

COYNESS, PHILANDERING AND STABLE STRATEGIES

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Abstract. An example put forward by Dawkins to describe the evolution of strategies in the conflict of the sexes over parental investment is discussed by means of a simple dynamic system. It is shown that the equilibrium of the strategies is not evolutionarily stable, but equal to the time average of the endlessly oscillating strategies.

The theory of games and the notion of evolutionarily stable strategies, as introduced by Maynard Smith & Price (1973), has proved to be very helpful for the understanding of the evolution of animal conflicts. Recently, Zeeman (1979), Taylor & Jonker (1978) and Hofbauer et al. (1979) have used a class of ordinary differential equations which makes the underlying dynamics of this approach more explicit. In this paper we show how to use this method to investigate situations leading to oscillations of genetically influenced social behaviour. Within the context of Trivers's (1972) theory of parental investment, we shall discuss an example introduced by Dawkins (1976) and also described by Wickler & Seibt (1977).

Suppose that the pure strategies for contests within one species are labelled $1, \dots, n$ and that a_{ij} is the payoff for the player using the pure strategy i when his adversary uses the pure strategy j . Then $\sum_j a_{ij}q_j$ is the payoff for the pure strategy i against the mixed strategy given by the probability vector $q = (q_1, \dots, q_n)$, and $\sum_{i,j} a_{ij}p_iq_j$ is the payoff for the strategy $p = (p_1, \dots, p_n)$ played against q . Let A denote the payoff matrix (a_{ij}) and let

$$S_n = \{x = (x_1, \dots, x_n) \in \mathbb{R}^n : \sum_j x_j = 1, x_i \geq 0 \text{ for all } i\}$$

be the simplex of all possible strategies.

A strategy $p \in S_n$ is called an evolutionarily stable strategy if, whenever a population using this strategy is perturbed by a mutation introducing a small population with strategy $q \neq p$, then p fares better (in the new, mixed population) than does q . Equivalently, in the definition of Maynard Smith (1978), p is an evolutionarily stable strategy if for all $q \neq p$ one has $p \cdot Ap \geq q \cdot Ap$, with $p \cdot Aq > q \cdot Aq$ in the case of equality.

In the words of Selten (1980), p is a best reply against itself, and fares better against any alternative best reply q , than does q against itself.

If the strategies are genetically determined, then the success of strategy i will be reflected in its success in reproduction, i.e. its rate of increase. In a population with strategy $x = (x_1, \dots, x_n)$ the payoff for strategy i is

$$\sum_j a_{ij}x_j$$

while the average payoff is

$$\sum_{k,j} a_{kj}x_kx_j$$

It is natural to assume that the rate of increase \dot{x}_i/x_i is equal to the difference between these two payoffs. Thus we obtain the system of ordinary differential equations

$$\dot{x}_i = x_i \left(\sum_j a_{ij}x_j - \sum_{k,j} x_k a_{kj}x_j \right) \quad i = 1, \dots, n \quad (1)$$

on the state space S_n . (It is easy to check that the simplex S_n and its faces are invariant for (1).) It can be shown quite simply (see Hofbauer et al. 1979 or Zeeman 1979) that if $p \in S_n$ is an evolutionarily stable strategy, then p is an equilibrium state of (1) which is asymptotically stable (all orbits in the neighbourhood of p converge to p). The converse is not true, however.

Let us now consider an aspect of the 'battle of sexes', as described by Dawkins (1976). At the moment of conception, the female invests more in the offspring than the male since her gametes are larger. The father is faced with the temptation to leave her 'holding the baby' and to look for a new mate. The female should prevent this by choosing a faithful husband, and the simplest way to do this would be to insist on a long engagement period in order to test the fidelity and the perseverance of her mate. Thus it would pay for her to be coy. A deserting male, among a

population of coy females, will have to face another long and arduous courtship. This puts a selective pressure on males to be faithful. Among faithful males, however, a fast female would fare better than a coy one, since she skips the courtship. Her genes will therefore spread. If there are too many fast females around, however, then philandering males will find rich pickings and spread in their turn. But in a population where faithful husbands are rare, a female would do well to be prudent and coy. So we are back at the beginning. As Maynard Smith & Price (1973) have shown in their well-known model of 'hawks' and 'mice', a superficially similar situation does not lead to oscillations but to convergence towards an evolutionarily stable equilibrium. In the example of Dawkins, however, we shall indeed obtain endless oscillations.

For our model, we shall use the same numerical values as did Dawkins (1976) and Wickler & Seibt (1977): the benefit for raising a child successfully is + 15 for each parent; the total costs for looking after the child are - 20; and the cost of a prolonged courtship is - 3. The gist of the model is largely independent of the actual choice of numerical values. Males have the two strategies X_1 (faithful) and X_2 (philanderer); females have the two strategies Y_1 (coy) and Y_2 (fast).

If a faithful male meets a coy female, then the payoff for both of them is + 2 (namely + 15 (the child) - 10 (they share the costs of looking after it) - 3 (the courtship)). If a faithful male encounters a fast female, the courtship is omitted and both earn + 5. But a philandering male meeting a fast female makes off with + 15 (no costs for him), while the female gets - 5 (she has to bear all the costs of raising a child). If a philanderer meets a coy female, nothing happens, so the payoff for both is 0.

More generally, suppose that a_{ij} is the payoff for a male using strategy X_i against a female playing strategy Y_j , and b_{ij} the payoff for a female using strategy Y_i against a male playing strategy X_j ($i, j = 1, 2$). Thus the game is described by the two matrices A and B . Let x_i be the proportion of males playing strategy X_i , and y_i be that of females playing strategy Y_i , for $i = 1, 2$. Obviously $x_1 + x_2 = y_1 + y_2 = 1$, and $x_i \geq 0, y_i \geq 0$ for $i = 1, 2$. The payoff for a male using strategy X_i against a female population described by (y_1, y_2) is

$$a_{i1}y_1 + a_{i2}y_2 \tag{2}$$

and the average payoff for a male population (x_1, x_2) against a female population (y_1, y_2) is

$$a_{11}x_1y_1 + a_{12}x_1y_2 + a_{21}x_2y_1 + a_{22}x_2y_2. \tag{3}$$

The expressions for the payoff expected by females are similar. In Dawkins's example, the two matrices are

$$A = \begin{bmatrix} 2 & 5 \\ 0 & 15 \end{bmatrix} \quad B = \begin{bmatrix} 2 & 0 \\ 5 & -5 \end{bmatrix} \tag{4}$$

The payoff for faithful males is $2y_1 + 5y_2$, the payoff for philanderers is $15y_2$, and these payoffs are equal if and only if $(y_1, y_2) = (\frac{5}{8}, \frac{1}{8})$. It follows that the payoff for any male strategy (x_1, x_2) against the female strategy $(\frac{5}{8}, \frac{1}{8})$ is the same, namely 2.5. A similar computation shows that the payoff for any female strategy (y_1, y_2) against the male strategy $(x_1, x_2) = (\frac{5}{8}, \frac{1}{8})$ is always 1.25. Thus indeed it pays for neither male nor female population to deviate from the equilibrium state given by the male population $(\frac{5}{8}, \frac{1}{8})$ and the female population $(\frac{5}{8}, \frac{1}{8})$.

On the other hand, however, there is no penalty for deviating either. Our players are not rational. There is no conspiracy to stick to the equilibrium. If a fluctuation changes, say, the male population from $(\frac{5}{8}, \frac{1}{8})$ to (x_1, x_2) , then its payoff against the female population $(\frac{5}{8}, \frac{1}{8})$ remains 2.5. The payoff for the female population $(\frac{5}{8}, \frac{1}{8})$, however, will change to $\frac{5}{8}(3x_1 - x_2)$, and will therefore decrease if the proportion x_1 of faithful males has been decreased by the fluctuation. There is no selection pressure on the males to change strategy, but there is on the females, rewarding an increase of the proportion y_2 of fast females. If, for example, the new male population is $(\frac{4}{8}, \frac{4}{8})$, then the 'old' female strategy has as payoff $\frac{5}{8}$. The female strategy $(\frac{1}{2}, \frac{1}{2})$, for example, has a higher payoff, namely $\frac{1}{2}$.

Another way to see why the equilibrium pair $(\frac{5}{8}, \frac{1}{8})$ and $(\frac{5}{8}, \frac{1}{8})$ is not stable is as follows. The state of the 'total' population (males and females) is obviously described by x_1 and y_1 , and thus by a point $q = (x, y)$ of the unit square

$$Q_2 = \{(x, y) \in \mathbb{R}^2 : 0 \leq x \leq 1, 0 \leq y \leq 1\}$$

where $x = x_1$ and $y = y_1$. The equilibrium population, as found by Dawkins, is described by the point $p = (\frac{5}{8}, \frac{5}{8})$. Let us define the payoff for a total population as the sum of the payoff for the males and the payoff for the females. Then a simple computation shows that the payoff for population $q = (x, y)$ against the equilibrium

population $p = (\frac{5}{8}, \frac{5}{8})$ is independent of q , namely

$$E(q,p) = 3.75$$

But the payoff for population p against population q is given by

$$E(p,q) = \frac{1}{15}(95 + 40x - 90y)$$

while the payoff for q against itself is

$$E(q,q) = 10 - 10y - 4xy$$

Hence

$$E(p,q) - E(q,q) = 4(x - \frac{5}{8})(\frac{5}{8} - y)$$

It follows that if either $x > \frac{5}{8}$ and $y > \frac{5}{8}$, or $x < \frac{5}{8}$ and $y < \frac{5}{8}$, one has

$$E(q,q) > E(p,q)$$

In this case, q is an alternative best reply to p , but q fares better against itself than does p against q . Hence the population $p = (\frac{5}{8}, \frac{5}{8})$ is not evolutionarily stable.

We shall presently see that the equilibrium $p = (\frac{5}{8}, \frac{5}{8})$ is still highly relevant, and stable in another sense. It turns out, indeed, that the populations will oscillate, but have p as a mean. We shall need slightly more complex arguments to prove this.

Let us first set up, in general context, the differential equations corresponding to the game given by the two matrices A and B . We do this by simply mimicking the way of obtaining (1). The rate of increase \dot{x}_1/x_1 of the population using strategy X_1 , for example, will be just the difference between the payoff for strategy X_1 (given by (2)) and the average payoff for the males (given by (3)). Hence

$$\dot{x}_1 = x_1(a_{11}y_1 + a_{12}y_2 - (a_{11}x_1y_1 + a_{12}x_1y_2 + a_{21}x_2y_1 + a_{22}x_2y_2))$$

Similarly

$$\begin{aligned} \dot{x}_2 &= x_2(a_{21}y_1 + a_{22}y_2 - (a_{11}x_1y_1 + a_{12}x_1y_2 + a_{21}x_2y_1 + a_{22}x_2y_2)) \\ \dot{y}_1 &= y_1(b_{11}x_1 + b_{12}x_2 - (b_{11}x_1y_1 + b_{12}y_1x_2 + b_{21}y_2x_1 + b_{22}y_2x_2)) \\ \dot{y}_2 &= y_2(b_{21}x_1 + b_{22}x_2 - (b_{11}x_1y_1 + b_{12}y_1x_2 + b_{21}x_1y_2 + b_{22}y_2x_2)) \end{aligned} \quad (5)$$

This system of equations can be greatly simplified.

First of all, one has $(x_1 + x_2)' = 0$ if $x_1 + x_2 = 1$, and $(y_1 + y_2)' = 0$ if $y_1 + y_2 = 1$. Thus, reasonably enough, the set which interests us (satisfying the conditions $x_1 + x_2 =$

$1, y_1 + y_2 = 1, x_i \geq 0, y_i \geq 0$ for $i = 1, 2$) is invariant. We may henceforth consider the restriction of (5) to this set.

Next, one can easily check that by adding a constant to each of the columns of A and B , one does not change the restriction of (5). Thus we can, without restricting generality, assume

$$A = \begin{bmatrix} 0 & a \\ b & 0 \end{bmatrix} \quad B = \begin{bmatrix} 0 & c \\ d & 0 \end{bmatrix}$$

For Dawkins's example (4), for instance, we obtain, by adding the constants -2 and -15 to the first and second column of A , and by adding the constants -2 and $+5$ to the first and second column of B , the matrices

$$A = \begin{bmatrix} 0 & -10 \\ -2 & 0 \end{bmatrix} \quad B = \begin{bmatrix} 0 & 5 \\ 3 & 0 \end{bmatrix} \quad (6)$$

Finally, remember that we are only interested in two variables, say x_1 and y_1 , which we again denote by x and y . Then, after a short computation, (5) becomes

$$\begin{aligned} \dot{x} &= x(1-x)(a - (a+b)y) \\ \dot{y} &= y(1-y)(c - (c+d)x) \end{aligned} \quad (7)$$

which we consider on the unit square Q_2 .

This square and its edges (corresponding to pure strategies) are invariant. There exists a unique equilibrium

$$P = \left(\frac{c}{c+d}, \frac{a}{a+b} \right)$$

in the interior of Q_2 if and only if $ab > 0$ and $cd > 0$. If this is not the case, then (7) is trivial, since \dot{x} or \dot{y} will never change sign. In this case x or y will be either constant, or else monotonic.

Thus from now on we shall only consider the case with unique equilibrium. The Jacobian of (7), evaluated at P , is

$$J = \begin{bmatrix} 0 & -(a+b) \frac{cd}{(c+d)^2} \\ -(c+d) \frac{ab}{(a+b)^2} & 0 \end{bmatrix}$$

If $ac > 0$, the eigenvalues of J are real numbers $\pm \lambda$, where

$$\lambda = \sqrt{\frac{abcd}{|a+b||c+d|}}$$

In this case P is a saddle. The theory of Poincaré & Bendixson implies that there is no closed orbit in Q_2 . Depending on the sign of a , either $(0, 0)$ and $(1, 1)$, or $(1, 0)$ and $(0, 1)$ are sinks, and almost all orbits in the interior of Q_2 will have these sinks as ω -limits (see Fig. 1 for a typical phase portrait).

If $ac < 0$, we see that the eigenvalues of J are $\pm i\lambda$, and hence on the imaginary axis. We may assume, up to time reversal, that a is negative. Then b is also negative, while c and d are positive. The numerical values chosen by Dawkins correspond to this situation. Equation (7) is then

$$\begin{aligned} \dot{x} &= x(1-x)(-10+12y) & (8) \\ \dot{y} &= y(1-y)(5-8x) \end{aligned}$$

and P is the equilibrium $(\frac{5}{8}, \frac{5}{8})$.

The function

$$V(x, y) = x^c(1-x)^d y^{-a}(1-y)^{-b}$$

vanishes on the boundary of Q_2 , is strictly positive in the interior and has P as unique maximum. It is easy to check that $\dot{V} = 0$. (This means that if $x(t)$ and $y(t)$ are solutions of (7), then the time-derivative of the function $t \rightarrow V(x(t), y(t))$, given by $(\partial V/\partial x)\dot{x} + (\partial V/\partial y)\dot{y}$, is equal to 0.) It follows that V is constant along every orbit. The orbits are closed and correspond to the constant value levels of V (see Fig. 2 for

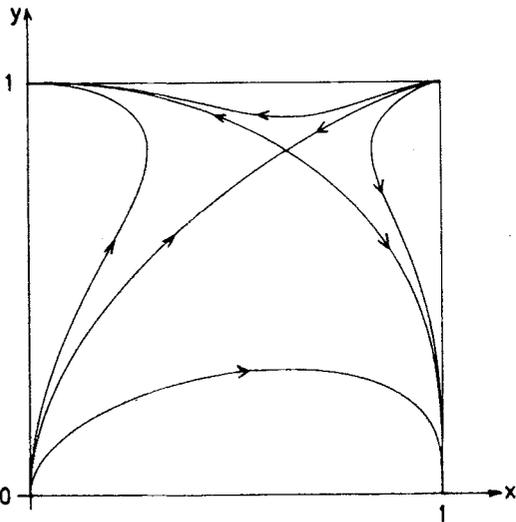


Fig. 1. Phase portrait of the equation $\dot{x} = x(1-x)(10-12y)$, $\dot{y} = y(1-y)(5-8x)$.

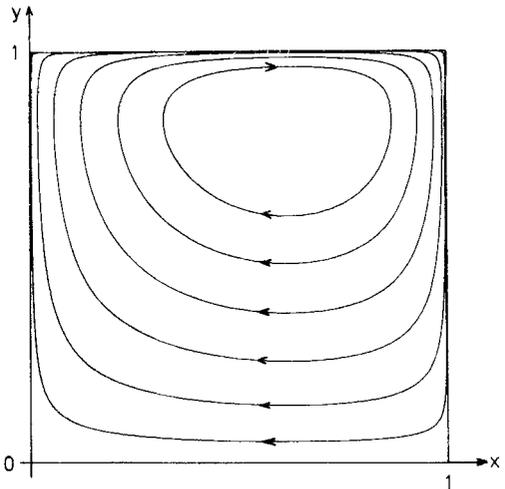


Fig. 2. Phase portrait of the equation $\dot{x} = x(1-x)(-10+12y)$, $\dot{y} = y(1-y)(5-8x)$.

the phase portrait corresponding to Dawkins's example).

The equilibrium P is stable (every neighbourhood U of P contains a neighbourhood U' such that no orbit issued in U' leaves U), but it is not asymptotically stable, and a fortiori not evolutionarily stable.

Thus the model of Dawkins leads to endless oscillations. Even if the system had started at equilibrium, small mutations would be bound to occur and would soon have sent it into an oscillatory state.

The equilibrium P is nevertheless most important, because it corresponds to the time-average along every orbit. Indeed, the first equation of (7) can be written

$$\frac{\dot{x}}{x(1-x)} = a - (a+b)y$$

The left-hand side is just the time derivative of $\log(x/(1-x))$. If we integrate along an orbit of period T , and note that $x(0) = x(T)$, we obtain

$$0 = \log \frac{x(t)}{1-x(t)} \Big|_{t=0}^T = aT - (a+b) \int_0^T y(t) dt$$

and hence, dividing by T ,

$$\frac{1}{T} \int_0^T y(t) dt = \frac{a}{a+b}$$

and similarly

$$\frac{1}{T} \int_0^T y(t) dt = \frac{c}{c + d}$$

This time-average, then, is independent of the initial conditions. It is not affected by mutations. Moreover, it corresponds to actual measurements. If, for example, one studies a population of grey geese for a very long time and finds that 60% of the males are faithful (see, e.g. Wickler & Seibt 1977), then one is dealing with a time average rather than with an evolutionarily stable state.

Other authors, for example Maynard Smith & Parker (1976), Maynard Smith (1977), Grafen & Sibly (1978) and Taylor (1979), have also studied animal conflicts between two populations by using the game-theoretic approach. Our differential equations apply to some of their models. Here, we only consider a contest between male and female of one insect species, as described by Parker (1979). In a given encounter, males are often under selection to mate, and simultaneously females are under selection to refuse mating. A sex-limited gene gives a competitive mating advantage M to males, but the male behaviour associated with the gene inflicts some cost $-R$ upon the female (e.g. direct damage) which may be felt by the progeny. Parker assumes that the females have two strategies, namely to reject, Y_1 , or to remain passive, Y_2 ; the males have also two strategies, namely to persist, X_1 , or not, X_2 . Let $-S$ be the cost for the female if the male persists, and $-U$ the cost of persistence for the male. We shall assume that the probability of a mating in an encounter between a passive female and a non-persisting male is $\frac{1}{2}$, and the probability of a mating in an encounter between a rejecting female and a persistent male is r .

The payoff matrix for the males is given by

	Y_1	Y_2
X_1	$rM - U$	M
X_2	0	$\frac{M}{2}$

and the payoff for the females by

	X_1	X_2
Y_1	$-S - rR$	0
Y_2	$-R$	$-\frac{R}{2}$

Thus we use the two matrices

$$A = \begin{bmatrix} 0 & \frac{M}{2} \\ U - rM & 0 \end{bmatrix} \quad B = \begin{bmatrix} 0 & -\frac{R}{2} \\ R(1 - r) + S & 0 \end{bmatrix}$$

The condition for mixed equilibrium, $ab > 0$ and $cd > 0$, is now

$$r < \frac{U}{M} \text{ and } r > 1 - \frac{S}{R}$$

The fixed point, then, is a saddle ($ac < 0$) and we have the situation depicted in Fig. 1. In this case, the outcome — which sex will win — depends on the initial condition.

Parker (1979) also describes in this context an ‘opponent-independent costs’ game which, although not directly describable in terms of equation (7), possesses some similar features. Each population has six different strategies, corresponding to different levels of escalation (and thus of cost). Here, numerical simulations lead to what Parker calls ‘unresolvable evolutionary chases’, i.e. there is no evolutionarily stable strategy, but the frequencies of the various strategies fluctuate. Thus Parker seems to have been the first to consider the possibility of endlessly oscillating behaviour. He cautions that ‘it is extremely difficult to know whether such cyclical chases exist in nature’.

We close with a few remarks.

Von Neumann & Morgenstern (1953) have already stressed that their theory of games is thoroughly static. In a study of evolution, a more dynamic theory seems to be preferable, and this is not only from a mathematical point of view. The simple biological example in this paper shows how ordinary differential equations can easily handle situations which cannot be

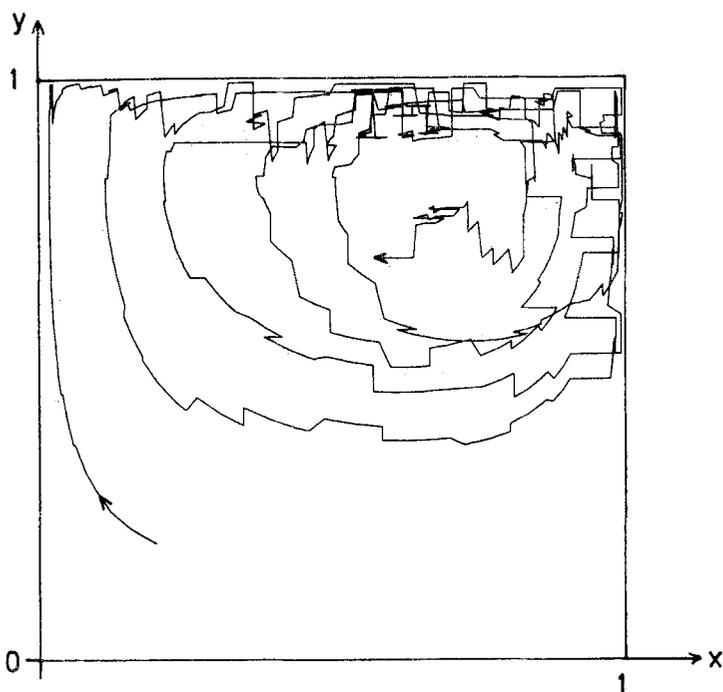


Fig. 3. A trajectory of the same dynamical system as in Fig. 2, with random fluctuations superimposed.

fully discussed in static terms alone. It seems that, at least for asymmetric contests, the notion of evolutionarily stable strategy has to be supplemented by a more dynamic approach.

Equations (1) and (7) are not very different from familiar equations in theoretical ecology. In particular, up to the factors $(1-x)$ and $(1-y)$, equation (8) looks just like an equation of Lotka-Volterra type describing the evolution of two populations of predator and prey (see for example, Hirsch & Smale 1974). Here again, the unique equilibrium is surrounded by periodic orbits and is equal to the time-average along these orbits.

Equation (8), of course, reflects only part of the dynamics underlying the model of Dawkins. Superimposed on the deterministic dynamical system (8) is a stochastic process corresponding to mutations. The evolution of the system will then be described by paths consisting of pieces of orbits of (8) and small random perturbations. In Fig. 3 we have simulated such an evolution by computer. The picture is reminiscent of Brownian motion and shows that (8) is in some ways quite unpredictable. The time average,

however, is not affected by the perturbations.

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.

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