

Book Reviews

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A comprehensive review of North America's most imperiled faunal group: setting the framework for new hypotheses

Haag, Wendell R. 2012. **North American freshwater mussels: natural history, ecology, and conservation.** Cambridge University Press, New York. xvi + 505 p. \$140.00, ISBN: 978-0-521-19938-4.

Key words: biogeography; host use; life history; species loss; unionid.

As more ecological work is being conducted on freshwater mussels, we are coming to appreciate the importance of this secretive fauna to ecosystem function and structure. Yet we still lack an understanding of the factors that control the distributions of this group, their reproductive strategies, the fish hosts they use, and the factors causing their decline. This book provides a thorough literature review of the available information, and a detailed analysis and synthesis of this information. Haag does a magnificent job at compiling this information, summarizing it, and attempts to make some important inferences based on the available data. Whether or not one is a freshwater mussel enthusiast, this book provides a comprehensive review of the literature on these inconspicuous animals that will be useful for both novices and experts alike. Wendell Haag, a USDA ecologist, has done an excellent job pulling together the beginnings of the study of freshwater mussels and the current status of our understanding. Haag's poignant review and respect for these creatures is made apparent in the preface of the book and is a common theme throughout. This nicely laid-out book spotlights the amazing diversity of mussels, their life history strategies, their importance in the ecosystem, and the unfortunate loss and continued loss of many mussel species. Yet this book does not only serve as a resource for pulling pertinent literature together, it synthesizes this information and serves as a meta-analysis of much of this work to invigorate new research in the field.

The book is split into 11 chapters, with each giving an overview of some component of the history of the study of unionids, mussel life history, mussel ecology, and the past and current stressors that have led to their decline. The book will be pleasing to read for both scientists and history buffs alike. Not only does this book focus on the study of these organisms, but also the early fascination of native peoples with mussels and the pearl and button industries of the late 19th and early 20th centuries. Figures such as the one showing mussel harvesting camps are fascinating and illustrate the over harvest of mussels during the early 1900s for the button industry. The first three chapters serve as an introduction to mussels, the history of their study, and the global distributions of these animals. Chapters 4–7 focus on the habitats required by mussels, reproductive strategies, life history, and population biology. Through these chapters, the author develops a framework for classifying mussel species based on their life history traits and then develops a conceptual framework to determine assemblage structure. Chapter 8 tries to combine all this information to understand assemblage patterns and niche partitioning in

mussel communities. The final chapters discuss human exploitation, declines of mussels, and conservation challenges for mussels in the future. The book is well organized throughout and includes 21 color plates that illustrate shell and nacre color variation, sexual dimorphism, and astounding mantle lures. Additionally, the pictures and figures that accompany each chapter are well done and illustrate points made throughout.

I think the most important contribution of this book is the conceptual framework Haag terms the host-habitat continuum. To outline this conceptual framework, Haag lays the groundwork by categorizing various mussel species into three strategy categories (opportunistic, periodic, and equilibrium) based on many of their life history characteristics presented in Chapter 7. This framework is useful for researchers to build upon and to make predictions regarding population dynamics and recruitment following disturbance. He uses these life history traits along with various means of niche partitioning, including competition for fish hosts, food, and habitat, to help determine assemblage structure. The all-encompassing literature review that makes up a large proportion of this book culminates with the role life history and host strategy play in determining mussel assemblage structure and outlines how these three strategies may be distributed across the river continuum. This summation stimulates the reader to think about the traits that lead to the patterns we see in assemblage structure and how these vary with habitat types due to niche partitioning. With the concept of the host-habitat continuum, Haag provides testable hypotheses to guide future research in mussel ecology.

Overall, the book is a fantastic contribution to the ecological literature and a very nicely produced book. However, some of the analyses that Haag presents are inadequately described and some additional detail would have aided an interested reader. Furthermore, while some of Haag's conclusions are supported by multiple studies, other inferences made within the book are not fully supported by current data. Although some portions of the book contain some speculative claims made regarding certain patterns, this speculation is included to provide a framework for future inquiry and study. While the book is unfortunately very much North American-centric, this slant occurs because the diversity of freshwater mussels as well as the study of this faunal group is centered primarily in the United States. The book does a great job of clearing up some common misperceptions of unionid freshwater mussels—even for those that work in the field of mussel biology (e.g., the issue of longevity). As more work is being done across the globe on these animals, I think we are going to discover a large variety of traits and hosts associated with mussels that will take our understanding further.

In the final chapter Haag states, "The value of any wild creature is inseparable from its context within the ecosystem of which it is an integral component." Given the highly imperiled status of freshwater mussels, this idea is essential if we wish to protect this fauna and to articulate their importance within the ecosystem. This book is an important contribution to our understanding of diversity within the natural world because it shows that within this faunal group of seemingly similar species there is a great variety in life history traits, strategies, and

habitats. Although a large portion of this book focuses on the imperilment of freshwater mussels and how we have gotten to this point, Haag ends on a positive note in the last chapter, leaving the reader with a sense of optimism that we may maintain much of what we have left. Given the wealth of information within this book and the thought-provoking synthesis, this book should be a part of every aquatic ecologist's bookshelf.

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Is character displacement central to ecology and evolutionary biology?

Pfennig, David W., and Karin S. Pfennig. 2012. **Evolution's wedge: competition and the origins of diversity**. Organisms and Environments, no. 12. University of California Press, Berkeley, California. xiv + 303 p. \$75.00, ISBN: 978-0-520-27418-1 (alk. paper).

Key words: character displacement; competition; eco-evolutionary dynamics; genetic assimilation; sexual selection.

Theory and empirical data increasingly emphasize the need to unify ecological and evolutionary thinking. The ongoing synthesis between ecology and evolution—often referred to as “eco-evolutionary dynamics”—promises to have important and lasting effects on both fields. In *Evolution's wedge: competition and the origins of diversity*, David and Karen Pfennig attempt to synthesize ecology and evolution by viewing a wide range of phenomena through the lens of character displacement. Although I found myself disagreeing with the authors on some topics, I recommend the book to anyone interested in evolutionary ecology; it is sure to spur discussion and future research, which is really the primary goal of any book directed towards practicing scientists.

Because of the central role that character displacement plays in their view of evolution, Pfennig and Pfennig begin with a general historical overview and review of current evidence for character displacement. Their overall view is that character displacement is widespread. This perspective contrasts somewhat with more recent review of character displacement by Yoel Stuart and Jonathan Losos (2013. Ecological character displacement: glass half full or half empty? *Trends in Ecology and Evolution* 28:402–408), who discuss the “rise, fall, and resurrection” of ecological character displacement and, reviewing empirical evidence, express some skepticism about the amount of support for this process in the natural world. Stuart and Losos characterize Pfennig and Pfennig's views on character displacement as “glass half full” and their own as “glass half empty,” which seems like a fair comparison that leaves open the possibility that character displacement is actually common but only rarely fully documented. *Evolution's wedge* also includes a useful table synthesizing the criteria for demonstrating both ecological and reproductive character displacement from observational data.

Early in the book Pfennig and Pfennig also introduce perhaps the two most controversial aspects of *Evolution's wedge*. First, the authors argue that ecological and reproductive character displacement are two categories of a general phenomenon. They define character displacement as “trait evolution that arises as an adaptive response to resource competition [ecological character displacement] or deleterious

reproductive interactions [reproductive character displacement] between species.” Bringing these two processes, typically considered separately from one another, together in a unified framework has both pros and cons. The main benefit of this perspective is that one can apply the same criteria to understand these two processes, which have distinct consequences for evolution. Additionally, the authors' discussions of the potential interactions between ecological and reproductive character displacement is interesting and often novel. At the same time, I felt that trying to include both forms as specific examples of a common phenomenon was, at times, confusing, and discussions of their complex interactions convinced me of the need for more mathematical modeling in this area. Still, on the whole, I found the unified approach to reproductive and ecological character displacement valuable. Second, Pfennig and Pfennig emphasize the role of phenotypic plasticity in understanding patterns of character displacement, and introduce a few ideas about character displacement and reaction norms that are developed further in later chapters. This is an interesting perspective that was at its strongest when applied to examples from the Pfennigs' own work. However, I do have some doubts about how plasticity and selection might interact and whether genetic assimilation is common or rare across the tree of life (see more detailed comments below).

Evolution's wedge includes a lengthy section on character displacement itself. This discussion includes a summary of the driving forces for ecological and/or reproductive character displacement, emphasizing competitive interactions both within and among species; a discussion of why some populations and species are more likely to undergo character displacement than others; ideas and examples on how ecological and reproductive character displacement might interact, either facilitating or impeding one another depending on circumstance; and a review of the mechanisms by which character displacement might occur. I found this part of the book interesting and useful. I was a bit surprised when the authors devoted relatively little attention to what I think of as “standard” genetic models for character displacement, including both the evolution of traits from standing genetic variation and new mutations during character displacement. They call such models “genetically canalized,” and argue that they may be the exception rather than the norm. As an alternative, Pfennig and Pfennig spend a substantial amount of space discussing a “plasticity-first” hypothesis for character displacement, where the process of character displacement begins with traits that show phenotypically plastic responses to environmental cues, which then undergo genetic assimilation (i.e., no longer respond to environmental cues) to result in fixed differences among forms (this process is also called “genetic hardening” in the book). This perspective shares some major themes with Mary Jane West-Eberhard's book, *Developmental plasticity and evolution* (2003).

Oxford University Press, New York) and I found the hypothesis challenging and interesting but, in some ways, a bit speculative. First, as Pfennig and Pfennig state, plasticity can either promote or constrain adaptation, depending on details of circumstance. Second, if one holds the plasticity-first explanation to the same standards as other examples of character displacement, then one must show both genetic variation in plasticity within species and natural selection on reaction norms, among other things. This is quite a high bar that, I think, has rarely been met. Furthermore, evidence for the process of genetic assimilation is somewhat scarce. In any case, the book presents an interesting perspective, but we do not yet know if the authors' "plasticity-first" mechanism is common or rare.

The second half of the book focuses on the consequences of character displacement. I particularly liked the discussion of the ecological consequences of character displacement, including evolution of the niche, community structure, and species range evolution. This is the chapter in the book that, to me, makes the strongest connections between ecology and evolution. The authors also discuss sexual selection (both how character displacement affects sexual selection and the reverse) and speciation. Finally, integrating much of the discussion of previous chapters, the authors attempt to connect the micro-evolutionary processes described through the rest of the book to long-term macroevolutionary patterns. As someone who frequently works over very long time scales, I appreciated the effort to explore the long-term consequences of the book's framework.

One thing I really liked about the structure of this book is the authors' decision to include a box with "suggestions for future research" at the end of each chapter. The book also ends extremely well with a chapter entitled "Major themes and unsolved problems." This last chapter is a relatively even-handed summary of major themes in the book, but also highlights major unsolved problems and future areas for research that might prove fruitful. Even in areas where I might have some disagreement with the book's perspective, I tended to agree whole-heartedly with the future research directions suggested by the authors.

I found that the book's strengths and weaknesses were often closely related. For example, throughout the book, the authors take the general approach of defining or describing some phenomenon, and then arguing for its importance through a "case-study" approach. This approach is a strength of the book, as the examples are well developed and will connect to the intended audience of biologists. Examples are taken from a wide range of systems. Examples from spadefoot toads (genus *Spea*) that draw on the Pfennigs' previous research are particularly interesting, applicable, and developed. However, this case-study approach also has some drawbacks. For

example, the book does not include meta-analyses over a range of datasets, which can make arguments for the generality (or not) of phenomena more convincing. Second, the book only occasionally includes references to mathematical models, and does not delve into the details of mathematical results. I do realize that this book is not about theoretical models; at the same time, I found it hard to follow the authors' verbal descriptions of how several phenomena (e.g., natural selection, sexual selection, and plasticity) might interact to influence evolutionary outcomes.

To me, the main weakness of the book is that connections to current ideas in ecology, especially relating to the importance of competition in communities and ecosystems are not as strong as they could be. In particular, long-standing ecological controversies about species coexistence and, in particular, the importance of competition are given relatively short shrift in the book. I think that ecologists reading this book might be surprised at the relative ease by which Pfennig and Pfennig invoke competition, given the typical standards of evidence expected in ecological studies. Additionally, ecologists have many and varied ideas of how and why species can coexist in local communities. The authors emphasize competitive exclusion and character displacement, and do not focus on other coexistence mechanisms that are known to be important in natural communities (e.g., competition-colonization trade-offs, facilitation, neutral community drift, and many others).

Overall, *Evolution's wedge* makes a good case that competition and character displacement are important and well-documented processes. The book presents an interesting framework to think about how they might influence phenomena from a wide range of spatial and temporal scales. But evolution and ecology are extraordinarily rich and diverse fields; so fundamentally, the ultimate question is whether we should give special priority to competition and character displacement when considering ecological and evolutionary phenomena. Although I remain unconvinced that character displacement can (or should) play such a central role, I admire the authors' ambitious scope. This book provides a rich source of testable ideas to spur the ongoing synthesis between ecology and evolution.

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The secret lives of nesting birds revealed

Ribic, Christine A., Frank R. Thompson III, and Pamela J. Pietz, editors. 2012. **Video surveillance of nesting birds**. Studies in Avian Biology No. 43. University of California Press, Berkeley, California. xv + 223 p. \$65.00, ISBN: 978-0-520-27313-9 (alk. paper).

Key words: avian breeding behavior; nest monitoring; nest predation; nest success; predator identification; video.

Not long ago, many ecologists cast doubt on the idea that mice (e.g., genus *Peromyscus*) could be important and pervasive predators on eggs and nestlings of birds. Now, not only is there evidence that mice are common predators of many species' nests, but also that voles, deer, elk, cows, western meadowlarks, and even (fire) ants and certain species of beetles can and will depredate bird nests. Moreover, many parent birds will risk serious injury or death to defend nest contents against nest invaders often much larger than themselves to increase the probability that at least some of their young will successfully

fledge. Such information on the mysterious lives of nesting birds has been revealed by the types of studies and video camera technology highlighted in the recent book *Video surveillance of nesting birds* edited by Christine Ribic, Frank Thompson III, and Pamela Pietz.

The book is divided into four sections: "Synthesis/overview" (three chapters), "Breeding behavior" (six chapters), "Behavioral responses to predation/predator identification" (five chapters), and "Technology" (one chapter). Chapters 1 and 3 provide excellent summaries of the types of critical discoveries that have been made via video surveillance of (grassland) songbird and gamebird nests. All chapters are appropriate in length, well written, and quite palatable. While the majority of the book is focused on the value of using video techniques to learn more than can be gleaned from standard nest monitoring, it is balanced by mention of current technological limitations and pitfalls that can lead to frustration and lost data. Cox et al., in the final chapter, generously lay out their detailed experiences with different nest camera systems and offer suggestions in terms of selection of appropriate equipment for one's study objectives and technological improvements that could be made to facilitate future research.

Predation is usually the main cause of nest mortality in birds. A primary focus of many of the chapters is therefore the identification of the predators responsible for nest losses, with the rationale that understanding mechanisms underlying temporal (diurnal, seasonal, annual) and spatial variation in nest fates requires understanding of specific predators and their autecology. Authors of several of the chapters (1, 2, 10, 11) astutely point out that few general trends have emerged in the literature in terms of relating nest predation rates to habitat and landscape features, which may be explained by local and regional variation in nest predator assemblages. Indeed, Davis et al. (Chapter 14) report very little overlap in predators of grassland bird nests in Saskatchewan and Montana, despite the similarity in habitat across sites. Cameras have revealed many previously undocumented nest predators and called into question the importance of others previously assumed to be important. Another major contribution of studies employing camera technologies at nests has been demonstrating that characteristics of post-predation nest remains cannot be reliably used to infer predator type or species. Many predators leave no evidence, and the same predator species can leave variable evidence at different nests. Moreover, multiple predators can visit a single nest. One anecdote, described in Chapter 1, provides a powerful example. Over the course of two days, a western meadowlark nest was first visited by a brown-headed cowbird that tossed out three eggs and punctured two, then insects and a red fox scavenged the remains. The remaining small egg fragments (resembling a small mammal depredation) belied the complexity of what had ensued at that nest site. These types of discoveries will be integral to the development of future studies and improving understanding of the linkages between nest predators and nest survival across different contexts.

Another major contribution of nest camera studies covered in Part 2 of the book is improved information on parental care behaviors at nests. The extent and timing of parental care behaviors has important implications for the evolution of life history strategies and trade-offs such as those between current and future reproduction. Ellison and Ribic in Chapter 12 evaluate the extent to which parents of different grassland songbird species attempted nest defense against certain types of predators and the frequency with which defense behaviors resulted in the survival of at least some young. Detailed information on life history traits such as lengths of different

nesting stages, moreover, is important for comparative analyses and has practical implications such as accurate determination of nest fates. For example, by video-monitoring nests, Pietz et al. (Chapter 4) expanded the published range of fledging ages for clay-colored sparrows and bobolinks. Quantification of incubation attentiveness can be difficult for species with biparental care without video data because parental switches are too quick to register on temperature-sensing devices placed in nests. Using video data, Smith et al. (Chapter 8) were able to show that uniparental shorebird incubators had about a 33% reduction in available foraging time compared to biparental incubators, which has implications for understanding the nature of trade-offs across breeding strategies. Another novel contribution, in my view, was Slay et al.'s (Chapter 9) documentation of nocturnal behaviors of parents on nests. Parent birds are vulnerable to predation while on nests at night, so sleep patterns may represent an interesting trade-off between balancing rest and maintaining vigilance.

While the book's minor shortcomings pale in comparison to its merits, I will briefly mention two minor reservations I have. First, many of the tables could have summarized data into proportions for ease of comparison. Second, the conclusions of several of the featured studies were tentative and the results often descriptive in nature rather than tests of explicit hypotheses, partly due to small sample sizes of nests and/or recorded events of interest. That said, one must acknowledge the logistical and financial constraints of locating substantial numbers of nests of certain species, as well as the building and deploying of fairly complicated camera set-ups in the field. Hopefully, continued advances in the pricing and sophistication of video monitoring equipment for wildlife usage will facilitate larger sample sizes and fewer instances of data lost to various technical malfunctions.

In summary, for any student of ornithology, and particularly those interested in the study of nesting birds at all stages of their careers, I would encourage the cover-to-cover reading of this book. The chapters are a treasure trove of new questions raised as a result of observations from video monitoring of avian nests that can be pursued with further technological advances and clever hypothesis testing. For example, cameras on several species of grassland birds (Chapter 4) revealed 15 instances of early fledging of young due to predator and researcher visits, which raises the question of how early fledging may influence post-fledging survival. In my opinion, a good scientific book provides inspiration and new knowledge, and for me, this book accomplished both. As a professional interested in furthering understanding of the mechanisms underlying variation in avian nest success and particularly nest predation, I was grateful to read a summary of much of what has been learned to date by video-monitoring nests. Even more importantly, I am now even more excited to continue to pursue many of the frontiers in understanding of nesting bird ecology and the synergisms that may occur with on-going habitat change, while taking advantage of what can be learned from the previously less-explored secret lives of nesting birds.

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