

Towards a dynamics of social behaviour: Strategic and genetic models for the evolution of animal conflicts

Peter Schuster[†] and Karl Sigmund[‡]

[†]*Institut für Theoretische Chemie und Strahlenchemie und* [‡]*Institut für Mathematik
der Universität Wien, A-1090 Wien and IIASA, Laxenburg, Austria*

Persistence of behavioural traits in animal societies rather than optimality of reproductive success is described in terms of the game-theoretic notion of evolutionarily stable strategy. Game dynamics provides a suitable framework to accommodate for the dynamic aspects of permanence and uninvadability, to model the evolution of phenotypes with frequency dependent fitness and to relate the strategic models of sociobiology to the mechanisms of inheritance in population genetics.

Introduction

Classical ethology provided numerous investigations of animal populations exhibiting social phenomena based on 'altruistic' behaviour. In this non-anthropomorphic context, an act performed by an animal is called altruistic if it increases the fitness of some other animal at the cost of its own. Such behaviour was often explained by notions such as 'group selection' and 'benefit of the species' (for example, see Wynne-Edwards, 1962). But while there is no logical inconsistency in viewing groups or species as units of selection, it seems well established that Darwinian evolution acts much more commonly through selection of the level of individual organisms or eventually genes. The explanation of many altruistic traits in terms of individual selection has, therefore, to be viewed as a major success of sociobiology.

Roughly speaking, there are three approaches which proved to be fruitful. They may be designated as genetic, economic and strategic, and attributed to Hamilton (1964), Trivers (1972) and Maynard Smith (1974), respectively, although the principles go back to Haldane and Fisher, and arguably to Darwin himself.

(1) The genetic explanation is based on the notion of kin selection. A gene complex programming altruistic acts which benefit relatives may well spread, since it occurs, with a certain probability, within the relatives whose reproductive success is increased.

(2) The economic explanation relies on the notion of reciprocal altruism. If the altruistic act is likely to be returned at some later occasion, then the behaviour may become established, especially so if there is individual recognition between members of the population preventing 'cheaters'.

(3) The strategic explanation, finally, uses the panoply of game theory to show how the fitness of an individual may depend on what the other ones are doing. An act which in certain situations would be called altruistic need not, in other situations, decrease the reproductive success of the organism performing it.

In this paper, we shall deal exclusively with the third approach stressing its dynamical aspects. It must, however, be stated at the outset that the game-dynamic approach described here constitutes only a fraction of the game-theoretical analysis of animal behaviour. Our discussion is accordingly biased. The theory of games covers many applications in biological evolution. Some of them do not easily fit into the mould of ordinary differential equations. For a balanced survey of these topics, we may refer to a recent book by Maynard Smith (1982).

Our paper consists of two parts. The first one discusses, within the static context of game theory, the crucial notion of evolutionarily stable strategy (ESS), which centres on aspects of permanence rather than optimality. The second part uses game dynamics to obtain broader notions of permanence, to model the evolution of behavioural strategies and to relate them to genetic mechanisms.

Before we start our discussion of strategic models in sociobiology we have to comment on the evolutionary aspects of this approach. The actual mathematical models used in sociobiology as well as those of population genetics discuss the spreading of mutant genes in populations. The causes of mutations are considered as external factors and not as part of the system under consideration. A proper description of the evolutionary process, however, is complete only if it includes the mechanism of mutant formation. At present, such complete theories of evolution exist for polynucleotides in laboratory systems (for example, see Eigen & Schuster, 1979; Biebricher *et al.* 1982; Küppers, 1983) and eventually for simple viruses (Weissmann, 1974). The replication of bacteria follows a much more complicated mechanism. Already ten enzymes or more are required for DNA copying. Although not all the mechanistic details of local mutations and DNA rearrangements in bacteria are known yet, the basic features of bacterial evolution are established in principle and we can expect a complete molecular theory to become available in the not too distant future.

In case of higher, multicellular organisms we encounter new sources of complications which obscure the relation between mutations and their manifestation in phenotypic properties. The major problem concerns the unfolding of the genotype: higher organisms obtain final form and shape through morphogenesis. This is a complicated dynamical process which is not completely understood at present and to which the genes contribute markers and other regulatory signals for intercellular communication apart from the ordinary duties in cell metabolism and cell division. Any complete theory of evolution of higher organisms hence has to deal explicitly with the influence of mutations on morphogenesis, which is far outside the bounds of present possibilities. Behavioural traits are exceedingly complex phenotypic features which apparently cannot be traced down to single genes. The notion of 'mutant genes' leading to changes in behaviour has to be understood as a metaphor. Mutations actually operate within complicated networks of gene actions which are converted into the properties of the phenotype by a highly complex transformation during morphogenesis.

Evolutionarily stable strategies

The term 'evolutionarily stable strategy' was introduced by Maynard Smith and Price (1973) to describe certain genetically determined traits of animal behaviour which are

uninadable by mutants. The basic idea was to describe such evolutionary stability in terms of the mathematic framework of game theory. This method was subsequently used to analyse a wide variety of biological conflicts, both within and between species, and can be rightly considered to be a cornerstone of theoretical biology.

Game theory and biology

Ever since von Neumann and Morgenstern's (1953) classical treatise first published in 1944, the methods of game theory have been applied to the modelling of all kinds of conflicts in human societies. The applications to conflicts within animals and plants, however, date back to the last ten years. There were a few forerunners using game theoretic notions in biology, but in a context quite different from the one described here. With the benefit of hindsight it seems astonishing that biological 'games' were neglected for so long in favour of political, military or economic ones. Indeed, there are at least two reasons which make human conflicts more difficult to analyze than their 'natural' counterparts in biology:

- (1) The payoff in human systems is often doubtful, since it is hard to evaluate money, social prestige, health and other factors on a single utility scale. In the evolutionarily weighted contests in biology, Darwinian fitness is the only relevant quantity. Although this notion presents considerable difficulties for theoretical analysis and empirical measurement it provides in principle, at least, a scalar estimate of reproductive success.
- (2) The 'rationality axiom' frequently sets empirical and theoretical game theorists at odds. The investigation of animal behaviour is unhindered by such an assumption. Biological conflicts tend to be fairly straightforward, compared with all but the simplest human conflicts of any real interest. The possibilities for conspiracy, fraud, lunacy, etc. are greatly reduced

It is interesting to note, however, that the notion of evolutionarily stable strategy in biological contests is quite close to that of Nash equilibrium strategy for noncooperative games between rational players (cf. the section on 'Characterizations of evolutionary stable strategies (ESS)' below). In Parker & Hammerstein (1984), this is interpreted as 'quasi-rationality' of selection. In our view, the convergence of the two concepts is rather due to the fact that both 'blind selection' and 'rational decision' lead to adaptive solutions. After all, rational behaviour itself is a product of selection.

Strategies and phenotypes

The shift in the application of game theory from human to animal conflicts entails a shift in the meaning of the two basic notions of 'strategy' and 'payoff'. 'Payoff', as we have said, now corresponds to Darwinian fitness, i.e. the number of offspring or—in subtler situations—the number of copies of genes transmitted to the next generation. [For an elaborate analysis of the notion of fitness we refer to Dawkins (1982).] 'Strategy', in the context of chess, or war games, suggests a nicely calculated sequence of moves. This aspect of plotting and scheming was replaced by the notion of an innate trait of fighting behaviour (Maynard Smith & Price, 1973). It was soon realized that this viewpoint was useful, not only in the analysis of aggressive encounters, but in the modelling of any clash of interests: in the parent-offspring conflict, for example, concerning the length of the weaning period, or in the male-female conflict about the respective share in parental investment (Trivers, 1972). A strategy, thus, became a genetically programmed way of behaviour in pairwise contests. But such contests form only a small fraction of 'subgames' of the struggle for life. Differences in resource allocation, size of the litter, dispersal rate etc., affect the fitness of an individual in quite another way. In such cases,

the success is determined, not through playing against a particular opponent, or a series of opponents, but through 'playing the field' (see Maynard Smith, 1982).

A strategy, then, is any behavioral phenotype, or may be any phenotype at all. Indeed, game theory has been successfully applied to desert shrubs in order to discuss the relative merits of catching rain water by spreading horizontal roots near the surface, or of tapping ground water by sending a vertical root deep below: the success obviously depends on what the neighbours are doing (see Riechert & Hammerstein, 1983). From there it is only a small step to the protective colouring of moths or the familiar features of Mendelian peas. Thus, any phenotype may be viewed as a 'strategy', as long as we wish to analyze it by game theoretical methods or, to put it less subjectively, as long as its fitness is frequency dependent, (which means that it depends on the distribution of phenotypes in the population considered).

On the other hand not every strategy is a phenotype. In particular, a 'mixed strategy'—consisting in playing different strategies with preassigned probabilities—need not be realized as phenotype. In order to avoid confusion, we shall therefore keep the distinction between phenotype and strategy, even if this implies some modifications in the standard terminology of ESS theory.

Optimum phenotypes and genetic constraints

It is tempting, and often useful, to view selection as an optimization process. In elementary situations, as for example with asexually and independently replicating units, this is indeed the case (see the section on 'Asexual inheritance: optimization and the game-dynamical equation' below).

The term 'optimum', of course, has meaning only with respect to a given environment. There is no reason to expect that under continuously changing conditions, selection would lead to an optimum response to the instantaneous situation. Furthermore, since the environment includes all other members of the population, adaptation to an environment will change this environment. It is easy to exhibit corresponding population genetical models where the frequency dependent fitness will not, on the average, increase. This is actually the main theme of this paper.

But even if each phenotype had constant fitness, one could not expect, in general, that the phenotype with highest fitness would prevail. In particular, if this optimum phenotype corresponds to a heterozygous genotype, as may easily be the case, then at least one half of its offspring will be suboptimum. It is true that according to Fisher's fundamental theorem, the average fitness will never decrease, and even increase, provided the composition of the gene pool changes at all. However, the maximum average fitness of the population may be much lower than the fitness of the optimum phenotype. Furthermore, a population may be 'trapped' in a state where a local, but not global maximum is attained. Moreover, the fundamental theorem rests upon the assumption that fitness corresponds to the probability of survival from zygote to adult stage and that this probability depends on a single genetic locus. For many-loci models involving recombination, and for fecundity models where reproductive success is a function of the mating pair, the average fitness will not increase, in general (for example, see Ewens, 1979).

Selfinterest and optimization

Apart from genetic constraints, there may also be strategic obstacles to an optimization of the 'good of the species', i.e. of the mean fitness of a population. Selection acts through differential reproductive success of individuals, which may be quite opposed to the

welfare of the group. Even in human games allowing forethought and deliberation, the self-interest of two players may in some cases lead without failure to an outcome which is disastrous for both.

This is best shown by the well known paradigm of the 'prisoners' dilemma'. Two prisoners kept in separate cells are asked to confess a joint crime. If both confess, both will remain in jail for seven years. If only one confesses, he will instantly be freed, while the other one gets sentenced to ten years. If none of them confesses, both will be detained for one year. This latter solution is optimum but it will not be obtained. Each prisoner, indeed, will confess: it is the better option, no matter what the other one is going to decide. As a result, both will have to spend seven years in jail. [For a recent application of the prisoners' dilemma to the problem of cooperative behaviour in biology see Axelrod and Hamilton (1981).]

The prisoners' dilemma is a game between two opponents. Similar results hold for games where an individual is 'playing the field'. The best known example, in this respect, is Harding's 'tragedy of the commons', where the common meadow is ruined by overexploitation, each villager trying to increase his payoff. [We refer to Masters (1982) who bases his sociobiological discussion of political institutions on the 'prisoners' dilemma' and the 'tragedy of the commons'.]

Evolutionarily stable phenotypes

If adaption leads to an equilibrium at all, it will be characterized by stability rather than optimality. An evolutionarily stable phenotype, in Maynard Smith's definition, is a phenotype with the property that if all members of the population share it, no mutant phenotype could invade the population under the influence of natural selection.

One possible way of formalizing this is the following one (Maynard Smith, 1982). Let us denote by $W(I, J)$ the fitness of an individual I -phenotype in a population of J -phenotypes and by $pI + (1 - p)J$ the mixed population where p is the frequency of I -phenotypes and $1 - p$ that of J -phenotypes. A population of I -phenotypes will be evolutionarily stable if, whenever a small amount of deviant J -phenotypes is introduced, the old phenotype I fares better than the newcomers J . This means that for all phenotypes $J \neq I$,

$$W(J, \varepsilon J + (1 - \varepsilon)I) < W(I, \varepsilon J + (1 - \varepsilon)I), \quad (1)$$

for all $\varepsilon > 0$ which are sufficiently small.

It must be mentioned that this definition has to be modified if the population is small. In such a case, a deviant individual would change the composition of the population by a notable amount, and not just by some small ε . This situation has been analysed by Riley (1979). In our context, we shall always assume large population sizes, thus avoiding this problem and, moreover, the effects of sampling errors.

By letting $\varepsilon \rightarrow 0$ we obtain from inequality (1) that

$$W(J, I) \leq W(I, I), \quad (2)$$

for all J , which means that no individual fares better against a population of I -phenotypes, than the I -phenotype itself. The converse is not true in general: (2) does not imply (1).

Evolutionarily stable states

Now we restrict our attention to those biological games which satisfy the following two assumptions:

(1) They consist in one or repeated pairwise contests, rather than in 'playing the field'. This implies that the payoff W is an affine function of its second variable, i.e. that for any three phenotypes E , I and J and any $p \in (0, 1)$:

$$W(E, pJ + (1 - p)I) = pW(E, J) + (1 - p)W(E, I). \quad (3)$$

Indeed the probability that an individual E -phenotype matches up against a J -phenotype, in the mixed population $pJ + (1 - p)I$, is just p ; and its payoff, in this case, is $W(E, J)$. Here, we have tacitly assumed random matching of opponents. In some situations—e.g. games against relatives—this will be not valid. [For a discussion of this case we refer to Hines and Maynard Smith (1979).]

(2) There are only finitely many phenotypes E_1, \dots, E_n . This assumption may look innocuous. But there are situations where it is quite misleading, even as an approximation. As an example, we mention the so called 'war of attrition', a contest where the prize goes to the player who invests more time—or energy—than his opponent. The set of strategies consists of a continuum of waiting times and its discretization may be as ill-advised as the replacement, say, of the bell shaped probability density of body sizes by a finite subdivision.

The loss of generality entailed by these two assumptions is compensated in a way by an increase in mathematical convenience. We may now describe the game in normal form, with the help of a payoff matrix.

By x_i we denote the frequency of the phenotype E_i in the population. The point $\mathbf{x} = (x_1, \dots, x_n)$ describes the state of the population. Since the x_i s are frequencies, \mathbf{x} lies on the unit simplex $S_n = \{\mathbf{x} = (x_1, \dots, x_n) : x_i \geq 0, \sum x_i = 1\}$. By a_{ij} we denote the average payoff, i.e. the expected change in fitness, for an E_i -individual matched against an E_j -opponent. The $n \times n$ -matrix $\mathbf{A} = (a_{ij})$ is called the payoff matrix. The average payoff for the phenotypes E_i is

$$(\mathbf{Ax})_i = a_{i1}x_1 + \dots + a_{in}x_n = \sum_k a_{ik}x_k. \quad (4)$$

If \mathbf{x} and \mathbf{y} describe two populations, then the average payoff for a \mathbf{y} -member opposed to an \mathbf{x} -member is

$$\mathbf{y} \cdot \mathbf{Ax} = y_1(\mathbf{Ax})_1 + \dots + y_n(\mathbf{Ax})_n = \sum_k \sum_l y_k a_{kl} x_l, \quad (5)$$

and in particular, the average payoff for contests within the \mathbf{x} -population is

$$\Phi(\mathbf{x}) = \mathbf{x} \cdot \mathbf{Ax} = x_1(\mathbf{Ax})_1 + \dots + x_n(\mathbf{Ax})_n = \sum_k \sum_l x_k a_{kl} x_l. \quad (6)$$

There is an alternative interpretation of distributions of strategies. In game theory, E_1 to E_n are viewed as 'pure strategies'. They correspond to the corners \mathbf{e}_i of the unit simplex S_n . By \mathbf{e}_i we denote the i th unit vector: all components are 0 except the i th one which is 1. We may interpret now a point $\mathbf{x} \in S_n$ as a 'mixed strategy' which consists in playing E_i with probability x_i ($i = 1, \dots, n$). The expression $\mathbf{y} \cdot \mathbf{Ax}$ is the payoff of a \mathbf{y} -strategist playing against an \mathbf{x} -strategist. In the sequel, we shall make use of both interpretations. Points of S_n will correspond, according to the context, either to strategies or to states of the population.

Under our assumptions, the phenotype E_i is evolutionarily stable iff

$$\mathbf{e}_j \cdot \mathbf{A}(\varepsilon \mathbf{e}_j + (1 - \varepsilon) \mathbf{e}_i) < \mathbf{e}_i \cdot \mathbf{A}(\varepsilon \mathbf{e}_j + (1 - \varepsilon) \mathbf{e}_i), \quad (7)$$

for all $j \neq i$ and all $\varepsilon > 0$ which are sufficiently small.

One may extend this definition, just as one extends the notion of a pure strategy to that of a mixed one. A strategy (or state) $p \in S_n$ is evolutionarily stable (or an ESS) iff for all $y \in S_n$ with $y \neq p$,

$$y \cdot A(\varepsilon y + (1 - \varepsilon)p) < p \cdot A(\varepsilon y + (1 - \varepsilon)p), \quad (8)$$

for all $\varepsilon > 0$ which are sufficiently small, i.e. smaller than some appropriate $\delta(y)$.

Characterizations of evolutionarily stable strategies (ESS)

Equation (8) may be written as

$$(1 - \varepsilon)(p \cdot Ap - y \cdot Ap) + \varepsilon(p \cdot Ay - y \cdot Ay) > 0. \quad (9)$$

This implies that p is an ESS iff the following two conditions are satisfied:

(1) equilibrium condition

$$y \cdot Ap \leq p \cdot Ap \quad \text{for all } y \in S_n; \quad (10)$$

(2) stability condition

$$\text{if } y \in S_n, \quad y \neq p \quad \text{and} \quad y \cdot Ap = p \cdot Ap, \quad \text{then} \quad y \cdot Ay < p \cdot Ay. \quad (11)$$

This is the original definition from Maynard Smith (1974). The equilibrium condition states that the strategy p is a best reply against itself. It corresponds to the notion of Nash equilibrium familiar to game theorists. In Dawkin's (1982) terms 'an ESS ... can be crudely encapsulated as a strategy that is successful when competing with copies of itself'. This property alone, however, does not guarantee uninvadability, since it permits that another strategy y is an alternative best reply to p . In fact, if p is 'properly mixed', i.e. if $p_i > 0$ for all i , then any $y \in S_n$ is a best reply. The stability condition states that in such a case, p fares better, against y , than y against itself. The same argument leads to the following characterization: a phenotype E_i is evolutionarily stable iff

(1) equilibrium condition

$$a_{ii} \geq a_{ki} \quad \text{for all } k; \quad (12)$$

(2) stability condition

$$\text{if } a_{ii} = a_{ki} \quad \text{for } k \neq i, \quad \text{then } a_{ik} > a_{kk}. \quad (13)$$

A third equivalent definition of ESS, probably the most useful for computations, is the following one (Hofbauer *et al.*, 1979): $p \in S_n$ is an ESS iff

$$p \cdot Ax > x \cdot Ax \quad (14)$$

for all $x \neq p$ in some neighbourhood U of p in S_n .

There are examples of games admitting no ESS, or several ones. If there is an ESS in the interior of S_n , however, then it is the only ESS. Indeed, in such a case expression (14) must be valid for all $x \neq p$.

The 'hawk-dove' game and mixed strategies

Let us now consider the famous 'hawk-dove' game, a model devised by Maynard Smith and Price (1973) to explain the prevalence of ritual fighting in innerspecific conflicts. We do not attempt to repeat here the considerable amount of work done on this model (Maynard Smith, 1972; 1974; 1982; Zeeman, 1979; Schuster *et al.*, 1981), but describe it in its most rudimentary form in order to elaborate the distinction between mixed strategies and mixed populations.

We shall assume that there are two phenotypes. E_1 ('hawk') escalates until flight of the opponent or injury decides the outcome. E_2 ('dove') is only prepared to fight in a ritual way, without risking or inflicting injury. The prize of the contest corresponds to a gain G in fitness, while an injury reduces fitness by $|C|$ *. The effort expended in a ritual contest costs $|E|$. A natural and self-explanatory order relation among these parameters is

$$G > 0 \geq E > C.$$

Then a_{11} is $(G + C)/2$ —each 'hawk' has the same chance to win or to get injured; a_{22} is $(G + E)/2$ since only one of the 'doves' can win, a_{12} is G and a_{21} is 0—the 'dove' retreats when it meets a 'hawk'. Furthermore we restrict our discussion to the case $|C| > G$. Thus

$$\mathbf{A} = \begin{bmatrix} \frac{G+C}{2} & G \\ 0 & \frac{G+E}{2} \end{bmatrix}.$$

Clearly, no phenotype is evolutionarily stable. A population of 'doves' can be invaded by 'hawks' and vice versa.

The unique ESS of the population $\mathbf{p} = (p_1, p_2)$ is a mixture of p_1 'hawks' and $p_2 = 1 - p_1$ 'doves', with

$$p_1 = \frac{E - G}{E + C}. \quad (15)$$

This follows from the fact that

$$(\mathbf{p} - \mathbf{x}) \cdot \mathbf{A}\mathbf{x} = \frac{1}{2}(G - E + (E + C)x_1)^2 \quad (16)$$

is positive for all $\mathbf{x} = (x_1, x_2)$ with $x_1 \neq p_1$. Note that this state is not optimal. The average fitness

$$\mathbf{x} \cdot \mathbf{A}\mathbf{x} = \frac{1}{2}(G + E - 2Ex_1 + (E + C)x_1^2)$$

is largest for $x_1 = E/(C + E)$. A numerical example is shown in Fig. 1.

What happens if we introduce a third phenotype E_3 , which plays the mixed strategy corresponding to the ESS: $p_1\mathbf{e}_1 + p_2\mathbf{e}_2$? (For simplicity, we set $E = 0$). The payoff matrix now is

$$\mathbf{A} = \begin{bmatrix} \frac{G+C}{2} & G & \frac{G(G+C)}{2C} \\ 0 & \frac{G}{2} & \frac{G(G+C)}{2C} \\ \frac{G(G+C)}{2C} & \frac{G(C-G)}{2C} & \frac{G(G+C)}{2C} \end{bmatrix} \quad (17)$$

Conditions (12) and (13) show that E_3 is evolutionarily stable and cannot be replaced by neither E_1 nor E_2 phenotype. The corresponding state \mathbf{e}_3 , however, is not an ESS, and neither is $p_1\mathbf{e}_1 + p_2\mathbf{e}_2$, in this extended game: condition (11) is not satisfied

* We measure all parameters on the same value scale. Hence, gains like G are positive and losses like C or E negative quantities.

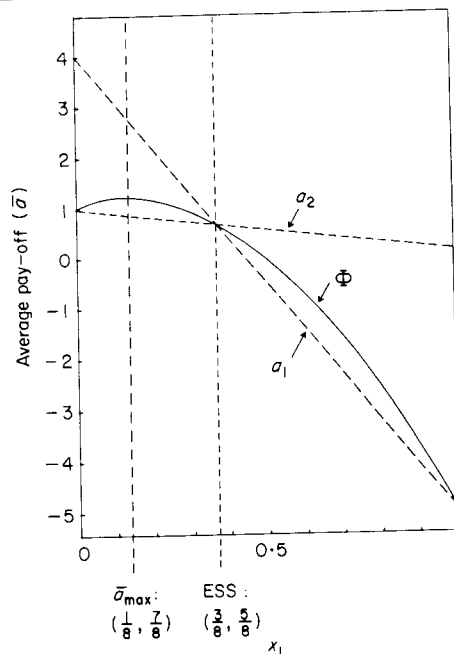


Fig. 1. The 'hawk-dove' game $G = 4$, $C = 14$, $E = 1$. \bar{a}_1 and \bar{a}_2 are the frequency dependent payoffs for 'hawks' and 'doves', while Φ is the average payoff for the total population consisting of x_1 'hawks' and $x_2 = 1 - x_1$ 'doves'

(cf. also the section 'Some examples'). Indeed, e_3 is not protected against the mixture and vice versa.

We may consider other 'mixed' phenotypes corresponding to mixed strategies $x_1 e_1 + x_2 e_2$ which are not the ESS in the hawk-dove game (i.e. $x_1 \neq p_1$). Such phenotypes are not evolutionarily stable: the population could be invaded, either by 'hawks', or by 'doves'. Furthermore, such 'mixed' strategies could not invade E_3 . All this is easy to check.

Continuing along these lines, one could analyze populations with several phenotypes corresponding to different mixtures of the 'hawk' and the 'dove' strategies. There is no reason, however, to stop at a finite number of such phenotypes. In the most natural set up, all possible mixed strategies would correspond to phenotypes competing with each other, but we prefer to stick to a finite set of phenotypes here and shall not pursue this question any further, referring instead, to Zeeman, (1981) and Akin, (1983).

How plausible, anyway, are phenotypes corresponding to mixed strategies? This is a delicate problem to which Maynard Smith (1982) devotes several chapters. His conclusion is roughly that such phenotypes are most important when 'playing the field', e.g. in the 'sex ratio' game, but probably of rather minor importance in the pairwise contests we are considering here.

On the other hand, does one find mixed states of the population which are evolutionarily stable? Again, this is not an easy matter. Mixed states are of course extremely common, but we are looking for strategic equilibria, consisting of several phenotypes for which the frequency dependent fitness values are equal. This is obviously difficult to verify. The safest empirical evidence, at present, seems to be found in Hamilton's, (1979) investigation of figwasps.

Asymmetric contests

So far we have considered contests which are symmetric, in the sense that both opponents play the same role. Many conflicts are asymmetric however: within the same species we have conflicts between males and females, between young and old, between owners and intruders of a habitat, and so on. The methods apply equally well to interspecific conflicts, e.g. between predators and preys. If we assume again that the contests are pairwise and the numbers of phenotypes finite, we are led to bimatrix games.

Thus let E_1, \dots, E_n denote the phenotypes of population X , and F_1, \dots, F_m those of population Y . By x_i we denote the frequency of E_i , and by y_j that of F_j . Hence, \mathbf{x} is a point in S_n and \mathbf{y} in S_m . If an E_i -individual is matched against an F_j -individual, the payoff will be a_{ij} for the former and b_{ji} for the latter. Thus the game is described by two payoff matrices $\mathbf{A} = (a_{ij})$ and $\mathbf{B} = (b_{ji})$. If the population X is in the state \mathbf{x} and the population Y in the state \mathbf{y} , then $\mathbf{x} \cdot \mathbf{A}\mathbf{y}$ and $\mathbf{y} \cdot \mathbf{B}\mathbf{x}$ are the respective average payoffs. If the phenotype E_i is stable in contests against the population \mathbf{y} , then it must do as well as all competing phenotypes. Thus $\mathbf{e}_i \cdot \mathbf{A}\mathbf{y} \geq \mathbf{e}_k \cdot \mathbf{A}\mathbf{y}$ for $k = 1, \dots, n$. But what if equality holds? There is nothing, then, to prevent E_k from invading. Thus, in contrast to the symmetric case, we cannot allow several 'best replies'. This leads to the following definition. A pair of phenotypes (E_i, F_j) is said to be evolutionarily stable iff

$$a_{kj} < a_{ij} \quad \text{for } k \neq i \quad (18)$$

and

$$b_{ki} < b_{ji} \quad \text{for } k \neq j \quad (19)$$

Similarly, a pair of states (or strategies) (\mathbf{p}, \mathbf{q}) with $\mathbf{p} \in S_n$ and $\mathbf{q} \in S_m$, is said to be evolutionarily stable if

$$\mathbf{p} \cdot \mathbf{A}\mathbf{q} > \mathbf{x} \cdot \mathbf{A}\mathbf{q} \quad \text{for all } \mathbf{x} \in S_n, \mathbf{x} \neq \mathbf{p} \quad (20)$$

and

$$\mathbf{q} \cdot \mathbf{B}\mathbf{p} > \mathbf{y} \cdot \mathbf{B}\mathbf{p} \quad \text{for all } \mathbf{y} \in S_m, \mathbf{y} \neq \mathbf{q} \quad (21)$$

It is easy to see that such a pair (\mathbf{p}, \mathbf{q}) must consist of pure strategies. Thus, in contrast to the symmetric case, a mixed strategy can never be evolutionarily stable. This has been shown for a considerably wider class of asymmetric games by Selten (1980). It also reflects on symmetric contests since it is often quite possible that a small, seemingly irrelevant difference can break the symmetry between the opponents and transform the originally symmetric contest into an asymmetric one (Maynard Smith, 1976; Hammerstein, 1979). This could explain why mixed strategies are rather rare in pairwise contests. On the other hand, if the population X interacts, not only with the other population Y , but also with itself, then mixed ESSs become possible again (Taylor, 1979; Schuster *et al.*, 1981a, b)

Nash equilibria and the 'coyness-philandering' game

A pair of strategies (\mathbf{p}, \mathbf{q}) (with $\mathbf{p} \in S_n$, $\mathbf{q} \in S_m$) is called a Nash equilibrium pair if

$$\begin{aligned} \mathbf{p} \cdot \mathbf{A}\mathbf{q} &\geq \mathbf{x} \cdot \mathbf{A}\mathbf{q}, & \forall \mathbf{x} \in S_n, \\ \mathbf{q} \cdot \mathbf{B}\mathbf{p} &\geq \mathbf{y} \cdot \mathbf{B}\mathbf{p}, & \forall \mathbf{y} \in S_m. \end{aligned} \quad (22)$$

Nash equilibria play an important role in classical game theory, since for rational players there is no reason to depart from the strategies \mathbf{p} and \mathbf{q} , as long as their opponent sticks

to it. We shall presently see, however, that in biological games, Nash equilibria are not invasion proof.

Indeed, let us consider another famous example, the 'coyness-philandering' game by Dawkins (1976). Let us suppose that the successful raising of an offspring increases the fitness of both parents by G . The parental investment $|C|$ will be entirely borne by the female if the male deserts. Otherwise, it is shared equally. The female strategy to counter male desertion is 'coyness', i.e. the insistence upon a long engagement period, which costs $|E|$ to both partners. Again we measure all parameters on the same value scale and have $G > 0$; $C, E < 0$. There are two phenotypes in the male population X , namely E_1 ('philandering') and E_2 ('faithful') and two phenotypes in the female population Y , namely F_1 ('coy') and F_2 ('fast'). The payoff matrices are

$$\mathbf{A} = \begin{bmatrix} 0 & G \\ G + \frac{C}{2} + E & G + \frac{C}{2} \end{bmatrix}, \quad \mathbf{B} = \begin{bmatrix} 0 & G + \frac{C}{2} + E \\ G + C & G + \frac{C}{2} \end{bmatrix} \quad (24)$$

No pair of phenotypes is evolutionarily stable, and no state of the population is an ESS (we have only to check the pure states). There exists a unique pair of mixed strategies \mathbf{p} and \mathbf{q} in Nash equilibrium, given by

$$p_1 = \frac{E}{E + C + G}, \quad q_1 = -\frac{C}{2(E + G)}, \quad (25)$$

(with $\mathbf{p} = (p_1, p_2) \in S_2$, $\mathbf{q} = (q_1, q_2) \in S_2$) provided $|E| < G < |C| < 2(G + E)$. This equilibrium is not stable, however. If a fluctuation decreases, say, the amount of philandering males, then the payoff for the males will not change: each phenotype still has the same payoff, which depends only on the female population. One cannot expect the frequency of philanderers to return to p_1 . The payoff for the female population will actually increase: but 'fast' females gain more than 'coy' ones, since their risk of being deserted decreases. It is only when the amount of 'fast' females increases that the male payoffs change. Again, they increase: but 'philanderers' gain more than the 'faithful' males; hence, more 'philanderers'; hence more 'coy' females; hence, less 'philanderers', and so on. This looks like an oscillating system. The static approach of game theory is no longer sufficient to deal with this situation.

Game dynamics

Evolution is dynamic, and hence any evolutionary model must present dynamical aspects. For the study of equilibria and persistence, however, such aspects may well remain implicit, as they do in the game theoretical approach. Indeed, a straight application of the inventory of dynamical systems used in population genetics may be quite off the point, in certain situations. In particular, ESS theory is essentially phenotypic rather than genotypic. It is, incidentally, quite interesting that a major part of sociobiology—a science which reputedly delivers everything, including humanity, into the clutches of selfish genes—derives its interest from taking a strategic rather than genetic point of view.

The present state of knowledge does not allow anything definite to be said about the genetic mechanism behind a given behavioural trait; and to tie such a trait arbitrarily to some hypothetical genotype may well confuse things. The Mendelian machinery could

override the frequency-dependent regulation at the strategic level which one wants to investigate. To avoid such interference, it will therefore be quite appropriate to assume asexual reproduction at least as a first approximation. Most game-theoretical models in biology concern sexual populations, of course; but this may eventually lead to irrelevant complications based not on a necessary constraint but on speculations about the inheritance of behaviour.

Asexual inheritance: optimization and the game-dynamical equation

Let us consider a population with n phenotypes. The point $\mathbf{x}(t) \in S_n$ denotes the state of the population at time t . Asexual reproduction means 'like begets like'. The better the phenotype E_i is adapted, the higher its rate of relative increase

$$\frac{1}{x_i} \dot{x}_i = \frac{1}{x_i} \frac{dx_i}{dt}$$

If the fitness of the phenotype E_i is given by a constant λ_i , then the average fitness of a population in state \mathbf{x} is given by $\Phi(\mathbf{x}) = \lambda_1 x_1 + \dots + \lambda_n x_n$. It is natural to assume that the rate of relative increase of E_i is given by the difference between the fitness λ_i of E_i and the average fitness $\Phi(\mathbf{x})$. Thus the equation

$$\dot{x}_i = x_i \{\lambda_i - \Phi(\mathbf{x})\}, \quad i = 1, \dots, n, \quad (26)$$

restricted to the invariant set S_n , will describe the evolution of the distribution of phenotypes in the population.

This equation plays an important role in the theory of Eigen and Schuster (1979) on prebiotic evolution. The population, in this case, consists of n types of selfreplicating macromolecules, RNA or DNA, in a flow reactor. It can easily be shown that the average 'fitness', i.e. the mean reproduction rate, increases monotonically. Indeed, the time derivative of Φ is just the variance of the 'fitness' in the molecular population. The molecular types with less than average fitness will be eliminated, and the average fitness thereby increased. In the limit, only the molecules with the highest fitness will remain. In populations with asexual replication and frequency independent fitness, selection is a global optimization process.

The above results are valid for 'error-free' replication. In more detailed studies (Eigen, 1971; Thompson & McBride, 1974; Jones *et al.*, 1976; Swetina and Schuster, 1982) mutations were taken into account. In this case, the average fitness Φ is not, in general, optimized. However, the state reaches a unique stable equilibrium, and this implies that there exists some (Ljapunov) function which increases monotonically. Actually, Jones (1978) displayed a function of this type which is closely related to the average fitness.

Let us now return to the 'error-free' case, but assume that the fitness of phenotype E_i is frequency dependent, i.e. a function of \mathbf{x} . More precisely, let us assume that it is given by the game theoretical payoff $(\mathbf{Ax})_i$, as derived in the section on 'Evolutionary stable states' above. The average fitness then is

$$\Phi(\mathbf{x}) = \mathbf{x} \cdot \mathbf{Ax}$$

according to equation (6). To be correct, $(\mathbf{Ax})_i$ and $\mathbf{x} \cdot \mathbf{Ax}$ are not to be viewed as fitness but as increase in fitness resulting from the conflict. The differential equation (27) given below, however, is invariant to the addition of constants to the columns of \mathbf{A} and hence remains unchanged when we replace differential fitness by total fitness.

The equation of 'game dynamics'

$$\dot{x}_i = x_i \{(\mathbf{A}\mathbf{x})_i - \Phi(\mathbf{x})\}, \quad i = 1, \dots, n, \quad (27)$$

restricted to the invariant set S_n (the unit simplex) describes the evolution of the distribution of phenotypes (Taylor & Jonker, 1978). In writing down a differential equation for game dynamics we made two implicit assumptions: (1) complete mixing of generations and (2) infinitely large population size. By infinitely large we mean in this context so large that fluctuations can be neglected.

Equation (27) plays a central role for many models of selection in fields as diverse as prebiotic evolution, population genetics and mathematical ecology (see Schuster & Sigmund, 1983). Its usefulness in sociobiology is a new facet of its widespread applicability.

In general, the average fitness Φ will not increase monotonically. Maxima of Φ need not coincide with fixed points of equation (27). Moreover, the dynamics of equation (27) may admit limit cycles, i.e. persistent oscillations (examples are discussed in Hofbauer *et al.*, 1980), and strange attractors, i.e. seemingly chaotic, highly irregular oscillations with extreme sensitivity to the choice of initial conditions (see Hofbauer, 1981, Arneodo *et al.*, 1980). Every game theoretical equilibrium, i.e. every point \mathbf{p} on S_n which satisfies equation (10) is a fixed point of equation (27), and every ESS, furthermore, is asymptotically stable in the sense that every state which is sufficiently close by will converge towards it (Taylor & Jonker, 1978; Hofbauer *et al.*, 1979; Zeeman, 1980).

Thus, small perturbations of evolutionarily stable states will be offset by the dynamics of the evolution. The converse, however, is not true: there are asymptotically stable fixed points of equation (27) which cannot be found as an ESS by the game theoretical approach (Hofbauer *et al.*, 1979; Zeeman, 1979).

Some examples

In a special case, namely when $a_{ij} = a_{ji}$ holds for all i and j , the average fitness Φ will always increase. Games whose payoff matrix satisfies this condition are called partnership games: both players always share the outcome fairly. Indeed, it can easily be checked that the rate of increase of Φ corresponds, again, to the variation of the fitness in the population. It is, of course, no surprise that in partnership games, in contrast to the 'prisoners dilemma' and the like, an optimization principle holds.

The ESS of the 'hawk-dove' game, $\mathbf{p} = p_1 \mathbf{e}_1 + (1 - p_1) \mathbf{e}_2$ with $p_1 = (E - G)/(E + C)$ as described by equation (15) is globally stable. In the extended 'hawk-dove' game given by Expression (17) with the phenotype E_3 corresponding to this ESS, there exists a line F of fixed points through \mathbf{e}_3 and \mathbf{p} (see Fig. 2).

All orbits converge to F , remaining on the constant level curves of the function

$$Q(\mathbf{x}) = x_3 x_1^{-p_1} x_2^{-p_2}. \quad (28)$$

There is an argument (Hofbauer, private communication) that random drift will cause the state to approach \mathbf{e}_3 , leading to fixation of the phenotype E_3 . Indeed the constant level curves of Q are concave. If the state of the population has approached some fixed point \mathbf{q} on F , and if a random perturbation sends it away, then the differential equation will lead it back to some point \mathbf{q}' on F . The probability that \mathbf{q}' is between \mathbf{q} and \mathbf{e}_3 is slightly larger than 1/2 (see Fig. 2). In this way, a sequence of small fluctuations will drive the state towards \mathbf{e}_3 . This, however, depends upon the assumption of fluctuations with radial symmetry.

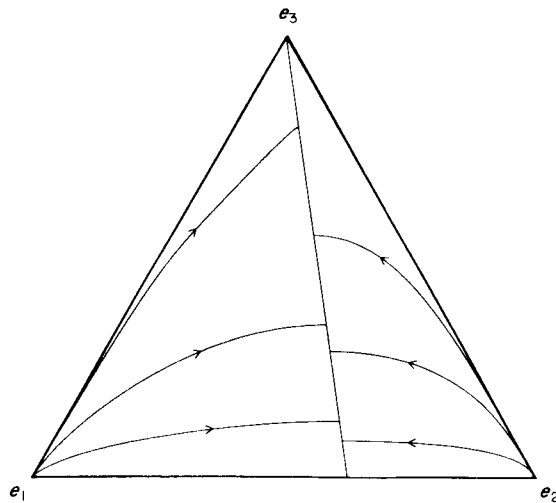


Fig. 2. Strategies e_1 and e_2 correspond to 'hawk' and 'dove' phenotypes, e_3 to a phenotype playing a mixed strategy, acting as 'hawk' with probability p_1 and as 'dove' with probability p_2 (where p_1 and p_2 are given by the ESS $\mathbf{p} = (p_1 e_1 + p_2 e_2)$ of the 'hawk-dove' game). The line from e_3 to \mathbf{p} consists of fixed points. Random drift might lead the state of the population, through fluctuations along the line, closer to e_3 .

We recall from equation (17) that phenotype E_3 is not evolutionarily stable. A more stricting example for such a situation is obtained with

$$\mathbf{A} = \begin{bmatrix} 0 & 10 & 1 \\ 10 & 0 & 1 \\ 1 & 1 & 1 \end{bmatrix}, \quad (29)$$

(see Fig. 3). E_3 is stable against invasion by E_1 alone, or by E_2 alone, but not if both phenotypes invade simultaneously.

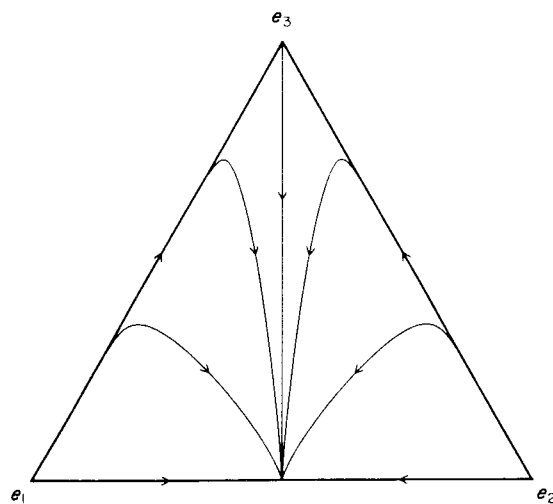


Fig. 3. The game-dynamical equation (27) with matrix given by (29)

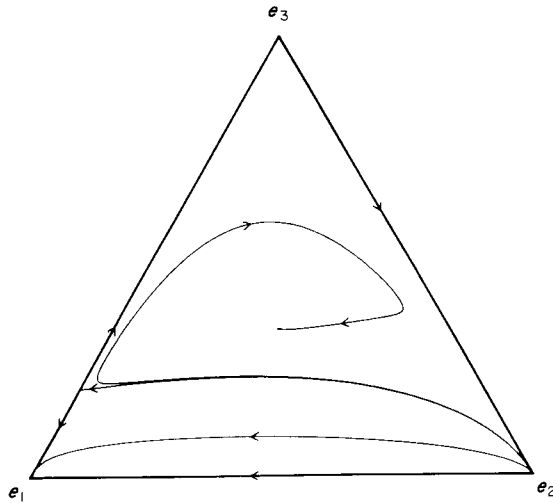


Fig. 4. The game-dynamical equation (27) with matrix given by (30)

Another interesting example due to Zeeman (1981) is given by the matrix

$$\mathbf{A} = \begin{bmatrix} 0 & 6 & -4 \\ -3 & 0 & 5 \\ -1 & 3 & 0 \end{bmatrix} \quad (30)$$

In this case, equation (27) admits two asymptotically stable equilibria, namely $e_1 = (1, 0, 0)$ and $m = (1/3, 1/3, 1/3)$ (see Fig. 4). The former point is easily checked to be an ESS. Hence the latter one, which lies in the interior of S_1 , cannot be an ESS.

Permanence and uninvasibility in terms of dynamical systems

As mentioned before, the orbits of a game-dynamical equation (27) need not converge to an ESS. They may converge to an equilibrium which is asymptotically stable but not an evolutionarily stable strategy in the sense of game theory, or they may settle to a persistent oscillatory regime, or exhibit chaotic behaviour. In the two latter cases it can be shown that the time averages of the phenotype frequencies converge to an equilibrium value (see Schuster *et al.*, 1981a).

Of course, one cannot hope to measure such time averages directly, since they would have to include a large number of generations. If the population is subdivided into many such populations (or demes) which oscillate out of phase with each other, then the mean value (at a given instant) of the phenotype frequencies of the different demes gives a plausible estimate of their time-averages and hence of the equilibrium.

The game dynamical approach suggests two eventualities:

- (1) the existence of equilibria which, although not 'evolutionarily stable', are nevertheless relevant and persistent features of the model, either because they are asymptotically stable and hence perturbation-proof, or because they correspond to the time averages of regular or irregular oscillations, and
- (2) the existence of asymptotic regimes which, although not static, are nevertheless robust features of the system.

Whether such phenomena occur in situations of biological interest is still open, but the possibility should be kept in mind.

In any case it is not difficult to describe, within the framework of population dynamics, the notions of permanence and uninvasibility in a non-static way which generalizes the concept of evolutionary stability. Roughly speaking, the n phenotypes E_1 to E_n are *permanent* if there is some minimum level $q > 0$ such that, if initially all phenotypes are present, i.e. if $x_i(0) > 0$ for all i , then after some time their frequencies $x_i(t)$ will be larger than q . These frequencies could oscillate or converge: the only relevant property, in this context, is that random fluctuations which are small and occur rarely are not able to wipe out some of the phenotypes.

The society can be termed *uninvasive*, with respect to some further phenotypes E_{n+1} to E_{n+k} , if it is permanent and if all initial conditions with sufficiently low frequencies $x_{n+1}(0)$ to $x_{n+k}(0)$ lead to the ultimate vanishing of these phenotypes. Permanence and uninvasibility, in this sense, mean protectedness against disturbance from within and from without. We refer to Schuster and Sigmund (1984) for a more detailed discussion of these notions and their applicability to models of biological evolution.

Dynamics for asymmetric games

Let us turn now to asymmetric contests, i.e. to games described by two payoff matrices **A** and **B** (see the section on 'Asymmetric contests' above). The same argument which led to the game-dynamical equation (27) now yields the differential equation

$$\begin{aligned}\dot{x}_i &= x_i[(\mathbf{A}\mathbf{y})_i - \mathbf{x} \cdot \mathbf{A}\mathbf{y}], & i &= 1, \dots, n, \\ \dot{y}_j &= y_j[(\mathbf{B}\mathbf{x})_j - \mathbf{y} \cdot \mathbf{B}\mathbf{x}], & j &= 1, \dots, m,\end{aligned}\quad (31)$$

describing the evolution of the population states $\mathbf{x}(t) \in S_n$ and $\mathbf{y}(t) \in S_m$ (see Schuster *et al.*, 1981b).

If one of the populations contains only one phenotype, equation (31) reduces to equation (26) and hence to an optimization problem.

In the general case, selection leads usually to the fixation of one genotype in each population. This reflects the fact that there exist no mixed ESS for asymmetric games. In the case $n = m$, however, it may also happen that the frequencies oscillate periodically. This is the case, for example, in the 'coyness-philandering' game of Dawkins (Schuster & Sigmund, 1981; see also the section on the 'Nash equilibria and the coyness-philandering game' above). Again, the time averages converge to the game-theoretic equilibrium, which is not evolutionarily stable.

Discrete game dynamics

Difference equations are the appropriate tool to study infinite populations with distinct generations. Thus, they apply to situations in which premise (1) for the validity of equation (27) is not fulfilled. Often, blending of generation is prevented by the action of some internal or external pacemakers for the reproductive cycle. An obvious example for the latter case is the periodicity of seasons.

The most straight-forward candidate for discrete-game dynamics of symmetric contests is the equation

$$x'_i = x_i(\mathbf{A}\mathbf{x})_i(\mathbf{x} \cdot \mathbf{A}\mathbf{x})^{-1}, \quad i = 1, \dots, n. \quad (32)$$

Here $\mathbf{x}' = (x'_1, \dots, x'_n)$ denotes the state of the population in the next generation. It is somewhat disturbing that this class of difference equations, in contrast to the differential

equations discussed above, does not seem to fit ESS theory very well. Indeed, equation (32) behaves rather badly in several cases. We consider as an example the 'hypercycle' game with $n = 3$ given by

$$\mathbf{A} = \begin{bmatrix} 0 & 1 & 0 \\ 0 & 0 & 1 \\ 1 & 0 & 0 \end{bmatrix}. \quad (33)$$

It has $\mathbf{m} = (1/3, 1/3, 1/3)$ as an ESS. The fixed point \mathbf{m} is not asymptotically stable, however. This is surprising, since the continuous analogue of expression (32), namely

$$\dot{x}_i = (\mathbf{x} \cdot \mathbf{Ax})^{-1} x_i [(\mathbf{Ax})_i - \mathbf{x} \cdot \mathbf{Ax}] \quad (34)$$

has the same trajectories as the game-dynamical equation (27). For asymmetric games, the difference equation

$$\begin{aligned} x'_i &= (\mathbf{x} \cdot \mathbf{Ay})^{-1} x_i (\mathbf{Ay})_i, \\ y'_j &= (\mathbf{y} \cdot \mathbf{Bx})^{-1} y_j (\mathbf{Bx})_j \end{aligned} \quad (35)$$

corresponds to the differential equation

$$\begin{aligned} \dot{x}_i &= (\mathbf{x} \cdot \mathbf{Ay})^{-1} x_i [(\mathbf{Ay})_i - \mathbf{x} \cdot \mathbf{Ay}], \\ \dot{y}_j &= (\mathbf{y} \cdot \mathbf{Bx})^{-1} y_j [(\mathbf{Bx})_j - \mathbf{y} \cdot \mathbf{Bx}], \end{aligned} \quad (36)$$

which need no longer be equivalent to equation (31). In particular, the inner fixed point (\mathbf{p}, \mathbf{q}) of the 'coyness-philandering' game is now asymptotically stable (Hofbauer, see Maynard Smith, 1982, appendix J). This may be viewed either as a misleading trick of the dynamics—after all, (\mathbf{p}, \mathbf{q}) is not an ESS—or as a remarkable vindication of Dawkins early claim (1976) that the strategies do converge to (\mathbf{p}, \mathbf{q}) . Of course, there are no empirical dates to decide which of the two equations (31) or (36) is more correct.

An interesting approach has been proposed by Eshel and Akin (1983). It consists in assuming that the sign of \dot{x}_i (or, in the discrete case, of $x'_i - x_i$) is that of the difference $(\mathbf{Ay})_i - \mathbf{x} \cdot \mathbf{Ay}$, without writing down an explicit equation like equation (31) or (36). The dynamics, then, is only incompletely specified, but should reflect the basic traits of the model; surely, the last word on difference equations, differential equations and ESS has not been said yet.

So far, we have accepted the simplification that 'like begets like'. More sophisticated discussions have to take account of the Mendelian mechanism of inheritance.

Sexual models

Although the strategic and the genetic point of view are to some degree disjoint, it is nevertheless of interest to check their compatibility, even if this requests assumptions which are quite hypothetical.

It is obvious that a genetic constraint can prevent the population from attaining an ESS. In particular, an evolutionarily stable phenotype which is only realized by a heterozygote genotype can never become fixed. Such a case of 'overdominance' leads to different predictions of game theory and population genetics. So far only one locus models have been studied (Maynard Smith, 1981; Eshel, 1982; Hines, 1980; Bomze *et al.*, 1983). In this case it was always overdominance which led to divergences from ESS results. In many-locus models one may expect other genetic constraints as well.

Let us consider first the frequency independent case. We assume that there are k alleles A_1 to A_k in the gene pool. Their frequencies are denoted by p_1 to p_k . The fitness of the genotype $A_i A_j$ is given by some constant w_{ij} which corresponds to the probability of survival from the zygote to the adult stage. Introducing the laws of Mendelian genetics we obtain the classical selection equation of Fisher for the evolution of the gene distribution

$$\dot{p}_i = p_i \{ (Wp)_i - \Phi(p) \}, \quad i = 1, \dots, k. \quad (37)$$

The differential equation is invariant on S_k , $W = (w_{ij})$ is the 'viability matrix' and $\Phi(p) = p \cdot Wp$ represents the average fitness in a randomly mating population with the gene distribution $p = (p_1, \dots, p_k)$. This equation is a special case of equation (27). Precisely, it corresponds formally to the (game) dynamical version of a partnership game since $w_{ij} = w_{ji}$. Accordingly, the average fitness Φ increases monotonically. Selection can be visualized as optimization of the mean reproductive success. There is nevertheless an important difference with respect to the nature of the optimization process in equation (37) and in the asexual case described by equation (26). In the latter case optimization was global on S_n . Here, selection does not lead in general to a global optimum of Φ . Consider for example the particularly simple case $n = 2$. The average fitness is of the form

$$\Phi = (w_{11} - 2w_{12} + w_{22})p_1^2 + 2(w_{12} - w_{22})p_1 + w_{22}.$$

In case $w_{11} > w_{12}$ and $w_{22} > w_{12}$, Φ has a minimum on the interval $0 < p_1 < 1$ and hence, there are two optima coinciding with the pure states $p_1 = 0$ and $p_1 = 1$. Depending on the initial conditions either allele A_1 or allele A_2 will be selected.

We turn now to the frequency dependent case and consider equations which combine the game theoretical model with population genetics. It will be appropriate to carry out the analysis on two levels, the phenotypic and the genotypic one. We shall assume that the population consists of n phenotypes E_1 to E_n and that each genotype $A_i A_j$ corresponds to one of those phenotypes, or possibly to a probability distribution $p(ij) = (p_1(ij), \dots, p_n(ij))$, where $p_k(ij)$ is the frequency of $A_i A_j$ —individuals of phenotype E_k . The converse, however, need not be true: as it happens in the case of dominance, two or more genotypes may give rise to the same phenotype.

The payoff is given as before by the $n \times n$ -matrix A . Now we have to specify how it is related to reproductive success. This is a rather delicate point which cannot be decided without a closer inspection of the situation to be modelled. Two alternative simple cases are:

(1) The payoff is independent of sex, and the number of offspring of a given couple is proportional to the product of parental payoffs. This situation corresponds to fights which are not sex-specific, like contests for food. Maynard Smith (1981) considered such a model.

(2) The expression of the genotype is sex-specific although the relevant genes are carried by both sexes. The number of offspring of a given couple again is proportional to contributions from both parents. The parent who carries the silent genes now contributes a constant factor. Such a model is appropriate for fights within the male population, e.g. contests for females, breeding grounds or other resources. A detailed discussion of this approach can be found in Hofbauer *et al.* (1982).

In any case one is led to fecundity models. To set up the corresponding (discrete or continuous) equations for the time evolution of genotype or phenotype frequencies is immediate, but the analysis of the resulting systems is in general difficult.

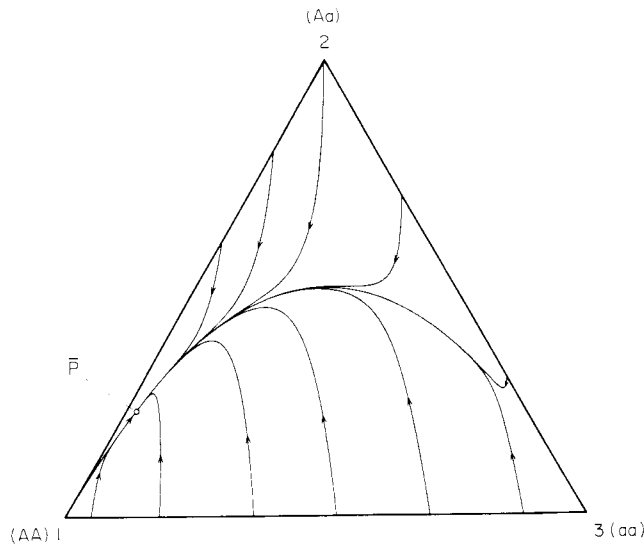


Fig. 5. A diagram describing a typical evolution of genotypes AA, Aa and aa (corresponding to the corners e_1, e_2, e_3) if the reproductive success depends on differential fecundity. The state of the population converges very quickly to a 'Hardy-Weinberg' parabola, and evolves through frequency-dependent selection along the parabola towards an equilibrium \bar{P} [for details, see Hofbauer *et al.* (1982)]

In some cases, however, the investigation is simplified by the fact that a Hardy-Weinberg equilibrium gets established: in case (1) if the model is discrete (nonoverlapping generations) and in case (2) if it is continuous (generations blending into each other, see Fig. 5). Thus the frequency of genotype $A_i A_j$ is given by the product of the frequencies of the corresponding genes A_i and A_j . (More generally, it often happens that the mating system—random or assortative—leads to relations between the genotype frequencies). This allows to reduce the problem to the time evolution of gene frequencies. The corresponding equations are similar to equation (37), except that the w_{ij} are now polynomials in p_1 to p_k . The average fitness will not increase in general.

An analysis of two-strategy games (see Maynard Smith, 1981; Hofbauer *et al.*, 1982; Eshel, 1982) shows, essentially, that if the genetic constraints allow the ESS to be realized at all, then it will asymptotically be reached indeed. If, for example, one of the alleles is dominant, then the outcome predicted by the simple game theoretic considerations of the section on 'The 'hawk-dove' game and mixed strategies' above will also be obtained by the genetic model. (It is worth mentioning in this context that Bürger, 1983, using a model of Sheppard, 1965, has shown that dominance may be established, if the selection pressure is sufficiently high, by the action of a secondary gene locus. Thus the genetic mechanism itself may evolve towards a suppression of the genotypic obstacles to phenotypic adaptation).

One may similarly investigate genetic models for asymmetric contests. In Bomze *et al.* (1983); the 'coyness-philandering' model is discussed at some length. We briefly sketch it, as an illustration. Let us assume that two alleles A_1 and A_2 determine the male behaviour, and that P_0, P_1 and P_2 are the probabilities that the male genotypes $A_1 A_1, A_1 A_2$ and $A_2 A_2$, respectively, are faithful. Then, if p denotes the frequency of A_1 ,

$$b = p^2(P_0 + P_2 - 2P_1) + 2p(P_1 - P_2) + P_2$$

is the frequency of faithful males within the male population. Similarly, let the alleles B_1 and B_2 determine female behaviour and let Q_0 , Q_1 and Q_2 be the probabilities that the female genotypes B_1B_1 , B_1B_2 and B_2B_2 , respectively, are fast. Then, if q is the frequency of B_1 ,

$$\beta = q^2(Q_0 + Q_2 - 2Q_1) + 2q(Q_1 - Q_2) + Q_2$$

is the frequency of fast females. It is easy, now, to compute the 'payoffs' a_1 and a_2 for faithful and philandering males, respectively, as function of β and the 'payoffs' α_1 and α_2 for fast and coy females, respectively, as function of b . If one assumes that the payoff corresponds to fertility, one can check that Hardy-Weinberg relations hold. Simple computations lead to the differential equations

$$\dot{p} = \frac{1}{2}p(1-p)[p(P_0 + P_2 - 2P_1) + P_1 - P_2](a_1 - a_2)$$

$$\dot{q} = \frac{1}{2}q(1-q)[q(Q_0 + Q_2 - 2Q_1) + Q_1 - Q_2](\alpha_1 - \alpha_2).$$

The strategic component—i.e. the terms depending on the payoff matrices—reduce to the factors $a_1 - a_2$ and $\alpha_1 - \alpha_2$. This facilitates the analysis of the gene frequencies. We shall only describe the interesting case of 'overdominance'. If $P_0 - P_1$ and $P_2 - P_1$ have the same sign, as well as $Q_0 - Q_1$ and $Q_2 - Q_1$, then the orbit in the 'state-space' (p , q) will be periodic (see Fig. 6). There are four possible oscillatory regimes, depending on initial conditions, but the time averages of the strategies will quickly converge to the equilibrium values obtained in Equation (25) by simple game theoretic considerations. This may well be a typical situation: complicated features on the 'microscopic' level of gene frequencies yield a simple result on the 'macroscopic' level of phenotypes. (For a detailed discussion see also Bomze *et al.*, 1983). Asymmetric conflicts between two different species can also be modelled in similar ways. The first paper in this direction, which apparently found only little attention in the literature, seems to be due to

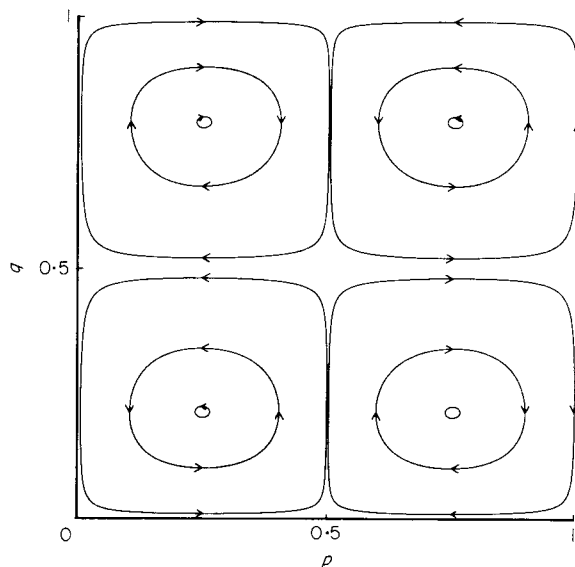


Fig. 6. A possible dynamics for the 'coyness-philandering' game. The gene frequencies p and q governing male and female behaviour oscillate endlessly, but the corresponding payoffs converge, in the time average, to the game theoretic equilibrium (25) (see Bomze *et al.*, 1983, for details)

Stewart (1971) and investigates dimorphism in two coevolving populations of predators and prey. His 'game' between cats which can stalk or watch and mice which can run or freeze, is similar in structure to the 'coyness-philandering' game. In its emphasis on game theoretic aspects it is a remarkable forerunner of ESS theory: it also offers an analysis of dynamical models based on sexual and asexual genetics, which fully agrees with the Nash equilibrium solution obtained from strategic considerations alone.

Results of this type strongly suggest that one may confidently stick to the phenotypic level, as long as there is no solid candidate for the underlying genotypic mechanism.

Concluding remarks

The considerations concerning the role of intrinsic constraints on the evolutionary optimization process can be subsumed with the help of Fig. 7. The mean reproductive success in populations of independently and asexually reproducing individuals is optimized through evolution. This will be modified by two mechanisms:

- (a) The rules of Mendelian genetics restrict the dynamics of selection onto the Hardy-Weinberg surface or onto a 'near Hardy-Weinberg' submanifold (see Ewens, 1979). Other distributions of genotypes are evolutionarily unstable for genetic reasons.
- (b) Direct interactions of replicating elements lead to constraints on the optimization process. The result is a displacement of the evolutionarily stable distribution from that which is characterized by the maximal reproductive success.

In populations in which both constraints are in operation, the genetic and the strategic one, we observe a superposition of both effects. In the sexual models considered so far, many cases (e.g. dominance) lead to situations which are indistinguishable from the corresponding asexual ones. This justifies a posteriori the various static or dynamic asexual models.

Of course the situations analysed so far are characterized by oversimplification. One could introduce further complications without end, but often without gaining further insights.

Basically, the game dynamical models incorporate features of highly developed fields, namely population genetics and game theory. A further emphasis on genetic aspects

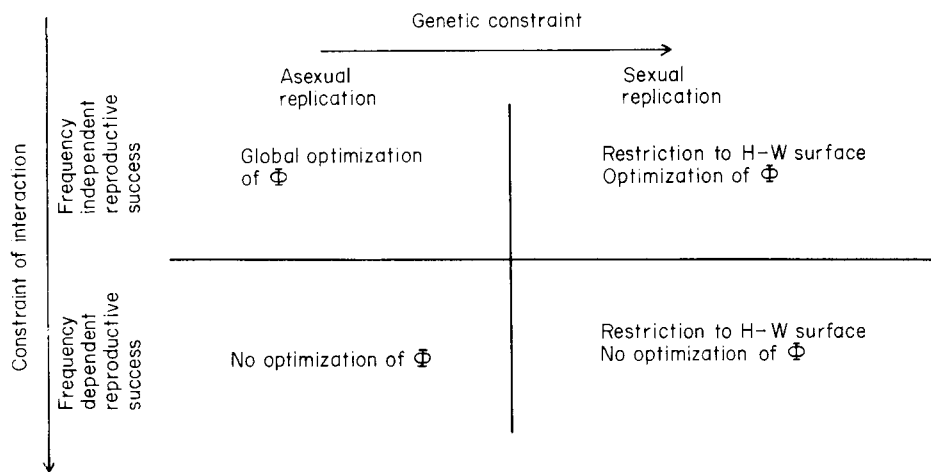


Fig. 7. Constraints on optimization. The genetic mechanism of sexual reproduction leads to relations between gene and genotype frequencies (e.g. the Hardy-Weinberg equation). This reduces the state space of genotype frequencies to a subset of lower dimension. Frequency dependent fitness parameters preclude optimization through strategic constraints

leads to intricate frequency dependent population genetics, and a stressing of game theoretic aspects to the subtle constructions of extensive games and subgames (see Selten, 1983). In its present state, game dynamics is a compromise between these two directions, trading elaborate sophistication in one or the other direction for broadranged compatibility between both aspects. It aims at acquiring an intuitive insight into biological conflicts, without too many technical details.

It seems very difficult to derive from field data valid estimates for the parameters involved in the payoff matrix. Some remarkable results have been obtained, however [we refer to Maynard Smith (1982) and Riechert and Hammerstein (1983) for surveys]. Moreover, it has been shown in several cases that the dynamics consist of a few types only, which are valid for wide ranges of the parameters. Thus, diverse sexual and asexual models of variations of the 'hawk-dove' conflict lead to a very small number of possible outcomes (see Schuster *et al.*, 1981*a, b*). It seems possible, in such cases, to relate (at least qualitatively) empirical data with some of the few theoretically possible cases.

Finally, we mention that the assumption of genetical determination of behaviour can be relaxed. In particular, the effect of learning can be incorporated into the game theoretical models [for example, see Harley (1981) and the notion of 'developmentally stable strategy' DSS by Dawkins (1980)]. It seems possible, therefore, that the dynamical approach sketched in this paper can be adapted to the modelling of complex behaviour in highly developed social structures (for example, see Wilson, 1975, Masters, 1983).

Acknowledgements

The work has been supported financially by the Austrian 'Fonds zur Förderung der Wissenschaftlichen Forschung' Project P 4506 and P 5286. We would like to thank Prof. John Maynard Smith and Dr Peter Hammerstein for fruitful discussions.

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