

The use of multiplayer game theory in the modelling of biological populations

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Abstract

The use of game theory in modelling the natural world is widespread. However this modelling mainly involves two player games only, or ‘playing the field’ games where an individual plays against an entire (infinite) population. Game theoretic models are common in economics as well, but in this case the use of multiplayer games has not been neglected. This paper outlines where multiplayer games have been used in evolutionary modelling and the merits and limitations of these games. Finally we discuss why there has been so little use of multiplayer games in the biological setting and what developments might be useful.

1 Introduction

In this section we start with an overview of important game theoretic concepts. In later sections the various multiplayer games used to model evolutionary processes are broken down into categories and discussed in turn. In Section 2 we discuss true multiplayer games. Section 3 describe contests which comprise pairwise games built into a dependence structure and hence a single multiplayer conflict. In Section 4 we see some related models which share some of the characteristics of the dependent games of Section 3 but are not truly multiplayer games. Finally in the discussion we look at the collection of models available and examine the considerable room for development of the idea of multiplayer game modelling.

1.1 Game Theory

The theory of games is a mathematical theory of conflict situations where the outcome is determined by the choices of two or more interacting individuals, originating with Von Neumann and Morgenstern (1944). Each player has some, but not total, control over the outcome. The investigation of such games has been very extensive and in a number of formulations. We briefly discuss two methods of describing a game which prove useful in the later sections.

Games in Normal Form

A game in normal form is defined by a set of players, a set of strategies for each player and a reward or *payoff* function which defines the reward to each player for each set of choices made by all players. A very common example is the bi-matrix game, which concerns the situation where there are two players, player 1 having a finite set of *pure strategies* $\{1, \dots, m\}$, which are the options that the player can choose to play in a particular game, and player 2 having a finite set of pure strategies $\{1, \dots, n\}$. Players make a simultaneous choice and if player 1 plays i and player 2 plays j then the first player receives a_{ij} and the second receives b_{ij} . The payoffs can then be grouped into payoff matrices $A = (a_{ij}), B = (b_{ij})$. Players may play mixed strategies, i.e. $\mathbf{p}^T = (p_1, \dots, p_m)$ is the strategy where player 1 plays i with probability p_i , for all i . A strategy pair (\mathbf{p}, \mathbf{q}) is called a *Nash Equilibrium* if and only if neither player can profitably alter their strategy (i.e. increase their payoff) unilaterally.

Extensive Form Games

In some contests individuals do not make single simultaneous decisions. Either they choose sequentially, or one or more individuals may have more than one decision to make. These contests are best described using a game tree, which is a finite tree with a single origin node and other nodes follow sequentially on paths. At every point where a decision is made by one of the players (or an outcome is decided by chance) there is a branching of the tree. The end nodes of the tree denote the end of the game, and each has a payoff vector determining the reward at this point to all players. Each player has a set of nodes where it makes a choice and a set of choices for each such node; its strategy is the collection of choices it will make at all of these nodes. Such a game is said to be in *extensive form* (see Selten, 1983 or van Damme, 1991). The method of dynamic programming is used to work backwards from the final solutions to find the best strategy to employ at each node, and hence at the origin node (see Mangel and Clark, 1988). This idea is used in several of the models described in this paper. It is possible to rewrite an extensive form game in normal form, but this will typically be non-generic and some of the Nash equilibria prescribe an irrational sequence of choices.

1.2 Evolutionary Game Theory

Game theory has been widely used to model the natural world, particularly in the area of animal conflicts. It has provided explanations for apparently paradoxical situations, for example 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 and Grafen, 1990b). Some important texts are Cressman (1992), Hofbauer and Sigmund (1998) and Maynard Smith (1982). Of particular significance has been the concept of an Evolutionarily Stable Strategy (ESS) which was introduced by Maynard Smith and Price (1973). An ESS is a strategy, which if adopted in a conflict by a population, cannot be invaded by any other strategy played by a small mutant group. The ESS is thus stable and persists through time, provided that all the payoff parameters and the set of available pure strategies remain unchanged.

A standard formulation for modelling a conflict amongst an animal population leads to the consideration of *matrix games*, and is as follows. Consider a population of animals competing for some resource e.g. food or mates. Individuals compete in pairwise games for a reward. Assume that all members of the population are indistinguishable (in that they are of the same size and strength etc.) and each individual is equally likely to face each other individual. There are a finite number of pure strategies available to the players to play in a particular game. These strategies are labelled $1, \dots, n$. Given the strategies played the outcome is determined; if player 1 plays i against player 2 playing j then player 1 receives reward a_{ij} (player 2 receives a_{ji}) representing an adjustment in Darwinian fitness. The value a_{ij} can be thought of as an element in the $n \times n$ payoff matrix \mathbf{A} (thus these games are referred to as matrix games). This corresponds to the bi-matrix game with $m = n$ and $B = A^T$.

An animal can play a mixed strategy represented by a probability vector \mathbf{p} . The expected payoff to player 1 playing \mathbf{p} against player 2 playing \mathbf{q} , which is written as $E[\mathbf{p}, \mathbf{q}]$, is

$$E[\mathbf{p}, \mathbf{q}] = \sum a_{ij} p_i q_j = \mathbf{p}^T \mathbf{A} \mathbf{q} \quad (1)$$

Suppose that \mathbf{p} is played by almost all members of the population, the rest of the population being a small mutant group constituting a fraction α

of the total population playing \mathbf{q} . \mathbf{p} is said to be *evolutionarily stable* (ES) against \mathbf{q} if

$$E[\mathbf{p}, (1 - \alpha)\mathbf{p} + \alpha\mathbf{q}] > E[\mathbf{q}, (1 - \alpha)\mathbf{p} + \alpha\mathbf{q}] \quad (2)$$

for all sufficiently small α . Thus \mathbf{p} does better against the mean population strategy than \mathbf{q} does.

This implies that

$$(i) E[\mathbf{p}, \mathbf{p}] \geq E[\mathbf{q}, \mathbf{p}] \quad (3)$$

and if (i) is satisfied with equality, then

$$(ii) E[\mathbf{p}, \mathbf{q}] > E[\mathbf{q}, \mathbf{q}] \quad (4)$$

The vector \mathbf{p} is said to be an Evolutionarily Stable Strategy (ESS) if \mathbf{p} is ES against all $\mathbf{q} \neq \mathbf{p}$. Thus if all members of a population play \mathbf{p} , it cannot be invaded by any other strategy.

The *support* of \mathbf{p} is the set $S(\mathbf{p}) = \{i : p_i > 0\}$. An ESS \mathbf{p} is an *internal* ESS if $S(\mathbf{p}) = \{1, \dots, n\}$ so that every pure strategy is involved in the ESS. A payoff matrix can have many ESSs (see for example, Broom, 2000). There are restrictions on which strategies can be ESSs of the same payoff matrix, and this has been investigated using the concept of a *Pattern of ESSs* (see Cannings and Vickers, 1988; Vickers and Cannings, 1988). If $\mathbf{p}_1, \mathbf{p}_2, \dots, \mathbf{p}_N$ are the ESSs of A , then A has *pattern* $P = \{S(\mathbf{p}_1), S(\mathbf{p}_2), \dots, S(\mathbf{p}_N)\}$. It is shown in Bishop and Cannings (1976) that no ESS can have support which is a subset of the support of another ESS of the same matrix; this result is often known as the *Bishop-Cannings Theorem*, although the true theorem gives a rather more powerful result; for the full theorem, see Bishop and Cannings (1976). A method for finding all the ESSs of a matrix is given by Haigh (1975).

2 True Multiplayer Games

In this section we consider games which demonstrate genuine multiplayer behaviour in the sense that more than two players make simultaneous decisions which decide the reward to each of the players, in contrast to later sections which consider interactions of non-independent pairwise games. This type of game has only been considered twice in the evolutionary setting to my knowledge, although it is more common in economics.

2.1 The N-player War of Attrition

The War of Attrition was one of the earliest game theoretic models used to investigate the behaviour of animals (Maynard Smith, 1974).

Two contestants compete for a prize of value V , and the winner is the one who is prepared to wait the longest. Both players pay a cost equal to the length of the time spent waiting. Letting $E(x, y)$ be the reward to an individual prepared to wait for time x against one prepared to wait y ,

$$E(x, y) = \begin{cases} V - y & x > y \\ -x & x < y \end{cases} \quad (5)$$

$$E(x, x) = V/2 - x \quad (6)$$

The game has a single ESS, namely to choose x drawn at random from an exponential distribution with mean V .

Haigh and Cannings (1989) extended this model to a multiplayer setting, considering four different models, with different assumptions. This is the earliest example of a multiplayer game applied to a biological setting (though see Palm, 1984, for a discussion of a general notion of a multiplayer ESS).

Model A: n players compete for a single reward value V ; each must pick their own value of x at the start of the game, the largest value gains the reward, all other players pay the time that they waited until dropping out. Thus

$$E(X_1; X_2, \dots, X_n) = \begin{cases} V - W_1 & X_1 > W_1 \\ -X_1 & X_1 < W_1 \end{cases} \quad (7)$$

where $W_1 = \text{Max}(X_2, \dots, X_n)$. The rewards to other players follow similarly. Here using analogous reasoning to the two-player game, there is a unique ESS found by considering the only possible distribution to give an equal payoff to any value of x played, which means that each player chooses a value independently from the distribution function

$$G(x) = (1 - \exp(-x/V))^{1/(n-1)} \quad (8)$$

Model B: The scenario is as in A, except that when a player drops out, all remaining players may reassess their strategy in light of the new situation. It turns out that in this situation the best play involves all but two players dropping out immediately (assuming they effectively do this sequentially, so that one leaves first and then the remaining players can then change their minds) the two players then playing an immediate war of attrition. This again follows from the fact that the expected reward when two players remain is zero, so that with more than two players this is not worth any time investment at all. This model is a special case of

Model C: The scenario is as in B, except there is a set of rewards available $V_n < V_{n-1} < \dots < V_1$, the player leaving when there are exactly j animals left receiving reward V_j . There is a unique ESS to this game, namely with j players remaining, wait for time X , where X is exponential with mean $(j-1)(V_{j-1} - V_j)$ for each $j : 2 \leq j \leq n$.

Model D extends the game by considering scenario C, but with only a single decision available at the start of the game as in scenario A and is the most complex (and probably the least realistic) of the four models.

Model C is an important theoretical contribution and seems the most realistic of the models. In particular the lack of reassessment in A and D when presented with obvious cues does not seem very plausible. The special case of C that is model B gives the most generally well-known phenomenon from this extension of the war of attrition, that all but two players pull out immediately so that the multiplayer game reduces to the two player one. One application of this idea is the modelling of juvenile dispersal from a territory, e.g. badgers (see Blackwell, 1997).

2.2 Multiplayer matrix games

Broom *et al* (1997b) extended the idea of the matrix game to the multiplayer setting. This is the most general in character of the multiplayer models, and considers general results for relatively simple cases. The assumption is that the order of opponents is irrelevant and so rewards only depend on how many opponents of any particular strategy a player faces, and not which order they appear in (thus there is a melee, rather than sequential pairwise contests, see Section 3). In an n -player game, $E[\mathbf{p} : \mathbf{q}^j, \mathbf{p}^{n-j-1}]$ is the payoff to a player playing \mathbf{p} against j opponents playing \mathbf{q} and all other opponents

playing \mathbf{p} . \mathbf{p} is ES against \mathbf{q} , at level j , if

$$E[\mathbf{p} : \mathbf{q}^j, \mathbf{p}^{n-j-1}] > E[\mathbf{q} : \mathbf{q}^j, \mathbf{p}^{n-j-1}] \quad (9)$$

and

$$E[\mathbf{p} : \mathbf{q}^i, \mathbf{p}^{n-i-1}] = E[\mathbf{q} : \mathbf{q}^i, \mathbf{p}^{n-i-1}] \quad \forall i < j \quad (10)$$

\mathbf{p} is an ESS if it is ES against all $\mathbf{q} \neq \mathbf{p}$ and is a level j ESS if it is ES against all $\mathbf{q} \neq \mathbf{p}$ where there is some \mathbf{q} against which \mathbf{p} is ES at level j , but no \mathbf{q} against which it is ES at level k for any $k > j$.

All pure ESSs must be level 0. The higher level ESSs ($j \geq 2$) are non-generic (mixed ESSs are of level 1 in the generic case) and so the more restricted definition of an ESS is

$$(i) E[\mathbf{p} : \mathbf{p}^{n-1}] \geq E[\mathbf{q} : \mathbf{p}^{n-1}] \quad (11)$$

and

$$(ii) E[\mathbf{p} : \mathbf{p}^{n-1}] = E[\mathbf{q} : \mathbf{p}^{n-1}] \Rightarrow E[\mathbf{p} : \mathbf{q}, \mathbf{p}^{n-2}] > E[\mathbf{q} : \mathbf{q}, \mathbf{p}^{n-2}] \quad (12)$$

for all $\mathbf{q} \neq \mathbf{p}$.

It is shown that the Bishop-Cannings Theorem is violated for any number of players greater than two, and indeed for four or more players it is possible to have two ESSs with the same support (although this is not possible for three players).

The two-strategy n -player case is investigated completely, and it is shown that there can be up to $n/2 - i$ internal ESSs and i pure ESSs, for each of $i = 0, 1, 2$ for an n player game. Despite the violation of Bishop-Cannings, there are still restrictions on which patterns can occur; Broom *et al* (1997b) goes on to look at the 3-player and 3-strategy case in detail showing which patterns are attainable and which are not (with one left unknown). The dynamics of these games in the case of completely symmetric payoffs (all animals involved in any contest receive the same payoff) is also investigated. It is shown that a ‘catalyst’ strategy, which when introduced to a population can invade the current ESS, can move the population to a new ESS in which it does not feature; a result not possible for two-player games. It is possible to have an ESS which is not attainable by a sequential introduction of strategies and so very unlikely to ever appear in a real population (this is

possible even for ESSs with a large basin of attraction); again a result which does not happen for two players. The problem of identifying which of several equilibria actually occur is a common problem in economics and is clearly a problem for biological systems as well. Many models yield but a single ESS so this problem does not occur, but we see that as the number of players increases the potential for multiple solutions (including some which turn out to be dynamically unreachable) grows and this problem comes more to the fore. This is a general feature of many multiplayer games.

This early work for the generalization of the concept of matrix games points the way to possible more general extensions and there is much room for development. Widely held ideas based upon two-player results are violated and it seems clear that much of what we believe to be true because of this simplified modelling will prove to be false.

3 Multiplayer games as structures of pairwise contests

In this section we consider games with a finite number of players who interact not in a single contest as in the last section but in pairwise games. These games are embedded in a structure so that the result of each game can influence both the final reward and which player the next game will be against. This non-independence means that the pairwise games are in fact part of one larger multiplayer conflict, with all the added complications that that implies.

3.1 A sequential-arrivals model of territory acquisition

Broom *et al.* (1997a) modelled the arrival of birds at a colonial nest-site. A set of n birds B_1, \dots, B_n arrive sequentially at n nest sites S_1, \dots, S_n . The value of the site S_i is $V_i (\geq 0)$ for the bird occupying that site at the end of the process, i.e. when all birds are settled on a site, where $V_i \geq V_j$ if $i < j$.

When a bird arrives it has the choice of going to any vacant site or challenging the occupier of any occupied site. A challenge is a simple contest where the challenger wins with probability $p \leq 0.5$, otherwise the occupier wins. The winner becomes the occupier of the contested site, the loser pays

a cost $C > 0$ (receives a payoff of $-C$) and must retreat to an unoccupied site of its choice.

The contest finishes after the arrival of the final bird. The payoff to a bird is the value of the site it occupies at the end of the contest minus any penalties it has received for losing challenges. It is possible to imagine a more complicated model (for example variable values of C or p depending upon the value of the site), but this model has the most important feature (choose a free site or fight) and is amenable to analysis.

The optimal play in a particular example is shown in Table 1. Thus bird B_7 arrives to find the top six sites occupied, it challenges on S_4 and goes to S_7 if it loses. Its expected reward is 5.134.

TABLE 1 ABOUT HERE

In Broom *et al* (1997a) the birds played rationally conditional upon the positions of all the birds which had arrived before them and upon the assumption that all subsequent birds would also behave rationally. The strategies which resulted were very complicated, but did possess some important general features, for instance the threshold phenomenon whereby all birds arriving before the threshold do not challenge and all birds arriving after it do. Broom *et al* (2000c) considered three, relatively simple, types of strategy, dividing sites into good sites ($1, \dots, I$), medium sites ($I + 1, \dots, J$) and poor sites ($J + 1, \dots, n$). For Type 1 strategies, a bird will occupy the best free site if a good or medium site is available. However, if only poor sites are free it will challenge for a good site chosen at random with each site having an equal probability of being chosen. If the bird loses a contest, whether as challenger or challenged, it occupies the best free site. Thus a strategy is described by an integer pair (I, J) . Type 2 and Type 3 strategies were refinements of this model. By comparing the values of the parameters I and J obtained to the theoretical results from Broom *et al* (1997a), it was noticed that the simple strategy is generally a good approximation to the optimal strategy.

Broom *et al* (1996) considered this model and allowed three strategies to be played; a strategy S of the form described in Broom *et al* (2000c) where birds choose the better sites and then challenge if only poor sites are available. A strategy T where birds pick the worst available site, unless they find an occupied site of higher value than a free one, in which case they

challenge the occupier of the higher site. Strategy U simply chooses the worst free site. T is both courteous and punishing, with S playing the part of a cheating strategy. U is courteous but does not punish cheats. T seems a perverse strategy, but if all birds play T, then S cannot invade. However in a population with a small non-zero mutation level, which introduces birds playing the other strategies, U birds can invade a population of Ts and the population goes from all T to many Us and few Ts, allowing Ss to quickly invade and eliminate the others.

The optimal strategy generated by Broom *et al* (1997a) was extremely complicated, and it seems unreasonable that any organism could play it. But in Broom *et al* (2000c) we see that quite simple rules can produce behaviour which effectively mimics the best strategy. This might be a common feature of evolution: life is complex and situations can change without warning so that it may be best not to try to solve the full problem, but to find simple robust rules which work well most of the time.

Some of the general features of this model were observed in Severinghaus (1996), who studied the behaviour of Brown Shrike *Lanius cristatus* arriving at a breeding ground. The locations of the territories of early arrivals tended to be scattered throughout the study area, and later birds filled the gaps between them. Initially there was little aggression between birds, but as the breeding ground filled up this aggression increased and some territory owners had to defend their territories several times. This agrees with the general predictions of the first birds occupying good sites, and later birds challenging for a site only when only poor sites remain free, and in particular closely approximates the threshold phenomenon found in Broom *et al* (1997a). It was also noticed that prior residence granted the defender an advantage in any contest, again as in the model. Of course, this is in no way comparable to fitting the model to data, and merely indicates that the broad thrust of the model is correct, rather than an accurate model of behaviour. Indeed, for such complex behaviour it would be very difficult to generate a model which could be accurately tested in this way.

3.2 A model of dominance hierarchy formation as a round-robin contest

The model of Mesterton Gibbons and Dugatkin (1995) considered a game where every individual interacted with every other one exactly once, called a *round-robin* or *all-play-all* contest, and the result of this interaction decided the dominance relation between the two animals. They were particularly interested in whether this situation led to a linear dominance hierarchy where A dominates all others, B dominates all but A, C dominates all but A and B etc. They introduced asymmetries into the relevant abilities, or Resource Holding Potential (RHP), of the individuals and evaluated the influence of this on the probability that a linear hierarchy was produced. Landau (1951) and Chase (1974) came to the conclusion that this was unlikely to occur through such a round-robin tournament because of the large number of contest ($n(n - 1)/2$) all of which had to go the ‘right’ way. Both of these papers assumed that a genuine contest would occur in all cases with each animal trying its best to win. Mesterton Gibbons and Dugatkin (1995) consider a more explicitly game-theoretic situation whereby if an animal knows that it is inferior, then it might choose to give up without a fight (rather than risking injury for a minimal chance of success) and so some contests might be decided with probability 1. This also raised the question of whether animals could tell that others were inferior/ superior and that the resulting contests might depend greatly upon how much this was the case. They consider both situations where assessment of differences is perfect and where it is non-existent.

It is assumed that if an animal of RHP X meets one of RHP Y then the difference $Z=X-Y$ is crucial in determining the outcome of a contest. In particular each contest takes the form of the classical *Hawk-Dove* contest (see Maynard Smith, 1982) where each individual has two pure strategies available, Hawk(H) and Dove(D). In this contest, the winner always obtains V, and the loser -C in a Hawk v Hawk contest and 0 otherwise. A player playing Hawk always beats one playing Dove and DvD contests are decided by the toss of an unbiased coin. In the classical game the winner of a Hawk versus Hawk contest is also decided by an unbiased coin toss, but in Mesterton Gibbons and Dugatkin (1995) the X animal wins a HvH contest

with probability

$$E(x, y) = \begin{cases} \frac{1}{2}e^{\alpha Z} & Z \leq 0 \\ 1 - \frac{1}{2}e^{-\alpha Z} & Z > 0 \end{cases} \quad (13)$$

The parameter α is a measure of the reliability of RHP, in the sense that the larger α the more reliable it is in determining the winner of a contest. RHP could be horn size, for example, and Mesterton Gibbons and Dugatkin (1995) give values of α estimated from data for different measures of size.

They found the probability of linear hierarchy formation from a round-robin contest dependent upon group size, the reliability of RHP, the coefficient of RHP variation (a measure of how variable RHP is within the group) and the aggression threshold (which is determined by the relative size of reward and cost in any Hawk Dove contest as well as victory probability if they both play Hawk) in the two situations where RHP is assessed or not. Without assessment this probability becomes very small as n increases for realistic parameter values, and such a hierarchy is virtually impossible for $n = 10$. With assessment this probability can remain quite large; this is due to the fact that weaker animals back down in many contests. Indeed there can be a high probability of the ‘correct’ hierarchy (in order of RHP) emerging, whereas this is very unlikely for the non-assessment case. The authors comment that a weakness of their analysis is the assumption that RHP is perfectly observable so that animals cannot bluff about their size (this is common to most models where animals are asymmetric, whether multiplayer or two player). They point out that the lack of data means that it is not known to what extent parameter values vary within species, although some life-history parameters are relatively invariant across species (Charnov, 1993).

This model has the same lack of structure prevalent in two player games in the sense that all contests are resolved independently. The paper works on this assumption and then explores the hierarchy after formation is complete and examines its structure and so gives insight into the type of results that are consistent with this independent formation. It shows the relative stability of small populations as opposed to larger ones, but also shows that even large populations can be linear if a sufficient number of contests result in one of the contenders giving way; the conditions for when this is likely to occur are also found. A potential problem is the large number of contests,

especially for big groups; see for example the knockout contests of the following section for a comparison (although different problems confront this type of model in large populations). This model makes a good null hypothesis; essentially that of no structure to the contests in the formation phase of a dominance hierarchy, and should be considered as a possibility before more complex ideas are mooted.

3.3 Knockout contests

A knockout contest is a multiplayer game which is composed of a number of pairwise games, and was used as a model of dominance hierarchy formation in Broom *et al* (2000a, 2000b). Initially there are 2^n players who form 2^{n-1} pairs and fight so that in each fight there is a ‘winner’ and a ‘loser’. The losers are 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. Round k was defined 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 to work with. Losers in round k gain the reward V_k , the overall winner receiving V_0 , assuming that $V_k \geq V_{k+1}$ ($k = 0, \dots, n - 1$). A population which has a large (essentially infinite) set of such conflicts was envisaged, with sets of 2^n players selected at random from the infinite population of players. If there were only a finite number of such tournaments then finite population size would require a different type of analysis (see Riley, 1979 and Thomas and Pohley, 1981).

The main advantages of the knockout model are that it breaks down a contest between a large number of individuals into a collection of pairwise games, has a simple structure with every individual starting from an identical position and generates a single overall winner (and a unique runner-up) with a relatively small number of contests. This is important to minimize injuries and unnecessary energy wastage. The hierarchy of individuals becomes less distinct further down the order, but in many animal societies this is not important; the division of reproductive rights (*reproductive skew*, see Vehrencamp, 1983, and Keller and Reeve, 1994) amongst communally-living animals is often very uneven (e.g. Moehlman, 1979 and Rood, 1980), so that the top few animals receive the vast majority of the overall pay-off. Note

that this is not always the case (see Vehrencamp *et al.*, 1988).

The pairwise games which were played in the knockout contest were as follows (but could be any game which has a winner and a loser); Suppose that in each round there are available m options labelled O_1, \dots, O_m . The *strategy* of a player specifies which option is to be used for each round should the player progress to that round. This specification may be probabilistic, involving various options in each round. The winner in a round progresses to the next round, the loser receives a payoff appropriate to that round and may also receive a cost; this cost and the probability of each animal progressing depending upon its strategy and that of its opponent (the Hawk-Dove game is an example of this game).

There are various versions of the knockout games which might be considered. Broom *et al* (2000a) considered the *fixed option* version in which each player must use the same option in each round. At the other extreme (*variable option*, in Broom *et al*, 2000b) players might vary their option freely from round to round.

For the Hawk-Dove game in the fixed option case, setting $D_k = V_k - V_{k+1}$, there is a unique ESS number of Dove players q given by

$$\sum_{k=0}^{n-1} \frac{1 - q^{2^{k+1}-1}}{2^{k+1}} D_{n-k-1} = C \left((1 - q) - \frac{1 - q^{2^n}}{2^n} \right). \quad (14)$$

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. This was done for the 2 round case and the method used can be generalized to more rounds, but calculations quickly become complicated. There is an interesting correspondence between the knockout model and the extensive two-person game of Selten (1983), which deserves to be explored further.

The probability of playing Hawk in round k , p_k , satisfies $p_k = \text{mid}(0, 1, z_k)$ where

$$z_{k+1} = \frac{z_k}{2} + \frac{D_k}{C} - \frac{p_k^2}{2} \quad (15)$$

If we further suppose that $D_k/C = b < 1$, then $p_1 = b$ and it is easy to show that z_k must always lie between 0 and 1 i.e.

$$p_{k+1} = b + \frac{1}{2}p_k(1 - p_k). \quad (16)$$

TABLE 2 ABOUT HERE

This yields the expected number of violent Hawk versus Hawk contests as shown in Table 2. The corresponding values for the fixed 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 structures.

The knockout model provides an example of a situation where all conflicts in a population are pairwise, but are organized 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* (2000a) 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 Broom *et al* (2000b) 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.

One disadvantage of the knockout model is that it is not realistic for a large group of animals to form themselves into fighting pairs in such an ordered way. However, assuming that the outcome of each contest is observed by every contestant, 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 may have already formed a hierarchy, and groups re-forming may well have a memory of other individuals (see, for example, Barnard and Burk, 1979). Thus the model may be most useful

in considering groups which form for the first time. A possible scenario is that of birds gathering at a lek (Hoglund and Alatalo, 1995).

3.4 Animal societies and multiplayer games

In Section 3 we have seen models of groups of animals that are organized as structures of pairwise contests where the results of contests are not independent. This must surely be true of all animals which live in groups where individuals interact over time. The dominance relationship between a pair of animals must affect how a third animal sees itself in relation to them. Indeed in some groups coalitions form so that games can be truly multiplayer in character with three or more players involved simultaneously. Possibly this starts out as a pairwise contest and then each side may obtain allies either through the hope of gaining support in later contests or because an animal is supporting a relative and its improved position will gain the animal indirect fitness benefits. Such interactions are common in primate groups, for example (see Harcourt and de Waal, 1992). This behaviour is not restricted to dominance hierarchies, however; even more transitory groupings such as herds have a dynamic which is more complicated than mere independent contests which may work best for species which are comprised of lone animals which meet sporadically.

4 Other structured evolutionary games

This section considers games where the results of pairwise contests influence the subsequent opportunities which an animal has so that contests are non-independent, but where there is no finite structure of contests comprising the overall game as in the previous section. Thus some, but not all, of the features of a multiplayer game will be present, but there is enough similarity to justify its inclusion.

4.1 The Finite-Horizon War of Attrition

The classical war of attrition model has assumed a contest over a single item with a cost paid proportional to the time used; effectively postulating

an unlimited time available to play such contests. In many real situations however there is a finite length of time available and strategies may depend significantly upon how much time there is to play (e.g. the brood care example of Houston and McNamara, 1999, in section 4.2).

Cannings and Whittaker (1995) consider a population playing war of attrition type contests where there is only a finite available time to play them in; thus the longer is spent in a particular contest, the shorter the remaining time to play in other contests. The model is difficult to analyze precisely and for the sake of computability they considered a discrete-time strategy space of total length n time units with an infinite population of individuals i.e. each individual was only allowed to pick a single integer k which governed the length of time it was prepared to play a contest for (regardless of the time remaining). At each time point some contests end and individuals not involved in a contest are repaired with others at random (there is thus a delay of one time period between successive contests). A contest is decided by an individual leaving due to its maximum time occurring, the reward then going to the remaining player. Contests where both leave simultaneously or where both are playing when the end time n is reached are drawn with the reward shared. There is no direct time penalty for being involved in contests (but there is the indirect one of not being able to fight in other contests). Contests were discounted so that rewards became less valuable the later that they were acquired.

A complex structure of equilibrium and invasion resulted from this potentially simple idea and it is clear that the introduction of the fixed end point has a huge effect. The smaller the discounting factor (so the greater the discrepancy in value from round to round) the larger the chosen strategy time in general (it is more valuable to win early rewards than later ones). It is also true that for large discounting factors complex behaviour occurs, but for a sufficiently small discounting factor there is a unique stable mixture of strategies involving $(1, 2, 3, \dots, n - 2, n)$ (i.e. all but $n - 1$ which is dominated by n).

One interesting feature of this model is that players who play shorter time lengths are involved in more contests, yet the optimal strategy in the war of attrition is based upon meeting randomly selected opponents. Thus a player is more likely to face a given individual playing a short time period than one who plays a longer time period, so that to make the overall distribution exponential, there should be a smaller number of short time length players

than expected (random individuals play shorter time periods less often than you would think). The other main feature is the finite time available to play the game. This would have only an indirect effect to many games (see the following section; Houston and McNamara, 1999) but has a more direct impact here because of the time factor central to the war of attrition.

4.2 State-based models of adaptive behaviour

Houston and McNamara (1999) consider a range of models where behaviour is dependent upon state, so that at any time an organism is characterized by its state and its behaviour may depend upon this state. An animal will make a sequence of decisions and each decision influences its state at the next decision point, and so its next decision (and possibly its next opponent if games are organized in such a way). An organism has a behavioural strategy which specifies how it behaves in every possible circumstance or state.

There is a wide range of real situations which can be modelled in the way that is proposed in Houston and McNamara (1999). We only touch on these briefly here, since it is not a multiplayer game as such. However, the strategy that an animal plays has a consequence for subsequent games and so the dependence structures that exist in multiplayer structures such as the knockout models of Broom *et al* (2000a, 2000b) also occurs in state-based models. One such situation where state can be important is in the modelling of food gathering and predator avoidance. In particular there is a trade-off between the two risks of predation and starvation which changes with an animal's state, which can be characterized by its energy reserves for simplicity. One of the situations considered is simply maximizing the probability of survival (for instance over a long period involving no reproduction, e.g. winter). An animal dies if it is eaten or its reserves fall to zero. The second risk is obviously larger the smaller the reserves, so the level of predation risk that an animal is willing to undergo for an item of food is larger if reserves are low. Time may also complicate the issue, as if survival to the end of winter is the aim, then as an animal's goal approaches behaviour may well change, so that time is also part of its state. This situation becomes game-theoretic in nature when animals can feed in groups and spend a proportion of their time feeding and the rest looking out for predators. The optimal strategy depends upon various parameters such as predation rate, but also on the strategies of other animals and an animal's own energy reserves. Note that

since the strategies of others depends upon their energy reserves then the strategy of an animal depends indirectly upon the energy reserves of others.

Another example is the game of brood care and desertion. Two animals mate to produce offspring but both need not stay to raise the brood. If both parents leave then the offspring die, but if one stays and the other leaves the leaver may have a chance to mate again. When is it best to leave, and when to stay? This depends upon whether the choice is made simultaneously or whether one partner has the opportunity to choose first (e.g. the male may be able to desert a pregnant female). It also depends upon the length of time into the breeding season that the decision is made; desertion may be more profitable early on when later mating chances are more plentiful. Thus the value of taking a particular course of action may vary with time, so potentially altering the optimal decision. Also the animal's state when it makes its next decision depends upon the decision it makes here, since the timing of its next decision depends upon this one.

The main relevance of this work to the multiplayer case is the non-independence of subsequent opponents which is a key characteristic of the multiplayer structures as well. The dynamic programming approach is common to both types of system and this idea is very applicable. Following Houston and McNamara (1999) there are many examples of how such a state-based approach can expand our understanding which will not be mentioned here, but for those interested in multiplayer games there is likely to be a consistent overlap between the two areas.

4.3 Game theoretic models of kleptoparasitism

Kleptoparasitism occurs when one individual steals food from another. Interspecific and intraspecific kleptoparasitism are widespread amongst vertebrates, especially birds. Ruxton and Moody (1997) developed a model of intraspecific kleptoparasitism. Each bird could be in one of three states, handler (with a food item), searcher (trying to find a food item or a handler with an item) and aggressive, involved in a fight over a food item (either as a handler or one attacking a handler). The behaviour is purely deterministic in the sense that every individual would try to steal if given the opportunity. Broom and Ruxton (1998) introduced a game-theoretic element, allowing birds to choose whether to try to steal or not (and in a second model how

to allocate their time between searching for handlers and food items). This model is state-dependent in the sense that a decision to fight or not decides whether a bird becomes an aggressive individual or remains a searcher which then indirectly influenced later opportunities. The time spent fighting is essentially wasted (it cannot be used to search for food) and so the more kleptoparasitism there is, the worse the population as a whole performs in food gathering. In particular the optimal strategy of when to challenge is found (it is best to always challenge when food levels are low, never to challenge when they are high, and there is a point of instantaneous transfer from one state to the next), which generates a step function for the rate of food consumption of the population, denoted by γ , which is obtained from the expression $\gamma = H/Pt_h$.

The equilibrium level of H , the density of food handlers, is given by

$$\left(\frac{H}{P}\right)^2 pD + \frac{H}{P}(C + 1) - C = 0 \quad (17)$$

where t_h is the mean handling time, $t_a/2$ is the mean fighting time, f is the food density, ν_f is the searching rate for new food items, ν_H is the searching rate for handlers, p is the probability that a bird challenges any handler that it observes and P is the total population density; $C = t_h f \nu_f$, $D = t_a P \nu_H$.

Fighting is optimal and so $p = 1$ if $t_a f \nu_f < 1$ otherwise $p = 0$ is optimal.

Later extensions have complicated analysis further by allowing birds to know the handling status of an item (how much extra handling it requires) and allowing for different types of food item, those which can be consumed as they are handled and those which must be consumed only after lengthy handling.

This model is similar to the previous ones in one key respect; the result of a contest alters the state of the player which in turn has a bearing on which opponent they are likely to meet next, and thus it falls within the general remit of a state-based model, although possessing its own unique features.

5 Discussion

In this paper we have looked at a number of multiplayer models (and related ideas) which are applied to biology. The multiplayer war of attrition model C provides a particularly elegant way of modelling a simple situation with greater than two players and demonstrates how logical extensions of two-player games to the multiplayer case need not always be highly complex and that a complete solution can be found.

The extension of matrix games to the multiplayer case in Section 2.2 provides a very different situation to the war of attrition in that it represents the early steps of a potentially large field. As well as the logical framework of how to consider such games and what constitutes an ESS, only the simpler situations, two strategies with many players and three strategies with three players were analyzed (and the latter by no means completely) yet several general results from two-players games are violated and it is clear that the whole situation will be much more complex. Indeed this is one of the reasons that the multiplayer field has been neglected for so long. Two player games are both much simpler and (apparently at least) provide good models for varied natural situations, so that it is perhaps unsurprising that attention has concentrated on them.

However, pairwise interactions may also not be as simple as they seem, as we saw in Section 3. If they take place in a group of individuals who interact with each other then these games can form part of a complex structure where the results of games influence each other, thus rendering them effectively part of a more complex multiplayer game. The clearest examples of this are the knockout models of Section 3.3 which provides a simple (but of course simplistic) structure into which games are slotted and results determine which games subsequently occur. More varied and complicated behaviour occurs but there is still enough structure to obtain some results which may generalize to other situations, for example the more freedom an animal has to vary its strategy the more aggressive on average it will be to the detriment of the whole group. Indeed the existence of a structure of pairwise games makes the population more aggressive than for independent pairwise games in this free choice case (but not necessarily in the case of fixed choices). This is perhaps a good first point to start thinking about the possibility of complex structures of pairwise games in different settings.

The structure of the round-robin of Section 3.2 is rather different in the sense that results do not affect the opponents that are played subsequently so that one of the key features of the structure idea is missing, that of dependence. Which games are played and which are not (in the sense of one of the participants backing down) are decided by outside factors and not by previous results. In this sense it provides an extreme case of the dominance hierarchy formation idea where the effect of the structure is at its weakest, but the results of individual games still determine the dominance relations of the hierarchy collectively which determines the rewards to the participants, possibly in a very non-linear way.

Section 4 constitutes models which are not multiplayer as such, considering essentially infinite populations, rather than finite groups of greater than two individuals, but have some of the characters of multiplayer games. Induced dependence between games due to extra conditions such as time constraints, as in the finite horizon war of attrition, is one such feature. The whole idea of state as described in Section 4.2 generates the type of structure that occurs in Section 3 and enriches our understanding of animal behaviour by introducing more realistic features to modelling. There is a strong parallel here with the idea of the multiplayer game.

Data investigations generally point to the kind of non-independence that features in multiplayer models. Experimental work in the laboratory shows that linear hierarchies are common and also that the results of successive contests are correlated. In particular if an animal loses a contest, it is more likely to lose a subsequent contest with this not being explicable by it being a weaker individual (the converse is not necessarily true for winners). Our own work predicts a similar result (losers should get less aggressive, but winners should not necessarily be more aggressive) so that this trend may be for logical not psychological reasons. Chase and Rohwer (1987) modelled the interactions between groups of house sparrows, particularly investigating triads (the results within subgroups of three individuals), and found cycles (A dominates B dominates C dominates A) to be much less likely than expected (see also Chase *et al*, 1994). Bekoff and Dugatkin (2000) investigated these winner and loser effects for groups of young coyotes and showed that whether such effects exist (and which type of effect) depends upon the rank of the individual concerned. They went on to develop a model to explain their findings. There is as yet no method for incorporating a system for fitting data to model hierarchy formation and the analysis is

qualitative only. However, the model of Mesterton-Gibbons and Dugatkin (1995) uses a formation model of independent contests and so provides an ideal null hypothesis for formation situations against which to test a variety of more structured models.

This lack of fitted models is a consistent theme for multiplayer games at the present time. In a sense this is very reasonable, since the extra complexity of multiplayer models makes data fitting much harder. However to make real progress in understanding this complex behaviour, such methods must be developed.

References

- Barnard, C.J. & Burk, T.E. (1979). Dominance hierarchies and the evolution of individual recognition. *J. Theoret. Biol.* **81**, 65-73.
- Bekoff, M. & Dugatkin, L.A. (2000) Winner and loser effects and the development of dominance relationships in young coyotes: An integration of data and theory *Evol. Ecol. Res.* **2** 871-883.
- Bishop, D.T. & Cannings, C. (1976). Models of animal conflict. *Adv. Appl. Prob.* **8**, 616-621.
- Blackwell, P.G. (1997). The n -player war of attrition and territorial groups. *J. Theoret. Biol.* **189** 175-181.
- Broom, M. (2000). Bounds on the number of ESSs of a matrix game *Math. Biosci.* **167** 163-175.
- Broom, M., Cannings, C. & Vickers, G.T. (1997a). A sequential-arrivals model of territory acquisition. *J. Theoret. Biol.* **189**, 257-272.
- Broom, M., Cannings, C. & Vickers, G.T. (2000c). A sequential-arrivals model of territory acquisition II. *J. Theoret. Biol.* **207**, 389-403.
- Broom, M., Cannings, C. & Vickers, G.T. (1996). Choosing a nest site: contests and catalysts. *Am. Nat.* **147**, 1108-1114.
- Broom, M., Cannings, C. & Vickers, G.T. (2000a) Evolution in knockout contests: the fixed strategy case *Bull. Math. Biol.* **62** 451-466.
- Broom, M., Cannings, C. & Vickers, G.T. (2000b) Evolution in knockout contests: the variable strategy case *Selection* **1** 107-123.
- Broom, M., Cannings, C. & Vickers, G.T. (1997b). Multi-player matrix games. *Bull. Math. Biol.* **59**, 931-952.
- Broom, M. & Ruxton, G.D. (1998) Evolutionarily stable stealing: game the-

- ory applied to kleptoparasitism. *Behav. Ecol.* **9** 397-403.
- Cannings, C. & Vickers, G.T. (1988). Patterns of ESS's 2. *J. Theoret. Biol.* **132** 409-420.
- Cannings, C. & Whittaker, J.C. (1995). The finite horizon war of attrition. *Games and Economic Behaviour* **11**, 193-236.
- Charnov, E.L. (1993) *Life history invariants*. Oxford University Press.
- Chase, I.D. (1974) Models of hierarchy formation in animal societies. *Behav Sci* **19** 374-382.
- Chase, I.D. & Rohwer, S. (1987) Two methods for quantifying the development of dominance in large groups with applications to Harris' sparrows. *Anim. Behav.* **35** 1113-1128.
- Chase, I.D., Costanza, B. & Dugatkin, L.A. (1994). Aggressive interactions and inter-contest interval: how long do winners keep winning? *Anim. Behav.* **48** 393-400.
- Cressman, R. (1992). The Stability Concept of Evolutionary Game Theory: A Dynamic Approach. Lecture Notes Biomath., 94, Springer-Verlag, Berlin.
- Grafen, A. (1990a). Sexual selection unhandicapped by the Fisher process. *J. Theoret. Biol.* **144**, 473-516.
- Grafen, A. (1990b). Biological signals as handicaps. *J. Theoret. Biol.* **144**, 517-546.
- Haigh, J. (1975). Game theory and evolution. *Adv. Appl. Prob.* **7**, 8-11.
- Haigh, J. & Cannings, C. (1989). The n -person war of attrition. *Acta. Applicandae Mathematicae* **14**, 59-74.
- Harcourt, A.H. & de Waal, F.B.M. (eds) (1992). *Coalitions and alliances in humans and other animals* Oxford University Press
- Hofbauer, J. & Sigmund, K. (1998). *Evolutionary Games and Population Dynamics*. Cambridge University Press.
- Hoglund, J. & Alatalo, R.V. (1995) *Leks* Princeton University Press.
- Houston, A.I. & McNamara, J.M. (1999) *Models of Adaptive Behaviour* Cambridge University Press.
- Keller, L. & Reeve, H.K. (1994) Partitioning of reproduction in animal societies *Trends Ecol. Evol.* **9** 98-103.
- Landau, H.G. (1951) On dominance relations and the structure of animal societies. I Effect of inherent characteristics *Bull. Math. Biophysics* **13** 1-19.
- Mangel, M. & Clark, C.W. (1988) *Dynamic modeling in Behavioral Ecology* Princeton University Press.
- Maynard Smith, J. (1974) The theory of games and the evolution of animal conflicts *J. Theoret. Biol* **47** 209-221.

- Maynard Smith, J.(1982) *Evolution and the Theory of Games* CUP.
- Maynard Smith, J. & Price, G.R. (1973). The logic of animal conflict. *Nature* **246**, 15-18.
- Mesterton-Gibbons, M & Dugatkin, L.A.(1995) Toward a theory of dominance hierarchies: effects of assessment, group size, and variation in fighting ability *Behav. Ecol.* **6** 416-423
- Moehlman, P.D. (1979) Jackal helpers and pup survival *Nature* **277**, 382-383.
- Palm, G.(1984). Evolutionarily stable strategies and game dynamics for n -person games. *J. Math. Biol.* **19** 329-334.
- Riley, J.G.(1979), Evolutionary equilibrium strategies. *J. Theoret. Biol* **76** 109-123.
- Rood, J.P.(1980) Mating relationships and breeding suppression in the dwarf mongoose *Anim. Behav.* **28** 143-150.
- Ruxton, G.D. & Moody, A.L. (1997) The ideal free distribution with kleptoparasitism *J. Theoret. Biol* **186** 449-458.
- Selten, R. (1983). Evolutionary stability in extensive two-person games. *Math. Social Sciences* **5** 269-363.
- Severinghaus, L.L. (1996). Territory strategy of the migratory Brown Shrike *Lanius cristatus*. *Ibis* **138**, 460-465.
- Thomas, B. & Pohley, H.J. (1981) ESS theory for finite populations. *Biosystems* **13** 211-221.
- van Damme, E. (1991) *Stability and Perfection of Nash Equilibria* Springer-Verlag.
- Vehrencamp, S.L. (1983) A model for the evolution of despotic versus egalitarian societies *Anim. Behav.* **31** 667-682.
- Vehrencamp, S.L., Koford, R.R. & Bowen, B.S. (1988) in *Reproductive success*, T.H.Clutton-Brock (Ed.), Chicago University Press.
- Vickers, G.T. & Cannings, C. (1988) Patterns of ESS's 1 *J. Theoret. Biol* **132** 387-408.
- Von Neumann, J. & Morgenstern, O. (1944). *Theory of Games and Economic Behaviour*, Princeton Univ. Press.

Table 1

Bird	B_1	B_2	B_3	B_4	B_5
Site	S_1	S_2	S_3	$\text{Ch}S_1(S_5)$	$\text{Ch}S_2(S_4)$
Payoff	5.956	5.952	5.864	5.796	5.850
Bird	B_6	B_7	B_8	B_9	B_{10}
Site	$\text{Ch}S_1(S_6)$	$\text{Ch}S_4(S_7)$	$\text{Ch}S_3(S_8)$	$\text{Ch}S_2(S_9)$	$\text{Ch}S_1(S_{10})$
Payoff	5.476	5.134	4.934	4.734	4.534

The optimal arrivals strategy when $n = 10$, $V_i = 11 - i$, $i = 1, \dots, 10$, $p = 0.4$.

Table 2

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

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