Richard Dawkins' Battle of the Sexes Model

Frank Wang, LaGuardia Community, CUNY

fwang@lagcc.cuny.edu

"Battle of the sexes" is the title of Chapter 9 in Richard Dawkins' *Selfish Gene*, in which he advocated the gene-centered view of evolution. The central thesis is that an organism is expected to evolve to maximize the number of copies of its genes passed on globally, and as a result, populations will tend towards an *evolutionarily stable strategy* (ESS). The concept of ESS was introduced by John Maynard Smith, in collaboration with George R. Price. They used the branch of mathematics called "game theory" to understanding the logic of animal conflict. Dawkins took their method of analyzing aggresive contests among animals of the same species and applied it to sex; he found a stable proportion of males and females playing some hypothetical strategies. In the second edition of *Selfish Gene*, Dawkins acknowledged a misstatement, based on Peter Schuster and Karl Sigmund's differential equations corresponding to Dawkins' game. The ratio Dawkins found was not asymptotically stable, but oscillatory. This worksheet utilizes Maple's **LinearAlgebra**, **VectorCalculus**, **DEtools** packages, in addition to other basic commands, to investigate the type and stability of the fixed point of the equations by Schuster and Sigmund. This example serves to supplement the topic "nonlinear differential equations and stabilities" covered in standard undergraduate textbooks such as that by W. E. Boyce and R. C. DiPrima.

No one can describe Dawkins' model better than he himself. Excerpt of Chapter 9 Battle of the Sexes (pages 151-153, 2nd edition) is reproduced below.

...Our two female strategies will be called coy and fast, and the two male strategies will be called faithful and philanderer. The behavioural rules of the four types are as follows. Coy females will not copulate with a male until he has gone through a long and expensive courtship period lasting several weeks. Fast females will copulate immediately with anybody. Faithful males are prepared to go on courting for a long time, and after copulation they stay with the female and help her to rear the young. Philanderer males lose patience quickly if a female will not copulate with them straight away: they go off and look for another female; after copulation too they do not stay and act as good fathers, but go off in search of fresh females. As in the case of the hawks and doves, these are not the only possible strategies, but it is illuminating to study their fates nevertheless.

Like Maynard Smith, we shall use some arbitrary hypothetical values for the various costs and benefits. To be more general it can be done with algebraic symbols, but numbers are easier to understand. Suppose that the genetic pay-off gained by each parent when a child is reared successfully is +15 units. The cost of rearing one child, the cost of all its food, all the time spent looking after it, and all the risks taken on its behalf, is -20 units. The cost is expressed as negative, because it is 'paid out' by the parents. Also negative is the cost of wasting time in prolonged courtship. Let this cost be -3 units.

Imagine we have a population in which all the females are coy, and all the males are faithful. It is an ideal monogamous society. In each couple, the male and the female both get the same average pay-off. They get +15 for each child reared; they share the cost of rearing it (-20) equally between the two of them, an average of -10 each. They both pay the -3 point penalty for wasting time in prolonged courtship. The average pay-off for each is therefore +15-10-3 = +2.

Now suppose a single fast female enters the population. She does very well. She does not pay the cost of delay, because she does not indulge in prolonged courtship. Since all the males in the population are faithful, she can reckon on finding a good father for her children whoever she mates with. Her average pay-off per child is +15 - 10 = +5. She is 3 units better off than her coy rivals. Therefore fast genes will start to spread.

If the success of fast females is so great that they come to predominate in the population, things will start to change in the male camp too. So far, faithful males have had a monopoly. But now if a philanderer male arises in the population, he starts to do better than his faithful rivals. In a population where all the females are fast, the pickings for a philanderer male are rich indeed. He gets the +15 points if a child is successfully reared, and he pays neither of the two costs. What this lack of cost mainly means to him is that he is free to go off and mate with new females. Each of his unfortunate wives struggles on alone with the child, paying the entire -20 point cost, although she does not pay anything for wasting time in courting. The net pay-off for a fast female when she encounters a philanderer male is +15 - 20 = -5; the pay-off to the philanderer himself is +15. In a population in which all the females are fast, philanderer genes will spread like wildfire.

If the philanderers increase so successfully that they come to dominate the male part of the population, the fast females will be in dire straits. Any coy female would have a strong advantage. If a coy female encounters a philanderer male, no business results. She insists on prolonged courtship; he refuses and goes off in search of another female. Neither partner pays the cost of wasting time. Neither gains anything either, since no child is produced. This gives a net pay-off of zero for a coy female in a population where all the males are philanderers. Zero may not seem much, but it is better than the -5 which is the average score for a fast female. Even if a fast female decided to leave her young after being deserted by a philanderer, she would still have paid the considerable cost of an egg. So, coy genes start to spread through the population again.

To complete the hypothetical cycle, when coy females increase in numbers so much that they predominate, the philanderer males, who had such an easy time with the fast females, start to feel the pinch. Female after female insists on a long and arduous courtship. The philanderers flit from female to female, and always the story is the same. The net pay-off for a philanderer male when all the females are coy is zero. Now if a single faithful male should turn up, he is the only one with whom the coy females will mate. His net pay-off is +2, better than that of the philanderers. So, faithful genes start to increase, and we come full circle.

As in the case of the aggression analysis, I have told the story as though it was an endless oscillation. But, as in that case, it can be shown that really there would be no oscillation. The system would converge to a stable state. If you do the sums, it turns out that a population in which 5/6 of the females are coy, and 5/8 of the males are faithful, is evolutionarily stable. This is, of course, just for the particular arbitrary numbers that we started out with, but it is easy to work out what the stable ratios would be for any other arbitrary assumptions.

The payoffs in Dawkins' model are recapitulated as follows. If a faithful male meets a coy female, then the payoff for both of them is +2. If a faithful male encounters a fast female, both earn +5. But a philandering male meeting a fast female makes off with +15, while the female gets -5. If a philanderer meets a coy female, nothing happens, so the payoff for both is 0. This result can be expressed in matrices A and B, where $a_{i,j}$ is the payoff for a male using strategy X_i against a female playing strategy Y_j, and $b_{i,j}$ the payoff for a female using strategy Y_i against a male playing strategy X_j.

```
> restart:
> A := <<2|5>,<0|15>>;
```

$$A := \begin{bmatrix} 2 & 5 \\ 0 & 15 \end{bmatrix} \quad (1)$$

```
> B := <<2|0>,<5|-5>>;
```

$$B := \begin{bmatrix} 2 & 0 \\ 5 & -5 \end{bmatrix} \quad (2)$$

Let x_i be the proportion of males playing strategy X_i, and y_i be that of females playing strategy Y_i. Obviously $x_1 + x_2 = 1$ and $y_1 + y_2 = 1$. We focus on two variables, say x_1 and y_1, which we denote by x and y.

```
> x1 := x; x2 := 1-x1;
```

$$x1 := x$$
$$x2 := 1 - x \quad (3)$$

```
> y1 := y; y2 := 1-y1;
```

$$y1 := y$$
$$y2 := 1 - y \quad (4)$$

The rate of increase $\frac{d}{dt}\, x1(t)$ of the population using strategy X_1 will be the difference between the payoff for strategy X_1, given by $a_{1,1} y_1 + a_{1,2} y_2$, and the average payoff for the males, given by $a_{1,1} x_1 y_1 + a_{1,2} x_1 y_2 + a_{2,1} x_2 y_1 + a_{2,2} x_2 y_2$. Similar argument applies to $\frac{d}{dt}\, y1(t)$.

```
> f := x1*(A[1,1]*y1 + A[1,2]*y2 - (A[1,1]*x1*y1 + A[1,2]*x1*y2 + A
  [2,1]*x2*y1 + A[2,2]*x2*y2));
```

$$f := x\left(-3y + 5 - 2xy - 5x(1-y) - 15(1-x)(1-y)\right) \quad \textbf{(5)}$$

```
> factor(f);
```

$$-2x(6y-5)(-1+x) \quad \textbf{(6)}$$

```
> g := y1*(B[1,1]*x1 + B[1,2]*x2 - (B[1,1]*x1*y1 + B[1,2]*y1*x2 + B
  [2,1]*y2*x1 + B[2,2]*x2*y2));
```

$$g := y\left(2x - 2xy - 5x(1-y) + 5(1-x)(1-y)\right) \quad \textbf{(7)}$$

```
> factor(g);
```

$$y(-1+y)(8x-5) \quad \textbf{(8)}$$

For a system of differential equations
$\frac{d}{dt} x(t) = f(x, y)$ and $\frac{d}{dt} y(t) = g(x, y)$, the fixed points are obtained by solving the equations
$f(x, y) = 0$ and $g(x, y) = 0$.

```
> solve({f=0, g=0}, {x, y});
```

$$\{x=0, y=0\}, \{x=0, y=1\}, \{x=1, y=0\}, \left\{x=\frac{5}{8}, y=\frac{5}{6}\right\}, \{x=1, y=1\} \quad \textbf{(9)}$$

The set $x = \frac{5}{8}$ and $y = \frac{5}{6}$ are what Dawkins found: 5/6 of the females are coy, and 5/8 of the males are faithful. To analyze the stability, we form the Jacobian matrix at this fixed point:

```
> JM := VectorCalculus[Jacobian](<f, g>, [x,y]=[5/8, 5/6]);
```

$$JM := \begin{bmatrix} 0 & \frac{45}{16} \\ -\frac{10}{9} & 0 \end{bmatrix} \quad \textbf{(10)}$$

```
> LinearAlgebra[Eigenvalues](JM);
```

$$\begin{bmatrix} \frac{5}{4} I\sqrt{2} \\ -\frac{5}{4} I\sqrt{2} \end{bmatrix} \quad \textbf{(11)}$$

The eigenvalues of this locally linear system are pure imaginary, thus the stability is indeterminate. Let us examine the direction field.

```
> with(DEtools):
> f := unapply(f, [x,y]); g := unapply(g, [x,y]);
```

$$f := (x, y) \rightarrow x\left(-3y + 5 - 2xy - 5x(1-y) - 15(1-x)(1-y)\right)$$

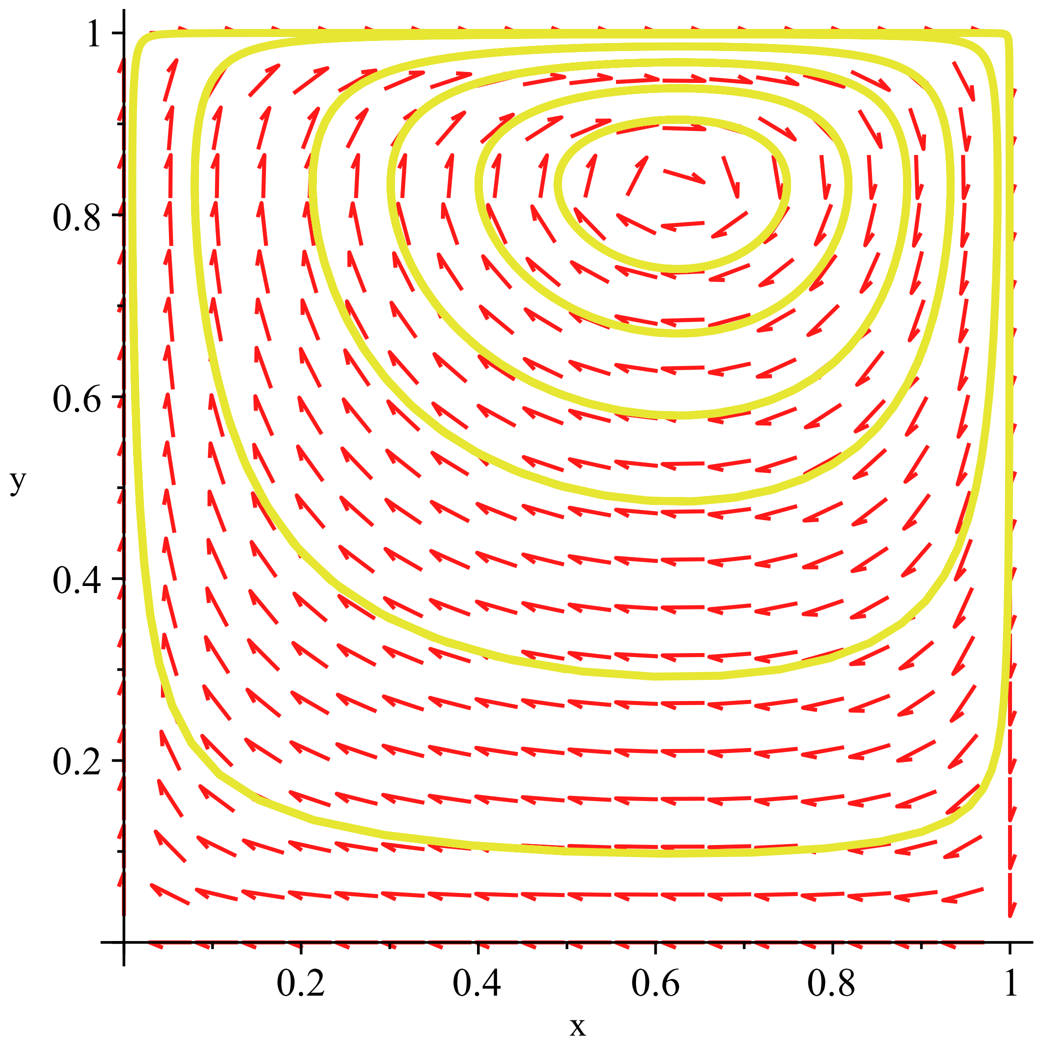
$$g := (x, y) \rightarrow y\left(2x - 2xy - 5x(1-y) + 5(1-x)(1-y)\right) \quad \textbf{(12)}$$

```
> Eqs := [diff(x(t),t) = f(x(t), y(t)), diff(y(t),t) = g(x(t), y(t))
  ];
```

(13)

$$Eqs := \left[\frac{d}{dt} x(t) = x(t) \, (-3\, y(t) + 5 - 2\, x(t)\, y(t) - 5\, x(t)\, (1 - y(t)) - 15\, (1 - x(t))\, (1 - y(t))), \frac{d}{dt} y(t) = y(t)\, (2\, x(t) - 2\, x(t)\, y(t) - 5\, x(t)\, (1 - y(t)) + 5\, (1 - x(t))\, (1 - y(t))) \right] \quad (13)$$

```
> DEplot(Eqs, [x(t), y(t)], t=0..10, x(t)=0..1, y(t)=0..1, [[x(0)=
  0.5, y(0)=0.1], [x(0)=0.5, y(0)=0.3], [x(0)=0.5, y(0)=0.5], [x(0)=
  0.5, y(0)=0.6], [x(0)=0.5, y(0)=0.7], [x(0)=0.5, y(0)=0.8]],
  numpoints=200);
```



From the trajectories in the phase plane, it appears that the fixed point is a center. To ensure that the orbits are indeed closed, we notice that this system $\frac{d}{dx} y(x) = \frac{g(x,y)}{f(x,y)}$ is separable and can be integrated.

```
> Int((-10+12*y)/(y*(1-y)), y) = Int((5-8*x)/(x*(1-x)), x);
```

$$\int \frac{-10 + 12\, y}{y\,(1-y)}\, dy = \int \frac{-8\, x + 5}{x\,(1-x)}\, dx \quad (14)$$

```
> value(%);
```

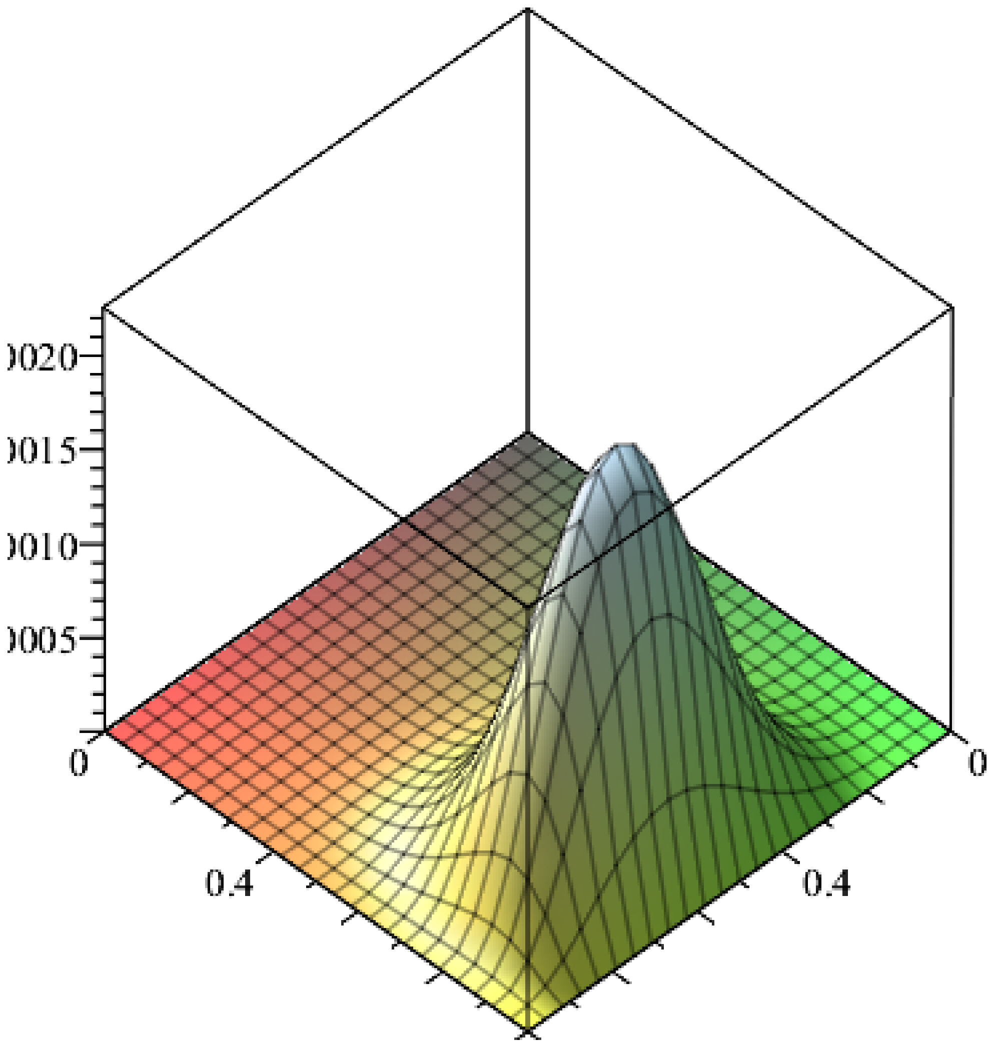
$$-2\ln(-1+y)-10\ln(y)=3\ln(-1+x)+5\ln(x) \quad (15)$$

Based on this result, we construct the function $V(x, y)$

```
> V := (x, y) -> x^5*(1-x)^3*y^10*(1-y)^2;
```

$$V := (x, y) \rightarrow x^5 (1-x)^3 y^{10} (1-y)^2 \quad (16)$$

```
> plot3d(V(x,y), x=0..1, y=0..1);
```



It is easy to check that the time derivative of V is zero.

```
> Vdot := diff(V(x,y),x)*f(x,y)+diff(V(x,y),y)*g(x,y);
```

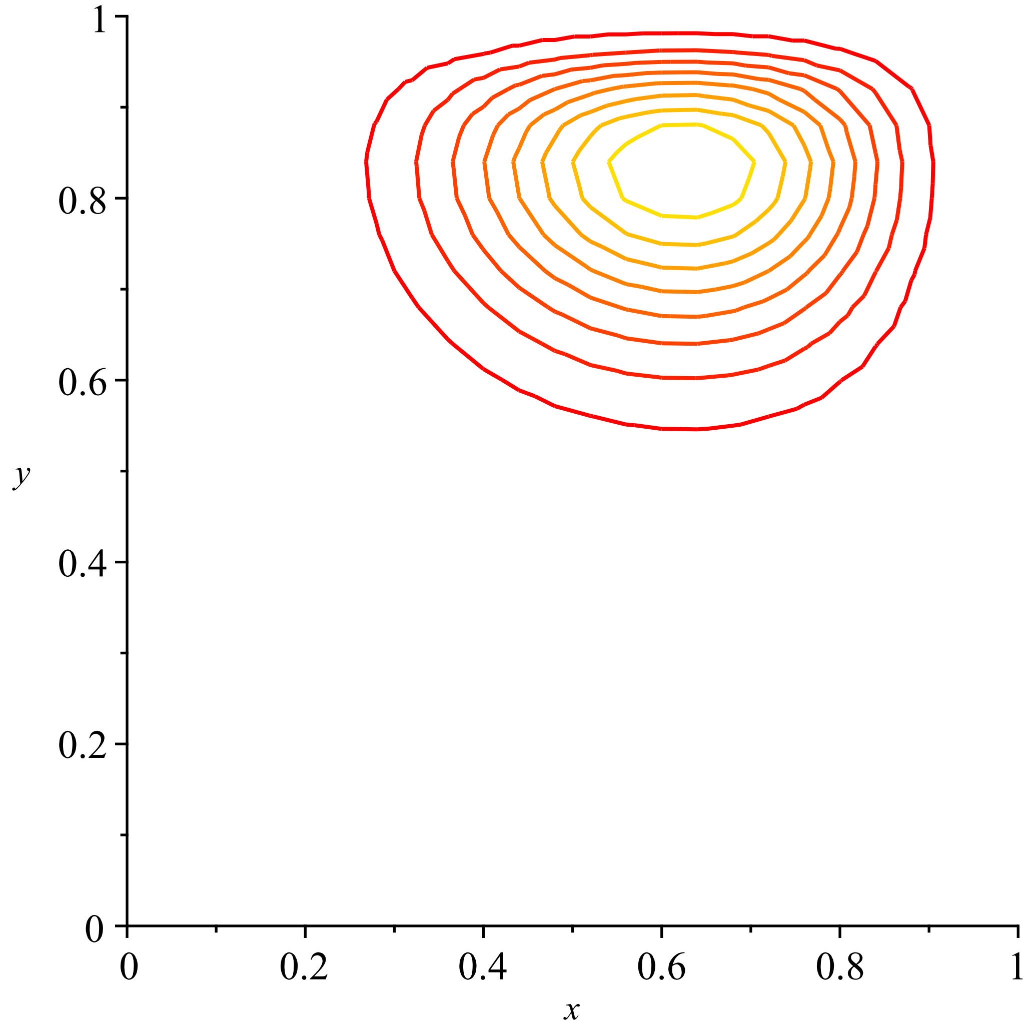
$$Vdot := \left(5x^4(1-x)^3y^{10}(1-y)^2 - 3x^5(1-x)^2y^{10}(1-y)^2\right)x(-3y+5-2xy-5x(1-y)-15(1-x)(1-y)) + \left(10x^5(1-x)^3y^9(1-y)^2-2x^5(1-x)^3y^{10}(1-y)\right)y(2x-2xy-5x(1-y)+5(1-x)(1-y)) \quad (17)$$

```
> simplify(Vdot);
```

$$0 \quad (18)$$

Along every orbit, V is constant. The orbits are closed and correspond to the constant value levels of V.

```
> plots[contourplot](V(x,y), x=0..1, y=0..1, view=[0..1, 0..1]);
```



The model of Dawkins leads to endless oscillations. This kind of oscillation looks just like the Lotka-Volterra equation describing the evolution of two populations of predator and prey introduced in many differential equations textbooks.

Schuster and Sigmund ended the paper with this statement.

Briefly, then, we can draw two conclusions:
(a) that the battle of sexes has much in common with predation; and
(b) that the behaviour of lovers is oscillating like the moon, and unpredictable as the weather.
Of course, people didn't need differential equations to notice this before.

References

1. Richard Dawkins, *The Selfish Gene*, 2nd ed. (1989). pp 151-153, p. 303.
2. Peter Schuster and Karl Sigmund, "Coyness, Philandering and Stable Strategies," *Animal Behaviour* **29**, 186-192 (1981).
3. W. E. Boyce and R. C. DiPrima, *Elementary Differential Equations and Boundary Value Problems*, 9th ed. (2009). Chapter 9.