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EVOLUTIONARILY STABLE STRATEGIES WITH TWO TYPES OF PLAYER

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Abstract

   A definition of ESS (evolutionarily stable strategy) is suggested for games in which there are two types of player, each with its own set of strategies, and the fitness of any strategy depends upon the strategy mix, of both types, in the population as a whole. We check that the standard ESS results hold for this definition and discuss a mate-desertion model which has appeared in the literature in which the two types are male and female.

ESS; PLAYERS OF TWO TYPES; MATE DESERTION

   A number of papers have recently appeared (Dawkins and Carlisle (1976), Maynard Smith (1977), Grafen and Sibly (1978)), which discuss parental invest-ment models (male versus female) using the concept of an evolutionarily stable strategy or ESS. The game being considered in these models has the following form. There are two types of player, male and female, each with its own set of possible strategies. The fitness of a strategy adopted by either type of player depends upon the strategy mix, of both types, in the population as a whole. However, it does not seem to be made clear just what the appropriate definition of ESS should be, for games of this general nature (more than one type of player).

   In this paper we propose a general definition of ESS for games with more than one type of player. We present versions of the basic ESS results which hold in this more general situation. In particular we observe that our ESSs are dynamically stable (Taylor and Jonker (1978)). Finally we discuss an example of mate desertion of Grafen and Sibly (1978) and find all the ESSs of this model. A model of this type was also considered by Maynard Smith (1977). The above authors restricted themselves to pure state ESSs, but we show that it is possible that one sex might play a mixed strategy at an ESS: some players deserting immediately, and others staying for a suitable common time.

The ESS theory

   Suppose we have a game with two types of player, I and J. Let $i = 1, 2, \cdots, m$ be the possible I-strategies and $j = 1, 2, \cdots, n$ be the possible J-strategies. At

any moment let p_i and q_j be the proportions of I and J individuals playing strategies i and j respectively. Then $p = (p_1, \cdots, p_m)$ and $q = (q_1, \cdots, q_n)$ are probability vectors which together describe the state of the population as a whole.

Now suppose that the fitnesses $F(i)$ and $G(j)$ of strategies i and j both depend upon the state (p, q) of the population. Thus we have fitness functions $F(i \mid p, q)$ and $G(j \mid p, q)$. If the population is in state (p, q) and a sub-population is in state (r, s) we will denote by $F(r \mid p, q)$ and $G(s \mid p, q)$ the average fitness of the I and J players respectively in the subpopulation:

$$F(r \mid p, q) = \sum_i r_i F(i \mid p, q)$$

$$G(s \mid p, q) = \sum_j s_j G(j \mid p, q).$$

For example, I and J may refer to two competing species. The success of a strategy adopted by any member of one species depends not only upon what those of his own species, but also what those of the other species are doing. Or I and J may refer to the male and female members of a single species.

When is a state to be an ESS? Recall that, in qualitative language, a state is called an ESS if whenever a small subpopulation arises in an alternative state, its average fitness in the whole population is strictly less than the average fitness of the original state. For a state (p, q) to be an ESS it must certainly be true that if we hold q constant and think about the resulting game played only by the I-players, then p must be an ESS for this game. And the same the other way round. Thus, for an alternative state $r \neq p$ we want $F(r \mid \bar{p}, q) < F(p \mid \bar{p}, q)$ for sufficiently small $\varepsilon > 0$ where $\bar{p} = (1 - \varepsilon)p + \varepsilon r$ is the perturbed I-state. Also if $s \neq q$, we want $G(s \mid p, \bar{q}) < G(q \mid p, \bar{q})$ for sufficiently small $\varepsilon > 0$ where $\bar{q} = (1 - \varepsilon)q + \varepsilon s$. But these two conditions are not enough to guarantee the stability of (p, q). We must be protected against simultaneous perturbations of p and q. We propose the following definition. A state (p, q) is an ESS if for all states (r, s) for which $r \neq p$ or $s \neq q$ we have

(1) $$F(r \mid \bar{p}, \bar{q}) + G(s \mid \bar{p}, \bar{q}) < F(p \mid \bar{p}, \bar{q}) + G(q \mid \bar{p}, \bar{q})$$

for all sufficiently small $\varepsilon > 0$ where $\bar{p} = (1 - \varepsilon)p + \varepsilon r$ and $\bar{q} = (1 - \varepsilon)q + \varepsilon s$.

Let us see how this definition fits in with some of the standard ESS results. First of all, we will consider linear games, which form an extensively studied special case. A game is called linear if the fitness functions $F(i \mid p, q)$ and $G(j \mid p, q)$ depend linearly on the state variables (p, q). In this case there are matrices A, B, C and D such that $F(r \mid p, q) = r(Ap + Bq)$ and $G(s \mid p, q) = s(Cp + Dq)$ for every p, q, r, s, and it is easy to show that the state (p, q) is an ESS if for every $(r, s) \neq (p, q)$

(2) $r(Ap + Bq) + s(Cp + Dq) \leqq p(Ap + Bq) + q(Cp + Dq)$

and in case equality obtains,

(3) $r(Ar + Bs) + s(Cr + Ds) < p(Ar + Bs) + q(Cr + Ds).$

This may be compared with the standard definition for the linear case as found, for example, in Maynard Smith (1974).

A state (p, q) is called an *equilibrium state* if all I-strategies present have the same fitness as all the J-strategies present. In symbols, $F(i \mid p, q) = F(p \mid p, q)$ and $G(j \mid p, q) = G(q \mid p, q)$ if $p_i > 0$ and $q_j > 0$. It is clear that an ESS is always an equilibrium point.

A result of Haigh (1975) provides a simple matrix criterion to tell when, for a linear game, an equilibrium point is an ESS. The generalization of his result to our situation is the following. Suppose (p, q) is an equilibrium point with $F(i \mid p, q) \leqq F(p \mid p, q)$ and $G(j \mid p, q) \leqq G(q \mid p, q)$ for all i in I and j in J. Let I' and J' be the set of indices for which equality obtains. Then (p, q) is an ESS if and only if

(4)
$$[x \ y] \begin{bmatrix} A & B \\ C & D \end{bmatrix} \begin{bmatrix} x \\ y \end{bmatrix} < 0$$

for all $(x, y) \neq 0$ with $x_i = y_j = 0$ for $i \notin I'$ and $j \notin J'$ and $\Sigma x_i = \Sigma y_j = 0$. For non-linear games the 'if' part of the above result is true if the matrices A, B, C and D are the suitable matrices of partial derivatives. A discussion of the non-linear aspects of this result is found in Taylor and Jonker (1978).

Finally let us look at dynamic stability. Taylor and Jonker (1978) produce a system of non-linear differential equations to describe the evolution of the population state vector. They prove that, under a certain non-degeneracy assumption, an ESS is a strictly stable equilibrium of this dynamical system. For games with two types of player the corresponding system is

(5)
$$\dot{p}_i = p_i(F(i \mid p, q) - F(p \mid p, q))$$
$$\dot{q}_j = q_j(G(j \mid p, q) - G(q \mid p, q)),$$

and the proof of the above result, suitably modified, shows that an ESS (p, q) is strictly stable for (5). Indeed, Condition (4) is just what is needed to make the modified proof go through, and this counts as a major justification of our definition (1).

Let us finally point out that there are two directions in which these ideas readily generalize. One is the situation where there are n types of player for $n > 2$. The other is the situation where there are an infinite number (for example a continuum) of pure strategies for each player to choose from. In this case, rather than work with vectors and sums, we work with distributions and integrals. Indeed the example which follows is of this type.

A mate-desertion model

The following model was constructed by Grafen and Sibly (1978). Under some simple qualitative assumptions, we will find all the ESSs.

There are two types of player, male and female. We assume continuous breeding: when an individual deserts its brood, it finds another mate as soon as it can and breeds immediately. Each player must choose a time after breeding to remain with the brood. Let s denote a typical male time and t a typical female time. These are the pure strategies which we called i and j in the general theory. The state of the population is defined by the distributions μ and ν of the times s and t respectively over the population (of course we restrict attention to breeding individuals). Denote by $T(\mu) = \int s d\mu(s)$ and $T(\nu) = \int t d\nu(t)$ the average times chosen by males and females for any state (μ, ν). Now assuming a 1 : 1 sex ratio, the average cycle time for males and females must be the same. If we suppose $T(\mu) < T(\nu)$, then each male will have to wait, on average, a time $T_0 = T(\nu) - T(\mu)$ between leaving one brood and finding an available female to start the next. For notational convenience we will always suppose $T(\mu) < T(\nu)$: it is the males that must do the waiting. We will not consider the degenerate situation in which $T(\mu) = T(\nu)$.

Now let $f(s, t)$ be the payoff to each parent of a brood if the father plays s and the mother t. Then in a population in state (μ, ν), assuming random mating, the fitnesses of a male playing s and a female playing t are the average payoffs per unit time:

(6)

$$F(s \mid \mu, \nu) = \int f(s, t) d\nu(t)/(s + T_0)$$

$$G(t \mid \mu, \nu) = \int f(s, t) d\mu(s)/t$$

where $T_0 = T(\nu) - T(\mu)$ and is assumed positive. Observe that these functions are not linear in the state variables because T_0 in the denominator depends upon μ and ν.

Let us remark that the basic ESS results for the case of finitely many pure strategies generally have valid continuous analogues which we shall be using here. For example if (μ, ν) is an ESS then it is an equilibrium state: $G(t \mid \mu, \nu) = G(\nu \mid \mu, \nu)$ for all t in supp (ν), where the support of a probability measure is the smallest closed set on which it has mass one.

When is a state (μ, ν) an ESS? The first thing to observe is that if (μ, ν) is an ESS with $T(\mu) < T(\nu)$ then ν must be a pure state (concentrated at a single value of t). Indeed if the population is in state (μ, ν) consider a small perturbing subpopulation in state (μ, t) where t is in supp (ν). (By abuse of notation we identify t with the probability distribution concentrated at t.) Then if $\nu \neq t$, we

have by (1) that $G(t \mid \bar{\mu}, \bar{\nu}) < G(\nu \mid \bar{\mu}, \bar{\nu})$ for small $\varepsilon > 0$ (since, in the notation of (1), $p = r$), where $(\bar{\mu}, \bar{\nu})$ is the perturbed state. But

$$G(t \mid \bar{\mu}, \bar{\nu}) = G(t \mid \mu, \nu) = G(\nu \mid \mu, \nu) = G(\nu \mid \bar{\mu}, \bar{\nu})$$

where the first and third equalities hold since $\mu = \bar{\mu}$ and at or near ν, G is independent of the second state variable, and the middle equality holds since $t \in \mathrm{supp}(\nu)$. This is a contradiction.
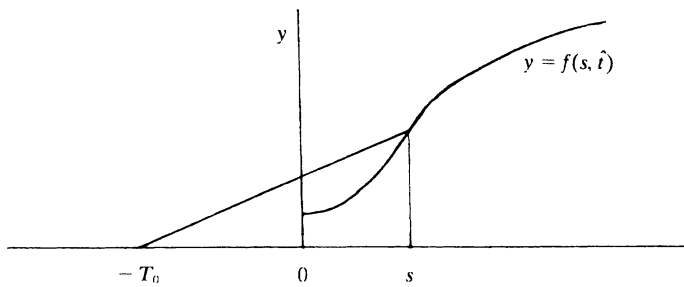

Figure 1.

The payoff for a brood to a male if he stays till time s and the female stays till $\hat{t}$. The payoff $F(s \mid \mu, \hat{t})$ is the slope of the line drawn from $-T_0$.

Thus an ESS must be of the form $(\mu, \hat{t})$ for some $\hat{t}$. To see what are the possibilities for μ, the best thing to do is to look at the graph of $f(s, \hat{t})$, which gives the different possible payoffs for a male bird when all the females are playing $\hat{t}$. Let us assume, as in Figure 1, that the graph is increasing for all s, and is concave up at first and then concave down. This corresponds to the biological situation in which the male's contribution per day is somewhat less immediately after or a long time after breeding, than at an intermediate time when, perhaps, young offspring are being fed and guarded.

The fitness of a male choosing s is

$$F(s \mid \mu, \hat{t}) = f(s, \hat{t})/(T_0 + s)$$

which is given by the slope of the line drawn from the point $-T_0$ on the s-axis to the point on the graph above s (Figure 1). If (μ, t) is to be an ESS it must certainly be true that the $F(s \mid \mu, \hat{t})$ are all equal for s in $\mathrm{supp}(\mu)$ and are at least as big as any $F(s \mid \mu, \hat{t})$ for s not in $\mathrm{supp}(\mu)$. It can be seen that, with the qualitative features of Figure 1, there are the following three possibilities for μ. (i) All males play $s = 0$ (desert immediately after copulation). In this case $T_0 = \hat{t}$. (ii) All males play some common time $\hat{s}$. In this case $T_0 = \hat{t} - \hat{s}$. (iii) A proportion p play $\hat{s}$ and $1 - p$ play 0. In this case $T_0 = \hat{t} - p\hat{s}$. These possibilities are illustrated in Figures 2(i), (ii) and (iii).

(i) all males play $s = 0$

(ii) all males play $s = \hat{s}$

(iii) p males play $s = \hat{s}$
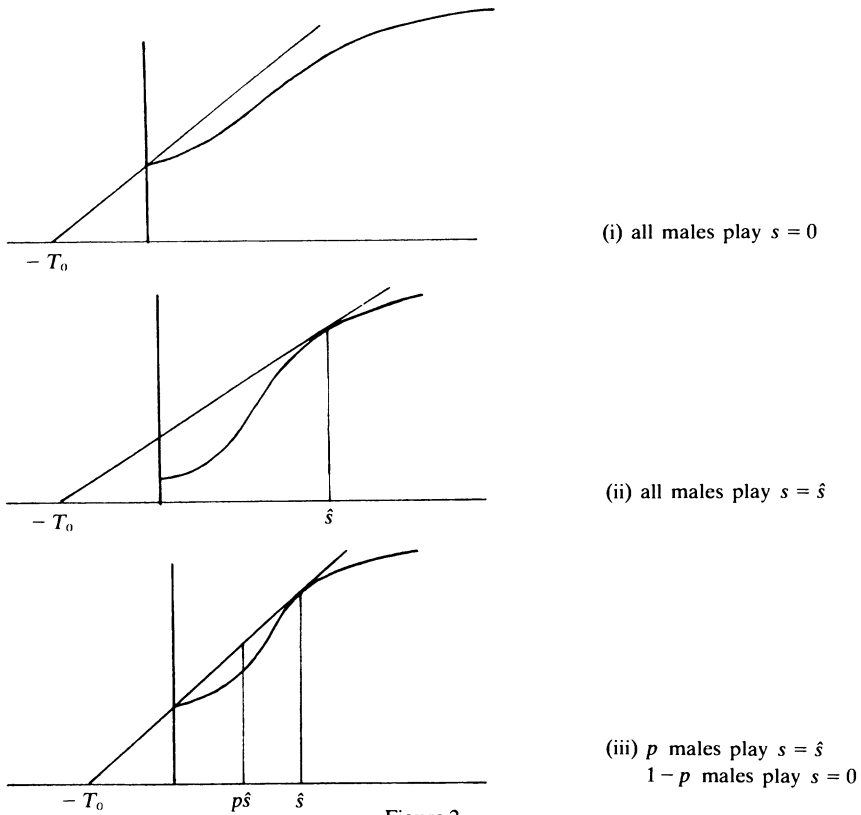 $1 - p$ males play $s = 0$

Figure 2
Possible male ESSS. In each case the curve drawn is $y = f(s, \hat{t})$.

Let us check that each of these cases represents an ESS. We assume that $G(t \mid \mu, \hat{t})$, attains a strict maximum at $t = \hat{t}$. Because of the qualitative assumptions we have made about the form of the curves, it is seen that in each of the three cases $F(s \mid \mu, \hat{t}) < F(\mu \mid \mu, \hat{t})$ for all s not in supp (μ). In Cases(i) and (ii) where μ is a pure state, it follows immediately that $(\mu, \hat{t})$ is an ESS. For Case(iii) in which μ is concentrated at two states, 0 and $\hat{s}$, we must examine the effect of perturbations towards 0 or $\hat{s}$. For example, suppose in Case(iii), a small subpopulation arises playing only $\hat{s}$. Thus the perturbed population has a larger value of p than the original. This causes T_0 to decrease to some smaller $\bar{T}_0$, which causes the slope of all lines to increase. But the line to the point above $p\hat{s}$ is steeper than the line to the point above $\hat{s}$. In symbols,

$$F(s \mid \bar{\mu}, \hat{t}) = \frac{f(\hat{s}, \hat{t})}{\hat{s} + \bar{T}_0} < \frac{pf(\hat{s}, \hat{t}) + (1 - p)f(0, \hat{t})}{p\hat{s} + \bar{T}_0} = F(\mu \mid \bar{\mu}, \hat{t})$$

which, according to (1), is what we need.

Thus, if we assume that it is the males who must wait for the females, then at an ESS, all females play the same time $\hat{t}$, and the males either all desert immediately, or all play some time $\hat{s}$, or some proportion desert immediately and the rest play $\hat{s}$.

Let us say a word about Case(iii). One might think that the configuration of (iii), although mathematically an ESS, and therefore stable within the given game, was in fact *structurally* unstable (under slight changes in the game parameters) and therefore biologically implausible. Such is not, however, the case. If the *payoff function $f(s, t)$* undergoes perturbations, then the effect on the graph (iii) will be to modify the curve slightly causing a small change in T_0 and $\hat{t}$. But the new curve will have the same qualitative features as the old, for a slightly altered $\hat{s}$, and p.

This is a difficult point, but it is important, so let us give an example. If a change in the function $f(s, t)$ had the effect of raising the curve slightly at $\hat{s}$ (in Figure 2(iii)), then this would cause p to increase ($\hat{s}$ has greater success), and would cause a slightly greater net cycle time for males which would decrease average male waiting time T_0, causing the sloping line (which for a moment was above the curve at $s = 0$) to fall back down at $s = 0$ until it is again a secant on $[0, \hat{s}]$ (for a slightly altered $\hat{s}$). Of course p has increased somewhat, but for small perturbations will not have had a chance to increase to 1. Thus we have not shifted to Case(ii), but have a new Case(iii). We conclude that an ESS of this type is structurally stable and therefore biologically plausible.

Discussion

We have provided a notion of ESS which applies to games with more than one type of player. This might provide a useful tool for analysing male–female conflicts or interactions between several species. As an example we consider a mate-desertion game of the kind studied by Maynard Smith (1977) and Grafen and Sibly (1978). We find that there are two types of ESSs, pure state ESSs which are those found by the above authors, and an ESS where one sex always plays the same time, and the other sex divides its players in some proportion between two times, one of which is an immediate desertion strategy.

We shall make two comments.

1. Our example is similar to Maynard Smith's (1977) parental investment model for the case of continuous breeding. This model considers some extra factors such as searching time for a new mate, and recovery time between broods. It is also accompanied by a substantial biological discussion with examples. However it is simpler than our example in two important ways. It works with simpler curves, using only payoff curves with one and two parents (whereas we use the function $f(s, t)$ of two variables) and it restricts its consideration to pure state ESSs (all members of each sex playing the same time).

In order to handle mixed-state ESSs for this model one really needs to use our approach. This approach, as has been pointed out, is due to Grafen and Sibly (1978), although they too restrict attention to pure state ESSs.

We might point out that if attention is restricted to pure state ESSs, then there is an obvious notion of ESS, which the above papers have implicitly used: $(\hat{s}, \hat{t})$ is an ESS if $F(s \mid \hat{s}, \hat{t}) < F(\hat{s} \mid \hat{s}, \hat{t})$ for all $s \neq \hat{s}$ and $G(t \mid \hat{s}, \hat{t}) < G(\hat{t} \mid \hat{s}, \hat{t})$ for all $t \neq \hat{t}$. It is only when one begins to consider mixed-state ESSs that one has to be careful about definitions.

2. There is a possible problem in applying our simple game-theoretic model to male–female conflicts. In the general game set-up, strategies propagate according to their fitness because I-players produce identical I-offspring, and J-players produce identical J-offspring. But in male–female conflicts, every male presumably carries a (possibly unexpressed) female strategy which he may hand to his daughters, and similarly females have male strategies which they may hand to their sons. Thus the state of the population is not determined by the numbers p_i and q_j, but by the numbers p_{ij} of individuals (half male and half female) of type (i, j). If $F(i)$ and $G(j)$ are average fitnesses of a male and female exhibiting strategies i and j respectively then the actual fitness of strategy i will be $(\frac{1}{2})(F(i) + \Sigma p_{ij}G(j))$. Even if $F(i)$ and $G(j)$ depend only on the p_i and q_j (as may be the case with random mating), the above expression will not, unless the p_{ij} do (e.g. I and J are independent: $p_{ij} = p_i q_j$). One can of course try to look for an ESS of the form $(\hat{p}_{ij})$, but this does not fit well into the standard game-theoretic framework because genotypes do not beget identical genotypes. It is the same problem one encounters when trying to build a diploid ESS theory. Perhaps the ESS idea really belongs in a haploid environment, where it is a useful conceptual tool, and if we want to model faithfully the spread of real genes, we should go back to the systems of differential or difference equations which exactly describe our situation.

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