City Research Online

City St George's, University of London

Citation: Broom, M., Cannings, C. & Vickers, G. T. (2000). Evolution in Knockout Contests: the Variable Strategy Case. Selection, 1, pp. 5-21.

This is the unspecified version of the paper.

This version of the publication may differ from the final published version. To cite this item please consult the publisher's version.

Permanent repository link: https://openaccess.city.ac.uk/id/eprint/990/

Copyright and Reuse: Copyright and Moral Rights remain with the author(s) and/or copyright holders. Copies of full items can be used for personal research or study, educational, or not-for-profit purposes without prior permission or charge, unless otherwise indicated, provided that the authors, title and full bibliographic details are credited, a hyperlink and/or URL is given for the original metadata page and the content is not changed in any way. For full details of reuse please refer to City Research Online policy.

City Research Online: http://openaccess.city.ac.uk/ publications@citystgeorges.ac.uk

Selection 1(2000)1–3, 5–21
Available online at http://www.akkrt.hu

Evolution in Knockout Contests: The Variable Strategy Case

M. BROOM[1]*, C. CANNINGS[2] and G. T. VICKERS[3]

[1]*Centre for Statistics and Stochastic Modelling, School of Mathematical Sciences, The University of Sussex, Sussex, UK*
[2]*Division of Molecular and Genetic Medicine, School of Medicine, Royal Hallamshire Hospital, The University of Sheffield, Sheffield, UK*
[3]*Department of Applied Mathematics, School of Mathematics and Statistics, The University of Sheffield, Sheffield, UK*

(Received: 11 February 2000, Accepted in revised form: 16 June 2000)

In a previous paper we introduced a model of a multi-player conflict in the form of a knockout tournament. Groups of individuals resolved their disputes in a tournament in which in each round the remaining contestants formed pairs who competed against each other: in such a contest between two individuals using behaviours x and y there was a probability that each would win, and a cost incurred by the loser, both of which depended on x and y. The winner progressed to the next round of the tournament and the loser was eliminated; a player received a reward which depended on how far that individual progressed. Individuals were constrained to adopt a fixed play throughout the tournament. In this paper we extend the model by allowing individuals to vary their choice of behaviour from round to round. The complexity of such systems is investigated and illustrated by both special cases and numerical examples. It is shown that in this case behaviour is very different to the fixed strategy case.

Keywords: Multi-player games, dominance, ESS, knockout tournament, local strategy

1. Introduction

Game theory has a relatively short but valuable history in modelling the natural world, especially in the area of animal conflicts. It has provided explanations for apparently paradoxical situations, such as the practice of heavily armed animals engaging only in ritualistic contests (Maynard Smith, 1982) and the tendency of (especially male) animals to develop extremely costly signals to acquire mates (Grafen, 1990a, b). The concept of an Evolutionarily Stable Strategy (ESS), introduced by Maynard Smith and Price (1973) has been especially useful, and has been central to a large body of literature; some important examples being (Haigh 1975; Bishop and Cannings, 1976; Maynard Smith, 1982; Cressman, 1992; Hofbauer and Sigmund, 1998). Most of this work has concentrated on games between only two players.

* M. Broom is also a member of the Centre for the Study of Evolution at the University Sussex.

Corresponding author: M. Broom, Centre for Statistics and Stochastic Modelling, School of Mathematical Sciences, The University of Sussex, Sussex, UK, E-mail: m.broom@sussex.ac.uk

Game theory has its roots in economics originating with von Neumann and Morgenstern (1944) (also see Alexrod and Hamilton, 1981 and Binmore, 1992), and multi-player games have always been central to its theory. See Luce and Raiffa (1957) for a general discussion, and a description of its application to voting schemes. The authors have recently written a series of papers developing multi-player models of biological situations (Broom et al., 1996, 1997a, b, 2000). If it is supposed that individuals come together in groups of size n and that each individual freely selects its play, then it is necessary to specify the payoff of each possible play against every possible combination of plays chosen by the other $(n-1)$ individuals in the group. In Broom et al. (1997b) this specification was made tractable by the choice of the particular structure imposed, namely symmetric finite contests [also see Cannings and Whittaker (1994) for a similar treatment of the multi-player war of attrition]. The others only allow 'fights' between pairs, but have these fights embedded within a structure [for another example, see Mesterton-Gibbons and Dugatkin (1995) who adopted a round-robin approach in modelling a dominance hierarchy]. This paper, following on

from Broom et al. (2000), adopts the latter approach, modelling a multi-player conflict as a set of pairwise games in a knockout tournament format. Of course this will not reflect the precise behaviour of any real population but will capture certain aspects of importance. For a more detailed rationale, see Broom et al. (2000).

There now follows a reiteration of some two-player game theory which is of relevance to work later in the paper.

In the classical two-player conflict models it is assumed that individuals compete in pairwise games for some reward, food or mates perhaps. In the symmetric version, which is our concern here, all members of the population are indistinguishable and each individual is equally likely to meet each other individual. There is a set **S** of choices available to each player to play in a particular game, referred to as *pure strategies.* Each contest results in a payoff to each of the protagonists which is specified by some $a(x, y)$, the payoff to an individual who plays strategy x when opposed by an individual who plays y; $x, y \in \mathbf{S}$.

Individuals do not need to play the same pure strategy every time, they can play a *mixed strategy* i.e. play x with probability (or probability density) p_x for each of $x \in \mathbf{S}$. The payoffs are presumed to be additive over both the first and second argument, so that, for example, if $\mathbf{S} = (S_1, \ldots, S_n)$, the payoff to an individual playing **p** against an individual playing **q**, which is written as $E[\mathbf{p}, \mathbf{q}]$, is given by

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

where **A** is the matrix whose (i, j)-element is $a(S_i, S_j)$.

p is an ESS of **A** if and only if, for all $\mathbf{q} \neq \mathbf{p}$,

(i) $E[\mathbf{p}, \mathbf{p}] \geq E[\mathbf{q}, \mathbf{p}]$ and

(ii) if $E[\mathbf{p}, \mathbf{p}] = E[\mathbf{q}, \mathbf{p}]$ then $E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}]$.

See Maynard Smith (1982) or Haigh (1975) for a more detailed explanation.

The vector **p** is a *Nash equilibrium* if it satisfies condition (*i*) above against all $\mathbf{q} \neq \mathbf{p}$, but not necessarily condition (*ii*) (see Hofbauer and Sigmund, 1998). The concept of an ESS can easily be extended to the multi-player case (see Palm, 1984 and Broom et al., 1997b).

The model developed in Broom et al. (2000) provided a number of predictions. For the case where the pairwise games were the classical Hawk–Dove game the more players, and hence the more rounds that were played, the smaller the frequency of the aggressive Hawk strategy amongst the population. However, the frequency of individuals playing Hawk in a particular contest could rise, since Hawk individuals were more likely to progress to the later rounds. In general the structure of the tournament had a large bearing on the overall level of aggression, which could be both less than or greater than that for independent games (and the difference could be fairly large). The model also predicted a relationship between the level of aggression in a population and the degree to which rewards are unevenly split amongst individuals, the concept of *reproductive skew* first developed in Vehrencamp (1983).

It was shown that there may be many ESSs for the type of knockout model described in Broom et al. (2000), although if there are only two options available it is impossible to have no ESS. It was shown that for the Hawk–Dove case, there is a unique ESS, which can be evaluated numerically via a formula given in Broom et al. (2000).

1.1. The structure of knockout games

A knockout contest is a multi-player game which is composed of a number of pairwise games. Initially there are 2^n players each of whom plays another player in a pairwise game in which there is a 'winner'. The winners are then repaired in the next round and this continues until there is one overall winner. Players receive a reward according to which round they were eliminated from the competition, usually increasing with the number of rounds the player survives. Opponents in each round are chosen at random, and we assume here that players do not differ in any aspect which affects their performance, other than the selection of strategies. Thus the organisation is similar to many human competitions, such as the Wimbledon Lawn Tennis Championships, although at Wimbledon individuals are not of equal quality and there is a seeding system which keeps apart the stronger players in the early rounds.

The main advantages of the knockout model are that it breaks down a contest between a large number

of individuals into a (relatively small) collection of pairwise games, and it has one of the simplest conceivable structures of pairwise games where every individual starts from an identical position. However, as we shall see, interesting phenomena can be observed from groups of as few as 4 players. The disadvantage is that it is not realistic for a large group of animals to form themselves into fighting pairs in such an ordered way, although it is not unreasonable to think that a structure approximating to the knockout model might occur in some circumstances. In addition large groups that are stable will have already formed a hierarchy, and groups reforming may well have a memory of other individuals (see, for example, Barnard and Burk, 1979). So the model may only be useful in considering groups which form for the first time.

Initially there are 2^n players who play a pairwise game with one opponent such that there is a 'winner' and a 'loser'. The loser is eliminated from the competition and the winner enters the next round, where the process is repeated with 2^{n-1} players. This continues until the final round with only two players. Define round k as the round with 2^k players remaining, i.e. the players start in round n, and the final round is round 1. This is the opposite to the round numbering system used in most sporting contests, but is mathematically more convenient. Losers in round k gain the reward V_k, the overall winner receiving V_0. It is assumed that $V_k \geq V_{k+1}$ ($k = 0, \ldots, n-1$).

The pairwise games which are played in the knockout contest could be any game which has a winner and a loser. As in Broom et al. (2000), we consider a very simple game in this paper. The pairwise game which is played in each round is defined as follows:

Suppose that in each round there are available m strategies labelled $O_1, \ldots, O_m$. These shall henceforth be referred to as *options*. Terms such as *mixed option* will be used. The term *strategy* will be reserved for the overall strategy specifying which option is to be used for each round should the player progress to that round. This specification may be probabilistic, comprising all the options from each round. Let the probability that a O_i-player beats a O_j-player be $\frac{1}{2} + \Delta_{ij}$, so that $\Delta_{ij} + \Delta_{ji} = 0$ and $\Delta_{ii} = 0$. In addition if a O_i-player loses to a O_j-player it incurs a cost c_{ij} (a reward $-c_{ij}$), which might correspond to an injury, or loss of time or energy.

In Broom et al. (2000) each player used the same option in each round. In this paper players may vary their option from round to round. Note that the two cases can be thought of as the two extreme cases out of a set of possible types of game (see Broom et al., 2000). Our conflicts each involve 2^n individuals and we envision a population which has a large (essentially infinite) set of such conflicts. The set of 2^n players are selected at random from the infinite population of players.

2. A variable strategy

In this paper we allow players to change their option from round to round. As opposed to the fixed strategy case, and as in any two-player conflict, we do not need to differentiate in any round as to whether individuals are playing pure or mixed options; it is only the overall population play which matters. We find a recurrence relation for the evolutionary stable play in round k conditional on all lower numbered rounds (i.e. rounds later in the competition). The term Evolutionarily Stable Option (ESO) is coined for such play (formally defined in Section 2.2) and we show that a collection of ESOs for each round forms a Nash equilibrium. In Sections 2.3–2.6 we consider the 2 and 3 option cases in more detail.

The type of contest that we consider has a lot in common with *extensive two-person games* described by Selten (1983) (see also Van Damme, 1991). Both games use a dynamic programming approach, finding optimal play at any stage of the game conditional upon optimal play at later stages. Selten (1983) uses the term *local strategy* for what we call an option and any collection of local strategies is referred to as a *behaviour strategy*. In case of extensive two-person games the same two players play at every stage, whereas in our game only one player gets through to the next stage, and the probability of qualification depends upon the option used. Nevertheless, there are many similarities between the two games, and these are commented upon throughout the paper.

2.1. The equivalence of different strategy combinations

For n rounds and m options, which we label O_1, ..., O_m, there are m^n pure strategies (a selection of an option for each round). However, the same population structure can be obtained from different mixtures of these.

Consider the case where $m = n = 2$. The four possible pure strategies are S_{11}, S_{12}, S_{21} and S_{22} (the first subscript is the option played in round 1, the second in round 2). Let the proportions of S_{ij} at the start be r_{ij}, so that

$$r_{11} + r_{12} + r_{21} + r_{22} = 1$$

Further, let the proportion of O_1-players in round 2 be $p_2 = r_{11} + r_{21}$, and the proportion in round 1 be p_1. The probability of a O_1-player reaching round 1 is $\frac{1}{2} + \Delta(1 - p_2)$ and for a O_2-player it is $\frac{1}{2} - \Delta p_2$, where $\Delta = \Delta_{12}$. Therefore

$$p_1 = [1 + 2\Delta(1 - p_2)]r_{11} + (1 - 2\Delta p_2)r_{12}.$$

Together with the equation $p_2 = r_{11} + r_{21}$, this gives two equations in three free variables, so that there may exist a family of pure strategies which give the same values of p_1 and p_2. One can prove that there always exist such a solution with valid r_{ij}. For example, in case $\Delta = 1/2$, $p_1 = 1/2$ and $p_2 = 1/2$ we have such a family defined by $r_{11} = x$, $r_{12} = 1 - 3x$, $r_{21} = 1/2 - x$ and $r_{22} = 3x - 1/2$ for $x \in [1/6, 1/3]$. More generally there are m^n pure strategies (i.e. $m^n - 1$ free variables) and only n equations. This phenomenon also occurs for extensive two-person games, and is referred to as *spurious duplication* in Selten (1983).

In general a strategy is of the form $(\mathbf{p_1}, \ldots, \mathbf{p_n})$, where the vector $\mathbf{p_i}^T = (p_{i1}, \ldots, p_{im})$ and p_{ij} is the probability of playing option j in round i. When $m = 2$ a strategy is of the form $(p_1, \ldots, p_n)$, p_i being the probability that the player adopts option 1 in round i.

2.2. Evolutionarily stable options

Assuming that we know which strategies are going to be played in later rounds, we can work out exactly the expected payoff to a player for any given course of action in the current round given the action of the current opponent.

An option (i.e. the play in a particular round) can be represented by a vector, and similarly the mean option in a particular round is also represented by a vector, with its kth entry representing the probability that a randomly chosen opponent plays pure option O_k. We define an ESO for round j conditional upon the mean option of the population played in later rounds. As in Broom et al. (2000), we assume an effectively infinite array of contests between 2^n players. Define the payoff $E[\mathbf{r_i}, \mathbf{v_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}]$ as the expected payoff to a player playing $\mathbf{r_i}$ against an opponent playing $\mathbf{v_i}$ in round i, when the mean population option in round j is $\mathbf{r_j}$ $\forall j < i$.

We define the ESO in a similar manner to an ESS in a two-player game, as indeed a single round with future behaviour fixed is just such a conflict. $\mathbf{p_i}$ is an ESO for round i conditional upon $\mathbf{r_1}, \ldots, \mathbf{r_{i-1}}$ if, for all $\mathbf{q_i} \neq \mathbf{p_i}$,

(i) $E[\mathbf{p_i}, \mathbf{p_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}] > E[\mathbf{q_i}, \mathbf{p_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}]$ and

(ii) if $E[\mathbf{p_i}, \mathbf{p_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}] = E[\mathbf{q_i}, \mathbf{p_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}]$ then

$$E[\mathbf{p_i}, \mathbf{q_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}] > E[\mathbf{q_i}, \mathbf{q_i}; \mathbf{r_1}, \ldots, \mathbf{r_{i-1}}].$$

$\mathbf{p_i}$ is a Nash equilibrium option if it satisfies condition *(i)* for all $\mathbf{q_i} \neq \mathbf{p_i}$ (it need not satisfy (ii)).

Hence we can work backwards from the final contest using results from two-player game theory to find an ESO for each round conditional upon ESOs in later rounds (there may be none, in which case the process breaks down, or more than one). These options then, collectively, form a Nash equilibrium strategy (and possibly an ESS) for the whole game. Such a collection is referred to as a *Locally Stable Strategy* (LSS) in Selten (1983). Note that to have a Nash equilibrium all that is required is a Nash equilibrium option in each round conditional on future rounds. It is proved by van Damme (1991) that for the extensive 2-person game, any ESS is also an LSS. It is easy to show that the corresponding result is true here; namely that $(\mathbf{p_1}, \ldots, \mathbf{p_n})$ is an ESS only if $\mathbf{p_j}$ is an ESO in round j, conditional on lower numbered rounds, for all j. This is true since if $\mathbf{p_1}, \ldots, \mathbf{p_{j-1}}$ are ESO's of their respective rounds then $\mathbf{p_j}$ must be an ESO as well, otherwise there is a $\mathbf{q_j}$ s.t. $(\mathbf{p_1}, \ldots, \mathbf{p_{j-1}}, \mathbf{q_j}, \mathbf{p_{j+1}}, \ldots, \mathbf{p_n})$ invades $(\mathbf{p_1}, \ldots, \mathbf{p_n})$.

Note that only strategies of this form are resistant to invasion from strategies 'a single mutation away' from them i.e. $(\mathbf{p_1}, \ldots, \mathbf{p_{j-1}}, \mathbf{q_j}, \mathbf{p_{j+1}}, \ldots, \mathbf{p_n})$ any $\mathbf{q}$,

some j. This only prevents the invasion of these specific strategies, however, so that the condition is necessary but not sufficient, as we see in Section 2.4.

2.3. The two-option case

We now consider the variable option case with just two options. We define some terms useful for working out the ESO(s) in a given round (as a function of the payoff parameters and W_k, the expected reward for winning in round k). A recurrence relation is developed which finds the ESO(s) in round k conditional on the ESO in round $k-1$ and all later payoffs, and thus finds all candidate ESSs for the whole game. We proceed to find when the candidate ESS for the 4-player (2 round) case is an ESS (Section 2.4) and show how the dynamics of the system work when it is not (Section 2.5).

Let W_k be the expected reward for winning in round k **(including the costs expected to be incurred)**, i.e. for a player entering round $k-1$ (e.g. $W_1 = V_0$), and let $\Delta = \Delta_{12}$ as earlier and in Broom et al. (2000). Further define the following terms:

$$C_1 = \frac{c_{22} - c_{12}}{2} + \Delta c_{12},\ C_2 = \frac{c_{11} - c_{21}}{2} - \Delta c_{21},$$

$$y_k = C_1 + \Delta(W_k - V_k),\ y_k^* = C_2 - \Delta(W_k - V_k),$$

$$a_k = \Delta(V_k - V_{k+1}) + \frac{1}{2}C_1,$$

$$v_k = \sum_{i=1}^{k-1} \frac{V_i}{2^{k-i}} + \frac{V_0}{2^{k-1}}.$$

Thus C_i is the expected cost incurred by a O_2-player when playing an O_i-player minus that of a O_1-player playing an O_i-player. v_k is the mean reward of a player winning in round k *not including future costs.* The relevance of y_k, y_k* and a_k will be seen shortly.

It is now shown that the ESO for round k depends upon y_k and y_k* in a simple way. The payoffs for round k are given by the matrix,

$$M_k = \begin{bmatrix} \frac{1}{2}(W_k + V_k - c_{11}) & \frac{1}{2}(W_k + V_k - c_{12}) + \Delta(W_k - V_k + c_{12}) \\ \frac{1}{2}(W_k + V_k - c_{21}) - \Delta(W_k - V_k + c_{21}) & \frac{1}{2}(W_k + V_k - c_{22}) \end{bmatrix}.$$

For example, when a O_1-player plays a O_2-player, the probability of winning is ½ + Δ with reward W_k, and the probability of losing is ½ – Δ with reward $V_k - c_{12}$ so that the O_1-player's expected payoff is

$$\left(\frac{1}{2} + \Delta\right)W_k + \left(\frac{1}{2} - \Delta\right)(V_k - c_{12}).$$

The above is equivalent to a single-round two-player game. For such a game with payoffs

$$\begin{bmatrix} a & b \\ c & d \end{bmatrix}$$

there is a pure ESO (1, 0) if $c - a < 0$, a pure ESO (0, 1) if $b - d < 0$ and a mixed ESO $(p, 1-p)$ where

$$p = \frac{b - d}{b + c - a - d},$$

when both $c - a > 0$ and $b - d > 0$. We shall, as in Broom et al. (2000), assume that neither $c - a$ nor $b - d$ are zero (these are non-generic cases). For matrix $\mathbf{M_k}$

$$c - a = \frac{c_{11} - c_{21}}{2} - \Delta c_{21} - \Delta(W_k - V_k) = C_2 - \Delta(W_k - V_k) = y_k^*$$

$$b - d = \frac{c_{22} - c_{12}}{2} + \Delta c_{12} + \Delta(W_k - V_k) = C_1 + \Delta(W_k - V_k) = y_k$$

$$c + b - a - d = y_k + y_k^* = C_1 + C_2.$$

This means that for round k there are ESOs as follows: $y_k^* < 0$ yields a pure O_1, $y_k < 0$ yields a pure O_2 and $y_k > 0$, $y_k^* > 0$ yields a mixed ESO (the proportion of O_1-players being $y_k/(C_1 + C_2)$). There are two different cases to consider:

(*i*) $C_1 + C_2 > 0$, when an internal ESO is possible and
(*ii*) $C_1 + C_2 \le 0$ (if $C_1 + C_2 < 0$ then two pure ESO's are possible).

Thus if we can find the set of values of y_k (and thus $y_k^* = C_1 + C_2 - y_k$) for all values of k, i.e. $(y_1, \ldots, y_n)$, we can find the set of ESOs and thus the corresponding candidate ESS. As we shall see, there may be more than one such set $(y_1, \ldots, y_n)$, and so more than one candidate ESS.

Defining X_k as the expected cost incurred by a player in round k, in Appendix A it is shown that y_k satisfies the following recurrence relation

$$y_{k+1} = \frac{y_k}{2} + a_k - \Delta X_k. \quad (1)$$

Thus we have a recurrence relation for y_k which also includes a term a_k which is known and X_k which is a function of p_k which is itself a function of y_k. Considering the two separate cases;

$$(i)\ C_1 + C_2 > 0.$$

We define b_k and z_k as follows:

$$b_k = \frac{a_k}{C_1 + C_2},\ z_k = \frac{y_k}{C_1 + C_2}.$$

Using the recurrence relation (1) for y_k, we obtain

$$y_{k+1} = \frac{y_k}{2} + a_k + \Delta(C_1 + C_2)p_k(1 - p_k) - \frac{1}{2}\Delta[c_{11}p_k + c_{22}(1 - p_k)]$$

$$\Rightarrow z_{k+1} = \frac{z_k}{2} + b_k + \Delta p_k(1 - p_k) - \frac{1}{2}\Delta\frac{c_{11}p_k + c_{22}(1 - p_k)}{C_1 + C_2} \quad (2)$$

and using the signs of the y_k and inferring similar signs for the z_k we have that p_{k+1} takes the value z_{k+1} if this is between 0 and 1, the value 0 if z_{k+1} is less than zero and the value 1 if z_{k+1} is greater than 1. So if we know z_k and p_k we can find z_{k+1} and p_{k+1} i.e. if the values of p_1 and z_1 are known then all the values of p_k ($k = 1, \ldots, n$) can be found. p_1 follows immediately from z_1 which clearly follows from $y_1 = a_0 + C_1/2$ ($W_1 = V_0$), i.e.

$$z_1 = \frac{2a_0 + C_1}{2(C_1 + C_2)}.$$

So there is a unique ESO for each round, and thus a unique candidate ESS.

Example 1

Consider the following set of payoffs.

$V_0 = 7.5$, $V_1 = 6.5$, $V_2 = 0$, $c_{11} = 25$, $c_{12} = 0$, $c_{21} = 11$, $c_{22} = 1$, $\Delta = 0.5$. For $k = 1$, that is the final round, we have

$$\mathbf{M_1} = \begin{bmatrix} -5.5 & 7.5 \\ -4.5 & 6.5 \end{bmatrix}$$

so that since $c > a$ and $b > d$ there is an internal ESO, with $p_1 = 0.5$. The payoff to each option, and hence to any mixed strategy, in a population playing the ESO is 1. Thus $W_2 = 1$ and so the payoff matrix for round 2, in a population which plays 0.5 in round 1 is

$$\mathbf{M_2} = \begin{bmatrix} -12 & 1 \\ -11 & 0 \end{bmatrix}$$

giving an ESO with $p_2 = 0.5$ and thus an overall candidate ESS $\mathbf{p} = (0.5, 0.5)$ and expected payoff –5.5 for the whole contest.

$$(ii) \quad C_1 + C_2 \le 0.$$

In this case there cannot be any p_k which is not equal to 0 or 1, i.e. $p_k(1 - p_k) = 0$. If $p_k = 1$ then $X_k = c_{11}/2$, and if $p_k = 0$ then $X_k = c_{22}/2$ i.e.

$$p_k = 1 \Rightarrow y_{k+1} = \frac{y_k}{2} + a_k - \Delta\frac{c_{11}}{2},$$

$$p_k = 0 \Rightarrow y_{k+1} = \frac{y_k}{2} + a_k - \Delta\frac{c_{22}}{2}.$$

We obtain the following relationship between p_k and y_k.

If $y_k^* < C_1 + C_2$ then $p_k = 1$ is the ESO.

If $C_1 + C_2 < y_k^* < 0$ then $y_k < 0$ and thus both $p_k = 0$ and $p_k = 1$ are ESOs.

If $0 < y_k^*$ then $y_k < 0$ and so $p_k = 0$ is the ESO.

As in case (i) if we have the values of p_k and y_k we can also find the values of p_{k+1} and y_{k+1}. Similarly it is easy to find the value of p_1 (the value of y_1 is $a_0 + C_1/2$ as before). However, in this case, the values of p_k may not be unique. If y_k lies between $C_1 + C_2$ and 0 then p_k can be either 0 or 1, which in turn generates two values of y_{k+1}, which generates more then a single set of ESOs. This implies that while in case (i) there is a unique candidate ESS ($p_1, \ldots, p_n$) in case (ii) the number of candidate ESSs lies between 1 and 2^n. In fact for case (ii), all candidate ESSs are really ESSs, due to the fact that all of the ESOs are pure strategies. If in any round k an individual does not play a pure ESO, the value of W_k for that individual falls, and thus the payoff matrix $\mathbf{M_k}$ for that individual is dominated by that for an individual playing the ESO, which in turn implies that the same is true for $\mathbf{M_n}$ the payoff matrix for round n (the start of the game).

We will now consider some simpler examples which can be evaluated more thoroughly. In all of the following examples we will assume that the V_k's decrease linearly with k, i.e. $V_{k-1} - V_k$ is constant so that $b_k = b \forall k$.

a) The Hawk–Dove game

We examine the knockout tournament where the pairwise contests follow the classical Hawk–Dove game of Maynard Smith (1982). In this game the values of the parameters are as follows:

$$\Delta = 1/2,\ c_{11} = C > 0,\ c_{12} = c_{21} = c_{22} = 0 \Rightarrow$$
$$\Rightarrow C_1 = 0,\ C_2 = C/2.$$

$C_1 + C_2 > 0$ so that this game is of type (*i*), and thus has exactly one candidate ESS. Thus the recurrence relation for z_k becomes

$$z_{k+1} = \frac{z_k}{2} + b_k + \frac{1}{2}p_k(1-p_k) - \frac{\frac{1}{4}Cp_k}{\frac{1}{2}C} = \frac{z_k}{2} + b - \frac{p_k^2}{2}.$$

If we further suppose that $b < 1$ (otherwise $p_k = 1\ \forall k$) then $p_1 = b$ and it is easy to show that z_k must always lie between 0 and 1 i.e.

$$p_{k+1} = b + \frac{1}{2}p_k(1-p_k).$$

We first prove that the p_k converge to some p as $k \to \infty$. If this is true, then we require $p = b + p(1-p)/2$, and so $p^2 + p - 2b = 0 \Rightarrow$

$$p = \frac{\sqrt{1+8b}-1}{2}$$

gives the equilibrium mixed strategy. Substituting for b in the original recurrence relation, we obtain

$$\begin{aligned} p_{k+1} &= p - \frac{1}{2}p(1-p) + \frac{1}{2}p_k(1-p_k) \\ \Rightarrow p - p_{k+1} &= \left(\frac{1}{2} - p\right)(p - p_k) + \frac{1}{2}(p-p_k)^2 \\ \Rightarrow |p - p_{k+1}| &\le \left|\frac{1}{2} - p\right||p - p_k| + \frac{1}{2}|p-p_k|^2 \\ &< |p-p_k|\left(\frac{1}{2} + \frac{1}{2}|p-p_k|\right) \le |p-p_k| \end{aligned}$$

with equality only if $p_k = p$, that is p_k converges to p. (If b_k is not equal to b but converges to it, the same argument will apply for p_k provided that k is sufficiently large.)

It can be shown that there are three different cases depending upon the value of b:

(a) $0 < b \le 3/8$: p_k increases to a limit, p, say.
(b) $3/8 < b < (5 - \sqrt{17})/2$: p_k initially increases towards p and then approaches it in an oscillatory fashion.
(c) $(5 - \sqrt{17})/2 < b < 1$: p_k approaches p in an oscillatory fashion.

In Broom et al. (2000) the case where $V_k - V_{k+1} = D\ \forall k$ was considered for both $C = 2D$ and $C = 4D$, each for $n = 1, \ldots, 6$. We now revisit this example and compare the two models. Note that here b_k is constant over k, and that $b = D/C$; we can thus use the above working to find the candidate ESS for each case. The ESO value of the probability of playing Hawk in each round is shown in Table 1. The ESO with k rounds to go is not affected by the total number of rounds, and so the best play for any number of rounds n less than 6 is given by columns headed 1, …, n in Table 1.

TABLE 1

$C = 2D$, $C = 4D$ the probability of playing Hawk in round k

k	1	2	3	4	5	6
$C = 2D$	0.5	0.625	0.617	0.618	0.618	0.618
$C = 4D$	0.25	0.344	0.363	0.366	0.366	0.366

This yields the expected number of violent Hawk versus Hawk contests as shown in Table 2. The corresponding values for the fixes strategy case are shown by way of comparison. It is clear that there is far more conflict in the variable strategy case than the fixed strategy case, for identical tournament

TABLE 2

The proportion of Hawk v Hawk contests over the whole conflict; $C = 2D$ and $C = 4D$

n	1	2	3	4	5	6	∞
$C = 2D$, Fixed	0.25	0.282	0.280	0.270	0.262	0.257	0.252
$C = 2D$, Variable	0.25	0.344	0.365	0.374	0.378	0.380	0.382
$C = 4D$, Fixed	0.063	0.078	0.079	0.072	0.064	0.056	0.041
$C = 4D$, Variable	0.063	0.100	0.118	0.126	0.130	0.132	0.134

structures. Thus extra choice has greatly reduced the payoffs to individuals. Of course, in a population of fixed option players, an individual who plays a suitably varied strategy would invade; evolution can reduce the fitness of the population.

b) Degenerate cases

b(i) If $\Delta = 0$ then a player has a probability of winning of ½ whichever opponent it is playing i.e. the reward V_i attained is independent of the play so that the game reduces to a series of pairwise games with payoff matrix.

$$\begin{bmatrix} -c_{11} & -c_{12} \\ -c_{21} & -c_{22} \end{bmatrix}.$$

b(ii) If all the costs are zero then $C_1 + C_2 = 0$ and $y_{k+1} = y_k/2 + a_k$. All the a_k's are positive (since $\Delta > 0$) so that $p_k = 1\ \forall k$.

c) Symmetric costs with

$$c_{12} = c_{21} = 0,\ c_{11} = c_{22} = C > 0.$$

Here players incur a cost if losing to an opponent playing the same strategy, but not if they lose to an opponent playing the other strategy, as is perhaps reasonable since the latter can be easily and quickly resolved.

$$c_{11} = c_{22} = C \Rightarrow C_1 = C_2 = C/2 > 0$$

$$z_{k+1} = \frac{z_k}{2} + b_k + \Delta p_k(1 - p_k) - \frac{1}{2}\Delta\frac{c_{11}p_k + c_{22}(1 - p_k)}{C_1 + C_2} = \frac{z_k}{2} + b_k + \Delta p_k(1 - p_k) - \frac{1}{2}\Delta.$$

We have assumed that $V_k - V_{k+1}$ is constant over all values of k. Define α by letting $C\alpha = V_0 - V_1$, then $b_k = 1/4 + \Delta\alpha$ so that

$$z_{k+1} = \frac{z_k}{2} + \Delta\alpha - \frac{1}{2}\Delta + \frac{1}{4} + \Delta p_k(1 - p_k).$$

For a very large number of rounds p_k will tend to a constant value which is given by the equation

$$p = \frac{p}{2} + \Delta\alpha - \frac{1}{2}\Delta + \frac{1}{4} + \Delta p(1 - p),$$

if α is sufficiently small (otherwise $p = 1$ is the equilibrium value). In case of the game when $\Delta = 1/2$ i.e.

$$p = p - \frac{1}{2}p^2 + \frac{1}{2}\alpha \Rightarrow p = \sqrt{\alpha}$$

for $\alpha < 1$, otherwise $p = 1$. It follows that even though the rewards are increasing in value and O_1-players have a better chance of progressing further in the competition than O_2-players for small α the overwhelming number of players in the equilibrium case play O_2 despite the symmetric appearance of the costs. The reason for this is that for large values of C the priority of the players is to leave the game without incurring a cost, and for $\Delta = ½$ the only way of achieving this is playing O_2 against a O_1-player.

We now examine when such a candidate ESS from case (*i*) is actually an ESS, considering the simplest non-trivial case, namely the game with two rounds.

2.4. Unstable equilibria

Consider the knockout game where there are two rounds and two options. We assume that there is a candidate ESS, labelled **p**, with (internal) ESOs p_1 in round 1 and p_2 in round 2. Suppose that a group of size $\in$ playing $\mathbf{q} = (q_1, q_2)$ tries to invade a population all of whose members play **p**. We evaluate the expected payoff to a **p**-player minus the expected payoff to a **q**-player and thus show when **q** can invade. In particular we find conditions for when no such **q** can invade i.e. when **p** is an ESS.

The mathematical arguments involved to show this are in Appendix B. It is shown when **q** can invade **p**, and that **p** is an ESS, if and only if

$$\Delta\left\{2\Delta(V_0 - V_1) + \left(\frac{1}{2} + \Delta\right)c_{21} - \left(\frac{1}{2} - \Delta\right)c_{12}\right\} < 2^{\frac{1}{2}}(C_1 + C_2).$$

Note that V_2 does not appear in this inequality, so that the value of V_2 does not affect whether our candidate ESS is in fact an ESS (of course V_2 affects the value of p_2; in particular p_2 is not internal unless V_2 lies within a certain range). For Example 1, we have $C_1 + C_2 = 2$ so that the right-hand side of the inequality is $2\sqrt{2}$, while the left-hand side is 6, so that the equilibrium strategy is not an ESS.

There is a parallel with extensive two-person games here, although not an exact one. Van Damme (1991) showed that an LSS is not always an ESS (see Cressman and Schlag, 1998 for a discussion on when backwards induction is a useful method to solve extensive form games). He constructed an example, similar to the knockout idea, where players either played a second stage or stopped after the first stage, depending upon play at the first stage. In this game either both players play a second stage or neither do, the mutant invading by playing so that mutant v mutant contests were likely to play the second stage, and playing cooperatively in the second stage. In our game the situation is different; a player can only increase its chances of progressing at the cost of its opponent. The mutants either play aggressively at first, so that more mutants reach the next stage, and then play passively or the converse, as in Section 2.5. Thus the mutant can indirectly make it marginally more (or less) likely that the next opponent it faces is also a mutant, and behave accordingly. This is a less effective mechanism than that available in the two-person extensive games, so it is reasonable to think that the knockout models are more likely to have ESSs.

2.5. Petal dynamics in knockout games

2.5.1. The replicator dynamic

Suppose that for a particular evolutionary game, the strategies which a player may play are $S_1, \ldots, S_n$ (these may be pure strategies, or 'allowable' mixtures as in the example we consider). Let the proportion of players of S_i at a particular time be p_i ($i = 1, \ldots, n$), so that the average population strategy is the vector $\mathbf{p} = (p_i)$, with the expected payoff (in terms of Darwinian fitness) of an S_i-player in such a mixture being $f_i(\mathbf{p})$ and the overall expected payoff in the population being $F(p) = \sum p_i f_i(p)$. Then the standard replicator dynamic (continuous) is defined by the differential equation

$$\frac{dp_i}{dt} = p_i[f_i(p) - F(p)].$$

Thus the proportion of players which play the better strategies increases with time (what determines a good strategy depends upon the composition of the population). A point in n-dimensional space, represented by the vector $\mathbf{p}$, is locally stable if it is an ESS [this is not necessarily true for the discrete dynamic (Zeeman, 1980)]. The replicator equation has been applied in very many situations (see Hofbauer and Sigmund, 1988).

We shall revisit Example 1. The parameters are as follows:

$$V_0 = 7.5,\ V_1 = 6.5,\ V_2 = 0,$$

$$c_{11} = 25,\ c_{12} = 0,\ c_{21} = 11,\ c_{22} = 1,\ \Delta = 0.5.$$

We have previously shown that (0.5, 0.5) is a Nash equilibrium but not an ESS. In order to study the possible invasion of a population playing $\mathbf{v}$ by some alternative playing $\mathbf{u}$ we need to evaluate $W_2(\mathbf{u}, \mathbf{v})$ the expected future payoff to a $\mathbf{u}$-player who wins in round 2. We have $\mathbf{u} = (u_1, u_2)$ and $\mathbf{v} = (v_1, v_2)$ and $W_2(\mathbf{u}, \mathbf{v})$ depends only on u_1 and v_1, and is given by

$$W_2(\mathbf{u}, \mathbf{v}) = (u_1, 1 - u_1)\, \mathbf{M_1}\, (v_1, 1 - v_1)^T. \qquad (3)$$

To illustrate we shall consider the set of nine possible strategies r_{ij}, ($i, j = 1, 2, 3$) where r_{ij} plays x_i in round 1 and x_j in round 2, where $x_1 = 0.1, x_2 = 0.5$ and $x_3 = 0.9$. Thus r_{22} is the Nash equilibrium. Under this regime, we have from equation (3) that

$$W_2(r_{ij}, r_{kl}) = (x_i, 1 - x_i)\, \mathbf{M_1}\, (x_k, 1 - x_k)^T,$$

which we denote by $W_2(i, k)$, since there is no dependence on j or l, and the matrix $\mathbf{W_2}$ of $W_2(i, k)$ elements for $i, j = 1, 2, 3$ is given in this case by

$$25\mathbf{W_2} = \begin{bmatrix} 137 & 25 & -87 \\ 145 & 25 & -95 \\ 153 & 25 & -103 \end{bmatrix}.$$

Now consider round 2. For strategies which play i and k in round 1 we have payoff matrix $\mathbf{M_2}(i, k)$ in round 2 given by

$$\mathbf{M}_2(i,k) = \begin{bmatrix} (W_2(i,k) - 25)/2 & W_2(i,k) \\ -11 & (W_2(i,k) - 1)/2 \end{bmatrix},$$

which we write as

$$\mathbf{M_2}(i, k) = W_2(i, k)\, \mathbf{A} + \mathbf{B} \qquad (4)$$

where $\mathbf{A}$ is the matrix of probabilities of winning and $\mathbf{B}$ is the matrix of expected costs. Thus the ex-

pected payoff for r_{ij} in a population of r_{kl} players, which we denote by $M_2(r_{ij}, r_{kl})$ is given by

$$M_2(r_{ij}, r_{kl}) = (x_j, 1 - x_j)\, \mathbf{M_2}(i, k)(x_l, 1 - x_l).$$

Substituting from equation (4) we have

$$M_2(r_{ij}, r_{kl}) = A_2(j, l)W_2(i, k) + B_2(j, l)$$

where $A_2(j, l) = (x_j, 1 - x_j)\mathbf{A}(x_l, 1 - x_l)$ and $B_2(j, l) = = (x_j, 1 - x_j)\mathbf{B}(x_l, 1 - x_l)$, $A_2(j, l)$ and $B_2(j, l)$ being the probability of winning in round 2 and the expected costs, for a j-player against an opponent playing l in that round. The matrices $\mathbf{A_2}$ and $\mathbf{B_2}$, are given by

$$\mathbf{A}_2 = \begin{bmatrix} 0.5 & 0.3 & 0.1 \\ 0.7 & 0.5 & 0.3 \\ 0.9 & 0.7 & 0.5 \end{bmatrix},$$

$$25\mathbf{B}_2 = \begin{bmatrix} 38 & 145 & 252 \\ 35 & 150 & 265 \\ 32 & 155 & 278 \end{bmatrix}.$$

The relative values of $M_2(r_{ij}, r_{kl}) = (x_l, 1 - x_j)\mathbf{M_2}(i, k)(x_l, 1 - x_l)$ are given in Table 3.

TABLE 3

Relative payoff of strategy (*i, j*) (row-label), in a population of (*l, k*)-players (column-label)

	(1, 1)	(2, 1)	(3, 1)	(1, 2)	(2, 2)	(3, 2)	(1, 3)	(2, 3)	(3, 3)
(1, 1)	305	–255	–815	–1039	–1375	–1711	–2383	–2495	–2607
(2, 1)	345	–255	–855	–1015	–1375	–1735	–2375	–2495	–2615
(3, 1)	385	–255	–895	–991	–1375	–1759	–2367	–2495	–2623
(1, 2)	609	–175	–959	–815	–1375	–1935	–2239	–2575	–2911
(2, 2)	665	–175	–1015	–775	–1375	–1975	–2215	–2575	–2935
(3, 2)	721	–175	–1071	–735	–1375	–2015	–2191	–2575	–2959
(1, 3)	913	–95	–1103	–591	–1375	–2159	–2095	–2655	–3215
(2, 3)	985	–95	–1175	–535	–1375	–2215	–2055	–2655	–3255
(3, 3)	1057	–95	–1247	–479	–1375	–2271	–2015	–2655	–3295

By inspecting the entries in Table 3, we can identify those strategies which can invade any population. A strategy **u** can invade a population playing **v** if, in column-**v** (that is the column corresponding to **v**) the entry in row-**u** exceeds that in row-**v** (i.e. $E[\mathbf{u}, \mathbf{v}] > E[\mathbf{v}, \mathbf{v}]$, or if these are equal then if, in column-**u** (that is the column corresponding to **u**) the entry in row-**u** exceeds that in row-**v** (i.e. $E[\mathbf{u}, \mathbf{u}] > E[\mathbf{v}, \mathbf{u}]$). For example only (1, 3) and (3, 1) can invade (2, 2); that is only (0.1, 0.9) and (0.9, 0.1) can invade the Nash equilibrium (0.5, 0.5). Table 4 contains the complete set of information regarding which strategies can invade which monomorphic populations; if the entry in row (*i*, *j*) and column (*k*, *l*) is + then the former can invade a population of the latter.

TABLE 4

Specification of invasions possible

	(1, 1)	(2, 1)	(3, 1)	(1, 2)	(2, 2)	(3, 2)	(1, 3)	(2, 3)	(3, 3)
(1, 1)	0	–	+	–	–	+	–	+	+
(2, 1)	+	0	+	–	–	+	–	+	+
(3, 1)	+	–	0	–	+	+	–	+	+
(1, 2)	+	+	–	0	–	+	–	+	+
(2, 2)	+	+	–	+	0	+	–	+	+
(3, 2)	+	+	–	+	–	0	–	+	+
(1, 3)	+	+	–	+	+	–	0	–	+
(2, 3)	+	+	–	+	–	–	+	0	+
(3, 3)	+	+	–	+	–	–	+	–	0

If (and only if) the entry is + for row-label (*i, j*) and column label (*l, k*) then the strategy (*i, j*) can invade a population of (*l, k*)-players.

We observe that there are sequences of strategies, labelled $\{s_1, s_2, \ldots, s_u\}$ say, such that s_u invades s_1 and s_i invades s_{i+1} for $i = 1, \ldots, u - 1$. In particular

$$\{(0.5, 0.5), (0.5, 0.1), (0.9, 0.1)\}$$

is such a set and we investigate the dynamics of this particular set in more detail below.

2.5.2. Phase portraits for three strategies

For games with three strategies, the proportion in the population of each of the strategies can be represented upon an equilateral triangle of unit height. Since the triangle is equilateral the sum of the perpendicular distances from each edge is equal to the height of the triangle, and thus is 1. Each strategy, therefore, can be represented by one of the vertices with the proportion of this strategy being the perpendicular distance from the opposite edge. For example, if the population all play strategy 1, then the corresponding point in the triangle is the vertex representing that strategy; if the population plays strategies 2 and 3 with equal probability, the corresponding point is midway along the edge between the vertices associated with strategies 2 and 3.

If we make a small disturbance away from the equilibrium (adding a small proportion of players of the other two strategies), the behaviour follows the

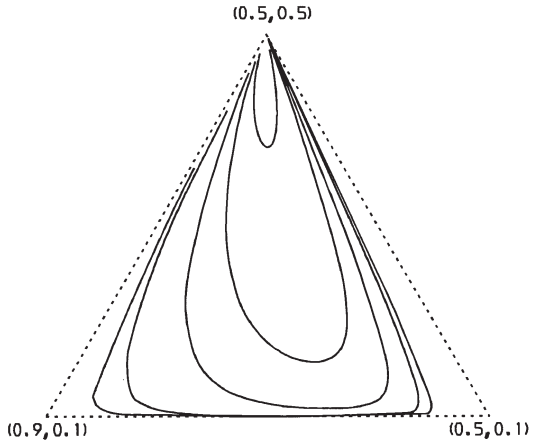

FIG. 1. Trajectories of the composition of the population for a 2-round knockout game with three strategies. The marked trajectories represent invasions into a population of (0.5, 0.5)-players by a small group containing (0.9, 0.1)-players and (0.5, 0.1)-players. As the proportion of (0.9, 0.1)-players increases the petal enlarges

pattern in Figure 1, with its path in the shape of a petal (at least for small disturbances). The population can move very far from the equilibrium if most of the introduced group plays (0.9, 0.1) no matter how small the disturbance (if the group is entirely (0.9, 0.1) then the population follows the edge of the triangle until the whole population plays (0.9, 0.1)). The size of the 'petal' decreases the larger the (0.5, 0.1) component in the added group, however as long as this component is non-zero the population always returns to the equilibrium. Hence even for a small disturbance, the population can spend a long time away from the equilibrium (which is unstable), but the dynamic will move the population back to the equilibrium eventually. This 'petal' phenomenon was discussed in Hofbauer (1993). There is another parallel with extensive two-person games here. Cressman (1997) proved that under certain conditions solutions obtained using backwards induction, as in Selten (1983), were *locally asymptotically stable*, so that the evolutionary dynamic eventually returned the population to such a solution, even if it was not an ESS; this is precisely what happens in our case.

2.6. The three-option case

We now briefly examine the knockout game where there are three options to show how the ideas already discussed can be adapted to consider more than two options. The payoff matrix for players in a particular round conditional upon future rounds is shown and an outline of how to find ESOs is given. In general there may be up to three (or indeed no) ESOs of a round for the three-option case, conditional on the play in lower numbered rounds. We then describe the conditions for which every ESO includes all three options (and is thus unique).

Finding the ESOs

The rewards, costs and the probability of victory against other strategies are as described earlier in this section. Let W_k again be the expected payoff for winning in round k. For 2-player matrix games, subtracting a constant from every element in a column of a matrix does not affect the ESSs of that matrix (Zeeman, 1980). Thus subtracting a constant from the matrix of payoffs for round k does not affect the ESOs of that round. We shall subtract the leading diagonal element from each column. Then the three-player game has the following payoff matrix for round k:

$$M_k = \begin{bmatrix} 0 & 1/2(c_{22} - c_{12}) + \Delta_{12}(W_k - V_k + c_{12}) & 1/2(c_{33} - c_{13}) - \Delta_{31}(W_k - V_k + c_{13}) \\ 1/2(c_{11} - c_{21}) - \Delta_{12}(W_k - V_k + c_{21}) & 0 & 1/2(c_{33} - c_{23}) + \Delta_{23}(W_k - V_k + c_{23}) \\ 1/2(c_{11} - c_{31}) + \Delta_{31}(W_k - V_k + c_{31}) & 1/2(c_{22} - c_{32}) - \Delta_{23}(W_k - V_k + c_{32}) & 0 \end{bmatrix}.$$

Three strategy games and their ESSs are discussed in Vickers and Cannings (1988), and their results can be readily used to find the ESOs of the above matrix.

An internal ESO is one in which the probability of playing a given pure option is greater than zero for all of the options. We can find a recurrence relation between ESOs in successive rounds in a similar manner to Section 2.3. Defining $r_k = W_k - V_k$ and $D_k = V_k - V_{k+1}$ then equation (1) yields the following recurrence relation for r_k.

$$2r_{k+1} = r_k + 2D_k - 2X_k$$

Thus, since $r_1 = V_0 - V_1$, we can find the value of r_k for every round and it is shown in Appendix C that there is an internal Nash equilibrium (p_{1k}, p_{2k}, p_{3k}) where

$$p_{ik} = \frac{y_{ik}}{y_{1k} + y_{2k} + y_{3k}}$$

and

$$y_{1k} = \Delta_{23}\Delta r_k^2 + C_{11} r_k + C_{12}$$
$$y_{2k} = \Delta_{31}\Delta r_k^2 + C_{21} r_k + C_{22}$$
$$y_{3k} = \Delta_{12}\Delta r_k^2 + C_{31} r_k + C_{32}$$

if $y_{ik} > 0 \forall_i$, where all the parameters C_{ij} and Δ_{ij} are defined in Appendix C.

The Nash equilibrium is also an ESO if the matrix satisfies the negative-definiteness condition of Vickers and Cannings (1988). This depends upon the costs only, and so if satisfied for one round it is satisfied for all and vice versa. Thus it is possible to generate the unique Nash equilibrium for the whole game.

3. Discussion

The knockout model provides an example of a situation where all conflicts in a population are pairwise, but are organised into a structure and thus not independent. This is not necessarily a realistic model of the way natural populations behave, but rather gives an insight into natural conflicts and how (and in what way) behaviour may be much more complex than that predicted by classical 2-player game theory. The dependence between games leads to behaviour which is qualitatively different to that from contests where the pairwise contests are independent.

It was shown in Broom et al. (2000) that there may be more or less aggression in a population playing a contest with a knockout format than in independent pairwise games, providing that there is no possibility of adjusting the strategy from round to round, depending upon the number of players and the rewards and costs involved. In Section 2.3 we see that when there is free choice of behaviour from round to round, the level of aggression increases the more rounds there are, and is more than for independent contests. Thus this freedom is damaging to the individuals, but will nonetheless evolve into the population.

In Section 2.3 it is shown that for a population organised into an n round knockout tournament with two available options, in the variable option case there may be as many as 2^n ESSs, but there is a simple commonly satisfied condition which if satisfied guarantees at most one ESS. It is shown in Section 2.4 that there might be no ESS at all (in 2-player game theory there is always an ESS when there are two strategies). It appears that any Nash equilibrium is less likely to be an ESS than for classical theory, since even the existence of a sequence of *ESO*s is not sufficient to guarantee an ESS. Thus there are extra conditions to be met for a strategy to be an ESS than in 2-player game theory. In particular a completely internal equilibrium is especially susceptible to invasion; the more pure options involved in the ESOs which make up the Nash equilibrium strategy the more susceptible it is (similarly, the more rounds, the more susceptible it is). Thus in real populations the number of observed options which occur in reality might be lower if there is a structure to the games that are played. However, it should be noted that there is a reverse tendency as well, since different pure options may be involved in the ESO for different rounds, thus increasing the overall number of pure options used in total.

As we have seen, the game can be very complex if players are able to change their strategies from round to round. For two options, strategies are vectors not just single numbers (for more than two options they are matrices rather than vectors). A recursive dynamic programming method was found which specifies all the candidate ESSs of a game. Showing when a candidate ESS is actually an ESS is a harder problem. In Section 2.4 we do this for the 2 round case. The method used can be generalised to more rounds, but calculations quickly become complicated. Section 2.5 shows that the dynamics of these games is also more complex than those for 2-player games. Indeed the example given is the simplest possible non-trivial knockout game (2-round, 2-option $\Delta = ½$) and it is to be expected that even more complicated behaviour will result from a more complex game. There is an interesting correspondence between the knockout model and the extensive two-person game of Selten (1983), which deserves to be explored further.

Acknowledgements

One of the authors (MB) acknowledges the help of Nuffield grant SCI/180/97/125/G in completing this work. MB also was supported by a BBSRC research grant reference number GR/J31520 when some of this work was done.

APPENDIX

A) A recurrence relation for y_k

The following argument finds a recurrence relation for y_k. In general for a population playing the mixed strategy $(p_1, \ldots, p_n)$ each placer has a probability of ½ of being eliminated in any round, and the expected cost for a player in round k is

$$X_k = p_k^2 \frac{c_{11}}{2} + (1-p_k)^2 \frac{c_{22}}{3} + p_k(1-p_k)\left[\left(\frac{1}{2}+\Delta\right)c_{21} + \left(\frac{1}{2}-\Delta\right)c_{12}\right].$$

It follows that

$$W_k = \frac{V_{k-1}}{2} + \frac{V_{k-2}}{4} + \ldots + \frac{V_1}{2^{k-1}} + \frac{V_0}{2^{k-1}} - \sum_{i=1}^{k-1} X_i \frac{1}{2^{k-1-i}} = v_k - Y_k$$

where

$$Y_k = \sum_{i=1}^{k-1} \frac{X_k}{2^{k-1-i}}$$

Y_k is thus the expected future cost incurred by a player which wins in round k and

$$Y_k = \sum_{i=1}^{k-1} \frac{X_k}{2^{k-1-i}} \Rightarrow Y_{k+1} = \frac{Y_k}{2} + X_k.$$

It is now possible to find y_{k+1} in terms of y_k.

$$W_{k+1} = v_{k+1} - Y_{k+1} = \frac{v_k}{2} + \frac{V_k}{2} - \frac{Y_k}{2} - X_k(2v_k = V_k + v_{k-1})$$

$$\Rightarrow W_{k+1} = \frac{W_k}{2} + \frac{V_k}{2} - X_k$$

$$\Rightarrow 2(W_{k+1} - V_{k+1}) = (W_k - V_k) + 2(V_k - V_{k+1}) - 2X_k$$

$$\Rightarrow 2C_1 + 2\Delta(W_{k+1} - V_{k+1}) = \Delta(W_k - V_k) + C_1 + 2\Delta(V_k - V_{k+1}) + C_1 - 2\Delta X_k$$

$$\Rightarrow y_{k+1} = \frac{y_k}{2} + a_k - \Delta X_k$$

(a_k is as defined in Section 2.3).

We now rearrange the expression X_k to get it into a more manageable form.

$$X_k = p_k^2 \frac{c_{11}}{2} + (1-p_k)^2 \frac{c_{22}}{2} + p_k(1-p_k)\left[\left(\frac{1}{2}+\Delta\right)c_{21} + \left(\frac{1}{2}-\Delta\right)c_{12}\right]$$

$$= p_k^2(C_1 + C_2) + p_k\left(-C_1 - C_2 + \frac{c_{11}}{2} - \frac{c_{22}}{2}\right) + \frac{c_{22}}{2}$$

$$\Rightarrow X_k = -(C_1 + C_2)p_k(1-p_k) + \frac{1}{2}[c_{11}p_k + c_{22}(1-p_k)].$$

B) Conditions for an ESS for the 2 round 2-player game

Notation

We define and then evaluate a series of terms which help us to find whether **p** is an ESS.

- h_i: the proportion of O_1-players in round i, $i = 1, 2$.
- $g_i(\mathbf{r})$: the probability of an **r**-player playing in round i winning, $i = 1, 2$, $\mathbf{r} = \mathbf{p}$ or $\mathbf{q}$.
- $v_i(\mathbf{r})$: the expected contribution to the payoff of an **r**-player of a loss in round i, $i = 1, 2$, $\mathbf{r} = \mathbf{p}$ or $\mathbf{q}$.
- $E(\mathbf{r})$: the expected total payoff of an r-player in the game, $\mathbf{r} = \mathbf{p}$ or $\mathbf{q}$.

Also define $u_1 = (p_1 - q_1)[1 - 2\Delta(p_2 - q_2)]$ and $u_2 = (p_2 - q_2)$.

The above expressions can be used to find the payoff functions $E(\mathbf{p})$ and $E(\mathbf{q})$, and in particular their difference.

$$E(\mathbf{p}) = v_2(\mathbf{p}) + v_1(\mathbf{p}) + g_2(\mathbf{p})g_1(\mathbf{p})V_0,$$

$$E(\mathbf{q}) = v_2(\mathbf{q}) + v_1(\mathbf{q}) + g_2(\mathbf{q})g_1(\mathbf{q})V_0$$

$$\Rightarrow E(\mathbf{p}) - E(\mathbf{q}) = [v_2(\mathbf{p}) - v_2(\mathbf{q})] + [v_1(\mathbf{p}) - v_1(\mathbf{q})] + [g_2(\mathbf{p})g_1(\mathbf{p}) - g_2(\mathbf{q})g_1(\mathbf{q})]V_0. \quad (5)$$

ESS conditions

Thus we nee to evaluate all the terms given in (5). These equations are labelled (6–18); some lower numbered equations are required to solve those which come later. An indication of which (if any) are required is given after each equation.

$$h_2 = p_2(1-\varepsilon) + q_2\varepsilon = p_2 - \varepsilon u_2 \tag{6}$$

$$g_2(\mathbf{p}) = \frac{1}{2} + \Delta(p_2 - h_2) = \frac{1}{2} + \Delta\varepsilon(p_2 - q_2) = \frac{1}{2} + \Delta\varepsilon u_2 \tag{7}$$

using (6).

$$g_2(\mathbf{q}) = \frac{1}{2} + \Delta(q_2 - h_2) = \frac{1}{2} - \Delta(1-\varepsilon)(p_2 - q_2) = \frac{1}{2} - \Delta(1-\varepsilon)u_2 \tag{8}$$

using (6).

$$h_1 = 2(1-\varepsilon)p_1 g_2(\mathbf{p}) + 2\varepsilon q_1 g_2(\mathbf{q})$$
$$= p_1 - \varepsilon(p_1 - q_1) + 2(1-\varepsilon)\varepsilon\Delta(p_2 - q_2)(p_1 - q_1)$$
$$= p_1 - \varepsilon u_1 - 2\varepsilon^2\Delta u_2(p_1 - q_1) \tag{9}$$

using (7) and (8).

$$g_1(\mathbf{p}) = \frac{1}{2} + \Delta(p_1 - h_1) = \frac{1}{2} + \Delta\varepsilon u_1 + 2\varepsilon^2\Delta^2 u_2(p_1 - q_1) \tag{10}$$

using (9).

$$g_1(\mathbf{q}) = \frac{1}{2} + \Delta(q_1 - h_1) =$$
$$= \frac{1}{2} - \Delta(p_1 - q_1) + \Delta\varepsilon u_1 + 2\varepsilon^2\Delta^2 u_2(p_1 - q_1) \tag{11}$$

using (9).

$$v_2(\mathbf{p}) = \frac{1}{2}(V_2 - c_{11})p_2 h_2 + \left(\frac{1}{2} - \Delta\right)(V_2 - c_{12})p_2(1-h_2) + \left(\frac{1}{2} + \Delta\right)(V_2 - c_{21})(1-p_2)h_2 + \frac{1}{2}(V_2 - c_{22})(1-p_2)(1-h_2) \tag{12}$$

using (6).

$$v_2(\mathbf{q}) = \frac{1}{2}(V_2 - c_{11})q_2 h_2 + \left(\frac{1}{2} - \Delta\right)(V_2 - c_{12})q_2(1-h_2) + \left(\frac{1}{2} + \Delta\right)(V_2 - c_{21})(1-q_2)h_2 + \frac{1}{2}(V_2 - c_{22})(1-q_2)(1-h_2) \tag{13}$$

using (6).

$$v_1(\mathbf{p}) = g_2(\mathbf{p})\left\{\frac{1}{2}(V_1 - c_{11})p_1 h_1 + \left(\frac{1}{2} - \Delta\right)(V_1 - c_{12})p_1(1-h_1) + \left(\frac{1}{2} + \Delta\right)(V_1 - c_{21})(1-p_1)h_1 + \frac{1}{2}(V_1 - c_{22})(1-p_1)(1-h_1)\right\} \tag{14}$$

using (7) and (9).

$$v_1(\mathbf{q}) = g_2(\mathbf{q})\left\{\frac{1}{2}(V_1 - c_{11})q_1 h_1 + \left(\frac{1}{2} - \Delta\right)(V_1 - c_{12})q_1(1-h_1) + \left(\frac{1}{2} + \Delta\right)(V_1 - c_{21})(1-q_1)h_1 + \frac{1}{2}(V_1 - c_{22})(1-q_1)(1-h_1)\right\} \tag{15}$$

using (8) and (9). We can now combine the above expressions and then substitute into equation (5).

$$v_2(\mathbf{p}) - v_2(\mathbf{q}) = (p_2 - q_2)\left\{\left[-\frac{1}{2}c_{11} + \left(\frac{1}{2}+\Delta\right)c_{21} + \left(\frac{1}{2}-\Delta\right)c_{12} - \frac{1}{2}c_{22}\right]h_2 + \frac{1}{2}c_{22} - \left(\frac{1}{2}-\Delta\right)c_{12} - \Delta V_2\right\}$$

$$= (p_2 - q_2)[-h_2(C_1 + C_2) + y_2 - \Delta W_2]$$

$$= u_2[\varepsilon u_2(C_1 + C_2) - \Delta W_2]$$

using (12) and (13).

$$v_1(\mathbf{p}) - v_1(\mathbf{q}) =$$

$$(g_2(\mathbf{p})p_1 - g_2(\mathbf{q})q_1)[-h_1(C_1 + C_2) + y_1 - \Delta W_1] +$$

$$[g_2(\mathbf{p}) - g_2(\mathbf{q})]\left[h_1(V_1 - c_{21})\left(\frac{1}{2}+\Delta\right) + (1-h_1)(V_1 - c_{22})\frac{1}{2}\right]$$

$$= \left[\left(\frac{1}{2} + \Delta\varepsilon u_2 - \Delta u_2\right)(p_1 - q_1) + \Delta u_2 p_1\right]$$

$$\{[\varepsilon u_1 + 2\varepsilon^2 \Delta u_2(p_1 - q_1)](C_1 + C_2) - \Delta V_0\} + \Delta u_2\left\{p_1(V_1 - c_{21})\left(\frac{1}{2}+\Delta\right) + (1-p_1)(V_1 - c_{22})\frac{1}{2} - [\varepsilon u_1 + 2\varepsilon^2 \Delta u_2(p_1 - q_1)]\left[(V_1 - c_{21})\left(\frac{1}{2}+\Delta\right) - (V_1 - c_{22})\frac{1}{2}\right]\right\} \quad (17)$$

$$g_2(\mathbf{p})g_1(\mathbf{p}) - g_2(\mathbf{q})g_1(\mathbf{q}) =$$

$$\left(\frac{1}{2} + \Delta\varepsilon u_2\right)\left(\frac{1}{2} + \Delta\varepsilon u_1\right) - \left(\frac{1}{2} - \Delta(p_1 - q_1) + \Delta\varepsilon u_1\right)\left(\frac{1}{2} - \Delta(1-\varepsilon)u_2\right)$$

$$= \frac{1}{2}\Delta u_2 + \frac{1}{2}\Delta u_1 + \Delta^2 \varepsilon u_2[u_1 + (p_1 - q_1)] + O(\varepsilon^2). \quad (18)$$

Using the equations (16)–(18) we can express equation (5) as follows (ignoring terms in ε^2 and higher orders).

$$E(\mathbf{p}) - E(\mathbf{q}) = \Delta\{-u_2 W_2 + \frac{1}{2}u_2 V_0 + u_2\left(p_1(V_1 - c_{21})\left(\frac{1}{2}+\Delta\right) + (1-p_1)(V_1 - c_{22})\frac{1}{2} - \Delta V_0 p_1\right)\} +$$

$$\varepsilon\{u_2^2(C_1 + C_2) + \Delta^2 u_2(u_1 + (p_1 - q_1))V_0 - \Delta u_2 u_1\left((V_1 - c_{21})\left(\frac{1}{2}+\Delta\right) - (V_1 - c_{22})\frac{1}{2}\right) + \frac{1}{2}u_1^2(C_1 + C_2) - \Delta^2 u_2(p_1 - q_1)V_0\}. \quad (19)$$

The constant term in equation (19) is Δu_2 multiplied by ($-W_2$ + the payoff to a O_2-player in the final when everyone plays $\mathbf{p} = (p_2, p_1)$). Note that the probability of winning in the final for a O_2-player in this case is $\frac{1}{2} - \Delta p_1$. But W_2 is the expected payoff to a player which wins in the first round, i.e. reaches the final when everyone plays $\mathbf{p}$. Since $\mathbf{p}$ is the equilibrium strategy the payoff to O_1-players in the final is the same as that to O_2-players, and thus equals W_2. Hence the constant term is zero.

Therefore the difference in the payoffs $E(\mathbf{p}) - E(\mathbf{q})$ reduces to the term in ε, i.e.

$$E(\mathbf{p}) - E(\mathbf{q}) = \varepsilon\left\{u_2^2(C_1 + C_2) + \frac{1}{2}u_1^2(C_1 + C_2) + \Delta u_1 u_2[\Delta(V_0 - V_1) + p_1(C_1 + C_2) + \left(\frac{1}{2}+\Delta\right)c_{21} - \frac{1}{2}c_{22}]\right\}.$$

Using the fact that

$$p_1 = \frac{\Delta(V_0 - V_1) + C_1}{C_1 + C_2},$$

$$E(\mathbf{p}) - E(\mathbf{q}) = \varepsilon\{u_2^2(C_1 + C_2) + \frac{1}{2}u_1^2(C_1 + C_2) + \Delta u_1 u_2\left[2\Delta(V_0 - V_1) + \left(\frac{1}{2}+\Delta\right)c_{21} - \left(\frac{1}{2}-\Delta\right)c_{12}\right]\}. \quad (20)$$

Using an alternative substitution we obtain

$$E(\mathbf{p}) - E(\mathbf{q}) = \varepsilon\{u_2^2(C_1 + C_2) + \frac{1}{2}u_1^2(C_1 + C_2) + \Delta u_1 u_2\left[(2p_1 - 1)(C_1 + C_2) + \frac{1}{2}c_{11} - \frac{1}{2}c_{22}\right]\}.$$

From (20) the third term is positive when $\Delta = ½$ i.e.

$$(2p_1 - 1)(C_1 + C_2) + \frac{1}{2}c_{11} - \frac{1}{2}c_{22} > 0$$

$$\Rightarrow \frac{1}{2}c_{11} - \frac{1}{2}c_{22} > -(C_1 + C_2).$$

The expression (21) is thus positive if u_1 and u_2 have the same sign. For a strategy $\mathbf{q} = (q_1, q_2)$ to invade the equilibrium, therefore, the probability of playing option O_1 must be greater than that for the equilibrium in one round and less than that for the equilibrium for the other round. It is possible under some conditions to find such a strategy (see below).

Expression (20) is a quadratic equation in u_1 and u_2. It is positive for all u_1 and u_2, i.e. **p** is an ESS, if and only if

$$\Delta\{2\Delta(V_0 - V_1) + \left(\frac{1}{2} + \Delta\right)c_{21} - \left(\frac{1}{2} - \Delta\right)c_{12}\} < 2^{\frac{1}{2}}(C_1 + C_2)$$

(in fact u_1 and u_2 are bounded, but u_1/u_2 is not).

C) 3-strategy ESOs

We define the following parameters:

Let $c^*_{ij} = c_{ij}(1 - 2\Delta_{ij}) \forall i, j$ and let $\Delta = \Delta_{12} + \Delta_{23} + \Delta_{31}$. Further let C_{ij} $i = 1, 2, 3; j = 1, 2$ be defined as follows:

$$C_{11} = \frac{1}{2}(-c^*_{12} - 2c^*_{23} + c^*_{13} - c_{22} + 2c^*_{32} + c_{33}),$$

$$C_{12} = \frac{1}{4}(c^*_{12}c^*_{23} + c^*_{13}c^*_{32} + c_{22}c_{33} - c^*_{12}c_{33} - c^*_{13}c_{22} - c^*_{23}c^*_{32}),$$

$$C_{21} = \frac{1}{2}(-c^*_{23} - 2c^*_{31} + c^*_{21} - c_{33} + 2c^*_{13} + c_{11}),$$

$$C_{22} = \frac{1}{4}(c^*_{23}c^*_{31} + c^*_{21}c^*_{13} + c_{33}c_{11} - c^*_{23}c_{11} - c^*_{21}c_{33} - c^*_{31}c^*_{13}),$$

$$C_{31} = \frac{1}{2}(-c^*_{31} - 2c^*_{12} + c^*_{32} - c_{11} + 2c^*_{21} + c_{22}),$$

$$C_{32} = \frac{1}{4}(c^*_{31}c^*_{12} + c^*_{31}c^*_{21} + c_{11}c_{22} - c^*_{31}c_{22} - c^*_{32}c_{11} - c^*_{12}c^*_{21}).$$

In Vickers and Cannings (1988) the 3-strategy payoff matrix is written as

$$\begin{bmatrix} 0 & a & b \\ c & 0 & d \\ e & f & 0 \end{bmatrix}$$

and it is shown that for there to be an internal ESO it is required that

$$ad + bf - df > 0,$$

$$ae + cf - ac > 0,$$

$$\text{and } bc + de - be > 0.$$

Let $y_{1k} = ad + bf - df$, then

$$y, k = \frac{1}{4}(c_{22}c_{33} + c^*_{12}c^*_{23} - c^*_{12}c_{33} - c_{22}c^*_{23} + c_{22}c_{33} - c^*_{13}c_{22} - c^*_{32}c_{33} + c^*_{13}c^*_{32} - c_{22}c_{33} - c^*_{23}c^*_{32} + c_{22}c^*_{23} + c^*_{32}c_{33})$$

$$+(W_k - V_k)^2(\Delta_{12}\Delta_{23} + \Delta_{23}\Delta_{31} + \Delta^2_{23})$$

$$+\frac{1}{2}(W_k - V_k)(c_{22} - c^*_{12} + c_{33} - c^*_{23} - c_{33} + c^*_{13} - c_{22} + c^*_{32} + c_{33} - c^*_{23} - c_{22} + c^*_{32})$$

$$= (W_k - V_k)^2\Delta_{23}\Delta + (W_k - V_k)C_{11} + C_{12}.$$

Defining $y_{2k} = ae + cf - ac$ and $y_{3k} = bc + de - be$ and using cyclic symmetry it is easy to show that

$$y_{2k} = (W_k - V_k)^2\Delta_{31}\Delta + (W_k - V_k)C_{21} + C_{22}$$

and $y_{2k} = (W_k - V_k)^2\Delta_{12}\Delta + (W_k - V_k)C_{31} + C_{32}$

i.e.

$$y_{1k} = \Delta_{23}\Delta r_k^2 + C_{11}r_k + C_{12},$$

$$y_{2k} = \Delta_{31}\Delta r_k^2 + C_{21}r_k + C_{22}$$

and $y_{3k} = \Delta_{12}\Delta r_k^2 + C_{31}r_k + C_{32}$.

If $y_{ik} > 0$ $\forall$i then (p_{1k}, p_{2k}, p_{3k}) is an internal Nash equilibrium where

$$p_{ik} = \frac{y_{ik}}{y_{1k} + y_{2k} + y_{3k}}.$$

Note that for this strategy to be an internal ESS, the matrix must satisfy the negative-definiteness condi-

tion that $\sqrt{(a+c)}$, $\sqrt{(b+e)}$ and $\sqrt{(d+f)}$ must form a triangle. Each of these terms only depends upon the costs c_{ij}, so that if the condition is satisfied by $\mathbf{M_k}$ for any k, it is satisfied for all k.

References

AXELROD, R. and HAMILTON, W. D. (1981): The evolution of cooperation. *Science* **211**:1390–1396.

BARNARD, C. J. and BURK, T. E. (1979): Dominance hierarchies and the evolution of individual recognition. *J. Theor. Biol.* **81**:65–73.

BINMORE, K. (1992): *Fun and Games (A Text on Game Theory)*. Heath, Lexington.

BISHOP, D. T. and CANNINGS, C. (1976): Models of animal conflict. *Adv. Appl. Prob.* **8**:616–621.

BROOM, M., CANNINGS, C. and VICKERS, G. T. (1996): Choosing a nest site: Contests and catalysts. *Amer. Nat.* **147**: 1108–1114.

BROOM, M., CANNINGS, C. and VICKERS, G. T. (1997a): A sequential-arrivals model of territory acquisition. *J. Theor. Biol.* **189**:257–272.

BROOM, M., CANNINGS, C. and VICKERS, G. T. (1997b): Multiplayer matrix games. *Bull. Math. Biol.* **59**:931–952.

BROOM, M., CANNINGS, C. and VICKERS, G. T. (2000): Evolution in knockout conflicts: The fixed strategy case. *Bull. Math. Biol.* **62**:451–466.

CANNINGS, C. and WHITTAKER, J. C. (1994): The finite horizon war of attrition. *Games and Economic Behaviour* **11**: 193–236.

CRESSMAN, R. (1992): *The Stability Concept of Evolutionary Game Theory: A Dynamic Approach.* Lecture Notes Biomath. 94, Springer-Verlag, Berlin.

CRESSMAN, R. (1997): Dynamic stability in symmetric extensive form games. *Int. J. Game Theory* **26**:525–547.

CRESSMAN, R. and SCHLAG, K. H. (1998): The dynamic (in)-stability of backwards induction. *J. Econ. Theory* **83**: 260–285.

GRAFEN, A. (1990a): Sexual selection unhandicapped by the Fisher process. *J. Theor. Biol.* **144**:473–516.

GRAFEN, A. (1990b): Biological signals as handicaps. *J. Theor. Biol.* **144**:517–546.

HAIGH, J. (1975): Game theory and evolution. *Adv. Appl. Prob.* **7**:8–11.

HAIGH, J. and CANNINGS, C. (1989): The *n*-person war of attrition. *Acta Applicandae Mathematicae* **14**:59–74.

HOFBAUER, J. (1993): Ecological differential equations: Permanence and heteroclinic cycles. *Proceedings Equadiff.,* Bratislava.

HOFBAUER, J. and SIGMUND, K. (1988): *The Theory of Evolution and Dynamical Systems*. Cambridge Univ. Press.

HOFBAUER, J. and SIGMUND, K. (1998): *Evolutionary Games and Population Dynamics*. Cambridge Univ. Press.

LUCE, R. D. and RAIFFA, H. (1957): *Games and Decisions.* Wiley.

MAYNARD SMITH, J. (1982): *Evolution and the Theory of Games*. Cambridge Univ. Press.

MAYNARD SMITH, J. and PRICE, G. R. (1973): The logic of animal conflict. *Nature* **246**:15–18.

MESTERTON-GIBBONS, M. and DUGATKIN, L. A. (1995): Towards a theory of dominance hierarchies: Effect of assessment, group size and variation in fighting ability. *Behav. Ecol.* **6**:416–423.

PALM, G. (1984): Evolutionary stable strategies and game dynamics for *n*-person games. *J. Math. Biol.* **19**:329–334.

SELTEN, R. (1983): Evolutionary stability in extensive two-person games. *Math. Social Sciences* **5**:269–363.

VAN DAMME, E. (1991): *Stability and Perfection of Nash Equilibria.* Second edition. Springer-Verlag, Berlin.

VEHRENCAMP, S. L. (1983): A model for the evolution of despotic versus egalitarian societies. *Anim. Behav.* **31**:667–682.

VICKERS, G. T. and CANNINGS, C. (1988): Patterns of ESS's 1. *J. Theor. Biol.* **132**:387–408.

VON NEUMANN, J. and MORGENSTERN, O. (1944): *Theory of Games and Economic Behaviour*. Princenton Univ. Press.

ZEEMAN, E. C. (1980): Population dynamics from game theory. In NITECKI, A. and ROBINSON, C. (eds): *Global Theory of Dynamical Systems.* Springer, New York.