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Evolution in Knockout Conflicts: The Fixed Strategy Case

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A group of individuals resolve their disputes by a knockout tournament. In each round of the tournament, the remaining contestants form pairs which compete, the winners progressing to the next round and the losers being eliminated. The payoff received depends upon how far the player has progressed and a cost is incurred only when it is defeated. We only consider strategies in which individuals are constrained to adopt a fixed play throughout the successive rounds. The case where individuals can vary their choice of behaviour from round to round will be treated elsewhere. The complexity of the system is investigated and illustrated both by special cases and numerical examples.

1. INTRODUCTION

Game theory has featured strongly in modelling 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,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 have been discussed in Bishop and

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Cannings (1976), Cressman (1992), Haigh (1975), Hofbauer and Sigmund (1988) and Maynard Smith (1982). Most of this work has concentrated on games between only two players. This is understandable for two reasons:

(i) Many natural conflicts involve only two players and thus the theory of pairwise games is widely applicable.

(ii) The mathematics involved in pairwise games is simpler than that for multi-player games, and thus it is easier to obtain results both in theory and in practical applications. The theoretical understanding of two-player games is now well advanced, at least as far as the understanding of evolutionarily stable strategies (ESSs) is concerned, though much remains to be done with respect to dynamical considerations.

It is clear however that many, possibly most, biological situations cannot be modelled by pairwise games. This is either because more than two individuals compete simultaneously or alternatively that though all the conflicts are between pairs of individuals, these occur within a structure which effectively makes them multi-player, e.g., dominance hierarchies in social animals (Barnard and Burk, 1979) or birds nesting at a colonial breeding site (Broom *et al.*, 1997b,a). Even in classical examples such as the competition of males for mates, the pairwise contests involved are likely to be dependent.

Game theory has its roots in economics originating with von Neumann and Morgenstern (1944) [also see Axelrod 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. However, there has been relatively little work in the area of multi-player game theory as applied to biological situations. Examples include Broom *et al*. (1997b), Cannings and Whittaker (1994), Haigh and Cannings (1989) and Mesterton-Gibbons and Dugatkin (1995).

Of the papers just cited above, two, Broom *et al*. (1997b) and Haigh and Cannings (1989), specify the payoff for each possible play against each possible set of plays by the opponents, this being possible by virtue of the particular structure chosen for the conflict; respectively symmetric finite conflicts and the War of Attrition. The other two, Cannings and Whittaker (1994) and Mesterton-Gibbons and Dugatkin (1995), only allow ‘fights’ between pairs but have these fights embedded within a structure. This paper adopts the latter approach, modelling a multi-player conflict game as a set of two-player 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. A group of individuals struggling for a position in a hierarchy may well, at the start of the season, interact initially in pairs, establishing thus some winners and losers; the losers might be inhibited from continuing to compete, while the winners continue. Thus a kind of knockout tournament might result. Obviously it would not function in the precise manner of such an organized human tournament but analysis of this type of game should give an initial insight into certain aspects of complex conflicts. A round-robin (all-play-all) approach was adopted by Mesterton-Gibbons and Dugatkin (1995) to model a dominance hierarchy. Our model would be appropriate for a population of birds splitting up into small groups, perhaps those which go to distinct sets of nest sites, and then competing for specific sites which have different intrinsic values in terms of reproductive success.

The paper is divided into four sections. This section is a general introduction to multi-player game theory. Section 2 describes the type of knockout games we shall be considering, which is a generalization of the Hawk–Dove game introduced in Maynard Smith (1982). The form of the contest is that generally used in sporting contests, where in each round players are paired together and the winners qualify for the next round. In particular, we examine fixed option games where players must play the same pure strategy in each round (Section 3), and conditions for the existence of pure and mixed ESSs are found, for the case where there are only two pure strategies. Section 4 is a brief discussion of knockout games.

2. 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 re-paired in the next round and this continues until there is one overall winner. Players receive a reward according to which round they are 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 particular strategies. Thus the organization is similar to many human competitions, such as the Wimbledon Lawn Tennis Championships, although there, of course, individuals are not of equal quality and there is a seeding system which keeps the stronger players apart in the early rounds.

It is possible to think of simpler structures of pairwise games, e.g., the first two players play, then the third plays the winner and so on; however in that game the players start from an unequal position and so the best strategy will depend upon an individual’s position in the ordering. The model could be extended so that losers also play other losers in the next round and in subsequent rounds players with the same result profile, e.g., win, win, lose, or the same number of wins, play each other so that we can generate an entire hierarchy of players with 2^n different rewards. We shall not consider such models (the latter type is called a Swiss tournament).

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, and that it has one of the simplest conceivable structures of pairwise games where every individual starts from an identical position. A single overall winner (and a unique runner-up) is found with a relatively small number of contests, when compared with an all-play-all competition. 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. There is growing interest in the concept of *reproductive skew*, originating with Vehrencamp (1983), which considers how reproductive rights are divided amongst communally living animals. This division is often very uneven [e.g., Moehlman (1979) and Rood (1980)], so that the top few animals receive the vast majority of the overall payoff. Note that this is not always the case, see Vehrencamp *et al*. (1988). Keller and Reeve (1994) developed a model where subordinate individuals are granted limited mating rights, known as *stay and peace incentives*, in order not to challenge for dominance or leave the group. The size of these incentives depends upon a number of factors, including the relatedness of the group members (Emlen, 1996; Reeve and Keller, 1996).

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).

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 winners enter 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 to work with. Losers in round k gain the reward V_k, the overall winner receiving V_0. We shall assume in this paper that $V_k \geq V_{k+1}$ ($k = 0, \dots, n-1$). Note that in the case of high reproductive skew, V_0 will be large, and each succeeding value of V_k will be small compared with the previous one, so that only the top few rewards are worth winning.

The pairwise games which are played in the knockout contest could be any game which has a winner and a loser. 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 choices labelled $O_1, \dots, O_m$. These will be referred to as *options* and 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, involving various options in each round. Let the probability that an O_i-player beats an O_j-player be $1/2 + \Delta_{ij}$, so that $\Delta_{ij} + \Delta_{ji} = 0$ and $\Delta_{ii} = 0$. The winner in a round progresses to the next round, the loser receives a payoff appropriate to that round. In addition, an O_i-player who loses to an O_j-player incurs a cost c_{ij} (a reward $-c_{ij}$), which might correspond to an injury, or loss of time or energy. The Hawk–Dove game is an example of this game with $m = 2$, $\Delta_{12} = 1/2$, and $c_{11} = C, c_{ij} = 0$ otherwise, played over one round, $V_0 = V$, $V_1 = 0$ (some versions have $c_{22} \neq 0$).

There are various versions of the knockout conflict which might be considered. Here we consider the version (fixed option) in which each player must use the same option in each round. At the other extreme (variable option) players might vary their option freely from round to round. More generally, players could play strategies which allowed a maximum of M changes of option (e.g., there are species which change sex but can only do this once), but we consider here the case $M = 0$ so that no changes are possible and shall treat the case where $M = n - 1$, n being the number of rounds, elsewhere. In the sections which follow we consider general values of Δ_{ij} and c_{ij}, but restrict the number of options m to 2.

Our conflicts each involve 2^n individuals and we envision a population which has a large (essentially infinite) set of such conflicts. The sets of 2^n players are 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)].

3. EVOLUTIONARILY STABLE STRATEGIES (ESSS)

In order to find the optimal strategy all rounds must be considered simultaneously. We shall refer to strategies rather than options because, due to the inability to change option from round to round, they are identical in this case. We consider the game where the number of strategies available is two, labelled S_1 and S_2. We shall set $\Delta = \Delta_{12}$ for notational simplicity.

Since there are only two strategies, and payoffs satisfy certain continuity conditions, there is at least one ESS, as we demonstrate below [also see Broom *et al.* (1997b)]. Further, once the parameter values have been specified there is only one variable, namely the proportion of S_1-players in round n, from which we can infer the proportion in round $n - 1$, and so on, and hence compute the expected payoff to each of the two strategies. The proportion of S_1-players which gives an ESS can then be inferred, although in practice this can only be found numerically.

3.1. ***The general two-strategy game.*** Suppose that the proportion of S_1-players in round k is t_k. We find the proportion of S_1-players in round $k - 1$ conditional on the proportion in round k, and hence on the proportion in round n. Recall that we have an infinite set of conflicts, each involving 2^n players. Thus in round n, each group of 2^n is formed as a random sample with probability t_n for S_1-players, so the number of S_1-players per group has a binomial distribution with parameters 2^n and t_n. Since a player in round k is the winner of a knockout tournament in which there were 2^{n-k} players randomly picked from the population in round n, the number of S_1-players in round k has a binomial distribution with parameters 2^k and t_k. The set of 2^k players in that round are thus independently selected with the appropriate probability that a S_1-player wins such a randomly formed tournament. It is, however, simple to derive the appropriate probabilities recursively. Given that the proportions of contests involving two, one and zero S_1-players are t_k^2, $2t_k(1-t_k)$ and $(1-t_k)^2$, respectively, the probability that a round-k winner is an S_1-player is

$$t_{k-1} = t_k^2 \cdot 1 + 2t_k(1-t_k) \cdot \left(\frac{1}{2} + \Delta\right) + (1-t_k)^2 \cdot 0 = t_k + 2\Delta t_k(1-t_k). \quad (1)$$

This recurrence relation cannot be solved neatly for general Δ. The case $\Delta = 0$ is trivial and $\Delta = 1/2$ (equivalent to $\Delta = -1/2$ if the options are relabelled) is considered later.

We derive sufficient conditions, in the general case, for the existence of an internal ESS (i.e., one involving both strategies), for there to be one pure ESS, and for there to be two pure ESSs. We then examine in more detail the case $\Delta = 1/2$, proving in that case that there is at most one internal ESS and giving necessary and sufficient condition for its existence.

Suppose we have specified the parameters of the conflict, i.e., n, the V_i, Δ and the c_{ij}. We consider the mean payoff to S_1-players and S_2-players when the population is almost entirely composed of S_1-players or almost entirely composed of S_2-players. This allows us to specify the conditions for the existence of the two pure ESSs. We relabel t_n as t to simplify the notation. Since no player may change its strategy in later rounds, the values of $t_{n-1}, \dots, t_1$ are determined once t is given, and so the expected payoff to an S_i-player, which we denote by $E_i(t)$, is a function of t alone. Since we have a large (essentially infinite) array of such contests between 2^n players, it is possible to have a strategy played by an arbitrarily small proportion of the population. Thus the impact of a mutant group has negligible effect upon the payoff to the established strategy, and for there to be a pure ESS with strategy S_1 we need $E_1(1) - E_2(1) > 0$ (if S_1-players do better in a population when almost all the opponents are S_1-players than S_2-players do, then the population of S_1-players cannot be invaded by S_2-players). For there to be a pure ESS with strategy 2 we require $E_1(0) - E_2(0) < 0$. It is possible that both pure strategies may be ESSs. $E_1(1) - E_2(1) < 0$ and $E_1(0) - E_2(0) > 0$ implies that there is an internal ESS [that this is sufficient is shown in Broom *et al.* (1997b)], although there may be an internal ESS even if these conditions are not satisfied. There is thus at least one ESS in this game. Note that in general multi-player games, when there are at least four players, there can be more than one internal ESS [see Broom *et al.* (1997b)], and this possibility cannot be excluded here. In fact the payoff to an S_1-player will be a polynomial function of degree $2^n - 1$ and so the possibility arises of up to 2^{n-1} internal ESSs.

Consider the expected payoff to an S_1-player in a population of S_2-players [we aim to find $E_1(0)$]. In each round the probability of the S_1-player being eliminated is $1/2 - \Delta$, so that the probability of it being eliminated in round k is $(1/2 + \Delta)^{n-k}(1/2 - \Delta)$ in which case it receives $V_k - c_{12}$ (if it loses it must be to an S_2-player). If it wins the competition it receives V_0 and it does this with a probability $(1/2 + \Delta)^n$. The overall expected payoff is thus

$$E_1(0) = \sum_{k=1}^{n} \left(\frac{1}{2} - \Delta\right)(V_k - c_{12})\left(\frac{1}{2} + \Delta\right)^{n-k} + \left(\frac{1}{2} + \Delta\right)^{n} V_0. \tag{2}$$

The working is similar for the other cases and the payoffs yielded are as follows:

$$E_1(1) = \sum_{k=1}^{n} \frac{1}{2}(V_k - c_{11})\left(\frac{1}{2}\right)^{n-k} + \left(\frac{1}{2}\right)^{n} V_0 \tag{3}$$

$$E_2(0) = \sum_{k=1}^{n} \frac{1}{2}(V_k - c_{22})\left(\frac{1}{2}\right)^{n-k} + \left(\frac{1}{2}\right)^{n} V_0 \tag{4}$$

$$E_2(1) = \sum_{k=1}^{n} \left(\frac{1}{2} + \Delta\right)(V_k - c_{21})\left(\frac{1}{2} - \Delta\right)^{n-k} + \left(\frac{1}{2} - \Delta\right)^{n} V_0. \tag{5}$$

Letting $D_k = V_k - V_{k+1}$, then equation (2) becomes

$$E_1(0) = \sum_{k=0}^{n-1} D_k \left(\frac{1}{2} + \Delta\right)^{n-k} - c_{12}\left(1 - \left(\frac{1}{2} + \Delta\right)^{n}\right) + V_n.$$

We can interpret this expression in the following way; a player survives to reach round k with probability

$$\left(\frac{1}{2} + \Delta\right)^{n-k}$$

and in each round collects $D_k = V_k - V_{k+1}$, having been given V_n at the start. In particular, the player collects D_k if and only if it survives to round k. The player also incurs a cost of c_{12} unless it wins the whole contest, which it does with probability

$$\left(\frac{1}{2} + \Delta\right)^{n}.$$

Expressions (3), (4) and (5) become

$$E_1(1) = \sum_{k=0}^{n-1} D_k \left(\frac{1}{2}\right)^{n-k} - c_{11}\left(1 - \left(\frac{1}{2}\right)^{n}\right) + V_n$$

$$E_2(0) = \sum_{k=0}^{n-1} D_k \left(\frac{1}{2}\right)^{n-k} - c_{22}\left(1 - \left(\frac{1}{2}\right)^n\right) + V_n$$

$$E_2(1) = \sum_{k=0}^{n-1} D_k \left(\frac{1}{2} - \Delta\right)^{n-k} - c_{21}\left(1 - \left(\frac{1}{2} - \Delta\right)^n\right) + V_n.$$

If $E_1(1) = E_2(1)$, a non-generic case, then S_1 may or may not be an ESS. The performance of the strategies against $(2^n - 2)$ S_1-players and one S_2-player would have to be compared. We do not consider this further.

We see that the condition for S_1 to be a pure ESS is

$$c_{11} < \frac{1}{1 - \left(\frac{1}{2}\right)^n}\left(\sum_{k=0}^{n-1} D_k \left[\left(\frac{1}{2}\right)^{n-k} - \left(\frac{1}{2} - \Delta\right)^{n-k}\right] + c_{21}\left[1 - \left(\frac{1}{2} - \Delta\right)^n\right]\right).$$

Similarly, the condition for S_2 to be a pure ESS is

$$c_{22} < \frac{1}{1 - \left(\frac{1}{2}\right)^n}\left(\sum_{k=0}^{n-1} D_k \left[\left(\frac{1}{2}\right)^{n-k} - \left(\frac{1}{2} + \Delta\right)^{n-k}\right] + c_{12}\left[1 - \left(\frac{1}{2} + \Delta\right)^n\right]\right).$$

There is at least one internal ESS if both of the above inequalities are reversed. In the case $\Delta = 0$, a players choice of strategy does not affect their chance of winning any round and so does not affect their expected winnings. The conditions reduce to expressions solely dependent on the costs and thus there is a unique internal ESS, given by

$$\frac{t}{1-t} = \frac{c_{22} - c_{12}}{c_{11} - c_{21}},$$

provided that both the numerator and denominator of the right-hand side are positive.

In the special case where $D_i = D\ \forall i$, i.e., the extra reward for winning any given round is constant over all rounds, and letting $n \to \infty$ (the number of players is very large) we have the following conditions which together guarantee an internal ESS:

$$c_{11} - c_{21} > \frac{4\Delta}{1 + 2\Delta} D, \qquad c_{22} - c_{12} > \frac{-4\Delta}{1 - 2\Delta} D.$$

3.2. ***The case when $\Delta = 1/2$.*** We consider the special case where $\Delta = 1/2$, so that when an S_1-player meets an S_2-player, the S_1-player always wins (e.g., the Hawk–Dove game). Note that c_{12} has no meaning since it is impossible for an S_1-player to lose to an S_2-player. It is immediate that the S_1-player will always invade a population of S_2-players from the earlier conditions. From equation (1) we know that

$$t_{k-1} = t_k + 2\Delta t_k(1 - t_k) \Rightarrow 1 - t_{k-1} = (1 - t_k)^2.$$

Let $1 - t_n = 1 - t = q$, then $1 - t_{n-1} = q^2$ and in general

$$1 - t_{n-k} = q^{2^k}.$$

The probability of any given S_2-player reaching round $n-k$ is the expected number of S_2-players in round $n - k$ divided by the original number of S_2-players, which is thus

$$\frac{q^{2^k} 2^{n-k}}{q 2^n} = \frac{q^{2^k-1}}{2^k}.$$

An alternative argument is to observe that an S_2-player can only survive for k rounds if it is placed in a pool of 2^k players all of whom are S_2-players which has probability q^{2^k-1}, and wins through which has probability 2^{-k}.

Every player in round n (i.e., every player in the game) receives at least V_n if we ignore costs. An S_2-player then has probability $1 - q$ of meeting an S_1-player and losing, picking up a cost c_{21} and no extra reward. In addition, it has probability $q/2$ of meeting an S_2-player and losing, incurring a cost c_{22} and a probability of $q/2$ of meeting an S_2-player and winning, picking up an extra reward of at least $V_{n-1} - V_n$. Similarly, any S_2-player reaching round $n - k$ (probability $q^{2^k-1}/2^k$) meets an S_1-player with probability $1 - q^{2^k}$ incurring a cost c_{21}, meets an S_2-player and loses with probability $q^{2^k}/2$ incurring a cost c_{22} and meets an S_2-player and wins with probability $q^{2^k}/2$ receiving an additional reward $D_{n-k-1} = V_{n-k-1} - V_{n-k}$. Hence

$$E_2(1-q) = \sum_{k=0}^{n-1} \frac{q^{2^k-1}}{2^k} \left(\frac{q^{2^k}}{2}(D_{n-k-1} - c_{22}) + (1 - q^{2^k})(-c_{21}) \right) + V_n.$$

Similarly, the probability that an S_1-player reaches round $n - k$ is

$$\frac{(1-q^{2^k})2^{n-k}}{(1-q)2^n} = \frac{1-q^{2^k}}{(1-q)2^k} \tag{6}$$

$$\Rightarrow E_1(1-q) = \sum_{k=0}^{n-1} \frac{1-q^{2^k}}{(1-q)2^k} \left(q^{2^k} D_{n-k-1} + \frac{1-q^{2^k}}{2}(D_{n-k-1} - c_{11}) \right) + V_n.$$

There will be a pure ESS ‘play S_1’ if $E_1(1) > E_2(1)$ (equality will require additional analysis). Mixed equilibria are obtained by equating the two expressions giving

$$\sum_{k=0}^{n-1} \frac{1-q^{2^{k+1}-1}}{(1-q)2^{k+1}} D_{n-k-1} - c_{11} \sum_{k=0}^{n-1} \frac{(1-q^{2^k})^2}{(1-q)2^{k+1}} + c_{22} \sum_{k=0}^{n-1} \frac{q^{2^{k+1}-1}}{2^{k+1}}$$
$$+ c_{21} \sum_{k=0}^{n-1} \frac{q^{2^k-1}(1-q^{2^k})}{2^k} = 0$$

which can be solved numerically for any particular set of parameters, giving potentially many solutions. As q increases from 0 to 1, the equilibria alternate between ESSs and non-ESSs.

For the Hawk–Dove game, $c_{11} = C$ and $c_{21} = c_{22} = 0$, so the above equation becomes

$$\sum_{k=0}^{n-1} \frac{1 - q^{2^{k+1}-1}}{(1-q)2^{k+1}} D_{n-k-1} = C \sum_{k=0}^{n-1} \frac{(1-q^{2^k})^2}{(1-q)2^{k+1}} \Rightarrow$$

$$\sum_{k=0}^{n-1} \frac{1 - q^{2^{k+1}-1}}{2^{k+1}} D_{n-k-1} = C \sum_{k=0}^{n-1} \frac{1 - 2q^{2^k} + q^{2^{k+1}}}{2^{k+1}} = C\left((1-q) - \frac{1-q^{2^n}}{2^n}\right). \tag{7}$$

If we divide both sides by the term

$$\left((1-q) - \frac{1-q^{2^n}}{2^n}\right)$$

we obtain

$$F_n(q) = \sum_{k=0}^{n-1} f_k(q) D_{n-k-1} = C$$

where the $f_k(q)$ are strictly increasing for $q \in [0, 1)$, and $f_k(q) \to \infty$ as $q \to 1$ for all k. Thus for the knockout contest which has the Hawk–Dove game as its pairwise game, if $F_n(0) \geq C$ there is no value of $q \in (0, 1)$ which solves the equation and if $F_n(0) < C$ there is a unique value.

We have now shown that there is an internal ESS in the Hawk–Dove game if and only if

$$C > \frac{1}{(1-2^{-n})} \sum_{k=0}^{n-1} \frac{D_{n-k-1}}{2^{k+1}} = \frac{1}{(1-2^{-n})} \left(\frac{V_0}{2^n} + \sum_{k=1}^{n-1} \frac{V_k}{2^{n+1-k}} - \frac{V_n}{2} \right).$$

This result is analogous to the one-round result that Hawk will constitute a pure ESS for values of the cost C below some threshold, but when the cost rises sufficiently then Dove is also a viable strategy. We can rewrite the above inequality as

$$(2^n - 1)C > (V_0 - V_n) + \sum_{k=1}^{n-1} 2^{k-1}(V_k - V_n);$$

the left-hand expression being the total cost and the right-hand side the total additional reward above the base value of V_n for losing in round n, in a population of Hawks. Thus there is a mixed strategy if the cost exceeds this additional reward in an all-Hawk population.

In the classical two-player Hawk–Dove game, $n = 1$, $V_0 = V$ and $V_1 = 0$, and the above condition reduces to $C > V$. Similarly, in the case where $D_i = D$ for all i, the condition for an internal ESS in the Hawk–Dove model is simply $C > D$. Note that the ESS value of q depends on n.

Table 1. $C = 2D$, $\langle$frequency of Hawk strategy$\rangle$ and probability of Hawk reaching round k for n-round conflict.

	$k =$	6	5	4	3	2	1	0
	6	⟨0.27⟩	0.87	0.66	0.43	0.23	0.12	0.06
	5		⟨0.29⟩	0.86	0.65	0.41	0.22	0.11
$n =$	4			⟨0.32⟩	0.84	0.62	0.38	0.20
	3				⟨0.37⟩	0.82	0.57	0.33
	2					⟨0.44⟩	0.78	0.51
	1						⟨0.50⟩	0.75

Examples. We shall consider the case where $D_i = D\lambda^i$ where $0 < \lambda \leq 1$. Thus if $\lambda = 1$, the extra reward gained for winning a round is constant over all rounds, giving low reproductive skew as discussed in Section 2. However, if $\lambda < 1$, the reward for winning each round grows; in particular if λ is small, we have high reproductive skew. Recall that the knockout contest produces a unique winner and a unique runner-up, the lower positions being more indeterminate (joint 3–4th, joint 5–8th etc.). In this situation, the overall winner of the contest will obtain a large reward, the runner-up a far smaller reward, and subsequent rewards may be negligible. Thus the important positions (first and second) are uniquely determined, the ordering of the other animals being irrelevant.

Equation (7) now becomes

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

Firstly we look at the case where $\lambda = 1$ and so $D_i = D$ and examine the cases where (1) $C = 2D$ and (2) $C = 4D$, and take n, the number of rounds, from 1 to 6. Tables 1 and 2 give the frequency of S_1-players (Hawks) in the populations and the probability of an individual playing Hawk reaching successive rounds, and winning overall, i.e., reaching round $k = 0$ [found using equation (6)]. The advantage of considering this case is that every extra game provides an extra reward D, so that results for different numbers of rounds are comparable. In general, the frequency of Hawk players in the population will be smaller the larger C is (compare Tables 1 and 2), as we would expect. In addition, the frequency of Hawk players in the population will decrease as n increases. This is also to be expected since Hawk players are more likely to progress than Dove players, so that later rounds will involve many Hawk–Hawk contests.

A more pertinent comparison is to compare the expected proportion of plays which are Hawk throughout the whole conflict, or alternatively the expected number of Hawk vs Hawk contests, which is given in Table 3. Note that there is not a simple relationship between the two, due to the dependence between contests. These are found as follows: we know that the proportion of Dove players in round

Table 2. $C = 4D$, $\langle$frequency of Hawk strategy$\rangle$ and probability of Hawk reaching round k for n-round conflict.

	$k =$	6	5	4	3	2	1	0
	6	$\langle 0.07 \rangle$	0.96	0.90	0.79	0.61	0.40	0.22
	5		$\langle 0.09 \rangle$	0.95	0.87	0.73	0.54	0.33
$n =$	4			$\langle 0.12 \rangle$	0.94	0.83	0.66	0.45
	3				$\langle 0.17 \rangle$	0.92	0.78	0.58
	2					$\langle 0.21 \rangle$	0.89	0.72
	1						$\langle 0.25 \rangle$	0.88

Table 3. Expected proportion of Hawk plays and Hawk vs Hawk contests over whole conflict; $C = 2D$ and $C = 4D$.

$n =$	1	2	3	4	5	6	∞
$C = 2D$ H plays	0.50	0.519	0.500	0.477	0.461	0.451	0.441
$C = 2D$ H vs H	0.25	0.282	0.280	0.270	0.262	0.257	0.252
$C = 4D$ H plays	0.25	0.268	0.253	0.224	0.193	0.166	0.119
$C = 4D$ H vs H	0.063	0.078	0.079	0.072	0.064	0.560	0.041

$n - k$ is q^{2^k}. It follows that the total proportion of Hawk plays is one minus the proportion of Dove plays and is thus

$$1 - \frac{1}{2(2^n - 1)} \sum_{k=0}^{n-1} 2^{n-k} q^{2^k}.$$

Using the fact that in any tournament the number of Hawk vs Hawk contests is one less than the number of Hawks in round n, unless there are no Hawks at all, the expected number of such contests is

$$(1 - q)2^n - 1 + q^{2^n}.$$

It should be noted that these proportions do not vary monotonically with n; as n increases there is first an increase and then a decrease in both the proportion of Hawk plays and the proportion of Hawk vs Hawk contests. The discrepancy is large, given that every contest, in effect, is for an extra reward D. For instance when $C = 4D$, the proportion of Hawk vs Hawk contests for $n = 3$ is almost double the asymptotic value.

We now consider $\lambda < 1$. Table 4 gives the frequency of Hawks in the population and the probability of an individual playing Hawk reaching successive rounds, and winning overall when $\lambda = 0.5$ and $C = 2D$.

The number of Hawk players falls away more sharply as the number of rounds increases than in Table 1, since as the number of rounds increases the overall reward increases sub-linearly.

Table 4. $C = 2D$, $\lambda = 0.5$, ⟨frequency of Hawk strategy⟩ and probability of Hawk reaching round k for n-round conflict.

	$k =$	6	5	4	3	2	1	0
	6	⟨0.03⟩	0.98	0.96	0.90	0.80	0.65	0.45
	5		⟨0.06⟩	0.97	0.92	0.82	0.66	0.46
$n =$	4			⟨0.11⟩	0.95	0.85	0.70	0.49
	3				⟨0.19⟩	0.90	0.75	0.53
	2					⟨0.33⟩	0.84	0.61
	1						⟨0.5⟩	0.75

Table 5. Frequency of Hawk strategy for various λ; $C = 2K$.

$\lambda =$	0	0.1	0.25	0.5	0.75	1
$D(\lambda)/K$	4	3.21	2.13	1	0.49	0.27
Hawk frequency	0.18	0.17	0.15	0.11	0.08	0.06

Note that we cannot fairly compare the effect of altering λ and thus the reproductive skew by simply comparing Tables 1 and 4, since the total reward available is larger for Table 1. A fair comparison would come from having the total extra reward above V_n the same for each value of λ. Thus D must change as λ is varied. We set $D_i = D(\lambda)\lambda^i$, so that the total extra reward is

$$2^{n-1}D(\lambda)\lambda^{n-1} + 2^{n-2}D(\lambda)\lambda^{n-2} + \cdots + 2D(\lambda)\lambda + D(\lambda)$$

which is equal to $nD(\lambda)$ if $\lambda = 0.5$ and

$$D(\lambda)\frac{1-(2\lambda)^n}{1-2\lambda}$$

otherwise. Suppose that $D(0.5) = K$ and $C = 2K$. If $n = 4$, the total extra reward is $4K$ and

$$D(\lambda) = 4K\frac{1-2\lambda}{1-(2\lambda)^4}$$

ensures that the total extra reward is the same for all λ. Table 5 shows the proportion of Hawk players in the contest for various values of λ ($'\lambda = 0'$ represents the limiting case).

For a population of animals the total reward available to the group, the expected cost of an escalated fight, and the reproductive skew should, according to our model, determine the level of aggression involved in contests.

Our model predicts that the higher the reproductive skew, the greater the proportion of Hawk players in the population. In particular, for the two cases we considered earlier, when $\lambda = 0.5$ the number of Hawk players is just under twice that when $\lambda = 1$. The number of injuries due to Hawk–Hawk contests in fact increases by a factor of 2.8.

4. DISCUSSION

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. We do not claim this to be a precise model of the way natural populations behave, but claim that in some circumstances it can be a reasonable approximation, and that it gives some insight into natural conflicts. We see, for example, that the more rounds that are to be played, i.e., the more players involved in a conflict, the smaller the frequency of the more aggressive strategy, Hawk, amongst the population. On the other hand, the frequency of individuals playing Hawk in individual contests may rise. For example, for the case when $C = 2D$ the population frequency of Hawk is 0.5, 0.437 and 0.367 for $n = 1$, $n = 2$ and $n = 3$, thus decreasing substantially, while the proportions of plays which are Hawk over the complete set of $n = 1$, $n = 2$ and $n = 3$ rounds are 0.500, 0.5186 and 0.5004, respectively. Tables 1, 2 and 3 give further numerical examples, and while the general behaviour illustrated by the values in Tables 1 and 2 seems intuitive that in Table 3 is interesting; the frequency both of Hawk plays and Hawk vs Hawk contests converges as $n \rightarrow \infty$ but not in a monotonic manner. The proportion of Hawk–Hawk contests varies greatly, and the asymptotic level may be either less than or greater than that for independent contests. Thus the structure of the game has a heavy bearing on the overall level of aggression. The effect of changing the cost C is also affected by the structure. For independent contests, the proportion of Hawk–Hawk contests when $C = 2D$ is four times that when $C = 4D$. When $n = 3$ it falls to 3.5 times, but as n tends to infinity the limit is over 6 times as many violent contests.

Table 5 shows the effect of dividing a fixed total group reward in different ways on the overall level of aggression within the population. The more unevenly the rewards are split, the higher the expected level of aggression. This mirrors the findings of Keller and Reeve (1994), but whilst their model had a threshold for when aggression would pay for an individual, our model gives a sliding scale of aggressiveness as a function of reproductive skew. Thus our model can make a prediction about the level of aggression in different populations as a function of the reproductive skew in that society, provided that the other parameters of the model are known (or at least a prediction of relative levels of aggression if the other parameters can reasonably be assumed constant over different populations).

It is possible to have many ESSs in the model discussed in this paper, as one might anticipate from earlier work (Broom *et al.*, 1997b). For the case where only two options are available, it is not possible to have no ESS, and conditions for the existence of the pure ESSs are found as are conditions which guarantee a mixed ESS. It may be possible to have more than one mixed ESS, although in Section 3.2 it is shown that for the Hawk–Dove game if there is a mixed ESS, then it is unique.

Other ways of structuring pairwise games can be imagined, but the one considered here is the simplest with the property that all players start from an equal position. We intend to present work on the case where an individual can alter its strategy between rounds in a later paper.

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