Phenomenological Models in the Age of Systems Biology

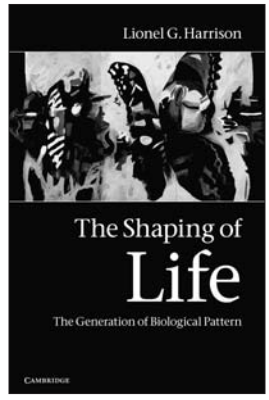
The Shaping of Life: The Generation of Biological Pattern. Lionel G. Harrison. Cambridge University Press, 2011. 272 pp., illus. $99.00 (ISBN 9780521553506 cloth).

Lionel Harrison was a physical chemist at the University of British Columbia whose interests turned to developmental biology when he was in his late 40s. He sustained that interest until his death in 2008 and first wrote a more-technical volume about his work, entitled *Kinetic Theory of Living Pattern* (1993). *The Shaping of Life: The Generation of Biological Pattern* was drafted shortly before Harrison's death in 2008 and was later completed by a consortium of his former students and postdoctorate researchers.

Harrison's goal was to produce a volume that was focused on the same ideas as was his 1993 book but to accomplish this in a less-technical and more-accessible way, using simple mathematical methods to understand how living organisms develop. As the writing progressed, *The Shaping of Life* became more of a commentary on how to bridge the gap between phenomenological models and molecular biology. The result is an interesting but uneven volume that should stimulate thinking about the role of phenomenological models in the age of systems biology.

Throughout his career, Harrison observed a gulf between theorists (those modeling macroscopic patterning) and empiricists (those studying molecular detail), although, toward the end of his life, he became optimistic about bridging this gulf. He believed that one could understand biological patterns through the use of phenomenological models, rather than a detailed knowledge of molecular biology. He saw a plentitude of both data and theory on opposite sides of this great intellectual chasm, but the challenge of building the bridge was daunting:

> Trying to cross disciplinary boundaries, one is beset with many perils. Some of these are rather trivial things to do with word usage.… But crossing boundaries becomes much more difficult when it involves [the] rapid and fluent comprehension of a new set of principles—whether these are ones that have to be expressed in mathematical terms or… by using the panoply of terminology of molecular genetics. (pp. 41–42)



The Shaping of Life is permeated with the attitude that although they must, biologists cannot do mathematics: "I don't generally anticipate that plant breeding in culture vessels and model breeding in computers will be done most usually by the same person" (p. xii), which becomes a self-fulfilling prophecy. However, Harrison believed that in the proper pursuit of the scientific method—when it is applied to developmental biology—experiment and theory would be equally time consuming.

But if the purpose of the book is to bridge the gap between empiricists and theoreticians, the treatment of mathematics is too cavalier to help. Harrison introduces the first equation in the book with "Consider these equations for a wavelength" (p. 38); those not in the know will emerge knowing essentially nothing more. Here and elsewhere (pp. 64, 70, 86), Harrison misses an opportunity to teach about dimensional analysis and dimensionless numbers. The classical diffusion equation is not given until page 111, and it too is presented with little explanation.

Harrison began his work in developmental biology as he began this book—by watching plants grow. He worked with Patrick von Aderkas studying developing somatic embryos of hybrid larch. In a later chapter, he shows that he knew his *Acetabularia*, and he subsequently provides superb summaries of experiments and observations on a variety of systems.

In the second part of the book, Harrison turns to animals but begins with a bit of a historical survey of the works of Sir D'Arcy Wentworth Thompson, Sir Vincent Brian Wigglesworth, and then Alan M. Turing. Chapter 8 is called The Dreaded Fruit Fly and is so named because Harrison found a particularly strong dislike of the phenomenological theory among *Drosophila* researchers. He discusses the earliest gene expression and protein concentrations in *Drosophila* eggs and pairs this with a reaction–diffusion model that creates a similar pattern. He also investigates those parts of the development of vertebrates that are likely to have important relationships with the development of plants or of lower animals and those parts that are so intrinsically different that no parallels can be drawn. In the course of this work, we are treated to the interesting biology of amphibia.

Harrison saw development as the process of breaking the symmetry that establishes the organism and, for this reason, was a great fan of the Turing (1952) model of morphogenesis: "The molecular–genetic approach is to collect details until one has a schematic of

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the whole reaction network and then examine its dynamic properties [where math may be needed]" (p. 45), whereas "the reaction–diffusion approach is to try to establish the presence of the motif that confers on the network the symmetry-breaking or pattern-forming property [i.e., that the pattern is formed by chemical dynamics]" (p. 46).

I found chapter 6 on the Turing equations to be somewhat long and wordy; later in the book (p. 159), however, there is a list of possible Turing morphogens of organisms ranging from slime molds to plants to vertebrates. Harrison asks the question, "When one has devised such a mechanism, what kind of experimental evidence does one try to match with it?" (p. 191) and answers by explaining that what we need in order to link theory to experimentation are careful measurements of the rates of change, the amount of time of transitions, sizes, and the number of parts in a pattern. Throughout the book, he offers the simplest models of complex dynamics, with the notion that one should apply Occam's razor to each explanation.

Because of his own training in physical chemistry, Harrison focuses on the pattern that a reaction–diffusion mechanism generates, and he does this through linear analysis—compared with James D. Murray's two-volume *Mathematical Biology* (2002), for example, where a more-complete treatment is given. But computation is essential even here. Harrison believed that to understand development properly, one needs to plunge into the equations that describe the processes. In this regard, he was hampered by an admitted lack of knowledge of partial differential equations, but he saw software as a possible answer, the idea being that it can assist in bringing experiment and theory together by letting individuals explore the interaction among geometry, chemistry, and growth rates without their having had to master the mathematics. To my mind, this is like teaching kids to use a calculator without explaining arithmetic—few of the concepts will sink in.

Turing's (1952) model applies to no particular species; for this reason, it applies to many. It represents a mathematical exploration of the phenomenon that is highly idealized, and it and its extensions (i.e., reaction–diffusion equations) often generate patterns that are similar to what we see in nature. An objection to using these applications is that it is easy to conclude that a matching pattern means a discovered mechanism, but clearly this is not so. The potential confusion is heavily outweighed, however, by the simple and profound insights that such phenomenological models generate.

In today's world, an impression is often given that if we can just take things completely apart, we will understand how they work as a whole. This is not likely to be the case, and, as Harrison intimated, our greatest understanding will come by combining molecular details, phenomenological models, and evolutionary thinking (Dorit 2011). There is no better example of this unified approach than the recent success in using the *Wolbachia* bacteria to suppress the transmission of dengue fever. These papers (Barton and Turelli 2011, Hoffman et al. 2011, Walker et al. 2011) are the seamless blending of the approaches that Harrison calls for in *The Shaping of Life*. The gap was bridged sooner than he could have realized.

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ECOLOGICAL AND SOCIAL CONSEQUENCES OF THE VOID IN MANGROVE CONSERVATION

Let Them Eat Shrimp: The Tragic Disappearance of the Rainforests of the Sea. Kennedy Warne. Island Press, 2011, 166 pp., illus. $25.95 (ISBN 9781597266833 cloth).

Let Them Eat Shrimp: The Tragic Disappearance of the Rainforests of the Sea is designed to draw attention to the devastating effects of industrial aquaculture—shrimp ponds in particular—and of land reclamation on mangroves around the world. These issues are presented as case studies—as informative as they are interesting, as diverse as they are insightful. Author and journalist Kennedy Warne has produced a highly readable but somewhat frightening account of the damage done to this ecosystem, and the patterns of destruction appear to be similar worldwide—with the exception of one or two glimmers of hope.

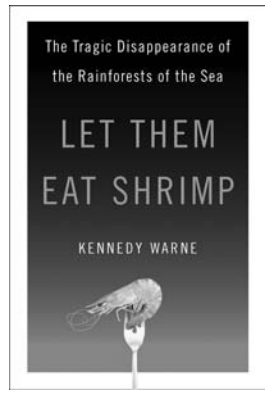
The book begins with an excellent introduction to the unique features of mangrove plants and their environment. The associated fauna is also introduced, as are the communities that live among and depend on mangroves. However, the underlying claim of the book that "without mangroves there would be no shrimp" (p. 29) is misleading. Mangroves are important for a part of the life cycle of some species of shrimp, but shrimp are not wholly dependent on mangrove forests and their waterways.

The evaluation of shrimp yield and mangrove data by Lee (2004), who used principal-components analysis, showed that shrimp yield is most strongly correlated with tidal amplitude, which suggests that shrimp catch is influenced by the amount of intertidal area available and not merely by the area of mangroves. Moreover, no significant relationship was noted between shrimp catch and relative mangrove area. Dietary evidence

supports this view: Stable-isotope studies have shown that the proportion of mangrove matter used as food for shrimp declines farther offshore, where phytoplankton and microalgae form the bulk of a shrimp's diet.

Although most of the case studies in *Let Them Eat Shrimp* are well researched and colorfully described, additional detail could have been helpful for one or two. For example, in the case study of the mangroves of the Rufiji Delta, Warne neglects to mention that in 1904, the colonial state of German East Africa (modern-day Tanzania) supplanted the local community's use of these mangroves with its own. Having pronounced the mangrove forests to be "ownerless, uninhabited, and off-limits to peasant use" (Sunseri 2003), the aim of the colonial government was to tax the communities of the Rufiji and to regulate the production of sisal hemp, coffee, and cotton as cash crops. The pivotal Maji Maji rebellion of 1905–1907 was the result of this policy, the first large-scale movement of resistance to colonial rule in East Africa. From this historical illustration, a lesson could perhaps have been gained: How acceptable should it be now for governments to restrict or ignore the rights of access of local communities to mangrove resources?

Similarly, the Sundarban mangroves are given deserved credit in the book for minimizing damage and loss of life during cyclones, but the valuable benefits of the planted mangrove greenbelts on the remaining parts of the Bangladesh coast are also worthy of mention. The extensive protection offered by the sustainable management of both natural and planted mangroves cannot be disputed. In addition, the minimal damage suffered by the coastal areas of Bangladesh from the Indian Ocean tsunami on 26 December 2004 can be attributed simply to the good condition of both the natural mangroves and the planted mangrove greenbelt of that country (Saenger 2011). The damage in other neighboring countries, where greenbelts do not exist or where natural mangroves had been severely degraded, was immense, sadly resulting in a great loss of property and lives. It is my view that the planting of mangrove greenbelts should be more actively and globally promoted—particularly in a world concerned with the possibility of rising sea levels. Planted mangrove habitats would also offer the added bonus of biodiversity conservation. The book touches on this



point but argues that system functionality is not restored for about 30 years (p. 109)—a time frame I have found to be much shorter (i.e., 4–6 years).

Despite my role as a mangrove ecologist and one who is generally wary of unfettered industrial aquaculture, I was disappointed by the book's treatment of industrial aquaculture and land development as being quintessentially evil, whereas subsistence extractive use—whether it be timber, fish, crustaceans, honey, thatch, or molluscs—is painted in Arcadian hues. The fact remains that without good management (both of the resource itself and of the political process governing it), both types of land use, when they are taken to extremes, can be destructive (Din et al. 2008). In the Middle East, for example, traditional camel herders have caused extensive mangrove destruction through severe overgrazing, and the loss of certain mangrove tree species (e.g., *Heritiera littoralis*, *Bruguiera gymnorhiza*, and *Ceriops tagal*) to traditional dhow construction has reduced the spread of these mangroves by hundreds of kilometers. Although these traditional practices appear at first glance to be sustainable, they are no more so than the commercial shrimp ponds for the giant tiger prawn *Penaeus monodon*.

It seems to me that many of the destructive activities in mangroves are the result of poor governance, based on incompetence, incomplete or improper valuation, or corruption. It is the politicians, therefore, who must be convinced that mangroves are valuable and in need of protection. Sending a message to politicians that mangroves are "green machines," tirelessly providing valuable environmental services, rather than "green cathedrals" (the approach stressed in the book), in which only some of us can worship, would be a useful step toward sustainable land-use practices.

Let Them Eat Shrimp succeeds admirably, however, at bringing the decline of mangroves and the resultant plight of dependent communities into public focus. It is not only the fate of the mangroves at stake but also the social consequences of their loss. The book raises many questions that we will ponder long after reading it.

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A FEATHER IN THE CAP OF SCIENCE

Feathers: The Evolution of a Natural Miracle. Thor Hanson. Basic Books, 2011. 336 pp., illus. $25.99 (ISBN 9780465020133 cloth).

Who among us has not marveled at the structure of a feather, the way its barbules can be unzipped and then locked back together to perfectly restore its vanes? Who has not envied the power of flight that the feather gives to a bird? In the book *Feathers: The Evolution of a Natural Miracle*, author Thor Hanson builds on these common denominators of human experience to take his readers on a broad-ranging tour of what experts know about (and how we make use of) feathers. From basic research about bird biology and the evolutionary origins of feathers to falconry, couture, and bioinspiration in industrial design, the book treats us to a series of engaging essays about feathers, both on and off of the bird.

Hanson is a conservation biologist, as well as an accomplished nature writer, and he has drawn on his scientific training and his extensive field experience in animal behavior and ecology to write *Feathers*. In the book, Hanson weaves his prior encounters with birds and his experiences as a scientist into the text, offering lively anecdotes about his student days and subsequent life as a professional grant-seeking field biologist. He is particularly adept at portraying how science really works: It is about first having an inquisitive mind and then satisfying it by gathering data and experimenting. Ever thus, Hanson has his hands in what he writes about, whether he is pulling the feathers off a road-killed winter wren or taking the temperature of a deceased woodpecker's plumage in both sunshine and shade.

From his current home in the San Juan Islands, where much of the book's action takes place, Hanson tackles an assortment of feather-related topics. But he also interviews experts ranging from fellow scientists to manufacturers of jackets and comforters to feather-clad Las Vegas showgirls, who all offer unique perspectives. Hanson's prose is polished, lively, and evocative. The outcome is a book that is easy and entertaining to read, yet one that is able to satisfy our intellectual curiosity. With Hanson's "up close and personal" approach *Archaeopteryx*'s discovery is revealed from the perspective of a nineteenth-century quarry worker. We then learn more about birds and dinosaurs from the thoughts of a curator of the most recently discovered specimen of *Archaeopteryx* in Thermopolis, Wyoming. While considering bird flight, we meet a falconer who has clocked his peregrine at 272 miles per hour in a streamlined free dive.

On other occasions, Hanson turns to the wisdom of our scientific predecessors. An explanation of the use of plumage in mating displays is introduced via Alfred Russel Wallace's field observations of birds-of-paradise. The topic of sexual selection by way of female mate choice opens with Charles Darwin's original observations and theories. Hanson also keeps good scientific company when doing research: He contemplates heat retention in tiny golden-crowned kinglets during a Vermont winter while taking Bernd Heinrich's famous winter ecology course. He reaches into a broad-billed prion burrow in the Falkland Islands under the tutelage of seabird expert Peter Harrison. He extensively interviews Richard Prum about his model for feather development and about his theory of the evolutionary stages of feathers. He also interviews Xing Xu about the types of filaments and feathers that are turning up on Mesozoic birds and dinosaurs from China.

One unfortunate aspect of *Feathers* is that the topic of birds' evolutionary relationship with dinosaurs is, once again, presented as a contentious scientific battle with winners and losers. With all the new fossil material that has come to light in recent years, the study of Mesozoic filaments and feathers and the animals that possessed them is becoming more empirical and inevitably moving away from its past emphasis on argumentation, but this recent shift is not apparent in *Feathers*.

Much of the book is devoted to human interactions with feathers. Hanson traces the roots of human fascination with feathers, starting with a long-eared owl depicted at Chauvet Cave in southern France. Readers consider the history of feathers used in manufacturing, including fletching on arrows, the once-essential feather quills used for writing, fly tying for trout fishing, and of course clothing and bedding made with astonishingly insulative downy feathers. We learn that manufacturers of waterproof clothing are still trying to decipher how structure alone conveys waterproofing in duck feathers. Although Hanson is a conservationist, the book is far from a conservationist tract. He presents the history of human exploitation of birds with surprising humor, leaving judgment up to the reader. Still, it is a dark chapter that recounts the exploitation of egrets, ostriches, and other birds for women's hats in the late nineteenth and early twentieth centuries, including the obscure fact that the most valuable cargo on the Titanic was 40 cases of fine plumes.

In *Feathers*, Hanson is remarkably successful at offering something for everyone. Readers from young adults to professional ornithologists and from those interested in nature to those

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more interested in human culture will enjoy this book. I should add that it is nicely illustrated with black-and-white drawings and includes chapter notes, a bibliography, and an index. Ultimately, *Feathers* is a book to read for pleasure, but along the way, we gain knowledge and insight into nature and our relationship with it.

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NEW TITLES

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