The Shaping of Life: The Generation of Biological Pattern

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Phenomenological Models in the Age of Systems Biology

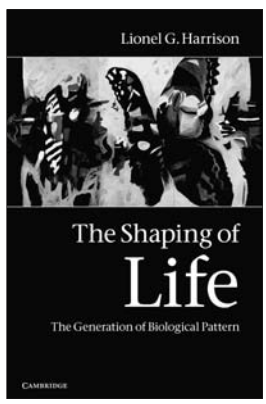
The Shaping of Life: The Generation of Biological Pattern. Lionel G. Harrison. Cambridge University Press, 2011. 272 pp., illus. $99.00 (ISBN 9780521553506 cloth).

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