BOOK REVIEW

J. Hofbauer and K. Sigmund, *The Theory of Evolution and Dynamical Systems*, Cambridge U. P., New York, 1988, viii + 341 pp, cloth $65.00, paper $19.95.

The steadily increasing collection of facts from molecular biology to ethology makes it clear that a rigorous physical and mathematical theory of evolution is a task of vast proportions. What gives hope is that the situation was hardly better in many other scientific disciplines that have by now evolved into a stage of remarkable explanatory power. Obviously it is a sound procedure to first focus on modest problems compared to the ultimate aims. This has been done on several levels of evolutionary theory: population genetics, population ecology, molecular (prebiotic) evolution, and animal behavior (sociobiology). There is a recurrent theme in discussions of genes, members of populations, self-replicating polymers, and strategic phenotypes: reproductive success of the corresponding entity or, as in the latter case, of its bearer. Hofbauer and Sigmund focus in their book on ordinary differential equations that model this aspect. The first half of the book consists of four parts, each dealing with one of the topics mentioned above.

After the obligate Hardy–Weinberg law has been presented, Part I introduces dynamical systems by means of the discrete time versions of Fisher's selection equation and the fundamental theorem. The latter states that the average fitness increases as long as the population is not in equilibrium. Part II is a primer on population ecology as modeled by the Lotka–Volterra equation. Predator–prey relations, competitive interactions, and food chains are briefly considered. At the same time the qualitative theory of differential equations as a major tool for investigating dynamical systems is presented. The qualitative theory seeks to establish the asymptotic behavior of solutions. This allows the characterization of the phase portrait and of robust features pertaining to the system. Hence stability becomes the central notion. The principle of linearized stability and the Ljapunov function concept are introduced.

Part III begins with the replication and mutation of noninteracting polynucleotides, which leads to the molecular counterpart of the selection–mutation equation for asexually reproducing individuals. Eigen's explicit inclusion of replication accuracy as a parameter sets a threshold to the length of a molecular information carrier, beyond which its line faces extinction. The resulting "information crisis" is the starting point for considering the Eigen–Schuster solution of this problem. An autocatalytic network might allow for the coexistence of its n members if each needs at least one other member in order to replicate. If the

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mutual help is cyclic, then the network is addressed as a "hypercycle." Global stability of the internal fixed point of hypercycles up to $n = 4$ is proved. The existence of periodic solutions for $n \geq 5$ has been proved only recently (not included in the present edition of the book). Lacking the latter fact it was essential for the validity of the hypercycle concept that, given the initial presence of all members, their individual concentrations would not vanish in the long time limit. Hofbauer and Sigmund coin the term *permanence* for isolating the notion of the boundary of the state space being a repellor. This feature of a dynamical system becomes a major theme in the second half of the book. At this stage the first sufficient condition is introduced as a function whose time average acts like a Ljapunov function. A generalized version of the hypercycle equation is shown to be permanent.

Part IV adopts the view of evolutionary game theory. Fitness as a measure of reproductive success of a phenotype P will certainly depend on what other phenotypes are likely to interact with P. Thus fitness will be frequency-dependent in the same way as the payoff of a strategy depends on how the other players behave during the game. Accordingly a phenotype may be viewed as a strategy. Maynard Smith's notion of an "evolutionary stable strategy," that is, a phenotype that is immune against invasion from mutants, is formally made precise. The authors move on to emphasize the dynamical aspects of game theory. Let x_i, $i = 1, \ldots, n$, be the frequency of a (strategic) phenotype and $f_i(\mathbf{x})$ its fitness (payoff) in a population whose phenotypic distribution is $\mathbf{x}$. The Darwinian view, then, identifies the growth rate $\dot{x}_i / x_i$ with the difference between the fitness of i and the mean fitness level of the population:

$$\dot{x}_i = x_i\Big(f_i(\mathbf{x}) - \sum_i x_i f_i(\mathbf{x}) \Big), \qquad i = 1, \ldots, n. \qquad (*)$$

This is a dynamical system on the unit simplex $S_n = \{\mathbf{x} = (x_1, \ldots, x_n) \in \mathbf{R}^n\colon \Sigma_i x_i = 1,\ x_i \geq 0 \text{ for } i = 1, \ldots, n\}$. Hofbauer and Sigmund proceed to show that the n-dimensional Lotka–Volterra equation can be mapped onto the orbits of (*). The time-continuous version of Fisher's selection equation is also of the form (*), and so is the hypercycle equation. Most of the book deals with binary interactions. Thus $f_i(\mathbf{x})$ takes on the linear form $(A\mathbf{x})_i$ with some suitably defined $n \times n$ matrix A. Four distinct phenomenological levels of evolutionary inquiry are described by the same type of equation. Actually this happened independently in each field and reflects a common view of natural selection. Equation (*) has been termed the replicator equation, thereby using a notion proposed by Dawkins.

The parts of this first and more introductory half of the book are extensively motivated, and the exercises remain feasible. The second half is definitely more advanced.

In the game dynamical equation (*), every evolutionarily stable strategy is an asymptotically stable equilibrium. The converse, however, does not hold. The very fact that the solutions of the replicator equation need not converge to evolutionarily stable states points to a more general stability concept captured by the above-mentioned permanence.

Part V, the longest part of the book, is entirely devoted to permanence. The Poincaré index is briefly introduced as a topological tool for obtaining information about the existence and number of critical points. Necessary and sufficient conditions for permanence are subsequently derived. The possibility of checking permanence by essentially computing eigenvalues of finitely many boundary equilibria is particularly intriguing. A chapter on the stability of n-species Lotka–Volterra equations exploits extensively the algebraic properties of the interaction matrices and leads to their classification according to the different kinds of stability they ensure. The exercises now become increasingly a collection of results.

Part VI resumes the theme from population genetics beginning with a close look at the time-continuous selection equation of the form (*) with $f_i(\mathbf{x}) = (A\mathbf{x})_i$ and symmetric matrix A. In view of the fundamental theorem, it is tempting to look for the existence of a potential and to ask which replicator equations qualify as gradient systems. It turns out that some replicator systems are indeed gradient vector fields if one gives up the Euclidean metric. A redefinition of the inner product, which essentially amounts to redefining the angle between two nonzero vectors, leads to a (Riemannian) metric—the Shahshahani metric—in which the replicator equation exhibits a potential if the functions $f_i(\mathbf{x})$ satisfy certain quite severe conditions. At the end of part VI, Hofbauer and Sigmund consider some selection models that result from relaxing the Hardy–Weinberg assumptions by taking into account nonrandom mating and fertility differences of the mating pairs. Multiplicative and additive fertility models lead again to equations of the replicator type.

Up to now the game dynamical analysis did not take into account any genetic mechanism. The last part of the book, Part VII, adds sex to the games. It becomes evident that the genetic constraints superpose the Hardy–Weinberg relation for genotype frequencies on the underlying game of strategies.

The recurrent implicit biological message of the book states that the "struggle for life" is much less dominated by seeking optimality than by seeking stability. The book, which is based on the many contributions of the authors to the subject, is written lucidly for a target group that ranges from the advanced undergraduate student in mathematics up to the research level. The avoidance of an overly technical language is a wise concession to the mathematically inclined reader coming from the life sciences.

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