

Putting the \times in Biology: A Review of *The Mathematics of Life*

Reviewed by John Adam

The Mathematics of Life

Ian Stewart

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Charles Darwin's 1859 work *On the Origin of Species* contained no equations. But that does not mean mathematics has no role to play in the science of life; in fact, the field of biomathematics is burgeoning and has been for several decades. Ian Stewart's new book does an admirable job of unfolding the mathematics undergirding so much of the research being carried out today in the many fields that comprise the subject of biology. Stewart sets the context by noting five great revolutions that have changed the way scientists think about life. These five revolutions are: (i) the microscope; (ii) classification; (iii) evolution; (iv) genetics, and (v) the structure of DNA. The sixth, Stewart says, is well on its way. It is mathematics.

I'm ashamed to admit it, but I did not pass my high school biology exam (in the UK it was called the "Ordinary Level" exam, or "O" Level). Reading Chapter 2 of the book ("Creatures Small and Smaller") brought back a lot of horrible memories about, well, memorization, particularly the names of all the components of a cell. Stewart does a good job of describing material I should have

known then but never did, and much more. By my standards at the very least, he knows and writes about a great deal of biology. Some years ago I was invited to give a talk about the philosophy and methodology of mathematical modeling at a conference on the topic of cancer biology. Most of the talks following mine were about maps of protein networks and pathways of gene expression for various types of cancer; the subject seemed (and is) incredibly intricate and complicated. I left the meeting feeling quite discouraged about the apparent mismatch between the kind of modeling I had presented and the sheer complexity of molecular pathways. So can mathematics bring some structure to this complexity? Indeed it can.

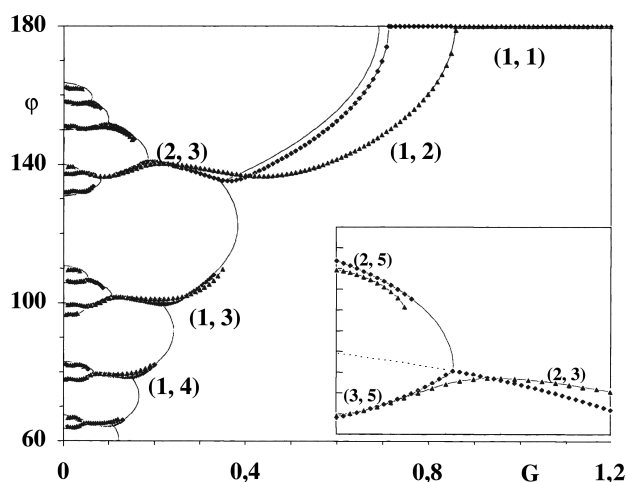
The application of serious mathematics to biology began perhaps with the foundational work of Sir Ronald Fisher, Sewall G. Wright (an American geneticist), and John B. S. Haldane on theoretical population genetics. Fisher's seminal 1937 paper [3], entitled "The wave of advance of advantageous genes", laid the groundwork for much of the interest in reaction-diffusion equations in later decades. It is well worth reading for both historical and mathematical reasons. Haldane, incidentally, wrote the popular article about the problem of scale, "On being the right size". More recently, William D. Hamilton, John Maynard Smith, and others continued this line of investigation. Hamilton was a theoretical evolutionary biologist whose work in the mid-1960s on the genetic evolution of social behavior is widely referenced. He is

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considered to be one of the forerunners of sociobiology, popularized by the American biologist E. O. Wilson in 1975. Smith wrote many articles and a book on the role of game theory in animal evolution. Curiously, Stewart doesn't refer much to this early work (though he does mention the game-theoretic contributions of Maynard Smith to evolutionary biology) but concentrates on more recent developments in the subject.

This is a review of Stewart's book, but rather than summarizing the material it contains or commenting on the writing style (which is up to his usual high standard, by the way), I shall take some liberties with several topics in the book by pursuing them in more detail. I shall do this primarily by taking excursions into the literature cited by Stewart in the extensive chapter notes at the conclusion of the book but also by assembling some of his comments about what modeling can do and what it does not do. These are scattered throughout the book, but together they comprise a unified account of the nature of a model and would in my view be valuable for any biologist wishing to work in the field of mathematical (as opposed to statistical) modeling. I make the latter point because at one time I gave a "grand rounds" talk about modeling at a nearby medical school (yes, it was pretty much the same talk as the above-mentioned one). The audience apparently stayed awake and was very polite, so much so that I thought I had made something of a breakthrough in their appreciation of the topic, until an MD researcher came up to me and suggested that I could help him analyze statistically all the data he had recently acquired....

The starting point for my first foray into the recently known is Chapter 4 ("Florally Finding Fibonacci"). To foreshadow the collection of comments about modeling, I note that in this chapter Stewart makes an important distinction between *descriptive* and *explanatory* models in connection with "the strange numerology of the plant kingdom", namely *phyllotaxis*—the arrangement of plant organs such as leaves, petals, branches, bracts, scales, and florets [5], [6], [12]. Collectively these are called *primordia* in their infancy stage. The connection of such patterns with the golden ratio, the golden angle, and the Fibonacci sequence is probably the best-known occurrence of a mathematical pattern in nature (at least, in my experience). Scattered throughout the book are references to this important distinction, including many examples of such models and our reasonable expectations arising from them. Thus, in connection with mathematical biology in early Victorian times, such as it was, he points out that the numerical patterns in plants were described in considerable detail—but that was as far as it went. Explanations (or at least explanatory models) for



This diagram from [2] shows the steady divergences ϕ ($\phi > 0$) obtained as a function of G for two energy profiles $1/d^3$ (triangles) and $\exp(-d/l)$ with $l = 0.1$ (squares). The solid line shows a diagram obtained using the geometrical condition. Inset: Detail of a transition. (Figure reprinted with permission from S. Douady and Y. Couder, "Phyllotaxis as a physical self-organized growth process", *Phys. Rev. Lett.* Copyright 1992 by the American Physical Society. Readers may view, browse, and/or download material for temporary copying purposes only, provided that these uses are for noncommercial personal purposes. Except as provided by law, this material may not be further reproduced, distributed, transmitted, modified, adapted, performed, displayed, published, or sold in whole or part, without prior written permission from the Amer. Phys. Soc.)

these patterns would have to wait many decades, as we shall see.

In the simplest case, primordia are formed near the apex of the plant—the tip of the growing center—and move outward. The spiral resulting from connecting chronologically successive primordia is called the *genetic* (or generative) spiral, but this is not noticed when looking at a sunflower head, for example. There appear instead two conspicuous sets of intersecting spirals called *parastichies* (sounding rather like it should be the name of a Scottish pub). One set runs clockwise and the other counterclockwise, and the number of spirals in each set are, in the vast majority of cases, consecutive terms in the Fibonacci sequence. Thus a fairly large sunflower head might have fifty-five clockwise spirals and thirty-four counterclockwise; a smaller head might contain thirty-four and twenty-one, respectively. But all is not lost for the genetic spiral, despite its illusory ostentatious cousins: the so-called *divergence angles* (relative to the apex) between two successive primordia on this spiral are close to the golden angle of $2\pi/(1 + \Phi)$ radians, or $\approx 137.5^\circ$. Indeed, the sequence $2\pi/(1 + n\Phi)$, $n = 1, 2, 3$, generates the divergence angles for what is sometimes called first, second, and third phyllotaxis [13]. The latter two are approximately 99.502° and 77.955° , respectively.

In 1992 a fascinating paper was published in the *Physical Review Letters* [2], and its findings significantly invigorated, even galvanized, the phyllotaxis research community. The authors, Stéphane Douady and Yves Couder, were able to obtain phyllotactic patterns, previously only observed in botany, in both a physics laboratory experiment and a numerical simulation. They showed, in effect, that the patterns arise from self-organization in an iterative process; they were studying a dynamical system.

The experimental arrangement was as follows. Identical mutually repelling drops of a magnetic fluid (a “ferrofluid”) were dropped periodically (with adjustable period T) at a given radius R_0 from the center of a plane surface. By means of a radial gradient of the imposed vertical magnetic field, the drops were radially advected away from the center with speed V_0 . The results were characterized by a single dimensionless parameter, $G = V_0 T / R_0$. The speed was adjusted by varying the magnetic field gradient. As drop after drop fell, spiral patterns developed under the combined influence of radial advection and mutual repulsion. This became particularly evident as the drops fell more frequently (i.e., as G decreased). The numerical simulations were designed to mimic the experimental setup, and this time the repulsive forces between particles were varied. The “repulsive energy” laws used were, as stated in the paper, $1/d$, $1/d^3$, and $\exp(-d/l)$, where d was the inter-particle distance; the results were all qualitatively the same.

Both the experiment and the simulation yielded similar results. They found that as G was decreased, the spiral pattern underwent transitions—symmetry-breaking bifurcations—from parastichy numbers (i, j) to $(j, i + j)$. For each pair of initial conditions, the simulation produced curves $\alpha(G)$ that converged for $G = 0$ toward the corresponding divergence angle (note that I am using α where Douady-Couder used ϕ). The primary curve corresponded to the golden angle of 137.508° , but another converged to the Lucas angle 99.502° , one to 77.955° , and some to angles not mentioned above. The ordering is interpreted as the system’s tendency to avoid rational organization, leading to a convergence toward (primarily) the golden number and hence the toward the golden angle. Jean [5] makes the following interesting comment:

This experiment shows that a hypothesis for the physiological process of the interaction of the primordia is not necessary, and that the various patterns do not seem to be directly encoded in genes. The existence of the patterns seems ...to transcend the degrees of botany...This is also

the conclusion to which Levitov (1991b) [8] arrives. His study of the “phyllotaxis” of flux lattices in layered semiconductors concerns a physical system quite unrelated to botany, yet it gives rise to structures very similar to those known in phyllotaxis.

The literature that exists on the topic of phyllotaxis is immense, and while the vast majority (perhaps as much as 98%) of known occurrences in nature involve rational approximations to the golden angle [5], there are exceptions. (In his book *Introduction to Geometry*, H. S. M. Coxeter referred to these occurrences as a “fascinatingly prevalent tendency”.) A divergence angle of $\approx 99.5^\circ$ is not *extremely* rare, as the above percentage indicates; this is associated with the *Lucas sequence* 1, 3, 4, 7, 11, 18, ..., satisfying the same difference equation as the Fibonacci sequence. Indeed, one can define the *generalized* Fibonacci numbers as

$$\begin{aligned} G_{p,q}(n) &= G_{p,q}(n-1) + G_{p,q}(n-2), \\ G_{p,q}(1) &= p; G_{p,q}(2) = q. \end{aligned}$$

The *Binet solution* for this difference equation is [9]

$$G_{p,q}(n) = \frac{1}{\sqrt{5}} \left\{ \left[\Phi^n - (-\phi)^n \right] p + \left[\Phi^{n-1} - (-\phi)^{n-1} \right] (q - p) \right\},$$

where $\Phi = (1 + \sqrt{5})/2 \approx 1.618$ and $-\phi = (1 - \sqrt{5})/2 \approx -0.618$ are the roots of the quadratic equation $x^2 - x - 1 = 0$. It is readily seen that

$$G_{p,q}(n) = pF_{n-2} + qF_{n-1}.$$

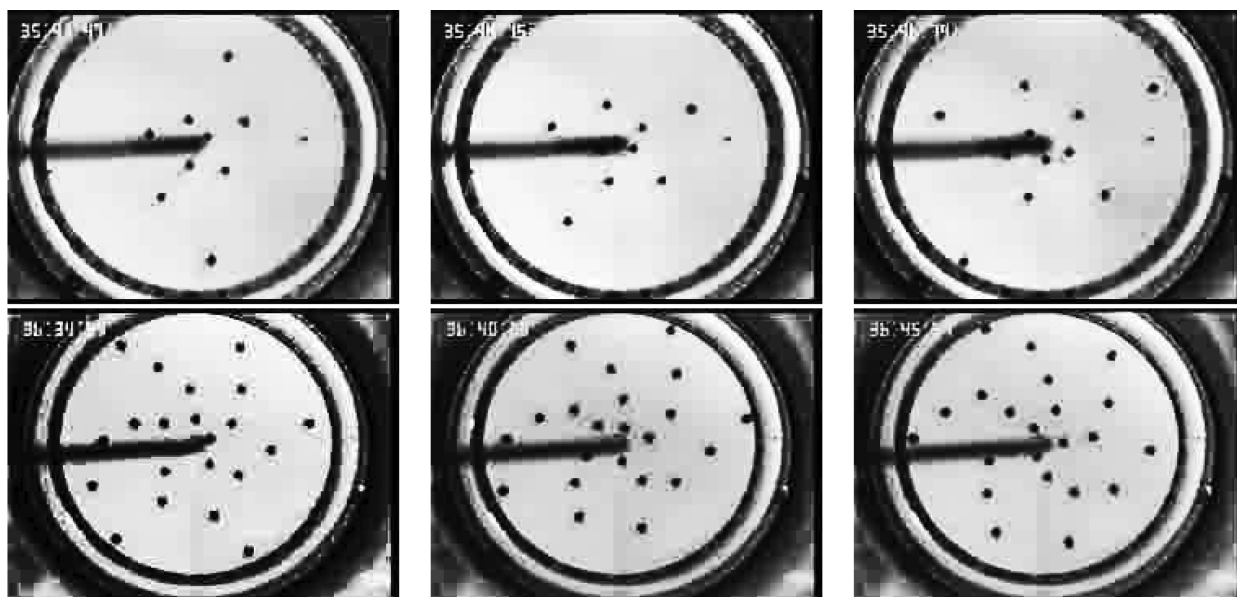
There is a fascinating connection with Farey numbers here. (The Farey series of order N , $\mathcal{F}(N)$, is the ascending series of irreducible fractions in $(0, 1)$ whose denominators do not exceed N .) In [9] Sy-Sang Liaw proved the following theorem and used it to determine the divergence angle of *any* pattern with a parastichy pair:

$G_{a,a+b}(n-1)/G_{p,q}(n)$ and $G_{a,a+b}(n)/G_{p,q}(n+1)$ are two consecutive Farey numbers in $\mathcal{F}(N)$ for $G_{p,q}(n+1) \leq N \leq G_{p,q}(n+2)$ if and only if p/q and b/a are consecutive in $\mathcal{F}(M)$ for $\max(q, a) \leq M \leq q + a$.

He then established for parastichy pair $[p, q]$ that the divergence angle is

$$\begin{aligned} \alpha &= \lim_{n \rightarrow \infty} \frac{G_{a,a+b}(n)}{G_{p,q}(n+1)} \\ &= \lim_{n \rightarrow \infty} \frac{aF_{n-2} + (a+b)F_{n-1}}{pF_{n-1} + qF_n} = \frac{a + b\phi}{q + p\phi}. \end{aligned}$$

The proof of the theorem requires that $|pa - qb| = 1$. Since p and q are usually small integers, a and b (and hence α) are readily found. Thus for $[1, 1]$ and $[1, 2]$, $\alpha \approx 137.508^\circ$; for $[1, 3]$, $\alpha \approx 99.502^\circ$; for $[1, 4]$, $\alpha \approx 77.955^\circ$; and for $[2, 5]$, $\alpha \approx 151.136^\circ$.



In the Douady-Couder experiment, drops of magnetically sensitive material are inserted into the center of a disk in a magnetic field at a fixed rate. The drops are attracted to the edge of the disk and repelled by each other. When inserted, they adjust themselves in the field of repulsions established by previous drops, and then move radially outwards. As the rate of insertion is increased (as from the top row to the bottom one), they are influenced by more neighbors, and the pattern changes qualitatively. Neighbors form apparent spirals, just as sunflower seeds do. (We thank Stéphane Douady for permission to use these images extracted from the film DouadyCouderExp5.9MB.mov, which can be found on the Internet. See for example Julie Rehmeier's article "The Mathematical Lives of Plants" on the *Science* website.)

Liaw was also able to reproduce the patterns of spiral phyllotaxis via a numerical simulation (for other aspects of the research inspired by the Douady/Couder paper, see [4], [7], [8], [13]). A very comprehensive site for all things Fibonacci is that developed by Ron Knott at the University of Surrey, UK: <http://www.maths.surrey.ac.uk/hosted-sites/R.Knott/Fibonacci/>.

In the above models, primordia are represented experimentally as floating droplets and numerically as discrete point-like objects. By contrast a "continuum" model enables mechanical forces to be distributed in a continuous manner over a surface. The subject of elasticity theory then becomes of prime importance in answering the question, How do surfaces deform under spatially and temporally varying forces? In 2004 two University of Arizona mathematicians, Patrick Shipman and Alan Newell [15], sought to use elasticity theory to see if they could reproduce phyllotaxis as surface deformations arising from a minimum of the strain energy buckling pattern on a compressed shell (thus mimicking the plant's growing tip). They showed that the strain energy is minimized by the superimposition of certain triads of wave patterns. They write, "We reproduce a wide spectrum of plant patterns, all with the divergence angles observed in nature, and show how the occurrences of Fibonacci-like sequences and the golden angle are natural consequences."

Thus there was indeed a pitchfork bifurcation of sorts from the nineteenth-century descriptive models to explanations based on dynamical systems and mechanochemical models. As Stewart points out, "there is a complex set of feedback loops between biochemistry and mechanics, mechanics and geometry, and geometry and biochemistry...undreamt of in Victorian times."

My next foray into the book commences with Stewart's fourteenth chapter ("Lizard Games"). Like most of the others, it contains much fascinating discussion. In particular, he highlights some important work on models of speciation. To set the scene, note that as early as 1952, the seminal paper on pattern formation by Alan Turing [17] demonstrated that the dynamics of so-called *reaction-diffusion* systems can be very sensitive to spatial inhomogeneities. The importance of spatial inhomogeneities has also become increasingly apparent in theoretical ecology; in particular, what are the effects of crowding on pattern formation? In a paper published in the *Brazilian Journal of Physics* [1] (see also [14]), a research group analyzed this question with a view to understanding the role of competition in the process of demes formation (and ultimately more about genetic diversity and speciation). In biology, a *deme* is a term for a local population of organisms of one species that actively interbreed with one another and share a distinct gene pool. When demes are

isolated for a very long time, it is thought that they can become distinct subspecies or species.

Crowding was modeled by decreasing the birth rate at large population densities with three different types of “crowding functions”, and they also investigated how the sharpness of the boundaries of the local territories for competition and mating affected the resulting patterns. The choices of (per capita) crowding functions were logistic, exponential, and Gaussian. For computational convenience they considered space to be discrete, with the population located in a square lattice with periodic boundary conditions and iteratively solved for the local population on each site at time $t + 1$ in terms of its population at time t . The stability of spatially independent solutions was first investigated, followed by the stability of small spatial perturbations. The subsequent analysis is very interesting; in particular, the polylogarithm function

$$\text{Li}_s(z) = \sum_{k=1}^{\infty} \frac{z^k}{k^s}$$

(a generalization of the Riemann zeta function) with $s = 2$ makes several appearances. But tempting as it is, it would take us too far afield to go there. The authors concluded that of the three crowding functions chosen, the logistic leads to the most rapid deme formation and is also the most robust against changes in the smoothness of territory boundaries. Nevertheless, if the boundary becomes too “fuzzy”, then even this choice cannot guarantee that such spatially isolated groups will spontaneously form.

There is much to note in this chapter, including a fascinating discussion of speciation as an example of symmetry breaking and the onset of instability. Indeed, Stewart notes that symmetry breaking “provides a very general mechanism for the formation of nature’s patterns. Those patterns are the explicit realizations, in specific physical systems, of the abstract symmetries that are implicit in the laws that describe those systems.” But I love the “kicker”: “Multiple solutions open the door to symmetry breaking. What shoves the mathematics through that door is instability” (p. 205).

As a further aside to this chapter, I was intrigued by Figure 59, which shows a Stewart-generated scatterplot for beak size versus wingspan in a group of birds. The figure shows two clusters and an outlier; Stewart uses this to introduce us to cluster analysis. Years ago I encountered a similar situation in connection with a pattern-recognition algorithm. The question that arose was, Given such a scatterplot, is there a preferred direction along which the data sets will be best separated? In principle, at least, the higher the dimension of the space, the more opportunity there will be for selective directional viewing. A major problem of medical diagnosis is that of pattern recognition

and subsequent classification; at the simplest level, that of distinguishing between two pattern sets. More than two decades ago, oncologist William H. Wolberg and mathematician Olvi L. Mangasarian published a paper on the application of a multi-surface method (*MSM*) of pattern recognition to breast cancer diagnosis [10], [11], [18]. Fundamental to *MSM* is the role of linear programming as the key algorithm for generating data-separating (hyper) planes. The authors used these hyperplanes iteratively to construct a piecewise linear surface that separated benign B from malignant M cases (the “training set”) in a breast cancer study. The surface thus constructed classified points into (in this instance) two subspaces denoted by B and M . In general, the convex hulls of the sets B and M intersect, so the idea is to construct a pair of parallel planes that are as “close” to each other as possible, such that only the region between them contains points from both subspaces. The “outer” regions are eliminated from the method, and the process is repeated on the remaining interior points with a new set of parallel hyperplanes. In this way an ordered finite set of parallel hyperplanes eventually separates the two data sets. This set then constitutes a piecewise linear discriminant function that completely separates the given training set. That function is then used to predict whether or not a new data point is benign or malignant, depending on which side of the ordered half-space it is found on. Given the success of the technique described in [10], [11], it appeared that this technique could be a valuable tool in cancer diagnosis.

Chapter 15 is called “Networking Opportunities”. Efficient transport networks are crucial (and hence ubiquitous) in social and biological systems. In modern society, it is deemed imperative to have a multidimensional infrastructure designed to move people, resources, and information while optimizing efficiency and cost in some measurable way. And if one does not have a Facebook account, one is often considered to be “beyond the pale”, especially by students. (The answer may be to have an account with no friends specified.) However, the large but single-celled slime mold organism *Physarum polycephalum* makes LinkedIn and Facebook look like amateurs in the game of networking, social or otherwise. It forages for patchily distributed food sources by means of a tubular network (behind a “foraging” boundary) linking the discovered food sources. By so doing, it can find the shortest distance through a maze and connect different arrays of food sources efficiently, yet with low total length and short average distance between pairs of food sources. According to an article in the journal *Science* [16], it does all this with a high degree of “fault tolerance” to accidental disconnection. One is tempted to respond to this impressive résumé by shouting “It’s a bird, it’s a plane, it’s *P. polycephalum*!”

The team of Japanese researchers studied how *P. polycephalum* would “behave” when confronted with a laboratory arrangement that placed food sources at spots representing the geographical distribution of cities in the Greater Tokyo area and compared the results with the actual rail network in that region of Japan. What occurred was quite remarkable. They found that the *Physarum* network exhibited a structure similar to that of the rail network (in terms of the above-mentioned characteristics), but it accomplished it through self-organization without a “control center” (or, indeed, explicit global information). It did this by selective reinforcement of preferred routes and removal of redundant connections. On the basis of these results the authors developed a mathematical model to reproduce the observed behavior. They used the theory of Hagen-Poiseuille fluid flow to model the flux of protoplasm through the tubes. They suggest that such biologically inspired models can produce solutions with properties at least as good as many existing infrastructure networks (including remote sensor arrays and wireless networks).

Here is a compilation of some statements Stewart makes about mathematical models and modeling. This list is probably not exhaustive, and they are scattered throughout the book, so it seemed sensible to gather them all into an itemized list here. I have annotated them with some reflections of my own; I hope the author won't mind.

(i) “*Mathematical models will apply within some range of validity, but it's not sensible to expect them to apply everywhere*” (p. 55).

(ii) “*Mathematical models [as opposed to the limitations of verbal descriptions] ...clarify the concepts, the assumptions and the relations between them. That is what models are for*” (p. 234). A model that tries to explain everything about a phenomenon would be as complicated as the phenomenon itself and would, as René Thom has said, explain nothing.

(iii) “*Science is seldom about direct observation: it is nearly always about indirect inference*” (p. 221). If a murder is committed when no one apart from the victim and the murderer are present, relatively few people doubt the conclusion of the inferential process if it is carried out properly (except possibly the family and friends of the above parties.) The all-too-common and somewhat specious argument that “we weren't there, how can we possibly know what happened?”, when applied to subjects such as evolutionary biology, paleontology, and cosmology, represents a remarkably low and narrow view of the nature of science. In connection with models of the 2001 outbreak of foot-and-mouth disease on British farms, Stewart again reminds us that:

(iv) “*Even in the physical sciences, models mimic reality, they never represent it exactly.... It is pointless to expect a model of a biological system to do better*” (p. 273). In essence he is saying that different models of a phenomenon, each focusing on a different aspect of the problem, when combined, can provide complementary levels of both description and explanation.

(v) “*What counts is what the model predicts, not what it leaves out*” (p. 318). In other words, the value of any given model is not how consistent it is with existing data (important though that is) but its predictive capability.

There are also sections in the book that have both philosophical and logical implications for some of the more extreme “intelligent design” hypotheses (including the confusion of “necessity” with “sufficiency”), but finding these is left as an exercise for the interested reader!

I enjoyed the opportunity to read this book. I did find Chapters 7 and 8 to be a little dry, but that is not a reflection on the author's generally easy-going style; it is more a commentary about my genetic predisposition to struggle with genetics and taxonomy (though my high school experience with biology didn't help). I was also disappointed that there was nothing about modeling tumor growth and wound healing in the book. The nearest Stewart comes to this, in a mathematical sense at least, is in Chapter 13 (“Spots and Stripes”), though some of the researchers who have made significant contributions to these areas are also mentioned in Chapter 15 (in connection with certain patterns observed in insects, nematode worms, chickens, and frogs). There is obviously much in the book that I have not even touched upon. It would make a wonderful topic for a graduate discussion group. Thankfully, the role of mathematics in biology is becoming more and more appreciated (though I know of some holdouts). Almost a decade ago a colleague in biology and I team-taught a course in mathematical ecology (using *Elements of Mathematical Ecology* by Mark Kot). It was open to mathematics students for undergraduate credit and to graduate biology students for graduate credit. The class consisted of fourteen mathematics and zero biology students! Those days are long gone (I hope). I would suggest that anyone pressed for time would do well to read Chapter 1 of the book (“Mathematics and Biology”), especially pages 9–12. And then read the rest of it.

I'll end with a final quote from the author: “The complexity of biological systems, often presented as an insuperable obstacle to any mathematical analysis, actually represents a major opportunity” (p. 274). For whom? For biology, mathematics, biologists, and mathematicians. *This* is Stewart's sixth revolution.

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Applications are invited for appointment as Associate Professor/Assistant Professor in the Department of Statistics and Actuarial Science and the Department of Mathematics, from January 1, 2012 or as soon as possible thereafter. The post will initially be made on a three-year term. Appointment with tenure will be considered during the second three-year contract. This is a joint appointment of the above two Departments.

Applicants should possess a Ph.D. degree or equivalent. Those whose research lies in the broad area of theoretical/applied probability, stochastic analysis, or mathematical finance will be considered. For enquiries on the existing research activities and the specific job requirements, please write to Professor W.K. Li, Head of the Department of Statistics and Actuarial Sciences (e-mail: hmtlwk@hku.hk).

Applicants should indicate clearly the reference number and which level they wish to be considered for.

A globally competitive remuneration package commensurate with the appointee's qualifications and experience will be offered. At current rates, salaries tax does not exceed 15% of gross income. The appointment will attract a contract-end gratuity and University contribution to a retirement benefits scheme, totalling up to 15% of basic salary, as well as leave, and medical/dental benefits. Housing benefits will be provided as applicable.

Applicants are requested to apply on-line at <https://jobs.hku.hk>. Please also upload a C.V. with a detailed publication list, a research plan, and a statement on teaching philosophy via the on-line application system. **Review of applications will start from January 31, 2012 and will continue until the post is filled.** Candidates who are not contacted within 3 months of the closing date may consider their applications unsuccessful.

The University is an equal opportunity employer and is committed to a No-Smoking Policy