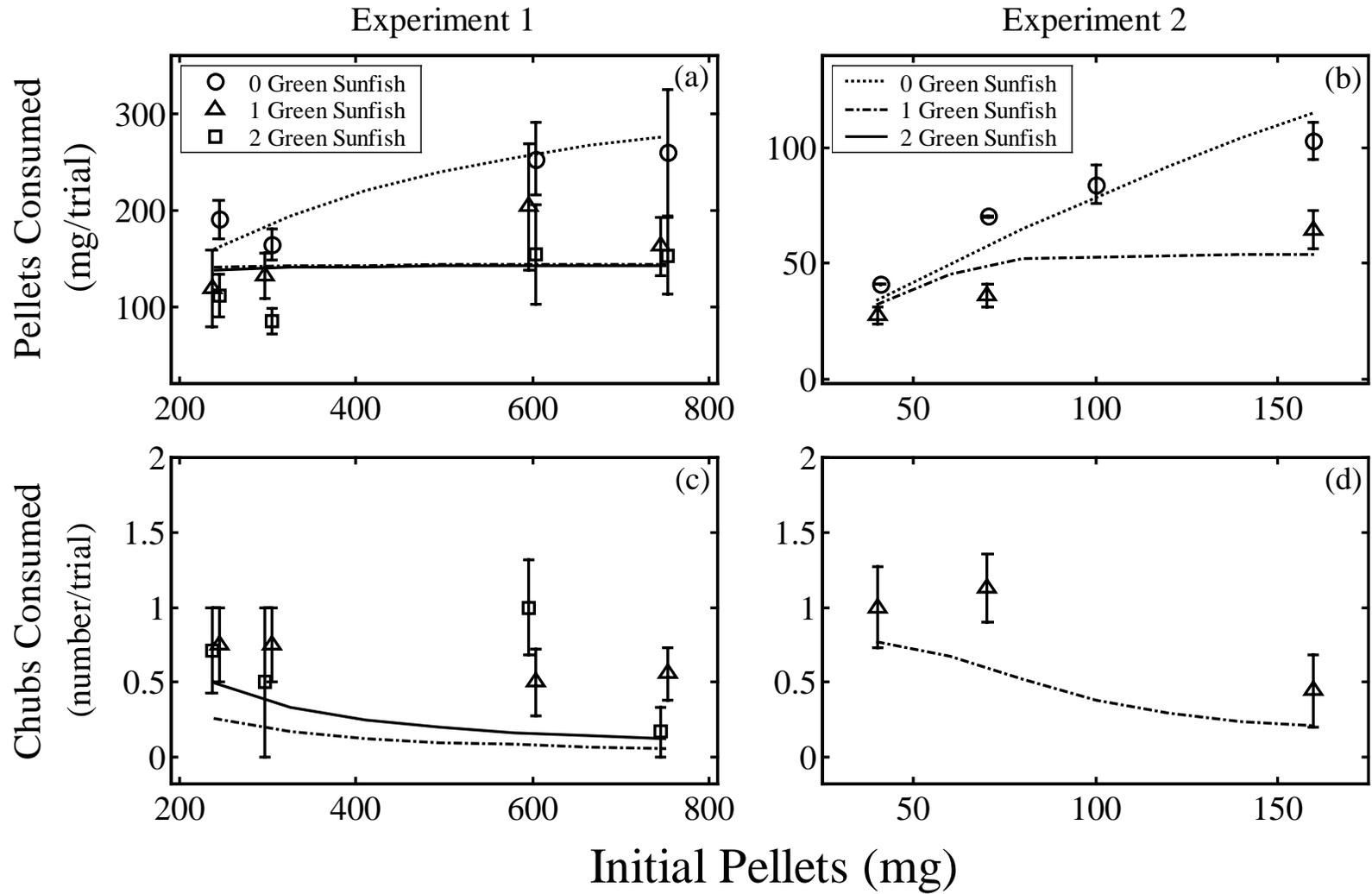


Figure 5

Model 4 (maximize $\theta g - \mu$)

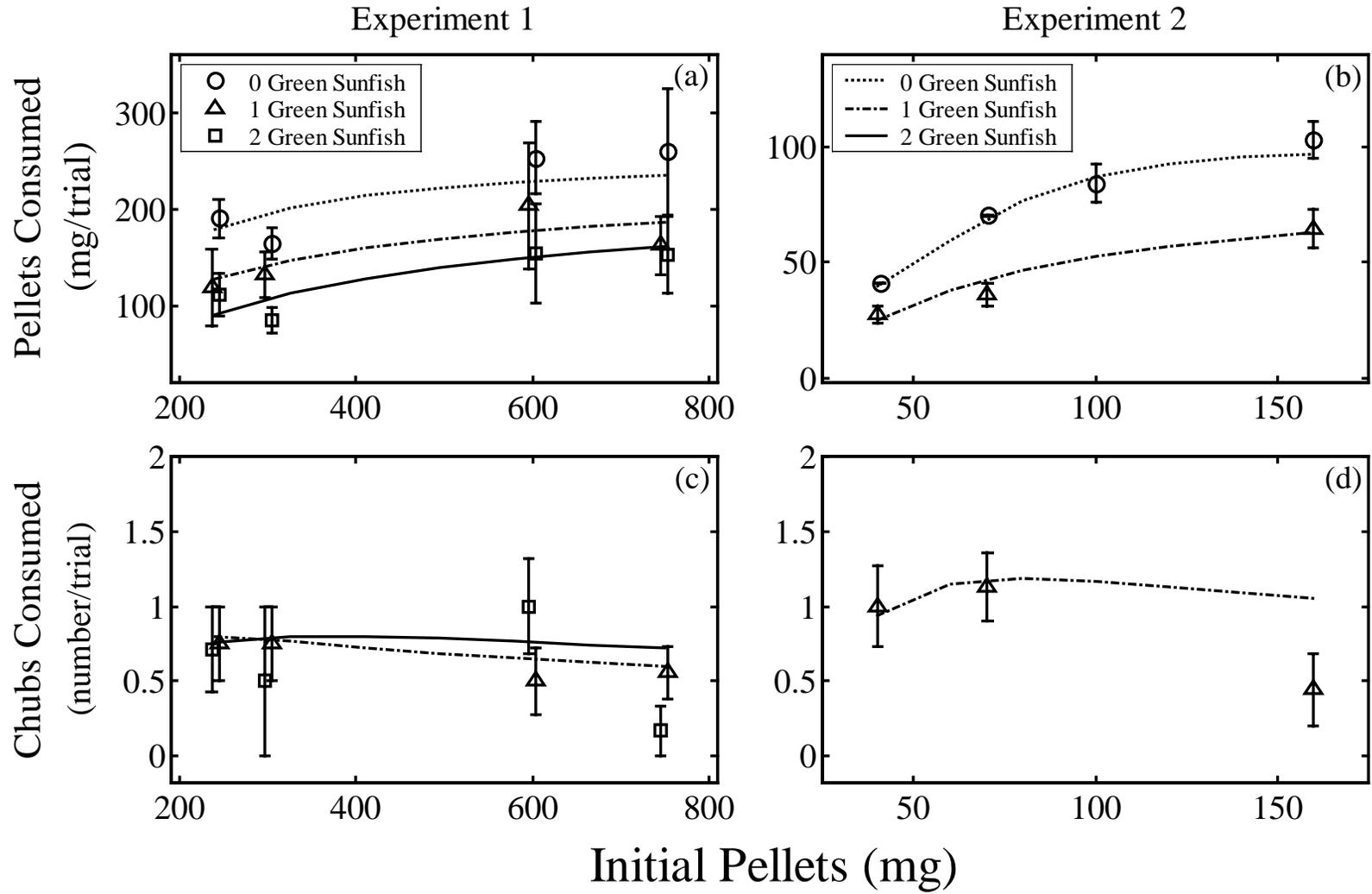


Figure 6