Shahshahani Gradients

Abbas Edalat

It is one of the dreams of any working mathematician to make such a significant research contribution in some subject that it ultimately finds its way in some textbook of mathematics. In fact, with the explosive increase in the number of mathematicians and the rapid specialization of mathematics in the past few decades, such fundamental and lasting contributions to any mathematical subject have become ever more difficult and quite rare. Even highly talented mathematicians remain content if they can publish their work in prestigious journals that are studied merely by the specialists in the field. Only very few of them will see any of their work eventually appear in some textbook. In 1998, a textbook on game theory and mathematical biology was published by Cambridge University Press [7] in which Siavash Shahshahani became one of these few enviable mathematicians.

In 1979, Shahshahani published a paper on mathematical biology with the title "A New Mathematical Framework for the Study of Linkage and Selection" which appeared as a single issue of the Memoirs of American Mathematical Society [13]. We will briefly review the main construction of this paper which, twenty years later, became a standard textbook material named after him.

Recall that a Riemannian metric on a manifold M associates a symmetric positive definite matrix $g(x) = (g_{ij}(x))$ to each point $x \in M$ in a smooth manner and the inner product of two vectors u and v in the tangent space T_xM at x is given by

$$\langle u, v\rangle_x = \sum_{ij} g_{ij}(x) u_i v_j = u \cdot (g(x)v)$$

where $a \cdot b$ is the Euclidean inner product of the vectors a and b. If M is an open subset of $\mathbb{R}^n$, then $T_xM = \mathbb{R}^n$. If M is the n-simplex $S_n = \{x \in \mathbb{R}^n \,|\, \sum_i x_i = 1\}$, then, for $x \in \operatorname{int} S_n$, we have $T_xS_n = \mathbb{R}^n_0 = \{u \in \mathbb{R}^n \,|\, \sum_i u_i = 0\}$. Recall also that the derivative of a real-valued smooth function $F : M \to \mathbb{R}$ at $x \in M$ is a linear map $DF(x) : T_xM \to \mathbb{R}$. Hence, there exists a unique vector $\nabla_g F(x) \in T_xM$ in the tangent space, called the *g-gradient* of F such that $\langle \nabla_g F(x), v\rangle_x = DF(x)u$ for all $u \in T_xM$. We thus obtain a dynamical system or vector field $\dot{x} = \nabla_g F(x)$ and F is said to be the *potential* of the vector field. When g is the identity matrix we get the Euclidean inner product and the usual gradient ∇F with components $\frac{\partial F}{\partial x_i}(x)$. When M is an open subset of $\mathbb{R}^n$ then the g-gradient is given by $\nabla_g F = g^{-1}\nabla F$.

Shahshahani introduced a general Riemannian metric $\sum_i (|x|/x_i) dx_i \otimes dx_i$, in the positive orthant $\{x = (x_1, \ldots, x_n) \in \mathbb{R}^n | x_i > 0\}$, with $|x| = \sum_{i=1}^n x_i$. This metric, now called after him the *Shahshahani metric*, is equivalent to the metric induced by the inner product, now called the *Shahshahani inner product*, on the tangent space given at the point x by $(u, v) \mapsto u \cdot (g(x)v)$ where g is the diagonal matrix with

$g_{ij}(x) = |x|\delta_{ij}/x_i$. Any g-gradient is also called a *Shahshahani gradient.*

The metric can be applied, as Shahshahani did in his paper, to the study of a genetic system consisting of n types of reproductive cells or gametes with x_i giving the number of gametes of type i. By changing the variables from the number x_i to the frequency $x_i/|x|$ of the ith gamete with $|x| = \sum_{i=1}^n x_i$, the dynamics of the population is analysed in the open simplex $S_n = \{(x_1, \dots, x_n) | \sum_{i=1}^n x_i = 1, x_i > 0\}$.

In pure selection, i.e. in the absence of cross-over, when the chromosomes are tightly linked, the dynamics of the genetic system can be modelled by a symmetric matrix $(A)_{ij}$ such that for each unordered pair (i, j), the number $A_{ij} \in \mathbb{R}$ gives the pay-off or the selective advantage of the pair. The pay-off to, or the fitness of, the ith gamete against the population x is then given by $\sum_j A_{ij}x_j = (Ax)_i$, whereas the the pay-off to population x against itself is $\sum_i x_i(Ax)_i = x \cdot Ax$. The dynamics of the population of gametes is then obtained by equating the rate of growth $\dot{x}_i/x_i$, of the ith gamete, with its advantage namely (pay-off to i) $-$ (pay-off to x):

$$\frac{\dot{x}_i}{x_i} = (Ax)_i - x \cdot Ax$$

which gives

$$\dot{x}_i = x_i((Ax)_i - x \cdot Ax).$$

This vector field, called the *replicator system*, is a Shahshahani gradient with potential $\frac{1}{2}x \cdot Ax$ and satisfies both Fisher's theorem that mean fitness increases on its nontrivial trajectories and Kimura's theorem that natural selection acts so as to maximize the rate of increase in the mean fitness of population. The replicator system also models dynamics of animal conflicts, is equivalent to the well-known Lotka-Volterra system and has been intensively studied in the past quarter of a century; see for example [14, 1, 6, 5, 8, 12, 10, 2, 9, 11]. For $n = 2$ the dynamics is trivial; for $n = 3$ the 19 stable classes of the system have been classified [15, 3], whereas for $n = 4$ numerical solutions already indicate some kind of chaotic motion [7, Page 210].

In fact a much larger class of vector fields applicable in game theory are Shahshahani gradients. Given any vector field $\dot{x}_i = f_i(x)$ on $\mathbb{R}^n$, consider the *generalized replicator system*

$$\dot{x}_i = \hat{f}_i(x) = x_i(f_i(x) - \bar{f}(x)), \tag{1}$$

with $\bar{f}(x) = \sum_i x_i f_i(x)$. It is easily checked that if $\dot{x}_i = f_i(x) = \frac{\partial V}{\partial x_i}$ is a gradient system then the vector field (1) is a Shahshahani gradient with the same potential V.

It is well-known that a vector field $\dot{x}_i = h_i(x)$ $(i = 1, \dots n)$ in $\mathbb{R}^n$ is a Euclidean gradient system iff the integrability condition

$$\frac{\partial h_i}{\partial x_j} = \frac{\partial h_j}{\partial x_i}$$

holds for all $i, j = 1, \dots n$. The question now is if we can characterize Shahshahani gradients of the form in Equation (1) in a similar way. The following theorem in [7] gives the required answer.

Suppose the vector field (1) is defined in a neighbourhood of S_n in $\mathbb{R}^n$. Then we can define the Jacobian bilinear form $H_x\hat{f}$ with respect to the Shahshahani inner product on the tangent space at $x \in S_n$:

$$H_x\hat{f}(u,v) = \langle u, D_x\hat{f}(v)\rangle_x,$$

for $u, v \in T_xS_n = \mathbb{R}^n_0$. Then we have the following:

Theorem 1 *For the vector field $\hat{f}$ defined by (1) in a neighbourhood of S_n in $\mathbb{R}^n$, the following conditions are equivalent:*

(i) $\hat{f}$ is a Shahshahani gradient on $\operatorname{int} S_n$.

(ii) There exist functions $V, G : U \to \mathbb{R}$ such that

$$f_i(x) = \frac{\partial V}{\partial x_i} + G(x),$$

for $x \in \operatorname{int} S_n$.

(ii) The Jacobian bilinear form $H_x\hat{f}$ is symmetric at all $x \in \operatorname{int} S_n$.

(vi) The relation

$$\frac{\partial f_i}{\partial x_j} + \frac{\partial f_j}{\partial x_k} + \frac{\partial f_k}{\partial x_i} = \frac{\partial f_k}{\partial x_i} + \frac{\partial f_k}{\partial x_j} + \frac{\partial f_j}{\partial x_i}$$

is satisfied on $\operatorname{int} S_n$.

The above theorem provides a convenient tool to check whether a given vector field is a Shahshahani gradient. It is used as such in several chapters in [7] including in the dynamics of mixed strategies (Section 19.6), continuous time selection-mutations (Sections 20.3, 20.4 and 20.5) and frequency-dependent selection equation for Mendelian populations (Section 22.1).

The wealth of applications of Shahshahani gradients in various areas of evolutionary games indicates why this notion has become a well-established paradigm in the subject. Nevertheless, reading the introduction of Shahshahani's original paper, one cannot help feel impressed by his humility and generosity in giving a large credit to Charles Conley, one of his collaborators, who according to Shahshahani, "is not a co-author of this paper only by his own choice." The quotation is a an excellent code of conduct in research collaboration quite opposite in spirit to the one Halmos, so regrettably for him, describes in his memoirs [4].

But Shahshahani did not wait some 20 years for the fruit of his encounter with mathematical biology to appear finally in a textbook and thus gain him recognition. Although he chose not to work on the subject any longer, he must have been, as a young mathematician, deeply affected by his experience in life sciences. So much so that it provided him with the real choice of his life: He married a biologist, formed a family that has borne him two sons and then lived happily ever after!

References

[1] E. Akin. Domination or equilibrium. *Math. Biosciences*, 50:239–250, 1980.

[2] I. M. Bomze. Non-cooperative two-person games in biology: a classification. *J. Math. Biol.*, 30:73–87, 1986.

[3] A. Edalat and E. C. Zeeman. The stable classes and the codimension one bifurcations of the planar replicator system. *Nonlinearity*, 5(4):921–939, 1992.

[4] P. R. Halmos. *I want to be a mathematician.* Springer, 1985.

[5] J. Hofbauer. A general cooperation theorem for hypercycles. *Monatsh. Math.*, 91:233–240, 1981.

[6] J. Hofbauer. On the occurrence of limit cycles in Volterra-Lotka equation. *Nonlinear Analysis*, 5:1003–1007, 1981.

[7] J. Hofbauer and K. Sigmund. *Evolutionary Games and Population Dynamics.* Cambridge University Press, 1988.

[8] J. Maynard Smith. *Evolution and the Theory of Games.* Cambridge University Press, 1982.

[9] J. Nachbar. 'Evolutionary' selection dynamics in games: convergence and limit properties. *Intern. J. of Game Theory*, 19:59–89, 1990.

[10] G. Palm. Evolutionary stable strategies and game dynamics for n-person games. *J. Math. Biol.*, 19:329–334, 1984.

[11] K. Ritzberger. The theory of normal form games from the differentiable viewpoint. *Int. J. Game Theory*, 23:201–236, 1995.

[12] P. Schuster and K. Sigmund. Replicator dynamics. *J. Theor. Biol.*, 100:533–538, 1983.

[13] S. Shahshahani. A new mathematical framework for the study of linkage and selection. *Memoirs Amer. Math. Soc.*, 17(211), 1979.

[14] P. D. Taylor and L. Jonker. Evolutionary stable strategies and game dynamics. *Math. Biosci.*, 40:145–156, 1978.

[15] E. C. Zeeman. Population dynamics from game theory. In *Lecture Notes in Mathematics*, volume 819, pages 471–97. Springer, 1980.