## ON THE CALCULATION OF EVOLU-TIONARILY STABLE STRATEGIES

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**Abstract:** A simple procedure is developed in order to calculate all evolutionarily stable strategies not involving at most three pure strategies. By means of this procedure especially all evolutionarily stable strategies of an at most four-dimensional payoff matrix can be determined.

Applying game-theoretical methods to problems in population dynamics, Maynard Smith and Price ([15]) introduced the notion of an evolutionarily stable strategy (ESS). Such a strategy is in some sense robust against new strategies invading the population. For literature concerning theoretical investigations on ESS's cf. e.g. [1]–[14] and [16]. The aim of this paper is to give a simple necessary condition for ESS's and to show how one can determine for a given payoff matrix all ESS's with "large" support.

In the following let n denote a positive integer and let  $I = \{i_1, \ldots, i_s\} \subseteq N := \{1, \ldots, n\}$  with  $i_1 < \ldots < i_s (0 \le s \le n)$ . If not stated otherwise, all indices run from 1 to n. Let  $A = (a_{ij})$  and  $B = (b_{ij})$  be real matrices with  $b_{ii} = 1$  and  $b_{ij} = b_{ji}$  for all i, j. Further let  $a, b, c \in \mathbb{R}$  and put

$$C:=egin{pmatrix} 1 & a \ a+1 \end{pmatrix} \quad ext{and} \quad D:=egin{pmatrix} 1 & a & b \ a & 1 & c \ b & c & 1 \end{pmatrix}.$$

A fundamental problem in evolutionary biology is the determination of E(A) for a given payoff matrix A. The following lemma says that for the sake of determining N(A) or E(A) we can restrict ourselves to matrices having 0 in their main diagonal:

**Lemma 1** (cf. [3]). 
$$N(A) = N((a_{ij} - a_{jj}))$$
 and  $E(A) = E((a_{ij} - a_{jj}))$ . **Proof.**  $\sum_{i,j} (x_i - y_i)(a_{ij} - a_{jj})z_j = (x - y)^T Az$  for all  $x, y, z \in S$ .  $\Diamond$ 

A further simplification of the problem of determining E(A) is provided by the following lemma:

Lemma 2 (cf. [2] and [13]). The supports of two different ESS's of A are incomparable.

**Proof.** Assume there exist two distinct ESS's p,q of A with supp  $p \subseteq \subseteq \sup q$ . From  $qAq^T = \sum q_i(e_iAq^T) \le \sum q_i(qAq^T) = qAq^T$  it follows that  $e_iAq^T = qAq^T$  for all  $i \in \sup q$ . Since  $\sup p \subseteq \sup q$ , we would have  $pAq^T = \sum p_i(e_iAq^T) = \sum p_i(qAq^T) = qAq^T$  and hence, because of  $q \in E(A)$ , also  $qAp^T > pAp^T$ . But this contradicts  $p \in E(A)$ .  $\Diamond$ 

Next we want to characterize the Nash equilibria of A:

**Theorem 3** (cf. [13]). Let  $p \in S(I)$ , assume  $k \in I$  and put  $p_0 := -e_k A p^T$ . Then t. f. a. e.:

- (i)  $p \in N(A)$ .
- (ii) (a) and (b) hold:
  - (a)  $(p_0, p_{i_1}, \ldots, p_{i_s})$  is a solution of

$$\begin{pmatrix} 0 & 1 & \dots & 1 \\ 1 & a_{i_1 i_1} & \dots & a_{i_1 i_s} \\ \vdots & \vdots & & \vdots \\ 1 & a_{i_s i_1} & \dots & a_{i_s i_s} \end{pmatrix} \begin{pmatrix} x_0 \\ x_{i_1} \\ \vdots \\ x_{i_s} \end{pmatrix} = \begin{pmatrix} 1 \\ 0 \\ \vdots \\ 0 \end{pmatrix};$$

(b)  $(p_0, \ldots, p_n)$  is a solution of

$$\begin{pmatrix} 1 & a_{11} & \dots & a_{1n} \\ \vdots & \vdots & & \vdots \\ 1 & a_{n1} & \dots & a_{nn} \end{pmatrix} \begin{pmatrix} x_0 \\ \vdots \\ x_n \end{pmatrix} \leq \begin{pmatrix} 0 \\ \vdots \\ 0 \end{pmatrix}.$$

**Proof.** (i)  $\Rightarrow$  (ii):

 $pAp^T = \sum p_i(e_iAp^T) \leq \sum p_i(pAp^T) = pAp^T$  shows that  $e_iAp^T = pAp^T = e_kAp^T = -p_0$  for all  $i \in I$  and that  $e_iAp^T \leq pAp^T = e_kAp^T = -p_0$  for all i.

 $(ii) \Rightarrow (i)$ :

$$xAp^T = \sum x_i(e_iAp^T) \le \sum x_i(-p_0) = \sum p_i(-p_0) = \sum p_i(e_iAp^T) = pAp^T \text{ for all } x \in S.$$

Now we are going to show a way of calculating all ESS's of A: **Theorem 4** (cf. [1] and [4]). Let  $p \in S(I)$ , assume  $k \in I$  and put  $p_0 := -e_k A p^T$ . Then t. f. a. e.:

- (i)  $p \in E(A)$ .
- (ii) (a) (c) hold:
  - (a)  $(p_0, p_{i_1}, \ldots, p_{i_s})$  is the unique solution of (1) over  $\mathbb{R}$ ;
  - (b)  $(p_0, \ldots, p_n)$  satisfies (2);
  - (c) if |J| > 1 then  $(a_{ik} + a_{kj} a_{ij} a_{kk})_{i,j \in J \setminus \{k\}}$  is strictly  $(J \setminus I)$ copositive, where  $J := \{i | (e_k e_i)Ap^T = 0\}$ .

**Proof.** Assume  $p \in E(A)$ . Then, by Th. 3,  $(p_0, p_{i_1}, \ldots, p_{i_s})$  is a solution of (1) over  $\mathbb{R}$ . Suppose, there exists another solution of (1) over  $\mathbb{R}$ . Then there would exist such a solution  $(q_0, q_{i_1}, \ldots, q_{i_s})$  with  $q_i > 0$  for all  $i \in I$ . But then  $q \in \mathbb{R}^n$  defined by  $q_i := 0$  for all  $i \notin I$  would be an element of  $S \setminus \{p\}$  with  $qAp^T = -p_0 = pAp^T$  and  $pAq^T = -q_0 = qAq^T$  contradicting  $p \in E(A)$ . Hence (1) is uniquely solvable over  $\mathbb{R}$ . The rest of the proof follows from Th. 3 and [12].

**Remark.** Let F denote the matrix in (1) and assume  $k \in I$ . Then |F| can be expanded in the following way: Subtract the row corresponding to k from the rows corresponding to the elements of  $I \setminus \{k\}$ , expand the resulting determinant along the first column, subtract the column

corresponding to k from the columns corresponding to the elements of  $I \setminus \{k\}$  and expand the resulting determinant along the first row. This shows  $|F| = (-1)^{|I|} |(a_{ik} + a_{kj} - a_{ij} - a_{kk})_{i,j \in I \setminus \{k\}}|$ , the latter determinant being positive in case there exists some  $p \in E(A)$  with support I, according to [12]. Hence  $(-1)^{|I|}|F| > 0$  in this case and therefore, using Cramer's rule, (a) and (b) can be translated in this case into equations and inequalities involving certain determinants.

The next problem is to decide whether a given quadratic matrix is I-copositive. First we remark that for the sake of investigating strict I-copositiveness of a quadratic matrix we can restrict ourselves to symmetric matrices having 1 in their main diagonal:

**Lemma 5** (cf. [11]). T. f. a. e.:

- (i) A is strictly I-copositive.
- (ii) (a) and (b) hold:

  - (a)  $a_{ii} > 0$  for all i; (b)  $(\frac{a_{ij} + a_{ji}}{2\sqrt{a_{ii}a_{jj}}})$  is strictly I-copositive.

**Proof.** We have  $a_{ii} = e_i A e_i^T$  for all i, and in case  $a_{ii} > 0$  for all i we have  $\sum_{i,j} \frac{a_{ij} + a_{ji}}{2\sqrt{a_{ii}a_{jj}}} (x_i \sqrt{a_{ii}}) (x_j \sqrt{a_{jj}}) = xAx^T$  for all  $x \in \mathbb{R}^n$ .

The following lemma shows how one can reduce strict I-copositiveness of an n-dimensional matrix in case  $n > \max(1, |I|)$  to strict Icopositiveness of a matrix of dimension n-1:

**Lemma 6.** Assume n > 1 and  $k \notin I$ . Then t. f. a. e.:

- (i) B is strictly I-copositive.
- (ii)  $(b_{ij} b_{ik}b_{jk})_{i,j\neq k}$  is strictly I-copositive.

**Proof.** 
$$xBx^T = (x_k + \sum_{i \neq k} b_{ik} x_i)^2 + \sum_{i,j \neq k} (b_{ij} - b_{ik} b_{jk}) x_i x_j$$
 for all  $x \in \mathbb{R}^n$ .

By Lemma 6, strict *I*-copositiveness of an *n*-dimensional matrix can be reduced to strict I-copositiveness of a matrix of dimension  $\max(1,|I|)$ . Hence, in order to settle the case  $|I| \leq 3$  completely, one has to characterize strict copositivity of matrices of dimension two and three. This is done by the following theorem:

Theorem 7 (cf. [11]).

- (i) C is strictly copositive iff a > -1.
- (ii) D is strictly copositive iff a,b,c > -1 and (a+b+c > -1) or |D| > 0 (or both)).

**Proof.** (i) follows from  $xCx^T = (x_1 - x_2)^2 + 2(a+1)x_1x_2$  for all  $x \in \mathbb{R}^2$ and (ii) was proved in [11].

Concluding remark. By the described method, for a given n-dimensional payoff matrix all ESS's with a support of cardinality  $\geq n-3$  can be determined. Especially, all ESS's of an at most four-dimensional payoff matrix can be calculated in this way.

## References

- [1] ABAKUKS, A.: Conditions for evolutionarily stable strategies, J. Appl. Prob. 17 (1980), 559-562.
- [2] BISHOP, D. T. and CANNINGS, C.: Models of animal conflict, Adv. Appl. Prob. 8 (1976), 616-621.
- [3] BISHOP, D. T. and CANNINGS, C.: A generalized war of attrition, J. Theor. Biol. 70 (1978), 85-124.
- [4] BOMZE, I. M.: On supercopositive matrices and their application to evolutionarily stable strategies, Techn. Report 29, Inst. for Statistics and Informatics, Univ. of Vienna, 1985.
- [5] BOMZE, I. M. and PÖTSCHER, B. M.: Game theoretical foundations of evolutionary stability, Springer Lect. Notes Economics Math. Syst. 324, Berlin, 1989.
- [6] CANNINGS, C. and VICKERS, G. T.: Patterns of ESS's II, J. Theor. Biol. 132 (1988), 409-420.
- [7] CANNINGS, C. and VICKERS, G. T.: Patterns and invasions of evolutionarily stable strategies, Appl. Math. Comput. 32 (1989), 227-253.
- [8] HAIGH, J.: Game theory and evolution, Adv. Appl. Prob. 7 (1975), 8-11.
- [9] HOFBAUER, J. and SIGMUND, K.: The theory of evolution and dynamical systems, Cambridge Univ. Press, Cambridge, 1988.
- [10] LÄNGER, H.: When are pure strategies evolutionarily stable? ZAMM 69 (1989), T63-T64.
- [11] LÄNGER, H.: Strictly copositive matrices and ESS's, Arch. Math. 55 (1990), 516-520.
- [12] LÄNGER, H.: A characterization of evolutionarily stable strategies, Math. Pann. 4/2 (1993), 225-233.
- [13] MAYNARD SMITH, J.: The theory of games and the evolution of animal conflicts, J. Theor. Biol. 47 (1974), 209-221.
- [14] MAYNARD SMITH, J.: Evolution and the theory of games, Cambridge Univ. Press, Cambridge, 1982.
- [15] MAYNARD SMITH, J. and PRICE, G. R.: The logic of animal conflict, *Nature* 246 (1973), 15-18.
- [16] VICKERS, G. T. and CANNINGS, C.: Patterns of ESS's I, J. Theor. Biol. 132 (1988), 387-408.