doi:10.1111/j.1558-5646.2010.01080.x

CORRECTING DARWIN'S OTHER MISTAKE

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Received June 14, 2010
Accepted June 14, 2010

Review of: *Experimental Evolution: Concepts, Methods and Applications of Selection Experiments*. Edited by Theodore Garland, Jr. and Michael R. Rose, 2009. Univ. of California Press, Berkeley, California. 752 pp. Hardcover ISBN 9780520247666, $75.00; Paperback ISBN 9780520261808, $45.00.

It has become a cliché to say that evolutionary biologists need multiple types of approaches to be effective. Comparative approaches help us identify interesting patterns, theoretical approaches help us clarify important processes, and experimental approaches help us infer causation between processes and patterns. Because of their complementary strengths and limitations, different approaches are more effective when used together than separately. With his well-known *Anolis* lizards, for example, Jonathan Losos has elegantly demonstrated the power of the combined use of comparative and experimental approaches (Losos 2009; Vamosi 2010). Many evolutionary biologists, however, practice only one or two types of approaches, even though they may consult findings by others who use other approaches. This is understandable, given the difficulty for an individual to master all existing approaches, but perhaps because of the limited use of different approaches by individual researchers, there is still ongoing discussion and even confusion in the literature regarding which approach can do what.

Experimental Evolution: Concepts, Methods and Applications of Selection Experiments, edited by Theodore Garland, Jr. and Michael Rose, is a collection of chapters by practitioners of experimental approaches. The primary goal of the book is to "foster selection experiments and experimental evolution as a central component of evolutionary biology." The editors have come up with a catchy way of introducing this goal: in the introductory chapter, they say that the book is about "correcting Darwin's other mistake." Because Darwin got most key points right about evolution, the few mistakes he did make get highlighted, and rightly so, because his mistakes are as illuminating as his correct discoveries. Darwin's primary mistake was, of course, to think of blending inheritance as a mechanism of heredity. Rose and Garland point out that another major mistake was to assume that natural selection always act very slowly, with its effect too miniscule to be observed in experiments. The editors suspect that, as a consequence of this mistake by Darwin, experimental approaches have not been as fully exploited by evolutionary biologists as comparative or theoretical approaches. The book's purpose is to remove what the editors refer to as the "Darwinian inhibition," that is, the incorrect notion that evolutionary changes always happen too slowly to manipulate and observe in action in experiments. In doing so, they seek to promote a wider and better use of experiments in evolutionary biology.

The book covers an impressively wide range of topics including behavior, morphology, demography, life history, ageing, altruism, evolution of sex, speciation, adaptive radiation, phylogenetics, and genome evolution. The coverage of topics is so comprehensive that it seems as though any evolutionary biologist can find their favorite subject in this book. As such, the book readily succeeds in showing how effective experiments can be in studying evolution. Case studies used are also highly variable, with a broad taxonomic spread of study organisms ranging from bacteria to insects to mammals. Study organisms are, however, dominated—although by no means entirely—by a handful of model organisms, such as *Eschericia coli*, *Pseudomonas fluorescens*, *Saccharomycetes cerevisiae*, *Drosophila* species, and

Mus musculus, reflecting the trends in experimental evolution as a field.

Chapters are grouped into five Parts. Part I (Introduction to Experimental Evolution) includes three chapters that discuss the role of experimental approaches relative to other approaches. Parts II (Types of Experimental Evolution), III (Levels of Observation in Experimental Evolution), and IV (Applications of Experimental Evolution) contain 17 chapters in total, each showcasing experimental studies on a particular topic of interest, mainly those studies by the chapter authors themselves. Part V (Conclusion) consists of two concluding chapters, which return to the general theme of the role of experimental studies in evolutionary biology discussed in Part I.

My favorite chapters are those that explicitly compare experimental approaches to other approaches in their strengths and weaknesses. For example, the critical assessment of experimental phylogenetics by Todd Oakley in chapter 21 is helpful in clarifying the strengths and weaknesses of experimental approaches compared with computer simulation as an alternative approach. Chapter 3 by Derek Roff and Daphne Fairbairn on modeling experimental evolution using individual-based, variance-components models shows, using case studies with sand crickets, how experiments can be particularly powerful when combined with the generation of theoretical predictions that inform experimental design. Similarly, chapter 19 by Benjamin Kerr presents a compelling case for a combined use of theoretical and experimental approaches to understand the evolution of altruism.

I believe it is worth noting that there is an edited book similar in purpose and style to *Experimental Evolution*, although this one is on ecology, the sister discipline of evolutionary biology: *Experimental Ecology: Issues and Perspectives*, edited by William Resetarits, Jr. and Joseph Bernardo (Resetarits and Bernardo 1998). Even though this book is now 12 years old, I find that *Experimental Ecology*'s treatment of conceptual issues surrounding the advantages and limitations of experiments and the combined use of experimental approaches with other approaches remains as relevant today as it was when the book was published. Ecology as a field shares the same logistical constraints, if somewhat less severe, of time scale with evolutionary biology. Experiments on ecological dynamics are possible, but not with any organisms, owing to too long generation times. For this reason, like evolutionary biology, ecology demands multiple approaches.

Comparison of such closely related, but not yet completely integrated fields as ecology and evolutionary biology may shed light on how each can make more rapid advance. Looking at the two books, I believe a main difference is that experimental evolution focuses more on using well-characterized model organisms, whereas experimental ecology places greater value on studying, collectively, a diversity of organisms. What may underlie this difference if it does exist? I suspect it may reflect a conceptual difference between the two fields. Evolutionary biologists have the Modern Synthesis as a unifying fundamental framework, and much of their research seems directed toward testing and refining basic general principles within the paradigm provided by the Modern Synthesis. On the other hand, ecologists do not really have an equivalent of the Modern Synthesis. Instead, most of them seem to rely on the tacit belief that generality, if any, can emerge only through comparison of results of experiments on many kinds of systems (Morin 1998). The increasing popularity of meta-analysis as a method among ecologists over the past decade or so seems to attest this belief.

Another marked difference seems that evolutionary experiments are more often done in the laboratory than ecological experiments, many of which are done in the field. Of course, there are important exceptions (see, e.g., chapter 8 by Duncan Irschick and David Reznick in the *Experimental Evolution* book), but this difference is evident, and is probably due to logistical constraints to a large extent: evolutionary experiments often require a higher level of control than do ecological experiments. However, I wonder if this difference may also be a by-product of the conceptual difference discussed above, namely that it is less essential to ensure natural conditions in testing basic principles than in getting data that will contribute to drawing generality through meta-analytical synthesis.

Given these differences, what can experimental evolutionists learn from experimental ecologists, and vice versa? In experimental evolution, the pendulum may have swung too much toward relying on the control afforded in the laboratory and away from grounding the research in what Raymond Huey and Frank Rosenzweig call "ecological realism" in the concluding chapter of the *Experimental Evolution* book. Huey and Rosenzweig lament that "embarrassingly little is known about the natural history of the very organisms most suitable for experimental evolutionary studies." Even though logistically harder than laboratory experiments, more field experiments, such as those discussed in chapter 8 by Irschick and Reznick, can bring fresh insights into evolutionary dynamics, and field experimental ecology has a wealth of methodological and conceptual guidance to offer, as evident in the *Experimental Ecology* book.

On the other hand, experimental ecology, or ecology in general for that matter, may benefit from adopting the Modern Synthesis view of the world, by viewing the ecological community as something that is formed through two general classes of processes—one that brings species to the community (immigration) and one that determines which species get to stay in the community (local interaction)—if their goal is to develop a general theory of ecology. As Joan Roughgarden (2009) explains well, this view is akin to the Modern Synthesis view of evolution, in which mutation brings variation, whereas natural selection determines which variant stays. With this emphasis on processes shaping community structure, ecologists will need more experiments on community assembly, to directly manipulate both immigration and local interaction. Analyses of patterns alone, which are too often the focus of ecological research, will not suffice to understand processes responsible for patterns.

In any case, recent research shows that the traditional disciplinary distinction between ecology and evolutionary biology is artificial, and that ecological dynamics cannot be ignored to understand evolutionary dynamics and vice versa. The time scales at which ecological and evolutionary dynamics occur were once thought distinct, with the former much shorter than the latter, but this assumption has proven incorrect in many recent studies. Ecological and evolutionary dynamics can feed back to influence each other intricately (Fukami et al. 2007). The "eco-evolutionary dynamics" (Pelletier et al. 2009) driven by "rapid evolution" (Hairston et al. 2005) has recently become a hot topic, naturally necessitating a union of ecology and evolutionary biology, which was, paradoxically, one of the strengths of Darwin's synthetic research. I expect that the merging of experimental evolution and experimental ecology will play a key role over the next decade in evolutionary biology.

Any skeptic of the utility of experimental evolution, anyone who still has the "Darwinian inhibition," would need only to read *Experimental Evolution* to be convinced otherwise. For those who are already convinced, which I suspect the majority of evolutionary biologists may actually be, the goal of the book set out by the editors, namely to remove the Darwinian inhibition, had already been achieved before this book. Still, the book should provide useful conceptual perspectives and methodological hints for designing and interpreting experiments. Better yet, to look ahead, I recommend reading both *Experimental Evolution* and *Experimental Ecology*. If you cannot afford reading both, I would recommend evolutionists to read *Experimental Ecology* and ecologists to read *Experimental Evolution*.

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Book Review Editor: J. Thompson