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C. R. Biologies 328 (2005) 403-412

http://france.elsevier.com/direct/CRASS3/

# Biological modelling / Biomodélisation

# Evolutionary games with variable payoffs

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Received 26 October 2004; accepted after revision 14 December 2004

Available online 5 February 2005

Presented by Pierre Auger

#### Abstract

Matrix games, defined by a set of strategies and a corresponding matrix of payoffs, are commonly used to model animal populations because they are both simple and generate meaningful results. It is generally assumed that payoffs are independent of time. However, the timing of contests in real populations may have a marked effect on the value of rewards. We consider matrix games where the payoffs are functions of time. Rules are found which hold in this more general situation, and the complexity of possible behaviour is underlined by demonstrating other conditions which do not hold and an illustrative game. *To cite this article: M. Broom, C. R. Biologies 328 (2005).* 

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#### Résumé

Jeux évoliutionnels avec gains et coûts variables. Les jeux matriciels prennent en compte un ensemble de stratégies avec une matrice de gain et de coûts. Ces jeux sont fréquemment utilisés pour modéliser les populations animales parce qu'ils sont simples et génèrent des résultats dont l'interprétation est aisée. Dans ces modèles, il est habituellement supposé que les gains et les coûts sont indépendants du temps. Cependant, la durée des rencontres entre individus dans les populations réelles peut avoir un effet important sur la valeur des gains. Nous considérons des jeux matriciels pour lesquels les gains et les coûts sont fonctions du temps. Nous obtenons des règles valables dans ce cas plus général. La compléxité du comportement est souligné en recherchant d'autres conditions dans le cas non autonome et en présentant un exemple de jeu illustratif de la méthode. *Pour citer cet article : M. Broom, C. R. Biologies 328 (2005)*.

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Keywords: Evolutionarily stable strategy; Replicator dynamic; Environmental change; Bimatrix games; Darwinian fitness

Mots-clés: Stratégie évolutivement stable; Dynamique du réplicateur; Changement environnemental; Jeux à deux matrices; Avantage sélectif darwinien

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#### 1. Introduction

We start by explaining some of the basic concepts of evolutionary game theory, introduced in the classic paper [1] (see also [2]), which will be of use in the rest of the paper. In particular we discuss matrix games between symmetric players and their equivalent between asymmetric players, bimatrix games. We also use the concept of the replicator dynamic to consider the evolution of strategies as a function of time.

### 1.1. Matrix games

The following idea is useful for modelling a population of animals which compete in pairwise conflicts for some resource, which could be food or mates, for example. It is assumed that all members of the population are indistinguishable 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. Let **U** be the set of pure strategies so that  $\mathbf{U} = \{1, \dots, n\}$ . 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 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, ..., n. Thus the strategy played by an animal is represented by a probability vector  $\mathbf{p}$ . The expected payoff to player 1 playing  $\mathbf{p}$  against player 2 playing  $\mathbf{q}$ , which is written as  $E[\mathbf{p}, \mathbf{q}]$ , is

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

A strategy **p** is a *Nash equilibrium* if  $\mathbf{q}^T \mathbf{A} \mathbf{p} \leq \mathbf{p}^T \mathbf{A} \mathbf{p}$  for all alternative strategies **q** (so a strategy is a Nash equilibrium if it is a best reply to itself).

The *support* of **p** is defined as  $S(\mathbf{p}) = \{i: p_i > 0\}.$ 

**p** is an *internal strategy* if  $S(\mathbf{p}) = U$ .

**p** is thus a Nash equilibrium if  $(Ap)_i = \lambda$ ,  $i \in S(\mathbf{p})$ ,  $(Ap)_i \leq \lambda$ ,  $i \notin S(\mathbf{p})$  for some constant  $\lambda$  and is thus an internal Nash equilibrium if  $S(\mathbf{p}) = U$  and  $(Ap)_i = \lambda$   $\forall i$ .

A strategy  $\mathbf{p}$  is an Evolutionarily Stable Strategy (ESS) if

(i) 
$$\mathbf{q}^{T} \mathbf{A} \mathbf{p} \leq \mathbf{p}^{T} \mathbf{A} \mathbf{p}$$
 and  
(ii) if  $\mathbf{q}^{T} \mathbf{A} \mathbf{p} = \mathbf{p}^{T} \mathbf{A} \mathbf{p}$  then  $\mathbf{q}^{T} \mathbf{A} \mathbf{q} < \mathbf{p}^{T} \mathbf{A} \mathbf{q}$ 

for all alternative strategies q.

A matrix may possess a unique ESS, no ESSs or many ESSs. See [3,4] for a discussion of the possible complexity of the ESS structure of a matrix.

#### 1.2. Bimatrix games

The assumptions underlying the bimatrix game model are the same as for the matrix game model, except that pairwise contests are fought between individuals in asymmetric positions, so that the individual designated player 1 has a different set of pure strategies  $\mathbf{U}_1$  to the set available to player 2 ( $\mathbf{U}_2$ ). If player 1 plays its strategy i against player 2 playing its strategy j, then player 1 receives reward  $a_{ij}$  and player 2 receives reward  $b_{ji}$ . The payoffs combine to form the payoff matrices A and B. In the same way individuals can play mixed strategies, so that if player 1 plays  $\mathbf{p}$  and player 2 plays  $\mathbf{q}$ , the rewards to the players are  $\mathbf{p}^T A \mathbf{q}$  and  $\mathbf{q}^T B \mathbf{p}$ , respectively.

The two strategy pair  $\mathbf{p}_1$ ,  $\mathbf{p}_2$  is a Nash equilibrium pair, if

$$\mathbf{p}_1^{\mathrm{T}} A \mathbf{p}_2 \geqslant \mathbf{q}_1^{\mathrm{T}} A \mathbf{p}_2$$
 and  $\mathbf{p}_2^{\mathrm{T}} B \mathbf{p}_1 \geqslant \mathbf{q}_2^{\mathrm{T}} B \mathbf{p}_1$ 

for any alternative strategies  $\mathbf{q}_1$ ,  $\mathbf{q}_2$ .

The strategy pair  $\mathbf{p}_1$ ,  $\mathbf{p}_2$  is an ESS if it is a Nash equilibrium pair,

and whenever 
$$\mathbf{p}_1^T A \mathbf{p}_2 = \mathbf{q}_1^T A \mathbf{p}_2$$
  
then  $\mathbf{p}_1^T A \mathbf{q}_2 > \mathbf{q}_1^T A \mathbf{q}_2$   
and whenever  $\mathbf{p}_2^T B \mathbf{p}_1 = \mathbf{q}_2^T B \mathbf{p}_1$   
then  $\mathbf{p}_2^T B \mathbf{q}_1 > \mathbf{q}_2^T B \mathbf{q}_1$ 

which is only possible if both these strategies are pure [5].

#### 1.3. Replicator dynamics

Let us assume that individuals can only play pure strategies, and let the proportion of players of pure strategy i at a particular time be  $p_i$  (i = 1, ..., n), so that the average population strategy (the *population state*) is the vector  $\mathbf{p} = (p_i)$ , with the expected payoff (in terms of Darwinian fitness) of an i-player in such

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