Review of[1]
The Mathematics of Life
by Ian Stewart
Basic Books/Profile Books, 2011
358 pages, Hardcover
US$16.68 on Amazon.com

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1 Introduction

Ian Stewart is one of the premier popularizers of mathematics. He has written over twenty books about math for lay audiences, including the well-received *Flatterland* and *Professor Stewart's Cabinet of Mathematical Curiosities*. He has also co-authored science fiction, and books on the science of science fiction (three books on "the science of discworld"). In his newest effort, *The Mathematics of Life*, Stewart focuses his talents on the mathematics of biology, and the result is superb. In an easy, flowing read, with dozens of diagrams and scholarly footnotes—but without a single formula—he introduces the reader to a wide range of interactions between mathematicians and biologists. I heartily recommend this book.

2 Summary

The Mathematics of Life contains 19 chapters. Chapter 8, "The Book of Life," focuses on the Human Genome Project, and algorithmic challenges of DNA sequencing. However, as this possibly the area most familiar to SIGACT News readers, I will only mention it briefly, and, instead, focus on chapters that introduced me to areas of mathematical biology I had not previously encountered.

Perhaps the most direct connection to (the roots of) theoretical computer science comes in Chapter 13, "Spots and Stripes," where Stewart considers Alan Turing's famous paper, *The Chemical Basis of Morphogenesis*, and sketches the development of biological thought about animal markings since Turing's groundbreaking proposal. As Stewart says:

> For half a century, mathematical biologists have built on Turing's ideas. His specific model, and the biological theory of pattern-formation that motivated it, turns out to be too simple to explain many details of animal markings, but it captures many important features in a simple context, and points the way to models that are biologically realistic.

Turing proposed"reaction-diffusion" equations to model the creation of patterns on animals during embryonic development. As noted by Stewart, Hans Meinhardt, in *The Algorithmic Beauty of Seashells*, has shown that the patterns on many seashells match the predictions of variations of Turing's equations. The mathematician James Murray extended Turing's ideas with wave systems, and proved the following theorem: a spotted animal can have a striped tail, but a striped animal cannot have a spotted tail. Intuitively, this is because "the smaller diameter of the tail leaves less room for stripes to become unstable, whereas this instability is more likely on the larger-diameter body."

In the very next chapter, "Lizard Games," algorithmic game theory makes an appearance. Stewart introduces us to Barry Siverno's studies of side-blotched lizards. These lizards come in three morphs: orange-throated, blue-throated and yellow-throated. The orange males are the strongest, while the yellow males are the smallest and most female-colored. The blue males are the best at pair-bonding. So the oranges win when they fight the blues, the blues are preferable to the yellows, and—the kicker—the yellow males sneak away with the females while the oranges fight the blues. This suggests an evolutionary game where

- orange beats blue
- blue beats yellow
- yellow beats orange.

Stewart introduces von Neumann's minimax theorem, Smith's definition of evolutionarily stable strategies, and other game-theoretic concepts. He then discusses what "survival of the fittest" means in a context where there is no one clear winner. (One of Stewart's themes throughout the book is an attempt to give the reader a more sophisticated understanding of Darwinian evolution.)

Also in this chapter, Stewart gives many examples of evidence for evolution, and ways in which evolutionary theory has developed since the time of Darwin. For example, the conventional biological wisdom at one time was that *sympiatric speciation* was impossible. Roughly, sympiatric speciation occurs when one species develops into two distinct species in a single geographic area. For many years, it was believed that groups of animals had to be geographically separated for speciation to occur. Nevertheless, this conventional wisdom appears to be false, both because of empirical evidence, and more sophisticated mathematical models. In Stewart's words:

> There are two main forces that act on populations. Gene flow from interbreeding tends to keep them together as a single species. Natural selection, in contrast, is double edged. Sometimes it keeps the species together, because collectively they adapt better to their environment if they all use the same strategy. But sometimes it levers them apart, because several distinct survival strategies can exploit the environment more effectively than one. In the second case, the fate of the organisms depends on which force wins. If gene flow wins, we get one species. If natural selection *against* a uniform strategy wins, we get two. A changing environment can change the balance of these forces, with dramatics results.

There are other computer-science-related chapters: "Networking Opportunities," which introduces graph theory; "What is Life?" which introduces cellular automata and von Neumann's replicating automaton. However, I will use the remaining space in this review to discuss a chapter that relates more to pure mathematics.

Chapter 10, "Virus from the Fourth Dimension," tells the story of scientists identifying viruses with X-ray diffraction and similar methods. In several chapters, Stewart discusses the mathematical importance of symmetry and symmetry-breaking, and this chapter is no exception: the herpes simplex virus is mirror-symmetric and has 120 symmetries. It turns out that many viruses are coated with chemicals in the shape of an icosahedron. These *icosahedral virus coats* are made of triangular arrays 9of capsomers, small self-assembling proteins.

Unfortunately, the mathematics of pure icosahedra did not quite match what was empirically observed. Inspired by the geodesic domes of Buckminster Fuller, Donald Caspar and Aaron Klug in 1962 proposed a theory of *pseudo-icosahedra* to model virus coats. (Expert geometers were already familiar with pseudo-icosahedra, but most mathematicians were not.) While this provided an excellent model of many viruses, over the next forty years, research teams found structures that could not be explained using the Caspar-Klug theory. Finally, starting in the year 2000, the mathematician Reidun Twarock and co-authors proposed a unifying framework, using higher-dimensional geometry.

Twarock introduced a *viral tiling theory* that uses the six-dimensional icosahedral symmetry group, then takes a cut from that 6D lattice and projects it into three dimensions. This approach accurately "predicts" both the pseudo-icosahedral virus coats, and also the exceptional virus coats that were observed after 1962.

3 Opinion

This book is full of great material I did not mention at all. Most of the early chapters are short, and introductory, which is why I focused on the later chapters in this review. The prose style is friendly and clear throughout, without talking down to the reader.

I consider this to be an excellent introduction to the mathematics of biology, for both amateurs and professionals. Seasoned researchers are likely to learn "teasers" about areas unfamiliar to them, and smart people "afraid of math" can read the book and enjoy the material. Highly recommended. I will conclude this review with the same words Stewart used to conclude the book:

> Instead of isolated clusters of scientists, obsessed with their own narrow specialty, today's scientific frontiers increasingly require teams of people with diverse, complementary interests. Science is changing from a collection of villages to a worldwide community. And if the story of mathematical biology shows anything, it is that interconnected communities can achieve things that are impossible for their individual members.
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> Welcome to the global ecosystem of tomorrow's science.