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Patterns of evolutionarily stable strategies: the maximal pattern conjecture revisited

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Abstract. A conflict is defined by a set of pure strategies $\{1, \ldots, n\}$ and a payoff matrix, and may have many evolutionarily stable strategies (ESSs). A collection of subsets of the set of pure strategies is called a pattern. If there is an $n \times n$ matrix which has ESSs whose supports match those of the pattern, then that pattern is said to be attainable. Much of the work on patterns of ESSs relied upon an unproved conjecture. Subject to some relaxation of the definition of attainability, this conjecture is proved.

1. Introduction

1.1. Evolutionarily stable strategies

The mathematical modelling of biological populations using game theoretic methods has proved remarkably successful. Some important texts are [6],[8],[9]. Of particular significance has been the concept of an evolutionarily stable strategy (ESS) which was introduced by Maynard Smith and Price [10]. An ESS is a strategy, which if adopted in a conflict by a population, cannot be invaded by any other strategy played by a small mutant group. The ESS is thus stable and persists through time, provided that all the payoff parameters and the set of available pure strategies remain unchanged.

A standard formulation for modelling a conflict amongst an animal population is as follows:

Consider a population of animals competing for some resource e.g. food or mates. Individuals compete in pairwise games for a reward. Assume that all members of the population are indistinguishable (in that they are of the same size and strength etc.) and each individual is equally likely to face each other individual. There are a finite number of pure strategies available to the players to play in a particular game. These strategies are labelled $1, \ldots, n$. Let $\mathbf{U}$ be the set of pure strategies so that $\mathbf{U} = \{1, \ldots, n\}$. Given the strategies played the outcome is determined; if player 1 plays i against player 2 playing j then player 1 receives reward a_{ij} (player 2

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receives a_{ji}) representing an adjustment in Darwinian fitness. The value a_{ij} can be thought of as an element in the $n \times n$ matrix **A**, the *payoff matrix*.

An animal need not play the same pure strategy every time, it can play a *mixed strategy* i.e. play i with probability p_i for each of $i = 1, \ldots, n$. This means that the strategy played by an animal is represented by a probability vector **p**. The expected payoff to player 1 playing **p** against player 2 playing **q**, which is written as $E[\mathbf{p}, \mathbf{q}]$, is

$$E[\mathbf{p}, \mathbf{q}] = \sum a_{ij} p_i q_j = \mathbf{p}^T \mathbf{A} \mathbf{q}$$

Suppose that **p** is played by almost all members of the population, the rest of the population being a small mutant group constituting a fraction α of the total population playing **q**. **p** is said to be *evolutionarily stable* (ES) against **q** if

$$E[\mathbf{p}, (1-\alpha)\mathbf{p} + \alpha\mathbf{q}] > E[\mathbf{q}, (1-\alpha)\mathbf{p} + \alpha\mathbf{q}]$$

for all sufficiently small α. Thus **p** does better against the mean population strategy than **q** does.

This implies that either

(i) E[**p**,**p**] > E[**q**,**p**]
or
(ii) E[**p**,**p**] = E[**q**,**p**] and E[**p**,**q**] > E[**q**,**q**]

The vector **p** is said to be an evolutionarily stable strategy (ESS) if **p** is ES against all $\mathbf{q} \neq \mathbf{p}$. Thus if all members of a population play **p**, any small invading group playing a different strategy have a lower fitness than the original population members, so that the strategy **p** persists as the dominant strategy through time.

1.2. Patterns of ESSs

1.2.1. Definition Suppose that **p** = (p_i) is an ESS of the payoff matrix **A**. The *support* of **p**, $S(\mathbf{p})$ is the set

$$S(\mathbf{p}) = \{i : p_i > 0\}$$

Thus the support of **p** is the set of pure strategies that are played by a **p**-player.

There may be more than one ESS for a particular payoff matrix (the possible number of ESSs increases exponentially with the number of pure strategies available, see [2], [13]). The ESSs which can occur will have supports which are restricted in various ways. In particular no two ESSs can have the same support (see section 1.4 for a stronger result). To explore these restrictions, the concept of a *pattern of ESSs* (or a *pattern* for short) was introduced by Vickers and Cannings [12].

1.2.2. Definition Any collection of subsets of **U** with no repeated elements is called a *pattern*. A particular pattern is the *pattern of* **A** if it is the same as the collection of supports of the ESSs of **A**.

1.2.3. Definition A pattern is said to be *attainable* on n strategies if there is some $n \times n$ matrix $\mathbf{A}$ which has that pattern.

1.3. Haigh's Theorem

It was shown by Haigh [7] that the conditions for $\mathbf{p}$ to be an ESS are equivalent to the following;
There is a constant λ and a set $R(\mathbf{p})$, $S(\mathbf{p}) \subseteq R(\mathbf{p}) \subseteq \mathbf{U}$, such that

(i) $(\mathbf{Ap})_i = \lambda \quad \forall i \in R(\mathbf{p})$.
(ii) $(\mathbf{Ap})_i < \lambda \quad \forall i \notin R(\mathbf{p})$.
Supposing, without loss of generality, that $R(\mathbf{p}) = (1, 2, \ldots, k)$. We define the matrix $\mathbf{C}$=$(c_{ij})_{i,j=1,\ldots,k-1}$ by

$$c_{ij} = a_{ij} + a_{ji} - a_{ik} - a_{ki} - a_{kj} - a_{jk} + 2a_{kk}$$

(iii) Then $\mathbf{C}$ is negative definite.

An ESS is said to be *regular* if $R(\mathbf{p}) = S(\mathbf{p})$ [11].

The usefulness of this result lies in the fact that to investigate whether $\mathbf{p}$ is an ESS it is sufficient to check whether it satisfies the above conditions, as opposed to considering its performance against all possible alternative strategies $\mathbf{q}$.

Note that adding a constant term to all the entries in a column of the payoff matrix leaves all ESSs unaltered, so that the set of ESSs of $\mathbf{B} = (b_{ij})$, where $b_{ij} = a_{ij} + c_j \quad \forall i, j$ is the same as that of $\mathbf{A}$. In particular, setting $c_j = -a_{jj} \forall j$, the set of ESSs of a matrix is the same as that of its *reduced matrix*, the matrix formed by adding a constant to each column to make the leading diagonal terms b_{jj} equal to zero. This result is due to Zeeman [14]. Henceforth it is assumed that all matrices are of the reduced form.

1.4. The Bishop Cannings Theorem

If $\mathbf{p}$ is an ESS with support I and $\mathbf{r} \neq \mathbf{p}$ is an ESS with support J, then $I \not\supseteq J$. This result is a simplified version of a more general theorem proved by Bishop and Cannings [1].

The Bishop Cannings Theorem is of great importance when considering which patterns are attainable, since it eliminates from consideration any pattern which contains two supports, one of which is a subset of the other. The discussion of which ESSs can coexist and thus which patterns are attainable is the subject of a series of papers by Cannings and Vickers and various collaborators (see, for example, [3],[4],[5],[12]).

The biological relevance of this concept relates to the behaviour of animals in a population divided into separate habitats, which have no contact with one another, for example the mating strategies of frogs in separate pools. These isolated habitats will henceforth be described as *niches*. For a particular conflict, defined by the set of pure strategies and the payoff matrix, the population may develop different ESSs in the separate niches (due to different initial conditions or random effects).

It is thus of interest to know what range of different strategies is possible. Similarly observation of different strategies in the separate niches may imply different payoff matrices, due to the incompatibility of the supports of these strategies.

For example suppose that there are two possible pure strategies 1 and 2, and in one niche the population plays a mixed strategy containing both of these. If the environmental conditions are the same in another niche, the population there cannot play either pure strategy, but must play (the same) mixed strategy, due to the Bishop Cannings Theorem. If another niche is observed where the individuals do play a pure strategy, then, according to our model, the environmental conditions there must be different.

It is also of interest to know how many different ESSs may exist for a given number of pure strategies, and how large the supports of these ESSs may be.

2. The maximal pattern conjecture

2.1. Introduction

2.1.1. Definition An attainable pattern P is described as $maximal$ if there is no $P^* \supset P$, which is attainable.

An important idea of Cannings and Vickers [4] was the conjecture that if P is an attainable pattern and $P^* \subset P$ then P^* is also attainable. No proof of this conjecture has been found, but neither have any counter-examples. This conjecture is a key element of the theory of Patterns of ESSs, and if it were not true then the task of identifying attainable patterns would become much more difficult. Under the assumption of the truth of the conjecture the complete set of attainable patterns can be specified by the complete set of maximal patterns only. This is a significant saving in work, especially when the number of strategies is large.

In Theorem 1 a weaker result is proved, which nevertheless is a useful contribution to the general theory. A revision of the theory is proposed which enables Theorem 1 to prove the maximal pattern conjecture.

Theorem 1. *If P is an attainable pattern for n pure strategies and $P^* \subset P$ then P^* is attainable for $n + k$ strategies for all $k \geq K$ for some positive integer K.*

Proof. Suppose that the pattern $(S_1, \ldots, S_m, \ldots, S_{m+t})$ is attainable on strategies $1, \ldots, n$. Further suppose that $\mathbf{A} = (a_{ij})$ is a matrix with this pattern.

Let $x = 1 + max_{ij}(a_{ij})$, and let M be large compared to x.

Now consider the matrix $\mathbf{B} = (b_{ij})$ on strategies $1, \ldots, n + t$. Define

$$
\begin{aligned}
& b_{ij} = a_{ij} \quad i \leq n, \quad j \leq n \\
& b_{(n+i)j} = x \quad j \in S_{m+i}, \quad 1 \leq i \leq t \\
& b_{(n+i)j} = -M \quad j \notin S_{m+i}, \quad j \leq n, \quad 1 \leq i \leq t \\
& b_{j(n+i)} = -M \quad j \leq n, \quad 1 \leq i \leq t \\
& b_{jj} = 0 \quad j > n \\
& b_{(j+1)j} = 1 \quad n < j < n + t \\
& b_{(n+1)(n+t)} = 1 \\
& b_{ij} = -M \quad \text{for all other } j > n, i > n
\end{aligned}
$$

It is clear that $b_{ij} + b_{ji} < 0$ for $j > n$. For i and j to be in the same ESS support of **B** requires $b_{ij} + b_{ji} > 0$ and so none of the strategies $n + 1, \ldots, n + t$ can be involved in ESSs other than as pure ESSs. However, for $j > n$

$$b_{(j+1)j} = 1 > b_{jj} \quad (b_{(n+1)(n+t)} = 1 > b_{(n+t)(n+t)})$$

so that none of $n + 1, \ldots, n + t$ can be pure ESSs either.

Consider the ESS with support S_{m+i}. For the elements of this support the $n+i$th row dominates every row corresponding to a strategy of the support, i.e. condition (ii) of Haigh's Theorem is violated and the ESS with support S_{m+i} is invaded by strategy $n + i$ for all $1 \leq i \leq t$.

Now consider $S_l, \quad l \leq m$. S_l is not a subset of any other support (by the Bishop Cannings Theorem), so for each row $n + i$ at least one of $b_{n+ij} = -M, \quad j \in S_l$ and so none of these rows can invade the ESS of S_l.

Suppose that a strategy's support is a subset of the set of pure strategies of a particular conflict, but that the strategy is not an ESS of the conflict. If extra pure strategies are added to the set of strategies, the strategy is not an ESS of the new conflict either. Thus in our conflict no other ESSs can be introduced, so that the pattern of **B** is $S_1, \ldots, S_m$.

In the original pattern the supports could have been ordered in any way, and m and t are arbitrary, so that any subpattern of the pattern is attainable on some larger set of strategies. This completes the proof. □

Corollary 1. *If $(S_1, \ldots, S_m)$ is a pattern which is attainable on $\{1, \ldots, n\}$ then for some positive integer K, $(S_1, \ldots, S_m)$ and all its subpatterns are attainable on $\{1, \ldots, n + k\}$ for $k \geq K$.*

Corollary 2. *There is a K such that every subpattern of any maximal pattern for n strategies is attainable on $n + k$ strategies $\forall\, k \geq K$.*

Proof. The number of ESSs for n strategies cannot exceed 2^n, since no two ESSs can have the same support and the total number of supports is 2^n. In the proof of Theorem 1 it was shown that an extra strategy was sufficient to invade every ESS whose support was contained in the maximal pattern but not in the subpattern. Hence less than 2^n new strategies are required to ensure than the subpattern is attainable. Thus there is a $K \leq 2^n$ for which all subpatterns of attainable patterns for n strategies are attainable on $n + k$ strategies, $\forall\, k \geq K$. □

The study of Patterns of ESSs aims to show which patterns are/are not attainable, the biological implications of which are briefly discussed in Section 1.4. Restrictions upon which strategies can be ESSs of the same payoff matrix in turn impose restrictions upon the possible behaviour of different populations in isolated niches under the same environmental conditions.

Thus;

(i) If we have information about the behaviour of animals in one or more niches, and given that they have the same set of pure strategies and payoff matrix, the possible strategies of new niches can be found conditional upon the strategies in the old ones.

(ii) if the strategies of populations in several niches are found, it can be deduced whether their behaviour is consistent with all having the same pure strategies and payoff matrix.

Cannings and Vickers have proceeded under the assumption that the maximal pattern conjecture is true, namely that all the subpatterns of maximal patterns are attainable. Theorem 1 provides extra evidence that this conjecture is likely to be true. It also has a deeper significance. The consequences of the conjecture being false are that some patterns which are unattainable are assumed attainable. Theorem 1, however, shows that any such pattern is indeed attainable, if only upon a larger set of pure strategies. Corollary 2 shows that for any number of strategies n, there is a k such that if an extra k strategies are introduced, then all subpatterns of all maximal patterns on n strategies are attainable upon $n + k$ strategies. In any natural situation the observed strategies may be catalogued, but there may well be many other strategies (existing at a very low level or having the potential to occur). The strategies used in the proof of Theorem 1 had payoffs which enabled them to invade other strategies, but were never able to be part of an ESS themselves. Therefore these strategies would never exist above a low level in a real population for an extended period of time and would thus be unlikely to be observed, although mutation might introduce such strategies from time to time.

It may thus be sensible to consider possible invasion from unknown strategies as a factor in finding which patterns are attainable. This would involve not specifying the number of strategies n upon which a pattern is attainable as in Definition 1.2.3, although obviously this must be at least as great as the total number of strategies which appear in the supports. Thus Definition 1.2.3 would become

2.1.2. Definition A pattern is said to be *attainable* if there is some matrix $\mathbf{A}$ which has that pattern.

Thus if a pattern is said to be attainable on five strategies, it is meant that it has a total of five or less distinct strategies in its supports.

It is known that every attainable pattern is also attainable upon any larger set of strategies. Thus the only consequence of introducing these ‘phantom’ strategies is to ensure the attainability of all subpatterns of attainable patterns. In particular no new maximal pattern on n strategies can be introduced. Thus, in effect, Theorem 1 would give us the maximal pattern conjecture. Note that if the maximal pattern conjecture in its original form turns out to be true, the two specifications are identical.

3. Discussion

The maximal pattern conjecture [4] is an important unproven result for the study of patterns of ESSs, which has generally been assumed to be true. Much previous work has made use of the conjecture, and the whole problem becomes considerably more difficult if it is not assumed. Theorem 1 provides a proof of a weaker result which is important for two reasons. Firstly the attainability of all subpatterns of any given pattern upon a larger strategy set increases the evidence in support of the maximal pattern conjecture being true. Secondly, if the problem of finding all the patterns which are attainable on n strategies for a given n, which is the original problem as stated by Cannings and Vickers [12] is amended to considering such patterns with the addition of extra 'potential' invading strategies (which might occur due to mutation), then the maximal pattern conjecture is proved by Theorem 1, and thus all previous work on patterns of ESSs which has assumed the conjecture is validated.

If, as seems likely, the maximal pattern conjecture is true, then the revised theory in effect reduces to the original theory and so nothing has been lost. If, however, the conjecture is false, then the revision saves much work which would otherwise have been either incomplete or, in part, false.

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