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in Asymmetric Animal Conflicts

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A Note on Evolutionarily Stable Strategies in Asymmetric
Animal Conflicts

by

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In a seminal paper by J. Maynard Smith and G.R. Price the notion of an evolutionarily stable strategy has been introduced as a game theoretical tool for the analysis of animal conflicts. (Maynard Smith - Price 1973). The concept of an evolutionarily stable strategy is closely connected to that of a symmetric equilibrium point (Nash 1951). The important game theoretical innovation consists in an additional stability requirement concerning deviation strategies which are alternative best replies to the evolutionarily stable strategy. It is necessary to impose this condition in order to exclude the proliferation of such mutants.

Asymmetric animal conflicts are situations where the opponents assume different roles like "owner" and "intruder" in a territorial contest (Maynard Smith - Parker 1976). The roles may be defined by a combination of several variables like ownership and size. Information may be incomplete in the sense that the opponent's role is not perceived with perfect accuracy.¹⁾

It is assumed that the two opponents in a contest never find themselves in the same information situation. This assumption will be referred to as information asymmetry. A sufficient condition for information asymmetry is satisfied if the two opponents in a contest always have roles which are different from each other.

It is the purpose of this paper to show that for the models of asymmetric animal conflicts considered here, evolutionarily stable strategies must be pure strategies. It is worth pointing out that this result crucially depends on the information asymmetry assumption.

The intuitive reason for the instability of properly mixed strategies which belong to symmetric equilibrium points can be seen in the fact that it is always possible to find an alternative best reply which deviates in just one information situation. Consider a mutant who plays an alternative best reply of this kind. The success of his strategy will be the same as that of

1) I am grateful to Peter Hammerstein from the biology department of the university of Bielefeld whose work on models of this kind made me aware of the question answered in this note.

the equilibrium strategy where both coincide. In view of information asymmetry there will be no difference with respect to that information situation where he deviates either, since there he always meets opponents whose behavior coincides with that prescribed by the equilibrium strategy whether they are mutants or not. Therefore, nothing prevents the mutant's proliferation by genetic drift.

1. Population games

Originally, the concept of an evolutionarily stable strategy has been defined for games in normal form. The normal form has the disadvantage that in games with choices in more than one situation spurious distinctions are made between mixed strategies which are indistinguishable with respect to observable behavior.²⁾ This is clear in view of Kuhn's theorem which is applicable to the models considered here, since they can be looked upon as extensive games with perfect recall (Kuhn 1953), (Selten 1975).

In order to avoid the disadvantages of the normal form, a different game form will be introduced under the name of "population game". The population game is similar to the agent normal form discussed elsewhere (Selten 1975). Some explanations of auxiliary concepts will precede the definition of a population game.

Information situations: The definition of a population game explicitly reflects the idea that choices may have to be made in more than one situation. The situations differ with respect to the information of the chooser. Therefore we speak of information situations. (Information situations correspond to information sets in the extensive form).

2) An unpublished paper "On Evolutionary Stable Strategies in Populations with Subpopulations Having Isolated Strategy Repertoires" by Heinz-Joachim Pohley and Bernhard Thomas at Köln University takes a normal form approach which avoids these disadvantages. They prove non-existence of completely mixed evolutionary stable strategies for a related but narrower class of models. Their analysis is based on Haigh's criterion (Haigh 1975). The methods used here are different and yield stronger and more general results.

The set of all information situations in a population game is denoted by U . The set U is assumed to be finite and non-empty.

Choices: At every information situation u the chooser has a finite non-empty set C_u of available choices. The function C which assigns to every $u \in U$ its choice set C_u is called choice set function.

Local strategies: A local strategy p_u for information situation u is a probability distribution over the choice set C_u at u . The notation $p_u(c)$ is used for the probability assigned to a choice $c \in C_u$ by p_u . The set of all local strategies p_u at u is denoted by P_u .

Behavior strategies: A behavior strategy p is a function which assigns a local strategy $p_u \in P_u$ to every $u \in U$. This definition closely corresponds to that of a behavior strategy for extensive forms (Kuhn 1953), (Selten 1975). The set of all behavior strategies is denoted by P .

Payoff function: The payoff function E of a population game assigns a real number $E(p,q)$ to every pair (p,q) of behavior strategies in P . The functional form of $E(p,q)$ depends on the biological model which gives rise to the population game.

Population game: A population game $G = (U,C,E)$ consists of a set U of information situations, a choice set function C and a payoff function E , where U,C and E have the properties described above.

Interpretation: In social science applications of game theory it is generally relatively easy to identify the players. Biological games are more difficult in this respect. The focus is on strategies rather than players.

It seems to be adequate to think of a player as a randomly selected animal. The payoff $E(p,q)$ is the expected incremental fitness obtained by this random animal in conflict situations covered by the model if he behaves according to p and all the other animals behave according to q .

These are two ways of further elaboration of this interpretation. Suppose that there are N animals in the population. We imagine that the game is played by N players who are randomly assigned to the N animals. Each player

has equal chances to become each one of the N animals. We call this the "many player interpretation". (N is a large number).

In the many player interpretation E is a partially specified payoff function of a symmetric game. A player's payoff is defined only for those cases where all other players use the same strategy. For all other cases the payoff can be left unspecified since evolutionarily stable strategies are defined in terms of deviations of one player from a commonly used strategy.

Another interpretation is based on the idea that there are only a small number of players, say n , where n is the number of players maximally involved in a conflict covered by the model. In the models of asymmetric animal contests considered here we have $n = 2$, but this is not the most general case which may be of interest (e.g. we may think of conflicts between siblings). We imagine that a conflict is picked at random with the appropriate probability from a universe of possible conflicts and that m of the n players are selected randomly and then randomly assigned to the m animals actually involved in the conflict. Each player has the same chance to be any one of these animals. We call this the "few player interpretation".

In the case $n = 2$ the few player interpretation has the advantage that $G = (U,C,E)$ becomes a symmetric two person game with a fully specified payoff function. For the models considered here it seems to be natural to adopt this interpretation.

As far as formal definitions and results are concerned, we need not choose one of both interpretations. The analysis always focuses on one player who may or may not deviate from a commonly used strategy. In a sense the number of players does not really matter and therefore need not be specified as a parameter of the population game $G = (U,C,E)$.

A game theorist who reads the biological literature may easily be misled to believe that the game which is played directly models the conflict between a population and an invading mutant. This is not the case. The mutant-population conflict is captured by the solution concept and not by the game. This is clear from the interpretation of an evolutionarily stable strategy (Maynard Smith - Price 1973).

2. Evolutionarily stable strategies

The definition of an evolutionarily stable strategy will be expressed in a way which emphasizes its close connection to the concept of a symmetric equilibrium point (Nash 1951).

Best reply: Let q and r be two behavior strategies for $G = (U, C, E)$. The strategy r is called best reply to q if the following is true:

$$(1) \quad E(r, q) = \max_{p \in P} E(p, q)$$

Equilibrium strategy: A strategy p for $G = (U, C, E)$ is called equilibrium strategy for G if p is a best reply to p .

Alternative best reply: Let p be an equilibrium strategy. A best reply r to p is called an alternative best reply to p if r is different from p .

Evolutionarily stable strategy: A strategy p for $G = (U, C, E)$ is called an evolutionarily stable strategy if the following conditions (a) and (b) are satisfied

- (a) Equilibrium condition: p is an equilibrium strategy for G .
- (b) Stability condition: For every alternative best reply r to p the following inequality holds:

$$(2) \quad E(p, r) > E(r, r) .$$

The equilibrium condition (a) requires that p is the equilibrium strategy in a symmetric equilibrium point in the sense of Nash. The stability condition (b) secures stability against mutants whose strategies are alternative best replies to p .

3. Models of asymmetric animal conflicts

In the following a class of models for asymmetric animal conflicts and the population games arising from such models will be described. In these models two animals are involved in every conflict. We shall adopt the few player interpretation of the population game.

Roles: A player may find himself in a number of roles $1, \dots, I$. One may think of examples like "small owner" and "big invader" in a territorial conflict.

Perceptive stimuli: It is not necessary to restrict one's attention to models where the opponent's role is perceived with perfect accuracy. Therefore we assume that there are S perceptive stimuli $1, \dots, S$ whose probabilities depend on the role of the opponent. A stimulus s may be thought of as an animal's inaccurate perception of his opponent's role.

Information situations: A role i together with a stimulus s constitutes the information on the basis of which a contestant must choose his course of action in a contest. Therefore the information situations have the form of pairs (i, s) where with $i = 1, \dots, I$ and $s = 1, \dots, S$. The set U of information situations is a non-empty subset of the set of all these pairs. We do not wish to include those pairs into U which never occur as information situations.

Contest situations: A contest situation (u, v) is a pair where u and v are information situations. The set of all contest situations (u, v) with $u \in U$ and $v \in U$ is denoted by X . A contest situation describes the information of both opponents at the beginning of a contest.

Basic distribution: In the few player interpretation a contest is randomly selected and player 1 is randomly assigned to one opponent and player 2 to the other. With this interpretation let w_{uv} be the probability that contest situation (u, v) occurs with player 1 in information situation u and player 2 in information situation v . It is assumed that w_{uv} does not depend on the strategies used.

In view of the symmetry involved in the interpretation we must require the following symmetry condition:

$$(3) \quad w_{uv} = w_{vu} \quad \text{for all } (u, v) \in X$$

The models considered here have the information asymmetry property that two opponents never find themselves in the same information situation:

$$(4) \quad w_{uu} = 0 \quad \text{for every } u \in U$$

It can be assumed without loss of generality that for each $u \in U$ a $v \in U$ with $w_{uv} > 0$ can be found. (If this is not the case, U can be narrowed down). Y denotes the set of all (u,v) with $w_{uv} > 0$

Choices: A player in an information $u \in U$ is assumed to have B_u choices $1, \dots, B_u$. Thus $C_u = \{1, \dots, B_u\}$ is the choice set at u . Choices are interpreted as possible courses of action like "attack", "display" or "flee".

Situation payoff: $h_{uv}(b,c)$ is player 1's payoff (in terms of incremental fitness) if he is in information situation u and takes choice b and player 2 is in information situation v and takes choice c . We may think of h_{uv} as a payoff matrix with B_u rows and B_v columns. Such matrices are assumed to be given for all $(u,v) \in Y$.

If player 1 and 2 use local strategies p_u and q_v , respectively, then player 1 receives the following expected situation payoff:

$$(5) \quad H_{uv}(p_u, q_v) = \sum_{b \in C_u} \sum_{c \in C_v} p_u(b) q_v(c) h_{uv}(b,c)$$

Local payoff: Let p_u be a local strategy and let q be a behavior strategy. Player 1's local payoff for (p_u, q) at u is defined as follows:

$$(6) \quad H_u(p_u, q) = \sum_{v \in U} w_{uv} H_{uv}(p_u, q_v)$$

where q_v is the local strategy assigned to v by q .

Total payoff: Let p and q be two behavior strategies. The payoff $E(p,q)$ is defined as follows:

$$(7) \quad E(p,q) = \sum_{u \in U} \sum_{v \in U} w_{uv} H_{uv}(p_u, q_v)$$

where p_u and q_v are the local strategies assigned by p and q to u and v , respectively. Equation (7) can be rewritten as follows:

$$(8) \quad E(p,q) = \sum_{u \in U} H_u(p_u, q)$$

Obviously $E(p,q)$ is player 1's expected payoff if he uses p and player 2 uses q . Player 2's expected payoff for this strategy pair is $E(q,p)$. This is clear in view of the symmetry of the situation.

Models: A model of the class considered here can be characterized by a quintuple

$$(9) \quad M = (I, S, U, w, h)$$

where I is the number of roles, S is the number of perceptive stimuli, U is the set of information situations, C is the choice set function, w is the basic distribution, and h is the payoff matrix function which assigns a payoff matrix h_{uv} to every (u,v) with $w_{uv} > 0$. (It is not necessary to mention C and Y since h and w contain the relevant information). Let K be the class of all models of this kind which have the properties described above.

Population game of a model: Every model $M \in K$ gives rise to a population game $G = (U, C, E)$ where U , C and E are defined as above. This game G is called the population game of the model M .

4. Results

In this section definitions and lemmata refer to a game $G = (U, C, E)$ of a model $M = (I, S, U, w, h)$ in the class K .

Pure strategies: A local strategy p_u is called pure if p_u assigns probability 1 to one of the choices $b \in C_u$ and zero to all other choices. A behavior strategy p is called pure if all local strategies p_u prescribed by p are pure.

Properly mixed strategies: A Local strategy or a behavior strategy is called properly mixed if it is not pure.

Notational convention: If a choice $b \in C_u$ is used as an argument in H_{uv} or H_u , then b stands for the pure local strategy which assigns probability 1 to b .

Locally optimal choices: A choice $b \in C_u$ is called locally optimal against q if we have

$$(10) \quad H_U(b, q) = \max_{c \in C_U} H_U(c, q)$$

Local best replies: $r_U \in P_U$ is a local best reply to $q \in P$ if the following is true:

$$(11) \quad H_U(r_U, q) = \max_{p_U \in P_U} H_U(p_U, q)$$

Lemma 1: A local strategy r_U is a local best reply to q if and only if every choice $b \in C_U$ with $r_U(b) > 0$ is locally optimal against q .

Proof: The lemma expresses a well known basic game theoretical fact which can be derived easily if one makes use of the following relationship:

$$(12) \quad H_U(r_U, q) = \sum_{b \in C_U} r_U(b) H_U(b, q)$$

Equation (12) can easily be derived from (5) and (6). We shall say that r_U can be improved upon if a strategy p_U with $H_U(p_U, q) > H_U(r_U, q)$ can be found. It follows by (12) that r_U can be improved upon if and only if for at least one b which is not locally optimal we have $r_U(b) > 0$.

Lemma 2: A behavior strategy r is a best reply to a behavior strategy q if and only if every local strategy r_U assigned by r to an information situation $u \in U$ is a local best reply to q .

Proof: We shall say that r can be improved upon if a behavior strategy p with $E(p, q) > E(r, q)$ can be found. It follows by (8) that r can be improved upon if and only if at least one of the local strategies r_U prescribed by r is not locally optimal.

Lemma 3: Let p be a properly mixed equilibrium strategy. Then p has a pure alternative best reply.

Proof: For every $u \in U$ let $b_u \in C_U$ be one of the choices which are locally optimal against p . Consider the pure strategy k whose local strategies k_u select these choices b_u with probability 1.

By lemma 1 each of the k_u is a local best reply to p . Therefore by lemma 2 the pure strategy k is an alternative best reply to p .

Lemma 4: Let p be an equilibrium strategy and let r be an alternative best reply to p . Then an alternative best reply m to p can be found whose local strategies m_u disagree with those of p only for one information situation.

Proof: Let v be an information situation with $r_v \neq p_v$. A v of this kind can be found since r is different from p . Let m be the behavior strategy whose local strategies m_u are as follows: $m_v = r_v$ and $m_u = p_u$ for all $u \neq v$. It follows by lemma 2 that m is an alternative best reply to p .

Lemma 5: Let p be an evolutionarily stable strategy. Then no alternative best reply to p exists.

Proof: Suppose that an alternative best reply to p exists. Then by lemma 4 we can find an alternative best reply m which differs from p only at one information situation v . The information asymmetry property (4) has the consequence

$$(13) \quad H_v(q_v, p) = H_v(q_v, m) \quad \text{for all } q_v \in P_v$$

This follows by the fact that p_u and m_u agree for all information situations of opponents of a player who is in information situation u . Since in view of lemma 2 both p_v and m_v are local best replies to p we have

$$(14) \quad H_v(m_v, p) = H_v(p_v, p)$$

According to (13) we can substitute m for p in (14):

$$(15) \quad H_v(m_v, m) = H_v(p_v, m)$$

Since p_u and m_u agree for $u \neq v$ we have

$$(16) \quad H_u(m_u, m) = H_u(p_u, m) \quad \text{for } u \neq v$$

Equation (15) and (16) together with (8) yield

$$(17) \quad E(m,m) = E(p,m)$$

It follows by (17) that m is an alternative best reply to p which does not satisfy inequality (2) in the definition of an evolutionarily stable strategy. Therefore condition (b) in this definition cannot be satisfied unless no alternative best reply exists.

Theorem: Let $G = (U,C,E)$ be the game of a model $M \in K$ and let p be an evolutionarily stable strategy for G . Then p is a pure strategy. Moreover, no alternative best reply to p exists.

Proof: The non-existence of alternative best replies follows by lemma 5. If p were properly mixed then an alternative best reply would exist by lemma 3. Therefore p must be pure.

References

- Dawkins, R., The Selfish Gene, Oxford 1976
- Haigh, J., Game Theory and Evolution, Advances of Applied Probability, 7, 1975
- Harsanyi, J., Games with Incomplete Information Played by "Bayesian" Players, Part I Management Science, Vol. 14 (November 1967), pp. 159-182. Part II, ibid. (January 1968), pp. 320-334. Part III, ibid. (March 1968), pp. 486-502
- Kuhn, H.W., Extensive Games and the Problem of Information, in H.W. Kuhn and A.W. Tucker (eds.): Contributions to the Theory of Games, Vol. II, Annals of Mathematics Studies, 28, pp. 193-216, Princeton 1953
- Maynard Smith, J. and G.A. Parker, The Logic of Asymmetric Animal Contests, Animal Behavior (1976), 24, pp. 159-175
- Maynard Smith, J. and G.R. Price, The Logic of Animal Conflict, Nature (1973), 246, pp. 15-18
- Nash, J.F., Non-cooperative Games, Annals of Mathematics, 54, pp. 155-162, 1951
- Neumann, J.v. and O. Morgenstern, Theory of Games and Economic Behavior, Princeton 1944
- Selten, R., Reexamination of the Perfectness Concept for Equilibrium Points in Extensive Games, International Journal of Game Theory, Vol. 4, Issue 1, pp. 25-55, 1975

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