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Predation and its Consequences:
Insights into the Modeling of Interference

A Dissertation Presented

by

Christopher Jon Jensen

to

The Graduate School

in Partial Fulfillment of the

Requirements

for the Degree of

Doctor of Philosophy

in

Ecology and Evolution

Stony Brook University

May 2007

Stony Brook University

The Graduate School

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Abstract of the Dissertation

Predation and its Consequences: Insights into the Modeling of Interference

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Ecology and Evolution

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2007

Ecological theory depicts predators and their prey as instantaneously interacting particles, a way of looking at predation with a historical footing in chemical kinetics. A series of recent models that consider mutual interference between predators to be an important factor in determining consumption rate and therefore predator-prey dynamics have challenged this view of predation.

In this dissertation I investigate the importance of interference and design experiments to contrast between competing models of predator-prey interaction. After laying out the history of this theoretical controversy and the data that accompanies it, I establish the importance of using appropriately simple models in light of limited ecological data. I then present a rationale for questioning traditional theory. In order to provide a full understanding of the competing models, I present a detailed exploration of their stability space and equilibriums based on numerical simulations. These explorations establish that models of predation can be contrasted across two biological parameters: the prey growth rate (r) and the prey carrying capacity (K). I discuss their meaning and show that they can be effectively manipulated in the laboratory. I argue that the time scale of predation rates is not universal and show that the degree of predator interference detected depends on the time scale on which predation is measured. Based on the experimental and theoretical insights of my work, I conclude with a novel predator-prey model designed to bridge the gap between historically competing representations of predation.

In honor of my father Robert Jensen
a man of intense intellectual curiosity
who would have wanted to share
in the joy and accomplishment of my own

Table of Contents

List of Illustrations

Acknowledgements

Lev Ginzburg has been an incredibly supportive advisor throughout my graduate career. I have enjoyed our varied conversations and the many collaborative projects we have worked on. I am thankful for Lev's optimism and continual push forward; on many occasions he has believed in my work more than I have. Much of the success of this dissertation is due to Lev's ideas and enthusiasm.

I am grateful for the work of my dissertation committee. Jessica Gurevitch has provided me with important perspective and support. Her compassion has shone through on a number of occasions, and I will always think warmly of her. Leo Luckinbill took the time out of his busy life to guide me and to travel to Stony Brook. Leo has modeled for me what it means to be a generous scientist. Stephan Munch was my man in the clutch, joining my committee late in the game and providing me with an impressive array of ideas and analysis. When I think about what I want to be when I grow up, Steve's on the list of role models.

The graduate students of Stony Brook's Department of Ecology and Evolution have provided an immense amount of support throughout my six-year career here. Toni Lyn Morelli and Melissa Mark provided the inspiration and ideas that fueled my decision to pursue a Ph.D. The other members of my cohort (Jennifer Verdolin, J. Matt Hoch, Paul Bourdeau, Cathy McGlynn, Adam Ehmer, Chris Noto, Eliza Woo, Annie Green, and Sybil Gotsch) nurtured my early career and provided the friendship needed to push towards this final goal. I am particularly thankful for the Gaia-care provided by Annie, Melissa, Dusty, Eliza, and J. Matt. Dan Stoebel was a constant friend and role model who patiently guided me through laboratory protocols and provided invaluable feedback on my work. I have also enjoyed the intellectual and emotional support provided by Ramona Walls, Dusty Brisson, Leone Brown, and Roberta Harnett.

Jeff Yule was my fearless co-conspirator whose constant confidence in me often reinforced my own sometimes-lagging self-appraisal. He helped me to believe in my work and believe in my own career prospects in science. Jeff provided wonderful feedback on my writing, a myriad of fun and interesting ideas, and plenty of opportunity to explain theoretical and mathematical concepts. I don't know where my graduate trajectory would have led if not for Jeff's entry into the Ecology and Evolution Department.

Chapter 1

Introduction to the Dissertation:
Gause, Luckinbill, Veilleux and What to Do

Introduction

If we place a population of predators with a population of their prey in a closed system supplying constant food to the prey, we know the possible outcomes. The predators may consume every prey individual, after which the predator population will starve to death ("dual extinction"). The predators may die off, leading to an "escape" by the prey population, which will equilibrate at a carrying capacity determined by its food supply ("predator extinction" or "prey escape"). Or, for some indefinite time, the predator and prey populations may persist, either equilibrating or oscillating with some amplitude around equilibrial abundances ("coexistence").

What determines the qualitative outcome achieved by a predator-prey system? Given that our system is free from external influences or internal complexity, it must be characteristics of the predator and prey populations. Mathematical models of predator-prey systems incorporate and quantify these characteristics as prey and predator parameters, the values of which determine whether the system will maintain coexistence or terminate with either predator- or dual extinction. As predator-prey models have evolved, a fairly common set of parameters has emerged describing critical predator and prey characteristics: (i) the per capita intrinsic growth rate of the prey population (r); (ii) the carrying capacity of the prey population in isolation (K); (iii) searching efficiency of the predator population (a or α); (iv) the per prey-item handling time (h); (v) the conversion efficiency of the predator population (e); and (vi) the death rate of predators in the absence of prey (d).

What extremes of these parameters destabilize the predator-prey system, leading to an extinction event? For some parameters, intuition may inform our answer to this question. For instance, we have an intuitive sense of how the death rate of the predators (d) should influence system stability. If the predators die off very quickly (high d), we expect that they will not be able to consume and reproduce fast enough to offset death, and predator extinction will be the outcome. On the other hand, if the predators die off very slowly (low d), we expect that the predator population may grow large enough to consume the entire prey population, and dual extinction may be the outcome. The absolute value of d at which the transition from coexistence to extinction occurs is determined by the relative value of d to other parameters. For example, we may have the intuitive sense that if the predators attack very frequently (high a or α), then the value of d that produces predator extinction will have to be lower relative to the d value producing predator extinction in a system in which predators attack very infrequently (low a or α).

How do we test whether our intuition is correct? Ecologists have addressed this question in two main ways: by building mathematical models and by conducting empirical tests. Models incorporate our basic assumptions as mathematical arguments of simple equations that lend themselves to formal analysis. Often analysis of these models simply serves to confirm our intuition – the idealized mathematical system behaves just as we suspect the natural system does. Sometimes, however, modeling reveals counter-intuitive or

unexpected behaviors. We call these behaviors "paradoxes" because they contradict our intuition. The classic paradox of population ecology is the "paradox of enrichment" discovered by Michael L. Rosenzweig (1971). Intuition suggested that a highly-enriched system (one with high K) should be more stable, as predators should find abundant available prey. Rosenzweig demonstrated that increasing the carrying capacity of a modeled predator-prey system actually destabilized the system, leading to dual extinction.

Mathematical modeling is of great value to ecology. The move from verbal to mathematical models allows for explicit description of often-complex system behaviors. As demonstrated by the work of Rosenzweig (1971) and Robert M. May (1974), modeling also significantly influences ecological thought. In its most successful forms, modeling can reshape our intuition. This value and success, however, does not come without risks. In the end, the value of a given model is determined not by its elegance, but by how consistent its predictions are with the real outcomes of natural systems. All mathematical models must eventually face empirical testing.

In the ideal world of scientific inquiry, mathematical modeling and empirical testing are in dialogue. Modeling presents explicit predictions that can be tested via controlled experiments. Experimental results suggest new model formulations. Without models, empiricists would lack clear direction for their experiments. Without experimental results, theorists would lack clear direction for their model-building. Ongoing dialogue between theorists and empiricists continually improves the quality of our scientific understanding.

The history of population ecology dedicated to the understanding of predator-prey systems is rich with theoretical and empirical progress. In this dissertation I endeavor to contribute to this progress by uncovering new empirical directions inspired by the current state of dialogue between theoreticians and empiricists. In particular, I will shed new light on a contemporary debate regarding which *functional response* is best to incorporate into predator-prey equations.

Critical empirical outcomes in the *Paramecium-Didinium* system

Mathematical representations of predator-prey dynamics remove many of the complexities of natural systems. These equations assume that the prey population is provided with a constant resource supply and that a single obligate predator provides the only threat. They assume that refuges, structural complexity, and immigration or emigration are not at play. These equations may seem unrealistic, but their simplicity allows them to address a critical question: "Fundamentally, how do populations of prey and predators interact?" Of course, their simplicity limits the arena in which these equations can be tested. It is not advisable to use a natural system – one that violates the assumptions of a basic predator-prey model – to determine how prey and predator populations fundamentally interact. To get at this question, we need a system that meets the assumptions of a closed, two-species predator-prey model. As a laboratory-based system that can be maintained without complexity, the *Paramecium-*

Didinium system fits the bill. The simple *Paramecium-Didinium* system has an historical position as mediator of the dialogue between theoretical and empirical population ecology.

Gause's influential book *The Struggle for Existence* (1934) set the stage for modern population ecology through a series of experiments that allowed the protozoan predator *Didinium* to prey upon *Paramecium* in a controlled laboratory environment. As with many later population ecologists, Gause's primary motivation for utilizing this "predator-prey in a jar" system was to test contemporary ecological theory. In Gause's time (the 1930's), the equations of Alfred J. Lotka (1925) and Vito Volterra (1926) were state-of-the-art and had not yet been scrutinized via empirical testing. The Lotka-Volterra equations predict that all predator-prey systems should coexist, with a variety of cycles possible depending on initial conditions (**Figure 1a**).

Contrary to this prediction, Gause found that he could not produce coexistence in a closed system; his *Didinium-Paramecium* systems consistently crashed after completing less than one cycle (**Figure 1b**), with complete consumption of the prey followed by predator extinction. Gause's solution to this apparent conflict between theoretical predictions and empirical results was to modify the conditions of his experiment. Not surprisingly, he found that coexistence was possible if small abundances of prey were allowed to "immigrate" into the system. This approach of adding to contemporary theory rather than questioning its fundamental validity would continue: Gause *et al.* (1936) and Flanders (1948) added prey refuges and Huffaker (1958) added physical complexity to achieve experimental coexistence.

Forty years passed before another ecologist successfully revisited Gause's predator-prey experiments. Again, the evolution and influence of contemporary theory was central to the direction of empirical work. The theoretical work of Holling (1959) and Rosenzweig and MacArthur (1963) produced the state-of-the-art equations of the time. In contrast with the consistent coexistence produced by the original Lotka-Volterra equations, these modifications allowed for a variety of predator-prey outcomes. Predator extinction, coexistence, and dual extinction were all possible, depending on the value of critical parameters (K, e, a, d, h). Informed by these new theoretical insights, Leo S. Luckinbill endeavored to show that added complexity of the kind employed by Gause, Flanders, and Huffaker was not necessary to produce coexistence.

Luckinbill (1973) devised an exceedingly simple modification of the Gause system to produce coexistence without immigration: he thickened the medium using methyl cellulose. Luckinbill showed that this modification reduced the rate of interaction of predator and prey *without* changing the relative ability of prey to escape predators or adding structural complexity and/or refugia to the system. Assuming that this reduction in interaction translates to a decrease in searching efficiency, the addition of methyl cellulose should potentially allow for coexistence under the Rosenzweig-MacArthur equations. Luckinbill found, however, that reducing searching efficiency alone was not sufficient to produce coexistence.

4

Under the methyl cellulose treatment, the predator population consistently went extinct. In order to modify this outcome, Luckinbill reduced the enrichment of the system by lowering the amount of food available to the prey. This combination of lowered interaction and lowered enrichment produced long-term coexistence in the *Didinium-Paramecium* system.

Several years later, Brendan G. Veilleux provided a more comprehensive picture of this transition from dual extinction to coexistence (1979). Adding methyl cellulose and modifying system enrichment, Veilleux showed how the Gause system can be manipulated to move from dual extinction to predator extinction to coexistence to predator extinction. Veilleux completed a large number of trials, showing that under most conditions the qualitative outcome of the system does not vary. Unfortunately, Veilleux's work would not provide conclusive support for existing predator-prey theory. Manipulations of system enrichment were shown to affect a variety of different parameters (including r, K, e, and a), making it difficult to conclude why reduced enrichment moves the system from dual extinction to coexistence. In addition, Veilleux observed the same inexplicable system behavior that Luckinbill encountered: while the transition from dual extinction to coexistence can be made by reducing the enrichment of the system, a consistent zone of predator extinction exists for intermediate levels of enrichment.

Shortly after the publication of Luckinbill's paper, George William Salt produced a little-known work (1974) describing another experimental approach to the *Didinium-Paramecium* system. While Gause, Luckinbill, and Veilleux (GLV) were primarily interested in qualitative outcomes, Salt was intrigued by a quantitative question: What is the role of predator interference in the functional response? He devised a set of simple "arena" experiments that monitored the short-term consumption of *Paramecium* by *Didinium* at various manipulated densities of predator and prey. The results of his experiment suggested that the *Didinium-Paramecium* system increases in predator density lead to a decrease in per capita consumption rate. Like Gause, Luckinbill, and Veilleux, Salt did not benefit from the insights of modern theory, and for that reason his experiment – while demonstrating that predator interference is present – cannot answer the question "Which functional response best represents consumption in the *Didinium-Paramecium* system?"

The work of the *Didinium-Paramecium* system remains incomplete. In particular, the emergence of the Arditi-Ginzburg predator-prey model (1989) has suggested new problems that can be solved within the *Didinium-Paramecium* system. The power to move this system through the parameter space of a proposed predator-prey model, afforded by manipulations of interaction rate and system enrichment, makes it ideal for exploring the validity of competing models. Just as Gause's unanswered questions were addressed by the new perspectives of Luckinbill and Veilleux, a series of new *Didinium-Paramecium* system applications have the potential to address those questions left unanswered by Luckinbill, Veilleux, and Salt.

Competing functional responses

Lotka and Volterra formulated a simple set of differential equations to represent the consumption of prey by a single obligate predator. A general form of these equations (Abrams and Ginzburg 2000) is given below:

$$\mathrm{d}N/\mathrm{d}t = r(N)N - f(\cdot)P \qquad (1)$$
$$\mathrm{d}P/\mathrm{d}t = g(f(\cdot))P - dP \qquad (2)$$

Here, $f(\cdot)$ represents the functional response of the predator population. Assuming that reproduction is a function of consumption, $g(f(\cdot))$ represents the numerical response of the predator population. Some versions of these equations (Leslie 1948, Berryman 1990, Turchin and Hanski 1997) decouple the functional response from the numerical response by allowing the $g(\cdot)$ of the predator equation to be independent of the $f(\cdot)$ of the prey equation, but this means of formulating the predator-prey equations has been called into question for violating the assumption that reproduction is a function of consumption (Ginzburg 1998).

The equations employed by Rosenzweig-MacArthur (1963), as heir to the legacy of Lotka and Volterra, assume that consumption of prey is solely a function of prey abundance. Modern versions of these equations use the functional response outlined by Holling (1959). This assumption has been challenged by alternative models that incorporate predator abundance into the functional and numerical responses of the predator population. These alternative models include the predator-dependent equations of Hassell and Varley (1969), Beddington (1975) and DeAngelis *et al.* (1975), and the ratio-dependent equation of Arditi and Ginzburg (1989). **Table 1** summarizes these functional responses.

The Beddington-DeAngelis (BD) and Hassell-Varley-Holling (HVH) equations are both capable of producing intermediate functional responses that depend on both prey and predator abundances. Although Hassell and Varley did not include predator satiation via handling time in their original equation, contemporary use of their N/P^m argument does (Arditi et al. 2001, Jost and Arditi 2001, Skalski and Gilliam 2001); I will refer to this saturating version of the equation as "Hassell-Varley-Holling" (Jost and Arditi 2001). For the extreme of no interference ($m = 0$), the equation produces the Holling function, while for the extreme of complete prey sharing (i.e. very strong interference or $m = 1$) it produces the ratio-dependent Arditi-Ginzburg function (Abrams and Ginzburg 2000). The BD form is also theoretically capable of producing both extremes: when the interference parameter $i = 0$, the equation becomes the Holling function, and when iP approaches infinity, the equation becomes the Arditi-Ginzburg function (See **Chapter 6** for more information).

Which of these predator-dependent forms is superior remains a subject of debate. The HVH equation creates a more simple distinction between ratio- and prey-dependence but has been criticized for lacking a mechanistic derivation. The BD form can be mechanistically derived from several sets of assumptions (Huisman and DeBoer 1997) but produces ratio-dependent behavior in a less

definitive manner than the HVH equation. Both have been used to fit to the data of Luckinbill and Veilleux (Jost and Ellner 2000, Jost and Arditi 2001, Skalski and Gilliam 2001).

The ratio- and prey-dependent extreme depictions of predator-prey interaction can be considered idealized abstractions of the actual functional response that drives natural predator-prey systems. Neither model is a perfect description of natural predator-prey interaction (Salt 1974, Abrams and Ginzburg 2000); however, each extreme suggests different system behaviors, and we would like to determine which behaviors are most accurate. Simple, idealized opposites of this nature were characterized as "limit myths" by Quine (1976, 1980, 1995), leading us to ask the question: "Which model represents the best *limit myth*?" (Colyvan and Ginzburg 2003b, a).

How advocates of predator-dependence view these *limit myths* varies, even amongst the two ecological theorists who first suggested the ratio-dependent functional response (Arditi and Ginzburg 1989). Roger Arditi has consistently pointed out that ratio-dependence (i.e. values of m approximating one) emerges from a system governed by prey-dependent interactions whenever spatial and/or temporal heterogeneities are significant (Arditi and Saiah 1992, Cosner et al. 1999, Arditi et al. 2001). In doing so, Arditi allows for prey-dependence as the fundamental model of interaction but maintains that this functional response can only be appropriately employed in idealized systems that are homogenously-mixed and perfectly continuous in time and space(Arditi et al. 2001). Arditi favors the use of the ratio-dependent function response in part because the idealized systems (i.e. prey-dependent) do not exist outside of the laboratory. Rather than considering predator-dependence an emergent property, Ginzburg sees ratio-dependence as a reflection of the fundamental invariancy of predator-prey interaction. Under ratio-dependence, proportional increases in predator and prey abundances have no effect on their interaction; only through other factors, such as the carrying capacity, is the system sensitive to proportional abundance changes. The invariant property of ratio-dependence is not shared by prey-dependence, where changes in abundance affect both the predator-prey interaction and the influence of other factors (such as carrying capacity). In Ginzburg's opinion, these invariant properties of ratio-dependence present a more parsimonious and ultimately more accurate portrayal of predation (Ginzburg and Colyvan 2004).

Understanding the unresolved controversy

Although the generalized model of Hassell-Varley (1969) followed the Holling and Rosenzweig-MacArthur formulation by only a few years, its publication did not generate substantial debate regarding which functional response form to incorporate. Similarly, interest in the BD function is a recent phenomenon. In fact, it was not until the 1989 publication of the Arditi-Ginzburg ratio-dependent functional response that the controversy was born. Since that time, a large number of papers have attempted to answer the question: "Which functional response is most appropriate to incorporate into our predator-prey

models?" A general summary of this debate was provided by Abrams and Ginzburg (Abrams and Ginzburg 2000).

On theoretical grounds, a number of disagreements persist. Many have argued that in the instantaneous time interval of differential equations, since predators can only react to the abundance of prey around them, the prey-dependent form is the only logical functional response to incorporate (Murdoch et al. 2003). This view has been labeled as "instantist" and criticized for interpreting the meaning of differential equations too literally (Ginzburg and Colyvan 2004, Jensen and Ginzburg 2005). Theorists also differ in their taste for purely-mechanistic models: the ratio-dependent functional response has been criticized for being too phenomenological because the mechanism behind ratio-dependence has not been made entirely explicit (Abrams 1994). A related issue hinges on the importance of auxiliary data. Theorists differ on whether particular mechanisms can be incorporated into models when empirical data has not clearly demonstrated their importance.

One might hope that theoretical disagreements could be mediated by effective experimental work, but this has not been the case. One reason is that direct measurements of predator-prey interaction are difficult to obtain. Those few studies providing functional response data that can be interpreted along the prey- to ratio-dependent continuum suggested by the generalized HVH equation provide equivocal results (Arditi and Akçakaya 1990, Osenberg et al. 1999). Because the predictions of prey- and ratio-dependence are so similar under equivalent static parameter values (when they allow for coexistence), fitting may not be sensitive enough to distinguish the two (Jost 1998). This weakness is compounded by the very noisy nature of most predator-prey data sets, prompting some authors to reject the fitting approach altogether:

> Given that in real life there would be substantial variation around the respective functions, because of stochastic environmental effects, population censusing errors, and variation in parameters among different ecosystems, we submit that the subtle difference in predictions of the prey- versus ratio-dependent models is minor and would not be detectable using simple regression tests. (Lundberg and Fryxell 1995)

Gary Harrison, who used a least-squares algorithm to fit the Luckinbill data, found that prey-dependence provided a better fit than ratio-dependence (Harrison 1995). Christian Jost, who applied a more complex fitting algorithm to the GLV data, also found that prey-dependence provides a better fit to Luckinbill's data but discovered that ratio-dependence provides a better fit to Veilleux's larger data set (Jost 1998, Jost and Ellner 2000, Jost and Arditi 2001). The equivocal results provided by the fitting approach suggest that its potential to mediate this debate has been exhausted.

An extensive literature chronicling the effects of nutrient supply on predator-prey systems has prompted some to look for solutions to the functional response dilemma using qualitative rather than quantitative clues. Because the prey- and ratio-dependent forms predict very different responses to enrichment,

experiments that employ nutrient input manipulations have the potential to suggest which functional response is appropriate in a given system. Unfortunately, these studies have also proved inconclusive. Because most take place in fairly complex natural systems (e.g. ones with multiple species at each trophic level), these experiments may not allow for controlled comparison of the two *limit myths*. However, their shift from comparison of quantitative values to comparison of qualitative outcomes merits further pursuit and suggests potential for experiments conducted in less complex systems.

Meaningful contrasts: how the two models differ in qualitative terms

Both the prey- and ratio-dependent forms can account for all of the expected qualitative outcomes of a simple predator-prey system. However, the explanations of these outcomes provided by each model differ significantly. These differences play out in three main arenas: i) whether or not extinction occurs as a deterministic outcome; ii) whether or not initial conditions influence the outcome of a particular system; and iii) the effect of the prey population growth rate (r) on the stability of the system.

Both *limit myths* predict that predator extinction and dual extinction are possible outcomes contingent on the value of critical parameters. However, their explanations for dual extinction differ. While both models can account for predator extinction as a deterministic outcome, only the ratio-dependent form predicts dual extinction as a deterministic outcome. The prey-dependent form (as well as all forms of the generalized HVH predator-dependent form for values of m less than one) relies on a non-deterministic explanation of dual extinction.

The non-deterministic explanation of extinction rests on reasonable assumptions but renders the bifurcation between coexistence and extinction in real systems ambiguous. If the trajectory of the system brings the prey population very close to the N- or P-axis (see **Appendix A**), the prey or predator populations may go extinct by one of two mechanisms: i) the discrete nature of real populations; or ii) the stochastic nature of real populations. Because the differential equations employed in these predator-prey models ignore the inherently discrete nature of individual organisms, it is possible for a system to persist (mathematically) with fractions of an individual. This property of these equations is obviously biologically unrealistic: if the system produces fluctuations where the actual number of organisms per system drops below 1.0, we consider this an extinction event. Demographic or environmental stochasticity may also cause extinction when populations drop to low abundances. The absolute threshold at which low abundances cause extinction by stochastic mechanisms is unknown but depends on either the reproductive properties of the organism, the magnitude of environmental noise, or both.

Non-deterministic extinction is also a possible outcome for the ratio-dependent model. As with the prey-dependent form, if the population trajectory brings the prey population close to zero, a system that should theoretically persist may go extinct. The ratio-dependent form simply does not rely on this explanation for all outcomes of dual extinction; deterministic dual extinction is a

9

mathematically possible outcome under ratio-dependence. To date, no one has explored the role of non-deterministic extinction in the ratio-dependent model.

Under the ratio-dependent model, initial conditions can influence the outcome of the system. There are two separate regions within the ratio-dependent parameter space in which two different outcomes are possible depending upon the initial densities of predator and prey – one region allows for either predator extinction or dual extinction, while another allows for either coexistence or dual extinction (Berezovskaya et al. 2001). Prey-dependent models do not display this kind of behavior, as a single outcome is predicted for a given set of parameters (regardless of initial population densities).

The last key difference between the two *limit myths* centers on their response to changes in various critical parameters. The stability properties of the prey-dependent system have been well-understood since the analysis of Rosenzweig and MacArthur (1963). The stability properties of the ratio-dependent system, however, were not fully understood until the publication of a paper by Berezovskaya *et al.* (2001). For a more comprehensive summary of the stability analyses of both models, see **Appendix B.**

In comparing the qualitative predictions of these two models (**Table 2**), only one parameter – the per capita growth rate of the prey population (r) – actually provides a meaningful contrast. In the ratio-dependent parameter space (see **Appendix B**), decreases in r mediate the transition from coexistence to dual extinction. The effect of changes in r in the prey-dependent space is a slightly more delicate and potentially more contentious issue. Traditionally, the stability of the prey-dependent model system is considered to be invariant to changes in r (a quick look through the prey-dependent inequalities in **Appendix B** confirms that r does not participate in any of them). However, the carrying capacity (K) is a critical parameter in determining the stability of the system, with increases in K leading to destabilizing effects described in the famous Rosenzweig paper (1971) on "The Paradox of Enrichment" (notice that the inequalities governing ratio-dependence listed in **Appendix B** are scale-invariant, so K is not involved in transitions between various states). I suggest, in an argument outlined in **Chapter 3**, that the parameters K and r are interdependent, with increases in r driving increases in K. Experimental evidence from the GLV system supports this positive correlation between r and K (Luckinbill 1979). Because of its sensitivity to scale, the prey-dependent model necessarily uses K as a proxy for r, suggesting that any changes due to r will be played out as changes in K. For this reason, I interpret increases in r in the same manner as Rosenzweig interpreted increases in K: as destabilizing to the prey-dependent system.

In stating that changes in the growth rate of the prey population (r) provide the only contrast in qualitative outcomes, I do not mean to suggest that the prey- and ratio-dependent systems are otherwise identical. Strong quantitative differences in response to changes in some or all of the critical parameters may exist, but they have not been explored theoretically or empirically. One complicating factor in making such a quantitative comparison is that the units of the per capita predator searching efficiency (*a* or α) differ between models. The

other problem is that quantitative differences between the model predictions may be too small to detect with available empirical tools. For these reasons, I have focused on the most dramatic difference between the predictions of the two models: qualitative response to changes in r.

Simple quantitative differences: getting beyond trajectory fitting

While curve-fitting has failed to provide an unambiguous answer to the question "which functional response should I use?", this does not mean that the potential of all quantitative approaches has been exhausted. Simple quantitative differences exist between the prey- and ratio-dependent extremes, and the transition between these extremes (using either the BD or HVH models) can also be understood in quantitative terms. Both extremes suggest an invariancy with the potential to be empirically tested. The prey-dependent functional response is invariant to predator density: given a fixed number of prey, the per-capita consumption rate of the predator should be the same regardless of predator abundance. The ratio-dependent functional response is invariant to overall density of predator and prey: given a fixed ratio of prey to predators, the consumption rate of the predator should be the same regardless of overall abundance.

Competing views of *Gause, Luckinbill,* and *Veilleux*

Have the experiments needed to effectively contrast the prey- and ratio-dependent functional responses already been done? One way to answer this question is to consider how the experiments of Gause, Luckinbill, and Veilleux might be interpreted under each model. Does one of these *limit myths* provide a more parsimonious explanation of the GLV results? Do the GLV results provide strong evidence in favor of one of these two functional responses?

Gause's experiment, in which dual extinction occurred consistently, does little to mediate the dispute. Both models predict that under certain conditions the system will consistently go extinct. As noted above, r is the only parameter that has different qualitative effects on system stability under the two different *limit myths*. Given that Gause's experiment occurred at a "point" in the overall parameter space of both models, we cannot gain insight into how changes in parameters might affect the stability of the system. The only informative evidence emerging from Gause's work can be seen in phase space plots of his experimental runs (**Figure 1**). These are the aforementioned "Gause loops": extinction events that occur before a full oscillation can be completed. Both functional responses can produce such a loop. Under prey-dependence, this loop would only be produced when the non-deterministic forces are strong enough to prevent any oscillation, as would be predicted in a very small or very noisy system. Under ratio-dependence, this loop is the consistent profile of dual extinction (see **Appendix B**).

The work of Luckinbill *does* demonstrate a transition between stable and unstable states and therefore has the potential to contrast the *limit myths*. The addition of methyl cellulose was the first step towards producing coexistence in

11

the Gause system. The most likely parameter to be affected by the addition of methyl cellulose is the per capita searching efficiency (a or α) of the predator (Harrison 1995). This assumption remains untested, because Luckinbill made no direct measurement of critical parameters. Depressing a or α has the same effects in both models: the system moves from dual extinction towards coexistence or predator extinction. So both models can account for the effects of methyl cellulose with equal parsimony.

To produce coexistence, Luckinbill had to reduce the availability of prey food. Presumably, this should reduce K and r. The prey-dependent *limit myth* provides a fairly parsimonious explanation of this result, as further reductions of K can pull the limit cycle away from the N- and P-axes, eliminating extinction. The ratio-dependent *limit myth* has a similarly clear interpretation of methyl cellulose addition but also fails to provide a simple explanation of the coexistence that accompanies reductions in r. Under ratio-dependence, reducing r cannot move a system from predator extinction to coexistence. The only way to account for the Luckinbill result is to assume that another parameter, the handling time (h), is being reduced as prey food availability is reduced. Luckinbill did not make direct measurements of h, so the validity of this assumption cannot be assessed.

Veilleux's data are more comprehensive and allow us to gain insight into how parameters change within his experimental system. Veilleux demonstrated a continuum of parameter changes, summarized in **Table 3**, by making incremental changes to the prey food concentration added to the system. The stability of the system was consistently determined by the food supply for all but one treatment, which appears to be at the transition between two outcomes (dual extinction and predator extinction). Veilleux discovered a transition between dual extinction and predator extinction that was consistent with the data of Luckinbill and through further reductions of food supply was also able to produce coexistence.

The prey-dependent model is consistent with Veilleux's data. In comparing the parameter changes shown in **Table 3** with the predicted outcomes listed in **Table 2**, we see that all three are consistent with the prey-dependent model. The only uncertainty lies in determining the degree to which each parameter change drives the transition between outcomes. Are we seeing strong paradox of enrichment effects associated with changes in r, or are the searching efficiency (a) and efficiency (e) exerting a more powerful effect on system dynamics? Despite their comprehensive nature, Veilleux's data cannot provide us with insight into this question.

The ratio-dependent model provides a less parsimonious version of Veilleux data, but it cannot be completely ruled out. Because the ratio-dependent model predicts that decreasing r should move the system towards dual extinction rather than away from it, the results of Veilleux are inexplicable in terms of r. However, the fact that two other parameters – e and a – decrease alongside r makes impossible to falsify the ratio-dependent model. In any parameter space, it is the relative effect of parameter changes that determines any change in system properties. If we assume that the change in r is small relative to changes in e and a, we can account for the basic transition from dual extinction to coexistence to

predator extinction. Explaining the predator extinction that seems to be occurring for a brief interval between dual extinction and coexistence is not possible within this space unless we invoke a non-deterministic outcome similar to that assumed for prey-dependence. Given the trajectories demonstrated by the analysis of Berezovskaya *et al.* (2001), it is possible to imagine that non-deterministic extinction of the predator population could occur within the space that deterministically coexists. Unfortunately, the experiments of Veilleux offer no insight into the likelihood of this explanation.

When considering the extent to which the GLV experiments can mediate the dispute between advocates of competing functional responses, it is important to remember that none of these experiments were designed to address this problem. The ratio-dependent functional response was unknown at the time of all three experiments. Because the manipulation of prey food supply affected three critical parameters, we cannot separate their effects on the system, and thus cannot select with confidence between the competing *limit myths*.

Each of these empiricists had a clear goal: to see if simple experimental systems could replicate the behavior of contemporary theory. Towards this goal, all three experiments provide an exemplary trajectory. I hope to gain new insight from the data left behind by these scientists and to find inspiration in their experimental system for new empirical work.

What to Do Analytically

Given that the prey- and ratio-dependent abstractions yield very different parameter spaces, we should be able to contrast the GLV results with each model space to consider which abstraction best accounts for the data. Parameters can be estimated from predator and prey trajectory curves for each of the experimental runs contained in the GLV data set; several attempts to fit the Luckinbill and Veilleux data to these models provide estimates of these parameters. These parameter combinations can then be located in the parameter space of both models. The relative success of each model at predicting the experimental outcome can then be considered. An equivocal result – where the two models both predict results with comparable success – is a possible outcome of such an analysis. However, it is also possible that such an analysis might show that the qualitative outcomes of the GLV data consistently conform to the predictions of either prey- or ratio-dependence.

Two limitations could potentially hamper such an analysis. The first problem emerges directly from the contrast between prey- and ratio-dependent functional responses. One parameter – the searching efficiency (a or α) – cannot be directly compared between models. For this reason, the algorithms used to estimate this critical parameter from the GLV data sets will have to be different; this necessary inconsistency has the potential to confound the comparison, as the results of this analysis will depend completely on the ability of these differing algorithms to accurately estimate the searching efficiency from existing data. A second problem is the relatively small number of replications present in the GLV data. Gause recorded only 6 runs, all of which exist only in graphical form.

Luckinbill recorded 2 runs producing dual extinction, 6 runs producing predator extinction, and 1 run producing coexistence. Veilleux's data set is the largest, with 23 runs producing dual extinction, 41 runs producing predator extinction, and 50 runs producing coexistence. Only the Luckinbill data is available in numerical form, and only a small subsample of the Gause and Veilleux data can been digitized from their publications. Given the small number of available GLV runs, there is some concern that there may not be enough data to clearly distinguish prey- and ratio-dependent predictions.

A second analytical task of great importance to my proposed experiments is to understand the behaviors of the BD and HVH models "in between" the prey- and ratio-dependent *limit myths*. Using numerical simulations that take into account the finite nature of a real biological system, these models can be explored across values of the interference parameters m and i. These simulations will allow me to understand: i) the role of non-deterministic extinction in the prey-dependent and predator-dependent models, and whether non-deterministic extinction plays a role in the ratio-dependent model; ii) how dependence on initial conditions emerges at higher levels of predator interference; and iii) the shift from a prey-dependent system stabilized by reductions in r to a ratio-dependent system destabilized by reductions in r. By exploring gradations of predator interference, these simulations will provide important insights into the potential outcomes of my experimental manipulations.

What to Do Empirically

Despite the limitations of their data, Gause, Luckinbill, Salt, and Veilleux all contributed greatly to the understanding of laboratory-confined predator-prey systems. In particular, Luckinbill's introduction of methyl cellulose and Veilleux's manipulation of prey food supply provide tools that greatly expand the potential of the GLV system for exploring the nature of predation. Several simple experiments that take advantage of these tools have the potential to clarify or even resolve the functional response debate.

Salt revisited

The only shortcoming of Salt's experiment (1974) is that it failed to provide an array of initial conditions that was suitably diverse. Given more combinations of predator and prey abundance, particularly combinations that allow us to test the invariancies predicted by the prey- and ratio-dependent models, such an experiment could suggest the short-term nature of *Didinium*'s functional response.

The Paradox of Enrichment *in reverse*

One valuable experiment investigates the paradox of enrichment phenomenon. This paradox has maintained a prominent theoretical presence despite glaring lack of empirical support (Jensen and Ginzburg 2005). The paradox highlights the key difference between prey- and ratio-dependent

depictions of predation. Under prey-dependence, increases in the growth rate of prey (r) either have no effect on system stability or cause system instability (via the paradox of enrichment phenomenon). In contrast, under ratio-dependence, increases in r should lead to greater stability.

Because enrichment has such a multivariate effect on the overall parameter space of the GLV system, other means of regulating r must be employed. One such means is through the enforcement of proportional mortality on the prey population. By removing a consistent fraction of the prey population, both r and K can be simultaneously reduced without affecting other key parameters of the system (see **Chapter 3**). Using this approach, one can in principle see how the GLV system responds to decreases in prey growth rate (r). Using manipulations of methyl cellulose and prey nutrient inputs, the system can be altered such that long-term stable coexistence can be maintained. Once this coexistence has been achieved, proportional mortality can be imposed to determine the effect of reducing r.

We expect that if we impose a high enough mortality on the prey, eventually the prey population will go extinct. However, the level of reduction required to achieve this extinction is of critical importance. Under prey dependence, reductions in r can only lead to prey extinction if r falls below zero. Under ratio dependence, reductions in r will lead to prey extinction with small but positive values of r. An additional distinction between the models can be explored through reduction of r. Under prey dependence, if K is sufficiently reduced, the predator can go extinct. Predator extinction cannot occur with reduction in r under ratio dependence; it emerges only when the prey goes extinct first. We can interpret outcomes of reducing r in terms of these two extreme theoretical abstractions. If the predator consistently goes extinct and prey escape, we can conclude that prey dependence is the better abstraction. If the prey goes extinct first, while r remains positive, we can conclude that ratio-dependence is the better abstraction.

Reversing The Paradox of Enrichment

The preceding experiment places much of the burden of proof on the ratio-dependent abstraction. In order to falsify the prey dependent hypothesis, the results of the Paradox of Enrichment *in reverse* experiment must be consistent with the predictions of strong predator dependence. To complement such an experiment, it would be valuable to perform a second experiment with the potential to falsify the ratio-dependent abstraction.

Many attempts to demonstrate the paradox of enrichment have been ineffective (Jensen and Ginzburg 2005), although a few studies provide suggestive evidence in favor of the phenomenon (Fussmann et al. 2000). These attempts have relied on increased nutrient inputs to increase carrying capacity (K); as discussed above, this approach suffers from the confounding effect that nutrient inputs affect multiple parameters. I suggest a new approach, again utilizing the tools developed by Gause, Luckinbill, and Veilleux. As the chief challenge of performing an experiment that demonstrates the paradox of

enrichment is achieving an increase in K without affecting other parameters, this experiment also takes advantage of the enforced proportional mortality method to modify r and K.

Taking advantage of methyl cellulose and prey food concentration manipulations, a *Didinium-Paramecium* system will be established that exhibits consistent dual and/or predator extinction. In order to depress K and allow for stable coexistence, the system will be subjected to various levels of enforced proportional mortality (see **Chapter 3**). The prey-dependent prediction is that sufficient reduction in K should allow for coexistence. If the system can be moved into a region of coexistence by decreasing the carrying capacity, we can falsify the ratio-dependent abstraction.

Why use a laboratory microcosm?

Our eventual goal, as ecologists, should always be to improve our understanding of natural systems. As such, it is reasonable to question the relevance of all laboratory work to natural communities. Why not answer the question of which functional response works best by manipulating natural populations? While this approach probably still retains untapped potential, it also suffers from a number of problems. Changing one parameter at a time, which is difficult enough to accomplish in the laboratory, is a practical impossiblity in natural systems; perhaps this is why enrichment experiments in the field continue to produce equivocal trophic cascade results. Intensive theoretical work suggests that any number of factors that increase the complexity of the system (e.g. spatial heterogeneity, presence of multiple predator and/or prey species) remove the Paradox of Enrichment. Because the overall goal of my work is to determine the nature of predation itself, introducing the complexity that typifies most natural systems is problematic. Work within microbial microcosms has a rich history of contributing to our ecological understanding (Jessup et al. 2004).

Conclusion:

Population ecologists continue to struggle with the question of which functional response to incorporate into their predator-prey models. The extensive and inconclusive nature of theoretical debates, paired with the inadequacy of natural observational data to provide unequivocal results, suggests that simple empirical work is needed to mediate the controversy (Abrams and Ginzburg 2000). Complexity is at the heart of the issue. It has become increasingly clear that some form of predator dependence emerges as systems become more complex. The question remains, however, whether this predator dependence is truly an emergent property, or actually a fundamental property of even the most simple predator-prey systems. If predator dependence is an emergent property, we need to know at what level of complexity it emerges. By considering those parameters that actually provide a contrast between the *limit myths*, and by examining both qualitative and quantitative outcomes, my work has the potential to uncover the nature of predation in the least complex system imaginable.

Tables

Table 1. Alternative Forms of the Functional Response

Original Publication	Abbreviation Used	Functional Response
Lotka 1925, Volterra 1926	**LV**	$f(\cdot) = aN$
Holling 1959	**H2**	$f(\cdot) = aN / (1+ahN)$
Hassell-Varley 1969	***n/a***	$f(\cdot) = \alpha_m(N/P^m)$
"Hassell-Varley-Holling"	**HVH**	$f(\cdot) = \alpha_m(N/P^m) / [1+(\alpha_m h N/P^m)]$
Beddington-DeAngelis 1975	**BD**	$f(\cdot) = aN / [1+ ahN +ahiP]$
Arditi-Ginzburg 1989	**AG**	$f(\cdot) = \alpha_m(N/P) / [1+(\alpha_m h N/P)]$

Table 2. Comparison of prey- and ratio-dependent outcomes based on decreases in fundamental parameters.

     The only parameter change that results in opposite qualitative predictions is that of r, the per capita growth rate of the prey population. Note that the predicted prey-dependent outcome assumes that r and K are linked. *Abbreviations used:* **DE** = 'dual extinction', **CoEx** = 'coexistence', **PE** = 'predator extinction/prey escape'.

Change in Parameter	Prey-Dependent Outcome	Ratio-Dependent Outcome
$a/\alpha \downarrow$	**DE → CoEx → PE**	**DE → PE**; or **DE → CoEx**
$r \downarrow$	**DE → CoEx;** or **PE → CoEx***	**CoEx → DE**
$K \downarrow$	**DE → CoEx → PE**; or **PE → CoEx**	*none*
$d \downarrow$	**PE → CoEx → DE**	**PE → CoEx → DE**
$e \downarrow$	**DE → CoEx → PE**	**DE → CoEx → PE**
$h \downarrow$	**PE → CoEx → DE**	**PE → CoEx → DE**

* unlike other parameter shifts, changing *r* in the prey-dependent system does not cause the system to cross a bifurcation; rather, reducing *r* only shrinks the size of the limit cycle, which is interpreted as reducing the probability of extinction.

Table 3. The results of Veilleux (1979).

Increases in food concentration led directly to changes in the parameters r, a, and e. These parameter changes moved the system from Dual Extinction to Coexistence to Predator Extinction.

Parameter Changes			Food Concentration	Number of Runs	System Outcome
high r	high a	high e	1.80	17	Dual Extinction
↓	↓	↓	1.58	9	Dual Extinction (6x) and Predator Extinction (3x)
			1.35	18	Predator Extinction
			0.68 to 1.13	50	Coexistence
low r	low a	low e	0.18 to 0.45	20	Predator Extinction

Figures

Figure 1. Expected and actual outcomes of Gause's experiment with *Didinium* and *Paramecium*.

Based on the Lotka-Volterra equations, Gause expected to find that *Didinium* and *Paramecium* coexist indefinitely **(a)**. Gause's actual results demonstrate a "Gause loop", consistent extinction of the prey followed closely by predator extinction **(b)**.
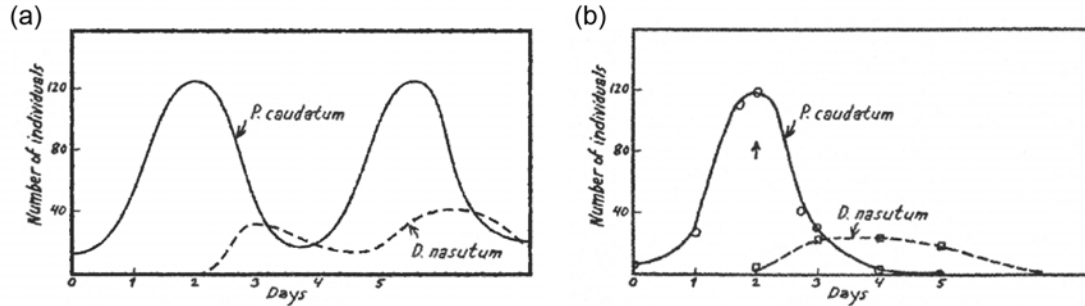
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Chapter 2

Paradoxes or theoretical failures? The jury is still out.

Christopher X J. Jensen and Lev R. Ginzburg

Context:

One of the hallmark behaviors of the historically-standard prey-dependent functional response is the paradox of enrichment. This destabilization caused by prey growth conditions that are "too good" has become a standard lesson in ecological education, but enjoys almost no observational or experimental support. The standard theoretical approach to the biological absence of the paradox of enrichment is to build a more complex model on the foundation of the traditional predator-prey depiction. We explore the possibility that this foundation is itself the source of incompatibility with data, and argue for further consideration of predator-dependent models that eliminate the paradox of enrichment at the simple level of functional response.

Introduction

Observations that confirm intuition – that are consistent with presumptions – rarely attract attention. But when observations defy intuition in a surprising manner, they attract scientific interest. Counterintuitive observations are labeled "paradoxes" and the pursuit of their resolution has been a key source of scientific innovation.

The classic paradox emerges when empirical observations are at odds with a stated and accepted theory. If observations are reliable, such empirical paradoxes must be resolved by modifying the theory so that it is consistent with evidence.

In the absence of complete or appropriate data, theory is often employed to yield understanding. Usually, such theories are self-fulfilling prophecies: a model is constructed based on logical assumptions, and the model outputs behavior that confirms intuition. Occasionally, theoretical predictions prove to be inconsistent with intuition. Such theoretical paradoxes can only be resolved by comparison to appropriate data.

We contend that paradoxes of both the theoretical and empirical varieties are important. The comparison of intuition with theory and theory with empirical observations yields progress in understanding and suggests a logical cycle that has been repeated throughout history: intuition leads to a theory and that theory is compared with empirical observations. When the properties of a theory contradict intuition, empirical observations must be made to resolve the paradox. When empirical observations contradict prevailing intuition or a prevailing theory (or both), intuition is reconfigured. This cyclic process continually modifies intuition until intuition, theory, and empirical observations are harmonized.

Theoretical and empirical paradoxes should not remain paradoxical. Once a theory proves consistent with empirical observations, intuition evolves and no longer remains in conflict with observations. The paradox disappears once intuition, theory, and empirical observations are made mutually consistent.

We focus on two theoretical paradoxes in ecology that have remained paradoxical for a substantial period of time: the *paradox of enrichment* and the *enrichment response*. Both make predictions that contradict an intuitive sense of how ecosystems should behave and both have therefore attracted significant attention. Neither, however, has been appropriately assessed in light of available data. It is for this reason that these paradoxes, and the theory that underlies them, have remained unquestioned for several decades.

The paradox of enrichment

This paradox, based on what has become a standard textbook generalization of the Lotka-Volterra-derived model of MacArthur and Rosenzweig (1963), states that when the prey carrying capacity of a stable predator-prey system is increased sufficiently, the system begins to cycle (Rosenzweig 1971). In fact, mathematically, the emerging structure is a limit cycle. As prey carrying capacity is increased further, this cycle brings one or both populations closer and closer to zero. As conventionally interpreted, when the limit cycle is sufficiently

large, one of the species can go extinct. If the prey species goes, predator extinction will follow; if the predator species goes, a trophic level is lost. Cited over 450 times, Rosenzweig (1971) has captured the imagination of countless ecologists and is upheld as a classic example of an ecological paradox.

While we find Rosenzweig's (1971) theoretical work innovative and important, the manner in which it has been handled since publication by the field of ecology is somewhat unnerving. Notwithstanding a few notable exceptions (Arditi and Berryman 1991), the paradox of enrichment has been widely accepted based on very little empirical evidence. For reasons we find difficult to comprehend, the paradox of enrichment quickly achieved the status of an ecological axiom, an assumed property that can only be overturned by proof that it does not exist. Without substantial comparison to empirical observations, the paradoxical theory *became accepted intuition.*

In particular, the community of theoretical ecologists has enthusiastically embraced the paradox of enrichment. This unjustified enthusiasm is epitomized by the manner in which the word "paradox" has come to be interpreted in the phrase "paradox of enrichment". For Rosenzweig, the "paradox" was that enrichment – intuitively perceived as beneficial – had the potential to destabilize an ecosystem. In more recent use, ecologists speak of "resolving" or finding "a solution to" the paradox of enrichment (Jansen 1995, Genkai-Kato and Yamamura 1999, Petrovskii et al. 2004, Vos et al. 2004); the "paradox" is that actual systems do not behave as accepted models predict they should. Even authors who are aware of this transformed meaning are forced to invent new terminology to precisely refer to the phenomena: our favorite is the "enigma known as Rosenzweig's paradox of enrichment" (Petrovskii et al. 2004).

The paradox of enrichment continues to exert a strong influence on theoretical work (Yodzis and Innes 1992, Abrams 1993, Huisman and DeBoer 1997, Boer et al. 2001, Murdoch et al. 2003) and any student of ecology will have to search heartily for a textbook that does not present the paradox of enrichment as biological fact. We have reviewed the literature on experimental attempts to demonstrate the paradox of enrichment and found a disturbingly small number of studies in favor of the phenomenon. The majority of the empirical work that is suggestive of the paradox of enrichment has been done within the last decade; at least two decades passed before this theoretical prediction was exposed to experimental testing. We contend that the need for experimental verification of the phenomenon is far from exhausted.

What evidence is there for the paradox of enrichment? Several commonly-misinterpreted examples, as well as several experiments that begin to answer the question "does the paradox of enrichment exist?", merit discussion.

A commonly suggested example of the paradox of enrichment is the process of lake eutrophication. Enrichment of aquatic systems does appear to increase the carrying capacity of producers, producing a bloom that covers the lake. This bloom deprives the lake bottom of light, increasing aerobic decomposition and lowering the oxygen content of the water. It is this reduction

in dissolved oxygen – not trophic destabilization – that can cause the subsequent loss of top predators.

While eutrophication does involve enrichment, its results are not paradoxical. If oxygen availability limits growth, any change that further reduces oxygen availability is expected to destabilize the system, particularly at trophic levels occupied by consumers. Clearly the only connection to consumption present in the phenomenon of eutrophication is the fact that consumers require oxygen. Other than this trivial similarity, eutrophication bears no resemblance to the predator-prey phenomenon described by Rosenzweig. We are puzzled by the fact that many ecologists still believe that eutrophication and the paradox of enrichment are connected. Enriched ecosystems generally display reduced complexity, but we have yet to encounter a case where this simplicity was the result of trophic level destabilization of the kind predicted by Rosenzweig (1971).

Since Rosenzweig proposed that increasing the carrying capacity of a prey species could destabilize a predator-prey pair, a number of experiments have tested this prediction. The first empirical work was performed in the *Didinium-Paramecium* system by Luckinbill (1973) and Veilleux (1979). Both authors showed that the system of Gause (1934) could be modified to produce coexistence of predator and prey. They found that two modifications to the system were required to prevent the predator from consuming all of the prey: (i) the interaction rate of predator and prey within the system had to be reduced by the addition of methyl cellulose, which serves to thicken the medium and presumably reduces the capture efficiency of the predator; and (ii) the availability of prey food (i.e. enrichment) had to be reduced. This second condition is commonly misinterpreted as clear evidence for the paradox of enrichment, as it appears at first glance to be the 'paradox of enrichment in reverse'— the system goes from instability to stability when nutritional inputs are reduced (Harrison 1995).

More recently, an experiment performed in a *Rotifer-Algae* system by Fussman et al. (2000) showed that predator extinction resulted from enrichment. Like the Luckinbill and Veilleux experiments, the results of this experiment showed that reducing nutrient input can bring the system from a region of consistent predator extinction to a region of coexistence; unlike these much earlier experiments, the work of Fussman et al. did not demonstrate a region of consistent dual extinction. Nevertheless, these experiments do make a coarse argument in favor of the paradox of enrichment; increasing nutrient inputs does seem to destabilize the system.

However, *how* this increase in available nutrients destabilizes the system remains unclear. During his experiments, Veilleux showed that adding nutrients to the system not only increased the carrying capacity and growth rate of the prey but also increased the conversion efficiency and capture efficiency of the predator. With so many parameters potentially moving in response to a single manipulation, a variety of competing models (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989) can lay claim to the results of Luckinbill, Veilleux, and Fussman et al., and there is no reason to

assume that the Rosenzweig model should be considered the superior explanation.

We find it remarkable that extinction has been shown in only three enrichment experiments. In lieu of demonstrating the extinction events predicted by the paradox of enrichment, many researchers have used increasing amplitude of oscillation as a proxy for actual irreversible destabilization. We find this substitution unsatisfactory, because the notable prediction of the paradox of enrichment is the loss of one or more trophic levels, not changes in the oscillation pattern of the system. Marshall and Peters (1989) show that the magnitude of oscillations is greater in eutrophic than oligotrophic lakes, but provide no evidence that greater oscillations can or will translate to extinction of consumers. In order for evidence of the kind presented by Marshall and Peters to be convincing, it would have to be shown that further eutrophication has the potential to lead to *destabilizing* oscillations (i.e. extinction). Ethical and logistical concerns surrounding artificial eutrophication place understandable limitations on manipulations of this sort in natural systems; however, the laboratory – which is free from such limitations – ought to be the ideal environment in which to produce irreversible destabilization. Unfortunately, laboratory microcosm work (Bohannan and Lenski 1997, Kaunzinger and Morin 1998, McCauley et al. 1999) also conflates increased amplitude of oscillation with extinction. We wonder why such studies fail to show that massive nutrient inputs do not produce the extinction predicted by the paradox of enrichment.

When ecologists have looked for evidence for the paradox of enrichment in natural and laboratory systems, they often find none (Walters et al. 1987, McCauley et al. 1988, Watson and McCauley 1988, Leibold 1989, McCauley and Murdoch 1990, Watson et al. 1992, Persson et al. 1993, Mazumder 1994). Obviously negative results receive less attention than positive ones, but we are surprised by just how minimal the impact of these results has been.

Why do researchers fail to observe this paradox in most experimental or any natural systems? If it is assumed that the paradox of enrichment *could* exist, the logical conclusion is that most of the experimental or natural systems in which it has been sought are not sufficiently simple. In other words, experimental conditions did not meet the theoretical assumptions and this is why experiments failed to demonstrate the paradox. Alternatively, if it is assumed that the paradox of enrichment *does not* exist, the logical conclusion is that new models of trophic interactions – ones that do not produce paradoxical destabilization under enrichment – must be sought.

The vast amount of theoretical effort in this area has been directed at the former explanation, producing a rich body of work showing that the paradox of enrichment can in theory be eliminated by any number of complicating mechanisms. The list of these potential mechanisms is long and continues to grow, as it has been shown that the paradox can be effectively eliminated by expanding the model to include: edible/inedible algae (Phillips 1974, Leibold 1989, Kretzschmar et al. 1993, Genkai-Kato and Yamamura 1999); density-dependence of the predator death rate parameter (Gatto 1991); refuges and

immigration (Abrams and Roth 1994); vulnerable/invulnerable prey (Abrams and Walters 1996); spatial heterogeneity (Nisbet et al. 1998, Petrovskii et al. 2004); life-history traits that allow consumers to buffer the effects of low prey densities (McCauley et al. 1999); and inducible defenses (Vos et al. 2004).

Generally, these theoretical explanations for the absence of the paradox of enrichment remain untested; some may even be untestable. Those few attempts to empirically confirm some of these increased complexity hypotheses have been unsuccessful (Murdoch et al. 1998), but faith in the paradox of enrichment persists. Theorists continue to provide models built upon MacArthur-Rosenzweig theory, confident that the proper complicating factors can be identified so that the conspicuous absence of the paradox of enrichment can be satisfactorily explained.

Models that incorporate various levels of additional complexity are difficult to falsify. With this additional complexity (and the associated addition of parameters) the danger of overfitting increases and authors risk drawing invalid conclusions (Ginzburg and Jensen 2004). Algae species do differ in their edibility, some prey may be more vulnerable than others, and spatial heterogeneity and/or refuges are bound to be present in most natural systems. But we wonder: is there no system, in nature or the laboratory, which is sufficiently free from all of these possible complicating factors? Is the lack of evidence for the paradox of enrichment an indication that – despite an underlying Lotka-Volterra mechanism – no system will ever abide by the assumptions of MacArthur-Rosenzweig dynamics?

Why have ecologists stood so loyally beside this as-yet-unsubstantiated theory? One explanation returns to the question of intuition. Perhaps, contrary to the implied meaning of Rosenzweig's nomenclature, the idea that enriched systems contain fewer trophic levels *is* intuitive. After all, many enriched systems are exceptionally simple, containing relatively few trophic links. Examples of such ecosystems can be found in both aquatic and terrestrial systems, including the aforementioned eutrophic lakes. We do not deny that such a trend exists – we simply do not find credible evidence that Rosenzweig's paradox of enrichment explains this enriched/simple configuration.

The enrichment response

The term "trophic cascade" is widely used by an array of ecologists and its meaning varies with context (Ponsard et al. 2000). We will be concerned with only one meaning, the response of the trophic chain to enrichment at the bottom; we refer to this phenomenon as the "enrichment response". As was the case with Rosenzweig's paradox of enrichment paper, a particular theoretical paper has considerably influenced ecological thought about enrichment responses; Oksanen et al. (1981), which expanded upon early work by Fretwell (1977), has been cited well over 500 times. We focus on two theoretical predictions made by Oksanen et al.: (i) noticeable additions in the number of trophic levels as productivity increases; and (ii) a curious behavior of the four-level system (**Figure**

1a). We believe that both phenomena emerging from Oksanen et al. theory contradict available data.

First, we find the idea that the number of trophic levels is a function of overall enrichment problematic. As proposed by Oksanen et al. (1981), new trophic levels are added and producer populations equilibrate at new abundances as enrichment at the bottom increases. At very low levels of enrichment, no consumer exists. As enrichment increases slightly, a primary consumer species can be sustained, but at abundances too low to support a secondary consumer species. Further trophic levels are added only as ecosystem enrichment occurs. While this unproven hypothesis seems logically possible, it is at odds with available data: a large-scale review of a wide variety of ecosystems suggests that no relationship exists between primary productivity and the number of trophic levels (Cohen et al. 1990). For us, this observed pattern is the true paradox: why should the number of trophic levels be independent of primary productivity? This paradox has yet to be resolved.

A second paradoxical behavior emerges when the effects of enrichment on the equilibrial abundance of each trophic level are considered. According to conventional theory, enrichment can cause the abundance of particular trophic levels to either increase, remain constant, or decrease. The four-level system yields the greatest insight into this behavior. As shown in **Figure 1a**, enrichment of a four-level system causes the top (secondary) carnivore to increase in abundance, while the primary carnivore remains fixed in abundance. Herbivores increase, while producers *decrease* in abundance. No intuitive explanation can account for this strange pattern. Not surprisingly, most discussions of this phenomenon are limited to the more palatable three-level system, which does not suffer from this prediction of decreasing abundance with increasing enrichment.

Oksanen et al. (1981) discuss a single purported example of a four-trophic-level system that is consistent with their theoretical predictions. The example, from a study performed by Arruda (1979), appears to show the expected results for the four-trophic-level system shown in **Figure 1a**. For several reasons, we remain unconvinced by these results as they are presented. First, there appears to be an error in the transfer of results from Arruda (**Figure 1b**) to Oksanen et al. (**Figure 1c**); in the third trophic level (primary carnivore), the data points appear to shift, changing a clear decrease in equilibrial abundance with increased productivity to an apparent constant abundance. The error changes the meaning of the results: instead of showing the constancy in equilibrial abundance, Arruda's results actually display a significant decrease in abundance in response to enrichment. Such a result cannot be explained any currently popular theory of predator-prey interaction.

Another concern arises when the significance of the curve fits are considered. All but one of the theoretically-derived curves of Oksanen et al. require at least three parameters to depict mathematically (one for the breakpoint and two for the linear trend). These curves are overlaid on the five Arruda data points (**Figure 1c**), giving the impression that data are consistent with

predictions. This impression is false, as it is impossible to reliably fit a three-parameter model to only five data points (Ginzburg and Jensen 2004).

A final worry concerns replication: if Arruda's results truly demonstrate that a four-trophic-level system could be consistent with the theoretical construct of Oksanen et al., we would expect other researchers to attempt to replicate them using a larger-scale approach more likely to yield statistically significant results. We know of no such replication in over 20 years and therefore question whether Arruda's apparent results resulted from anything more than chance.

In the absence of field data we turn to the results of laboratory microcosm work, much of which claims to produce results consistent with the predictions of Oksanen et al. Two recent examples are by Bohannan and Lenski (1997) and Kaunzinger and Morin (1998). As shown in **Figure 1a**, the theoretical predictions of Oksanen et al. suggest that in a simple two-trophic-level system, enrichment should cause no change in prey abundance and an increase in the predator population. What the papers by Bohannan and Lenski and Kaunzinger and Morin show are significant increases in both predator and prey abundance, a result that is inconsistent with the Oksanen et al. predictions. Such results are more consistent with predator-dependent models (Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989), which predict that in response to enrichment all trophic levels will increase in abundance with differing slopes (the highest levels increase the most, while successively lower levels respond with smaller and smaller increases) (Akçakaya et al. 1995). The smaller-yet-significant increases in prey abundance shown by these experiments demonstrate that the Oksanen et al. theory is at odds with biological observations.

The most compelling empirical argument in favor of Oksanen et al. theory comes from the second experiment of Kaunzinger and Morin (1998). In this three-trophic-level system, they showed that the top predator was consistently excluded from the microcosms with the lowest nutrient inputs. To our knowledge, this experiment remains the only evidence for thus prediction of Oksanen et al. While we find these results interesting, we worry that they could arise from a rather large departure from the assumptions of standard predator-prey theory. Like all batch culture systems, the microcosms of Kaunzinger and Morin violate the assumption of continuous nutrient input. We recognize the practical concerns that govern such a violation (and find little solace in the more complex alternative: the continuous system of the chemostat) but we fear that the magnitude of this violation – rather than an underlying mechanism consistent with MacArthur-Rosenzweig theory – may have produced the extinction of the top predator. The microcosms were refreshed every four days; given that in this four day span one can get nearly fifty generations of the bacteria that occupy the producer level, we are concerned that starvation between nutrient pulses may be the reason for the elimination of the top predator from the microcosms with the lowest nutrient inputs. The approach of Kaunzinger and Morin was ingenious; we would like to see it replicated with a more frequent (i.e. closer to continuous) input of nutrients.

The literature on top predator removal experiments has generated considerable confusion. A series of experiments has shown consistently that the abundances of lower trophic levels can be dramatically affected by the removal or addition of a top predator. Often, the results of these removal experiments look superficially like the predicted results of enrichment described by Oksanen et al. For example, Shapiro and Wright (1984) showed that the elimination of planktivorous fish resulted in a reduction in the steady-state abundance of phytoplankton. Viewed without consideration of causality, this transition from a system with three trophic levels to a system with only two resembles the predicted difference between the three- and two-level systems shown in **Figure 1a**. When causality is considered, the resemblance is rendered meaningless: the fact that predator removal produces results that are similar to those predicted under enrichment does not show that these predictions are confirmed in actual trophic systems. When it comes to the results of predator removal experiments, many other models of predation (including the ratio-dependent extreme) make predictions identical to those of the traditional prey-dependent form (H.R. Akcakaya, pers. comm.). Because model predictions in this area do not differ, these experiments do not allow us to distinguish between various predation models. While we do not question the importance of these studies for understanding the effect of predators on lower trophic levels (so-called "top-down" effects), we hasten to point out that experiments of this kind have no relevance to the question of whether or not enrichment responses follow the pattern predicted by Oksanen et al..

Evidence from a variety of ecosystems suggests that comparable communities, varying in nutrient input level, differ only in overall abundances at each trophic level and show none of the paradoxical behaviors predicted by accepted theory (Ginzburg and Akçakaya 1992, Akçakaya et al. 1995). Both intuition and evidence suggest that enrichment causes increases in the overall abundance of all trophic levels.

Origins of the paradox: how the field got this far astray

Both the paradox of enrichment and the enrichment response emerge as the result of the same assumption about consumer-resource systems. The vertical predator isocline, a consequence of linking trophic levels with a prey-dependent (i.e. Lotka-Volterra) functional response, is the theoretical construction which produces these enrichment phenomena. Under prey dependence, the functional response of the predator depends on the abundance of prey, not the abundance of consumers. This assumption has been questioned (Abrams and Ginzburg 2000) but remains a prominent component of most predator-prey models. Predator dependence seems to be more of a common case than an exception (Arditi and Akçakaya 1990, Jost and Ellner 2000, Jost and Arditi 2001, Skalski and Gilliam 2001, Vucetich et al. 2002, Schenk et al. 2005). Under predator-dependent models, such as that of Beddington-DeAngelis (Beddington 1975, DeAngelis et al. 1975), as interference increases so too does the carrying capacity at which destabilization occurs (Huisman and DeBoer

1997). Ratio dependence, an extreme form of predator dependence, emerges at the opposite end of the spectrum from prey dependence (Arditi and Ginzburg 1989). At this opposite extreme, the paradox of enrichment is theoretically absent (Arditi and Berryman 1991).

So when we ask "why have these enrichment paradoxes remained unquestioned for so long?" we are really asking the question: "why hasn't the prey-dependent axiom been widely questioned?". The paradox of enrichment and the enrichment response both emerge because of the assumption of a purely prey-dependent functional response. For many authors (Abrams 1994, King and Shaffer 2001, Murdoch et al. 2003), this construction is beyond question – prey dependence is the only logical form and need not be confirmed by empirical inquiry.

The fallacy of instantism

The unquestioned acceptance of prey-dependence is often justified by a simple but dangerous assumption about the nature of the differential equations employed in modeling predator-prey interactions. When a population is modeled by considering its change over time, dN/dt, exactly what dt means needs to be defined. Of course by using differential equations, mathematically it is assumed that change occurs continuously and instantaneously and therefore dt represents an infinitely small time step. The question is: should mathematical constructions be taken literally? In using instantaneous equations, should theorists be constrained to considering only processes which transpire in an instant? Many theorists answer "yes" to these questions and constrain their instantaneous models to capturing instantaneous phenomena; we call such mathematical formalism *instantism* (Ginzburg and Colyvan 2004).

Instantism has been used to argue that only the prey-dependent functional response can be logically nested within predation models. As the argument goes, in an infinitely small time step, predators cannot interfere with each other: they can only respond to the instantaneous abundance of prey. Interference is a factor that only emerges when times steps larger than an instant are considered. Murdoch et al. (2003) effectively summarize the instantist argument in favor of prey-dependence, noting: "… ratio dependence sometimes emerges in a natural way in a discrete-time framework… We do not believe that it makes ecological sense, however, to insert ratio-dependent functional responses into continuous time models which, by their nature, describe instantaneous rates… (p. 103)." Under this instantist view, the only natural functional response to use in continuous-time models is the prey-dependent form. We question this assertion and point out that predator interference has been successfully incorporated into differential equations that model only instantaneous interaction (Beddington 1975, DeAngelis et al. 1975).

We also feel that the instantist view is fallacious. We can conceive of few if any organismal processes that literally occur in instantaneous time. Organismal behaviors are by and large discrete in nature and for this reason differential equations cannot be considered or used as literal depictions of biological

33

processes. At best, differential equations are apt metaphors and so any consideration of which metaphor (time scale) to employ should be based on comparison of their relative utility, not on their conformation to instantist orthodoxy.

It also should be noted that the instantists are not fully consistent. While one might legitimately argue that consumption occurs instantaneously, it is much more difficult to justify literally the instantaneous conversion of food into offspring (if for no other reason than that reproduction is commonly a discrete process). Given that consumption is instantaneous and reproduction is discrete, the correct mathematical formalism should be an integro-difference equation. Such equations may be more 'realistic' but this realism comes at great cost: integro-difference equations are difficult to interpret analytically. That theorists who uphold the prey-dependent axiom usually do not use these cumbersome equations calls into question the consistency and validity of the instantist argument.

Literalism in using mathematical constructs

Instantism, as described above, is a special case of a larger problem which can be termed *literalism* in applying mathematical constructs to biology. A good example is partitioning of actual biological species into discrete and continuous categories, an approach endorsed by Murdoch et al. (2003). Discrete species are, in their judgment, those that reproduce every spring, for instance. Whether these species are iteroparous or semelparous does not matter: as long as reproduction is periodic, they are discrete. Other species, like *E. coli*, humans, or *Daphnia* are continuous: they reproduce at any time without a specified frequency. The authors consider differential equations the correct abstraction for continuous species and difference equations the correct abstraction for discrete species.

We find such a literalist projection of the mathematical construct into biology very restrictive and unreasonable. Depending on the time scale appropriate to the particular case, the same species can be described by both constructs. Darwinian natural selection is a prime example. It does not matter whether a geometric series (discrete) or exponential growth (continuous) is invoked to deduce the idea of natural selection from Malthusian law. The law is just a caricature that captures the necessary properties of the process in either form.

To use an artistic metaphor, we feel that literalist theorists are attempting something akin to photorealism. If data were abundant and perfect, it might be reasonable to impose a literalist aesthetic and require that all 'images' of ecological phenomena be photorealistic. Unfortunately, because data are so limited and often imperfect, information adequate to 'paint' photorealistic pictures in ecology is not available. Imposing a strict literalist constraint only serves to guarantee that the resulting image will be distorted and nonsensical; in essence, a high-resolution image must be reconstructed from a very small subset of data 'pixels'. Such an approach will only work if: (i) the domain of the image that one

aims to depict is very small (i.e. a specific, non-generalizable model is produced); or (ii) there is data sufficient to 'paint' a complete image. It seems clear to us that the former case is the best portrayal that photorealist theorists can hope for (considering the limited nature of existing data) and that such portrayals do little to advance the field.

We consider good theoretical work to be akin to impressionism. Rather than interpreting our mathematical constructions as literal depictions, we see them as metaphors for more complex underlying details. It is for this reason that we allow our models to relax some of the literalist constraints in pursuit of a more valuable albeit imperfect impression. For instance, we utilize differential equations but allow for mechanisms such as particular forms of predator dependence that emerge most prominently in time steps that are larger than instantaneous. Certainly, inclusion of such mechanisms violates literalist rules, but the resulting metaphors often work (Arditi and Akçakaya 1990, Akçakaya 1992, Ginzburg and Akçakaya 1992, Akçakaya et al. 1995, Jost and Ellner 2000, Ponsard et al. 2000, Jost and Arditi 2001, Skalski and Gilliam 2001, Vucetich et al. 2002, Schenk et al. 2005). What results is an image that is less sharp but more meaningful. It is our judgment that this approach will achieve more with less – theorists will construct more valuable pictures out of the limited available data.

While we understand why many theorists impose a literalist constraint (they honestly believe that the resulting models are more accurate that way), we call for models that are far too rough to depend on such delicate detail. Taken to its logical extreme, literalist thinking often requires that models portray levels of detail which far outweigh the complexity of the simple questions that are asked (Ginzburg and Jensen 2004). In relaxing literalist constraints, we hope to make theoretical work more practical and tractable – the goal is to produce rough but meaningful models in a world constrained by limited data. In this sense, we see the metaphorical approach to modeling as being far more realistic than the literalist alternative.

Intuition, evidence, and math

Theoretical paradoxes can only provide a starting point for further inquiry. While it may be interesting when verbal or mathematical models suggest paradoxical behaviors, to assess their validity these models must be exposed to empirical tests. **Figure 2** suggests two out of many possible paths that such an inquiry might take. Once relevant data can be brought to bear on a theoretical paradox, data re-informs either intuition (**Figure 2(b)(c)**), theory (**Figure 2(d)(e)**), or both. When relevant data are absent, the paradox remains. Neither intuition nor theory can be assumed correct when data is absent or incomplete.

The prevailing acceptance of enrichment paradoxes violates this tenet of empirical science. Data in favor of existing theory is either weak or completely absent, and in some cases data are in agreement with alternative theories (Akçakaya et al. 1995). For some reason, a particular theory has been accepted without empirical confirmation, leading to unjustified alteration of intuition on a

massive scale. In what seems to us a bizarre turn of events, an entire field has come to embrace a theory based not on data but on the beauty of theory itself.

In this sense, perhaps the work of theorists like Rosenzweig and Oksanen et al. is too good. The simple mathematical elegance of their theoretical discoveries, mistakenly associated with unrelated phenomena, has lulled many ecologists into complacent acceptance. Mathematical discoveries were confused with empirical discoveries. In order to return to a more regular path of inquiry, these enrichment phenomena and the underlying prey-dependent functional response that drives them must be subjected to proper empirical testing.

The potential hazards of blind faith

Continuing unwarranted acceptance of the paradox of enrichment and the enrichment response phenomena presents ecology with problems beyond the theoretical. Applied ecologists, taking cues from colleagues who provide basic theory, include enrichment paradoxes in their models (DeFeo and Rinaldi 1997, Choi and Patten 2001). If these enrichment phenomena are as unsubstantiated as they appear to be, many of the management strategies based on them will fail. As the demand for more applied use of theory increases, selection against incorrect theories will increase (Ginzburg and Jensen 2004). However, this selection process has intrinsic costs: every poorly-informed strategy has the potential to result in the mismanagement of an ecological system. The costs associated with such errors on an applied scale are much higher than those associated with theoretical reconsideration.

One need only look at the number of papers explaining away the empirical absence of these enrichment phenomena to begin to realize how much effort may have been wasted on upholding these paradoxes. Even though the occasional pursuit of dead-ends is a vital part of scientific exploration, we suggest that the benefits associated with upholding these paradoxes may have been exhausted.

Acknowledgements

Figures

Figure 1. The enrichment response. (a) Response of trophic levels to enrichment in the MacArthur-Rosenzweig predator-prey system. As enrichment occurs, primary productivity increases; however, abundances of producers, herbivores, and/or carnivores do not always respond to productivity (after Arditi and Ginzburg 1989). (b) Arruda (1979) explored the relationship between productivity and equilibrial abundance but found significance only in the third trophic level (labeled "C2"). (c) The same data, redrawn in Oksanen et al. (1981), suggests that the theoretically-derived predictions presented in the paper are consistent with Arruda's data, despite the non-significant nature of any attempt to fit a three-parameter curve to five data points.

(a)

Number of Trophic Levels	Response of each trophic level to enrichment			
	1st "Producer"	2nd "Herbivore"	3rd "Primary Carnivore"	4th "Secondary Carnivore"
2	constant	**increase**		
3	**increase**	constant	**increase**	
4	*decrease*	**increase**	constant	**increase**

(b)

(c)

37
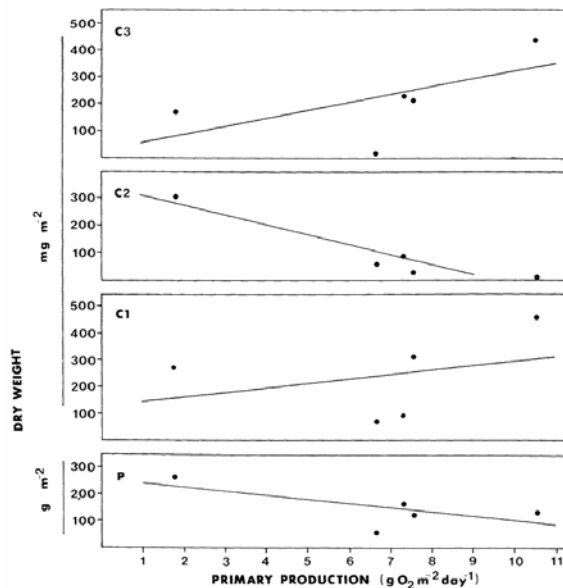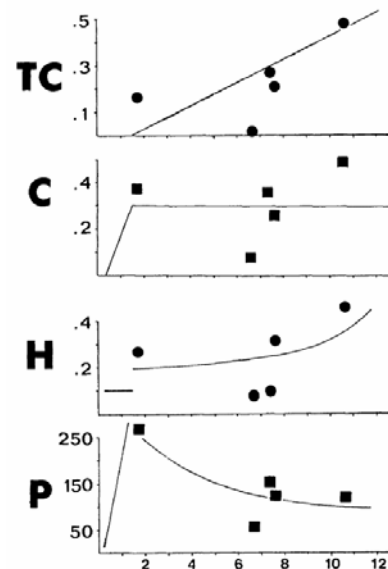
Figure 2. Theoretical paradoxes and their resolution by comparison with data (matching shades signify agreement; mismatching shades signify disagreement). **(a)** A paradox emerges when intuition and theoretical predictions disagree and can only be resolved when the theory is compared with appropriate data. **(b)** In one scenario, data agrees with theory. **(c)** When theory and data are in agreement, intuition is informed by data and thereby altered, making intuition, theory, and available data consistent. **(d)** In the alternative scenario, data disagrees with theory. **(e)** If theory is inconsistent with data, theory is informed by data and thereby altered until a theory that is suitably agreeable with data can be identified. If this theory is consistent with previous intuition, intuition need not be altered.
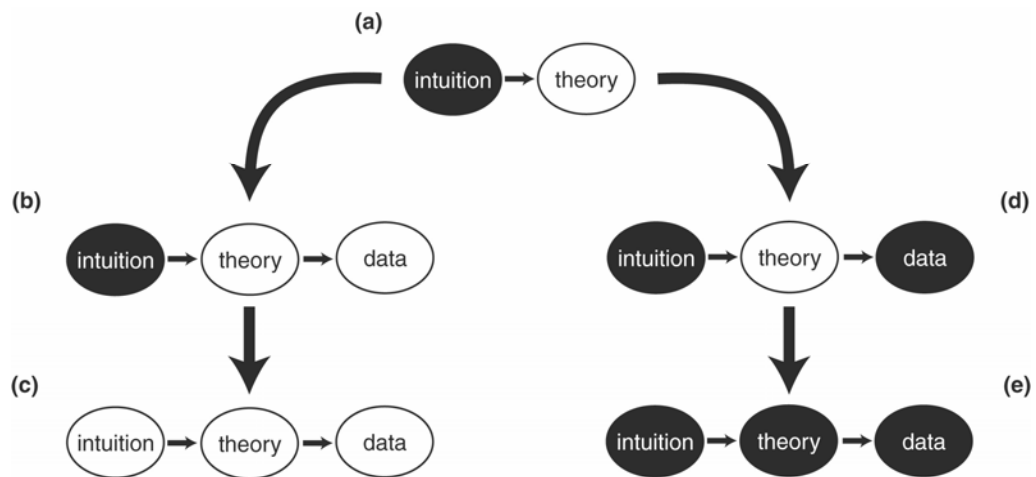
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Chapter 3

The Interdependence of r and K

Christopher X J. Jensen and Alex Luryi

Context:

A key difference between traditional prey-dependent functional responses and predator-dependent alternatives lies in predicted model responses to changes in the prey growth rate (r) and carrying capacity (K). We combine theoretical analysis with experimental manipulations of *Paramecium* to show that r and K can be simultaneously manipulated through a simple filtration scheme.

Introduction

The logistic equation has been a fundamental component of population growth equations for well over a century (Berryman 1992). Although it is a standard assumption of countless population models, its use is not without controversy (Berryman 1992a, Ginzburg 1992, Mackenzie 1992, Olson 1992, Watkinson 1992, Young 1992, Getz 1993, Ginzburg 1993, Taneyhill 1993, Turchin 1993). The logistic has survived in part because it provides the simplest imaginable depiction of a commonly observed phenomenon in natural systems: as any positively growing population increases, competition for resources will inevitably halt growth at some population size. We call this critical population size the carrying capacity (K) and assume that while populations at very low densities can grow at their maximum growth rate (r), the actual realized growth rate of a resource-limited population is always lower than this maximum.

Originally, the logistic equation representing prey growth was written by Pierre Verhulst (1838) as follows:

$$\frac{dN}{dt} = rN - \gamma N^2 \tag{1}$$

Under this formulation of the logistic, two parameters determine the growth of prey: (i) the per capita growth rate of prey in absence of limitation (r); and (ii) the degree of intraspecific interference between prey individuals (γ). Raymond Pearl and LJ Reed (1920) modified this version of the logistic, providing a new version with more immediate biological meaning:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) \tag{2}$$

This equation is now recognized as "the" logistic. The parameter K is interpreted as the carrying capacity of the system and is expressed as an abundance of individuals. The modern assumption is that K is related to the delivery rate of some limiting resource, with increases in this delivery rate (i.e. "enrichment") leading to increases in the number of individuals that can be stably supported by the system. Whether changes in K also lead to changes in r depends on whether or not we assume that the level of intraspecific competition (γ) is dependent on the rate at which limiting nutrients are delivered to the system.

While the inclusion of K makes the behavior of the logistic easier to understand, it has also been the source of confusion resulting from the fact that r and K are not independent of each other. In removing γ from the equation, the modern logistic gives the false impression that intraspecific interference is no longer a critical property of the system. Yet as shown below, γ is embedded in the derived parameter K:

$$\frac{dN}{dt} = rN - \gamma N^2 = rN\left(1 - \frac{N}{K}\right) \tag{3a}$$

$$rN - \gamma N^2 = rN - \left(\frac{r}{K}\right)N^2 \tag{3b}$$

$$\gamma = \frac{r}{K} \tag{3c}$$

$$K = \frac{r}{\gamma} \tag{3d}$$

Viewed in this manner, K can be modified by changing either r or γ and so should not be considered an independent parameter. If we assume that the level of intraspecific competition (γ) is relatively constant, we must conclude that changes in the growth rate (r) will lead to direct changes in carrying capacity (K). However, if we assume that γ decreases when the rate of resource delivery is higher, it is possible for K to increase without changes in r. A clarification of the relationship between γ, r, and K in real systems is needed.

Which parameter is independent of r: K or γ? One way to answer this question is to look at how depressions of r affect population growth patterns. If the Verhurst version of the logistic is accurate, then γ is invariant to changes in r and K will decrease when r is decreased (**Figure 1a**). However, if the Pearl-Reed version of the logistic is accurate, r and K are independent. Decreases in r will only change the rate at which the growing population reaches K (**Figure 1b**). Such a pattern of growth implies that as the growth rate (r) increases so does the level of intraspecific competition (γ). To date no experiments have been aimed at answering this basic question.

Enrichment has been shown to increase both the growth rate (r) and the carrying capacity (K) of experimental systems (Veilleux 1979). However, enrichment has the undesirable effect of changing other parameters in the system: predator conversion efficiency (e), predator per capita capture efficiency (a), and perhaps the per-prey item handling time (h). If we truly want to understand the effects of varying levels of K in real systems, we need an experimental manipulation with the potential to change r and K without modifying other parameters. Enforced proportional mortality has the potential fill this need.

The effects of proportional mortality on r and K can be understood by looking at the logistic prey growth equation. Without enforced mortality, the equation is:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) = rN - \left(\frac{r}{K}\right)N^2 \qquad (4)$$

Adding mortality (p) in proportion to prey abundance (N), the equation becomes:

$$\frac{dN}{dt} = rN - \left(\frac{r}{K}\right)N^2 - pN \qquad (5)$$

This equation can be rewritten as follows:

$$\frac{dN}{dt} = (r - p)N - \left(\frac{r}{K}\right)N^2 \qquad (6a)$$

$$\frac{dN}{dt} = (r - p)N\left(1 - \frac{rN}{K(r - p)}\right) \qquad (6b)$$

$$\frac{dN}{dt} = (r - p)N\left(1 - \frac{N}{K\left(1 - \frac{p}{r}\right)}\right) \qquad (6c)$$

Under proportional mortality, the prey growth rate (r_p) and the carrying capacity (K_p) are reduced:

$$r_p = (r - p) \qquad (7)$$

$$K_p = K\left(1 - \frac{p}{r}\right) \qquad (8)$$

The main disadvantage of the enforced proportional mortality method is that it can only be used to depress r and K; enforced mortality cannot increase these parameters. Problems associated with this limitation in the *Didinium-Paramecium*

system can be overcome through other system manipulations, such as methyl cellulose concentration (Luckinbill 1973, Veilleux 1979).

In this study we employed enforced proportional mortality to determine whether r and K are independent. Using *Paramecium*, a model organism in the field of population biology, we asked the question "Can a change in growth rate (r) affect the equilibrium abundance (i.e. K) of a monospecific population?" Because we use a mechanical depression of r, we can be confident that our manipulation is not affecting other key properties of the system. Our experiment creates conditions consistent with the basic assumptions of the logistic growth equation and therefore has the potential to test basic properties of the model.

Methods

We prepared buffered leaf infusion media (bLIM) at concentrations of 0.5 and 3.0 g/L by boiling cereal grass media (Carolina Biological Supply) in artificial pond water (ddH$_2$O containing 0.1 mM CaCl$_2$, 0.1 mM NaCl, 1.0 mM KCl, Total Molarity = 0.0012 M) for 15 minutes. Following boiling, we filtered the medium through cotton batting and then through #413 qualitative filter paper (VWR) to remove particulate matter. To buffer this solution, we added 4.7 mL of a 0.1 M solution of Na$_2$HPO$_4$ and 0.3 mL of a 0.1 M solution of NaH$_2$PO$_4$ to the filtered media. To ensure correct concentration, we brought the entire solution back up to 1 L with ddH$_2$O. We aliquoted and sterilized the resulting media by autoclave for 30 minutes.

We innoculated experimental bottles containing 100 mL of 0.5 g/mL bLIM with *Enterobacter aerogenes* and allowed the bacterial suspension to grow for ~24 hours. After using an increase in turbidity as a check for successful bacterial growth, we added 500 μL from stock cultures of *Paramecium aurelia* (Carolina Biological Supply) to each experimental bottle. We inoculated 4 bottles for each of three treatments (0%, 20%, and 40% enforced mortality). Bottles were incubated at 25º C.

On a daily basis we swirled each bottle to mix and removed 1 mL of media. For the first four days of the experiment we removed four 250 μL samples; on subsequent days we removed eight 125 μL samples in order to reduce the overall number of *Paramecia* to be counted in a single sample. For each bottle we obtained total abundances for four samples using five second video clips taken on a video microscope. After sampling, 1 mL of 3.0 g/L bLIM that had been inoculated with *Enterobacter aerogenes* in the past 24-72 hours was added to each bottle to maintain constant volume and provide food for the *Paramecium* at a constant rate.

Populations reached relatively constant abundances by Day 10 of the experiment, and on Day 12 we subjected each population to one of three enforced proportional mortality treatments: 0%, 20%, or 40%. We used a 50 mL syringe to remove 20 or 40% of the media in each of the bottles subject to mortality treatment. We then used an inline syringe filter cartridge containing a single Pall 10 μm polypropylene separator (part #61756) to catch *Paramecia* but allow for the return of dissolved media and any free-living bacteria in the

suspension. We performed these enforced mortality treatments daily (immediately after subsampling for counting) until the termination of the experiment on Day 24.

We used *MS Excel* to organize and plot our data and performed ANOVA using *R*. Raw data, calculations, and data analysis are available by request from Christopher Jensen.

Results

Figure 2 displays the trajectories of all twelve replicate bottles throughout the 24-day experiment. Clear differences can be seen in the trajectories and final abundances during the interval between Day 12 and Day 24 when the enforced proportional mortality treatment was applied. In this experiment our goal was to assess how enforced mortality affects equilibrial abundances; to make this assessment we used aggregated data from various windows of time. **Table 1** shows the average abundances for the last three, five, seven, and ten days of the experiment. Using a 2-way ANOVA to analyze aggregated data from the last four days of the experiment, we compared the effect of individual replicate bottles to the enforced mortality treatment. Boxplots for this aggregated data set are shown in **Figure 3**. The enforced mortality treatment effect was highly significant, while differences between bottles were not (**Table 2**).

In order to assess whether our actual equilibrial abundances matched those predicted by theory, we used empirically-derived values of r and K to compare predicted equilibria for the two treatments that employed enforced proportional mortality to actual equilbria under experimental treatment. We determined the carrying capacity (K) and average growth rate (r) by fitting the data from Bottles 1-4 (no enforced mortality treatment) using the *Solver* function of *MS Excel* to minimize the sum-of-squares error between log-transformed predicted and observed *Paramecium* densities. The best fit K was 135.9 individuals per mL, and the best fit r was 0.646 offspring per individual per day. Predicted values of K_p under enforced proportional mortality were calculated using equation (8). As **Table 3** shows, the actual and predicted values are more similar for the 20% removal treatment than the 40% treatment.

If the enforced mortality treatment is only affecting the equilibrial abundance of the population, we expect that the intraspecific competition constant, γ, should be constant. γ can be estimated for each of the enforced mortality treatments using the following equation:

$$\gamma = \frac{p}{N_0{}^* - N_p{}^*}$$

(9)

Where p is the level of enforced mortality, $N_0{}^*$ is the equilibrial abundance without enforced mortality, and $N_p{}^*$ is the equilibrial abundance at the level of enforced mortality p. Using equation (9) and the best-fit estimate of K for the zero-

49

enforced-mortality treatments, we estimated the constant γ for each set of four replicates in the 20% and 40% enforced mortality treatments (**Table 4**). Using a one-tailed paired t-test, we detected a significant difference (P=0.002) between the two treatments.

Discussion

Our experiment demonstrates that enforced proportional mortality can be used to abiotically decrease the effective carrying capacity (K) of protozoan populations. Populations at equilibrium respond rapidly to the experimental manipulation (**Figure 2**), with clear and significant (**Table 2**) differences between various levels of treatment. For the 20% enforced proportional mortality, abundances predicted by theory approximate actual abundances (**Table 3**). While the actual abundances of the 40% enforced proportional mortality do not as closely match the predicted values, this treatment still had a significantly larger effect on equilibrial abundance than the 20% treatment.

Our results cannot be used to resolve why the larger of the two enforced mortality treatments produced equilibriums that are above those predicted by equation (8). Three potential factors deserve future investigation. First, subsequent experimental work has suggested that some *Paramecia* are able to escape through the filter. If the filter is not 100% efficient, actual mortality rates (p) will be lower than expected based on the volumes removed. Second, based on the apparent trajectories shown in **Figure 2**, is seems reasonable to assume that additional time under the 40% treatment might have led to further decreases in abundance. Because we started each population at or near the natural carrying capacity (K), it will take longer for populations under the higher enforced mortality treatment to equilibrate to the adjusted carrying capacity (K_p). A final possibility is implied by the results shown in **Table 4**. The assumption of equation (8) is that changes in r directly affect K, which means that the intraspecific competition parameter (γ) remains constant. Our results suggest that under the higher mortality treatment, intraspecific competition is significantly increasing. Why or how this is happening is unclear, and the direction of the change (higher intraspecific competition in the population which is being thinned more) is counterintuitive.

The main value of our experiment is its demonstration of a novel experimental manipulation, enforced proportional mortality. Using this manipulation, experimenters can artificially depress r and K through purely abiotic means. The alternative – biotic depression of these parameters through the reduction in the delivery rate of the limiting nutrient – has the undesirable effect of depressing other vital rates. Being able to change r and K but maintain static values of other parameters is potentially useful in distinguishing between the predictions of competing models. For instance, the ratio-dependent depiction of predation predicts that predators will completely consume prey at a sufficiently low value of r (Berezovskaya et al. 2001) whereas the prey dependent model predicts that complete consumption is only possible at high values of K (Rosenzweig 1971).

Our experiment does not provide definitive evidence that r and K are related in natural systems. In order to understand how r and K are interrelated, we need to perform experiments that modify only one component of the pair. For instance, our understanding of carrying capacity (K) is that it is a function of the delivery rate of the limiting nutrient. To determine whether this delivery rate also affects the growth rate (r), we need to measure the effects on r and K under various levels of reduced nutrient input. The opposite approach is also possible: if growth rate (r) can be reduced in a manner that keeps the nutrient input constant, we can look for effects on the carrying capacity (K). Our experiment may appear to have this effect, but in essence it depresses both r and K because it simultaneously reduces the growth rate (by removing a fraction of individuals that were produced by reproduction) and reduces the carrying capacity (by effectively reducing the nutrient input rate via removal of biomass). To determine how r and K are interrelated, we need experiments that compare r and K over a range of nutrient inputs, with particular attention to the early (exponential) phase of growth where growth rates (r) can be compared.

Conclusion

The current experiment demonstrates that enforced proportional mortality can be used to abiotically reduce r and K in laboratory protozoan microcosms. While this manipulation does not produce reductions that exactly match mathematical predictions, it does significantly decrease r and K. Further work is needed to determine if r and K are similarly related in natural systems.

Acknowledgements

Tables

Table 1. Effect of enforced mortality on final abundances of replicate treatments.

		0% enforced mortality				20% enforced mortality				40% enforced mortality			
		Bottle 1	Bottle 2	Bottle 3	Bottle 4	Bottle 5	Bottle 6	Bottle 7	Bottle 8	Bottle 9	Bottle 10	Bottle 11	Bottle 12
Last 10 Days	*Average*	135.4	135.2	135.4	134.2	101.6	98.2	98.8	99.2	74.2	74.2	73.2	76.2
	S.D.	5.0	3.9	2.8	3.9	2.8	7.0	4.9	7.6	4.4	6.0	7.5	4.9
Last 7 Days	*Average*	135.1	134.9	135.4	134.9	102.0	96.6	97.1	97.7	72.6	71.1	70.3	74.0
	S.D.	6.0	3.6	3.2	4.6	2.3	7.7	4.7	8.6	2.5	3.8	6.3	4.0
Last 5 Days	*Average*	135.6	135.2	134.0	134.4	102.4	94.4	98.8	96.4	72.4	70.8	70.8	74.8
	S.D.	5.9	4.1	2.4	5.4	2.6	8.2	3.0	10.1	3.0	4.4	7.6	4.4
Last 3 Days	*Average*	132.7	136.0	134.7	130.7	103.3	93.3	98.0	93.3	71.3	70.0	66.0	76.7
	S.D.	6.1	4.0	3.1	1.2	3.1	8.1	3.5	13.0	3.1	6.0	5.3	4.6

Table 2. 2-way ANOVA of the Aggregated Last 4 Days of Abundances.

	df	Sum of Squares	Mean Sqaures	F Value	Prob.
Enforced Mortality Treatment	2	126,821	63,410	205.63	$<2\times10^{-16}$
Bottles	9	1,303	145	0.47	0.8937
Residuals	180	55,508	308		

Table 3. Actual Versus Predicted Abundances Under Enforced Mortality Treatment.

Abundances are expressed as individuals per mL for each of four time windows (last 10, 7, 5, and 3 days). Predicted densities are derived from the actual abundances for the 0% treatment (K) and estimated r between Day 4 and Day 6 using equation (8).

	0% em	20% em		40% em	
	Actual	Actual	Predicted	Actual	Predicted
Last 10 Days	135.05	99.45	93.24	74.45	51.43
Last 7 Days	135.07	98.36	93.25	72	51.44
Last 5 Days	134.8	98	93.07	72.2	51.33
Last 3 Days	133.5	97	92.17	71	50.84

Table 4. Estimation of the intraspecific competition constant (γ) for both enforced mortality treatments.

		N_p^*	enforced mortality (p)	Intraspecific competition constant (γ)
20% enforced mortality	Bottle 5	101.6	0.2	5.83 x 10^{-3}
	Bottle 6	98.2	0.2	5.31 x 10^{-3}
	Bottle 7	98.8	0.2	5.39 x 10^{-3}
	Bottle 8	99.2	0.2	5.45 x 10^{-3}
40% enforced mortality	Bottle 9	74.2	0.4	6.48 x 10^{-3}
	Bottle 10	74.2	0.4	6.48 x 10^{-3}
	Bottle 11	73.2	0.4	6.38 x 10^{-3}
	Bottle 12	76.2	0.4	6.70 x 10^{-3}

Figures

Figure 1. Logistic Growth Under The Verhulst and Pearl-Reed Equations
        Logistic growth can be represent in two manners: **(a)** under Verhurst's depiction, decreases in growth rate (r) lead to decreases in carrying capacity (K); and **(b)** under Pearl and Reed, decreases in growth rate (r) simply slow the rate at which the unchanged carrying capacity (K) is reached.

(a)

(b)
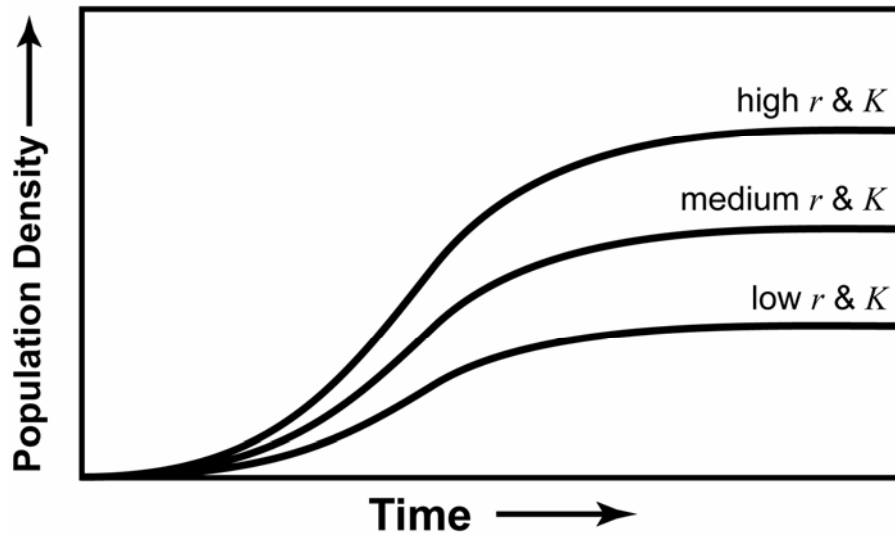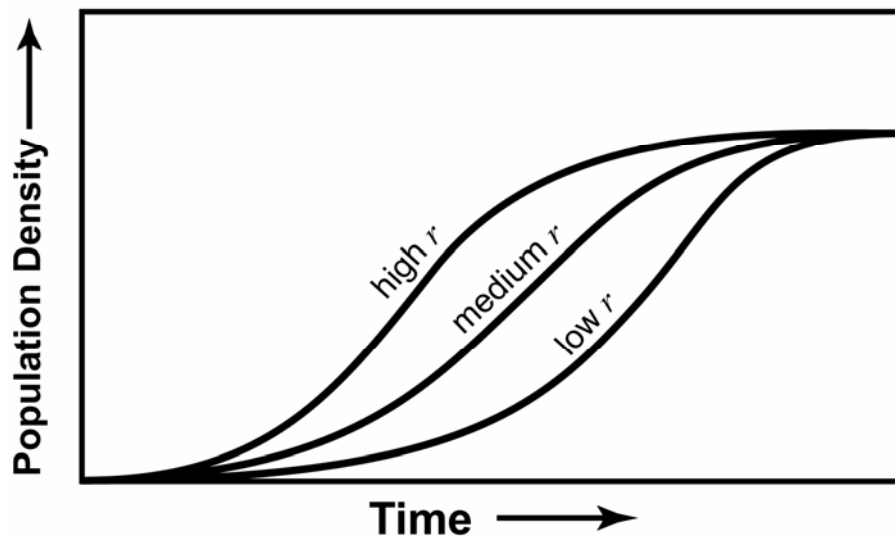
Figure 2. Effect of Enforced Mortality on Paramecium Growth.
We estimated *Paramecium aurelia* densities daily, and at Day 12 we subjected each bottle to one of three mortality treatments (0, 20, or 40%).

Effect of Enforced Mortality on *Paramecium* Growth

Legend:
- 0% em (#1)
- 0% em (#2)
- 0% em (#3)
- 0% em (#4)
- 20% em (#5)
- 20% em (#6)
- 20% em (#7)
- 20% em (#8)
- 40% em (#9)
- 40% em (#10)
- 40% em (#11)
- 40% em (#12)

Y-axis: Individuals per mL
X-axis: Day
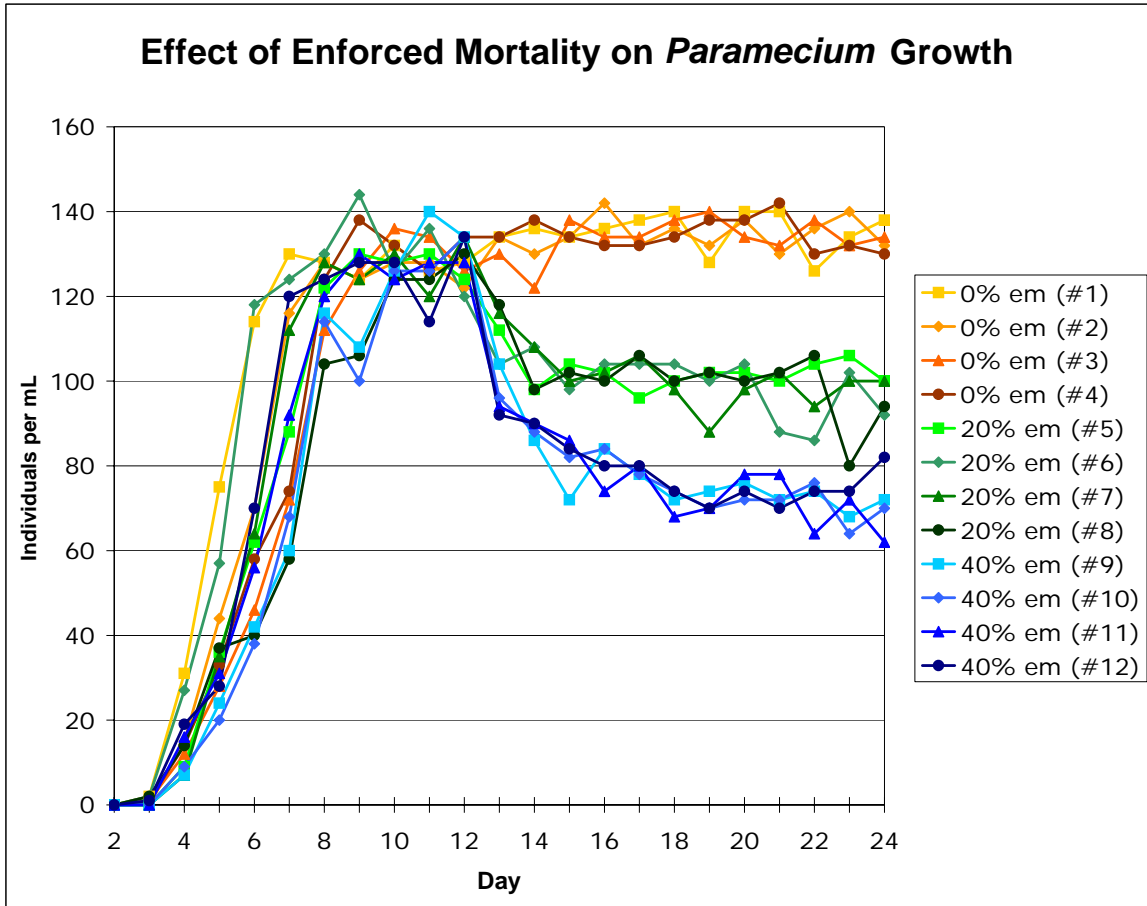
Figure 3. Boxplots for the Last 4 Days of Growth by Enforced Mortality
Treatment.

We used aggregated data from the last four days of growth of each bottle
to construct boxplots for the 40% (forty), 20% (twenty), and 0% (zero) enforced
mortality treatments. The dark line represents median density for each treatment,
with 50% of values incorporated within the boxes and 75% of the values
incorporated within the whiskers. Outlier values are displayed as circles.
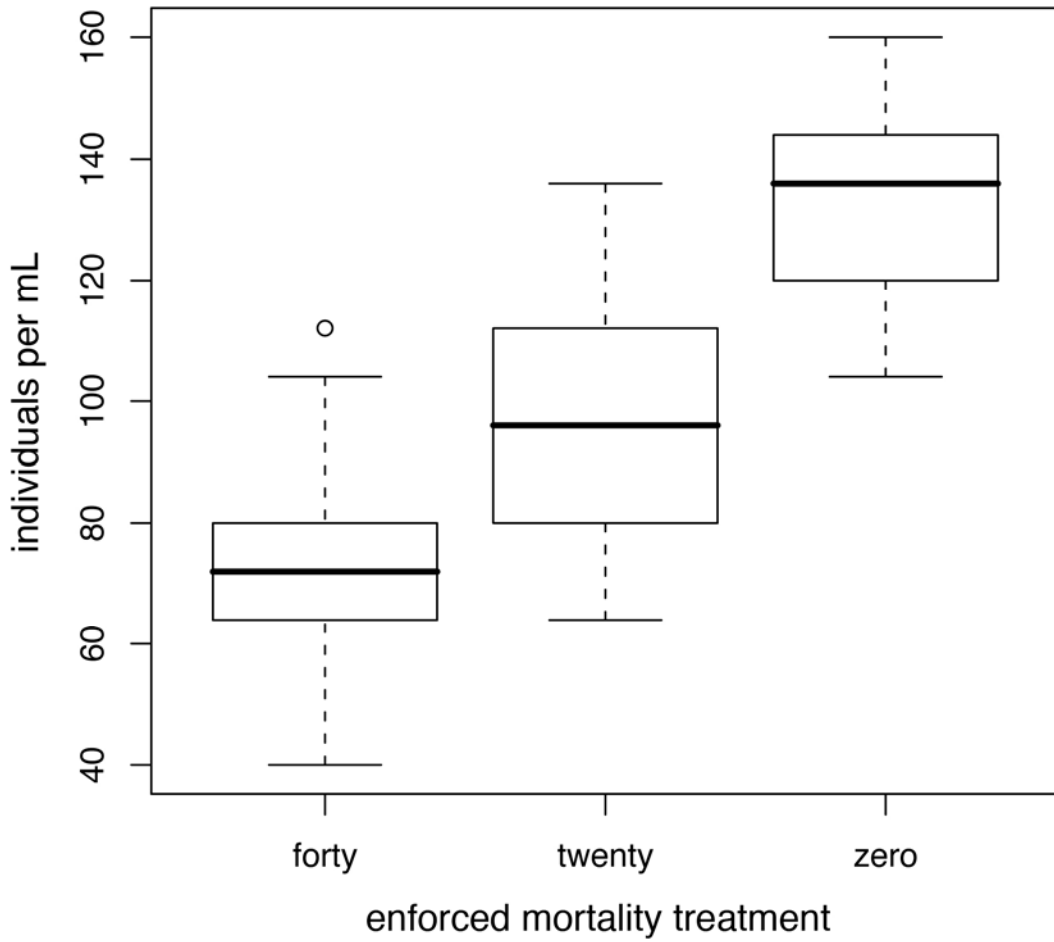
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Chapter 4

The Consequences of Functional Response Choice: Differences in Stability and Equilibrium

Context:

     If we are to convince ecologists whose focus is beyond the narrow world of predator-prey modeling that functional response choice is important, we need to establish that there are consequential differences between the competing theoretical representations. Using stochastic simulations based on the *Paramecium-Didinium* system, I show that different functional responses produce qualitatively different outcomes in terms of system stability and equilibrial trophic response to basal enrichment.

Introduction

The importance of predator interference has been heavily debated in a series of articles on prey dependence, ratio dependence, and predator-dependent intermediates (e.g. Arditi and Ginzburg 1989, Arditi et al. 1991, Akçakaya 1992, Arditi and Saiah 1992, Berryman 1992, Ginzburg and Akçakaya 1992, Matson and Berryman 1992, Ruxton and Gurney 1992, Abrams 1994, Gleeson 1994, Akçakaya et al. 1995). However few attempts have been made to experimentally contrast these competing depictions of predator-prey interaction. My goal in this paper is to theoretically substantiate an appropriate test for the presence of predator interference in a real biological system.

A major turning point in the debate over the importance of predator dependence came with the publication of a "reconciliation paper" by Abrams and Ginzburg (2000). Both authors – traditionally at odds over how consumption should be depicted – agreed that real systems probably exhibit behaviors that are intermediate between the prey- and ratio-dependent extremes. While many functional response forms incorporate interference (Jeschke et al. 2004), two forms have dominated the literature: i) Beddington-DeAngelis (Beddington 1975, DeAngelis et al. 1975) and ii) Hassell-Varley-Holling (Hassell and Varley 1969). These forms have gained importance in part because they represent forms of "intermediate interference" between the traditional prey-dependent model (which incorporates no interference) and the upstart ratio-dependent model (which makes the extreme assumption that interference causes complete sharing of prey by predators).

The Beddington-DeAngelis (BD) functional response is of the form:

$$f(N) = \frac{aN}{1 + ahN + iahP} \tag{1}$$

Where N is the abundance of prey, P is the abundance of predators, a is the capture efficiency of predators on prey, h is the per prey handling time, and i is the interference parameter. In this equation, i represents the importance of time spent encountering and interfering with other predators relative to time spent searching for, capturing, and handling prey. The HVH functional response is of the form:

$$f\left(\frac{N}{P^m}\right) = \frac{\alpha_m\left(\dfrac{N}{P^m}\right)}{1 + \alpha_m h\left(\dfrac{N}{P^m}\right)} \tag{2}$$

Where α_m is the capture efficiency and m is a parameter expressing the degree of predator interference, generally assumed to be between zero (where the model

simplifies to the Holling Disc Equation) and one (where the model simplifies to the ratio-dependent model).

As explained in **Chapter 1**, the prey- and ratio-dependent extremes differ in their predictions of: i) system stability and ii) equilibrial response to basal enrichment. Strangely, almost all theoretical work in these two important arenas has been confined to the extreme functional responses (i.e. Rosenzweig and MacArthur 1963, Oksanen et al. 1981, Arditi and Ginzburg 1989, Berezovskaya et al. 2001). Very little work has been done to analyze the stability and equilibria of the BD and HVH models. Arditi and colleagues analyzed the effect of increasing interference on the stability of these models (Arditi et al. 2004), but did so in a purely deterministic framework. While this information is valuable, there are two problems with practically applying analytical approaches to the stability of the BD and HVH models. First, destabilization in these systems usually arises from the production of large-scale limit cycles that bring predator and/or prey abundances very close to extinction. As explained in **Appendix A**, such destabilization results in non-deterministic extinction events. If we want to depict an actual biological system, we cannot predict when this destabilization will result in a real extinction unless we make assumptions about the threshold abundance at which extinction occurs. A second shortcoming of the purely analytical approach is that it ignores the effects of natural variation, which may be very important especially in small-scale systems.

My approach to exploring the effect of intermediate levels of predator interference was to allow both models to operate in a discrete, probability-based predator-prey system. Assuming that both the BD and HVH models are viable representations, my goal was to simulate the range of possible system behaviors in a real predator-prey system. I chose the laboratory-based *Didinium-Paramecium* system for its historical importance (e.g. Gause 1934), range of stability behaviors (Luckinbill 1973, Veilleux 1979), and importance to the predator-interference debate (e.g. Harrison 1995).

Because of its rich experimental legacy, the *Didinium-Paramecium* system provides ample information for parameterizing the model. Parameters have been determined from fitting to data (Harrison 1995), and the simulations are based on the real experiments of Luckinbill (1973) and Veilleux (1979). As such the simulation environment can be initiated with the same starting abundances, run under the same conditions, and allowed to produce dynamics for the same period of time. In addition, alternative scenarios can be explored to reveal potentially valuable experimental manipulations.

Because the prey growth rate and carrying capacity parameters provide the critical contrast between the prey- and ratio-dependent extremes, it is most efficient to explore the parameter space of each model over a range of simultaneously varying values of r and K. For this reason I have linked these two parameters by the following relation:

$$K = \frac{r}{\gamma}$$

(3)

As outlined in **Chapter 3**, this connection is supported both theoretically and experimentally.

Methods

In order to simulate conditions comparable to a real *Didinium-Paramecium* system, I used input parameters derived from fitting to Luckinbill's data (Harrison 1995) and initial predator abundances identical to those of each experimental protocol (Luckinbill 1973, Veilleux 1979). **Table 1** summarizes these values. The Beddington-DeAngelis (BD) model is a simple derivative of the traditional Holling Disc Equation to which Harrison fit his parameters, so these parameters can be used directly in BD simulations.

For the Hassell-Varley-Holling (HVH) model one parameter, α_m, cannot be easily estimated. For the purely prey-dependent form of HVH at $m = 0$, the parameters a and α_0 are equivalent. For all other values of m, a and α_m have different units and are not comparable. Even different values of α_m are not comparable, as changes to the parameter m continuously change the units of the capture efficiency (see **Appendix C**).

Because my main concern was comparing qualitative outcomes, I chose a capture efficiency (α_1) that destabilized the ratio-dependent model at a similar value of r and K as the prey-dependent model. For intermediate levels of interference, α_m was assumed to be:

$$\alpha_m = \frac{a}{\xi^m}$$

(4)

Where ξ is the factor relating the prey-dependent capture efficiency (a) to the chosen ratio-dependent capture efficiency (α_1).

My initial approach to understanding the HVH and BD models was to analyze the stability and equilibrium response via deterministic numerical simulations, which allowed for real number abundances of predator and prey. This approach was tractable for the BD model, but proved problematic for the HVH model. The HVH functional response contains the following rational expression:

$$\frac{N}{P^m}$$

(5)

Because the predator abundance (P) can approach zero when we allow real number abundances and the exponent m is also assigned very small values (always less than or equal to one), the inclusion of this expression can sabotage numerical simulation algorithms. Attempting to numerically simulate the trajectories of systems depicted by HVH produced error messages. These error messages indicated that the HVH functional response was generating rates

approaching infinity consistent with very low values of P and m. Output from these simulations was nonsensical and in light of the error messages was deemed untrustworthy.

As an alternative approach, I switched to simulations of discrete population growth that allowed for demographic stochasticity. These simulations were built on two basic tenets: i) individuals were considered discrete, so only integer values representing the total number of prey and predators in the system were allowed; and ii) the relevant processes of growth and death were modeled as probabilistic events. Not only did this approach allow both models to be explored by eliminating the inclusion of predator abundances close to zero, it also enabled me to consider the role that very simple variability can play in this relatively small system.

Figure 1 displays the basic algorithm used to generate each replicate population trajectory. The simulation produces a series of asynchronous discrete events until either the predator or prey population drops to zero or the experimental time limit of 30 days is reached. In the original experiments of Luckinbill and Veilleux, only one of five events could occur at any moment: i) a single prey individual can die of starvation; ii) a single prey individual can reproduce; iii) a single prey individual can be consumed; iv) a single predator individual can die of starvation; or v) a single predator can reproduce. To appraise the value of a possible laboratory manipulation, I also allowed for a sixth event: removal of a single prey individual by an experimenter ("enforced mortality").

Table 2 shows the rate functions used for each of these potential events. The prey growth function (**g**) was modeled after the logistic equation, and allows for both prey reproduction (when $N < K$) and prey death by starvation (when $N > K$). The consumption function (**c**) was modeled after either the BD or HVH models, and both predator death due to starvation (**d**) and mortality enforced on the prey (**emR**) were modeled as linear functions of abundance. Rather than making reproduction a probabilistic event, I created a cache that produced a single predator every time that a sufficient number of prey (assumed to be the inverse of the conversion efficiency or $1/e$) had been consumed.

All of the rate functions are density-dependent, so as prey and predator abundances fluctuate through time absolute rates also fluctuate. At any given time step, absolute rates were converted into relative probabilities. For instance, the prey growth function (**g**), which can be positive or negative, has the following relative probability:

$$\text{Prob}[\mathbf{g}] = |\mathbf{g}| \, / \, (|\mathbf{g}| + \mathbf{c} + \mathbf{d} + \mathbf{emR}) \tag{5}$$

Because absolute rates vary through time, the time step employed also varies and was modeled as:

$$t_{step} = (|\mathbf{g}| + \mathbf{c} + \mathbf{d} + \mathbf{emR})^{-1} \tag{6}$$

In other words, this simulation models the average time between events as the inverse of summed absolute rates, which allows for greater frequency of events when total rates are higher. I also ran these simulations using a time step modeled as an exponential random variable; the results of these simulations were indistinguishable from those which employed a deterministic time step.

In order to identify differences in stability, modules were programmed to explore parameter space in two dimensions: i) over a range of r and K and ii) over a range of interference (i or m). The simulations linked r and K through the relationship described in equation (3). For each combination of parameters, 25 replicate simulations were performed and the relative frequencies of each outcome (coexistence, predator extinction, or dual extinction) outputted. As **Figure 2** explains, these relative frequencies were use to generate an RGB color and displayed in the parameter spaces of **Figures 3**, **4**, and **5**.

In order to compare equilibrial responses to enrichment, modules were programmed to explore ranges of r and K for various values of i in the BD model and m in the HVH model. For each value of r and K, 100 replicate simulations were performed for a time period of 30 days, generating average final predator and prey abundances. Standard deviations provided an assessment of the degree of variability in each set of final abundances.

All simulations were performed using *Mathematica* version 5.2.0.0 and are available on request. See **Appendix D** for more information on the specific calculations and code employed in these simulations.

Results

These simulations illuminate the differences between the BD and HVH models as well as differences in stability between various intensities of predator interference. As **Figure 3** shows, both models produce consistent regions of coexistence, dual extinction, and predator extinction. For most areas of the parameter space, the boundaries between these regions are relatively distinct. A quick comparison of **Figure 2** (which shows the color-coded range of possible outcomes in this system) with the range of color-coded outcomes displayed in **Figure 3** suggests that both models have a low degree of uncertainty, even when we allow for demographic stochasticity within relatively small populations. The greatest uncertainty occurs in both models where predator interference is very low.

The key difference between the BD and HVH models relates to the manner in which each represents dual extinction. In the HVH model at low levels of interference, increases in r and K shift the system from predator extinction to coexistence to predator extinction to dual extinction. The transition from coexistence to either predator- or dual extinction is the classical "paradox of enrichment." In both models, increasing predator interference eliminates the paradox of enrichment. For the BD model, as shown by **Figure 3a**, increases in predator interference effectively remove the possibility of dual extinction and allow for coexistence for all values of r and K above the minimum prey carrying capacity required for predator persistence. In contrast, increases in interference

64

in the HVH model introduce the potential for dual extinction to emerge at the lowest values of r and K. For the ratio-dependent extreme at $m = 1$, the HVH model produces predator extinction solely as a rare boundary outcome at the interface along the r and K continuum where the regions of dual extinction (for low r and K) and coexistence (high r and K) meet.

      Figure 4 demonstrates the importance of initial condition in the HVH model. Results for the BD model were similar and are not shown. Not surprisingly, the model is most extinction prone when initial abundances of predators are high and prey are low (**Figure 4a**) and most extinction averse when initial abundances of predators are low and prey are high (**Figure 4d**). Interestingly, these differences in stability only occur when interference values are low. As the level of interference increases, sensitivity to initial conditions decreases, and the outcomes of all four models in **Figure 4** are virtually identical for interference values of $m > 5$. The initial abundance of predators appears to have a stronger effect on outcomes than the initial abundance of prey: **Figure 4a** and **Figure 4c** are more similar to each other than the other spaces, as are **Figure 4b** and **Figure 4d**. Because the number of replications per parameter combination (25) is relatively low, some differences between these four spaces could be due to chance, but the relative consistency of outcomes suggests that these comparisons are valid.

      Figure 5 suggests that the "enforced proportional mortality" experimental protocol has a strong effect on both the BD and HVH models. When we remove an average of 50% of the prey per day in the BD (**Figure 5d**) and HVH (**Figure 5c**) models, we produce changes in the system stability. For both models, the region of coexistence shifts towards higher values of r and K, which suggests that the actual effect of the experimental manipulation matches the intended effect (simultaneous reduction of r and K). For lower values of interference in the HVH model and all values of interference in the BD model, the region of predator extinction at low r and K expands. For higher values of interference in the HVH model (those near to or at the ratio-dependent extreme), the region of dual extinction at low r and K expands. The threshold for dual extinction at lower values of interference also shifts towards higher values of r and K in both models.

      The average equilibrial response of predator and prey abundances to increases in r and K can be seen in **Figure 6**. For zero interference, both the HVH (**Figure 6a**) and the BD (**Figure 6g**) model show the classic response to enrichment associated with the prey-dependent functional response: while the predator abundance increases in response to enrichment, the prey abundance remains unchanged. Notice however that when the system approaches the region where dual extinction begins to be important, multiple runs of stochastic simulations produce an average decline in prey abundance. For interference values that preclude dual extinction in the HVH (**Figure 6c-e**) and BD (**Figure 6i-l**) models, predator and prey abundances show simultaneous and comparable increases. At the ratio-dependent extreme we see an exception to this rule (**Figure 6f**), where regions of low r and K produce dual extinction and the

predator and prey abundances show very strict proportional increase at higher values of r and K.

Discussion

Treating predator and prey abundances as discrete and allowing for demographic stochasticity enabled these simulations to reveal a number of previously unexplored system behaviors. First, we can see that although stochasticity is incorporated, these systems behave in a highly predictable manner for most parameter combinations. Second, we can clearly compare the behaviors of the BD and HVH over a range of possible predator interference values. Third, we can compare the experimental results of Luckinbill and Veilleux to the outcomes predicted by the simulation with a particular focus on variable results.

In areas of parameter space at the interface between two consistent outcomes we see some variability, but this variability is only pronounced in the regions of lowest interference. For both the BD (**Figure 3a**) and HVH (**Figure 3b**) model simulations, the purely prey-dependent region at $i = 0$ or $m = 0$ failed to display any region of consistent coexistence, suggesting that the prey-dependent model is highly unstable for all parameter combinations. For most other regions of the parameter space, there is a small boundary over which outcomes are variable but the predominant outcome resembles the prediction of the deterministic model.

Both models show that at low values of predator interference, system enrichment first produces predator extinction and then dual extinction (**Figure 3**). This pattern, which is highly relevant to experimental results (see below), is only made apparent via this non-analytical approach. Both extinction events are caused by a shift towards a stable limit cycle; clearly, this limit cycle changes subtly from a trajectory in which prey escape extinction but predators do not to a trajectory in which predators completely consume their prey and then starve to death. This pattern can only be discovered under conditions of non-deterministic extinction.

Increases in interference stabilize both models, increasing the threshold for extinction at high values of r and K. Even at moderate levels of interference ($m \approx 1$ and $i \approx 0.25$), dual extinction in this system is practically absent, since it could only occur at biologically unrealistic values of r and K. This finding is consistent with the analytical finding of Arditi and colleagues (Arditi et al. 2004). Dual extinction is a rare outcome for laboratory and field systems: the rather unique ability of *Didinium* to completely consume its prey sets it apart from other predators, even in the protozoan world. It seems likely that for most predators moderate levels of interference would remove the potential for dual extinction caused by enrichment. In fact, experimental evidence for destabilization due to enrichment is completely absent from the natural world (Jensen and Ginzburg 2005).

Consideration of the regions of higher interference reveals the principle difference between the BD and HVH models. At high interference, the BD model

simply loses its region of dual extinction at high values of r and K (**Figure 3a**). At low values of r and K, the pattern of predator extinction is consistent throughout all levels of interference. The simulations displayed here employ a maximum interference value of $i = 5$. This represents a relatively high level of interference, as the rough meaning of this value is that "the probability of wasting time bumping into other predators is five times greater than the probability of spending time searching for and handling prey." Simulations on values of i up to 100 suggest that the BD never produces dual extinction at low values of r and K. This finding suggests that although the BD model theoretically collapses to an approximation of the ratio-dependent model at the limit of $P \rightarrow \infty$ (see **Chapter 6**), for all imaginable practical conditions it does not share the stability properties of ratio dependence.

In contrast, the HVH model produces a continuum of behaviors that bridges the gap between the prey-dependent model at $m = 0$ and the ratio-dependent model at $m = 1$ (**Figure 3b**). Consistent with previous analytical findings (Berezovskaya et al. 2001), my simulations demonstrate that under ratio dependence, low values of r and K produce dual extinction. Although it is barely detectable at the resolution of these simulations, a small region of predator extinction emerges at the boundary between consistent coexistence and consistent dual extinction. Approaches to ratio dependence (Berezovskaya et al. 2001) do not predict this boundary region; it is apparently a product of non-deterministic extinction.

Interestingly, the region of dual extinction in the HVH model emerges only at the very highest levels of interference ($m > 0.75$). In regards to stability, the HVH model only differs qualitatively from the Beddington-DeAngelis model when the system approaches ratio-dependence. As **Figure 3b** suggests, predator extinction is the sole outcome at lower values of interference. One of the problems in comparing the BD and HVH models revolves around their capture efficiencies. For BD capture efficiency (a) is consistent throughout the simulations, but for HVH the capture efficiency (α_m) necessarily varies throughout the range of interference (m). Because our assumption about how α_m varies is arbitrary, it is impossible to make accurate comparisons of the BD predictions across ranges of r and K with analogous regions of the HVH space. What we are left with is a truly qualitative comparison: BD doesn't produce dual extinction at high levels of interference whereas HVH can when it approximates ratio-dependence.

Because they are based on actual experimental data, these simulations allow us to ask the question: what parameters best represent the experiments of Luckinbill (1973) and Veilleux (1979)? Based solely on fitting data, Harrison (1995) argued that the prey-dependent model was a better fit than the ratio-dependent model to Luckinbill's data, with models that incorporated intermediate predator interference superior to both extremes. Similarly Jost and Arditi (2001) found that both data sets were better fit by prey dependence than ratio dependence. In contrast, studies of the Veilleux data that take into account reproductive delays suggest that ratio dependence may be a superior fit (Jost

and Ellner 2000). By comparing the fit of outcomes rather that the fit of trajectories, these simulations can shed new light on this debate.

Both models were fit using Harrison's estimated parameters (Harrison 1995) from the Luckinbill experiment (Luckinbill 1973). Consistent with Harrison's conclusions, my results suggest that moderate interference is necessary to produce the Luckinbill results. As shown in **Figure 4c**, starting with Luckinbill's initial abundances it is impossible to produce consistent coexistence with a purely prey-dependent model. These simulation results were consistent regardless of whether the HVH or BD model was employed: without moderate interference, the only two outcomes produced with any frequency across the range of r and K explored were predator extinction and dual extinction.

In producing his results across a range of system enrichment, Veilleux modified Luckinbill's experiment slightly. One of his chief modifications was to increase the abundance of both predators and prey initially introduced into the system. In contrast to Luckinbill (**Figure 5a,b**), Veilleux's initial abundances (**Figure 5c,d**) allow for some relatively consistent coexistence even when predator interference is absent. As with the Luckinbill data, the simulations that incorporated small amounts of predator interference provide the best account of Veilleux's experiments (shown in **Table 3** of **Chapter 1**). At low levels or interference ($0 < i < 1$ or $0 < m < 0.3$), we can travel across the continuum of r and K and see the predator extinction, coexistence, mixed predator/dual extinction, and dual extinction regions Veilleux discovered experimentally.

In order to fully understand the role that initial abundances play in these systems, simulations were performed at all four combinations of prey and predator abundances used by Luckinbill and Veilleux. **Figure 4** shows the effect of changing the initial abundance of predators and/or prey in the HVH model; analogous simulations in the BD model produced similar results. Based on these results, the initial abundance of prey seems to have a much stronger effect on the stability pattern of the model than initial predator abundance. The simulations with high P and low N (**Figure 4a**) are virtually identical to those with low P and low N (**Figure 4c**), whereas both are different from simulations that employed high P and high N (**Figure 4b**) or low P and high N (**Figure 4d**). Increasing the initial abundance of prey reduces the incidence of predator extinction in areas with low interference and moderate levels of r and K, presumably by preventing prey overexploitation during the early stages of the simulation. For prey-dependent or moderately predator-dependent systems, systems of coexisting predator and prey often trace limit cycles. When initial abundances fall far outside the area traced by the limit cycle, trajectories can bring abundances close to zero before joining the limit cycle, leaving open the possibility of extinction due to the effects of initial conditions. This finding opens up the possibility for some interesting experimental work using the Luckinbill/Veilleux system. Finding differences based on initial abundances would further aid in locating this system across the continuum of predator interference.

It should be noted that none of the simulations suggest that ratio dependence or even predator-dependent systems with relatively high

interference can satisfactorily explain the results of Luckinbill and Veilleux. This is because ratio dependence explains dual extinction as a phenomenon of low r, whereas Luckinbill and Veilleux both found lower values of r to be stabilizing to the system. While this does not bode well for the ratio-dependent system, several complications merit further investigation. First, it should be noted that increases in basal enrichment change parameters other than prey carrying capacity (K) and growth rate (r). The rate at which food was delivered to the prey affects conversion efficiency (e), capture efficiency (a or α_m), and death rate (m) of the predator. As such, these experiments offer an imperfect test of the functional response.

Simulations that incorporate an experimenter-enforced proportional mortality, the results of which are shown in **Figure 5**, suggest an alternative approach. As shown in **Chapter 3**, when prey are removed proportionally from the system, the effect is an abiotic reduction in r and K. As expected, reducing r and K in this manner causes a shift in system behavior. In both the BD and HVH systems, the entire parameter space "shifts" to the right. For instance, regions of coexistence at lower values of r and K (**Figure 5a, b**) may produce predator or dual extinction when prey are subjected to high enforced proportional mortality (**Figure 5c, d**).

The advantage of abiotically modifying r and K is that other parameters should not be affected by this manipulation, as it does not affect the supply of food to prey or the individual quality of prey. Such a test would allow for a definitive comparison of the prey- and ratio-dependent *limit myths*. Each could be easily falsified by a simple experiment. In the case of prey-dependence, a system that lies just within the dual extinction region should be shifted to coexistence if prey are subject to sufficiently high enforced proportional mortality. For ratio-dependence, a system that lies in the coexisting region with the lowest r and K should be destabilized to dual extinction by sufficiently high levels of enforced proportional mortality. These kinds of experiments have the potential to distinguish between the predictions of prey- and ratio dependence in other systems as well as microcosm experiments.

A number of laboratory microcosm experiments demonstrate that increasing basal food supply causes increases in both predator and prey abundances, usually with predators responding more strongly to enrichment than prey (Bohannan and Lenski 1997, Kaunzinger and Morin 1998). My simulations suggest that these experiments are best depicted by versions of the BD and HVH model that incorporate moderate interference. As shown in **Figure 6**, the purely prey- and ratio-dependent models fail to account for these patterns. For prey-dependent systems and those with very low interference (**Figure 6a,b,g,h**) prey abundances either decline or do not respond to enrichment. Only at higher levels of interference (**Figure 6c,d,i,j**) do we see moderate increases in the prey abundance paralleled by larger responses in the predator abundance. At the highest levels or interference (**Figures 6e,k,l**) prey and predator abundances tend to increase at the same rate, causing the "net difference" between predator and prey abundances to be similar. The predicted response of the ratio-

dependent system (**Figure 6f**) is farthest from observed results, as it predicts that prey will increase in abundance at a rate higher than the predators.

The equilibrium response of ratio dependence, like its stability profile, is unique. As shown in **Figure 6f**, the response of a ratio-dependent system is highly predictable, even in the presence of stochastic variation. This response, with predators and prey increasing proportionally to enrichment with independent slopes, differs significantly from the responses predicted by the HVH model at lower values of interference (**Figure 6a-e**) or the BD model at any value of interference (**Figure 6g-I**). Because it displays such a clear pattern, ratio dependence should be easy to detect. Data from enriched and non-enriched estuarine systems suggests that this response pattern has been observed (Bishop et al. 2006), but further data (particularly from systems with more than two levels of enrichment) would augment the case for ratio dependence in natural systems.

These simulations suggest that the BD model is significantly easier to work with than that of HVH. Even with reliable field data, estimating capture efficiencies is difficult to do using the HVH model. The formulation of the model presents a sort of "Catch-22": in order to know the capture efficiency we need to know the interference coefficient, but an accurate estimate of the interference coefficient may require that we know the capture efficiency. For analytical approaches that simply fit the entire equation to the data (e.g. Arditi and Akçakaya 1990, Jost and Ellner 2000, Jost and Arditi 2001) this may not be a problem, but for the preferred approach of empirically determining parameters this quality of the HVH model represents an obstacle. The simulations employed here considered populations as discrete and allowed for demographic stochasticity, the benefits of which have been already trumpeted thoroughly. The downside of these kinds of models is that they are much more costly to run; many of the parameter spaces displayed in **Figures 3-5** took weeks to complete, even though the system modeled was relatively small and simple. For more complex problems, differential equations remain an important tool. I have discovered that differential equations that incorporate the HVH model are not very amenable to numerical simulation. As such, everyday ecologists who wish to use numerical simulation tools (rather than stability analysis) to consider the behavior of predator-prey models will find the HVH model unusable. Of course the real issue is which model is most appropriate, a question that remains unanswered by this simulation study.

One unrealistic assumption of these simulations is that captured prey "accumulate" to produce new predators. For real predators including *Didinium*, a more realistic depiction would track the actual consumption rate of individual predators relative to their metabolic loss rate. Such a model would have to shift from the population-level analysis used in these simulations to an individual-based model. These models have been employed to answer similar questions in similar systems (e.g. Holyoak et al. 2000) and could be of use in the *Didinium-Paramecium* system. The ratio-dependent model has been suggested as a good approximation when there are large reproductive lags in a predator-prey system

(Arditi and Ginzburg 1989, Jensen et al. *In Press*); simulations of prey-dependent systems incorporating significant predator reproductive lags could assess the validity of this claim by comparing results of an IBM with lags to the predictions of the ratio-dependent model.

Conclusion

Numerical simulations parameterized with experimental data show that both the Beddington-DeAngelis (BD) and Hassell-Varley-Holling (HVH) models can adequately explain the experimental results of Luckinbill and Veilleux when they incorporate low levels of predator interference. Neither the prey- nor ratio-dependent extremes provide a satisfactory depiction of these experimental systems. Experiments that proportionally remove prey or manipulate the initial abundances of predators and prey have the potential to further illuminate the degree to which predator interference affects the stability and equilibria of systems.

Acknowledgements

Tables

Table 1. State variables and parameters employed in these simulations

State Variable or Parameter	Symbol Employed	Value Employed	Source
Capture Efficiency (BD)	a	0.0150	Harrison 1995
Capture Efficiency (HVH)	α_m	0.015 – 3.0	---
Conversion efficiency	e	0.486	Harrison 1995
Enforced mortality rate	ε	0 or 50%	---
Prey competition coefficient	γ	0.000343	Harrison 1995
Handling time	h	0.0392	Harrison 1995
Degree of interference (BD)	i	0 – 5	---
Prey carrying capacity	K	0 – 17,475	Harrison 1995
Degree of interference (HVH)	m	0 – 1	---
Predator death rate	μ	2.07	Harrison 1995
Initial Prey abundance	N_i	90	Luckinbill 1973
		300	Veilleux 1979
Initial Predator abundance	P_i	35	Luckinbill 1973
		100	Veilleux 1979
Prey growth rate	r	0.0 – 6.0	Harrison 1995
HVH conversion factor	ξ	0.00499	---

Table 2. Rates for asynchronous discrete event simulations

Process Modeled	Applicable Functional Response Form	Rate Function
Prey growth (**g**)	ALL	$\mathbf{g} = r\,N\,(1 - N/K)$
Consumption of prey (**c**)	Beddington-DeAngelis	$\mathbf{c} = \dfrac{aNP}{1 + ahN + iahP}$
	Hassell-Varley-Holling	$\mathbf{c} = \dfrac{\alpha_m\left(\dfrac{N}{P^m}\right)P}{1 + \alpha_m h\left(\dfrac{N}{P^m}\right)}$
Predator death (**d**)	ALL	$\mathbf{d} = \mu\,P$
Enforced mortality on prey (**emR**)	ALL	$\mathbf{emR} = \varepsilon\,N$

Figures

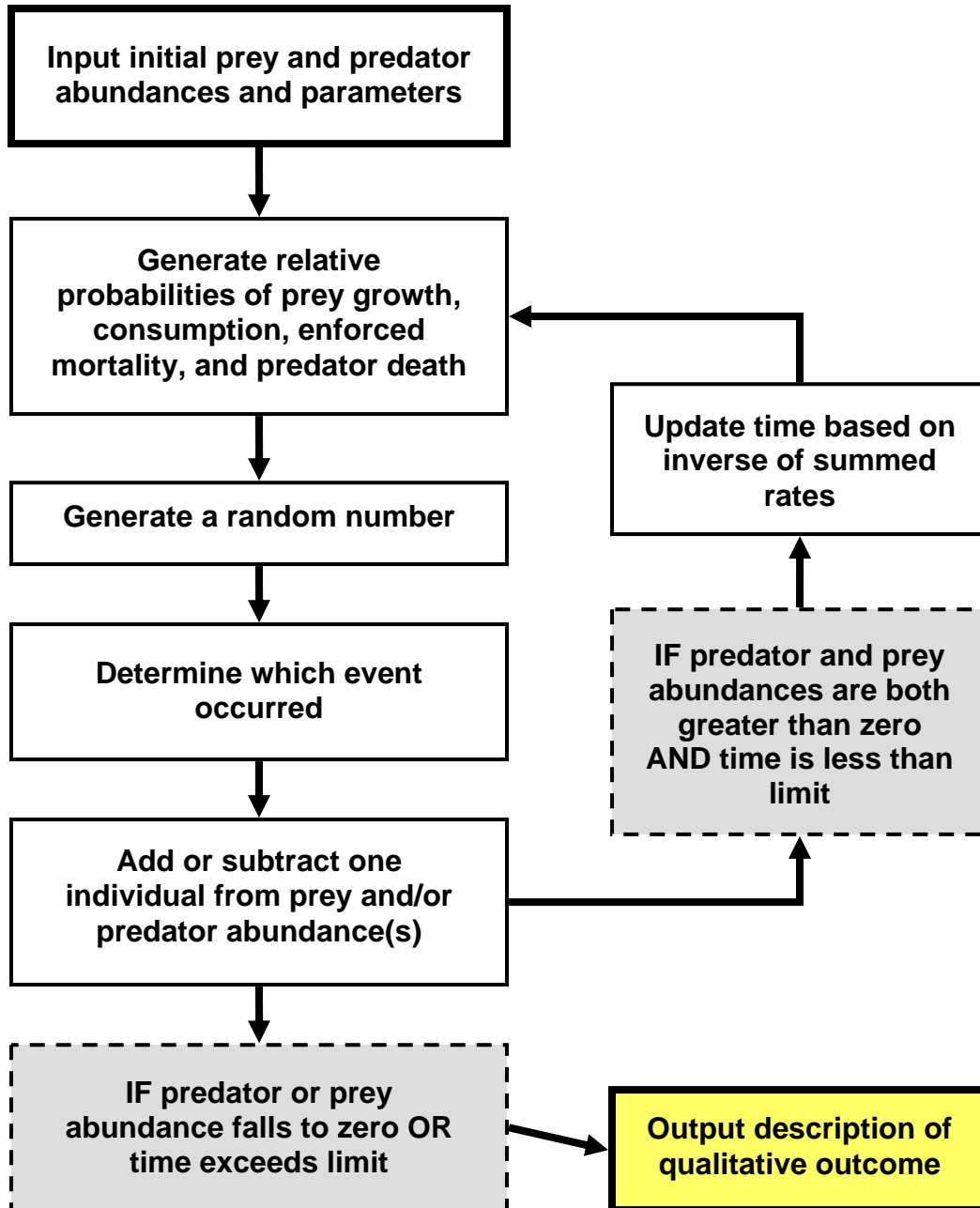**Figure 1.** Flow diagram for asynchronous discrete event simulations

Figure 2. Color guide for understanding replicate outcomes in stochastic simulations

     Because parameter space was explored using replicated stochastic simulations, each particular parameter combination can potentially produce mixed results. These mixed results are displayed by assigning each possible outcome to a channel on the RGB (red, green, blue) color system. For my simulations the three possible outcomes were: i) predator extinction (assigned RED); ii) coexistence of predator and prey (assigned GREEN); and iii) dual extinction of predator and prey (assigned BLUE). Mixed outcomes are displayed by producing a single color composed of the appropriate proportions of R, G, and B. The guide below shows a range of possible colors assigned to a variety of mixed outcomes.
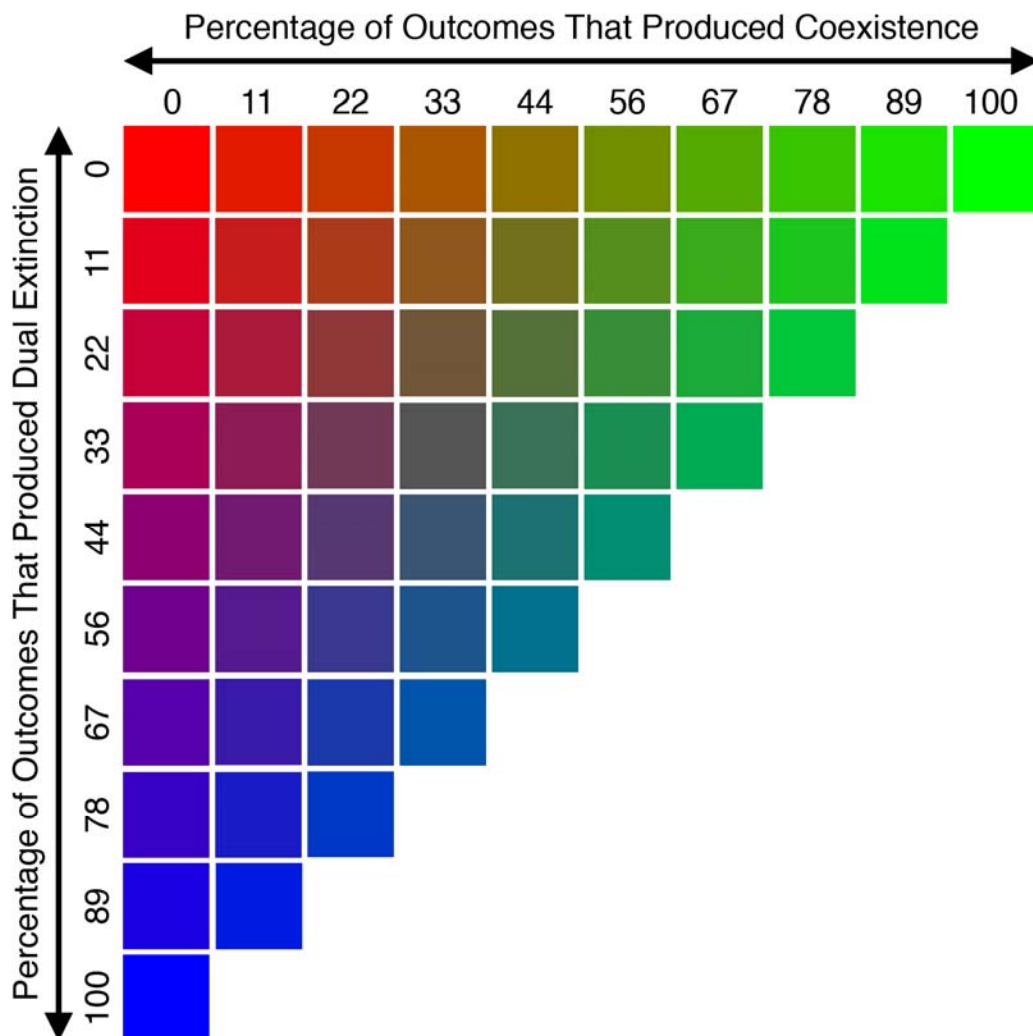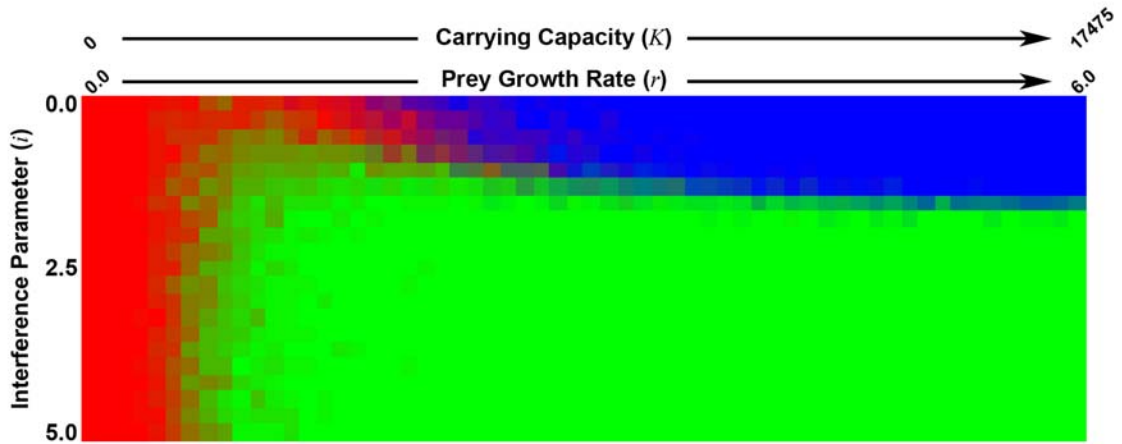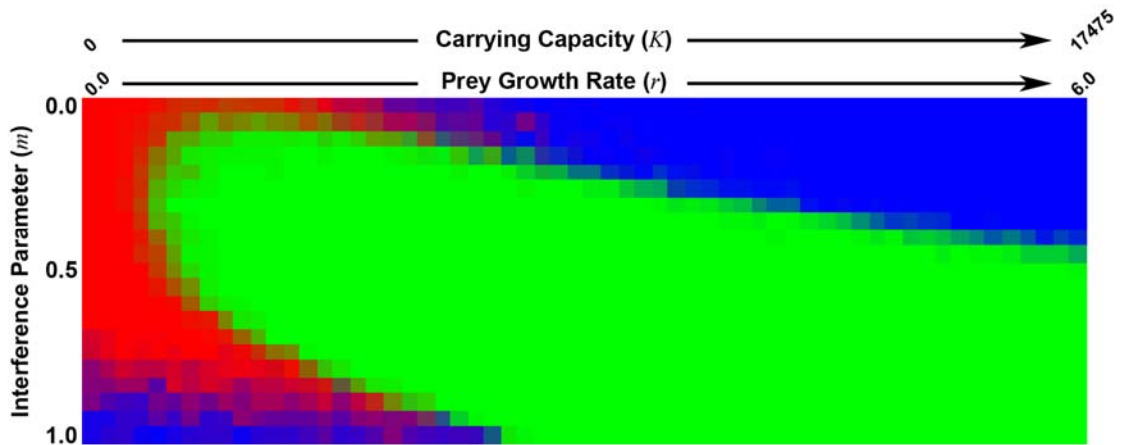
Figure 3. Stability properties of Beddington-DeAngelis versus Hassell-Varley-Holling models

Parameter spaces for the BD and HVH models using the parameters listed in **Table 1**, with 0% enforced proportional mortality. See **Figure 2** for a guide to interpreting these color-coded spaces.
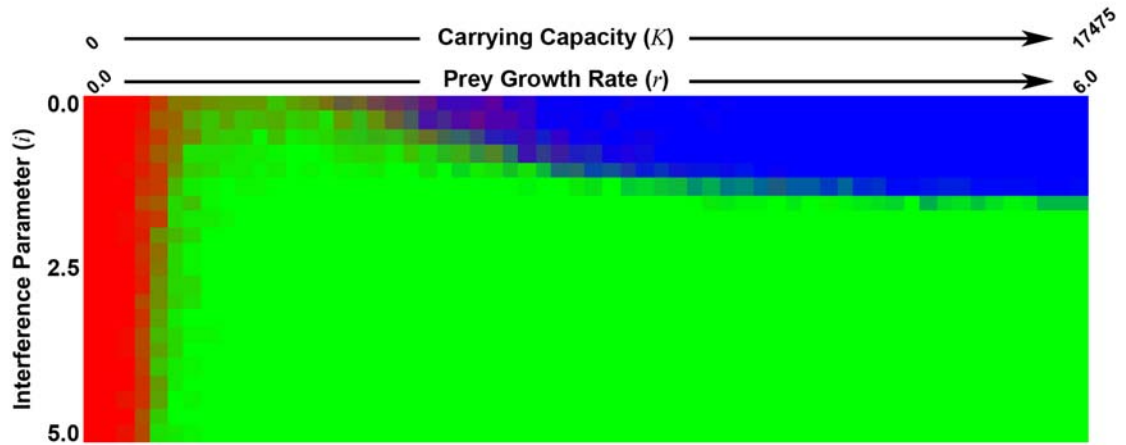
(a) Beddington-DeAngelis model with low prey (90) and low predator (35) initial abundances

(b) Hassell-Varley-Holling model with low prey (90) and low predator (35) initial abundances

(c) Beddington-DeAngelis model with high prey (300) and high predator (100) initial abundances

(d) Hassell-Varley-Holling model with high prey (300) and high predator (100) initial abundances
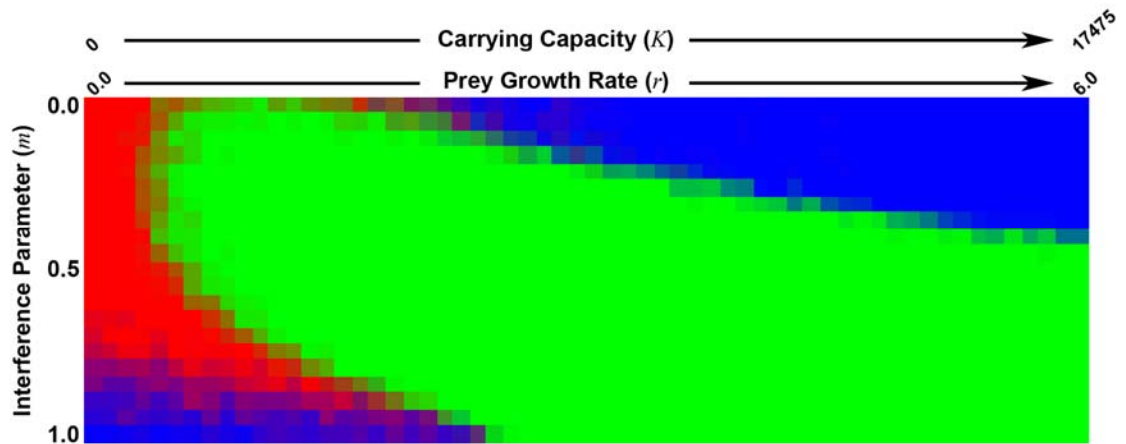
Figure 4. Effect of initial conditions on the stability properties of the Hassell-Varley-Holling model
    Parameter spaces for the HVH models using the parameters listed in **Table 1**, with 0% enforced proportional mortality and various predator and prey initial abundances. See **Figure 2** for a guide to interpreting these color-coded spaces.

(a) High Predator, Low Prey
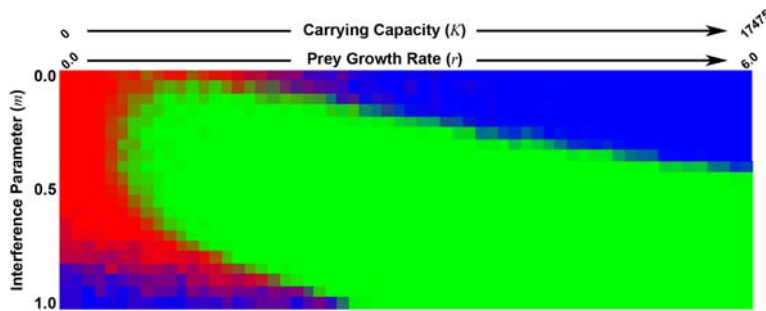
(b) High Predator, High Prey
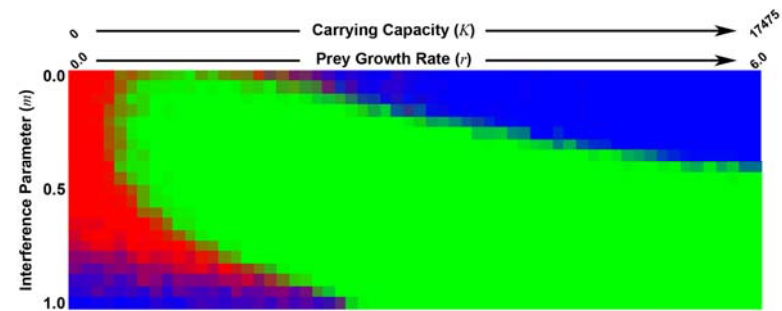
(c) Low Predator, Low Prey
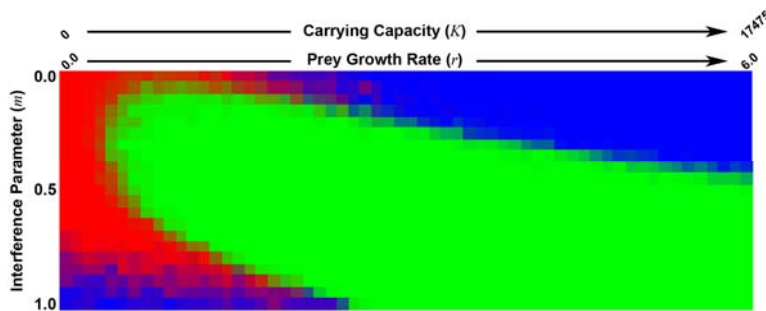
(d) Low Predator, High Prey
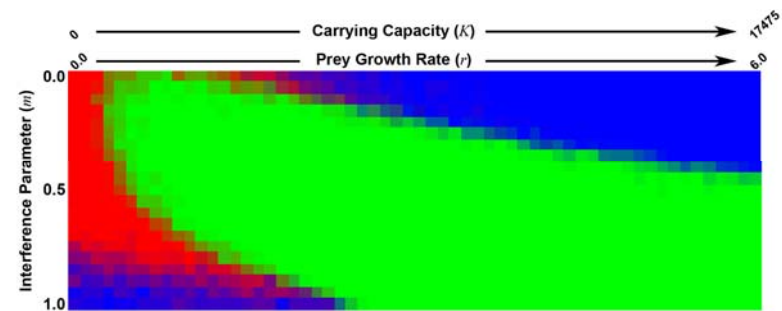
Figure 5. Effect of enforced proportional prey mortality on the Hassell-Varley-Holling and Beddington-DeAngelis models

Parameter spaces for the BD and HVH models using the parameters listed in **Table 1**, with 0% or 50% enforced proportional mortality and the high prey (300) and low predator (35) initial abundances. See **Figure 2** for a guide to interpreting these color-coded spaces.

(a) 0% prey mortality, Hassell-Varley-Holling
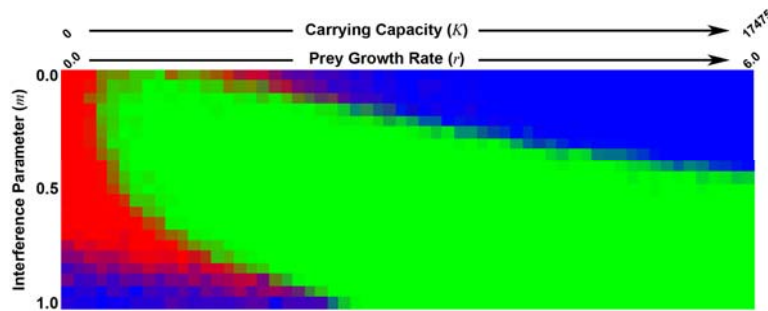
(b) 0% prey mortality, Beddington-DeAngelis
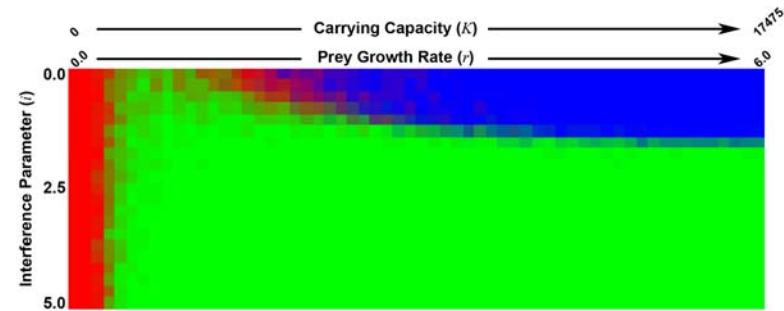
(c) 50% prey mortality, Hassell-Varley-Holling
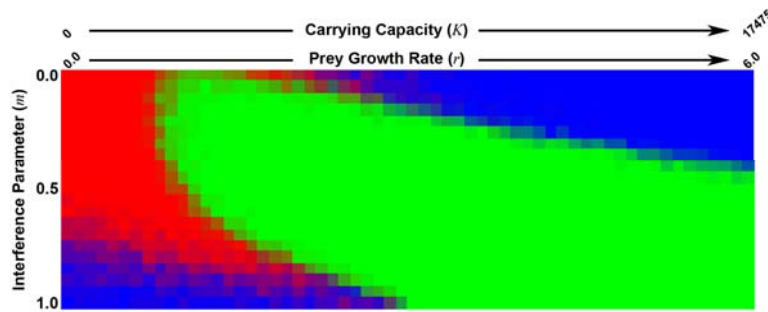
(d) 50% prey mortality, Beddington-DeAngelis
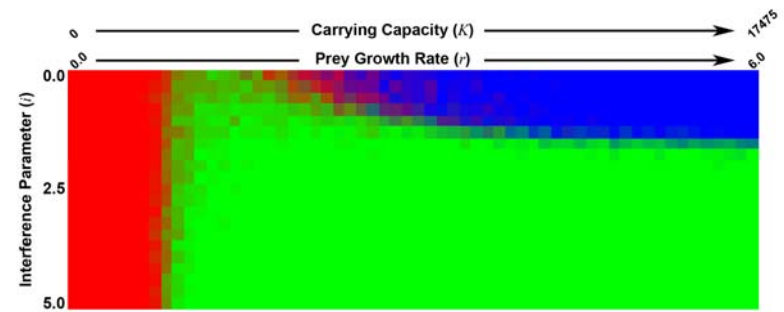
Figure 6. Large-scale equilibrial response to enrichment in the Hassell-Varley-Holling and Beddington-DeAngelis models

I have plotted response of prey (triangles) and predator (circles) abundances to increases in r and K. I display K as the independent variable; r follows the relation shown in equation (3). For various levels of interference I show the response in the HVH **(a-f)** and BD **(g-l)** models.
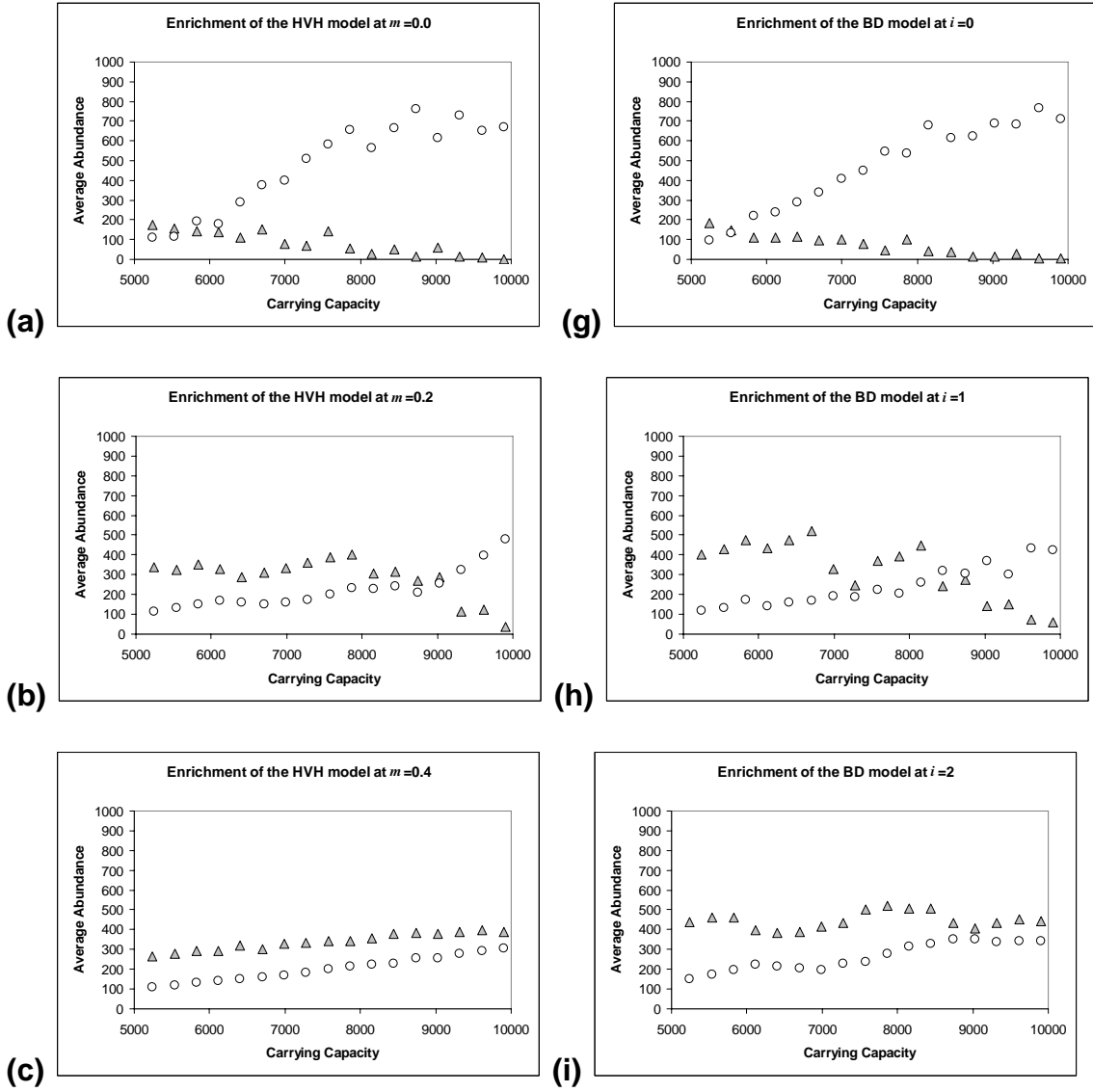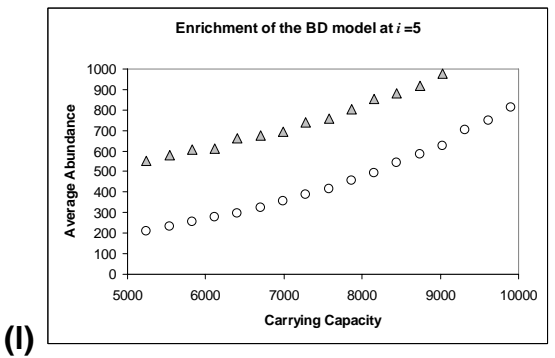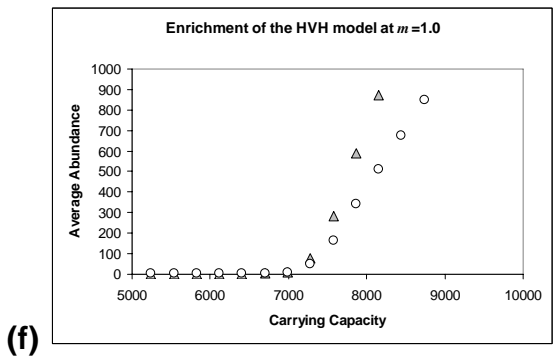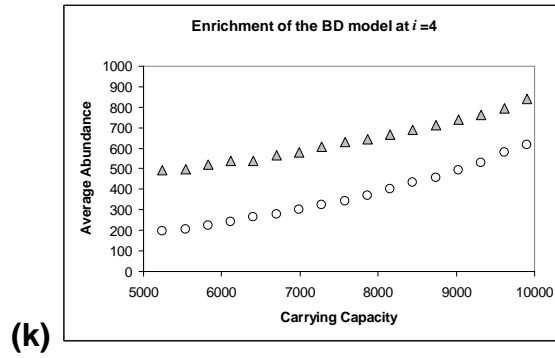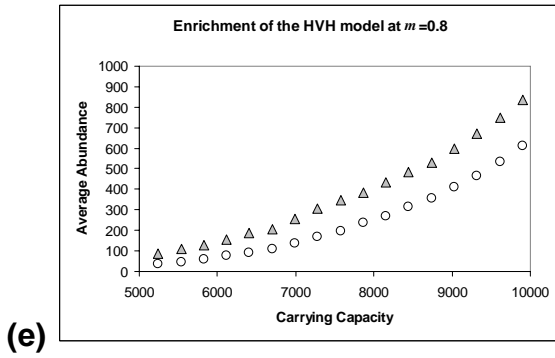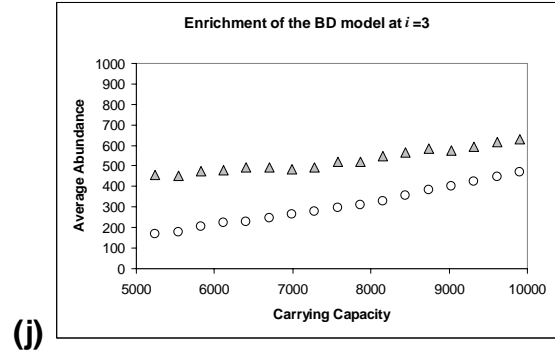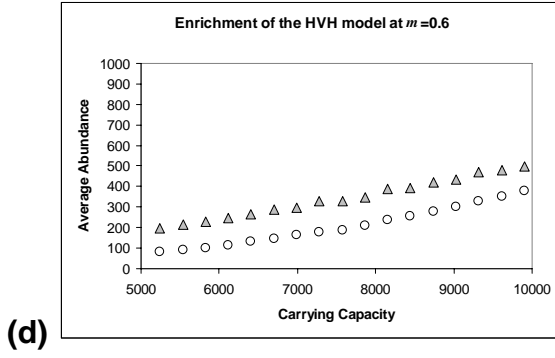
(a)

(g)

(b)

(h)

(c)

(i)

80

(d) Enrichment of the HVH model at $m = 0.6$

(j) Enrichment of the BD model at $i = 3$

(e) Enrichment of the HVH model at $m = 0.8$

(k) Enrichment of the BD model at $i = 4$

(f) Enrichment of the HVH model at $m = 1.0$

(l) Enrichment of the BD model at $i = 5$

81

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Chapter 5

A Direct, Experimental Test of Resource vs. Consumer Dependence: Comment.

Christopher X J. Jensen, Jonathan M. Jeschke, and Lev R. Ginzburg

Context:

Proponents of traditional prey-dependent theory think about predation in a manner that is fundamentally different from proponents of predator-dependent theories. This difference centers on how each side of the debate regards the time scale of consumption. In this short response to a recent experimental paper that provided direct measures of consumption, we establish that there is no *a priori* time scale of consumption. We suggest that only experiments that simultaneously measure consumption over different time scales and assay important system properties (such as stability or equilibrial response to enrichment) can resolve the debate over which functional response should be employed.

Consumer-resource system dynamics hinge upon the rate at which consumers capture, consume, and convert resources into biomass. In classical functional and numerical response theory, this rate is assumed to depend on resource density but not on consumer density (reviewed in Jeschke et al. 2002). In assuming that both densities determine this rate, consumer-dependent functional responses (e.g. Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989) challenge the resource-dependent tradition. This challenge has produced a long-standing debate (reviewed in Abrams and Ginzburg 2000). The traditional approach of fitting functional response models to time series data has yielded equivocal results (e.g. Jost and Arditi 2001) and may not be capable of resolving the debate (Lundberg and Fryxell 1995). In a recent issue of *Ecology*, Fussmann et al. (2005) tried to enrich the debate with empirical data. They described functional response experiments in the rotifer-algae system *Brachionus calyciflorus – Monoraphidium minutum* that detected consumer dependence only at unnaturally high *Brachionus* densities and concluded that consumer dependence plays only a minor rule for planktonic rotifers in natural environments. Here we outline why this conclusion is an over-interpretation of their results. Their experimental approach only considers direct physical interference between *Brachionus* and excludes all other and more important forms of consumer-dependent effects (e.g. chemically mediated interference, induced responses in the algal resource, resource depletion). Fussmann et al.'s results cannot therefore be considered as evidence against consumer dependence.

In contrast with the traditional resource-dependent form, the inclusion of a consumer-dependent functional response changes both the equilibria (Ginzburg and Akçakaya 1992, Akçakaya et al. 1995) and stability (Berezovskaya et al. 2001) of a trophic system. We agree that consumer density determines how important interference will be in a consumer-resource system (Arditi and Ginzburg 1989, Abrams and Ginzburg 2000). At very low consumer density, the functional response will be resource-dependent. At very high consumer density, the functional response will be consumer-dependent. In seeking to determine the threshold consumer abundance at which a trophic system switches from resource to consumer dependence, Fussmann et al. have correctly framed one unanswered question of consumer-resource dynamics.

However, the only form of consumer dependence detectable by their approach is direct physical interference between consumers. All other forms of interference (e.g. chemically mediated interference, induced responses in the algal resource, resource depletion) were excluded. The results of Fussmann et al. show that physical interference is not significantly influencing *Brachionus* consumption rate at naturally occurring *Brachionus* densities, but they provide no evidence for or against other more important consumer-dependent effects. Therefore, the results cannot be considered as evidence against consumer-dependent consumption.

The philosophy underlying Fussmann et al.'s experiment provides an illustrative example of a theoretical error we call *instantism* (Ginzburg and

Colyvan 2004, Jensen and Ginzburg 2005). Whenever theorists use differential equations they make assumptions about what comprises an "instant," as the *dt* in such equations represents this "instant". Our main concern is that the "instant" be consistent with the time scale of consumer reproduction, which drives the dynamics of any consumer-resource system. In contrast, instantism assumes that because in theory differential equations describe instantaneous rates, we should consider the *dt* in ecological models to *literally* represent infinitely small intervals. This modeling perspective has strong advocates (e.g. Murdoch et al. 2003) but has been questioned for decades (e.g. Arditi and Ginzburg 1989, Jensen and Ginzburg 2005). Fussmann et al. clearly advocate the instantist view when they criticize previous studies for taking a "non-instantaneous approach to the problem"; we prefer these so-called non-instantaneous approaches, as they address the more biologically relevant time scale of consumer reproduction.

A key issue addressed by Fussmann et al. is the phenomenon of resource depletion: when consumption intervals increase, resource abundance decreases over the period during which consumption is measured. Fussmann et al. treat resource depletion as a source of error in measuring the functional response; to minimize this error the experimenters have monitored consumption over an extremely short time interval. The scale of this interval is clearly designed to observe behavioral phenomena, ignoring the fact that the reproductive time scale (i.e. the *dt* in the consumer equation) involves a much longer interval (Arditi and Ginzburg 1989). Given that the generation time of *B. calyciflorus* is approximately 5 days (Fontaine and Gonzalez 2005), the four-minute consumption interval Fussmann et al. used is three orders of magnitude smaller than the focal consumer's reproductive interval. This massive discrepancy between the measured (behavioral) time scale and a biologically and dynamically relevant (reproductive) time scale leads us to question whether these results provide any evidence for using the resource-dependent functional response in dynamic models of this or any other system .

Consumer-resource models should accurately capture the consequences of consumption: whether or not the systems are stable, and the densities at which stable systems equilibrate. These consequences result from both the functional response and the numerical response. Even organisms like *Escherichia coli*, which seemingly reproduce continually, do not respond *numerically* to changes in resource abundance instantaneously (i.e. on the time scale of cell division). A delay always exists between changes in consumption and the resulting effects on reproduction, and this delay introduces the potential for resource-depletion effects. Consumer-dependent functional responses may account for these delays and bridge the gap between the time scales of consumption (i.e. functional response) and reproduction (i.e. numerical response).

Resource depletion should not be treated as an error but as a biologically important phenomenon. The experiments of Salt (1974) provide an illustrative example. Salt measured the consumption rate of *Didinium* on *Paramecium* at hourly intervals. While this time scale is still about one order of magnitude

smaller than the reproductive time scale of *Didinium* (Veilleux 1979), it allowed Salt to observe clear consumer dependence in his functional responses. Even when every consumptive and reproductive act can be monitored, as is the case with wolf and moose on Isle Royale (e.g. Vucetich et al. 2002), the time interval over which consumption is integrated influences the degree of consumer dependence observed (Ginzburg and Colyvan 2004, Jost et al. 2005). Because the functional response can vary in response to the chosen consumption interval, the debate over which functional response form to use really centers on identifying the appropriate consumption interval. This unanswered question is not a question for Fussmann et al.: they assume that the smallest consumption interval is the only biologically relevant interval. All we can learn from the experiment of Fussmann et al. is that physical interference is not important at natural densities in this system: their experiment does not address the dynamic consequences of functional response, so we cannot conclude that the consumptive interval employed is correct for even this system.

Accordingly, we reject the contentions of Fussmann et al. that their experiment represents "treatment of the most general case" and warn ecologists against their suggestion that "[resource] dependence… should be the norm in dynamical mathematical models." If we want to use the results of short-term experiments like that of Fussmann et al. to parameterize our model, we need to make the model consistent with the varying time scales of consumption and reproduction. Such an "instantaneously realistic" model would have to take into account the discrete nature of reproduction (we suggest an integro-differential equation), spatial heterogeneity, and a host of other potential mechanisms that, over biologically reasonable time periods, appear to produce a degree of consumer dependence. Such a model would be overly complex, heavily over-fitted, and impossible to parameterize with any confidence (Ginzburg and Jensen 2004). Instead of taking the instantist stance and using the resource-dependent functional response as the building block of a complex, analytically intractable model, we suggest that ecologists consider using the appropriate consumer-dependent functional response (e.g. Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Arditi and Ginzburg 1989). In doing so, we are suggesting that ecological modeling should broaden its understanding of mechanism beyond the behavioral time scale.

Fussmann et al. assert that "it is obviously true that consumption will be exclusively resource-dependent if consumer density is extremely low because interference cannot occur." We suggest that it is almost equally obvious that consumption will be resource-dependent if the measured consumptive interval is very low (only direct physical interference, which is usually relatively unimportant, produces detectable consumer dependence). Over appropriate time intervals – those closer to the consumer's generation time – natural densities of consumers will produce consumer-dependent effects. We already have strong experimental evidence (as reviewed in Fussmann et al. 2005) that over longer consumptive intervals, consumer dependence emerges. An important unanswered question remains: "What is the appropriate time interval over which to measure the

functional response?" If we want to use functional responses to better understand or even predict population dynamics, we should also measure functional responses on the time scale of population dynamics. Most of the 814 responses recently reviewed by Jeschke et al. (2004) were not measured on this time scale, and those that were did not discriminate between resource and consumer dependence. A few experiments have contrasted the predictions of resource and consumer-dependent functional responses in terms of predicted equilibria (Bohannan and Lenski 1997, Kaunzinger and Morin 1998) and stability (Fussmann et al. 2000), but these experiments did not measure the functional response, even over a single time interval. In order to provide better advice to ecologists who want to build models of trophic interaction, we need experiments that simultaneously compare the functional response measured at a variety of time intervals with the equilibrial and stability properties of a dynamic system. For instance, the experimental system of Fussmann et al. could be used to explore the effect of system enrichment on equilibrial resource abundance (Oksanen et al. 1981, Ginzburg and Akçakaya 1992); contrasting this result with direct measures of functional response over varying consumptive intervals would provide a more valuable insight into what form functional response should take. Results of this kind are more likely to suggest a biologically relevant functional response.

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Chapter 6

Direct measurements of functional response over varying time intervals in the Paramecium-Didinium system

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and Aby Joseph

Context:
Using consumption data gathered at a variety of predator densities and over variety of time intervals, we demonstrate that per capita consumption rate decreases with increasing predator density. Our experiments provide a basis for future work with the potential to link the short-term predator consumption patterns to long-term dynamic predator-prey outcomes.

Introduction

While the prey- and ratio-dependent models have garnered the most attention from theorists, the functional response that most likely represents natural systems lies somewhere between these extremes (Abrams and Ginzburg 2000). Unlike the prey-dependent limit myth, predator-dependent functional responses (e.g. Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975) incorporate mutual interference between predators. Unlike the ratio-dependent limit myth, the Beddington-DeAngelis (BD) and Hassell-Varley-Holling (HVH) models allow for the incorporation of low to moderate levels of interference between predators.

Each of these models can theoretically act as intermediates between the prey- and ratio-dependent limits. The HVH model has the form:

$$f\left(\frac{N}{P^m}\right) = \frac{\alpha_m\left(\dfrac{N}{P^m}\right)}{1 + \alpha_m h\left(\dfrac{N}{P^m}\right)} \tag{1}$$

where N is the abundance of prey, P is the abundance of predators, h is the handling time per prey, α_m is the capture efficiency, and m is a parameter expressing the degree of predator interference. For the HVH model, the interference parameter (m) creates a clear continuum between the traditional prey-depenendent model (for which $m = 0$) and the newer ratio-dependent alternative (for which $m = 1$).

The BD model does not bridge the gap between the extreme models with such simplicity. Its most basic formulation is:

$$f(N) = \frac{aN}{1 + ahN + iahP} \tag{2}$$

where a is the capture efficiency of predators on prey and i is the interference parameter. In order for this model to produce ratio dependence we must assume that $P \to \infty$, as follows:

$$f(N) = \frac{aN}{1 + ahN + iahP} \tag{3a}$$

$$= \lim_{P \to \infty} \frac{aN}{1 + ahN + iahP} \tag{3b}$$

$$= \frac{aN}{ahN + iahP} \tag{3c}$$

$$= \frac{\frac{1}{ih}N\big/P}{1 + \frac{1}{i}N\big/P} \tag{3d}$$

This interpretation is problematic in that it does indicate how dense predators need to be in order to approximate ratio dependence. One of the goals of this study is to consider how increasing predator density influences the form that the functional response should take.

Experiments that directly measure consumption have been used for decades to estimate functional response. Only a small subset of these studies vary both predator and prey abundances (e.g. Salt 1974, Mills and Lacan 2004, Schenk et al. 2005), a prerequisite for determining the degree of predator interference. Although these studies often detect significant predator interference, they have been criticized (Fussmann et al. 2005) for ignoring the effects of predator depletion. Whether or not prey depletion is a biologically important process that should be taken into account by the functional response (Jensen et al. *In Press*) or a source of experimental error leading to false detection of predator dependence (Fussmann et al. *In Press*) remains an important unanswered question. The common point of agreement in this debate is that functional response ought to be measured over a period of time that leads to meaningful predictions of the predator-prey dynamics.

Our goal was to ascertain the effect of consumption interval on the degree of predator interference detected in a commonly-studied predator-prey system. We used the *Didinium-Paramecium* system to consider how varying numbers of predators affect the per capita consumption rate over three different consumption intervals. By understanding how prey depletion functions in a real system, we hope to eventually make the link between measuring functional response and accurately predicting dynamic behavior.

Methods

Throughout this experiment, we used the bactiverous protozoan *Paramecium aurelia* (ATCC) and its predator, *Didinium nasutum* (Carolina Biological Supply). We cultured *Paramecium* in 100 mL volumes of 0.45 g/L protozoan pellet medium with two wheat seeds (Carolina Biological Supply). We allowed cultures to grow for at least 7 days before using them for experimental runs. In order to maintain sufficient predator stocks, we introduced *Didinium* to dense cultures of *Paramecium*, transferring a subsample of each system to a fresh culture once *Didinium* had completely consumed all prey.

93

Twenty-four hours prior to each experimental run, we washed *Paramecium aurelia* in artificial pond water (ddH$_2$O containing 0.1 mM CaCl$_2$, 0.1 mM NaCl, 1.0 mM KCl, Total Molarity = 0.0012 M) in order to remove all nutrient sources from their surrounding media and thereby prevent fission during experimental runs. To perform these washings, we withdrew 20 mL of *Paramecium* in protozoan pellet media into a 50 mL syringe. In order to minimize the amount of particulate matter entering the syringe, we allowed ample time for settling prior to removing the sample. We pushed this sample through an inline syringe filter cartridge containing two Pall 10 μm polypropylene separators (part #61756), trapping the *Paramecium* on the filter. Using a second syringe, we pushed 5 mL of artificial pond water through the filter. Finally, using a third syringe (also containing artificial pond water) attached to the outlet side of the inline filter cartridge; we expelled the *Paramecium* into 3 spot depression plates. Through a series of pilot studies (A. Joseph, personal communication) we demonstrated that growth by fission ceased in these cultures well within the twenty-four hour period their use in our experiment.

At the beginning of each experimental run, we transferred thirty (30) washed *Paramecium aurelia* via mouth pipet into each of fourteen (14) depression plate wells each containing 100 μL of artificial pond water. We then transferred by mouth pipet variable numbers of *Didinium nasutum* (zero, two, five, or ten individuals) in a spatially randomized pattern. For each run of the experiment, we used four wells for each of the three *Didinium* densities and two wells for the control containing no *Didinium*. Each well was sealed with several drops of paraffin oil to prevent evaporation. For each well we established a known start time by censusing *Paramecium* and *Didinium* and using mouth pipetting to bring abundances back to original numbers of thirty prey and zero, two, five, or ten predators.

We re-censused each well every sixty (60) minutes and returned the system to its original abundances by transfer of new individuals. We interpreted all decreases in *Paramecium* abundance as due to consumption by *Didinium*. We generally ran the experiment for a total of four 60-minute periods, producing four replicate consumption rates per well. We ran the same protocol on June 14th, 16th, 19th, and 23rd of 2006; only three intervals were run on the 14th. In total there were 180 replicates, 60 for each predator number treatment.

To determine the consumption rate over longer time intervals, we used modified protocols that incorporated 30 and 120 minute consumption intervals. For the 30 minute protocol, we used half as many replicates per experiment (2 per treatment plus 1 control) and eight rather than four intervals per day. The 30-minute experiments were run on July 3rd and 10th of 2006, producing a total of 96 replicates, 32 per predator number treatment. For the two-hour protocol, we doubled the length of the experimental "day" by retaining four 120 minute intervals and the same number of replicates as the 60-minute protocol. The 120-minute experiments were run on June 28th and 30th and July 7th of 2006, producing a total of 144 replicates, 48 per predator number treatment.

We used *MS Excel* to organize our data and produced plots and performed ANOVA using *R*. Raw data, calculations, and data analysis are available by request from Christopher Jensen.

Results
All three time intervals showed a decrease in per capita consumption rate at higher predator densities (**Table 1**). The severity of this effect varied, with the largest decreases in consumption rate at the longer intervals. As **Figure 1** demonstrates, the 30- and 60-minute interval experiments showed comparable decreases in consumption rate with increasing predator density; the depression of consumption rate was greater over the 60 minute interval but only slightly. The overall consumption rate for the 120-minute interval was much lower than that of the 30- or 60-minute intervals. Average consumption rates per interval (30, 60, or 120 minutes) are shown in **Table 2**. As expected, the total number of prey consumed during the 60 minute interval was greater than for the 30-minute interval. Unexpectedly, the total number of prey consumed during the 120-minute interval was less than during the 60-minute interval; because the experiment was not blocked for time interval, we cannot rule out the possibility that conditions varied significantly between intervals.

For ANOVA we employed a factorial model that considered the number of predators per experimental arena, date of the experiment, and sequence in experimental run as treatments. We corrected for the error associated with individual wells as repeated measures over the sequence in each experimental run. **Table 3** shows the ANOVA for the 96 replicates of the 30-minute treatment; none of the differences in consumption rate were significantly accounted for by any of the factors considered. **Table 4** displays the ANOVA for the 180 replicates of the 60-minute treatment; for this set of experiments, the number of predators, date of experiment, and a date of experiment-by-sequence of experimental run interaction were all significant contributors to differences in the consumption rate. **Table 5** shows the ANOVA for the 144 replicates of the 120-minute treatment; for this set of experiments, we detected significant treatment effects for the number of predators and sequence in experimental run.

Discussion
Inspired by the work of George Salt (1974), our goal was to determine if the *Didinium-Paramecium* system can be used to understand explicitly the role that prey depletion plays in a predator-prey system. If the effects of prey depletion can be adequately understood in these systems, we can begin to determine whether or not the dynamic properties of the system are best predicted by functional responses that exclude (i.e. the Holling Disc Equation) or include (i.e. predator-dependent forms) prey depletion as an important process (Jensen et al. *In Press*).

This work is clearly in its early stages. Although we were able to replicate Salt's basic finding that higher predator densities lead to lower per capita consumption rates (**Table 1**), our methodology lacks the refinement required to

truly tackle this problem. We did not block our interval treatments because doing so would have added an intractable level of complexity to an already-difficult experiment. An ideal protocol would have allowed for the simultaneous running of 30-, 60-, and 120-minute treatments; while this is not impossible, in practice we found it difficult to design and run such an experiment. Our hope was that the laboratory conditions we maintained would be uniform enough to prevent significant error due to running different treatments on different days. In reality, we found that predator consumption rates did vary from day to day. This can be seen most clearly by considering the overall consumption rate averages per interval for each time interval treatment (**Table 2**). While prey depletion can reduce the number of prey consumed per unit of time, we still expect that more prey will be consumed over longer periods of time. In our experiments, we found that this was not the case: during the 120-minute interval *Didinium* actually showed a lower total amount of consumption than in the 60-minute interval. We have found that the quality and viability of *Didinium* varies significantly from week to week, and our findings suggest that experiments of this type must be adequately blocked in order to discover the effect of consumption interval on consumption rate.

While we were not able to compare the effects of different consumption intervals, we were able to analyze the role of various factors within each interval treatment. If prey depletion is the chief factor accounting for the appearance of interference in these systems, we expect that the effects of predator number should be strongest in the longest treatment. This is only in part true. For the 30-minute consumption interval (**Table 3**), the number of predators was not a significant predictor of consumption rate. For both the 60- (**Table 4**) and 120-minute (**Table 5**) treatments, predator number was a significant predictor, although this significance was marginal for the 120-minute interval. This is counter to our prediction, which states that the effect of predator number should be strongest in the longest interval. Again, we suspect that temporal variation in *Didinium's* consumptive ability led to uncontrolled variation between experimental runs.

Interestingly, only the 60-minute interval treatment showed a significant effect of date of experiment. The 60-minute experiments were the first that we ran (see **Methods**). The 30- and 120-minute experiments were intermixed at later dates, and apparently there was less variation in these experimental dates. If there was not a significant effect of experimental date within either of these two intermixed experimental treatments, why did the 120-minute treatment produce such lower consumption rates? One explanation would be a change in the predatory efficiency of *Didinium*, a phenomenon we have indirectly observed during periods of time where *Didinium* cultures crash even under ideal conditions. A second explanation is predator satiation, an effect that should be stronger in the 120-minute experiments, which ran for twice as long as the other experiments. Further explanation of predator satiation is important, as in experiments of this kind its effects can be mistaken for interference between predators.

96

An additional methodological problem lies in the unbalanced nature of our experiments. While we suspect that the lack of significance in the 30-minute treatment arises from less prey depletion over the shorter time period (suggesting that much of the "apparent interference" we see is simply due to prey depletion), the fact that our three treatments were replicated at different levels prevents their accurate comparison. In order to level the playing field in terms of experimental power, we also ran ANOVA's on the 60- and 120-minute treatments for data sets that had been reduced to 96 replicates by the arbitrary removal of data from one or more experimental dates. For the 60-minute interval, number of predators was still a significant factor in explaining consumption rate. For the 120-minute interval, reducing the statistical power removed the significance of the number of predator treatment. Clearly, in the future the level of replication used in the 60-minute treatments should be used in a design that blocks for consumption interval.

One noteworthy feature of our experiments is that they subject particular wells of predators to a sequence of repeated consumptive intervals. We controlled for this in our analysis by introducing an error term for individual wells that considered how the experimental sequence influenced the measured rate. We found that the influence of wells was generally not significant; only in the 120-minute treatment (**Table 5**) was the sequence of consumption rates influenced by the well.

If we are to link direct measurements of functional response to experiments that assay critical dynamic properties of predator-prey systems, we need to discover systems in which both measurements can be made. Although our experiments require refinement, they represent a first step towards making laboratory estimates of functional response in a system that can also be used to understand dynamic properties (e.g. Luckinbill 1973, Veilleux 1979). Future studies need to meaningfully contrast the dynamic predictions of competing functional responses and then match those predictions to the measured consumption patterns of real systems. In particular, we would like to know whether measuring functional response over longer intervals leads to more or less accurate predictions of dynamic behaviors.

Tables

Table 1. Average consumption rates per hour for varying numbers of predators and consumption intervals

Number of Predators	30 minute interval		60 minute interval		120 minute interval	
	Per Predator Consumption Rate	Decline from Two-Predator Rate	Per Predator Consumption Rate	Decline from Two-Predator Rate	Per Predator Consumption Rate	Decline from Two-Predator Rate
2	2.64	*n/a*	2.61	*n/a*	1.04	*n/a*
5	1.88	0.71	2.05	0.78	0.64	0.62
10	1.62	0.61	1.27	0.49	0.53	0.51

Table 2. Total average consumption per interval for varying numbers of predators and consumption intervals

Number of Predators	Per Interval Consumption Rate (30 minutes)	Per Interval Consumption Rate (60 minutes)	Per Interval Consumption Rate (120 minutes)
2	2.64	5.22	4.15
5	4.70	10.24	6.44
10	8.11	12.71	10.56

Table 3. Analysis of Variance for 30 Minute Interval

Source of Error	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Probability Value (>F)
Error: Well					
Number of Predators	1	15.018	15.018	1.575	0.2449
Date of Experiment	1	12.930	12.930	1.356	0.2778
Number of Predators x Date of Experiment	1	17.454	17.454	1.830	0.2131
Residuals	8	76.282	9.535		
Error: Well x Sequence in Run					
Sequence in Run	1	12.164	12.164	1.379	0.2740
Number of Predators x Sequence in Run	1	2.118	2.118	0.240	0.6372
Date of Experiment x Sequence in Run	1	11.816	11.816	1.340	0.2805
Number of Predators x Date of Experiment x Sequence in Run	1	2.946	2.946	0.334	0.5792
Residuals	8	70.554	8.819		
Error: Within					
Residuals	72	588.40	8.17		
TOTALS	95				

Table 4. Analysis of Variance for 60 Minute Interval

Source of Error	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Probability Value (>F)
Error: Well					
Number of Predators	1	54.290	54.290	18.468	**0.0001**
Date of Experiment	1	15.035	15.035	5.114	**0.0290**
Sequence in Run	1	5.226	5.226	1.778	0.1896
Number of Predators x Date of Experiment	1	2.771	2.771	0.943	0.3372
Number of Predators x Sequence in Run	1	2.663	2.663	0.906	0.3467
Residuals	42	123.468	2.940		
Error: Well x Sequence in Run					
Sequence in Run	1	13.041	13.041	3.261	0.0778
Number of Predators x Sequence in Run	1	8.763	8.763	2.191	0.1459
Date of Experiment x Sequence in Run	1	25.633	25.633	6.410	**0.0150**
Number of Predators x Date of Experiment x Sequence in Run	1	10.440	10.440	2.611	0.1133
Residuals	44	175.951	3.999		
Error: Within					
Residuals	84	147.030	1.750		
TOTALS	179				

Table 5. Analysis of Variance for 120 Minute Interval

Source of Error	Degrees of Freedom	Sum of Squares	Mean Squares	F Value	Probability Value (>F)
Error: Well					
Number of Predators	1	5.584	5.584	3.944	**0.0557**
Date of Experiment	1	1.200	1.200	0.848	0.3641
Number of Predators x Date of Experiment	1	2.524	2.524	1.783	0.1912
Residuals	32	45.313	1.416		
Error: Well x Sequence in Run					
Sequence in Run	1	4.131	4.131	9.691	**0.0039**
Number of Predators x Sequence in Run	1	0.0820	0.0820	0.1923	0.6639
Date of Experiment x Sequence in Run	1	0.0840	0.0840	0.1971	0.6601
Number of Predators x Date of Experiment x Sequence in Run	1	0.0526	0.0526	0.1234	0.7277
Residuals	32	13.6408	0.4263		
Error: Within					
Residuals	72	25.479	0.354		
TOTALS	143				

101

Figures

Figure 1. Average per capita per hour consumption rates for the three interval experiments.
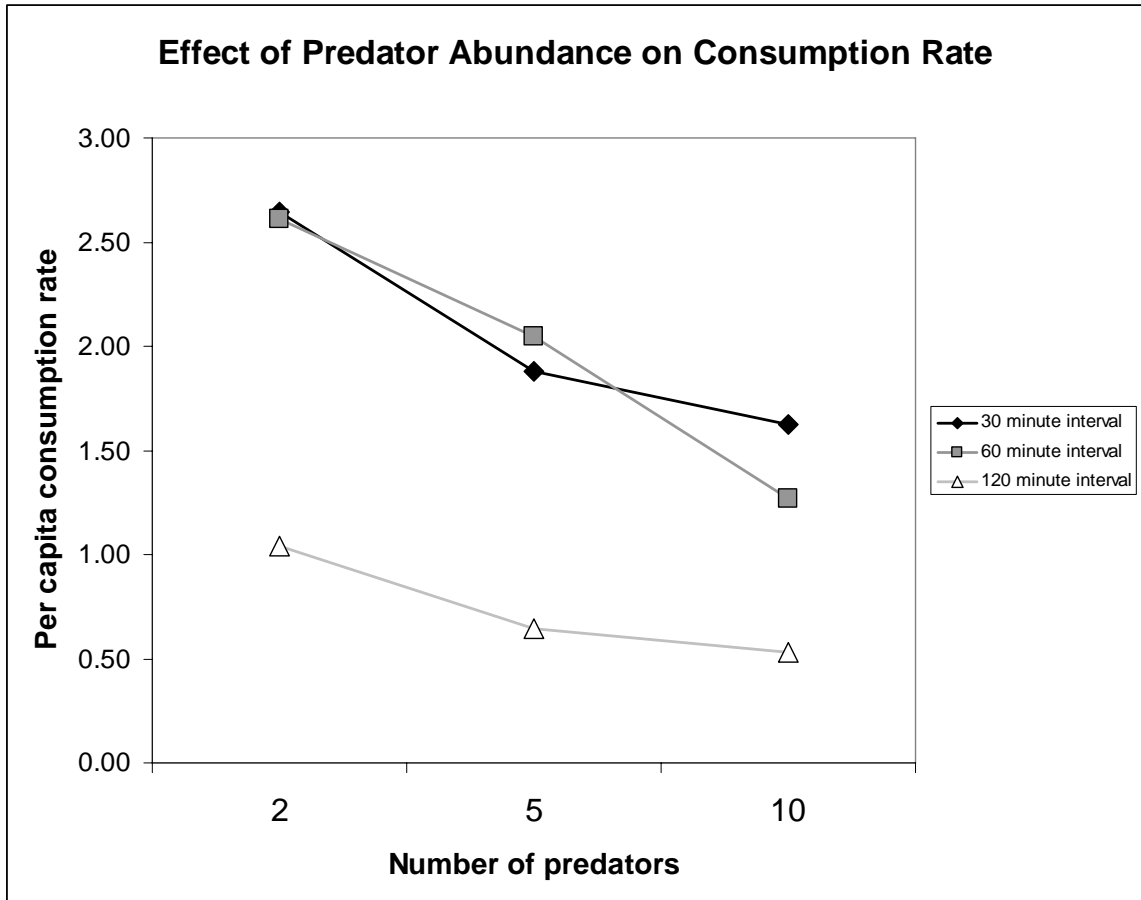
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Appendices

**Appendix A.** The non-deterministic explanation of dual extinction and predator extinction

Under the prey-dependent model, true deterministic prey extinction is a mathematical impossibility. As shown below, a vertical predator isocline that intersects with the prey isocline far to the left of its apex produces a limit cycle that comes very close to but never actually touches the predator and prey axes:
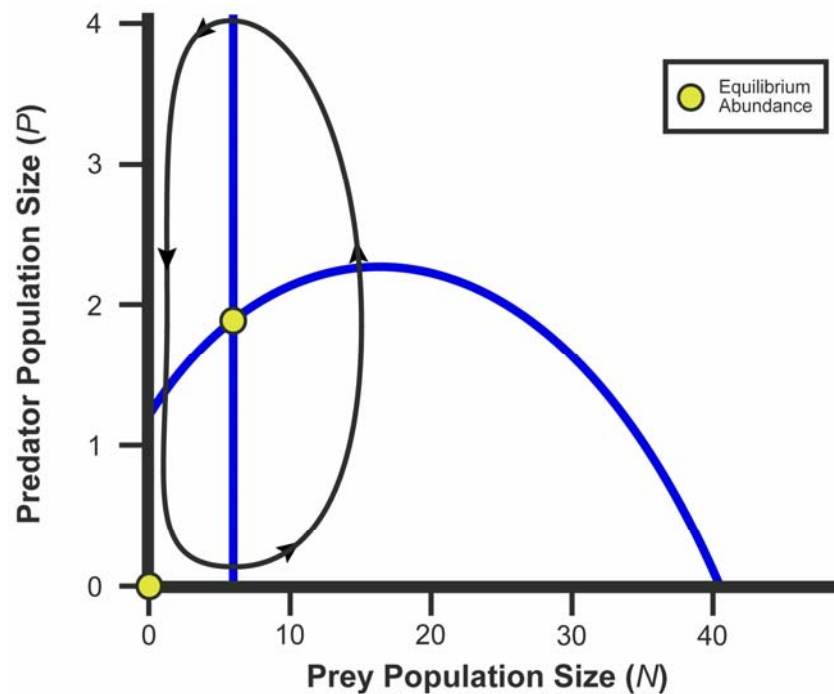
Because deterministic extinction is not possible under prey-dependence, non-deterministic explanations of extinction must be invoked. Two forms of non-deterministic extinction are reasonable: (i) extinction due to the discrete nature of natural populations; and (ii) extinction due to stochastic forces. As the phase space above suggests, the trajectory of the two populations may bring the system to abundances below one individual. While such abundances may make mathematical sense, they do not make biological sense. When limit cycles bring a population to levels below one individual, extinction occurs.

Stochasticity can also produce extinction when limit cycles pass near the predator and/or prey axes. If demographic or environmental variations produce regular perturbations of the system, small populations will be expected to crash to zero with some calculable risk. As stochasticity increases and/or the limit cycle passes closer to zero, the probability of extinction should increase.

No clear experimental test for these explanations of extinction has been performed. One means of testing these explanations would be to increase the scale of the system. Such a scale change would involve only two modifications: (i) an increase in the volume of the experimental system (i.e. using a larger Petri dish); and (ii) an appropriate proportional increase in the volume of experimental media (i.e. an increase in the absolute amount, but not overall concentration, of prey food). If extinction is non-deterministic, scaling up should reduce the probability of extinction due to both discreteness and stochasticity. The system below, scaled up by a factor of ten, provides an illustrative example:
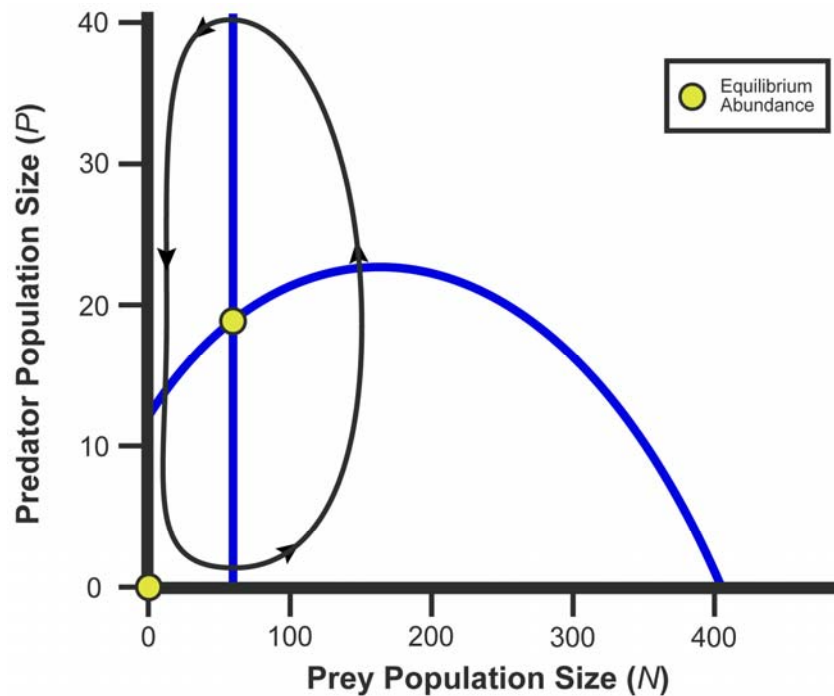

Assuming that scaling up changes the size of the system but *not* the predator and prey parameter values, the limit cycle's shape remains the same. However, the distance of this limit cycle from the axes (measured in numbers of individuals) is now greater by a factor of ten. In the hypothetical example considered above, extinction of the prey population due to the discrete nature of actual populations no longer occurs but may still be possible for the predator population. If the discrete nature of actual populations is a factor in extinction, we expect scaling up of this hypothetical system to remove prey extinction as a regular outcome.

If all other experimental conditions remain the same as we scale up the system, the scale of stochastic variation should not change. If stochastic forces account for extinction, increasing the scale of the system should reduce the probability of extinction. Whereas small perturbations were sufficient to cause the smaller system to go extinct, only larger perturbations can cause extinction in the large system, leading to a lower overall probability of extinction.

Appendix B. More on the difference in qualitative outcomes between the prey- and ratio-dependent *limit myths*

Extinction under Prey-Dependence:

The prey-dependent model can be easily understood by considering the predator and prey isoclines it produces:
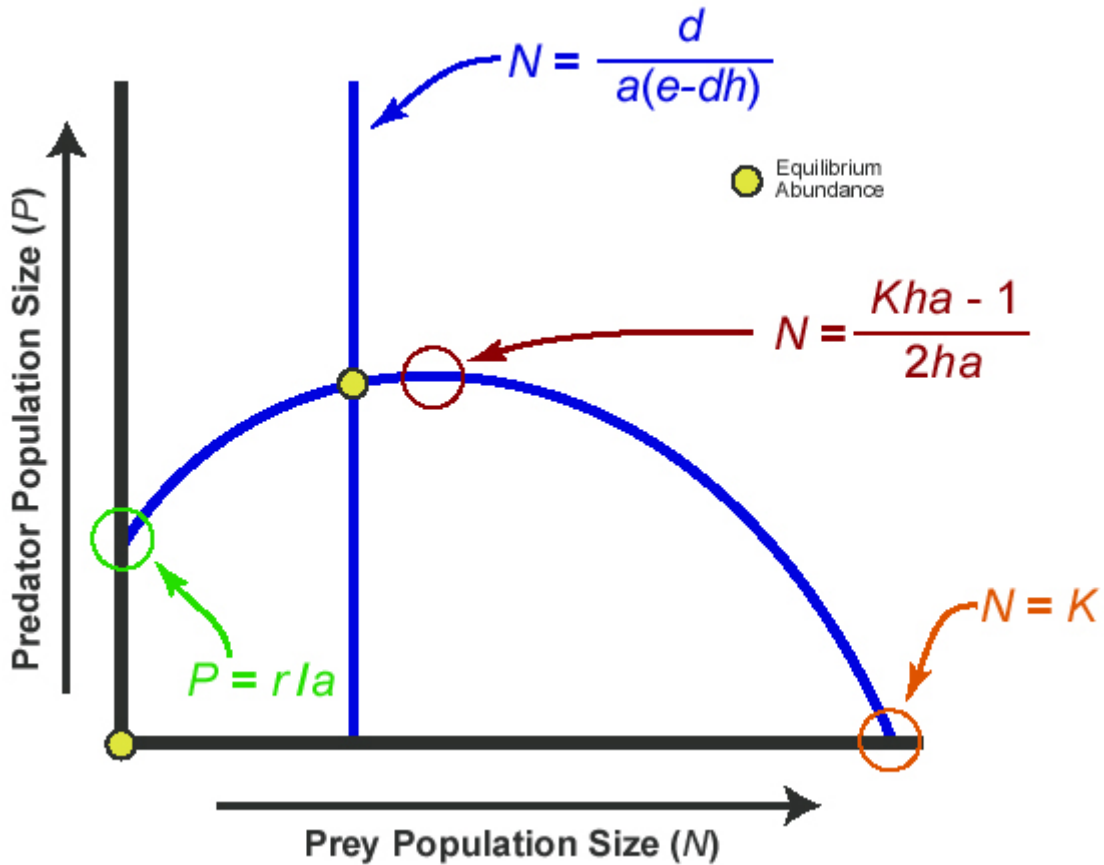

One of the most interesting properties of these isoclines is that none contain the prey growth rate parameter (r). This has mistakenly led many to conclude that the stability of the prey-dependent system is invariant to r, when in fact r is one of two parameters from which K – a critical parameter for consideration of stability – is derived (see **Chapter 3** for more on this interdependence of r and K).

Under prey-dependence, predator extinction occurs as a deterministic outcome when the vertical predator isocline is located to the right of the prey isocline zero-intersection point. Mathematically, these conditions are:

$$K < d\,/(a[e-dh])$$

In a phase space diagram, these conditions produce the following isoclines:
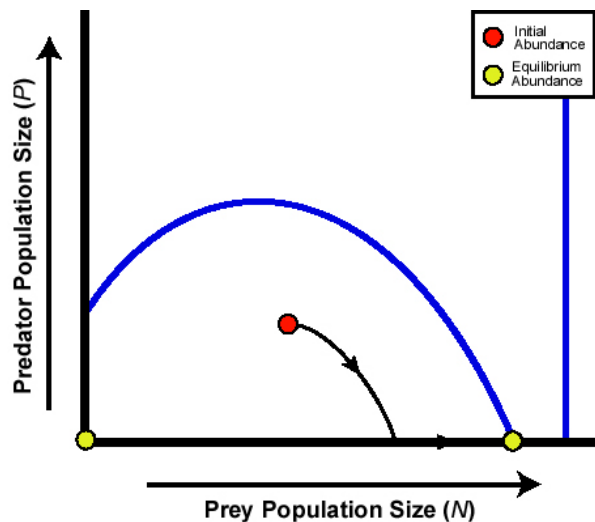
A second explanation of predator extinction, outlined in **Appendix A**, involves system trajectories that bring the predator population close enough to zero abundance that non-deterministic factors can cause extinction.

Certain coexistence in the prey-dependent model occurs when the vertical predator isocline is located between the apex and righthand zero-intersection of the prey isocline. Mathematically, these conditions are:

$$(\textit{Kha} - 1) / 2\textit{ha} < \textit{d} /(\textit{a}[\textit{e} - \textit{dh}]) < \textit{K}$$

A system in this portion of the parameter space will experience dampened oscillations towards equilibrium. In graphical form, this looks as follows:
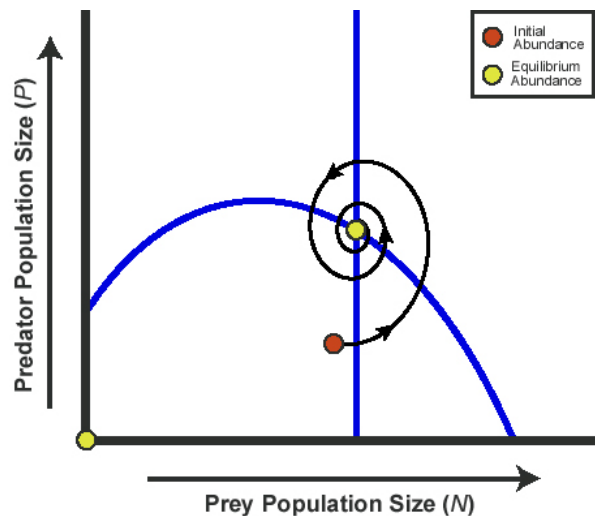

When the predator isocline is located to the left of the apex of the prey isocline,

coexistence is also possible. In general, limit cycles emerge under these conditions:

$$d\,/(a[e - dh]) < (Kha - 1)\,/\,2ha$$

If the resulting limit cycle does not come near either the predator or the prey axes, the system will experience stable oscillations. However, if this limit cycle approaches an axis, prey extinction can occur. Graphically, this looks as follows:
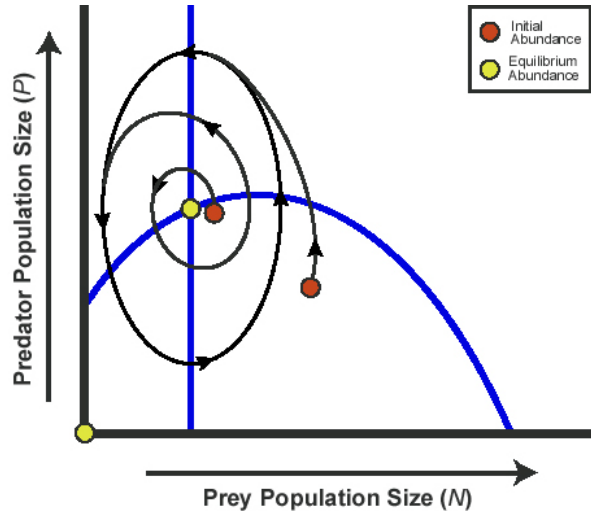
**Appendix A** discusses in greater detail the rationale behind this kind of extinction.

One problem with this non-deterministic explanation of extinction is that the transition through parameter space from coexistence to dual extinction is poorly defined. In fact, because non-deterministic extinction can result from stochastic processes, there is no true bifurcation between coexistence and dual extinction in the prey-dependent model.
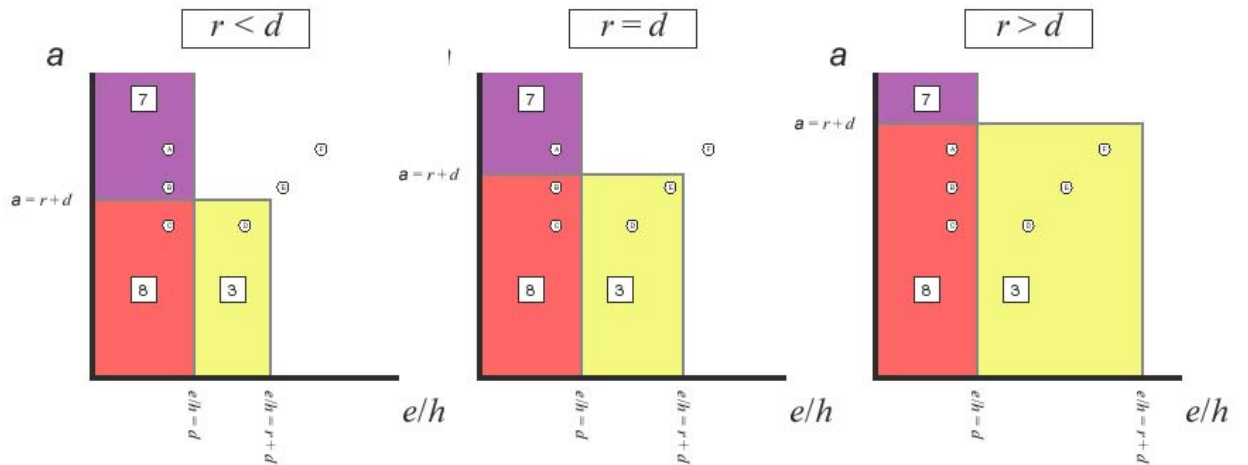
Extinction under Ratio-Dependence:

Since its introduction, the ratio-dependent model of predator-prey interaction has stimulated a flurry of mathematical effort aimed at defining its parameter space. Because the ratio-dependent model displays complex behavior around the origin, defining stability conditions is difficult. Whether or not this behavior at zero is powerful or pathological has been a source of theoretical discussion (Abrams 1994). However one considers the ratio-dependent "zero problem", one thing is clear: these behaviors prevented full understanding of the ratio-dependent model for more than a decade after its introduction.

Berezovskaya *et al.* (2001) provided a comprehensive view of the ratio-dependent parameter space. This parameter space, including the inequalities

that govern major bifurcations, is shown below:
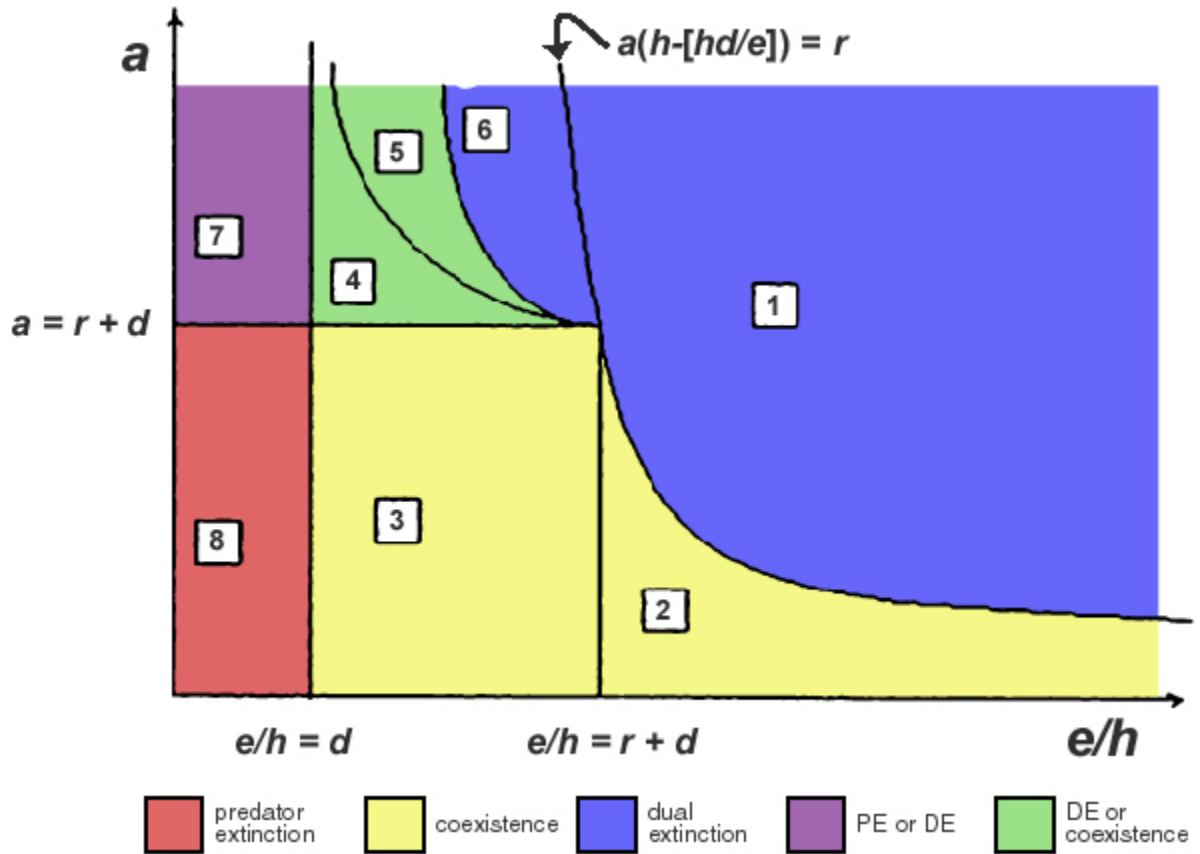
As this diagram suggests, the boundaries between different qualitative outcomes are clearly defined in the ratio-dependent model. The effect of changing parameters a, e, and h are readily apparent, as these parameters dictate movement along the axes. As the entire parameter space is scaled to the predator death rate (d), changes in this parameter serve to "shrink" or "expand" the space. The effects of changing r, a critical participant in all of the major inequalities separating outcomes, are more subtle. The relative value of r and d have a major effect on outcomes beyond the $e/h = d$ line (which separates predator extinction from coexistence), but changes in r have no effect on whether or not predators go extinct. The effect of changes to r and d can seen in the following diagram:

As r increases, the region of coexistence increases, causing the outcome of some systems to move from dual extinction into coexistence.

One interesting consequence of ratio-dependent predation is the dependence of qualitative outcomes on initial conditions. When capture efficiencies (α) are sufficiently high, we enter an area of the parameter space where qualitative outcomes depend on the initial abundances of predator and prey. This property of ratio-dependence provides an important contrast to the prey-dependent model, for which initial conditions do not determine the qualitative outcome.

In comparing the qualitative outcomes predicted by the prey- and ratio-dependent models, one reality becomes clear: only one parameter, the prey growth rate (r), provides radically different predictions in each model. Under ratio-dependence, increasing r leads to system stability. Under prey-dependence, increasing r has a destabilizing effect by increasing the carrying capacity (K).

Appendix C. Understanding capture efficiency in the Hassell-Varley-Holling models

The Hassell-Varley-Holling model employs linked parameters: capture efficiency (α_m) and interference (i). This is in contrast the capture efficiency (a) employed by the Beddington-DeAngelis (BD) model. The units of the BD capture efficiency are as follows:

$$a \equiv \frac{1}{time \bullet predator}$$

This set of units applies to the full spectrum of possible BD behaviors, from the extreme of $i = 0$ of prey dependence through $i = \infty$.

In contrast, the HVH model is constructed in such a way that its units shift with its interference parameter (m):

$$\alpha_m \equiv \frac{1}{time \bullet \left(predator^{(1-m)}\right)}$$

This capture efficiency is difficult to interpret and difficult to empirically parameterize. While the a of BD has a clear meaning (the number of successful captures per predator per time), the α_m of HVH is much less clear (because the predator to a power in the denominator is completely counterintuitive). This ambiguity in the HVH model also leads to a fundamental problem when trying to use actual data to determine α_m. For BD it is sufficient to know the number of successful attacks performed by a known abundance of predators on a known abundance of prey in a given time period. In order to actually calculate the HVH capture efficiency, we also need to know the interference parameter, which has no biological meaning and therefore can only be discovered by fitting.

An exception in HVH model is the extreme case of ratio dependence at $m = 1$, where the units of capture efficiency are:

$$\alpha_1 \equiv \frac{1}{time}$$

If we can safely assume that ratio dependence is an accurate depiction of the system, we can now use empirical data to parameterize our models: under ratio dependence, the capture efficiency is calculated as the total number of successful attacks per time.

Appendix D. Coding and parameterization of *Mathematica* simulations

For the simulations presented in **Chapter 4**, I programmed *Mathematica* to explore parameter spaces using three basic modules: i) **Module A** produced outcomes for a single run of a given set of parameters; ii) **Module B** harnessed **Module A** to produce multiple outcomes for a given set of parameters; and iii) **Module C** explored parameter space using **Module B** to output the results of multiple runs at each of many parameter combinations.

Both simulations used this basic structure, with the main difference between them being the data outputted from **Module A**: for the stability studies, the module outputted qualitative outcomes, and for the studies of equilibrial response the module outputted final abundances. I used the following code for **Module A** in the stability studies:

```
ADS [iR_, iC_, rR_, e_, u_, K_, aR_, hR_, em_, i_, tL_] :=
 Module[
  {t, nC, nR, OffCache, g, c, d, proBg, proBc,
   proBd, trial, AggListLength, AggList, ListSpot, Outcome},
  t = 0;
  nC = iC;
  nR = iR;
  OffCache = 0;
  Outcome = 0;
  While[(t < tL && Outcome == 0),
   g = rR nR (1 - nR / K);
   c = (aR nR nC) / (1 + aR hR nR + i aR hR nC);
   d = u nC;
   emR = em nR;
   proBg = Abs[g] / (Abs[g] + c + d + emR);
   proBc = c / (Abs[g] + c + d + emR);
   proBd = d / (Abs[g] + c + d + emR);
   proBemR = emR / (Abs[g] + c + d + emR);
   trial = Random[];
   If [trial ≤ proBg,
    If [g > 0, nR = nR + 1,
     If [g < 0, nR = nR - 1]
     ]
    ];
   If [(trial > proBg) && (trial ≤ (proBg + proBc)),
    nR = nR - 1;
    OffCache = OffCache + e];
   If [(trial > (proBg + proBc)) && (trial ≤ (proBg + proBc + proBd)),
    nC = nC - 1];
   If [trial > (proBg + proBc + proBd),
    nR = nR - 1];
   If [OffCache ≥ 1,
    nC = nC + 1;
    OffCache = OffCache - 1];
   t = t + 1 / (Abs[g] + c + d + emR);
   If[nC == 0, Outcome = 1,
    If[nR == 0, Outcome = 2]
    ]
   ];
  Outcome
  ]
```

This code employs the Beddington-DeAngelis functional response; the Hassell-Varley-Holling can be constructed substituting the appropriate rate function from **Table 2** in **Chapter 4**. I used the following code for **Module B** in the stability studies:

```
ADSMult [iRM_, iCM_, rRM_, eM_, uM_, KM_, aRM_, hRM_, emRM_, iM_, tLM_, numsims_] :=
 Module[
  {},
  simnum = 1;
  OutcomeList = {};
  While [simnum ≤ numsims,
   NewOutcome = ADS[iRM, iCM, rRM, eM, uM, KM, aRM, hRM, emRM, iM, tLM];
   simnum = simnum + 1;
   OutcomeList = Join[OutcomeList, {NewOutcome}]
  ];
  CoExPer = Count[OutcomeList, 0] / numsims;
  PredExPer = Count[OutcomeList, 1] / numsims;
  DualExPer = Count[OutcomeList, 2] / numsims;
  OutcomeSummary = {N[CoExPer], N[PredExPer], N[DualExPer]};
  OutcomeSummary
 ]
```

I used the following code for **Module C** in the stability studies:

```
MakeMyADSpace[iRMs_, iCMs_, g_, eMs_, uMs_, aRMs_, hRMs_, emRMs_,
 tLMs_, numsimss_, mHigh_, mStep_, rHigh_, rStep_, FilePathName_] :=
 Module[
  {TotalSimList, TempList, TempArray, TotalArray, m, r, K, OutcomePalette
  },
  TotalSimList = {};
  TotalArray = {};
  m = 0 - mStep;
  While[(m < mHigh),
   m = m + mStep;
   r = 0;
   TempList = {};
   TempArray = {};
   While[(r < rHigh),
    r = r + rStep;
    K = r / g;
    OutcomePalette =
     ADSMult [iRMs, iCMs, r, eMs, uMs, K, aRMs, hRMs, emRMs, m, tLMs, numsimss];
    RED = Part[OutcomePalette, 2];
    BLUE = Part[OutcomePalette, 3];
    GREEN = Part[OutcomePalette, 1];
    TempArray = Join[TempArray, {RGBColor[RED, GREEN, BLUE]}];
    TempList = Join[TempList,
      {{r, K, m, OutcomePalette}}]
   ];
   TotalSimList = Join[TotalSimList, TempList];
   TotalArray = Join[{TempArray}, TotalArray]
  ];
  Export[FilePathName, TotalSimList];
  Show[Graphics[RasterArray[TotalArray], AspectRatio → Automatic]]
 ]
```

For the studies of equilibrial response, I used the following version of **Module A**:

```
ADS [iR_, iC_, rR_, e_, u_, K_, aR_, hR_, em_, i_, tL_] :=
 Module[
  {t, nC, nR, OffCache, g, c, d, proBg, proBc,
   proBd, trial, AggListLength , AggList , ListSpot, Outcome},
  t = 0;
  nC = iC;
  nR = iR;
  OffCache = 0;
  While[(t < tL) && (nR > 0) && (nC > 0) ,
   g = rR nR (1 - nR / K);
   c = (aR nR nC) / (1 + aR hR nR + i aR hR nC );
   d = u nC;
   emR = em nR;
   proBg = Abs[g] / (Abs[g] + c + d + emR);
   proBc = c / (Abs[g] + c + d + emR);
   proBd = d / (Abs[g] + c + d + emR);
   proBemR = emR / (Abs[g] + c + d + emR);
   trial = Random[];
   If [trial ≤ proBg,
    If [g > 0, nR = nR + 1,
     If [g < 0, nR = nR - 1]
    ]
   ];
   If [(trial > proBg) && (trial ≤ (proBg + proBc)),
    nR = nR - 1;
    OffCache = OffCache + e];
   If [(trial > (proBg + proBc)) && (trial ≤ (proBg + proBc + proBd)),
    nC = nC - 1];
   If [trial > (proBg + proBc + proBd),
    nR = nR - 1];
   If [OffCache ≥ 1,
    nC = nC + 1;
    OffCache = OffCache - 1];
   t = t + 1 / (Abs[g] + c + d + emR)
  ];
  {nR, nC}
 ]
```

As with the stability studies, this is the Beddington-DeAngelis version, but it can be easily converted to the Hassell-Varley-Holling model by substituting for the existing consumption rate function. For the equilibrial response version of **Module B**, I coded as follows:

```
ADSMult [iRM_, iCM_, rRM_, eM_, uM_, KM_, aRM_, hRM_, emRM_, iM_, tLM_, numsims_] :=
 Module[
  {},
  simnum = 1;
  OutcomeList = {};
  PreyList = {};
  PredatorList = {};
  While [simnum ≤ numsims,
   NewOutcome = ADS[iRM, iCM, rRM, eM, uM, KM, aRM, hRM, emRM, iM, tLM];
   simnum = simnum + 1;
   OutcomeList = Join[OutcomeList, {NewOutcome}];
   PreyList = Join[PreyList, {Part[NewOutcome, 1]}];
   PredatorList = Join[PredatorList, {Part[NewOutcome, 2]}];
  ];
  N[{KM, Mean[PreyList], Mean[PredatorList],
   StandardDeviation[PreyList], StandardDeviation[PredatorList]}]
 ]
```

I used the following code for **Module C** in the equilibrial response studies:

```
EnrichX [iRX_, iCX_, eX_, uX_, aRX_, hRX_, emRX_,
 iX_, tLX_, rHigh_, rStep_, gX_, numsimsX_, FilePathName_] :=
Module[
 {},
 EnrichList = {{Carrying Capacity, Prey, Pred, Prey SD, Pred SD}};
 r = 0;
 While[(r < rHigh),
  r = r + rStep;
  K = r / gX;
  OutcomeList = ADSMult [iRX, iCX, r, eX, uX, K, aRX, hRX, emRX, iX, tLX, numsimsX];
  EnrichList = Join[EnrichList, {OutcomeList}]
 ];
 Export[FilePathName, EnrichList];
 EnrichList
]
```

All *Mathematica* notebooks employed in these studies as well as outputted data are available by request from the Christopher Jensen.

Appendix E. Modeling prey depletion in the Beddington-DeAngelis functional response

We can model the process of prey depletion in the Beddington-DeAngelis (BD) model in a system where prey growth has been arrested using the following equation:

$$\frac{dN}{dt} = -\frac{a_N NP}{1 + a_N h_N N + a_P h_P P} \qquad (1)$$

Where N is the abundance prey, P is the abundance of predators, a_N is the capture efficiency of predators on prey, h_N is the time predators require to handle prey, a_P is the probability of two predators interfering with each other, and h_P is the time wasted by each predator during each episode of interference. This equation can be rearranged as follows:

$$\frac{dN}{dt} = -\frac{1}{h_N} \frac{a_N h_N NP}{1 + a_N h_N N + a_P h_P P} \qquad (2a)$$

$$\frac{1 + a_N h_N N + a_P h_P P}{a_N h_N N} dN = -\frac{1}{h_N} P dt \qquad (2b)$$

$$\left(\frac{1 + a_P h_P P}{a_N h_N N} + 1 \right) dN = -\frac{1}{h_N} P dt \qquad (2c)$$

We can integrate this equation to determine the effect of prey depletion over a known interval of time (t):

$$\int_0^t \frac{1 + a_P h_P P}{a_N h_N} \frac{1}{N} dN + \int_0^t dN = -\frac{P}{h_N} \int_0^t dt \qquad (2d)$$

$$\left(\frac{1 + a_P h_P P}{a_N h_N} \right) \ln\left(\frac{N(t)}{N(0)} \right) + N(t) - N(0) = -\frac{P}{h_N} t \qquad (3)$$

Where $N(t)$ is the number of prey remaining after the consumption interval (t) and $N(0)$ is the initial number of prey introduced into the system.

Equation (3) can easily be modified to represent the Holling Disc Equation by removing the predator-dependent term:

$$\left(\frac{1}{a_N h_N}\right) \ln\left(\frac{N(t)}{N(0)}\right) + N(t) - N(0) = -\frac{P}{h_N}t \tag{4}$$

Equation (3) can also be rewritten to approximate ratio-dependence:

$$\left(\frac{a_P h_P P}{a_N h_N}\right) \ln\left(\frac{N(t)}{N(0)}\right) + N(t) - N(0) = -\frac{P}{h_N}t \tag{5}$$

These equations can be used to model the effects of prey depletion and compare these effects between various models.