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G. J. BUTLER'S RESEARCH IN MATHEMATICAL BIOLOGY

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ABSTRACT. Dr. Butler's work in mathematical ecology and ecogenetics is discussed. In particular, his fundamental work in dealing with competition in the chemostat is examined in some detail. Other works of his include analysis of predator-prey systems and the dynamics of a population with different fertility frequencies among its genotypes.

1. Introduction. Geoff Butler became interested in mathematical biology in the same way that I did: through the influence of Paul Waltman.

Geoff spent the fall term of 1975 on leave visiting Paul at the University of Iowa. Anyone who spends time with Paul cannot help but succumb to his magic. Geoff was no exception, and, by the time he left Iowa, he had started a whole new line of investigations, occupying a large portion of his research time and energy from that moment until his untimely end.

In the pages that follow, I will try to describe some of Geoff's marvelous ideas in mathematical biology and the research that resulted. All references are to the publication list that appears earlier in this Proceedings.

2. Predator-prey systems. The first of Geoff Butler's research in mathematical biology to appear was a paper in the proceedings of a conference on "Modelling and Differential Equations in Biology" [**25**] in 1980 on predator-prey systems. Altogether, he published three papers on predator-prey systems [**25, 28, 34**], with the main results contained in [**28**].

In 1979, Geoff and I read some papers of Jim Cushing in which he considered Lotka-Volterra systems with periodic coefficients and obtained criteria for the existence of a positive periodic solution. We

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felt that we could extend Cushing's results to more general Kolmogorov systems.

Consequently, we considered a system of the form

$$\begin{aligned} \frac{dx}{dt} &= xf(t,x,y), \quad x(0) \ge 0 \\ \frac{dy}{dt} &= yg(t,x,y), \quad y(0) \ge 0 \end{aligned} \tag{1}$$

where $f(t+\omega,x,y) = f(t,x,y)$, $g(t+\omega,x,y) = g(t,x,y)$. Here x represents the prey population and y the predator.

Under the usual prey assumptions, it can be shown by Massera's theorem that the system

$$\frac{dx}{dt} = f(t,x,0) \tag{2}$$

has a positive periodic solution of period ω, denoted $\varphi(t)$. Let $\mu = (1/\omega)\int_0^\omega g(t,\varphi(t),0)\,dt$. If $\mu < 0$, then $\varphi(t)$ is asymptotically stable. As μ increases through zero, a bifurcation theorem due to P. Rabinowicz gives a positive periodic solution for $\mu > 0$.

It turned out that, even in the Lotka-Volterra case, our results were more general than Cushing's. However, turnabout is fair play, and shortly after our paper appeared, Jim Cushing published a paper improving our results.

3. Ecogenetics.

Geoff wrote one paper in the area of ecogenetics [**30**], a joint effort with Paul Waltman and myself. The paper was based on some earlier work that I had done with Paul on predator-prey systems with different prey genotypes and was inspired by some previous work of Karl Hadeler's at Tubingen and two of his coworkers.

The idea was to model a single species with three genotypes and different fertilities among the genotypes. We hoped to show that the dynamics of the system were only trivial, i.e., all solutions approached a polymorphism (steady state) as $t \to \infty$.

At first we tried to consider a system where all nine possible pairings among the three genotypes could have different fertilities. This proved too difficult. We got nowhere! Indeed, this is still an open problem.

Next, we attempted to consider the symmetric case, i.e., fertility is the same when the i^{th} genotype mates with the j^{th}, no matter which one is the male or female. This reduced the number of fertility parameters from nine to six, but we still couldn't do it.

Finally, we decided to consider the "supersymmetric" case, i.e., assume the same fertility whenever a homozygote mates with a homozygote. Now we were down to three fertility parameters, and we solved the problem.

If x_1, x_3 are the homozygote populations, x_2 the heterozygote population, and $y_i = x_i/x$, where $x = x_1 + x_2 + x_3$, we were led to the system

$$
\begin{aligned}
\frac{dy_1}{dt} &= \alpha(y_1^2 - 2y_1^2 y_3 - y_1 y_3^2 - y_1^3) + \beta\left(\frac{1}{4}y_2^2 - y_1 y_2^2\right) \\
&\quad + \gamma(y_1 y_2 - 2y_1^2 y_2 - 2y_1 y_2 y_3) \\
\frac{dy_2}{dt} &= \alpha(-y_1^2 y_2 + 2y_1 y_3 - 2y_1 y_2 y_3 - y_2 y_3^2) \\
&\quad + \beta\left(\frac{1}{2}y_2^2 - y_3^2\right) + \gamma(y_1 y_2 - 2y_1 y_2^2 + y_2 y_3 - 2y_2^2 y_3) \\
\frac{dy_3}{dt} &= \alpha(-y_1^2 y_3 - 2y_1 y_3^2 + y_3^2 - y_3^3) + \beta\left(\frac{1}{4}y_2^2 - y_2^2 y_3\right) \\
&\quad + \gamma(-2y_1 y_2 y_3 + y_2 y_3 - 2y_2 y_3^2),
\end{aligned}
\tag{3}
$$

$$y_1 + y_2 + y_3 = 1.$$

α, β, γ are the three fertility parameters. Depending on their relative values, we could show that there could be three or five equilibria. The tricky part was to show that only trivial dynamics could occur.

The research started during the summer of 1981, when Paul visited the University of Alberta for a few weeks. At that time, we thought we have proved our result.

During the 1981–82 academic year, Paul took a leave of absence and spent the year at the University of Southern California. He and his charming wife, Ruth, had a small apartment in Santa Monica, not far from the beach. In February, 1982, Geoff and I went to visit him for a week, for the express purpose of writing up this paper.

The second night we were there, we started writing up the paper, and, much to our dismay, realized that our "proof" in the last and trickiest case was no good.

We started reproving this last case at 8:00 P.M. At midnight, Paul gave up and went to bed. The last I remember was checking the time at 2:00 A.M. At 5:00 A.M. (so I am told) I was awakened by a loud **EUREKA**! Geoff had found the proof (which did hold up to next day's scrutiny).

I refuse to discuss what were the consequences of us stopping on the way back to Edmonton for a few days in Las Vegas.

4. Chemostat Modeling.

By far and away, Geoff Butler did more work in mathematical biology in models devoted to investigating competition in the chemostat, than in any other aspect. He worked with Paul Waltman [**29**], Paul and his former student Edwin Hsu (now at Tsinghua University in Taiwan) [**35, 41**] and wrote a series of papers with Geoff's former student Gail Wolkowicz (now at McMaster University) [**36, 42, 48, 53, 55**]. (In this regard, both Paul and Geoff were blessed with exceptionally fine students, as time has shown).

Edwing Szi-Bi Hsu was just completing his Ph.D. under the supervision of Paul Waltman at the University of Iowa, when Geoff was visiting there. (That was also the time when Geoff and his lovely wife, Karen, got married.) As usual, Geoff took a keen interest in everything that was going on around him, and so it should not surprise you that Geoff was intensely aware of Edwin's research on chemostat modeling (as well as the research of three other of Paul's students at that time).

Subsequently, Geoff collaborated with Paul and Edwin on chemostat models with Michaelis-Menton uptake dynamics involving n competitors for a nutrient of the form

$$\begin{aligned} \frac{dS}{dt} &= \gamma S\left(1-\frac{S}{k}\right) - \sum_{i=1}^{2} \frac{m_i}{y_i}\frac{Sx_i}{a_i+S} \\ \frac{dx_i}{dt} &= \frac{m_i S x_i}{a_i+S} - D_i x_i, \quad i=1,2, \end{aligned} \tag{4}$$

as well as the case $d_i = D_i(t)$, a periodic washout, obtaining specific criteria for periodic solutions and for a competitive food chain of the type

$$
\begin{aligned}
\frac{dS}{dt} &= 1 - S - \frac{m_1 x S}{a_1 + S} \\
\frac{dx}{dt} &= x\left(\frac{m_1 S}{a_1 + S} - 1 - \frac{m_2 y}{a_2 + x} - \frac{m_3 z}{a_3 + x}\right) \\
\frac{dy}{dt} &= y\left(\frac{m_2 x}{a_2 + x} - 1\right) \\
\frac{dz}{dt} &= z\left(\frac{m_3 x}{a_3 + x} - 1\right).
\end{aligned} \tag{5}
$$

In 1984, Geoff and I were particularly fortunate in having exceptionally good graduate students complete their Ph.D.'s, Gail Wolkowicz and Joseph So (now my colleague), respectively. Geoff collaborated with Gail both during and after her graduate student days to write the five above mentioned papers.

One extremely important aspect of their work was to replace Michaelis-Menton uptake by general uptake functions, not necessarily monotonic. A second aspect was to consider several complementary resources. This allowed the possibility of inhibition among competing microbial populations.

The models examined included many types of food webs (too numerous to detail here), and the various analyses are mathematically difficult, stimulating and informative.

The reader is referred to [**42, 48, 53**] for the details of this tremendous work.

5. Persistence. Geoff wrote four papers in persistence theory [**44, 45, 51, 56**], the last of which was submitted by Paul Waltman after his death.

His work in this area began with another Paul Waltman visit in the spring of 1984. Paul and I had defined "persistence" of a dynamical system (specifically a system of autonomous ordinary differential equations) as having the property that the omega limit sets of orbits with positive initial values did not intersect the coordinate planes. We also defined both a weaker (termed "weak persistence") and a stronger (termed "uniform persistence") version. Uniform persistence meant that the distance between the coordinate planes and *all* such omega limit sets was greater than some fixed value.

At the same time, work was being carried out by Vivian Hutson and coworkers at the University of Sheffield and Josef Hofbauer and coworkers at the University of Vienna on "permanent coexistence," later termed "permanence," both equivalent to uniform persistence of both continuous and discrete systems. Stimulated by their work, we posed the question, "when will persistence imply uniform persistence?"

We set to work on that question and, a week or so later, we had the answer, and much more, since Geoff was able to generalize our results for generalized definitions of persistence and uniform persistence in abstract locally compact metric spaces. Originally, I had my doubts about Geoff's proof. So the three of us sat down one afternoon, Geoff as theorem prover, myself as devil's advocate whose job it was to try and shoot down the proof at each step, and Paul as referee. It was an afternoon I shall never forget. At the end of the day, when we were all satisfied that the theorem was valid, we went out and celebrated by hoisting an appropriate number of "scoops."

Subsequent to this work, Paul and Geoff were able to extend the results even more, eliminating the local compactness assumption and allowing for discrete dynamical systems as well as continuous semidynamical systems.

Did I mention that Geoff had one of his prior results named after him? Arising out of a course he gave in the late 1970's, he proved an interesting result concerning when a rest point is part of the omega limit set of a dynamical system. He meant to write it up, but never did. The result was also proved in the early 1980's by Richard McGehee of the University of Minnesota. He also never published it. This result is now known as the "Butler-McGehee lemma" and is crucial in obtaining persistence theorems.

6. To be continued. Even though Geoff Butler is no longer with us, his work lives on.

Joseph So wrote his thesis partly on the basis of Geoff's work in ecogenetics. The Butler-McGehee lemma continues to be improved, generalized, and used in persistence theory. Gail Wolkowicz has continued her career as a fine mathematician and has extended their joint work in chemostat modeling.

Geoff left some notes outlining ideas in what he termed "almost persistence," in which there is a singular orbit which approaches the boundary, all others staying away. Hopefully, one day the notes will come to fruition and Geoff's results in this area will be completed and published.

In the minds and hearts of his students, colleagues, and friends, Geoff Butler, his humor, his work, his insight, and his general Geoffness continue to go on.

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