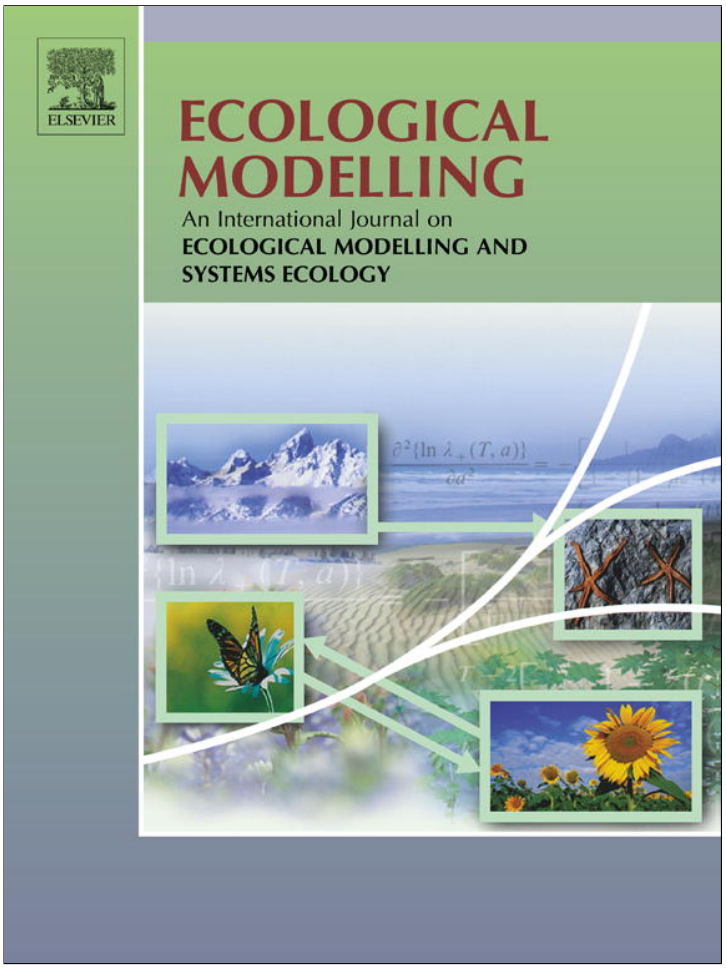

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Ecological Modelling 246 (2012) 103–104

Contents lists available at SciVerse ScienceDirect

Ecological Modelling

journal homepage: www.elsevier.com/locate/ecolmodel

Book review

Ratio dependent predator–prey theory: Aged, mellowed, and distilled

How Species Interact: Altering the Standard View on Trophic Ecology, R. Arditi, L.R. Ginzburg. Oxford University Press (2012). ISBN-13: 978-0-19-991383-1, 170 pp., $59, Hardback

In 1989, Roger Arditi and Lev Ginzburg came together to publish a paper in the *Journal of Theoretical Biology* with the simple title "Coupling in predator dynamics: ratio dependence". The paper presented a provocative idea: the Lotka–Volterra equations, bedrock of traditional predator–prey theory, were the wrong representation of this fundamental ecological interaction. Arditi and Ginzburg argued that the per capita consumption of prey should be a function of the ratio of prey to predators rather than being based solely on the density of prey. Others had published similar ideas (and both authors had published their own separate works on the topic), but the 1989 paper made an impact on the field of predator–prey modeling because it illuminated the strong contrast between the default prey-dependent functional response and the proposed new ratio-dependent form.

As one of the fundamental modules of any predator–prey equation, the functional response describes the rate at which the prey population is decreased by predator consumption. This rate determines not only the trajectory of the prey population, but also that of the predator, as in most models the growth or decline of predators is logically a function of prey consumption. As such, the functional response employed by a given predator–prey model has the potential to fundamentally alter that model's predictions. Models that assume that the success of a particular predator is determined solely by the density of the prey population (the so-called prey-dependent functional response) can produce very different dynamics than those that assume that predator density also determines individual hunting success (so-called predator-dependent functional responses, which include the particular ratio-dependent form).

This importance of the functional response assumption is the central focus of Arditi and Ginzburg's new book *How Species Interact: Altering the Standard View on Trophic Ecology*. Synthesizing the last two decades of theoretical and empirical work that explores predator dependence, the book makes a provocative argument for including predator densities in the functional response. While a lot of this material can be found scattered throughout the previous papers of Ginzburg and Arditi, the book organizes their accumulated arguments into a mellowed, well-synthesized, and organized collection. Because many of the important papers explaining predator dependence were published in rather obscure locations, this book also provides an invaluable service by sewing together the disparate pieces needed to understand this alternative view of predation.

In less than 150 pages of text (including appendices), *How Species Interact* provides the reader with a broad introduction to the formulation of and evidence for predator-dependent functional responses. "Standard" and "alternative" theories of trophic interaction are reviewed in the first chapter, while the second and third chapters are dedicated to exploring direct and indirect empirical evidence in favor of predator dependence. The final three chapters are increasingly philosophical. The fourth chapter is dedicated to explaining the variety of mechanisms that can cause predator- or ratio-dependence to emerge, the fifth chapter provides a series of arguments in favor of the ratio-dependent approach, and the final chapter ("It Must Be Beautiful") establishes an aesthetics of theory that casts a better light on the authors' favored functional response. Predominantly clear, well-organized, and concise, the book's text provides the fundamental arguments and plenty of citations to allow any interested reader to assess whether ratio-dependent functional responses deserve to upend the established canon of Lotka and Volterra.

While the book mostly reviews arguments already presented in the primary literature, it does provide some new material. Most prominent are sections on how predator dependence can lead to donor control in predator–prey systems, particularly when prey are at relatively low densities. Arditi and Ginzburg suggest that donor control may resolve a variety of theoretical dilemmas, including the question of why complex ecological communities appear to be far more stable than predicted by theory. The short sections that present the donor control argument have the potential to be swept up in larger argument for predator- and ratio-dependence, but their provocative implications should not be ignored: if *How Species Interact* is correct about the prevalence of donor control in nature, the role and importance of predator–prey interactions in ecological communities will have to be reassessed.

I found the fourth chapter, which explores how various spatial and temporal heterogeneities yield predator-dependent outcomes, to be the most interesting section of *How Species Interact*. The importance of spatial heterogeneity has been uncovered in a variety of theoretical areas of study, and often theoretical predictions are dramatically changed when space is considered explicitly. Arditi and Ginzburg show that a variety of mechanisms that depend on spatial or temporal heterogeneity can cause the emergent functional response to be predator- or ratio-dependent in nature, even when there is no direct interference between predators. This emergence presents a real dilemma for modelers, who aim to reduce interactions between predators and their prey to simple, easy-to-analyze differential equations. Because space is difficult to consider explicitly and realistically in such formulations, the spatial dynamics of the interaction may be missed by conventional theoretical representations. Similarly, time lags such as those that probably separate bursts of predator consumption from bursts of predator reproduction are difficult to represent in analytically tractable

0304-3800/$ – see front matter
http://dx.doi.org/10.1016/j.ecolmodel.2012.07.026

forms. Arditi and Ginzburg's solution to these problems is to use the ratio-dependent functional response as a proxy for the explicit consideration of space and/or time lags; skeptics may ask why – if heterogeneity in space or time is so important – models are not just built to consider clustering explicitly. The book's final chapter provides the counter-argument that simple models with minimal free parameters are the only ones that will lead to meaningful theory, but the fact that predator dependence emerges when heterogeneity is considered explicitly could also be used to argue for the abandonment of differential equations as the chief tool of predator–prey modelers.

How Species Interact does not claim to provide a comprehensive review of predator–prey theory, and instead reviews only the literature that appears to favor predator-dependent functional responses. As such, the book ignores a large body of theory that assumes prey-dependence, much of which claims to provide practical and/or accurate representations of real systems. Because it does not actively refute this literature, *How Species Interact* is unlikely to make converts of the many theoreticians who have spent lifelong careers building models based on the prey-dependent functional response. In particular, there is a large body of theory dedicated to explaining how apparent "paradoxes" between conventional theory and observed patterns in nature can be resolved by adding additional complexity to predator–prey models, and the only claim that *How Species Interact* levels against these formulations is that they are over-parameterized. I suspect that many will remain unconvinced by this argument.

If using a ratio- or generically predator-dependent functional response may be more appropriate in a substantial number of ecological scenarios, modelers need better education on how to do so. For instance, in a food web with multiple predators sharing multiple prey, interference effects will be the result of both predator populations competing for multiple prey populations. The prey-dependent functional response lends itself well to tackling this applied problem because it assumes no interference between predators, an assumption that allows the functional response of each predator to be separately added to the differential equations representing each population. But if ratio dependence results from various mechanisms causing mutual interference within a predator population, it should also arise as different predator populations compete for prey. How should such multi-species interference be incorporated? Such applied questions are beyond the scope of this book, a fact that might prevent it from strongly influencing those modelers looking at real-world questions. This is unfortunate, and might point the direction for future ratio-dependent modeling efforts: if ratio dependence is often the best approximation of real systems, we need to know how to incorporate it into ecological scenarios that go beyond one species of predator consuming one species of prey.

Those familiar with the initial controversy surrounding the introduction of the ratio-dependent functional response will discover a noticeable change in perspective in *How Species Interact*. Although much of the original work on predator dependence (including some of the papers I have co-authored with Lev Ginzburg) contentiously argued that ratio dependence should replace prey dependence, this book strikes a more even-handed, conciliatory tone that aims to explore where and when predator dependence might emerge. Make no mistake: this is a book advocating a particular point of view. The authors offer strong evidence that under most real-world conditions a predator-dependent functional response is the best representation of predation rates, and suggest based on both experimental and philosophical grounds that ratio-dependence should replace prey-dependence as the default functional response. The book even includes a not-so-subtle appendix section called "How a Revised Ecology Textbook Could Look" that basically tells textbook authors how to update their sections on predator–prey theory to better reflect the perspective of Arditi and Ginzburg. But what makes this book different – and better – than the authors' previous work is its nuance. Rather than arguing that ratio dependence is the way of nature, *How Species Interact* explores and explains the many different ways in which nature can produce ratio and predator dependence. And although the authors contend that the applicable domain of traditional prey-dependent theory is limited, this book most clearly delineates the rationale for these limits.

Insightful readers will discover a number of interesting issues lurking between the lines of explicit argument in *How Species Interact*. The book's central thesis depends in part on arguing that the time scales described by differential equations cannot be taken literally, a perspective that calls into question swaths of ecological modeling far larger than just predation theory. Analogous problems are uncovered when homogenous mixing is assumed, as spatially explicit realities may not be well-represented by non-spatial representations. The book also struggles with the question of how to deal with model complexity, as the relevant complexity of systems generally far exceeds our ability to validate such complex models with actual observations. Arditi and Ginzburg argue that "impressionistic" models are needed to aggregate a variety of complicating factors and preserve model simplicity, but one could just as easily conclude that until more comprehensive data can be obtained most modeling of predator–prey systems will remain conjectural. As much of the argument of the book rests on pointing out the inability of current-day models to effectively capture the important dynamics of predator–prey theory, one could easily expand the critique beyond just prey-dependent theory to predation theory in general: perhaps the hope for generalized theory based on simple equations is misguided.

While theorists should consider many of the issues raised here, especially as they design applied theories, experimental biologists represent the most important audience for this book. In particular, those working in highly manipulable and easily observable laboratory and field mesocosms have the potential to test the provocative ideas of Arditi and Ginzburg. After all, only through experimental testing of ratio-dependent predictions – and not additional theoretical rhetoric – will the field of ecology arrive at the most appropriate mathematical means of representing trophic interactions. *How Species Interact* is filled with clear opportunities to use experiments to resolve the theoretical disputes presented in the book, including new insights on invariancies that seem ripe for empirical assessment.

This book should be required reading for all whose research includes consideration of predation and its consequences. It provides an important alternative to the paradigmatic equations of Lotka and Volterra (and Holling), and nicely lays out issues that any modeler of predator–prey should consider. While readers new to predation theory may find this book insufficiently explanatory, most others will find its well-organized distillation of predator-dependent theory to be a valuable resource.

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