

Book Reviews

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The great predator–prey debate

Arditi, Roger, and Lev R. Ginzburg. 2012. **How species interact: altering the standard view on trophic ecology.** Oxford University Press, New York. ix + 170 p. \$59.00; ISBN: 978-0-19-991383-1

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Few topics are as central to ecology as the study of predator-prey dynamics. Starting with the pioneering studies of Vito Volterra, Alfred Lotka, and Georgii Gause, ecologists have long struggled with understanding, and more importantly predicting from first principles, how predators influence populations of their prey and vice versa. A pivotal concept in most empirical and theoretical studies of predation is the functional response, depicting the (generally) curvilinear relationship between predator feeding rates and population density of prey. Following a well-trodden set of textbook examples, many ecologists have long accepted that feeding rates measured on short time scales are unaffected by the local abundance of predators competing for prey. Nonetheless, there is a well-developed set of alternative theoretical formulations (so-called predator- or ratio-dependent models) that predict that the presence of other predators should depress feeding rates below the levels expected from prey abundance acting alone.

How species interact provides a fascinating history of this debate, as well as a multi-faceted exploration of its ecological ramifications. The authors have devoted major parts of the past three decades to developing predator- and ratio-dependent theory, as well as testing model predictions using a mixture of lab and field data, mostly gleaned from the published literature. The book, structured in six chapters, covers several different elements of their own intellectual journey. Chapter 1 provides an overview of many of their arguments. In many ways, this is the closest thing to a current review on the topic that is available in the published literature and would be well worth reading even by ecologists with only a casual interest in the subject. Chapter 2 reviews the empirical evidence for alternate forms for the functional response, comparing the degree of fit provided by the classic prey-dependent case with the alternate forms based on predator dependence or ratio dependence. While some of this material has received previous coverage in the literature, the breadth of comparison in this chapter is particularly impressive. Not surprisingly, the authors conclude that prey-dependent models fare considerably less well than predator-dependent and ratio-dependent models in explaining outcomes of functional response trials conducted with multiple predators.

The third chapter focuses on implications of the prey-dependent and ratio-dependent models with respect to expected patterns of equilibrium abundance of predators vs. prey and responses of predator and prey to changes in productivity of the environment. Here the weight of evidence is particularly intriguing: there exists a wealth of comparative data demonstrating positive co-variation in predators and prey biomass in a

variety of taxa and biomes, consistent with expectations from ratio-dependent models, but inconsistent with purely prey-dependent models of trophic interactions. Moreover, the authors correctly identify the lack of strong experimental evidence for the paradox of enrichment, a theoretical prediction that purely prey-dependent interactions with predators should lead to wild oscillations in enriched ecosystems vs. those with lower levels of nutrient loading. Although there are well-executed studies demonstrating how population oscillations can be induced through nutrient enrichment, these examples are truly rare.

In the final two chapters, the authors adopt a more reflective tone, musing on the logical underpinning of alternate models, their scaling properties, and implied differences in the way that time enters the models. While providing excellent food for thought, many readers may join this one in concluding that such philosophical considerations are unlikely to alter perceptions about the relative value of the different concepts for the functional response.

There is much to admire in this book. It is rare that ecological models are explained with the clarity presented here. While the arguments themselves are necessarily quantitative in nature, the authors have been remarkably careful not to overwhelm readers with mathematical detail. Helpful figures are used to illustrate important concepts, lending a pleasant tone to the overall presentation. The inclusion of line drawings of important contributors to the historical evolution of these ideas was a nice aesthetic touch, although one cannot imagine why Buzz Holling, the originator of the ecological functional response, did not receive similar treatment. The combination of clarity, mathematical simplicity, and short length of this book should make it accessible to most ecologists, regardless of background. I found the nature of the debate refreshing—it is rare in my experience that ecologists think about the weight of evidence in support of their favored hypotheses.

But therein lies the chief weakness of the book, for I'm afraid these authors care a little too much for their own baby, the ratio-dependent model. To quote a single example, in their concluding chapter the authors argue that, "an alternative predator-prey interaction theory can be built on the ratio-dependent foundation," with an accompanying histogram demonstrating the range in variation in interference values from experimental trials. This conclusion would be fine, except that the data actually suggest substantial variation in outcomes, with most levels of interference (18 of the 22 studies considered) falling below the magic value of 1 predicted by the ratio-dependent model, albeit well above the magic value of 0 predicted by purely prey-dependent models. There are many flexible predator-dependent formulations that can explain such variability better than the ratio-dependent model, yet the authors persistently call for this special case as the true "null" model. While the authors acknowledge this viewpoint in the text, with particular effectiveness in Chapter 4, such evenhandedness often seems to disappear whenever they arrive at summary statements.

I was also somewhat disturbed by the poor degree to which the authors acknowledge competing models that are well developed in the literature. In postulating a causal mechanism

to explain why predator-dependent processes occur, the authors describe fascinating recent work in their own lab on diffusive movement models for predators and prey. While these studies are no doubt important contributions, there is a rich theoretical and empirical literature on the subject dating back to the 1950s that is scarcely acknowledged. If space were at a premium, one could understand such limitations, but in a 170-page book with a breezy presentation style, I suggest it represents an unacceptable level of professional scholarship.

In spite of these weaknesses, I strongly recommend this book, not only to specialists in predator-prey dynamics, but across the wider discipline. I do so for two reasons. First, ecologists might well benefit from a more solid commitment to testing theory. What more relevant place to start than the most basic models of consumers and their resources? Second, I think this book will do much to stimulate reader thinking about the underlying behaviors that can dictate the statistical outcome of population interactions, whether these be mutualism, compe-

tion, or predation. If nothing else, these authors have achieved much in reminding us how variable the patterns of predation can be and postulating a number of intriguing explanations for such departures from simple expectations. While the answer may not necessarily lie in ratio dependence, it may well lie in the behavioral details that shape the interactions themselves.

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