The Theory of Evolution and Dynamical Systems,* Josef Hofbauer and Karl Sigmund. Cambridge University Press, 1988. $65.00 (cloth), $19.95 (paper), 341 pp.

R. A. Fisher began his *Genetical Theory of Natural Selection* by observing that with Mendelian inheritance genetic variance is preserved in the absence of selection. He thus ended a controversy which had pitted the "Darwinians" against the "Mendelians". Looking back we find this dispute incomprehensible because we have all learned from Fisher that, instead of contradicting the hypothesis of natural selection, Mendel's genetics solves what Darwin regarded as the most serious problem with his theory. For under the alternative, blending, view of inheritance the variance is halved with each generation.

Bob May once remarked that great applied mathematics is often very simple mathematics applied to an unrealistic model which nonetheless provides great insight about reality. The analogue in art would be a great caricature rather than a portrait or photograph. Rather than showing how something did happen, an argument like Fisher's frees our imagination when we are otherwise trapped, unable to see how some phenomenon could have occurred at all. The early, elementary portions of the population genetics theory developed by Fisher, Haldane and Wright are examples of such ice-breaking mathematics as are the recent applications of economics and game theory to ecology by MacArthur, Maynard Smith and May himself.

Nearer to portraiture are quantitative genetics and biostatistics whose detailed and even busy models are justified by their close relationship with (ugh!) data. Here the pictures are realistic enough to test biological hypotheses. Even more sophisticated, and quite elegant, mathematics is used by Kimura and Ohta in developing and defending the neutral gene theory as well as by Ewens and Gillespie in criticizing it.

Most of these people were biologists who developed the mathematics they felt the problems required. Some, like Maynard Smith and May, were immigrants from other areas and Fisher maintained a dual citizenship. (Statisticians are surprised to hear him identified as a biologist.) Recently, the field has been discovered by tourists. We itinerant mathematicians have produced reams of technical paper ostensibly addressed to biologists, who are unable to read the stuff much less judge its quality.

Some of this work is both useful and beautiful, especially where an intimate connection with a particular biological problem is maintained. Examples are Peskin's heart model and a few of the applications of chaotic dynamics. But I have read, or at least picked up, a lot of papers which are unhelpful as biology

* English translation of *Evolutionstheorie und dynamische System: Mathematische Aspekte der Selektion.* Paul Parey Verlag, Hamburg, 1984.

and unbeautiful as mathematics, but which were published, I suspect, because the jargon and notation appeared impressive.

In every academic area (not just mathematical biology) one finds this general problem of quality and, in particular, the purveyance of rubbish gilded with fancy language. The new problem for our subject is the changing relationship between mathematics and the biology even in good work.

Consider evolutionary games. To a biologist I would recommend: read Maynard Smith's *Evolution and the Theory of Games* and some chapters from Dawkins. After that go straight to the biology, reading the papers in Krebs and Davies *Behavioral Ecology* both for content and bibliography. I would mention only in passing all the lovely mathematics due to Taylor, Jonker, Hines, Zeeman, Hofbauer, Sigmund and me (among others).

Lyubich in the introduction to his recent *Mathematical Structures in Population Genetics* contrasts the older mathematics *for* biology with the more recent mathematics *from* biology. We may be inspired by biology but what we are doing is mathematics and it should be judged as such. Occasionally, results will emerge which could be of genuine interest to the biologist. When that happens, it is up to us to produce a readable, mathematically simplified report rather than expect the biologists to learn topology and differential geometry for our sakes.

Hofbauer and Sigmund's new book, an extensive revision as well as translation of the 1984 German original, describes a number of classical models from population genetics, ecology and evolutionary games, but it is definitely a mathematics book. With these applications in mind it is not pure mathematics but its content is purely mathematical. The authors demand a mathematical reader and are thus able to broaden their scope. They assume a familiarity with linear algebra and ordinary differential equations as well as a willingness to work through calculations. They supply in return an organizing theme for the subject and supplement it with lots of tasty side topics and examples. I want to be precise here so I don't scare off appropriate readers: if you are not familiar with, even comfortable with, systems of ode's and their linear theory, you will find this book too hard. However, such ideas as Hopf bifurcation and Riemmanian metrics are used only after they have been nicely introduced. Thus, the use in a proof of the stable manifold of an equilibrium is preceded by an earlier discussion. I would have preferred an explicit cross-reference of the "Recall from p. 53 . . ." variety but the index is quite good and the entry "manifold, stable" directs the reader back to the right place. The references are also very good. Reading the discussion of index theory, I thought "I hope they refer to Milnor's 'Topology from the Differentiable Viewpoint'." They do. Perhaps their tastes merely happen to agree with my own but that is my definition of good taste.

The book opens with a quick survey of the elements of genetics. The authors

are in a hurry to get to the good stuff and commit a few amusing gaffes. But the reader is equally impatient so these are of little consequence. Then commences a lovely survey of a wide class of models in ecology, population genetics and evolutionary games. Except for a quick glance at branching processes the models are deterministic, applying, in parallel, differential and difference equations. Suitable for a good student, the treatment is well balanced between general description and special cases or examples, e.g. the one-locus n-allele model is highlighted by two-allele results. Here, and throughout, there are a lot of pictures.

Halfway through comes an "Interlude" where the central theme, the replicator equation, is described. The differential equations version is a system on the positive orthant $\mathbb{R}_+^n = \{x \in \mathbb{R}^n : x_i \geqslant 0\}$, of the form $\dot{x}_i = x_i f_i(x)$, or on the simplex $\Delta^{n-1} = \{p \in \mathbb{R}_+^n : \sum_1^n p_i = 1\}$ of the form $\dot{p}_i = p_i(f_i(p) - \bar{f}(p))$ with $\bar{f}(p) = \sum_1^n p_i f_i(p)$.

At first glance, this seems silly, To begin with, any smooth function F on $\mathbb{R}^n$ which vanishes when $x_i = 0$ can be written as $F(x) = x_i f(x)$ by defining the smooth function:

$$f(x) = \begin{cases} F(x)/x_i & x_i \neq 0, \\ \partial F/\partial x_i & x_i = 0. \end{cases}$$

So any vectorfield which leaves the boundary faces invariant can be written in "replicator" form. Then too, a large number of effects like mutation and recombination do not fit the replicator conditions.

Despite this, I share the authors' opinion of the central role of the replicator form. For a large number of models in economics as well as biology the state is described by measuring the size or quantity of each of n types and for the dynamics we prescribe the relative growth rate of each type: hence x_i and f_i. In then examining the competition between the different types it is natural to project to the simplex Δ^{n-1} by defining $p_i = x_i/|x|$ (with $|x| = \sum_1^n x_i$). It often happens, e.g. with suitable homogeniety assumptions, that each $f_i - \bar{f}$ is a function of p—at least up to multiplication by a common positive function (see below).

Related to this projection, which discards information about the change in the total population size $|x|$, there is a procedure due to Hofbauer which retains the full description. Introduce a new variable x_0 with $f_0 = 0$, i.e. $\dot{x}_0 = 0$ and regard x_0 fixed at 1. The above projection now maps $\mathbb{R}_+^n$ homeomorphically into the simplex Δ^n in $\mathbb{R}_+^{n+1}$ by:

$$p_0 = x_0 / \sum_0^n x_j = 1/1 + \sum_1^n x_j,$$

$$p_i = x_i / \sum_0^n x_j = x_i/1 + \sum_1^n x_j \ (i = 1, \ldots n).$$

In effect, $\mathbb{R}^n_+$ is compactified by attaching the face $p_0 = 0$ in Δ^n. In particular, this useful device lets us go back and forth between the Lotka–Volterra and evolutionary game models.

Here arises a mild expository flaw. While this transformation is used repeatedly, the reader is only warned once about that common (but not constant) positive factor which is then omitted. If $\mathbf{X}(x)$ is a vectorfield and $a(x)$ is a positive function then the systems:

$$\frac{dx}{dt} = a(x)\mathbf{X}(x) \quad \text{and} \quad \frac{dx}{d\tau} = \mathbf{X}(x),$$

are related by the "time change":

$$\frac{d\tau}{dt} = a(x),$$

and so the solution paths of one system are just reparametrizations of the solution paths of the other. The particles move along the same point sets but at different speeds. As the dynamics are similar, the authors feel free to drop such a positive factor, switching from one system to the other. This is fine but I would have appreciated an occasional reminder.

The latter half of the book investigates in detail the replicator equations, especially the Lotka–Volterra equations on $\mathbb{R}^n_+$ and their projection, the evolutionary game equations, on Δ^{n-1}. This part is a gold mine for special topics of which I will describe two.

For many models the relative rate $f_i(x)$ is naturally specified only up to a positive multiple and there is no reason why the proportionality constant should be the same for different values of i. Linearizing at equilibrium to get $\dot{h} = Ah$ for a column vector h and a square matrix A we arrive at the question: when is A not only stable but remains stable after multiplication by all positive diagonal matrices $\mathbf{D}$? Except for some quibbles about boundary cases, strict vs weak inequalities, etc. the following related results are true: $\mathbf{VA}$ is stable for every positive definite symmetric (p.d. for short) matrix $\mathbf{V}$ if and only if $A + A^T$ is negative definite. On the other hand, A is stable if and only if $(\mathbf{V}_0 A) + (\mathbf{V}_0 A)^T$ is negative definite for some p.d. matrix $\mathbf{V}_0$. Finally, one can show easily that $\mathbf{DA}$ is stable for all positive diagonal $\mathbf{D}$ provided that $(\mathbf{D}_0 A) + (\mathbf{D}_0 A)^T$ is negative definite for some positive diagonal $\mathbf{D}_0$. I kept badgering Hofbauer with my hopes for the converse which he assured me was false. In the book, he and Sigmund investigate both conditions in some detail and provide a nice class of examples illustrating the gap (in Exercise (!) 11 on p. 209. It has, however, a sign error in the statement: $(b-c)^2$ should read $(b+c)^2$).

I also especially recommend the discussion of permanence and related conditions. A major question for these systems is whether a type initially

present is competitively eliminated, i.e. $\lim_{t \to \infty} x_i(t) = 0$. If there is a positive equilibrium which attracts all solution paths having positive initial points, then, of course, no type is eliminated. When such a globally stable equilibrium does not occur, one needs alternative conditions. Permanence is a natural property to look for. In the simplex case it says that the boundary is a repellor, or, equivalently, there exists a $\delta > 0$ such that every orbit with $x_i(0) > 0$ for all i satisfies $\liminf_{t \to \infty} x_i(t) \geqslant \delta$ for all i. On $\mathbb{R}^n_+$ we also assume uniform boundedness, i.e. there exists a D, independent of $x(0)$, such that $\limsup_{t \to \infty} x_i(t) \leqslant D$. Permanence plus uniform boundedness on $\mathbb{R}^n_+$ is exactly equivalent to permanence for the transformed system on Δ^n. A number of sufficient conditions are given for permanence of a Lotka–Volterra system including one which only requires looking at the boundary equilibria and which is consequently computable in a practical way. (It is a linear programming problem.) The related conditions persistence ($\liminf x_i(t) > 0$) and weak persistence ($\limsup x_i(t) > 0$) are also considered.

Finally, another word about the bibliography. Of course the literature of Western Europe is well described, but also there are a fair number of Soviet references. This is helpful in correcting an American tendency to ignore foreign work. I became familiar with Lyubich's work, for example, after I had published a result which he had proved in a paper which had already been translated into English. The need to translate Hofbauer and Sigmund's German original is perhaps another symptom of the same problem. I am, however, grateful that they have thus catered to my linguistic provincialism. Perhaps a similar difficulty accounts for the fact that Darwin did not read the copy of Mendel's paper he received.

ETHAN AKIN
Mathematics Department
The City College
137 Street and Convent Avenue
New York, NY 10031, U.S.A.